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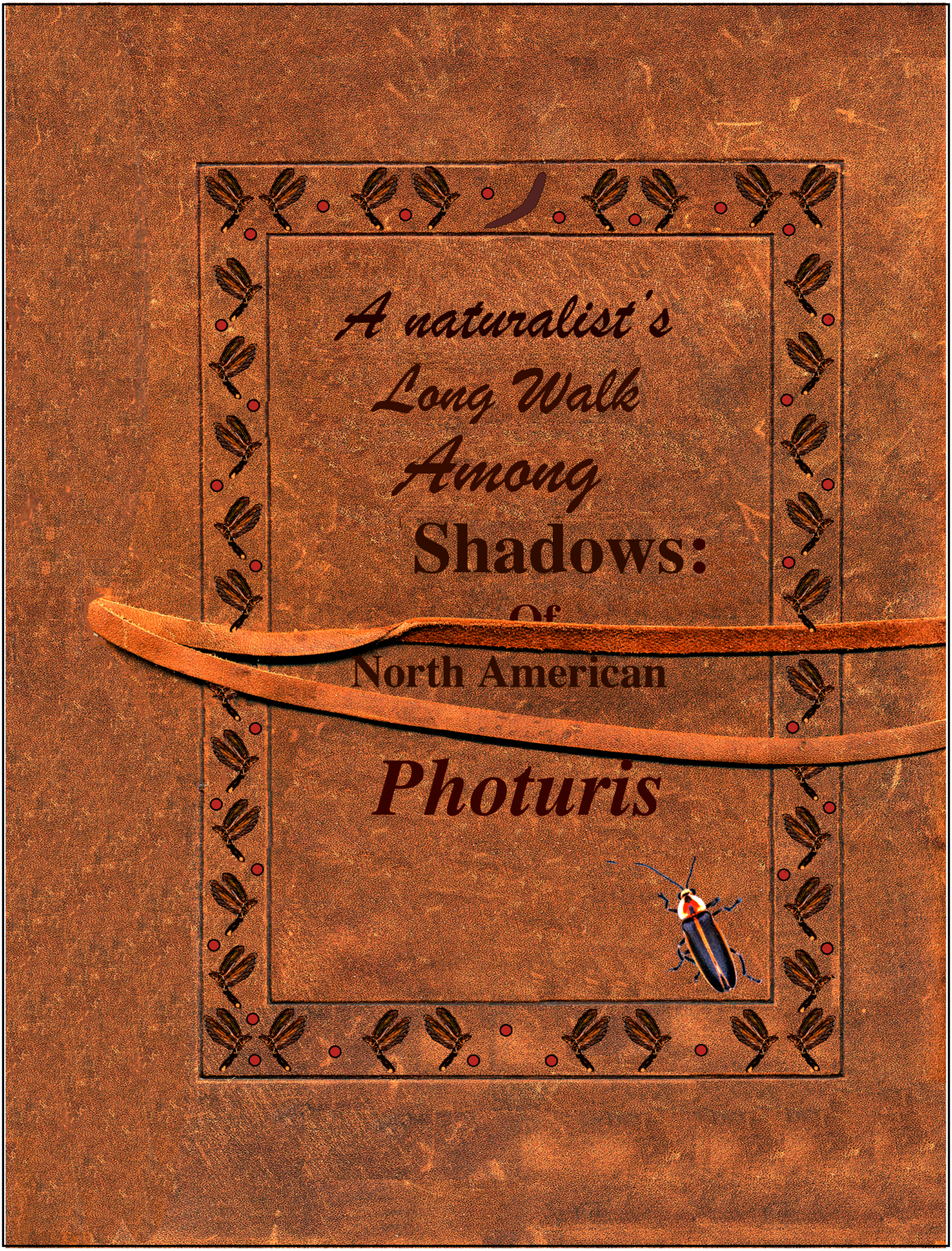

A naturalist's Long Walk Among Shadows:
Of North American
Photuris

A naturalist's ***Long Walk Among*** **Shadows:**

* * *

Of ***NORTH AMERICAN Photuris***

—Patterns, Outlines, Silhouettes … Echoes

DESCRIPTIONS, ILLUSTRATIONS, notes AND CONSIDERATIONS— FROM A LONG–HUNTER'S OVERLAND EXPLORATION AND ADVENTURE FROM A DIFFERENT AGE

15 April 2018
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at the Bridgen Press

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Department of Entomology
and Nematology, uf.
Gainesville, Florida
32611

In Memoriam

Photograph of the last
Passenger Pigeon-female-
taken in year 1911 in
The Cincinnati Zoological
Garden, Cin.,O. The bird
died at 2o'clock P. M. on
Saturday August 29th, 1914,
it being the last of a flock
of seventeen captured in 1876.

LAST PASSENGER PIGEON

Died at Cincinnati, O., Zoo, August 29, 1914.

"Within the memory of men still living, countless millions of wild pigeons passed over Pennsylvania in their migratory flights. Old residents can recall the time when from horizon to horizon flying birds were seen in flocks so large and so compact as to obscure the sun. Fifty years ago wild pigeons were still common game birds and thousands of them could be observed in their seasonal flights, but today it is admitted that the last passenger pigeon in the world, so far as is known, died in the Cincinnati Zoo during the fall of 1914.

"Large rewards were offered for a mate for the last wild pigeon in the hope that the species might be saved from total extermination. But not one could be found. And in order that the bird might be properly mounted upon its death, the keeper carefully saved the feathers dropped each year for the taxidermist. So the bird has been preserved—by taxidermy—but the species is now totally extinct."

John C. French, 1919. The passenger pigeon in Pennsylvania, page 128. Altoona Tribune Co., Altoona PA. (photo 223)

DEDICATION

*To **Frank A. McDermott** (1885-1966),*
a quiet, perservering Scholar and
Long-Hunter who went on ahead;
Father of Lampyrid Semiosystematics
and Victorian Gentleman, who,
in a better world, would have brought
Honor and Dignity to a
University as Professor of Entomology;
I don't expect to meet another like him.

*

To the Independent and Energetic
*Spirit of **Willis S. Blatchley** (1859-1940),*
Undaunted and Dedicated
Insect Taxonomist and Philosopher
who knew.

*

To the investigative Insight,
Skill, and Courage of
***Herbert S. Barber** (1882-1950) ;*
a Companion in the Field,
though we never met;
*and to **John Wagoner Green** (1889-1968),*
Master Taxonomist, who, as those above,
Taught by example, and was always
in spirit, beside me, in the field
and at the Bench..

*

To the sharp and probing Intellect
*and wit of **Richard D. Alexander** who*
more than anyone, ever,
taught me how to Think.

* * *

*To my parents **Ann and Harry Lloyd***
for the incredible outdoor and
diversified life experience they gave
me for my first 18 years and their
continued love and support for a
half-century more.

* * *

*And, To **Dorothy**, whose spouse*
I am; My brightest Light and
constant Companion,
through all these decades.

* * *

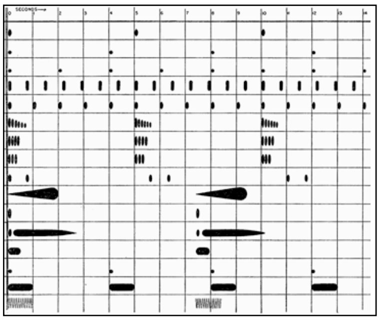
I hope this study meets with their approval,
for to each of them goes Credit
for its completion.

Preface

When this project began the scientific goal was to resolve the taxonomy of fireflies of the genus *Photuris*, and if possible, find the reasons for the fact that one seemingly speciose section of this genus had escaped a satisfying taxonomic resolution for more than a century. Field studies began in Florida in the spring of 1967. Preparation had been a warming-up exercise on the genus *Photinus*—and to a lesser extent *Pyractomena* (1963-1966). One section of the genus *Photuris*, recognized here as Division II, had long been referred to and lumped under the name "*pennsylvanica"* (this spelling since returned to DeGeer's original, and under the Rules the legitimate form, *pensylvanica*). The "*pennsylvanica*" aggregation actually included all but a very few of our many North American *Photuris.*

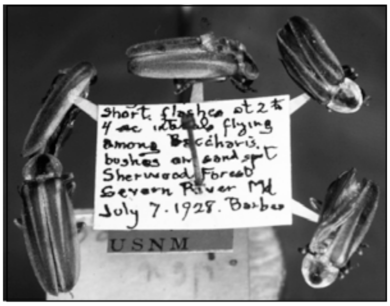
An example of *Photuris* "*pennsylvanica*.".

Inspiration and approach methods were found in the pioneering study by H. S. Barber in the 1920s—not published until 1951. He applied the earlier discovery of F. A. McDermott that males of some firefly species could sometimes be distinguished by the patterns of light (signals, *flash patterns*, FPs) they emit as they fly about their habitats seeking mates. Barber found that several *Photuris* species were actually present in his bailiwick, the lower Potomac River and adjacent Chesapeake Bay area, and that he could morphologically distinguish some of them by subtle body color and size differences. He collected series of FP vouchers, which were subsequently archived for future reference—he also received FP-vouchers from Minnesota, Wisconsin, and Nova Scotia, collected by friends and colleagues.



Diagrams of Barber's *Photuris* flash patterns.

Before the revelatory field studies of Barber, there seemed no way the taxonomy of *Photuris* could be resolved, because when archived *Photuris* carcasses were closely examined, and certainly several taxonomists had done this locally over many decades, there seemed continuous variation with no apparent differentiation that would allow for a clear separation of even a few defensible suggestions for species distinction. Nor was anything found that would permit the descriptions of even species that had been named by iconic European science in Colonial times—DeGeer in Sweden and Fabricius in Germany—to be associated with specimens now residing in brittle rows in American museum cabinets. Eventually, most *Photuris* were subsumed under the senior (oldest/priority) name, DeGeer's *pensylvanica*; there they remained until Barber. Surely, *Photuris "pennsylvanica"* had become a "phenom," a 6-legged, flashing enigma of mythological reputation.



Barber's *Photuris salina* vouches; wheels are not now recommended.

As detailed in this paper, the flashing behavior of a certain few of these "*pennsylvanica*" (in Division II) *Photuris* are far more complex than anyone could have suspected. This complexity has evolved as a consequence of what originally was discovered/suspected by Barber himself: that females of some *Photuris* species prey upon males of other firefly species by imitating, that is, by having evolved imitations of the mating signals of the females of their intended prey. This *biological mimicry* ala Wickler (1968), again discussed and delineated by Pasteur (1982:169), is "*unconscious* biological mimicry." However, and contrariwise, in a few cases it may actually go a little further than this, and might involve ad hoc simulations with subsequent fine-tuning? Reflections on mimicry origins have led to this (working) conclusion. Predation via signal mimicry here falls under the rubric of *aggressive mimicry*—less commonly/rarely (in lit.) referred to by other names—where the resemblance of certain features of an organism to those of another, permits/facilitates the exploitation of the other, the so-called *dupe* (Peckham, 1889; Wickler, 1968; Pasteur, 1982). Obviously this behavior potentially affects all flashing species in the domains of these predators. In a more contemporary allusion, these femmes fatales truly and inescapably are the *Jaws* of firefly signal ecology, and their influence must be expected/anticipated to be significant in the signaling of flashing fireflies of the Western Hemisphere.

Female predation via mimicry has been responsible for another *Photuris* mimicry behavior that has greatly complicated the use of FPs for taxonomy: Males of various species emit *adjunct* FPs (extra, supernumerary, additional FPs) that are matches/mimicries of the FPs of their females' prey. And, the same/identical adjunct FP is used by more than one *Photuris* species: For example, some use combination flicker FPs of *Pyractomena angulata* and *dispersa*. A species in Florida precisely matches the flicker of *angulata*, and two other match the long-glow signal of *angustata*. Further, *Photuris* males emit these FPs varyingly, depending upon the species: during certain times of evening, at some sites and not others, in varying proportions through evenings and over days, and on some evenings and not others. The primary explanation for adjunct FPs must be that they locate hunting females and seduce/induce them to switch to a mating mode from a hunting mode (jel, 1980). When a male's adjunct FP is flash-answered with a decoy simulating his female's response, the male will switch (default) to his species' own FP. Adjunct-FP development, involving an adaptation that is at once connected to the acquisition of sustenance, defensive compounds, mating success and fecundity, and predator avoidance, may well have driven the rapid evolution and divergence of signaling in regional often contiguous populations of *Photuris*. In suggesting this I am invoking the regional, ecological fine-tuning considerations of Paul Erlich and Peter Raven (1967), as one mechanism driving signal divergence and speciation.

During this study several hundred populations ("demes") of *Photuris* across eastern North America from Nova Scotia, Cape Cod, and Long Island to North Dakota and Nebraska; and from Florida to southwest Texas, were sampled/ studied. (An imaginary "deme" [local population] would seem to be the proper unit of evolution and for dissecting biodiversity.) FPs were noted and electronically recorded, temperatures taken, and voucher specimens preserved. Unlike the earlier survey of *Photinus*, where morphology and behavior usually matched, were generally in agreement, and ranges could be mapped, a different *Photuris* seemed to appear "almost" at every stop, sometimes with only subtle variations from what was noted elsewhere. What then, should be recognized as a species?, and where to formally recognize distinctions among such populations?, seemed to be unanswerable questions. Perhaps only DNA analysis can find happy answers. But, perhaps the genetic diversity and partitioning of *Photinus* and *Photuris* are not very different, but are reflected in the signals of one and not the other? How are such populations/entities to be "made available," identifiable, as normally would be accomplished in a key? How can a key to FPs be constructed when they are varied in time and space as noted above?: (**1**) I have not seen and thus cannot illustrate repertoires existing in all populations sampled here; (**2**) brief observers in many cases will not see all FPs in a population's repertoire; (**3**) and certain FPs are common to the repertoires of several otherwise distinctive demes. Finally, (**4**) to which demes should formal names be given, and which should be given nicknames? I have used degrees of difference, geographic separation, and intuition/ suspicion to make decisions, all of which have at times been found unreliable? Those named are as reference points …

All of the species Barber and McDermott recognized are retained. New species, those 30+ formally recognized here, are sometimes clear and distinctive. Others will require further field observation with attention given to certain, previously-overlooked, specific details, and often over several evenings. **For identification**: (**1**) First, to distinguish *Photuris* from other genera, see the morphological guides to the three major flashing **genera** in North America, on pages 22, 136. (**2**) Note on page 64 the crude flash-chart of FPs of certain *Photuris*—superficial and not reliable for serious work? See also instructions on page 65. (**3**) All known FPs of all *Photuris* are placed in one of the nine (AA-II) structural groups of Chapter 8; then ID yet may remain difficult. The recognized FP structures will lead to various species chapters. OTUs in the "refined *pennsylvanica*" group, which includes emitters of dot-dash FPs (Barber's designated *pensylvanica*), and certain long-flash FPs—(Barber's *caerulucens*)—will be the most difficult and problematic. (**5**) Wing it, with patience, intuition and inspiration. And, there are many variants/variads yet to be found.

The Bridgen homestead in the Cowaselon Valley in the 1950s, where *Photuris* FPs presented strange and sometimes borrowed variations in the 1970s?

At Plummer's Island camp, Barber, and his mentor and colleague E. A. Schwarz, circa 1911. Table setting for 2 and Barber's dangling foot suggest that Barber, known to be a photographer, took a time-delayed exposure.

Eunice Myers and Robert Boland, collectors in 1927 of Barber's MN and WI *Photuris* vouchers, at my campsite in 1970, across the highway (background) from one of their *caerulucens* localities.

Acknowledgments

I gratefully acknowledge and do especially and forever thank the many who extended support of one kind or other, were of special significance, or provided meaning in my education and firefly experience during and over the past half century and more. They were: Dick Alexander, Elena Alyanaya, Lesley Ballantyne, Awinash Bhatkar, Herr Green Bean, Bill Biggley, Bob Boenig, Robert Boland, Marc Branham, Bill Brown, Drion Boucias, John Capinera, Pat Carlysle, Jim and Muriel Case, Skip Choate, Charles Decker, Mark Deyrup, S. and D. Durland, Ken Eddy, Tom Eisner, Durland Fish, Howard Frank, David Furth, Tim Forrest, Mr. Fritz, Erin Gentry, Al Higgins, Nick Hostettler, Fred Hough, Pam Howell, Theodore Hubbell, Oliver Keller, Abner Lall, Norm Lepla, Ann and Harry Lloyd, Dorothy Lloyd, Robert and Florimel Lloyd, Flora McColl, Frank McDermott, Jim Maruniac, Fowden Maxwell, Frank Mead, Jane Medley, Tom Moore, Glenn Morris, Julia Moutron, Eunice Myers, Jim Nation, Dan Otte, Ann Pace, Don Pafka, John and Anna Pafka, Larry Patrie, Barbara Polacek, Bard Prochaska, Arwin Provonsha, Paul Rupert, Nancy Sanders, Howard Seliger, Dan Shankland, Blair Siegfried, John Sivinski, Paul Skelly, Grover Smart, MaryAnn Smith, Fred Sparrow, Kate Stanger-Hall, Gladys and Willard Stanley, Bo Svenssen, Mike Thomas, Henry and Marjorie Townes, Herb Wagner, David Wahl, Tom Walker, Howard and Camilla Weems, Kay Weigel, Rick Wilkerson, Gary Williams, Steve Wing, and George Zimmer. A special note of gratitude must be extended to the inventers and makers of *Macintosh* computers; the production of this and other firefly contributions would not have been possible without their technology, and that of the applications they have supported since their beginning—I wish there had been more compatability among their changing generations. Also, a special nod is due to the creators of *Intellidraw*; they should recieve a medal for creating an incredibly intuitive graphics program; unfortunately it went out of production, apparently a victim of vulture capitalism—without consideration for the art. Among other key applications were *Excel, Word, Eazy-Draw, Photoshop, StatView*, and *DeltaGraph*—all of these could be used to the end because of the genius of the Department's Mac Guru Nick Hostettler. Finally, I was once, in my inexperience, critical of the inclusion of a criticism of an unnamed uncooperative colleague in the introduction to Willis Blatchley's "Coleoptera Of Indiana"; I am wiser and more understanding now, having met and experienced such bastards myself, some in unexpected and important places. Also, the *Kodak* outfit deserves serious rebuke for having discontinued the production of *Kodachrome-25*, and not planning for continued availability of this art medium via some other, perhaps a family-operated organization! Finally, two small NSF grants five decades ago, before "academic" administrations got out of hand, helped get things off to a good start, and did not lead to addiction—but NSF-funded trips to New Guinea and Indonesia with Scripps, and to Thailand via the National Geographic Society, were incredibly important in the overall view of things.

The following individuals/institutions loaned specimens, some of which were retained for many many years too long, and a few I have yet to finish, but will: Albert Allen/Boise ID; Fred Andrews/Div. Plant Ind. Sacramento CA; Diomedes Quintero Arias/Smithsonian TRI, Univ. Panama; Allan Ashworth/Geology Dept. NDSU, Fargo ND; Cheryl Barr/Essig Museum of Entomol. Univ. CA. Berkeley; Charles Bartlett/Dept. of Entomol. Univ. of DE; Derrick Blocker/Dept. Entomol. Kansas S.U. Manhatten KS; Nancy Boase/Can. Nat. Coll.; Edward Barrows/Georgetown Univ. (Dyke Wildlife Preserve VA); Jim Cane/Col Forestry, Syracuse Univ. NY; Wayne Clark, Gary Mullen, Mike Williams/Dept. Entomol. Auburn Univ., Auburn AL; David Foster/Entomol. Texas Tech. Univ. Lubbock TX; Paul Freytag/Dept. Entomol. Univ. Ky, Lexington KY; David Furth/USNM Washington DC; Eugene Hall/Div. Entomol. Univ. Nebraska State Mus., Lincoln NE; Steve Haydon/Bohart Mus. of Entomol., Univ. CA. Davis; Roland Fischer, Gary Parsons/Entomol. Dept. MI State Univ. E. Lansing MI; Diane Hartzler/Dept. Entomol. OH St. Univ.; Lee Herman/ AMNH NY; Carolus Holtzschuh/Pohigasse, Wien, Austria; Charles Hunt, Geology Dept., Johns Hopkins Univ.; Boris Kondratieff/CO. St. Univ. Boulder CO; Peter Kovaris/Cent. BioControl. FL A&M Univ. Tallahassee FL; Frank Kurczewski/ SUNY Syracuse NY; Nicky Ladkin/Mus. Texas Tech. Univ. Lubbock TX; Paul Lago/Dept. Biol. Univ. MS; R. E. Lewis/Dept. Entomol. Iowa St. Univ. Ames IA; Per Lindskog, SMNH, Stockholm, Sweden; Kathryn McGiffen/INHS Champaign IL; Jean McNamara/Can. Nat. Coll. Ottawa Ont. CAN.; Steve Marshall, Steven Paiero/Univ. of Guelph, Ont. Can.; Ole Martin, Zoology Museum, Copenhagen, Denmark; Silverio Medina-Gaud, Jorge Santiago-Blay/Univ. Puerto Rico; Charlie Messenger/Div. Entomol. Univ. Nebraska State Mus.,Lincoln NE; Patricia Miller/Mississippi Entomol Mus. Starkville MS; Mark O’Brien/UMMZ Univ. MI; Stewart Peck/Carleton Univ. Ottawa CAN.; Jane Borges Pinheiro/ CTAP Sau Paulo Brazil; Jerry Pliny/Univ. Waterloo, Ont. CAN.; R. L. Post/NDSU Fargo ND; Hugh Powell/Staten I.

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And, in celebration of and gratitude to the many hundreds/thousands of collectors whose names appear on archived firefly specimen labels, here is but a tiny sample: E. B. Southwick 1891, G. D. Bradford 1892, J. L. Zabroski 1897, E. Lilejeblad 1904, L. B. Woodruff 1904, W. M. Wheeler 1905, VanDuzee 1908, G. R. Pilate 1918, Siepmann 1921, A. W. Andrews 1921, Latham 1921, S. Moore 1921, Hatch 1925, A. E. Brown 1926, J. C. Pallister 1926, F. M. Schott 1927, D. S. Bullock 1929, R. R. Dreisbach 1929, L. K. Gloyd 1930, K. Sloop 1930, E. G. Linsley 1930, K. G. Silvey 1931, H. E. Milliron 1934, I. J. Cantrall 1936, Standish-Kaiser 1937, J. P. Brimley 1937, John Naz 1937, Hubbell-Friauff 1938, F. E. Guyton 1938, W. J. Gertsch 1941, J. Bastion 1944, H. B. Cunningham 1944, C. D. Michener 1944, T. H. Hubbell 1945, J. A. Mooney 1946, S. Emslie 1946, K. Bohnsack 1947, M. Cazier 1948, Robert Kyle 1948, A. E., Rioji Namda 1948, Thompson 1949, H. K. & M. Townes 1950, L. Lacey 1952, Dozier 1953, B. L Fisher 1956, R. W. Hodges 1957, G. C. Eickwort 1959, A. R. Thornhill 1968, H. M. Graham 1972, K. L. Hays 1974, H. & A. Howden 1974, C. Scholtz 1985 …


Tom Walker


Les Ballantyne


Bill (Ant) Brown


Tim Forrest


Clyde Mather


Durland Fish


Howard Weems


Ken Eddy


Barb Polacek


WFS

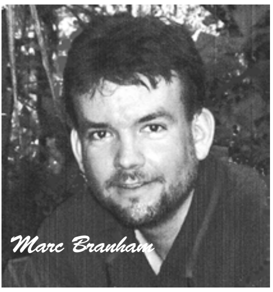

Aquatic Fireflies, Behavior, 1967


Steve Wing

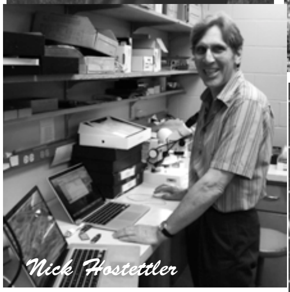

RDA

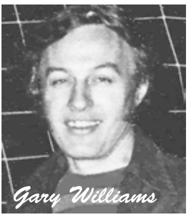

George Zimmer


Fred Hough


Marc Branham


Bob Boenig


Nick Hostettler


Gary Williams


Seeking borealis


Bean


Larry Patrie

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Partial Index To Miscellaneous Fillers, Notes

Index To Species & Identification Aids

Chapter 1

Homage To Pioneers: Their *Photuris* History

Two early 20th-Century fireflyers are among those to whom I dedicate this study. They deserve our special appreciation for their insight and industry toward the advancement of lampyrid knowledge. Key contributions are in the two lists below. They especially deserve our scientific recognition, gratitude, and respect, because neither received these during their own lifetimes, being decades ahead in their thinking and industry. One could say, and with good reason, that both were intellectually abused, denigrated and exploited by their contemporaries. The studies of Herbert Spencer Barber, published in 1951 after his death, though primarily done more than 20 years earlier, put the insights of Frank Alex McDermott into application. Barber's methods, as well as his reserved suspicions as a naturalist, are the foundation not only of this study, but for anyone who takes up the proper study of fireflies.

Mr. Mac

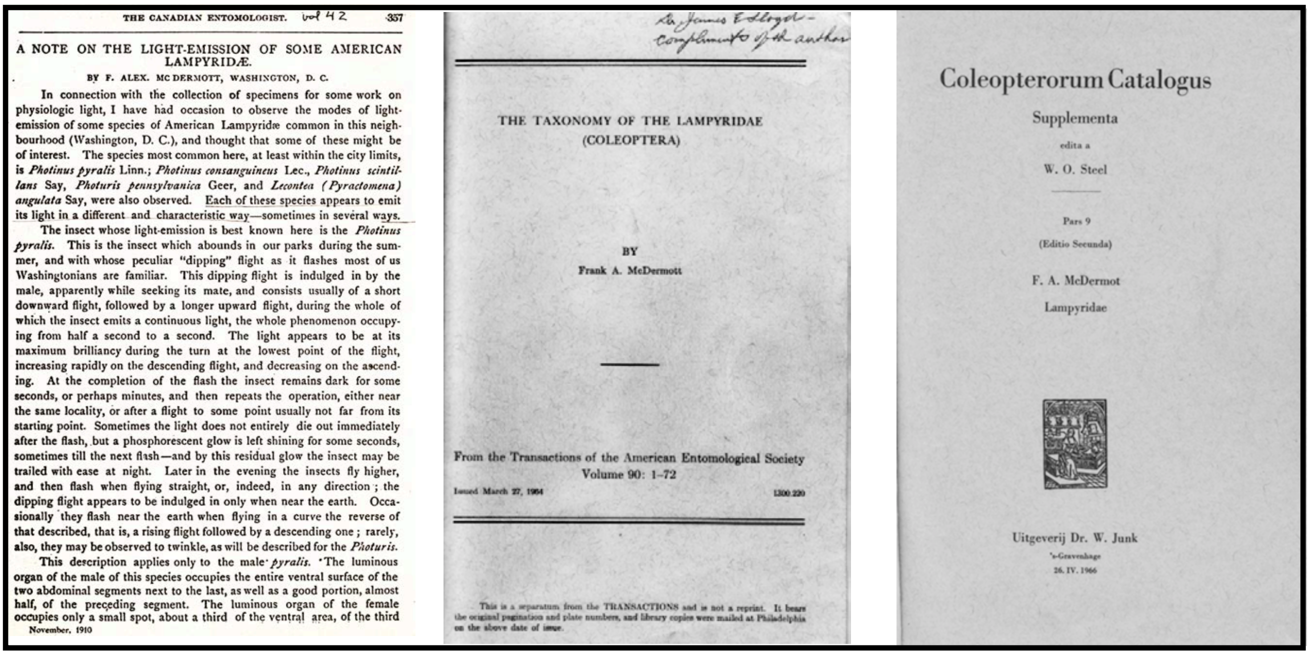
Frank Alex McDermott When I met Mr. McDermott in 1964 I didn’t know enough and probably was too intimidated to ask how he, an industrial chemist, came to recognize that flying male fireflies of different species flash in different patterns, an observation no zoologist or entomologist had previously made note of—nor later pursued!—nor why he happened to be out watching fireflies. Mr. Mac, as some knew him, was not intimidating, but physically small and you can even say of delicate stature. He was incredibly polite and gentle, a Victorian, and showed great interest in my firefly studies. I had the manuscript of my first aggressive mimicry paper with me when I first visited him at his home in the suburbs of Wilmington, and he read it as we sat on the grass under a small tree on his front lawn—and he approved! Later we lunched together with Mrs. McDermott. While I was a graduate student, in his letters he referred to me as “doctor” and when I advised him that I had not yet received such degree, he replied that doctor meant teacher and that I was teaching him. And then he was taken away … but I had some of his thoughts in letters, on postcards, and in the papers and major works that he had published.

I should have asked him if it were only the chemical nature of their bioluminescence that initially attracted his attention, and was it a eureka moment when he first noticed different flashing patterns and associated these with morphological (species) differences. Nor did I even ask him the simplest of questions—how he got to his study sites. It was 1908 or earlier, many revolutions in transportation ago, a different world than we can ever know. Was it a horse and buggy, a trolley, a Model-T pickup, a bicycle with a big front wheel, or were there fields, woods, and streams close around the house where he lived? Even more to the point, what was his thinking after he had a few years of experience with *Photuris*, in 1914 maybe, with respect to the different flash patterns he saw being emitted by the conglomerated "*pennsylvanica*" of the time. I suppose we shall never know. Years later when I contacted his daughter for biographical notes, a short biography, she was reserved and said little. She could never know how important he and the visits I had with him were to me and perhaps to the path of firefly study in years to follow.

Even more unfortunate than this for me personally, in 1962 I missed the opportunity to suggest that he should be the one to give a paper at the annual meeting of Entomological Society of America in Philadelphia—I was dodging a scary request that I give a paper in a behavior symposium, and I suggested another, much to my later regret. But, I was a novice graduate student, originally from a tiny teachers college and had never even seen a scientific meeting. Nor at the time had I discovered what a significant contribution Mr. Mac had made. Further compounding my error, this was at that very time he was completing two major works, a catalogue and a taxonomic overview of the Lampyridae of the World. There was much he could have told us; he would have appreciated the invitation to Philadelphia and the long overdo recognition, and firefly history made richer—maybe he would have talked about his discoveries—gems, bioluminescent emeralds for his successor, H. S. Barber, to place in a green-flashing *Photuris* setting.

McDermott Discovered/Realized:

1. **Some species of lightningbugs can be identified by the patterns of flashes they emit.**
2. **That what was then recognized as *Photuris pennsylvanica* actually emitted more than one flash pattern (not to be confused with Barber's later discovery).**
3. **That ambient temperature influences flashing rates—the colder the evening the slower the rates.**
4. **That comparative studies of populations are valuable for revealing significant behavior differences—female delays in *Photinus pyralis* vs. *marginellus*.**
5. **That observed differences in flashing behavior deserve consideration toward formal changes in formal taxonomic nomenclature.**



THE CANADIAN ENTOMOLOGIST. vol 42 357

A NOTE ON THE LIGHT-EMISSION OF SOME AMERICAN LAMPYRIDÆ.

BY F. ALEX. MC DERMOTT, WASHINGTON, D. C.

In connection with the collection of specimens for some work on physiologic light, I have had occasion to observe the modes of light-emission of some species of American Lampyridæ common in this neighbourhood (Washington, D. C.), and thought that some of these might be of interest. The species most common here, at least within the city limits, is *Photinus pyralis* Linn.; *Photinus consanguineus* Lec., *Photinus scintillans* Say, *Photuris pennsylvanica* Geer, and *Lecontea (Pyractomena) angulata* Say, were also observed. Each of these species appears to emit its light in a different and characteristic way—sometimes in several ways.

The insect whose light-emission is best known here is the *Photinus pyralis*. This is the insect which abounds in our parks during the summer, and with whose peculiar "dipping" flight as it flashes most of us Washingtonians are familiar. This dipping flight is indulged in by the male, apparently while seeking its mate, and consists usually of a short downward flight, followed by a longer upward flight, during the whole of which the insect emits a continuous light, the whole phenomenon occupying from half a second to a second. The light appears to be at its maximum brilliancy during the turn at the lowest point of the flight, increasing rapidly on the descending flight, and decreasing on the ascending. At the completion of the flash the insect remains dark for some seconds, or perhaps minutes, and then repeats the operation, either near the same locality, or after a flight to some point usually not far from its starting point. Sometimes the light does not entirely die out immediately after the flash, but a phosphorescent glow is left shining for some seconds, sometimes till the next flash—and by this residual glow the insect may be trailed with ease at night. Later in the evening the insects fly higher, and then flash when flying straight, or, indeed, in any direction; the dipping flight appears to be indulged in only when near the earth. Occasionally they flash near the earth when flying in a curve the reverse of that described, that is, a rising flight followed by a descending one; rarely, also, they may be observed to twinkle, as will be described for the *Photuris*.

This description applies only to the male *pyralis*. The luminous organ of the male of this species occupies the entire ventral surface of the two abdominal segments next to the last, as well as a good portion, almost half, of the preceding segment. The luminous organ of the female occupies only a small spot, about a third of the ventral area, of the third

November, 1910

Dr. James E Lloyd –
compliments of the author

THE TAXONOMY OF THE LAMPYRIDAE
(COLEOPTERA)

BY
Frank A. McDermott

From the Transactions of the American Entomological Society
Volume 90: 1–72
Issued March 27, 1964 1300.220

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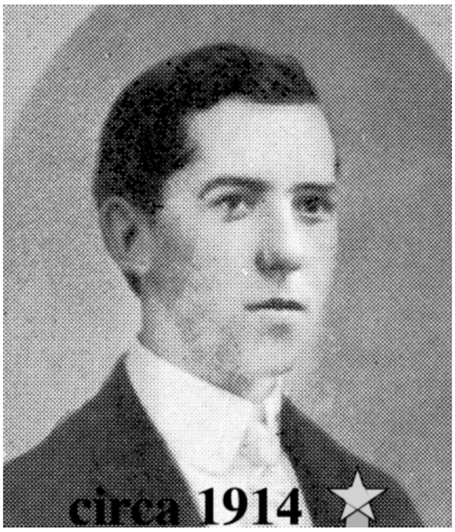
Coleopterorum Catalogus
Supplementa
edita a
W. O. Steel

Pars 9
(Editio Secunda)

F. A. McDermot
Lampyridae

Uitgeverij Dr. W. Junk
's-Gravenhage
26. IV. 1966

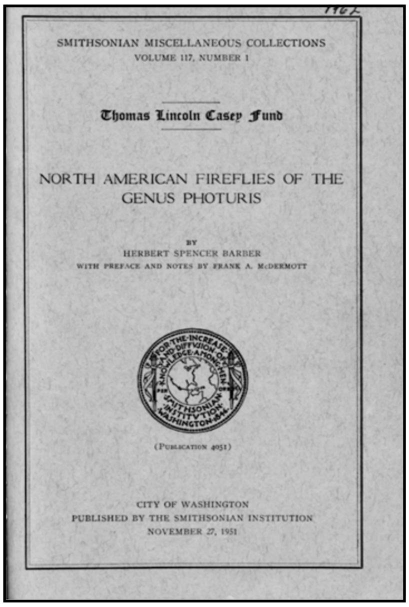
Herbert Spencer Barber was a naturalist and entomologist, an outdoor man that hunted, fished, and canoed on the Potomac River. A man with probing curiosity, intellect and energy. His mentor, E. A. Schwarz, was a Prussian born, well-educated taxonomic entomologist. They camped and collected on Plummer's Island in the Potomac near Washington and watched fireflies along its grassy, tree-lined shores. They discussed McDermott's discoveries and the *Photuris* "*pennsylvanica*" problem—from their campfire they could easily see the distinctive flash-trains of fireflies that Barber later would name *Photuris potomaca*, the crescendo flashes of his *Photuris lucicrescens*, and the tremulous flicker of his *Photuris tremulans*. Given this experience for inspiration, insight, and encouragement, for these three fireflies can be morphologically distinguished once you have separated FP-vouchers of them, it would have been surprising had Barber not sought FPs elsewhere in what we will appreciate as his bailiwick, and collected vouchering specimens of each. When quizzed by McDermott in an ad hoc lab practicum, Barber was able to tell him how his "unknowns" had flashed, except for one he had not yet met (McDermott, in Barber, 1951).



By studying the flashing patterns of *Photuris* fireflies in the field Barber began the semiosystematic analysis of the genus. In addition to emphasizing important working methods and habits, he asked rhetorical questions of his students, that is, those of us who would take up the *Photuris* problem, which he knew he would never resolve. He made it very clear that there was something out of the ordinary, something inexplicable in *Photuris* signaling. His work, published posthumously, transformed the *Photuris* "*pennsylvanica*" problem into an incipient enigma of transcendent interest—and he "warned" that it *is far more complicated than you think, and we are still far from the truth* (Barber, 1951:v).

Though Barber studied *Photuris* in the mid 1920s, his view, as expressed in his paper in 1951 (ibid: iii), was New Synthesis in orientation. He sought Biological Species with care, caution, and replication, and emphasized his strong but then unpopular belief in the scientific need for taxonomists to seek and formally recognize populations in nature, not merely the distinctive morphs of their cabinets. As a matter of fact he apparently was quite belligerent about this, and critical to the point of being disagreeable and marginalized, even morose, so I was told by a younger contemporary whom Barber had mentored. An excerpt from Barber's letters to and quoted by McDermott in his introduction to Barber-51 make some of this very clear:

> *Taxonomy from old mummies which fill collections is a misguided concept. It leads to the misidentification of rotten old samples in collections. How these poor fireflies would resent being placed in such diverse company—among specimens of enemy species—if they were alive and intelligent! What contempt they would feel for the "damned taxonomist.* (McDermott's Preface in Barber, 1951:v)



SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 117, NUMBER 1

Thomas Lincoln Casey Fund

NORTH AMERICAN FIREFLIES OF THE GENUS PHOTURIS

BY
HERBERT SPENCER BARBER
WITH PREFACE AND NOTES BY FRANK A. McDERMOTT

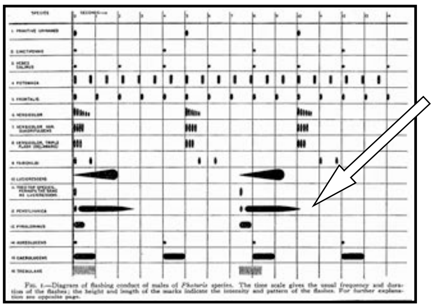
(Publication 4051)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 27, 1951

Today Barber’s bio-taxonomic perspective remains completely satisfactory and theoretically sound. His purview was for the most part non-dimensional, that of an expert local naturalist (demes), his field universe being within a 100 mile radius of Washington, DC—except for incidental samples from other domains. Such narrow and focused field-studies of local populations are the elements toward getting a grasp of evolutionary biodiversity and speciation itself, and the stuff understanding grows from.

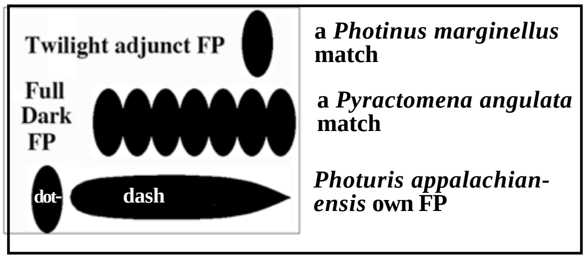
Barber Discovered/Realized:

1. **That aggressive mimicry apparently occurred.**
2. **That some *Photuris* species emit more than one distinctive flash pattern.**
3. **That the *Photuris* behavior and thus taxonomy was far more complex than anyone had realized.**
4. **That a less formal writing style, was more appropriate for describing field observations.**
5. **That voucher specimens were important and he left *Photuris* voucher specimens with notes to anchor and document his studies.**
6. **That taxonomy from archived specimens alone was inadequate for understanding species or for serving the requirements of other areas of biology.**



Among Barber’s captures was a little dot-dash flasher (i.e. <short flash>-break-<short glow) that he found inhabiting brackish wetlands. After comparing his voucher series with DeGeer's morphological description of *pensylvanica and* noting cryptic historical mentions of local ecology and flashing behavior, Barber decided that his dot-dash flasher was “*the*” *Photuris pensylvanica*— that is, belonged to the same species that Charles DeGeer had in hand in 1774, when he assigned the name. McDermott thought Barber was incorrect about this.

Barber’s most important taxonomic legacy, not forgetting his suspicion that *Photuris* females were firefly predators via mimicry, was certainly one that frustrated him to the core, gave him second thoughts and sleepless nights, and could have been one explanation for his not publishing his discoveries earlier. Why, he asked, did his *lucicrescens* at one site use both of its flash patterns but at another site use only one? And why did his *tremulans* most commonly emit a single-flash FP, but occasionally use the flicker he recognized when naming it? He mused, envied the wings of bats, that he might follow his fireflies and know with certainty. What he couldn’t know was that a dot-dash flasher in western Maryland—herein named *Photuris appalachianensis*—would present a 3-FP repertoire, and that *quadrifulgens* and its apparent offshoot, *eureka* in Florida, may be even more complicated. Or that another *Photuris* with an even more remarkable flashing repertoire occurs in the northeast: a variad of his *Photuris versicolor,* it *w*ould have made Long Island the *Photuris* utopia he once imagined. There he would have found one very common and abundant *Photuris* that he could study in detail without the confusion of other flashers. Not surprisingly, and, as to be expected with *Photuris*, there is also hidden away on this great, glacier island of two faces, perhaps hiding in reclusive marshes near the Sound, another dot-dash flashing firefly—it was found in a stream-side marsh near a bridge not far from Stonybrook.



In August of 2014 the International Group of fireflyers gathered in Gainesville, Florida. In my discussion of who might have attended such a meeting, were one to have been held in 1914, I recognized McDermott and Barber as our special honorees—too late, not enough. But all present were reminded of the Pioneers' spirit and contributions.

Chapter 2

Some Firefly Natural History

If a photon could talk, we could not understand it.
Jack Kelly

photons speak to me, and … Barber;
i have understood a little.
Jim Lloyd

Fireflies are beetles (Class Insecta, Order Coleoptera), of the Family Lampyridae (-idae, family ending). Fireflies that emit light in flashes are termed lightningbugs. Fireflies and kin are currently/recently placed in the Superfamily Elateroidea (-oidea=superfamily ending) with click beetles (Elateridae). In older literature find them in Cantharoidea, which included: soldier beetles (Cantharidae), giant glowworm beetles (Phengodidae), net-winged beetles (Lycidae), and a few poorly known forms such as long-lipped beetles (Telegeusidae). Worldwide nearly 2,000 species of fireflies (lampyrids) have been formally described and named (McDermott, 1966). About half this number are from tropical America, where there is a great variety of form and flashing. In North America there may be as many as 275-300 (working) species, that is, those that deserve recognition with formal Latinized names (DNA?). The actual number of firefly species in the world that deserve such formal/scientific/utilitarian recognition could be as many as 10,000.


Luminescent click beetle, Elateridae

It is useful to recognize three basic types of North American fireflies, though the fit of this scheme with evolutionary relationships is not congruent: (**1**) In lightningbug fireflies, males of nearly all species emit patterns of flashes of light (flash patterns, FPs) and females respond to these patterns with species-characteristic flashed answers. (**2**) In glowworm fireflies females emit the initial soliciting luminescent signals and in some species they also emit pheromones. Male glowworm fireflies are typically non-luminescent, however, males of our most common eastern glowworm firefly, *Phausis reticulata*, emit light, and their glows—and that of a penlight—will elicit glow responses from females that are unlit at the moment. (**3**) Adults of only one daytime dark firefly is known to emit light: males of *Lucidota luteicollis* apparently locate females by their pheromones during daylight and inactive at night; they glow from their tails and pronota, which they have been seen to stick beneath the sand when "digging out a female!? Most daytime dark fireflies probably use pheromones for sexual signaling.


Lightningbug firefly, *Photinus pyralis*

Fireflies of eastern North America seem to have their genealogical connections with the American tropics via an old and enduring eastern Mexico passageway, and show little or no close connection with fireflies of the Caribbean—this in spite of their seeming proximity and the common occurrence of hurricane winds with bug-bearing potential, both aloft and aboard drift such as logs.

The Bahamas apparently have received a few species from southeastern North America. Some Western North American fireflies have a connection with western Mexico (*Microphotus*) and two, remotely, maybe with Asia or elsewhere in the "Old World" (*Brachylampis*). Two somewhat well-represented (speciose) western genera, *Ellychnia* and *Phausis*, have a few formally-named representatives in eastern North America. Our oldest archived specimens from North America are represented by two pronota tentatively identified as those of incredibly tiny Winter Fireflies (*Ellychnia corrusca*); they were found in sphagnum/peat with fragments of other insects. These fossils were collected in what now is southern Ontario, Canada, but lived near and were buried in a marsh more than 10,000 years ago, as the glacier melted northward.


A daytime "dark"(?) *Lucidota luteicollis* female.


Day-time Dark firefly, *Lucidota atra.*

Habiti of fireflies, from left to right: *Pleotomodes knulli* male, a glowworm firefly; four daytime dark fireflies,*Tenaspis angularis*, *Ellychnia corrusca*, *Pyropyga nigricans* (with ticks), and *Pyropyga minuta*.

Natural History. Lampyrids are holometabolous—have four distinct life stages: egg, larva, pupa, and adult. The pupal stage is a key adaptation of such insects. At pupation the larva—often the only only feeding stage—"melts down," and rebuilds in a form that will be the *dedicated reproductive* and often *emigration* stage, the adult.

Female glowworm firefly, a *Phausis*, with eggs.

Eggs. In some lampyrids eggs are deposited a few at a time over several days or weeks. This is probably the case in those Division II *Photuris* species whose females are hunters and acquire egg-building nutrition and sustenance over an extended period; some (Florida *Ph. harrannorum*) may deposit a few eggs in each of several prey sites. Females of *Photinus pyralis* and *Photinus umbratus*, species of the grass- and herb-land of early-successional ecological stages, may likewise place their eggs in two or more different sites. In some species the eggs are all laid at one time, as in *Photinus collustrans*, in which the brachypterous (short-winged hence flightless) females live briefly after ovipositing, and die in their burrows (Wing, 1987). The eggs of some species glow dimly, from luminous material placed on the eggs in the mother's egg canal, but later with development of larval light organs, embryos within the eggs are reported to emit light (Buschman, 1984b).

Larvae. As far as known, larvae of all fireflies are luminescent, even those of daytime-dark species. Several functions have been suggested, and aposematism has been demonstrated. Some are snail specialists (*Pyractomena*, *Micronaspis floridana*). They stun prey with a poison (anesthetic) that is injected via bites to the neck that render them briefly immobile. *Photinus* fireflies, being subterranean, presumably are earthworm specialists. *Photuris* larvae are omnivorous and scavengers. A firefly from Sri Lanka (Ceylon in lit.) was unsuccessfully released as a biological control agent against the African snail in Hawaii and New Britain in the Solomon Islands; and two Japanese *Luciola* species were released in Hawaii to control snails harboring cattle-attacking liver flukes, but apparently did not become established (Bess, 1956, and misplaced ref.). Larvae of *Pleotomodes* species live in ant nests (as do *Pelania* larvae in Morocco), perhaps feeding on the food or young of the ants, or other nest inhabitants (Sivinski et al, 1998).


Photinus


Py. nigricans


Micronaspis


***Pyractomena* larva, kissing a snail**


***Photuris* pupa**

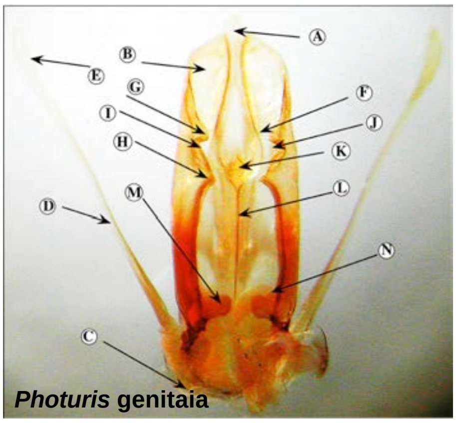
Photuris and *Pyractomena* larvae are often seen luminescing, *Pyractomena* especially on damp, rainy nights on twigs and branches of low woody plants in damp woods. Glowing larvae of marsh and pond inhabiting *Pyractomena* have been observed glowing underwater and on emergent vegetation (see L. Buschman and his refs. for *Pyractomena* and *Photuris* larval biology). *Py. ecostata* larvae glow along damp roadsides within 20 miles of Florida and southern New Jersey coastlines. *Photuris* larvae are the most commonly seen, usually along damp roadsides, paths and streams. It was certainly *Photuris* larvae that the early botanical explorer Peter Kalm remarked upon in the report of his “Travels In North America” (1753, Vol. I: 184):

> Glowworms. *Towards night we found some glowworms in the wood. … The color was brown and the segments joined in the manner as the onisci or woodlice* [sowbugs]. *… When the insect crept, its hindmost segments were dragged on the ground, and helped its motion by pushing. The extremity of the tail contains a matter which shines in the dark with a greenish light … It had rained considerably all day, yet they crept in great numbers along the bushes, so that the ground seemed as if it were sown with stars.*

Pyropyga nigricans larvae occur along stony and sandy shores of lakes and streams, amongst and under stones; *Ellychnia* and perhaps *Lucidota* juveniles occur in leaf litter and rotting logs, especially pine perhaps, near the horizon with the soil and within. Find them at night with dark-adapted eyes, by carefully pulling apart logs (also look for the tiny sparks of luminescent Collembola (springtails) that occur and may interact with them (?). *Micronaspis* larvae occur at the edges of black-needle-rush marshes in coastal Florida; they have diagnostic projections on their dorsal plates.

Pupae. Most larvae seek or make sheltered places to pupate. Pupation generally lasts from one to three weeks, depending upon the species and ambient temperature. *Photuris* and *Photinus* larvae pupate in chambers they make at or under the surface of the soil (Buschman, 1984ab). *Pyractomena* larvae hang up in herbaceous vegetation and on tree trunks. This seems an adaptation for living in habitats where rising water would flood chambers in the soil, such as in river forests. *Py. borealis* larvae in north-central Florida pupate in cool/cold January-March and select the southern exposure of larger trees; this shortens pupation time, and adults are sometimes seen in late February, perhaps avoiding early *Photuris* predators; also, their first-stage larvae may avoid competition from larvae of another species (*Py. limbicollis*) during early development (jel, 1997). *Py. limbicollis* larvae pupate on the north side and lower on smaller trees. *Aspisoma* species probably also hang up to pupate; they are almost exclusively tropical but single specimens of two species have been collected at southern-most localities in Florida and Texas.

At the far left are two *borealis* pupae hanging out of their larval skins from a broken twig in a swamp forest in Gainesville, Florida. One has just emerged and has not yet tanned. At the near left is a *borealis* pre-prepupa, a larva hanging, beginning pupation.



***Photuris* genitaia**

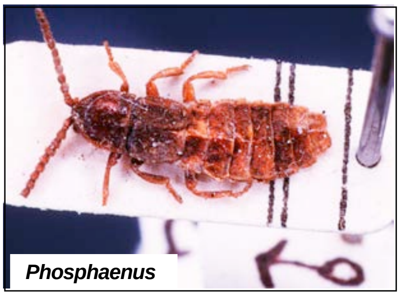
Adults. The reproductive activities of adult fireflies are: mate-finding and selection, copulation, oviposition, and dispersal. Females of *Photuris* fireflies—and possibly males too, although evidence is equivocal—are predators of other fireflies. Females of a few *Photinus*—with none yet known in *Pyractomena* or *Photuris*—are flightless and not known to have long-winged forms, nor known nor suspected to be transported by males or other means, other than floodwaters and organic drift, such as sod islands and logs. Known females of glowworm fireflies are flightless; those of daytime dark fireflies are winged, excepting those of a certain few *Pyropyga nigricans* populations found occasionally along lake-side strands, wetland sites, and montane valleys (jel, 1999), and *Lucidota luteicollis*. There are no documented cases of parthenogenesis, either obligately or facultatively. Male genitalia are of taxonomic value and are used to distinguish among working/operational species or species groups. They are especially useful in *Photinus* and *Pyractomena*; extrusion or extraction of them is simple in freshly-killed specimens. They hold some promise in *Photuris*, and voucher series are being examined/compared.


***Photinus cooki* site in sw Missouri.**


***Photinus cooki* site in s Mississippi.**


***Photinus indictus*, sniffing, near Lake Champlain NY**

Daytime Dark Fireflies. Habiti of five genera are shown on pages 4 and 5. Males typically seek mates by *homing* in on chemical signals or cues that females emit. In some species (*Ellychnia corrusca*, *Lucidota atra*, *Pyropyga nigricans*, *Photinus indictus*), males have been observed to fly to gauze-caged (captive) females—after detecting female pheromones males fly upwind, which takes them ("crudely?") toward the source. Then, some probably use visual cues (reflected light) when they near the source, such as a black body against a green leaf. Black-body visual orientation may be the only method used by the Fairy-Ring Firefly (*Photinus cooki*), a "recently" evolved day-time dark species that that does not appear to use long-distance pheromones, but instead has twice been seen in numbers at the leafy tips of branches near a creek and a lake in *late* afternoon. Support for such black-body orientation comes from observations on a twilight-active lightningbug: Theodore Burk found that males of the Big Dipper Firefly (*Photinus pyralis*) were more apt to aim their FPs toward vegetation that had a female-like dark spot on a leaf. A single specimen of the male/female flightless European *Phosphaenus hemipterus* was found in the 1950s in Nova Scotia, presumably its ancestors having been dumped along shore with shipping ballast during the Napoleonic Wars, along with many other insects and plants. This dark firefly apparently has spread beyond its initial introduction, or had a separate introduction, for it has since been collected further west in Canada. Single specimens of a Mexican species, the Broad Black Firefly (*Tenaspis angularis*), have been collected widely in North America since the mid 1800s, and until recently were suspected of being merely occasional immigrants that never successfully colonized. Collection of an occasional second specimen within a few years at a few localities, and the recent discovery of an apparent active population in Gainesville, Florida, suggest that this species may actually be established at certain locations. A climate change that totally eliminates deep freezes in the deep south could perhaps be the key to "naturalization."

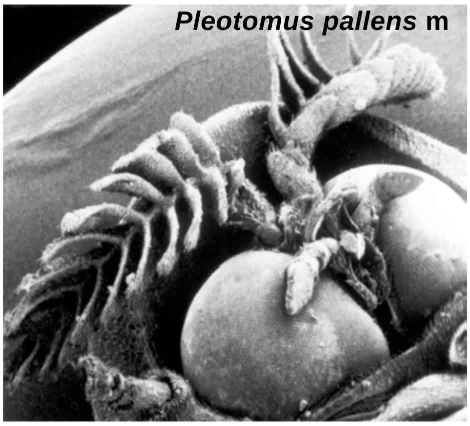

Phosphaenus

Glowworm Fireflies. Pioneers of firefly communication, Frank McDermott and K. G. Blair, made the distinction between System I, with an advertising attractor, and System II, where the attractor waits in the dark and emits her attractive signal-response when she sees the appropriate FP (originally referred to as systems a and b). In nocturnal species in which females emit light but mate-seeking males do not (*Pleotomodes*, *Pleotomus*, *Microphotus*, most

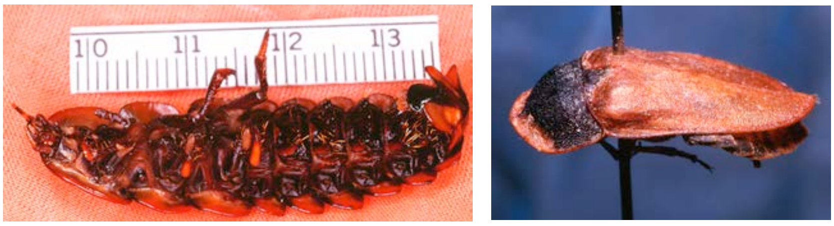
Phausis), males fly about their activity spaces seeking glowing females (Signal System I). Males of some glowworm fireflies have a distinctive appearance, with bulging eyes and pale bodies. The glowworm signal system is analogous to a pheromone system in that females broadcast the attracting signal, but the range is shorter. Males of *Pleotomodes* may light up after they have reached their glowing female; those of *Phausis reticulata* glow during aerial search and non-glowing females light up when they see an illuminated male; such a light-up-response is the *key element* of the Lightningbug Firefly flash-answer, signaling system.

In the glowworm firefly *Pleotomus pallens* a combination of signal channels may be used, with males first detecting a pheromone at a distance. Their huge and robust, branched antennae would presumably increase the surface area available for arrays of chemo-detector organs, though these may also be used in jousting. Species of *Microphotus*, *Phausis*, and *Pleotomodes* may also use pheromones, but their simple(?) antennae yet give no hint of this. Perhaps males of *Pleotomodes* cue in on odors emitted by ant nests and then see glowing females at nest entrances. Males of *Phausis*, *Microphotus*, and *Paraphausis* have a puzzling, seemingly structureless bead on their terminal antennal articles ("segments"). Two *Lamprohiza splendidula* specimens, a European species, turned up in the mid 19th century, one in Illinois and another in Maryland; perhaps they were hoaxes or from intentional introductions that failed—and/or were mislabeled. Occasionally large *Phausis reticulata* archived in collections have been misidentified *L. splendidula*.


***Phausis reticulata* m & f**


***Pleotomus pallens* m**


Lamprohiza splendidula



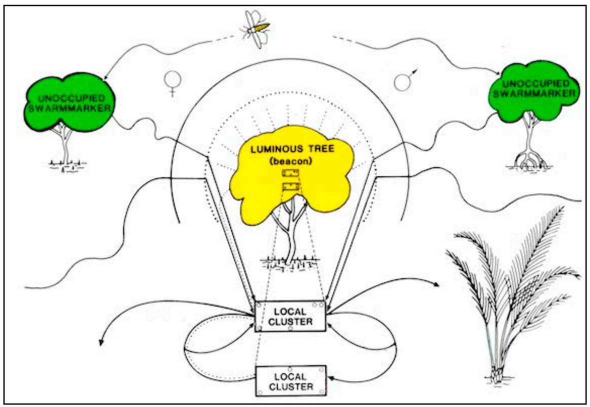
Larva, or female, and a male of Celonese *Lamprigera tenebrosus*, imported into Hawaii in the 1950s to control the African snail; these borrowed specimens courtesy of N. Ohba.

Lightningbug Fireflies. Males of many genera throughout the World, especially America and Asia, emit their mate-seeking flash patterns (FPs) as they fly about (patrol about/within) their habitat (activity space) in flight-paths that are characteristic and often diagnostic of their species. When females of such a species see the FP that is characteristic of males of their species, they flash the answer that is characteristic of their species. In America north of Mexico, flashing species belong to the genera *Photuris*, *Photinus*, *Pyractomena*, *Micronaspis*, and *Bicellonycha*—also, single specimens of *Aspisoma*, a Neotropical genus, were collected in southern Texas and at the southern end of the Florida Keys. There may also be an undiscovered mystery genus near *Luciola* (an Eastern Hemisphere lightningbug genus), near Uvalde, Texas; the original specimens reported by J.W. Green have not been relocated, and no populations were found in field searches during two seasons.

Other Continents/Hemispheres, Other ~~Systems~~ Protocols: Some Asian lightningbug species have mating behaviors of such apparent complexity that the use of the term *Signal System* as long understood, seems an inadequate generalization. I first used the term *protocol* when describing complex mating behavior of New Guinea *Luciola* and *Pteroptyx* (now *Medeopteroptyx*) Lloyd, 1972ab; 1973). The reason for the evolution of such complexity would seem to be that in the absence of *Photuris* predation there has instead been selection for factors relating to mate competence/quality and competition. Many species form sedentary swarms where males and females presumably examine/evaluate each other at length(?), and whatever they are learning is lost to the human viewer—humans cannot easily see, or smell or taste what might be influencing mating decisions. And, like the Age of Elegance on the Continent, in some species everything appears programmed and ritual. Photurines, *Photuris*, *Bicellonycha*, *Pyrogaster*, and others, would quickly eat such sedentary signalers—as perhaps they, that is, their ancestors, once did as they themselves were evolving their carnivory—were they to occur in the Americas.

Chao Phraya River, firefly mangroves of history.

Asian species and their protocols are important to examine because of the contrast the details their behavior provide for understanding the fireflies of the Americas, these latter being the products of an “American Wild West.” That is, there is a natural, inter-hemisphere experiment for such comparison. Here are two examples of easy Eastern-Hemisphere targets: **(1)** The mating behavior of the New Guinea Diamond-Back Firefly (*Pygoluciola* [nee *Luciola*] *obsoleta*, Madang region) includes an initial, perched-flashing period, and both aerial races and chases with bumping (combative dog-fights?) in its protocol; after further interaction at the landing site (dances), couples join and stay together until sunset the following day. Example **(2)**: Several species of bent-wing fireflies in New Guinea and southeast Asia gather in large groups, where the more renown species synchronize their flashes, thus producing a large beacon *effect* to which other fireflies are attracted. After close rapprochement, males of *Pteroptyx valida*, a non-synchronizer in Thailand, mount and display their genital regions to courted females, perhaps revealing their mating status or their previous successes, or availability of connubial gifts; after coupling they clamp females in a vise that is formed by the bent tips of their elytra (upper jaw) and sclerites at the ventral tip of the abdomen. Males then make internal adjustments and insert a mating plug (Wing et al, 1983; Lloyd, et al, 1989).

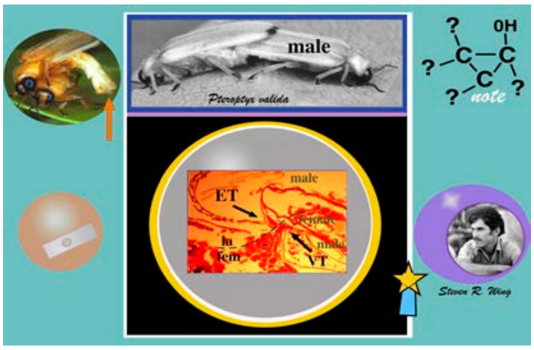


Synchronized flashes result in an epiphenomenal* magnet, composed of spatially integrated local arenas.
***epiphenomenal*: a secondary effect arising from but not causally influencing**

Mounted, then tail brought around to face

However, of special value and perhaps greatest importance for comparison with American lightningbugs may be the mating behavior of those Asian species that outwardly exhibit behavior similar to that found American species, but as far as known, have no history of natural selection by *Photuris* or *Photuris*-like predators. It should be reasonable to expect a complete absence of extreme counter-measures and deceptions in their signaling, excepting those relating to the avoidance of mate competition and the seduction of prospective partners.

Tail bent around, opened in face, clamp



Clamp: elytral tip and ventrite tip (ET, VT), female held, action inside, sectioning and study by Steve Wing (Symposium Slide)

Chapter 3

Methods & Technology

If a man keeps cherishing his old knowledge, so as continually to be acquiring new, he may be a teacher of others. (*The Analects,* XI, Confucius)

This chapter presents methods and basic technical procedures used and developed during this study, including conceptual and working principles adopted or modified from earlier fireflyers. This chapter must go beyond what M&T sections of taxonomic revisions typically present for these reasons: (**1**) The lampyrids offer taxonomic characters—their identifying flashes—that are different from what taxonomists usually work with, and involve unfamiliar methods and technology; (**2**) lampyrids hold interest for a broad range of amateurs, including and especially youngsters and their parents, who lack knowledge of standard taxonomic procedures, and these must be presented here; (**3**) because research biologists in many non-taxonomic specialities will find aspects of firefly biology interesting and attractive for research they will require unfamiliar information—methods for collecting, maintaining, and curating *voucher research specimens*; (**4**) new technology for signal analysis will be developed, and the technology and requirements addressed here will be insightful; (**5**) many research questions that might seem highly attractive may involve such an investment in time (nightly, seasonally, annually) that researchers pursuing academic degrees or satisfying administrative demands should anticipate logistic difficulties.

Fig. 1. Pup tent and vacant BSA camp, 8 June 1963, eastern PA.

Fig. 2. Tarp & PU truck, north- eastern IA, June 1980s.

Fig. 3. Private estate/conservation area north of Nashville TN, May 2012.

Figs. 4. Debriefing: field book, tape-recorder, killing bottles. Eastern TN?, 1970s.

With respect to making this study, beyond the pioneering ideas and methods of Frank McDermott, Herbert Barber, and John Wagoner Green, the tutelage of Richard D. Alexander and the perspectives of Charles Darwin, it was especially the Interstate Highway System, early Space Era electronics, and (once) free camping or 50-cent facilities at state parks and forests that had the greatest impact on field work **(Figs. 1-4)**. Interstates allowed quick access to a wider territory at low cost to be covered during the more limited season of the continent; electronic equipment for recording flashes was of incredible descriptive and analytical value, and was essential/critical for providing confidence that verbal notes of seemingly identical flash patterns observed by eye, were indeed—or indeed not—nearly or virtually identical. Through experience one will appreciate how gratifying it is on occasion to have photo-multiplier chart-records of flashes after the field season has passed and doubts about details and observations rise, and they always will. This is what Barber had in mind when he noted the importance of *repeated* observations. However important modern conveniences and technology were, most of the results achieved were accomplished through patience, persistent doubt, repetition of observation and measurement, and extensive note-taking via a pocket tape-recorder —another and most important Space Era marvel—and its subsequent “debriefing” into a field-book **(Figs. 4, 8)**.

1. Field Work. Field observations and experiments were made at hundreds of localities throughout eastern North America, and a few isolated localities in southwestern United States **(Fig. 5)**. Field studies in Colombia SA, Jamaica WI, southern Mexico, Thailand, and Papua New Guinea at various times were useful for the behavioral contrasts and similarities their fireflies presented. More than 2200 evenings of up to six hours each (average 2-3) were spent in the field—these totals were through the 1990s. Tens of thousands of miles were driven, more than 3000 pages of notes written, more than 5000 voucher specimens of fireflies that were captured, singly in the hand, curated and individually numbered and labeled, and about 48 hours of photo-multiplier (PM) records of firefly flashes were taped.

In addition to observations made in Alachua County, Florida, rather extensive and long-term field observations were made elsewhere. At Hines, Dixie Co. FL; Avon, Hartford Co. CT; Peconic and Shoreham, Suffolk Co. (L.I.), NY; Gee Creek Camp, Polk Co. TN; and Cedarville St. Forest, Charles & Prince Georges Cos.

MD. Study sites were often in or near State Parks or State or National Forests with a tent, camper, or truck. In later years, with rising expenses and park expectations of written reports, and change in work habits with increasing familiarity and focus with fireflies, fieldwork at various sites along highways was planned with the end-point each night near an Interstate Rest Area. A score of law and conservation officers questioned my suspicious behavior, in early years to see whether I had a gun, were a rustler or poacher, and later, whether I were a smuggler of controlled substances. I gave ad hoc firefly lectures and PM-gun demonstrations to Fish and Wildlife officers, a poacher, police, and other night people at the back of my vehicle on a number of occasions—the dim glow of the PM system having aroused suspicions **(Figs. 6 & 7)**. I also PM-recorded flashing police lights. Once I was “interrogated” on a coast road by a plain-clothes officer in an intimidating, long-hooded automobile (years later he, apparently was jailed in connection with the construction and use of my fireflying road for air-importing operations?).

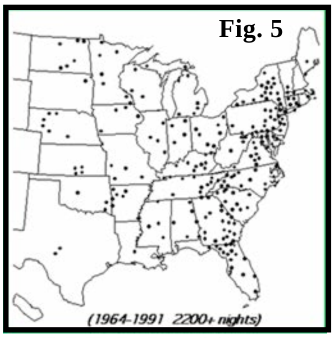


Fig. 5

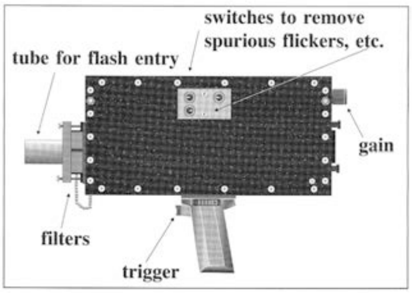


Fig. 6. Photomultiplier-"gun."

2. Data Taken. Typical semiosystematic activities at a site on a given evening included: noting the species of fireflies present, their times of activity and abundance; the collection of flash pattern (FP) data and voucher specimens, making PM-records of FPs; observing flight-paths and activity spaces used, scanning for court-ship and predation interactions; experimention with decoying males to penlight or flashpole simulations of female response flashes**;** and quantifying evening FP change-over profiles in various *Photuris* species (e.g., see *stevensae*). Much time was spent "merely" watching, motionless, trying to fit the flashing behavior seen into patterns (stereotypes) of previously observed demes, to see variations, and identify significant differences. It was a useful habit to quantify various aspects of behavior. More directed activities included, as examples, the quantification of male search-flight parameters such as flight speed and success, sampling and quantification of *Photuris* aerial attack behavior and success, quantification of bat occurrence, and the measurement of temperature variation within firefly activity spaces.

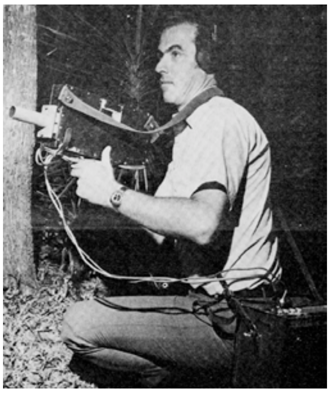


Fig. 7. Photo-multiplier gun in hand, aimed, and tape-recorder and power pack at the hip.

3. Pocket Tape Recorders (TRs). Field notes of an evening, were recorded on a pocket tape-recorder **(Fig. 8)**. Inexpensive recorders, or those with several complex controls or that must be viewed to be operated with certainty, or those with sound-sensitive starting, were not suitable. Thin recorders, that show a tiny red light when recording, that have a single, slide-RECORD-OFF switch, with a locking-OFF mechanism are best—one that fits a deep pocket of a shirt, and that can be leashed on a shoestring looped through a button-hole or epaulet so that it will not strike the ground or fall into water when it eventually slips from the pocket.

Fig. 8. Two TRs from a series of five used during 45 years.

4. Voucher Specimens, Field Books. Holotypes and paratypes will be deposited in the USNM.With experience it became easier to identify FPs on the wing. However, some species required special consideration, especially those of several *Photuris*. Some change FPs with time of night—and perhaps with competition level (male density), season, and habitat structure. Males of some *Photuris* species match FPs of other genera, and though they differ in color, human eyes/brain sometimes err. Some matched FPs belong to *Pyractomena* species and others, especially the FPs of twilight *Photinus* —*appalachianensis* at a western Maryland locality does both **(Fig. 9)**. To identify such *Photuris* species it is necessary to emit a decoy response (female imitation) flash after the male FPs: if his FP is a mimicked (adjunct) FP, the male will *default*, that is, will switch to his species "own" FP **(Fig. 9)**; *Photuris lucicrescens* is atypical, has two FPs (mark-release study) but is not known to default.

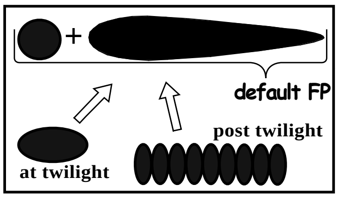


Fig. 9. Default (own) and adjunct FPs.

Fig. 10. KBs and Kill jar.

FP vouchers were collected singly in the hand, with practice, rather than with a net, which would result in a greater chance for error. When doubt or uncertainty existed, because the specimen had been dropped or something raised a suspicion of error, the insect was released or a note “possible chance for error” was recorded. Voucher specimens were placed in a numbered, 2-dram, glass, screw-cap (bottle **(Fig. 10)**. Caps of these "capture/killing" (KB) bottles had the paper cap-liner removed and 1/32" holes drilled in them. When voucher specimen capture notes were entered on the voice recorder the entry began with "KB" (kay-bee, an abbreviation for killing bottle), followed by the bottle's number. Saying "KB" first, identified the nature of the number that followed, and when the recorder was slow in starting (a characteristic of some recorders) only "K" or at most "KB" was lost, not the critical number itself. A night's collection of specimens in their numbered bottles was kept alive overnight in a humid chamber, moist air entering through the holes in the caps. Desiccation was found to be the major killer of captive fireflies—not lack of oxygen—and even when temporary "high"-temperature storage was unavoidable, fireflies remained alive in humid chambers. Vouchers were put in a closed plastic refrigerator box with a pad of damp paper toweling, and this was kept overnight in the camp icebox or vegetable drawer of a refrigerator.

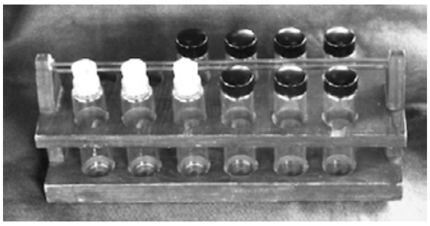


Fig. 11. Rack of 8-dram "live bottles.".

5. Keeping Specimens Alive, Kill-Jar. The morning after capture, specimens to be kept alive were put in numbered 8-dram, corked vials, with a tiny piece of fresh apple for humidity and nourishment **(Fig. 11)**. Specimens to be killed and pinned, were left in their 2-dram KBs, and put into a large killing jar **(Fig. 10)**. Potassium-cyanide is an effective killing agent for fireflies, which immobilizes them almost immediately and does not interfere with and may actually facilitate extraction of genitalia. Ethyl-acetate makes specimens too flexible(?).

This killing/keeping system kept specimens with their field identification KB numbers from the time of capture until they were pinned, without requiring bulky and inconvenient individualized killing bottles, as were used briefly in the beginning. I personally did all voucher collecting, note taking, transcribing, recording, labeling, and curating.

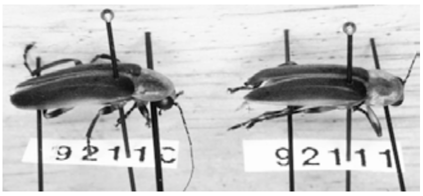


Fig. 12. Pinned, lifted, angle-boarded, with voucher/cabinet accession numbers.

6. Field-books. Notes on the pocket tape-recorder from an evening's observations were nearly always copied into the field-book the following morning. Books were 4"X 8" bound, record/note books. An evening's notes were headed by locality and date. The combination of date and KB# gave each bottled voucher-specimen a unique identification in the field-book entry. When the flashes of a specimen were electronically recorded on the PM's tape-recorder its KB# was associated with it via the PM’s voice-mode recorder; the KB# was at that moment also put on the pocket tape-recorder. At curating the date-KB# was associated in the fieldbook with a unique cabinet-accession number that was pinned to the specimen permanently **(Fig. 12).** All field-books are indexed for species and a few other topics of interest.

Fig. 13. Field-book copies, cabinet drawers.

Field-books were thermocopied and these were bound (in green covers) for insurance **(Fig. 13)**. In these, the specimen identification numbers were written over with a red ink marking pen, as they appear in the original fieldbooks, for quick location. Fieldbooks, most specimens, photographs, PM tapes and Scrapbooks of charts of PM-recordings (see below) will be archived when studies are ended—deposited in the USNM collection; examples of some will be distributed to various locations yet to be determined. Professor Marc Branham will be the administrator and authority.

7. Mounting Specimens, Extracting Genitalia, Safe-keeping. After killing, each specimen was mounted on a number-2 insect pin, with the pin passing through the right elytron just posterior and mesad the humeral angle, as usual for beetles. This avoided destroying a position-unique area potentially useful for identification. The pin is pushed through the specimen until 3/16"-1/4" remains above the elytron, with the impaled insect without pitch or roll. To expose the aedeagus hold the head of the pin between the index-finger and thumb, with the pinned male on its back over the crease between thumb and fingertip; extrude the genitalia by gently pressing, rolling, manipulating an insect pin on the terminal ventrites, toward the tail, easing the aedeagus from under the cylindrical clasper ventrite at the tip **(Fig. 14)**. This is easiest at low-power of a dissecting microscope. It may be necessary to hook the genitalia with the tip of a bent insect pin or *minuten nadln*, reaching between the apical ventrite and tergite and pricking the membrane anterior the basal piece.

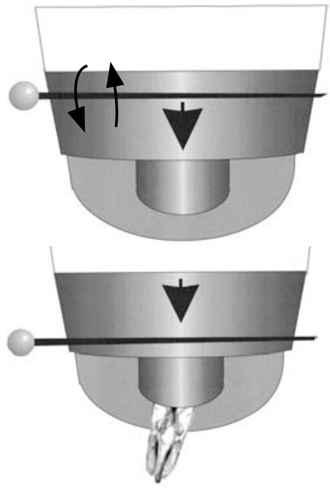


Fig. 14. Extraction/extrusion of aedeagus.

Care must be used not to damage the apical ventrites when pressing/rolling on them, because important characters for the identification of some species occur there. After extrusion, with pressure of the pin removed the aedeagus may slip back into the body. This can be prevented by carefully dragging the pin laterally across the tissue between the sclerotized genitalia and the body, causing the tissue to twist and stick or catch in the extruded position. The genitalia of freshly-killed specimens are left "tethered" to the specimen by the sperm-duct or other tissue, and slightly within the clasp of the ventrites and pygidium. This simple preparation will not usually work with older, museum preserved/relaxed specimens (see below).

If extracted genitalia or the abdomen broke or became separated from the pinned insect, they were glued on an insect point that was pinned immediately **below the specimen**. Following the procedure recommended by J. W. Green, detached genitalia should be glued standing erect, with basal-piece down **(Fig. 15)**. A water-soluble, white glue that dried clear (transparent) was recommended by an associate insect taxonomist. Clear finger-nail polish was easy to carry for field work, and was used.

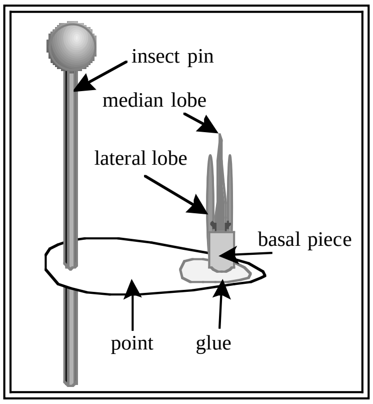


Fig.15. Green's method.

Genitalia were extruded for most specimens in genera other than *Photuris*, because they were found of great importance for the identification of certain species or species groups (*Pyractomena, Pyropyga,* and *Photinus* **(Fig. 16)**, see Green (1956, 1957). In the case of *Photuris*, male genitalia were historically presumed to be of no taxonomic value, and during early years of this study genitalia were seldom extruded. However, significant differences were found and in expectation that more would be seen with better microscopes, they were extruded in some freshly-caught specimens in most series, and close examination has revealed a number of possible sites for useful variation and characters **(Fig. 17)**. The dissection of dried then chamber-relaxed specimens or even those drenched with Barber's solution is nearly always very difficult and generally very damaging, most especially with *Photuris*.

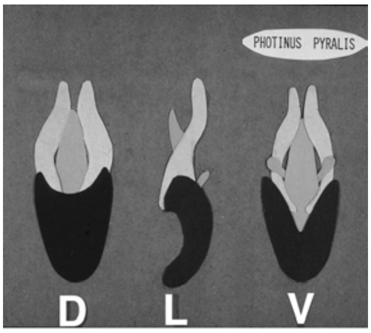


Fig. 16. Photinus pyralis aedeagus.

After genitalia were extruded specimens were pinned on an angle board, using a technique of UMMZ orthopterists: pins pushed into the back board (not through the specimen) lifted the pronotum and abdomen to lie horizontally **(Figs. 12, 18).** When on the road, angle boards were kept in a fitted Schmitt box, and on extended field trips when many specimens were collected, after they had dried they were pinned into space in the the bottom of the box or transferred singly to another **(Figs. 18, 19)**. At the lab vouchers were kept in several Cornell drawers in two cabinets. Specimen trays and specimens in the drawers have colored labels, indicating those PM-recorded and vouchers whose luminescent spectra had been measured by W. Biggley et. al. at John Hopkins (**Fig. 20**).

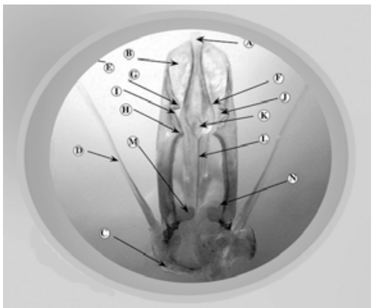


Fig. 17. *Photuris* aedeagus.

8. Relaxing/Extrusion—Archival Specimens. If specimens are dried or preserved in alcohol it is necessary to relax ("moisterize") them before the genitalia can be extracted. Various techniques were used, depending upon the nature of the specimen and how it was preserved. I prefer to keep such specimens in a humid chamber **(Figs. 21)** for 3-5 days and then apply a drop or two of Barber's solution directly on the terminalia and. This relaxes them sufficiently, and they can be handled and dissected carefully with only slight damage, **except** for ***Photuris***—

among lightningbugs. A chemical (Lysol®) is added to the damp sand in the humid chamber to prevent the development of mold and specimen damage. An ultrasonic bath was occasionally used to hasten relaxing **(Fig. 22)**, but when left unattended for a few minutes, will rapidly eroded, beginning with the tip of the abdomen, progressing anteriorly. A faster method of relaxation is to place the specimens in a mild (and warm), detergent solution (e.g. Kodak Photoflo®) for several minutes, but this is less satisfactory.

After relaxation, sometimes it was possible to tease or hook genitalia out far enough to see their diagnostic features. Often it was necessary to separate the ultimate dorsite (pygidium) from terminal ventrites on one side (of a relaxed specimen), with a sharp blade (e.g. a splinter from a razorblade or of broken glass fastened to a small handle), and then hook the genitalia out or push them out with the tip of the blade, pin, or forceps. Sometimes the entire tip of the abdomen will become detached and everything must be mounted on a point. Typically, in such cases, the genitalia including the basal piece with a bit of tissue, and lobes and ventrite 8 were completely removed from the specimen and pointed.

9. Cross-referencing. After the genitalia were extruded, the specimen's permanent and unique accession number was pinned below it on its pin **(Fig. 12)**. These numbers can be made with a laser printer in Excel® on archival paper. Specimen numbers begin with the last two digits of the calendar year, followed by a simple ordinal series. For example, for 1968, the first numbers of the year ran 681, 682 … 689, 6810, 6811 etc. The last number for that year was 681468. The identification number for each specimen was entered in red ink, next to the KB# entry in the field book (in Fig. 12, numbers 92110 & 92111). Thus, as explained above, a specimen's accession number can lead to the field-book and be associated with the specimen's notes, and through the associated date and KB# in the field-book, to a flash recording on the PM tape and in the flash-chart scrapbook (see below). On the other hand, when starting with the PM tape or scrapbook trace, the date and KB# lead through the dated field book, to the specimen accession number. Specimens are arranged in the cabinet alphabetically by genus and then species epithet.

Fig. 18. Balsa angle boards in a protective Schmitt box, with room remaining for already-dry specimens.

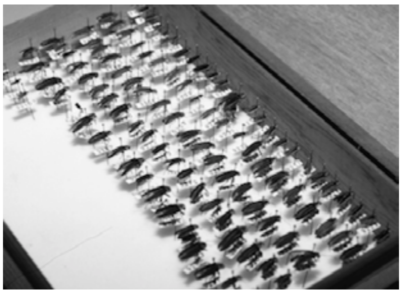


Fig. 19. Schmitt box with drying/secure box overflow.

Fig. 20.Trays of vouchers in four drawers.

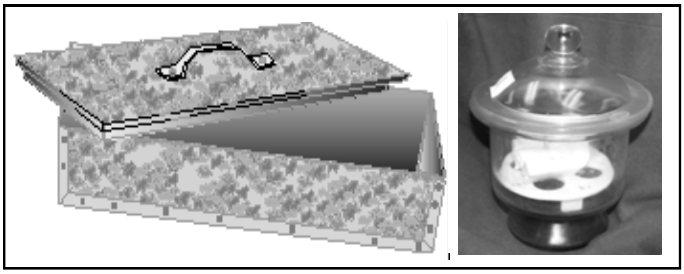


Fig. 21. Two types of relaxing chambers, not to scale!

Fig. 22. Ultrasonic cleaner/vibrator.

10. Alcohol and other Preservation. In the past certain specimens were preserved in 70% isopropyl alcohol: including firefly eggs, brachypterous, larviform, and other soft-bodied females, females whose eggs were to be examined later, specimens whose internal reproductive systems were to be examined, specimens that had died and slightly decomposed, and spiders and other firefly-associated organisms. Today 95% ethanol is always used because it will also preserve DNA in such specimens. Flight (hind) wings of many species were mounted on microscope slides for the examination of wing venation, and in particular, the wings of many micropterous and macropterous *Pyropyga nigricans* were so mounted for comparison and measuring.

11. Parasites. Diptera parasites (Phoridae, Tachinidae) emerged from fireflies, after pupating in a bottle,were killed and pickled in alcohol or mounted separately with reference numbers of the host. Such small, soft-bodied insects can be glued to a point, or *staged* by pinning them with a *minuten nadln*, which in turn is pinned to a pith block that is mounted (impaled) on the #2 pin below the firefly specimen. An additional data label can be attached beneath for bio notes/records and field-book references.

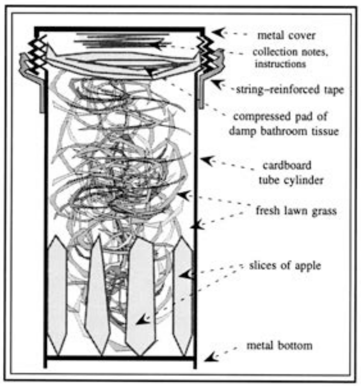


Fig. 23. Longitudinal section through a mailing tube.

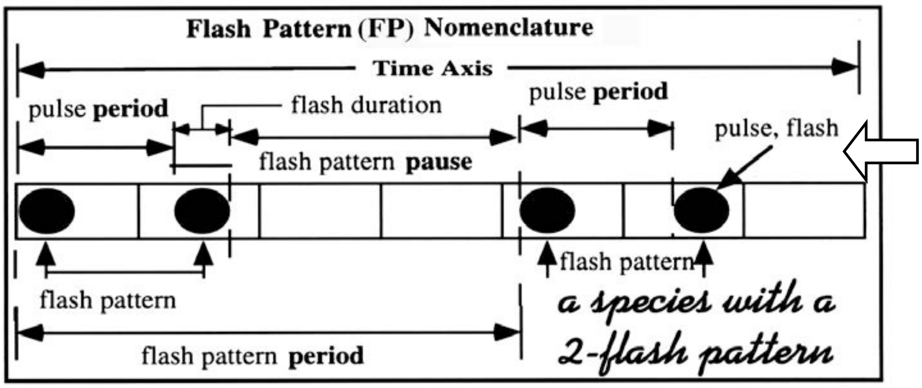
Fig. 24. Serum vials for collecting, and mailing tube.

12. Shipping Living Vouchered Specimens. When shipping live fireflies: On the night of capture fireflies were put into a metal-reinforced mailing tube that had been loosely stuffed with fresh grass **(Figs. 23/24).** Long thin slivers of washed apple were slid down the inner walls of the tube at four points, a damp pad of slightly compressed toilet-paper was placed over the top of the grass, and a descriptive note added on top. The metal cover was screwed on tightly and sealed with string-reinforced mailing tape. Tubes were airmailed special delivery, but not mailed Thursday or Friday when, at the time, they could possibly have been kept in a hot post-office or mail truck over the weekend.

13. Flash Pattern (FP) Configuration, Nomenclature & Measurement. Words and terms used for various aspects of firefly signaling have come into and rarely fallen out of usage, and an even rarer few have changed their meaning. Many definitions are in the Glossary; the following is an illustrated introduction and overview (**Fig. 25**). A flash is an emission of light, to be contrasted with a glow, and an indefinite distinction is made between them. Terms such *long flash, short glow*, glow of *indefinite duration*, are usefully ambiguous and usually understood from context.

It is important to take note of the fact that the parameters of bioluminescent emissions (duration, rate, period) are influenced by ambient temperature, and this must be taken into account when dealing with (observing/reporting) flashing behavior.

A **flash pattern (FP): (1)** is the **male** species-typical emission of light broadcast(ed) during mate search; that **(2)** is often the repeated unit of light emission that is useful to the naturalist for identifying species; **(3)** is the unit of emission that typically is the signal that females use to recognize males of their species and that will cause/influence them to flash respond; **(4)** is often only a single flash but may comprise two or more flashes (<11) which are termed **flashlets** or **pulses**. The **FP period** is the duration of time from the beginning of one FP to the beginning of the next consecutive FP. It is useful when used with other data for the identification of species. With **Figure 25** note the listed elements, defined graphically:



flash pattern (FP)
pulse/(flashlet)
flash duration
flash pattern period
flash pattern pause
pulse period
Note: Time and Relative Intensity (Y) Axes

Fig. 25. Terms used for elements of flashing patterns of fireflies.

FP **rate** is the reciprocal (1/period) of FP *period*, is recorded in **Hertz** (cps) and is useful for comparison, but also and especially for anticipating/estimating FP period/temperature slopes when few period (but temperature-spaced) data are available.

When the FP is composed of 2-9-11 pulses the pulse interval is nearly always and easily measured with a stopwatch **(SWAT; Figs. 26, 30, 31)**, and for purposes of field recognition is simply reported as pulse interval (**period**). For example, this is the case with the 2-pulse FPs of the several (and some confounding "species") in the *consanguineous* Group of *Photinus* **(Fig. 25)**. When collecting FP-vouchers, after **timing** pulse period, they are light-spotted and grabbed in hand **(Fig. 27/28)**. The FPs of certain *Photuris* species present two aspects for special mention: FPs of river-associated species (e.g., *potomaca, missouriensis, chenangoa*), and of most *Photuris* Division I species (e.g., *frontalis*,

Fig. 26. Fireflyer SWAT, a huge, ticking, split-timing turnip.

congener), are **trains** of single flashes—that is, long-continued, "almost" metronomic sequences of single short flashes with near-constant (only slightly irregular) periodicity. The element of communicative importance may be the/a rate established by a short sequence (pair?) of flashes, which itself slides or jumps along the train. Note that though the FP period is easily measured with a SWAT (> 0.5 sec), and is the more useful for field identification, the **rate** may be of more value for taxonomic/systematic comparisons—this may also be the case in all FP parameters. One FP (at high population densities?) of *Photuris fairchildi* (s. l.?) appears to be a flash train, but it demonstrates curious and virtually subliminal idiosyncrasies: **(1)** it does appear to be of indefinite length but no sequences longer than 30 pulses were noted; **(2)** pulses in a train gradually increase in intensity until toward the end of long trains; **(3)** pulse rate gradually increases along the "train."

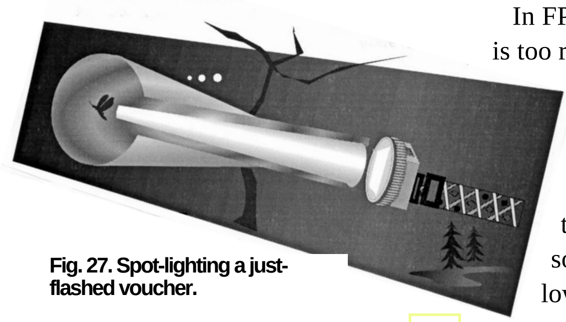


Fig. 27. Spot-lighting a just-flashed voucher.

In FPs of more than one pulse/flashlet in which the pulse repetition rate is too rapid for the eye to accurately distinguish/count individual pulses, thus be timed with a stopwatch (SWAT), the FP is termed a *flicker*, and the pulse rates are reported in Hertz. Pulse-rate in the FPs of *Pyractomena dispersa* are challenging in the field because it crosses the threshold of discernment within the span of temperatures that occur during *dispersa's* season. To the human eye the FPs of some species appear to twinkle, jerk, or hitch, especially or only at lower temperatures. In the bimodal flash of *Photuris hebes* the first mode is dimmer and often registers in PM recordings as merely a shoulder of the second. At lower temperatures when viewed from the side, the flash of a flying *hebes* hitches/jerks along, revealing its bimodality, but when *simuultaneously* view from the back, the other observer will see a short crescendo flash. Perhaps the two segments of the lantern do not flash in synchrony, and viewed from the side the spatial separation is resolved by the human eye(?). In one FP of *fairchildi* the 2-3 rapid pulses of rising intensity appear as a twinkle at warmer temperatures, and even more conspicuously, these FPs are repeated at a rapid rate, one quickly following the other and *appearing* to pause for merely “one missing beat.” Of importance here is the fact that the apparent FP period of *fairchildi*, as compared with those of other species, is an artifact, that is, seems not to be homologous, but perhaps derives secondarily from some other sequential element of, say, an ancestral train(?).

Fig. 28. Head-lamp near perfection.

Fig. 29. Armored (meat-case) thermometers.

The **female flash response** is usually a single flash of short duration (< 0.3 sec, and usually emitted with various and seemingly variable delays after the FP. However, close examination of and experimentation with female responses may eventually reveal that female delay is varied as part of signal codes that have evolved as countermeasures (CMs) to predation by *Photuris* females via aggressive (signal) mimicry. This context (CMs) may in fact eventually be recognized as the single most important feature of American (Western Hemisphere) signal codes, and will be discussed briefly elsewhere

Fig. 30. Data on the fly.

The measurement and terminology of FPs is straightforward and as noted/illustrated in **Figure 25**. It is of first importance that ambient temperature in the activity space be measured at intervals throughout the data-taking period, with the thermometer thoroughly equilibrated while hanging or held away from extraneous sources of heat—pavement, buildings, humans. I have used a variety of instruments, and favor a simple, calibrated, metal-cased “meat-case,” Fahrenheit thermometer **(Figs. 29/30;** more text below**),** and a "turnip," a huge, mechanical/wind-up, analogue SWAT, one that audibly ticked when eyes were focused elsewhere in the dark! **(Fig. 26)**

The split-timing feature is necessaryfor simultaneously/concurrently timing pulse periods and FP periods, as in FPs of fireflies in the *Photinus macdermotti-consanguineus* enigma. Electronic SWATs and thermometers are available **(Figs. 30-31)**.

Fig. 31. Electronic SWAT and thermometer.

14. Photo-Multiplier (PM) Recording, Measuring, Illustrating Flashes. PM-recorded voucher specimens were captured immediately after observation/ recording by illuminating them in the beam of the headlamp and grabbing them by hand. To do this, a headlamp with its spot focused at 2-4 feet is a necessity **(Figs. 27, 28)**. Many PM recordings were made while attracting flashing, flying males to simulated female flashes (decoying, penlight). This gave good exposure of the lantern to the PM-tube, and brought the fireflies near, to be captured in hand as vouchers. When recordings were made like this were compared with the flashes of non-attracted males no differences were noted—that is, differences that might be expected to exist between flashes emitted in the two different situations (search/ advertising versus courting). However, attracted/approaching males of many *Photuris* commonly dim their flashes, and often other flashing males approach the decoy, but no differences other than intensity and period/pause duration were noted in FPs.

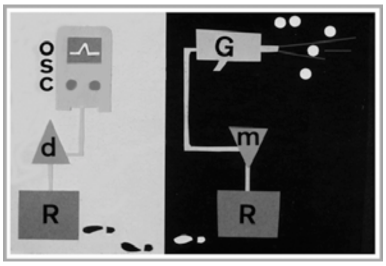


Fig. 32. PM-recording system.

The PM-recording system used continuously since 1967 operated as follows: Flashes were electronically detected by a PM-tube, transduced to frequency modulated signals that varied proportionally with detected intensity (as seen by viewers and PM, but not necessarily as emitted at the lantern), and recorded on magnetic tape (7.5" and later, 3.25"/sec). The PM unit (PM-gun) was hand-held like a pistol and aimed as one points a finger **(Figs. 7/33).** The PM-gun filtered streetlight and skylight flicker. The PM-system also automatically compensated for changes in background illumination, and could record (not simultaneously) voice notes. An audio side-tone while recording, via a built-in speaker/microphone, was used to adjust amplifier *gain*. When the recording sensitivity was too high and distorted the recorded signal, an alarm sounded. Chart and oscilloscope traces show this alarm as “grass” and other distortions. Detectors other than the a PM tube were investigated, anticipating the power demands (2 gel cells) would be smaller, but none then (1980s) compared with the PM tube with respect to sensitivity—by several factors.

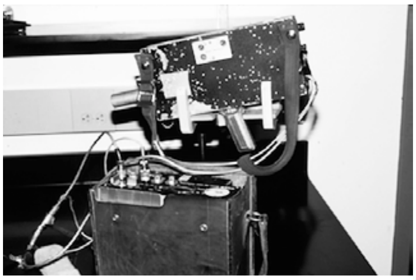


Fig. 33. PM-gun, batt. pack and tape recorder.

Data were retrieved from the PM-tapes in the following manner: The frequency-modulated signal—a 9-12 kHz whistle that changed tone proportionally with detected flash intensity changes—from the tape was demodulated, changed to a small voltage that varied in amplitude proportionally as the flash had varied in intensity/brightness. The demodulated signal, the small, varying, information-carrying voltage was then fed into a Tectronic® storage oscilloscope, where flashes appeared on the screen **(Figs. 32, 34, 35)**.

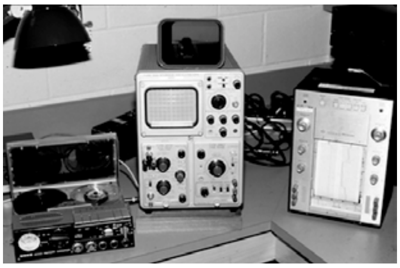


Fig. 34. Tape playback to view and chart flash records.

Four Uher® tape-recorders since 1967 were used and endured rough field experience, salt-air exposure, high humidity, and thousands of switch movements, with fingered reel-turnings, backward and forward to position taped records for precise positioning for display—that is, the tape was pulled backward via the reel while switched on PLAY and PAUSE. The backward low-frequency flash sounds (growls) were distinctive and recordings could be positioned precisely.

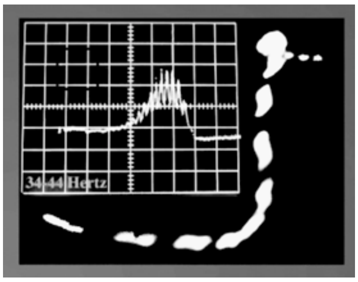


Fig. 35. Tape playback on the oscilloscope to view FP (flicker) of *P. lamarcki*; contrasted with film (camera hand-held near flying lantern) record of this flicker.

Such PM-records were the fed into a chart-recorder to prepare recordings for publication and comparison (**Fig. 36, 37**). First, chart records were snipped from the roll and pasted into a scrapbook: Snips were lightly pressed face down on a desk-blotter tablet lightly sprayed with a photomounting glue. When the blotter was full the back of the chart snips were sprayed and snips placed in chronological sequence on large scrapbook pages **((Figs. 38, 39).** Pages were removed from the scrapbooks and filed in (legal sized) folders and paginated **(Fig. 40)**. In recent years scrapbook records have been scanned directly into the computer for publication figures.

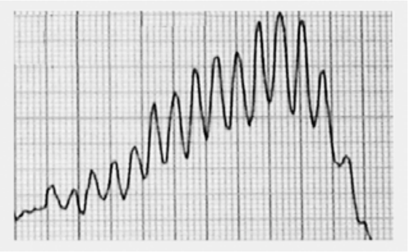


Fig. 36. Tape playback into ink/paper chart recorder (ala EKG) at 125 mm/sec (speed).

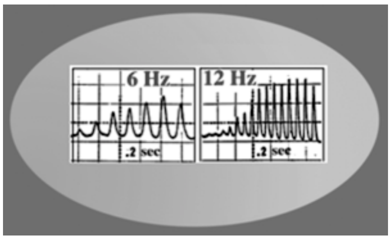


Fig. 37. Comparison of FPs of two species.

Fig. 38. Snipped and marked chart records attached face down on sticky sketch paper.

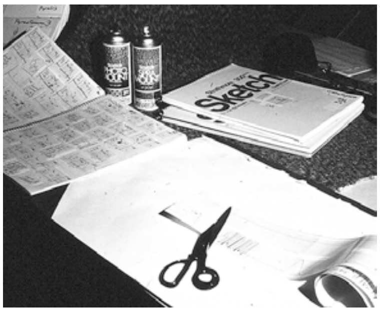


Fig. 39. Charting, from snipping to scrapbook.

Charts were measured in mm and converted to time. Modulation rates were rounded to the nearest one-tenth Hertz (cps), flash durations to the nearest one-hundredth sec, and flash intervals to the nearest one-tenth second. Points on flash traces from which measurements of duration were made were base duration and duration at half-maximum intensity. Several sources of variation for PM recordings of flying males are present. Variation in flash duration observed among the recordings of an individual or within a species are certainly due to the changing spatial relationships between the firefly lantern and the PM-detector: Recording distance varies as does the orientation of the firefly lantern with respect to the PM, thus the variations reported here must be viewed in this light. They are important when considering recording technique and signal fall-off or other circumstances of communication that may be of insectan significance, but they complicate the understanding of variance at the light-organ. It is obvious that the intensity changes seen in recorded flash patterns are relative, not absolute —light output (photons) at the firefly cannot even be crudely estimated without knowledge of firefly to PM distance, the orientation (aim) of the target LO, and the solid (3-dimensional) output of the organ. Thus, reported here are only general timing values and approximate range based upon a large number of observed recordings. The nature and refinement of firefly discrimination of flash duration and variation is known only crudely, as for example experiments on female discrimination in *Photinus* (e. g. Lloyd, 1966).

When available only strong and "clean" recordings were used for measurement. When poor records are used it is is noted. Tape-speed sometimes varied slightly between recording and playback. Since the resulting change in recording measurement was less than variation noted in the field due to intra- and inter-individual variation, which may be partly due to within-site moment-to-moment and point-to-point temperature variation, special calibration checks and procedures for tape-speed variation were not considered necessary or used after some experience with reality.

When more precise analyses of flash signaling are made, tape-speed checks (on site, crystal controlled), multiple detectors (2+ PMs at different angles feeding into or radio-transmitting back to multichannel recorders), and multiple temperature recordings in the firefly activity space may be desirable. Flash parameters other than durations are sometimes noted.

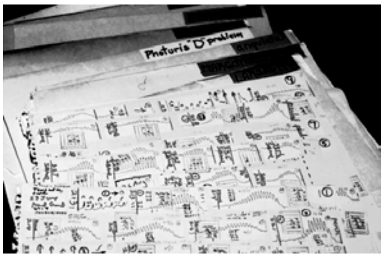


Fig. 40. Sketch-book pages with snips of PM-records..

15. Geographic and Seasonal Distribution (Phenology). Information on the geographic and seasonal distributions of North American fireflies is useful for finding active populations in the field, for recognizing undescribed species, and for comparison with new trends induced by climate change. Field data reported here were taken during two consecutive decades before 1985.

These data are of three general kinds, and are treated in three categories: (A) **GE**ographic—**SE**asonal—**DIS**tribution (***GESEDIS***) data, from reliable archival records, including museum specimen labels and species lists that judged to be reliable; (B) ***GE***ographic***—SE***asonal—***DIS***tri-bution—***OBS***ervational) (***GESEDISOBS***) data, from personal field studies in North America, beginning in 1963; and (C) **SE**a**S**onal—**OBS**ervational (***SESOBS***) data, from personal extensive "semi-systematized" observations of the occurrence and abundance of fireflies at several primarily Florida sites in the years 1964-1984 (sites near Gainesville in particular).

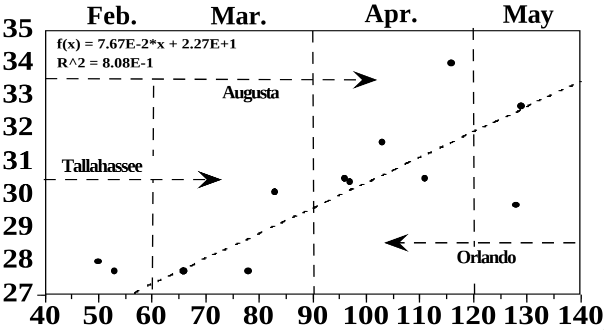


Fig. 41. GESEDIS (Latitude/DayOfYear).

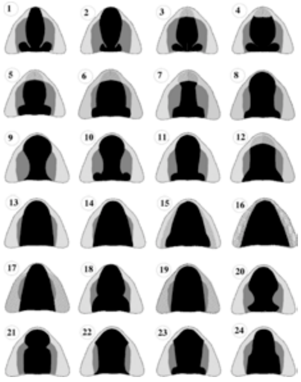


Fig. 42. PN sketches: *L. atra.*

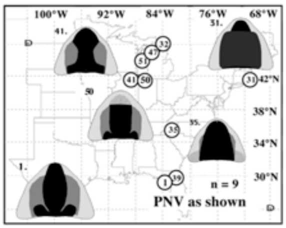


Fig. 43. PN distributions.

(A) GESEDIS Data (Fig. 41). These data show seasonal occurrence in latitudinal (south to north) progression. GESEDIS records were made as I examined and identified numerous archival holdings. Specimens were sometimes measured (pronotal length and width, elytral length), variable color patterns sometimes recorded **(Figs. 42)—**vittal forms of one in particular that offered insight into population differences geographically: *Lucidota atra* **(Fig. 43)—**regions revealed might also be or give information toward those of flashing species. Genitalia were extracted, and details on labels sometimes noted. Certain records were subsequently transferred to Exel® computer files and plotted with *DeltaGraph*®.

These computer files are termed "ALL" GESEDIS lists. (More selective, focused sub-lists were initiated to control for various archival biases but were not continued: "SELECTED", "EARLY".) In ALL files, numerical values for key data were entered. In most cases the latitude and longitude of the county of collection was estimated—to the nearest tenth degree—from inspection of the counties illustrated in a commercial atlas. For huge counties, as in Nevada and Arizona and a few other cases, estimates for the localities within the counties were used. In ALL files, years became 3-digit numbers (1776=776), month and day became a day-of-year (DOY) number (4 July=185), and a week-of-year (WOY) number was entered in a third column (4 July=27) (see A. Peterson, 1934:T-13, and Appendix below).

There are several sources of bias in GESEDIS records. Holiday areas (parks) and dates (Independence Day, 4 July); counties with agriculture colleges and entomology departments, or museums, may be expected to be have "over" representation. Some records are obviously flawed: archives retaining student collections have unusual dates and localities represented. For example, one locality in New York State near the Canadian border has, over several decades, produced *Photinus pyralis* specimens, yet other sources and field experience indicate that this species only rarely occurs north of Pennsylvania at this longitude. Other specimens seem to have been transported out of range and time, for their locality of collection. Interestingly, a *P. pyralis* adult labeled from near Tampa, Florida, 150 miles south of the southern-most known population for this species, was taken on an early date that would be seasonally appropriate (extrapolating the continental day-of-the-year/latitude regression) should the species occur there; it may have been transported as a larva in soil (flower pot?), and eclosed appropriately. A few specimens certainly were mislabelled. There is a Delaware record for a Caribbean firefly, given to me by an energetic, traveling graduate student. But then, this is a wide-ranging, sporadically occurring, vagabond "species"—perhaps it really did get to Delaware "by itself", that is by Gulf stream or hurricane winds?

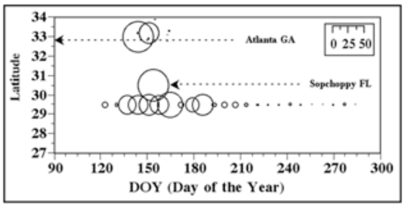


Fig. 44. GESEDISOBS, seasonal occurrence.

(B) GESEDISOBS Data (Fig. 44). Personal records (jel specimen labels, field books, PM-tapes) of sightings, their dates and localities, for each species during the years 1963 to ca 2005, were quantified, and tabulated. Such records for the north-central Florida region appear in the SESOBS section below. But for a very few localities elsewhere I experimented with the plotting form shown in **Figure 44**. Such 3-dimensional charts quantified seasonal abundance based on observations, but was not continued.

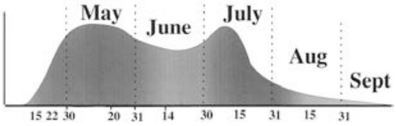


Fig. 45. Interpretive summary view of seasonal occurrence from SESOBS data shown in Figure 46.

(C) SESOBS Data (Figs. 45-46). During 1966-1984, sightings of species (males) were noted and sometimes quantified (males active) at several north Florida sites. These observations were primarily at sites in Alachua County: Gun Club and Airport Pond, both near the Gainesville Airport; Austin Cary Forest, near Waldo, Florida about 12 miles north of Gainesville; Medicinal Plant Garden, on the University campus near Lake Alice, a wildlife preserve; and Lake Place, along the western shore of Newnans Lake, including areas on

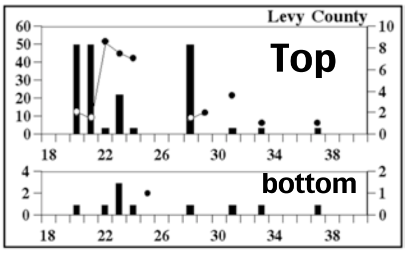


Fig. 46. Data-graph of seasonal occurrence of *Photuris beani*.

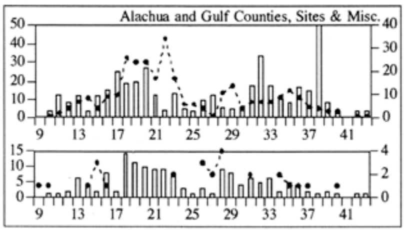


Fig. 47. SESOBS data-graph of a clearly bivoltine seasonal occurrence.

the bluff southwest of Palm Point. A general Gainesville "locality" combined records from several occasionally or incidentally visited sites. Severa sites were visited in the Gulf Counties Region, in Levy, Dixie, Lafayette, Taylor, and Gilchrist Counties. Records from them are combined variously as noted, and are phenologically distinct, usually being seasonally earlier than those of Alachua County. Individual sites in Gulf Counties Region were variously discovered, nicknamed, visited repeatedly, and abandoned over the years. Their names appear in the field books (Hogs' Delight, Shell Mound, 11-mile Bridge, Old Town, Hines, etc).

In quantifying firefly activity in early years I merely noted that a species was present (***sight*** records—note: unfortunately *sight* data were initially called *count*, which will appear in some files); I soon began to record the number of males that were flashing (***quant*** records), as scanned from a single station of view. *Quant* estimates distinguished several levels: 0, 1, F (few=2-7), S (several=8-20), M (many=50-100+), T (thousands=indefinitely, very high, rarely used). Number values were combined to give an average value for each week of the year (WOY) for each species' adult season, at each locality. Because my visits to sites across the years were "roughly" "random", these records may be used as reasonable first indicators of seasonal adult presence. Among-season differences in "early" and "late" make the spread of the indicated firefly seasons broader than would be observed on a single year, maybe by a factor of 1.5-2(?).

Fig. 48. US County map commonly used to show records of known occurrence.

Reading SESOBS charts: A simplified interpretation of a SESOBS data- chart is shown in **Figure 45**. Compare this with the data chart from which it was derived, **Figure 46**. Both record-types (sight, quant) of occurrence are given in the larger (top) graph in each set (**Fig. 46**, see TOP): the bar graph gives the average quant (quantity, read on the left Y axis) for the WOY (week of the year) shown below on the X axis.

Also in this TOP chart note the dots (weekly-consecutive dots are connected). These indicate the total sights (read on the right Y axis)—that is, this number tells how many times (over the years) I saw them during the week numbered below (X axis). The *bottom* (small) graph indicates two different types of data: the bars give the "n" (number of nights upon which the mean quant value in the TOP graph is based (read on left Y axis); the dots indicate how many times I looked specifically but saw **none**, that is, got a zero sight (read on the right Y axis). **Figure 47** is the SESOBS chart of a species with two generations per year (is bivoltine); the overlap seen results from variations among seasonal records that were combined, and because local demes are not phenologically synchronous.

Fig. 49. From Raisz US map of. U.S. landforms.

16. Geographic data, maps. Maps of geographic distribution are shown on a "standard" US county map, which were available through the UMMZ, Ann Arbor (**Fig. 48**). The landform and physiographic province maps used are the familiar one of Erwin Raisz (6th revision 1957, **Fig. 49**), though occasionally the more stylized rendition by Charles Hunt were use (by his permission, **Fig. 50**). Since Hunt's original maps no longer existed, those needed from his book (east and west U.S.A. and Canada) were combined, and retouched (J. Knobb). Since about 1963 geographic records of occurrence of most NA species have been kept in a (19" X 13") masonite-bound folder of UMMZ maps, with a backup copy kept at another site (**Fig. 51**).

Fig. 50. From Charles Hunt maps of N. A. landforms.

17. Morphological data. The pronotal median vitta (vitta-gram, **Figs. 52)** has been considered as a potential taxonomic character for *Photuris*; differences among them had been noted, and it is conveniently conspicuous. The next two chapters will discuss this character and its "coded forms", with suggestions for further analysis. General external features of the *Photuris* exoskeleton are mainly color and size. FP-voucher series were measured, ratios calculated, and colors of various sclerites coded and tabulated.

Fig. 51. Books with UMMZ maps of known geographic occurrence of working US species.

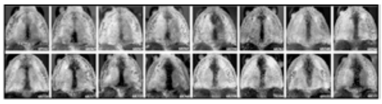
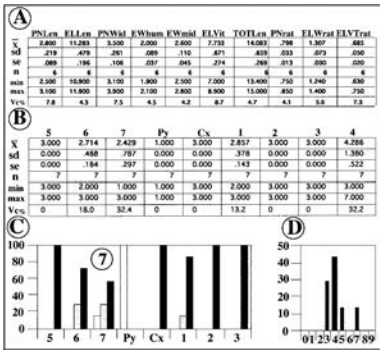


Fig. 52. Array of pronota from a series of *Photuris sivinskii* FP-vouchers, showing the range, an array, of median PN vittae (vittagrams). Note accession numbers.



Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.800	11.283	3.500	2.000	2.600	7.733	14.083	.798	1.307	.683
sd	.219	.479	.261	.089	.110	.671	.659	.033	.073	.050
se	.089	.196	.106	.037	.045	.274	.269	.013	.030	.020
n	6	6	6	6	6	6	6	6	6	6
min	2.500	10.900	3.100	1.900	2.500	7.000	13.400	.750	1.240	.630
max	3.100	11.900	3.900	2.100	2.800	8.900	15.000	.850	1.400	.750
Vc%	7.8	4.3	7.5	4.5	4.2	8.7	4.7	4.1	5.6	7.3

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.714	2.429	1.000	3.000	2.857	3.000	3.000	4.286
sd	0.000	.488	.787	0.000	0.000	.378	0.000	0.000	1.380
se	0.000	.184	.297	0.000	0.000	.143	0.000	0.000	.522
n	7	7	7	7	7	7	7	7	7
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	18.0	32.4	0	0	13.2	0	0	32.2

Table 53. Morphological data; measurement, ratios, color, and splash histograms.

The statistics given in the tables are used for both measurements and color evaluations: mean ($\bar{x}$), standard deviation (sd), standard error (se), number (n), minimum value (min), maximum value (max), coefficient of variation (Vc%=sd/x) Measurements were made with a Zeis microscope, in millimeters; specimens were hand-held for viewing and measuring with an eye-piece micrometer. Example measurement/ratio data from voucher samples are shown in **Table 53(A)**. The dimensions given are: pronotal length (PNLen); elytral length (ELLen); pronotal width (PNWid); elytral width at humerus (EWhum); elytral width at midlength (EWmid); elytral lateral vitta, measured from the anterior edge of the elytron (note, the two vittae often differ in length—then the average or in some cases the length of the left elytral vitta is used; total length (PNLen+ELLen); pronotal length/width ratio (PNrat=PNWid/PNLen); elytral width ratio (ELWrat= EWhum/EWmid); elytral vitta ratio (ELVrat), ELVit as a fractional proportion of elytal length (ELVit/ELLen); total length (PNLen+ELLen).

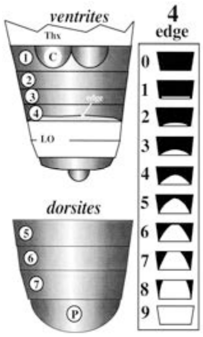


Fig. 54. (A) Elytral lateral vittae, (B) Key to dorsites, ventrites and pre-lantern ventrite "4" splash of pale.

Table 53(B-D below) shows color data numerically and histographically. The three color categories scored are, pale, dusky, and dark, translated as follows: (1) ivory/tan, "1"; (2) medium- to medium-dark, "2"; (3) dark brown/black "3". Green used the term piceous for dark pigment in *Photinus* and *Pyractomena*, but since this can include "pitch-like" with glossy and/or amber high-lights, I have not used it. In descriptions and text I have avoided traditional Latin adjectives, fuscous and flavous, but occasionally used "rufus" since it has a known and similar meaning in common English, ≈brick-red. The cuticular elements scored, as illustrated and numbered in **Figure 54** are: **Ventrites**, "1" first *visible* ventral plate; "2" and "3" ventral plates in sequence posteriorally; and plate "4", immediately anterior the lantern, is scored following the "4-edge" (splash) chart (**Fig. 54**), indicating the degree of splash/intrusion/encroachment of light color at the posterior margin. Hind coxae "C" are scored with the same color values as ventrites, as are **dorsites**, which with the pre-antepenultimate "5" and in sequence plates "6"-"7" (antepenultimate, penultimate) and finally the pygidium "P". The terms dorsite and ventrite are used and not sternite and tergite respectively because the sclerites involved are fusions with sclerites from the pleurae.

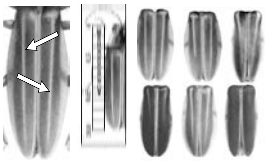


Fig. 55. With cladistic analysis perhaps possibilities.

Diagnostic characters are not evident, but with additional characters and reevaluations (**Fig. 55**) and from signaling behavior and DNA they may prove useful in the development of phylogenies, "surely there must be something of use."

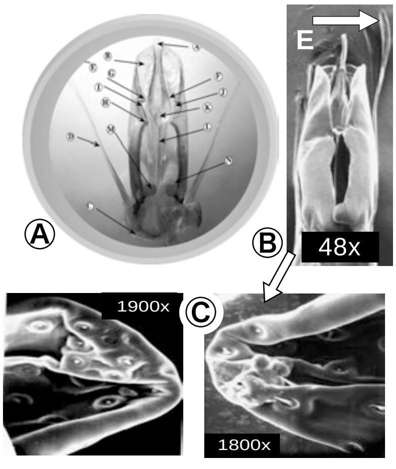


Fig. 55. Features G–J in A may especially hold some promise. E element at upper left in A and B shown at high mag. in C.

Genitalia. There are several points of taxonomic interest to be found in *Photuris* genitalia: these will be examined later in collaboration with Marc Branham. Those noted in particular are found in the ventral aspect of the lateral lobes (parameres in some lit.), which often has dominating cusps, inward swirls, fields of micro-cusps, and other noteworthy gadgets (**Fig. 55A, B**.

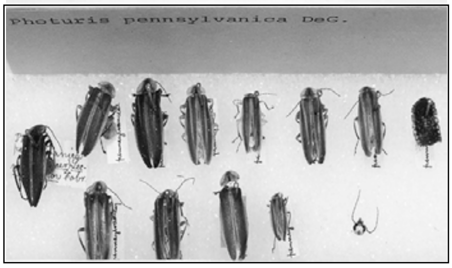


Fig. 56. LeConte's "pennsylvanica" tray in 1992,

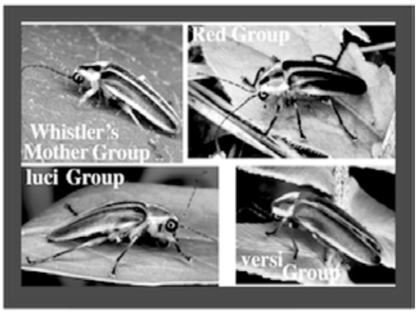
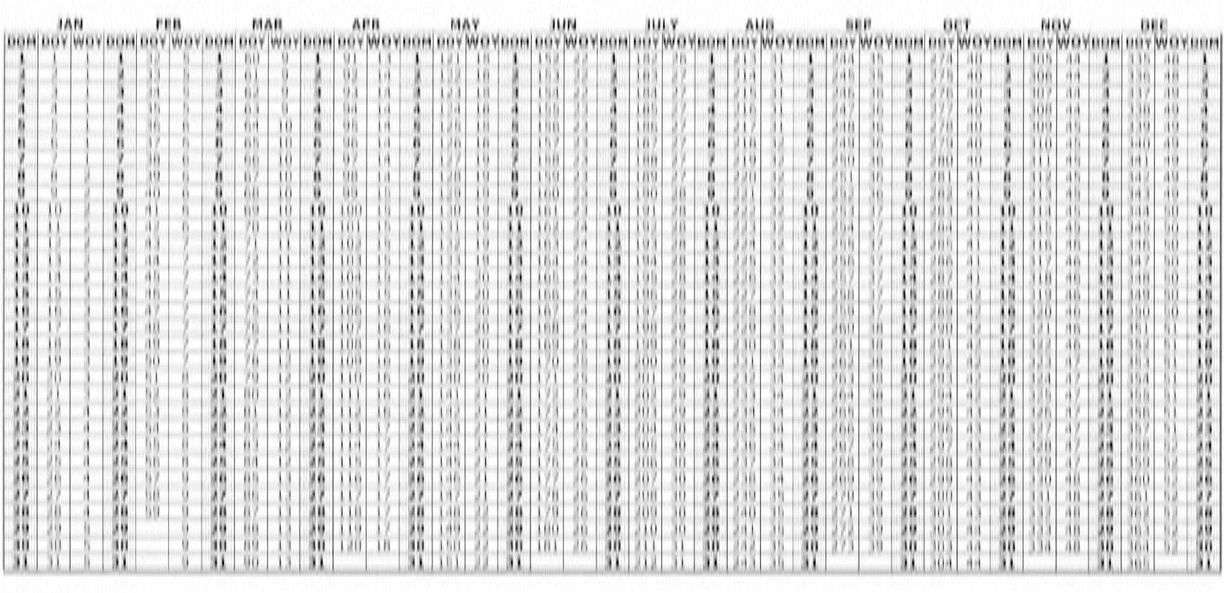


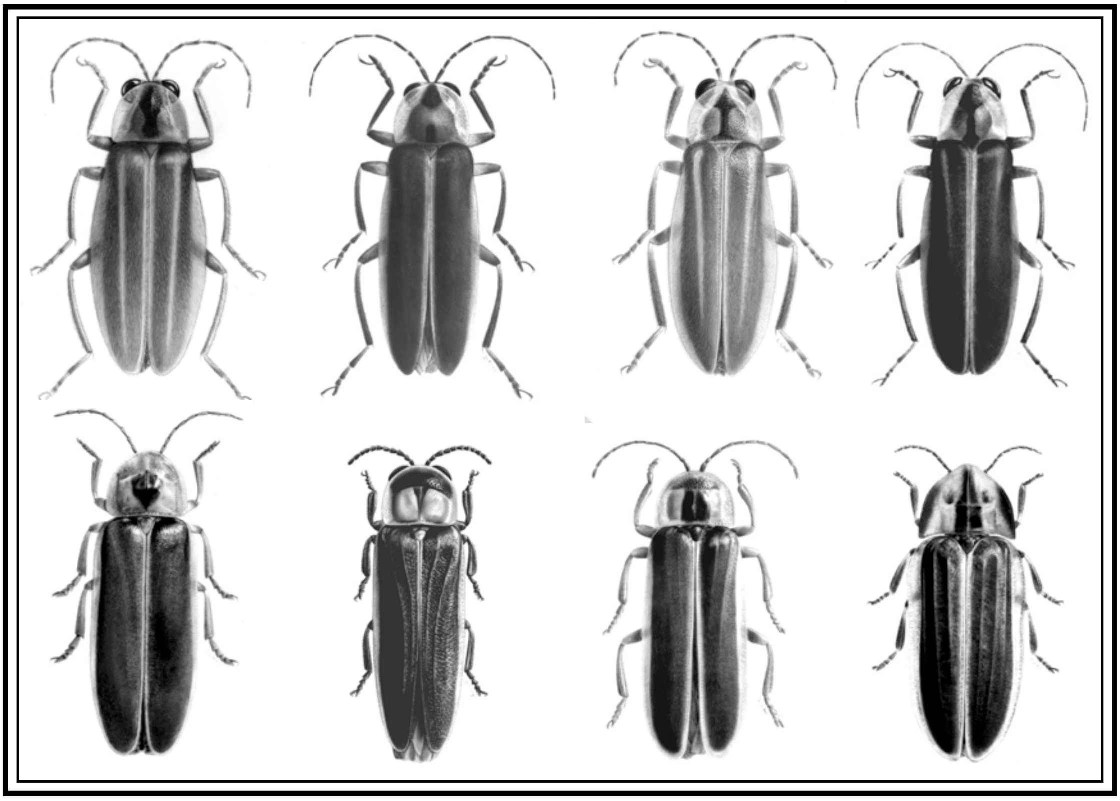
Fig. 57. In hand, some *Photuris* "sections" are recognizable— consistent infallible distinctions are elusive.

Although easily observed morphological characters are not likely to be broadly useful for ready identification of *Photuris*, it is obvious that there are differences and at least at the local level these may become apparent and useful. The LeConte tray of the aggregated "*pennsylvanica"* at the MCZ shows different forms (**Fig. 56**), but probably these are not the specimens LeConte at hand, more recent curators having added more recent acquisitions and made alterations. **Figure 57** shows some distinctive "morphs" of Division II *Photuris* that will be recognized in hand.

Appendix

Several charts as well a references to seasons and dates in text here used standard abbreviations as shown in this table. They are: DOM, day of the month; DOY, day of the year; WOY, week of the year. This table also is at the end of this paper for easier reference. For information on such charts, tables and entomological equipment construction see Peterson (1934).





Four Photuris, Three Photinus, and Pyractomena angulata

Chapter 4

Photuris Pronotal Vittae: Hieroglyphics, Vittagrams

in hoc signo vinces?

An impasse in *Photuris* bench/cabinet taxonomy began in the nineteenth century and continued, forever. Maybe, from time to time there was kindled in some forgotten taxonomist a glimmer of hope … the possibility that the dark insignias that adorn *Photuris* collars (**Fig. 1**), might, like crests sported along upward-curving stairways of aristocrats, have some yet-undiscovered recognition or phylogenetic implication. These vittagrams (median discal vittae of firefly pronota) appear in a variety of forms and have no yet-apparent adaptive significance for *Photuris* bearers—as heat absorbers to raise daytime cranial temperatures, to block light from cerebral ganglia, to provide eye-shades to occlude skylight … Not only do these vittae vary in general configuration, they also display embellishments that might just possibly, eventually, hopefully, say something to an attentive taxonomist. Hope must spring eternally, that there is a secret yet to be found; certainly … an anatomical feature with such Rorschach variation must be hiding something? Perhaps the secret lies in a duet or quartet of key features, or a simple suite of easily-remembered flourishes? Something, anything, that, that would permit the determination/identification of cabinet specimens that are not accompanied by details of their flashing comportment on a label (**Fig. 2**). This is important, because more than merely for firefly identification for its own sake, as for life lists, but because thousands of *Photuris* specimens with locality labels attached have historical-distributional and climatological stories to tell that are especially important now that their decendents and their world are disappearing in front of us, of them—we. These poor dead and mostly forgotten photurids wait silently, in countless cabinet trays and stacked Schmitt boxes in museum and university closets.

Figure 1. *La[mpyris] versicolor*: **Fabrician specimen ("type) labelled in Fabricius' hand. Carbon dust by Laura Line.**

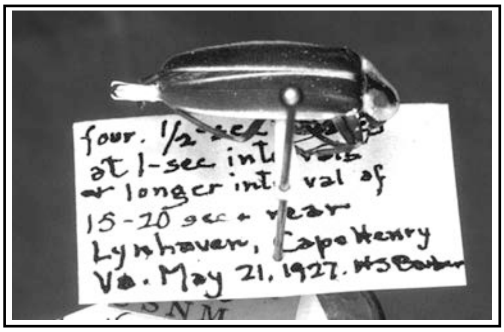


Figure 2. ***Photuris quadrifulgens,*** **FP voucher in Barber's hand**

This Chapter describes preliminary observations and makes suggestions toward making sense of the vittagram insignia enigma—with full cognizance that they may actually conceal nothing and bear no sense to be revealed. But firefly taxonomists must make an effort to remember that this is what was said of variations found among male genitalia whose many forms J. W. Green introduced, and whose known applications to insects themselves have been compared with those of Swiss Army knives—getting sperm to eggs one way or another, in any way whatsoever, in the face of female resistance and rival competition.

Vittagram arrays. It is obvious that graphic illustrations are necessary, but a sample of suitable size could be expensive to produce. Arrays of a few species were drawn by Laura Line, and examination of these and of a series of rapid pencil sketches made on standardized outlines indicated that neither a single element nor the entire vittagram was useful as a unitary guide. However, it appeared that *arrays* of sketches showed some promise. **Figures 3** and **4** show series of vittagrams of the perhaps-related crescendo-FP species *Ph. lucicrescens* and *Ph. carrorum*; they illustrate a range from the most reduced to the most expansive in their respective FP voucher series. Note that no pronotum in these series is totally lacking a vittagram, nor is any provided with a huge dark blob, extremes seen in the reference array (**Fig. 5, @ C2***); the male in the *lucicrescens* first position is missing a stem and has a much-reduced serif (page 232), and others show an assortment of individual variations.

Photographic production: A speedy photographic method for making vittagram illustrations used a *Nikon Cool-Pic*® camera

***unfortunately the alpha-numeric coordinate references (columns and rows) were reversed on Plate 1 (Figure 5)—they do not follow the convention used in computer spread-sheets.**

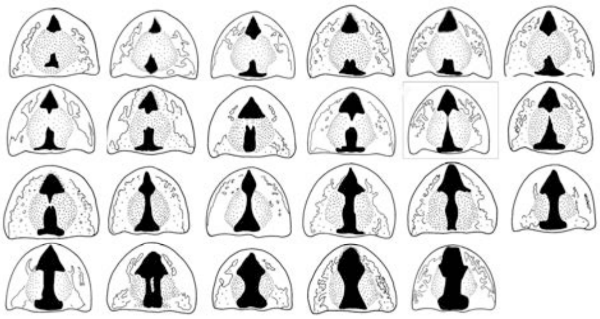


Figure 3 . *Ph. lucicrescens.*

held at the eyepiece of a Wild® binocular microscope. The camera was precisely manipulated and braced (in 3D) with the fingertips, which cushioned and aligned the camera near and above the lens, to produce a clear, centered, and appropriately magnified image on the screen. This produced reasonable and fast results. Photographs were adjusted for color and gathered to produce plates in *Photoshop*®. For monochrome (B&W) images, in *Photoshop*® the color image was first manipulated (*Image, Adjustment, Color Balance, Red, Black* menu selections) to produce maximim intensity (saturation) **contrast** between the red "spots" and black vittagrams. On each photo the specimen's cabinet number was placed at the lower right, in white print.

Figure 4 . *Ph. carrorum.*

Red oval spots: Before presenting details of the vittagram review, note that one pronotal character that has often been mentioned by taxonomists is the presence or absence of brick-red oval spots (shapes) that lie on each side of a vittagram. These are "absent" in Division I (*congener*, *frontalis*, etc.). The reality seems to be that there is one large median red spot that often has its center hidden by the black vittagram. Such a spot can be seen in its entirety in pronotum A1 in **Figure 5** (color on page 446**)**, where the vittagram is absent. (Axes in Figure 5 were reversed (alpha-numerically), this noted too late to rearrange.)

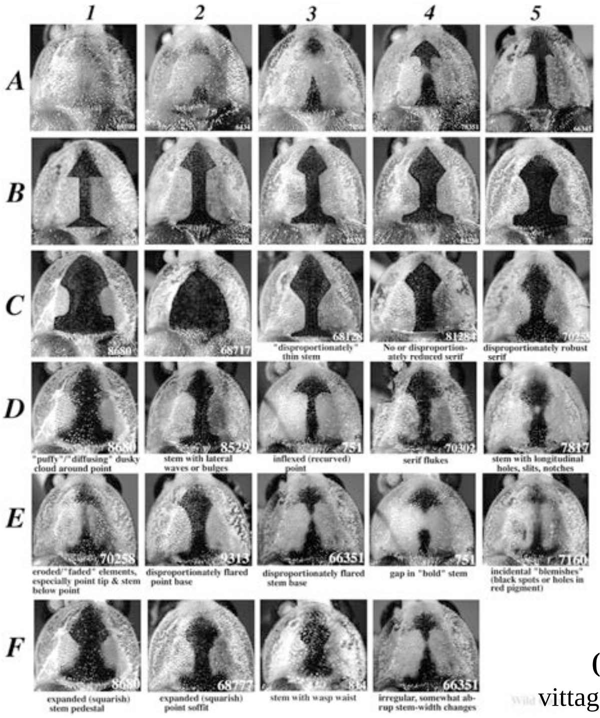


Figure 5. Selected all-species array.

Vittagram anatomy, evaluation: The generalized *Photuris* male vittagram can be seen, as a beginning, as having three basic elements (**Fig. 6**): apex (arrow head), stem (shaft), and serif (base). Any or all, or combinations of these three may be missing, exaggerated proportionally, decorated with flourishes, notched, or otherwise modified. These variations were divided into two basic sets, **1** and **2**:

(Set 1) Arranged assortment. Vittigram photos were selected to produce an array from the extreme of *complete absence* to the other extreme of *complete coverage* of the pronotal *disk* with dark/black color (**Fig. 5, A1-C2,** so also in **Figure 11**). Note that the array is not step-wise successional ("linear"); this is not possible because the three elements do not vary together but independently. Also, it would appear that the dark pigment of the vittae occurs both at the surface and within the cuticle, and also, seemingly, to the eye, sometimes to be exaggerated by a shadow within empty space beneath. This may result in a source of uncertainty or error from unaccounted variation.

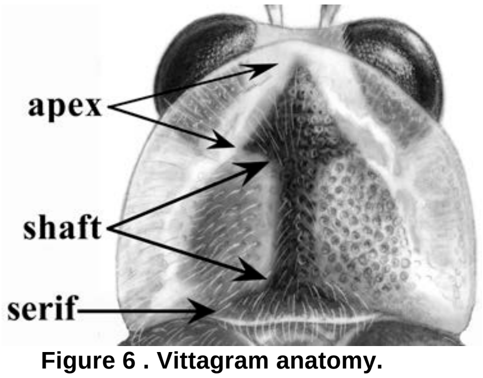


Figure 6 . Vittagram anatomy.

(Set 2) Idiosyncratic embellishments. These features of the vittagrams are shown in **Figures 5** and **11**, in **C3-F4**—note in the next section where the occurrence of these vittal characters is presented graphically for a few species, additional (wild card) features are mentioned (F5-F8). The features C3-F8 are as follows:

C3—stem disproportionately narrow when compared to proportions of the reference vittagram (B3).
C4—serif absent or disproportionately small.
C5—serif disproportionately robust.
D1—dusky, diffuse cloud around the apex.
D2—stem with lateral waves or bulges.
D3—posterolateral points of apex deflexed, down-turning.
D4—serif with upturned flukes.
D5—stem with longitudinal slits, holes, notches.

E1—faded elements, especially apex tip and stem below apex.
E2— disproportionately flared apex base, where joins stem.
E3— disproportionately flared stem where joins serif.
E4—gap in otherwise bold stem.
E5—incidental blemishes, black spots or holes in red “spots.”
F1—expanded stem at base, forming a “squarish” pedestal.
F2—expanded “squarish” apex base, a soffit.
F3—stem with narrowed waist.
F4—irregular somewhat abrupt stem-width changes.

WILD CARDS (incidental notations)

F5—inlet notches at PN base (in below-mentioned species and *lucicrescens*).
F6—in *lamarcki*, no serif, stem base rounded.
F6—in Iowa *caerulucens,* bulge on stem below apex.
F6—in *beanii*, bulge on stem above basal flare.
F6—in *carrorum*, narrowing of stem below sub-apex flare.
F6—in *forresti*, stem narrowing (erosion) below apex.
F7—in Iowa *caerulucens,* stem erosion above bulge below apex.
F7—in *lamarcki*, on pronotal marginal flange, tiny “fat-like” speckles except over eyes.
F8—in *forresti*, apex narrowed

Vittagram sample comparisons, frequencies of occurrence. Comparisons of vittagram features that are characteristic of species and local populations can be made visually by comparing the frequencies of occurrence of each of the variations (A1-F4-F8). As demonstration, samples of the vittagrams of voucher *Ph. lucicrescens* from four localities were examined, evaluated for each character, and tabulated; tabulation results were illustrated with histograms, with a bar for each character (**Fig. 7**). Horizontal axes show features in the three histograms (A1-C2, C3-D5, E1-F5); vertical axes show percent of sample showing the feature. Note that in the array A1-C2 the percentages total 100 since a single specimen could have only one general type of vittagram. In C3-F5 single specimens may show several idiosyncratic features, thus totals have no special meaning for the present, but can be imagined to actually indicate something of genetic variation. Compare especially the vittagrams of these *lucicrescens* variads with those of several *fairchildi* variads (**Fig. 8**). These two (Barber) species, judging from their flashing behavior and general coloration are only distantly related.

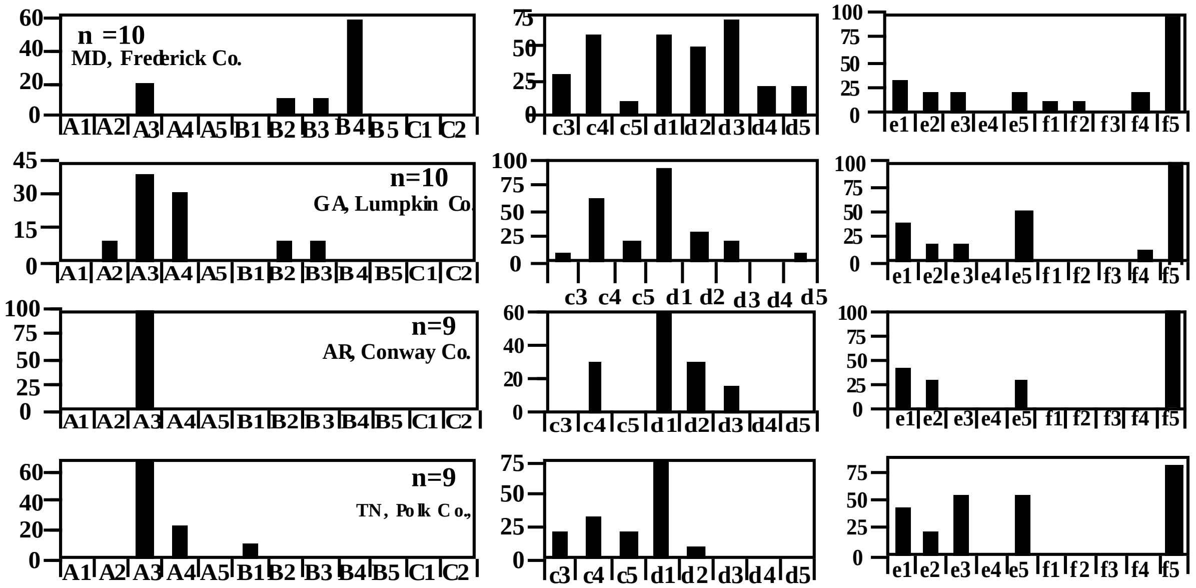


Figure 7 . Vittagram comparison of four voucher populations of *Photuris lucicrescens*.

Vittagram element combinations. Certainly various idiosyncratic elements must occur together and it may be combinations of them that will have taxonomic significance? **Figure 9** shows simplified contingency tables for more common elements found in samples of five species. Computer cladistic analyses could reveal the hoped-for combinations or perhaps put an end to such search. **Figure 10** stacks the vittagram arrays of the *Photuris* "Red Group" (*lineaticollis* and presumptive kin) for comparison.

Conclusion. The arrays of vittagrams A1-C2 are helpful auxiliaries when identifying *Photuris*, and cladistic analyses may reveal an even greater utility, but this is labor-intensive especially if large series of vouchers must first be collected after field experience and familiarity has properly prepared the collector. If analyses are to be made, a suggestion would be to begin with voucher series in the jel collection, and trials with data presented here.

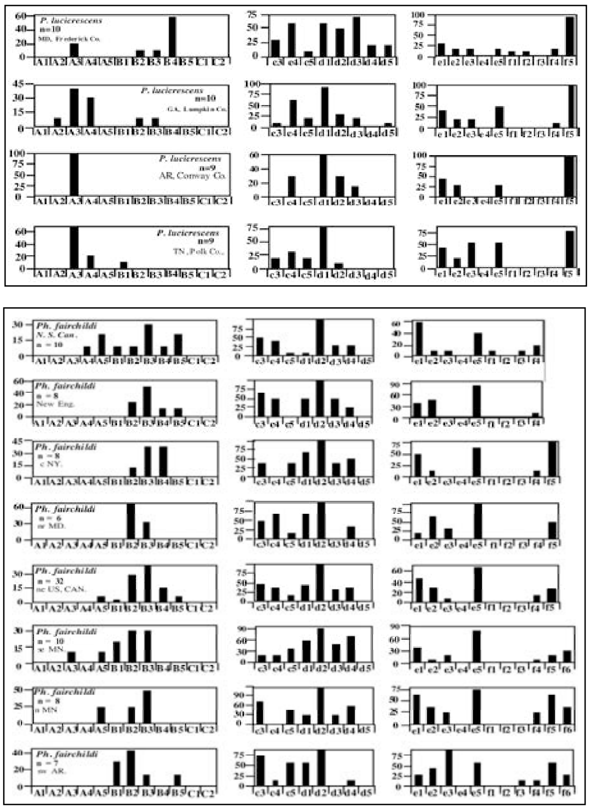


Figure 8 . Vittagram comparison of voucher populations of distant demes of two working species.

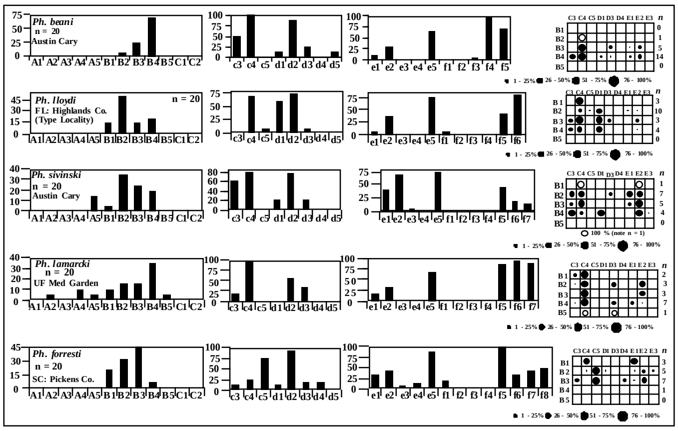
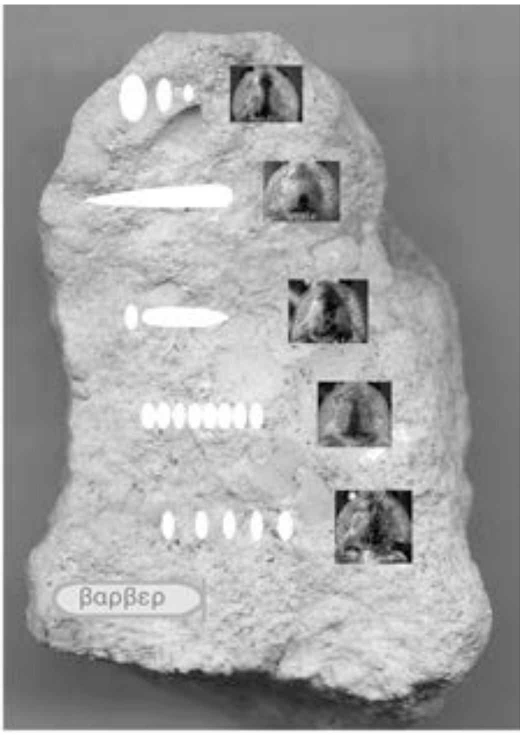
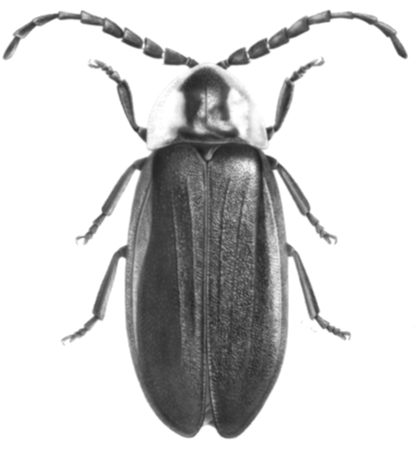


Figure 9 . Vittagram comparison of voucher populations of five working species, and their experimental contingency matrices.

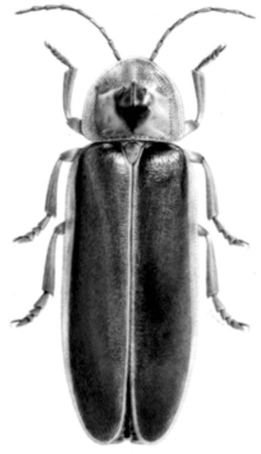
Epilogue. Some readers may be encouraged to begin DNA and cladistic analyses but lack field and natural history experience to begin properly and without hope of making a successful contribution. There is a nominal species of daytime dark firefly that holds promise as a place to start: Chapter 5 presents information on *Lucidota atra* (below), and focuses on geographic variation noted in its remarkably variable vittagrams. Another species of promise in this regard is the twilight-flasher *Photinus pyralis*, which is well-represented in American archives. The vittagrams of this firefly range from a near-goblet shape to mere and vanishing vertical slits and tiny spots, judging from cursory inspection. At the western edge of *pyralis*' range the vittagram is lost altogether, and the beautiful pink pigment seen in eastern populations becomes an unblemished, immaculate rufus. *Lucidota atra*, the subject of the next chapter, is as a hopeful model of what is sought in the pursuit of flash patterns and demes in *Photuris*.



Ala-Barber Stone?



Lucidota atra



Photinus pyralis

With discovery of the Rosetta stone writings left by ancient Egyptians did not immediately reveal their secrets. So also with the discoveries and insights of McDermott and Barber. One step in a long walk.

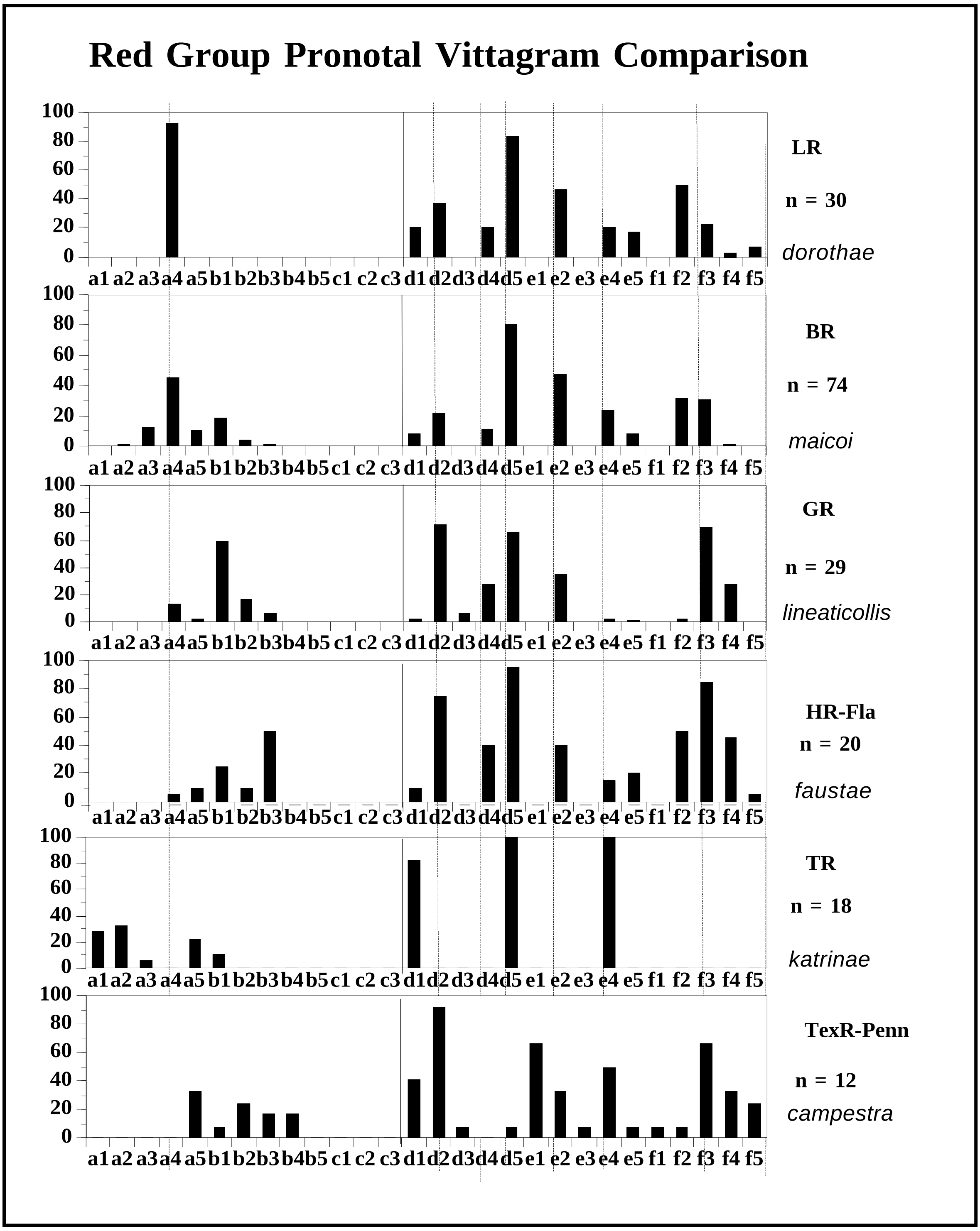


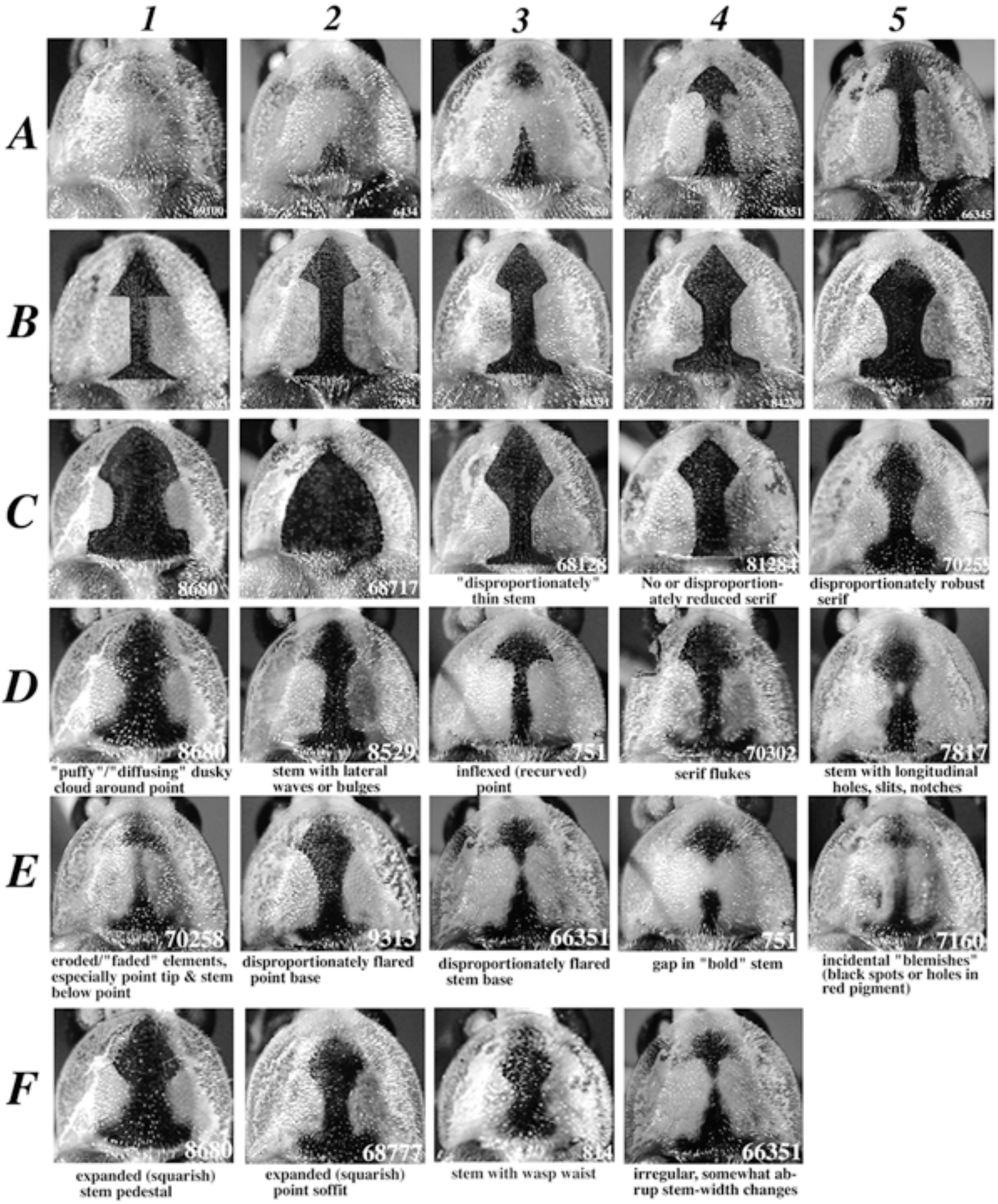
Figure 10. Histograms of vittagram features of the (operational) *Photuris* Red Group.

Figure 11. Selected all-species array—array as in monochrome in Figure 5.

Figure 11. Vittagram reference array, with basic range (A1-C2) and idiosyncratic embellishments (C3-F4).

201.2 PN Array

color on page 446



C3: "disproportionately" thin stem

C4: No or disproportionately reduced serif

C5: disproportionately robust serif

D1: "puffy"/"diffusing" dusky cloud around point

D2: stem with lateral waves or bulges

D3: inflexed (recurved) point

D4: serif flukes

D5: stem with longitudinal holes, slits, notches

E1: eroded/"faded" elements, especially point tip & stem below point

E2: disproportionately flared point base

E3: disproportionately flared stem base

E4: gap in "bold" stem

E5: incidental "blemishes" (black spots or holes in red pigment)

F1: expanded (squarish) stem pedestal

F2: expanded (squarish) point soffit

F3: stem with wasp waist

F4: irregular, somewhat abrup stem-width changes

Chapter 5

PNVs of *Lucidota atra* (G. A. Olivier) 1790:

In Particularized Perception

Halloween Firefly

Examination of the median pronotal vittae of several nominal firefly species suggested their possible value for recognizing geographic subpopulations. This could target regions for DNA analyses and comparison. Although too little was known of *Photuris* species or their vittagrams to use them for this purpose, archived collections hold large numbers of *Lucidota atra* with sufficient label data to use it as a model. Perhaps, it was speculated, that *atra's* regional markings/ divisions could provide clues to locations of similar divisions of other lampyrids. This daytime-dark firefly occurs broadly across eastern North America, from Quebec/Ontario/Manitoba to Florida, and the Atlantic Ocean to the eastern borders of Kansas/Nebraska (**Figs. 1, 2, 15, 16**). Note, there are three other medium-to-large, jet-black, attention-grabbing summer flyers: *Tenaspis angularis*, *Pollaclasis bifaria* and *Ellychnia corrusca* (**Fig. 14**). Over 1300 *atra* specimens from several archival collections were examined—the oldest individual was from 1883, Rockland County, New York. Collectors have in the past occasionally taken several at the same time, perhaps via malaise-traps, or by chance they collected at a local peak, a phenological moment; during the *Photinus*/*Photuris* studies only an occasional *atra* was seen.

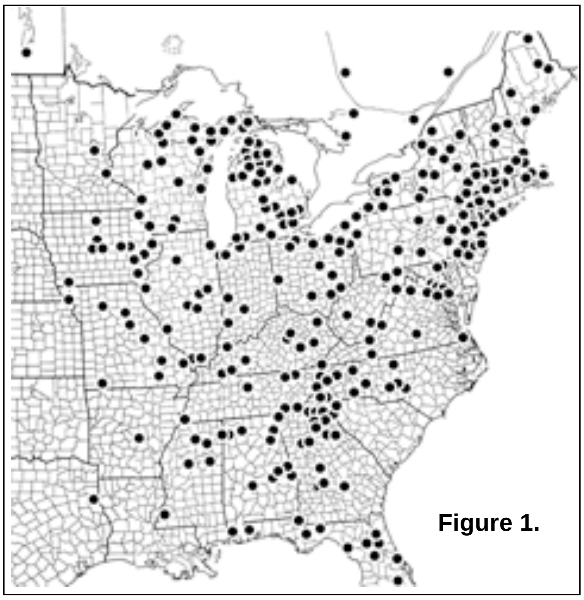


Figure 1.

Figure 3 shows the seasonal (Lat/DOY) occurrence of *atra* from archives and observation; as can be seen, the Halloween Firefly is a summer species, and does not make it to October 31. Both males and females are flyers; the sample's sex ratio (male fraction) is 0.76 (847/1108), the departure from an expected 50:50 probably resulting from time females spend during their adult lives perched, emitting pheromones or ovipositing (possibly at decaying woodland logs?). From cursory inspection the Lat/DOY sample does not clearly reveal an earlier emergence of male adults (protandry) as might be expected and is observed in some insects. In **Figure 4** the crowded central portion of the regression seen in Figure 3 was expanded to reveal individual data points, but a male-first appearance is still not evident. However, in Figure **5A-D** perhaps there is a slight indication of it; one sample is from regions (States) along a similar latitude and the other from Long Island, New York. Based on the length and breadth of male antennae, mate attraction would certainly seem to involve airborne signals, pheromones. Such antennae must have noteworthy effects on flight aerodynamics—perhaps the increased surface-area for pheromone-detectors, or even as used in male jousting, will eventually explain the size and serrations that balance the cost of any flight handicap.

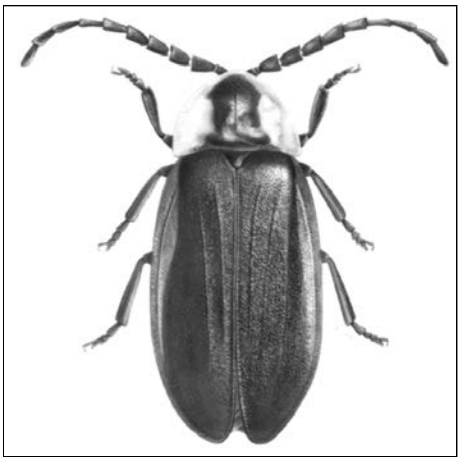


Figure 2. Carbon dust, by Laura. Line.

Pronotal PNVs. The appearance of this large and attractive coal-black firefly on the wing, with its bright pronotal exclamation, cannot help but capture the attention of amateur and professional alike—jet-black hieroglyphs against colorful pronotal shields (**Figs. 15, 16**). **Figure 6** is a short PNV sampler of "sketched" (colored onto template out-lines) from archived specimens. Color **Plates 1-3** show the complete collection.

The introductory sampler in **Figure 6** illustrates note-worthy points: (**1**) Some vittagrams are distinctive in their delicate and eye-catching appeal (A1, A4, B4), and one must, at the least, and even

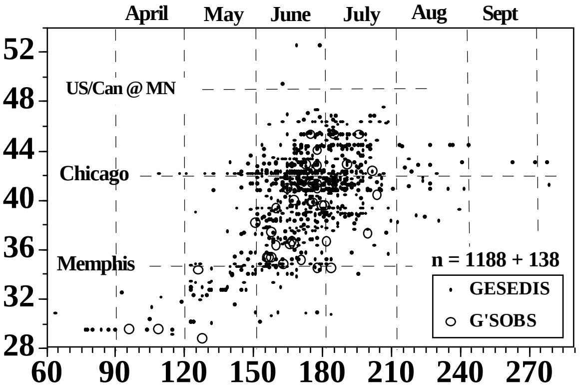


Figure 3. Seasonal/latitudinal occurrence of *atra* (AX: lat/DOY).

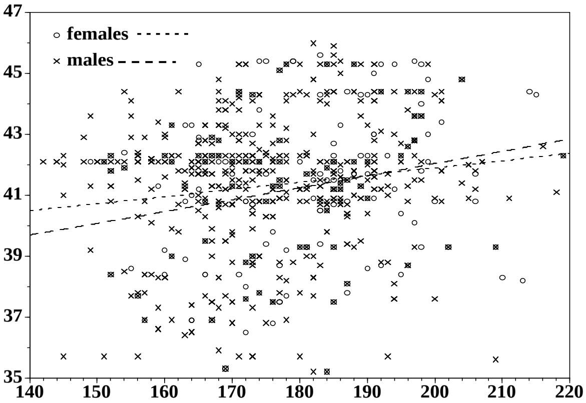


Figure 4. Expanded mid-season; sexual phenology appears to be similar (AX: lat/DOY).

wish that such remarkable variation will reveal something important biologically. (**2**) Some PNVs seem to be variations on a theme, conspicuous in a distinctive shared detail but with variation in another—note the presence of paired lateral-basal knobs with varying shaft development in A1, D2, D3, (A4?), C4, A5, B5, C5, D5. (**3**) Some glyphs are broad and obscure much or all of the underlying colors (B1, C1, C3, C4, D3, D4, D5), and some are themselves occluded or blemished by dark overlying dusky, dark, or other pigment (D1, A2, C2, B3). Consider, if bright PN colors serve an aposematic (warning) function, then it would seem that strong natural selection (pressure) in some other context would be necessary to reduce its conspicuousness? (**4**) A few individuals in the sample had asymmetrical vittagrams, such as D5 in **Figure 6** which combines elements from pronota numbers 25 and 3 (=25/3) in the arrays in **Figure 7** and **Plates**. Other noted example combinations were: 22/2, 14/2, 17/2, 22/2, 31/2, 32/2. Note in **Figure 6** that vittagrams A5 and C5 differ slightly in pronotal proportions (length/width, cf. B5)—are somewhat atypical. Perhaps these mentioned PNVs and proportions reveal a genetic or developmental disruption, or a general but otherwise overlooked disturbance (≈androgyny?).

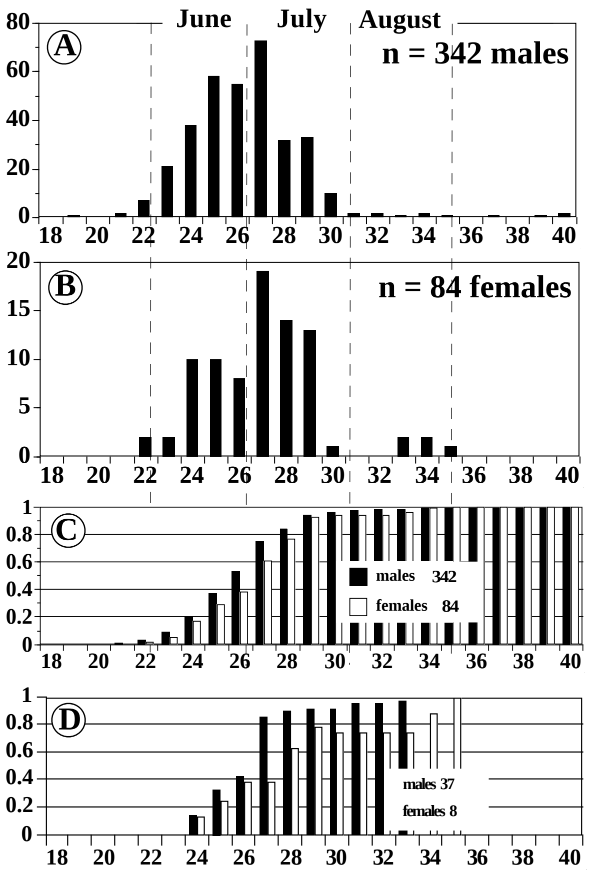


Figure 5. Sexual phenological data: A-C, from MA, CT, NH, NY (not LI), MI; D, from Long Island, NY (AX: y, count or fraction; x, WOY).

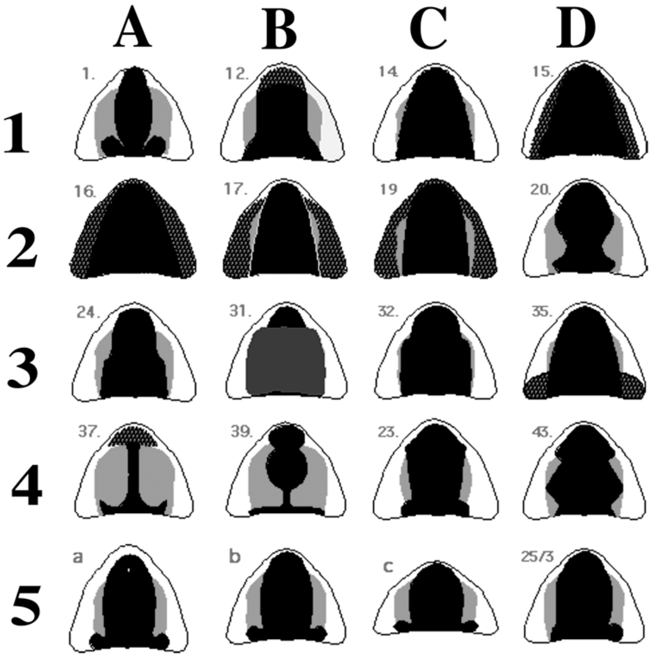
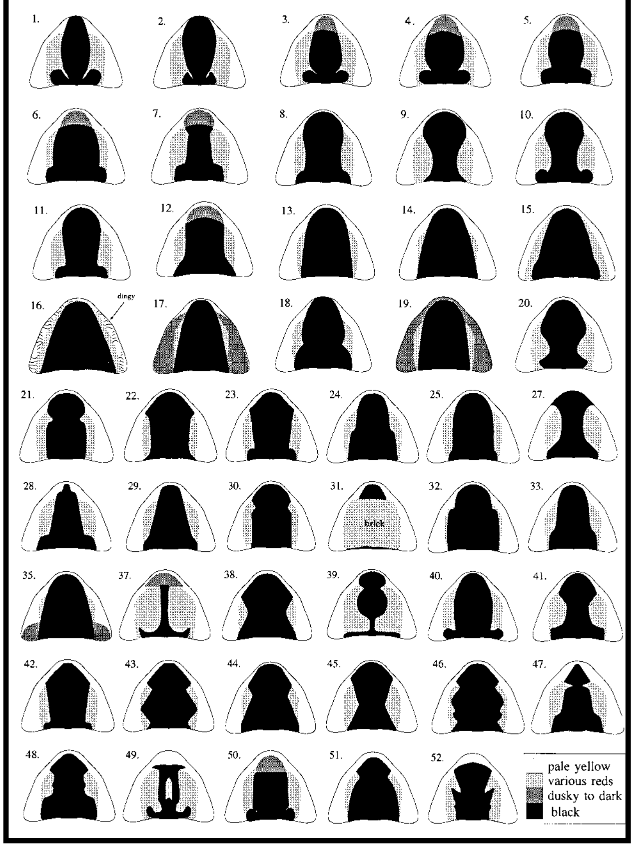


Figure 6. Vittagram sampler with alpha-numeric coordinates referred to in text and also PN number references as defined/associated in Figure 7 and Appendix Plates 1-3.

Figure 7. Complete array of pronotal glyphs from borrowed archived specimens. Missing numbers are those later recognized/appreciated as duplicates.



Altogether 52 vittagram variations were originally noted and sketched, but this number was subsequently reduced somewhat (**Fig. 7**; **Plates 1-3**). Some variations may be induced by environmental conditions, but others, upon which of course this inspection is predicated, are due to genetic differences. The following figures introduce the subject, and allow comparison and speculation toward more exacting examinations (3D-bar-coding), and progressive speculation. **Figure 8 (immediately below)** shows the number of each PNV in the sample (Y-axis), and arranges them according to their frequency of occurrence (number counted). **Figure 9** (**below left**) arranges **State** PNV compositions for regional/State comparison.

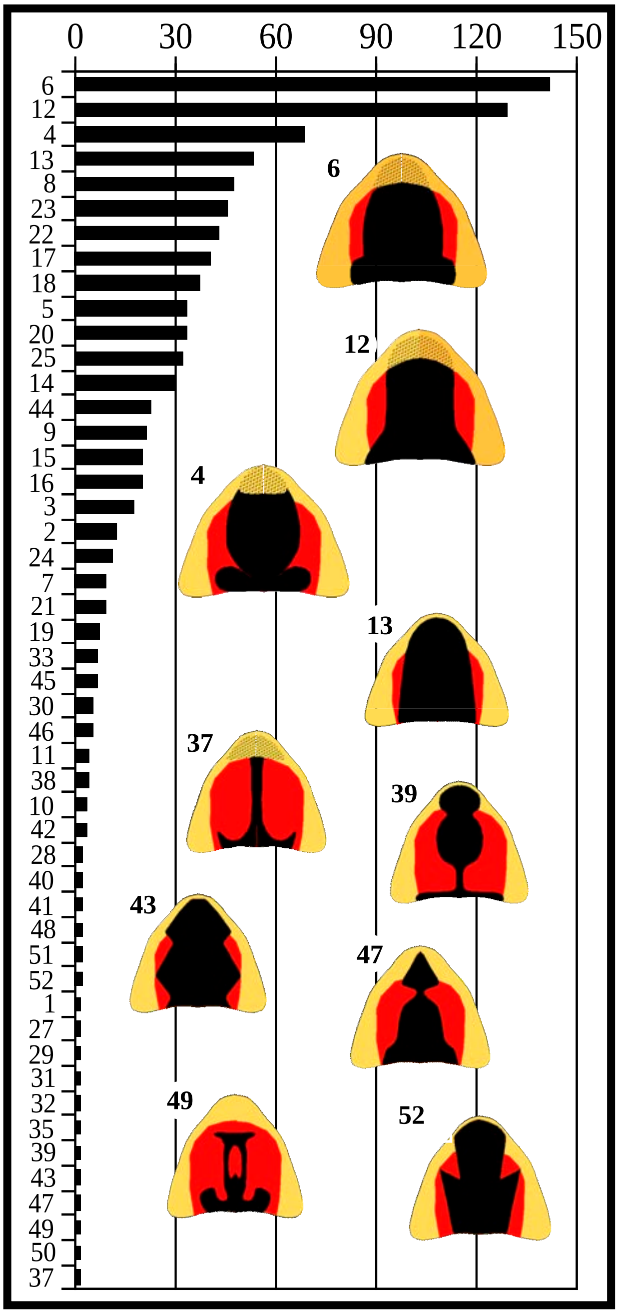
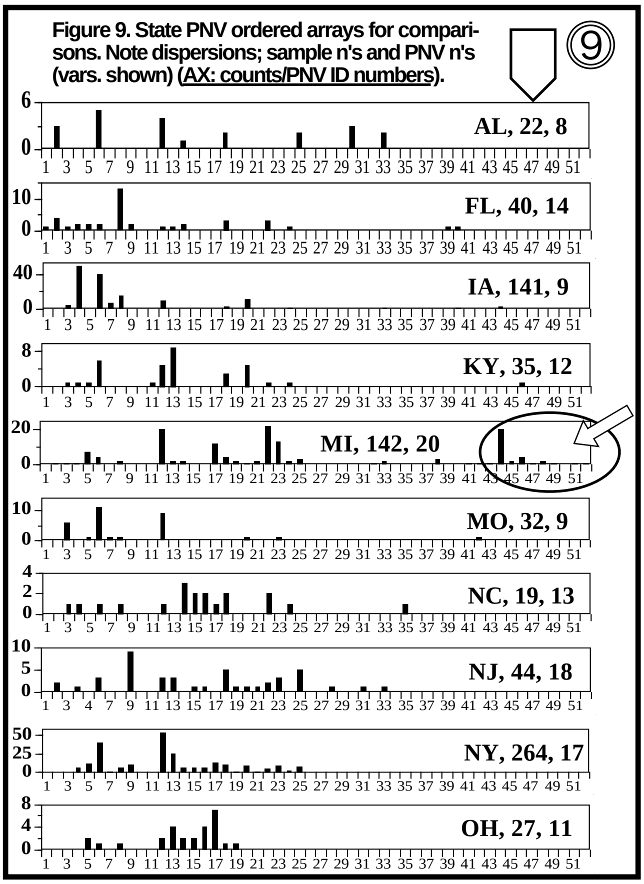


Figure 8. PNV frequency of occurrence from 839 specimens in the GESEDIS record, with most common at the top and odd forms at the bottom (AX: PNV#/count).

Figure 9. State PNV ordered arrays for comparisons. Note dispersions; sample n's and PNV n's (vars. shown) (AX: counts/PNV ID numbers).



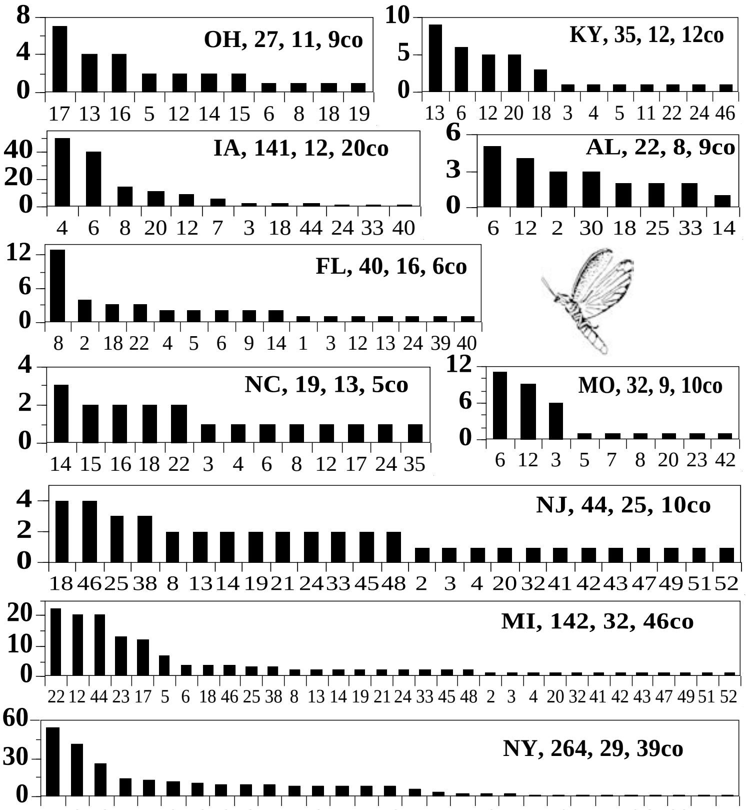


Figure 10. Prevalence of PNVs in example States: figures are n specimens, PNV forms (varieties), counties in sample (AX: count/PNV ID numbers).

Figure 10 arranges PNVs for each State according to prevalence in its sample. **Figure 11** shows PNVs from States with limited representation of examined archival material.

Consideration and reflections. (**1**) The bright colors of the pronotal disk are often subdued or nearly or entirely occluded by the vittagram or other over-lying pigments (**Plate 2: 15-17**, **19**; **Plate 2: 26, 31, 35, 38; Plate 3: 43, 44, 46, 52**). Selection might have been directly responsible (i.e., not pleiotropy), that is, favored such PN conditions to hide an attractive brilliance, say, from focused, poison-tolerant predators, or because dark/black color more efficiently converts short wave-lengths of light to sensible heat, of reproductive value for exothermal (“cold-blooded”) organisms in a sunlit but cool (montane) environment. Maps in **Plate 6** (**49-51**) show the geographic occurrence of pronota with such expanded PNVs and sooty shading (dinginess): note occurrence in mountainous and northern regions.

(**2**) In some maps there appear to be occurrences, perhaps even concentrations of darker pronota around certain urban areas: southeastern New York and northern New Jersey, western Pennsylvania, and southeastern Michigan. (**Plate 6**, **Maps 49-51**). These were perhaps areas of early and extended industry, with coal-burning steam locomotives, iron-smelters and steel manufacture, with pervasive soot. Such circumstances have been associated with the industrial melanism described for certain Lepidoptera, classically *Biston* in forests near Birmingham, England, described by Kettlewell in the 1950s, but also others, say in Livingston County, Michigan, in the 1960s by Dennis Owens. However, such a connection would not appear to be as simple and unfettered as explained for lepidoptera where camouflage was the key consideration.

(**3**) Now, toward what had been anticipated: compare the histograms in **Figure 9** and note the bars at the right end of the Michigan array, and that they are as a group without parallel in histograms of other States. In fact, even the individual PNVs are scarcely represented elsewhere. (Causally these are gathered “as a group” at the numbered high end simply because the Michigan collections was scored later in the process, when the form-count had reached the mid-forties.) Other rare PNVs occurring in Michigan, though not always exclusively, are: 19, 21, 25, 33, and 38. Collectively these rarer PNVs comprise about 11 percent of the State’s complement. While not all are unique to Michigan, some are, and taken together, Michigan’s Hallo-

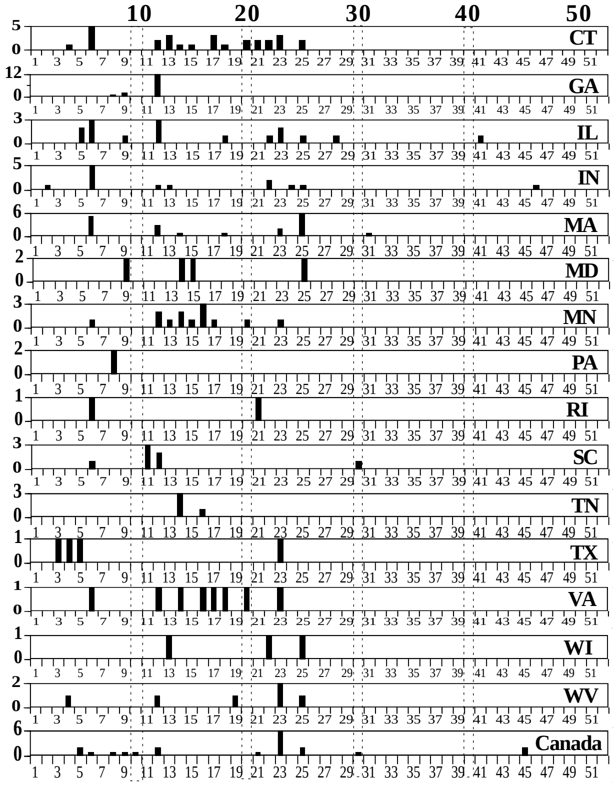


Figure 11. Ordered array of PNVs from States and 3-Provinces with but few specimens in the sample.

ween is perhaps worthy of special note. On the obverse, PNV-4 is third high in the overall frequency array (**Fig. 8**) but was not found in the Michigan sample; but Iowa, just around the corner of Lake Michigan, has 50 PNV-4s!, 35 percent of its PNV complement, and the comparison is almost as extreme with PNV-6, but the reverse with PNV-12. **Map 52** in **Plate 6** shows the county-based occurrence of members of Michigan's oddball subset. As can be seen, **Figure 10** gives the relative frequency of occurrence of PNVs in States with good archival representation that may suggest specific DNA comparisons.

(**4**) Though it was not the *atra* experience that suggested the possibility that Michigan's lightningbug fauna might also bear closer examination, it does provide encouragement to return to the northern regions, on both sides of the Straits, for there occurs a *Photuris* whose flashing behavior seems non-sensical. The name it has been given, in honor of a former UM professor and UMMZ Museum Director, was selected as encouragement for a closer look by students at the UM Bug Camp on Douglas Lake near Pellston (UMBS), and for another generation there to explain, along with the mysteries of *Lucidota atra*.

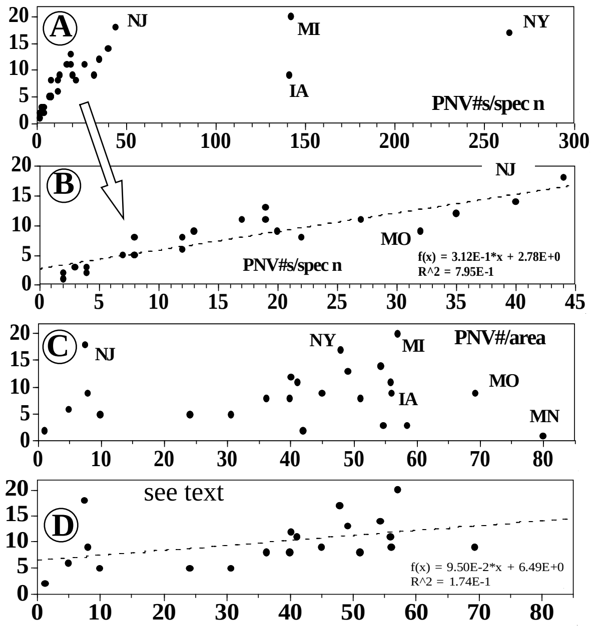


Figure 12. Variety of PNVs for each state a function of sample size (A, B), and area in square miles (X1000; C, D).

(**5**) The scatter diagrams in **Figure 12** are concerned with two ecological points: What is the smallest sample that can be taken to gain an understanding of a population? How many PNVs are needed to assess the "individuality" of diversity in a region? Also, when data are arrayed in a fashion to consider these questions, do deviants among the samples lead anywhere? The data allow a crude and somewhat flawed hint toward answers. In **Figure 12A** the number of PNV forms recognized in each State is regressed on the sample size for each State. At the left the number of PNV forms is seen to rise sharply with increased sample size, and then level off after the MI point. A key uncontrolled/unknowable variable influencing the samples is *atra*-habitat availability. In **Figure 12B** the rapid-rise segment in **12A** has been expanded and the graphing program asked to plot a linear function. The data were available so it was plotted, but the results don't reveal any secrets. *Post facto,* Michigan may not be far off an asymptotic line, sampled almost perfectly, Iowa and New York on the other hand either needlessly killed too many fireflies, or perhaps did not sample well?

In plots **Figure 12C** and **D** the numbers of PNVs types in each State's sample were regressed on the area (square miles), and the result is a scattering of points. The X-axis perhaps should have been the area of sampled counties, or habitat remaining. By removing samples with absurdly small n's (2 and 3, except RI) not much is changed (**Fig. 12D**). Ecological suitability and natural areas certainly matter most, and for this firefly maybe old cool forests of oak and beech-maple-hemlock? **FigTable 13** gives numbers. A source of variation not addressed was the number of specimens per year since 1900, but these data are in the files.

State	Spec Coll	PNVs	Area
AL	22	8	51.1
CT	12	6	4.9
FL	40	14	54.3
GA	4	3	58.5
IA	141	9	56
IL	17	11	55.9
IN	12	8	36.2
KY	35	12	40.1
MA	20	9	7.9
MD	8	5	9.9
MI	142	20	57
MN	2	1	80
MO	32	9	69.3
NC	19	13	49.1
NJ	44	18	7.5
NY	264	17	47.9
OH	27	11	41.1
PA	13	9	45
RI	2	2	1.1
SC	8	5	30.6
TN	4	2	42
VA	8	8	39.9
WI	3	3	54.7
WV	7	5	24.1
TX	5	2	263.6

FigTable 13. Data by State.

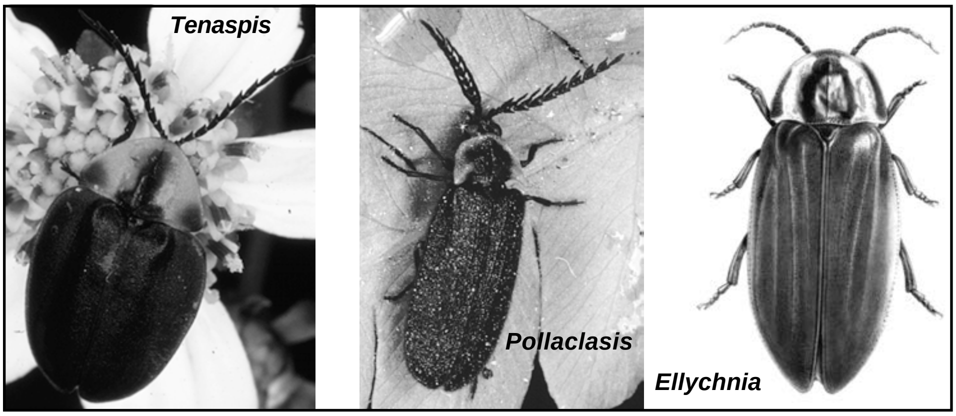


Fig. 14. Other medium to large daytime dark flyers—not *Lucidota atra*.

Figure 15. Halloween on a cattail.

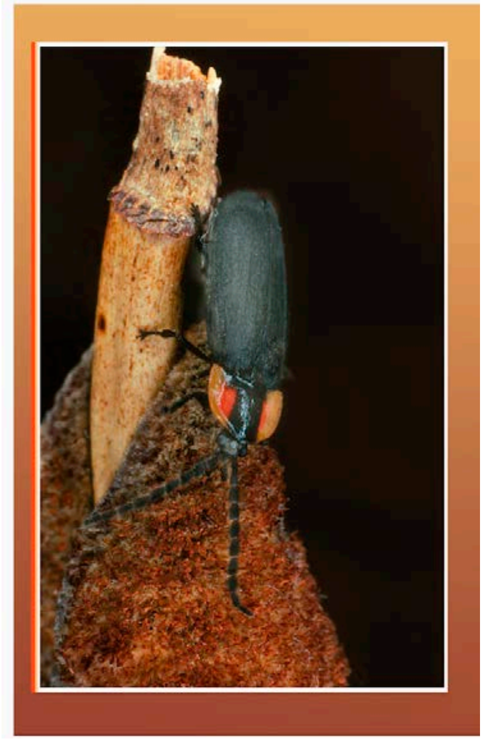


Figure 16. Halloween on a cattail #2.

* * *

Plate 1: PNV Forms 1-12

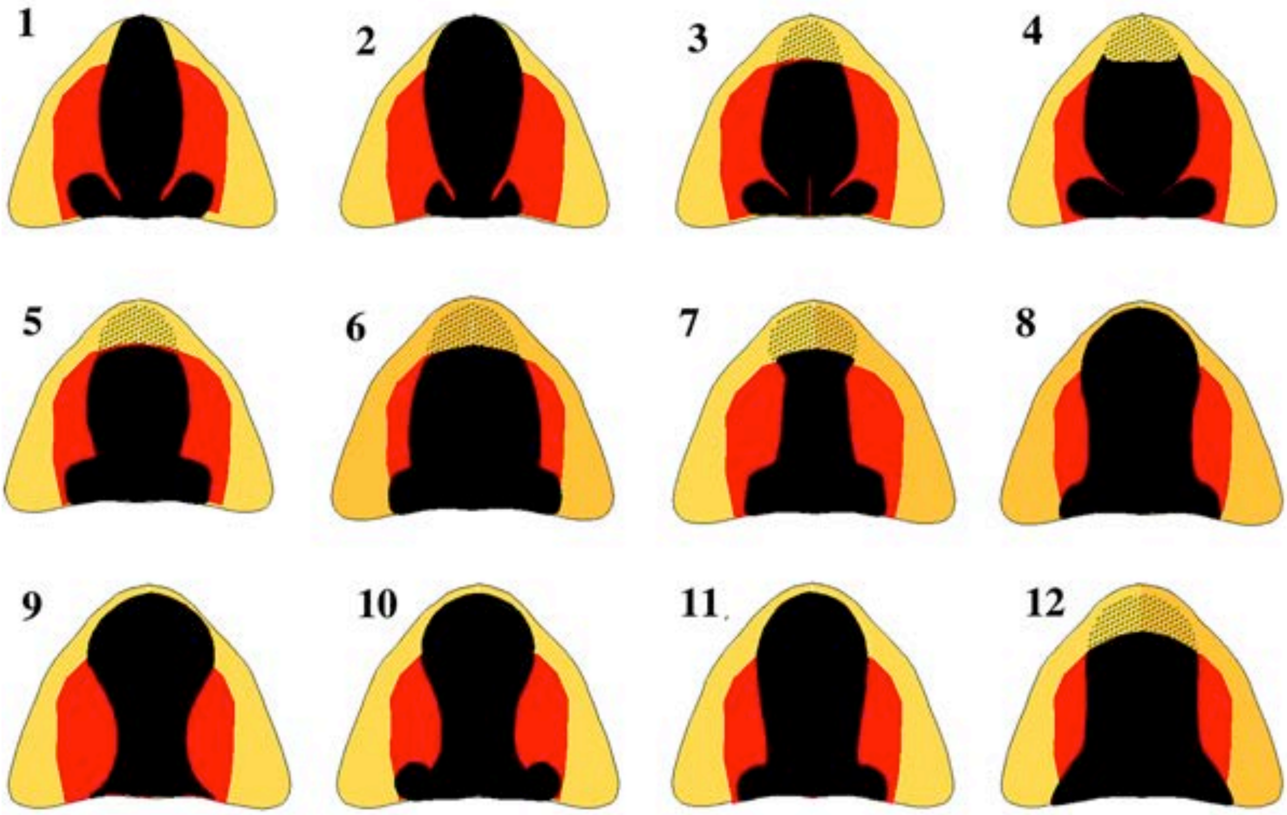


Plate 2: PNV Forms 13-39

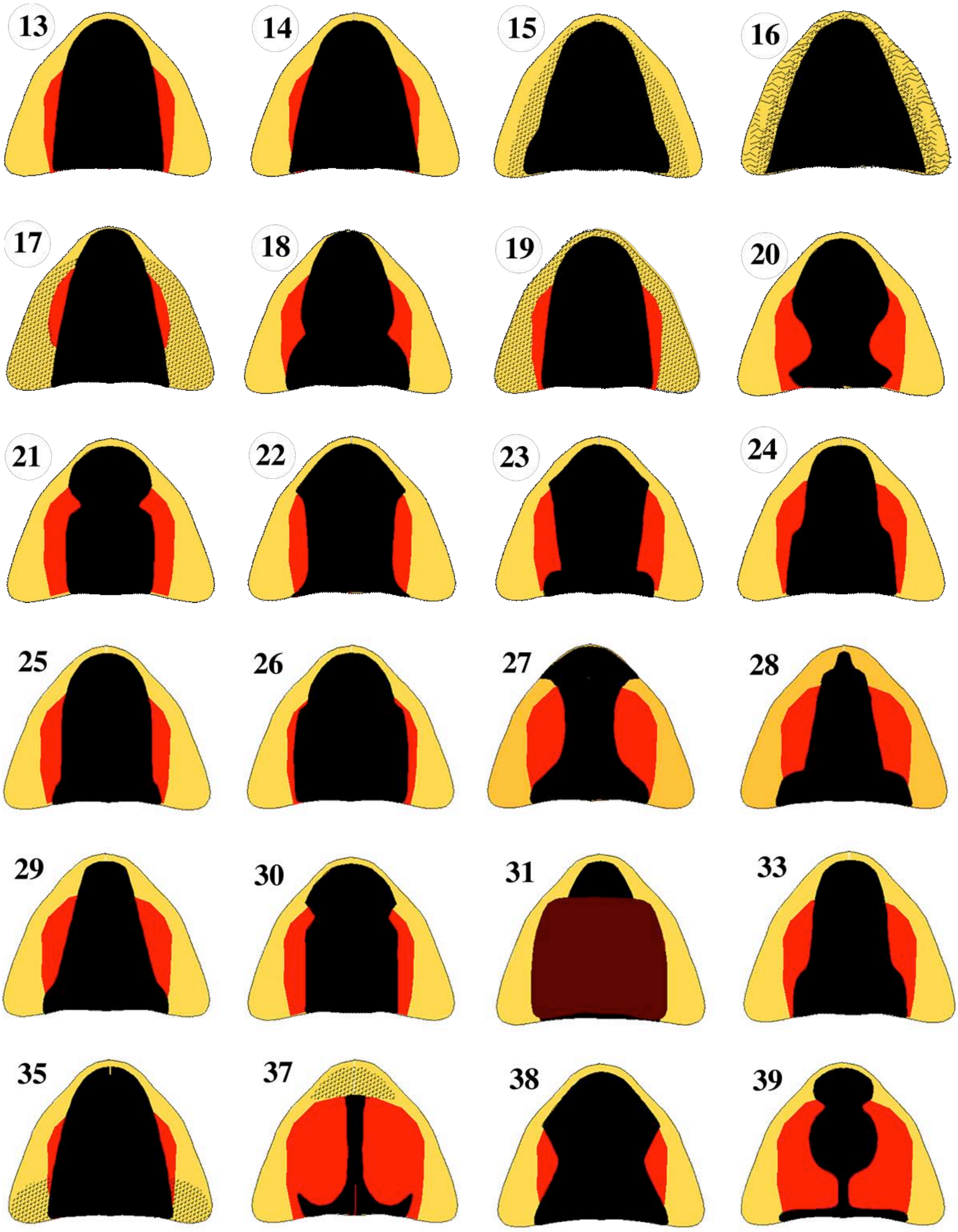


Plate 3: PNV Forms 40-52

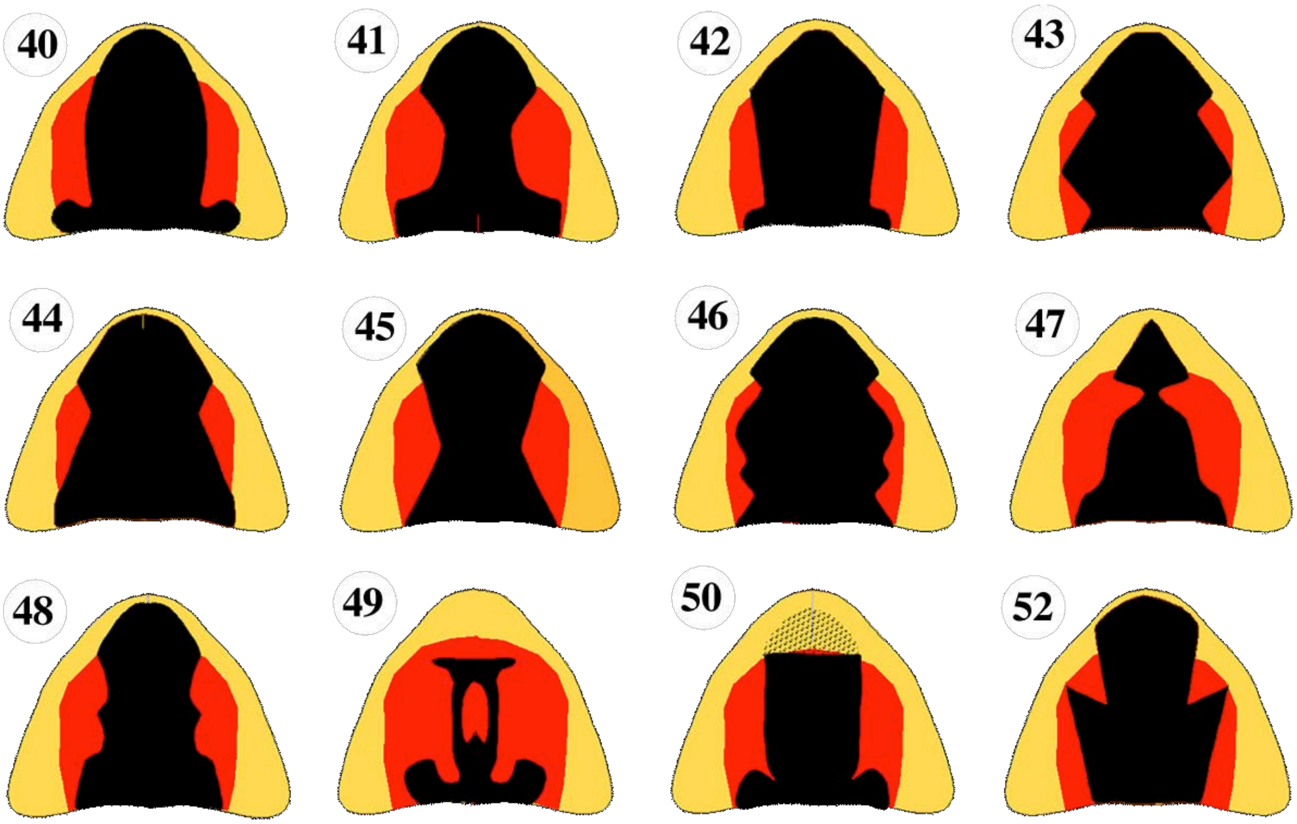


Plate 4: PNV Forms and Distributions 1-6.

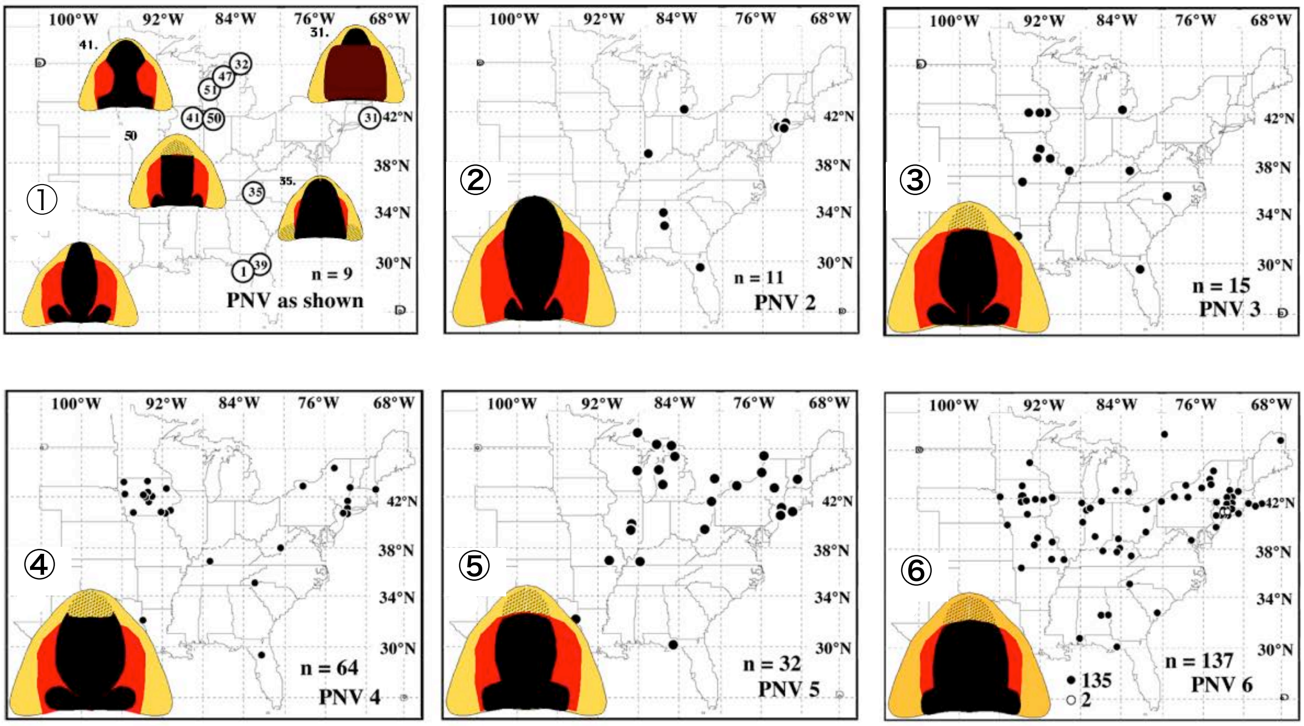
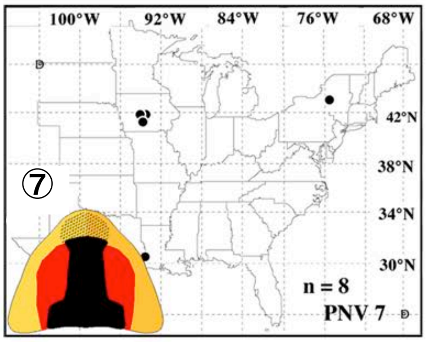
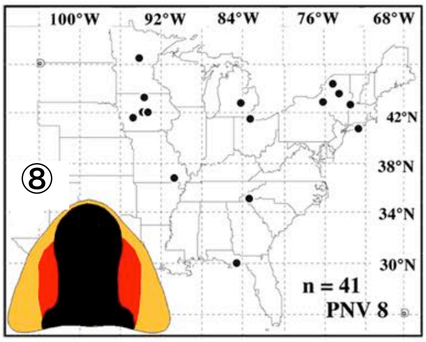
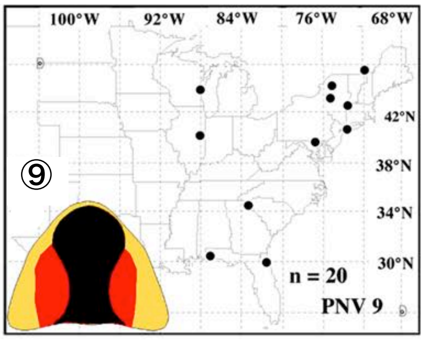
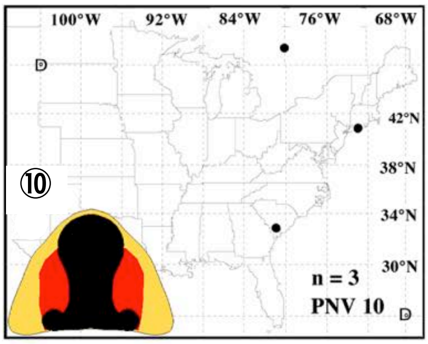


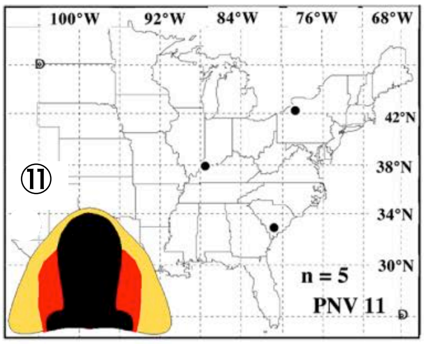
Plate 5: PNV Forms and Distributions 7-21.

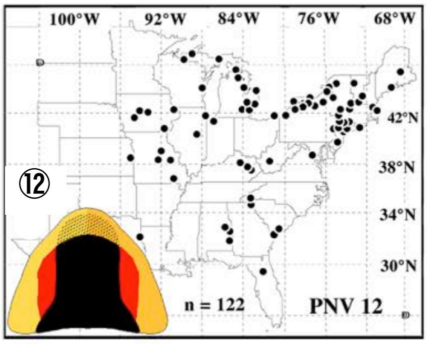


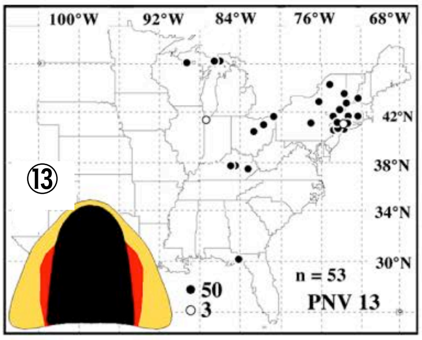


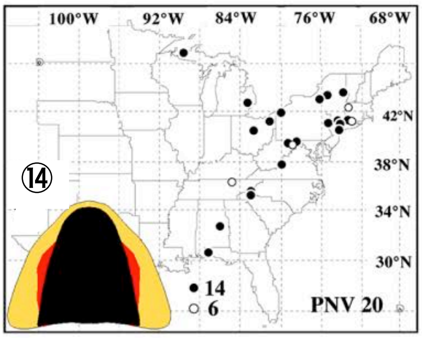


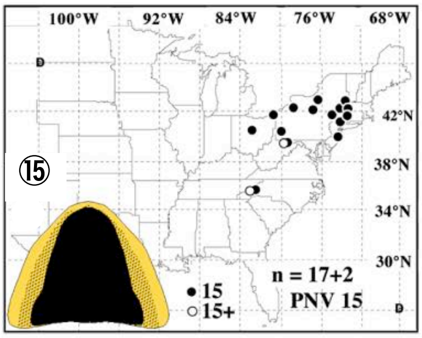


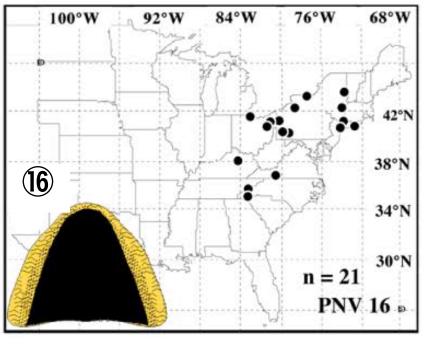


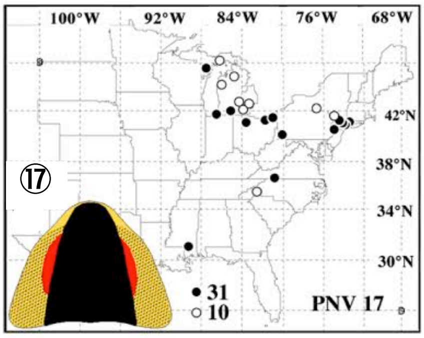


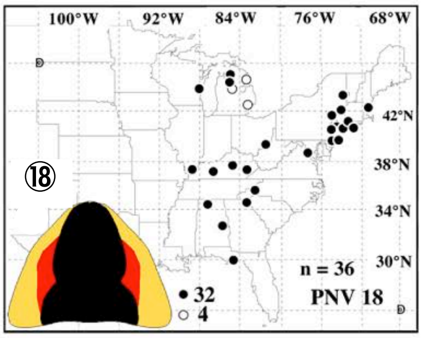


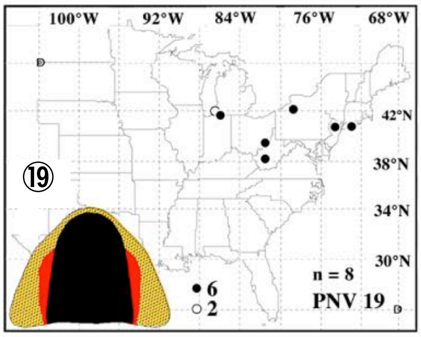


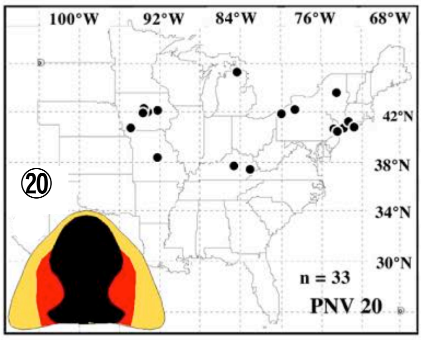












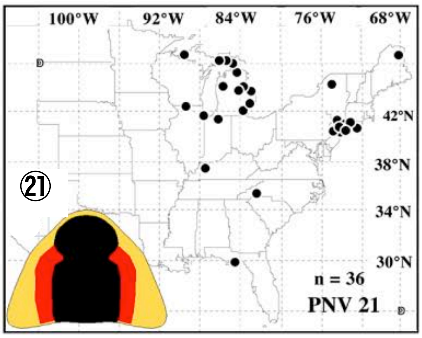
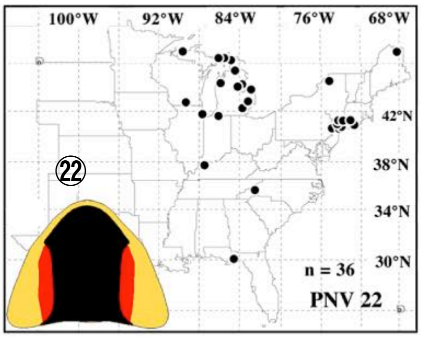
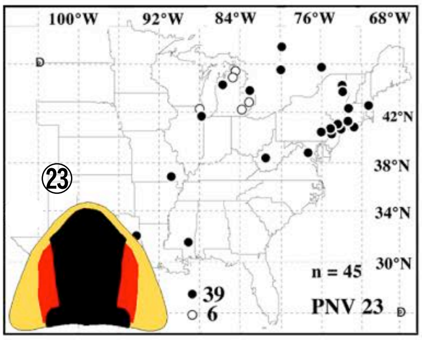
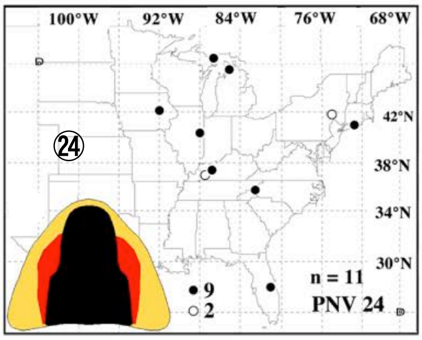
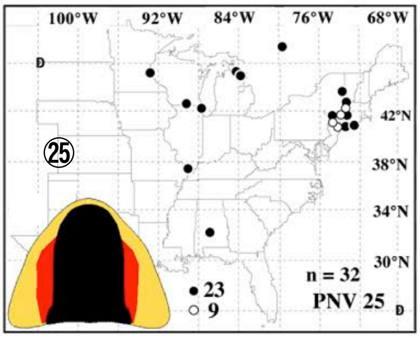


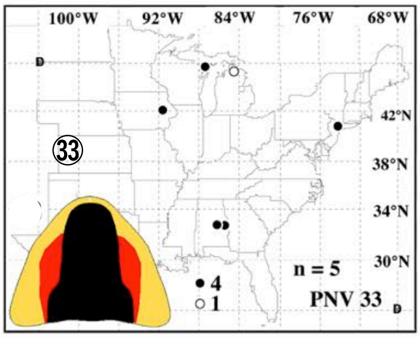
Plate 6: PNV Forms and Distributions 22-48.

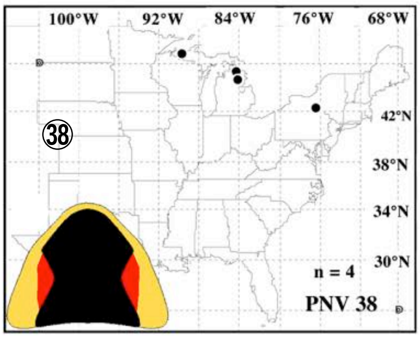


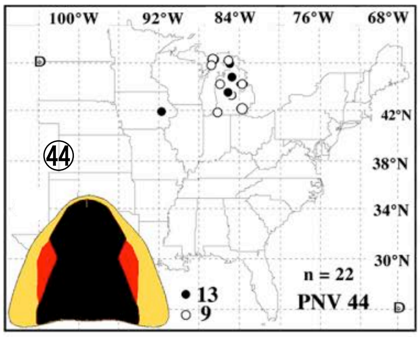


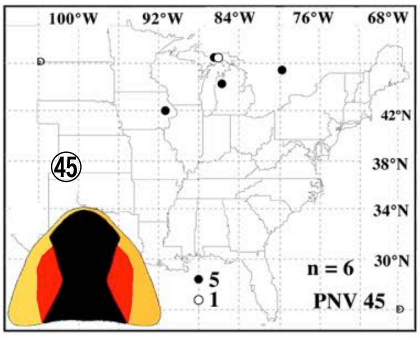


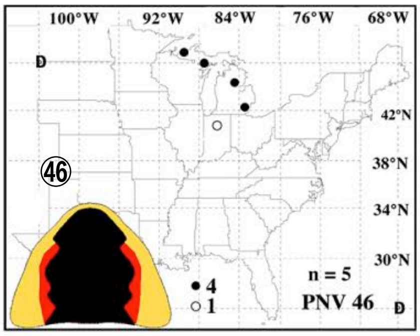


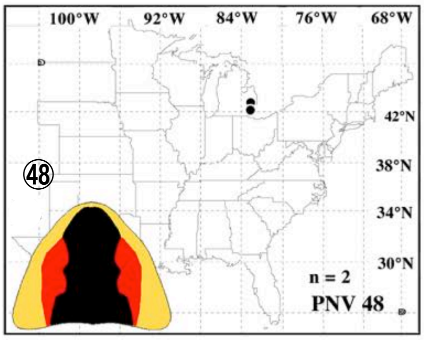


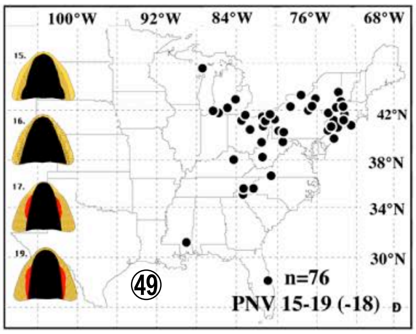


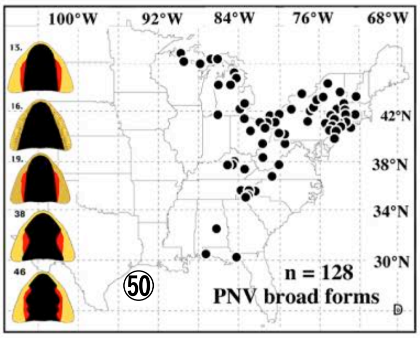


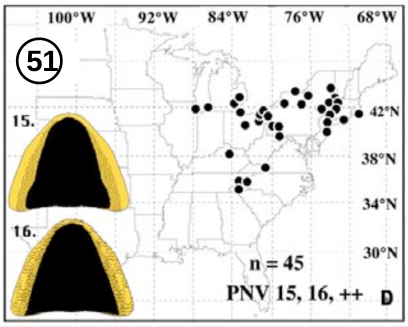


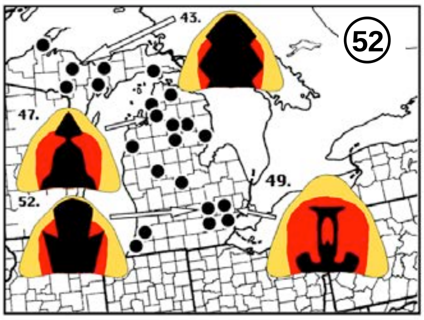












Guillaume Antoine Olivier
1756-1814

Photo ref. in Bibliography

Chapter 6

Fireflies & Two Epiphenomena: Beacon Trees & Species!—Dissection, Analysis

Facts are stubborn things; and whatever may be our
wishes, our inclinations, or the dictates of our
passion, they cannot alter the state of facts.
John Adams

A conspicuous consequence of a phenomenon can be mistaken to be the explanation for its occurrence. To argue the contrary, to dismiss the obvious, whether history's wisdom or habit, with scientific facts, one may expect to be met with resistance and rejection. A new perspective may provide insight and avenues to approach a question. This is appreciated in the use of the expression "thinking outside the box." In this and a related firefly study, new views were forced upon the author: (**1**) by an understanding of basic (natural) selection thinking, and (**2**) by knowledge and comparison of the behavior and ecology of dozens of firefly populations in the field. The epiphenomena addressed here are: (**1**) flashing swarms of fireflies in **beacon trees** as observed in southeast Asia; and (**2**) **species**, as defined and understood in the Biological Species Concept (BSC). The first is discussed in some detail as an illustrative model; the second as an analytical necessity, and takes the view of the BSC-species—the amalgamation of sub-populations—and stands it on its head, with the sub-populations (demes, variads) understood to be the operational and real units of evolution to be closely examined. That is, demes are the entities on which to focus thinking in field and lab research. To particularize, such studies should involve defining the geographic and genetic limits of these in the real outdoor world, and second, discovering connections and relations among them. The term *species* is used loosely for convenience, sometimes applied to a collection of "sub-populations"; and at other times to a single sub-population, with the important point being that "the species" is not usually a unit of biological "natural self-cohesion/organization." A comparison of selected demes and variads in three genera of flashing fireflies, *Pyractomena, Photinus* and *Photuris* may provide a different perspective toward understanding the real nature of biodiversity as it exists at their scale in nature.

Rhythmic synchronized flashing of thousands of fireflies was long reported to occur along Thailand’s estuarine shorelines (**Fig. 1**). These beacons were used for piloting by Thai boatmen, and obviously, it would appear, by fireflies seeking fireflies of their kind. In the early 20th Century several *Science* note-writers explained the spectacle, which they had not themselves seen: it was fermented sap causing drunken beetle revelry; a psychological tendency to see synchrony where there was none; quivering eyelids; a tale told by natives with flawed senses and extravagant imaginations. Much later, engineers invoked mathematical proof and the physics causing clocks in a room to tick-tock in unison. (Before the moon landing an argument/spoof in *Science* cautioned astronauts to be prepared for stepping into green cheese.) To the point explored here, as recently as the 1970s lab-bound biologists proposed and steadfastly insisted that mass synchrony was a *population* adaptation to help other fireflies avoid bats. The word *population* was never mentioned; to them, the observation of firefly-assisting beacons was explanation enough. Several explicitly and fervently rejected genetic reasoning and Darwinism specifically, *in toto*, quoting literally, as "simple-minded nonsense."


Fig. 1. Along the Chao Phraya near Bangkok.

There were other less than reasonable explanations proposed at the time for swarms of fireflies: mangrove swamps were too dense for flying-searching (patrolling) flash communication as in American fireflies—which can easily be seen flying and flashing over dense hayfields and treetops, around shrubs, amongst cattails and marsh grasses, and within tangles of prostrate vines before sunset?; and, the gatherings helped fireflies assess their abundance, adjust individual reproduction to local ecology and its carrying capacity, and avoid population extinction ("epideicticism"?).

It is reasonable, is expected that fireflies might be attracted to lights. Even in species that do not form sedentary aggregations, such as those in America, emigrating gravid females seeking new sites: say, upon leaving a deteriorating home-site, might be expected to approach a distant glow or flashing lights. A positive response to light, orientation and approach, could be an adaptation, benefiting the individual with the genes coding for this behavior. Genes could also code for a response to flashing lights of specific characteristics, say, flashes repeated at a particular rate or a group of flashes of a particular configuration. These behaviors can be examined, experimentally demonstrated to occur in individuals. Studies could also be designed to demonstrate their reproductive significance for individuals.

But, to demonstrate an adaptive significance of collective (mass) synchrony (the beacon effect) but no other benefit to the individuals that are actually responsible for synchrony, appears to be impossible: individual males would have to flash their lanterns in synchrony with neighbors to contribute to the beacon, but not derive individual benefit from doing so. If the mass effect were the adaptation, that is, individuals gained no selfish benefit, sneaky males that saved energy (cheated) by not flashing would have the advantage (their genes selected) by saving energy, living longer, and eventually the beacons would go out. Formally stated, in this discussion of flash synchrony, it is the *level* of adaptation—individual selection versus population (group) selection of genes/alleles—that is the point of focus.

Focusing attention on the real questions. The genes coding for flash synchrony are delivered through aedeagi of individual males that successfully compete for females that are attracted by the species-specific timing of the males' rhythmic trains, and then are receptive to further advances **(Figs. 2, 3**). To be successful a male of a species in which flash **rate** is key, must cooperate with his near rivals. If he did not, the identifying timing-signature of his signals (flash rate) would be unrecognizable in a muddle of flashes as seen by approaching, inflight females (jel, 1973ab). That is, the key ID signal pattern would be lost amidst the out-of-phase flash-trains of neighboring males and also by the "spurious" flash trains and solo FPs of other species active among them at the same time. To re-emphasize the key point: analysis of mass synchrony in Asian fireflies begins with a focus on synchronizing *individual* males with genes to inject, and individual females that are attracted to land near/amongst them, select one of them, and accept delivery of his genes.

Figure 2. Such egos, those of species with synchrony genes, also aim their invitations from mangrove leaves as does this *P. valida* , a non-synchronizer.

Figure 3. Courting male of *P. valida* atop a female bringing his tail around to her face, with a message.

This understanding of "mass synchrony" first began to emerge from observations on New Guinea *Medeopteroptyx* (nee *Pteroptyx*) males seen in separate, somewhat isolated clusters that occurred across bushes and trees (**Figs. 4**; jel, 1973ab**)**, and the timing that occurred within, between, and among the clusters. The interval between flashes in one species was about five seconds. Males within and those hovering near and closely approaching each cluster flashed in synchrony. Though the flash rate of all clusters was the same, the clusters were not in phase with each other; instead, when viewed from the road 100 feet above the valley, the sequential flashing of the out-of-phase clusters jerked/hopped across space in a time sequence—step-times between clusters were similar but not identical, and clusters closer to each other in space, were also closer in time. Note the figure legend.

In mass (whole tree, treeline) *Pteroptyx* synchrony—as seen along the Chao Phraya and other rivers near near Bangkok, inland along canals and at other damp places—functional "clusters" of competing egos may also occur but may be indistinguishable along a continuum, leaf to leaf, and because of "cluster" proximity, all are melded into a single, eye-catching phase. The flashes of some species are modulated, doubled, raising the question whether this is to facilitate synchrony, to aid in coding, or both. Also, perhaps there are constellations of competitive males, with super males and satellites. Other insects swarm at markers: flies that parasitize crickets were found gathering at a water tank towering above surrounding vegetation; desert insects use tall shrubs on ridges for *hill-topping* markers; and some flies swarm just off the ends of low-hanging branches at twilight. Certainly some firefly species use others' beacons?

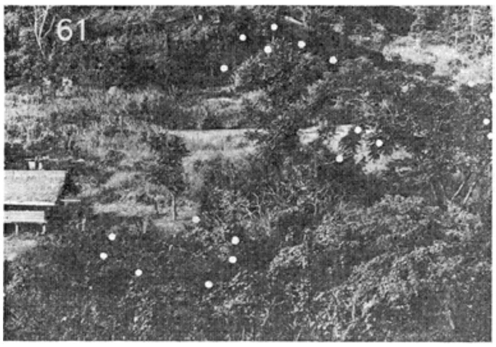


Fig. 4. A nightly panorama, looking down toward Namie Creek, each dot as a firefly. In each group (n = 5) they synchronized their flashes. The flashes these out-of-phase groups hopped across space. Groups near each other were more nearly in phase as would be expected since males moved between groups.

To understand the meaning of the mass synchrony an observer must get inside swarms **(Fig. 5)**, and from a ladder take photos and videos, and smear samples from males tails, this to learn whether they might be telling females something when they swing their tails around and over their faces (**Fig. 3**; also page 9)—tales of previous success, of nuptial gifts currently available from accessory glands … Simple novel observations can be important: the question once existed as to whether mangroves or other broad-leaved woody plants themselves had some feature that made them, but not the palms, platforms for swarms (**Fig. 6**). The answer, by chance, is yes they do. When tropical zephyrs moved through and waved palm fronds one evening, frond leaflets scissored against each other and dislodge males perched there. The bush behind the nippa palms in **Figure 7** is where photos were taken; the species in the photos is the non-synchronizing *P. valida.* (see also: pages 9, 129, 176, 178, 172, and 474)

photo by Steve Wing

Fig. 5. Over a Bangkok bush, surrounded by nippa palms.

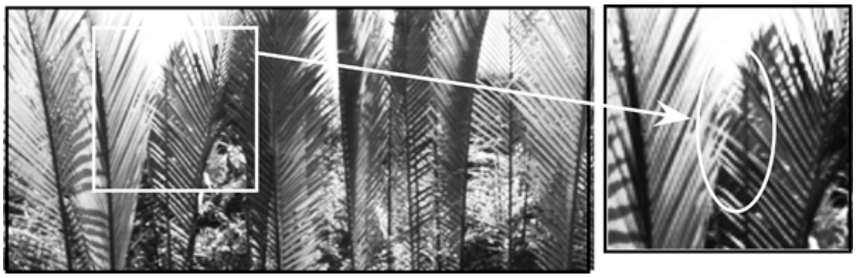


Figure 6. Scissors at a *Pteroptyx valida* site near Bangkok; the bush is behind the row of palms.

Species as epiphenomena. For most thinking humans and cultures, species are, long have been, and shall remain the obvious, recognizable and “logic”-satisfying elements of the natural scene. Insect collections have always labeled trays of pinned specimens that are identified as belonging to the same *species*. We will always see nature, each panorama before us and beyond the horizon, as consisting of many unitary, non-interbreeding entities. However, scientific understanding of the true biological nature of species, what they are and were and how defined, has changed greatly since John LeConte described his fireflies in the 1850s. With a developing understanding of genetics, species became constellations of genes (gene pools) of organisms of similar appearance, and interconnected local gene pools, potentially interbreeding. With this, concerns about the adequacy of gene flow to connect geographically separated pools, and the unitary nature of such fragmented species became a concern. Consistent variations among specimens in a tray that had different geographic origins sometimes led to species being divided into subspecies or “varieties” or “forma”. Under the Biological Species Concept (BSC), such populations or at least those with "permissible" variations—a matter for arbitration—were acceptable, and a unitary view of species carried forward. The question lives: how could local populations in some taxonomic groups that were separated across "significant" space/time (distance/vagility), remain so much alike—why didn’t mutations drive or drift them apart. Was natural selection similar at all sites for the key taxonomic details viewed, and/or could genes fly really fast enough to tie pools together? How much time was involved—in seasons or in generations?

In the view entertained and future research prepared for here, the situation as observed in *Photinus*—which easily fits into old understandings—is placed in contrast to what has been found in certain *Photuris* (especially, the dot-dash/long-flash Penn complex). This may provide an opportunity to explore the nature of biodiversity at a finer grain than offered by organisms lacking luminescent signals, and in particular, signals of such a range of complexity and diversity. Instead of putting *Photuris* vouchers with variations together in single trays, here some are separated, and sometimes given scientific names. Indeed, expecting genetic variations of interest to be found in DNA-vouchers from different "remote" sites, site-vouchers often receive separate trays even when their signals appeared to be identical—as example, my vouchers of Barber’s *Ph. hebes* are separated into 18 trays, all waiting to be “gelled” by someone as the next step.

Parallels can be drawn between the synchronous clumping of flashes in *Pteroptyx* beacon trees in Asia and the clumping nature of the BSC, both being taken as epiphenomena: the recommended way to study beacon-tree flashing is atop a ladder with broad comfortable steps and a railing to lean on, and watching individuals and any existing(?) “sub-clustering.” Similarly, one studies species by seeking local populations through space to identify the limits of functional demes, and seeking deme differences. Fireflies should be good for this sort of scrutiny—follow the flashes, for more than merely being guides to find them in the field, the flashes are of languages, with characters to be coded into cladograms.

In the field, learning each deme's territorial extent and interconnection with others presents new and unexamined problems for fireflyers—no one has sought or studied actual deme limits and the interdemic traveling ability or propensity of individual fireflies, say, young versus old males. Demes evolve, diverge, converge, reject intruders, exchange single individuals, and become extinct. They are the units where adaptation begins to occur. With the conclusions of Erlich and Raven (1967) in mind, and knowledge that aggressive mimic fireflies, for example, could put great local ecological pressure on prey populations, perhaps …

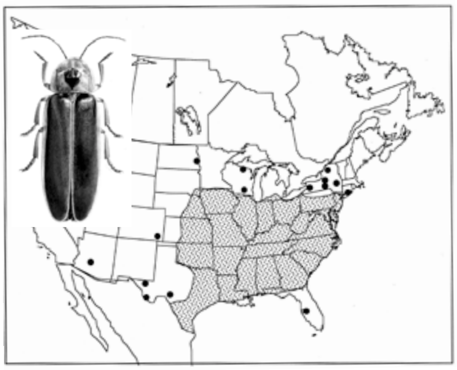


Figure 9. *Photinus pyralis* occurrence with "outlyers", some being from student collections and some perhaps transported in potted plants or bales of hay.

What is a deme? There's a rub, for though easily imagined for theoretical purposes, as in the thinking of population geneticists, in shifting balance theory and the illustrative 3D (inverted-cone) model, in the field it is more difficult to recognize the limits of demes and their separation and distances from one another. In practice, operationally only as a beginning, a deme is a local population observed and sampled (behavior measured, vouchers). In the present study hundreds if not thousands of such demes were sampled, differences and similarities sometimes noted, vouchers collected and labeled for future examination. But, in fact, in Alachua County FL, for example, whether the *Photuris carrorum* population at the Austin Cary Forest site belongs to the same deme as the Gun Club *carrorum* just down the road a few miles, is the question in its simplest form.

At the beginning of this firefly chase it was difficult to imagine that *Photinus pyralis* could travel and exchange genes fast enough to stitch populations together across the known range of nominal *pyralis* (**Fig. 9**). For decades this very common firefly was deliberately and closely observed at points throughout its range and seemed to belong to a single BSC species—as we have previously understood species, judging from morphology and sexual conduct. Only pronotal vittae showed any promise. The analysis of the PNV of *Lucidota atra*, Chapter 5, a daytime dark firefly, pursued the question of geographic diversity. The BSC idea seemed to hold true for all of the several *Photinus* that were observed across eastern North America in the 1966 field study. Perhaps because, from some literature, identical natural selection on isolated populations combined with some unexplained *tendency* to resist change ("genetic inertia", "ether", "formative causation", Sheldrake, 1981)? Whatever the explanation, it was also needed to explain several other fireflies, including most *Pyractomena* and certain *Photuris*, such as Division I *frontalis* and *congener*, and some others. But sampled demes of certain *Photuris* were really discomfiting, and eventually became the primary focus and concern of this study. It is these that defy taxonomic pigeon-holing that provide a space-time adventure. In this study several are outlined and sketched for further study, and will suggest/encourage methods for further pursuit—a reasonable way to start.

Practical and other notes on demes, variations. (**1**) Herbert Barber found that in a river-side deme of his *lucicrescens* the males used a single FP, a long crescendo flash (page 475 "I"), and in a "conspecific" deme a few miles away (a broad dale?) it used the crescendo **and** a short flash. He questioned this, and envied bats that he might follow individual fireflies and watch their flashes. In the present study, decades after Barber and 1000 miles to the west, in Missouri, mark-release-recapture studies on *lucicrescens* at a site where they sometimes flew low and were accessible, demonstrated that this Missouri *lucicrescens* was responsible for both FPs. (Note: *lucicrescens* does not default!—none has ever done so when asked!)

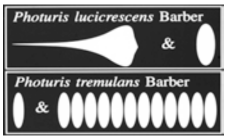
(**2**) In this paper variad populations have sometimes been given scientific names. Such judgment anticipated genetic reality and future convenience. Foremost in mind was taxonomic stability, utility, and simplicity, and the highest priority on the list of essentials was to anticipate what the next generation of taxonomist (DNA and field specialists) would find useful. I expect that decimal numbers not names will eventually be used. Sometimes a designator/nickname, from a regional name or FP appearance was applied, as in these two examples. (**A**) Along the Atlantic coast from Maryland south to Florida and at sites on or near the Gulf coast of Florida are populations of short flashers similar to what Barber described as *salina* ("*salinus*"). There are some differences among and miles between them. These are treated under *salina*. Understanding will require DNA analysis. (**B**) Three distinctive FPs were observed and PM-recorded in Ann Arbor marshes in the 1960s, during observational innocence: a dipper, a flickerer, a dot-dasher. These FPs could have been adjuncts and emitted by one species; or, the dot-dash flasher could also have emitted the *Py. sinuata*-similar long flicker as well as the *Py. linearis*-like long-flash dips; or the flickerers and dippers could have been different species. They all look the same on a pin. They are referred to, in Washtenaw Marshes Chapter 68, as AA flicker, AA dipper, and AA dot-dasher.

(**3**) There is an extensive literature on sexual reproduction as an individual adaptation, rather than the flawed supposition that it serves to provide variation for exigencies that future generations will face (Williams, 1975, 1992; Manning, 1976; Maynard-Smith, 1976; Hapgood, 1979). I mention this because the explanation for the apparent constancy of *Photinus* across space and the remarkable variation seen among certain *Photuris* might have some connection, and provide examples for comparison. Is the best predictor of what environment that offspring of a *Photinus* pair will face is that experienced by their parents?—what of changing and variable challanges from *Photuris* predators?

Chapter 7

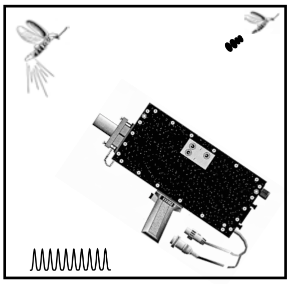
Found and Emerging Patterns In Firefly Semiosystematics

(Observations, Theory—Expectations)



> *Organismic diversity is not chaotic but patterned, revealing all sorts of regularities … These regularities have various causes, and it is one of the major tasks of systematics to discover the nature of the causation of these patterns.*
>
> Ernst Mayr

This Chapter is the heart, soul and raison d'etre of this study, and the most promising result of this half-century semiosystematic approach to the classic "*Photuris pennsylvanica* Problem"—that was initiated by Herbert S. Barber nearly a century ago. It is compilation of observations and ideas, and should provide clues in studies of local populations (demes) and eventually toward understanding their number, evolution and phylogenetic relationships. The significance of some patterns was not appreciated when they were first recognized, as in the case of similar flash patterns (FPs) seen in members of different genera. In fact, the very close-matching, theory-attracting nature of this particular phenomenon could not be recognized by pioneers Frank McDermott and Barber though they spent time in the field and thought deeply, because portable electronic FP-recording technology was not available. Though they were familiar with the flickers of both *Photuris tremulans* and *Pyractomena angulata*, the similarity if not identity of these FPs could not be recognized, draw their attention, and demand explanation. Color differences between match and model flickers might also have been a distraction because the color-blindness of fireflies, at least when viewing others at usual operating distances, was not known at the time—that is, the difference in color might have rendered observers blind to their (apparent) functional identity to fireflies. Also, until faced with the doubts and uncertainty of the reliability of observations of the previous night, that always arise in the light of the rising sun, one cannot appreciate the support and confidence provided by electronic records of impersonal photomultiplier and other recording instruments.



Predation Is Key: Because predation by Photurinae (subfamily) species on other fireflies is focused on signals and signaling behavior, predation emerges as the ecological pressure potentially most responsible for making semiosystematic studies most complex, interesting, and evasive to understanding. The hunting tactics of *Photuris* are the key to understanding FPs: females of the genus *Photuris* (**1**) attract and eat males of other species by mimicking the mating signals of the males' own females; and (**2**) attack them in the air, using the emitted light of their prey as a target. These deadly, omnipresent, and omnipotent predators are both **inside** their prey's coded signal systems using false messages, resulting in coded countermeasures to them, to which predators will in turn respond; and **outside**, using the signals as targets, just as pit vipers and sidewinder missiles home-in on energy emissions from their prey. It is certainly no coincidence that in *Photinus*, those species whose males emit (leak?) dim light between flashes, are the fast-flying searchers (*collustrans, stellaris;* p. 472 D*)*; or that males of some *Pyractomena,* which commonly "leak" dim glows between flashes, drop to the foliage or ground when they receive an answering flash. Further, there are other emerging dimensions of *Photuris* predation that deserve attention: (**3**) indirect evidence suggests that *Photuris* females prey upon males of their own species, in particular those with which they are copulating or are just completing intromission—perhaps as part of their sexual selection protocol; (**4**) they may hunt the hunting females of other *Photuris* species; and (**5**) they probably exploit (by proxy) flash responses of prey-species females to catch

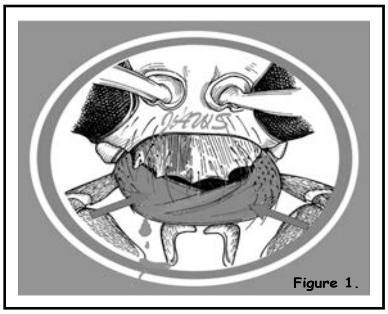
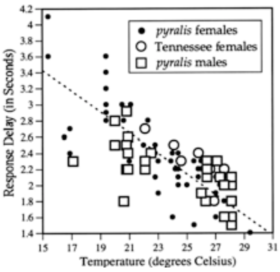


Figure 1.


Ph. carrorum, aggressive mimic

males the females are attracting, and perhaps prey upon these yolk-rich respondents themselves. Certainly more threads of this tangled web are to be expected. The fact that certain *Photuris* females have only recently been found to *routinely* exploit spiders by stealing prey caught in their webs (Faust et al, 2013; Barber, here page 475 J), confirming an early observation of Barber, gives a clue as to what we have yet to learn.

There are several other known and suggested predators of fireflies, including spiders, bats, and nocturnal birds, and undoubtedly they too have been responsible for selection pressure on firefly signaling (jel, 1973c). Fireflyers should examine suspicious dimensions of this drama: as example, when it was discovered that *Photuris tremulans* males sometimes emit (are even named for) a flash pattern (FP) that is a very good copy of that of a distasteful species, an ultrasonic emitter was used to simulate the echo-location signals of an approaching bat to see whether this would cause a mate-seeking *tremulans* male to switch from his mating-identification (own, default) FP and begin emitting his (“bad-tasting”) flicker pattern. The question was, would edible (*Photuris*) males use this FP to divert bats from attack? It was suspected at the beginning that the experiment had a low probability of success—fireflies are not known to have ears—but it was simple and inexpensive to try and would provide important insight if by remote chance it were true. But, even when the electronic emitter was held within a foot or so of the fireflies and its ultrasonic clicks presented in a rate-sweeping, approaching-bat-like manner, the fireflies did not switch to the (presumptive) aposematic flicker FP (jel, 1989; FLB 18).

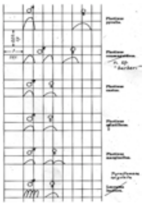


In another example, when a *Photinus pyralis* male hanging in a spider web was found responding like a female *pyralis* to the FPs of passing males of his species, the question raised was whether the spider was specifically adapted to using snared males to attract more males to the web—were firefly specialists using fireflies as penlights to decoy prey? *P. pyralis* males experimentally attached to spider webs and sticky tape showed that neither spider venom nor a tug on the web was necessary to trigger a female-like response from them (jel, 1997; FLB 19). It is not known *why* nor *how* males behave this way—(**1**) maybe it is nothing more than a physiological misfiring, their afferent (recognition) circuits becoming efferent, feminizing their flashing so to speak; and/or (**2**) in males this response has evolved because it is adaptive, for if another male approaches and accidentally knocks them free of the web … but this would seem unlikely if most spiders wrap their prey securely (page 475, J).

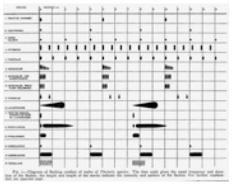
Some, a few, elements in the listing below of found and emerging patterns are universals, apply to all or nearly all Western Hemisphere lightningbugs. Others are found only in certain species groups: For example, though it is certainly predation by aggressive mimicry by *Photuris* females that has driven or led to many of the complexities observed, this behavior is not known to occur in *Photuris* of the *frontalis* group (e. g., *divisa*, *congener*, *frontalis*, *floridana*), nor yet seen in members of the *potomaca* "group," though *potomaca* itself might find targets aplenty along the river- and canal-adjacent areas in central Maryland, northern Virginia and West Virginia.

A Florida member of the *lucicrescens* Group(?), *lamarcki*, is an unrelenting hawker. In a deme near Ocala its own males often signal from perches rather then fly, and its females attack “flying” LED targets almost immediately (Warren Prince and associates)—one explanation for *lamarcki’s* wing-beat-like FP flicker is that it deters aerial hawkers because they avoid or are slow to launch an attack through beating wings, and the lantern’s flicker is similar in frequency to that of wingbeat shuttering … auto-mimicry? This flicker is unusual, extreme, with a rate far faster then any other North American firefly—perhaps it tapped into the wing-beat oscillator (Chap. 43).

⁂



The List: A Sketch



1. Luminescence in adult North American fireflies is used for sexual communication. Two major communication *systems* are recognized in North American fireflies (McDermott, 1909-1917). In **System I**, brachypterous or wingless, soft-bodied, often-burrowing females, glow and attract (typically non-luminous) males (the glowworm fireflies, *Microphotus, Phausis, Pleotomodes,* and *Pleotomus*; and *Pterotus*, a western species, formerly a lampyrid but apparently of uncertain affinity). Females of *Pleotomus* glowworm fireflies apparently use pheromones to attract mates from long range, and their glows provide targets and perhaps additional information at short range. Most daytime dark fireflies probably use chemical signals (pheromones) in System I fashion, with females attracting males from longer distances than glow signals would. In **System II**, which is almost universal in North American lightningbugs (*Photinus*, *Photuris*, *Pyractomena, Micronaspis, Bicellonycha, Aspisoma*), flying FP-emitting males are attracted to flashed responses from females perched below. These responses are usually single short flashes. Possibly *Micronaspis floridana* uses a combination system in its windblown, seaside, Florida needle-rush-habitat, and both flying females and males approach answering flashes. Unexpected/unusual signals occur in two North American *Photinus*; *they* have become dark and fly in daytime: *P. indictus* uses pheromones, and *P. cookii* (an afternoon firefly?) may use visual, reflected-light cues, the black form of females against green leaves, as recognized some time ago in the flash-aiming of a twilight-active flashing species by Ted Burk. This classification (systems I and II) is simple and useful, so far, for American species, but with the more complex mating behaviors as seen in Asian species it is better to speak of protocols, that include System I and System II elements but are far more complex than the simple signal-approach described (jel 1966, 1972, 1973ab).

2. Fireflies emit bioluminescence of different colors (Appendix 3). **Apparent** color of firefly light to humans is often misleading, caused by variations in viewer dark adaptation and ambient lighting: the yellow flashes of *Pn. pyralis* will appear green in sodium-vapor light or rosy sunsets. With one known exception (≈green *tanytoxus*), *Photinus* lightningbugs emit yellow light; *Pyractomena* lightningbugs emit orange-yellow or amber light, with two known green exceptions (*angustata* and *ecostata*); *Photuris* lightningbugs emit green (or blue-appearing?) light, except *frontalis*, which emits a yellow-shifted light. *Photuris* spectra match the sensitivity spectrum of the superposition eye found in day-active insects, and *Photuris* (Seliger et al, 1982a, b). However, *Photuris* light appears green, blue, or white?! The yellow light of twilight-active *Photinus* (Div. I and *pyralis* Group), with some with modification of eye filtering, enhances (monochromatic) signal reception against the (noisy) green background of foliage illuminated by twilight skylight (Lall et al, 1980). Red-shifted luminescence (amber, orange-yellow) in certain marsh-inhabiting *Photinus* and *Pyractomena* may be an adaptation to foggy air, common in their marshy habitats—long wavelengths are not reflected by fog droplets. Spectra are in Appendix 3 (mostly unpublished, J. Lloyd, W. Biggley, H. H. Seliger; see also Biggley et al 1967).

3. Flying males of many species can be identified by their (species-typical) mating signals (flash patterns, FPs) they emit while cruising about within (*patrolling*) their species-typical activity spaces. FPs vary among species with respect to pulse number, pulse rate, pulse configuration (shape), and repetition rate (McDermott, 1917; Barber, 1951; Lloyd, 1966; see Chapter 8). (When beginning, to ID seek/observe the same FP of many males flying together).

4. Individual *Photuris* males of a few species range widely, apparently seeking their hunting females in prey habitats/sites (see also 35). In Florida, hunting females of *Ph. harranorum* are often found singly perched in sites with prey species. Single males are often seen *roving*, flying through sites without resident conspecific populations. Males of at least two continental species appear to behave this way: *Ph. versicolor* and *Ph. fairchildi*. Their FPs are distinctive, of unmistakable form, and those of the latter are repeated at very short intervals appropriate to rapid mate-seeking flight.

5. Males that are seeking females via flashed responses to their emitted FPs, also recognize the flashed responses of females to the FPs of rival males. Rival males also move toward a responding (then-contested) female (p. 475 E). Males of many species dim their FPs upon receiving female flash responses, thus reducing such interloping.

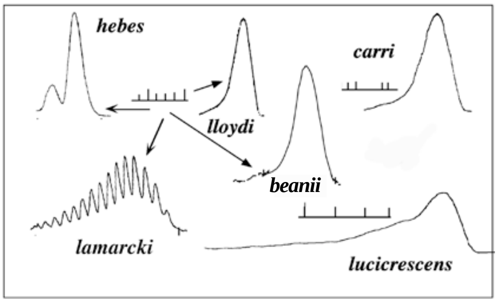
6. Female flash delay is sometimes part of a species' code. In P*hotinus ignitus* female delay is "extreme," <10 sec @15°/59°, but in most species it is rather short—in a few *Photinus*: *pyralis*, *aquilonius*, *umbratus*) it is 1-2 seconds or slightly more. After flashing, males of long-delay species hover or fly slowly to receive a response with the correct timing (McDermott, ibid; jel, 1966). It is important to emphasize that McDermott could discover/recognize this because he observed female responses in both *Pn. pyralis* and *Pn. marginellus*, the former having a 2-3 second delay, and the latter contrasting with a short <0.5+ sec delay—that is, the comparison (i.e., comparative method) would have brought the significance of this parameter to his attention. Contemporaries would not appreciate this.

7. Male approach-time varies greatly among species. After the initial exchange of signals, males may take several minutes and FP-response-flash connections, but two or three minutes is typical for many species. In certain circumstances it may take much longer: when several Florida *Pn. macdermotti* (s.s.) approach the same female they land and emit a variety of flashes "to" (that will sometimes) deceive rivals and determine whether their respondent is an aggressive mimic predator. On the other hand, *Photuris* males may reach females in a few seconds (n=3, *douglasae, hebes, lucicrescens* observed). This may explain why across a span of decades only a few *Photuris* attractions were caught in the act. When attracting male *Photuris* to the penlight or flashpole it requires from seconds to several minutes.

8. Flashing parameters change predictably with temperature, as incidentally noted/implied in early writings of McDermott and Barber, and measured by Jones and Jones (1921) for flash pattern periods in *P. pyralis*. This is likewise true of female delay, as noted in *pyralis* by McDermott (ibid.) and measured by Buck (1934). Pulse rate within multi-pulse FPs and flash duration also vary predictably with temperature (see also jel, 1966). Interval durations (e.g., **periods**), of FPs and of pulses within multipulse FPs across a range of temperatures vary in a curvilinear/exponential fashion, and the reciprocal, i.e. the **rate** (1/period) is nearly or virtually linear for flashing parameters. Ambient temperatures must be measured and accompany field flashing data to be useful for identification; flashing/temperature slope equations are potentially useful as taxonomic characters and also for understanding ecological adjustment ("adaptation" s. l., as in physiological "versus" evolutionary) to environmental circumstances (see *Ph. missouriensis*).

9. Signal puzzles are understood/resolved/clarified for testing by using a selective-thinking perspective. In one example, a flash-answer system could evolve from a continuous-glow system, via a response glow like that found in the glowworm-firefly *Phausis reticulata* (jel, 1966); as a more recent example, the code:: male <single flash>—female <very **long delay** then flash> of *Photinus ignitus* could have evolved from a 2-flash pattern like that of *Photinus macdermotti* (jel, 1966, 1984). Retrodiction and experimentation may suggest the extinct FPs of recent ancestors of some species, including one or two from glacier times ("paleo-*ignitus*", "paleo-*indictus"*; page 339-340).

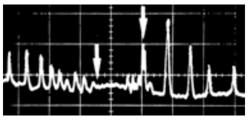
10. Flashed signals show phylogenetic relationship. Species that are judged to be related based on morphological features often have similar signals (jel, 1966). That is, signals corroborate existing evidence for taxonomic relationships; certain features of flashing behavior such as the two pulse FPs of members of the *Pn. consanguineus* group are apparent homologues. Parameters showing such relationship may be suspected of having coding significance (jel, 1966). This is strongly illustrated in Green's (morphological) species groups of *Photinus*: species of Division I all have a simple <1-flash>-short delay <short-flash> codes. The only embellishments of note are the durations of the male flashes. Species in the *Photinus ardens* group all have multiple-pulse FPs; those of the *consanguineus* group have 2-pulse FPs or, as experimentally demonstrated in one species, derivations from 2-pulse ancestors; and members of the *punctulatus* group all have "not short" 1-flash FPs and short female delays, excepting *umbratus* which is *deviant* in ecology and certain aspects of its morphology; such contrasts attract special attention, pursuit, and DNA scrutiny. A crescendo-flash connection of several *Photuris* species directs and invites DNA verification—*lucicrescens* Group; including *whistlerae and beanii*?



Crescendo FPs of the speculated *Ph. lucicrescens* Group

11. FPs comprising several flashes (pulses) have *variable* numbers, not fixed numbers. In no known case is there evidence that *specific* (fixed) pulse numbers of three or more (≥3) identify species—though 2-pulse-**only** FPs occur —that is, there are **no known** 3-pulse-only, or 4-pulse-only FPs, or other such numerically-coded FPs. Perhaps this generalization will be modified, in the context of defensive countermeasures, as when communicating pairs are closely approaching each other. In northern Virginia (Westmoreland Co.) and southern Maryland there may be a *P. consanguineus* Group species whose FP pulse interval is variable, via the occasional omission of the #2 or the #3 pulse of a 3-pulse FP?

12. Miscellaneous luminescent emissions may reveal taxonomic relationships. Flashed emissions other than FPs used in mate search may yet be found to be useful in semiosystematics, showing relationships at higher taxonomic levels; that is, similar neural mechanisms) may occur within clades at the variad/species-group levels. Examples are the glows, pulses, and twinkles (rapid erratic pulses) commonly emitted by *Photuris* females when landing, walking, constrained or entangled, manually stimulated, or in confined spaces; and male "twinkles" when they approach responsive decoys (females) through vegetation or other tangles. Also, the techniques used and prey species attacked by hunting *Photuris* females may be expected to be similar in closely related species. As a caution, unless previous experience and special knowledge provides otherwise, the apparent FPs of perched males should not be used for identification and especially for the certification of FP voucher specimens.



***Photuris* landing flashes.**

13. *Photuris* females are versatile aggressive-mimic predators. Such femmes fatales are known (presently observed) to occur only in some Division II *Photuris* (and in other Neotropical Photurinae genera). These females take perches in the activity sites of species in the genera *Photinus* and *Pyractomena,* and perhaps some *Photuris,* flash-respond to FP-emitting, mate-seeking males, attract them with false (mimicked) mating responses, and eat them. This has been demonstrated to occur widely; there may have been some disagreement between Barber and McDermott with respect to its universality in North American species, though both may have been somewhat correct: some species of

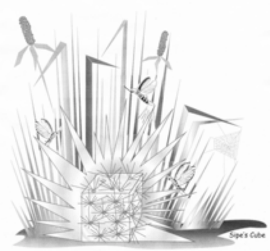
Division II (the classical "*pennsylvanica* section"), may not be predaceous (*potomaca* Gp)?

14. *Photuris* females may cannibalize conspecific males. Blinking, walking males on foliage dragging their aedeagi via the sperm ducts, leaving wet trails, have been seen three times. This suggests that females may sometimes seize mates after copulation and eat them—though no lucibufogens (sic) may be present, there is other nourishment.

15. *Photuris* females of some species are "polyglots/polyphots." Females of *Ph. harrannorum* and others can mimic the responses of more than one prey species. In some cases their responses, or some aspects of their responses appear hard-wired (but tunable?), which apparently is responsible for certain mistakes that have been observed during casual experiments (jel, 1975, 1981).

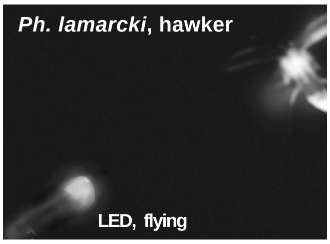
16. *Photuris* males in the *cinctipennis* Group may be aggressive-mimic predators. Flash responses of two *branhami* males to the *macdermotti* FP were like those emitted by *mac* females: one flashed answers to a *mac* male and the other to penlight simulations being used to collect *mac* females. The relationships among members of these two species groups in near-Gulf Florida counties is unresolved. Several timings of pulse pairs of both have been observed and measured, and recorded for reference in a large comb-binder on file with the voucher specimen collection.

17. Hunting *Photuris* females interact. During brief observations of hunting by *Photuris harrannorum* and *stanleyi*, T. Forrest and this author saw movement and approach by neighboring hunting females that suggested either mutual predation or other exploitation (ca 1980, Alachua Co., FL). *Photuris* females approach flashing lights on the ground, as demonstrated decades ago by UF entomology student Mike Sipe with an artistic bioplastic cube (10"x10"x10") with embedded, blinking LEDs and batteries.



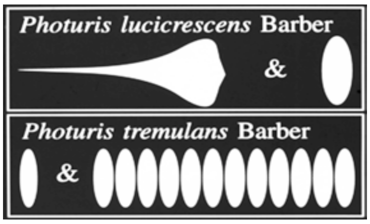
Mike Sipe's cube.

18. *Photuris* females are hawkers, and launch aerial attacks on luminescing males. This may occur in many species, but in Florida *Ph. lamarcki* and *beanii* were very active and perhaps more specialized in this predation. While filming with John Paling the aggressive mimicry responses of a *Ph. harrannorum* female to LED simulations of *Pn. macdermotti* FPs, she suddenly launched an aerial attack. In experiments, attacks are more rapid on hovering *glowers* (as with leaky lanterns) but only a few seconds slower on hovering *flashers* (Lloyd and Wing, 1983). Females pursued and attacked a moving, glowing LED target but not a simultaneously (i. e. competing) flashing (2-sec period) LED, nor the unlit control LED. Once, when two attackers struck the same decoy, they fought briefly and one decapitated (dethoraxed) the other. At a site east of Ocala at the Oklawaha River bridge, females attacked their own males in the air; males signaled from perches (pers. obs., W. Prince, T. Forrest, J. Sivinski, S.Wing, jel; see Note/Filler Index; pp. 461-462).



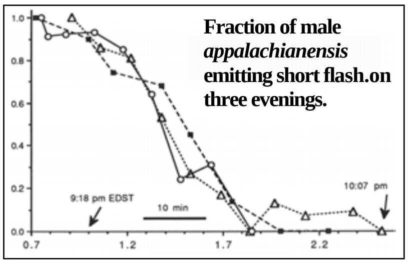
19. Males may travel/search (rove) as singles or in pairs or trios. This tactic for finding females may be the explanation for the observed "squadron" flights of two or three males that seem to pass together through previously inactive sites—perhaps resulting in tiny mobile leks. Also/instead, passing single males may cause perched watching/resting/waiting males to take flight (see Note/Filler Index, "Solo boradcasters").

20. Some *Photuris* males use two or more structurally different FPs. In *Photuris* Division II several species use two or more distinctively different FPs as they patrol their habitats seeking mates (Barber, 1951). The differences among *Photuris* FPs noted here are not merely changes in pulse numbers as seen in the FPs of *Photinus ardens*-Group species, or in the 2-pulse (-2-4-2-4-) versus continuous (-2-2-2-2-) flash "trains" of continental *Photinus macdermotti*-complex (jel, 1969b). Barber recognized this *Photuris* puzzle in three species: his *lucicrescens* emits single-short-flash and long-crescendo FPs; his *tremulans* emits a single short and 8-10-pulse flicker FPs; he also noted a third firefly but did not identify it or its patterns—based on lengthy study of *Photuris* in his bailiwick during several years, it could have been his *cinctipennis* or possibly *quadrifulgens*. He may have been suspicious or knew that—whichever of these two it might have been—it also, confusingly, emitted a flicker as did his *tremulans*.

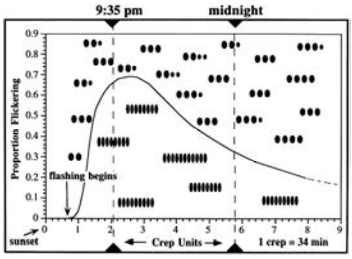


Barber's confusing FP repertoires in two of his species.

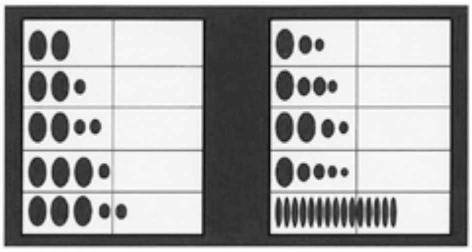
22. Males of some *Photuris* species use their different FPs in a time-predictable progression during an evening. In a population of *appalachianensis* in the mountains of Garrett County, western Maryland, males began activity each evening using their 1-flash FP (below, page 48, left); the proportion of males emitting this FP gradually diminished and the proportion using a dot-dash FP gradually increased, from zero at the onset of flight to "virtually" 100 percent by 40 minutes later—that is, except for two or three males at the site that emitted a flicker FP (these males identified as conspecific via *defaulting*, see **items below**). Similar behavior was observed in a *Photuris asacoa* in northeastern Iowa, which defaulted to a weak-crescendo FP. Males of *Photuris stevensae* (LIV) emit two **basic** FP **types**, a flicker and a range of pulsing configurations. Pulsing FPs vary in the number of pulses in an individual FP and the number and relative amplitudes of their **step-down** pulses. The proportion of males emitting the flicker FP increases from zero at the onset of evening flight to 30–80 percent an hour later; then, over the next few hours the percentage gradually declines. FP-profiles of this change on different nights was similar, with varying maxima, in sites in CT and on L. I., NY.



Fraction of male *appalachianensis* emitting short flash.on three evenings.



***Ph. stevensae* evening change-over.**



Sampling of *Ph. stevensae* repertoire (part).

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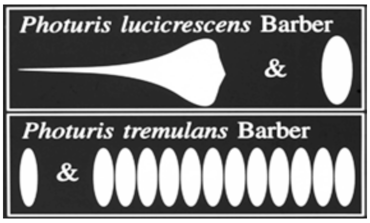
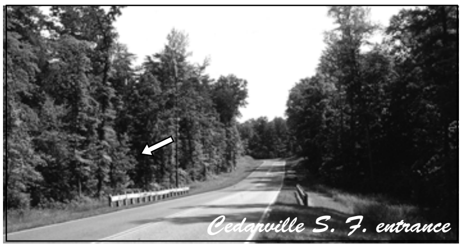
23. *Photuris* species with repertoires may not give a complete recital at each outing or site. A key question is whether all demes retain the same repertoire—and what would be the significance of this? From Barber: *The treetops are watched for the very short flashes … Two such places show only the crescendo flashes* [of *lucicrescens*]*, but about 6 miles west of Priest's Bridge we first see numbers of the very short explosions … A gust of wind disturbs the fireflies, and one comes down … a strong spotlight beam is abruptly thrown upon him … No chance this time to have netted the wrong firefly, but he looks no different from those taken in their long crescendo flash. Why were none of these flashes seen at Priest's Bridge or at two other stations? Why do both types of flash occur here and at some other places?* The Priest Bridge locality is along the Patuxent River presumably (see *lucicrescens* chapter); the second site Barber mentioned (6 miles west), possibly was a tree-lined slough/depression, as noted when sought five or so decades after Barber's observations. A mark-release-recapture study in southwestern Missouri demonstrated that individual male *P. lucicrescens* **there** emit both the short and crescendo patterns, with a tendency to use the short flash earlier in the evening. (Illustration at right shows FPs of Barber's two species; photo page 475, I)



In his second example, Barber noted that *Photuris tremulans* males use both a flicker FP and a short flash, and that the flicker was less commonly seen: *As dusk deepens … short, sharp flashes … from time to time there appear among them males … emitting long, tremulous flashes, less intense than the commoner sharp flash … followed by others, becoming more and more numerous, the shorter flashes disappearing until for a few minutes the long* [*tremulous*] *flashes dominate … or that a contagious emotional exuberance has changed the behavior of those males formerly emitting the short flashes. … described as but one species, tremulans* (1951: 7).

During the present study *tremulans* was observed in Barber's bailiwick at a forest edge 10 miles east of Washington (around low roadside trees and shrubs along the entrance drive of Cedarville S. F.; photo at left). Observations on all evenings were made at the same post-crepuscle time. Males emitted only the short flash on two evenings, but on the third nearly all emitted the flicker FP. On the fourth evening they emitted both FPs with the short flash being the more common. A trigger or other explanation for this variation was not apparent, and the number of flashing males appeared to be about the same over the four nights. Perhaps reproductive values or proclivities of available females was involved. Flickering males defaulted to the short flash when answered with a decoy (see below).



24. Explanation for the presence and use of multiple FPs by mate-seeking *Photuris* males: their (**1**) form/configuration and (**2**) times of use, are of major importance. These are the key elements in several of the following items, both factual and theoretical. Certain FPs of males, those termed *adjunct* FPs, are connected to the aggressive-mimic mode of hunting by their females—or once were, in their phylogeny. Evidence from several species together lead to the conclusion that *Photuris* males emit FPs like those of their females' prey and present these flashes at the times (e. g. twilight) and in the spaces (e. g. grassy forest edges) that prey males are active, and where the *Photuris*' females are hunting. While it is the reasons these FPs have evolved in *Photuris* that is of primary semiosystematic interest, the origin of their program (neural control) in the nervous-systems is a major unknown; a possibility suggested below especially invites experimentation.

25. One or more FPs in many *Photuris* repertoires match FPs of species of *Pyractomena* and *Photinus*. Models and matchers usually are known to occur in the same region, and are active in the same season and evening-time (jel, 1980). For example: *Ph. stanleyi* emits a flicker FP closely matching that of *Py. angulata*, and both fly at full darkness. Note the histograms with SESOBS data for *Py. angulata* and *Ph. stanley* at the same locations in north-central and Gulf-side Counties in Florida. Barber noted the similarity of the FP and spatial J-gesturing of *Photinus pyralis* to those of the firefly he named *Photuris pyralomima*. At his time such similarity in this single pair of species would have been understood *only* as an independent adaptation to the vegetation of the habitats. Now FP similarity/identity should be recognized as *potentially* being something more. Several *Photuris* species including *cinctipennis*, *tremulans*, *quadrifulgens*, and *stevensae*, emit a flicker FP that is sometimes a fairly accurate copy (except for color) of the pattern of *Pyractomena angulata* (termed the A-flicker), as determined via the comparison of many PM-recordings (but see below for added complexity). Some Florida *Photuris* species in the *cinctipennis* group compare closely with *Photinus* species in Green's *consanguineus* Group (see #16). Curiously, and certainly not by chance, both of these groups are taxonomically confusing and some that formerly might otherwise have been recognized as species are in this paper left in limbo, reported as variads of close affinity until more is known about repertoires and FP changing. During field studies near Cali, Colombia, other *Photuris* match-ups were noted. Most matching patterns discussed here presumably are **fixed**-matches, that is, are programmed into the male nervous systems and produced somewhat precisely by males without observing or calibration via the presence of the presumptive model. This, however, is an important question and is mentioned again below.

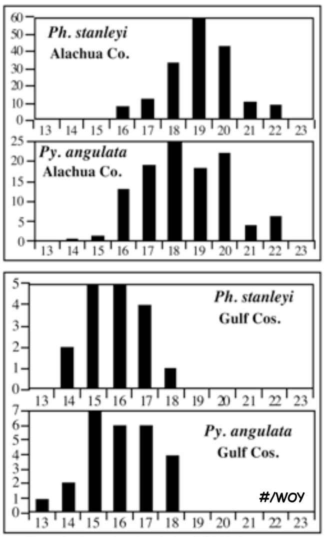
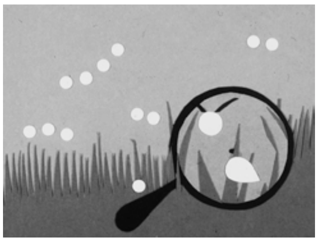


Figure 9. Comparing phenologies (SESOBS).

26. Some *Pyractomena* and *Photinus* species with *Photuris*-matched FPs are known to be prey of the *Photuris* own females (bottom p. 55**).** Recognition of this FP-connection provides a reasonable clue to one probable (adaptive) origin and significance of multiple FPs in *Photuris* species. FP matches between *Photuris* FPs and prey FPs include for example: in Florida the flicker of *Ph. stanleyi* matches that of co-active *Py. angulata*; in Florida, early evening male *douglasae* emit a long flash, and their females hunt *Pn. collustrans* males which have an early evening window and a similar FP; male *eureka* emit an ≈A-flicker (see Chapter 32) and long glow: (**1**) their females hunt *Py. barberi*, whose signal is the A-flicker, and also (**2**) *Py. angustata* whose "FP" is a long-continued glow—*eureka's* own-ID (*default*, see below) FP is a pulsing pattern similar to that of *Ph. quadrifulgens*. The variable-pulsed FP of *douglasae* males matches that of the minute' *Pn. lineellus* raising questions as to which species is the model, or whether both have reached the identical FP as an adaptation to signaling in a marshy tall-vegetation environment.

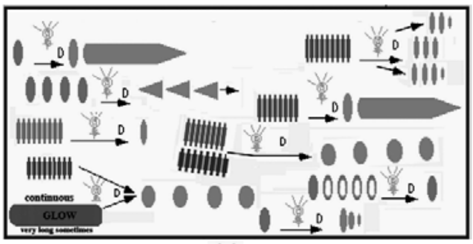
27. Mate-seeking *Photuris* males use prey-matching FPs to locate hunting females. The simplest explanation for FP matching is that males emitting matching FPs are seeking hunting females of their species and will ("attempt to") convert them to a mating mode. (Female mode option may be influenced by prey abundance, age and egg-status, and nature of stored sperm; male FP selection from a repertoire may be influenced by prey abundance, level of mate competition, phenology as related to "expected" female reproductive values.) This was one explanation for male mimicry *suggested* in the original paper (jel, 1980). Though observations that were convincing had been made, this explanation was mentioned as one of several possibilities for such FP matching. Females are long-lived, and their fitness (total reproduction) may be considerable if they are successful hunters, *continually* acquiring nutrition and defensive chemicals for continuing egg production, this not being limited to stores acquired as larvae. Though acquiring suitable sperm is a primary objective, finding prey potentially has great reproductive significance—is compar-able to the advantages of super males with extreme attractiveness in sexual selection perhaps—and finding a mate may usually be easier than finding prey. [Subsequent criticism in the "impact" journal of citation can now be recognized as having completely misrepresented and apparently manufactured a number and broad range of facts and details. Key behaviors that were suggested in the original (1980) paper, including defaulting (see 28) were found by the present author in the field near the campus where: (**1**) the critic had "performed his research," and (**2**) one of his referees and associate resided and lived long afterward. Further, (**3**) it was found in the region where another referee who was tutored by Barber himself had decades-long residence. There are more facts connected with this episode will be discussed in detail. The era of alternative facts and reality did not begin in 2017 in science.

28. When (decoy-) answered with a proper female simulation FP-matching *Photuris* soon begin emitting another FP from their repertoire. *Photuris* males of species with two or more FPs, one or more of which are the apparent match of a known *Pyractomena* or *Photinus* species, can be induced to change FPs. This is one of the easiest experiments to perform—in degree of difficulty easier than the attraction of *Photinus pyralis* males to a penlight. When a flashpole is used the operator can stand out of the approach path of the firefly being attracted. Among the many *Photuris* species that have been switched from one pattern to another are: *eureka* from the long-glow of *Py. angustata* to its pulsing pattern (by R. A. Lloyd, age 10, 1972), and others; *eureka* from the B/A-flicker FP of *Py. barberi*/*angulata* to its pulsing FP; spring generation *harrannorum* from the single short FP of *Py. limbicollis* to its J-3-4 pattern (T. & S. Forrest, jel); *quadrifulgens* from the A-flicker FP of *angulata* to its pulsing FP, and perhaps *quadrifulgens* from the D flicker FP of *Py. dispersa* to its pulsing pattern (see Chapter 60 for explanation of this confusion); *Ph. appalachianensis* from both the A-flicker (of *angulata*) and short FPs of twilight *Photinus* to its dot-dash FP; *Ph. stevensae* from its A-flicker FP of *Py. angulata* to a pulsing FP; *Ph. walkeri* from the long glow pattern of *Py. angustata* to its short-flash FP; *Ph. tremulans* from the A-flicker FP to its short flash.



It should be noted that defaulting behavior in some species on occasion may give mixed results that lead to more complexity. This was noted in *Ph. quadrifulgens* which emits as noted above, flicker pulse-rates like those of *Py. angulata* and *Py. dispersa*. Plots of recordings of a limited sample also show some pulse rates that fall between these two species' regressions. Whether this is an indication of a seasonal change-over, *dispersa* appearing earlier in the spring, or lack of fine-tuning, or other, remains to be determined. It may provide an opportunity to measure fine-tuning, and experimental manipulation with flickering LEDs. Note that *quadrifulgens*' Florida counterpart *eureka* also has two adjunct FPs matching FPs of two co-active *Pyractomena*, *barberi* and *angustata*, and also an indication of a *dispera* frequency being in the mix though *dispersa* is not known to be present in Florida.

29. When FP-matching *Photuris* males are answered and change FPs (item 28) they always(!?) change to their species-specific ID FP. The switched-to FP is the same for all members of an OTU, and is termed the ***default**** FP; the one **known** exception to this defaulting **rule(?)** is *Ph. lucicrescens*, which is attracted to decoy responses to both FPs in its known repertoire, and is **not known** to switch FPs. Defaulting clearly puts FP matching and FP switching in its historical context, and gives confidence in the explanation for this behavior. In the examples given in text **28** above and figure below, the FPs that males **change from** are obvious matches with the FPs of other species, as identified above by name. The FPs that males **change to** can thus be recognized/defined as the defaulter's **own,** species identifying FP. Should adjunct FPs of *Photuris* male repertoires be found not to match FPs of other species, they may: (**1**) eventually be found to match that of an unknown (extinct?) species, or (**2**) be found to be a general-template FP, or (**3**) be recognized to function as generalized chumming FP to elicit responses from hunting females, say, for trial and error exploration. For example, the single short FP of *beanii* may be a reasonably good but not precise simulation of the pattern of *Photinus macdermotti* or *Ph. branhami*, and the single short, early evening FPs of several dot-dash species and *asacoa* are presented in time and space as imperfect matches of early evening *Photinus* species (Green's morphological Division 1).



Defaulting after decoy response.

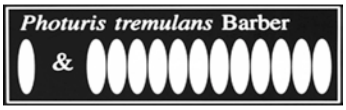
30. Males have little or no control in the situation. After a male defaults and identifies himself to the female, the female can stop flash-responding and hide or depart in the darkness of foliage. Males may become prey of their own females—though typically somewhat smaller, males could cause damage in a fight. They have not (yet) been found to carry protective chemicals acquired from *Photinus* or *Pyractomena* prey they have eaten (Eisner, 1997).

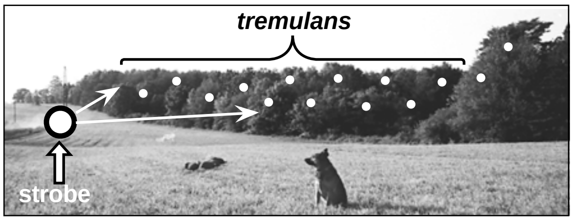
*** Definition, *Default FP*: FP that males begin emitting after receiving a flash response to another (adjunct) FP in their repertoire; it can be viewed, as a working understanding, as the species-recognition FP.**

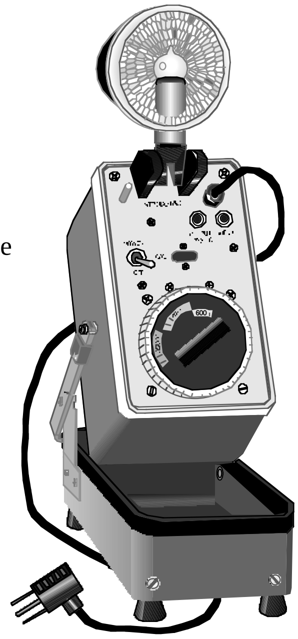
31. ***Photuris'*** **matching FPs may be emitted in the (extreme) absence of the model.** Male mimicry of prey FPs would appear from data at hand to have evolved as a mate-seeking tactic, but be anticipated/expected to have evolved beyond this in the (all-explanatory!?) context of sexual selection (jel, 1980). Females may assess a number of male qualities by the time, place, and finesse with which a male performs not only FP matching, but other aspects of his performance during his approach. Though matching and model species are sometimes seen flying together or in adjacent sites, and phenological records congruent, a matching FP is sometimes used when the model is absent and even—via archival evidence—historically very rare. It was, however, the simultaneous activity of *Photuris eureka* (sympatrically, synchronically, and syntopically) with two of its presumptive models, *Py. barberi* and *Py. angustata*, that *finally* brought awareness of this FP connection to this writer. The indication of a *Py. dispersa* influence in the flickers of *eureka,* though this species is not now known to occur in Florida, suggests a recent/remote(?) historical connection. In the more than 60 nights spent in the field with *stevensae* on Long Island, numbers of flickering males were always present, but the presumptive (ancestral) model, "*Pyractomena angulata*", was never seen—examination of many insect collections, including that of the very old Staten Island Collection that acquired specimens from members of two local Entomological Societies, only one L. I. *Py. angulata* was found. Yet, in many PM-recordings the modulation rate of the *stevensae* flickers was reasonably close to the established rate of the A-flicker of *angulata* at the comparable temperature. *Py. angulata* does occur to the north, across L.I. Sound, based on archived specimens, and genetic input from there may (doubtfully?) sustain the behavior on the Island? Perhaps, in some mystery twist, it is the absence or scarcity of *angulata's* amber flickers that (briefly) sustains the high level of flickering in L.I. *stevensae*?

One must also ask whether *stevensae* males, and males of other green-flickering *Photuris* can distinguish between flickers emitted by conspecific males and the amber flickers of *Py. angulata* males. As noted, the FP matching by *Photuris* males may have gone beyond the original function (adaptive significance) and explanation—that of locating hunting females and converting them to a mating mode.

32. ***Photuris*** **species with repertoires may emit one of its FPs exclusively for a long time.** Such periods (e.g. "long times") may be hours, days, or longer<(?). Because the reason for *Ph. tremulans* switching among FPs en masse, and with such "chaotic" irregularity, is unknown, when populations of exclusively short flashing *tremulans* are seen it cannot be known whether the conditions for the flicker FP are not locally/temporally/combinatorially met, or the flicker FP no longer occurs in that particular population, or that the firefly is not *tremulans*. In an attempt to induce a (reverse) change in the flashing (single-flash) of a presumptive *tremulans* populations that numbered in the hundreds across the forest tops seen from a side road in eastern Tennessee (Polk Co.), a laboratory strobe light was set to flash at the temperature-appropriate flicker rate and aimed across the canopy. It was powered through a DC/AC converter from the car battery, and its light spread across the treetops for considerable distance (hundreds of feet?). No changes in firefly behavior was noted—perhaps the strobe's flash was too short. On numerous occasions non-flickering populations of (presumptive) *tremulans* at localities from Maryland to Oklahoma were seen, but it can only said that the A-flicker **appears to** no longer exist in a *tremulans* variad(?) found in New England, herein named *Ph. margotooleae;* the suspected difference is that in New England the A-flicker is emitted by *Ph. stevensae,* a larger and very abundant firefly.







33. Adjunct FPs of ***Photuris*** **may disappear from repertoires of local populations**. As suggested in **item 30** to have occurred in *Ph. margootooleae*, a *Photuris* species that once had a matching (adjunct) FP may lose that FP, with their default FP then becoming their only FP. This is the first of two possible interpretations in the following example. The repertoire of Florida's *Photuris walkeri* near Otter Creek and Sopchoppy consists of two FPs: Its default FP is a single short flash emitted at 3-4 sec intervals; the adjunct FP is a long-continued glow that matches the "FP" of *Py.*

angustata, which occurs in regions of Florida with *walkeri*. Inland near Gainesville and Waldo, and elsewhere in Alachua County, where *Pyractomena angustata* does not occur, a firefly of virtually identical appearance, *Ph. lineaticollis*, emits only the single flash FP. One interpretation has a *walkeri*-like ancestor losing its adjunct FP in the absence of *Py. angustata*. Alternatively, the common ancestor of the two may have emitted only the single flash and after coming into contact with *angustata, walkeri* added the long-glow adjunct FP. I favor the second (alternative) sequence because the addition/innovation of FPs would seem to be, as invoked below, of some significance in the evolution of pattern-matching (via ad hoc learning) and a common theme in *Photuris*.

34. Adjunct FPs of *Photuris* may become the only FP in a repertoire. A population of *Photuris* in the mountains of northwestern South Carolina emits an FP like that of *Photinus carolinus*, an inhabitant of this range of mountains. When FPs of this species, herein named *Photuris forresti*, were answered with a decoy flash they approached and landed near the LED without defaulting to another FP. The hypothesized sequence of events is: (**1**) the *Photinus*-like FP was added to the ancestral repertoire as a mate-seeking option; (**2**) the default FP was lost. Specifically: pre-*forresti* (short flash) initially separated from "*tremulans*" in, say, mountain isolation, and gained a matching *carolinus* FP; then, in contact again with and over-whelmed by *tremulans* populations, a surviving population (pre)-*forresti* lost its conflicting single-flash default FP. Lynn Faust has noted a similar (*forresti*-like) *Photuris* further north, in Tennessee.

35. *Photuris* females of certain species range widely seeking prey populations; their males rove widely, seeking them (see also item 4). In Florida hunting females of *harranorum* are found singly in various prey sites. Single males are seen flying through/over various sites. **Roving**, solitary **males** of two other species are likewise seen on the continent. The following connecting hypotheses are suggested: (**1**) females of such species lay eggs in sites where they have successfully hunted; (**2**) *Photuris* larvae are omnivorous, known to eat various prey as well as berries, and are able to survive/thrive in a range of habitats; (**3**) hunting females become sexually responsive at intervals, and attract passing conspecific males to replenish sperm (sometimes cannibalizing mates); (**4**) males of such species have distinctive, unmistakable FPs that are readily recognized and distinguished from other FPs wherever they appear. Two continental species seem to fit this description: *Ph. versicolor* and *Ph. fairchildi*. The latter is of particular interest, for although as recalled, a female was observed in predation, the field note has not been found; the roving FP of males has a distinctive, unmistakable form and is repeated at very short intervals, appropriate for fast-flying search. Such males were frequently observed on the continent, but local flashing populations as found in other species were rarely encountered. In local populations on Cape Cod, MA, in Minnesota, and elsewhere in Massachusets, they usually used a different FP—a long, multipulsed phrase of changing rate and intensity. In Nova Scotia, near the *fairchildi* type locality only the shorter FP was noted.

36. *Photuris* males that are seeking females via flashed responses to their emitted FPs, also recognize flashed responses of females to prey-matching FPs in their own repertoires. (This may be the explanation for Barber's observation of a small (*hebes*) male and *versicolor* male being attracted to a *versicolor* female; p. 475, E). This suggestion is supported by the behavior of a male *Ph. stevensae* described below, and this incident **suggests** two other patterns that seem possible—they may have significance for eventually understanding the evolution of male FP matching. Discussions of these three (patterns 36-38) closely interrelate. First, field-book notes of the observation:

Observation: A male *Photuris stevensae* on Long Island (near Peconic) hovering about two feet from a hedge emitted the FP of *Pn. macdermotti* (complex, =*mac*) (2 flashes at about 2 sec interval, 20°C/68°F). A few *mac* males were also flashing close around the periphery of the hedge. A female *mac* perched in the hedge answered the *stevensae* male, which then flew closer and again emitted a *mac*-like 2-flash FP which the female again answered. He then defaulted to a 3-pulse *stevensae* pattern, she did not answer, ditto, then he flew away. (**First**) The *mac*-like FP emitted by this *stevensae* male perhaps is not a fixed-FP of their repertoire. During more than 60 nights of close observation and measurement of this species in a dozen sites on LI-NY, and additional sites and nights in New England, and just east of the Hudson River in Putnam Co., NY, no *stevensae* males were ever observed (of hundreds) to emit this precise *mac* FP, either singly or routinely as part of a species-typical evening profile of FPs. Perhaps *stevensae* has a 2-flash template in its neural program that can be tuned (ad hoc) to match any FP they observe being emitted by males in the vicinity. (The evolutionary origin of FP matching by *Photuris* males—as noted, is a major and fundamental puzzle and of considerable interest.)

37. Second, continuing from 36: Perhaps there is a **fixed** FP in the *stevensae* repertoire. Though males of *stevensae* were never seen to emit the *mac* FP, *Photuris* populations often do not use some FPs of their repertoires for days at a time and perhaps much longer. (As far as could be determined all of the FPs in the photo were emitted by *stevensae* in an oldfield near Norwich, CT.)

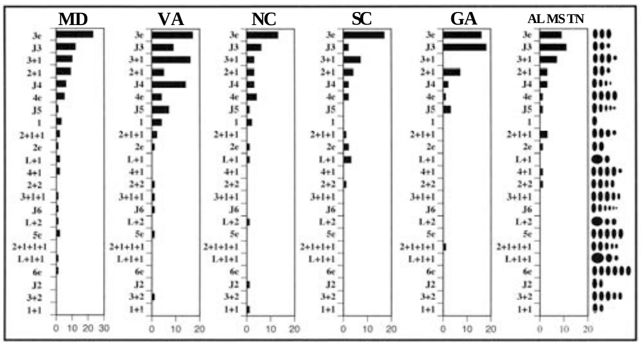
Flicker and pulsing FPs; but *mac* pairs, singles? CT site.

38. Third, *Photuris* males that see prey males receiving flash responses from females may be able to *de nova*/ad hoc-match the FP of prey species. (continued from pattern **36**:) Possibly the male described in 36 **copied** the observed *mac* pattern **ad hoc** after seeing males receiving answers from a female—then his failure to get a response to his *stevensae* (default) FP terminated the interaction. Perhaps this reveals/suggests an explanation for the early evolution of FP-matching by photurine males. Note two variations: **(1)** males have a *general template* in their repertoires and match patterns falling within the parameters of the template—e.g., a 2-pulse pattern, capable of matching **various** 2-pulse intervals; **(2)** and/or males have a "*tabula rasa*," that can copy, then drive “any” FP. The latter raises more questions of complexity, but the occurrence of some FPs emitted by *Photuris* seems inexplicable except via this pathway.

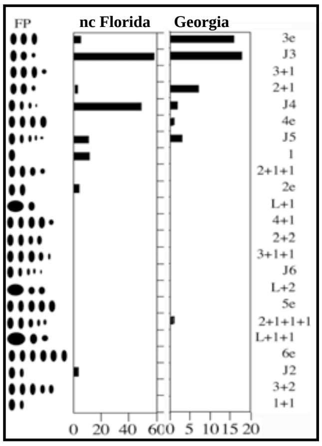
39. Complex FPs and repertoires, those revealing regional variation in particular, may be especially useful taxonomically for focusing DNA studies?—any biological/informational significance of such variation may remain inscrutible and even become doubtful. The *Ph. versicolor* complex is herein divided into three OTUs. Continental *Ph. versicolor s. s.,* is probably a complex of variads with wide distribution in the Atlantic states, south- and westward; Florida's *harrannorum* differs primarily in its lack of "**even**" (intensity) pulses and the presence of 6-pulsed FPs, which seem to be emitted when several males are in close proximity/competition in the tree-tops.

Ph. stevensae in New England and on Long Island differs in (**1**) possession of the A-flicker, which it emits in a repeated nightly pattern, and (**2**) the variable redundancy of stepped pulses, as though to make a (coded?) stepwise change more conspicuous. Pulsing FPs can be arranged in a series of increasing numbers of pulses with variably-even or -decreasing pulse intensity. Though the pulsing FPs of *stevensae* and *versicolor* appear similar in the charts, a very different impression was gained from field observations. In *stevensae*, an array of pulse variation is conspicuous and noted on many if not most evenings in local populations; this was not noted on the continent. If *stevensae* were derived from continental *versicolor* then this would seem to be a distinction to be examined in more detail for what it might reveal. (These frequency-of-occurrence charts are primarily based on incidental mentions in fieldbook notes from many localities and not systematic counts or surveys.)

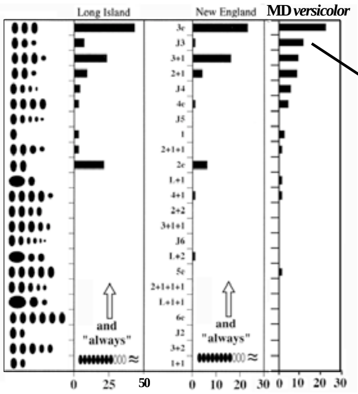
Non-systematically-noted arrays, Continental *versicolor*.

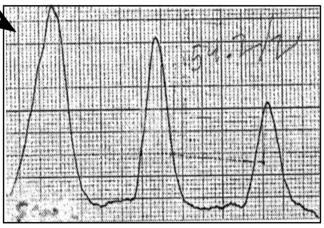


FL *Ph. harrannorum* vs GA *versicolor*



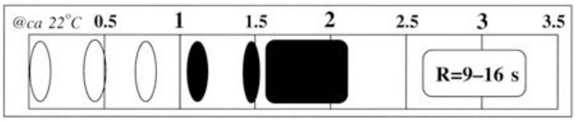
Compare L.I. NY and New England *stevensae* with northeastern *versicolor*.





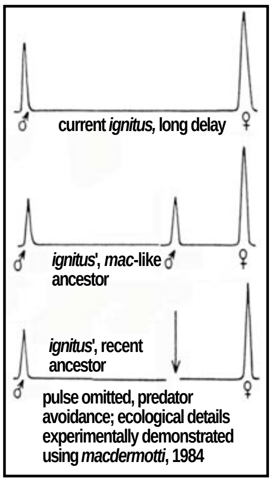
The J-3 (jagged 3) FP comon to all three nominal species of the *versicolor* Group.

40. Flash patterns may have evolved from combining two FPs into a single FP. The FP of *Photuris barberi* consists of a series of 3-6 short flashes followed by a dot-dash pattern—that is, a pulse series as seen in several species (*Photinus consimilis*, *Photuris quadrifulgens*), with a "*pennsylvanica*" dot-dash add-on. The preliminary pulses are emitted at a rate of about 3/sec; the dot-dash section was less than a second in duration, the dot being merely a wink followed by a very short OFF, this followed by the dash; all components were of apparent equal intensity. (No PM records, notes from few visual obs.; few of this firefly were seen, and only one voucher could be collected in their high flights of 20 or more feet.)



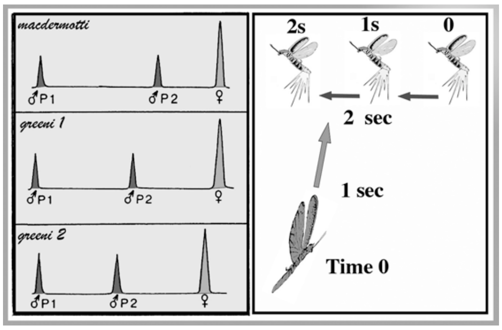
The dot-dash FP could be a composite pattern of a short-flash FP followed by an ancestral default long-flash FP—or the dash (glow) was initially emitted in the landing context for illumination. These would seem simple, logical, and situational sources. This itself raises the possibility that the widely separated geographic localities where the dot-dash FP occurs may not necessarily indicate a wide phylogenetic dispersion of single dot-dash taxon/genome, but instead, that a number of separate lineages have independently evolved a dot-dash.

41. Similar FPs of a clade may be the result of predators that have co-evolved with and driven the FPs of their prey along simiar pathways—members of a clade will have similar genomes/genetic-potential, ecology. By omitting the second pulse of a 2-pulse pattern a *Photinus* male provides a more difficult aerial target for hawking *Photuris*. It may also "confuse" an aggressive mimic that is tracking a 2-pulse FP. Experiments with *P. macdermotti* s.s. females have shown that after an initial species-typical 2-pulse stimulus females answered single-flash stimuli (omitted second flash), at the anticipated long delay. This could explain the evolutionary origins of the 1-flash codes of three or more species in the *consanguineus* group, those of *ignitus*, *aquilonius*, unnamed "falli," and a Florida "*ignitus*." Some may have similar origins from 2-flash species such as *P. greeni* complex forms.



42. Aerial-attack predation by *Photuris* females on FP-emitting males of other species may have had important consequences for signaling. This behavior puts strong selection pressure on the signaling of target-males and certainly has been responsible for changing some elements of their FPs as well as their flight, including speed, time of evening active, and places within a site that will be used or avoided. These potentials may be found/shared by members of a clade.

How decreasing the P1-P2 interval could avoid an aerial attack from a lagging hawker.



43. Lightningbugs that live in less complex photic environments may evolve simpler signals. Short-flashing, coastal species such as *Photuris salina* that occur in marshes from Maryland to Florida, including Florida's west coast, could have been derived from a common ancestor that spread along the coast, some then evolving different FP intervals as noted in Chapter 69. Alternatively, some may have been derived from short-flashing inland species, or species with more complex signals, and evolved simpler signals or dropped complex FPs from their repertoires. after moving into a less complex/different signaling environment?

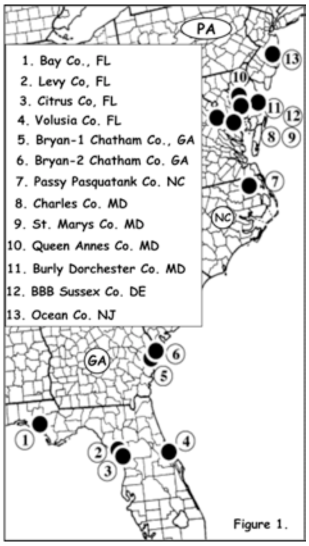


Figure 1.

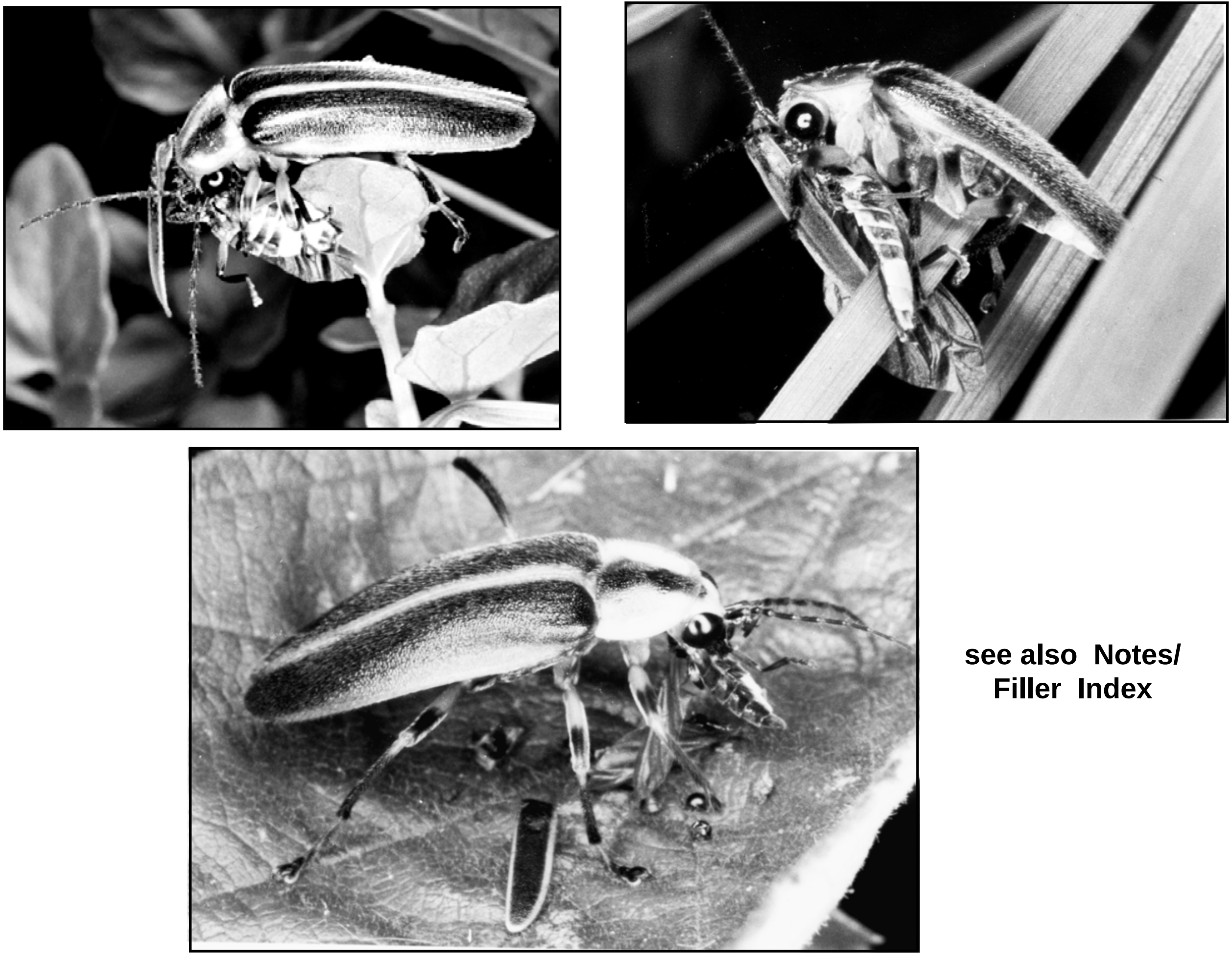
44. Engrams or ambient conditions might determine FP usage. The FP used from a repertoire at any given time by males of a *Photuris* species might be determined: (**1**) by an engram (a hardwired programmatic schedule), or (**2**) be *conditional*, i.e., determined by current local conditions, or some combination of these. Barber's description of male *tremulans* FP usage ("selection") from their known repertoire suggests that he was aware that both phenomena could be involved. In L.I. *stevensae*, the level of male competition may be significant, but we can know it was not the current presence of the presumptive model's FP (*Py. angulata*)—but could it have been its complete absence? Examined archival collections of L.I. fireflies of the past century had but one *angulata* specimen; none were seen during several weeks in six summers of field work there.

45. ***Photuris* males may see and repeat (*de novo*/ad-hoc) the FPs of other species**. This is mentioned in some detail with variations in items above. Such behavior **could be key** to understanding/explaining the enigmatic origin and evolution of FP matching in *Photuris*, that is, the photurine lineage. Although this may seen too complicated for an insect such excuses have been used for many animals for decades at any suggestion of complex **behavior** though incredible complexity in the details of insect adaptation is reported continually. Perhaps behavior is a special case, in the past, because humans must see themselves as unique and special in this regard. The prospects for finding special kinds of learning in males and females of *Photuris* may be very good, and worth exploring. It will be essential to use the right species for experimental examination.

46. Twilight use of the short-flash FP by *Photuris*. Recall that certain prey species seem to have evolved twilight flight in an escape from predators. Most Division-I *Photinus* fly soon after sunset, and Div. II *Pn. scintillans* males search for females in deep shade as early as one hour before sunset. *Photuris* males of some species also fly early, though beginning a bit latter than these *Photinus*, and emit an adjunct short-flash FP in *Photinus* spaces. Such early flight in, say, the population of *appalachianensis* noted in **Item 22** might be hard-wired, such that each male begins evening activity using it, and then with individual variation, and in experience, there is a gradual decrease in frequency over the next 40 minutes. It is also reasonable, more reasonable perhaps, that once short-flashing has begun individual males **monitor** local conditions of ambient light, habitat structure, and male-male visual encounters, and adjust their own mate search FP accordingly. What is suggested here, taking uncertain cues from Barber, is that both an engram, proximate releasers and variable inputs may be responsible for some observed evening FP profiles, and that such inputs modulate/ tune a basic engram. An *ultimate* explanation certainly must be evident to the uninitiated reader in cases where an early-evening, short-flash FP is similar to that of twilight-flashing *Photinus* species, which are known to be prey of *Photuris* females. Evening- as well as seasonal-changes in male behavior will relate to the varying occurrences of varying female conditions: unmated (newly eclosed); just-mated, now hunting; mated previously but requiring sperm replenishment; or manipulation of genetic characteristics of progeny—conditions especially relevant in some—*fairchildi*, *versicolor*?).

47. DNA analyses will reveal species/FP groups not apparent from FP configurations and provide insight to the evolution of FP configuration and signal coding.

***Photuris stanleyi* females with *Pyractomena angulata* males, at the Med Garden.**



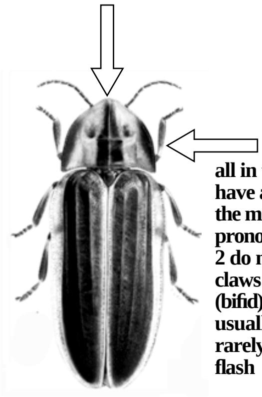
see also Notes/ Filler Index

Chapter 8

Photuris Lightningbug **ID** Via **FP** Morphology

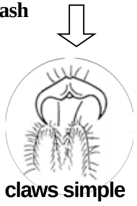
A study of Photuris is not the place for quick fixes, for those
who would seek the fast & dirty, easy way to publication . . .

The identification of about half of North America's lightningbugs is uncomplicated, and different from that of many other beetles only because flashed signals are added to the list of characters that can be used to recognize “operational species”—and probe phylogeny. When, as a graduate student at UM, I began studying fireflies and brought specimens of a fast-pulsing unknown to the Museum, Tom Moore, one of my professors and Hemiptera specialist, quickly extracted the aedeagus of a male, got out Green's 1957 key to *Pyractomena*, and in moments "we" had the ID—though, as it turns out *dispersa* is once again an unknown. In *Pyractomena* the aedeagi, with a few other characters, are sufficient to identify "species" to the current level of understanding, excepting for the known confusion in the *dispersa-linearis* suite, which involves geographic as well as morphological, flash pattern, and locale uncertainties. The same can be said for identifying *Photinus* with Green's 1956 masterful key. But, *Photuris* identification presents problems that could not have been anticipated before Barber, and many have come to light since his 1951 revolution. While the morphological appearance of some *Photuris* may ocassionally be somewhat reassuring after identification is reached via (male) flash patterns (FPs), it almost never can be relied upon with confidence for diagnoses without sufficient local knowledge, and this may be possible only in certain regions of North America. Species in *Photuris* Division I—such as *congener*, *divisa, polacekae*, and *frontalis*—can be identified via morphology, with locality being definitive for some. But some "cohorts" of *Photuris* Division II, the now-classical "*pennsylvanica*" side of the genus in North America, are amazing in the complexity of their signals and associated behavior; a certain few may be diagnosed via their FPs.



all in this genus have a keel down the midline of the pronotum; the other 2 do not; tarsal claws not 2-pronged (bifid); in hand usually calm, only rarely scramble and flash

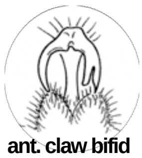
a *Pyractomena*



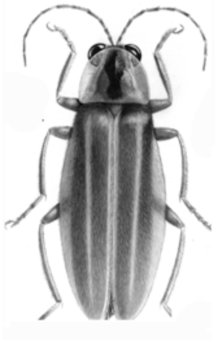
claws simple

midline of pronotum may have groove or be smooth; no tarsal claws are 2-pronged (bifid); in hand usually calm, do not scramble and flash

a *Photinus*



ant. claw bifid

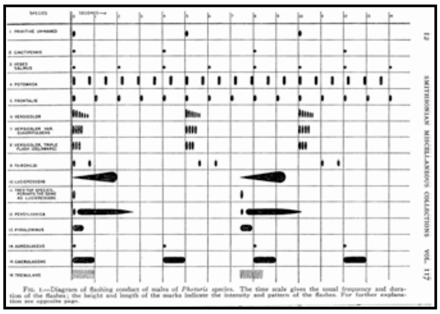


anterior tarsal claw on each foot is 2-pronged (bifid); in hand often/usually scramble and flash (not FP); elytra often with short or long midline stripes

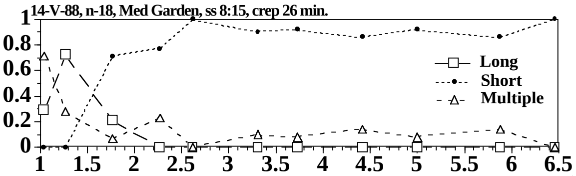
a *Photurus*

The charts below (**AA—II**) distinguish among structural details of the FPs of *Photuris* fireflies of North America. Details figuring into this FP taxonomy are: number and form of pulses (flashes, flashlets) within FPs, and in some cases, pulse repetition rate (1/pulse interval). Each chart leads to list of possibilities ("species," operational taxonomic units, OTUs). *Photuris* OTUs that are known to emit more than one *distinctively different* FP are cross-referenced, that is, may often be reached via the different FPs of their repertoires. Variations within the same type of FP, such as pulse number, are indicated in the charts. Chart **II** shows emissions that require further explanation—including certain glows that are the functional equivalents of FPs. Characters that morphologically distinguish *Photuris* from the other two major flashing genera of N. A. that will be encountered are shown in illustrations at the left. Following the **AA-II** FP guide is an abbreviated short key that includes a few additional notes toward ID (**Appendix I**, p. 63). **Appendix II** is an aid to the ID of several commonly-encountered/noticed fireflies in eastern North America. Note that in the **AA-II** guide some chart lines show *repeated* FPs of a species; others, *variations* in one or among species. Also, keep in mind that these keys are to entities (demes, local populations) that were encountered, to aid in associating what you find with what has been seen (maybe) and has accompanying notes (Chapters).

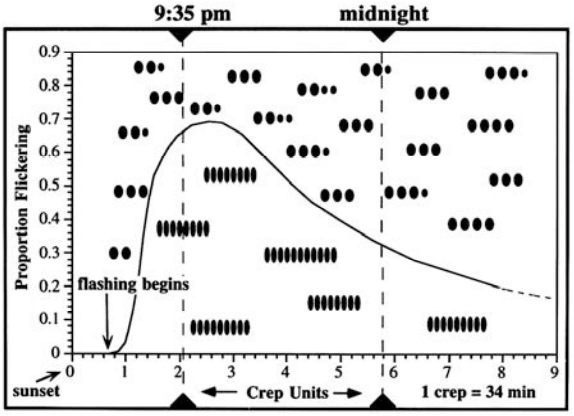
Herbert Barber’s *Photuris* monograph (1951), based primarily on his personal, local field study was delayed two decades before it was published. In the intervening near quarter-century he had time for reflection and consideration of what he had discovered. We can now further appreciate some of his solitary accomplishments: (**1**) he demonstrated a promising method toward resolving *Photuris* taxonomy; (**2**) he recognized OTUs worthy of formal taxonomic recognition via their flash patterns; (**3**) he revealed the existence of certain FPs that raised questions concerning the use of them in taxonomy; and (**4**) he reported his observation of a *Photuris* female answering the FPs of a *Photinus* male, leading him to *cautiously* venture whether she would attract him with false signals and eat him. Consider: if Barber had viewed this last point as merely an interesting tidbit in the natural history of his fireflies it is doubtful that he would have mentioned it; he was a very good naturalist and certainly must have recognized the impact that this behavior could have on firefly signals, on their complexity, and on our ability to understand and use them taxonomically! Considering the pressure this present writer was under when he raised this question in 1964, and the arrogance and ignorance encountered from some well-positioned "authorities" in the scientific community for many years, Barber's hesitancy in saying more can be appreciated—after all, to them he was merely a grunt taxonomist.


Barber's 1951 chart, the first/only guide to *Photuris* identification until the extensions reported in this paper.

From the foregoing there are two items in particular to be emphasized before continuing, as essential points of overview, introduction, and clarification: (**1**) as demonstrated for more than a century, the resolution of *Photuris* taxonomy by classical bench methods is not possible, and the only reasonable recourse is to use the signals (FPs) the insects themselves use for identification and that the two researching taxonomists have had to rely upon. This means that the identification of *Photuris* in each case is limited to careful, accurate, and aware knowledge and understanding of flashing behavior, and the inconvenient and problematic consequences of this. Further, local populations, with their variations however slight or difficult, *must* be the focus of attention. (**2**) This paper should be seen not as a solution, but merely as an extension and continuation of Barber's **outline,** a sketch, a chisel chipping at the masonry, only gradually tending/trending toward an understanding. The working asssumption is, as discussed in the previous chapter, that certain *Photuris* seem to be revealing the *real* operational ***units*** of evolution, at their scale of life, and though we presently stand in total ignorance of *Photuris* vagility and "deme" (local population) structure, a clue to a powerful force driving deme divergence is perhaps beginning to emerge in their predations (ala Erlich and Raven, 1967).



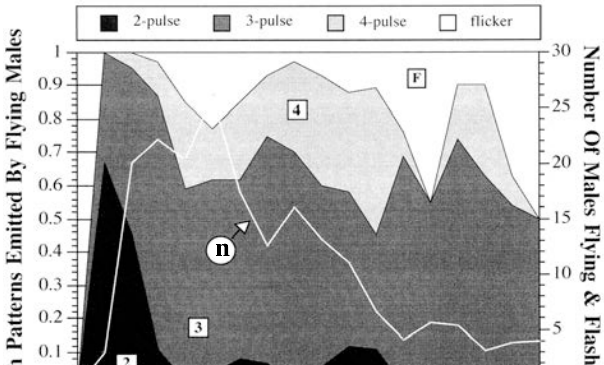
***Photuris douglasae* evening FP transitions, one evening on the UF campus (AX: fraction emitting/creps).**



***Photuris stevensae* evening transition with rise and later decline of the fraction of males emitting the flicker FP, Peconic, L. I., NY.**

After years of frustration chasing *Photuris*, initially with sunny expectations born of *Photinus*, and the BSC, this deme/variad view inspired a new vigor in the quest; it became obvious that what should be sought (next!) were local variads. This encouraged the view that all ("conspecific") demes were perched delicately on the threshold of evolutionary divergence. That these were what really exists in nature, that had usually lacked careful attention and description as operational units and "individuals."

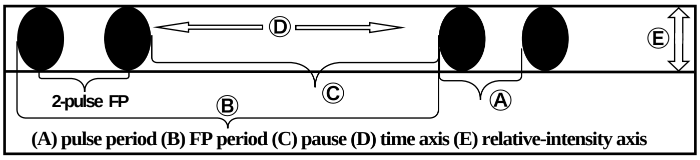
Variations in FPs and other elements of flashing behavior that occur among demes, and traffic among neighboring demes, in contrast to those with obvious and grand geographic separations, are especially what is lacking and need to be examined—Barber of course hinted at this long ago!



***Photuris stevensae* in a narrow roadside berm north of NYC in Putnam County.**

As examples of *silent* variation: FPs used by males of some *Photuris* OTUs vary with time of night, some being used only at twilight, during the window of twilight *Photinus* (*appalachianensis, douglasae*); another uses one FP in a "scheduled" variability through the night (*stevensae*). Demes of *tremulans* may use an FP for several nights and then on the next, some or all males use another FP from their repertoire. Some may not use one of their known FPs at some localities (*lucicrescens*). Identification and description of local populations depends upon being aware that such patterns may not be revealed except under specific local and ephemeral circumstances. Such conditions as vegetation, population density, phenological moment (female value, seasonal maturity), and prey availability may be key influences.

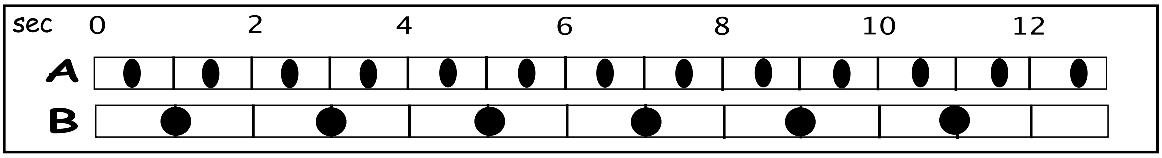
FP Anatomy in a 2-FP sequence of a 2-pulse FP



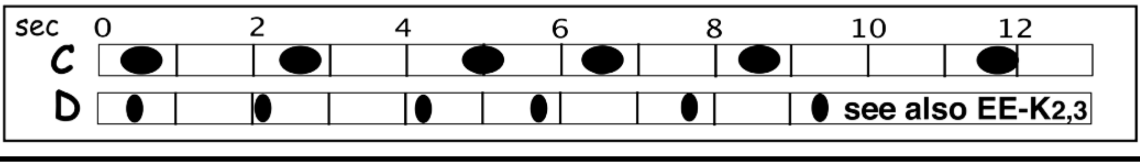
Flash Pattern Structure and Identification. (**1**) The charts below group FPs into element- or form-related types. (**2**) Many are known only from *Photuris,* and are not found in other flashing genera of North America. (**3**) Some *Photuris* species emit more than one FP type as well as variations within a type (species of *Photinus* and *Pyractomena* only emit variations *within* a type, with one "exception"—*Photinus macdermotti* complex). (**4**) The basic sets are: (**AA**) **Single**, **short** flashes emitted in noticeably **rhythmic** (≈metronomic) continuous **series**, and having flash periods usually less than 1.5 seconds in duration (**AA-A**). FPs at longer intervals sometimes have the appearance of such regularity; where confusions may arise it is noted. (**BB**) **Single, simple** flashes emitted at noticeably **variable intervals** of 2-5 Sec duration (longer at lower temperatures). (**CC**) **Pairs** of **simple** flashes. (**DD**) **Groups** with **varying** numbers (**2-11**) of **simple** flashes. (**EE**) **Groups** of flashes with **stepwise intensity** changes. (**FF**) **Single** or **groups** of flashes of **crescendo** form. (**GG**) **flickers**, that is, sequences of rapidly repeated pulses. (**HH**) **Combinations** of flash forms in a single FP. (**II**) **Miscellaneous luminescent emissions**. It is important to be constantly aware/consider that periods, rates, and durations of FP parameters vary predictably with ambient temperature—and often, *visually*, with flight speed and ambient lighting.

To associate a population (single (OTU) of fireflies with one reported here: (1) observe several individuals and form a mental concensis of their FPs (types, variations, transitions). (2) Test male FPs with experimental decoy responses to elicit defaulting. (3) Match what you have observed, with respect to Key Charaters, to one of the Sets described below (AA-II).

Set AA: Few species actually flash like this (see also **BB-D**). Single flashes are of simple-form, and emitted in long-continuing, **very rhythmic** sequences. Some are "longish" with durations like the blinks of directional signals on a car; some are short and snappy (60 mSec duration (**AA-A**). When individuals of such species fly near each other some precisely synchronize their flashes in flight; in synchrony flash interval may become even more constant/regular. Flash periods are typically less than 1.5-sec in duration in North American species. In such species the "true" FP may not be the single flash, but the rate established by a short sequence. Flashes in trains are often skipped when males fly over foot paths or roads, etc.. Continuous flash sequences with such near-perfect regularity of interval are termed **trains**. Rhythimic-appearing sequences of FPs at longer intervals occur in some species, but more variation is seen in the intervals. The FPs of *Pn. macdermotti* complex mentioned above, in some measurements indicate that every other period may be slightly longer—a clue to the origin of train-flashing in this complex? A confusing factor is flight speed: the human eye/brain misjudges the flash-duration of fast flyers, and can make a 250 mSec flash appear much longer. The flash of the twilight, fast-flying *Photinus collustrans* is about a quarter of a second long but appears longer.

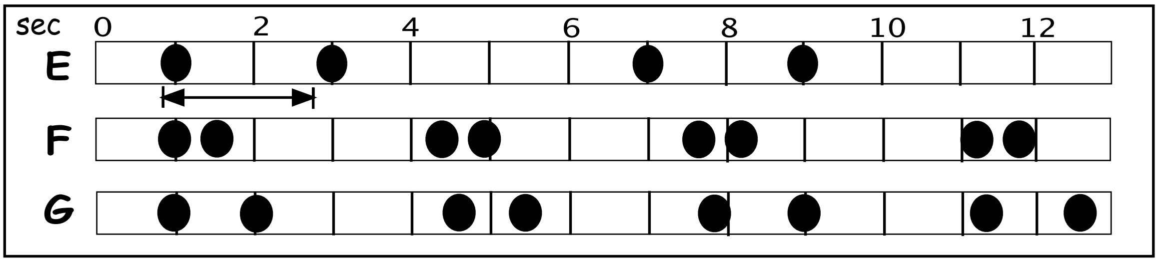


Set BB: Single flashes of simple-shape ("normal"), emitted in long-continuing, **non-rhythmic** sequences. Some are **long** flashes with durations of nearly a second or a bit more (**BB-C**, depending upon ambient temperature); some are like the blinks of directional signals on a car (**BB-D**), a few are snappy. Flash intervals vary from 1 sec to 5 or more, depending upon ambient temperature. When males fly fast or swoop through space during emission, flash duration is exaggerated to the human eye/brain. **CAUTION**: if *Photuris*, decoy with a short flash, look for defaulting—a switch to a **different** FP after a pause and/or 2 or 3 more short FPs.

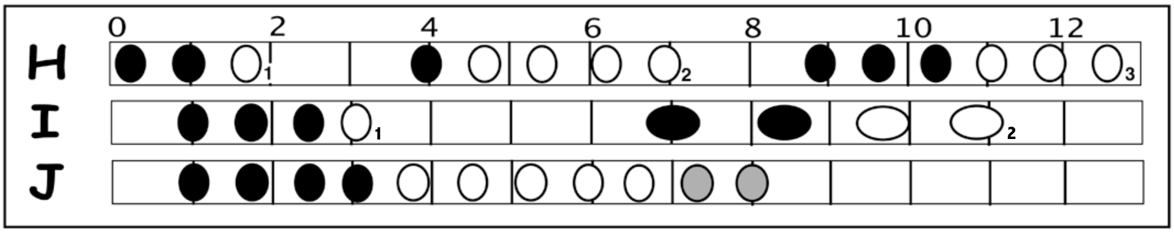


Photuris asacoa site in northeastern Iowa, with huge flashes drawn in position where the two flash-types of its known repertoire are emitted: at the shrub foliage the default FP, a weak crescendo (**Set FF**), and among the herbs at the edge of the mown area, the short (**BB**) flashes. The short is a generalized match of the flashes of the local *Photinus* Division-I species, *Pn. curtatus*, presumptive prey of *asacoa* females. For unknown reasons such twilight *Photuris* only begin their short-flashing minutes after *Photinus* males begin—predators: clubtail dragonflies, cardinals?

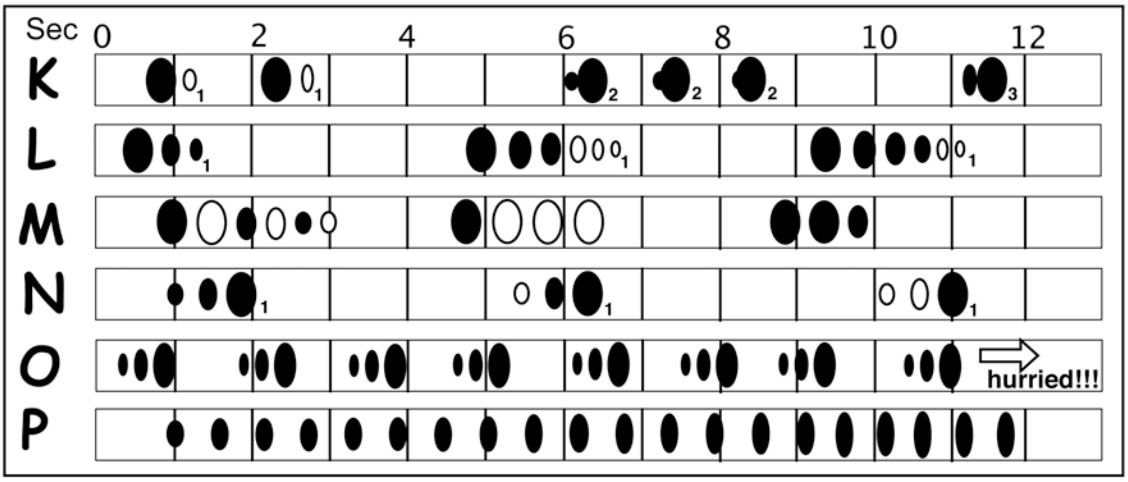
Set CC: Pairs of simple pulses. Pulses in all but one species are separated by **near-constant** intervals of species-characteristic (coded) durations. Some (**CC**-E) are 2 seconds or slightly more apart; inferential evidence might suggest that an ancestor of one extant species of *Photinus* had a 3-second interval. *Photuris branhami* emits pairs at about one-half sec intervals (F). *Photuris darwini* in the Appalachian Mountains emits 1-pulse and 2-pulse FPs, but its pulse **pairs**, unlike those in E and F are, curiously, more variable (G)—perhaps signal coding to trick predators?) Train-flashing *Photinus macdermotti* (complex; north of Florida) switches from continuous ≈2-sec intervals to (E) when flash-answered; ca 1-sec delay).



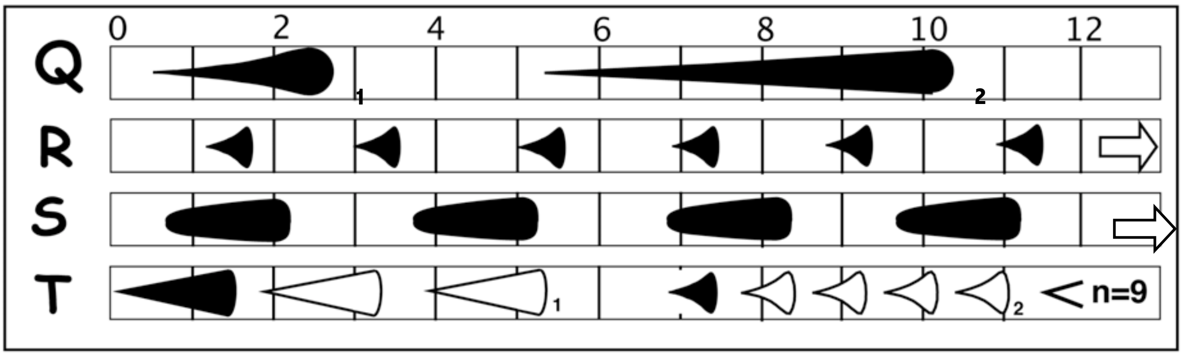
Set DD: Groups (phrases) of 2-11± simple, single pulses of **equal** intensity; pulse number, duration, and period vary among species. FPs are separated by pauses of various durations. These FPs are common in *Photuris* that have repertoires such as those in the *versicolor* Group and *douglasae*, but *Ph. forresti* emits such an FP and is not known to emit any other. Many *Photinus*, especially wetland inhabiting species in the *ardens* Group have pulsing FPs; some are used as examples in the chart.



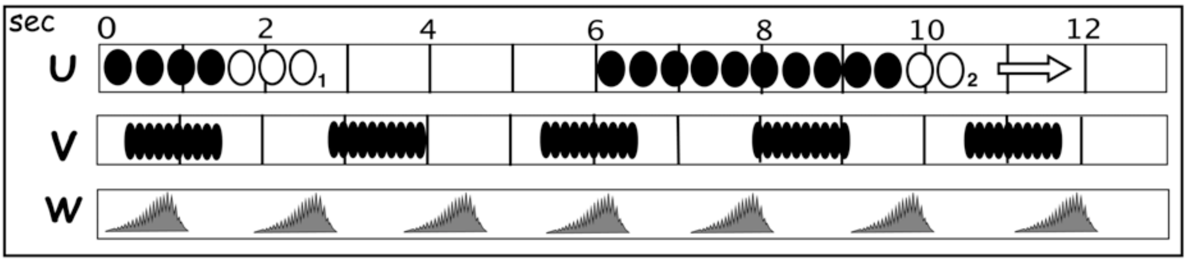
Set EE: Groups of pulses of **variable** intensity. (Three *Pyractomena* species emit 2-pulse **step-down** FPs (**EE**-K), with the second pulse varying in intensity and delay, and is often/usually? omitted.) Stepped pulses (L-M) of the *Photuris versicolor* Group are **never** step-up, but either **step-down** (or **even)** in intensity, with pulse number ranging to 6. The FP of *sivinskii* (N) is composed of 1 to 3 **step-up** pulses, with omitted pulses being the dimmer first two. FPs presently associated with *Photuris fairchildi* (O, P) are step-up; in one (O), "units" are repeated with **short pauses** between them; the rate/temperature regression is made confusing by the number of pulses in an FP—see text. The other FP (P), observed from Cape Cod to Minnesota, is typically a long series of pulses with two variables: pulses gradually increase intensity until near the end; they also decrease in rate. One *Photuris* emits "shouldered" (hitched) FPs (K_2) and another hitches as in K_3.



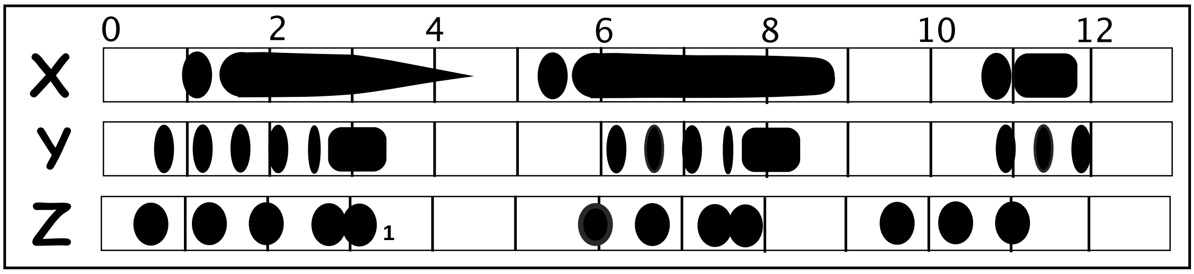
Set FF: Crescendo (ramp**)** flashes, emitted as singles (Q, R, S) or in groups (T). That of *Photuris lucicrescens* (Q2) is long, at cool temperatures sometimes reaching three or more seconds in duration; it is variable both in duration and intensity reached. Crescendos of some species are too short (judged from PM records) to usually be appreciated visually and of limited diagnostic value, but that of *Ph. lloydi* (R) is resolved by eye when exaggerated by spatial movements. Crescendos are sometimes grouped (T) as in *Ph. carrorum* (T1), *beanii*, and *whistlerae* (T2), and particularly useful for IDs. Occasionally crescendos are so weak as to pass unnoticed at first view (S), as in *Ph. asacoa*.



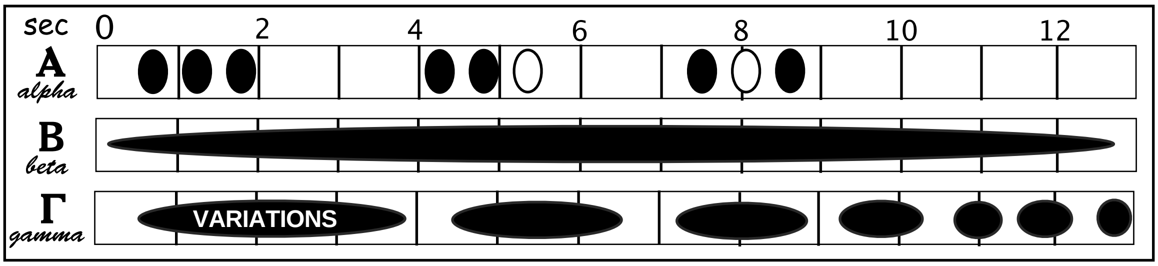
Set GG: Flickers, **rapidly repeated pulses** of various pulse-repeating frequencies (Hertz), from so low as to be clearly distinguishable by eye as discrete pulses at lower temperatures (U, V**,** @5-12 Hertz), and subliminal (W) (30-45 Hz). This rate is known only in *Photuris lamarcki*, and has a crescendo envelope. The flicker of a marsh species in southern Michigan is unusually long, sometimes with 18 pulses. Many flickers of *Photuris* species match those of three *Pyractomena*, and appear to be more precisely tuned **locally** than available data can usually determine (see *Ph. quadrifulgerns* and *eureka*). Ambiguity occurs because rapid discrete pulse appear as flickers at high temperatures.



Set HH: Combinations of **elements** and **configurations** found in other sets. All have a short flash as one element. In some (the "dot-dash set") a single short flash is followed by a longer flash (X), the "ubiquitous" dot-dash pattern; the dash may be short or long, with variations in intensity ranging from long-tapering, wavering(?), to with an abrupt termination. These variations are observed in local demes in central New York State, where some lack the initial dot. It must be expected that local demes may have fixed various of these FPs in scattered localities across northern United States and adjacent Canada. A Texas species, *Photuris barberi*, emits 2-4 short pulses followed (visually, not PM-recorded) by a dot-dash (Y) as illustrated, but may reveal variation and complexity when several males are seen competing. The dot appeared to be a shorter pulse than those preceding it—the rhythm was one-two-three-ker-choo. A Florida species, *Ph. dorothae*, emits an array of FPs from a single pulse to the full expression in Z1, left. Visibly and in PM records terminal elements sometimes are two *fused* short flashes.



Set II (eye-eye): Some emissions require special introduction to avoid confusion when they are first confronted in the field. (**1**) (**alpha**) apparently is a legitimate ***Photinus*** FP "repertoire" known primarily by occasional glimpses seen in tree-tops—southern Maryland (and northern Virginia?). This belongs to the *consanguineus* Group and may have something to reveal about the evolution of FPs in the group and CM coding as countermeasures to predaceous female *Photuris*. (**2**) Some species emit long-continued glows (**beta**), which are distinctive and must be mentioned because they are emitted by lightningbugs, *Pyractomena angustata* and its mimics, *Ph. walkeri* and *eureka.* This is also the emission of the glowworm firefly, *Phausis reticulata (*habitus below*)* and others. A common emission in grassy and damp sites is that of landing females (**gamma**). Males have never been seen attracted to these and they apparently are used mostly by females for illumination. They may differ among species, and their form may indicate relationships at a higher level, say species groups.



* * *

A Rough Guide To Species (working OTUs, "Demes")

Check Genus Via Morphology (page 56) Before Beginning

Listings below are not complete, and with some uncertainty

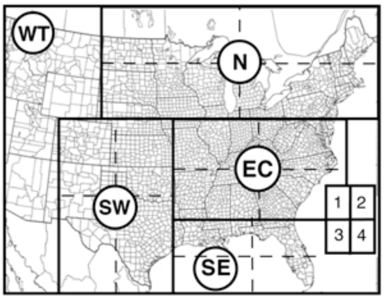
The letter and number codes after species names indicate geographic regions of known occurrence, localized within the region if appropriate or as presently known, by numbered quadrent. An asterisk after a species name indicates the species is known to emit other FPs, that is, has a repertoire. With tentative ID, consult chapter information.

AA: FPs Short-Flash Train Flashers. Division I. A: *congener* **[SE24 (on map)]**; *frontalis* **[EC234 SE12]**; *floridana* **[SE4]**—possibly *flavicollis* **[SW3]** and *polacekae* **[SW4]** **[**see also SULLIVAN below *divisa,* p. 142 **[N4]]** **Division II.** A: *chenangoa* **[N4]**; *missouriensis* **[N3 SW2 EC13]**; *potomaca* **[N4 EC24]**.

BB: FPs Single-Flashes @ Variable-Intervals. (SEE PAGE 114) Division I. D *divisa** **[EC1 SW2]**.

Division II. C *alleganiensis** **[N4]**; *asacoa** **[N3]**; *douglasae** **[SE24 EC4]**; Down-slider **[EC3]**; *pyralomima* **[N4 EC2?]**. D *appalachianensis** **[EC2]**; *aureolucens* **[N3]**; *beanii** **[SE2]**; *bethaniensis** **[EC2]**; *branhami** **[SE2]**; *cinctipennis*?* **[EC2]**; *cowaseloniensis** **[N2]**; *darwini** **[EC234]**; *dorothae** **[SE2 EC4]**; *douglasae** **[SE24 EC4]**; *fairchildi?** **[N EC SW2]**; *harranorum** **[SE24]**; *hebes** **[N234 EC SW2]**; *katrinae* **[SW34]**; *lineaticollis* **[SE2]**; "*lloydi**" **[SE24]**; *lucicrescens** **[N234 EC SW2]**; *maicoi* **[SE24]**; *margotooleae* **[NE4]**; *polacekae* **[SW4]**; *salina* and other coastal marsh singles **[NJ s to FL, & nFL Gulf]**; *sivinskii** **[SE2 EC24]**; *stanleyi** **[SE24]**; *stevensae** **[N4]**; *tremulans** **[EC N4 SE12]**; *walkeri** **[SE2]**.

Rough guide to geog. occurrence



CC: FPs Pairs Of Simple Flashes . Division I. F *billbrowni*?* **[SW4]**; *divisa** **[EC1 SW2]**.

Division II. F *bethaniensis** **[EC2]**; *branhami** **[SE2]**; *bridgeniensis* **[N4]**; *darwini** **[EC234]**; *dorothae** **[SE2 EC4]**; *douglasae** **[SE24 EC4]**; *fairchildi** **[N EC SW2]**; *stevensae** **[N4]**; *versicolor** **[N4 EC234 SE1]**.

DD: FPs Groups Of 3-11 Simple Flashes.

Division I. none known, with certainty, but *billbrowni*? **Division II.** H *dorothae** **[SE2 EC4]**; *douglasae** **[SE24]**; *eureka** **[SE2]**; Ozark Slow pulser* **[EC1]**; *quadrifulgens** **[EC]**; *stevensae** **[N4]**; *versicolor** **[N4, EX SE1]**. J *forresti* **[EC4]**.

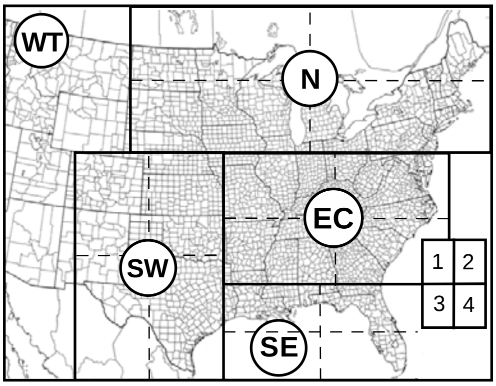
EE: FPs Groups Of Flashes Of Variable Intensity.

Division I. *billbrowni**? **[SW4]**. **Division II.** K2**:** "*hebes*" **[N4EC]**; K3**:** "*bridgeniensis*" **[N4 EC1]**; L1**:** *versicolor* **[N1 EC]**; *harrannorum** **[SE24]**; *stevensae** **[N4]**; N1**:** *sivinskii** **[SE4 EC3]**; O **&** P **in** *fairchildi** **[N, EC]**.

FF: FPs Crescendo Flashes, Single, and In Groups <9.

Division I. none known, not expected. **Division II.** Q1 *moorei* **[EC13]**; *paludivulpes** (with modulations) **[EC3]**; Q2 **in** *lucicrescens** **[EC]**; R **in** *lloydi* **[SE24]**; S**:** *alleganiensis** **[N4]**; *asacoa** **[N3]**; T1 **in** *carrorum* **[SE24]**; T2 **in** *beanii** **[SE2]**; *whistlerae* **[SE2]**.

Rough guide to geog. occurrence



GG: FPs Flickers and/or Very Fast-Pulsing.

Division I. none known. **Division II.** V**:** *alexanderi** **[N1]**; *appalachianensis** **[EC1]**; *cinctipennis** **[EC2]**; *eureka** **[SE2]**; *faustae** **[SE2]**; Ozark slow pulser* **[EC3]**; *paludivulpes** **[EC4]**; *quadrifulgens** **[EC SW +]**; *stanleyi** **[SE2]**; *stevensae** **[N4]**; *tasunkowitcoi** **[N1]**; *tremulans** **[EC +]**; W**:** *lamarcki* **[SE2]**; U2 *fairchildi** **[N EC]**.

HH: FPs with Combinations Of Elements and Configurations.

Division I. none known. **Division II.** X **in** *alleganiensis** **[N4]**; *appalachianensis** **[EC2]**; *campestris* **[SW12]**; *cowaseloniensis** **[N2]**; *hiawaseensis** **[EC234]**; *pensylvanica* **[EC2]**; Y **in** *dorothae** **[SE2 EC4]**; Z **in** *barberi*"*" **[SW4]**.

II (EYE-EYE): Miscellaneous Emissions.

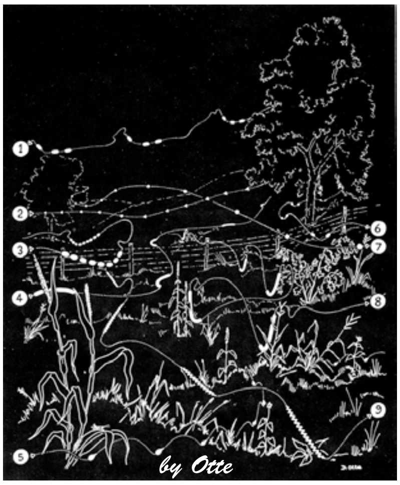
Division I. none noted, perhaps some form of **gamma** occurs, perhaps **beta**-like. **Division II. beta** as adjunct FP of *eureka** and *walkeri** **[SE3]**; **gamma** in some (all?) species.

Phausis reticulata

A glowworm firefly, not a lightningbug firefly.

Flicker FP (GG-V), pulsed FP (DD-J), and glow "FP" (II-β) will lead to possible IDs.

1: 2-3-pulser DD-H; 2: a train maybe? or a single flasher AA-A or BB-D; 3: a pulser DD-J; 4: a single flasher BB-C; 5: a single flasher BB-D; 6: a double pulser CC-e or F (need temp and swat measurements); 7: short flasher BB-D; 8: long-single flasher BB-C; 9: a flicker maybe? GG-V. No, abdomen shake probably, and BB.



Appendix I

A Short Trichotomous, Augmented Key To *Photuris,* Via Flash Patterns

"Findability": if sought in season and region at the right time of day

☑ probable
⊕ 50:50
☒ difficult

not all species included here

1. Flash pattern (FP) a single short or somewhat short flash or a somewhat longer "very short (1-sec) glow" (see AA and BB). **3**

1'. FP a series of <3 sec glows or a long continued glow >5 sec. (see **II**) [only known from Florida: ☒*eureka*, ☒*walker*] (don't confuse long glows of landing individuals or weak glows from light-leaking lanterns, or with model *Pyractomena angustata*!)

1". FP a shaped flash (crescendo), or group of crescendo flashes (see **FF**); OR a group of short flashes (see **DD**, **EE**); or a group/combination of flash types (see **HH**); OR a flicker (a "phrase" of very rapidly-repeated pulses) (see **GG**). **2**

2. FP a single crescendo flash or group of 2-9 such flashes, intensity rising rapidly or slowly, then usually ending rather abruptly (see **FF**). ☑*alexanderi*, [☑*lucicrescens*, ☒*beanii*, ⊕*carrorum*, ⊕*moorei*, ☒*paludivulpes*, ☒*whistlerae*—also weak crescendos: ⊕*asacoa*, ☑*alleganiensis,* ☑Portage, and two difficult crescendos, the very short ☒*lloydi,* and extremely-rapidly modulated ⊕*lamarcki.*

2'. FP a group of 2-9, and rarely many more short flashes. (see DD, EE, II) ☑*quadrifulgens*, ☑*versicolor*, ☑*stevensae*, ☑*harrannorum*, [☑douglasae (FL), ☒*forresti*, ⊕*fairchildi*, , ☑*billbrowni* Texas, ☒*eureka*, ☒*branhami*

2". FP a flicker: a group of fast-repeated pulses, repeated so rapidly as to run together or slightly slower such that individual pulses can be seen, especially a lower temperature. Often emitted as an adjunct FP— if so, when decoy-answered the emitter will default to a different FP. (see GG, esp. V) ☑*alexanderi*, ☑*tremulans*, ☑*quadrifulgens*, ☑*stevensae*, ☒*cinctipennis*, ☒*paludivulpes*, ⊕*tasunkowitcoi,*⊕*lamarcki* (really subliminal, as in GG:W)

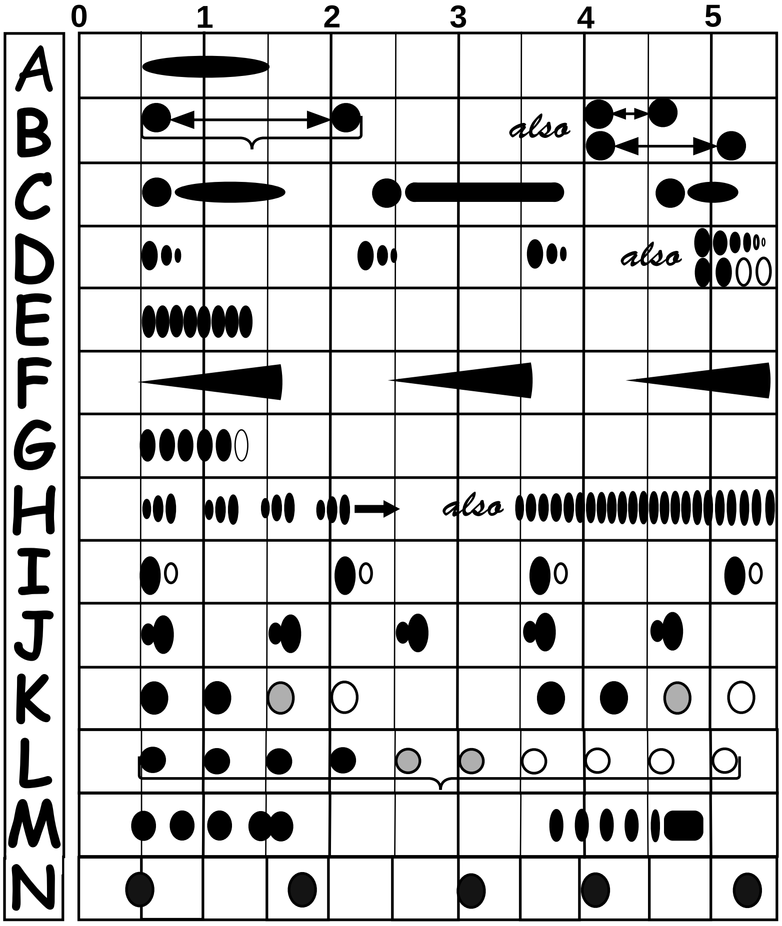
3. This "catch-all" section is comprised of several "recognizable," often troublesome sets. (**A**) Highly regular, rhythmic, "≈metronomic-like" flashers: some Division I species: ☑*congener*, ☑*frontalis*, ☑*floridana*, possibly some others. Certain Division II species: ☑*chenangoa*, ☑*potomaca*, ☑*missouriensis*. (**B**) Late twilight short-flashers, low, ecotone flyers that will default to their own FP when decoy-answered: ⊕*asacoa*, ⊕*cowaseloniensis*, ☒*appalachianensis*, ☑*alleganiensis*, ☑*caerulucens*, [⊕"*aureolucens*"??]. **(C)** Meadow and grassland long flashers (BB): *caerulucens*, Down-Slider. (**D**) Southern, often high-flyers with a <u>tawny</u> (brick-reddish) <u>trim/base color</u>: ☑*katrinae* (Texas); ☑*lineaticollis*, ☒*dorothae* (very tiny), ⊕*maicoi*, ☒*walkeri* (se US). (**E**) Often high flyers, appearing around and across tree crowns and in treetop open spaces, and lower around shrubs. Difficult to ID without specimen: *lucicrescens* (pale hind coxae, large); ☑*tremulans* (dark hind coxae); ☒spring *harrannorum*, Florida; ⊕*beanii* Florida. (**F**) Low flyer <10' over Florida roadside ditches, over fields, in parks and shady groves [☑*douglasae*. (**G)** Along and near Atlantic and Gulf, flying low over shoreline herbs and rushes ☑*salina* and others as in Chap. 61; *bethanienses* (Delaware). (**H**) Hitched flashers that reveal their modulated flash as they "jerk" along at lower temperatures ☑*hebes,* eastern US; ⊕*bridgeniensis* (east to west across central New York); note also ☑*billbrowni*, Texas.

Appendix II

Some Common or Distinctive FPs of 3 Genera—as guides, nothing is definitive

(For Pyractomena FPs see page 200, and 369 for Green's Key)

These FPs are either emitted by common species or are distinctive or have diagnostic elements that may lead directly to species identification. All species known to emit these FPs are not given, usually only those considered to be most likely to be encountered. ID usually takes time and concentration—more than merely a single, passing flasher seen for a brief moment. Because *Photuris* flashes, though green, often appear white, this is noted as a reminder of what is to be expected.



(**A**) Yellow, J-shaped or up-swept flashes at summer twilight over grassland: *Pn. pyralis*. Green/white down-sliding or level flashes after twilight over grassland: *Ph. caerulucens.*

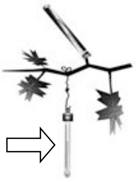
(**B**) Consistently-timed pairs of yellow flashes, *Pn. consanguineus* Group: @ 2 sec, *macdermotti* complex; nr 1.2 sec, *greeni* complex; @ 0.5 sec, *consanguineus* (Florida). Pairs of Green/white flashes, in Florida over roadside, especially wet ditches *Ph. douglasae*.

(**C**) Dot-dash, *Ph. pensylvanica* Group, several species; with a short electric dash, *Ph. hiawaseensis*.

(**D**) Down-step pulses: *versicolor* Group *versicolor* (continental), *harrannorum* (Florida), *stevensae* (New England, Long Island).

(**E**) Amber, rapidly-pulsed, flicker, singly/few in treetops, many low over marsh, *Py. angulata*; Green/white fast-flying around tree and bush foliage, over grassland: *Ph. tremulans*, *Ph. quadrifulgens*. *Ph. cinctipennis*, *Ph. appalachianensis*, *Ph. stevensae*, Ozark slow pulser; *Ph. stanleyi* and *eureka* in Florida. (**F**) Long, green/white: *Ph. lucicrescens*. Short green/white: *Ph. moorei* MO, GA. (**G**) Yellow, rapid pulses, low-wet grassland, spring, broadly: *Py. dispersa*; low, roadsides, FL, late summer, *Py. floridana*. (**H**) Green/white, step up, short FPs run together; rarely? long sequences with barely perceptible increase in intensity, at end a decrease in rate, broad occurrence, *Ph. fairchildi*. (**I**) Orangish-yellow singles and rare doubles: woodland, spring, broadly, *Py. borealis.* (**J**) Green/white, jerky flash at lower temperatures when viewed from side, and a very short crescendo when viewed from back, grassland and low herbs, *Ph. hebes*. (**K**) Orangish-yellow, marshes, northern US/s Can., *Pn. ardens* and *obscurellus*, both with chestnut pronota. (**L**) Orangish-yellow, variable flash number among species, *Pn. consimilis* Group: *consimilis* s.s., sw MO, *consimilis* complex broadly, *carolinus* in Appalachians, unnamed trio in FL and GA. Green/white, southern Appalachians, *Ph. forresti*. (**M**) Green/white, at left, north-central and toward Gulf in FL, with variations, *Ph. dorothae*. At right, east TX, with expected variations, *Ph. barberi*. (**N**) Either yellow or green, around edges (ecotones), low, at twilight: yellow, a *Photinus*, commonly *marginellus*; green, a *Photuris* of any of several species—answer with a penlight to see switch (default) to species ID FP.

Appendix III



Suggested Procedures/Rules for Field Identification

This guide assumes that the user has had very
little experience and needs very basic instruction.

First (after hanging out a thermometer):

1. The identification of solitary flashing individuals is problematic without experience. Seek populations of a dozen of more flying, flashing males, all emitting identical or very similar FPs (flash patterns).

2. Without local experience, do not rely upon (use the charts in this chapter) to identify the flashes of perched or stressed individuals—those trapped in spider webs, water, spanish moss.

3. Observe flashing individuals in the population for a few minutes, noting the area of the site they are using, height of flight, flight speed, interactions of males as they fly near each other or behavior as they near the edges of the activity space.

4. Do not be distracted, lose focus, by the flashes of perched individuals unless they follow quickly (<2 seconds) after the FP of a male—if so, watch again before intruding, to be certain that the proximity in time was not fortuitous. Note whether any change their FP to a different type.

Then (with SWAT [a split-timer stopwatch] in hand):

5. Turn attention to the travels of an individual male. With eyes on him only, note the unit of flashing that he repeats—is it a single flash, a pair of flashes, a group/phrase of several flashes/pulses—then, watching his presumptive path for him to repeat after a few moments or seconds, see him repeat the same unit/phrase/group—that is, his same advertising flash pattern (FP). Practice this.

6. With stopwatch, time the duration/interval from the beginning of an FP to the beginning of the next consecutive FP (FP period), and record its duration in seconds on a note pad or pocket tape-recorder (TR).

7. If the FP has more than one flash, with the stopwatch time the duration/interval between the flashes/pulses within the FP, and record.

8. Check the TR to be certain that it recorded. Record temperature on the TR following the FP measurements.

9. Take a larger sample (<10) of FP measurements.

10. At 8 am record site notes, space used, and data in a fieldbook.

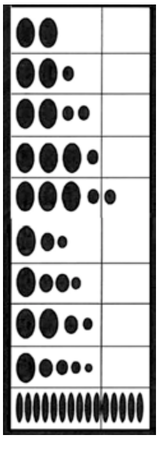
Preamble To *Photuris*

> *Things in themselves are wrapped*
> *in such a veil that not a few philosophers,*
> *and those of no mean caliber,*
> *have come to the conclusion that*
> *they are absolutely unknowable.*
> **Marcus Aurelius *Meditations* V.10 (121-180 C. E.)**

How can the incredibly variable and complex elements of behavior of *Photuris* as sketched in the preceding chapters —the awaited key to untangling the connections and sinuous entwining pathways of their genealogies on a long-abused and ever-changing continent—be explained and understood with mere words and still-life illustration? After 50 years of this focused study, *Photuris* remains almost as indescribable as it is inscrutable. I cannot be completely certain of that which I write, long seen and bent as it were through a species prism darkly. I try to keep in mind that this sketch must be of some improvement over the taxonomy long used for the genus. That was like the method my German tutor (Mr. Fritz) recommended for translation of the subjunctive mood, which, said he, could otherwise occupy a large percentage of instructional and study time, but occurs only rarely in German *science* texts. When confronted, he said, “simplify”, be formulaic, use what works: (1) *may*, (2) *might*, or (3) *must*. This certainly was the method used for *Photuris* over the century before Barber—alles ist *pennsylvanica*, almost. In darker moments of frustration, near acquiescence, I wondered whether the quest had entered a transcendent realm, and not realizable in normal experience … at the bench or in the field.

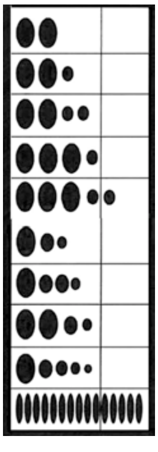
When Barber applied (circa 1926) the revolutionary insights of McDermott (1911-1917) and chased *flash patterns* (FPs) he accomplished more than he realized. His field work and voucher specimens, and later his comfortable writing style, provided a model for those who would follow—one that emphasized the necessity of a natural-history/evolutionary orientation. And, more to the point of the problem itself, he put his finger on aggressive mimicry, **and** the use of multiple flash patterns by individual males/species. Why, he certainly must have asked himself, if flashed signals were for mate identification, and both correspondents were presumed to have a shared interest in a successful outcome, why then should some of his species use two different FPs? It must have made no sense to him. Of course, the belated rebirth of evolution via Darwin's sexual selection was yet to come.

In 1951, clearly disappointed, and posthumously through McDermott’s annotated and augmented preparation of his manuscript, Barber observed that the *Photuris* problem was more complicated than anyone could possibly realize. At one point he mused, you might say, wished for a firefly site where there existed but a single *Photuris* species that could be studied without the interference of other species and their flashing. With the opportunity to travel further, or had he happened onto the right vacation spot he might have found his described fantasy island, for there is one in North America. In fact, the dominating resident species there is an exuberant "polyphot," that has a large vocabulary, and the only other *Photuris* seen there was a recluse in an out-of-the-way and perhaps safe hide-away. If Barber had found the former in 1926 it could have changed course of *Photuris* history. I compare this misfortune to one mentioned by Sir William Jones, a linguist of the late 18th century:



> *It is much to be lamented, that neither the Greeks, who attended Alexander into India, nor those who were long connected with it under the Bactrian Princes, have left us any means of knowing with accuracy, what vernacular languages they found on their arrival in this Empire. The Sanskrit language, whatever be its antiquity, is of a wonderful structure; more perfect than Greek, more copious than the Lati[n], more exquisitely refined than either, yet bearing to both of them a stronger affinity, both in the roots of verbs and in the form of grammar, than could possibly have been produced by accident; that no philologer could examine them all three, without believing them to have sprung from some common source, which, perhaps, no longer exists (1799).*

LIV



Chapter 9

Photuris alexanderi n. sp.

UMBS Firefly

In a coniferous, transition-bog between two small lakes at the northern tip of the mitten of Michigan, Cheboygan County, there occurs a *Photuris* with such unusual behavior that it might raise doubts whether the single elements of its flashing noted and recorded here, are part of a coherent signaling repertoire (**Fig. 1**), or mere remnants, pieces of a fragmented and disrupted yet operational program. This firefly "is clearly" derived from a *fairchildi*-like ancestor, and perhaps its isolation at the extreme northern end of a lake-bound peninsula (**Fig. 2**), which, on its landward, southern end experienced a major ecological transition following the Wisconsian glacial retreat a few thousand years ago, has permitted chaos to vacation there. This first acquaintance can only describe *alexanderi's* flashing elements, the timing of these elements, and some notes made on them.

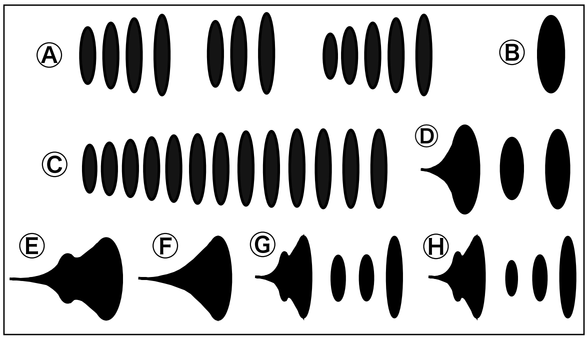


Figure 1. Repertoire or ad hoc assemblage (AX:rel int/time)?

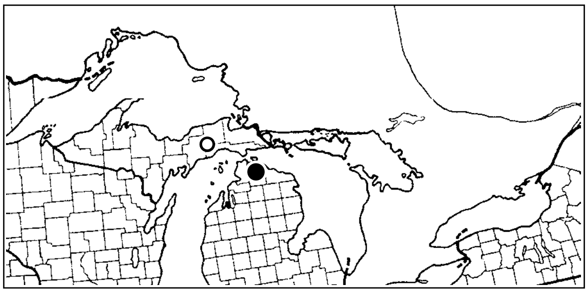


Figure 2 Circle marks uncertain sight-only record.

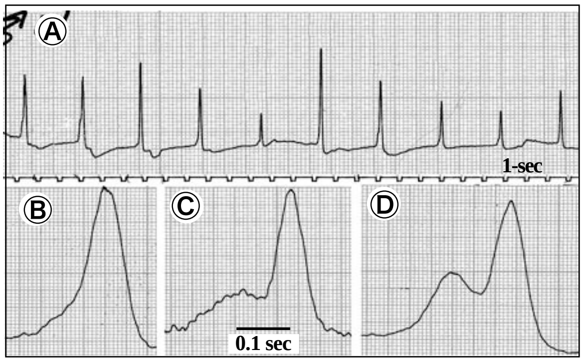


Figure 3. (A) Series of FPs emitted by a single male; (B) three forms of FPs (AX: ri/time).

Ecology and FPs. Small populations were found along a steep, ferny/grassy hillside under a power line, and over a nearby herby roadside along a dirt lane between a summer camp on Burt Lake and Reece's Bog. Observed season of flashing was 23 June to 28 July, during three years, 1971-73; **Fig. 22**). At the power-line males flew 1-6 feet above low vegetation and part way up against the face of an adjacent tree-line. One common FP was a continuing series of short flashes which to the eye appeared as short crescendos or bimodal hitches (**Fig. 1 EF**); PM-recordings confirm this impression, and that FP form varies between clean crescendos and distinct hitches among the FPs of individual males (**Fig. 3A-D**). Hitch modulation rate varies with temperature, as shown and extrapolated in **Figure 4** (based on PM records of 41 FPs and 11 males at 3 temperatures). FP period is about 2.2 seconds at 16°/61°; **Figure 5** shows period measurements, and then extrapolations (both a graphing program and rate conversion method) to extend the useful range for field ID and comparison. **Figure 6** shows interval rate from electronic measurements only.

The second common FP was a rapid series of shorter pulses, an FP similar to that of *fairchildi* (**Figs. 1A, 7**), with "less-than-perfect" signature profiles, possibly the result of changing lantern-PM alignment. These FPs had 4-8 pulses, were usually emitted in low flight over the ground, but sometimes during stationary hovering flight. Pulsing-FP period was similar to that of Minnesota *fairchildi*, a second or so longer than that measured elsewhere ("other"; **Figs. 8-11**). In **Figures 8** and **9** the durations of *alexanderi's* pulsing periods following 4 and 6 pulses are noted against regressions for *fairchildi*, both Minnesota and "other." In **Figure 10** *alexanderi* data are shown, lumped for a combined regression in **10A** and in **10B** period differences following lead-FP numbers are distinguished with symbols. **Figure 11** shows the rate trajectories for pulsing FPs, and though appearing chaotic at first, perhaps a rise-then-fall pattern is emerging?

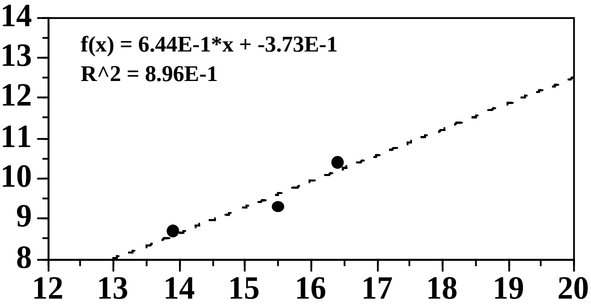


Figure 4. Hitch modulation rate (AX: Hz./temp).

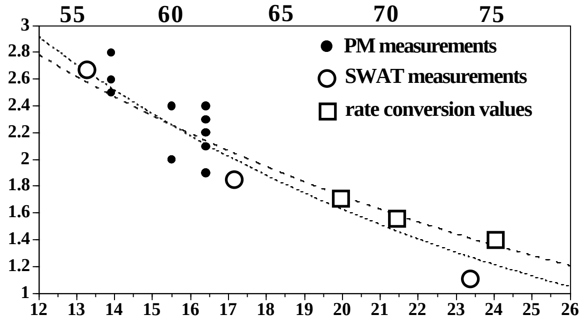


Figure 5. Cresc/short FP periods (AX: sec/temp).

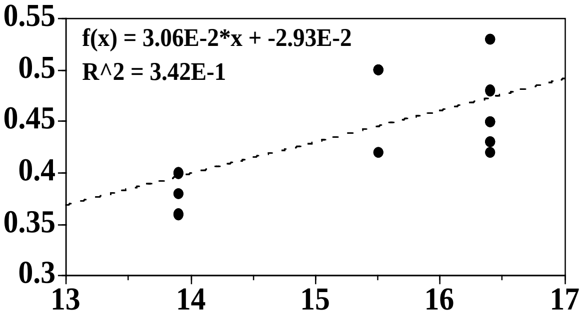


Figure 6 . Crescendo/short FP rate (AX: Hertz/Temp).

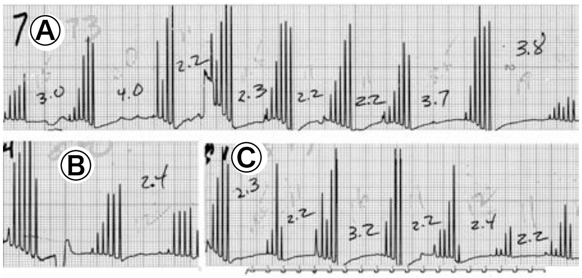


Figure 7. A-C, Pulsing-FP sequences from three different males showing the *fairchildi*-like signature (1-sec time marker in C applies to all:(AX:rel int/time).

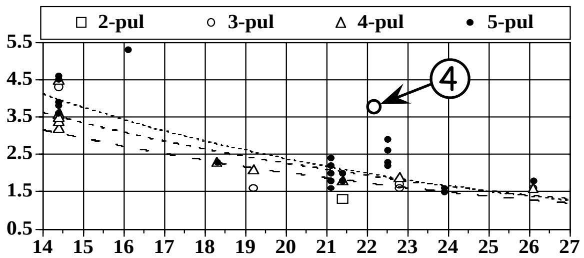


Figure 8. FP periods of *fairchildi*. Period-duration of 4-pulse FPs of *alexanderi* indicated (AX:sec/temp).

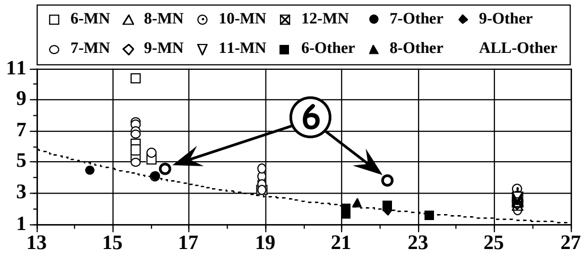


Figure 9. FP-period chart for 6-12-pulse FPs of *fairchildi* distinguishing between Minnesota (open symbols) and "other", and showing position of 6-pulse *alexanderi* (sec/temp)—see *fairchildi* for further discussion (AX: sec/temp).

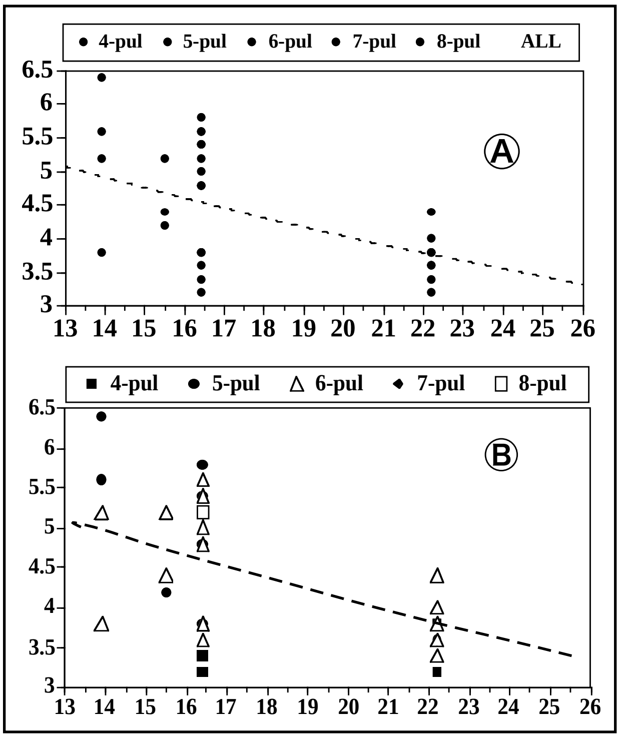


Figure 10. (A) All data points for *alexanderi* considered collectively and regressed (ALL line). (B) lead-FP pulse-number distinguished with symbols, ALL line transfered from A (AX: sec/temp).

On the second night of observation (24 June 1971) after the collection of a dozen pulsing vouchers, all were released when it was realized that pulsers of two forms had been included, *alexanderi's* two FPs not having been appreciated. However, both forms are emitted by *alexanderi*. The second form would appear to be a hybrid between the hitched/crescendo FP and the pulsing FP (**Fig. 1 DGH**). Visual impressions were confirmed and some variations were revealed in PM-records (**Fig. 12AB**). The Figure also shows part of a sequence of several phrases in **C** (1-sec marks), and an FP at 25mm/sec (**D**); **E** shows rate trajectories for FPs where PM-records permitted.

There was no indication that these different FPs were emitted at or dominated different windows through the evening. Through mark-release-recapture it was determined that individual males change among the observed FPs; such changes were also occasionally seen when flashing males were followed. Such changes are illustrated in **Figure 13**.

Incidental FPs of interest are shown in **Figure 14**: (**A**) A "normal" pulsing-FP for comparison at the 125mm/second scale; (**B**) a pulsing FP with one pulse having a down-stepping shoulder; (**C**) a *versicolor*-type down-stepping pattern though

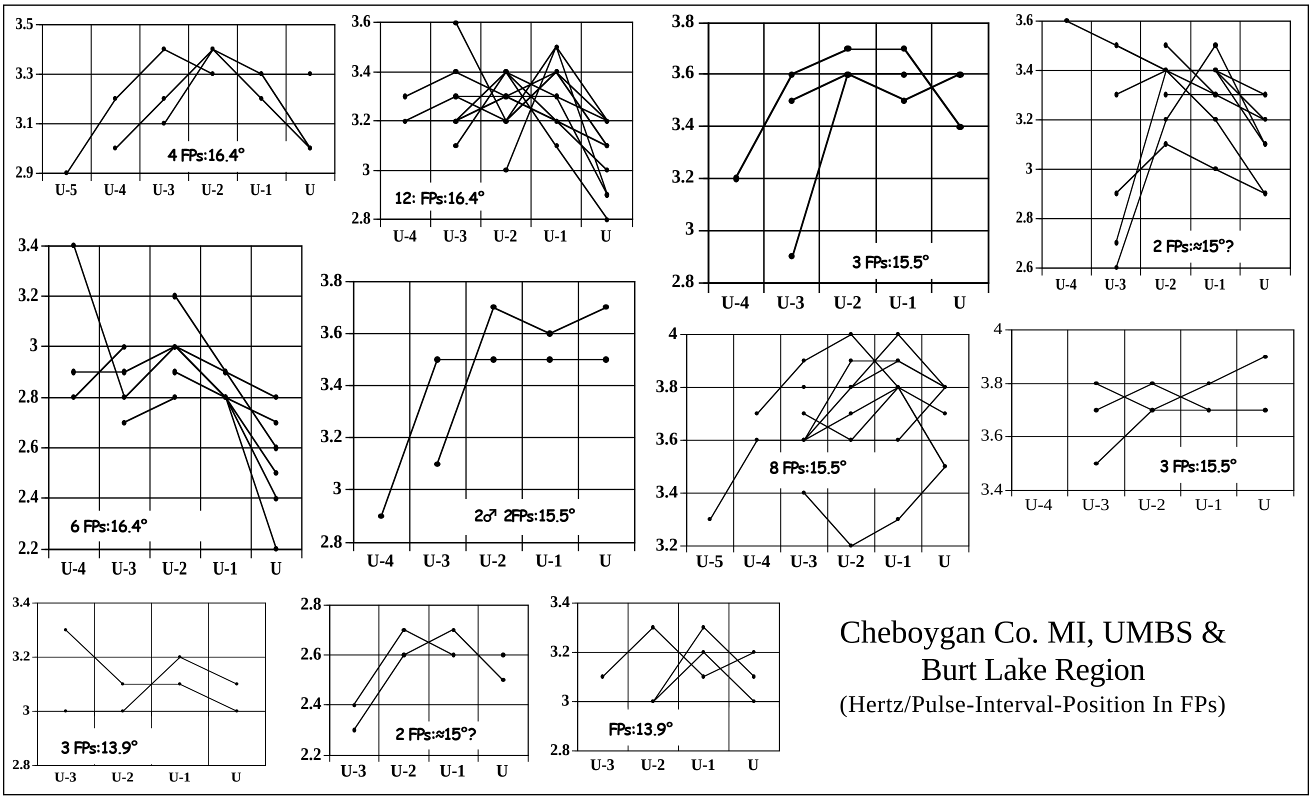


Figure 11. This collection of rate trajectories from individual males reveals an utter chaos as sometimes revealed in marginal populations, as compared with most "other" demes sampled—perhaps a rise-then-fall pattern is emerging (AX: Hz./pulse-interval-position in FPs).

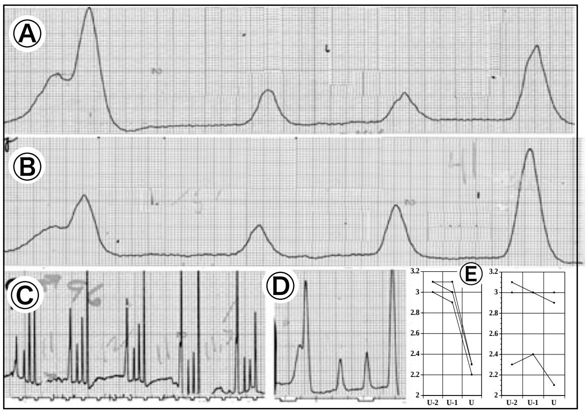


Figure 12. FPs, neural chimera, or both (AX:ri/time)?

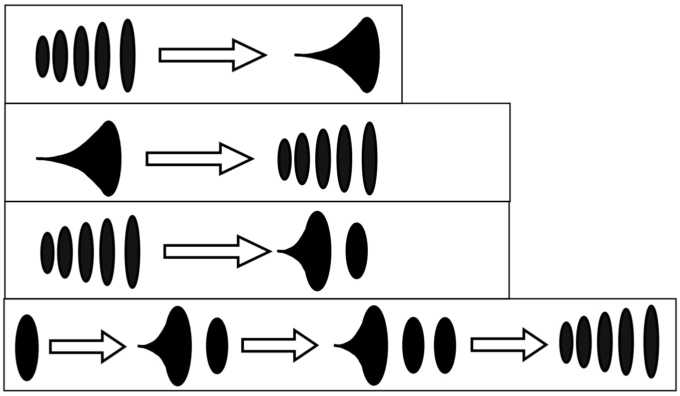


Figure 13. FP transitions observed (AX:ri/time).

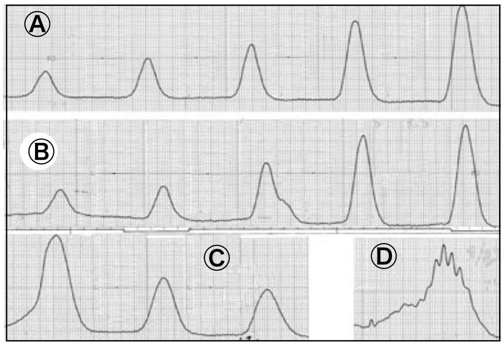


Figure 14. Incidental FPs of interest AX:ri/time).

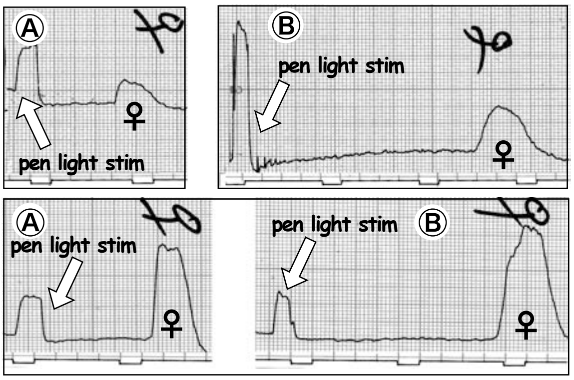


Figure 15. Responses of two females to prey-simulating FPs? (A) in both shows a short delay, and (B) in both shows a long delay. (B) of the top pair was the next response after (A); in the pair below the female emitted the two different delays in the same sequence but not consecutively (1-sec marker; AX:ri/time).

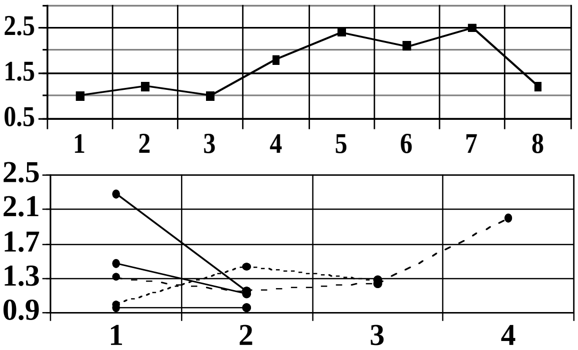


Figure 16. Durations of sequential female delays to penlight flashes—prey simulations? A single female above, four below (delay in seconds/stimulus position in presentation sequence).

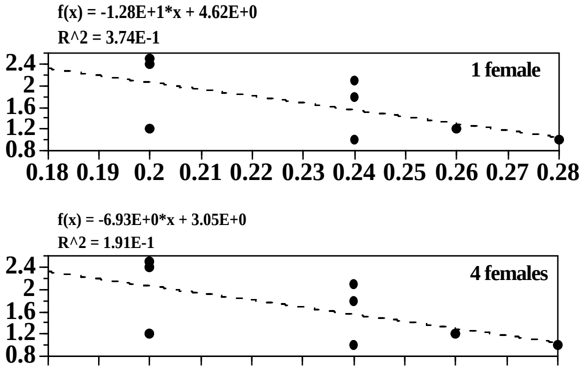


Figure 17. Correlation of female delay durations with penlight flash durations (delay/stim, in seconds).

Power Line Site

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.573	10.293	3.167	1.940	2.507	6.900	12.847	.811	1.309	.672
sd	.133	.465	.135	.159	.205	1.047	.476	.045	.148	.096
se	.034	.120	.035	.041	.053	.270	.123	.012	.038	.025
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.400	3.000	1.800	2.300	4.500	11.800	.740	.950	.420
max	2.800	10.900	3.400	2.500	3.100	8.500	13.500	.880	1.670	.820
Vc%	5.2	4.5	4.3	8.2	8.2	15.2	3.7	5.6	11.3	14.3

Burt Lake Site

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.610	10.830	3.300	1.940	2.480	6.840	13.430	.796	1.289	.631
sd	.137	.517	.170	.084	.063	.659	.562	.033	.074	.055
se	.043	.163	.054	.027	.020	.208	.178	.011	.023	.018
n	10	10	10	10	10	10	10	10	10	10
min	2.500	10.000	3.100	1.800	2.400	5.800	12.500	.750	1.180	.540
max	2.900	11.300	3.600	2.100	2.600	7.800	14.000	.850	1.430	.690
Vc%	5.3	4.8	5.2	4.3	2.5	9.6	4.2	4.2	5.7	8.7

FigTable 18. Morphology/measurements (Part A).

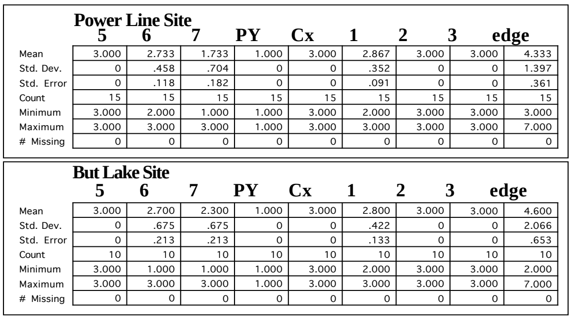
the first pulse is a crescendo and there are no *versicolor* of this sort for 300 miles or more; (**D**) a crescendo with wing-beats of 43.7 Hertz at 13.9°/57°.

Males were easily attracted to a flashed decoy that was flashed immediately after their FPs, and often to the tip of the decoy light. When attracting crescendo/short flashers, a slightly longer decoy flash was more successful than a short flash. Interloping males often approached the decoy. No defaulting was ever noted though many short and pulsing flashers were attracted. In one instance it appeared that a low-flying, circling male may have been responding to an answering female, and as he circled he emitted both short/crescendo and pulsing FPs, switching back and forth between them.

Female flash responses. Ad hoc penlight flashes (presumptive simulations of prey FPs) directed at perched and presumably hunting(?) females near Burt Lake produced suggestive/interesting results. PM-records showed that females varied their delays greatly from response to response (**Figs. 15, 16**)—possibly revealing a trial and error method to determine which delay worked for the prey firefly she was responding too (in her "mind"/neural circuitry). **Figure 15** shows the extreme difference in delays seen within PM-recorded sequences of the responses of two females. **Figure 16** shows the trajectories of delays of a single female and for four females. Possibly a relationship between the duration of the penlight's pulse and female delay is "weakly suggested" in **Figure 17**. Stimulus (prey FP duration) would be expected to have some influence on a female's selection of delay as she tunes her responses to different prey species. These sketchy data are shown merely to suggest that rather simple but carefully designed and equipped experiments could be worthwhile. But, perhaps female delay changes are associated with FP form or sequence?

Morphology. Data are shown for two sites in **FigTable 18 Parts A-D**, but these neighboring areas could probably be considered as one. Measurement means for the power-line site are (n=15): PNL 2.6, ELL 10.3, PNW 3.2, EWhum 1.9, EWmid 2.5, ELVit 69, TOTLen 12.8, PNrat 0.81, ELWrate 1.31, ELVTrat 0.67; colors are in **Part B** and color histograms in **Parts C** and **D**. **Figure 21** is key for anatomical elements and splashing on ventrite 4. A range of vittagrams is in **Figure 19**. Histograms in **Figure 20** show the vittagram analysis.

Holotype: male, voucher number 7139, collected 28 June 1971, Cheboygan County, Michigan. FB page 28: marked with a red 2, as a crescendo flashers, and recaptured emitting a 5-pulse FP. Morphological data: genitalia extruded, remain attached; from spread sheet —PNLen 2.6, ELLen 10.9, PNWid 3.1, ELWhum 1.9, ELWmid 2.6, LELVit 8.1, TotLen 13.5, PnRat 0.84, ElRat 1.40, VitRat 0.75; Colors: T 332, Py 1, Cx 3,V 333, Edg 4. Types will be deposited in the USNM.



Power Line Site

	5	6	7	PY	Cx	1	2	3	edge
Mean	3.000	2.733	1.733	1.000	3.000	2.867	3.000	3.000	4.333
Std. Dev.	0	.458	.704	0	0	.352	0	0	1.397
Std. Error	0	.118	.182	0	0	.091	0	0	.361
Count	15	15	15	15	15	15	15	15	15
Minimum	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
# Missing	0	0	0	0	0	0	0	0	0

But Lake Site

	5	6	7	PY	Cx	1	2	3	edge
Mean	3.000	2.700	2.300	1.000	3.000	2.800	3.000	3.000	4.600
Std. Dev.	0	.675	.675	0	0	.422	0	0	2.066
Std. Error	0	.213	.213	0	0	.133	0	0	.653
Count	10	10	10	10	10	10	10	10	10
Minimum	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	2.000
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
# Missing	0	0	0	0	0	0	0	0	0

FigTable 18. Morphology/color (Part B).

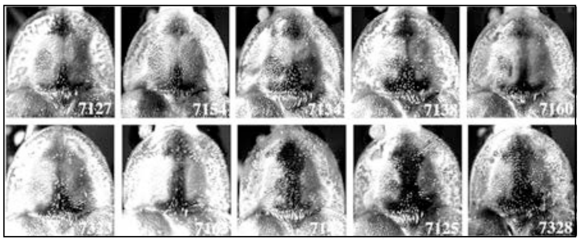


Figure 19. Vittagram array.

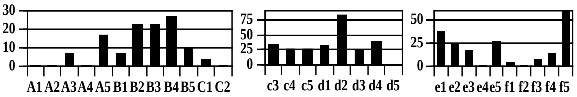


Figure 20. PN vittagram analysis.

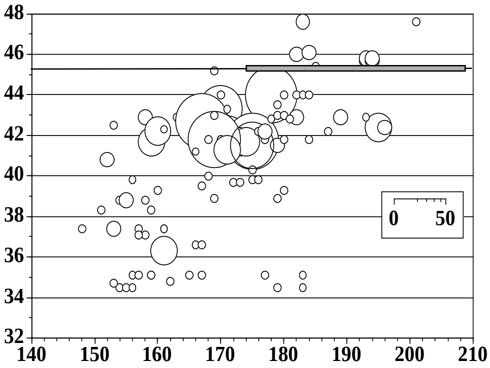


Figure 22. Observed occurrence of *alexanderi* (DOY 174-209) , a bar at 45.3°, shown against *fairchildi* GESEDISOBS records (AX:Lat/DOY).

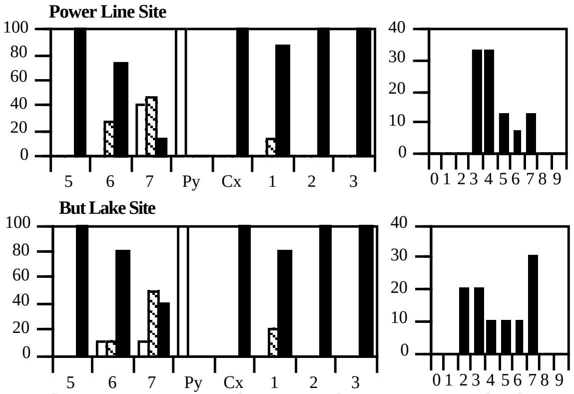


Figure 18. Morphology (Parts C and D).

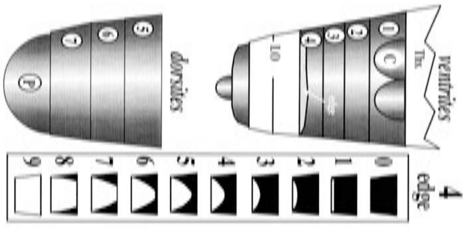
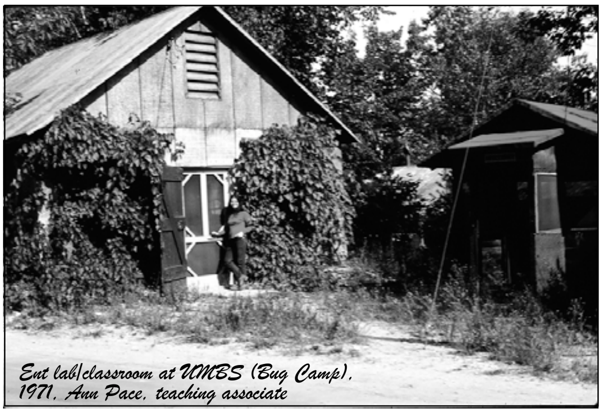
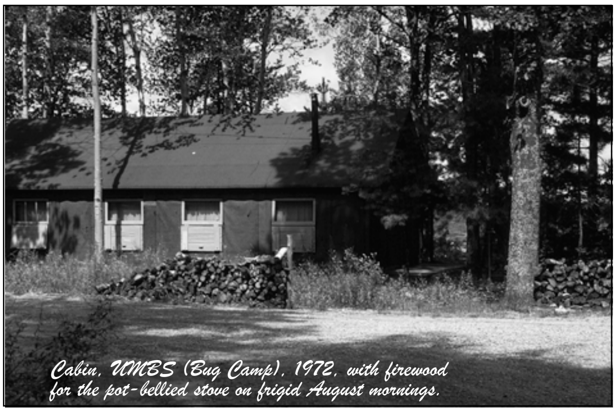


Figure 21. Topographic and splash keys.

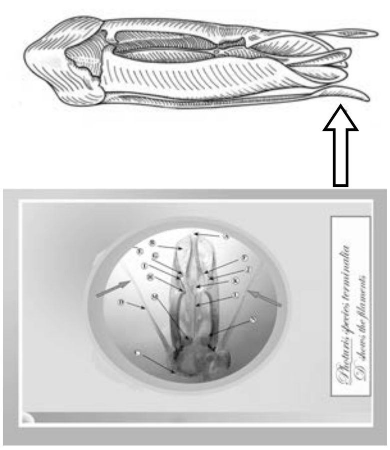
Nomenclatural Notes. This species is named in honor of Dr. Richard D. Alexander, my advisor at UMMZ in the early 1960s and mentor and confidant thereafter for many years. This firefly was selected from many possibilities, because it was complex, had an interesting evolutionary history, could attract and keep student attention as they studied insects in the field at UMBS (Bug Camp), and perhaps seduce them to field studies incorporating the pleasure of such studies, with all the complexity of evolutionary theory and behavioral ecology—outcomes my studies with RDA provided, for a lifetime. Without doubt Dick Alexander was the most important, creative, inspiring, and insightful teacher I ever had. I especially thank Dick and Laurie Alexander for their kind hospitality during many, and sometimes lengthy visits to Ann Arbor, to the Alexander farm, the fireflies, and museum.



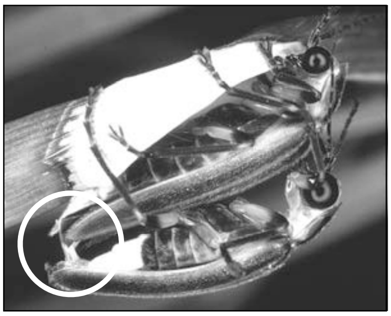
Ent lab/classroom at UMBS (Bug Camp), 1971, Ann Pace, teaching associate



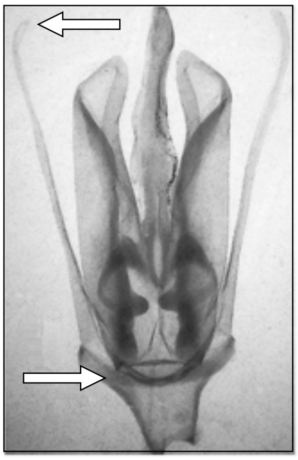
Cabin, UMBS (Bug Camp), 1972, with firewood for the pot-bellied stove on frigid August mornings.

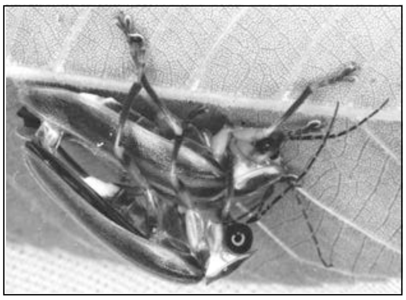


Photuris aedeagi and phylogenetic indications. First, the filamentous appendages of the basal piece would appear to have two functions: (**1**) They may function as guiding sensors, feelers used by males to align the aedeagus for insertion into the acute female terminalia at coupling—the filaments apparently are not themselves inserted; (**2**) during coupling, when aligned closely along the sides of the female abdomen, they detect movement of the female should she begin to turn to grab him to eat—to serve as her repast (quoting Barber from another context). In which of these two contexts might they have *first* evolved? The second seems more likely. If they originally had evolved as guides to insertion, their anatomical attachment would be at the probing/seeking tip of the aedeagus at the very moment of probing/seeking. However, if they originally had evolved as detectors of movement of the female after insertion was complete, they would be expected to have evolved and now occur at the point of contact with the female's external body/cuticle **after** coupling and insertion was complete. Their actual origin is the basal piece of the aedeagus, which remains just outside the body of the female after coupling and complete insertion is achieved. Note the figures showing filament attachment to the basal piece and placement outside the female abdomen during coupling.



Second, the two Divisions of North American *Photuris* have many differences. Female of Division I are not known to be predaceous, and in fact seem "gentle," and somewhat *Photinus*-like. However, the aedeagi of their males are like those of Division II males in having filaments, suggesting that if their function is to avoid predation by their females, as in (2) above, then there are predators in the ancestry of Division I. Certainly separation of Division I and II lineages occurred long ago, and probably somewhere south of the Rio Grande in tropical America.





In observed copulations females hung below a leaf, with males below them, with middle legs held away from the females; perhaps both manuevers were connected with female predation.

Chapter 10

Photuris alleganiensis n. sp.

This presumptive variad of *caerulucens* was seen only in Allegany State Park in western New York State, Cattaraugus County (**Figs. 1, 2**). It occurred in a roadside marshy area at a culvert, perhaps the inlet of a beaver pond, and also over a nearby hayfield. These sites were south of Quaker Lake (≈1.9 miles), route ASP-2. It emitted both a short flash FP at twilight and later a long flash FP. The long flash is variable in form, appearing as a slight crescendo, a slight decrescendo, and of even intensity throughout (**Fig. 4A-D**). A few long flashes were seen around boughs of trees but most were low over grassy areas. Short flashers answered with a decoy defaulted to a long flash, approached and landed near the light. The short flashing window was timed during one brief session that ended as a long-lasting storm moved in (**Fig. 3**). The short flash is similar to that of twilight *Photinus* species in Division I; short FP period averaged 2.3 seconds at 18.5°/65° (r=1.9-2.8, n=10; **Fig. 8**). On a mid-July visit to the site only long-flashing was seen.

Males flew at higher altitudes (8-10’) than than noted in other Penn-Group demes. SWAT durations of long flashes ranged 1.9-2.3 seconds at 14.4°/58°, n=4; **Fig. 5);** FP period, 5.6-7.0 seconds (n=5; **Fig. 6**). The FP interval of short flashes averaged 2.3 sec in duration, and ranged 1.9-2.9, at 18.3°/65°. Mid-flash intensity rises (**Figs. 4E**, **5CD**), as with those sometimes seen in other Penn-Group demes, are presumably caused by attitude changes by males as they aim their lanterns, increasing their field of broadcast. Visual judgment of long-flash form in the field is subjective and sometimes differs significantly from PM records, but in this case the PM records agree with what the eye observed: the four traces in **Figure 5** were all emitted by the same male: one is “normal” (**A**), one shows a sharp hump (D) and another (**B**) is greatly shortened and has an unusually sharp termination. All four traces show indications of wing-shuttering, averaging 45.4 Hz (r=43.8-46.9, 18.3°/65°). Long-FP period falls with the regression for the long FPs of other Penn-Group demes (**Fig. 6**, arrow; rate in **Fig. 7**, arrow); so also the twilight short flash (**Fig. 8**, arrow).

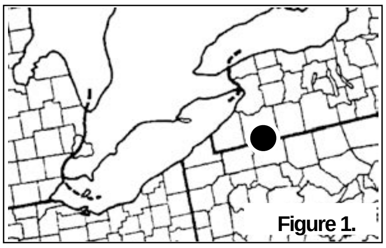


Figure 1.

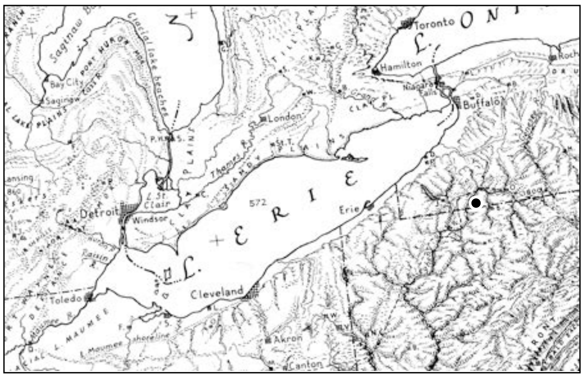


Figure 2. Physiographic view.

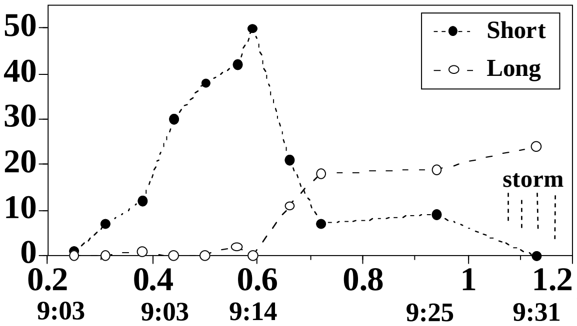


Figure 3. Evening FP change-over (AX: number/creps & EDST).

Morphological summary. Means (n=4): PNL 2.5, ELL 10.5, PNW 3.1, EWhum 1.9, EWmid 2.5, ELVit 7.7, TOTLen 13.0, PNrat 0.79, ELWrate 1.30, ELVTrat 0.73 (**FigTable. 9A**, with other stats); colors in **FigTable 9B-C**, pre-lantern ventrite splash in **9D**. **Figure 10** is key for anatomical elements and splashing on ventrite 4.

Figure 4. Long FPs of *alleganiensis*, observed (visual) variations.

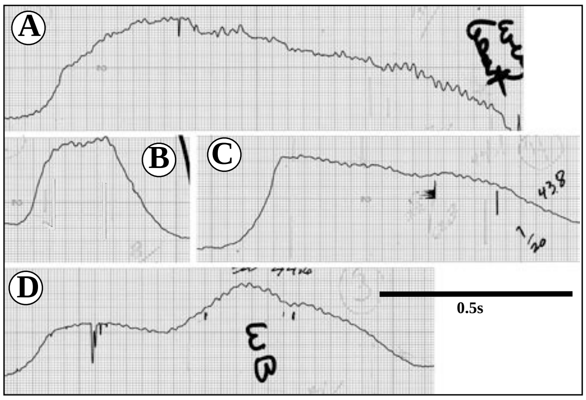
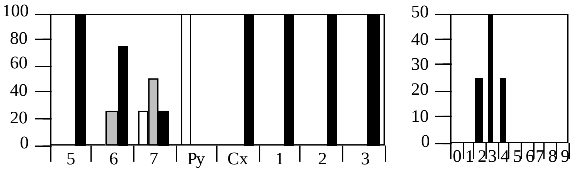


Figure 5. *P. alleganiensis* PM traces (AX: ri/sec).

Holotype. male, voucher number 9267, collected 2 July 1992, Cattaraugus County, New York, Allegany State Park, 1.9 miles south of (Quaker Lake/Red House) Lake on route 2. (FB page 70: "KB 42\9267—"long from 2nd bridge site, 1.9 m s, on rt 2, from loop road". Morphological data: genitalia partially extruded remain attached; from spread sheet—PNLen 2.6, ELLen 11.0, PNWid 3.4, ELWhum 1.9, ELWmid 2.6, LELVit 8.4, TotLen 13.6, PnRat 0.78, ElRat 1.40, VitRat 0.76; Colors: T 332, Py 1, Cx 3,V 333, Edg 4. Types will be deposited in the USNM.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.475	10.500	3.125	1.900	2.450	7.700	12.975	.792	1.300	.733
sd	.096	.663	.206	0	.129	.913	.741	.030	.085	.072
se	.048	.332	.103	0	.065	.456	.371	.015	.043	.036
n	4	4	4	4	4	4	4	4	4	4
min	2.400	9.600	2.900	1.900	2.300	6.600	12.000	.760	1.200	.660
max	2.600	11.000	3.400	1.900	2.600	8.500	13.600	.830	1.400	.820
Vc%	3.9	6.3	6.6	0	5.3	11.9	5.7	3.8	6.5	9.8

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.750	2.000	1.000	3.000	3.000	3.000	3.000	3.000
sd	0.000	.500	.816	0.000	0.000	0.000	0.000	0.000	.816
se	0.000	.250	.408	0.000	0.000	0.000	0.000	0.000	.408
n	4	4	4	4	4	4	4	4	4
min	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	4.000
Vc%	0	18.2	40.8	0	0	0	0	0	27.2



FigTable 9. Morphology: measurements, ratios, colors.

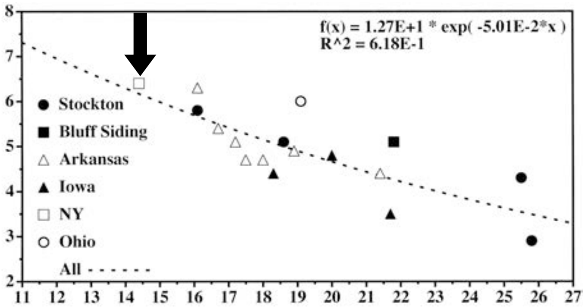


Figure 6. Long-FP period (AX: sec/temp).

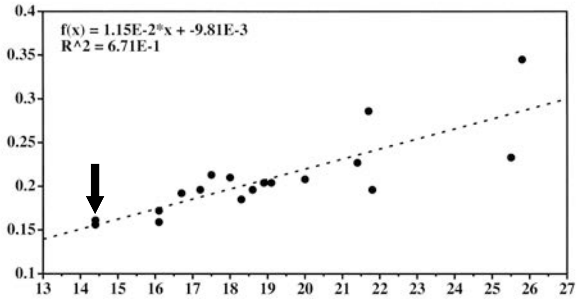


Fig. 7. Long FP period (interval) rate (AX: Hz/temp).

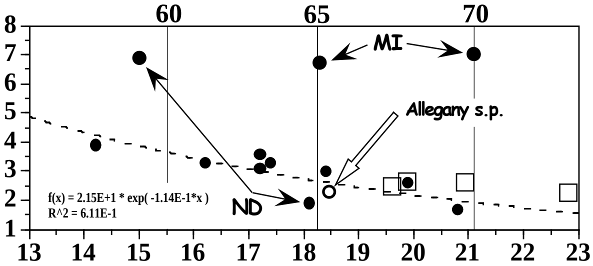


Figure 8. Short flash period, circle/arrow (AX: sec/temp).

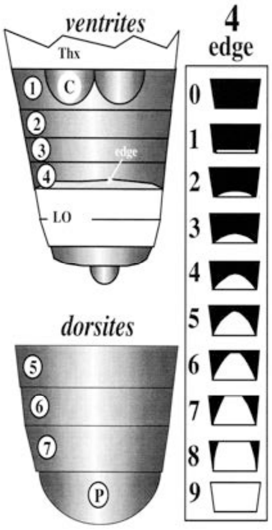


Figure 10. Topographic and splash keys.

Chapter 11

Photuris appalachianensis n. sp.

This firefly was recognized/found only in the Potomac River Forest in the Appalachian Mountains in Garrett County, at the western end of Maryland, and may have some similarities with *bridgeniensis* in central New York State (**Figs. 1, 2**). The diagnostic FP is the *pensylvanica* dot-dash accompanied by two adjunct FPs, one twilight and one later. In some PM-recordings the dot-dash is clear but not often sharp, with the break minimal. Observations were made from 29 June to 4 July, 1984 (**Fig. 3,** arrow). The main study area was a 40’X40’ mowed-grassy area at a bridge across a small and loud stream, Lost Land Run, and was probably intended as a campsite (**Fig. 4**). This was bordered on the creek side by a narrow margin of long grass where twilight (short FP) flight began and was centered. Dot-dash FPs appeared a few minutes later in the same area and also along the access road for some distance both ways, occasionally high against the forest wall. In addition to the dot-dash FP, and twilight short flash (**Fig. 5**), males emitted in late-evening the A-flicker. They defaulted from both the short and flicker to the dot-dash FP without exception in 20 or more trials, when answered with an LED-decoy flash at the tip of the flashpole (**Figs. 6, 7 also Fig. 10G-J; p. 472 C**). This firefly with its FP versatility is perhaps useful for connecting and understanding members of the *pensylvanica* Group, perhaps the most complex of them all.

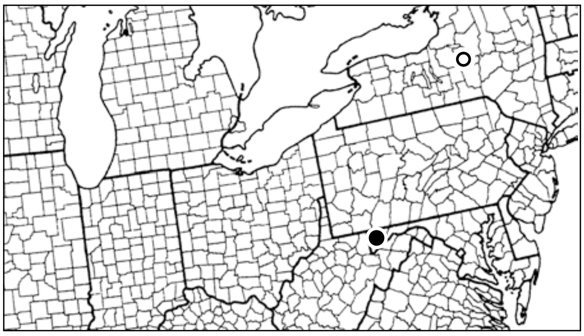


Figure 1. Dot, Garrett Co. MD; circle, Madison Co. NY.

Figure 2. Dot, Garrett Co. MD; circle, Madison Co. NY.

Figure 4. Center of activity, experiments.

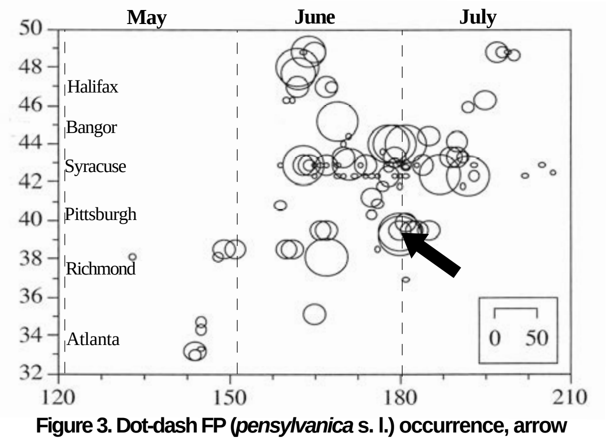


Figure 3. Dot-dash FP (*pensylvanica* s. l.) occurrence, arrow marks *appalachiensis* observations (AX: Lat/DOY).

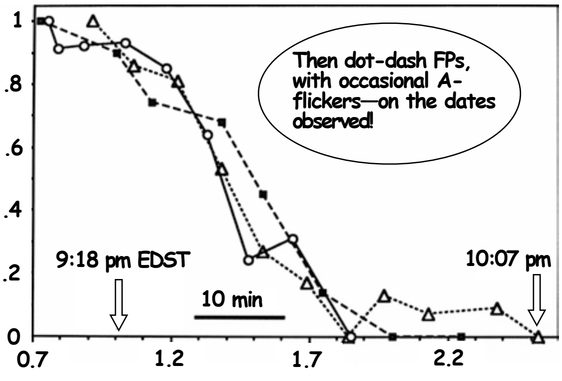


Figure 5. Fraction of males emitting twilight short FPs,on three evenings (AX: fraction/crep).

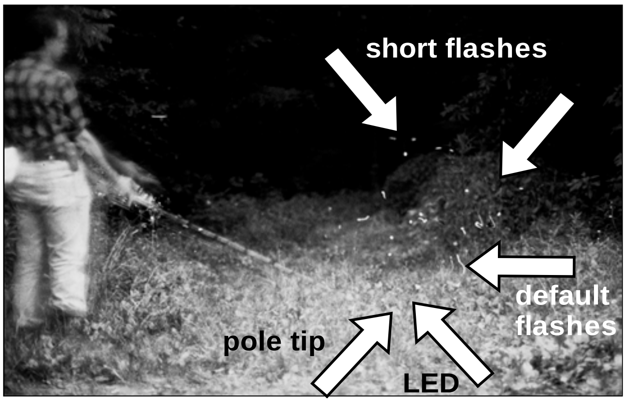


Figure 6. Flashpole defaulting experiment. Rival males move toward a decoy that is flashed in answer to only one of them.

Figure 7. Flashpole defaulting experiment up close; note apparent fusion of dots with dashes, and attraction of rival males.

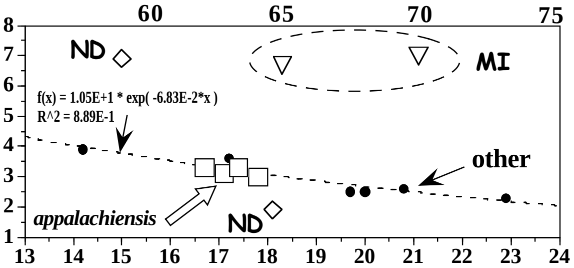


Figure 8. Short-flash FP (twilight) period with periods of other penn-Group OTUs (AX: sec/temp).

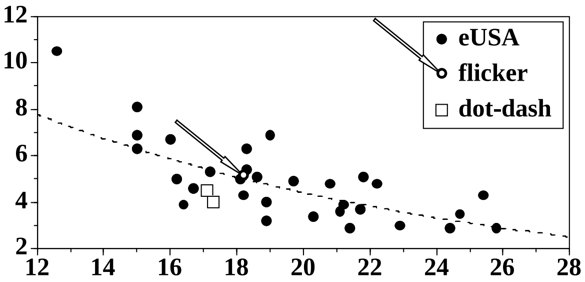


Figure 9. Dot-dash and flicker FP periods with all records.

Flashing behavior. At twilight males flew among the tips of and just over the un-mowed vegetation at the margin of the cleared area, and emitted the short flash; its period is shown in **Figure 8**). With increasing darkness they flew higher and further into the open space. Dot-dash FP period is shown in **Figure 9**); in Figure 9 note that flicker periods measured fell tightly within the dot-dash regression. **Figure 10** shows PM records of several FPs; descriptions and explanations:

10A, B. Twilight short-flash FPs; **10C, D**. Dot-dash FPs, note different relative intensities of two FP components, intensity variation during dash probably from flight movements with respect to the PM recorder. **10E**. Continuation of decoy attraction (note arrow) beginning in **F**. 1**0F-H, E**. Male's short flash seen at the beginning of **G** at a faster chart speed. **10G**. Male short flash answered with decoy, repeated twice, and finally male defaults to dot-dash in **E**. **10I**. Part of A-flicker seen at the beginning of panel **J** at a faster chart speed. **10J**. Male A-flicker FP answered with a decoy flash, male defaults to dot-dash FP. **10K**. Male A-flicker FP. **10L**. Hitched emissions of a male on the ground; he was attracted to land with a decoy. This pattern appears too "good" not to have some significance? **10M-O**. Dot-dash FPs with modulations from flight movements probably; in **10N** and **O** note the wingbeat ripples. None in **C**—they come and go!, perhaps controlled by males in circumstances where an aerial attack is a possibility? (see *lamarcki* text)

Morphological summary. Tables and histogram on next page Means are (n=14): PNL 2.6, ELL 10.8, PNW 3.3, EWhum 1.9, EWmid 2.5, ELVit 7.7, TOTLen 13.4, PNrat 0.80, ELWrate 1.32, ELVTrat 0.71 (**FigTable. 11**, with other stats); colors in **FigTable 11**, pre-lantern ventrite splash in **11D**. **Figure 12** is key for anatomical elements and splashing on ventrite 4.

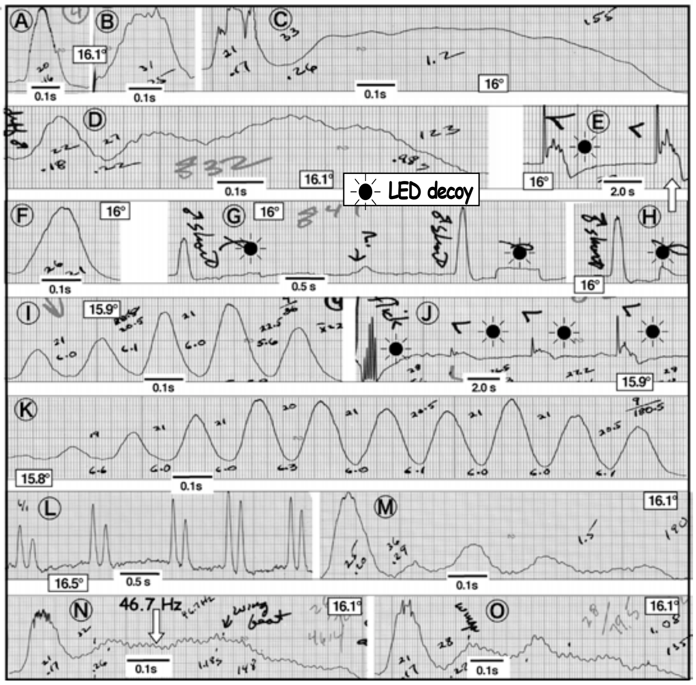
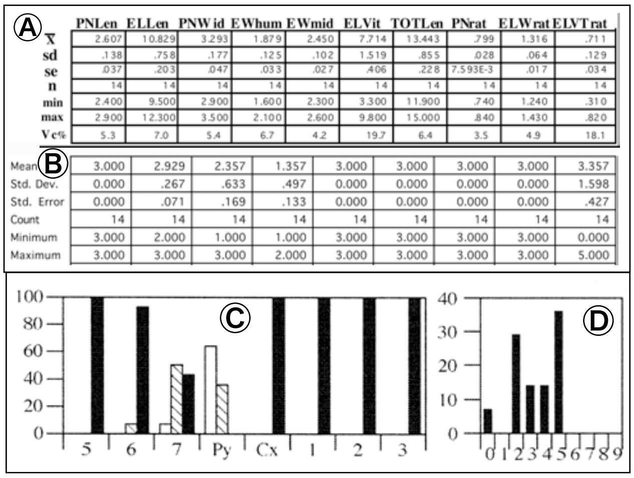


Figure 10. PM-records with temperatures and timings as noted on each panel.



	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.607	10.829	3.293	1.879	2.450	7.714	13.443	.799	1.316	.711
sd	.138	.758	.177	.125	.102	1.519	.855	.028	.064	.129
se	.037	.203	.047	.033	.027	.406	.228	7.593E-3	.017	.034
n	14	14	14	14	14	14	14	14	14	14
min	2.400	9.500	2.900	1.600	2.300	3.300	11.900	.740	1.240	.310
max	2.900	12.300	3.500	2.100	2.600	9.800	15.000	.840	1.430	.820
Vc%	5.3	7.0	5.4	6.7	4.2	19.7	6.4	3.5	4.9	18.1

Mean	3.000	2.929	2.357	1.357	3.000	3.000	3.000	3.000	3.357
Std. Dev.	0.000	.267	.633	.497	0.000	0.000	0.000	0.000	1.598
Std. Error	0.000	.071	.169	.133	0.000	0.000	0.000	0.000	.427
Count	14	14	14	14	14	14	14	14	14
Minimum	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	0.000
Maximum	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000

FigTable 11. Morphological data, measurements, ratios, color.

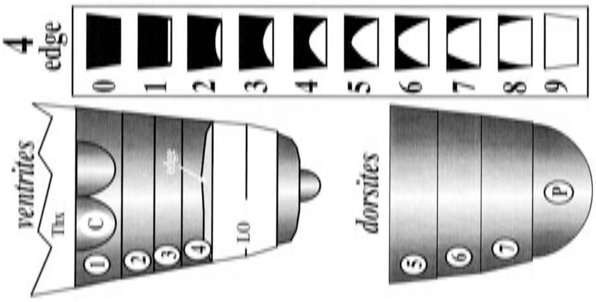


Figure 12. Key to anatomical elements and splash.

Holotype: male, voucher number 84251, collected 1 July 1984 Garrett County, Maryland, Potomac River Forest, Lost Land Run, at campsite near bridge (Fig. 4; FB page 111: "KB 10\84251 recorded short flash male--when I was holding him he gave long [dot-dash] flash in my fingers—a test?" Morphological data: from spread sheet—PNLen 2.8, ELLen 11.5, PNWid 3.4, ELWhum 2.1, ELWmid 2.6, LELVit 8.1, TotLen 14.3, PnRat 0.81, ElRat 1.24, VitRat 0.71; Colors: T 333, Py 2, Cx 3,V 333, Edg 2. Types will be deposited in the USNM.

4 July 1984, Lost Land Run

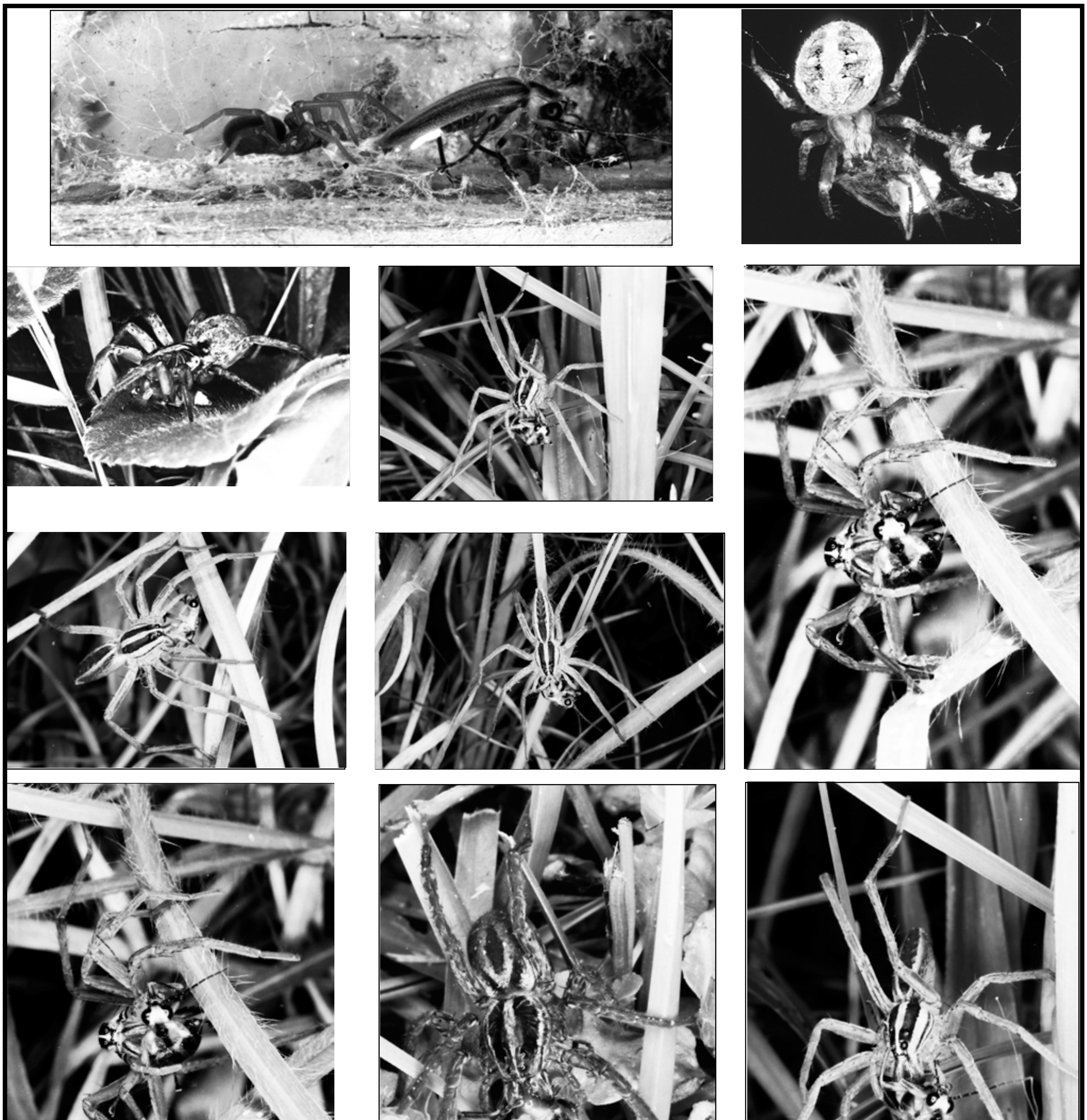
4 July 1984, Lost Land Run

4 July 1984, Lost Land Run, water hole

Bean

4 July 1984, Lost Land Run, Potomac State Forest, MD

Spider predation. Fireflies are trapped in the webs of spiders, as shown in the first two photos—one in a web against the siding of the old garden house at the Med Garden site; the other was taken in Jamaica, with a captured *Photinus pallens*. At the UF Med Garden lethal spider encounters usually involved wolf spiders (Lycosidae), and were brought to the attention by the flashing of captives. Flashes emitted by ambulating, ovipositing females may have attracted the spiders in these photos to the fireflies. Experimentation with this should be simple, but lights that don't also emit infra-red frequencies should be used. Some photos are of the same capture from different angles. Captures include *Photuris harrannorum* and *douglasae*. (See also page 475 J)



Chapter 12

Photuris asacoa n.s.

Leopold's Firefly

> *There will always be pigeons in books and in museums, but these are effigies and images, dead to all hardships and to all delights … But we, who have lost our pigeons, mourn the loss …*
>
> Aldo Leopold

This firefly was seen only in the gorge of Little Paint Creek, a trickle of the Mississippi River in the Yellow River State Forest, Allamakee County, in northeastern Iowa (**Figs. 1, 2**). It is similar to other regional *Photuris* in appearance (**Fig. 10**). Males began flashing 15-20 minutes after sunset in the shady stream-side forest and later over low fields outside the campground. They emitted both short symmetrical flashes and long crescendo flashes, with the proportion of short flashes perhaps being greater in early evening and the proportion of crescendo flashes increasing to virtually or nearly exclusive use about one hour after activity began. Males emitting crescendos were often perched near the ends of tree boughs whereas short-flashing males flew low amongst and over tall grasses and herbs (**Fig. 3**).

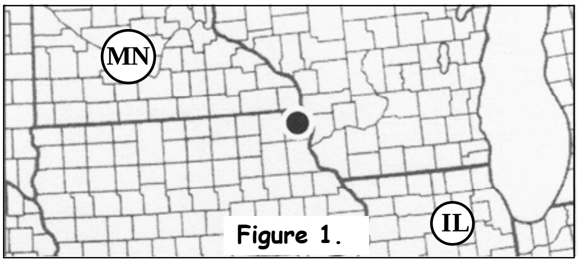


Figure 1.

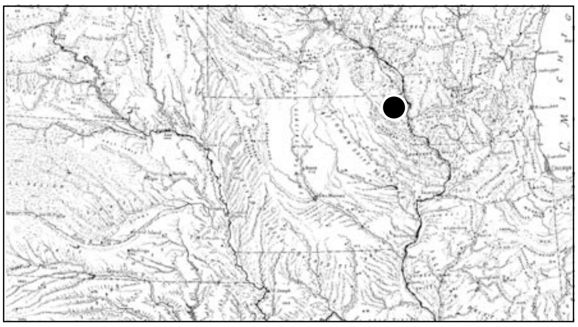


Figure 2. Physiographic localtion.

Figure 3. One end of site, with flashes drawn in place.

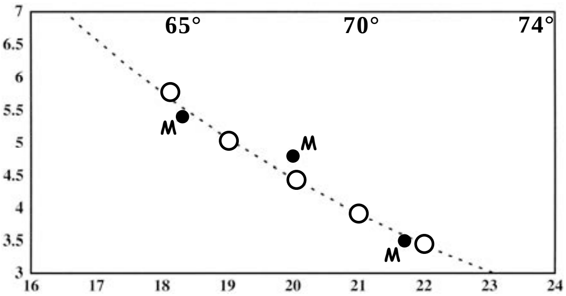


Figure 4. Cresc. FP period (AX: sec/temp).

The crescendo flash will be confused (only) with that of *Photuris lucicrescens*, which apparently does not occur as far north as Iowa, has pale hind coxae, and is larger. Short-flashing males default to the crescendo FP after receiving a flashed response; short flashing *lucicrescens* males are not known to default. This firefly may be diagnosed with confidence only by flashing behavior.

Flashing Behavior and Ecology. The observed population in the campground numbered fewer than 30 males during four evenings of observation, 19 June 1987 and 8-10 July 1990; they were more abundant in June 1987 than in July 1990. This firefly may occur only in bottom land, for I found none along the road climbing out of the gorge or in the adjacent highlands. Males began flying and flashing in the well-shaded, stream-side forest earlier than elsewhere—generally, small firefly populations and those in a high-sided valleys may vary considerably in onset of activity—at 0.29-0.45 creps (10-16 min after sunset).

In contrast with flashing in some populations of *penn*-Group fireflies, in which the adjunct FP (short) was used first in the evening for several minutes before the primary dot-dash pattern was first seen, *asacoa* may use both of its (known) FPs, the short (adjunct) and a crescendo (default) FP, at the beginning of activity. Short flashing seemed to end by 0.5-2 creps, and after 3 creps crescendo flashing was greatly diminished (**Fig. 3**).

In early evening, males emitting the short flash flew slow, meandering courses through/below the tops of tall, ecotonal, herbaceous vegetation, and FP periods were variable. Later and in shadier places they flew faster over the top of low vegetation —and probably with greater rhythmicity; with higher ambient light firefly males use vegetation clues for flying and directing flashes which results in greater period variance. Rarely short-flashing males flew up amongst the low boughs of small trees, 10-15 feet above ground. The period of short flashes averaged 2.3 sec at 21.7°/71°. Short flashes were nearly symmetrical in form, with only a slightly longer fall time, and averaged 84/148

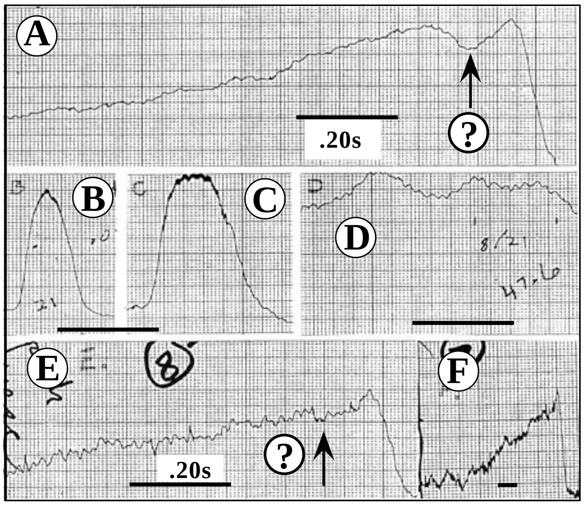


Figure 5. PM records (AX: rel. int./time; 20°/68°).

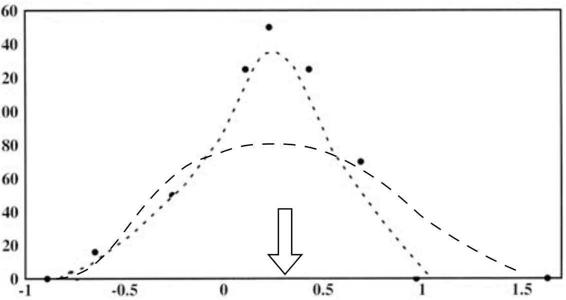


Figure 6. *Photinus curtatus* evening window (AX: number/creps).

mSec in duration at 20°/68° (15 short flashes recorded, 10 measured; **Fig. 5B**).

Crescendo flashes were emitted during slow, sometimes poising flight, over low vegetation in the river forest, with diminishing numbers at higher flight altitudes though one or two males could occasionally be seen at 50 feet or more around the high boughs and crowns of trees, poising, cruising and flashing in a manner of *P. lucicrescens.* Only occasionally did males emit crescendos over the open lawn. During the last part of their crescendo, males (viewed closely) sometimes seemed to waggle or oscillate back and forth in sinusoidal arcs (**Fig. 5D**, slow undulations). Males often emitted crescendos from perches, and at times half the FPs seen were emitted by such stationary males. Perhaps males alternate between flying and perched flashing through the evening (see page 82).

Crescendo FP period averaged 3.5 sec at 21.7°/71° (**Fig. 4**). Crescendos averaged 1.8 sec in duration at 21.7°/71° (n=10, range=1.7-2.5, s=0.3). To the eye, some crescendos appeared to reach maximum intensity and remain constant for a half second or more before ending. PM-recordings made of crescendo flashes unfortunately were often (inexplicably) very noisy (**Fig. 5E, F**). Two emitted by a perched (i.e. thus not wagging) male show a "notch" in intensity shortly before the maximum (**Fig. 5A**). Decay is rapid but not abrupt, and ranges 80-140 mSec in several readable PM-records (20.0°/68.0°).

Individuals were sometimes seen to change from one pattern to the other, when no stimulus/releaser was noted. When crescendo flashing males were answered (LED, see below) with a short flash immediately after their flash, they approached and landed near the decoy, indicating that this decoy simulation is probably similar to the sexual response of females. When short-flashing males were answered with a short flash immediately after their flash, they defaulted to the crescendo FP and approached the decoy (n=5).

Experiments with crescendo-emitting males used a 180 mSec (est.) flash with a green LED at the tip of a 6-ft flashpole. This was placed on the ground in front of flying males. In most cases, the LED was placed on mown grass near the edge of the coarse, herbaceous vegetation under overhanging boughs around the mowed area. When answered immediately after their pattern, males continued to emit their crescendo pattern (i.e., did not switch to a different FP, n=9). They emitted <4 more patterns while airborne, flew toward and landed 2-8 inches from the LED. With continuing answers, they walked toward the LED and eventually reached and stood upon it.

However, decoy response-flashes presented *during* crescendos were not long attractive (n=5). In one notable case the male landed 18 inches from the LED and after two more mid-crescendo answers, he took off; when he crescendo-flashed again and was answered correctly (n=2) he landed at 8 inches, and was attracted on foot, to stand upon the LED with 8 more correctly timed (post-crescendo) flashes.

Males of several species reduce the intensity of their flashes when they approach answering flashes—this reduces interference from competing males. One decoyed male perhaps revealed another simple tactic: he had flown to the ground 6 inches from the LED. Another male was overhead, 3 ft up and 6 ft over. After 30 sec the flying male had passed, and the approaching male (then) flashed another crescendo, 3 inches from the LED, having approached darkly. Other attracted males were noted to emit their crescendo FP at about 4-sec intervals during close approach. Perhaps the long pause of this resulted from the presence of a potential interloper, a suggestion easily tested experimentally with two flashpoles.

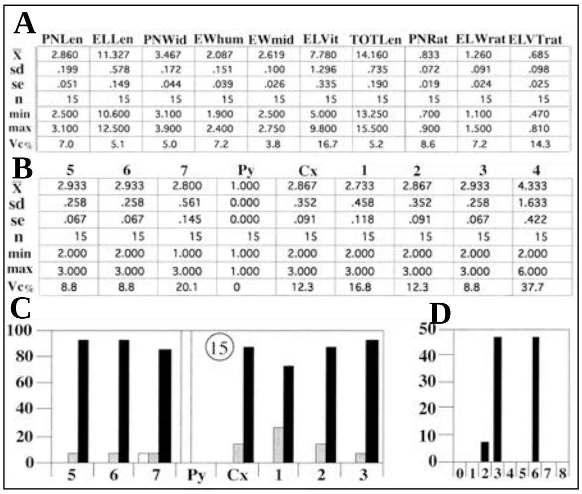
Adjunct FPs of several *Photuris* species bear resemblance to FPs of species that sometimes occur with them. The short flash of *asacoa* is not a precision copy of the co-active, probable prey species, *Photinus curtatus,* at the Little Paint Creek site (**Fig. 5, cf B & C**), but may be “good enough” and be or historically have been so. Flight/flashing activity of *asacoa* began about half way through the *curtatus* evening flight window tabulated at this site (**Fig. 6**).

Whether *Photuris* males become the prey of their own females and in particular of their own mates, is of some interest. The leg-raised position and external placement of the genital basal-piece filament noted during observed copulations (n=3) in *Photuris* may indicate an early warning-quick bailout/escape tactic. A perched *asacoa* male (#9060) emitting "twittery" flashes, was upon close examination found to have his aedeagus and a length of the spermatic duct extruded and dragging behind on the wet leaf (as noted in a *Photuris quadrifulgens* male at Appomattox VA). A few males have been observed completing copulation "normally", but such extrusion was not seen. Perhaps this *asacoa* male had barely escaped a turnabout cannibalistic (mate evaluating?) female.

A female was observed flashing while landing, with flashes est. 300 mSec in duration and at a period of est. 0.8 sec.

The beating wings of fireflies sometimes shutter their luminescence. Apparent wingbeats on one recorded *asacoa* crescendo show small sinusoidal waves riding atop wagging undulations, at a rate similar to that detected in other fireflies (47.6 Hz (20.0°/68°; **Fig. 5D**).

Morphological summary. Means are (n=15): PNL 2.9, ELL 11.3, PNW 3.5, EWhum 2.1, EWmid 2.6, ELVit 7.8, TOTLen 14.2, PNrat 0.83, ELWrate 1.26, ELVTrat 0.69 (**FigTable. 7A**, with other stats); colors in **FigTable 7B-C**, pre-lantern ventrite splash in **7D**. **Figure 9** is key for anatomical elements and splashing on ventrite 4. A range of vittagrams is in **Figure 8**. Figure 10 is a dot-dash flasher ("pensylvanica") of similar appearance.



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNRat	ELWrat	ELVTrat
$\bar{X}$	2.860	11.327	3.467	2.087	2.619	7.780	14.160	.833	1.260	.685
sd	.199	.578	.172	.151	.100	1.296	.735	.072	.091	.098
se	.051	.149	.044	.039	.026	.335	.190	.019	.024	.025
n	15	15	15	15	15	15	15	15	15	15
min	2.500	10.600	3.100	1.900	2.500	5.000	13.250	.700	1.100	.470
max	3.100	12.500	3.900	2.400	2.750	9.800	15.500	.900	1.500	.810
Vc%	7.0	5.1	5.0	7.2	3.8	16.7	5.2	8.6	7.2	14.3

B

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.933	2.933	2.800	1.000	2.867	2.733	2.867	2.933	4.333
sd	.258	.258	.561	0.000	.352	.458	.352	.258	1.633
se	.067	.067	.145	0.000	.091	.118	.091	.067	.422
n	15	15	15	15	15	15	15	15	15
min	2.000	2.000	1.000	1.000	2.000	2.000	2.000	2.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	8.8	8.8	20.1	0	12.3	16.8	12.3	8.8	37.7

Figure 7. Morphological measurements, ratios, colors.

IOWA: Allamakee Co.

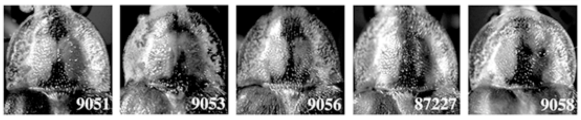


Figure 8.

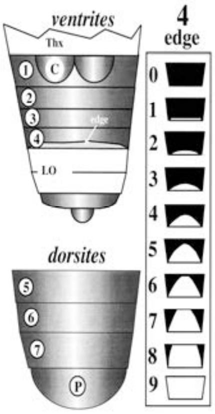
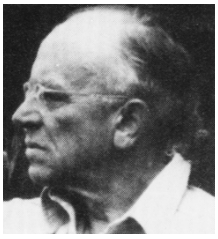


Figure 9.

Holotype: male, voucher number 87222, collected 19 June 1987, Allamakee County, Iowa, Yellow River State Forest, Big Paint Campground. FB page 8: "(2) KB 7—I ans short and he switch to crescendo!" Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 3.0, ELLen 11.5, PNWid 3.4, ELWhum 2.1, ELWmid 2.6, LELVit 9.0, RELVit 8.5, TotLen 14.4, PnRat 0.89, ElRat 1.24, VitRat 0.78; Colors: T 333, Py 1, Cx 3,V 333, Edg 6. Types will be deposited in the USNM.

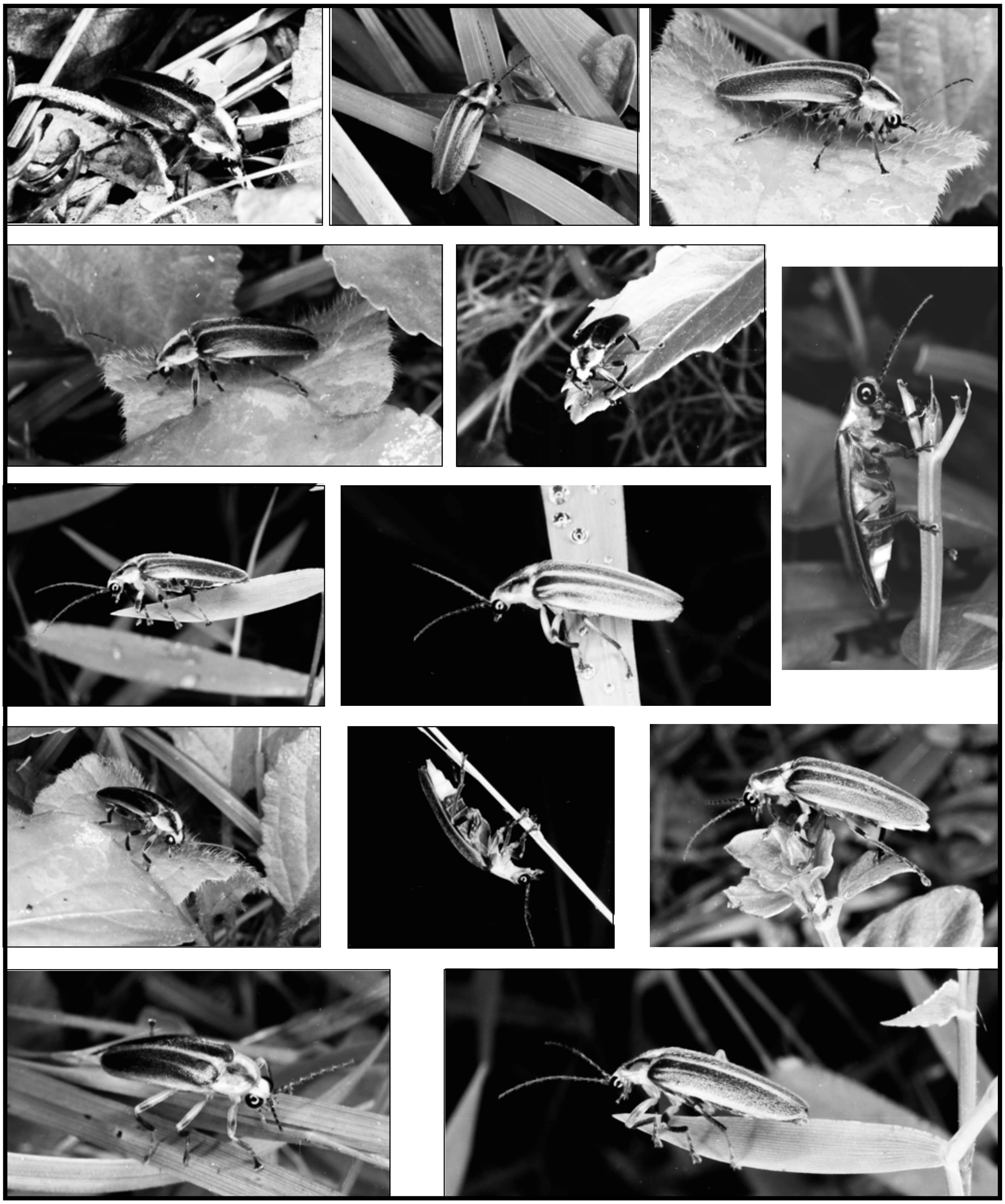
Taxonomic notes. The epithet is an acronym for Aldo Leopold's enduring observations on conservation, "A Sand County Almanac," and thought is quoted at the top of this chapter. His photo shown here appeared in the *Sierra*, Nov/Dec 1987, page 67.



Augmented figure legends. **4**. Period of crescendo FPs, measured and predicted (rate slope method), across a span of temperature. Line and open dots from period-to-rate conversions; M, measured period means. **5**. PM traces: **A**. Crescendo flash of a perched male showing a brief intensity dip near the end (20°/68°); **B**. Short flash of a flying male *asacoa* (20°/68°); **C**. Short flash of a *Photinus curtatus* male (18.9°/66°); **D**. Apparent wingbeats on a portion of the crescendo of a flying male, of 47.6 Hz (20.0°/68°); **E**. Crescendo flash of a perched male possibly showing a brief intensity dip near the end (20°/68°); **F**. Crescendo flash traced at a slower chart speed (25mm/s, 20.0°/68°). Bars indicate time scale; vertical axis, relative intensity. **6**. Evening activity profile of *P. curtatus*. Axes: number active/twilight time in creps. This (presumptive prey) firefly began activity more than 1 crep unit (=35 min) before *asacoa* began (18.3°-20.6°C). The lower curve is probably more typical.

Figure 10. A dot-dash flasher of similar appearance.

Soliloquising *Photuris* upon the grass at the old UF Med Garden. That *Photuris* fireflies perch and walk around blinking, and also "sit silently," has long been known. The three *versicolor* females the nephew of renown astronomer Herschel collected in South Carolina in the 1700s, and sent to his father in Germany, who then passed them along to Fabricius, who named them, were undoubtedly blinking on the ground, perhaps ovipositing; to collect otherwise would have been very difficult for a colonist with only an oil lamp or candle for illumination. When Barber took us to collect his *pensylvanica* he noted the blinking lights left in our wake through the deep marsh-grass (his p. 5, see 4 also). Illumination for egg-laying or predator deterrence is simple and obvious enough, but there is obviously more to *Photuris*' "hanging around" behavior. Both males and females do it, perhaps watching for prey or mate attractions to intrude upon, or to re-oxygenate muscles, to mention both proximate and ultimate explanations. This series of photos was taken mostly in 1974-75; some are "duplicates" of the same individual from a different angle, and most attracted attention by their blinking or glows. A number of experiments with LEDs could reveal hitherto hidden aspects of firefly behavior. Species shown are: *douglasae, harrannorum, lamarcki,* and *stanleyi*.



Chapter 13

Photuris aureolucens Barber 1951

A biosystematics project is never finished—
like an artist, the taxonomist finally stops …
(adapted from Picasso)

The two collectors of Barber's *aureolucens* Holotype series also provided him with his *caerulucens.* Information about them is in Chapter 20. They collected *aureolucens* in 1926 along a narrow berm and ditch and into the adjacent tamarack swamp near Bluff Siding, Buffalo County, Wisconsin (**Figs. 1, 2**). They took me to their sites in 1970. Barber recorded the following about the flashing of *aureolucens*: "… information kindly supplied by the collectors states that this species emits a single, short, yellowish flash not to be distinguished from that of *Photinus castus* [=*marginellus*, but possibly *curtatus* in Wisconsin], and flies about the tops of tall weeds in marshy ground, appearing in the dusk before *caerulucens*, with which it occurred but from which it is conspicuously different in the color and the duration of the flash." Barber was unable to find reliable morphological characters to distinguish the two *Photuris*. From data presently available Barber's *aureolucens* presents an interesting and unresolved prospect, and is retained as a named entity.

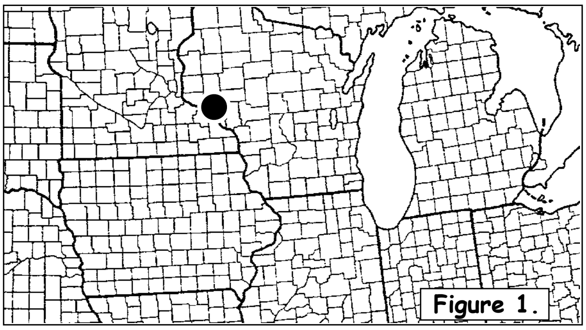


Figure 1.

Figure 2. Tamarack swamp locality near Bluff Siding WI, 1970.

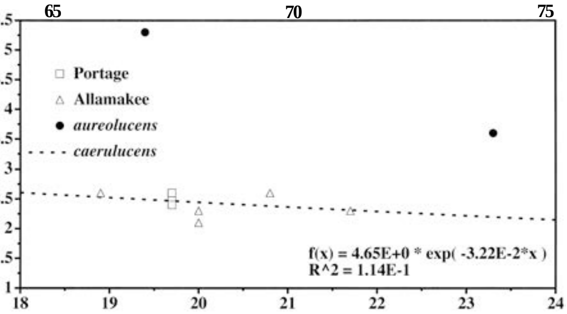


Figure 3. Mean FP periods, note species difference (AX: sec/temp).

Because this firefly so uncomplicated in behavior and not to offer difficulties or new and significant perspectives, only sketchy notes and observations were made. Later, when the possibility that *aureolucens* males might have defaulted to the long flash had they been asked to do so, that is, might actually be *caerulucens*, notes were reexamined, and these would indicate that *aureolucens* **is not** a twilight short-flashing *caerulucens*. Had defaulting behavior been known at the time and experiments made some of the following would be superfluous. Note underlined indications …

Flashing, ecology. Short-flashing *aureolucens* became active 15 and 23 minutes earlier(!) in the evening than resident *caerulucens*, and flew in slow hovering flight just above the tips of the grass and herby vegetation, flying 3-4' between flashing positions. The FP was about as Barber related and emitted each 3-5 seconds of flight (nr 21°/70°; **Fig. 3**). Males remained active well past twilight for two or more hours(!). A noted interaction from the fieldbook: "*aureolucens* [male] got answer [no default noted]—dropped down & landed—female flew in near male. (a different female?) could find her but not male." Bear in mind that *aerolucens* males were identified as such because they had emitted single, short flashes—in one case it was noted "single at 2 sec counted," an interval far too short according to **Figures 3** and **4**.

Freshly cyanide-killed, glowing males of short flashers (presumptive *aureolucens*) and long flashers (presumptive *caerulucens*, one from Stockton, MN and one from the *aureolucens* site) were viewed in the field and the short flashers appeared yellow by comparison—this comparison was made by two sets of eyes, the others, those of a biology student from a local college.

Perspective. Another interesting prospect for future examination involving this and other *Photuri* is the occurrence of short-flash-only populations around the periphery of North America's continental core with its extravagant flashers—those with crescendos, multiple-pulse FPs, adjunct FPs with and without defaulting, prey-matching FPs, flickers, and most importantly and especially, several predaceous, neurologically-athletic females that specialize on mate-seeking males. Perhaps *aureolucens* is as a peripheral isolate living on the northern Canadian edge, in a more tolerant and less complex environment?

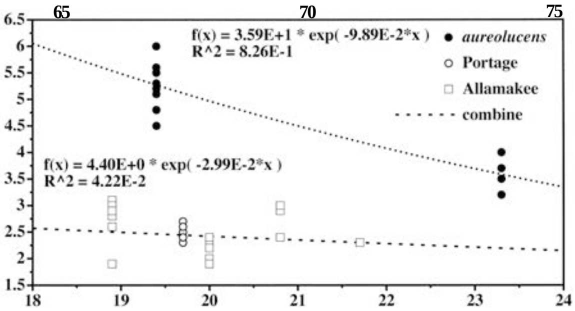
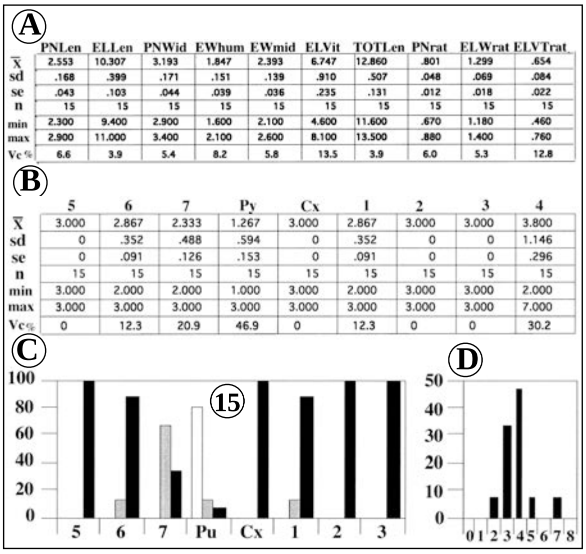


Figure 4. Single FP periods of individuals (sec/temp).

Morphological data. General morphological means: (n=15, WI): PNL 2.6, ELL 10.3, PNW 3.3, EWhum 1.9, EWmid 2.4, ELVit 6.8, TOTLen 12.9, PNrat 0.80, ELWrat 1.30, ELVTrat 0.65 (**FigTable 5A**). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae and splashing on ventrite 4 are shown numerically in **FigTable 5B**, graphically in **5C** and **5D**. **Figure 6** is topographic and splash (ventrite 4) guide. A range of vittagrams of *aureolucens* is compared with those of *caerulucens* in **Figure 7**.



Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.553	10.307	3.193	1.847	2.393	6.747	12.860	.801	1.299	.654
sd	.168	.399	.171	.151	.139	.910	.507	.048	.069	.084
se	.043	.103	.044	.039	.036	.235	.131	.012	.018	.022
n	15	15	15	15	15	15	15	15	15	15
min	2.300	9.400	2.900	1.600	2.100	4.600	11.600	.670	1.180	.460
max	2.900	11.000	3.400	2.100	2.600	8.100	13.500	.880	1.400	.760
Vc %	6.6	3.9	5.4	8.2	5.8	13.5	3.9	6.0	5.3	12.8

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	2.867	2.333	1.267	3.000	2.867	3.000	3.000	3.800
sd	0	.352	.488	.594	0	.352	0	0	1.146
se	0	.091	.126	.153	0	.091	0	0	.296
n	15	15	15	15	15	15	15	15	15
min	3.000	2.000	2.000	1.000	3.000	2.000	3.000	3.000	2.000
max	3.000	3.000	3.000	3.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	12.3	20.9	46.9	0	12.3	0	0	30.2

FigTable 5. Measurements, ratios, color.

Taxonomic and other notes. Barber obviously named this firefly "yellow light" from the description the collectors had given him. Though the bioluminescence apparently is slightly yellower than that of certain other *Photuris*, and in particular that of *caerulucens*, it is not as yellow as that of the *Photinus* they compared it to, 554 vs. 564 mmicrons.

Adjunct figure legends. **3**. Short-flash FP periods of *aureolucens* compared with short flashes of *caerulucens* (sensu lato) from two other sites. Unfortunately periods of short flashes were not measured in MN/WI *caerulucens*. Values shown are **means** of SWAT measurements of several males. **4**. Short-flash FP period of *aureolucens* with those of *caerulucens* from two sites—none were measured for WI or MN populations. Single interval measurements show the range of variation as males fly near the vegetation and probably adjust their flashing according to what they see. **FigTable 5**. Morphological data: (A) Basic measurements and ratios (rat); (B) Colors of abdominal ventrites and dorsites (see Fig. 6); (C) Histogram of sclerites (5-3) numerically quantified in B (n=15; (D) Histogram showing degree of pale splash on hind margin of visible ventrite 4. **7**. Comparison of pronotal vittagrams of *aureolucens* and *caerulucens*; note in particular that the rather uncommon inflected serif occurs in both arrays.

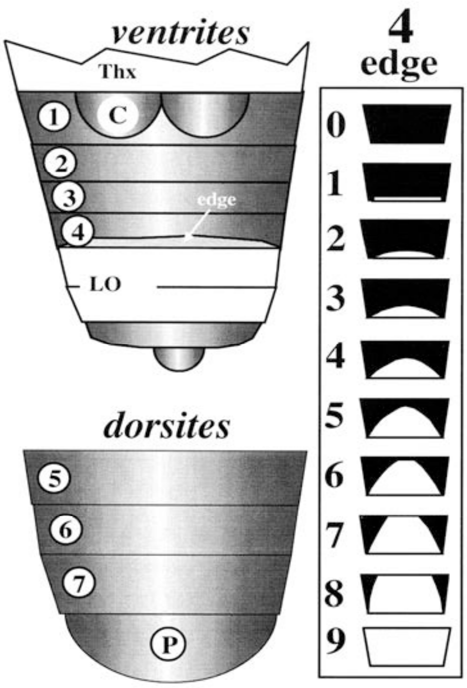


Figure 6. Topographic and splash keys.

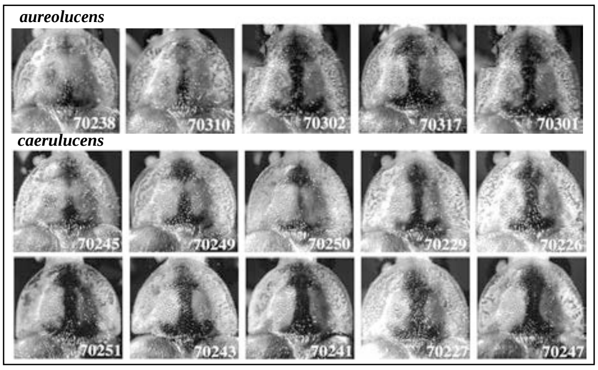


Figure 7. Vittagram syntopic comparison.

Chapter 14

Photuris barberi n. sp.

To be able to concentrate on the same matter for a considerable
time is essential to difficult achievement, and even to the
understanding of any complicated or abstruse subject.
Bertrand Russell

This firefly was found in disturbed areas at two sites in eastern Texas from 31 May to 3 June 1994 (**Fig. 1**). At one males flew 15 feet above ground along a narrow campground trail/roadway through a dense second-growth woods which began immediately at trail-edge. Trail-edge tree-lines rose sharply to 20 or more feet and reached over the roadway leaving a narrow flyway of about 15 feet. A few were seen flying along a lakeshore 100 yards distant at 10-20 foot altitudes and out from the shore about 30 yards where they briefly flashed around the crowns of small cypress growing there (**Fig. 2**). The other site was a roadside picnic area where they flew at the top of tall pines. It was nearly impossible to capture specimens; one voucher was obtained with a twenty-foot tropical net—when it missed and swept past high-flyers they stopped flashing and did not flash again in the same or adjacent space. Flashing was seen from 9 pm (CST) for two or more hours, in briefly increasing then decreasing numbers. Males emitted FPs consisting of 1–4 short flashes which were quickly followed first by a shorter then a followed a longer pulse, that is, a sequence of dots quickly followed by a rapid dot-dash (**Fig. 3**). The vittagram of the single voucher is distinctive (**Fig. 4**).

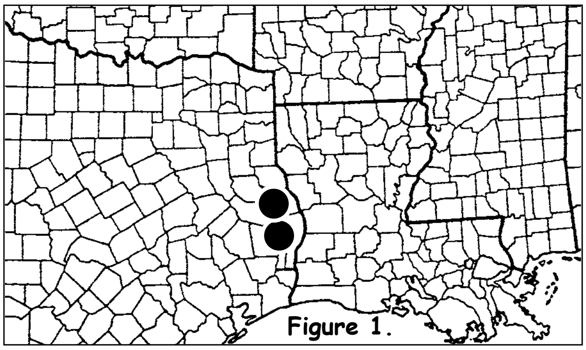


Figure 1.

Figure 2. FP targets.

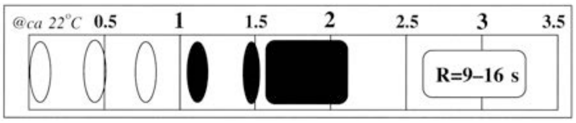


Figure 3. Flash pattern (intensity/time)

Flashing details. This firefly emitted a unique FP combining diagnostic elements of species in the (presumptive) *P. pennsylvanica* and *P. versicolor* groups. Its flash pattern begins with 1–4 pulses similar to those of *quadrifulgens* and ends with an electric dot–dash like that of *hiawasseensis* (**Fig. 3**). The preliminary dots *appeared* to have a duration of about 130 mS with rates near 2.5 Hz (nr 22°/72°). Dashes appeared to be about 500 mSec in duration, with a sharp ON and OFF, and to follow the terminal dot more quickly than dots succeeded dots—that is, the pause between the last dot and the dash resulted in a pattern ending with the appearance of a short "electric wink" in conspicuous contrast with previous pulse successions. The spoken phrase one–two–kerchoo) simulates the rhythm of a 3-dot + 1-dash pattern. This FP resembles one seen in a Jamaican *Photinus*, though simple pulse combinations occur in *dorothae, pennsylvanica*, and *hiawaseensis*. Males were not attracted to a variety of decoy flash-responses presented from overhanging boughs with the flashpole.

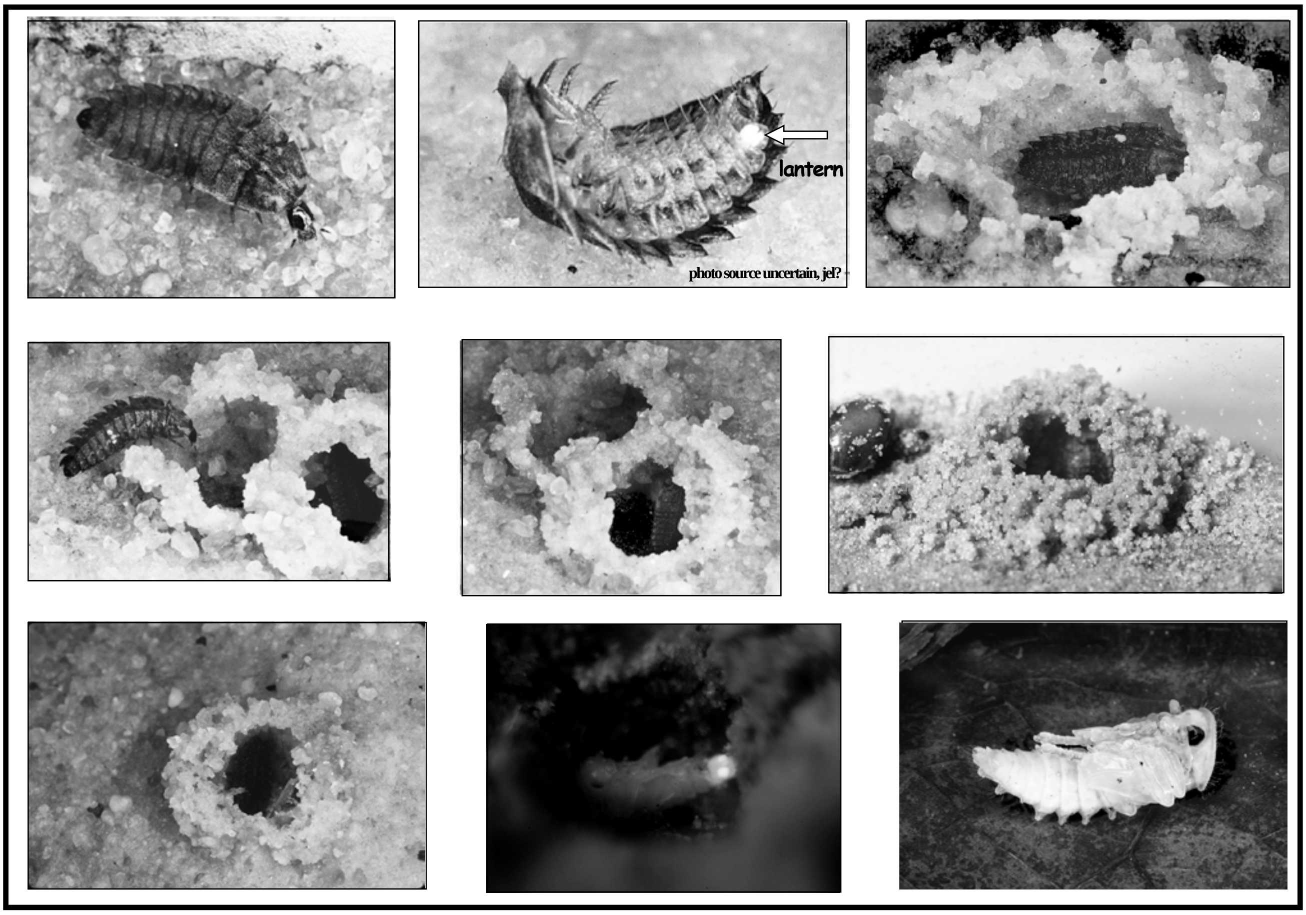
Taxonomic Notes. The specific epithet recognizes the pioneer of *Photuris* semiosystematic studies with an unresolved problem for the next *Photuris* addict, and is especially appropriate since the FP of *barberi* combines of two of the several FPs H. S. Barber significantly distinguished in his study.

Figure . 4. Holotype # 9474.

MiTab. FP Period. Jasper Co. TX. (counted) 1-VI-94, 22.3°C: 10 [sec], 15. 3-VI-94, 24.4°C: 9–16 sec. **Pulse Period.** (SWAT) 1-VI-94, 22.3°C: .35/1 [.35 sec per 1 per], .4/1; x=2.7 Hertz. 3-VI-94, 24.4°C: 1.2/3, 1.3/3, .65/2; x=2.6 Hertz.

Holotype description. The single voucher, male, voucher number 9474, collected 3 June 1994, Steinhagen Lake, rt 190, Jasper Co. Texas. Fieldbook notes: "KB 4 9474 versi-penn flash had net extended all the way. At 10:17" Aedeagus partially extruded. From spread sheet—PNLen: 2.5, ELLen 9.1, ELWhum 1.6, ELWmid 2.4, LELVit 0, TotLen 11.6, PnRat 0.83, ElRat 1.46, VitRat 0; Colors: T 322, Py 1, Cx 3, V 333, edg 7. Holotype will deposited in the USNM.

***Photuris* life history**. *Photuris* eggs are laid in the soil. Some species may deposit them in one place, but in other species they probably are placed in several sites. Shown are juveniles, larvae and pupae photographed in the lab. Larvae of some species make sand igloos at the soil horizon to change from one larval stage to the next, and dig chambers underground to metamorphose to adults. (See Buschman's study for details.) Pupae retain larval lights and will light up if disturbed in their digs. A pupa found between layers of damp leaves in a road/treeline ditch in Polk County, Tennessee, apparently made no igloo. Unlike certain *Pyractomena* pupae that are pigmented and concealed against the tree bark where they hang, *Photuris* pupae are white, and out of sight—economics?



Chapter 15

Photuris beanii n. sp.

Bean's Firefly

This firefly is presently known only from sites in Levy County, in northwestern peninsular Florida southwest of Bronson along route 24 (**Fig. 1)**, a region of mixed-hardwood swamp forests. The raised causeway that is route 24, from Otter Creek almost to Cedar Key provided access to more than 25 miles of this habitat, and in season the flashes of *beanii* could be seen in the hundreds over and around the crowns of the trees, which as a gallery forest bordered the causeway (**Fig. 2**). Toward the Gulf end of this highway, with higher elevation and the arid, scrubby ecology of old dunes, small numbers occurred in isolated depressions at culverts and ditches (**Fig. 3**). Identification requires observation of its crescendo FP (**Fig. 4**), one of the "two" FPs *beanii* is known to emit, though more than two definitive FPs may actually be involved (1-pulse, 2-pulse, crescendo). Identification is certain if defaulting from the short-flash FP to the crescendo is observed or caused via simulation of a female response flash (**Fig. 5**). Adult activity begins in mid April and may continue until early September (**Fig. 6**). As a summary of useful diagnostic field characteristics: (**1**) sequences of (typically non pumping) moderate crescendos that are given in typically lateral flight, and resemble the flashes of *Photuris lamarcki* but are brighter and without lantern modulation (except wing shuttering, **Fig. 11**); (**2**) the presence of short flashes at <±2-sec periods, commonly high in tree crowns and crossing spaces between them, commonly occurring with the crescendos described; (**3**) the general absence of unsolicited (non-default) crescendo *groupings* by nearly stationary, poising/pumping males as described for *P. carrorum* and *P. whistlerae*.

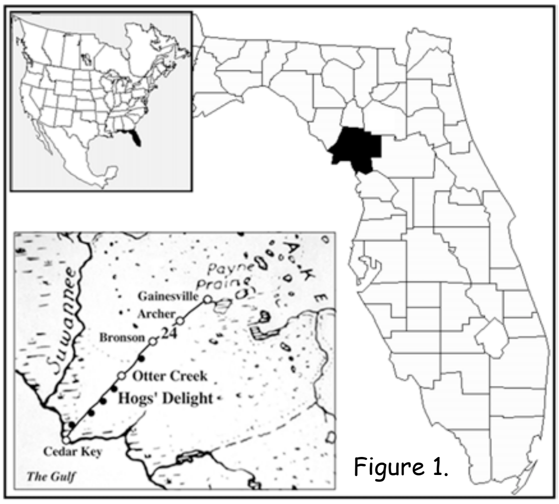


Figure 1.

Figure 2. Route 24, at Hogs' Delight.

Flashing behavior, ecology. The primary observation site (Hogs' Delight) was about 5 miles southwest of Otter Creek, on the backside of the gallery, at the edge of a shrub-overgrown pasture where sweetgums, sugarberry, and various other hardwoods of the gallery formed a backdrop (**Fig. 5**). Access was via an overgrown tunnel through the gallery. Evening flight began about the end of CT (1.1-1.3 creps, n=3).

Males emit two distinctive flash types, one a single short flash and the other a short crescendo flash (**Fig. 4**). Short flashes are often emitted in pairs forming 2-pulse FPs, of varying interval. Possibly only short flash FPs are emitted for the first 20 minutes of evening activity—that is, there may be a characteristic/ routine nightly FP profile in the appearance of short and crescendo flashes. The crescendo flash is the default pattern, and was first noted at 1.8–1.9 creps (n=2) and was more common later (3.4 creps). Crescendo flashes are emitted in long continued sequences but apparently also/rarely? in short groups by roving/patrolling males. In many trials, when short flashing males were answered with a decoy if they approached to 2-3 feet, with one questionable exception, they defaulted to the crescendo FP. Attracted crescendo males continued to emit crescendos, and at close range, in a short, swooping upward motion (pumping, **Fig. 5**). When males were attracted to a decoy, other males sometimes also approached the decoy, emitting the crescendo pattern. Only one of several prospective interlopers observed emitted a short flash—and once a short-flashing "interloper" was a female—hawking?

The crescendo pattern is emitted at temperature dependent periods ranging from about 2.7 sec at 17˚/ 62.6° to 1.7 sec at 25˚/ 77° (**Figs. 7,** rate in **8)**. Estimated crescendo duration ranges from ca 330 mSec at 21˚/ 69.8° to 250 mSec at 25˚/77°, based on inspection of 104 PM-recorded crescendo flashes, of which about half were of reasonably good quality. Visually, in action/appearance, this FP falls between those of *lloydi* and *lamarcki*. Crescendo form varies in better records, from a presumptive ideal, a log-like rise, to a flat ramp. When crescendo flashes are emitted males sometimes fly a 1-foot lateral swoop, slowing or stopping at the end. This movement emphasizes (to my eyes) the crescendo appearance and sharpens the abrupt OFF transient.

Figure 3. Culvert site near Cedar Key.

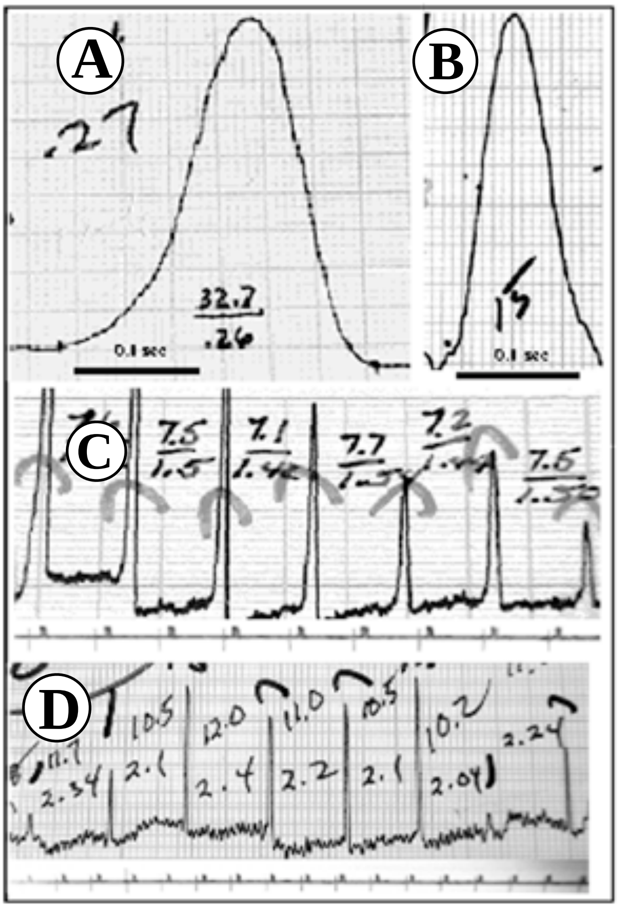


Figure 4. PM records (AX:rel.int/time).

Figure 5. Approach, then default pumping (a sketch).

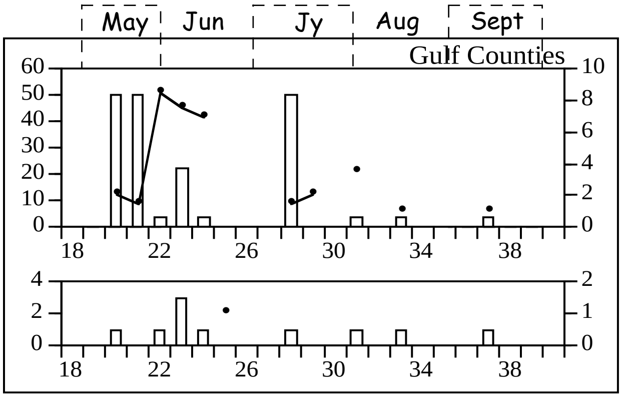


Figure 6. SESOBS.

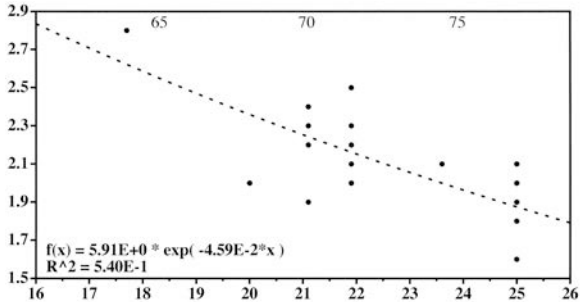


Figure 7. Crescendo FP period (AX:sec/temp).

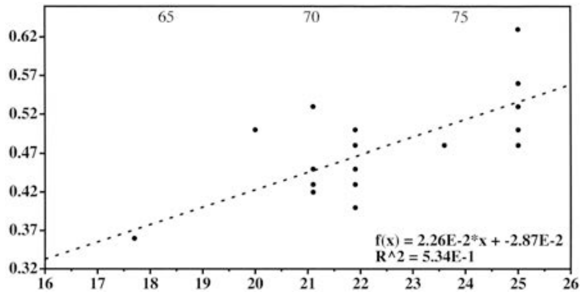


Figure 8. Crescendo FP period rate (AX:sec/temp).

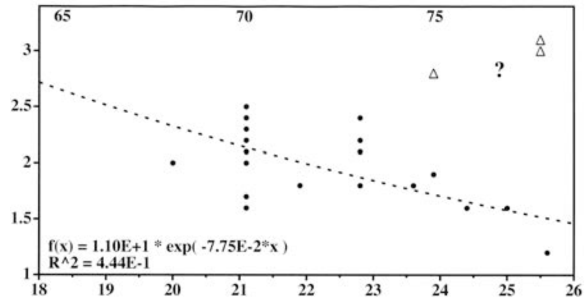


Figure 9. Short flash FP period (AX:sec/temp).

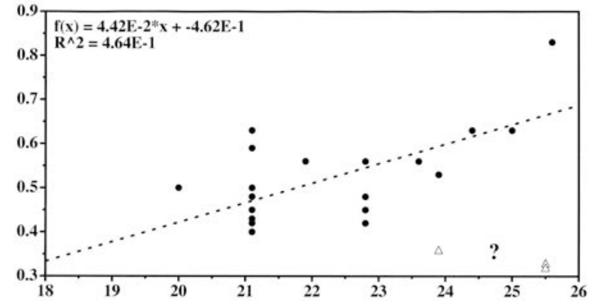


Figure 10. Short flash FP period rate (AX:sec/temp).

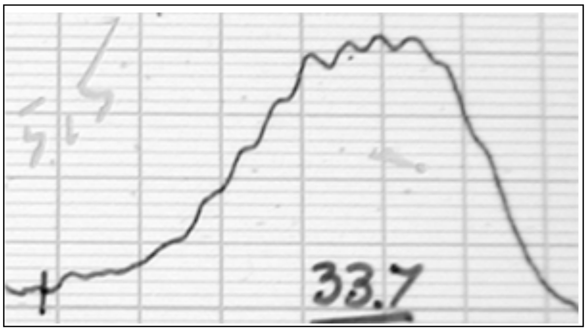


Figure 11. Wingbeats over crescendo (AX: rel.int./time).

Short flashes are emitted at mean temperature dependent periods ranging from about 2.4 sec at 17˚/62.6° to 1.2 sec at 26˚/78.8° (**Figs. 9,** rate in **10**). However, this flash period summary disregards the probable presence of two or more distinctive (programmatic or copied) 2-pulse FP periods—and consequent pause interval variation. That is, the regression probably incorporates short flash intervals from several contexts—including timings perhaps matching that of one resident *Photinus* (*greeni-macdermotti* complex). *P. beanii* males possibly adjust their FP periods on the basis of observed FPs in their site; at Hogs' Delight *Photinus* species in the mentioned complex were present with confusing variations in their FP pulse-period timings, perhaps part of coding countermeasures against tracking *Photuris*? Tim Forrest and I have both noted at least an occasional pairing of *beanii* short flashes resembling the FPs of the mentioned *Photinus* complex. Similar pairing also occurs in *Photuris branhami* (*whistlerae*-group variads) found in this region of Florida.

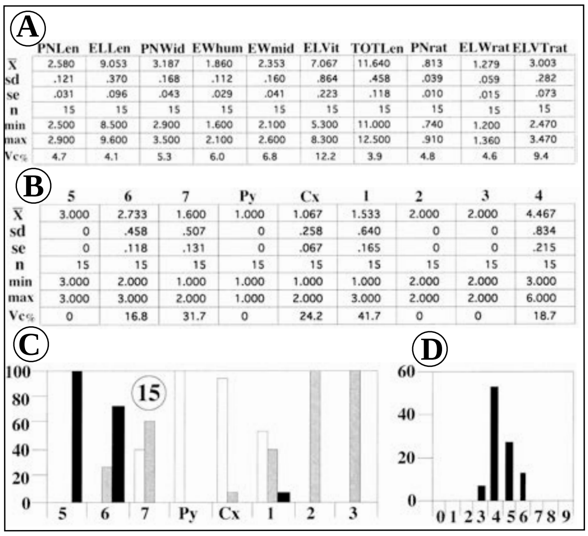
The mean estimated flash duration ranges from ca 70/140 mSec at 21˚/69.8° to 45/115 mSec at 26˚/78.8°, based on an inspection of 73 PM-recorded short patterns, of which about three-fourths seemed to be of suitable quality.

Decoying and Default Switching. Several males were attracted toward a flashpole decoy by emitting a short (<0.3 s) flash about a half-second after their patterns. Males that were emitting short flashes changed to the crescendo pattern at a range of 2-15 feet (n=>20). Often males emitted their crescendos in pumping flight within a yard of the LED, which was usually placed on the leafy crown of a shrub (**Fig. 5**). When males approached the decoy they sometimes emitted dimmer flashes, and when they switched they sometimes (n=4) appeared to emit dim "longer" flashes. Occasionally males landed in foliage, and approached by hopping/flitting through it. When crescendo flashing searchers were decoyed, they continued to emit the crescendo FP.

In PM–records of a few crescendo flashes there appear ripples interpreted as shuttering of the wings passing between the firefly lantern and the PM-tube. In one male the frequency ranged 55.7–57.7 Hertz, n=4 flashes, @ 24.4°/75.9°; in another male it was 55.8 Hz, n=1, @ 21.9°/71.4°; and another was 54.3 Hz, n=1, @ 25.6°/78.1° (**Fig. 9**). Curiously these rates are near that of electric lights but the site was miles from any artificial illumination other than head lamps and LEDs.

Research notes: (**1**) This species is a consummate aerial attacker, and should be a good subject for examination of the significance of the P1-P2 interval for attacker avoidance in members of the *Photinus greeni-macdermotti* complex. The Hogs' Delight study site is the most inland Florida locality presently known for fireflies now known (collectively) as "*Photinus greeni*." (**2**) The taxonomic relationship of *P. beanii* to other members of the *P. lucicrescens* group and in particular to *P. lamarcki* is of special interest because of its (i) unique default-switching, (ii) possible ad-hoc pattern-matching, and (iii) perhaps superficial but at least suggestive similarities to *P. lucicrescens* (short & crescendo patterns) and *lamarcki* (continuous-crescendo phrasing, and "eager" aerial hawking). (**3**) As a member of what seems to be a north-Florida *lucicrescens* species-swarm, *beanii* should be of interest for DNA analysis.

Morphology. General morphological means are (n=15): PNL 2.6, ELL 9.1, PNW 3.2, EWhum 1.9, EWmid 2.4, ELVit 7.1, TOTLen 11.6, PNrat 0.81, ELWrate 1.28, ELVTrat 3.0 (**FigTable 12A**, with other stats). Data for the colors of various apparent abdominal plates (sclerite combinations) and hind coxae are shown in **FigTable 12B-C**, and splash of the pre-lantern ventrite, in **12D**. **Figure 13** key to skeletal plates and degree of splashing on ventrite 4; array vittagrams in **Figure 14**.



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	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.580	9.053	3.187	1.860	2.353	7.067	11.640	.813	1.279	3.003
sd	.121	.370	.168	.112	.160	.864	.458	.039	.059	.282
se	.031	.096	.043	.029	.041	.223	.118	.010	.015	.073
n	15	15	15	15	15	15	15	15	15	15
min	2.500	8.500	2.900	1.600	2.100	5.300	11.000	.740	1.200	2.470
max	2.900	9.600	3.500	2.100	2.600	8.300	12.500	.910	1.360	3.470
Vc%	4.7	4.1	5.3	6.0	6.8	12.2	3.9	4.8	4.6	9.4

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.733	1.600	1.000	1.067	1.533	2.000	2.000	4.467
sd	0	.458	.507	0	.258	.640	0	0	.834
se	0	.118	.131	0	.067	.165	0	0	.215
n	15	15	15	15	15	15	15	15	15
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000
max	3.000	3.000	2.000	1.000	2.000	3.000	2.000	2.000	6.000
Vc%	0	16.8	31.7	0	24.2	41.7	0	0	18.7

Figure 12. Measurements, ratios, splash.

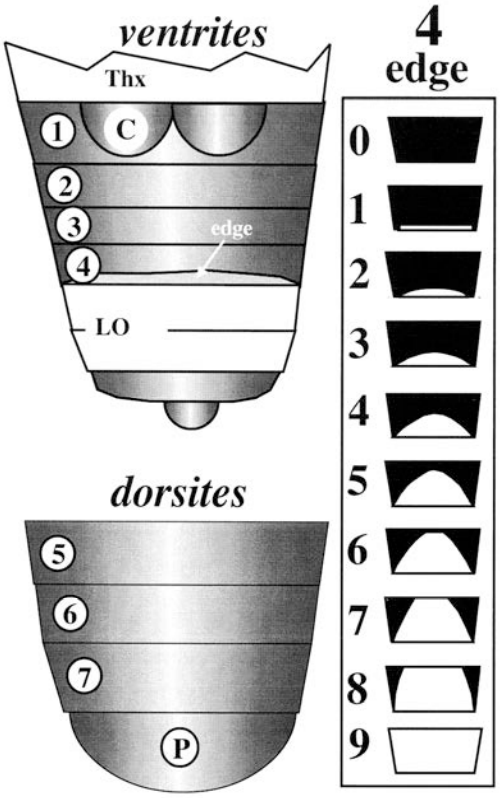


Figure 13. Key to sclerites, splash.

Holotype description: male, voucher number 83259DF, collected 17 July 1983, Levy County, Florida, Route 24, about 5.5 miles southwest of Otter Creek, on back side of tree row on se side of highway. Fieldbook page 61: "KB 64—single attr [attracted] to pl [penlight] in bush—he switched to a cresc [crescendo]. his intervals got longer as he appr [approached], his light dimmed o then to cresc, he moved back and forth during cresc." Morphological data from spread sheet: PNLen 2.6, ELLen 9.0, PNWid 3.3, ELWhum 1.9, ELWmid 2.3, LELVit 7.3, TotLen 11.6, PnRat 0.81, ElRat 0.83, VitRat 0.83; Colors: T 321, Py 1, Cx 1, V122, Edg 4. Types will be deposited in the USNM.

Taxonomic Note. The specific epithet and common name honor the memory of a faithful and best friend, research associate, guardian, and companion, who watched fireflies with me for a decade, between 1982 and 1992, and scarcely missed a firefly field trip from Baddeck, Nova Scotia to Shell Mound, Florida to Little Paint Creek, Iowa, until failing health brought our long partnership to a close.

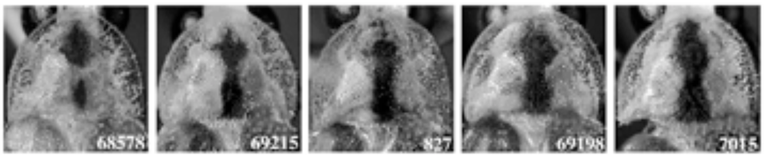
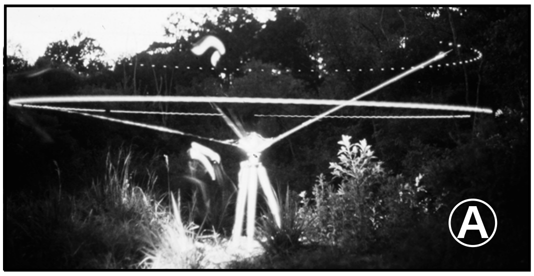
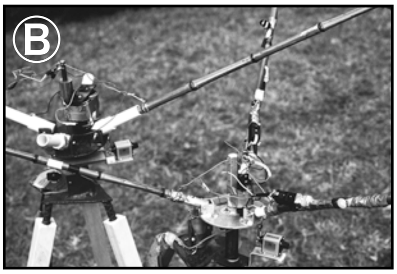


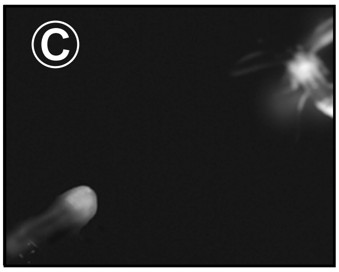
Figure 14. Vittagram array.

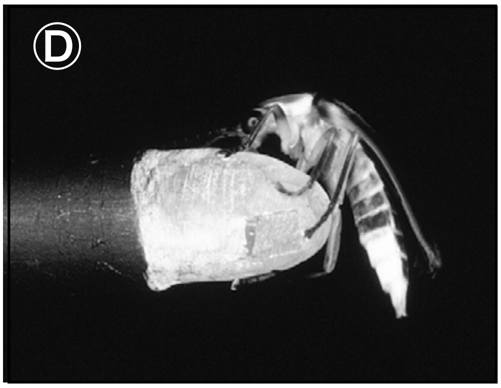
Adjunct figure legends. 4. PM-recordings of *P.beanii* FPs: A. crescendo flash, 18 July 1983, @ 25.0°/77°, 125mm/sec, bar 0.1 sec; B. short flash, 18 Jun 1980, @ 21.1°/70°, 125mm/sec, bar 0.1 sec; C. series of crescendo flashes, 15 June 1969, @ 24.4°/76°, 5mm/sec, 1-sec markers; D. series of short flashes, 18 June 1980, @ 22.8°/73°, 5mm/sec, 1-sec markers. **5**. View on the inner (southern) side of the roadside gallery near Hogs' Delight, showing (sketched-in) cruising short and crescendo FPs; across the center from right to left a short flasher is attracted to responding (larger) flashes from the bush and defaults to pumping crescendos. The actual Hogs'Delight site was not identified on a recent hasty visit—more than 25 years of growth have concealed original recognition markers. **7**. Crescendo flash–pattern period as it changes with ambient temperature. The dashed line is a prediction from the technique described in M&T. The broad variation of means is not surprising and (yet) tell us nothing as to whether the flash pattern period itself may convey information, or be a utilitarian adjustment to environmental circumstances (e.g., vegetation, rivals, predators). **9**. Short flash–pattern period as a function of ambient temperature—and other unknown but key variables. Dots are means of a given set of measurements at a single place/date/temperature. The dashed line is a prediction from the technique described in M&T. The broad variation of means is not surprising and is seen in males of many fireflies, however, in this species there is a reason to take special note: the enigmatic variation of flash-pairs described for Florida members of the *Photinus consanguieus* Group, coupled with similar variation in members of the P*hoturis cinctipennis* complex, caution against facile dismissal of such timing variations as observed here. In particular, the most extreme flash-pair variation of the *Photinus* mentioned were seen in this Hogs' Delight site. Adding to the confusion: (1) there are other short–flashing *Photuris* species in the area, and (2) even with voucher specimens doubt is not necessarily assuaged, since morphological similarity and near-identity is be anticipated. Finally, the three triangles are legitimate and puzzling records of short flashes at the site. **11**. Chart record of a PM-recording of a crescendo flash pattern emitted by a single male, with presumed shuttering of wing superimposed, @25mm/sec. Wing-beat frequency on this flash trace is 57.6 Hertz (cps; @24.4°C); see text).

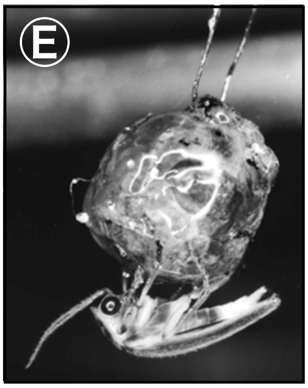
Aerial attack experiments. Over many years when attracting a firefly to a decoy penlight flash, a female *Photuris* would land on the hand, head, or shoulders. Suspecting that they were attacking the light this was tested with "flying" illuminated targets. First, LEDs in plastic capsules were placed at the tips of three bamboo poles (**A**) that were rotated around a hub (**B**) , powered by a slow, high-torque motor. One target glowed, one flashed, and one was OFF, as a control. All were coated with a sticky, foot-tangling "grease." Females attacked the glowing target (**C**), were caught (**E**), had their feet wiped clean and were released. After two or three captures at a site it was apparently "fished out." Next a bamboo pole with an LED inside a dangling, sticky, spherical bead (to provide equal illumination in all directions), was carried slowly along a row of bushes and flashed each 2-seconds (**F**)— composite photos in (**F**) show collaborator Steve Wing with the flash pole, a time exposure of flashes carried along the bush-row with city lights in the background to silhouette the action, and an attacking female on the illuminated bead. Finally, a male *Photinus* was threaded on a bendy, slippery wire below a naked LED (**G**), and this decoy was presented along the bush-row. An LED-attacking female found and began eating the male (**G**), as had been expected, while holding the male, slid down the wire (H) and both went to the leaf of a plant below (**I**). On one "run" two females attacked, fought jaw to jaw (**J**), until one worked down and severed her opponent's neck (**K, L**), and finally began eating at the loser's mid-section (**M**), enlarged in (**N**). See also color photos on pages 461-62.

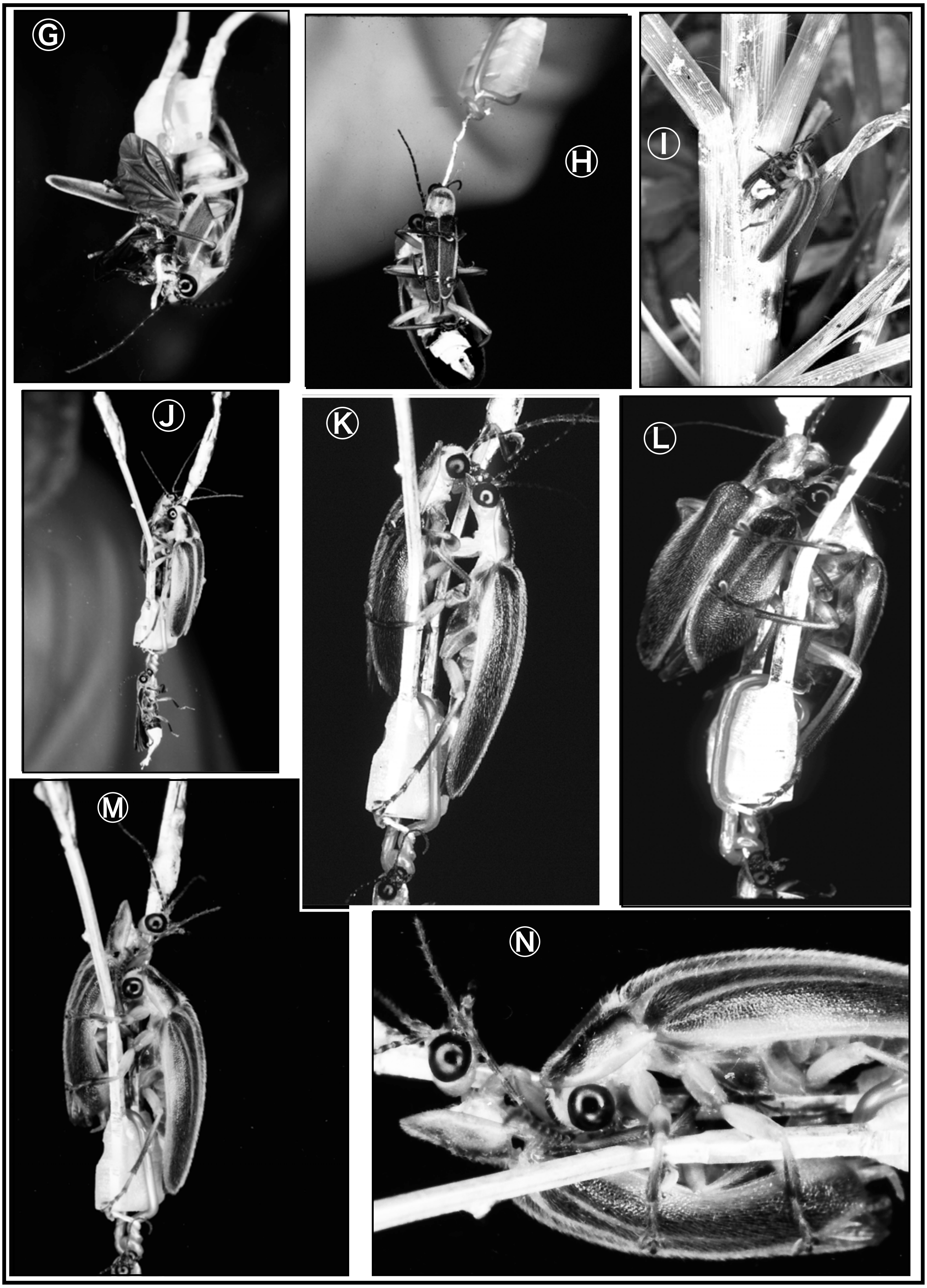











G
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Chapter 16

Photuris bethaniensis McDermott 1953

Frank McDermott described this firefly from Bethany Beach, Delaware (**Fig. 1**). From his paper: "… August 1949 … a very few instances of a double greenish flash were noted over grass in a large vacant area at the north end of the town and perhaps 1,000 feet from the ocean front. … black pigmentation on the pronotum different from any previously seen … earlier in the year nothing notable … July 1951 … again saw double green flash … differs from other photurids so far found in Delaware by the relatively small size, the distribution of the pronotal pigmentation [vittagram], and the rather distinctly different flash [FP] of the male. The pronotal black pigmentation, while rather variable, has a distinct tendency to be enlarged toward the apical margin, and in none of the specimens did this spot show the forms characteristic of those of *P. versicolor, P. lucicrescens* Barber, 1951, or *P. hebes* Barber, 1951 [species potentially confused at the time] … [the FP] much like that of *Photinus consanguineous* LeConte, 1851, two short, bright coruscations separated by a distinct interval perhaps somewhat longer than that of a single coruscation, but is quite greenish as compared with the yellow light of *consanguineous*. Occasionally the second coruscation may be much less bright than the first, even with the same specimen, and a few gave only a single flash but were [morphologically] indistinguishable from those giving the double flash." Other data: date first seen, 11 July, but two days later a "large colony"; about 2 miles south of town, bayberry both sides of town; not found inland, "seems to be a rather strictly seacoast, almost a sand-dune, form." Small, 9.0-10.75 mm; 3.5-4 mm wide; Type and paratypes, USNM 61469.

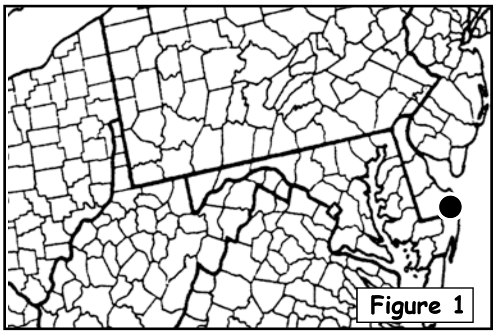


Figure 1

Observations offered here are generally in agreement with those of McDermott, but there exists some uncertainty because the 1-flash FP **period** as recorded here appears to have two modes, as noted for the single-flash coastal forms *Photuris* ("*salina* et al"; **Fig. 2**). (McDermotti did not report the FP periods of his specimens.) Measurements (of single flash FPs, not flash pairs) were made at populations along the road within a few miles of Bethany Beach; all of the several vouchers have the diagnostic PN vitta as described by McDermott. Many individuals flashed from perches and those that flew were often blown in gusts of wind, but the FP difference does not appear to be related to either circumstance. FP period measurement data are: x=2.5, range 2.1-3.0, n=12, 23.3°/74°, 29 June 1968; x=3.1, range 3.1-3.3, n=5, 24.7°/76.5°, 15 July 1968; x=2.1, range 1.8-2.4, n=4, 24.7°/76.5°, 15 July 1968. These are plotted with data from the coastal single-flash samples (**Fig. 2,** tiny dots with arrows).

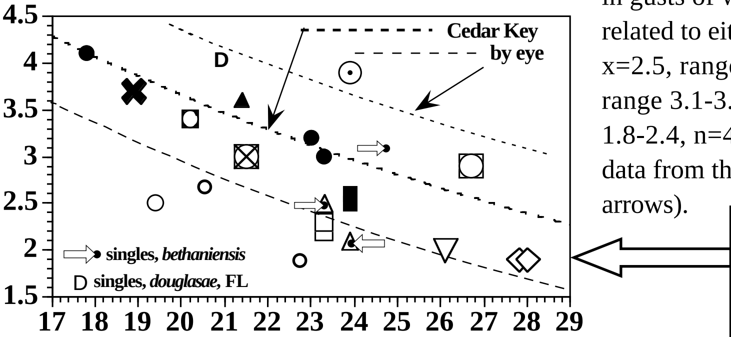
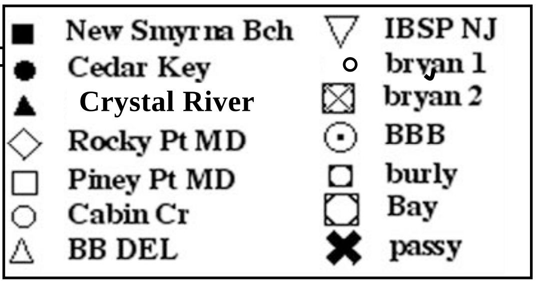


Figure 2. FP periods of coast singles (salina-like) and *bethaniensis* (AX: sec/temp). (see *salina* section)



The broad PNV is distinctive and similar to that of *Photuris douglasae* in Florida. This coupled with its central Atlantic coastal, even sub-beach occurrence and dark hind-coxae should be sufficient to identify this species. The only species noted flying in the area was a *Photuris salina* (*sensu lato*). *Ph. bethaniensis* in a strict sense is known only from Delaware though it is appears to be closely related to a coast-inhabiting population seen in Berkeley County, SC, and most particularly to *Photuris douglasae*, a more versatile flasher and the most abundant species occurring throughout Florida. In this it compares with the beach cricket, *Gryllus firmus*, which in Florida occurs broadly inland, throughout the peninsula—to some orthopterists Florida is all beach.

Ecology-flashing. The "primary" observation site was on the lagoon side of the highway near a parking area. The vegetation was of various grasses, burrs, a sedge, and small *Baccharis*. Males flew at full darkness, 3-5 feet above ground, occasionally below tips of vegetation, and emitted 1- and 2-pulse FPs. Those emitting the double flash flew more quickly than those emitting 1-flash FPs, and many flashed from perches. Males were strongly phototactic and when a beam was shone on them they darted quickly toward it. Individual flashes “looked peculiar” and sometimes they may have some substructure that was not resolved by eye (at 25°/77°). A female answered the flash of a perched male with a short flash at 1-1.5-sec delay.

This species is of special interest for two additional reasons: (**1**) populations at times emit only the single flash FP and without close attention (vittagram) will easily be confused with populations in the *salina* coastal-short set, though there appears to be a habitat ("type") difference; and (**2**), its unusual and diagnostic PN vittagram suggests that it may be related to *douglasae* in Florida, which has a similarly-timed 2-flash FP in its repertoire, and perhaps connected by populations that will reveal connecting behavior and DNA along the coast.

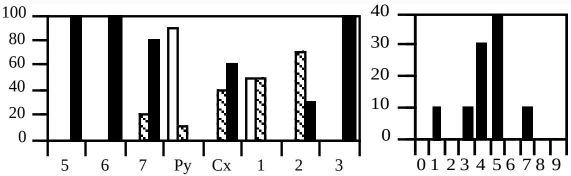
Morphology. Measurements, ratios, and sclerite color of a series of vouchers are shown in **FigTable 4**, morphology key in **Figure 5**; an array of *bethaniensis* PN vittae in **Figure 6;** in **Figure 7** a PN array of Bethany Beach "B" (BBB), enigmatic vouchers with a longer FP period and vitta that does not match that of either *salina* or *bethaniensis* (see **Fig. 2**); adjacent coastal regions "*salina*" vouchers in **Figure 8**; and a *bethaniensis* PN analysis histogram in **Figure 6**.

Ecological note. A *Google Earth*$^{©}$ view of Bethany Beach on 10 June 2015 (**Fig. 10**) revealed that there were none of the *bethaniensis* sites of McDermott or this study (1968) remaining/preserved; in fact, from the number of houses and people along and on the beach it was rather remarkable that neither McDermott nor jel observed/reported human procreative activity during their nocturnal visits to the area two generations ago.

bethaniensis DE

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.100	7.590	2.670	1.550	1.920	5.330	9.680	.784	1.234	.702
sd	.149	.448	.195	.118	.148	.678	.543	.032	.078	.078
se	.047	.142	.062	.037	.047	.215	.172	.010	.025	.025
n	10	10	10	10	10	10	10	10	10	10
min	1.900	6.900	2.400	1.400	1.600	4.000	8.900	.750	1.080	.580
max	2.300	8.300	3.000	1.800	2.100	6.300	10.500	.840	1.360	.820
Vc%	7.1	5.9	7.3	7.6	7.7	12.7	5.6	4.1	6.2	11.1

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	2.800	1.100	2.600	1.500	2.300	3.000	4.300
sd	0	0	.422	.316	.516	.527	.483	0	1.567
se	0	0	.133	.100	.163	.167	.153	0	.496
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	2.000	1.000	2.000	1.000	2.000	3.000	1.000
max	3.000	3.000	3.000	2.000	3.000	2.000	3.000	3.000	7.000
Vc%	0	0	6.6	3.5	5	2.8	4.8	0	2.7



FigTable 4. Measurements, ratios, colors.

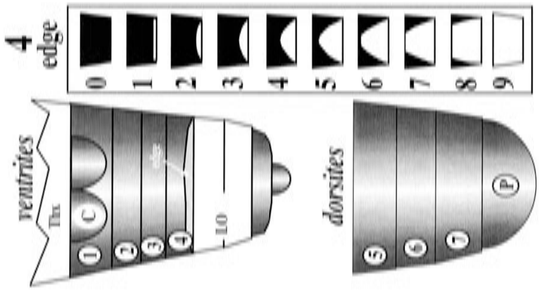


Figure 5. Topographic and splash key.

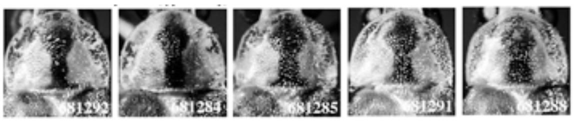


Figure 6. *bethaniensis* PN vittagram array.

Figure 7 PN vittagram array of Bethany Beach B (BBB).

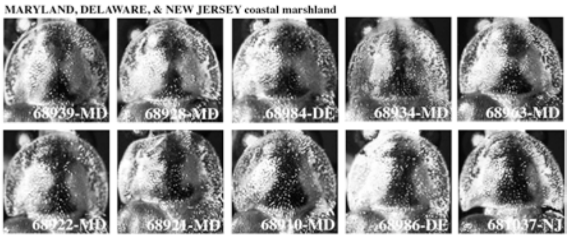


Figure 8 PN vittagram array/sampler of "*salina*" from adjacent coastal areas.

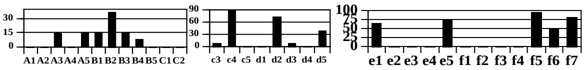


Figure 9. *bethaniensis* PN vittagram configurations, n=14.

Figure 10. *Google Earth*$^{©}$ Bethany Beach environs today, bewitched.

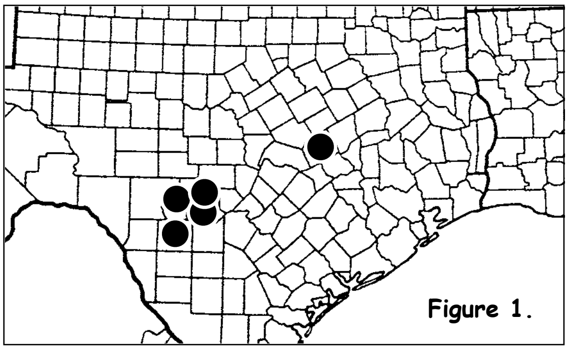
Chapter 17

Photuris billbrowni n. sp.

Bill’s Hitch

This firefly is known from five counties in south-central Texas (**Fig. 1**), above and just below the Balcones Escarpment (**Fig. 2**), in a variety of both damp and dry habitats in patches along highways (**Figs. 3, 4**); observed 4-9 July 1992. It apparently is the only Division-1 *Photuris* in central Texas, *flavicollis* occurring only in the extreme west, and *divisa* may possibly occur in northern Texas. The FP is a pair of short flashes emitted so rapidly that they appear to be a hitched single flash (**Fig. 5**); this FP is emitted at variable intervals averaging 1.0 to 1.8 second at temperatures near 28°/82° (**Fig. 6**), but sometimes in rhythmic (near metronomic) trains (**Fig. 5A**). Browns Hitcher lacks the rufus-red pronotal “spots” that are generally diagnostic of Division-2 fireflies, but pale spots (maculae) are present, and these are of a diffuse salmon color. This firefly superficially resembles a small (≈11mm) *Photuris frontalis*; the latter apparently does not occur in Texas and its train flashes are single, emitted at intervals shorter than one second, and passing males, and groups of males in high density synchronize their flashes; this was not seen in *billbrowni*.

Ecology, flashing behavior. This firefly was found in low woods, over dry roadside ditches, and along streams and rivers. Whether some of these sites of adult activity were suitable for larval development or were only sexual arenas may be of special interest; some sites seemed to be exceedingly dry and some may be subject to occasional or seasonal violent flooding (**Fig. 3**). Arenas noted in very dry sites were often within 100 yards of a wet or dry river/stream channel. Under a full and very bright moon male flashing flight was almost exclusively confined to shady places (**Fig. 4**). In one low and deeply shaded woods, the stratum of numerous low flying (< 3’) males strongly resembled *Photuris congener* and *frontalis*, though the flash rate in these two is twice that of *billbrowni*. Males flew from grass level up into and around low trees, from a few inches to a yard or more between flashes, and often in unpredictable paths, with rapid changes in direction that made PM-aiming a video game before the technology was generally available. They occasionally passed through a site of *Photinus sabinalensis* at the river; however, no *Photuris* adult of Division-1 is yet known to be a predator of fireflies.



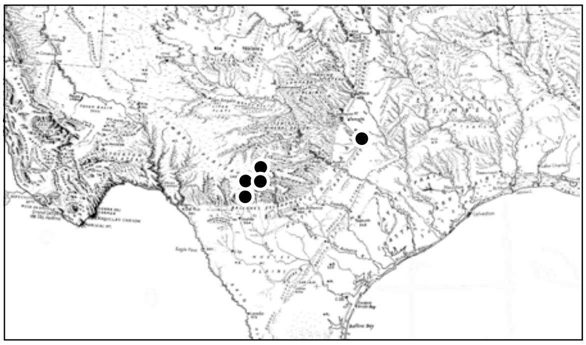


Figure 2. Pysiographic perspective.


Figure 3. Dry woods and roadside.

The FP resembles that of a yet-to-be-named *Photinus* and *Photuris bridgeniensis* but the hitching is somewhat more pronounced. The FP is emitted at variable intervals averaging from 1 to 1.8 seconds (at 28°/82°; e.g., for PM-recorded male #6: n=15, x=1.1, r=0.9-1.3, s=0.1, at 26.8° /80.2°. A period of about 0.5 sec was once noted, when a male was traveling rapidly down a stiff wind over a roadside ditch.

From inspection of 46 suitable flash patterns from 8 males the following were noted: The two flashes are of identical form, each with only a slight asymmetry, resulting from the slight tailing-off during the last one-third of the fall. The two flashes in an FP are usually of different intensity: in a small sample from Milam County the second was usually the brighter (**Fig. 5A-E**), and from Bandera Co. there was considerable variability with the first often being brighter (**Fig. 5F-J**). To illustrate, the overall ratio of intensity: for Milam Co. recordings (flash 1/ flash 2), n=5 males and 33 FPs, x=0.54, r=0.21-0.88, s=0.11), and for Bandera Co. records, n=4 males & 19 FPs, x=1.07, r=0.43-1.80, s=0.54. Flash base duration was about 36-56 mSec, and at half-max was 22-30 mSec (26.1°-26.8°C). With large intensity differences, the brighter flash was <9 percent longer.

The modulation frequency of flash pairs at 26.8°C averaged 17.1 Hz, based on 46 FPs from 6 males; and at 26.1°, 16.9 Hz, 20 FPs from 4 Milam Co., males. As examples of variability at 26.8°: male 6, n=14, x=16.3 Hz, r=15.6-17.6, s=0.6; male 7, n=17, x=17.2 Hz, r=16.7-17.9, s=0.4.

Morphological data. General morphological means from the Holotype locality are (n=8): PNL 2.5, ELL 8.2, PNW 3.2, EWhum 1.8, EWmid 2.5, ELVit 2.2, TOTLen 10.7, PNrat 0.77, ELWrate 1.25, ELVTrat 0.0 (**Fig. 7A**, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **Figure 7B-C**, and the color of the pre-lantern ventrite in **7D**. **Figure 8** is a reference for skeletal plates and numbers for degrees of splashing on ventrite 4. A range of vittagrams is shown in **Figure 9**.

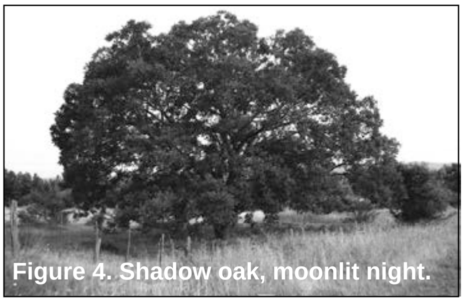


Figure 4. Shadow oak, moonlit night.

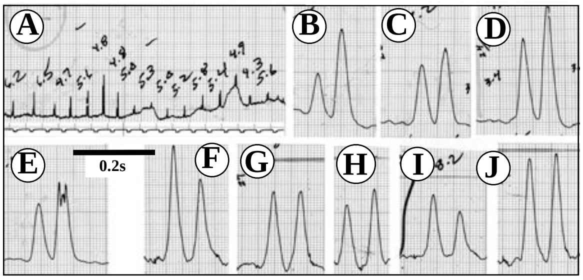


Figure 5. PM traces (AX: ri/time).

TEMP	PER	TEMP	Rate	n
26.8°	1.4	26.8°	0.71	9
26.8°	1.4	26.8°	0.71	2
26.8°	1	26.8°	1	2
26.8°	1.1	26.8°	0.9	3
26.8°	1.8	26.8°	0.6	4
26.8°	1.1	26.8°	0.94	15
29.2°	1.7	29.2°	0.59	11
26.1°	1	26.1°	1	6 males
26.1°	1.2	26.1°	0.86	10 males
26.1°	1.6	26.1°	0.63	4 males

FigTable 6. FP period.

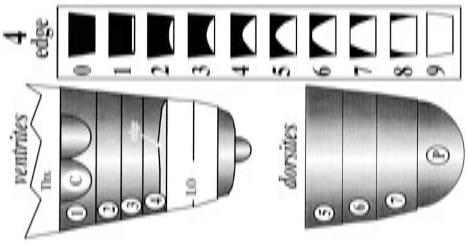
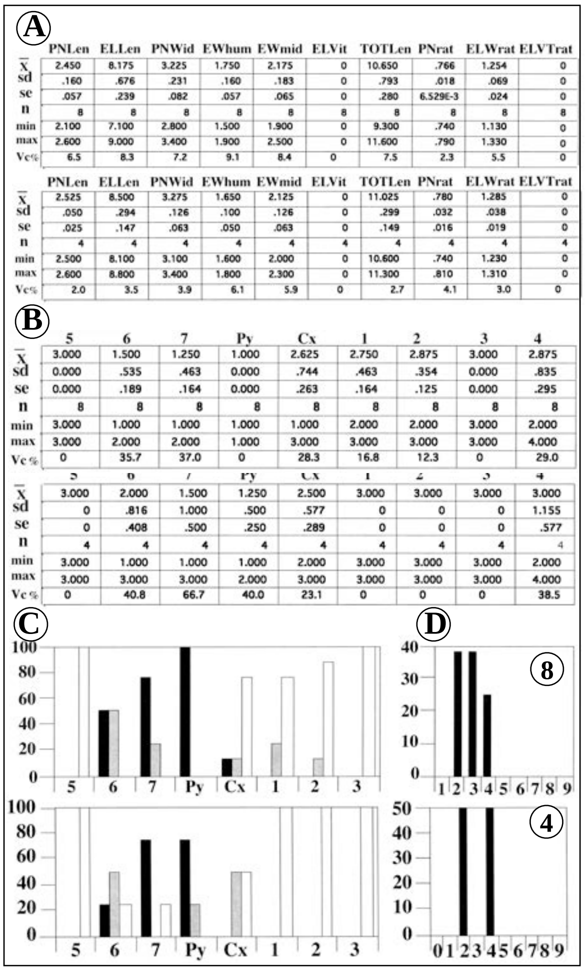


Figure 7. Topographic and splash key.

Holotype Description. male, voucher number 9283, collected 5 July 1992, Real Co., Texas, Rt 86, 6 mi s Leakey nr Buffalo Crk. FB page 216: FB notes. "in shade of large spreading tree (oak) ... 1 mi N of picnic area. Moon is bright by 1/4, & ff mostly in shade of tree. KB 46 9283 hitch at this site" (oak mentioned shown in Fig. 4) Morpholog-ical data: genitalia extruded, remain attached; from spread sheet—PNLen 2.5, ELLen 7.4, PNWid 3.4, ELWhum 1.6, ELWmid 2.1, LELVit 0.0, TotLen 9.9, PnRat 0.74, ElRat 1.31, VitRat 0.00/NA; Colors: D 322, Py 1, Cx 3, V 333, Edg 3. Types will be deposited in the USNM.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	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.450	8.175	3.225	1.750	2.175	0	10.650	.766	1.254	0
sd	.160	.676	.231	.160	.183	0	.793	.018	.069	0
se	.057	.239	.082	.057	.065	0	.280	6.529E-3	.024	0
n	8	8	8	8	8	8	8	8	8	8
min	2.100	7.100	2.800	1.500	1.900	0	9.300	.740	1.130	0
max	2.600	9.000	3.400	1.900	2.500	0	11.600	.790	1.330	0
Vc%	6.5	8.3	7.2	9.1	8.4	0	7.5	2.3	5.5	0

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.525	8.500	3.275	1.650	2.125	0	11.025	.780	1.285	0
sd	.050	.294	.126	.100	.126	0	.299	.032	.038	0
se	.025	.147	.063	.050	.063	0	.149	.016	.019	0
n	4	4	4	4	4	4	4	4	4	4
min	2.500	8.100	3.100	1.600	2.000	0	10.600	.740	1.230	0
max	2.600	8.800	3.400	1.800	2.300	0	11.300	.810	1.310	0
Vc%	2.0	3.5	3.9	6.1	5.9	0	2.7	4.1	3.0	0

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	1.500	1.250	1.000	2.625	2.750	2.875	3.000	2.875
sd	0.000	.535	.463	0.000	.744	.463	.354	0.000	.835
se	0.000	.189	.164	0.000	.263	.164	.125	0.000	.295
n	8	8	8	8	8	8	8	8	8
min	3.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000	2.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	4.000
Vc %	0	35.7	37.0	0	28.3	16.8	12.3	0	29.0

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.000	1.500	1.250	2.500	3.000	3.000	3.000	3.000
sd	0	.816	1.000	.500	.577	0	0	0	1.155
se	0	.408	.500	.250	.289	0	0	0	.577
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	2.000	3.000	3.000	3.000	2.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	4.000
Vc %	0	40.8	66.7	40.0	23.1	0	0	0	38.5

Figure 7. Morphological data (Kerr/Milam Cos).

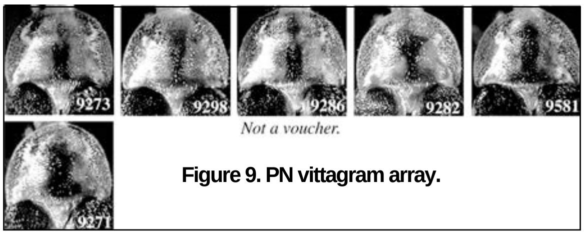
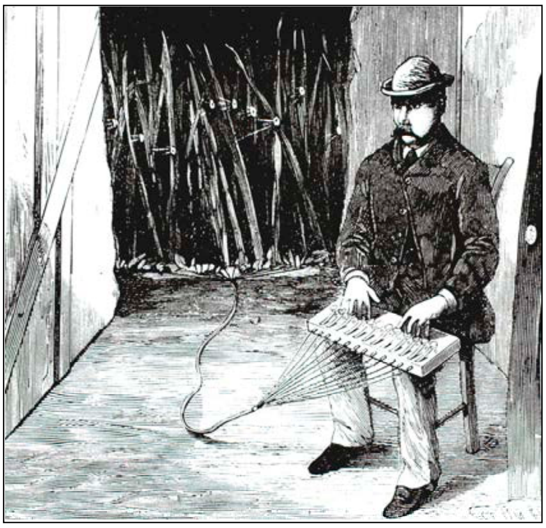


Figure 9. PN vittagram array.

Taxonomic note. The specific epithet is tribute to a teacher and friend at Cornell, Professor William L. Brown, who taught Evolutionary Biology from the perspective of someone who had spent many years thinking about the subject and its problems during a life's study of ants. As text, other than his own experience, he used E. Mayr's 1964 treatise, and though I now understand from my own experience that he had serious disagreements with fundamental elements of the book, he was always a gentleman about it—I now suspect that he perhaps felt the book set thinking about species back to a pre-Darwinian state. Bill is the one who read the draft of my dissertation, made helpful comments and deleted more than 100 definite articles, ran interference when I needed it, and offered an experienced perspective on scholarly matters—when I was finishing my dissertation, he observed that I should remember that it was only another beetle paper.

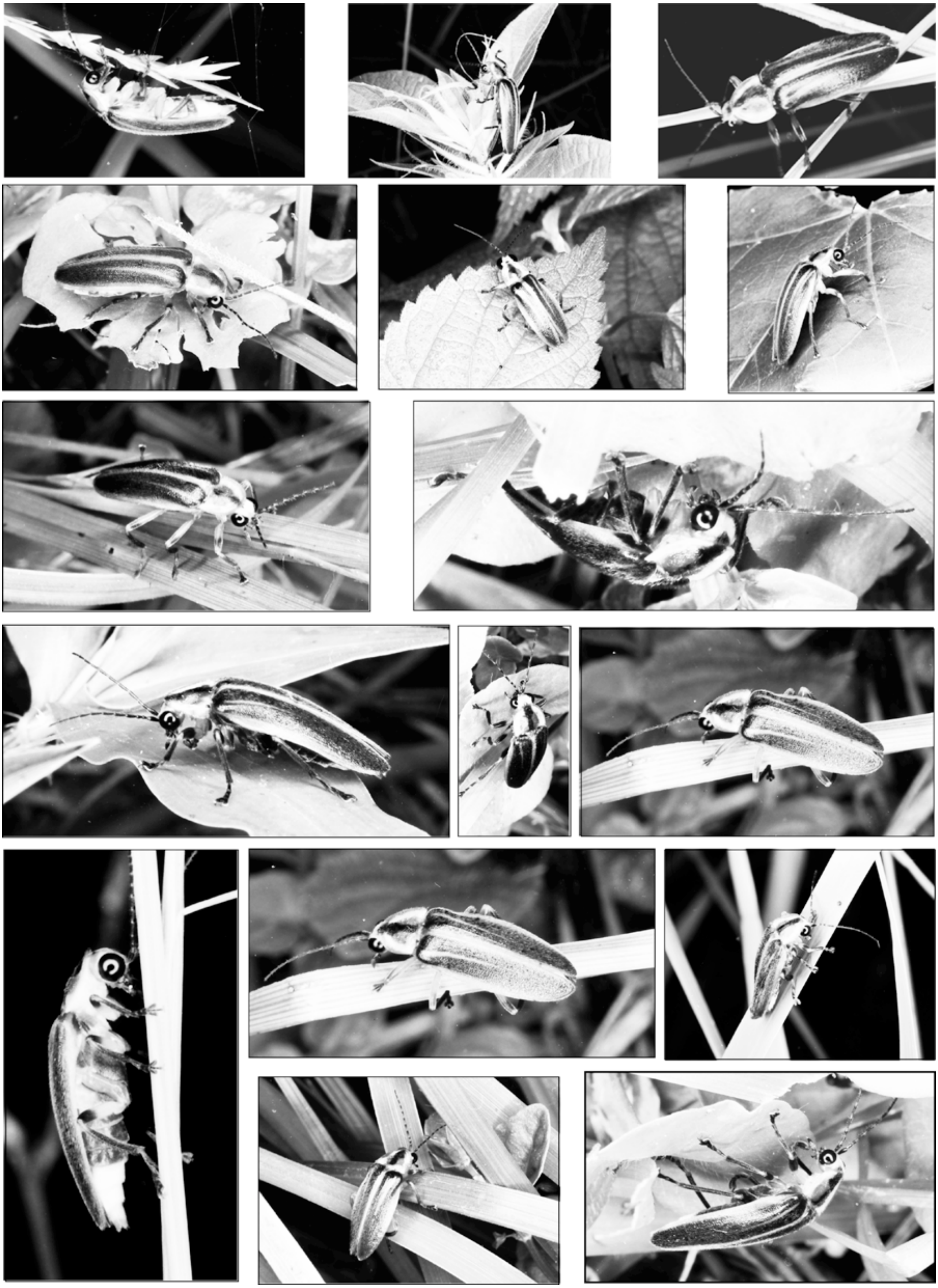
In our last interaction, which he perhaps thought was somewhat metaphysical, ants that I had found nesting in an extinct, uplifted, coral reef on the north shore of New Guinea, and apparently nurtured a firefly inquiline, arrived on his desk the day he was preparing the chapter on the group for a book he was completing.

Adjunct figure legends. **4**. A lonesome oak which on a moonlight night casts a shadow large enough to provide operational shade for 100 flashing fireflies. **5**. PM-records of *billbrowni* emissions: (**A**) a metronomic train of FPs with a rhythm almost as constant as the 1-sec markers on the line below; (**B-E**) FPs from the train in A. Note that the second pulse is brighter than the first in this consecutive array from Milam Co.(at 26.8°); (**E-J**) consecutive FPs emitted by a male in Bandera Co. (at 26.1°C). **6**. FP period data; the narrow temperature range did not make a graph possible. Shown at the top are means of 7 individual males, with n the number of FPs in the sample. The 3 bottom values are SWAT records with the number of FPs and males indicated. **7**. Morphological data: (**A**) Basic measurements and ratios; (**B**) Colors of abdominal ventrites and dorsites (see Fig. 8), using a 3-color discrimination: 1=pale, 3=dark), except ventrite 4 which indicates pale splash on posterior margin (see Fig. 78 (**C**) Histogram of sclerites (5-3, not 4) numerically quantified in B (n=8): bar position (l-c-r) and bar color indicate sclerite color (1-3); bar height indicates percentage in sample—note percents for each sclerite total is 100. (**D**) Histogram showing degree of pale splash on hind margin of visible ventrite 4, represented in array (0-9) at right in Figure 8. Circled number is n. **8**. Anatomical key to color-coded elements on abdomen. Note that the splash on illustrations of ventrite 4 is much generalized, and actually is very irregular or fragmented with strands and splotches.



Electric fireflies on stage. This illustration appeared in the book, *Magic: Stage Illusions and Scientific Diversions Including Trick Photography*, Arno Press, New York, 1997, page 337, first published in New York in 1897. The electric flashes appearing as fireflies flying in the marsh were controlled by a keyboard. By randomly striking several keys it would appear that several fireflies were in the marsh; if keys were struck in sequence it would appear that a single firefly was flying and flashing as it flew amongst the grasses in the marsh. If keys were struck simultaneously it would appear they were synchronously flashing *Pteroptyx* in southeast Asia, or perhaps *Photuris frontalis* in the Appalachians or Rock Creek Park in Washington, D.C.. The stage production was *The Kaffir Diamond*; the plot and other details remain to be researched.

Male and female *Photuris* seen upon the grass and herbs at the old UF Med Garden, Page 2: monitoring?



Chapter 18

Photuris branhami n. sp.

Double Mother (DM)

This Operational Species could well have more confusing elements in its flashing behavior in two or three Florida counties than all other *Photuris* have yet revealed collectively. On the other hand, it could be rather simple in its flashing behavior, and has merely become wildly and extravagantly variable in its 2-pulse FPs in the Gulf Counties explored. The first section of this chapter will describe Alachua County *branhami* (**Fig. 1**). For the near-Gulf situation no formal taxonomic decisions is made, except to make none. In *Photuris* peripherally located populations seem to have diverged as their mate seeking behavior, most notably their FP repertoires have: (**1**) tracked FPs of their females' prey species, or —and apparently not a factor in this case—(**2**) have dropped FPs that were used by other and "dominant" resident *Photuris*. This sketch offers a glimpse as to what might *possibly* await a dedicated fireflyer with several seasons to devote—and sufficient patience to endure. DM, with its near-Gulf variads could well give insight into insect communication ecology and fine-tuning not likely to be surpassed by many arthropods, except perhaps eusocial hymenoptera—but certainly not that of any other beetle, social or otherwise?

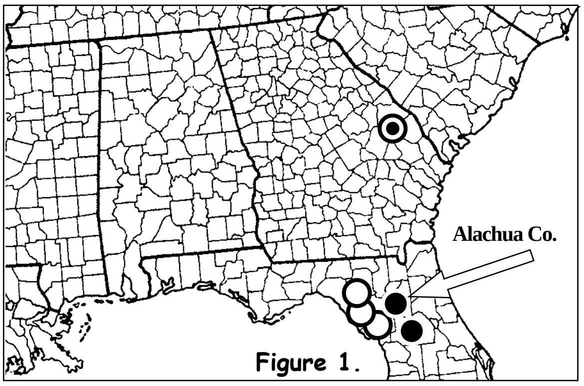


Figure 1.

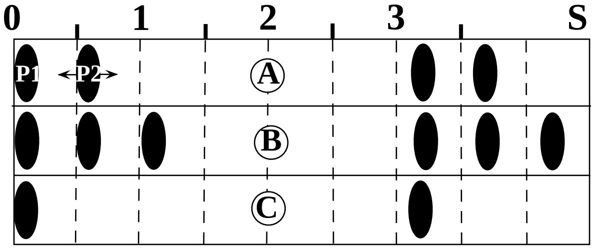


Figure 2. DM's known repertoire in Alachua Co. (AX: FP/sec).

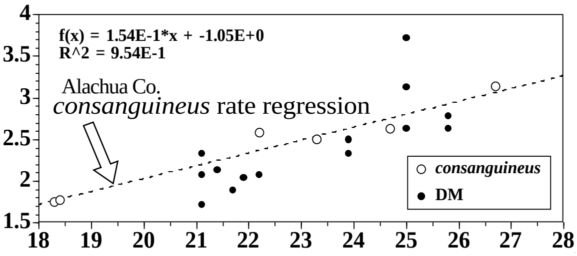


Figure 3. DM pulse (P1P2) period rate (AX: mean Hz/temp).

DM's basic and diagnostic FP is a pair of flashes similar but not identical to those of *Photinus consanguineus*; that is, P1-P2 *about* one-half second apart (**Fig. 2A**)—but showing greater variation. This FP is repeated at 3-5-second intervals. This discussion will mainly concern only the P1-P2 intervals, and not FP intervals. **Figure 3** shows means of Alachua DM's P1-P2 pulse rates along the *Photinus consanguineus* pulse-rate slope. ID confirmation following FP observation is in morphological appearance: DM is a rather small ($\bar{x}$=10.6-mm), delicate and rather beautiful *Photuris*, of distinctive appearance, with sharply delineated details in black and white/ivory (**Fig. 4**). Seasonal occurrence in Alachua County is shown in **Figure 5**.

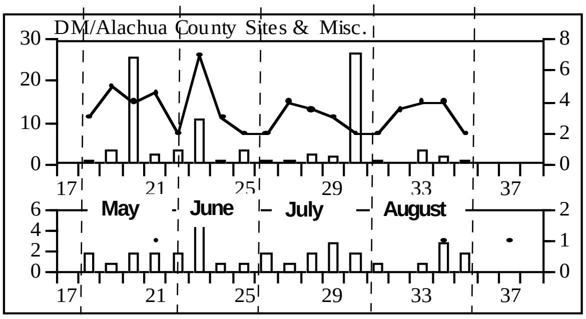


Figure 5. SESOBS records of Alachua seasonal occurrence.

Occurrence, ecology, flashing behavior. The geographic occurrence of DM is probably more extensive than shown with black dots in **Figure 1**, perhaps extending both north and south, and even into the near-Gulf Counties?; SESOBS records of occurrence for DM-like flashers in north-central and northwestern peninsular Florida are shown in the **Appendix, Part 1**.

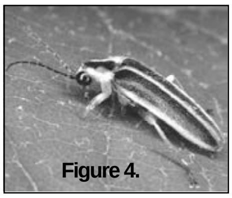


Figure 4.

In Alachua County: DM males emitting the 2-pulsed (diagnostic, signature) FP (**Figs. 2A, 6A-C**) flew around the crowns of bushes and tall trees of mesic hardwood forests (**Fig. 7**), but never in any numbers, and could easily be attracted toward a hand-held penlight decoy. Decoy flashes were emitted about 1 second after the -P2 of the FP. Pulse period ranged 0.3-0.5 seconds at 27°/81°-20°/68° (**Fig. 8**); rate in **Fig. 9**. In a small sample, the base duration of the P1 pulse

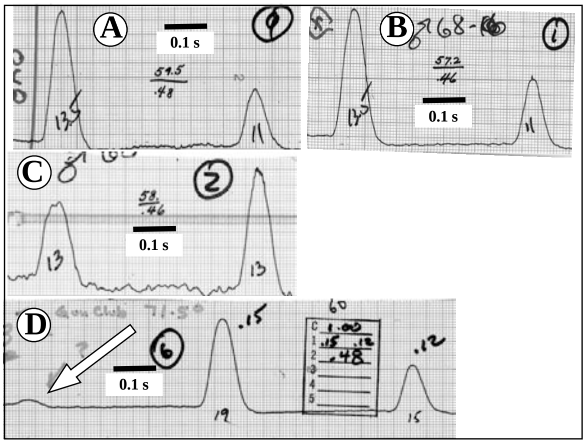


Fig. 6. Two common (73%), 1 reverse; and a 3-pulser (AX: ri/time).

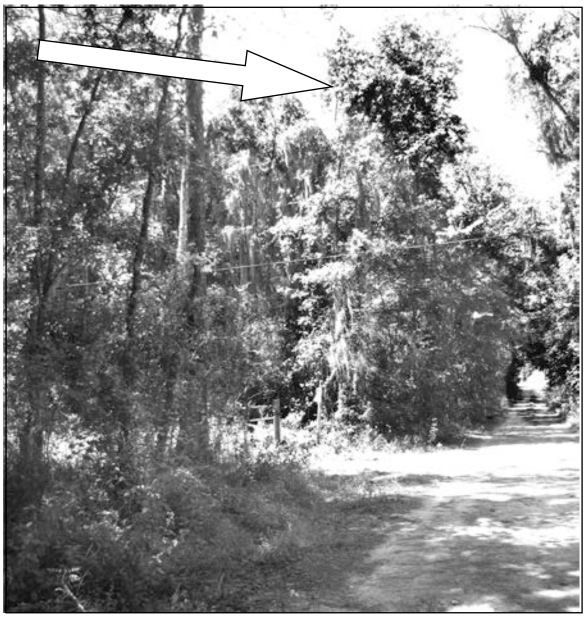


Figure 7. Treeline and roadside DM site.

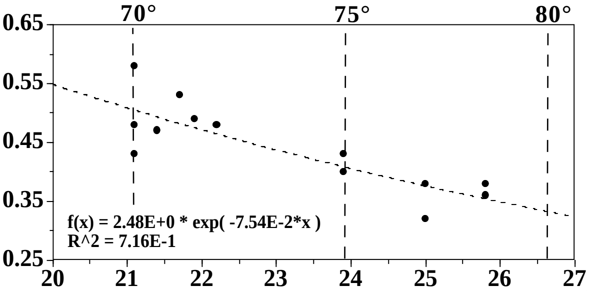


Figure 8. Pulse period (AX: sec/temp).

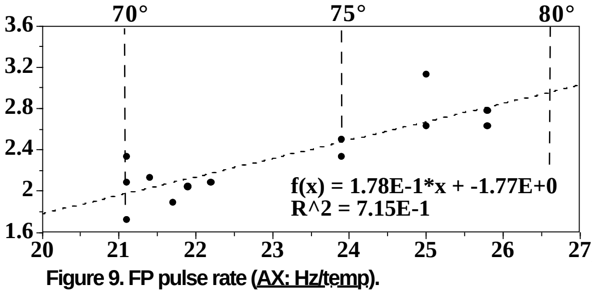
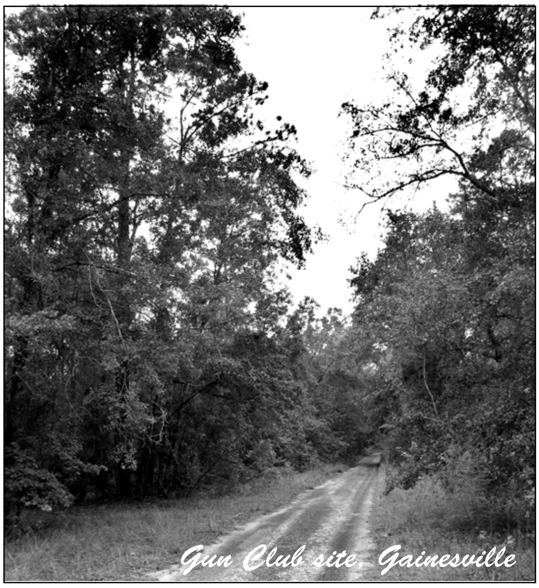


Figure 9. FP pulse rate (AX: Hz/temp).

was somewhat longer than that of P2: 110 mSec vs 90 (25°/77°, n =10). In about three-quarters of recorded pulse-pairs P2 on average was only 63 (38-88) percent as bright as P1 (**Fig. 6A**, **B**), the other quarter showing equal or reversed intensity (**Fig. 6C**). FP period of a small sample at 21.1°/70° averaged 4.6 seconds, and ranged 4.2-5.0). Unlike the enigmatic, white-*appearing* flashes of its cognate (Group-mate) WM/*whistlerae*, to my eyes the flashes of DM appeared pale green.

Occasionally but not rarely a 3-pulse FP was seen (**Figs. 2B, 6D**), but was never recognized to occur or be associated with any ecological circumstance—e. g., FPs of competitors or other species. The 1-pulse FP (**Fig. 2C**) was a different matter: it was seen several times when a decoyed, approaching male drew within a few feet, paused and hovered, retreated, or disappeared. It did not appear to be a default FP, but perhaps provides a clue to a counter-measure tactic—perhaps to an evolutionary origin of defaulting? The near-Gulf section below gives sketchy FP details of DM-connected *cinctipennis*-Group populations occur-ring there; these were variously and confusingly in fieldbooks termed DDM, WD, GRN, MM, etc., with apologies—which terms originally had reference to "matching?" nominal *consanguineus*-Group species, *greeni* and *macdermoti*, and those initially suspected to be "composites."

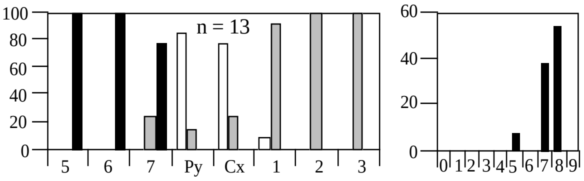
Two additional observations that are suggestive of the presence of a unique relationship among members of the *Photinus consanguineus* Group (a J. W. Green [1956] taxonomic grouping based on aedeagal structure) with those of the *Photuris cinctipennis* Group addressed here: from deep grass along the roadway shown in **Figure 7**, a **male** of the *cinctipennis* complex (DM) gave correctly-timed answers to a *macdermotti* male; and on another occasion while using a penlight simulation of the *macdermotti* FP along this roadside, seeking a female *macdermotti*, a perched DM **male** answered, timed as a *mac* female would.



Gun Club site, Gainesville

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.300	8.285	2.769	1.485	2.054	.192	10.569	.825	1.092	.022
sd	.252	.410	.149	.080	.105	.693	.578	.070	.054	.080
se	.070	.114	.041	.022	.029	.192	.160	.019	.015	.022
n	13	13	13	13	13	13	13	13	13	13
min	1.500	7.400	2.500	1.300	1.900	0.000	9.400	.600	1.000	0.000
max	2.500	8.800	3.000	1.600	2.300	2.500	11.300	.870	1.200	.290
Vc%	11.0	4.9	5.4	5.4	5.1	361	5.5	8.5	4.9	363.6

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	2.800	1.133	1.267	1.933	2.000	2.000	7.333
sd	0	0	.414	.352	.458	.258	0	0	.816
se	0	0	.107	.091	.118	.067	0	0	.211
n	15	15	15	15	15	15	15	15	15
min	3.000	3.000	2.000	1.000	1.000	1.000	2.000	2.000	5.000
max	3.000	3.000	3.000	2.000	2.000	2.000	2.000	2.000	8.000
Vc%	0	0	14.8	31.1	36.2	13.4	0	0	11.1



FigTable 10. DM morph data, Alachua Co. (AP/GC).

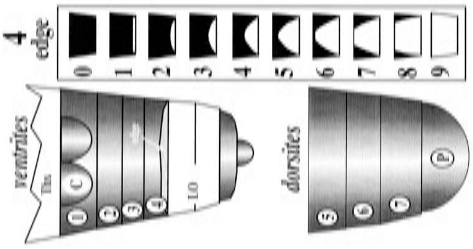


Figure 11. Key to morphology and splashing.

Morphology. **FigTable 10** gives morphological data for Alachua County DM (s.s.). **Figure 11** is the key to morphology; and **Figure 12** gives vittagram arrays for Alachua DM (see also **Figure 24**).

Holotype Description: male, voucher 68287, collected 18 May 1968, Alachua County, Florida, Gun Club locality. FB page 67: KB-69, PM-Recorded. Morphological data: not genitalia extruded; from spread sheet—PNLen 2.3, ELLen 8.0, PNWid 2.8, ELWhum 1.6, ELWmid 2.3, LELVit 0.0, RELVit 0.0, TotLen 10.3, PnRat 0.82, ElRat 0.72, VitRat 0.00; Colors: T 333, Py 1, Cx 1, V 222, Edg 8. Types will be deposited in the USNM.

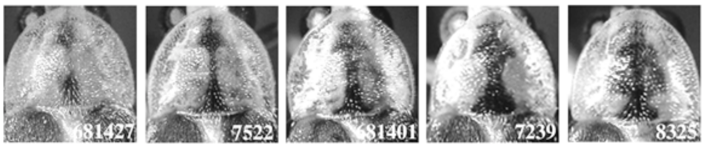


Figure 12. DM morph data, Alachua Co. (AP/GC).

Nomenclatural note. The selection of Dr. Marc Branham as the honoree for this firefly was, among other considerations, to encourage him and his future students to dig deeply, thoughtfully, and at length into the *cinctipennis* enigma described in the next section, before they disappear.

⁂

Photuris cinctipennis ("DM") Group, In near-Gulf Counties

Figure 13. Hog Pen site, far left, looking north, Rt 357.

DM-connected FPs of Levy, Dixie, and Taylor Counties.* At sites in "near-Gulf" counties west of Alachua (**Fig. 1**, circles; **Figs. 13, 14, 16, 17**), Gulf-DM emits 2- and 3-pulse FPs with pulse-intervals like those found in Alachua County, and also at other P1-P2 intervals (**Fig. 15**). Occurring with this Gulf-DM in near-Gulf counties are 2-flash members of Green's *Photinus consanguineus* Group that emit their two pulses at intervals not seen elsewhere, and also those with *macdermotti* and "*greeni*" intervals. Gulf-DM males vary their P1-P2 intervals greatly as they fly and search (**Fig. 18**). The time-base in **Figure 18** is measured

Fig.ure 14. Hog Pen site, Rt. 357, 4.1 miles north of the Dixie/LaFayette Co. line, in LaFayette Co..

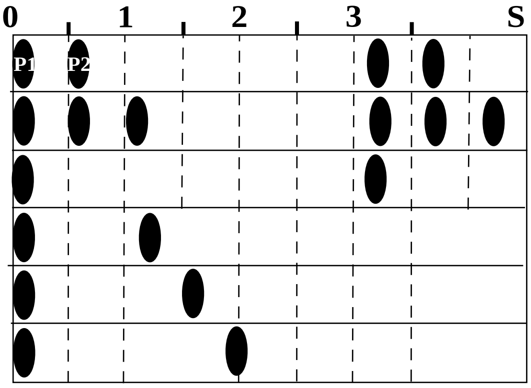


Figure 15. FPs noted in near-Gulf counties, generalizations and approximations.

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*Various mnemonic letters were long used for emerging near-Gulf P1-P2 OTUs and remain in text and some charts: M translates as *mother*. DDM=double double mother; GM=*greeni* mother, WM=*whistler's* mother, etc..

Figure 15. Cypress swamp/dome near Ellzey, Levy Co. FL.

Figure 16. Hogs Delight—not actual firefly photo.

mac-Value units, explained as follows:

***Mac*-value**. Because flash data recorded at different temperatures are not directly comparable when working with various timings connected with *macdermotti* itself—such as the competitive arena-emissions that congregations of landed, rival males (Florida-*macdermotti*) emit when approaching a contested female—a *mac*-value is used to permit comparisons of timing data when observation/experiment temperature is not controlled (Lloyd, 1984). However, because the rate/temperature **slopes** differ among the two "species-groups) of interest here (**Fig.19**), the correction equation appropriately used for *macdermotti*-like timings errs considerably with steeper slopes. But here, for the simple purpose of presenting a broad comparative view of the many P1-P2 variations, and most especially for P1-P2 **sequences** emitted by individual males, the *mac*-value correction was used; see also **Figure 18** legend. Proceeding: In **Figure 18** the bars on the time-line to the right of male identification numbers (e.g. 69-1), represent P1-P2 timings made in a **sequence** of PM-recorded FPs emitted by this individual male (male 69-1). Note/examine: (**1**) horizontally there seem at the least to be three sets (dashed vertical rectangles)—variance among the P1-P2 intervals of individuals is considerable, and greater than noted in corresponding P1-P2 intervals emitted by Alachua *Photinus* males; (**2**) some P1-P2 intervals there would seem to be leaps rather than slight adjustments (males 79-1, 82-3, 82-5, 82-6); and (**3**), it may be of significance to note that in none of the PM-recorded sequences did the males leap between vertical rectangular sets (prey species modes?). (**4**) Until a thorough analysis is made of the *consanguineus*-Group in this near-Gulf region and the timing of their P1P2 intervals, and most particularly the variations they adaptively introduce into their intervals, perhaps in the context of countermeasure to predators (tricking hunting females into making errors), or fishing/chumming to find a working P1-P2, it will probably be impossible to understand/interpret the significance of the variation described in Figure 18. (**5**) Note that the bottom sequence line is a collection of incidental stopwatch measurements.

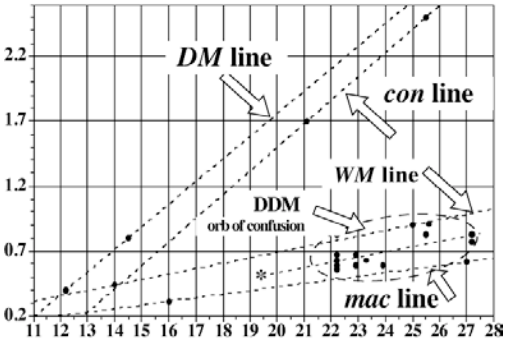


Figure 19. Pulse-rate regression comparisons (AX: Hz/temp).

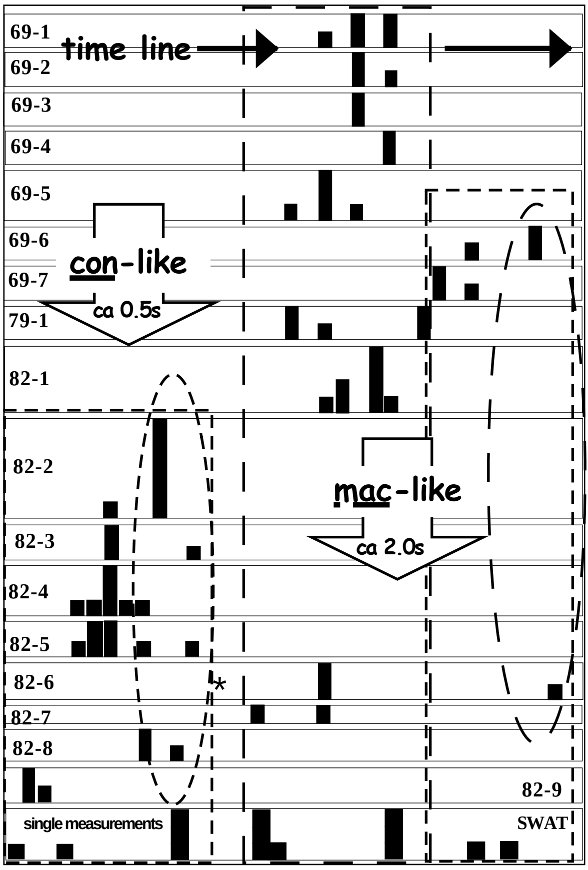
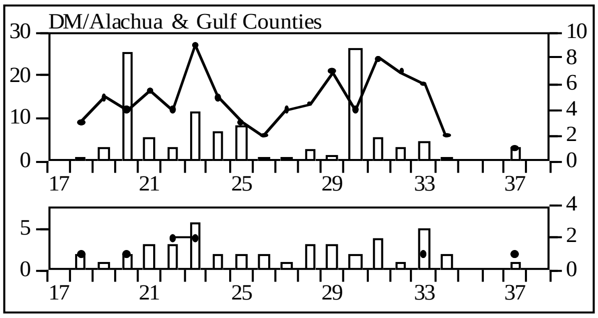


Figure 18. Individual variation among (PM-recorded) 2-pulse FP sequences of individual Gulf-DM males (AX: male number/mac-value). SWAT= incidental stopwatch measurements..Time-line is distorted at left end. See text above for explanation of *mac*-value.

APPENDIX Part 1. *Photuris branhami* SESOBS, Vittagrams



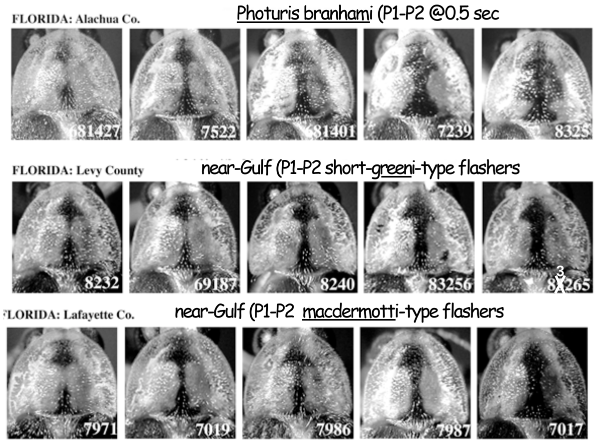
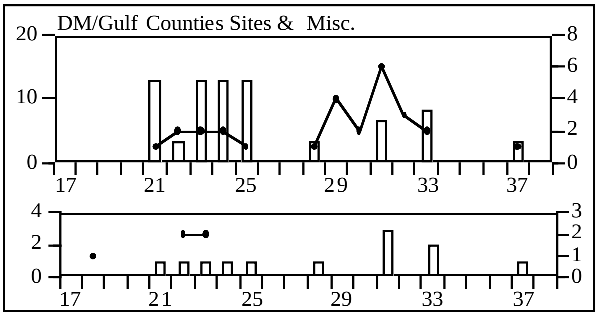
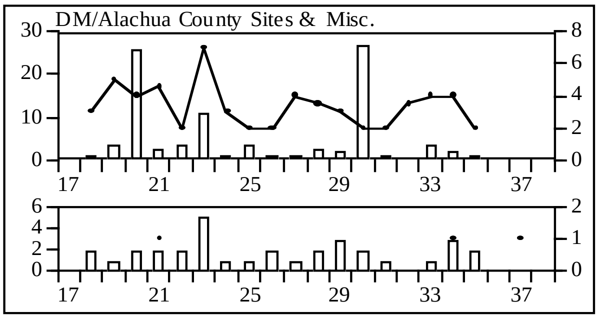
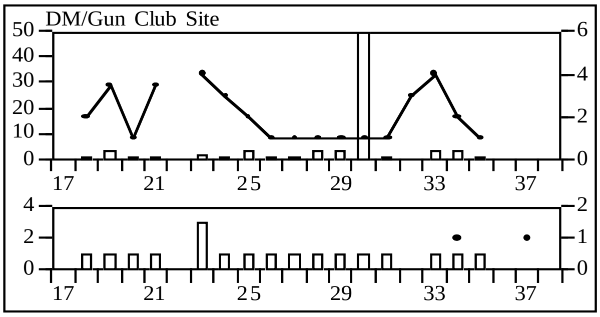
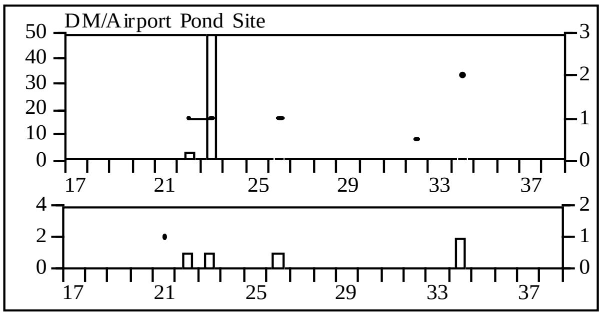


Figure 24. Vittagrams as noted; near-Gulf errors possible, unresolved distinctions.









APPENDIX Part 2. *Photuris branhami*; Morph Measurements, Ratios, Colors

GM 1.2: Ellzey, Levy. Co., n=10

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.302	8.150	2.810	1.570	2.100	0	10.450	.824	1.327	0
sd	.245	.540	.173	.106	.149	0	.740	.071	.078	0
se	.077	.171	.055	.033	.047	0	.234	.022	.025	0
n	10	10	10	10	10	10	10	10	10	10
min	1.750	6.900	2.500	1.400	1.900	0	8.900	.670	1.230	0
max	2.500	8.800	3.100	1.800	2.300	0	11.300	.910	1.500	0
Vc%	10.6	6.6	6.2	6.8	7.1	0	7.1	8.6	5.9	0

GM 1.2: Levy Co., Ellzey, n=10

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	2.300	1.000	1.400	1.600	2.100	2.000	6.500
sd	0	0	.483	0	.516	.516	.568	.667	2.506
se	0	0	.153	0	.163	.163	.180	.211	.792
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	2.000	1.000	1.000	1.000	1.000	1.000	2.000
max	3.000	3.000	3.000	1.000	2.000	2.000	3.000	3.000	9.000
Vc%	0	0	21.0	0	36.9	36.9	27.1	33.4	38.6

DM: Pinetop, Alachua Co., n=2

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.300	8.050	2.800	1.500	2.100	0.000	10.350	.820	1.090	0.000
sd	0.000	.071	0.000	0.000	0.000	0.000	.071	0.000	0.000	0.000
se	0.000	.050	0.000	0.000	0.000	0.000	.050	0.000	0.000	0.000
n	2	2	2	2	2	2	2	2	2	2
min	2.300	8.000	2.800	1.500	2.100	0.000	10.300	.820	1.090	0.000
max	2.300	8.100	2.800	1.500	2.100	0.000	10.400	.820	1.090	0.000
Vc%	0	0.88	0	0	0	0	0.7	0	0	0

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	3.000	1.000	1.500	2.000	2.000	2.000	7.000
sd	0.000	0.000	0.000	0.000	.707	0.000	0.000	0.000	0.000
se	0.000	0.000	0.000	0.000	.500	0.000	0.000	0.000	0.000
n	2	2	2	2	2	2	2	2	2
min	3.000	3.000	3.000	1.000	1.000	2.000	2.000	2.000	7.000
max	3.000	3.000	3.000	1.000	2.000	2.000	2.000	2.000	7.000
Vc%	0	0	0	0	47.1	0	0	0	0

GM 1.5: Levy Co., n=3

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.400	8.300	2.867	1.567	2.100	0.000	10.667	.840	1.347	0.000
sd	0.000	.200	.058	.058	0.000	0.000	.208	.017	.064	0.000
se	0.000	.115	.033	.033	0.000	0.000	.120	.010	.037	0.000
n	3	3	3	3	3	3	3	3	3	3
min	2.400	8.100	2.800	1.500	2.100	0.000	10.500	.830	1.310	0.000
max	2.400	8.500	2.900	1.600	2.100	0.000	10.900	.860	1.420	0.000
Vc%	0	2.4	2.0	3.7	0	0	1.9	2.0	4.8	0

GM 1.5: Levy Co., n=3

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	3.000	1.000	1.000	1.333	1.667	2.000	8.000
sd	0.000	0.000	0.000	0.000	0.000	.577	.577	0.000	0.000
se	0.000	0.000	0.000	0.000	0.000	.333	.333	0.000	0.000
n	3	3	3	3	3	3	3	3	3
min	3.000	3.000	3.000	1.000	1.000	1.000	1.000	2.000	8.000
max	3.000	3.000	3.000	1.000	1.000	2.000	2.000	2.000	8.000
Vc%	0	0	0	0	0	43.3	34.6	0	0

GM 1.5: Dixie/LaFayette Cos.., n=4

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.400	8.300	2.775	1.500	2.050	1.825	10.700	.863	1.380	.215
sd	.082	.469	.206	.082	.058	1.559	.542	.029	.101	.176
se	.041	.235	.103	.041	.029	.779	.271	.014	.050	.088
n	4	4	4	4	4	4	4	4	4	4
min	2.300	7.600	2.500	1.400	2.000	0	9.900	.830	1.230	0
max	2.500	8.600	3.000	1.600	2.100	3.800	11.100	.900	1.450	.430
Vc%	3.4	5.7	7.4	5.5	2.8	85.4	5.1	3.4	7.3	81.9

GM 1.5: Dixie/LaFayette Cos.., n=4

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	2.750	1.250	1.000	1.000	2.000	2.000	7.000
sd	0	0	.500	.500	0	0	0	0	.816
se	0	0	.250	.250	0	0	0	0	.408
n	4	4	4	4	4	4	4	4	4
min	3.000	3.000	2.000	1.000	1.000	1.000	2.000	2.000	6.000
max	3.000	3.000	3.000	2.000	1.000	1.000	2.000	2.000	8.000
Vc%	0	0	18.2	40.0	0	0	0	0	11.7

MM: Dixie Co., n=5 (with *macdermotti*-like P1-P2)

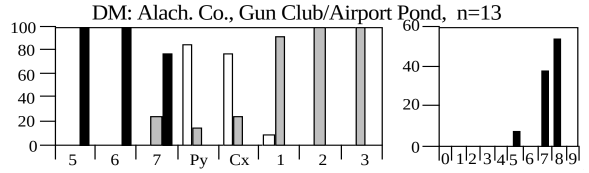
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.420	8.340	2.920	1.720	2.160	0.000	10.720	.822	1.266	0.000
sd	.110	.611	.217	.164	.182	0.000	.687	.053	.074	0.000
se	.049	.273	.097	.073	.081	0.000	.307	.024	.033	0.000
n	5	5	5	5	5	5	5	5	5	5
min	2.300	7.500	2.600	1.500	2.000	0.000	9.900	.760	1.200	0.000
max	2.600	8.900	3.100	1.900	2.400	0.000	11.500	.900	1.360	0.000
Vc%	4.5	7.3	7.4	9.5	8.4	0	6.4	6.4	5.9	0

MM: Dixie Co., n=5 (with *macdermotti*-like P1-P2)

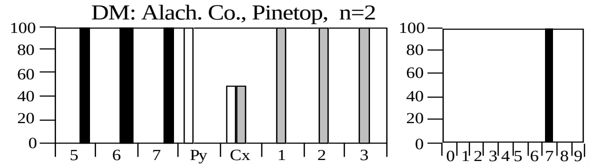
	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	3.000	1.000	1.000	1.600	2.000	2.200	4.600
sd	0.000	0.000	0.000	0.000	0.000	.548	0.000	.447	.894
se	0.000	0.000	0.000	0.000	0.000	.245	0.000	.200	.400
n	5	5	5	5	5	5	5	5	5
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	4.000
max	3.000	3.000	3.000	1.000	1.000	2.000	2.000	3.000	6.000
Vc%	0	0	0	0	0	34.3	0	20.3	19.4

Color Histograms

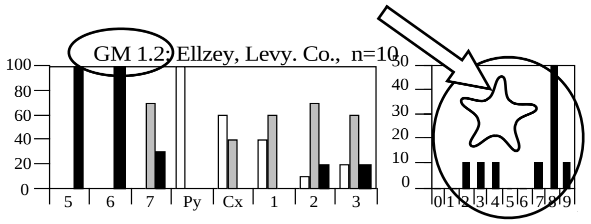
DM: Alach. Co., Gun Club/Airport Pond, n=13



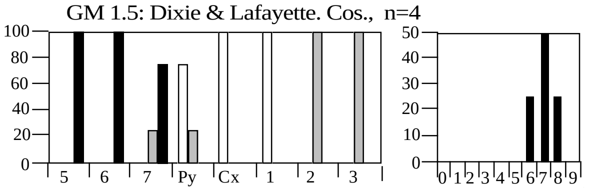
DM: Alach. Co., Pinetop, n=2



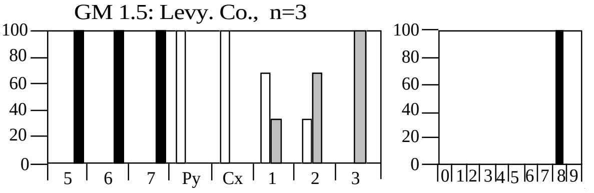
GM 1.2: Ellzey, Levy. Co., n=10



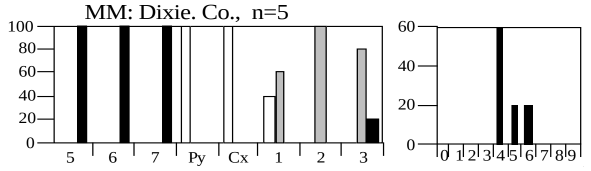
GM 1.5: Dixie & Lafayette. Cos., n=4



GM 1.5: Levy. Co., n=3



MM: Dixie. Co., n=5



Chapter 19

Photuris bridgeniensis n. s.

Hitched-Single (HS)

I travelled among unknown men,
In lands beyond the sea;
Nor, Bridgen! did I know till then,
What love I bore to thee.
Wordsworth, var.

This firefly occurs in abundance in the Cowaselon Valley of central New York State, an area described in detail for the Creek Firefly (**Fig. 1**). Its distinctive FP was also seen at other sites in western New York State. This bright and sharply-hitched FP (**Fig. 2**) often looks in space, when viewed from beneath, like an illuminated bowtie (▶◀) and often asymmetrical, with the first pulse appearing dimmer as found in PM records (▸◀); this impression, spatial separation, may indicate that the two segments of the lantern are not flashing synchronously? The hitched FP of *Photuris hebes* can sometimes be confused with that of HS, apparently when its first modulation is brighter than usual and has more separation. The hind coxae will permit separation of the two, those of *hebes* being pale and of *bridgeniensis,* dark. This species often occurs with Creek *Photuris* and some observations and PM-records suggested that the two could actually be the same species. However mark-release exercises and observations of in-flight flashes revealed no switching between the two FPs by individuals, nor did decoy-answered males default to the dot-dash FP. See also Creek *Photuris*, Chapter 26. A female identified as HS was seen flashing answers to a *hebes* male.

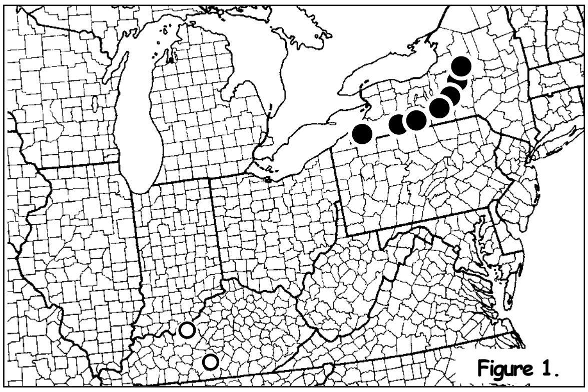


Figure 1.

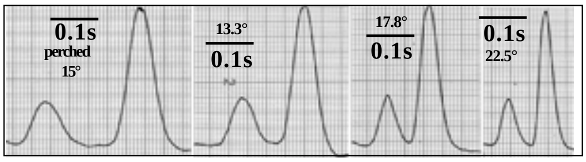


Figure 2. Flying FPs at 3 temps (AX: rel. int./time).

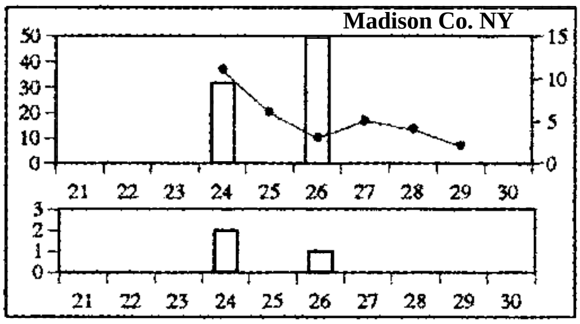


Figure 3. Sketchy SESOBS (AX: amt, cnt/WQY).

Ecology and flashing behavior. HS occurred in June and July (**Figs. 3, 4**), in low wet meadows and along marshes and streams (**Figs. 5, 13, 14**), where it flew low over grassy and herby vegetation and sometimes higher up among boughs of trees. Its jerky/hitched, bimodal emission is emitted continuously in indefinitely long sequences at 1-4-sec intervals (73°-52°: FP period, **Fig. 6**; FP rate in **Fig. 7**). These figures plot mean values; note that sequences are not rhythmic trains as often approximated in *hebes* and which seem characteristic of members of the *potomaca* and *frontalis* Groups, but instead show appreciable interval variation. As examples, note these means and ranges from continuous PM records: **1.6**, 1.4-2.2; **2.9**, 2.0-3.5; **2.9**, 2.6-3.4.

The temperature regression for the modulation rates of the 2-pulses of the ("standard/normal") FP is shown in **Figure 8**. At usual field temperatures the two modulations are not conspicuous as base-separated pulses (except perhaps as the bowtie viewed from beneath), though in most PM recordings they are seen to be separated by a deep rounded trough, more so, as expected, in recordings made at longer distances. Occasionally some are more closely joined than usual (**Fig. 9C**), but never with the first modulation as merely a soft shoulder as seen in *hebes* FPs—no inter-deme difference has been noted in this feature. Note FP differences in **Figure 9** (bars = 0.1 sec.): (**A**) Selected from an unbroken sequence of >25 FPs emitted by a single male, showing diversity of form; 13 were as in A2 and A3; 1 as in A4; 4 as in A1—17.2°/70°, Bridgen, NY site. (**B**) Four consecutive and "atypical" FPs emitted by a single male; unfortunately the only FPs recorded from this male—site as in A, 15.5°/60°. (**C**) Selected FPs from a sequence of 12 by one male, these three in particular showing reduced separation—site as in A, 21.1°/70°. (**D**) Sample from four FPs emitted by a perched male, showing separation not otherwise noted, even among perched males, from hundreds of PM recordings—site just north of Wampsville, NY, not cold, 67°/19.4°.

There is considerable variation in the relative intensity of the two modulations in PM FP-sequences of single males, but the first pulse is usually less bright. Although "reversals" of this in an occasional FP could be the result of lantern-aiming changes or momentary occlusion by a leaf or twig, it is clear that such reversals in HS also occur at lantern control, for PM-recorded FPs of perched males occasionally show this intensity relationship. A hasty/superficial review of 714 FPs in the PM scrapbook—which excluded those with intensity reversal—produced the values at the top of **Figure 9**—indicating that roughly 50% (0.33+0.17) of FPs emitted are like those seen in **Figure 9A2** and **9A3** (intensity ratios in or near the range 0.35-0.57). FPs **9A** and **9B** show varying pulse ratios selected from sequences of each of two males. Among questions inviting attention: (**1**) are asynchronous lantern segments the mechanical (neurological) means of producing modulated emissions as seen in HS and SH?; (**2**) are males coding or signaling something of significance to other fireflies by changes in pulse-intensity ratios, or influencing nearby rivals that monitor them. The following is toward answering the second question.

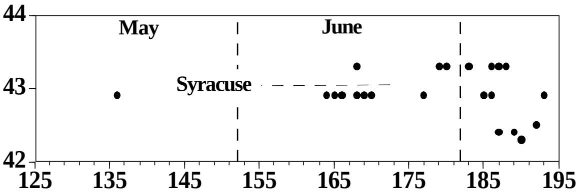


Figure 4. GESEDIS (AX: Lat/DOY).

Figure 5. JCT Creek and Mt. Hope Roads; creek, wet pasture.

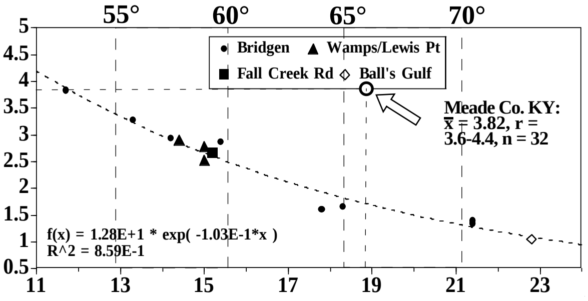


Figure 6. Mean FP period (AX: sec/temp).

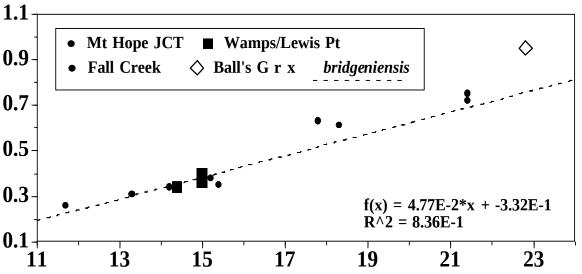


Figure 7. FP period rate (AX: Hz/temp; AFL).

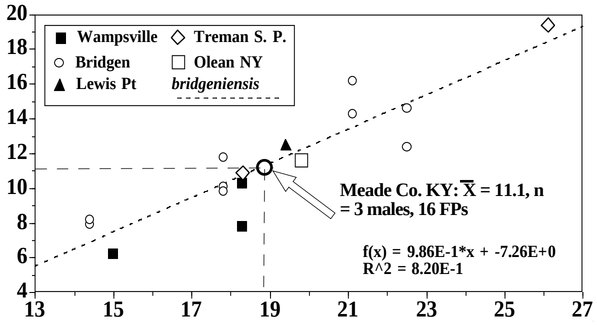


Figure 8. FP modulation rate (AX: Hz/Temp).

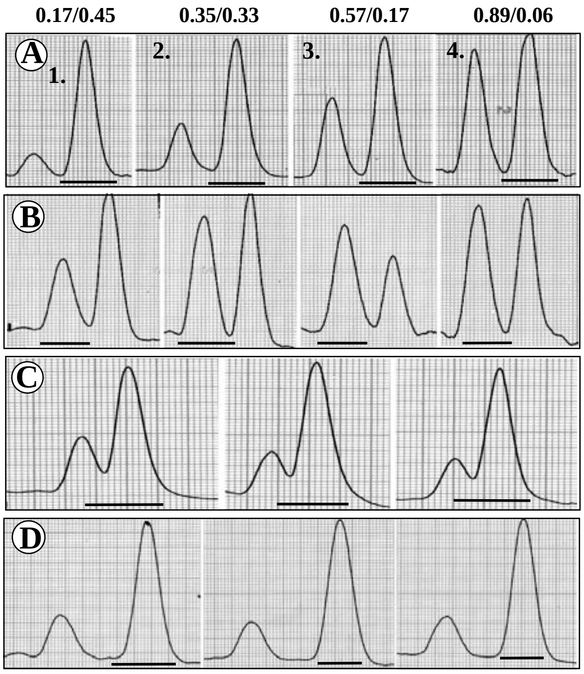


Figure 9. Selections from 4 male sequences. Numbers at top refer to traces in (A): mod amplitude ratio, est. occurrence in PM FP records. Bars = 0.1 sec. (AX:rel. inten./time)

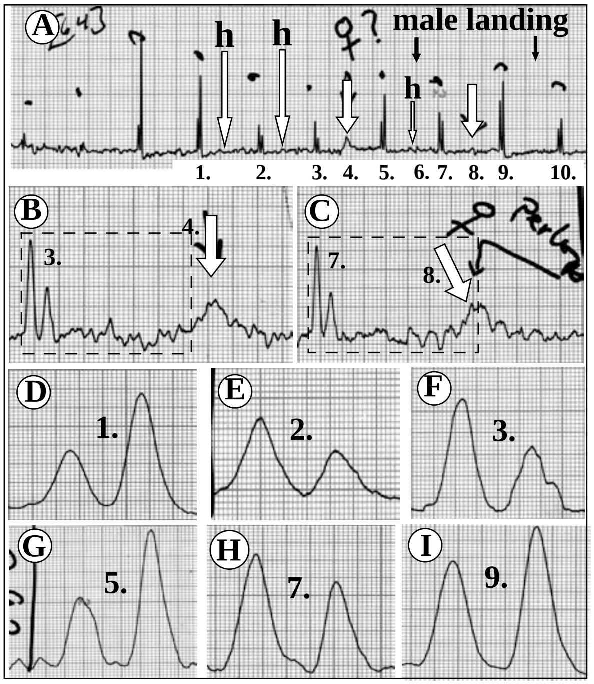


Figure 10. Male-female sexual communication (AX: rel. int./time).

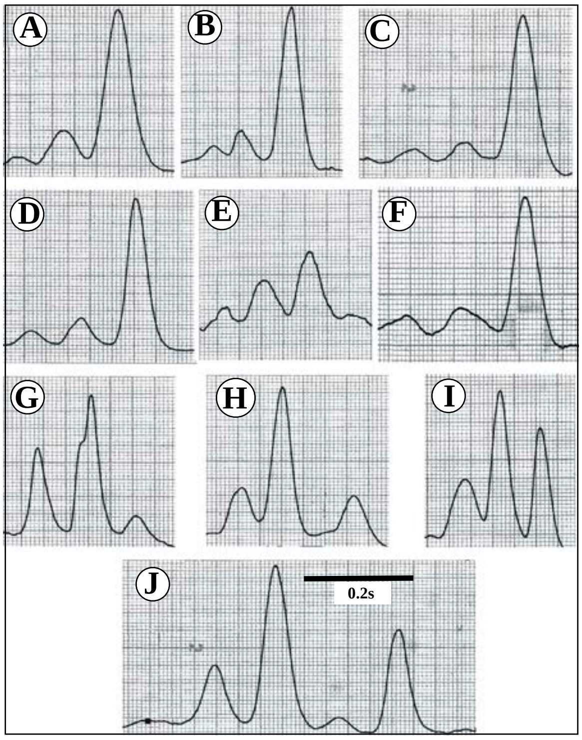


Figure 11. Sampler of mupli-pulse FPs mixed in sequences with 2-flash ("normal", bimodal) HS FPs (scale the same in all; AX: rel. int./time).

The only sexual flash-exchange and coming-together data at hand—after a chance/serendipitous detection—was “caught on the PM-recorder.” A flying flashing male received a >second-long, down-tapering flash-response, approached and after additional flash exchanges landed near the female (**Fig. 10A**); both were captured. Pulse-intensity ratios of the male’s FPs were *reversed* at times during his approach; the timing of two female response-flashes apparently were recorded (**Fig. 10B, C**; note key numbers below the trace in **10A** and referenced FPs below, in **D-I**). In **Figure 10A-B** white arrows indicate apparent female response flashes; black arrows (at top) in **A** indicate the time span during which the male presumably landed. Note the FP intensity-ratio reversals in reference to female flashes. They may have some significance, or followed a cue from the female?

During field PM-recording when FPs appeared unusual it was "flagged" (voice on tape) for later examination. Some looked to have as three modulations; examination revealed that one actually had three, but some had four, and the intensity ratios of included pulse-pairs varied. As experience is able to judge, none were the result of flashes of more than one individual simultaneously being PM-detected. **Figure 11** illustrates several of these. The time-scale is the same for all. Whether some are adaptive, have coding significance or confuse rivals is unknown.

Variad notes; Kentucky. Brief observations of a hitching firefly, supported by PM-records from nine males on 12 June 1967 in Meade County, revealed two interesting variations from New York *bridgeniensis*. Note that unit FPs from NY and KY are identical (cf traces **Fig. 12A** and **12B**), as demonstrated by many PM records: at similar temperatures (18.9°/66° and 17.8°/64°) the mean modulation rate of the KY sample (3 males, 17 FPs) was 11.1 Hz; and for the New York (Bridgen) sample at an only slightly lower temperature (3 males, 16 FPs was 10.6 Hertz. However, FP periods differ considerably: observe the sequences in **Figure 12C** and **12D** from which these compared FPs were taken, that the mean KY period/rate is 3.82 sec/0.26 Hz; and in the NY (Bridgen) sample is 1.6 sec/0.63 Hz. That is, the Kentucky FP period rate was less than half that of the Bridgen, New York sample. Though many New York HS were observed, not one was ever noted under any circumstance to emit their FPs at rates anywhere near those observed in the Kentucky population. The second difference noted in the Kentucky sample is the complete lack of pulse-ratio reversals, as discussed above or the appearance of 3-4-pulse FPs among any of the 40 FPs from nine males PM-recorded in Kentucky.

The **Ball's Gulf** variad in western New York State series had a longer FP period and the hitch more difficult to see; measured @ 22.8/73°: 2 2 2.3 2.2 2.2 2.4 2.3 2.8 2 2.4 2.3 2.3 2 2.1 2.3 1.8. 9 July 1966.

Nomenclatural Note. The scientific name is from the family “homestead” of 1940-1970, which derived its name from the name given by children in reference to the creek bridge leading to the house, barns, and 18 acrea of fallow firefly country. This site is in the Cowaselon Creek Valley, which drains the confining glacial hills of the terminal moraine of the Wisconsian Glacier to the Mohawk Valley, at Oneida Lake to the north.

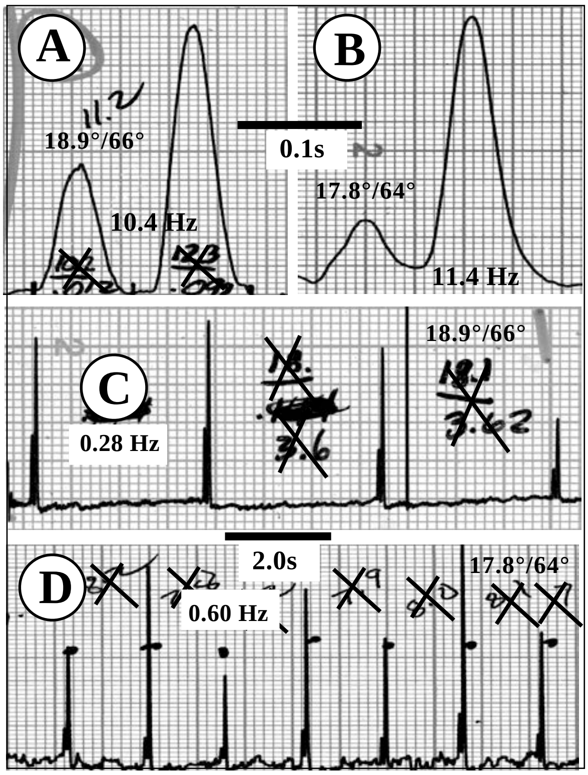


Figure 12. Comparison: KY: A, C; NY: B, D (AX: rel. int./time).

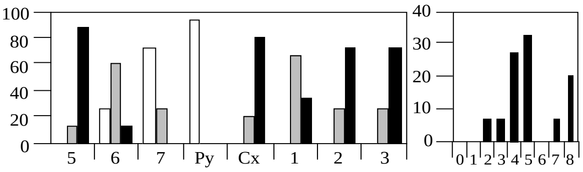
Figure 13. Expansive marsh near Vernon, Oneida County, NY.

Figure 14. Trestle site at Greene, Chenango County, NY.

* * *

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.527	10.707	3.273	1.913	2.460	7.280	13.220	.775	1.292	.682
sd	.096	.610	.139	.125	.145	1.074	.664	.030	.041	.093
se	.025	.158	.036	.032	.038	.277	.171	7.799E-3	.011	.024
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.800	3.100	1.600	2.100	5.000	12.100	.710	1.240	.460
max	2.800	11.800	3.500	2.100	2.800	9.100	14.400	.810	1.360	.810
Vc%	3.8	5.7	4.3	6.5	5.9	1.5	5.0	3.9	3.2	13.6

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	2.933	1.867	1.267	1.067	2.800	2.333	2.733	2.733	5.133
sd	.258	.640	.458	.258	.414	.488	.458	.458	1.846
se	.067	.165	.118	.067	.107	.126	.118	.118	.477
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	2.000	2.000	2.000	2.000	2.000
max	3.000	3.000	2.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	8.8	34.3	36.2	24.2	14.8	20.9	16.8	16.8	36.0



FigTable 15. Stats and colors, Madison Co. NY.

Morphological summary. Means (n=14): PNL 2.5, ELL 10.7, PNW 3.3, EWhum 1.9, EWmid 2.5, ELVit 7.3, TOTLen 13.2, PNrat 0.78, ELWrate 1.29, ELVTrat 0.68 (**FigTable. 15A**, with other stats); colors in **FigTable 15B-C**, pre-lantern ventrite splash in **15D**. **Figure 16** is key for anatomical elements and splashing on ventrite 4.

Holotype description. male, voucher number 68713, collected 15 June 1968, Madison County, New York, Creek Road at "the Bridgen homestead", about 5 miles southwest of Oneida. (FB page 124: "KB 39—hitched single recorded." Specimen with red-4 (@humerous right elytron, red paint dot); 1 of 5 so marked, flying, emitting hitched-single FP, 13 June 1968 (FB page 119). Morphological data: genitalia extruded remain attached; from spread sheet—PNLen 2.6, ELLen 10.8, PNWid 3.3, ELWhum 1.9, ELWmid 2.5, LELVit 7.5, TotLen 13.4, PnRat 0.81, ElRat 1.33, VitRat 0.70; Colors: T 222, Py 1, Cx 3,V 333, Edg 5. Types will be deposited in the USNM.

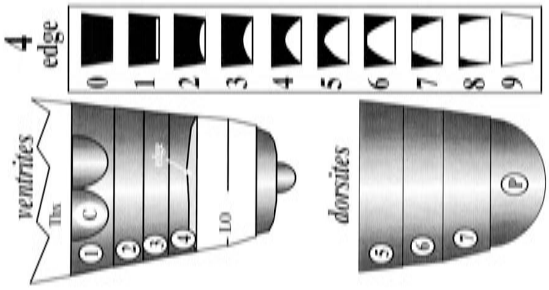


Figure 16. Topographic and splash keys.

Chapter 20

Photuris caerulucens Barber 1951

Slow Blue Firefly

Barber described *caerulucens* from specimens collected in low, damp areas near Stockton, Minnesota (**Fig. 1**), and just across the Mississippi near Bluff Siding, Wisconsin, the Type locality (**Fig. 2**). From Barber (p. 32): “According to the collectors, who called this firefly ‘Slow Blue,’ the normal male flash pattern [FP] is a steady bluish-green light of about a second’s duration, dimly visible for some time after the flash.” Barber illustrated this as shown in **Figure 3A**. In 1970, guided to the original *caerulucen's* sites by its two original collectors (Eunice Myers and Robert Boland, **Fig. 14**), 44 firefly generations after the fact, this writer had the opportunity to observe their firefly early in his *Photuris* pursuits, with them at both of their localities. Barber’s *caerulucens* is here operationally, tentatively viewed as but one of many diverged/diverging demes/variads in a Penn-Group that emit a variety of "Long-Flash" FPs (**Fig. 3A-K).** The diagnostic FP described by the original observers is the key recognition character of *caerulucens* FP. The dim after-glow Myers and Boland described was not noted, but is occasionally seen in males of all luminous genera—Barber did not include it in his figure. Also, though the original collectors perceived a bluish bioluminescence (*caeruleus*, L., blue); this was not noted (see also below). The adjunct twilight short-flash FP seen in some populations in the Penn-Group was not observed at the original Stockton site in 1970, but found to occur in 1991 at a nearby location. The short-flash FP is perhaps used *conditionally*, in some but not other habitat types, or at different stages in a phenological progression. A composite map showing all known Long-Flash and Dot-Dash occurrence records is shown in **Figure 4,** and **Appendix**.

Figure 1. Stockton, MN 1926 *caerulucens* site, in 1970.

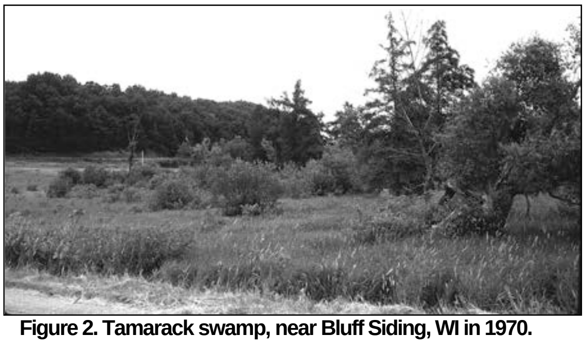


Figure 2. Tamarack swamp, near Bluff Siding, WI in 1970.

Potentially contributing to *caerulucens* confusion—in a narrowed but reasonable view from the bench—is that an argument might be made that Barber’s short-flashing *aureolucens* that were collected with *caerulucens* in 1926 and 1970 at the Bluff Siding site could be *caerulucens.* As noted in the *aureolucens* section, and as their Latin names indicate (*aureolus*, L., golden)—though human vision often errs seriously—luminescence color of the two does actually differ slightly, and in the appropriate direction—peaks as measured by Seliger and Biggley (551 versus 554 millimicrons); and also from side by side comparison of glows in a killing bottle, as determined by two observers (one an unknown biology student attending a local college who had stopped by the tamarack swamp).

Morphological comparisons indicate general similarity if not identity among the populations included here in the Long-Flash Set, though considering the history of *Photuris* taxonomy not too much should be made of this.

Flashing behavior. Males flew a few feet over the tops of grass and herbs in straight or slightly winding courses, and emitted their long flashes during slightly downward-sloping flight. They sometimes flew angularly-rotated path-segments whereby each successive FP was emitted along a slightly different azimuth, angled perhaps 5 degrees or so. The adaptive significance of this seems readily apparent, and its initiation may depend upon low male density when individual males can access more competition-free space with each FP. During each flash males slowed their flight, typically covering from a few inches up to three or more feet, but occasional they traversed up to ten feet during a flash. Males occasionally flew high in bordering trees.

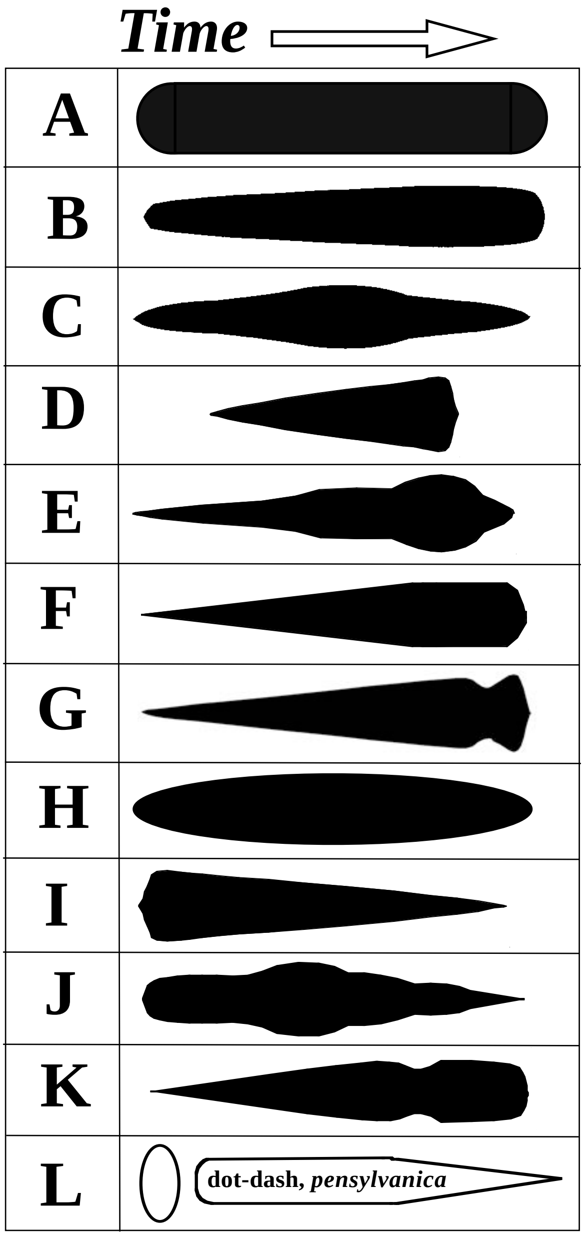


Figure 3. FPs of *caerulucens* s.l.(!) and operational kin-Group's iconic/brand FP, L.

The FP is not as simple as would be presumed from casual observation and as described and illustrated by Barber (**Fig. 3A**). At original localities a slight crescendo was often noted (**Fig. 3B**); some flashes appeared to be steady in intensity with a sharp OFF, others to have a tapered OFF; some appeared to have an intensity bump in the middle (**Fig. 3C**). The few PM-recordings suggest that such appearances may sometimes be misleading: two show a rapid-rise crescendo of about 700 mSec duration (**Fig. 5A, C, D**, 25.5°/78°; as in **Fig. 3D**), and one has a step (**Fig. 5A, B,** as in **Fig. 3E**). Some visual and PM intensity variations could perhaps be the result of males weaving and twisting in flight, enhancing broadcast over larger areas. Visual appearances are mentioned because they are useful in field identification and might otherwise be confusing, though they may be at some variance with actual intensity emitted at the lantern which may be closer to that seen by a female from below an approaching male.

SWAT measurements of long-flash duration varied considerably, and factors other than temperature, such as rival competition/density or vegetation type are probably involved. Note these SWAT-measured duration ranges at temperatures: r=0.9-1.1 sec, @25.8°/78.8°, n=7; r=1.1-2.0, @21.8°/71.3°, n=9; r=1-1.8, @18.6°/65.5°, n=8; r=2.1-2.7, @16.1°/61; one was timed at 2.3 seconds @14.4°/58°.

No indication of a “vestigial” bright or transitional *pensylvanica*-dot at the beginning of any *caerulucens* FP was ever noted; nor were any twilight short flashes observed in 1970 observations; but, in 1991 at a site a mile further west of the original Stockton site twilight short flashes were seen.

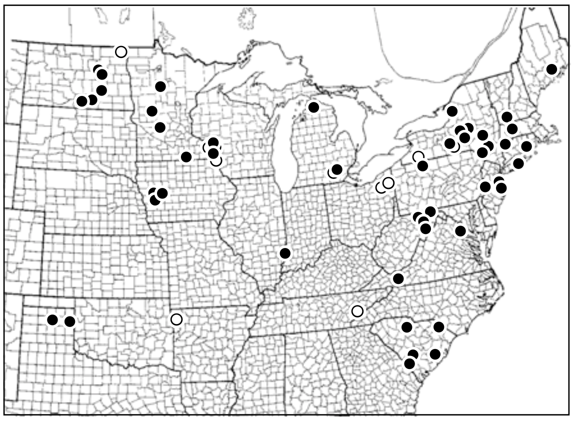


Figure 4. Dot-dash (dots) and long-flashing (circles) demes.

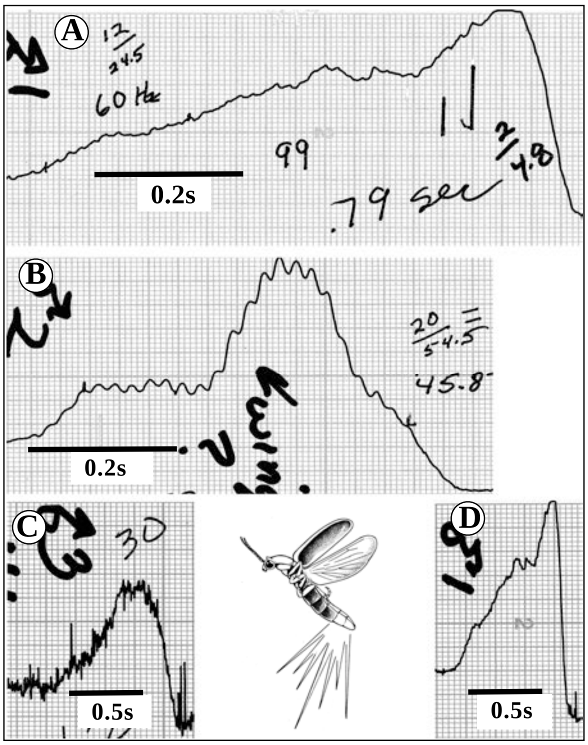


Figure 5. PM-traces (relative intensity/time).

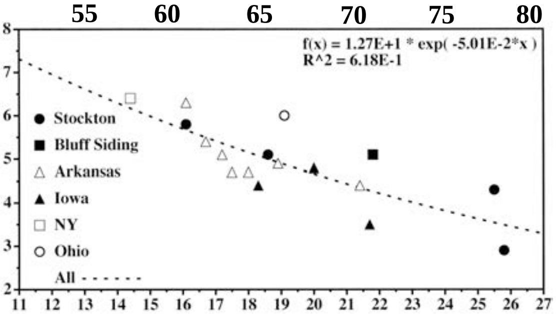


Figure 7. Mean Long FP periods of variads (AX:sec/temp).

This site was a narrow hayfield adjacent to an oldfield, gully and stream; a few dot-dash FPs were also were seen. Short flashers were few in number and appeared only at twilight. When answered with a short-flash decoy and by a responding female, they immediately defaulted and emitted long flashes of the weak-crescendo form (**Figs. 3B**); these were emitted at shorter intervals than when cruising, which is shown in **Figure 7** with data from other Long-Flash-Group variads. **Figure 8** shows the rate regression for these periods. No measurements were made of the short-flash periods but those of two "related" variads are shown (**Fig. 9**).

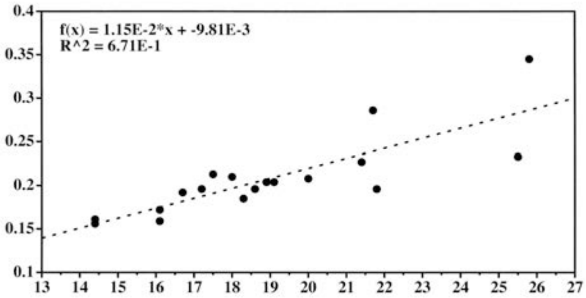


Figure 8. Mean FP (interval) rate (AX:sec/temp).

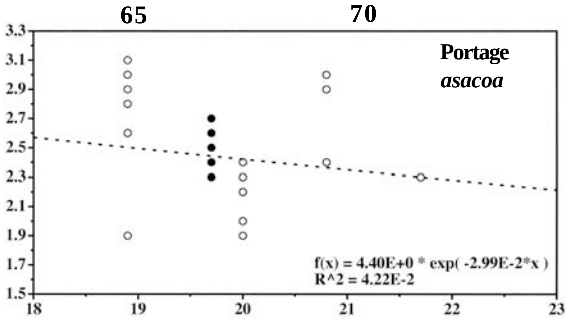


Figure 9. Short FP period (AX:sec/temp).

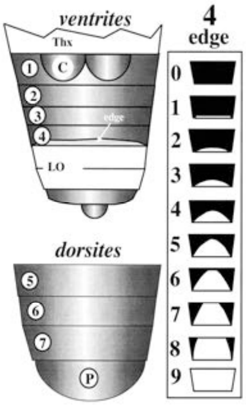


Figure 10. Topographic and splash keys.

Morphological Data. Figure 10 is a key to skeletal plates and splashing on ventrite 4; **FigTable 11** shows measurements, ratios, and colors for the MN and WI vouchers; **Figure 12** shows the PN vittagram arrays for the MN and WI vouchers. A comparison of regional Long-Flasher variads is discussed below and data for comparison are together in the **Appendix**.

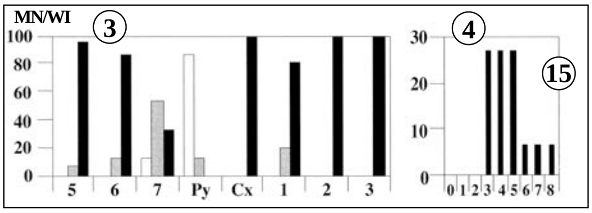
Taxonomic and other notes. The epithet of the scientific name of this firefly means blue light (L); Barber obviously took it from the flash color that the collectors of his specimens reported. The common name is that used by the original collectors Miss Eunice Myers and Bernard F. Boland (**Fig. 14**). I met them in 1970 when I visited the Stockton area to see Barber's species and relocate the sites where his specimens had been collected. Mr. Boland was listed in the Winona phone directory and we arranged to meet at the campground where I was staying and he brought Miss Myers. In 1926 she was a teacher and Boland one of her students. She had been Barber's technician in Washington and knew him well and confirmed what I had learned from others who were familiar with his experience at the museum—among other things, that he was under great pressure not to publish his firefly work. Miss Myers told me a detail about Barber's curating techniques that I had not heard; he used hair from between tiger toes to mount certain minute beetles that he studied. Miss Myers was able to recall the exact sites where they had collected Barber's *caerulucens* and *aureolucens* (**Figs. 1** and **2**). The horseshoe curve in the road near Bluff Siding was the key landmark that identified the tamarack swamp for her, and when I returned in 2003, 31 years after my first visit, it was the same, though a bridge nearby had been replaced. In the Figure one leg of this near-horseshoe curve can be seen in the distance part way up the hill toward the woods.

MN/WI ①

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.573	10.653	3.273	1.933	2.480	7.220	13.227	.790	1.294	.676
sd	.128	.678	.212	.176	.193	.836	.769	.036	.125	.060
se	.033	.175	.055	.045	.050	.216	.198	9.207E-3	.032	.016
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.600	2.900	1.500	2.100	6.300	12.000	.720	1.120	.580
max	2.900	12.000	3.600	2.300	2.900	8.800	14.600	.850	1.640	.800
Vc%	5.0	6.4	6.5	9.1	7.8	11.6	5.8	4.6	9.7	8.9

MN/WI ②

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	2.867	2.200	1.133	3.000	2.800	3.000	3.000	4.600
sd	0	.352	.676	.352	0	.414	0	0	1.502
se	0	.091	.175	.091	0	.107	0	0	.388
n	15	15	15	15	15	15	15	15	15
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	12.3	30.7	31.1	0	14.8	0	0	32.7



FigTable 11. Measurements, ratios, and colors for MN and WI vouchers.

Years later, probably in the late 1990's, when planning a trip to revisit the *caerulucens* sites, I spoke briefly with Mr. Boland by phone. I never managed to make the trip. Returns to sites worked after a long time long is informative though nostalgic, when so much time and ecology has passed.

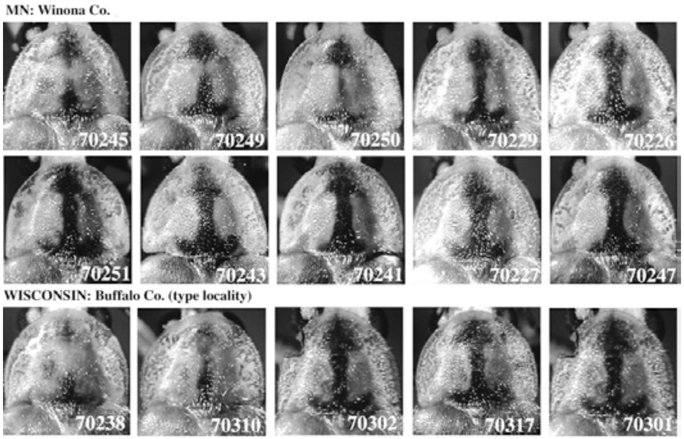
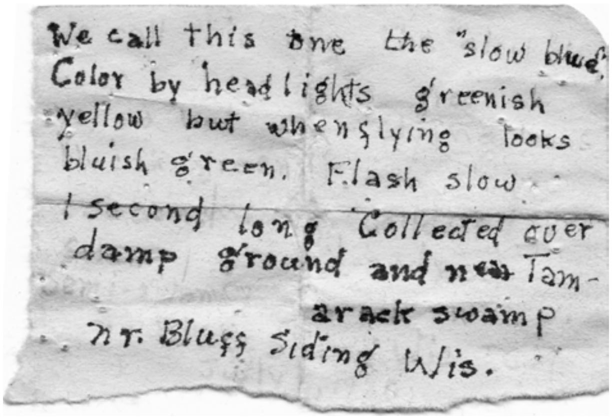


Figure 12. PNV arrays from two localities.



We call this ~~one~~ the "slow blue"
Color by headlights greenish
yellow but when flying looks
bluish green. Flash slow -
1 second long Collected over
damp ground and ~~near~~ Tam-
arack swamp
nr. Bluffs Siding Wis.

Figure 13. Descriptive note with specimens from Eunice Myers to Barber. The note appears to have originally been in a bottle of alcohol with specimens but when I saw it, it was pinned with one of the vouchers. Note the many pin-holes.

Figure 14. Miss Eunice Myers and her student, Mr. Bernard Boland, years earlier, in 1926. They provided Barber with *caerulucens* and *aureolucens* specimens with notes on their FPs. This photo was taken 44 years later, in 1970. Just beyond the highway that runs along the top of the raised berm behind them is the Stockton site (Fig. 1; scanned from a Polaroid® photo). Previously Myers had been Barber's technician, and perhaps the one who told this writer that Barber preferred to mount tiny beetles on hairs snipped from between tiger toes—a question for forensics perhaps, and part of firefly history.

❄ ❄ ❄

Appendix—Comparing Data Of the Long-Flasher Set of the Penn-Group

Text next page.

MN/WI

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
x̄	2.573	10.653	3.273	1.933	2.480	7.220	13.227	.790	1.294	.676
sd	.128	.678	.212	.176	.193	.836	.769	.036	.125	.060
se	.033	.175	.055	.045	.050	.216	.198	9.207E-3	.032	.016
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.600	2.900	1.500	2.100	6.300	12.000	.720	1.120	.580
max	2.900	12.000	3.600	2.300	2.900	8.800	14.600	.850	1.640	.800
Vc%	5.0	6.4	6.5	9.1	7.8	11.6	5.8	4.6	9.7	8.9

IA

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNRat	ELWrat	ELVTrat
x̄	2.860	11.327	3.467	2.087	2.619	7.780	14.160	.833	1.260	.685
sd	.199	.578	.172	.151	.100	1.296	.735	.072	.091	.098
se	.051	.149	.044	.039	.026	.335	.190	.019	.024	.025
n	15	15	15	15	15	15	15	15	15	15
min	2.500	10.600	3.100	1.900	2.500	5.000	13.250	.700	1.100	.470
max	3.100	12.500	3.900	2.400	2.750	9.800	15.500	.900	1.500	.810
Vc%	7.0	5.1	5.0	7.2	3.8	16.7	5.2	8.6	7.2	14.3

OH

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
x̄	2.800	11.283	3.500	2.000	2.600	7.733	14.083	.798	1.307	.685
sd	.219	.479	.261	.089	.110	.671	.659	.033	.073	.050
se	.089	.196	.106	.037	.045	.274	.269	.013	.030	.020
n	6	6	6	6	6	6	6	6	6	6
min	2.500	10.900	3.100	1.900	2.500	7.000	13.400	.750	1.240	.630
max	3.100	11.900	3.900	2.100	2.800	8.900	15.000	.850	1.400	.750
Vc%	7.8	4.3	7.5	4.5	4.2	8.7	4.7	4.1	5.6	7.3

AR

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
x̄	2.920	11.360	3.680	2.080	2.580	7.600	14.280	.802	1.242	.656
sd	.249	.853	.239	.148	.179	2.769	1.080	.030	.041	.218
se	.111	.382	.107	.066	.080	1.238	.483	.014	.019	.098
n	5	5	5	5	5	5	5	5	5	5
min	2.500	10.100	3.300	1.900	2.300	2.800	12.600	.770	1.200	.270
max	3.100	12.500	3.900	2.300	2.800	9.900	15.600	.830	1.310	.790
Vc%	8.5	7.5	6.5	7.1	6.9	36.4	7.6	3.7	3.3	33.2

NY

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
x̄	2.475	10.500	3.125	1.900	2.450	7.700	12.975	.792	1.300	.733
sd	.096	.663	.206	0	.129	.913	.741	.030	.085	.072
se	.048	.332	.103	0	.065	.456	.371	.015	.043	.036
n	4	4	4	4	4	4	4	4	4	4
min	2.400	9.600	2.900	1.900	2.300	6.600	12.000	.760	1.200	.660
max	2.600	11.000	3.400	1.900	2.600	8.500	13.600	.830	1.400	.820
Vc%	3.9	6.3	6.6	0	5.3	11.9	5.7	3.8	6.5	9.8

caerulucens
(s MN/WI)

asacoa
(ne IA)

ne OH

nw AR

sw NY

MN/WI

	5	6	7	Py	Cx	1	2	3	4
x̄	3.000	2.867	2.200	1.133	3.000	2.800	3.000	3.000	4.600
sd	0	.352	.676	.352	0	.414	0	0	1.502
se	0	.091	.175	.091	0	.107	0	0	.388
n	15	15	15	15	15	15	15	15	15
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	12.3	30.7	31.1	0	14.8	0	0	32.7

IA

	5	6	7	Py	Cx	1	2	3	4
x̄	2.933	2.933	2.800	1.000	2.867	2.733	2.867	2.933	4.333
sd	.258	.258	.561	0.000	.352	.458	.352	.258	1.633
se	.067	.067	.145	0.000	.091	.118	.091	.067	.422
n	15	15	15	15	15	15	15	15	15
min	2.000	2.000	1.000	1.000	2.000	2.000	2.000	2.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	8.8	8.8	20.1	0	12.3	16.8	12.3	8.8	37.7

OH

	5	6	7	Py	Cx	1	2	3	4
x̄	3.000	2.714	2.429	1.000	3.000	2.857	3.000	3.000	4.286
sd	0.000	.488	.787	0.000	0.000	.378	0.000	0.000	1.380
se	0.000	.184	.297	0.000	0.000	.143	0.000	0.000	.522
n	7	7	7	7	7	7	7	7	7
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	18.0	32.4	0	0	13.2	0	0	32.2

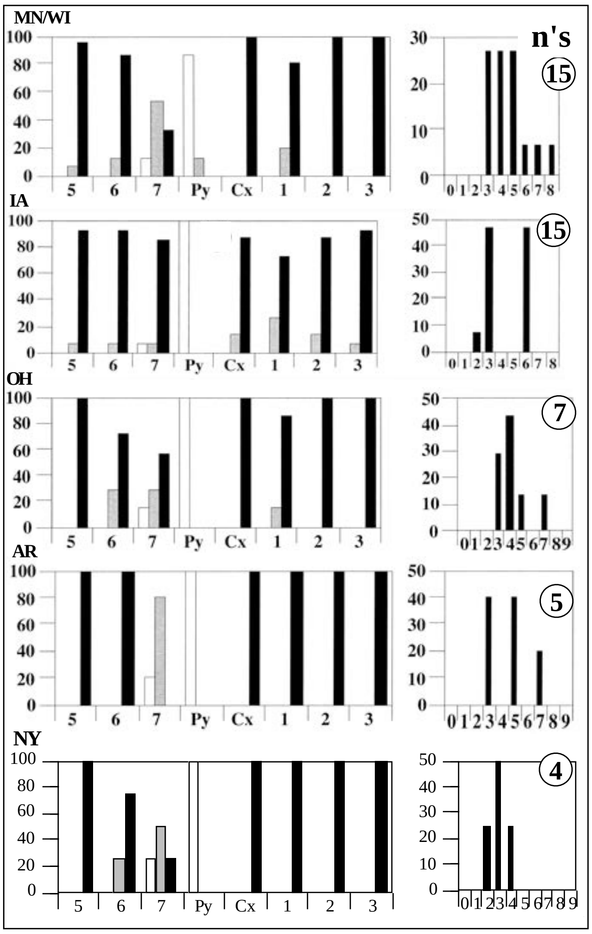
AR

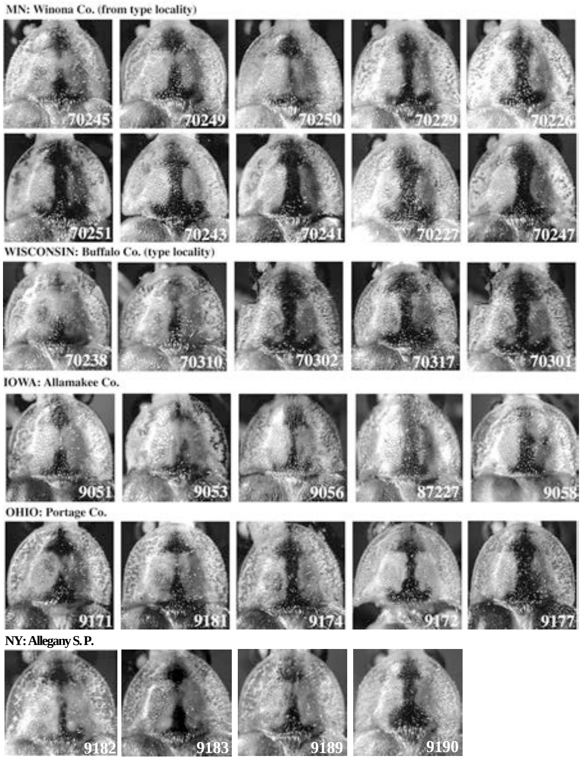
	5	6	7	Py	Cx	1	2	3	4
x̄	3.000	3.000	1.800	1.000	3.000	3.000	3.000	3.000	4.600
sd	0	0	.447	0	0	0	0	0	1.673
se	0	0	.200	0	0	0	0	0	.748
n	5	5	5	5	5	5	5	5	5
min	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	0	24.8	0	0	0	0	0	36.4

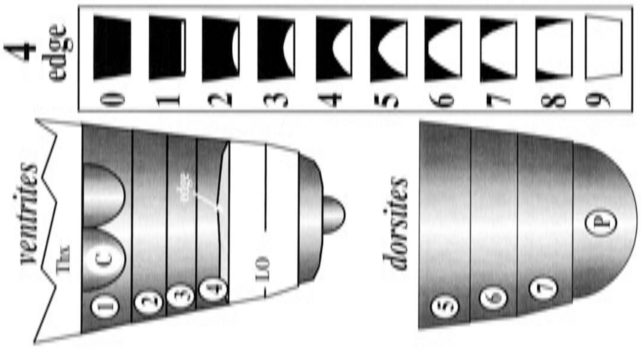
NY

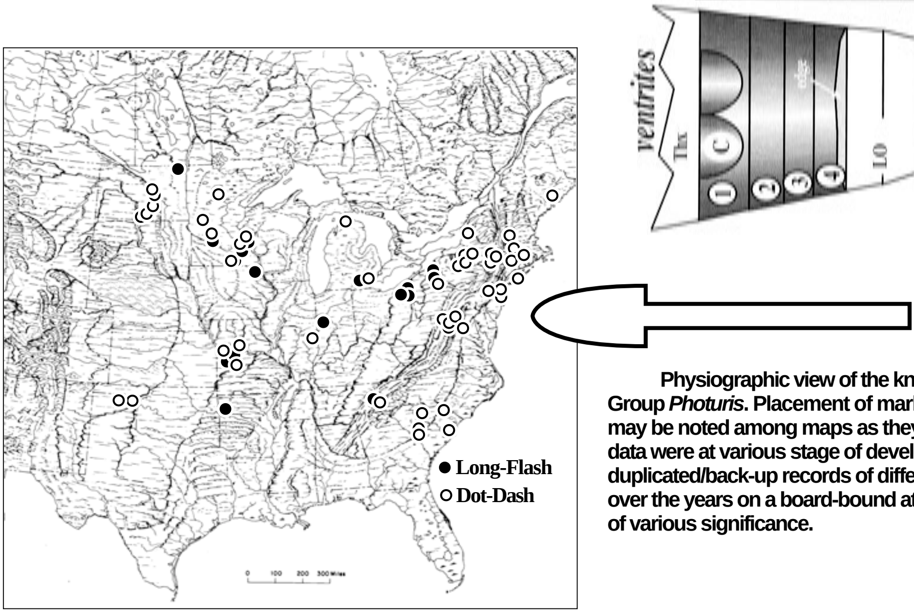
	5	6	7	Py	Cx	1	2	3	4
x̄	3.000	2.750	2.000	1.000	3.000	3.000	3.000	3.000	3.000
sd	0.000	.500	.816	0.000	0.000	0.000	0.000	0.000	.816
se	0.000	.250	.408	0.000	0.000	0.000	0.000	0.000	.408
n	4	4	4	4	4	4	4	4	4
min	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	4.000
Vc%	0	18.2	40.8	0	0	0	0	0	27.2

Long-Flashing Variads: tables, charts, and photos, for comparisons of measurements, ratios, colors, and vittagrams. A subjective scan of the numbers in the tables above left reveal no outstanding significant differences, though the Allegany (sw NY) population perhaps appears marginal. Numerical conversions for the colors of various abdominal plates (sclerite combinations) and hind coxae and splashing on ventrite 4 are shown numerically (above right) and graphically below, but attract no attention. Arrays of vittagrams from variad demes (below), reveal nothing eye-catching—but there are difference in the sample sizes of the compared populations; note there is only an occasional appearance of a flared serif—once a hoped-for Group indicator.









Physiographic view of the known/observed occurrence of Penn-Group *Photuris*. Placement of markers is approximate; some differences may be noted among maps as they were produced at different times when data were at various stage of development and scattered among duplicated/back-up records of different ages. Most, however, were plotted over the years on a board-bound atlas of UMMZ maps with scattered notes of various significance.

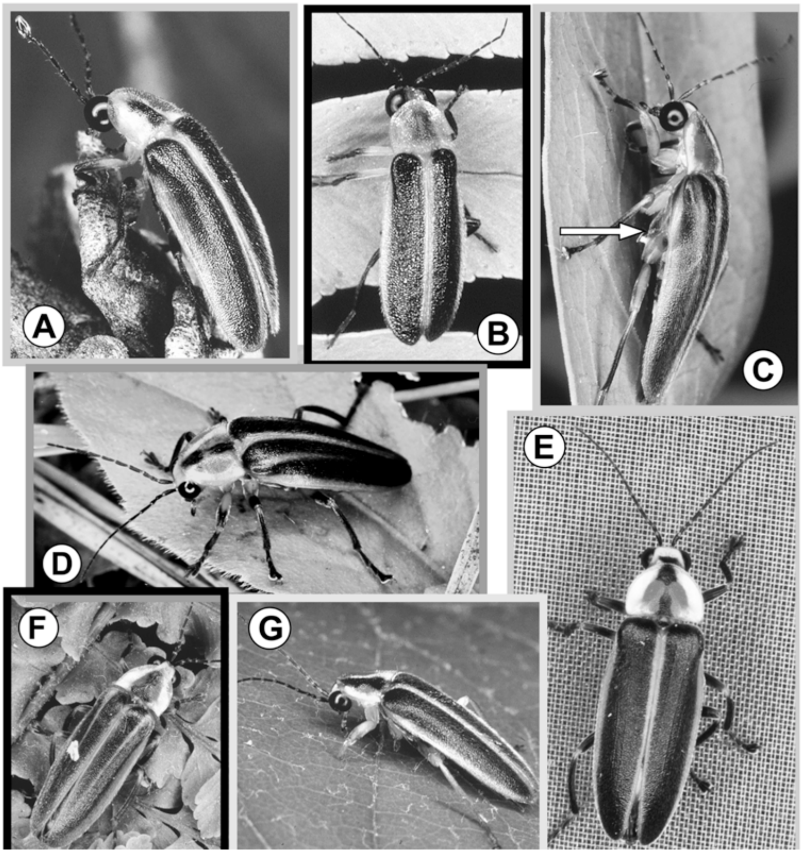
Read this before making identifications. For a century or more *Photuris* defied taxonomic resolution or even a rough beginning because of the lack of consistent characters that could be sorted into patterns. Knowledge of flash patterns finally permitted a preliminary sorting, and from this it was found that morphology can play a small role in identification. The morphology of *Photuris* with (non-train) 1-flash FPs (set BB in Chapter 8) can sometimes be used to make identification simpler. Some emit 1-flash FPs as an adjunct FP, and some will default to a recognizable FP if answered with a decoy flash. These are mostly, but not entirely late-twilight, forest-edge, low grass/herb flyers. When collecting vouchers of a 1-flash species, at that time check to see whether they will default to a distinctive recognizable FP—e. g. J3-4, the dot-dash, or crescendo. This provides an indespensible clue to ID.

A few *Photuris* have 1-flash FPs as their primary (default) FP, and they will require the use of other details, including geography, measurements, and ecology. Habiti, in a few cases, can narrow the search. When the guide to FP morphology is consulted there is long list of possibilities connected with choice BB, **non-train, single flash emitters**; do the following:

1. Following Barber-McDermott's couplet 1, exclude Division I species (examples in **Fig. 1 A, B; also** check genitalia, **Fig. 2**): *congener*, *divisa*, *flavicollis*, *floridana*, *frontalis*, *gentrae* (**2**). Check the color of the hind coxae: if pale or only slightly dusky or marked, this often will distinguish *hebes* and *lucicrescens* (**Fig. 1 C**). (**3**) In species of the "red group" the ground color/trim is a distinctive tawny color (brick red, rufus; **Fig. 1 D**): *dorothae*, *katrinae*, *lineaticollis*, *lynfaustae*, *maicoi*, *walkeri*. (**4**) **Figures 1 E** and **F** present variations in the general appearance of a number of species, but when the length is >14 mm either *fairchildi* or a member of the *versicolor* group is a possibility; the reality here is that **1 F** is a dot-dash species, large, and darkly pigmented enough to pass for a *versicolor*! (**5**) The distinctive, very attractive, "delicate," sharply defined firefly in **Figure 1 G** belongs to Barber's *cinctipennis* group, and though rare, especially north of Florida, the habitus is usually easily recognized.

Figure 1: (**A**) *Ph. frontalis*, Division I; (**B**) *Ph. congener* Division I; (**C**) *Ph. lucicrescens*; (**D**) *Ph. maicoi*, Red Group; (**E**) *Ph. harrannorum*, *versicolor* Group; (**F**) *Ph. cowaseloniensis* (dot-dash complex); (**G**) *Ph. branhami*, *cinctipennis* Group. **Figure 2**: *Ph. congener* aedeagus (Division I) **Figure 3**: *Photuris* ? aedeagus (Division II). Compare the indicated areas in Figures 2 and 3. The differences noted here at points G-J, that is, the simplicity in Figure 2, may hold for other species in Division I?

Figure 1.



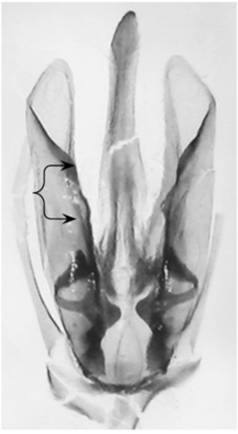


Figure 2.

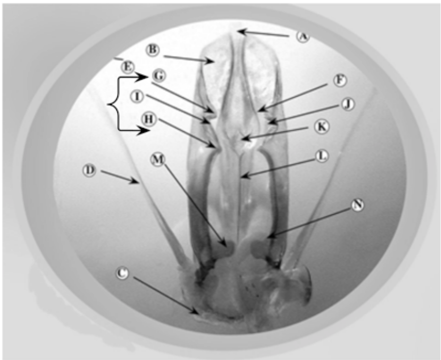


Figure 3.

Chapter 21

Photuris campestra n. sp.

Notch-Dash Flasher

Near the northeastern corner of the Texas panhandle is not where a "*penn*-like" firefly was expected (**Fig. 1**), and it perhaps is a stretch to consider this firefly "*penn*-like." Its ≈1-second-long flash sometimes appears to have a single notch of varying depths near the beginning or at various positions, rather than a preliminary dot (**Fig. 2**), and the notch is not always visible, though is often conspicuous at cool temperatures, especially with peripheral vision. It sometimes presents as a twinkle or hitch. Vouchers from two and possibly three or four demes are combined in this description. Two occurred at the back of dams: the outflow of the Meredith Dam was a very large marsh with tall vegetation, and at the Black Kettle National Grassland, a low, grass-covered, earthen dike with a small wet area below was the focus of activity. Toward the bottom of Bugbee Canyon near Meridith Lake *campestra* occurred in a damp tall-grassy area next to a stream that flowed under the road and down into the Canyon (**Fig. 3**), and again along the edge of a marsh/pond at the bottom of the Canyon (**Fig. 4**). These sites were in Hutchinson County, and near Lake Marvin, and in the Black Kettle N. G. in Hemphill County. Observations were made 31 May-2 June 1999. Others seen along the Canadian River at the big bridge in the town of Canadian probably are closely related but no FP-notch was apparent, perhaps because of the higher temperature.

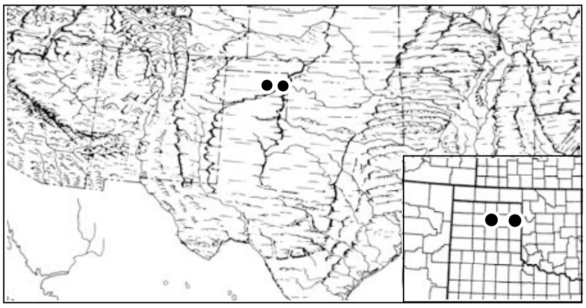


Figure 1. Wet spots on the prairie.

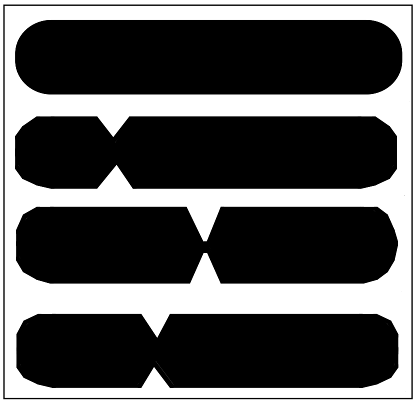


Figure 2. FP truncated and notched, twinkling and hitched, as per visual appearances.

The FP was emitted in a 1.5' stripe on a down-sloping, level, or slightly rising path at grass-tops or higher, up to four feet above the tips of cattails behind the dam; one night in the wind they flew up around the boughs of the very few cottonwoods adjacent to the Black Kettle site. FP period averaged about 3 seconds at 23.6°/74.5° (**Fig. 5**; rate in **Fig. 6**). The FP was not a flare, but of even intensity except for the notch and had fairly sharp transients at each end. A single mating-signal interaction was observed, and though the female response pattern was unusual, it may have been typical for the species(?), since it was repeated in identical form three times during the male's approach: it was a "syncopated" 3-flash response which can be described being like a 4-pulse pattern with the third pulse omitted—or else so dim it was not seen, or was aimed in a different direction (**Fig. 7**). The male repeated his FP at the same period used in searching flight as he approached, and landed about 6" from the female, atop an herb 16" above the ground.

Morphology. General morphological means are: PNL 2.8 , ELL 10.6, PNW 3.5, EWhum 2.0, EWmid 2.5, ELVit 8.1, TOTLen 13.4, PNrat 0.81, ELWrate 1.22, ELVTrat 0.76, n=4 (**FigTable 8A**, with other stats). Data for the colors of various apparent abdominal plates (sclerite combinations) and hind coxae are shown in **FigTable 8B-C**, and splash of the pre-lantern ventrite, in **8D**. **Figure 9** is a key to skeletal plates and degree of splashing on ventrite 4. **Figure 10** is a long-flash, no-notch(?) voucher (9959) from the bridge site in Canadian (see also **Fig. 12**). In the array of vittagrams in **Figure 11** only 9948 and 9951 are from the demes mentioned and vouchers for the notched long flash. The other two are from a river-side spit "under" the bridge in Canadian (9957, 9958); they emitted long flashes at 2-sec periods (25°/77°); the notch was not apparent, and it may have been present but the emission rate resulting from the higher temperature concealed it. The FP periods of the Canadian River specimens fall along the regressions from the other sites for visibly notched FPs. The data in **FigTable 8** are from FP-vouchers and do not include measurements from Canadian River specimens.

Figure 3. Roadside wet spot by a creek.

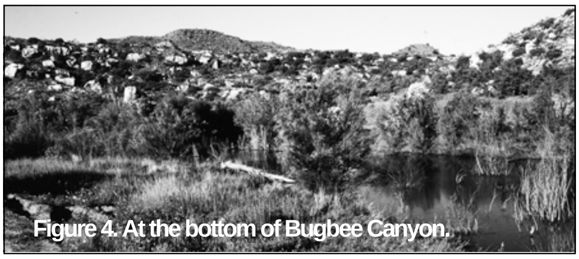


Figure 4. At the bottom of Bugbee Canyon.

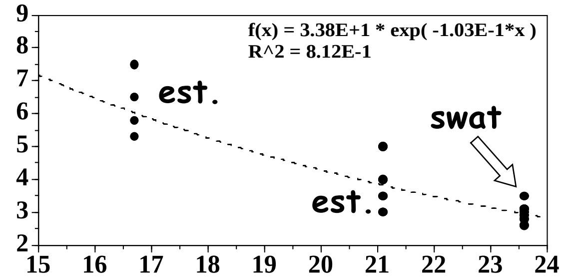


Figure 5. FP periods (intervals), indiv. values (AX:sec/temp).

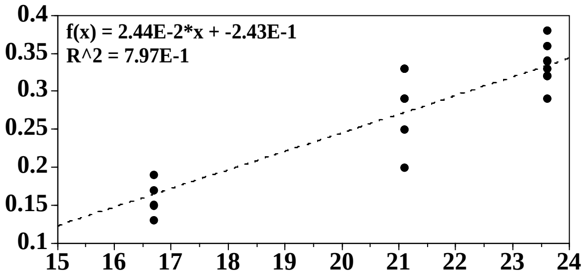


Figure 6. FP interval rates, indiv. values (AX: Hz./temp).

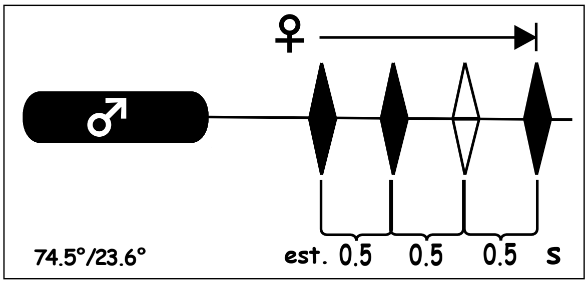


Figure 7. Observed FP and response, see text.

Holotype: male, voucher number 9950, collected 31 May 1999, Hutchinson County, Texas. FB page 118: "KB 78 ..."another voucher. midnight . back at Bugbee Canyon. penn—quite pronounced . see only 1. cool—[notch] easy to see with peripheral vision. 62°" Morphological data: genitalia well extruded, remain attached;—PNLen 2.6 ELLen 10.8, PNWid 3.3, ELWhum 2.0, ELWmid 2.4, LELVit 7.5, TotLen 13.4, PnRat 0.81, ElRat 1.19, VitRat 0.70; Colors: T 332, Py 1, Cx 3,V 333, Edg 2. Types will be deposited in the USNM.

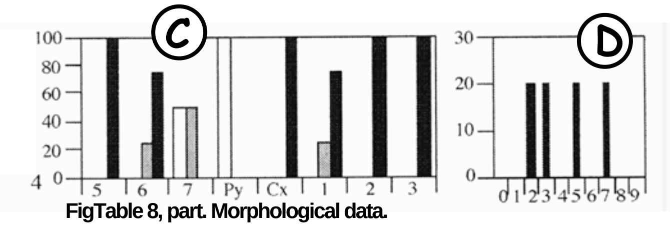
A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.825	10.600	3.525	2.000	2.450	8.050	13.400	.805	1.222	.762
sd	.171	.400	.206	.082	.058	.656	.432	.013	.044	.061
se	.085	.200	.103	.041	.029	.328	.216	6.455E-3	.022	.031
n	4	4	4	4	4	4	4	4	4	4
min	2.600	10.000	3.300	1.900	2.400	7.500	12.800	.790	1.180	.700
max	3.000	10.800	3.800	2.100	2.500	9.000	13.800	.820	1.270	.840
Vc%	6.1	3.8	5.8	4.1	2.4	8.2	3.2	1.6	3.6	8.0

B

Measured series and Paratypes: 9947, 9948, 9949 (+ Holotype).

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.750	1.500	1.000	3.000	2.750	3.000	3.000	4.250
sd	0.000	.500	.577	0.000	0.000	.500	0.000	0.000	2.217
se	0.000	.250	.289	0.000	0.000	.250	0.000	0.000	1.109
n	4	4	4	4	4	4	4	4	4
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	2.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	18.2	38.5	0	0	18.2	0	0	52.2



FigTable 8, part. Morphological data.

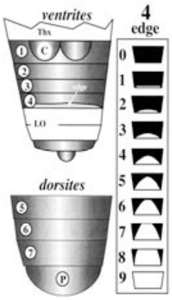


Figure 9. Key to sclerites and splash.

Figure 10. Presumptive voucher, 9959, but see text.

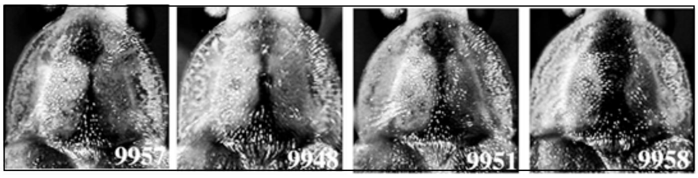


Figure 11. Vittagram array, see text.

A

Vcher#	PNLen	ELLen	PNWid	ELWhum	ELWmid	LELVit	TotLen	PnRat	ElRat	VitRat
9951	3.0	10.6	3.6	2.0	2.5	7.9	13.6	0.83	1.25	0.74
9952	2.6	10.1	3.3	1.8	2.5	7.4	12.8	0.81	1.43	0.73
9953	2.9	10.9	3.8	2.0	2.5	7.5	13.8	0.77	1.25	0.69
9954	2.8	10.4	3.4	2.0	2.5	10.4	13.1	0.81	1.25	1.00
9957	3.1	11.6	3.5	2.3	2.8	8.8	14.8	0.89	1.22	0.75
9958	3.1	11.1	3.9	2.3	2.8	8.4	14.3	0.81	1.22	0.75
9959	3.0	9.6	3.6	2.1	2.6	7.5	12.6	0.83	1.24	0.78

B

	DORSITES				Coxa	VENTRITES			
Vch #	5	6	7	Py	Cx	1	2	3	edge
9951	3	2	1	1	3	3	2	2	7
9952	3	2	1	1	3	3	3	3	7
9953	3	2	1	1	2	2	2	3	7
9954	3	2	1	1	3	3	3	3	4
9957	3	1	1	1	2	2	2	2	7
9958	3	2	1	1	3	2	3	3	5
9959	3	2	1	1	3	2	2	2	7

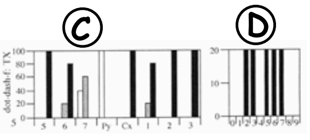


Fig. 12. Data from long-flash and other presumed *campestra* vouchers.

Chapter 22

Photuris carrorum n. sp.

Carrs’ Crescendo

This uncommon firefly is known from few sites, though perhaps it once may have occurred throughout deep southeastern pineland, in low wet places, around bayheads, along creeks, and in mesic hammocks with magnolias and bays. Presently, with one apparent exception in South Carolina, known sites are in northern Florida (**Fig. 1**), where the season of adult flashing extends from mid-May to mid-July (**Fig. 2**). In appearance *carrorum* is similar to other medium sized, crescendo-emitting *Photuris*, with pale hind coxae and 10-12 mm length, with the shaft of the vittagram reduced or interrupted in some individuals (**Figs. 3-4, 17**). Evening flashing began at full darkness, somewhat earlier in shady places. At the Austin Cary Forest (ACF) site, the Holotype locality, males flew within, throughout and closely around a small mesic copse (**Fig. 5**); in the corner of a tree-row of hardwoods (**Fig. 6**); along tree rows (**Fig. 7**); and occasionally scattered over adjacent pine where they conspicuously aimed their 1-3+-flash phrases of FPs at boughs of foliage (**Figs. 8**). Throughout the evening for two or more hours males flew from near the ground to the treetops, pausing and hovering or flying slowly around or off the ends of branches, moving slowly 3-4 inches during each flash and a few feet between phrases. Males emitted short crescendo flashes singly or in groups of up to five, rarely six. Phrases of two were the most common, and a census across a span of about a minute accounted for 90 percent of FPs seen.

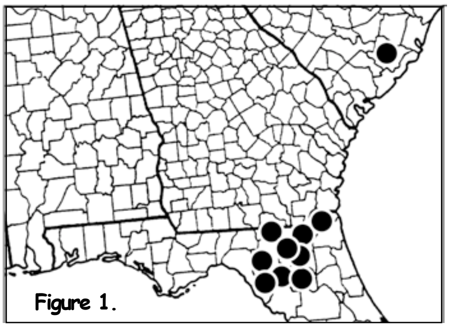


Figure 1.

Possibly—and suggesting with hesitant suspicion—at certain times, under certain, perhaps late-season conditions, males may emit *Photinus*-like *short* flashes at 2-4 second intervals(?), or 2-sec pairs of flashes; hence, for diagnosis, phrases of *crescendos* as described are necessary. Crescendo period within phrases averaged 1.7 sec (**Fig. 9**) and phrase period 7.8 sec @21°/70° (**Fig. 10**). This firefly appears clearly to belong to the working *Photuris lucicrescens* group. Females are extreme and versatile aggressive mimic and perhaps hawking aerial predators (**Figs. 11, 14**).

Flashing behavior, details. The diagnostic "FP" for *carrorum* is a group (*phrase*) of crescendos, but the term FP has a less restrictive meaning in this case: males usually emit two or more crescendos in each phrase; Example phrases are: 2-3-4-, 2-1-2-, -3-3-3-, -1-2-2. However, the functional (operative) unit for *carrorum* could be a single crescendo—perhaps under certain conditions, for enhanced advertising in coarse vegetation, or as countermeasure against female-mimicking predators, some coded arrangement or timing of crescendo groups is used.

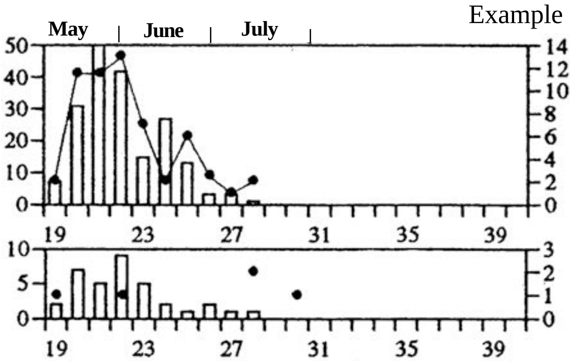


Figure 2. SESOBS Alachua County.

When attracting males to a decoy it was not necessary to flash a response after each crescendo in a phrase, nor do females themselves. In three observed attractions of males to answering females, the females flashed a short flash about a half-second after one or two crescendos of 4-flash phrases. Males rapidly darted/zipped in and landed where I had seen the responding flashes—however, no females were found in these three cases.

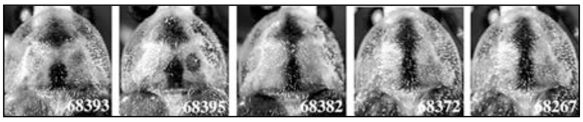


Figure 3. Vittagram array.

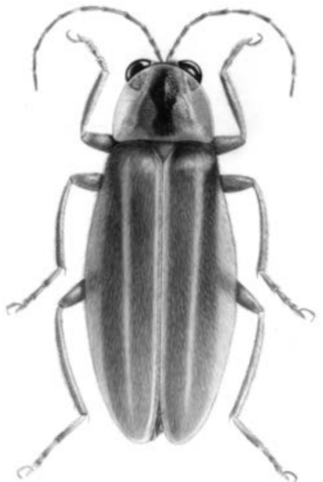


Figure 4. *Photuris carrorum*.

The crescendo, though brief, sometimes was striking and explosive in its increasing and larger-than-life brilliance, but at times intensity increase was barely noticeable, the

Figure 5. Small woods ACF site.

ramp appearing nearly flat. Sometimes a crescendo seemed to begin at half max, and when viewed from the tail-end it sometimes looked like a square wave or a simple, symmetrical flash. At higher temperatures the crescendo was more difficult to see, and it often appeared as a simple flash if the male did not move through space (swoop) during emission. Because these variations did not appear in PM-records, what the human eye sometimes sees—as also suggested for peculiarities seen in the flashes of *hebes* and others—perhaps is caused by non-synchronous flashing of the two lantern segments that are perceived separately from some directions—from the side.

Males emit *short* non-crescendo flashes at times, and dozens of evenings over several years passed at the ACF before this was seen. Suspicions were aroused when several “alien, hitherto

Figure 6. Treeline corner woods, ACF.

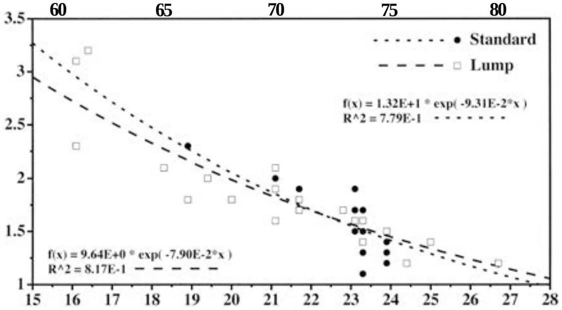


Figure 9. Intra-phrase FP period (AX: sec/deg).

Figure 7. Treeline toward corner woods, ACF; flashes sketched showing phrasing.

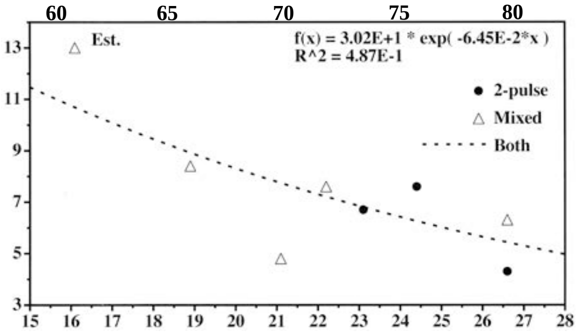


Figure 10. Phrase period and temperature (AX: sec/temp).

Figure 8. Scraggly pines and palmettos.

Figure 11. Aggressive mimic. *P. carrorum* hunter with *Photinus macdermotti*, duped prey, at the ACF.

Figure 12. Hunting area; behind building in Figure 7.

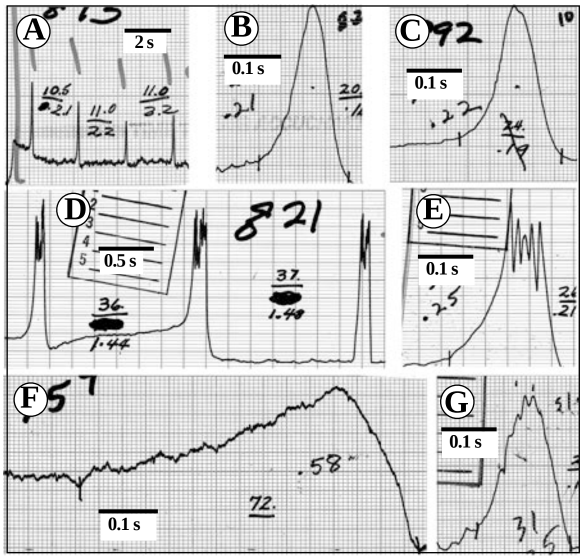


Figure 13. PM-records (AX: ri/time).

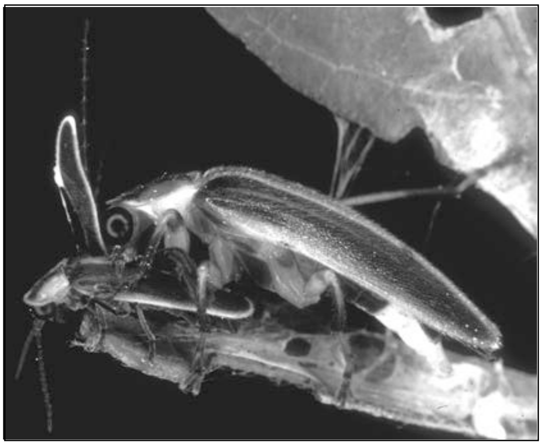


Figure 14. Aggressive mimic *carrorum* and a victim/dupe, a *macdermotti* male at the ACF.

unseen” male *Photuris* were observed emitting short flashes (or *macdermotti* pairs?) over palmettos at the edge of the main *carrorum* activity site. Subsequently, in herbs near the hunting area (**Fig. 12**), a short-flashing male received an answer, quickly approached the flash and switched FPs to an unmistakable *carrorum* 2-crescendo FP; immediately an illuminated firefly flew up out of the vegetation and away—it appeared to be male mimicry, a default and subsequent rejection—or a failed hunting deception by a female of *Ph. carrorum* or other.

From observations and PM-records the duration of the crescendo is clearly short, typically less than 1/3 secs, and from the examination of 122 PM-traces from 93 males, not all of which provided clear detail, at temperatures 22.2°-26.7°C, duration at half-max and base averaged 58/218 mSec. (**Fig. 13A-C**). The mean ratio of half-max/base duration in sets across a span of temperatures was 0.27 (r=24.6-29.5). In spite of the effort to record, measure, and carefully read and reread crescendo traces, and accumulate a reasonable sample, there remain doubts as to the accuracy of measurements because of the low and slow rise of the emission. When the gain of the PM-system was set very high purposely to detect the early moments of a crescendo—thus ignoring the loss of the (blown out) crescendo peak—and the PM-was still able to detect the decay of the flash—that is, not be electron-saturated and rendered inoperable—the crescendo was 20 percent longer (**Fig. 13D, E**). And, when a “log-PM” system was used for detection, the resulting PM-trace was even longer, but I suspect inaccurately so (**Fig. 13F**). Though it is difficult to accurately determine crescendo durations, realistically, it is probably not important to do so. What may be important to fireflies is the rise in intensity across a brief time span, one that is within the limits of even the durations that have been PM-detected, and more importantly one that establishes a level sufficient to define the OFF transient, perhaps the/a significant timing marker. This is to say, that the crescendo's slope focuses the attention of the legitimate (code-reading) receiver on the key element in time, and the OFF of the crescendo is that marker.

Aggressive mimicry, aerial predation. When one sees the hunting behavior of female *carrorum* they must reflect back to the original theorists of mimicry concepts in the 19th and early-to-mid 20th centuries—when the notion was met with strange and fierce resistance by back-benchers—and wish that Bates, Müller, and especially E. G. Peckham who introduced the concept of aggressive mimicry—though there is some confusion in the old records—could accompany them to the ACF to view the small patch of lawn and watch the proceedings (**Fig. 12**). Imagine, in wax myrtle bushes behind the grasses along the edge of the killing field a few wee *Photinus floridanus* male are seeking mates, though most have quit for the night. Over the palmettos on the far side of the shrubs and back into the scraggly pines *Photinus macdermotti* males were doing likewise. And *carrorum* females, perched in the herbs and on lawn, are dining out.

Sometimes they out-number the available *floridanus* females four to one (12/3). These lawn leopards leave their perches to fly up in front of a passing decoy light, emit their false signal while in flight, and then drop back to the vegetation, and sometimes walk down a stem to a position deeper within the herbage. Once, when trolling with a *macdermotti*–FP penlight decoy, one female hovered a foot from the decoy, then landed on my hand, and then two others appeared out of the dark and joined her. Another approached a long-flash *collustrans* simulation to three inches and hovered, waiting perhaps. When presented with a *floridanus* FP (single short flash) perched females answered, but their delay at 0.5 sec appeared a bit too long, and then, when presented with a *macdermotti* 2-pulse FP they would err the first time or two or three, but then answer correctly (**Fig. 15**).

Males of *floridanus* are so tiny that initially it was questioned whether they would be hunted, be worth the expended effort, time and energy. When the virtual identity of the signals of *Photuris douglasae* and the <*floridanus*-sized *Photinus lineellus* was recognized through PM-records, it was questioned whether the mimicry might not be better explained as *douglasae* copying little *lineellus* to escape aerial predation by *Photuris* females. Apparently even a tiny portion of poisonous blood and meat works in a tight budget. But the mimicry of *Photuris* females, though it sometimes appears to be perfect, cannot be, for males apparently detect flaws, and some are not deceived. As example: A *Pn. macdermotti*-hunting *carrorum* female on a six-foot high wax myrtle perch at the edge of the woodland copse, answered 25 passing males before she finally caught one, enjoying a success rate of merely 4 percent (**Fig. 14**). This is as expected, as packaged in a *life-dinner* aphorism: natural selection is stronger on prey, where lives are at stake, individuals sometimes totally losing out in reproduction; and, other things being equal, it is weaker on those that merely miss out on but a single meal.

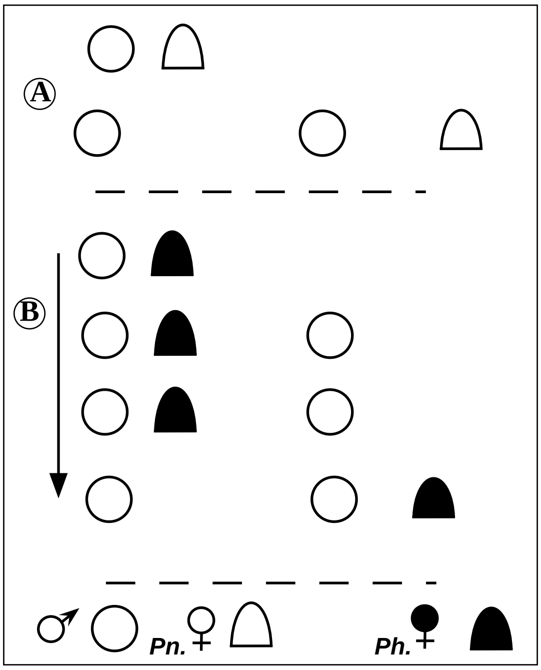
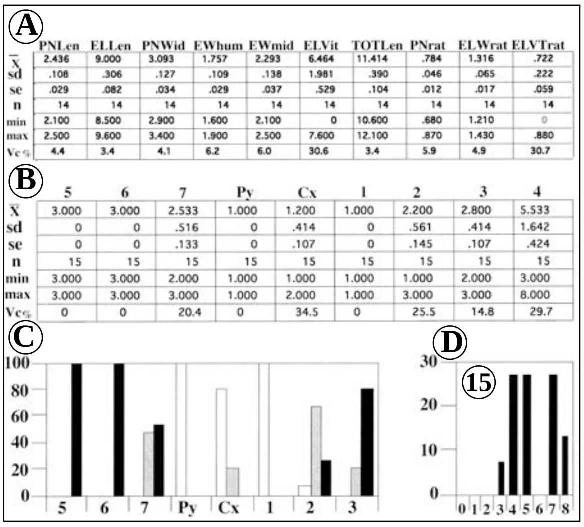


Fig. 15. Adjustment of a predator with a repertoire; as observed via penlight experimentation by UF firefly-class students on a campout.

At the ACF there were four *Photinus* prey species potentially available in *carrorum's* season—species that all presumably have the poison-laden blood with a rare and special currency. Though *carrorum* females were found flash-responding in the *collustrans* short grass area some 200 feet from centers of *carrorum* mating activity, and their flashed answers were timed nearly correctly, *carrorum's* flash did not linger on as a gradually-dimming glow for several seconds as would those of *Pn. collustrans* females. However, if a male in high competition landed or his grounded flashes attracted interloping males, *carrorum* might successfully scramble and find one on the ground. The single flashes of *Pn. umbratus* males were answered by *carrorum* females, but *umbratus* females delay their flashes for a few seconds and *carrorum* has only been seen to answer at a half-second delay. Answered males were not attracted. Though a dozen predators perched at the edge of the *floridanus* site, there were few *Photinus* males active by the time hunting started; probably the later-active *macdermotti* males, at least at the ACF site were the main prey for *carrorum* females.

Finally, as one last observation/consideration that may be useful when considering experimentation on the choices hunting *Photuris* females make when presented with a mating signal by a defaulting *Photuris* male: a female in the hunting mode flashed a response to the crescendo phrase of a passing male, and then, when presented with a short flash she immediately answered a prey FP simulation. This seems the best clue presently to the sexual strategy of *Photuris* females. The question: Might females of some species exclusively seek mates or prey first? Surely they must have the option, and select either depending upon individual circumstances. In the female mentioned, had she mated before?, were there sperm in her spermathecae?, and how many eggs remained in her ovary? The reproductive success of *Photuris* females is comparable, analogous to that of males: higher than average hunting success in competitively capturing males to eat probably results in the deposition of more viable and successful eggs, which is counterpart to higher mating success and more fertilizations in males competing and achieving multiple mating partners.



Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.436	9.000	3.093	1.757	2.293	6.464	11.414	.784	1.316	.722
sd	.108	.306	.127	.109	.138	1.981	.390	.046	.065	.222
se	.029	.082	.034	.029	.037	.529	.104	.012	.017	.059
n	14	14	14	14	14	14	14	14	14	14
min	2.100	8.500	2.900	1.600	2.100	0	10.600	.680	1.210	0
max	2.500	9.600	3.400	1.900	2.500	7.600	12.100	.870	1.430	.880
Vc %	4.4	3.4	4.1	6.2	6.0	30.6	3.4	5.9	4.9	30.7

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	2.533	1.000	1.200	1.000	2.200	2.800	5.533
sd	0	0	.516	0	.414	0	.561	.414	1.642
se	0	0	.133	0	.107	0	.145	.107	.424
n	15	15	15	15	15	15	15	15	15
min	3.000	3.000	2.000	1.000	1.000	1.000	1.000	2.000	3.000
max	3.000	3.000	3.000	1.000	2.000	1.000	3.000	3.000	8.000
Vc%	0	0	20.4	0	34.5	0	25.5	14.8	29.7

Table 2. Morphology.

Morphology. General morphological means are (n=14): PNL 2.4, ELL 9.0, PNW 3.1, EWhum 1.8, EWmid 2.3, ELVit 6.5, TOTLen 11.4, PNrat 0.78, ELWrate 1.32, ELVTrat 0.72 (**Table 2A**, with other stats). Data for the colors of various apparent abdominal plates (sclerite combinations) and hind coxae are shown in **Table 2B-C**, and the color of the pre-lantern ventrite, in **2D**. **Figure 16** is a general guide indicating the numbers used for various skeletal plates and numbers for degree of splashing on ventrite 4. A range of photographed vittagrams of *carri* is shown in **Figure 3**, and **Figure 17** shows a sampler of PN vittae, pen and ink drawings made when experimentally seeking a way to illustrate vittagrams. **Figure 18** shows histograms that code the vittagrams with respect to basic form (A1-C2) and unique features (c3-f5; ref: **Fig. 101.2**).

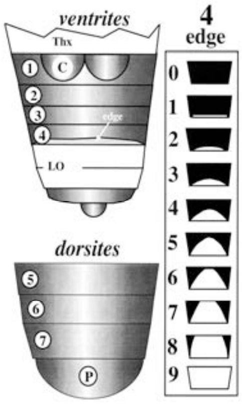


Figure 16. Topographic and splash keys.

Holotype Description: male, voucher number 67236, collected 16 May 1967, Alachua County, Florida; Univ. Florida Austin Cary Forest, near sawmill. FB page 53: One of a series of six, collected after emitting their crescendo FP; series voucher numbers 67234-67239. Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.4, ELLen 9.5, PNWid 3.1, ELWhum 1.6, ELWmid 2.1, LELVit 6.9, TotLen 11.9, PnRat 0.76, ElRat 0.76, VitRat 0.72; Colors: T 333, Py 1, Cx 1, V 133, Edg 8. Types will be deposited in the USNM.

Taxonomic and other notes. The scientific name and suggested common name for this firefly pays tribute Archie and Marjorie Carr, long time and devoted champions of conservation in Florida and elsewhere. I knew Archie personally, as a friend, naturalist, conservationist, and teacher, who should still be on campus to change things. I was fortunate enough to spend time with him, only briefly in the field, when he befriended a pigmy rattlesnake, but at length in a small group of faculty that met each week to discuss a new and comprehensive volume on evolution. I recall our first meeting when he was being baited by colleague Prof. Franz Sauer to stick his hand into a box of leaves—apparently they had a history of debate on whether the rattling sound of a burrowing owl was defensive and would invoke an innate avoidance response. As Archie stuck his hand in the box, Franz, who was a Messerschmitt pilot in WW2 and used that to explain his poor driving habits, played a recording of the burrowing owl's rattle through a speaker in the box. I don't recall Archie's response, but the question surely remained unresolved.

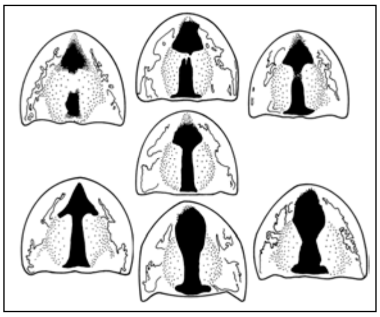


Figure 17. Pen & ink array.

Augmented figure/table legends. 11. A head-on view of a *carrorum* female eating a *macdermotti* male she attracted with *false* mating signals. **13**. PM-traces of crescendos of flying *carri* males. (A) Four crescendos of a 5-pulse phrase, @21.4°/70.5°; (B) crescendo @221.4°/70.5°; (C)) crescendo @18.9°/66°; (D) phrase with PM gain increased to detect dim beginnings of emissions yet remain functional for OFF transient @23.9°/75°; (E) gain increased, more ONSET detected though OFF abbreviated @22.2° / 72°; (F) PM-log recording @21.7°/71°; (**G**) wingbeats? atop a crescendo, ca 62.5 Hz @23.3°/74°. Bars indicate time in sec. **15**. (**A**) The mating signals of *floridanus* and *macdermotti*, in open symbols (see key at bottom), are shown above. (**B**) The predator (dark symbol) answers a *floridanus* simulation and then, when presented with a *macdermotti* simulation answers incorrectly twice, but then gets it right. Students in the firefly class have performed this experiment on females of *Photuris harrannorum*, the Florida variad of continental *versicolor*. **18**. Histogram summarizing the general shapes and certain unique features found in the vittagrams of a voucher series of *carrrum*. **Appendix.** Comparison of pronotal vittagams of species in "operational" *lucicrescens* Group, with those of *carrorum* in the box..

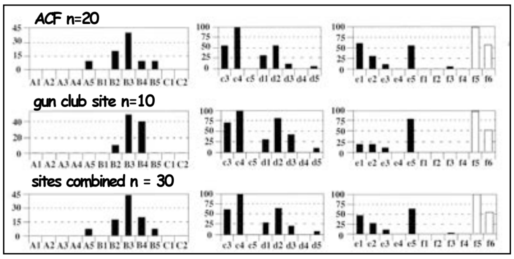
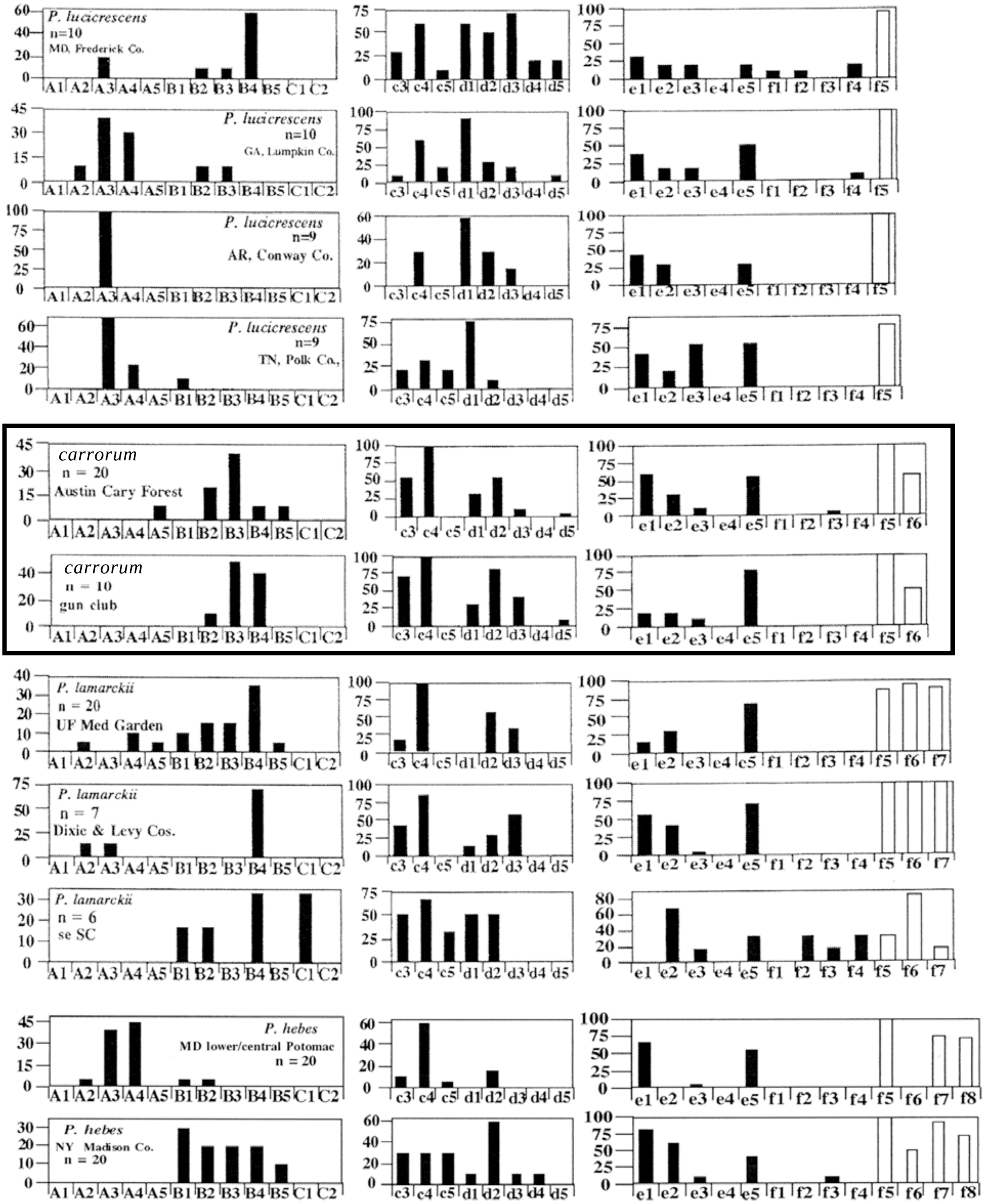


Figure 18. PN coded histograms.

Appendix: 4 Lucy-Group PN Vittae Comparisons



P. hebes "Wild Cards"
f5 inlet notches at PN base
f6 stem erosion, sub pt, mid
f7 above serif bulge
f8 "U" stem base visible through dusky serif

Chapter 23

Photuris chenangoa n. sp.

Photuris chenangoa is a northeastern representative of the *potomaca* "working group" (river train-flashers). As constituted here it occurs in the watersheds of the Hudson, Susquehanna, Delaware, St. Lawrence, and perhaps Connecticut Rivers (**Figs. 1, 2**). All known *chenangoa* sites were near streams where males flashed over adjacent grasslands and up into neighboring shrubs and trees (**Figs. 3, 4**), and sometimes flew 100' or more from streamside. This firefly is the only species within its known geographic distribution that emits trains of *simple* short flashes at or near 0.83 sec intervals (1.2 Hz) @21°C, **Figs. 5-7**), a timing that falls—across most temperatures—between those measured in *potomaca* and *missouriensis*; in F**igure 8** note that the slope of its rate/temp regression is near that of *potomaca* and crosses that of *missouriensis*—the two are not known to come into contact, i.e., to be sympatric. Its flashes may be confused with those of *P. hebes* and *P. bridgeniensis* but the subtly modulated flashes of the last two will often appear to hitch (jerk along), especially at lower temperatures, with the possible exception of a *hebes* seen at one locality, as noted. The geographic occurrence of *chenangoa* and *potomaca* may overlap to some extent in northeastern US. Neither habitus nor phenology is useful for identifying *chenangoa* (**Fig. 9**).


Figure 1.

Flashing Behavior and Ecology. All *chenangoa* sites apparently were along or near streams, and males flew over stream-side vegetation and adjacent herbs and grassland including hay- and old-fields, lush alfalfa fields, and up into adjacent trees, even very tall ones; they were occasionally seen 100 or more feet from streamside. At Treman State Park near Ithaca NY a few presumptive *chenangoa* were seen, and they were high in trees where they flew slowly around and along the canopy. (No vouchers were collected at this site.) As noted for a few other species, two or three males sometimes seem to travel together (*squadron*), for they would appear, moving through the treetops together and then disappear, seemingly continuing on out of sight. Males emit their short flashes in trains: a sample of lengths of unbroken series, that is, of continuous flashes at the species-typical rate, was 10, 10, 11, 9, 9, 10, and 21. Flash rate ranges between ≈0.8 Hz at 18°C and ≈1.8 Hz at 25°C, and the rate/temp regression is linear (**Fig. 7**).

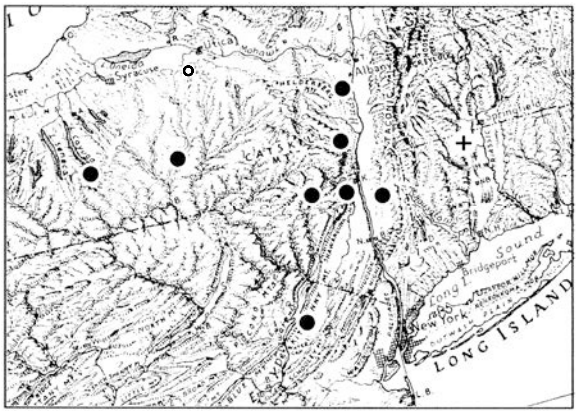


Figure 2. Physiographic occurrence.


Figure 3. Trestle at site just south of Greene, NY.

Flash form is similar to that of *potomaca* and *missouriensis*, nearly symmetrical, with a slightly shorter rise than fall-time (**Fig. 5**). In PM-records of flashes, the duration of flashes at 18.9° C is ca 33 mSec half-max and 79 mSec base (Albany Co. NY, 77 flashes of 7 males examined); and @ 26.1°C is ca 28 mSec half-max and 65 mSec base (Tompkins Co. NY, 11 flashes of 5 males examined). Recorded flashes of males at the Chenango County site were longer at their base than those of other localities (cf **Figs. 5B, C**): a sample of 19 averaged 7 percent longer than a sample of 95 flashes recorded in Greene Co. at a similar temperature. I suspect this difference could have a technical explanation—that is, not be biologically significant.

A female (Chenango Co.) in grass answered several but not all flashes of a flying male, with short flashes, emitted immediately after his. I did not see the outcome, and she may

Figure 4. Oldfield at west end of trestle at Greene.

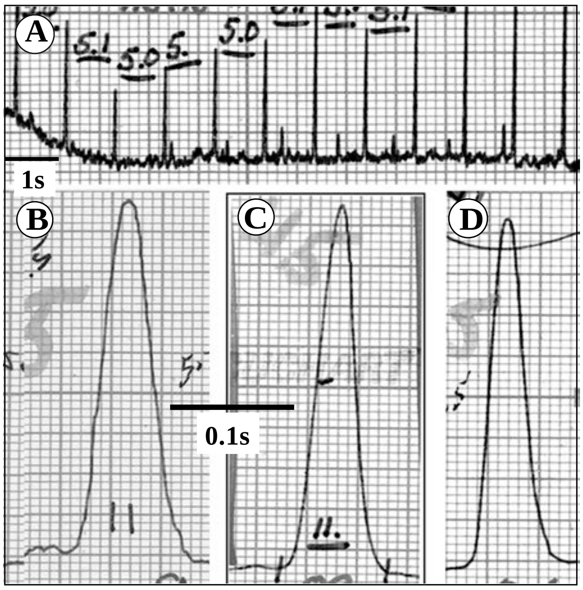


Figure 5. PM-traces of FPs (AX: rel. int./time; see text at right.

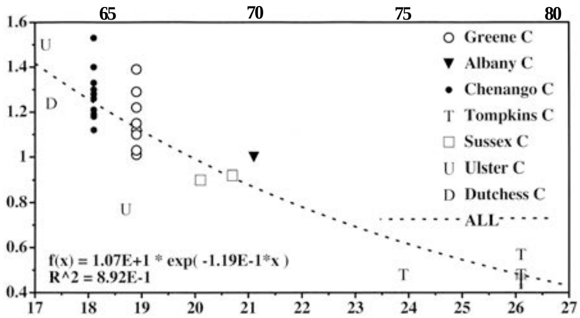


Figure 6. FP (flash) period (AX: sec/temp).

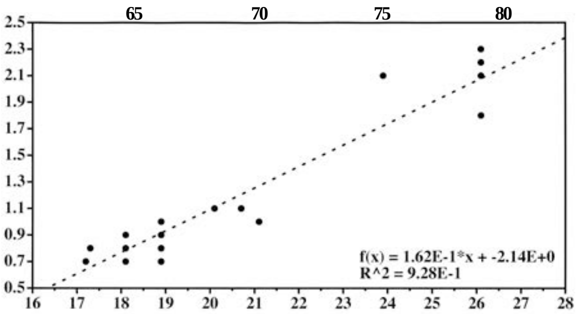


Figure 7. FP (flash) rate (AX: Hz/temp).

have been hunting *Photinus curtatus* x *marginellus* males that were in the area. She responded to short flashes of the penlight with similar answers. I was able to attract males to the penlight by flashing after their flashes. Curiously, inexplicably, one flying, flashing *chenangoa* "male" that I attracted to within 6 inches of the penlight was a female. Incidentally, the wooded copse shown in **Figure 4** in this 1985 photo was the northern-most, valley-floor locality of "pure *marginellus*" (see **Fig. 16**) of the two mentioned *Photinus* species; it was found during the original study in 1965 and again on two later visits at about 10-year intervals.

PM-traces of flashes of *chenangoa*. A. Train of flashes recorded in Greene Co., NY, 18.9°/66°; **B**. Chenango Co., NY, 18.1°/64.5°; **C**. Greene Co., NY 18.9°/66°; **D**. Tompkins Co., NY 26.1°/79°. Flashes recorded in Chenango Co. appear somewhat longer than might be expected from the only slightly lower temperature.

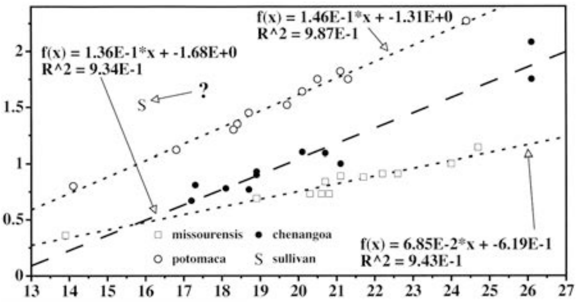


Figure 8. FP rate comparison. (AX: Hz/temp).

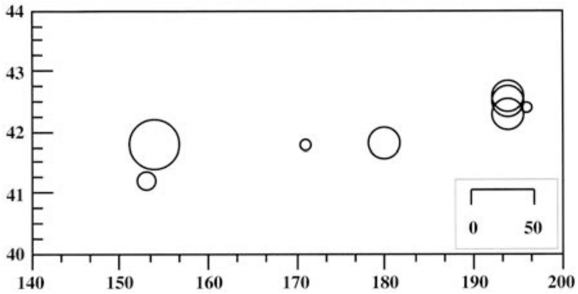
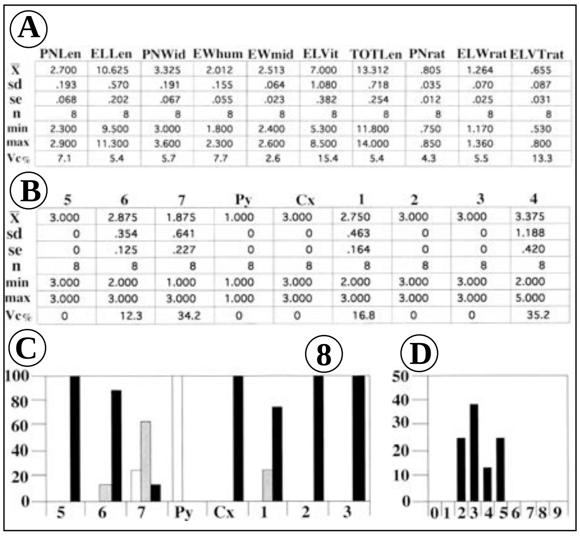


Figure 9. GESEDISOBS (AX: no. active / Lat./ DOY.

Taxonomic and nomenclatural notes. As constituted here, *chenangoa* was found south of Green (Chenango Co.) NY on the Chenango River (Holotype locality); Climax (Greene Co.) NY near Coxsackie Creek; at Selkirk (Albany Co.) NY near Vloman Kill; at Accord (Ulster Co.) NY on Rondout Creek; about six miles south of Pine Plains (Dutchess Co.) NY near Wappinger Creek; at Ithaca (Tompkins Co.) NY on Enfield Creek in Robert Treman State Park; south of Green (Chenango Co.) NY on the Chenango River; near Tranquility (Sussex-Warren Cos.) NJ, near Pequest River; and near New Paltz at Kleine Kill (Ulster Co.) NY.

This species is named for the river and valley that was worked extensively in the 1960s on *Photinus* Division I hybridization. This valley is also where two pioneers/notables of a large religious sect made a poor impression on settlers in the early 19th century; their remembered reflections are preserved in "Chenango Valley Tales".

Morphological data. General morphological means are (n=8): PNL 2.7, ELL 10.6, PNW 3.3, EWhum 2.0, EWmid 2.5, ELVit 7.0, TOTLen 13.3, PNrat 0.81, ELWrat 1.26, ELVTrat 0.66 (**Figure 10A**, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are in **Figure 10B-C**, and the color of the pre-lantern ventrite in **10D. Figure 11** is a generic sketch indicating the numbers used for various skeletal plates and degrees of pale splashing on ventrite 4. A range of vittagrams (pronotal vittae) of *chenangoa* is shown in **Figure 12** (see also **13** and **14**).



Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.700	10.625	3.325	2.012	2.513	7.000	13.312	.805	1.264	.655
sd	.193	.570	.191	.155	.064	1.080	.718	.035	.070	.087
se	.068	.202	.067	.055	.023	.382	.254	.012	.025	.031
n	8	8	8	8	8	8	8	8	8	8
min	2.300	9.500	3.000	1.800	2.400	5.300	11.800	.750	1.170	.530
max	2.900	11.300	3.600	2.300	2.600	8.500	14.000	.850	1.360	.800
Vc%	7.1	5.4	5.7	7.7	2.6	15.4	5.4	4.3	5.5	13.3

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.875	1.875	1.000	3.000	2.750	3.000	3.000	3.375
sd	0	.354	.641	0	0	.463	0	0	1.188
se	0	.125	.227	0	0	.164	0	0	.420
n	8	8	8	8	8	8	8	8	8
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	12.3	34.2	0	0	16.8	0	0	35.2

Figure 10. Morphological data, as described in text.

Holotype description. male, voucher number 7753, collected 13 July 1977, Chenango County, New York, 3 miles north of Chenango Forks, Rt. 12. FB page 20: One of several flying/flashing males along river bank and in adjacent hay-field, emitting FPs at about 1-sec period, #7753 FP was observed. Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.3, ELLen 9.5, PNWid 3.0, ELWhum 1.8, ELWmid 2.4, LELVit 5.3, TotLen 11.8, PnRat 0.75, ElRat 0.74, VitRat 0.55; Colors: T 331, Py 1, Cx 3, V 333, Edg 3. Types will be deposited in the USNM.

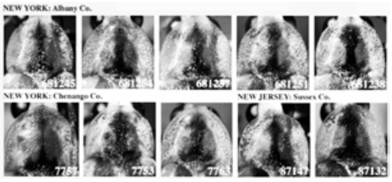


Figure 12. *P. chenangoa* FP-voucher arrays.

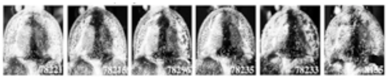


Figure 13. *P. potomaca*, MD & VA: variously along Potomac River, west to Pt. of Rocks, Maryland.

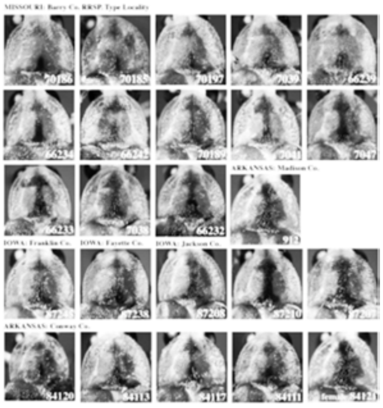


Figure 14. *P. missouriensis* FP-voucher pronotal arrays.

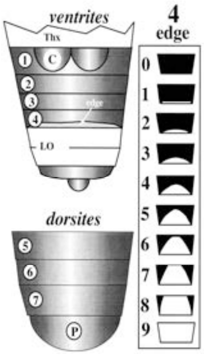
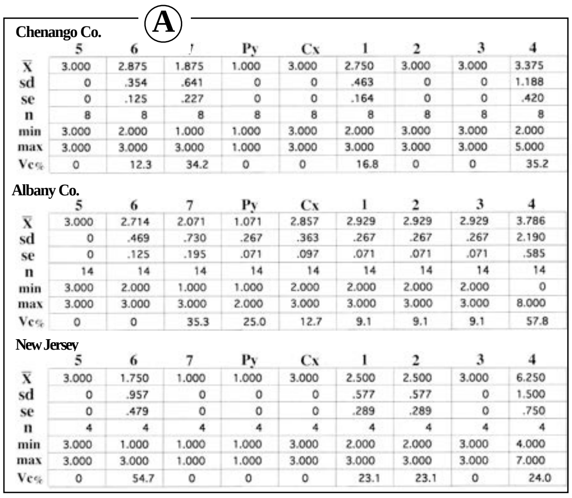


Figure 11. Anatomical/ Topographical key to data.



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Chenango Co.

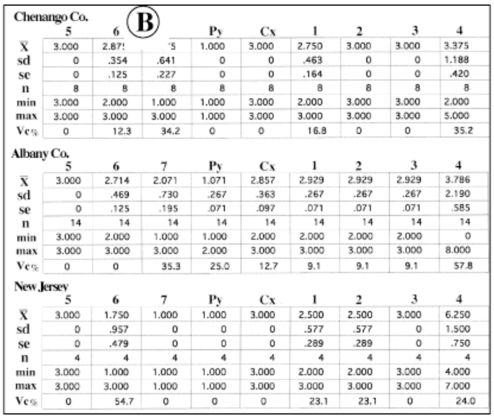
	5	6	!	Py	Cx	1	2	3	4
X̄	3.000	2.875	1.875	1.000	3.000	2.750	3.000	3.000	3.375
sd	0	.354	.641	0	0	.463	0	0	1.188
se	0	.125	.227	0	0	.164	0	0	.420
n	8	8	8	8	8	8	8	8	8
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	12.3	34.2	0	0	16.8	0	0	35.2

Albany Co.

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.714	2.071	1.071	2.857	2.929	2.929	2.929	3.786
sd	0	.469	.730	.267	.363	.267	.267	.267	2.190
se	0	.125	.195	.071	.097	.071	.071	.071	.585
n	14	14	14	14	14	14	14	14	14
min	3.000	2.000	1.000	1.000	2.000	2.000	2.000	2.000	0
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	0	35.3	25.0	12.7	9.1	9.1	9.1	57.8

New Jersey

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.750	1.000	1.000	3.000	2.500	2.500	3.000	6.250
sd	0	.957	0	0	0	.577	.577	0	1.500
se	0	.479	0	0	0	.289	.289	0	.750
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	3.000	2.000	2.000	3.000	4.000
max	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	54.7	0	0	0	23.1	23.1	0	24.0



Ⓑ

Chenango Co.

	5	6		Py	Cx	1	2	3	4
X̄	3.000	2.87!	'5	1.000	3.000	2.750	3.000	3.000	3.375
sd	0	.354	.641	0	0	.463	0	0	1.188
se	0	.125	.227	0	0	.164	0	0	.420
n	8	8	8	8	8	8	8	8	8
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	12.3	34.2	0	0	16.8	0	0	35.2

Albany Co.

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.714	2.071	1.071	2.857	2.929	2.929	2.929	3.786
sd	0	.469	.730	.267	.363	.267	.267	.267	2.190
se	0	.125	.195	.071	.097	.071	.071	.071	.585
n	14	14	14	14	14	14	14	14	14
min	3.000	2.000	1.000	1.000	2.000	2.000	2.000	2.000	0
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	0	35.3	25.0	12.7	9.1	9.1	9.1	57.8

New Jersey

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.750	1.000	1.000	3.000	2.500	2.500	3.000	6.250
sd	0	.957	0	0	0	.577	.577	0	1.500
se	0	.479	0	0	0	.289	.289	0	.750
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	3.000	2.000	2.000	3.000	4.000
max	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	54.7	0	0	0	23.1	23.1	0	24.0

Figure 15 A, B. Deme data of working conspecifics.

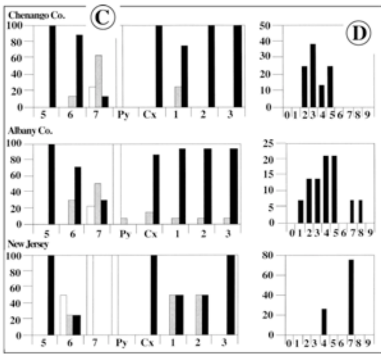


Figure 15 D, E. Deme data of working conspecifics.

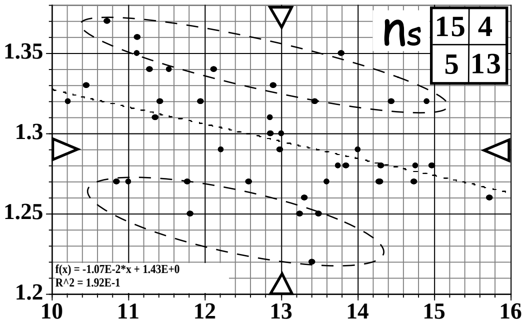
Brief Reflections On Tables of Means

These two spread sheets show mean values for morphological features of most Division II *Photuris* sampled in this study. In the table at the left demes are arranged alphabetically by epithet (column 1), and in the table at the right they are arranged by total body length (column 8). It is interesting that the two largest species would be considered closely related on the basis of flashing behavior. They are among the pairs of species that might have diverged, become distinct when the land mass that is now Florida was separated from the continent long ago. Going on in exploration, by regressing a character on another, clues into hidden aspects of adaptation and ecology may appear, or ideas tested. The reason that measurements of elytral width at the humeral angle and at the midpoint were made was because it was reasoned that during flight when the wing-covers are held aloft they must, in addition to being sails in the wind, probably influence flight dynamics, such as stability and lift—beating wings perhaps send drafts of air over them. Perhaps broader wings (higher ratios) also have greater camber, that is, have deeper airfoil arching, and are better for some flight modes than narrow wings. For example, for hovering flight during slow, hovering search or when setting up an attack on a flying luminescing target, perhaps broader wings provide lift and stability. The regression in **Figure 1** reveals outliers for further attention in this context. There is considerable scatter, and body length is a poor predictor of elytral width ratio, but larger males would appear to have narrower elytra (lower ratios), and smaller males tend to have broader elytra—perhaps they tend to search for mates in more sheltered places . The ellipses in the figure enclose extreme outliers named in the list.

SPECIES	PNLen	ELLen	PNWid	EWhum	Ewmid	ELVit	TOTLen	Pnrat	ELWrat	ELVTrat
alexanderi	2.57	10.29	3.17	1.94	2.51	6.9	12.85	0.81	1.31	0.67
alleganiensis	2.48	10.5	3.13	1.9	2.45	7.7	13	0.79	1.3	0.73
appalachian	2.61	10.83	3.29	1.88	2.45	7.71	13.44	0.8	1.32	0.71
aureolucens	2.55	10.31	3.19	1.85	2.39	6.75	12.86	0.8	1.3	0.65
branhami	2.3	8.15	2.81	1.57	2.1	0	10.45	0.82	1.33	0
campestris	2.83	10.6	3.53	2	2.45	8.1	13.4	0.81	1.22	0.76
carrorum	2.44	9	3.09	1.76	2.29	6.46	11.41	0.78	1.32	0.72
chenangoa	2.7	10.63	3.23	2.01	2.51	7	13.3	0.81	1.26	0.66
cinctipennis	2.43	9.13	2.94	1.65	2.24	1.3	11.53	0.82	1.34	0.14
darwini	2.68	10.93	3.29	1.97	2.48	2.49	13.59	0.82	1.27	0.23
dorothy	2.31	7.99	2.71	1.51	2	0.39	10.21	0.82	1.32	0.05
douglasae	2.78	10.47	3.38	1.98	2.46	1.94	13.24	0.82	1.25	0.18
eureka	3.18	12.57	3.89	2.29	2.87	2.72	15.72	0.82	1.26	0.22
fairchildi MN	2.93	11.44	3.62	2.06	2.69	8.05	14.44	0.81	1.32	0.7
faustae	3.23	11.67	3.94	2.19	2.79	0	14.75	0.82	1.28	0
forresti	2.43	9.51	2.95	1.71	2.26	0.54	11.94	0.83	1.32	0.06
hebes	2.53	9.58	3.15	1.82	2.41	6.55	12.12	0.8	1.34	0.68
hiawassee	2.49	9.34	3	1.8	2.19	2.06	11.81	0.83	1.25	0.221
harrannorum	2.73	9.85	3.43	1.95	2.46	2.85	12.57	0.8	1.27	0.29
katrinae	3.37	11.53	4.27	2.33	3.07	5.67	14.9	0.79	1.32	0.49
lamarcki	2.5	8.76	3.15	1.81	2.39	3.46	11.28	0.8	1.34	0.74
lineaticol alach	3.11	11.21	3.89	2.11	2.7	0	14.3	0.8	1.28	0
lloydi	2.3	8.7	2.84	1.63	2.06	5.92	11	0.81	1.27	0.68
ucicrescens md	3.2	11.54	3.91	2.22	2.82	7.93	14.73	0.82	1.27	0.69
mad dotdash	2.51	10.39	3.09	1.83	2.41	5.21	12.89	0.81	1.33	0.5
maicoi	3.16	11.14	3.93	2.08	2.65	6.95	14.29	0.81	1.27	0.63
margotoole	2.65	11.11	3.25	1.84	2.45	7.02	13.78	0.82	1.35	0.63
missouriensis	2.71	10.8	3.41	1.99	2.47	5.69	13.49	0.8	1.25	0.53
moorei	2.49	9.29	2.97	1.73	2.16	0.36	11.77	0.84	1.27	0.04
paludivulpes	2.3	8.83	2.79	1.55	2.09	2.91	11.11	0.83	1.35	0.32
potomaca	2.61	10.37	3.32	2	2.52	3.15	12.98	0.79	1.29	0.31
quadrifulgens	2.96	12.02	3.64	2.09	2.66	6.5	14.97	0.81	1.28	0.54
sivinskii	2.23	8.49	2.67	1.48	2.02	2.66	10.72	0.83	1.37	0.31
stanleyi	2.4	9	2.95	1.75	2.26	4.55	11.35	0.81	1.31	0.5
stevensae	2.97	11.31	3.68	2.17	2.77	8.19	14.28	0.81	1.27	0.73
tasunkowitcoi	2.76	11.12	3.36	1.92	2.42	7.2	13.84	0.82	1.28	0.65
tremulans md	2.45	9.75	2.98	1.8	2.29	4.58	12.21	0.82	1.29	0.47
versicolor md	2.88	10.86	3.53	2.13	2.73	6.45	13.74	0.82	1.28	0.59
walkeri	2.78	11.2	3.7	2.1	2.7	0	14	0.76	1.29	0
whistlerae	2.43	8.7	3	1.66	2.24	0.13	11.12	0.81	1.36	0.01

SPECIES	PNLen	ELLen	PNWid	EWhum	Ewmid	ELVit	TOTLen	Pnrat	ELWrat	ELVTrat
eureka	3.18	12.57	3.89	2.29	2.87	2.72	15.72	0.82	1.26	0.22
quadrifulgens	2.96	12.02	3.64	2.09	2.66	6.5	14.97	0.81	1.28	0.54
katrinae	3.37	11.53	4.27	2.33	3.07	5.67	14.9	0.79	1.32	0.49
faustae	3.23	11.67	3.94	2.19	2.79	0	14.75	0.82	1.28	0
lucicrescens md	3.2	11.54	3.91	2.22	2.82	7.93	14.73	0.82	1.27	0.69
fairchildi MN	2.93	11.44	3.62	2.06	2.69	8.05	14.44	0.81	1.32	0.7
lineaticol alach	3.11	11.21	3.89	2.11	2.7	0	14.3	0.8	1.28	0
maicoi	3.16	11.14	3.93	2.08	2.65	6.95	14.29	0.81	1.27	0.63
stevensae	2.97	11.31	3.68	2.17	2.77	8.19	14.28	0.81	1.27	0.73
walkeri	2.78	11.2	3.7	2.1	2.7	0	14	0.76	1.29	0
tasunkowitcoi	2.76	11.12	3.36	1.92	2.42	7.2	13.84	0.82	1.28	0.65
margotoole	2.65	11.11	3.25	1.84	2.45	7.02	13.78	0.82	1.35	0.63
versicolor md	2.88	10.86	3.53	2.13	2.73	6.45	13.74	0.82	1.28	0.59
darwini	2.68	10.93	3.29	1.97	2.48	2.49	13.59	0.82	1.27	0.23
missouriensis	2.71	10.8	3.41	1.99	2.47	5.69	13.49	0.8	1.25	0.53
appalachian	2.61	10.83	3.29	1.88	2.45	7.71	13.44	0.8	1.32	0.71
campestris	2.83	10.6	3.53	2	2.45	8.1	13.4	0.81	1.22	0.76
chenangoa	2.7	10.63	3.23	2.01	2.51	7	13.3	0.81	1.26	0.66
douglasae	2.78	10.47	3.38	1.98	2.46	1.94	13.24	0.82	1.25	0.18
alleganiensis	2.48	10.5	3.13	1.9	2.45	7.7	13	0.79	1.3	0.73
potomaca	2.61	10.37	3.32	2	2.52	3.15	12.98	0.79	1.29	0.31
mad dotdash	2.51	10.39	3.09	1.83	2.41	5.21	12.89	0.81	1.33	0.5
aureolucens	2.55	10.31	3.19	1.85	2.39	6.75	12.86	0.8	1.3	0.65
alexanderi	2.57	10.29	3.17	1.94	2.51	6.9	12.85	0.81	1.31	0.67
harrannorum	2.73	9.85	3.43	1.95	2.46	2.85	12.57	0.8	1.27	0.29
tremulans md	2.45	9.75	2.98	1.8	2.29	4.58	12.21	0.82	1.29	0.47
hebes	2.53	9.58	3.15	1.82	2.41	6.55	12.12	0.8	1.34	0.68
forresti	2.43	9.51	2.95	1.71	2.26	0.54	11.94	0.83	1.32	0.06
hiawassee	2.49	9.34	3	1.8	2.19	2.06	11.81	0.83	1.25	0.221
moorei	2.49	9.29	2.97	1.73	2.16	0.36	11.77	0.84	1.27	0.04
cinctipennis	2.43	9.13	2.94	1.65	2.24	1.3	11.53	0.82	1.34	0.14
carrorum	2.44	9	3.09	1.76	2.29	6.46	11.41	0.78	1.32	0.72
stanleyi	2.4	9	2.95	1.75	2.26	4.55	11.35	0.81	1.31	0.5
lamarcki	2.5	8.76	3.15	1.81	2.39	3.46	11.28	0.8	1.34	0.74
whistlerae	2.43	8.7	3	1.66	2.24	0.13	11.12	0.81	1.36	0.01
paludivulpes	2.3	8.83	2.79	1.55	2.09	2.91	11.11	0.83	1.35	0.32
lloydi	2.3	8.7	2.84	1.63	2.06	5.92	11	0.81	1.27	0.68
sivinskii	2.23	8.49	2.67	1.48	2.02	2.66	10.72	0.83	1.37	0.31
branhami	2.3	8.15	2.81	1.57	2.1	0	10.45	0.82	1.33	0
dorothy	2.31	7.99	2.71	1.51	2	0.39	10.21	0.82	1.32	0.05

Figure 1.



Lower left
billbrowni
lloydi
moorei
hiawassee
harrannorum

Upper right
appalachianensis
fairchildi MD
katrinae
margotooleae

Upper left
stanleyi
alexanderi
dorothae
carrorum
forresti
branhami
potomaca
penn NY
aureolucens
hebes
cinctipennis
lamarcki
paludivulpes
whistlerae
sivinski

Lower right
campestris
douglasae
missouriensis
chenangoa
darwini
maicoi
lucicrescens MD
versicolor MD
tasunkowitcoi
lineaticollis Alachua
faustae
quadrifulgens

Chapter 24

Photuris cinctipennis Barber 1951

Flicker Mother (FM)

Barber described this morphologically distinctive and rare species from specimens he collected in his bailiwick, but he was uncertain as to its FP. In his text he noted that not having recognized their unique appearance at the time of capture, he had not specifically noted the FP. As will be understood below, he might well have seen its flicker FP and presumed it was was his (already discovered) *tremulans*, and/or perhaps later concluded or observed that it emitted a single short flash at two second intervals (**Fig. 2**). Also, his text (p. 35) shows that at the time he had not yet decided what firefly Motschulsky (*lineaticollis*) had previously described, and seems to have considered his now-*cinctipennis* (FM?) a possibility. The latter uncertainty is here perhaps resolved, this resolution either being historically correct or if not, at least the simplest in the cause of nomenclatural stability. With respect to his FP uncertainty, if Barber's *cinctipennis* is not the flickering species discussed here, from his bailiwick (**Fig. 1**), and there another in the Group in the Potomac/Chesapeake region, patient field FP work will be necessary in an already human-infested region.

In morphological appearance FM is indistinguishable from other members of the Mother Group, which are otherwise known only from southeastern United States. FM itself is known from three Maryland Counties (**Fig. 1**), and was never seen among many hundreds/thousands of archived specimens examined. In this study it was found in Cedarville State Forest, just east of Washington, D. C., where perhaps as many as fifty were flying a flickering closely around and over a small, dense copse of bushes and low scraggly trees in an oldfield clearing. At this time, June 1978, this field was perhaps 150 feet in diameter, and surrounded by a regrowth forest of pines and hardwoods.

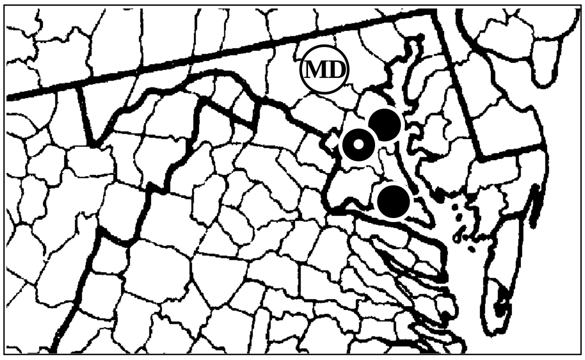


Fig. 1. Dots, Barber's records; donut, flicker.

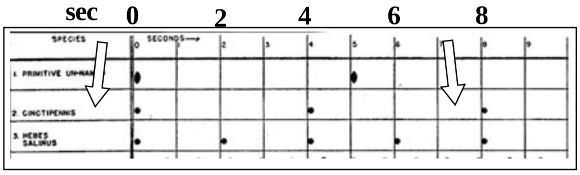


Fig. 2. From Barber's (uncertain) *cinctipennis* FP chart.

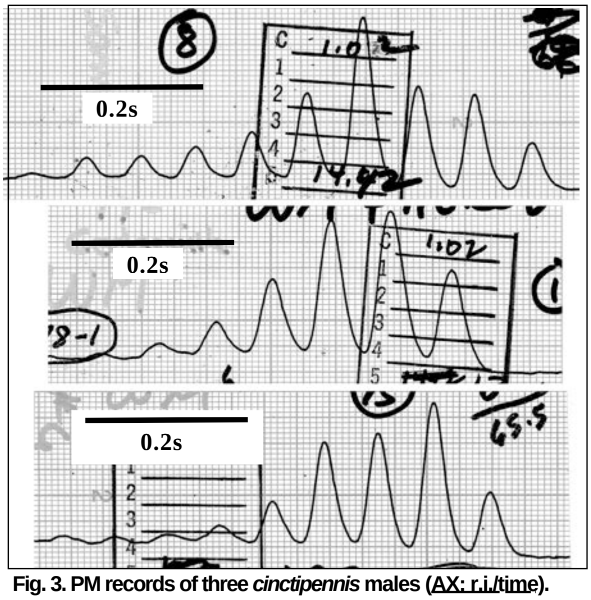


Fig. 3. PM records of three *cinctipennis* males (AX: r.i./time).

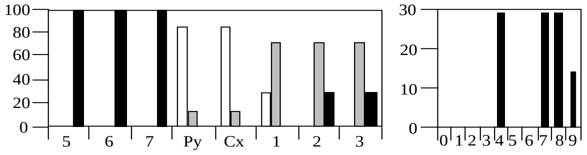
The flicker FP had a modulation rate similar to but not exactly that of *Pyractomena angulata* (**Fig. 3**), and likewise, similar to that of adjunct FPs of a few other *Photuris*. SWAT-measured FP mean period at 25.0°/77° was 2.5 sec, s.d. = 0.39, n = 7, r = 2.1-3.2. From 26 PM-recorded flickers (**Fig. 3**) emitted by ten males the following were determined: mean-mean modulation rate = 13.7 Hertz; overall range = 12.4-16.7 Hz. On one occasion a short bimodal flash was observed as an apparent (female) response to a male's flicker.

Before making these recordings, and at the site, what was presumed to be a *tremulans* male was decoyed with a penlight flash. It approached quickly and then emitted a single flash. No actual *tremulans* were known to be present. This observation occurred at the beginning of awareness of defaulting FPs of *Photuris*. Possibly Barber's-*cinctipennis'* repertoire consists of both a single short flash and a flicker.

Morphology. Morphological measurements and ratios for voucher FM are in **FigTable 4** and the array of their vittigrams in **Figure 7**. For comparison, the color histograms of two Florida *cinctipennis* Group species with those of flicker-vouchers are in **FigTable 6**. Data and histogram for for Barber's specimens are in **FigTable 5**.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.425	9.125	2.937	1.650	2.237	1.300	11.525	.824	1.341	.141
sd	.071	.341	.119	.093	.119	1.433	.365	.040	.060	.155
se	.025	.121	.042	.033	.042	.507	.129	.014	.021	.055
n	8	8	8	8	8	8	8	8	8	8
min	2.300	8.600	2.800	1.600	2.100	0.000	11.000	.760	1.290	0.000
max	2.500	9.500	3.100	1.800	2.400	3.400	11.900	.870	1.460	.360
Vc%	2.9	3.7	4.1	5.6	5.3	110	3.2	4.9	4.5	110

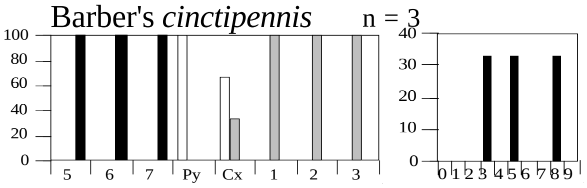
	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	3.000	1.143	1.143	1.714	2.286	2.286	6.714
sd	0.000	0.000	0.000	.378	.378	.488	.488	.488	1.976
se	0.000	0.000	0.000	.143	.143	.184	.184	.184	.747
n	7	7	7	7	7	7	7	7	7
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	4.000
max	3.000	3.000	3.000	2.000	2.000	2.000	3.000	3.000	9.000
Vc%	0	0	0	33.1	33.1	28.5	21.4	21.4	29.4



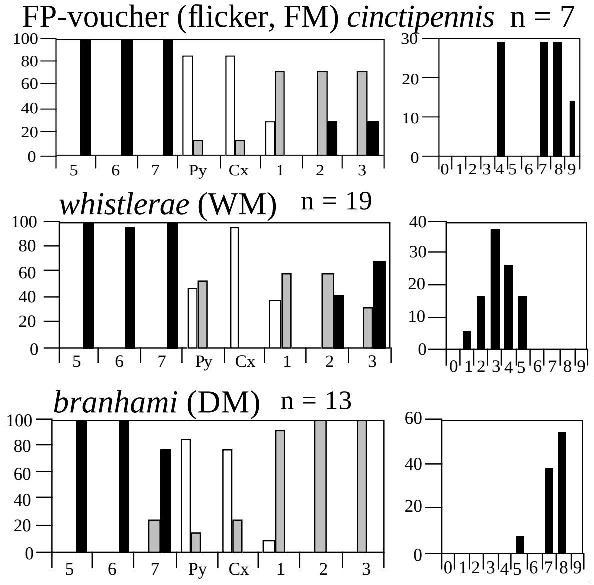
FigTable. 4. Morph data for *cinctipennis* (FM) vouchers.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNRat	ELWrat	ELVitRat
$\bar{X}$	2.467	8.867	2.100	1.533	1.867	3.267	11.333	2.777	1.173	.370
sd	.058	.451	1.473	.115	.513	3.465	.451	3.372	.240	.386
se	.033	.260	.850	.067	.296	2.000	.260	1.947	.139	.223
n	3	3	3	3	3	3	3	3	3	3
min	2.400	8.400	.400	1.400	1.300	0.000	10.900	.830	.910	0.000
max	2.500	9.300	3.000	1.600	2.300	6.900	11.800	6.670	1.380	.770
Vc%	.02	.05	0.7	0.08	0.27	1.06	0.04	1.21	0.20	1.07

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	3.000	1.000	1.333	2.000	2.000	2.000	5.333
sd	0.000	0.000	0.000	0.000	.577	0.000	0.000	0.000	2.517
se	0.000	0.000	0.000	0.000	.333	0.000	0.000	0.000	1.453
n	3	3	3	3	3	3	3	3	3
min	3.000	3.000	3.000	1.000	1.000	2.000	2.000	2.000	3.000
max	3.000	3.000	3.000	1.000	2.000	2.000	2.000	2.000	8.000
Vc%	0	0	0	0	0.43	0	0	0	0.47



FigTable. 5. Barber's specimens in USNM coll.



FigTable. 6. Color histograms of a Florida species for comp.

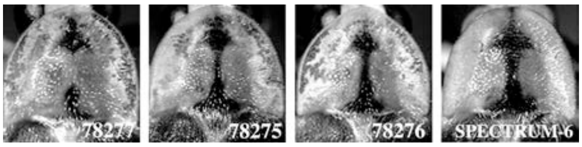


Fig. 7. PN array, *cinctipennis* s. s. vouchers.

Chapter 25

Photuris congener LeConte 1852

Of Florida's many firefly species this is the one most likely to be noticed, even by non-entomologists, though its adult season is brief, confined to a span of a few weeks—actual dates shift with latitude, the peak in central Florida just north of Lake Okeechobee occurring in March and in north-central Florida at Gainesville, in mid-April (**Figs. 9, 11**). When *congener* appears great pressure for "signal space" must be put on communication in other species in its habitat which becomes totally dominated by *congener's* (noisy/nuisance) flashes—some species may have shifted their adult season accordingly? *Congener's* flash pattern is a train of very short (60-80 mSec) flashes emitted at short intervals (0.5-1 sec), depending upon temperature (**Figs. 7, 8, 10**). The combination of repetitious spikes at short periods, large numbers of individuals, low flight (**Fig. 6**), and occasional/rarely, precise, flash synchrony make healthy populations at their peak remarkable, their silent choruses not-to-be-forgotten displays. The map in **Figure 1** is incomplete; *congener* certainly occurs in several additional counties. Below the southern end of *congener's* range there is a similar species, *Photuris floridana*, recognized by Barber as *Ph. brunnipennis*, with, seemingly, an identical FP; this firefly may have once been isolated on pine-islands and other elevated sites in the southern-most everglades. To the north, among FP-voucher samples were three that were identified as *congener* at the time, but flashed at much longer intervals as shown in **Figures 8** and **10**—apparently *frontalis*? Whether intergrades occur at their contiguity, along the FL/GA line (?) is unknown. Specimens of the two except at the frontier are easily distinguished (**Figs. 2, 4**). LeConte had second thoughts after naming both. Note in **FigTable 5** that the two differ in the color of their luminescence. See *frontalis* map and compare FP regressions in Chapter 36.

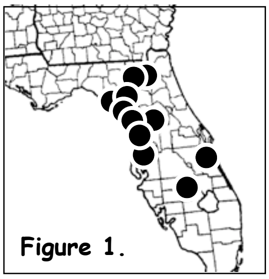


Figure 1.

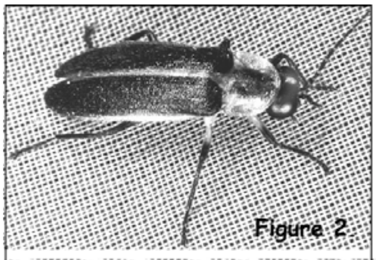


Figure 2

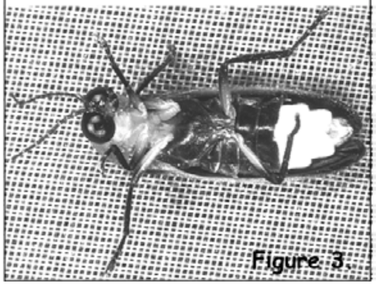


Figure 3.

Species	Date	Locality	n	Peak	Half Max		Wid/HMx
congener	2 V 67	nc FL	5	554	528.0	602.0	74.0
congener	22 IV 68	nc FL	10	551	527.0	602.0	75.0
congener	31 III 78	c FL	6	558	530.0	602.0	72.0
frontalis	11 VI 67	nw GA	5	568	539.0	611.0	72.0
frontalis	26 VI 78	e MD	4	571	540.0	619.0	79.0
frontalis	30 VI 81	e MD	4	571	540.0	616.0	76.0

FigTable 5. Color of luminescence compared.

Figure 6. Low flight over a hammock floor.

Morphology. **Figures 2, 3, 12-14** give measurements, colors, ratios; or illustrate elements for identification.

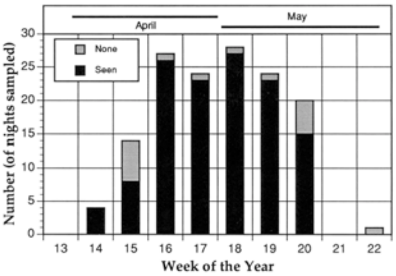


Figure 9. SESOBS for Alachua Co. (north central FL).

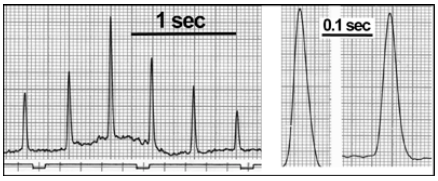


Figure 7. High. Ham. S. P., 21.8°/71.2° (AX: rel. int./time).

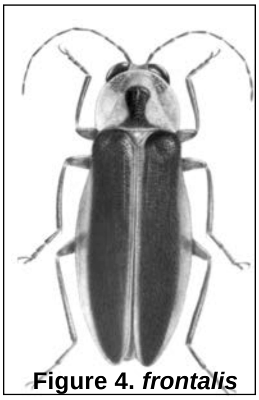


Figure 4. *frontalis*

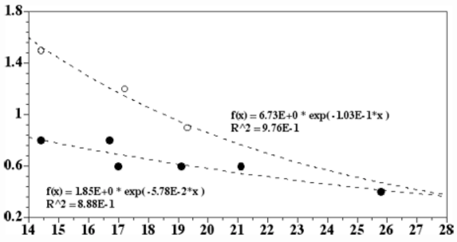


Figure 8. FP period (AX:sec/temp)..

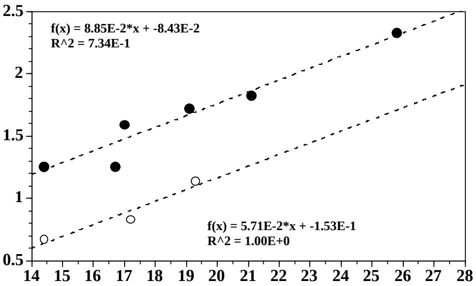


Figure 10. FP flash rate (1/per; AX: Hz/temp)..

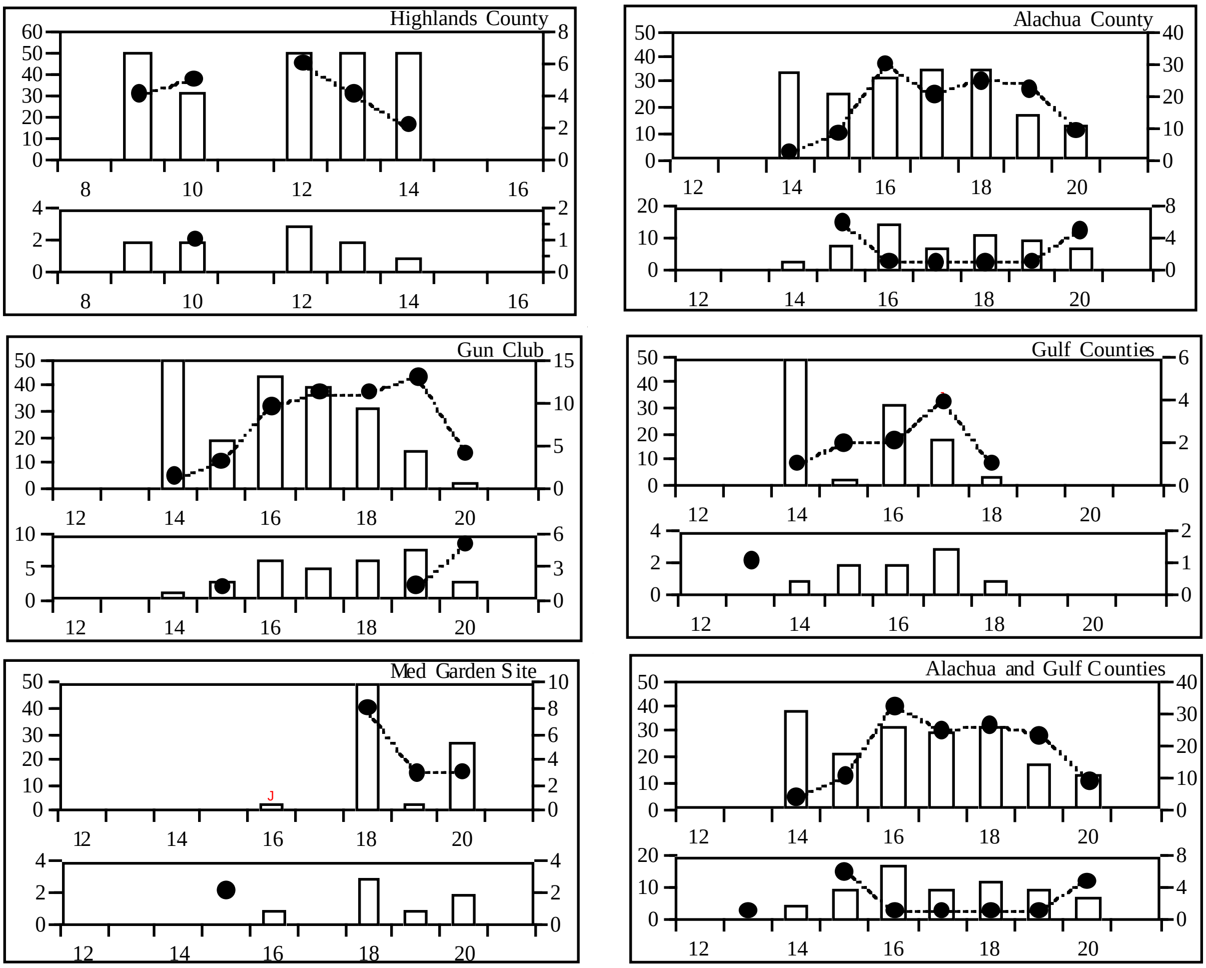


Figure 11. SESOBS from various sites and combinations.

congener HH

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.273	8.633	2.873	1.707	2.040	0.000	10.893	.791	1.207	0.000
sd	.240	.412	.139	.122	.106	0.000	.597	.065	.063	0.000
se	.062	.106	.036	.032	.027	0.000	.154	.017	.016	0.000
n	15	15	15	15	15	15	15	15	15	15
min	1.600	7.900	2.600	1.500	1.900	0.000	9.800	.590	1.070	0.000
max	2.500	9.400	3.100	1.900	2.300	0.000	11.900	.860	1.310	0.000
Vc%	10.6	4.8	4.8	7.2	5.2	0	5.5	8.2	5.2	0

congener HH

	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	2.800	2.067	1.200	1.000	1.467	2.267	2.800	3.000	1.267
sd	.414	.594	.414	0	.516	.458	.414	0	1.033
se	.107	.153	.107	0	.133	.118	.107	0	.267
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000	0
max	3.000	3.000	2.000	1.000	2.000	3.000	3.000	3.000	3.000
Vc%	14.8	28.7	34.5	0	35.2	20.2	14.8	0	81.5

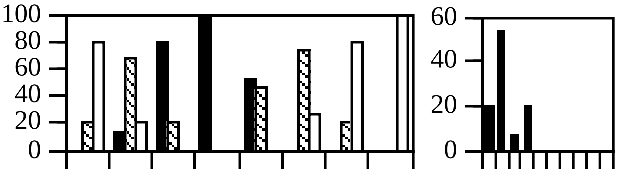


Figure 12. Measurements, colors, and ratios.

FLORIDA: (various sites)

Figure 13.

Figure 14. The filaments are missing/broken in this very old, stained preparation. The bracket indicates an area of the lateral lobe that is useful for distinguishing the two Divisions: In Division I, as shown here in *congener*, this area is usually simple, without elaboration.

Chapter 26

Photuris cowaseloniensis n. sp.

Creek-Penn Firefly

This dot-dash emitter and the sloppy repertoire it presented was found only in central New York State near Oneida, in Madison County (**Figs. 1, 2**). First, and simply, it emitted two basic FP types that are similar to those seen in other Group members, with much variation in the configuration of the dash and sometimes the dot was omitted, as also seen in other Group members (**Fig. 3A-C, Dab, 17A-G**). Other light-emission patterns ("FPs" emitted while perched or walking), could not be interpreted as to significance or sometimes sexual origin. It is because some of these resembled FPs emitted by species that were active in the area, in varying numbers and from time to time, is the resemblance not to be dismissed but suspected as possibly part of the puzzle to be resolved (**Fig. 3Dcd-G, 17H-K**).

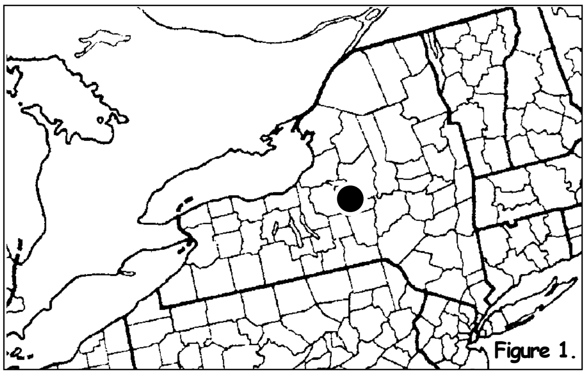


Figure 1.

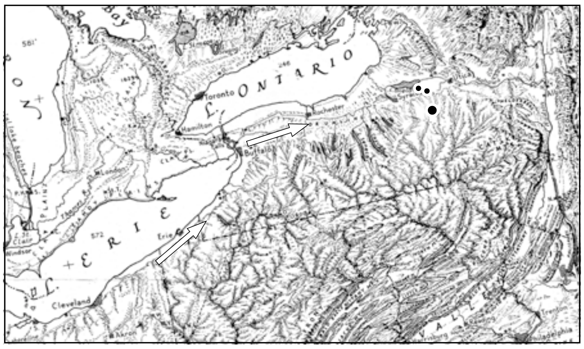


Figure 2. Locations in physiographic context.

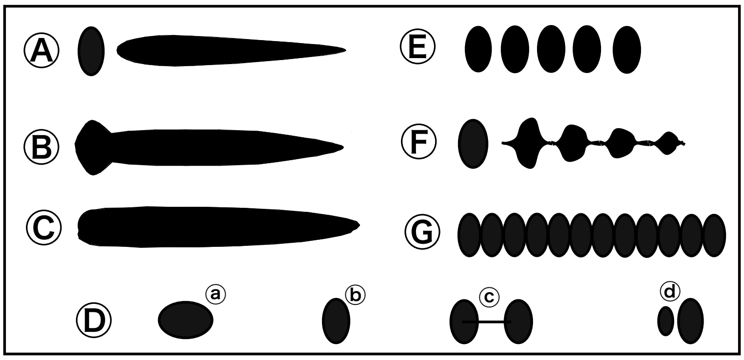


Figure 3. Sketches of FPs and a few other emissions ("FPs"?).

The possession of two basic FPs, the dot-dash and short-single, were determined by mark-release (**Fig. 4**). As to the "pseudo-FPs," there are four mentionable connections that might be kept in mind, as remote or unlikely as some may seem at the moment: (**1**) Some of these may be "hard-wired" copies of FPs of *Photuris* species that females of the Creek firefly prey upon, but their males only rarely emitted them at times of observation; (**2**) Two of the dominating OTUs (species) recognized at this locality may actually be members of a single genetic population, though a mark-release study did not reveal this; (**3**) some "curious, unlikely" FPs may result from the intrusion of genes from other species, these perhaps arriving in the area along the "steppe corridor" and prairie peninsula from the west after the last glacier—the common twilight *Photinus* in the region is a hybrid having such an origin (Lloyd, 1967). Finally, (**4**) some emissions may be *ad hoc* copies by males that had observed these foreign FPs. (**5**) Some observers will prefer to ignore these emissions as happenstance misfirings of the nervous systems to be disregarded, as perhaps they are.

Ecology. In the rather narrow Cowaselon Creek valley, often only 300 yards across and bordered by low and often forested, steep-rising, mostly non-arable hills and hillsides (**Fig. 5**), this firefly flew over the bottom-land with its low and soggy fields—such as often put into cow pasture (**Figs. 6, 7**). Occasional it occurred in drier grassy areas back from the creek (**Fig. 8**), and over sandbars and spits that had been reclaimed by oldfield vegetation along the creek's edges (**Fig. 9**). The Cowaselon flows a few miles to the north into a low damp region of the Mohawk Valley. In this region at localities near Wampsville and long the highway north toward Oneida Lake at Lewis

Point, dot-dash FPs were often seen in numbers across large areas of untilled and oldfield acres dominated by goldenrod (**Fig. 21**). Seasonal distribution records are shown in **Figures 10 and 11**.

Figure 4. A marked yellow-2 dot (dot-dash) flasher.

Figure 5. View east across the valley from atop the west hill where the pasture/ski slope marked the end of an otherwise long-continued, hillside woods.

Figure 6. Low wet pasture, Creek Road, Merrillsville, NY.

* * *

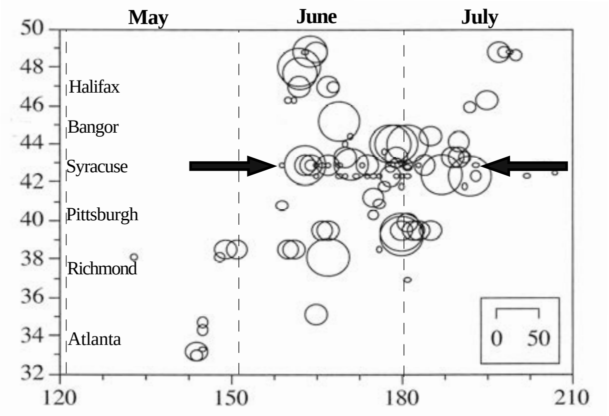


Figure 10. Gesedisobs records of dot-dashing populations (AX: Lat/WOY/number).

Figure 7. Another view of the pasture in Figure 6, looking north; one mark-recapture exercise was done here.

Figure 8. Firefly preserve, dry-to damp with the season and near the woods and a spring, back from the Creek 100 yards. See also Figs. 28, 29, and page 467).

Figure 9. Creek-side gravel-spit reclaimed by oldfield vegetation and occupied by Creek *Photuris*.

* * *

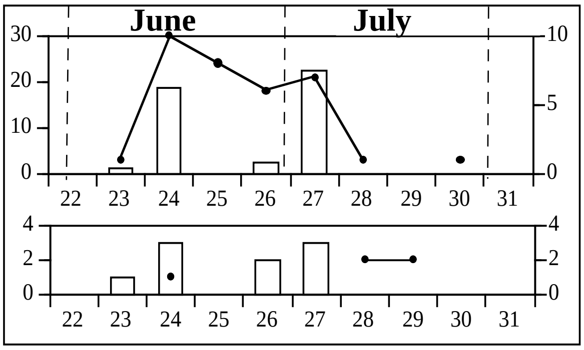


Figure 11. SESOBS for Madison County, NY (AX: #/WOY).

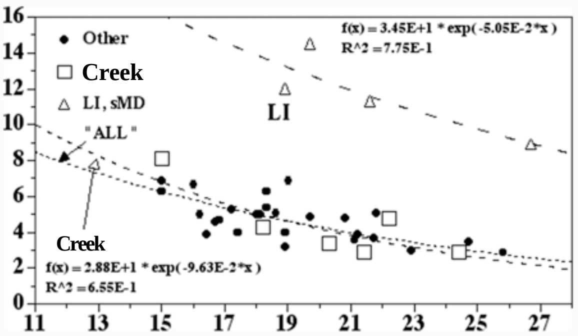


Figure 12. Dot-dash periods compared (AX: sec/temp).

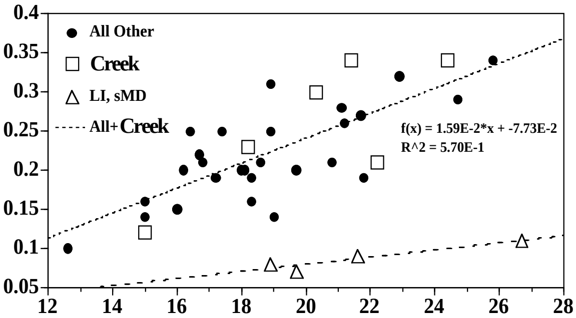


Figure 13. Dot-dash FP (period) rate combined (AX: Hz/temp).

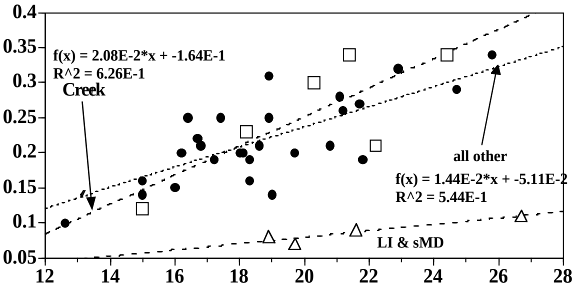


Figure 14. Dot-dash FP rate comparisons (AX: Hz/temp).

Flashing behavior basics. Search flight was commonly low over the grass-tops as described for others in the Group, with angularly-rotated progression, but often was higher and more rapid, sometimes leaving 3-4' stripes of light during the dot-dash, dash-only and variant FPs. FP period for dot-dashes (and variations) was like that for dot-dash demes across the US, excepting southern Maryland and Long Island demes (**Fig. 12**).

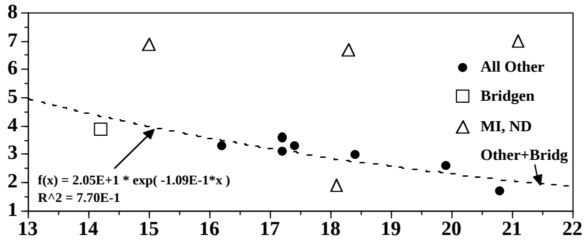


Figure 15. Short (twilight) FP period (AX: sec/temp).

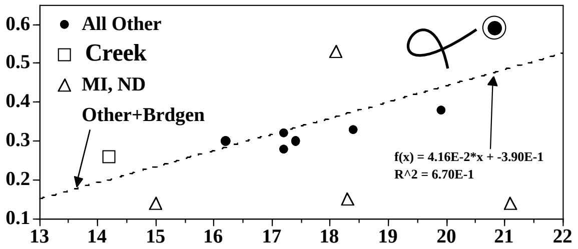


Figure 16. Short (twilight) FP (period) rate (AX: Hz/temp).

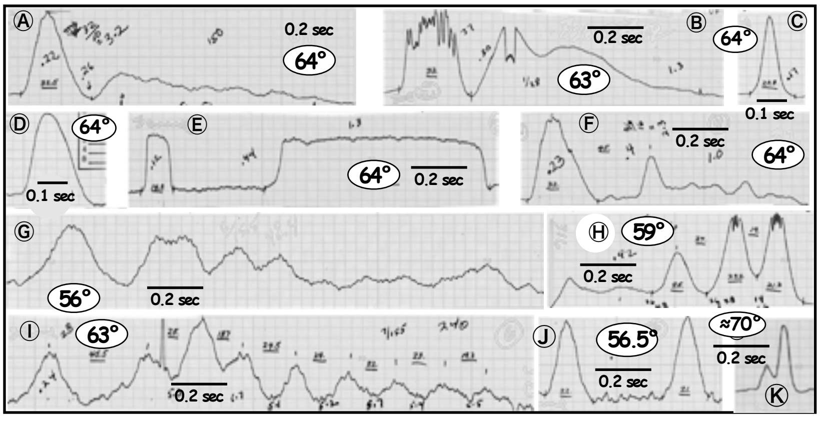


Figure 17. PM records of NY-penn; details, adjunct legend, in text (AX: rel. int./time).

Dot-dash FP (period) rates are shown and compared in **Figures 13** and **14**. For about 30 minutes at the beginning of evening flight many individuals emitted short flashes; short-flash period is shown in **Figures 15** and rate in **16**. To be certain that some individuals emitted both dot-dash and short FPs—and also as will be discussed later, not the bimodal FP herein attributed to *bridgeniensis* n. sp. (**Fig. 3Dd**)—more than 64 were marked and released for recapture (**Fig. 4**) to determine whether dot-dash flashers were also responsible for the early-evening short flashes. Both dot-dash n=37) and short-flashers (n=27) were marked, and demonstrated that individuals in the same population emit both. Apparently most short flashes of this firefly are a fairly close match to those of the twilight firefly in the region *Photinus curtatus X marginellus (*compare **Figure 17D, and Fig. 18A)**. The mark-release exercise failed to reveal FP switches between the FP here attributed to *bridgeniensis*, whose FP is the "hitched-single" (HS) like that shown in **Figure 17K**. However, on three occasions a switch-over from a dot-dash FP to an HS FP was (thought to be) visually observed, with intermediate flash durations appearing to occur progressively. A combination of the dot-dash and HS FPs that was PM-recorded is noted below. Individual HS-emitting males were followed for several consecutive flashes but no changes were noted. Run duration n's of these were: 14, 8, 26, 8, 17, 35, 35, 5, 100, 50. No default testing was done; whether defaulting does occur, or if it does, occurs every time in this population is beyond prediction—*Photuris lucicrescens* being an example of a 2-FP non-defaulter and the significance of this is unknown. As the next section will describe, the behavior of *cowaseloniensis* presents more *Photuris* complexities than encountered anywhere in this study, and invites and justifies imagination (Chapter 71).

Flashing behavior, complexities. PM-recorded FPs shown in **Figure 17** are a sampling, and illustrate some of the curiosities and unknowns encountered: **17C** is a much shorter flash than others (**D**) but cannot be associated with any other species active at the time; **17E** has an unusually long dot-to-dash pause; **17F** has a long pause and strongly modulated dash as does the dash in **17G** and as seen in many other PM records (**17H, I; Fig. 20**)—this pulsing and others, perhaps all of them, may be the result of abdomen wagging but should not be quickly dismissed, for such a mechanical means of producing flickers in fireflies could be connected evolutionarily to pulsing at the lantern, as discussed elsewhere. **17J** is one of three such paired-pulse emissions observed, one being a 3-pulser, each with a pulse interval of about 0.5 seconds; this invites attention in future field observations because this is the FP of a potential prey species in northern marshlands, the common *Photinus obscurellus* (*ardens* in Lloyd, 1966). **17K** is a reversal of the FP of *bridgeniensis*, and is similar to that of *Photuris hebes* that occurs in the region in great abundance. The FP connection among these three *Photuris* OTUs, whether it involves a *Photuris* species preying upon another, is unknown. Fortunately, *hebes* is morphologically distinct, via the pale color of the hind coxae, but close examination of the other two disclosed no differences.

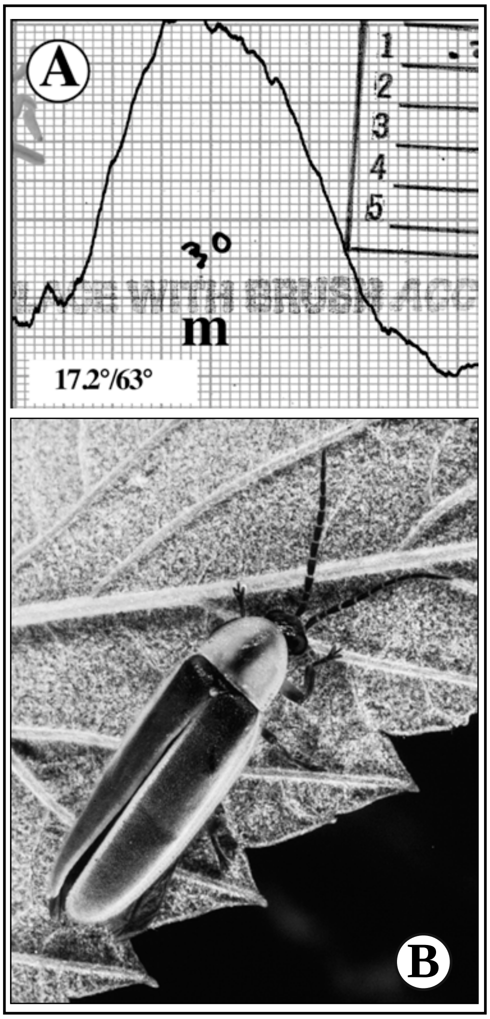


Figure 18. Twilight short-flashing prey species *Photinus curtatus* X *marginellus*, FP and habitus.

Figure 19 shows a series of FPs emitted by a *cowaseloniensis* male, beginning with the typical dot-dash, the dash being weakly (tail-wag?) modulated (**Fig. 19A**). The series shown is complete except some of the intervals between FPs were trimmed. Note below each trace the bracket indicating the dash duration (bracket identified with arrows in **A** and **D**); these were marker-inkpen indicators drawn at time the chart was transduced from the PM-tape. **Note** that the dots, beginning in **B,** became hitched strongly resembling the shouldered FPs of *hebes* (SH)!

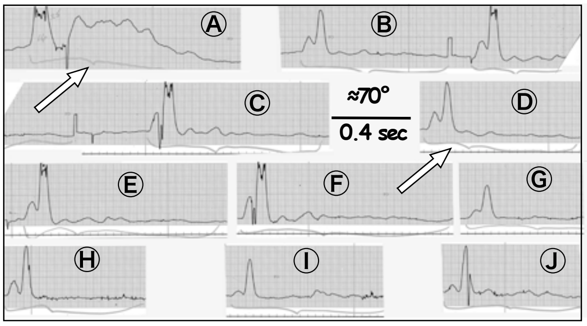


Figure 19. Continuous series of FPs with *cowaseloniensis* male using *bridgeniensis*-like dot.

Figure 21. Oldfield, goldenrod, fallow cropland, elm long gone, 1970s.

Figure 20 shows series of FPs of a *cowaseloniensis* male. Part of the sequence is shown in **A** at a different time-scale, as noted on the charts. Note the extreme degree of modulation and in some examples, its smooth regularity. These could not be produced by abdomen wagging alone? Arrows (**20 BFIJ**) indicate little peaks, which perhaps indicate two out-of-sync modulation-producing mechanisms? The modulation rate of these, as far as could be gained from the irregularities were: x=**5.5**, range = 4.2-7.2, n=9; with a selected sample of 5 having a mean of **5.4**, range = 5-5.7; (@15°/59°). The modulation rate of the flickered dash shown in **Figure 17I** is 6.0 Hz.

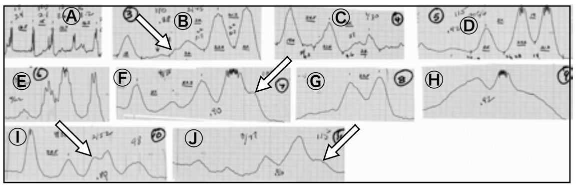


Figure 20. Dash of a *cowaseloniensis* with puzzling modulations.

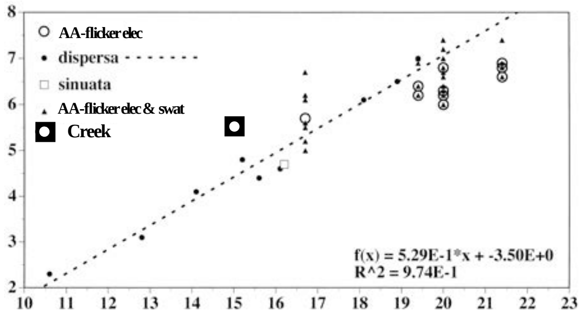


Figure 22. FP pulse rate of *cowaseloniensis*, the AA-flicker and possible *Pyractomena* connections (AX: Hz/temp).

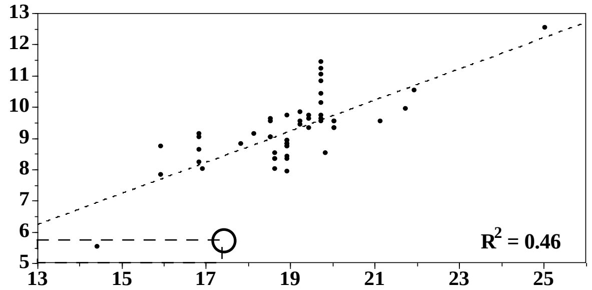


Figure 23. *Py. angulata* modulation rate, all data all localities (AX: Hz/temp).

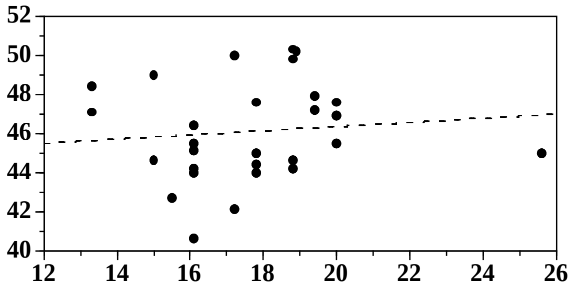


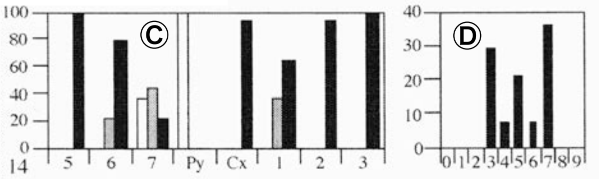
Figure 24. Wingbeat modulation rate of OTUs in the *pensylvanica* Group.(AX: Hz/temp).

Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.507	10.393	3.093	1.827	2.413	5.207	12.893	.807	1.329	.504
sd	.158	.581	.149	.116	.125	2.869	.653	.050	.072	.280
se	.041	.150	.038	.030	.032	.741	.169	.013	.019	.072
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.400	2.900	1.600	2.300	0.000	11.800	.760	1.190	0.000
max	3.000	11.600	3.400	2.000	2.800	7.900	14.300	.910	1.460	.770
Vc%	6.3	5.6	4.8	6.4	5.2	55.1	5.1	6.2	5.4	55.6

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	3.000	2.786	1.857	1.000	2.929	2.643	2.929	3.000	5.143
sd	0.000	.426	.770	0.000	.267	.497	.267	0.000	1.703
se	0.000	.114	.206	0.000	.071	.133	.071	0.000	.455
n	14	14	14	14	14	14	14	14	14
min	3.000	2.000	1.000	1.000	2.000	2.000	2.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	15.3	41.5	0	9.1	18.8	9.1	0	33.1



FigTable 25. Measurements, ratios, colors.

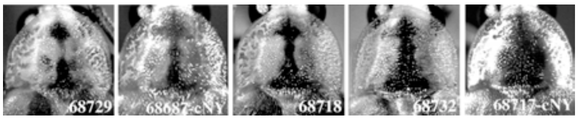


Figure 26. Vittagram array of the Creek *Photuris*.

These measurements put the modulations of *cowaseloniensis* (Creek) above the regression line shown for some fast-pulsing/slow-flickering *Pyractomena* in **Figure 22,** and below that for *Py. angulata* (**Fig. 23**). A fit with either of these might have provided a working hypothesis.

Flashing, wingbeats. Several of the FP PM-charts here have shown ripples atop traces. Such ripples are certainly from the shuttering of the luminescent emissions by the passing of the beating wings between the lantern and PM-receiver. **Figure 24** shows the modulation rate of these ripples in the FP-dashes of *cowaseloniensis* regressed on ambient temperature. Though fireflies are not furry, have no obvious insulation for their thorax and wing-muscles, it would appear that wingbeat frequency may show some independence from ambient temperature. The sample shown in **Figure 24** is for the *pensylvanica* Group, and includes record means from 19 males. There is no evidence that ambient temperature influences rate in wingbeat, and in contrast it does influence FP parameters such as duration and other flash-parameter rates. If the ganglia with circuits controlling both of these rates are in the thorax with the wing muscles, why the difference?

Morphological summary. Means are (n=15): PNL 2.5, ELL 10.4, PNW 3.1, EWhum 1.8, EWmid 2.4, ELVit 5.2, TOTLen 12.9, PNrat 0.81, ELWrate 1.33, ELVTrat 0.50 (**FigTable. 25A**, with other stats); colors in **FigTable 25B-C**, pre-lantern ventrite splash in **25D**. **Figure 27** is key for anatomical elements and splashing on ventrite 4. A range of vittagrams is in **Figure 26**

Holotype Description: male, voucher number 76155, FP recorded, then collected 22 June 1976, Madison County, New York, Creek Road at "Moon's pasture", about 7 miles southwest of Oneida. (FB page1147: "KB 1\76155 [recap penn flash both times; marked 21 June]." Specimen with yellow 2—@midway left elytron, yellow paint dot). Morphological data: genitalia partially extruded, remain attached; from spread sheet—PNLen 2.4, ELLen 9.8, PNWid 3.0, ELWhum 1.8, ELWmid 2.3, LELVit 6.3, TotLen 12.1, PnRat 0.79, ElRat 1.29, VitRat 0.64; Colors: T 333, Py 1, Cx 3, V 223, Edg 3. Types will be deposited in the USNM.

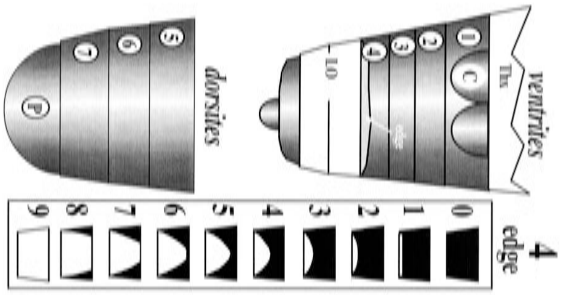
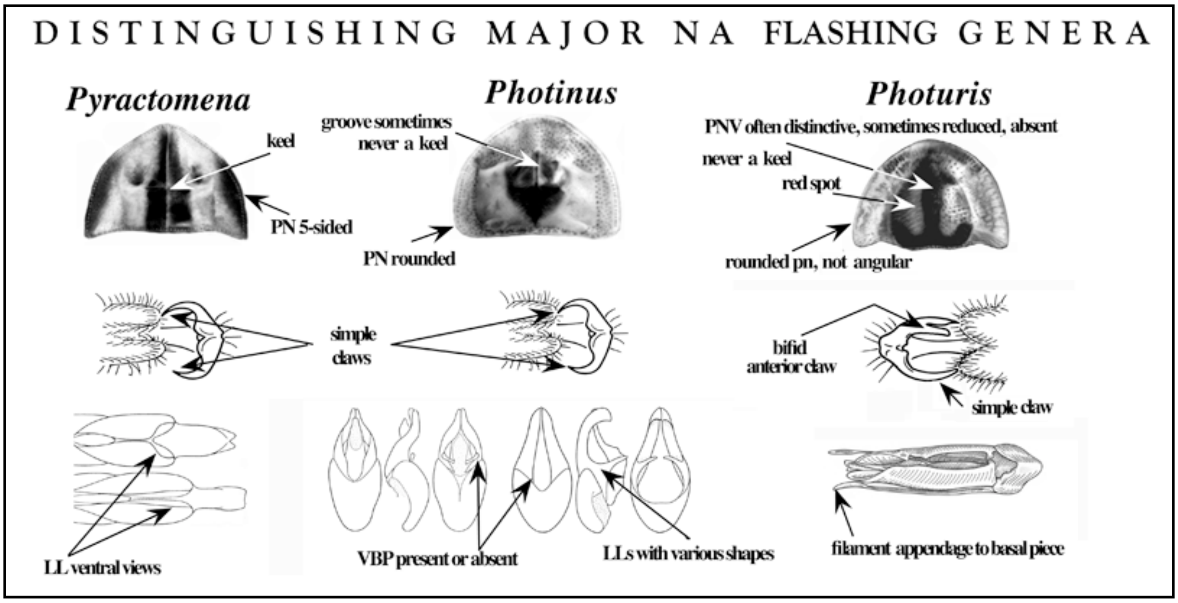
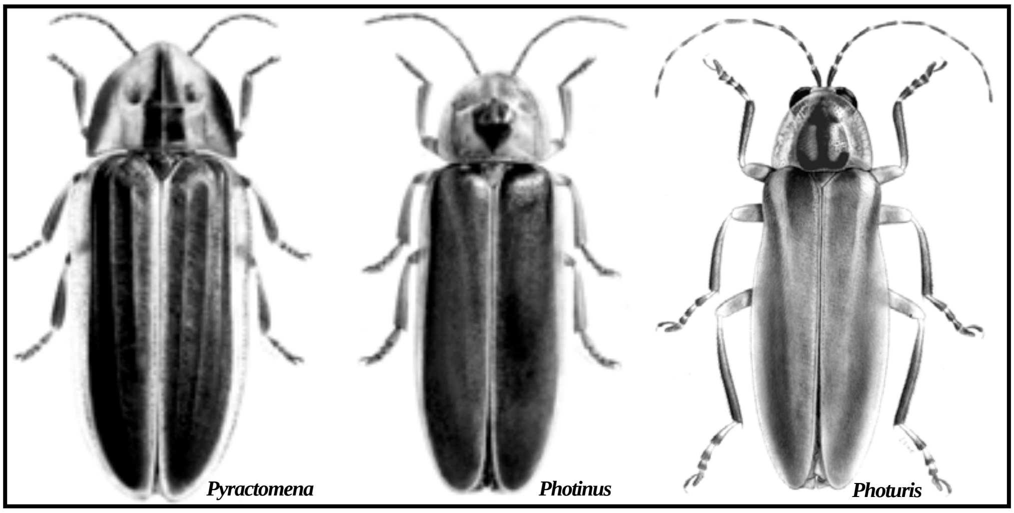


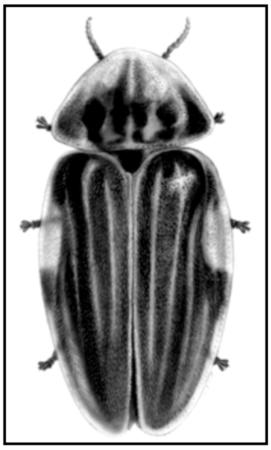
Figure 27 Anatomical key.

Figure 28. Another view of HAL firefly preserve shown in Figure 8. Later in the evening males moved beyond the long grass into adjacent short-grass and lawn areas, as shown in the foreground in Figure 29. Behind the camera 50 feet or so is Cowaselon Creek with more habitat. Harry Lloyd was responsible for this preserve, which is continued even now, 50 years later.

Figure 29. This entire site below the hill rising to the right was at various seasons damp and soggy, with lush grasses, and apparently ideal for these *Photuris* fireflies. Springs in the woods oozed into the "bottoms" here, with only a few trickles running down in tiny rivulets. The steep hill to the right, at the top (photo from top in Fig. 5) continued to gently rise a mile or more before falling away into the next valley. A tree just off camera or barely showing at the right foreground is the living fossil, *Gingko biloba*.







Tropical visitor: s TX, FL s Keys. genus *Aspisoma*

Chapter 27

Photuris darwini n. sp.

The occurrence of this firefly beyond southeastern Tennessee, where it was closely observed and vouchers collected, is based on voucherless (1 exception) but indicative field sightings of FPs; such localities are differentiated in **Figures 1** and **2**. The primary study site was Gee Creek Camp near Wetmore, Polk County. It included airspace over a small slough in a grove of trees (**Fig. 12**) and over an adjacent ditch that ran along a tree-line and drive leading to the boat ramp on the Hiawassee River (**Fig. 13**). Flashing males cruised slowly at the crown of the tree-row and occasionally flew beneath and within the canopy in the grove over the slough; occasionally they flew around the bushes along the tree-line, and a short distance into the adjoining meadow. At the Lumpkin County, Georgia site *darwini* flew along the crowns of a stream gallery. Active populations were never very large; the phenology shown in **Figure 10** is suggested from visits at various times over several years. Evening flight began about full darkness and continued with diminishing numbers two hours or more. It was often difficult to capture vouchers even at Gee Creek. Sometimes they could very easily be attracted close enough to grab in hand or net (see below), and at others they would not respond to “identical” decoy flashes. Males emitted 1- and 2-pulse FPs (**Figs. 3A-C, 11**), but identification depends upon observing the 2-pulse (P1-P2) interval, and there's the rub, for the key is the P1-P2 variability at temperature (**Fig. 8**). Unlike the "precision" timing of 2-pulse (p1-p2) intervals of some species—sometimes in *darwini* individual pulse pairs are conspicuously more variable in duration—possibly suggesting a conditional influence (**Fig. 8**; see Adjunct Legend). Sample means from measured varying intervals do reveal the expected temperature dependence (**Figs. 4-5**). As with other species, FP period is temperature dependent: 2-pulse FP periods averaged 8 sec at 19°/66° (**Fig. 7**, **9** rate). One-flash FPs had much longer periods and a different slope; 1-pulse possible defaults(?) have agreeable timing (**Fig. 7**, circles).

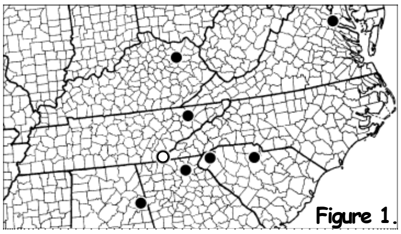


Figure 1.

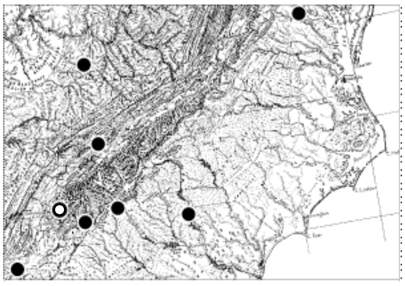


Figure 2. Physiographic perspective.

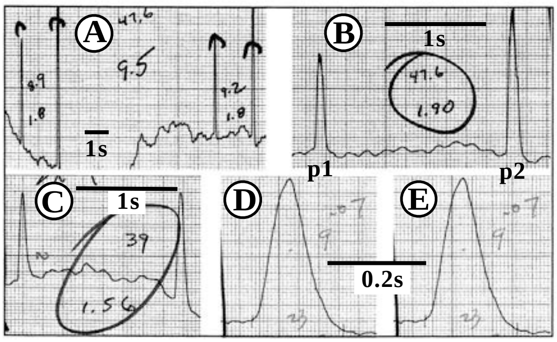


Figure 3. PM-records—see Augmented figure legends.

Flashing behavior, ecology. This species appears to have a stream-side/damp-site association. The slough and ditch sites at Gee Creek (**Figs. 12, 13)** rarely had standing water at times of observations, but were soggy. The unidentified *Photuris* pupa in **Figure 14** was found merely between layers of damp leaves—i.e. not underground in an igloo-dugout as noted in some species—in the tree-edged gully; perhaps these areas provide larval habitats and are an attractive element for male flashing, which is at times suggestive of hill-topping as described for various insect species.

P1-P2 intervals provide the best/only diagnostic clue: **Figure 4** illustrates pulse-period data from the Gee Creek and other sites; **Figure 5** combines and separates these data differently. Note that the Gee Creek *only* and the *combined* regressions are agreeable—data from unvouchered sites (as are included in the calculation of the *both* regression) are indicated with dots. Data from all sites are combined in the rate regression (**Fig. 6**).

The variable pulse period of *darwini* broadly overlaps that of the *Photinus macdermotti* **variad** that occurs in the area —note the asymmetrical and often considerable spread (i. e. weak central tendency) of values around the means in *darwini* (**Fig. 8**).

Flash form is asymmetrical with possibly a slight deflection at the peak, and fall-time 1.6X that of rise time; duration averages ca 180 mSec at the base and 70 mSec at half max at 20°C, based on an examination of 11 flashes of 7 males (**Fig. 3D, E**).

Though a 1-pulse emission often appears to be *the* or *a* default FP in LED attractions (≈50%), at other times attracted males apparently did not use it. The circles in **Figure 7** are estimates of the 1-pulse FP period by males approaching the decoy; note they fall near the regression established by the (questionable) intervals measured for flying 1-pulse FPs. The timing of the 2-pulse FP is presumably associated with the FPs of the *mac*-var (*Photinus macdermotti*-variad) in the area. Predation on *darwini* males by their own and other and large sympatric/syntopic(?) *Photuris* females—*versicolor*, *lucicrescens*, and *quadrifulgens*, and possibly even those of smaller species, *hiawasseensis* and *tremulans*—and sexual selection, most especially mate competition and interloping, may all be involved in the flashing and approach behavior of *darwini*, as described next.

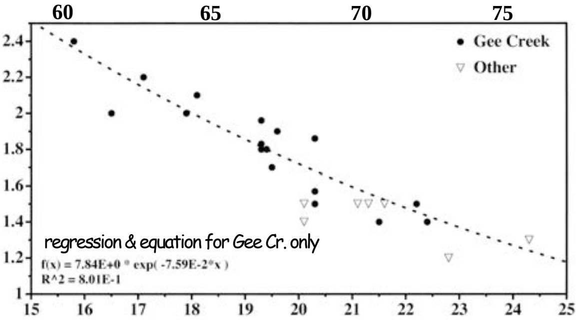


Figure 4. Pulse-period means (AX: sec/temp; see adjunct legends).

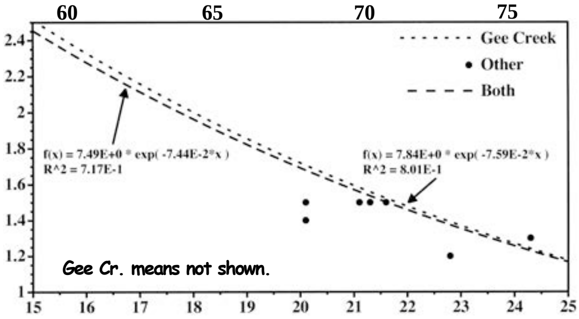


Figure 5. Pulse-period means (AX: sec/temp; see adjunct legends).

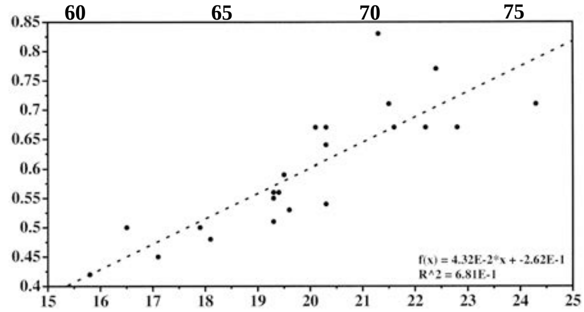


Figure 6. Regression of PP mean rates from all sites (AX: Hz/temp).

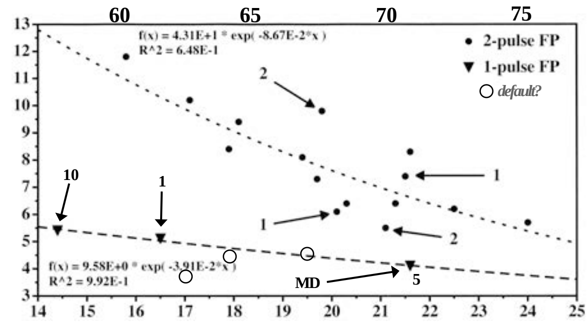


Figure 7. Periods for 1- and 2-pulse FPs (AX:time/temp).

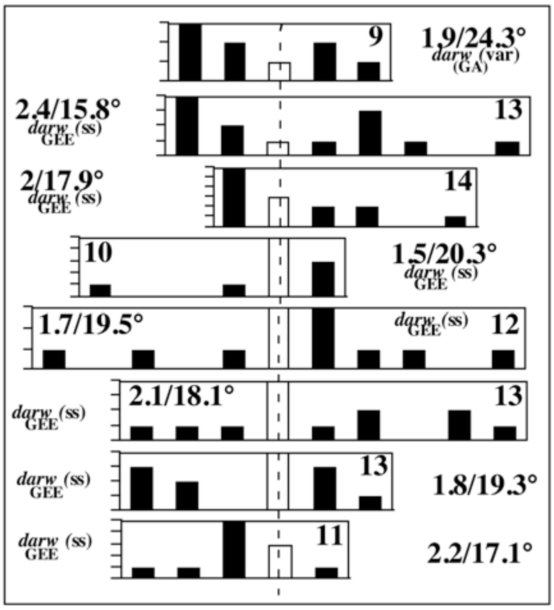


Figure 8. P1-P2 period means and noted spread variations. Is this wide variation connected with an anti-predator, counter-measure tactic (AX: number/timing)? (see adjunct legend)

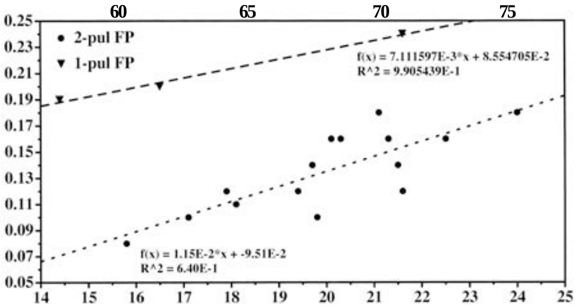


Figure 9. Rate regression (1/period) for 1- and 2-pulse FPs (AX:Hz/temp).

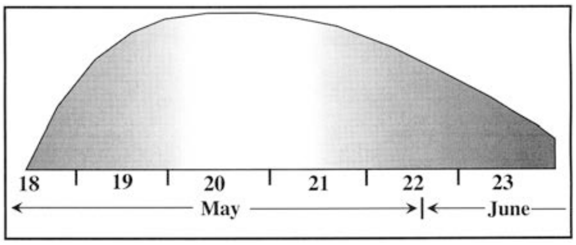


Figure 10. Seasonal occurrence from FB notes (AX: no./WOY).

Figure 11. *Ph. darwini*, as sketched in treetops in east TN.

Figure 12. Slough site, Gee Creek camp TN.

Figure 13. Treeline site, Gee Creek camp TN.

Fig. 14. *Photuris* pupa layered in leaves, tree-line ditch.

Decoy anecdotal observations. If there is a single operative word to describe *darwini* male behavior during their attraction to LED decoys in 20+ trials it is—anthropomorphically speaking—very, very wary, compared with most approaches by other decoyed males of other *Photuris* species. LED attractions noted here were all made in the grassy area by the slough (**Fig. 12**) with a flashpole. Once answered, males approached mostly in darkness, except for occasional FPs, and they commonly alighted without luminescing. Often the FP interval of flying and perched males increased greatly, noted at estimated 40 and 60 seconds, and another at two minutes. Only twice did males approach within a few inches of the decoy, though eleven landed within two feet. Ten landed males emitted a single, dim flash at 4-6-second intervals, which may be a default FP(?), made dim to reduce intrusion by rival males. None switched to a 1-pulse FP during flight approach. After landing one male circled around 90 degrees, remaining at a distance; when I accidentally flashed with another male's P2, he was never seen to flash again; when I answered another in a way I had not intended, he flew like a rocket into the boughs overhead, glowing all the way, and never seen to flash again. During such "experiments" males emitted a variety of flash combinations.

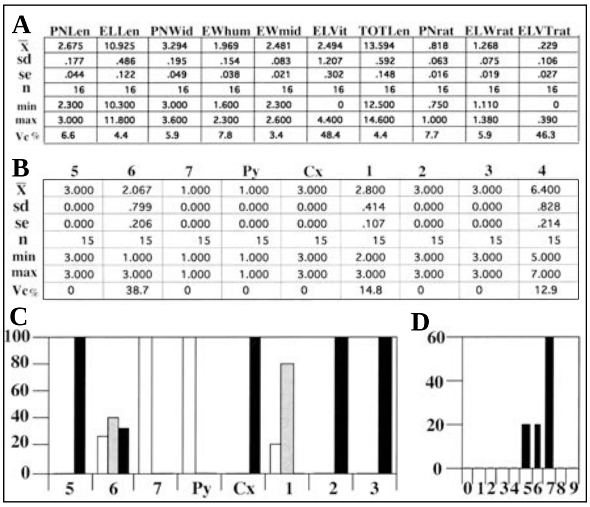
Finally, there must yet remain a small level of doubt about the occurrence of a 1-pulse FP in *darwini*, though the evidence for it strong: (**1**) Mark-release-recapture was unsuccessful because of the difficulty in capturing specimens; (**2**) on five occasions when 2-pulse emitters were observed, a few seconds later a 1-pulse FP was seen in the exact same air space with no other males nearby; (**3**) while visually following flights of 2-pulsing individual males, twice a 1-pulse FP appeared in the anticipated space ahead of where “they” had last flashed the 2-pulse FP; and (**4**) more than 10 decoyed males began emitting a 1-pulse FP after they had landed, and at approximately the same period (questionably) established via FPs of flying males (note **Fig. 8**). Presently, the conclusion is that predation upon *darwini* males by their own females or those of other *Photuris* is common and a strong selective force on their behavior.

Augmented figure legends. **3**. PM-scans of *darwini* FPs and elements, temperature as indicated: (A) two consecutive FPs; (B, C) 2-pulse FPs; (D, E) single flashes from 2-pulse FPs. **4**. Regression of FP pulse-periods on temperature; the curve and equation are for Gee Creek data. **5**. Regression of pulse-periods on temperature: data from Gee Creek *alone* and from *all* sites are plotted and curves fitted as indicated, and data points from sites other than Gee Creek are also shown separately. **7**. FP period for 1- and 2-pulse FPs, with descriptive equations for each provided by the graphing program. Numbers shown in the chart indicate sample size as it may contribute to deviance. The difference in slope must raise some question as to whether one sample (n=10) involved another species. **8**. Histograms showing P1-P2 interval means and variation in several samples at different temperatures at Gee Creek. Means are lined up vertically (dotted line, open bars); SWAT measurements at 0.1 sec intervals, with means, temperatures, taxonomic designation and locality; ss=sensu stricto. **9**. FP period shown as rate (1/period) for both 1- and 2-pulse FPs. **10**. Phenology of *darwini* at the Gee Cree locality, as suggested by a few observations and notes made during visits (1983-87).

Nomenclatural notes. The scientific name of this firefly pays tribute to the major author of biology's most important tool and most painful idea that man can ever know about himself. Wide though admittedly light reading on the activites of Darwin in biology has led me to an astonishing but radical and gratifying conclusion. It is common knowledge that he published many books of original research and thought in biology. It is part of the historical record that he avoided mixing to any extent with academic biologists of his time, this usually being attributed to some socially-problematic gastric illness—he thus spent most of his time at home at Down doing earthworms, carnivorous plants, barnacles and thinking. Apparently he received little academic acclaim from even his own alma mater, Cambridge, during his life and the feeling would appear to have been mutual. I suggest that he was actually sick of babbling, unthinking academicians and their games. An Englishman once said that an American is an Englishman that has been left alone. I think it fair to conclude that Darwin was a self-made American!

Tales told to me of the difficulties encountered by the original Park manager during early development of Gee Creek as a protected public facility are awing and inspiring—these were the times when it was first set aside and protected out of a land that for many generations had been the private hunting domain of uncooperative and reclusively independent souls.

Morphological data. General morphological means are (n=16): PNL 2.7, ELL 10.9, PNW 3.3, EWhum 2.0, EWmid 2.5, ELVit 2.5, TOTLen 13.6, PNrat 0.82, ELWrat 1.27, ELVTrat 0.23 (Table 1A, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in Table 1B-C, and the color of the pre-lantern ventrite in 1D, as explained and defined in Chapter __. **Figure 16** is a general sketch indicating the numbers used for various skeletal plates and numbers for degrees of splashing on ventrite 4. A range of vittagrams (pronotal vittae) pronotal of *darwini* is shown in **Figure 17**.



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.675	10.925	3.294	1.969	2.481	2.494	13.594	.818	1.268	.229
sd	.177	.486	.195	.154	.083	1.207	.592	.063	.075	.106
se	.044	.122	.049	.038	.021	.302	.148	.016	.019	.027
n	16	16	16	16	16	16	16	16	16	16
min	2.300	10.300	3.000	1.600	2.300	0	12.500	.750	1.110	0
max	3.000	11.800	3.600	2.300	2.600	4.400	14.600	1.000	1.380	.390
Vc %	6.6	4.4	5.9	7.8	3.4	48.4	4.4	7.7	5.9	46.3

B

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	2.067	1.000	1.000	3.000	2.800	3.000	3.000	6.400
sd	0.000	.799	0.000	0.000	0.000	.414	0.000	0.000	.828
se	0.000	.206	0.000	0.000	0.000	.107	0.000	0.000	.214
n	15	15	15	15	15	15	15	15	15
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	5.000
max	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	38.7	0	0	0	14.8	0	0	12.9

FigTable 15. Morphological measurementsm ratios colors.

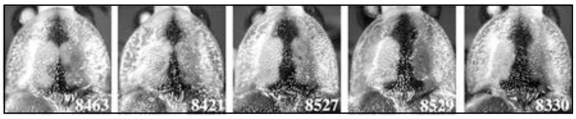


Figure 17. Array of voucher vittagrams.

Holotype Description. male, voucher number 8461, collected 20 May 1984, Polk County, Tennessee, at Gee Creek campground, at little "ravine" behind site B11. FB page 174, identified as "TN". Notes: "1.9 [sec, pul per] attr to fl from 12' to tip of light on gnd. he land 6" from LED on fish pole. up on veg 3" up. looking. gave dim singles at 4-5 s intervals." Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.5, ELLen 10.4, PNWid 3.0, ELWhum 1.6, ELWmid 2.3, LELVit 2.1, TotLen 12.9, PnRat 0.83, ElRat 1.38, VitRat 0.20; Colors: T 331, Py 1, Cx 3, V 333, Edg 7. Types will be deposited in the USNM.

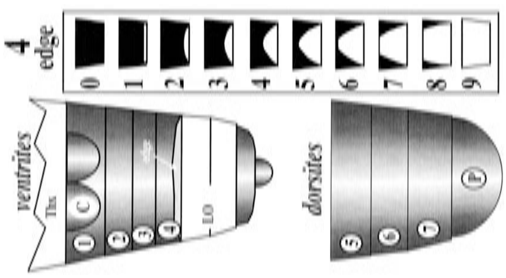


Fig. 16. Sclerite color and splash key.

Chapter 28

Photuris divisa LeConte 1852

This the most atypical or unusual of the North American *Photuris*: belonging to Division I, by all appearances, its flashed signals and presentation in the field are more like those of a *Photinus*. Its single short and pairs of such flashes were noted in southwestern Missouri along roadsides and over grassy areas, as previously had been described in some detail by Lawrent Buschman (1972, below), from studies made at sites in Lyne County, Kansas. He also experimented in the lab with *divisa's* flashed signals; his report should be consulted when making further studies on this firefly. Its documented occurrence is shown in **Figure 1**. The following is from Buschman's study (1972:83/160):

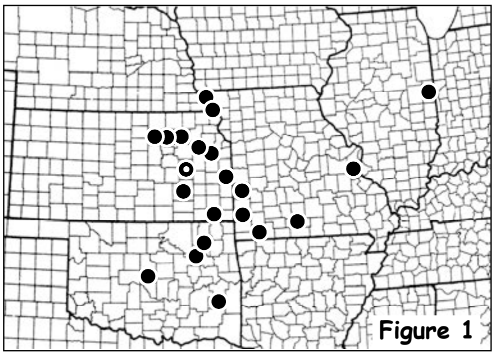


Figure 1

> *Adult Photuris divisa were seen in the field from mid May until late July* [Fig. 2] *in grassy habitats where the vegetation 1-2½ ft. tall. Male flashing activity began about 16 min. after sunset and lasted for about an hour. The first flashes were often single pulses emitted by males perched on the grass. A few minutes later males began to fly slowly, 1-2 ft. above the vegetation, emitting paired pulses about 0.4 sec apart at intervals of 4.6 sec (range 3.2-7.1 sec, n=32, 21-22.5°C). Females were found on vegetation about 6 inches above the ground where their flashes could be seen from above. Their response flash consisted of 2, 3 or more pulses spaced slightly farther apart than the male's pulses. They did not appear to flex the abdomen when answering as noted in Photinus … The females responded to male paired flashes after a delay of about a second. Flying males landed near responding females or flew back over and flashed again. After landing the male emitted paired flashes at irregular intervals. If the female responded he walked or flew to her. Several males were often attracted to one female. When the female responded to one male other males often moved toward her.*

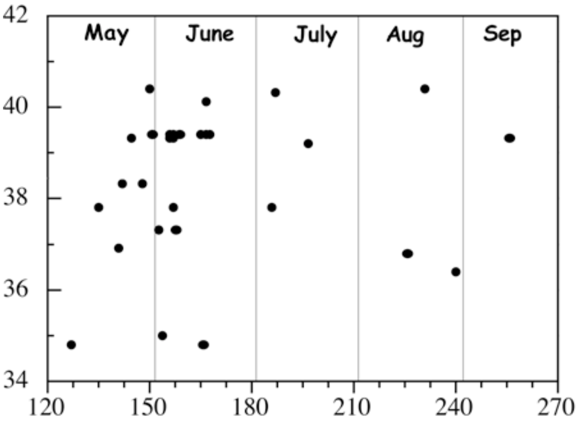


Figure 2. GESEDIS (AX: Lat/DOY).

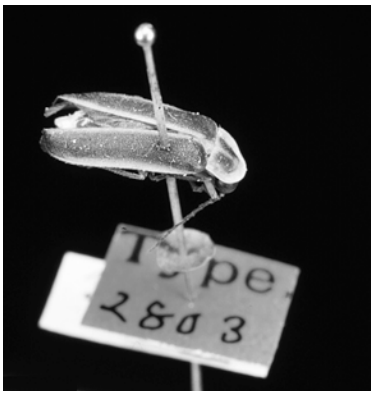


Figure 3. LeConte's "type" specimen of *Ph. divisa*.

The figure below is Buschman's **Fig. 1** with its legend that describes results from his lab experiments.

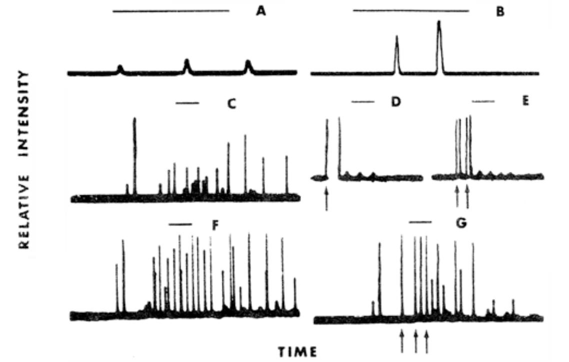


FIG. 1. Oscillogram of firefly flashes. A. A female response flash. B. A male paired flash pattern. C. A male paired flash followed by a female response flash and a burst of male single pulses. D. A female response to an artificial pulse 0.5 sec long. E. A female response to artificial pulses 0.4 sec apart. F. A male paired flash followed by another male single flash and a burst of male pulses. G. A male paired flash followed by artificial pulses and a burst of male pulses. Intensity of the above recordings does not reflect actual flash intensity. Arrows indicate artificial flashes. Scales show 1 second.

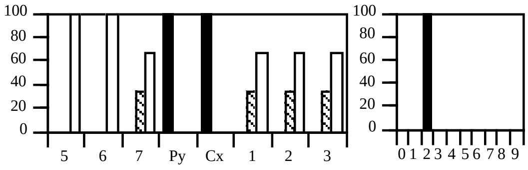
Morphological data of vouchers are in **Fig-Table 4** and key to morphological elements and splash are in **Figure 5**. PNV of vouchers are in **Figure 6**.

divisa O K KS

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.175	8.250	2.825	1.775	1.775	0	10.475	.785	1.003	0
sd	.150	.443	.050	.126	.126	0	.350	.030	.104	0
se	.075	.222	.025	.063	.063	0	.175	.015	.052	0
n	4	4	4	4	4	4	4	4	4	4
min	2.100	7.900	2.800	1.600	1.600	0	10.300	.770	.930	0
max	2.400	8.900	2.900	1.900	1.900	0	11.000	.830	1.150	0
Vc%	6.9	5.4	1.8	7.1	7.1	0	3.34	3.8	10.4	0

divisa O K KS

	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	3.000	3.000	2.667	1.000	1.000	2.667	2.667	2.667	2.000
sd	0	0	.577	0	0	.577	.577	.577	0
se	0	0	.333	0	0	.333	.333	.333	0
n	3	3	3	3	3	3	3	3	3
min	3.000	3.000	2.000	1.000	1.000	2.000	2.000	2.000	2.000
max	3.000	3.000	3.000	1.000	1.000	3.000	3.000	3.000	2.000
Vc%	0	0	21.6	0	0	21.6	21.6	21.6	0



FigTable 4. Measurement and colors, ratios.

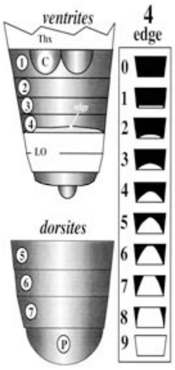


Figure 5. Key to anatomical/topo-graphical data.

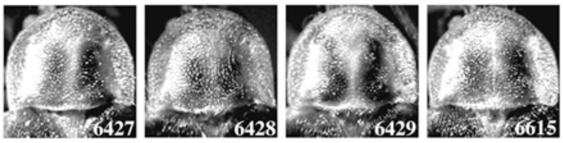


Figure 6. PN vitta array of specimens at hand.

Another Train-flasher? A train flashing firefly seen in the treetops along the road about a mile south of Phillipsport, Sullivan County NY (**Fig. 1**), early in the evening of 26 June 1991 is noteworthy. No vouchers were collected. Its unusually fast rate was immediately recognized as too fast for known train flashers in the northeast (*chenangoa*, *potomaca*). The fieldbook records four SWAT measurements of short flash sequences, but does not specifically indicate the number of individuals present or measured. The mean pulse period was 0.68 sec (1.47 Hz), @15.9°/60.7° (**Fig. 2**).

The following explanations come to mind: **1**. The firefly was perhaps emitting flashes at a faster rate than expected from any known species, specifically *potomaca*, because ambient temperature was measured near the ground and was lower than at treetops. Note in **Figure 2** that a differential of 3°C would have made the difference; this 3° difference is between the observation and the *mean potomaca* value, but considering *potomaca's* previously measured variation, it is possible. Temperature differences of such magnitude are noted and sensibly appreciated in the field. **2**. A second possibility is that a *fairchildi* was emitting its long FP, one previously seen only over grassland, and the typical amplitude change in this FP was not apparent. SWAT DATA: 26-VI-91, 15.9°C (nr ground). 2/1.2, 3/2.2, 3/2.0, 3/2.2, 5/3.2, 3/1.8 in trees; n=6, x=.66 (1.52), s=.06.

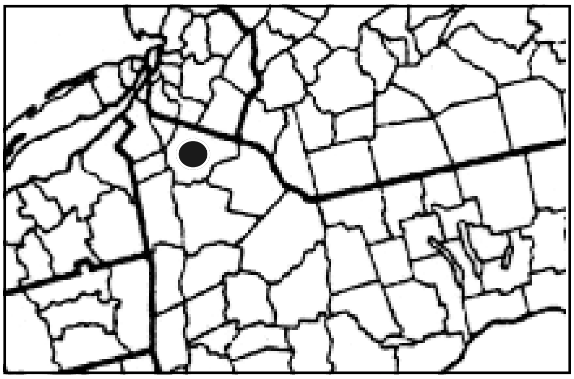


Figure 1. Sullivan Co., southeastern NY.

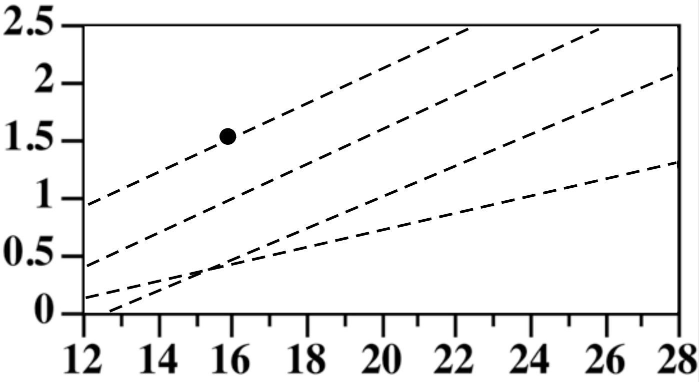


Figure 2. Flash rate comparison for train-flashing *Photuris* (AX: Hz/temp)

Chapter 29

Photuris dorothae n. sp.

Little Red

This species is one of the easiest fireflies of the genus to identify, from both its physical appearance—a beautiful rufus and black miniaturization of Big Red, *maicoi*—and its FP, which sometimes has the rhythm and configuration of the first four notes of Beethoven's Fifth Symphony (dot-dot-dot-dash)—at *largo* tempo. Geographic occurrence may be restricted to southeastern North America (**Fig. 1**), for I saw *dorothae* nowhere else in the field, but there are archived specimens that resemble it from Illinois and Indiana. Certain variations of *dorothae's* FP are diagnostic, but others are unreliable. Diagnostic FPs are those that include one or more dashes, that is, the longer "winked-pulses" that follow the 1-4 short flashes in some FP variations (**Figs. 2, 3**). The bimodal dash appears to be composed of two connected short pulses, the intensity "wink" between them plainly visible and eye-catching (**Fig. 3C, F**). When only short-pulse FP variations are seen specimens must be captured for positive identification. FP period and pulse period data are shown in **FigTable 1**. When first discovered *dorothae's* small size and resemblance to Big Red suggested that it might be an autumn generation of *maicoi*, and one can still imagine and find biological examples of life histories that involve such macro and micro generations (Florida's *Photinus macdermotti*). A distinctive feature often seen in populations of this firefly was the number of females landing, perhaps ovipositing and apparently also taking hunting stations on low vegetation. They responded readily to simulations of *Photinus* FPs and probably are important predators of *P. macdermotti*. Their distinctive landing flashing emission is a series of short pulses as they approach the ground at a steep angle followed by a 2-second long bright glow just before and during touch down. Adult season is from late May to mid-September **(Fig. 4)**. Vittagrams are distinctive and resemble those of *maicoi* (**Figs. 5, 12**).

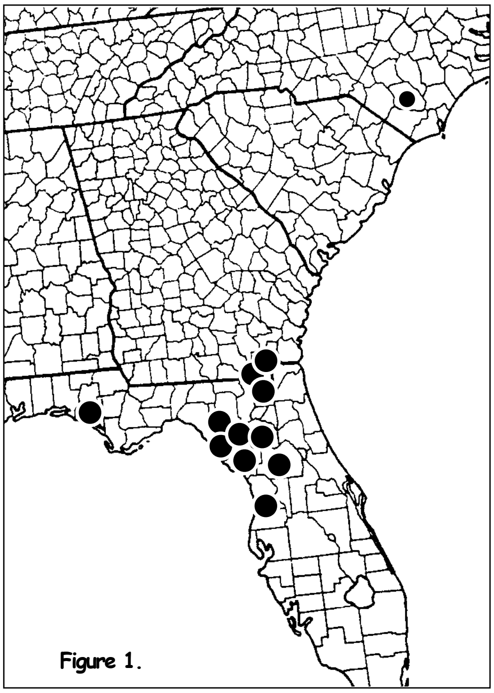


Figure 1.

Ecology, flashes, behavior. Like other Florida Red fireflies, *dorothae* seems to occur primarily in and near pineland. At the Austin Cary Forest (ACF) males flew over and among the crowns of tall pines within and along plantations (**Fig. 6**). In the Gulf Hammock, especially near Hines—a now-vanished lumber camp with a railroad siding of 100 years ago near Cross City, Dixie County—occasionally there were large numbers, and they flew over fields and berm, and along road-side shrubs (**Fig. 7**), as well as at pine crowns. As with other Reds, few specimens are in museum collections, and males in the voucher series were obtained by attracting males to penlight simulations that presumably approximated the female response flash.

The duration of the asymmetrical short flash in a small sample (n=2) was 115/265 mSec ≈23° (**Fig. 3A**), and the winked dash is nearly twice as long (**Fig. 3F**). An examination of PM-traces indicates that the dash is seemingly composed of two asymmetrical short flashes with the second a reversal of the first and perhaps a half-again longer (**Fig. 3F**): note the shapes of the short flash in **3A** and the two flashes in the winked-dash in **3F**. To construct Figure **3C** the short flash in **3A** was duplicated, the copy flipped horizontally, but not melded closely with the original, which made this fabrication longer than recorded traces of the winked-dash (cf **3C** and **3F**. Examination of 15 PM-traces of dashes, most of poor quality, from 8 males gives an estimated mean base of 500 mSec ≈23°. Pulse rate of the two

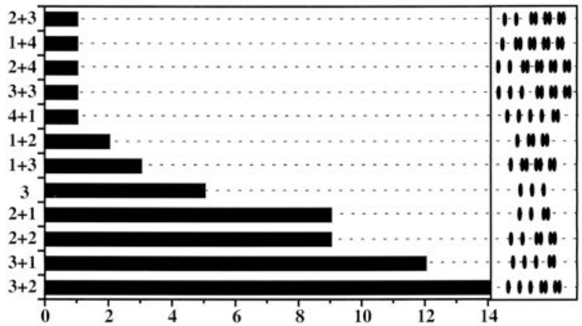


Figure 2. FP configurations (AX: form/frequency).

pulses in the winked-dash is speculated in **Figure 8** from measurements of 15 PM-traces from 10 males at two temperatures, and is in the range of 3-5 Hz near 23°. Any biological significance of this rate and the accuracy of the slope illustrated is unknown. Though the two modes in a winked-dash are probably of equal intensity, some PM-recordings show significant intensity differences (**Fig. 3 I**); presumably because males change the direction of their aim during the dash.

This firefly is one of the few fireflies known to combine two different flash forms in a single FP—some others being *Photuris pennsylvanica*, *barberi*, and *hiawaseensis*, and *Photinus ceratus* in Jamaica. Little Red's short and winked-dash pulses produce distinctive, diagnostic combinations. The crude frequency sampler of Little Red FPs arrayed in **Figure 2** is based on incidental notations made in fieldbooks, and is only an unsystematic estimate of occurrence in the field. Portions of some configurations were PM-recorded, and are shown in **Figure 3B, D, E, H**. Several ecological factors, including phenology, habitat type and structure, level of micro-local mate competition, and predator presence could be influencing factors.

There is no apparent clue to a functional or transition connection among the most frequently observed FP configurations. Among some acoustic insects there occur combinations of tics and buzzes that have been connected with male competition among acoustic neighbors. The most likely guesses for fireflies, from what is known about the conditions, problems, and hazards of mate search in fireflies, is that the number and proportion of "tics and buzzes" of *dorothae* could be connected with: (**1**) deterring nearby flashing rivals; (**2**) countermeasures for the avoidance of female-mimicking predators; and (**3**) structure of the immediate substrate—where receptive but obscured females may be perched.

The FP in **Figure 3G** was recorded at a *dorothae* site and possibly is an adjunct FP of mate-seeking males, an unwinked dash?

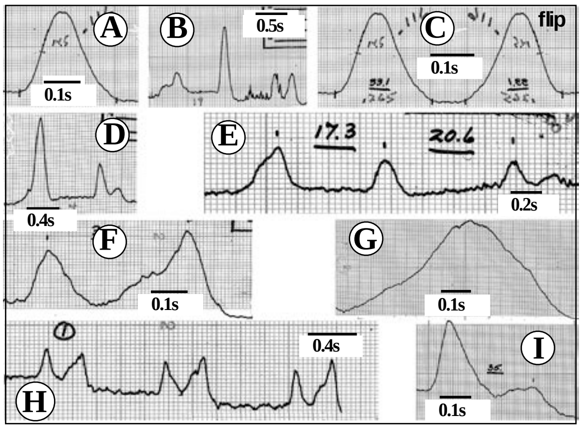


Figure 3. PM traces (AX: ri/time).

	FP Per	Pul Per
Mean	9.283	.634
Std. Dev.	1.603	.059
Std. Error	.654	.027
Count	6	5
Minimum	6.600	.550
Maximum	11.400	.700
Vc%	17.3	9.3

FigTable 1. FP stats @ 22.8°/73°—24.7°/76.5°.

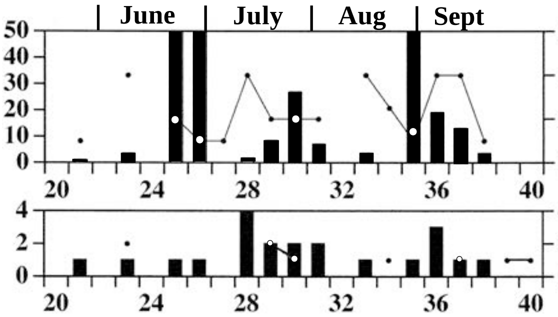


Figure 4. SESOBS, Alachua & Gulf Cos. FL

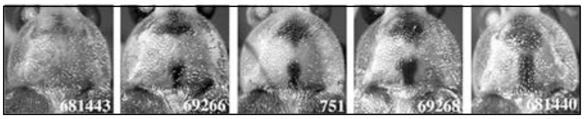


Figure 5. Vittagram array.

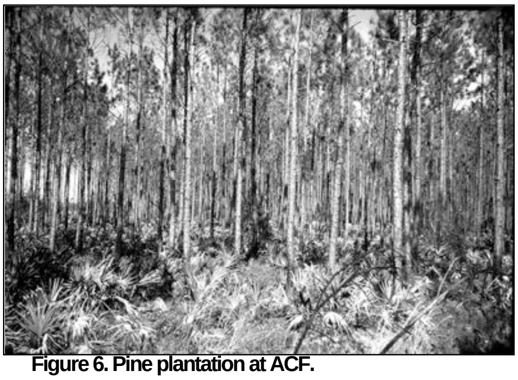


Figure 6. Pine plantation at ACF.

Figure 7. Firefly-rich berm near Hines, Dixie Co.

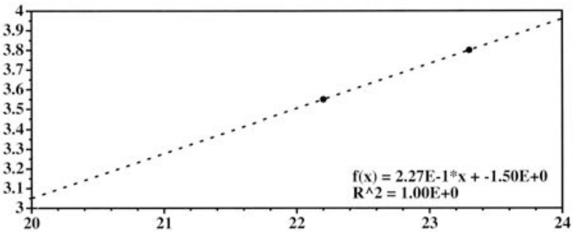
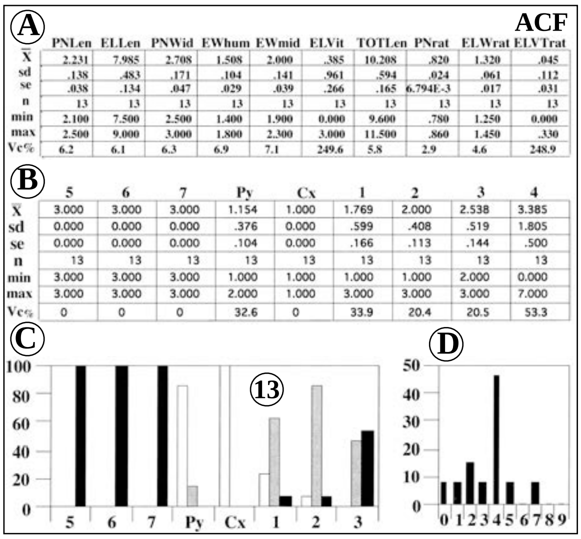


Figure 8. Regression for wink modulation rate (AX: Hz./temp).



	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.231	7.985	2.708	1.508	2.000	.385	10.208	.820	1.320	.045
sd	.138	.483	.171	.104	.141	.961	.594	.024	.061	.112
se	.038	.134	.047	.029	.039	.266	.165	6.794E-3	.017	.031
n	13	13	13	13	13	13	13	13	13	13
min	2.100	7.500	2.500	1.400	1.900	0.000	9.600	.780	1.250	0.000
max	2.500	9.000	3.000	1.800	2.300	3.000	11.500	.860	1.450	.330
Vc%	6.2	6.1	6.3	6.9	7.1	249.6	5.8	2.9	4.6	248.9

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	3.000	1.154	1.000	1.769	2.000	2.538	3.385
sd	0.000	0.000	0.000	.376	0.000	.599	.408	.519	1.805
se	0.000	0.000	0.000	.104	0.000	.166	.113	.144	.500
n	13	13	13	13	13	13	13	13	13
min	3.000	3.000	3.000	1.000	1.000	1.000	1.000	2.000	0.000
max	3.000	3.000	3.000	2.000	1.000	3.000	3.000	3.000	7.000
Vc%	0	0	0	32.6	0	33.9	20.4	20.5	53.3

FigTab. 9. Basic morphology.

Morphological data. General morphological means are (n=13): PNL 2.2, ELL 8.0, PNW 2.7, EWhum 1.5, EWmid 2.0, ELVit .39, TOTLen 10.2, PNrat 0.82, ELWrate 1.3, ELVTrat 0.045 (**FigTab. 9A**, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **FigTab. 9B-C**, and the splash of the pre-lantern ventrite in **9D**. **Figure 10** is the general sketch indicating the numbers used for various skeletal plates and numbers for degrees of splashing on ventrite 4. A range of vittagrams is shown in **Figures 5, 12**. **Figure 11** gives the results vittagram analysis for general form and idiosyncratic features, and **Figure 12** shows pen and ink.

Taxonomic and nomenclatural notes. The specific epithet recognizes the spirit, strength, support, industry, and companionship of Dorothy Lloyd, wedded partner since 1958, and the critical role she has played in the production and completion of this survey. Such a long study with its trials and tribulations would not be possible without such support. The common name is the one used for this species since its discovery in 1967, *Red* referring to its tawny color, and *little* referring to its small size as compared with other Red-group species associated it with in north central Florida—Big Red, Giant Red fireflies (*lineaticollis* variads and *maicoi*)—red ground-coloration compared to most *Photuris* species.

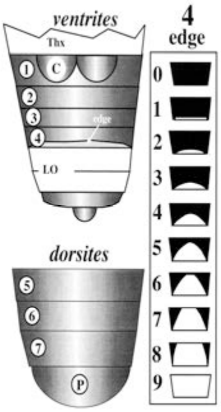


Figure 10. Topography and splash key.

Holotype Description. male, voucher number 681441, collected 19 August 1968, Alachua County, Florida, Univ. Florida Austin Cary Forest, near sawmill. FB page 216: FB notes. "KB 32 little red [male], gave 2 shorts & long then twice gave 2 pulse phrases, low over ground, 5'." Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.1, ELLen 7.8, PNWid 2.6, ELWhum 1.4, ELWmid 1.9, LELVit 0.0, TotLen 9.9, PnRat 0.81, ElRat 1.36, VitRat 0.00/NA; Colors: T 333, Py 1, Cx 1, V 222, Edg 4. Types will be deposited in the USNM.

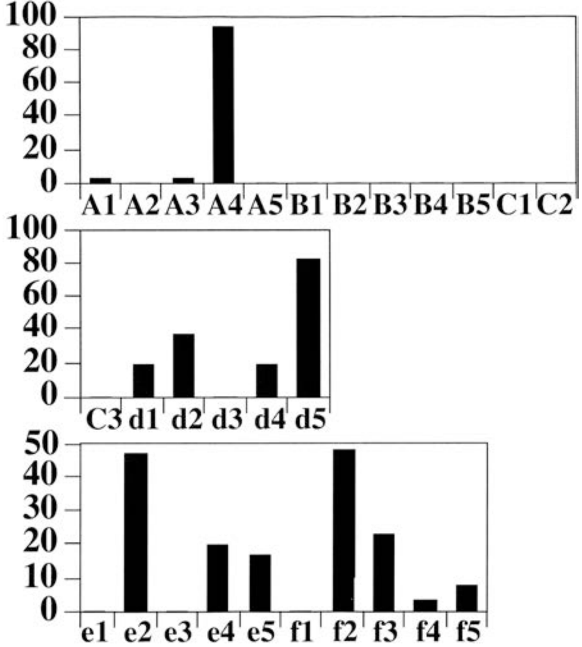


Figure 11. Vittagram evaluation, Chap. 4.

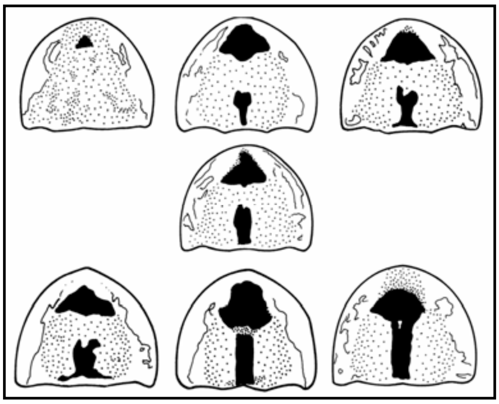


Figure 12. Vittagram array sketches.

Male and female *Photuris* upon the grass and herbs at the old UF Med Garden, Page 3: searching mode?















wsw across douglasae space toward lamarcki's damp corner

lamarcki sw corner with a douglasae


wnw across harrannorum hunting grove

Chapter 30

Photuris douglasae n. sp.

This “polyphot” lightningbug occurs primarily in Florida (**Fig. 1**), but eventually important demes should be found further north as instructional subsets—distinctive variads or intergrades—that occur rather near the Atlantic coast and perhaps intimately “connect” with McDermott’s *Photuris bethaniensis* in Delaware. A ribbon-like distribution coupled with the complexities and variations of this firefly’s flashing repertoire, as observed in Gainesville, could provide a readable natural experiment in geographic isolation and evolutionary divergence. In Florida, *douglasae* is ubiquitous, with adults present from February to October, from Miami to Jacksonville (**Fig. 2**), both along and across the State; it certainly must also occur in the Florida Keys. SESOBS records for latitudes near 29°-30° N (**Figs. 3** and **29**) suggest two generations per year, as also in **Figure 2**.

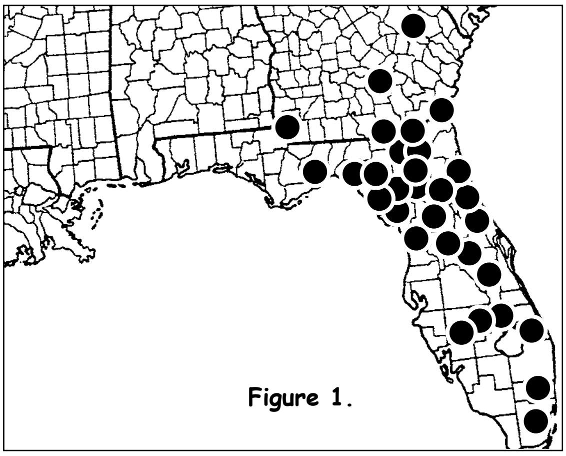


Figure 1.

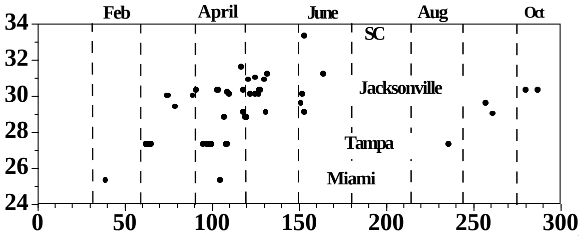


Figure 2. G'SOBS records of seasonal occurrance (AX: lat/DOY).

Though most often noticed along roadsides in cattail and other ditches, *douglasae* occurs over damp grassland, around lake margins, along roadway berms, across wetlands and beside salt marshes—and from along the causeway south to Flamingo in the Everglades to a grassy roadside north of Sopchoppy near Mack’s Landing in the Apalachicola National Forest on the Florida panhandle (**Figs. 4-6**). Rarely and then only briefly were males seen flashing very high above the ground as around low boughs of trees. **Figure 4** shows the grassy-grove of the main observation site, the Med Garden, on the UF campus; **Figure 3B** shows seasonal occurrence at this site across a span of nearly 20 years. *Ph. douglasae* appears to be an early successional (disturbed-land) species and appeared abruptly at grassy-herby margins of lakes that had recently retreated (**Fig. 10**), and around newly-formed borrow pits and drainage basins. At the Med Garden a population crash was noted to occur at about the same time an adjacent cattail- and herb-crowded rivulet was scalped, though the grassy-grove observation site itself appeared to remain the same. **Figure 11** is the wall of a small and antique, web-draped garden-house at the site—since gone—an adjunct substrate for certain resident arachnids to build entangling traps in 1967.

For confident diagnoses FPs must be observed and sometimes flashers interrogated with a decoy; in the absence of flashing notes, the combination of small size, dark coloration, dingy and somewhat patchy-fuscous or dark-brown hind coxae (**Figs. 7, 21**), and a sometimes unusually broad vittagram as in the arrays (below, **Figs. 27, 28**), with a habitat as described above

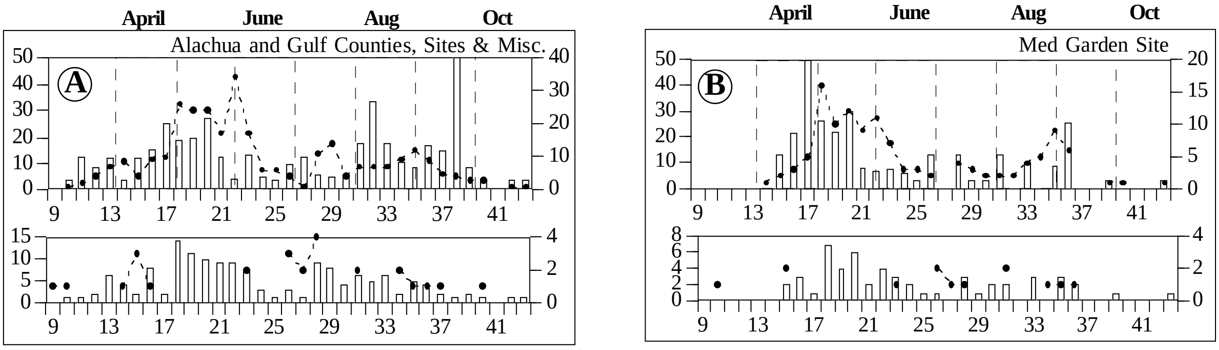


Figure 3. (A) SESOBS records for latitudes near 30° N, and (B) the main study deme in particular.

provide a tentative ID. **Figure 8** is a simplified sketch of the known FPs of *douglasae*. Those most commonly observed are the single-short (**Figs. 8C** and **9F, G, I, J**) and 2-pulse FPs (**Figs. 8A, 9B**). These are emitted at 3-4-sec intervals while a male cruises slowly or hurries quickly along a berm 6-10 feet above the ground (**Fig. 12** gives mean periods; **Fig. 13** shows FP mean period rates). Other PM-records of FPs in **Figure 9** are a 3-pulse FP (**9E**), a sequence of multi-pulse FPs (**9D**), the twilight long flash (**9A, C**), and the landing flickers of a male (**Figs. 8C, 9H**). The multipulsed FPs are, except for color, often indistinguishable from those of *Photinus lineellus*, and the two species are found in similar habitats; *lineellus* has apparently disappeared from sites in Alachua County where small populations were seen in the past.

Figure 4. Med Garden, UF campus.

Figure 5. Roadside ditch, east Gainesville.

Figure 6. Lush and low lake-side site.

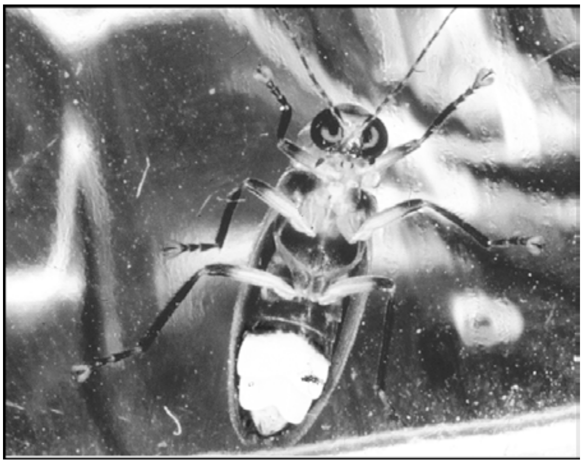


Figure 7. Mason jar, reflections, hind coxae.

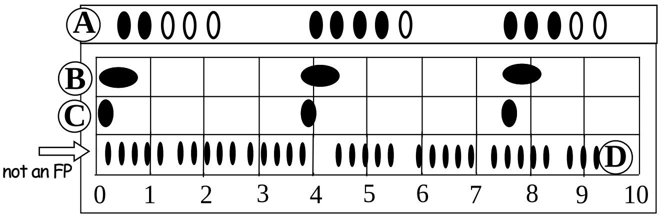


Figure 8. Simplified diagnostic flash chart, FPs and landing (AX: Rel int/sec).

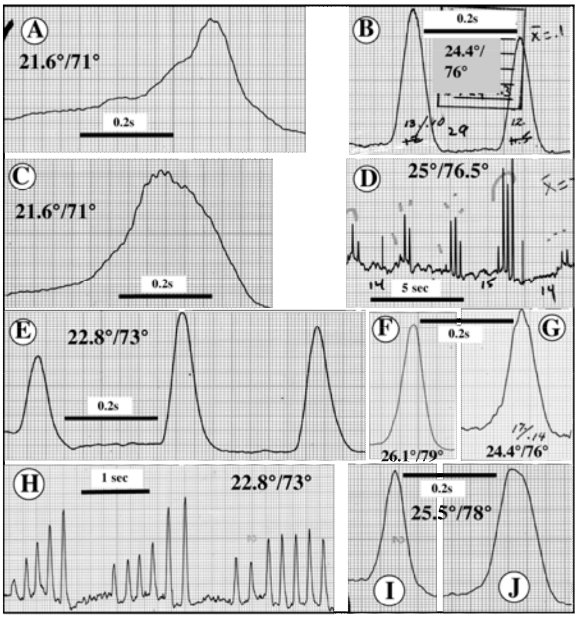


Figure 9. Long, multi-pulse and short FPs.

Figure 10. Receding shoreline in drought.

Figure 11. Garden-shed tangle-trap, operator and prey.

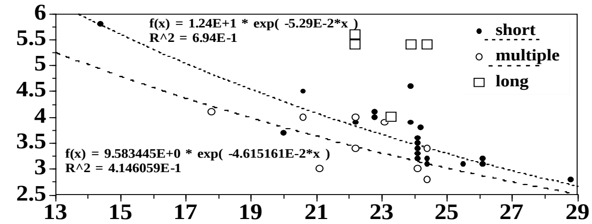


Figure 12. Mean FP periods (sec/temp).

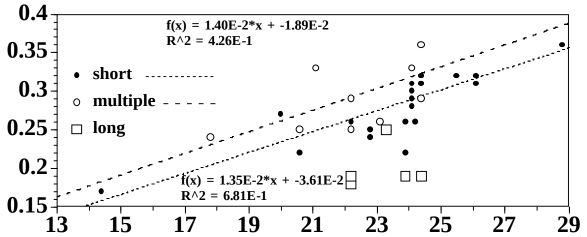
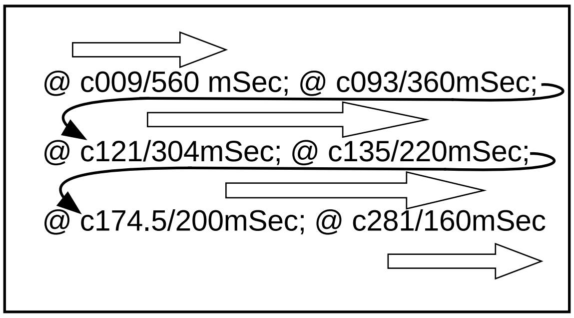


Figure 13. FP rates/positions (Hz/temp).

male #	$\bar{x}$(Hz)	n(FPs/Pps)	sd	range	temp
11	4.0	10/22	0.2	3.8-4.1	24.4°/76°
21	4.4	2/2	0.1	4.3-4.4	24.4°/76°
27	4.4	2/6	0.2	3.8-4.1	24.1°/75.5°
35	4.9	2/5	0	——	24.4°/76°
41	4.1	3/6	0.2	3.9-4.2	24.4°/76°

FigTable 14. Pulse rate in multi-pulse FPs: range = 0.20- 0.26 sec pulse period (e.g, 1/4.4 Hz = 0.23 sec.



@ c009/560 mSec; @ c093/360mSec;
@ c121/304mSec; @ c135/220mSec;
@ c174.5/200mSec; @ c281/160mSec

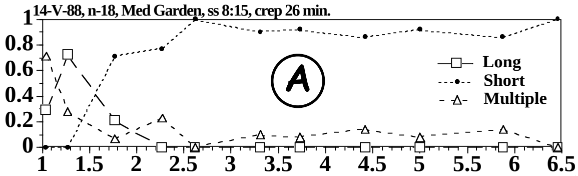
FigTable 15. Long to short FPs across first crep one evening in June 1967: c# = on-running tape-counter reference/duration in milliSeconds, see text).

Flashing behavior. This is one of two *Photuris* species in North America, known to me, to have *large* flashing repertoires and whose arena of flashing is primarily and conveniently non-arboreal—the other being *Photuris stevensae* in New England and on Long Island. Both species provide better than might be hoped-for access for scrutinizing and experimenting with the subtle details and complexity possible in their communication. Below are additional descriptive FP details toward accurate identification, and comparisons and sketches of behavioral complexities that may guide further analyses, with brief "methods, results, and discussion." Bear in mind the idiosyncratic nature of *Photuris* flashing found in many nominal species, with local demes often varying both in the presence and frequency of occurrence of FPs known to be present in regional repertoires—as noted by Barber in *lucicrescens* and *tremulans* and one other unnamed species (*quadrifulgens*?). This is particularly evident in *douglasae*, where, for example, at some sites the twilight long-flash may not appear at all, or momentarily be emitted and then only by, say, a single "uncertain" individual, i.e. an individual with confusing inputs?

The experiments, observations, and results described here, from which tentative conclusions about flashing behavior are drawn primarily for taxonomic/systematic purposes, should be viewed as but preliminary sketches to guide future fireflyers; detailed study such as site/FP-usage comparisons will perhaps reveal how habitats appear in the eyes and are analyzed in the computers of these illuminating subjects:

> *A beetle may or may not be inferior to a man—the matter awaits demonstration; but if he were inferior to a man by 10,000 fathoms, the fact remains that there is probably a beetle view of things of which a man is entirely ignorant.* Chesterton, 1901

More FP Basics: Mean FP periods are shown in **Figure 12** and their rates in **Figure 13**. In this species, as with most but not all others, there often is considerable variation around FP-repetition means—especially at late twilight before "complete" darkness—and depending upon ecology, and the species. Some individual periods may occasionally be twice the mean. Such extreme variation does not occur in pulse rates within multi-pulsed or flicker FPs. Pulse rate in *douglasae* multi-pulse FPs (**Fig. 9 B, D, E**) averaged 4.4 Hertz in PM-recordings at temperatures near 24.4°/76°; means of five males ranged 4.0-4.9 Hz. and the 41 individual intervals of the combined 19 FPs (phrases) ranged 3.8-4.9 Hz (**FigTable 14**). The mean pulse interval (1/4.4=0.23 sec) is too short to be accurately measured from pulse pairs by SWAT, but with 4- and 5-pulsed phrases more accurate averaging-estimates can be made. Mean flash base-duration of multi-pulse FPs at these temperatures averaged 0.08 seconds (81 mSec) and ranged 73-95 mSec. Half-max width of a small sample was about 65 percent of base width.



14-V-88, Med Garden, ss=8:15, crep= 26 min.

time	crep	long	short	multi	n sum
8:42	1.03	2 0.29		5 0.71	7
8:48	1.27	13 0.72		5 0.28	18
9:01	1.77	3 0.21	10 0.71	1 0.07	14
9:14	2.27		10 0.77	3 0.23	13
9:23	2.61		15 1.00		15
9:41	3.31		9 0.90	1 0.10	10
9:52	3.73		11 0.92	1 0.08	12
10:10	4.42		12 0.86	2 0.14	14
10:25	5.00		12 0.92	1 0.08	13
10:48	5.88		12 0.86	2 0.14	14
11:03	6.46		11 1.00		11

FigTable 16. Med Garden scan-sample chart, accompanied by the raw and transformed data (In each cell, n above and fraction below.)

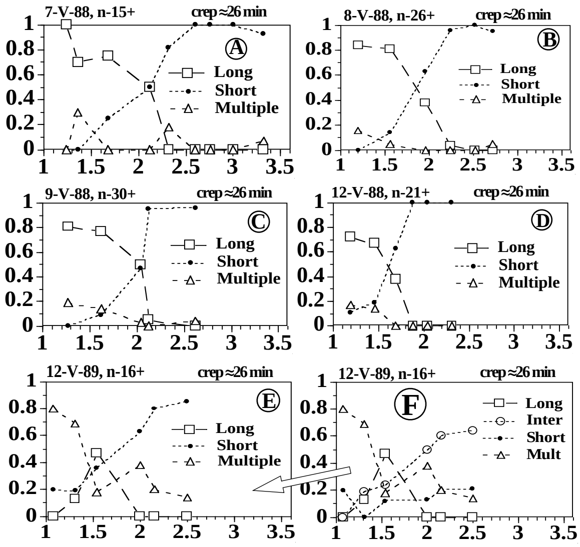


Figure 17. Six early-eve scan-samples (f/crep).

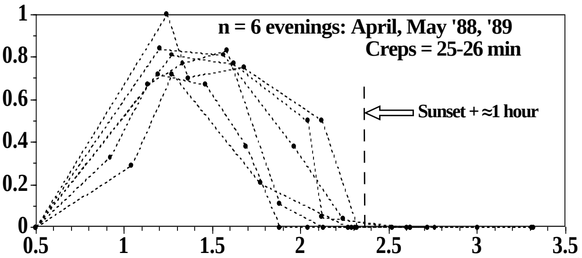


Figure 18. Twilight long flashes (freq/creps).

A small sample of short flashes (**Fig. 9 F, G**) averaged 120 mSec base duration and half max about 50 per cent of this at 24.1°/75.5°. The bioluminescent spectra of more than 18 males in four sets (1965-1978) had a mean peak at 550.8 millimicrons (range 549-553), and mean half maxima of 524.5 and 592.2 (ranging 523-526 and 590-596) (Biggley et al, 1967). **Figure 9H** is the PM-record of flickers of a landing male, the situation and mechanics suggesting a potential evolutionary origin of new FPs—or vice versa?

Flash complexity: durations, forms, evening sequences. The single, short-flash FP occurs throughout an evening, but sometimes there also are flashes of somewhat longer duration that appear briefly, close-upon and probably over-lapping the conclusion of early long-flash period. PM-records appear to show two different flash *forms* as well as intermediate-length flashes. Both duration and form variations are sometimes (appear to be) visually apparent in the field to the unaided, (practiced?) eye. With respect to symmetry of form, some are nearly symmetrical (**Fig. 15 @c135, @c281**) while others have a distinctive crescendo with a longer ON (rise times) than OFF transients (**Fig. 15 @c121, @c174.5**). During one evening at the UF-campus site these records were made across a span of several minutes, on 23 June 1967 at 22.8°/73°; **Fig. 4**). The "c" numbers in the PM panels of **Figure 15** are from the tape-transport counter and crudely indicate the evening-sequential timing of these recordings as the twilight long-flash period drew to a close.

More on evening FP sequences. The sequential appearance through the evening of the three basic FP types—long, short [combination short-intermediate], and multi-pulse—was quantified via scan samples (page 288) made at short time intervals. In scan-sample figures (**Figs. 16-20**) the fraction of a given FP type at each moment-scan was determined by dividing the number of that type observed by the total number of all FPs counted in that moment's scan (**FigTable 16** shows the table of calculations for the illustration above it, "**A**"). The n (of the n+ values) given above each sample is the maximum number of males observed from among all of the evening's series of moment-counts. Note from the **Figures 16-20**: (**1**) that, the long flash FP (**Fig. 9A, C**) is emitted only during early minutes of flashing, beginning about one crep (≈26 min) after sunset and ending about 40 minutes later (**Figs. 16, 18**); (**2**) that, the long flash is the only FP noted (presently known) in the repertoire to have a specific and restricted window of presentation; [note also that, this window falls during the activity period of *Photinus collustrans*, a species with a similar FP whose males are preyed upon by *douglasae* females—via flash responses similar to those of *collustrans* females [i. e., aggressive mimicry]; (**3**) that, the long flash is occasionally preceded briefly by and typically coincidental with short or pulsed FPs (**Fig. 17E**,

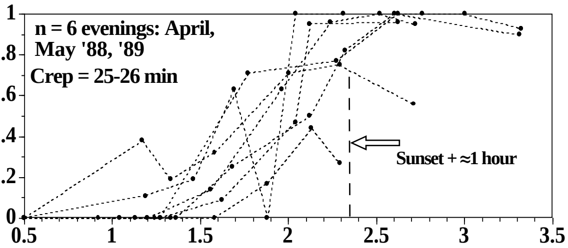


Figure 19. All short flash types (freq/creps).

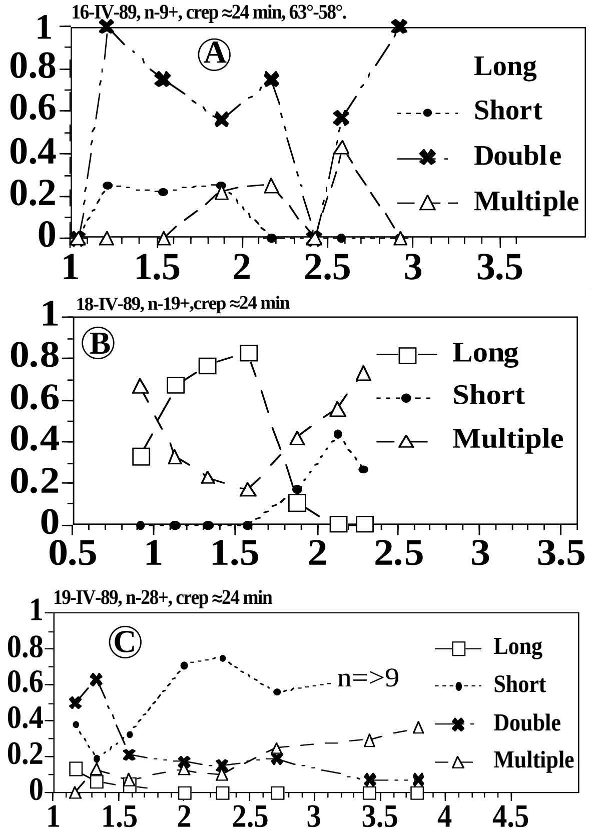


Figure 20. Three eves in April—note doubles.

FigTable 21. Copulation, hanging under, as apparently the usual in *Photuris*, based on a very limited sample.

note creps in 19); (**4**) that, pulsed FPs occur throughout the evening (**Fig. 16**); (**5**) that, the scan shown in **17F** attempts to visually distinguish and count separately flashes of intermediate length, as noted—these short and intermediate flashes were combined as "short" in **Figure 17E**; (**6**) that, in **Figure 20A** and **20C** that 2-pulsed FPs were distinguished from 3-5-pulsed FPs; (**7**) and in Figure **20A** only a few males were active and there were no long flashers.

FP Repertoires: Mark-release-recaptures were made at the beginning of observations on this species to determine: (**1**) whether a single (genetic) population (i. e. local species) was involved, that is, whether *individuals* switched among the observed FP categories, and (**2**) whether maturation or age was a factor in determining which FP an individual emitted. This was overkill, in retrospect, because individuals could often and easily be seen or induced to change between certain FPs—following one PM-record is this verbal note: "he gave 4, then 2, then 3, then back [i. e., to 1]." Markings were either tiny dots of colored airplane dope on one or both elytra, or an elytron had a tiny, coding-angle clipped from its tip; these coded for FP type and date of marking. At the UF campus 178 males were marked on six evenings, and recaptures were made throughout (**FigTab. 22**; marked totals: 85 long, 71 short, 22 multi-pulsed). Marking demonstrated that one population could account for all FP types and few males remain active in the population five days or longer—death or emigration? Might age be a factor in the type of FP emitted?: if older males have a tendency to fly faster or to emigrate and this behavior was accompanied by the emission of pulsing FPs, age could be associated with multi-pulsing. Or, might older males barter with females, insemination for nuptial cannibalism, and advertise this with a particular FP? In Highlands County where 22 individuals of a tiny deme were marked, results were similar.

FPs	mins	24h	48h	72h	96h	120h	144h
L→L		**8**	**3**	**2**	**1**	**1**	**1**
L→S	**8**	**5**	**4**	**7**			
L→P	**4**	**3**	**1**	**3**			
S→S	**1**	**7**	**5**	**4**	**1**		
S→L		**5**	**6**	**3**	**3**		
P→S	**6**	**7**	**3**				
P→L		**2**	**2**				

FigTable 22. FP change-overs over time; also P to P =4; S to P =1. Multi-pulse FPs were infrequent at this site.

Sexual interaction. When short-flashing males are answered they continue to emit the short flash and approach the responding light, often reaching it after a few exchanges; when pulsing males are answered, after one or a few more exchanges, they default to the short flash and approach. Male-female interactions have been seen many times as has defaulting in response to female and decoy response-flashes. When long-flashing males were answered with a flash of similar duration, two

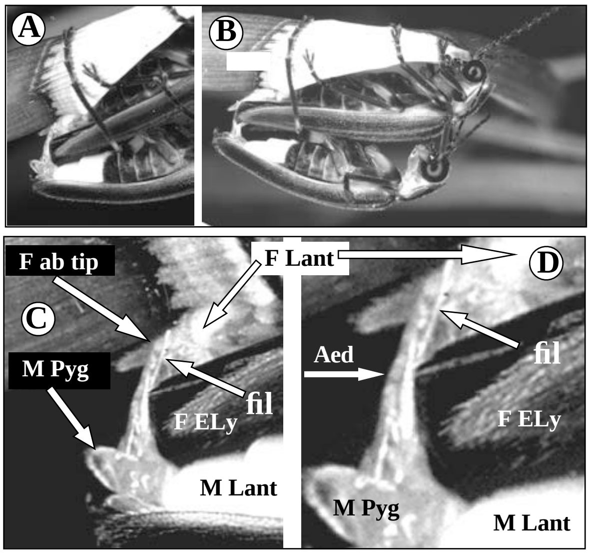


Figure 23. Filament (fil) function: orientation here in early intromission, and early warning later in copulation, though in reversed order in evolutionary sequence.

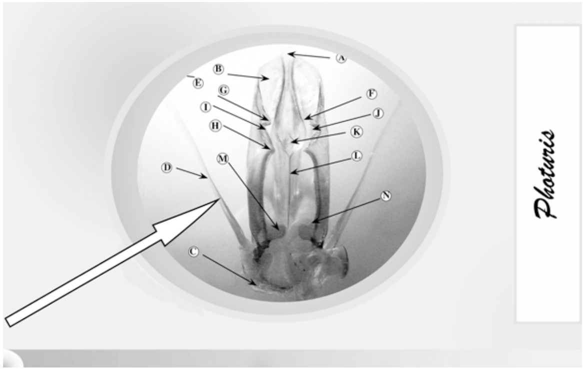


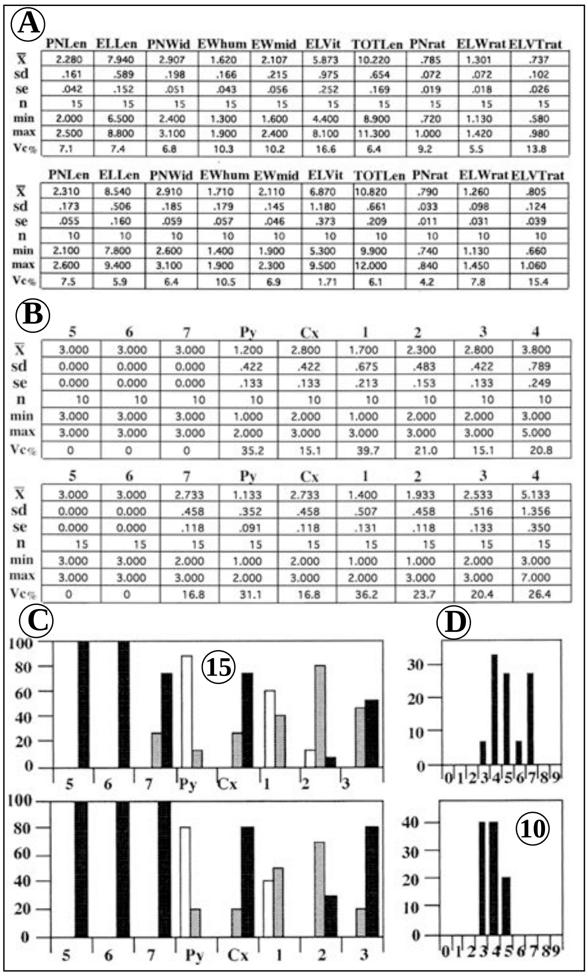
Figure 24. Complex *Photuris* aedeagus showing potentially useful characters for taxonomy and indicating the filament.

different signals were observed: as males approached they continued to use the long FP, or they defaulted to the short flash and continued the approach. Since these males are preyed upon by mimicking females of *Photuris stanleyi*, *lamarcki*, and *harrannorum*—all present in the Med Garden—a signaling counter-measure is to be suspected—and perhaps this is clue to the evolutionary context and origin of defaulting … a male *douglasae* courting a female *harrannorum*, was seen changing his flash lengths. Different delay-times were noted with response flashes, sometimes responses were almost instantaneous and sometimes delayed about one second. The following are paraphrases from fieldbook notes: (**1**) Highlands Co, 4 March 1967: <M[male]: single in air, F[female] answer from ground with flash like his; M again, F again, he land @ 3'; M flash, F dim longer ≈ ¼-sec flash @ 1 sec delay; M again, F response a barely perceptible glow; all dark, check @ 10 sec, in cop>. (**2**) Highlands Co, 8 April 1967: < M: single sharp in air, F answer from ground with 1 sec long flash @ 1 sec; repeated 6 X, w one skip; no more, not found>. (**3**) Med Garden , 8 May 1967: < M walk to responding F, mount, @ 3 min turn 180°, @ 30 sec uncouple, both flew off>; (**4**) Med Garden, 8 May 1967: < M attracted @ 3 exchanges landed, check @ 30 sec wolf spider had him; (**5**) Med Garden, 11 May 1980: <long-flashing M decoyed to ground w 1 sec @ 1 sec delay; repeated 2X; M short from same posit, then drop 6"; at ground M emit short [defaulting] @ 5", climbed up to decoy>. (**6**) Highlands Co, 19 April 1983: <M 2-pulser , F ans @ 1-1.5 sec; M apprch, default; M land @ 6", 10" up grass; [got camera] upon return found coupling> (**Figs. 21, 23,** see also **24**).

The two aedeagal filaments arising from the basal piece in *Photuris* are suspected of being proprio-receptive guides for aiding intromission, and also as detectors that warn males when a mate turns to grab (cannibalize) him during copulation. Some macro-photos of copulating *Photuris* have shown the visible (near-side) filament alongside the tip of the female abdomen. Photos of the coupling pair described above (**Figs. 21, 23**) show the filament at different points of contact with the female, presumably guiding intromission; **Figures 22C** and **22D** enlarge and label various anatomical elements, including lanterns, filament, pygidium, elytra, and aedeagal lobes. (See also pages 72 and 404).

Morphology. General morphological means for a series (n=15) from the Med Garden locality are: PNL 2.3, ELL 7.9, PNW 2.9, EWhum 1.6, EWmid 2.1, ELVit 5.9, TOTLen 10.2, PNrat 0.79, ELWrate 1.30, ELVTrat 0.74 (**FigTab. 25A).** Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **FigTab. 25B-C**, and the color (splashing) of the pre-lantern ventrite in **25D**—**Figure 26** is a reference sketch indicating the numbers used for various skeletal plates and numbers for degrees of splashing on ventrite 4. There is sample of vittagram illustrations for comparison, including arrays of drawings and photographs (**Figs. 27** and **28**).

Holotype. Male, voucher 6729, collected 4 March 1967, Highlands County, Florida, at marshy area, near Archbold Biological Station. FB page 6: "At a spot in [along] road about a mile from entrance to station." Both single pulsers and multi-pulsers active. Specimen 6729 a multipulser, one of six collected at the time—nos. 6725-6729 & 6741. Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.4, ELLen 8.4, PNWid 3.0, ELWhum 1.8, ELWmid 2.3, LELVit 7.0, TotLen 10.8, PnRat 0.79, ElRat 1.36, VitRat 0.84; Colors: T 333, Py 1, Cx 3, V 223, Edg 3. Types will be deposited in the USNM.



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̅	2.280	7.940	2.907	1.620	2.107	5.873	10.220	.785	1.301	.737
sd	.161	.589	.198	.166	.215	.975	.654	.072	.072	.102
se	.042	.152	.051	.043	.056	.252	.169	.019	.018	.026
n	15	15	15	15	15	15	15	15	15	15
min	2.000	6.500	2.400	1.300	1.600	4.400	8.900	.720	1.130	.580
max	2.500	8.800	3.100	1.900	2.400	8.100	11.300	1.000	1.420	.980
Vc%	7.1	7.4	6.8	10.3	10.2	16.6	6.4	9.2	5.5	13.8

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̅	2.310	8.540	2.910	1.710	2.110	6.870	10.820	.790	1.260	.805
sd	.173	.506	.185	.179	.145	1.180	.661	.033	.098	.124
se	.055	.160	.059	.057	.046	.373	.209	.011	.031	.039
n	10	10	10	10	10	10	10	10	10	10
min	2.100	7.800	2.600	1.400	1.900	5.300	9.900	.740	1.130	.660
max	2.600	9.400	3.100	1.900	2.300	9.500	12.000	.840	1.450	1.060
Vc%	7.5	5.9	6.4	10.5	6.9	1.71	6.1	4.2	7.8	15.4

B

	5	6	7	Py	Cx	1	2	3	4
X̅	3.000	3.000	3.000	1.200	2.800	1.700	2.300	2.800	3.800
sd	0.000	0.000	0.000	.422	.422	.675	.483	.422	.789
se	0.000	0.000	0.000	.133	.133	.213	.153	.133	.249
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	3.000	1.000	2.000	1.000	2.000	2.000	3.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	0	35.2	15.1	39.7	21.0	15.1	20.8

	5	6	7	Py	Cx	1	2	3	4
X̅	3.000	3.000	2.733	1.133	2.733	1.400	1.933	2.533	5.133
sd	0.000	0.000	.458	.352	.458	.507	.458	.516	1.356
se	0.000	0.000	.118	.091	.118	.131	.118	.133	.350
n	15	15	15	15	15	15	15	15	15
min	3.000	3.000	2.000	1.000	2.000	1.000	1.000	2.000	3.000
max	3.000	3.000	3.000	2.000	3.000	2.000	3.000	3.000	7.000
Vc%	0	0	16.8	31.1	16.8	36.2	23.7	20.4	26.4

Figure 25. Morph. data (Med Garden Alach. Co./Highlands Co.).

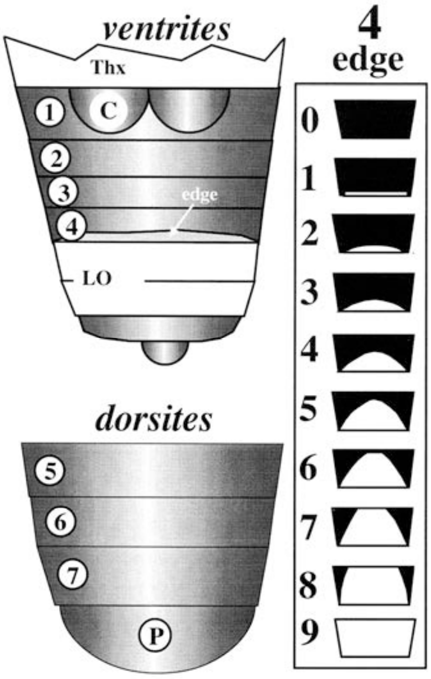


Figure 26. Topographic and splash key.

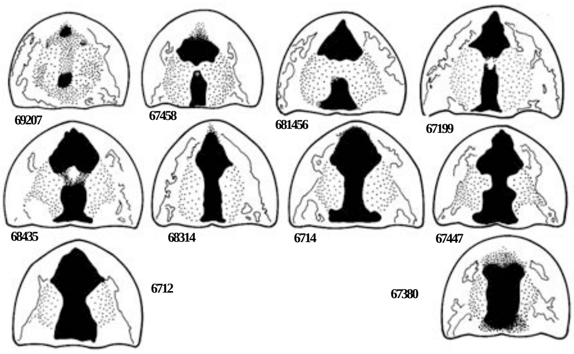


Figure 27. Sketched array of pronota (Laura Line).

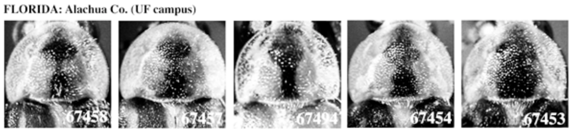


Figure 28 . PN vittagram array.

* * *

Taxonomic/nomenclatural notes. This firefly honors the memory and contributions of Marjory Stoneman Douglas, Woman of the Century (**Fig. 28**; Poole, 1998), "… matriarch of conservation in Florida and among the giants of conservation in the history of this country." *Photuris douglasae* occurs in numbers along roadways through and around her Everglades, and maybe it was born there. The Holotype was selected from the southern-most studied locality to increase likelihood that it would be from the domain of Ms. Douglas, should northern populations, such as those in Gainesville, later be considered to warrant separate, specific distinction.

Figure 29. Marjory Stoneman Douglas, 1890-1998.

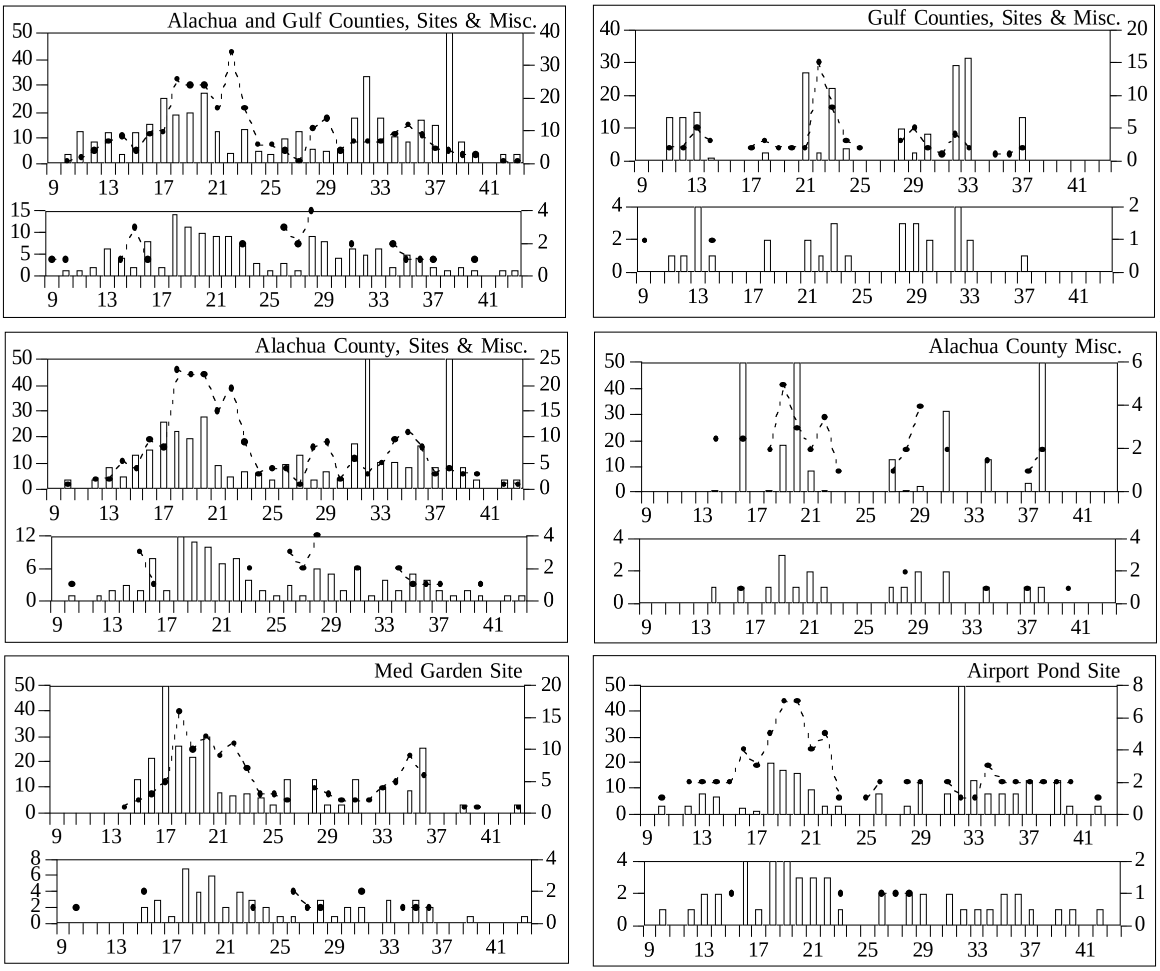
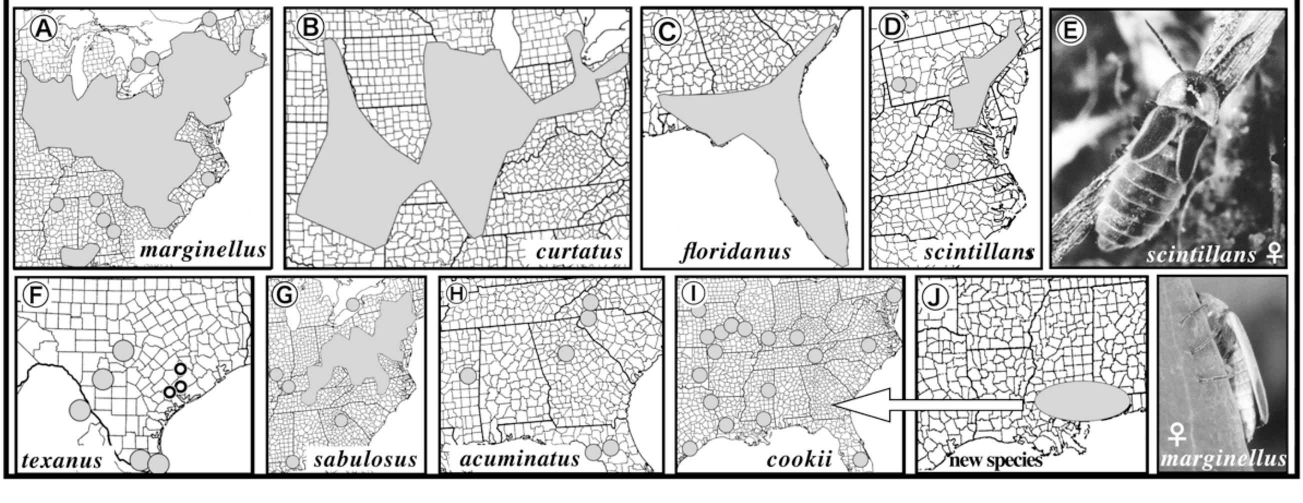


Figure 29. SESOBS data of seasonal occurrence from various regional populations.

Twilight prey of femmes fatales: victims & losers? Females of several *Photuris* species are presumed to be specialized predators of twilight-active, short-flashing *Photinus* based on observations and because FP repertoires of their males include short flashes that are emitted only at twilight and in the *prey-species* habitats. Using this as guide, and assuming that such predation could be an important factor in their survival, some working predictions and retrodictions may be made. The maps show the known occurrence of certain twilight *Photinus*, and others of interest. Maps **A-C** show the distributions of prey species that occur over large areas and are rather common. **D/E** probably evolved in sandy NJ, partly escapes into very shady, pre-twilight time space; **F** and related TX species occur with their predators along streams threading through inhospitably dry areas; **G** apparently escapes by flying in tree foliage, and later into the evening; **H** is losing, going extinct? though a **very**-early, very-sharp/bright-flashing, twilight flyer; **I** totally escaped, flies in afternoon and lost its lantern; **J** is like **I**, except is luminescent, and despite DNA evidence to the contrary (Stanger-Hall and jel, 20__), much evidence, including almost identical aedeagi, general morphology, and fairy-ring distribution in *cookii*, supports a recent and close derivation of **I** from **J**.



Chapter 31

Photuris Arkansas Down-Slider

AR Down-Slider

This long-flasher was seen over a site on low, flat bottomland (100+ acres) along the West Fork of the White River, in Washington County, Arkansas, along route 71 (**Fig. 1**). The site was a meadowland flood-plane that included an old-field and pasture with a bordering tree row. Many were active 28-31 May 2003. They flew a few feet above the vegetation and only rarely around the boughs of bordering trees. Their long FP measured (SWAT) 0.6-0.9 seconds in duration (±20°/68°) and was often emitted over a 1.5-2' slight down-slope; a similarity to Minnesota and Wisconsin *caerulucens* was noted. Though it appeared to be of simple structure, a slow rise and fall in amplitude, without transients, a 12-sec time exposure suggests that a crescendo envelope was actually present and that the OFF transient was rapid (**Fig. 2**, ASA 400, @f2.0). However, because male may slow flight speed during emission, perhaps this results in the apparent crescendo as recorded on film. Males sometimes flew angularly-rotated path-segments, with each successive FP emitted along a slightly different azimuth. Twilight short-flashing was sought but not seen.

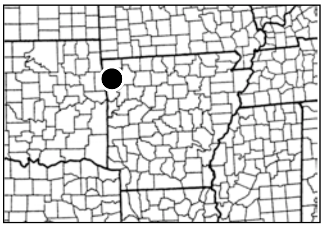


Figure 1.

Morphological summary. Means (n=5): PNL 2.9, ELL 11.4, PNW 3.7, EWhum 2.1, EWmid 2.6, ELVit 7.6, TOTLen 14.3, PNrat 0.80, ELWrate 1.24, ELVTrat 0.66 (**FigTable. 3A**, with other stats); colors in **FigTable 3B-C**, pre-lantern ventrite splash in **3D**. **Figure 4** is key for anatomical elements and splashing on ventrite 4. Specimens will be deposited in the USNM.

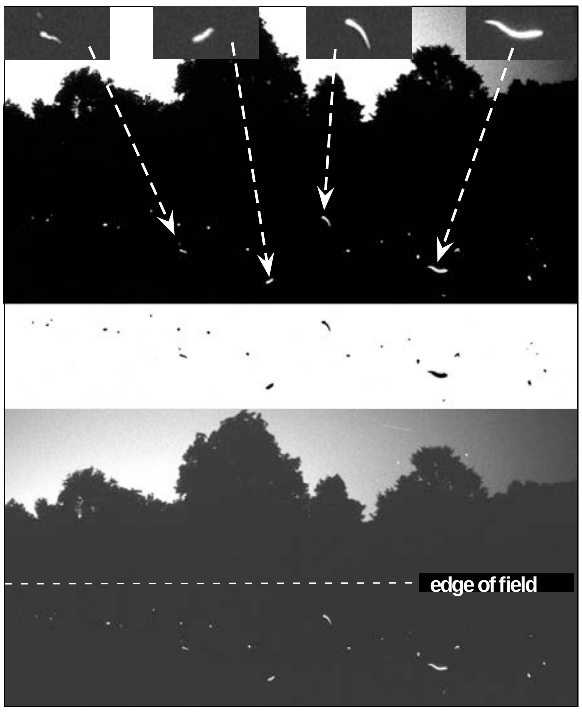
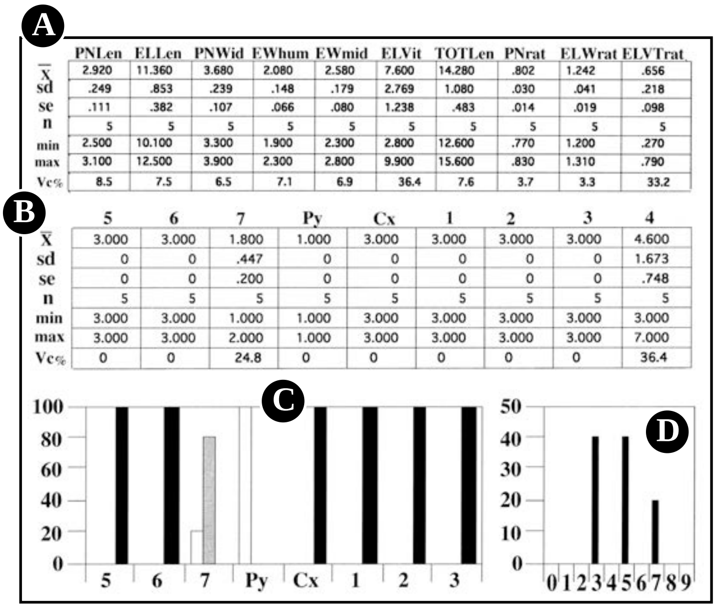


Figure 2. Downsliders appear to emit crescendos.



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.920	11.360	3.680	2.080	2.580	7.600	14.280	.802	1.242	.656
sd	.249	.853	.239	.148	.179	2.769	1.080	.030	.041	.218
se	.111	.382	.107	.066	.080	1.238	.483	.014	.019	.098
n	5	5	5	5	5	5	5	5	5	5
min	2.500	10.100	3.300	1.900	2.300	2.800	12.600	.770	1.200	.270
max	3.100	12.500	3.900	2.300	2.800	9.900	15.600	.830	1.310	.790
Vc%	8.5	7.5	6.5	7.1	6.9	36.4	7.6	3.7	3.3	33.2

B

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	1.800	1.000	3.000	3.000	3.000	3.000	4.600
sd	0	0	.447	0	0	0	0	0	1.673
se	0	0	.200	0	0	0	0	0	.748
n	5	5	5	5	5	5	5	5	5
min	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	0	24.8	0	0	0	0	0	36.4

FigTable 3. Measurements, colors, ratios.

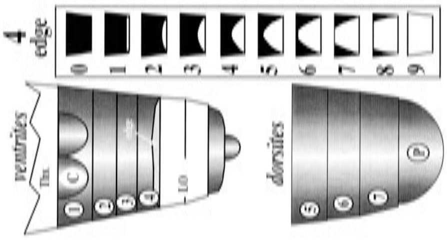
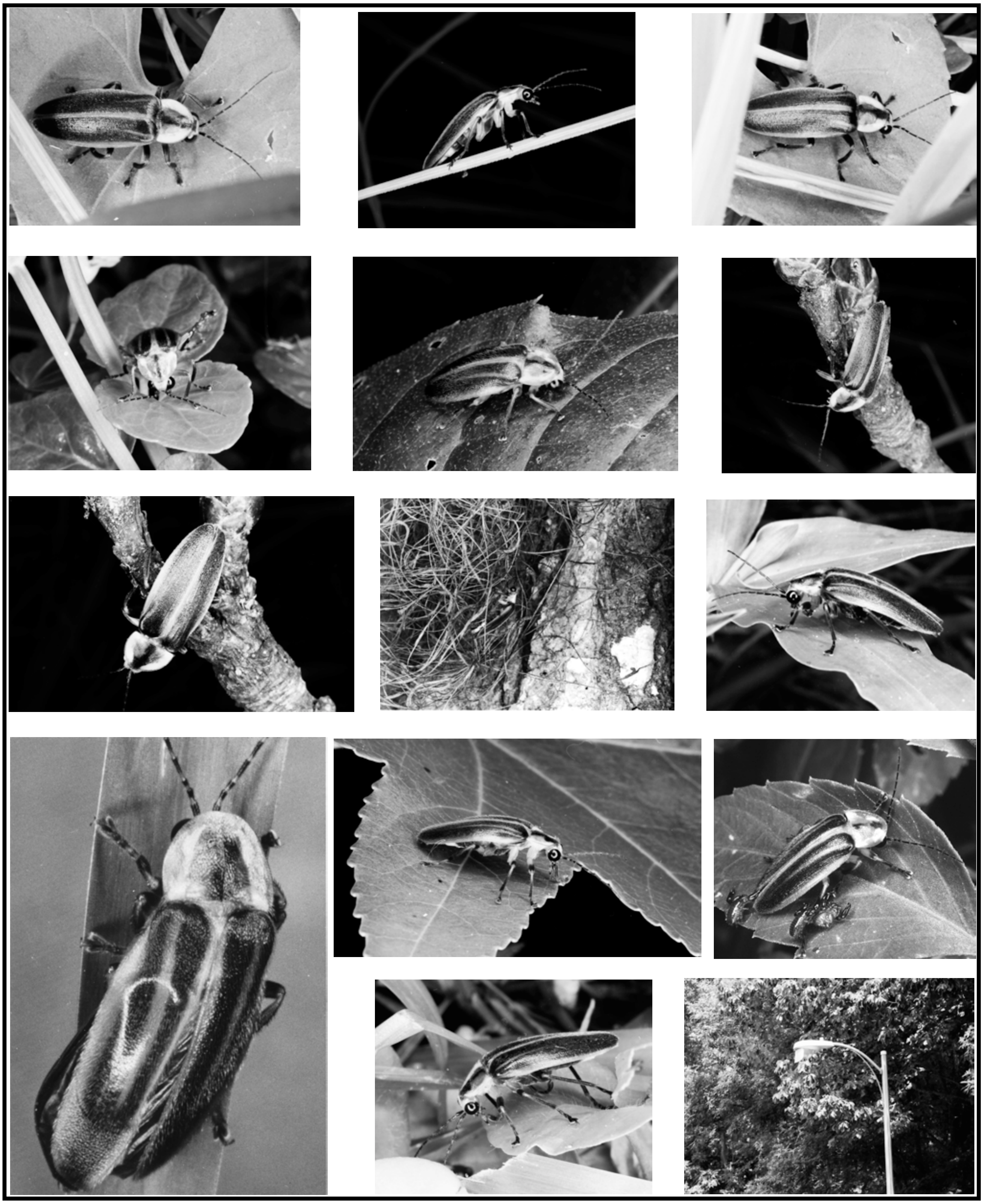


Figure 4. Key to sclerites and splash.

Male and female *Photuris* upon the grass and herbs at the old UF Med Garden, Page 4: searching mode? These four pages of *Photurus* fireflies were seen over a few nights. They suggest that for both mate-seekers and predators, and perhaps for resting or other necessities, such perching plays an important part in the biology of these fireflies and should not be dismissed without a look now and then.



The shielded streetlight at the lower right was one of a number provided/arranged for by the Director of Plants and Grounds, beginning in 1970. They permitted a light-free environment for fireflies and fireflyers in the Med Garden for many years. UF administrators were not cooperative (SOP).

Chapter 32

Photuris eureka n. sp.

Mallory Swamp Firefly

Known only from the Big Bend coastal area and western reaches of Mallory Swamp in Florida (**Figs. 1, 2**), and having several attention-grabbing peculiarities in flashing behavior that connect it to at least three and possibly four species of *Pyractomena,* and two or more of *Photuris,* this firefly is an enigma to spend time with in Florida every winter/spring (**Fig. 3**). In the 1970s and ‘80s *eureka* occurred widely and in numbers over the “grasslands” of pine replantings, around low wet areas of maturing plantations, and at bayheads and hammocks along a paved highway with wide swards through its Swamp (**Figs. 4-6**). Though remarkable in a number of respects, the most interesting is its promise for what it could reveal about: (**1**) the tuning and evolution of adjunct FPs, (**2**) the dynamics and consequences of conflicting selection pressures, (**3**) the scramble among species for space in the communication channel, (**4**) the nature and effects of predations that track and exploit mating signals and the evolution of countermeasures to them, and (**5**) the incorporation of elements of all of these into a sexual selection context. It was localized—but, now unseen for 15 years.

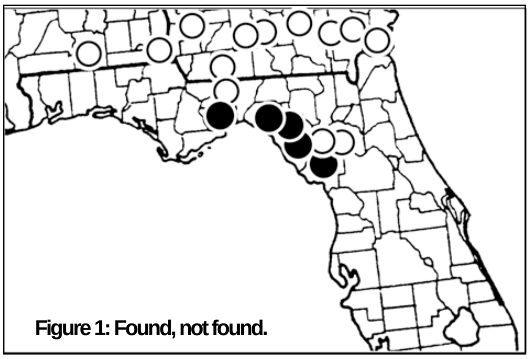


Figure 1: Found, not found.

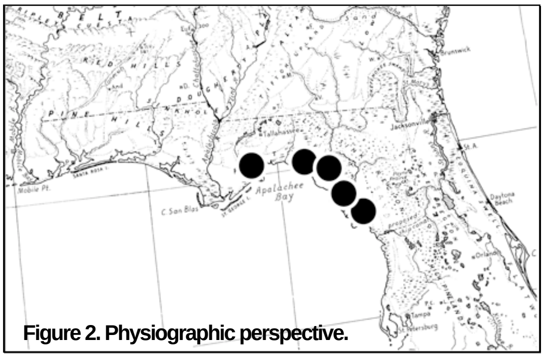


Figure 2. Physiographic perspective.

The *recognized* FPs of *eureka* include crude or indecisive mimicries of two flickering *Pyractomena* species that occur in season and space with it and another at its northern frontier—and apparently under certain circumstances *eureka* possibly uses one of these adjunct FPs—perhaps only mistakenly—as a “default” FP. Its own pulsing default FP is similar to that of continental *Photuris quadrifulgens* (**Fig. 7**).

Eureka's primary/default FP is a series of <7 slow pulses, each emitted at 0.6-1.1-sec periods (**Figs. 7, 8A, 9**; rate **Fig. 10**), with pulsing-FP periods of cruising males ranging at 5-10-sec periods (**Fig. 11;** rate **Fig. 12**). Adjunct FPs include a green “A-flicker” overlapping in modulation rate the orange flickers of coactive *Py. barberi,* the later *angulata,* and sometimes approaches the slower rate of the absent *Py. dispersa* (**Figs. 13-14**). This 6-8-modulation A-flicker FP has a phrase period ranging 1.5-3.5-sec (**Fig. 15**; rate **Fig. 16**). The other recognized *Pyractomena* "FP" match-up found in *eureka* is the long-glow emission/signal ("FP") of *Py. angustata*.

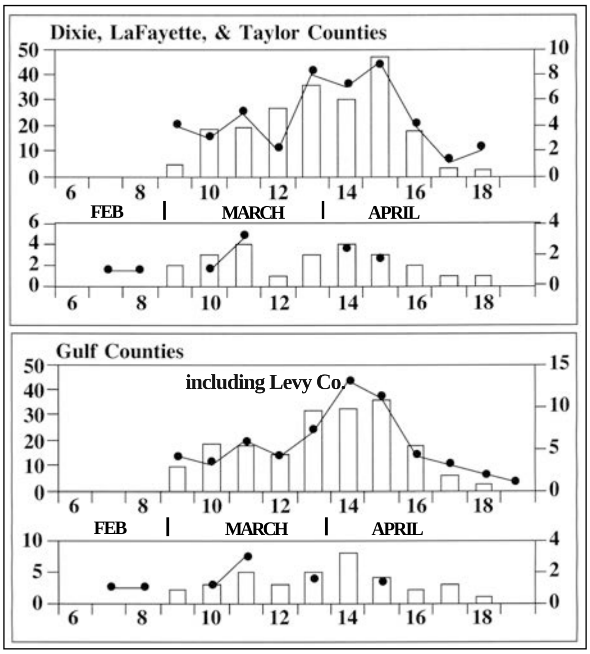


Figure 3. ***Ph. eureka*** **SESOBS.**

Py. angustata's **green** glow is identical to that of *eureka’s,* an atypical color for bioluminescence in *Pyractomena,* with the spectra of both peaking at 555 millimicrons. The two emissions cannot be distinguished in the field by any means—but when a green-glowing firefly was seen pursuing a green glow, the pursuing glow was always that of *eureka* (and sometimes a male?) These aerial "chases" perhaps explain the convergence of the luminescence of *angustata* on *eureka,* and aerial attack and color discrimination are worth investigating.

Figure 4. Hines study site.

Figure 5. Site near Old Town.

Figure 6. Pond in flood at site near Old Town.

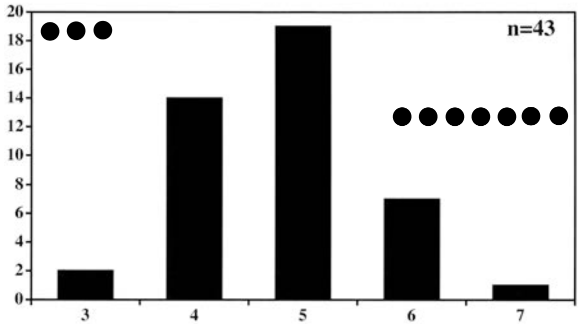


Figure 7. Pulse # scan sample (AX: male count/pulse number).

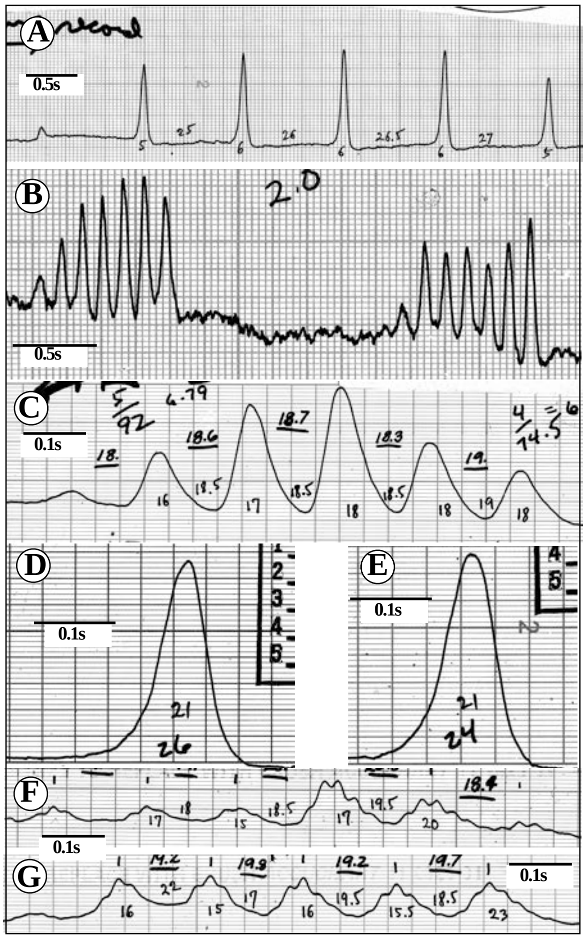


Figure 8. PM-records (AX: ri/time; see augmented figure legends).

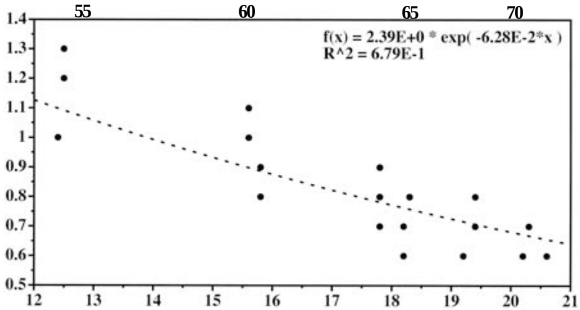


Figure 9. FP pulse period (interval) (AX: sec/temp).

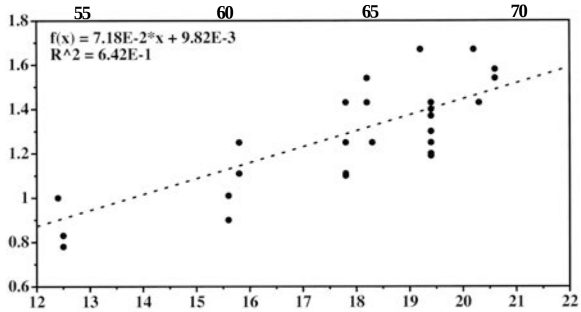


Figure 10. FP pulse period (interval) rate (AX: Hz./temp).

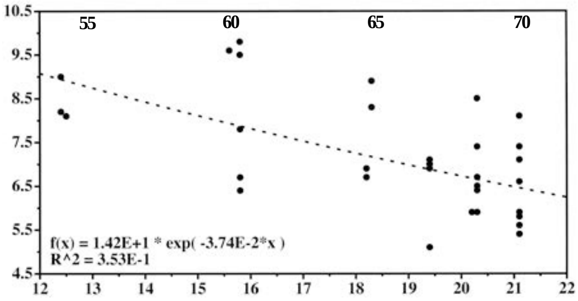


Figure 11. Pulsing-FP period (interval) (AX: sec/temp).

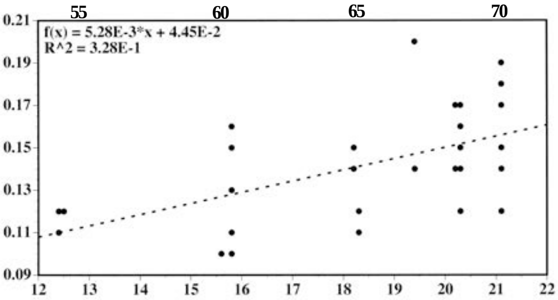


Figure 12. Pulsing-FP period (interval) rate (AX: Hz./temp).

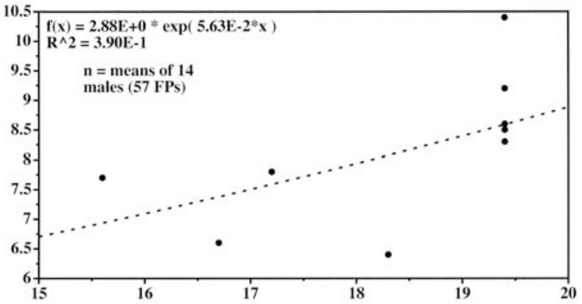


Figure 13. Flicker FP modultion rate (AX: Hz./temp).

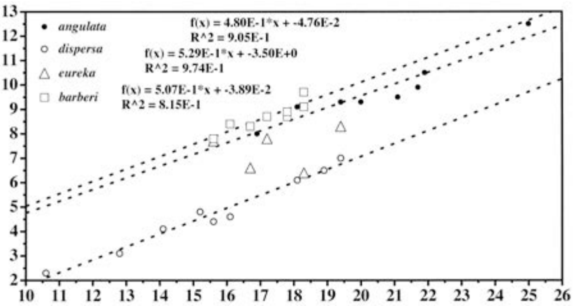


Figure 14. Flicker species-comparisons (AX: Hz./temp).

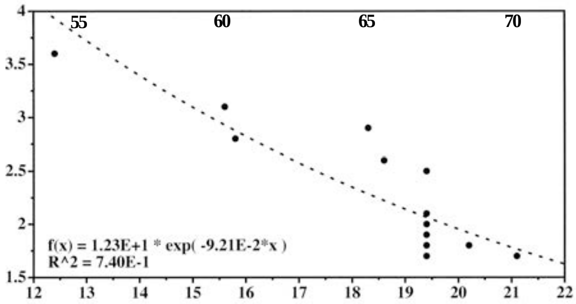


Figure 15. Flicker FP period/interval (AX: sec/temp).

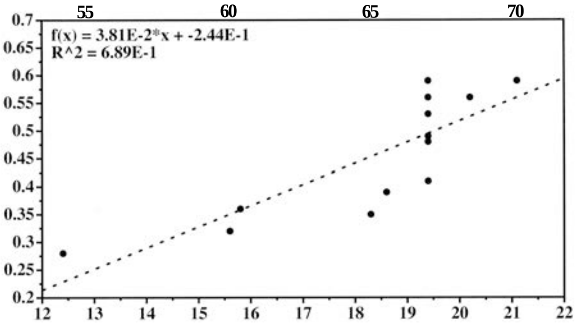


Figure 16. Flicker FP period/interval rate (AX: Hz./temp).

Figure 17 shows the SESOBS of these three unusual and rare species and others for comparison.

Observation of the pulsing FP is necessary for diagnosis. Another long-glowing (*Py. angustata*-like) *Photuris* occurs in this region of Florida, *Py. walkeri*. This may be connected with a problem not encountered with other *Photuris*: on three occasions when pulsing *eureka* were answered with a glowing decoy they switched ("defaulted") to the A-flicker; on another occasion, when a long-glowing *eureka* was answered with a glow he switched to the A-flicker and then immediately to the pulsing (default) FP—perhaps countermeasures? Usually, however, flickering and glowing *eureka* defaulted to the pulsing FP when answered with a decoy.

Helpful for *eureka* identification are: (**1**) the very early-spring adult season (**Fig. 3**), (**2**) limited geographic occurrence (**Figs. 1, 2**), and (**3**) when *eureka* flickers or glows it flies in the activity spaces of *barberi* and *angustata*, but when emitting its pulsing FP males usually fly higher, often at the crowns of tall trees (**Fig. 19**). Although green-glowers were occasionally seen at high altitudes identification was not possible unless they could be attracted down to a decoy and then defaulted (*eureka*) or could be captured. When flying *eureka* males are seen significantly changing flight altitude, an observer can predict an FP change will usually follow (**Figs. 18-20**).

Ecology. The most first-worthy observation to record about *eureka* is that during the past two decades its populations at monitored sites in and near Mallory Swamp seem to have disappeared, gone from abundance to extinction. Though *eureka* and its rare associates have been sought many times at the original Swamp sites of the 1970s and '80s, and as recently as March 2015, often accompanied by a van-load or two of students —with extra flash-seeking eyes—no active populations nor solitary individuals of either *eureka* or *angustata* have been seen. A lowered water table may be responsible, from increasing urban demands and "draw-down" by a very large city to the east. As a timely example, on 11 June 2011 the mourning paper reported approval for 163 million gallons per day to be taken from an area northwest of Gainesville for use by the mentioned city; the regional lake shown in the article was already down 20 feet. A relevant fact and food-chain connection here is that *Pyractomena* larvae are snail predators, and they require damp and marshy/ swampy habitats.

Another reason *Pyractomena* populations are reduced may be forest-management fires. *Natural* fires occur after pupation, but now human activity, especially forest-management burns could be responsible for fires during the time of pupation, and such fires would kill pupating *Pyractomena* low on stems of trees and shrubs.

Flashing behavior. The pulsing FP of *eureka* is similar to that of continental *quadrifulgens* in appearance though the latter most commonly (apparently) emits 4 pulses, with its 2- and 3-pulse FPs appearing earlier in the season and otherwise only for

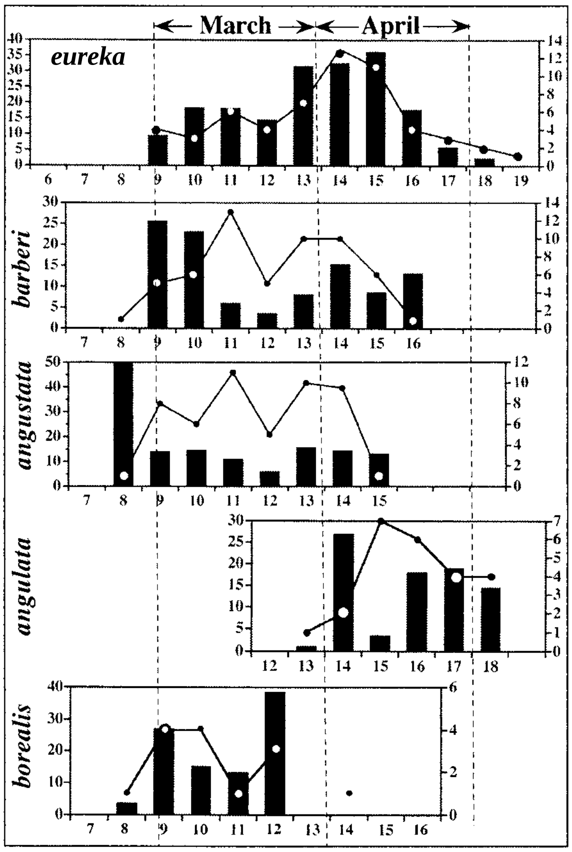


Figure 17. SESOBS comparisons.

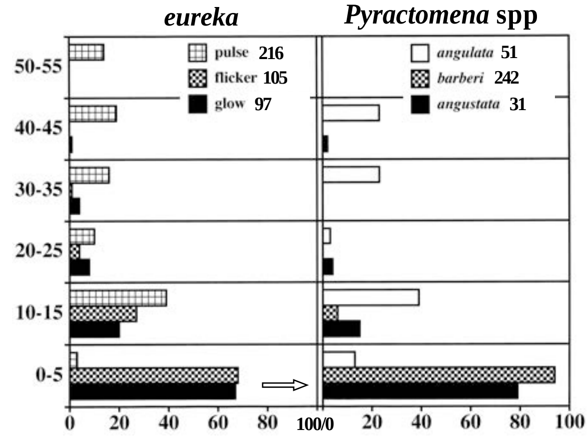


Figure 18. Flight heights and FPs (feet/%)

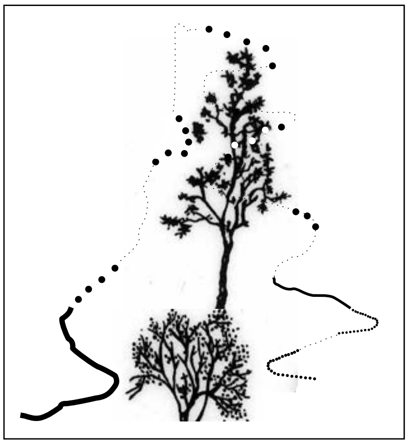


Figure 19. Changing altitude and FP switching.

a few minutes at the beginning of evening flight (Forrest and Eubanks, 1995). McDermott and Barber were familiar with both 3- and 4-pulse FPs in *quadrifulgens* but did not note that 3-pulse FPs sometimes or typically were transitional. Though 2- and 3-pulse FPs are termed transitional this is not to suggest they are not functionally significant, say, functioning as decoys to early-hunting females or females with ambivalent valences for hunting vs mating, virgin or otherwise.

A chronological transition, seasonal or nocturnal, was not noted in *eureka* but may exist. For example, *eureka's* use of the adjunct *angustata*-glow and A-flicker was high during the seasonal times of my observations—when glowing and flickering *Pyractomena* were in season—and together amounted to about half, in aggregate, of *eureka's* FPs in the several census counts that were made (**Fig. 18**; n=202 and 216). Only rarely were 1-flash FPs seen. Earlier, when *Py. borealis*, a predominately 1-flasher, is in season perhaps *eureka* emits 1-flash FPs more often (**Fig. 17**, note local *borealis* phenology).

The pulsing-FP mean period of *eureka* ranges broadly (**Fig. 11**), but only some of this can be explained by varying pulse numbers in the FPs in the periods sampled (**Fig. 7**). It is reasonable, from watching measured males cruise from crown to crown of tall pines, presenting each one with a pulsing FP, that they vary their FP intervals as they select targets and move varying distances along the line from tree to tree. Note the tall pines in the distance in **Figure 5** and imagine a necklace of slow pulses at one, and then a few seconds later a similar series at the next tree, and so on (**Fig. 19**).

A small sample of slow pulse PM-recordings reveals an asymmetrical somewhat crescendo form **(Fig. 8D, E**) and mean durations of 74/176 mSec at 19.4°/70° (n=7), and at 15.5°/60°, 80/204 mSec (n=5). PM-recordings of A-flickers show sinusoidal waves that do not go to OFF between modulations at the recording temperatures (**Fig. 8B, C, F, G**).

The confusing flicker FP. This discussion of the "A-flicker" of *eureka* is merely a sketch, far from complete. While the flight during the emission of the pulsing FP is slow and sometimes "drifting," even leisurely, on the other hand, for descriptive purposes, flight during the emission of the flicker FP often appears,"frantic" and one must run to keep pace. Flying rapidly and sometimes dangerously close to vegetation-tops and covering four or more feet **during** a flicker, males

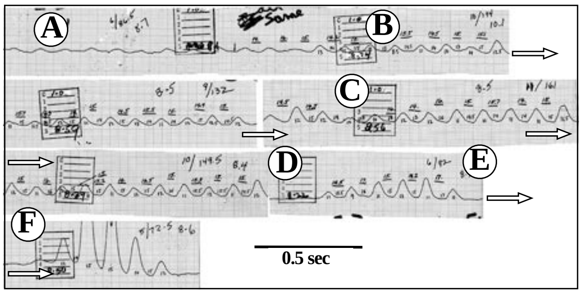


Figure 20. PM traces of FP transition (AX: ri/time).

Pyractomena angulata

travel in winding, undulating, sometimes rapidly reversing paths, their luminescence tracing parabolas, humps, hooks, esses and double-esses, often covering twelve or more feet between flickers, and casting their light in all directions along their pathways. Then suddenly they may slow, and easing into a long and gentle curve, gain altitude and begin pulsing. At times there will be no flickering and then abruptly, there will appear a spree of individuals doing so. They surely monitor the behavior of each other, rivals and intruders all.

An early generalization of the flicker FP as observed in several species of NA *Photuris*, including *eureka*, *tremulans*, *quadrifulgens*, *stanleyi*, *stevensae*, and *cinctipennis*, was that they were often closely but not always perfectly tuned to the flicker of *Pyractomena angulata*, a wide-ranging, fairly common though not abundant firefly. As more recordings and detailed comparisons were made of all PM and map records it began to appear that *Ph. quadrifulgens* possibly might be matching two flickering *Pyractomena* species, and perhaps tracking them seasonally. This remains unknown and will require extensive field PM recording and local, longitudinal studies.

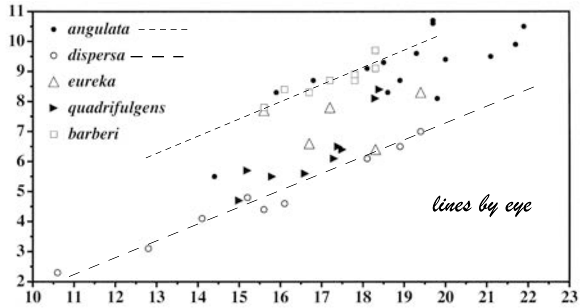


Figure 21. Flicker mod-rate comparison (AX: Hz./temp).

Similarly, it is not possible to interpret the broad variation in *eureka's* flicker frequency. *Py. dispersa* does not occur in Florida and records of it in southeastern United States are few. Note the flicker rates in **Figure 21**.

Figure 22 shows, at the left, the rates of each FP for four males; at the right the variation among 10 other males. Note that the five sets were recorded at different temperatures. Samples are small, but clearly show that variation exists in the flickers of individual males, and among the modulation rates of several males at the same temperature. **Figure 23** shows modulation rates of consecutive flickers emitted by four males; the fifth, rates from sequential segments of a very long transitional flicker as it changes from a long glow to a series of typical flickers (PM-trace in **Fig. 20**). These traces show that the flicker modulation rate in consecutive FPs emitted by single individuals can vary greatly. These meagre data invite experimentation with flickering LEDs.

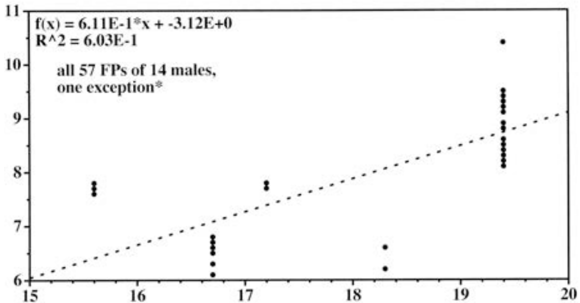


Figure 22. Flicker cps, all FPs (AX: Hz./temp).

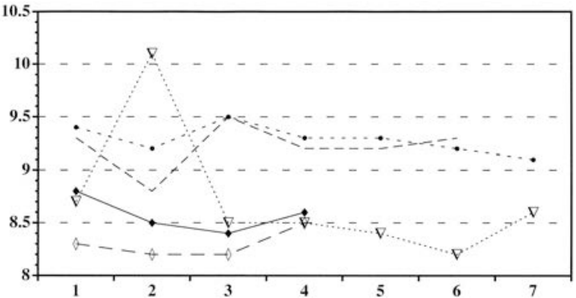
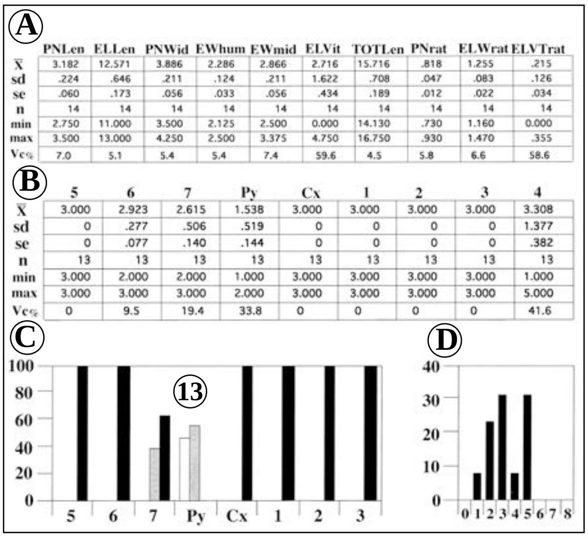


Figure 23. Flicker mod'-rate trails (AX: Hz/chronology).

Augmented figure legends. **8**. PM-traces of several of *eureka's* emissions: (**A**) A 6-pulse phrase, the pulsing FP, which is the primary default FP of this firefly; pulse numbers in FPs range 2-7. After the first pulse the PM-gun was aimed more accurately and more light was picked up—recorded at 16.9°/62.5°. (**B**) Two consecutive A-flickers from the same male recorded near Old Town, 17.2°/63°. (**C**) An A-flicker recorded near Steinhatchee at /16.9°62.5°. (**D, E**) Two consecutive flashes from the same phrase, recorded near Hines at 15.4°/60°; note the asymmetrical, crescendo form. (**F, G**) Two flickers in a series of flickers from one male, at Steinhatchee, in which all showed the wing-beat modulations to some extent—in these two the modulations were the most pronounced, both at about 38 Hertz at 16.9°/62.5°. **20**. PM-records of a *eureka* just as he ended his glow-FP and began to flicker, with the modulations at first continuous, then increasing in strength and changing slightly in frequency, and finally being broken into discrete flickers.**22**. Mod-rates of single FPs of individuals, showing variation among their FPs: At the left are four individuals at different temperatures and at the upper right several individuals ranged together and showing a broad 2.5 Hertz spread.

Morphological summary. Means are (n=14): PNL 3.2, ELL 12.6, PNW 3.9, EWhum 2.3, EWmid 2.9, ELVit 2.7, TOTLen 15.7, PNrat 0.82, ELWrate 1.26, ELVTrat 0.22 (**FigTable. 24A**, with other stats); colors in **FigTable 24B-C**, pre-lantern ventrite splash in **24D**. **Figure 25** anatomical key for skeletal plates and splashing on ventrite 4. **Figure 26** A range of vittagrams; **Figure 27** is a small collection of preliminary sketches of pronotal vittae.



Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.182	12.571	3.886	2.286	2.866	2.716	15.716	.818	1.255	.215
sd	.224	.646	.211	.124	.211	1.622	.708	.047	.083	.126
se	.060	.173	.056	.033	.056	.434	.189	.012	.022	.034
n	14	14	14	14	14	14	14	14	14	14
min	2.750	11.000	3.500	2.125	2.500	0.000	14.130	.730	1.160	0.000
max	3.500	13.000	4.250	2.500	3.375	4.750	16.750	.930	1.470	.355
Vc%	7.0	5.1	5.4	5.4	7.4	59.6	4.5	5.8	6.6	58.6

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.923	2.615	1.538	3.000	3.000	3.000	3.000	3.308
sd	0	.277	.506	.519	0	0	0	0	1.377
se	0	.077	.140	.144	0	0	0	0	.382
n	13	13	13	13	13	13	13	13	13
min	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	1.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	9.5	19.4	33.8	0	0	0	0	41.6

FigTable 24. Morphological stats.

Holotype: male, voucher number 7925, collected 18 April 1979, Dixie County, Florida, near Steinhatchee, on "infamous "road to nowhere" 4.7 miles south of Jena. FB page 12: One of a series of several collected after emitting their flickering or continuous-glow FP. From FB: "KB 28 *7925* flicker VR [= then nickname, variable red], 8:55 [pm], 1st one, low, 5'." The measured voucher (Paratype) series also represents, is from, a locality (deme) just north of Hines on route 357, off 358 just north of Cross City. Morphological data: from spread sheet—PNLen 3.4, ELLen 12.6, PNWid 4.1, ELWhum 2.5, ELWmid 3.4, LELVit 0.0, TotLen 16.0, PnRat 0.82, ElRat 1.35, VitRat 0.0; Colors: T 333, Py 1, Cx 3, V 333, Edg 3. Types will be deposited in the USNM.

Figure 26. Vittigram and PN array.

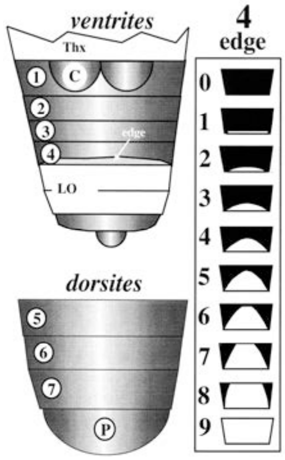


Figure 25. Topography and splash key.

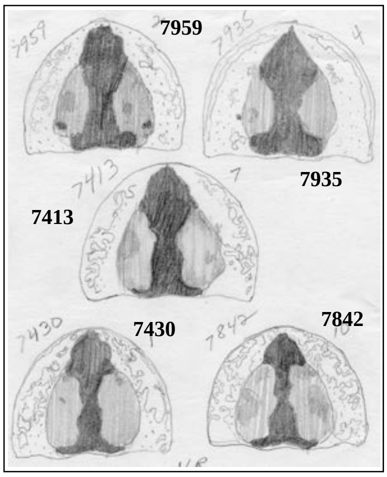


Figure 27. PN pencil sketches.

Nomenclatural and miscellaneous notes. The scientific name of this species recognizes a rare instant of insight, that occurred as I watched it emit FPs, and suddenly suspected that the adjunct/supernumerary FPs of *Photuris* species were copies of FPs of species in other genera. It only could have occurred at the moment I saw the particular *Pyractomena* that were flying with *eureka*, most especially the unique long-glow of *angustata*! I already had much evidence in files and recordings, but until these FPs were juxtaposed in flying luminescence I did not make a connection. With this notion I finally had a working explanation for Barber's question and dilemma, <why should the mate-finding and *identifying* context involve extra FPs>. If Barber could have chased his *tremulans* longer he would have seen it with *Pyractomena angulata* and I think he might have made the connection. Judging from his monograph (1951) he seems to have given more thought to the still-problematical, predaceous but non-defaulting *lucicrescens*. Perhaps notes in his archived files can tell us what he knew but hadn't yet told us before he left. And there was no one there at the time to tell his complete story …

Chapter 33

Photuris fairchildi Barber 1951

Cape Breton Firefly ("FRFP-versi")

Photuris fairchildi can be identified with certainty only when its diagnostic FP is observed. This, with some exceptions, consists of 3-10+ pulses; with shorter FPs there is an *unexpectedly*-short *pause* after the termination of one FP before the next begins. There are no FPs in North America that can be confused with this. Pulse intensity in each FP generally increases as it progresses, but sometimes this is difficult to see. Pulse *rate* in an FP generally decreases everywhere excepting in the northwestern corner of *fairchildi's* known range, Minnesota. However, this "*retardando"* (slow down) may also be difficult or impossible to see. FRFP appears to be the most widely distributed of all *versicolor*-complex species, its known range extending in the southwest from Barry County, Missouri (at least), to Nova Scotia (at least) in the northeast (**Fig. 1**). Geographically marginal/peripheral demes/variads may present a peculiar array of "FPs" and repertoires, as seen at the northern tip Michigan's southern peninsula (mitten). Records of seasonal occurrence are few and strongly biased by northern movement of fieldtrip excursions (**Figs. 18. and 19**). Larry Buschman (1974) made several important observations on the flashing behavior and predation of this firefly and his paper should be studied carefully before beginning field study.

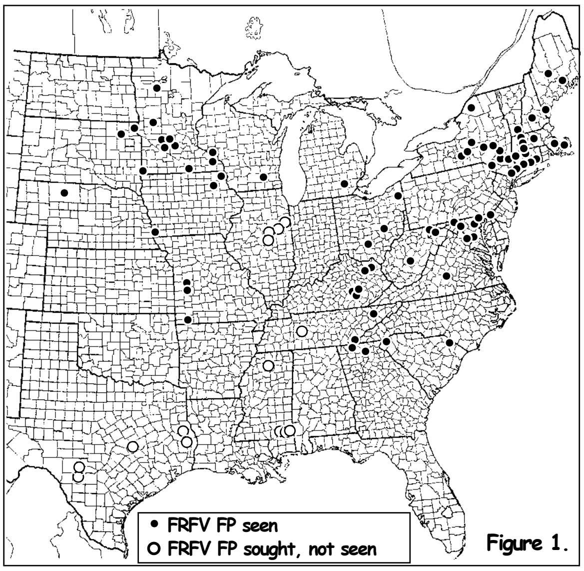


Figure 1.

Ecology, flashing behavior. A single individual of this firefly, as identified by its distinctive, most common FP—a phrase of 3-6 rapid pulses of rising intensity repeated at "unexpectedly" short intervals—will be seen passing quickly along woods' edges on half the nights a fireflyer is afield in its eastern area of occurrence (**Fig. 2**). Such individuals are also seen passing low over the ground as they zip through demes of other species, probably seeking their hunting females. In a visit to a tiny grassy field near Boston, the *Photinus* study site of fireflyer students in the area, while in conversation with the researcher a single *stevensae* male passed by quickly and moments later a FRFP raced through. Buschman noted single-flash FPs were common in demes he studied—though seemingly less common in the U.S., perhaps this was the identity of Barber's "primitive unknown." Simple 2-pulse FPs that may be attributable to *fairchildi* are occasionally seen.

Juveniles may often be woodland residents, and judging from the wide-ranging occurrence of individual flashing males, the speed that they fly, and the rapid redundancy of their FPs, females are expected to range broadly in their hunting and ovipositing. With respect to the short pause time relative to the duration of the FP-period itself (FP/FP+Pause), this atypical "*duty-cycle*" may permit an increase in flight speed during roving mate searches, with the coverage of more space during an evening.

Close FP scrutiny reveals inscrutable complexity, and the variability of certain elements makes description difficult. Data permit an overview but can only encourage further attention. (**1**) FPs sometimes *appear* to be separated by a *pause* scarcely longer than a single pulse, but measurement shows this not to be the case (**Fig. 3**). (**2**) FP period is temperature dependent and its duration is influenced by pulse number in the FP initiating/beginning the period measured: as would be expected, FP periods following 4-pulse FPs tend to be shorter than periods following 5-pulse FPs, and so on (**Fig. 4**). Periods of FPs of 2-6 pulses average about 2.2 seconds in

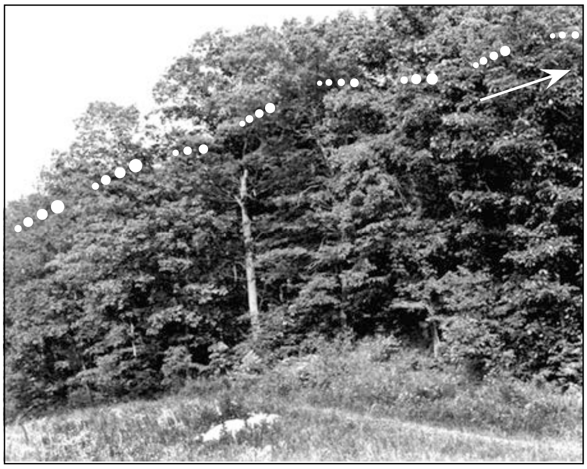


Figure 2. As zipping along a gasline, Harford Co. MD.

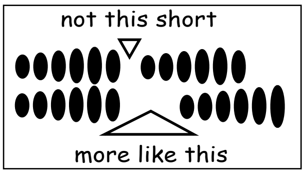


Figure 3. FP succession is often deceiving.

duration at 20°/68° (**Fig. 5, solid symbols**). (**3**) FP periods of demes in Minnesota average longer, this being more evident at lower temperatures (**Fig. 5, open symbols**), the difference being about 2 seconds at 15.5°/60°. A similar regional difference is shown in **Figure 6**, the regression of 6-12-pulse FP periods.

(**4**) Finally, with respect to apparent regional differences in FP periods, note that in Figure 5 the periods of 2-6-pulse FPs were regressed and in **Figure 6** the periods of 6-12-pulse were. Among distinctions of these two sets, the longer FPs, up to 18+ occur low over meadows and shorter FPs were emitted by faster flying and apparently roving males. In the sample from Minnesota there were many more 6-12-pulse FPs, and sites were often over grassland and along rural highways. Thus, the nature of habitats sampled may have resulted in this bias, and the shorter FPs measured perhaps were under the influence of this different ecology. Males flying over a meadow on the Fort Hill National Seashore on Cape Cod (**Fig. 7**), emitted FPs almost as long as those observed in Minnesota. However, as another variable, these two regions, Minnesota and Cape Cod, also share another feature of suspected importance in that they are fringe localities, somewhat isolated at the edge of the Continental melee of FPs and species, with its diversity of pulsed patterns and dangerous mimicries. (Incidentally, note in **Figure 1** the hiatus(?) that may be indicated from Michigan to Alabama?)

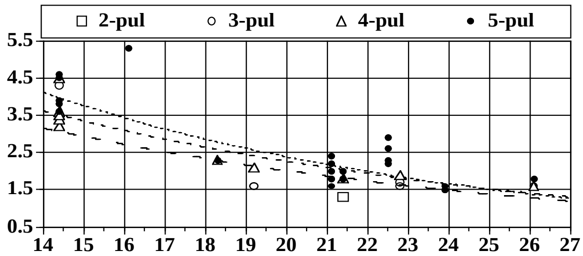


Figure 4. FP periods following 5-pulse FPs are longer than those following FPs with fewer pulses (AX: sec/temp).

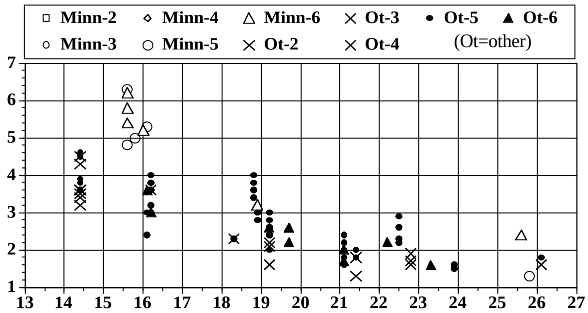


Figure 5. Regional difference of Minnesota FP periods; note pulse-number arrays in stacks of symbols (AX: sec/temp).

In **Figure 8** all data were incorporated in regressions: Data points from Minnesota are not shown, the upper dashed line shows their regression. Data points for “other US” are shown and the lower dashed line is their regression, with solid dots showing all periods following pulse-numbers except 5, and open circles showing periods following 5-pulse FPs; inexplicably, some 5-pulse samples fall neatly between the regressions. These demes were in Westchester County, New York, and Barry County, Missouri.

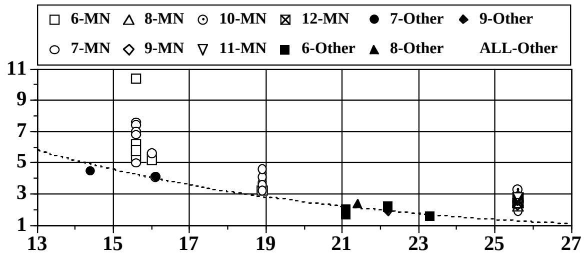


Figure. 6. FP period of 6-12-pulse FPs (AX: sec/temp).

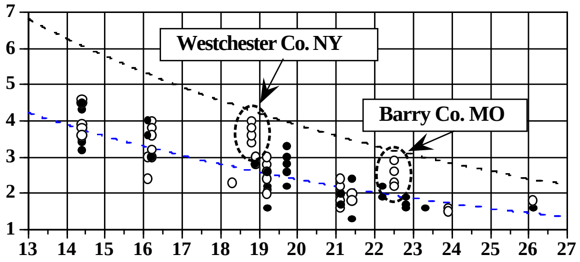


Figure 8. Above, FP period regression of Minnesota (from 41 data points, not shown); "other" below (103 data points). Circles show periods after 5-pulse FPs—note those in the middle, from two localities (AX: sec/temp).

Figure 7. Cape Cod meadow, Fort Hill National Seashore.

Pulse amplitude/intensity. The core though imperceptible *signature* of *fairchildi*, this FRFP-*versi* firefly, is the gradual increase in amplitude of pulses in FPs observed in some PM-records from all localities (**Fig. 9**). The significance of records/demes that do not show this feature or otherwise vary from the signature-form cannot be properly evaluated due to two uncontrolled variables during PM-recording: (**1**) as an FP progressed, particularly long ones at low temperatures, the sensitivity/gain may have been adjusted to improve the quality of the recording; (**2**) the aim of the lantern may have changed during the FP. Records from Minnesota show more deviation and variability than those from other localities, and in increasing occurrence in four (five!) localities recorded from south **to** north—Winona, Chagiyogi, Douglas, and Clearwater Counties.

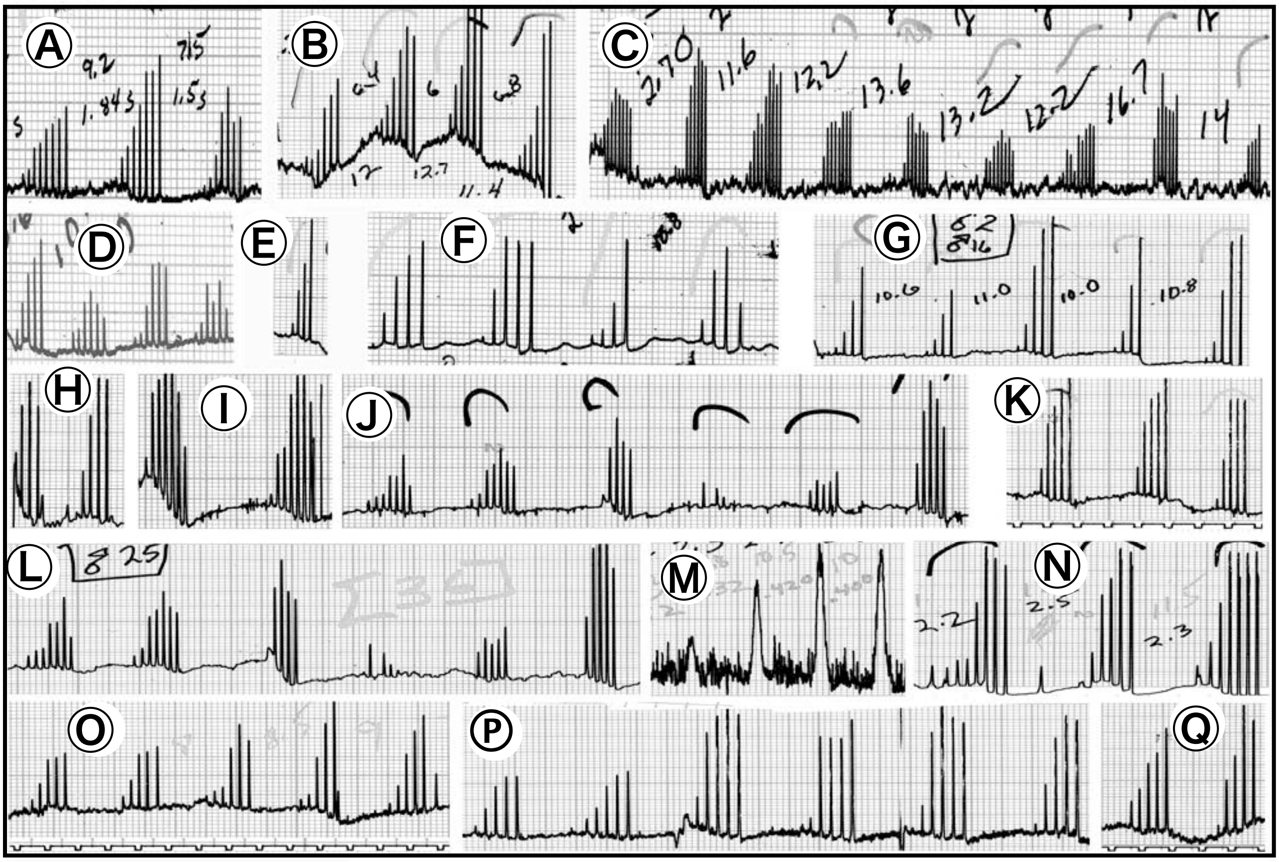


Figure 9. PM-records of FPs from demes across eastern North America showing the occurrence of the "signature" for OTU-fairchildi, sometimes in sequences with variations that doubtfully(?) were functional but perhaps caused by momentary lantern-PM alignment change, or irregular neural control systems. In all records except M chart speed was 5 mm/sec, as shown by the 1-second markers in K, O and Q: in M it was 25 mm/sec. The FP in N is from a variad deme that has been formally named (alexanderi). (A, B) Barry Co. MO (RRSP), 67.5°; (C) Winona CO. MN 25.6°; (D) Madison Co. NY, 21.7°; (E) Tompkins Co. NY, 18.3°; (F) Harford Co. MD, 14.4°; (G) Murray Co. GA, 19.5°; (H) Appomattox Co. VA, 18.3°; (I) Clearwater Co. MN, 18.9°; (J) Clearwater Co. MN, 18.9°; (K) Barnstable Co. MA, 19.3°; (L) Clearwater Co. MN, 18.9°; (M) Kennebec Co. ME, 13.9°; (N) Cheboygan Co. MI, 16.4°; (O) Washtenaw Co. MI, 16.3°; (P) Windham Co. VT, 16.2°; (Q) Westchester Co. NY, 18.9°.

Recordings in South Dakota were made at such a cold temperature, with only perched individuals flashing, that they cannot enter the consideration; and recordings from the far north of Minnesota—Lake-Of-the-Woods County—show only a different FP entirely, one that possibly connects with *alexanderi,* a northern Michigan variad of *fairchildi*: In Cheboygan County, Michigan, at the northern tip of the southern peninsula, and at a locality on the Upper Peninsula, a widely variant form was noted, and this population emitted the *signature* FP discussed here among the many other patterns it flashed. This variad is herein named *Photuris alexanderi*.

Finally, the deme at Baddeck, Nova Scotia, being the origin of the Holotype, will retain the name *fairchildi* when populations elsewhere are formally given rank. The FPs in **Figure 10** were emitted by a male on Cape Breton Island, 3.1 miles from the site where Dr. Alexander Graham Bell (Sandy) Fairchild, for whom the species is named,

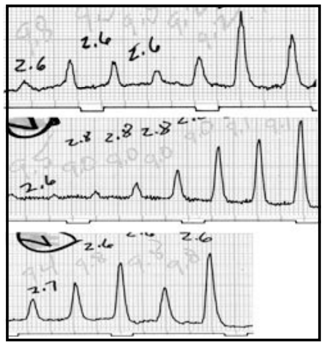


Figure 10. Consecutive FPs from a single male, at 14.4°/58° (AX: intensity/time, 1-sec markers).

collected the series from which Barber selected the Holotype. Sandy collected his series by his cabin and in a neighbor's yard. No *Photuris* were there when I visited the site, 30 June-31-1 July 1988, though *Photinus obscurellus* was present. At the recording site, along a road by a meadow, FPs with 1-5 pulses were observed, and an intensity increase was distinct (**Fig. 11**). One brief experiment with a decoy seemed to confirm Lawrent Buschman's conclusion that communication in this firefly is different and complex …

Pulse rate. This FP parameter has many moving parts: (**1**) Pulse rate decreases with temperature. The rate of the last two pulses in an FP—that is, the rate (reciprocal) of the duration of the **Ultimate** period (U, in **Fig. 12**)—is used to illustrate this temperature influence. In **Figure 13** the U-rates of FPs from demes across a broad region are regressed on temperature. In **Figure 14** the U-rates from Minnesota demes are separated from all others.

(**2**) Pulse rate, in general, gradually decreases through the duration of an FP, but there is variation in this among the FPs of an individual (**Fig. 15**), and among the FPs of different individuals (**Fig. 16**). **Figure 16** shows the change in pulse *interval* at the left and the deceleration of the reciprocal, the pulse *rate*, at the right, period by period, for three males at RRSP Missouri, at the same time and temperature. **Figure 17 (Parts 1-4, four pages)** shows such rate trajectories for males recorded at several sites and of several demes across eastern and midwestern United States. Note that in traveling north in Minnesota strange things happen. Pulse repetition rate averages about 5 Hertz at 20° and 2.5 Hertz at 14°, but such values much oversimplify reality.

Figure 11. Nova Scotia site, near Baddeck on Cape Breton Island.

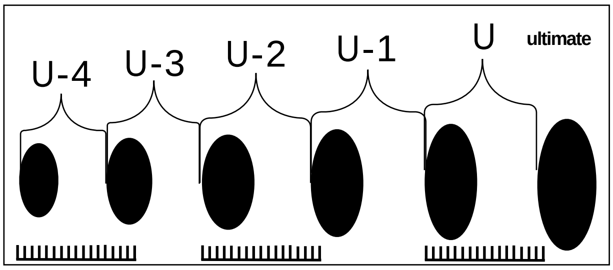


Figure 12. U-names of FP periods "U" = ultimate.

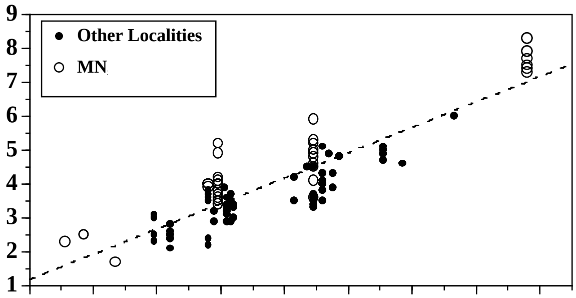


Figure 13. Rate/temp. regression of U periods in FPs (AX: Hz./temp).

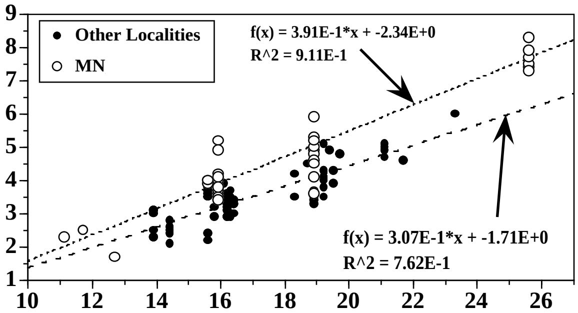


Figure 14 . Regression of rate of U (ultimate) pulse period on temperature (AX: Hz./temp).

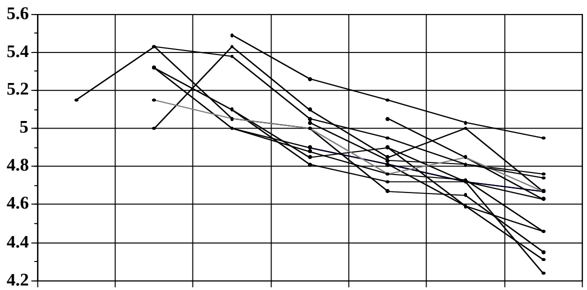


Figure 15. Through-FP rate decelerations in a sequence of FPs emitted by a single male (AX: Hz/period position; Barry Co. MO).

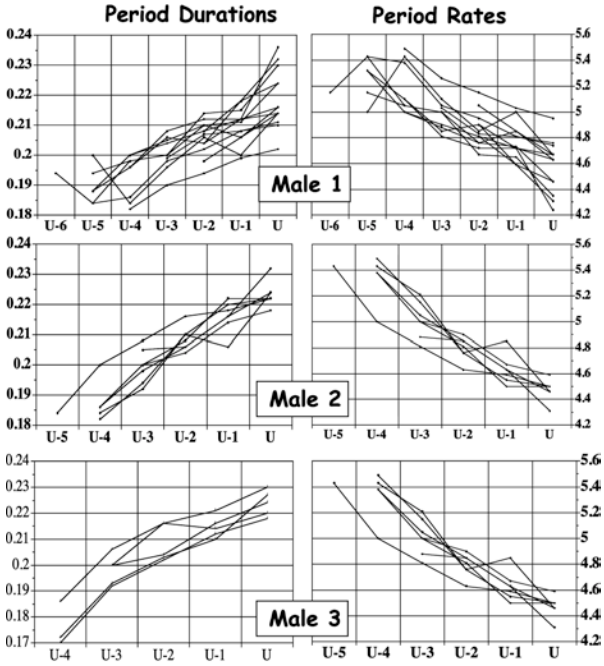
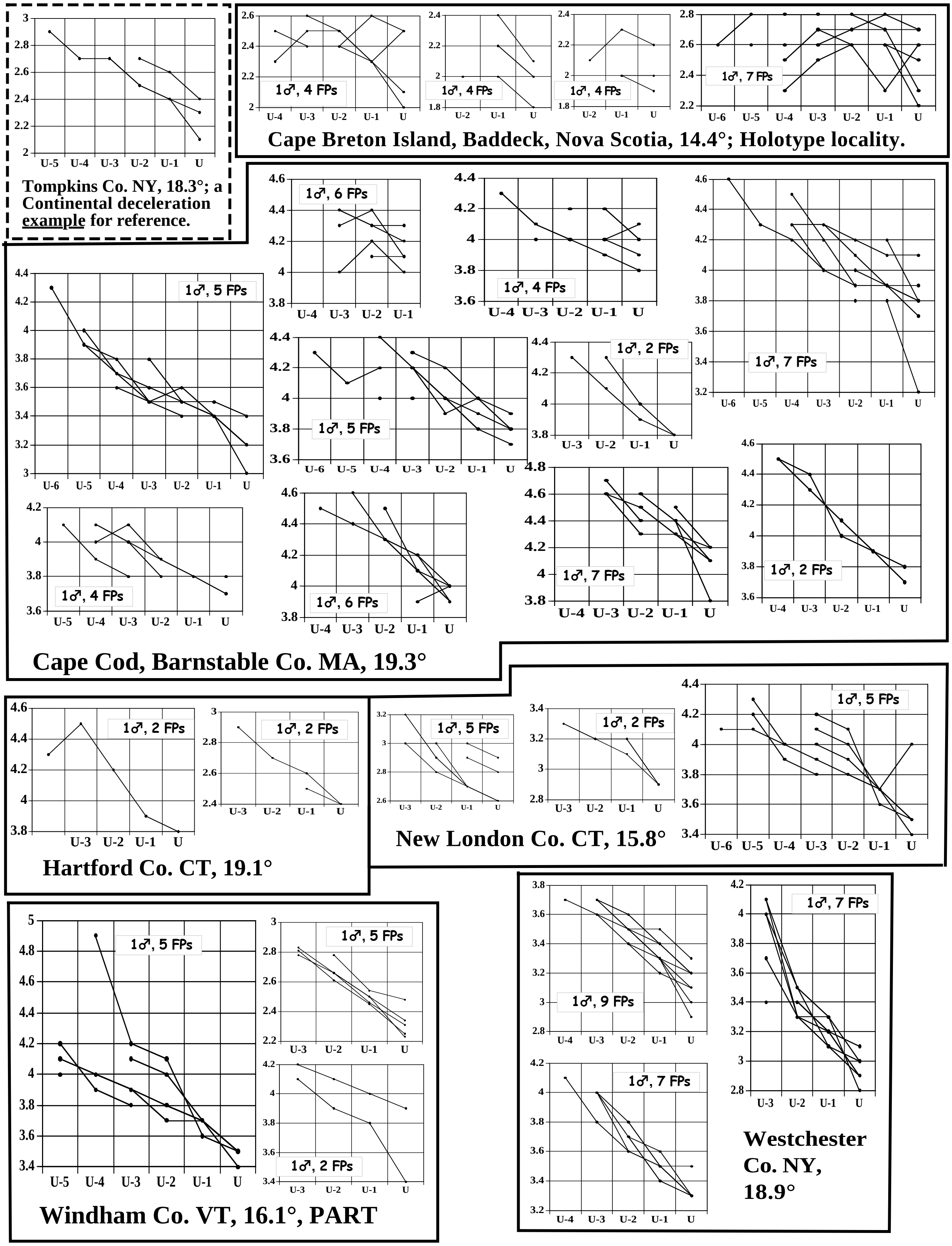
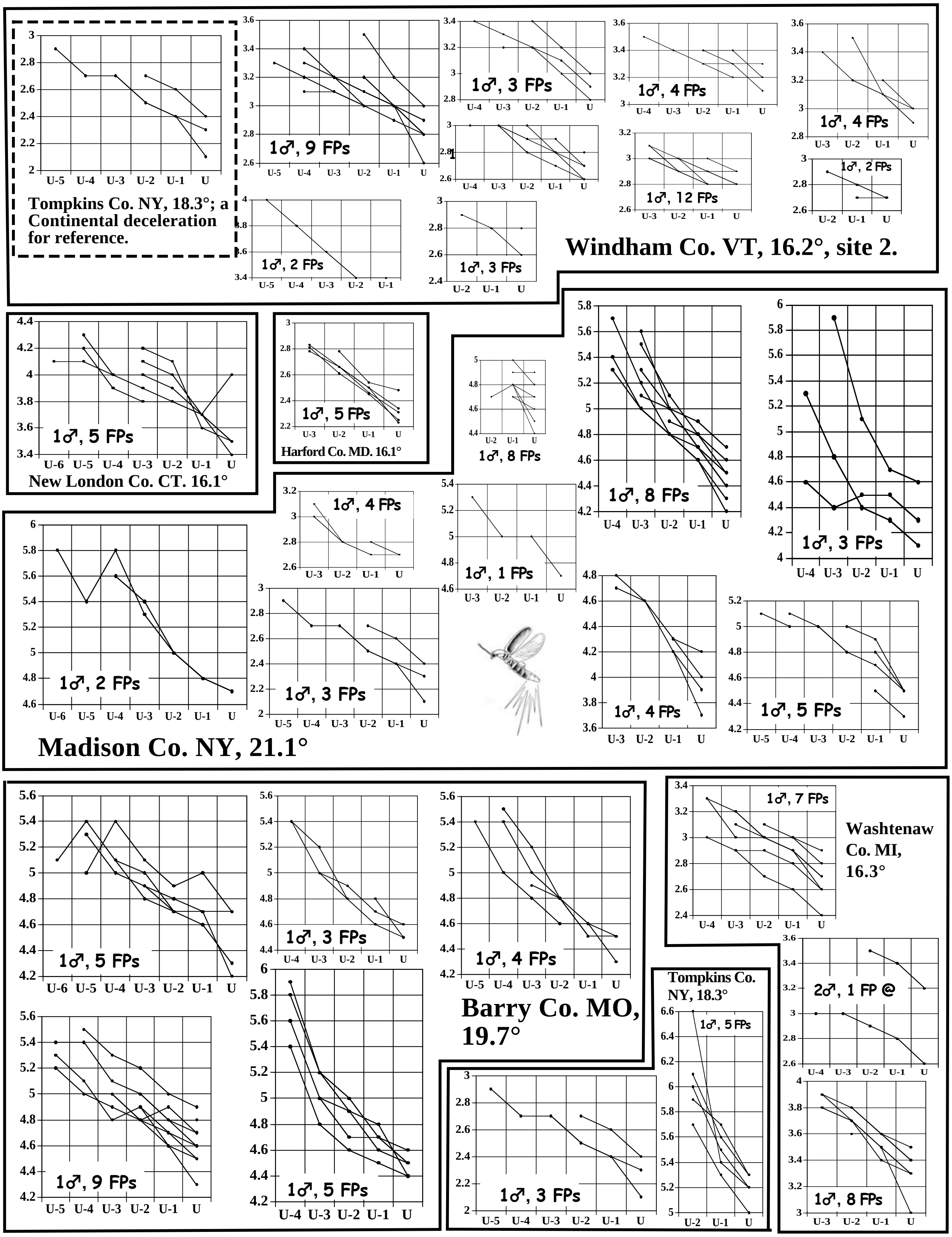


Figure 16. At the left is shown the through-FP increases in pulse periods in consecu-tive FPs of three males; graphs at the right show the through-FP rate (1/period) decelerations (AX: Hz/period position; Barry Co. MO).

Figure 17, Page 1. This collection of PM-recorded rate trajectories is from demes across the known range of OTU *fairchildi* and is merely a sketchy sampling, but suggests elements that may have significance.

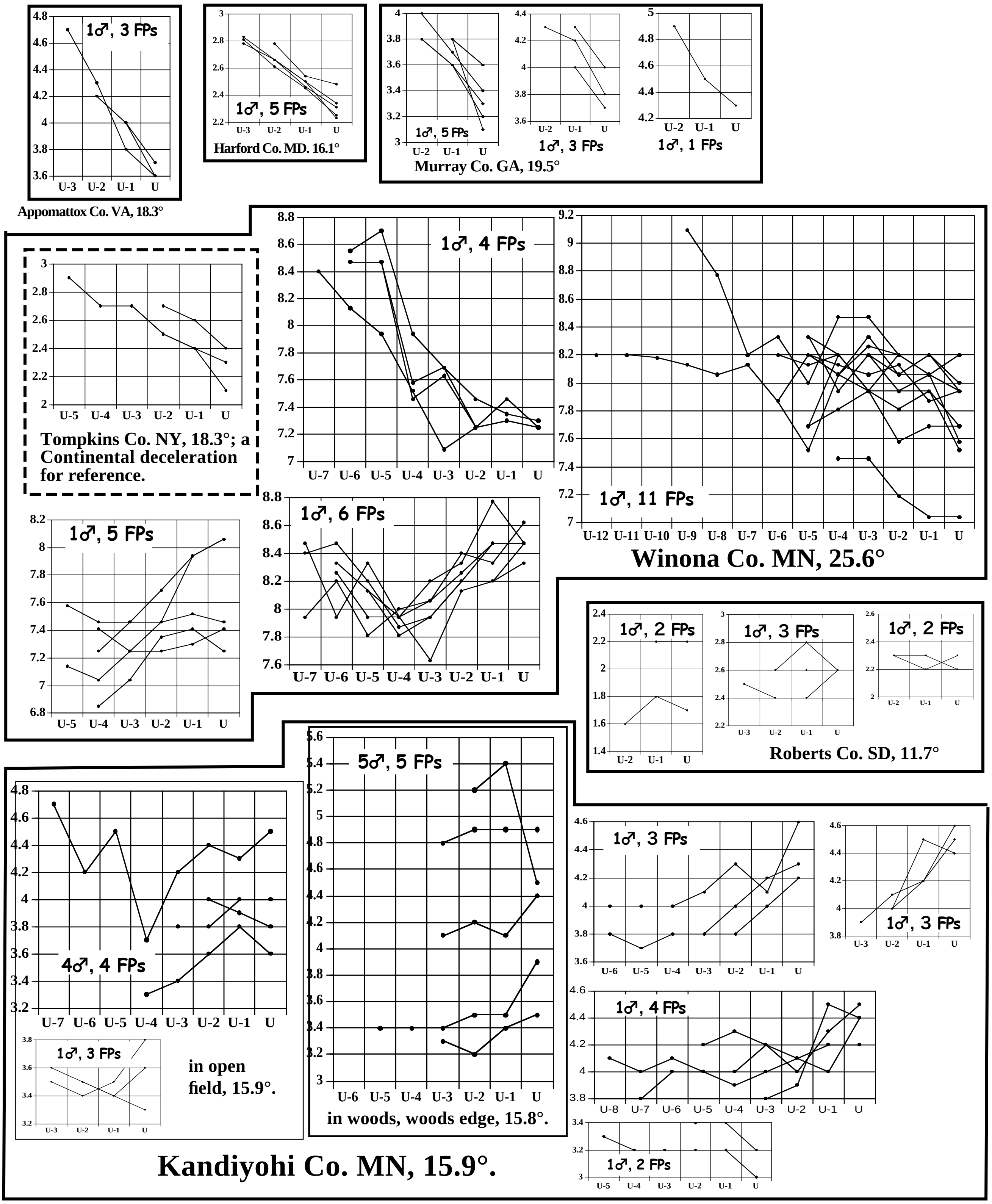


Pulse-Rate Trajectories: Figure 17, Page 2, more ne and the midwest



Pulse-Rate Trajectories: Figure 17, Page 3, the East, SD & MN (part)

Beginning with Winona County, in southeastern Minnesota, the demes sampled progressively northward show both a gradual disruption/disintegration of trajectory form and reversal of "polarity" that seems to be increasing in frequency, perhaps becoming established in Douglas and Clearwater Counties.



Appomattox Co. VA, 18.3°

Harford Co. MD. 16.1°

Murray Co. GA, 19.5°

Tompkins Co. NY, 18.3°; a Continental deceleration for reference.

Winona Co. MN, 25.6°

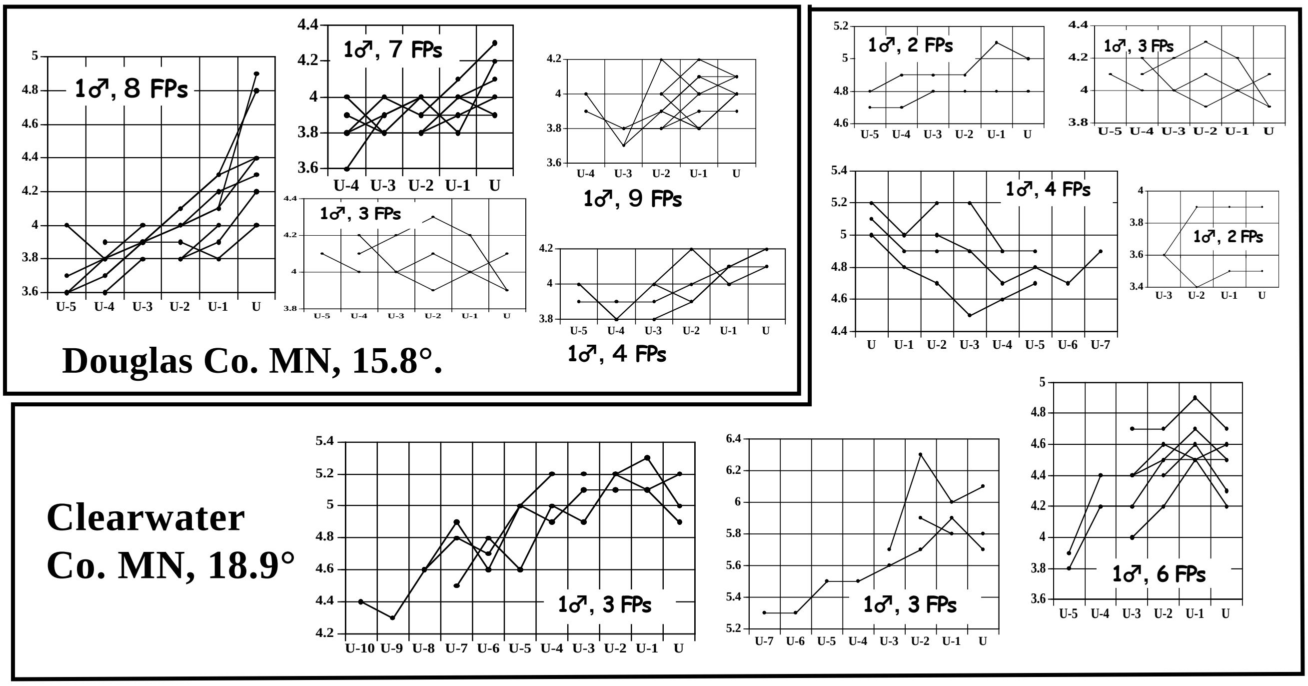
Roberts Co. SD, 11.7°

in open field, 15.9°.

in woods, woods edge, 15.8°.

Kandiyohi Co. MN, 15.9°.

Pulse-Rate Trajectories: Fig. 17, Page 4, MN (part)



When examining these trajectories keep in mind that occasionally the rate given as U—the ultimate (last) interval of an FP—that this judgement of position is based upon what was actually PM-detected and may have been one interval earlier in reality. That is, in some cases, few probably, the ultimate pulse may not have been recorded. This would account for some variation among terminal intervals of FPs within and among series. Also, note the occasional steepness of a trajectory, perhaps an indication that the male had encountered a different situation, perhaps temperature which varies on a micro-scale, or received a response, or rival interference. Finally, perhaps most interesting is the peripheral effect, where at the edges of the distribution, or the concentration of several species as previously mentioned, things seem to fall apart—or change course.

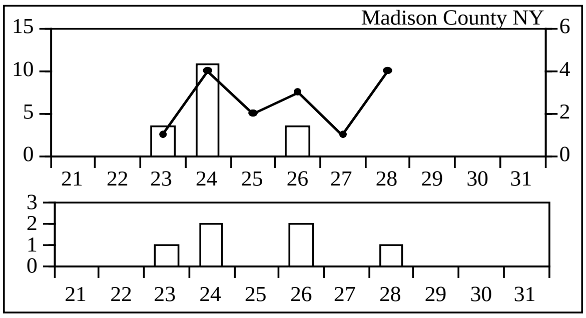


Figure 18. SESOBS based on limited observations.

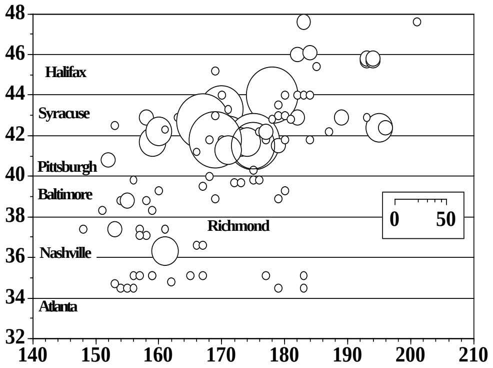


Figure 19. GESEDISOBS, *fairchildi*.

Nomenclatural Notes. The specific epithet recognized the collector, Dr. A.Graham Bell Fairchild, who collected Barber's type series, and noted that those of his series emitted a 2-flash FP. The common name refers to the type locality, on Cape Breton Island, Nova Scotia, and the mnemonic referents FRFV and FRFP-versi are those commonly used during this study. As can be understood from Sandy's name he had two famous grandfathers who, as I was told, shared ownership of the estate on the Island.

* * *

Morphology. Several measurements and other data were recorded from voucher specimens from several demes, including two series collected at the Holotype locality by two different fireflyers. The following pages have tables and figures that give these data.

fairchildi NS bush

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.510	9.850	3.040	1.840	2.310	5.840	12.360	.824	1.278	.590
sd	.074	.479	.070	.052	.152	1.098	.532	.027	.069	.097
se	.023	.151	.022	.016	.048	.347	.168	3.589E-3	.022	.031
n	10	10	10	10	10	10	10	10	10	10
min	2.400	9.400	2.900	1.800	2.100	3.800	11.800	.790	1.200	.400
max	2.600	10.800	3.100	1.900	2.500	7.300	13.400	.880	1.360	.690
Vc%	3.0	4.9	2.3	2.8	6.6	18.8	4.3	3.3	5.4	16.4

fairchildi NS jel

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.567	10.083	3.133	1.817	2.367	5.150	12.617	.812	1.308	.513
sd	.186	.371	.234	.117	.052	.764	.440	.025	.090	.086
se	.076	.151	.095	.048	.021	.312	.180	.010	.037	.035
n	6	6	6	6	6	6	6	6	6	6
min	2.400	9.800	2.800	1.600	2.300	4.300	12.300	.790	1.200	.410
max	2.800	10.800	3.400	1.900	2.400	6.000	13.500	.860	1.460	.620
Vc%	7.3	3.7	7.5	6.4	2.2	14.8	3.5	3.1	6.9	16.8

fairchildi MN kand

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.650	10.617	3.300	1.933	2.450	7.583	13.233	.797	1.275	.713
sd	.176	.776	.167	.103	.105	1.013	.882	.020	.072	.066
se	.072	.317	.068	.042	.043	.413	.360	3.028E-3	.030	.027
n	6	6	6	6	6	6	6	6	6	6
min	2.400	9.100	3.100	1.800	2.300	6.100	11.500	.760	1.180	.660
max	2.800	11.300	3.500	2.100	2.600	9.100	14.000	.810	1.360	.840
Vc%	6.6	7.3	5.1	5.3	4.3	13.4	6.7	2.5	5.6	9.3

fairchildi MO rrsp

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	3.329	12.529	4.171	2.357	3.086	9.329	15.843	.800	1.324	.746
sd	.170	.692	.293	.140	.121	.899	.846	.027	.057	.065
se	.064	.262	.111	.053	.046	.340	.320	.010	.022	.025
n	7	7	7	7	7	7	7	7	7	7
min	3.100	11.300	3.800	2.100	2.900	7.800	14.400	.770	1.250	.610
max	3.500	13.300	4.500	2.500	3.300	10.400	16.800	.840	1.410	.810
Vc%	5.1	5.5	7.0	5.9	3.9	9.6	5.3	3.4	4.3	8.7

fairchildi TN

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	3.200	12.380	4.040	2.300	2.860	7.200	15.580	.796	1.254	.580
sd	.187	.327	.329	.141	.182	1.407	.444	.038	.049	.116
se	.084	.146	.147	.063	.081	.629	.198	.017	.022	.052
n	5	5	5	5	5	5	5	5	5	5
min	3.000	12.000	3.500	2.100	2.600	5.400	15.000	.760	1.170	.440
max	3.400	12.800	4.300	2.500	3.100	8.800	16.100	.860	1.290	.730
Vc%	5.8	2.6	8.1	6.1	6.4	19.5	2.8	4.8	3.9	20.0

fairchildi MN stock

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.931	11.438	3.615	2.062	2.692	8.046	14.338	.812	1.323	.701
sd	.085	.669	.212	.189	.166	1.305	.730	.042	.114	.089
se	.024	.186	.059	.053	.046	.362	.202	.012	.032	.025
n	13	13	13	13	13	13	13	13	13	13
min	2.800	10.000	3.100	1.800	2.500	5.800	12.900	.760	1.180	.580
max	3.100	12.500	3.800	2.400	3.000	9.800	15.500	.920	1.500	.850
Vc%	2.9	5.8	5.9	9.2	6.2	16.2	5.1	5.2	8.6	12.7

Nova Scotia, Buschman

Descriptive Statistics

	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
Mean	3.000	3.000	3.000	1.200	3.000	2.800	2.900	3.000	4.800
Std. Dev.	0	0	0	.422	0	.422	.316	0	1.932
Std. Error	0	0	0	.133	0	.133	.100	0	.611
Count	10	10	10	10	10	10	10	10	10
Minimum	3.000	3.000	3.000	1.000	3.000	2.000	2.000	3.000	3.000
Maximum	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	7.000
# Missing	0	0	0	0	0	0	0	0	0

Nova Scotia, jel

Descriptive Statistics

	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
Mean	3.000	3.000	2.600	1.000	3.000	3.000	3.000	3.000	5.600
Std. Dev.	0	0	.548	0	0	0	0	0	2.408
Std. Error	0	0	.245	0	0	0	0	0	1.077
Count	5	5	5	5	5	5	5	5	5
Minimum	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	3.000
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	8.000
# Missing	0	0	0	0	0	0	0	0	0

Kandiyohi MN

Descriptive Statistics

	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
Mean	3.000	2.667	1.333	1.000	3.000	3.000	3.000	3.000	4.833
Std. Dev.	0	.516	.516	0	0	0	0	0	1.722
Std. Error	0	.211	.211	0	0	0	0	0	.703
Count	6	6	6	6	6	6	6	6	6
Minimum	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
Maximum	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
# Missing	0	0	0	0	0	0	0	0	0

RRSP MO

Descriptive Statistics

	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
Mean	3.000	1.571	1.143	1.000	3.000	2.857	3.000	3.000	5.286
Std. Dev.	0	.787	.378	0	0	.378	0	0	1.890
Std. Error	0	.297	.143	0	0	.143	0	0	.714
Count	7	7	7	7	7	7	7	7	7
Minimum	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
Maximum	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
# Missing	0	0	0	0	0	0	0	0	0

TN

Polk Co. TN.

Descriptive Statistics

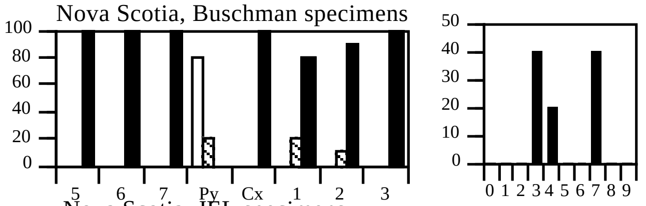
	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
Mean	3.000	2.600	1.400	1.000	3.000	3.000	3.000	3.000	5.800
Std. Dev.	0	.894	.548	0	0	0	0	0	1.095
Std. Error	0	.400	.245	0	0	0	0	0	.490
Count	5	5	5	5	5	5	5	5	5
Minimum	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	5.000
Maximum	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
# Missing	0	0	0	0	0	0	0	0	0

Winona Co. MN

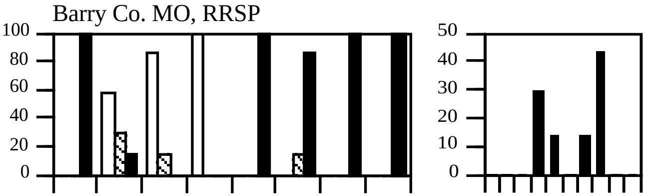
Descriptive Statistics

	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
Mean	3.000	2.308	1.462	1.000	3.000	2.923	3.000	3.000	5.846
Std. Dev.	0	.630	.660	0	0	.277	0	0	1.864
Std. Error	0	.175	.183	0	0	.077	0	0	.517
Count	13	13	13	13	13	13	13	13	13
Minimum	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	8.000
# Missing	0	0	0	0	0	0	0	0	0

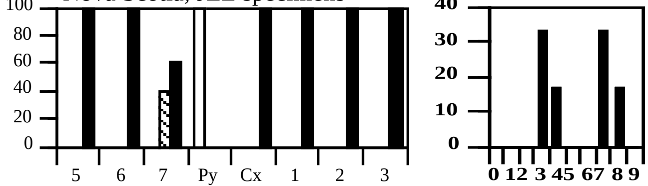
Nova Scotia, Buschman specimens



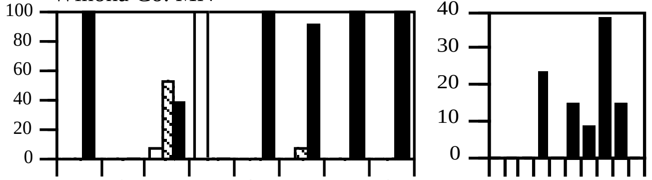
Barry Co. MO, RRSP



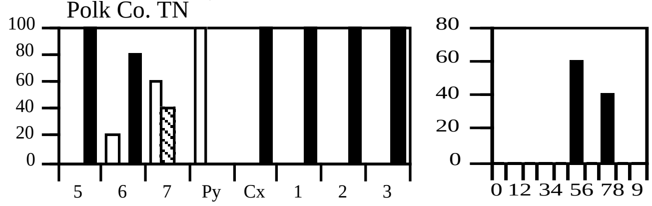
Nova Scotia, JEL specimens



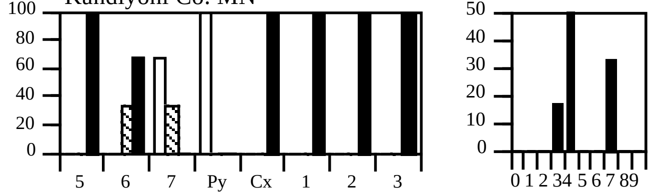
Winona Co. MN



Polk Co. TN

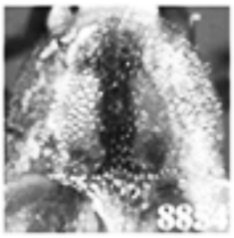


Kandiyohi Co. MN



NOVA SCOTIA: Cape Breton Isl., Baddeck (Type Locality)


8857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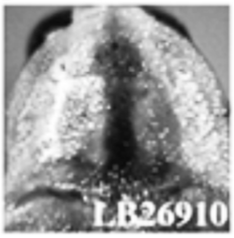
8855


8856

NOVA SCOTIA: Bridgewater (Lawrent Buschman coll.)


LB26934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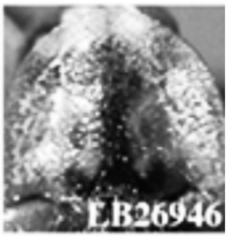
LB26921


LB26925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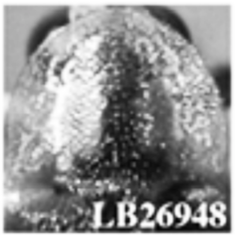
LB26939


LB26948


LB2699


LB26918

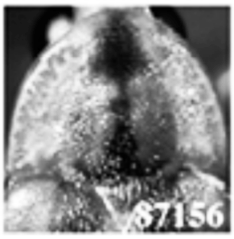

LB26931

NEW ENGLAND: Connecticut, Massachusets, & Vermont

CT: Hartford Co.


91119

MA: Barnstable Co.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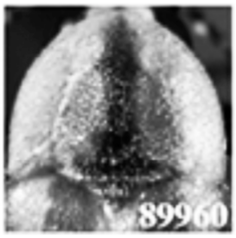
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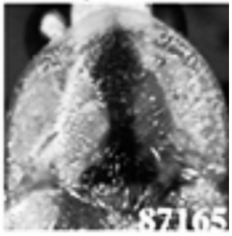
87155

MA: Plymouth Co.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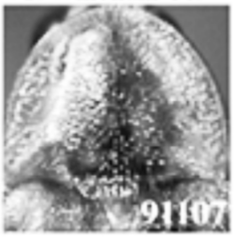
VT: Windham Co.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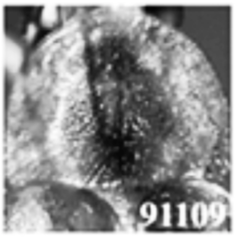
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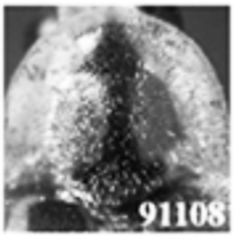
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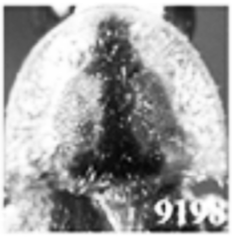
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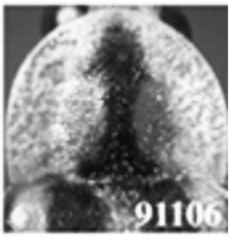
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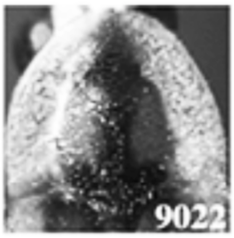
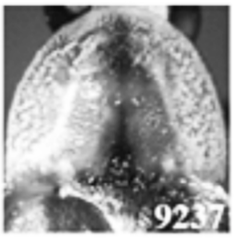
VT: Windham cont.'


9022

NEW YORK: Westchester Co. (east side of Hudson R.)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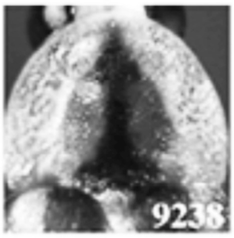
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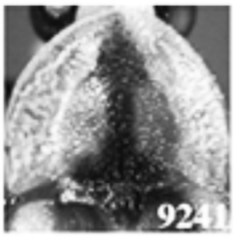
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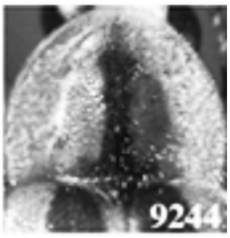
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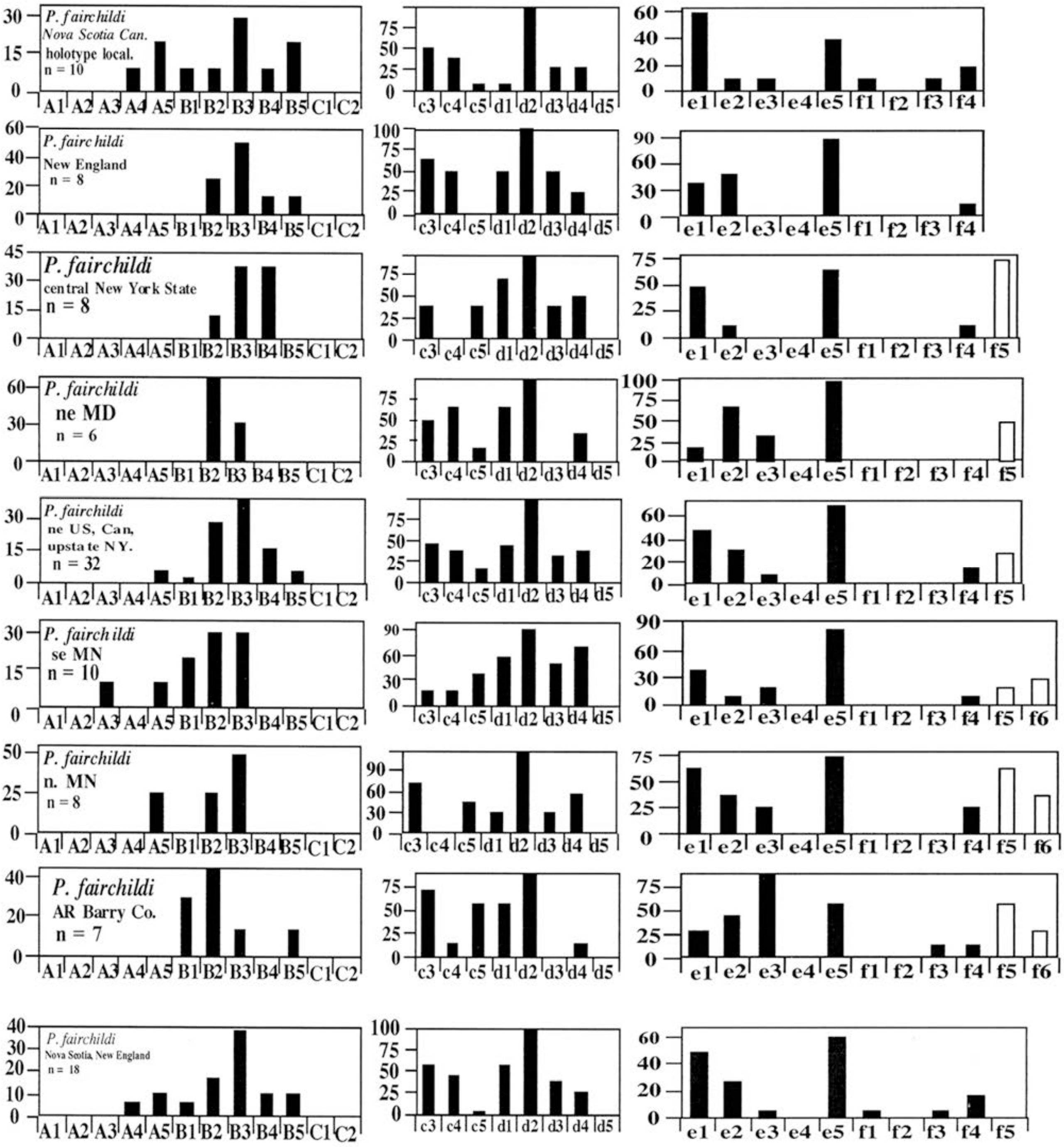
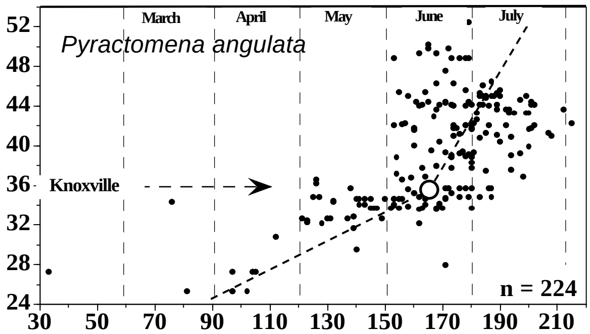
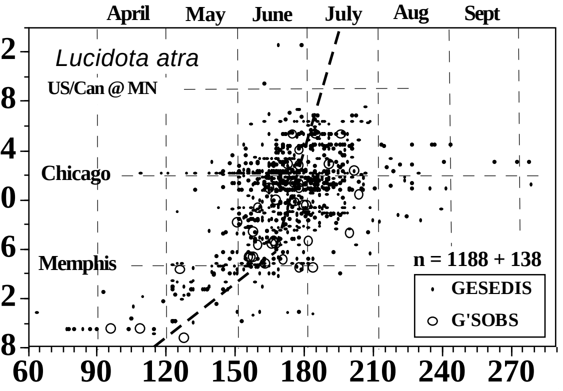
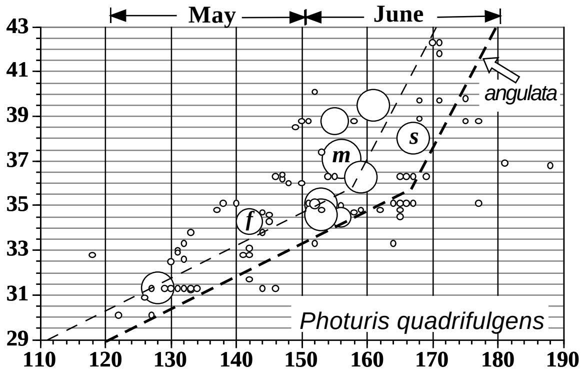
Pronotal evaluation histograms, as viewed from PN array x201.2



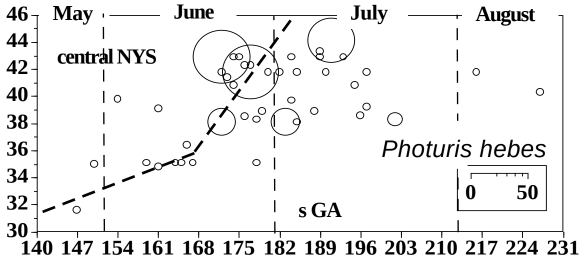
Firefly phenology: a reference model for prediction? With each new season the appearance of firefly adults, which begins in the southern part of the species' range, progresses slowly northward. This can be seen when latitude and date-of-collection for archived specimens are plotted for a species that has broad (north and south) geographical occurrence. This of course is subject to some bias—for example, relatively more may be collected on the Fourth of July or Labor Day, and the records from field observations (G'SOBS) will be biased by the dates of my northward travel over the years. Early plots used records selected to avoid such biases but this extra effort seemed unnecessary. Early in this study it was noticed that the slope of this plot sometimes seemed to bend "rather sharply" upward at a latitude near that of Knoxville, Tennessee, as is made conspicuous in the chart for *Pyractomena angulata*, below left—an extrapolated slope of appearance would bring summer fireflies out with fall colors in the north. The *angulata* line has been crudely placed (by eye) on DOY/Lat. (GESEDIS and/or G'SOBS) plots of a few wide-ranging species for comparison. Note that the regression for *E. corrusca* is different from others: *E. corrusca* is a complex of species, and in the population studied by Fred Hough near Accord, Dutchess County, New York, adults eclosed in late summer, overwintered as adults that sometimes during frigid months explosed themselves on the trunks of trees, perhaps killing internal parasites, and then mated in the spring. Note that adult records for July are few—perhaps most are larvae at that time. Keep in mind that these charts combine data from many seasons, and phenology varies somewhat from season to season—climate change will certainly necessitate adjustments in predictions.



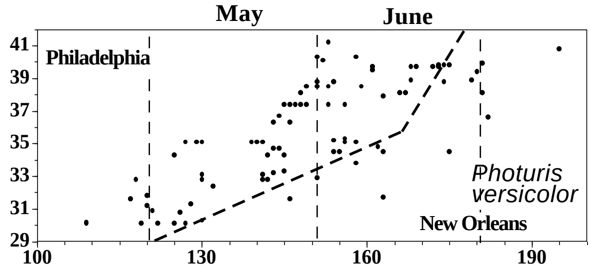




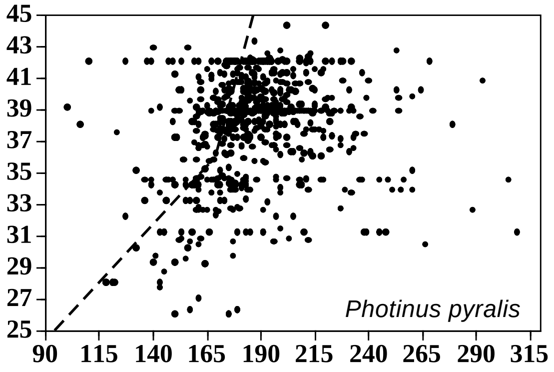
G'Sobs records (AX: Lat/DOY); noted < many.

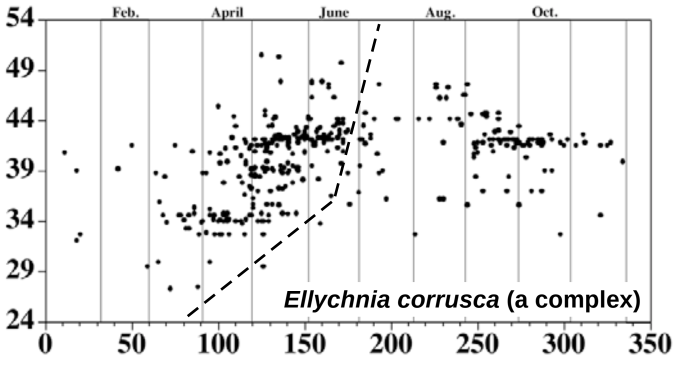


GESEDISOBS records (AX: Lat/DQY/n).



G'SOBS records of seasonal occurrence (AX: Lat/DOY).





Chapter 34

Photuris flavicollis Fall 1927

This firefly, an adventure never pursued, perhaps flashes like three other members of Division 1, with an FP like that of *Ph. floridana* and a congener that was considered by Barber to belong to the same species, or *Ph. congener* (**Fig. 4**). This to say, it may/probably? emit(s) a flash train, a continuous rhythmic/metronomic series of very short (60 mSec) flashes with intervals less than one second in duration. The following is from the original description by H. C. Fall:

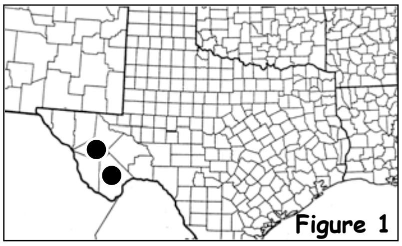


Figure 1

> *Prothorax orange yellow, the explanate margins of paler yellow; head, scutellum, metasternum and femora yellow; antennae, elytra, tibiae and tarsi black. … Elytra entirely black, distinctly closely punctate … Length 8.4 to 11.5 mm. / Alpine, Texas; three males, collected by O. C. Poling.*

Ph. flavicollis is presently only known from two counties in southwest Texas, a mountainous region (**Figs. 1, 2**). Seasonal occurrence of the short sample is confined to midsummer, June to early August (**Fig. 3**). Morphological data are in **Figures 5-7**.


Figure 2. *Ph. flavicollis* domain, near Marfa's lights!

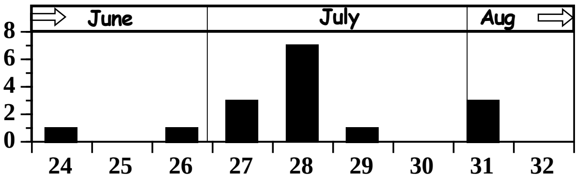


Figure 3. Dates of 16 archived specimens from Brewster and Davis Counties (AX: #/WOY).

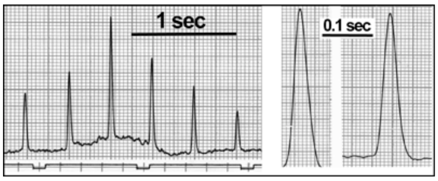


Figure 4. *Ph. congener* flashes, 21.8°/71.2° (AX: rel. int./time).

flavicollis

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.462	9.388	3.112	1.863	2.163	0	11.850	.790	1.161	0
sd	.074	.372	.189	.119	.160	0	.400	.031	.050	0
se	.026	.132	.067	.042	.056	0	.141	.011	.018	0
n	8	8	8	8	8	8	8	8	8	8
min	2.400	9.000	2.900	1.600	1.900	0	11.400	.740	1.070	0
max	2.600	10.000	3.400	2.000	2.300	0	12.500	.830	1.210	0
Vc%	3.0	4.0	6.1	6.4	7.4	0	3.4	3.9	4.3	0

flavicollis

	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	3.000	3.000	2.375	1.000	1.125	2.250	3.000	3.000	4.500
sd	0.000	0.000	.518	0.000	.354	.707	0.000	0.000	.756
se	0.000	0.000	.183	0.000	.125	.250	0.000	0.000	.267
n	8	8	8	8	8	8	8	8	8
min	3.000	3.000	2.000	1.000	1.000	1.000	3.000	3.000	4.000
max	3.000	3.000	3.000	1.000	2.000	3.000	3.000	3.000	6.000
Vc %	0	0	21.8	0	31.5	31.4	0	0	16.8

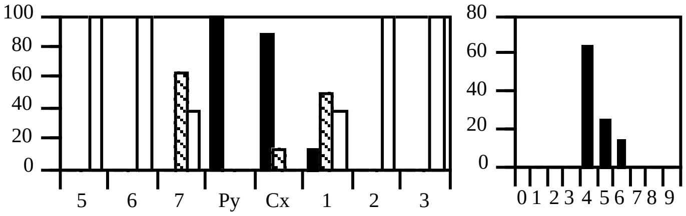
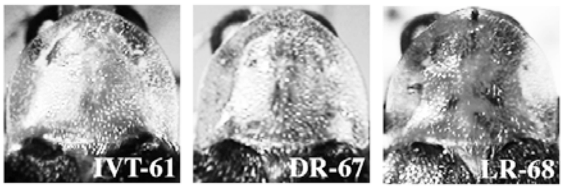


Figure 6. Measurements, ratios, color, and splash.



TEXAS: Jeff Davis Co.

Figure 5. Nearly immaculate yellow-orange PNs.

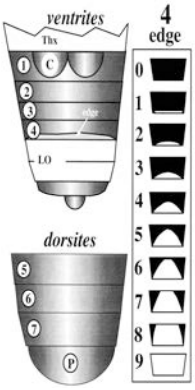


Figure 7. Key sclerites and splash.

Ecology of "mass synchronous" flashing. The phenomenon of synchronous flashing observed in large populations of fireflies has long attracted the attention of travelers and scientists, as illustrated by literature dating more than 300 years. From mangrove swamps in Southeast Asia, where *sedentary, rhythmic, beacon-like* flashing—once upon a time—involved thousands if not millions of individual fireflies along estuarine shorelines, to the wave-like appearance of *airborne* fireflies *in perpetual motion* over wet meadows in the southern Appalachians in North America, such phenomena have stirred much confusion among those who would attempt to explain or understand them. More than inept silliness is buried in scientific (peer-reviewed) publications concerning Asian manifestations, and not merely in times of journal infancy and adolescence at the turn of the 20th century. Such notions were contributed by "credentialated" academicians, and others sporting gray-matter documentation. Explanations varied, was sometimes culturally arrogant, psychologically or scientifically sophomoric, or misplaced expertise. Though certain elements and origins have already been examined (pages 39-40, 230, 268), a few important ecological fundamentals of the phenomenon have not been mentioned, or compared with behavior seen in other fireflies or insects (hill-topping, swarming). Here are some relevant points for consideration.

The question rephrased: *Why does mass flash synchrony, as seen in certain Asian ecological situations not occur in the Western Hemisphere?* **Working answer**: Western Hemisphere fireflies cannot usually perch in gatherings large or small—where individuals may examine each other at length when selecting mating partners—because firefly-eating/grazing photurines would make short work of them. In fact, it can reasonably be suggested, that the Photurinae lineage of the West acquired its predatory nature long ago by attacking perched flashers (pages 230, 266). Associated with this in producing the huge Asian displays that once were seen was a rich habitat that supported a super-abundance of individuals and convenient foliage to perch upon. Other species and other places will sharpen the focus: (**i**) occurring in numbers with *P. malaccae* in estuarine mangroves is the non-synchronizing *Pteroptyx valida*. Its advertising FPs are not single pulses or phrases that require synchrony to avoid disrupting an essential, identifying encoding rhythm. However, individual *valida* males and females, and those of other genera also, surely often use *malaccae's* beacon-mangroves—as once did Thai boatmen—and find conspecific mates waiting there. In New Guinea and elsewhere in the Eastern Hemisphere there are other species that form sedentary swarms. But, in the Western Hemisphere I know of only two: Joe Cicero reported that *Photinus knulli* in Arizona forms sedentary leks; he noted in connection with this behavior, that *Photuris* does not occur in the region. In the Andes Mountains of Colombia several individuals of an unnamed species (here nicknamed ascophengus; a new subfamily?), were found perched closely together in a tangle of vines over a trail, emitting trains of short glows. Because their lanterns are suspended from the abdomen like pockets, perhaps it may be conjectured that they emit light only when perched?

(**ii**) Occurring in small dispersed groups (20±) over the herbs and shrubs of the forest floor near Madang, New Guinea, occurs a species, *Pygatyphela* [nee *Luciola*] *obsoleta*, in which both sexes perch and flash their sexually distinctive soliloquies at length. After a long period of general introductions and overtures, females take flight and males chase them. In these flights males bump females as well as rival males as they fly short chases throughout the site. Upon landing, courtship (with dancing?) continues; some pairs remain coupled until the following evening. (**iii**) Synchronizing species of *Medeopteryx* in New Guinea gather in varying numbers in isolated trees and shrubs along waterways and

continued on page 178

Tidal mangrove/palm shoreline habitat along the Chao Phraya, south of Bangkok, in 1980.

Shrub/tree swarming platform with synchronizing fireflies on the Markham River at the bridge, near Lae, New Guinea, 1969.

A lone shrub with a few synchronizing fireflies by a small marsh on the Highlands Highway, near Goroka, New Guinea, 1969.

CHAPTER 35

Photuris floridana Fall 1927

Little is known about this firefly, but it appears much like *Ph. congener* in flashing and ecology. It is similar in coloration to *Ph. brunnipennis* in Cuba, and although Barber (1951) considered it a subspecies of *brunnipennis*, they are surely on their own separate evolutionary trajectories; in keeping with the general approach here, in appreciating and focusing on demes as the key unit of biodiversity, this firefly is again given species recognition. As to the more interesting question of its relationship with *congener*, their notable color difference—the very dark elytra and orange pronotum in *floridana* and drab dusky and fuscous appearance of *congener*—such color changes also occur at the southwestern margins of certain *Photinus*. During this study no special attention or evaluation of morphology was made to address this question, but instead *congener* and *floridana* (*brunnipennis*) were accepted as separate. One aspect of their biology should attract notice: *congener* has a rather restricted seasonal occurrence of adults at all latitudes (**Fig. 11**, in Chap. 24), while *floridana* adults have been collected in nearly every month in its limited latitudinal occurrence (**Fig. 1**).

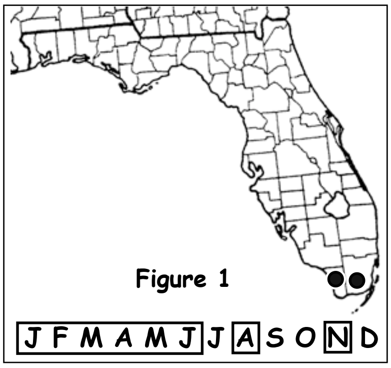


Figure 1

This firefly was seen in the field in the Everglades N. P., Dade County (1968, 1969), along a paved footpath leading to Royal Palm Hammock from the Anhinga Trail parking lot; and along the Pineland Trail near the Pine Key campground. It flew in numbers low over the ground amongst the palmettos. Flashes appeared much like those of *congener*, short sharp emissions at about half-second intervals at 19.3°/67°. In an apparent curious difference with *congener, floridana* often seemed to emit its flashes in groups of five. Males flying near each other often synchronized, as occasionally seen in *congener*. Many PM records were made and transcribed but apparently have been misfiled for later reference and not available at this writing. The similar FPs of *congener* and *frontalis* are shown (**Figs. 2 and 3**).

Notes on morphology and pronotal vittae are shown in the figures.

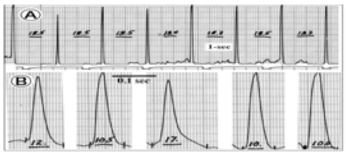


Figure 2. Flash train and flashes oif *Ph. frontalis* 19.4°/67°. (AX: rel. int./time).

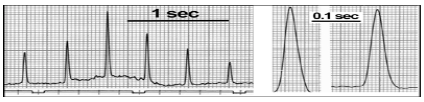
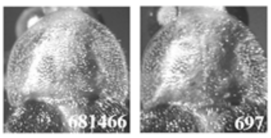


Figure 3. Flash train and flashes oif *Ph. congener* @ 21.8°/71.2°. (AX: rel. int./time).

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.479	8.893	3.143	1.764	2.179	0	11.364	.788	1.260	0
sd	.080	.489	.179	.134	.148	0	.512	.036	.075	0
se	.021	.131	.048	.036	.039	0	.137	.009618	.020	0
n	14	14	14	14	14	14	14	14	14	14
min	2.300	8.100	2.800	1.500	2.000	0	10.600	.710	1.130	0
max	2.600	9.500	3.500	1.900	2.400	0	12.100	.840	1.420	0
Vc%	3.2	5.6	5.7	7.6	6.8	0	4.5	4.6	6.0	0

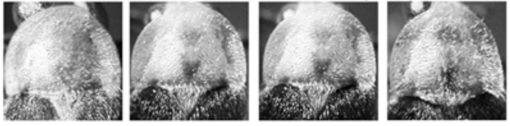
	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	2.429	1.571	1.000	1.000	1.214	2.071	2.643	3.000	1.571
sd	.514	.646	0.000	0.000	.426	.616	.497	0.000	1.399
se	.137	.173	0.000	0.000	.114	.165	.133	0.000	.374
n	14	14	14	14	14	14	14	14	14
min	2.000	1.000	1.000	1.000	1.000	1.000	2.000	3.000	0.000
max	3.000	3.000	1.000	1.000	2.000	3.000	3.000	3.000	3.000
Vc%	20.6	41.1	0	0	35.1	29.7	18.8	0	89.1

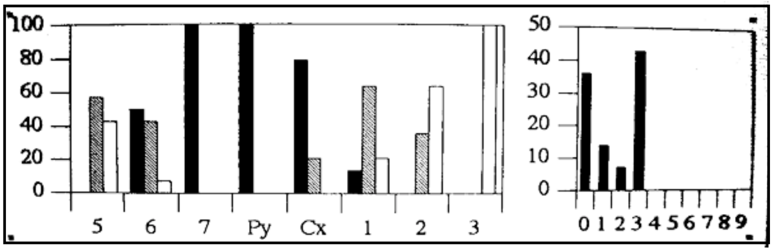
FLORIDA: Miami-Dade Co.

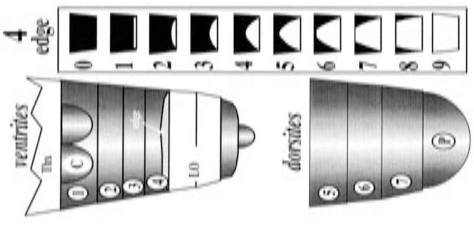


CUBA: Soledad (AMNH)

CUBA: Taco Taco (AMNH)







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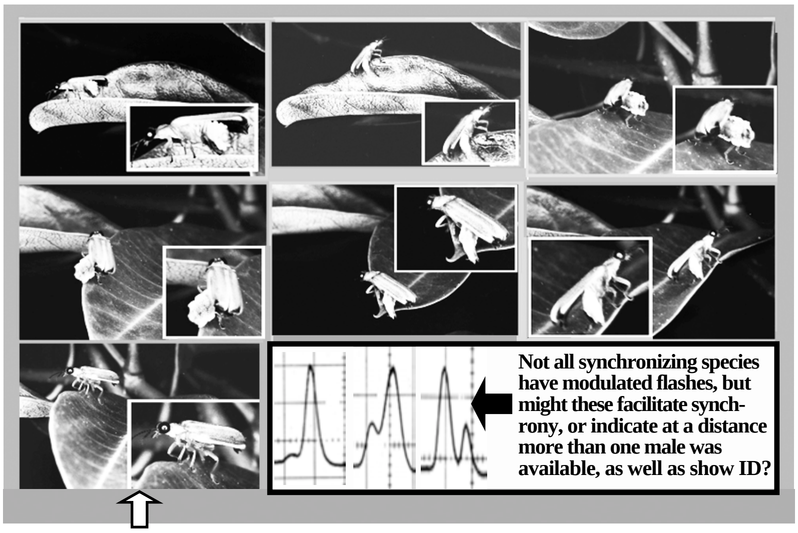
A broadcasting male *Pteroptyx valida* in a swarm shrub surrounded by Nippa Palms near Bangkok, aiming his lantern at something?

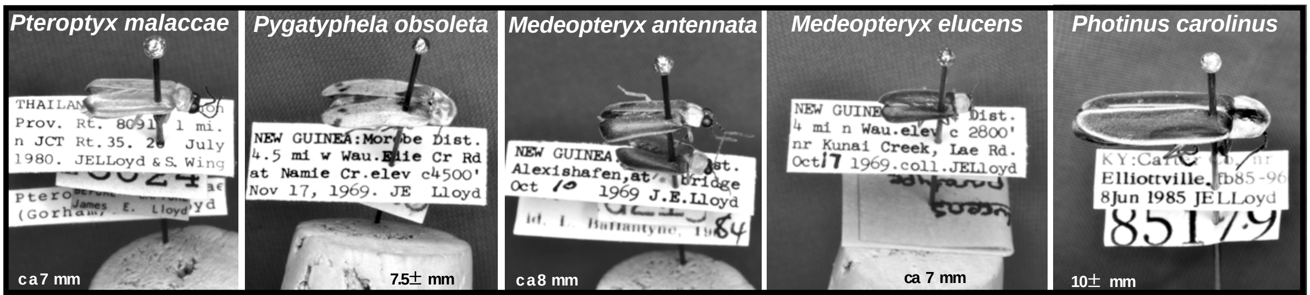


Not all synchronizing species have modulated flashes, but might these facilitate synchrony, or indicate at a distance more than one male was available, as well as show ID?

If *malaccae* males near Bangkok aim their lanterns in different directions as this *valida* male does, would they be protecting territories (leaves?) and warning nearby rivals, or facilitating their synchrony with him; surely a male would aim at incoming females. When females are not in the vicinity do males follow a time-based program in their aiming; do certain more troublesome neighbors get more of their attention?

sometimes in small groups in bushes at roadside marshes. From comparison of the above and other forms, some tentative conclusions may be drawn: Habitats that (**1**) produce large numbers of individuals of (**2**) species that encode species ID via flash rate, that (**3**) are able to perch without attacks from light-focusing predators, may/will form large sedentary swarms of synchronizing flashers.

In contrast, inflight flash synchrony of *Photinus carolinus* in the Appalachians arises from necessity and ancestry. In this species males patrol their habitat emitting their rate-coded flash phrases, finding/recognizing females via their delay-coded responses. Were they to flash from perches, attracting searching females to them, they would become targets for females of a number of *Photuris* species—*versicolor, tremulans, lucicrescens, forresti*, and others. Individual males synchronize their pulses with rivals flying near them, this (**i**) avoids disrupting the species-encoding pulse rate; (**ii**) may coordinate their female-delay-recognition-timer such that they will recognize a female flash-response from among the myriad of flashes occurring near them, including those of predators; and (**iii**) may increase the likelihood that an answering female will aim her lantern in their direction, on average putting rivals at a disadvantage. The ancestry of *carolinus*, as understood via the signals of others in their clade (Green's *ardens* Group) perhaps has "obligated them" to (**1**) emitting their pulses in phrases rather than in continuous trains, and (**2**) retaining a flash-delay-answer form of exchange rather than having the female response being an identifying unit in itself, that is, without a time reference to the male emission. (**3**) Note also, that the ancestral phrasing of pulses may provide/facilitate a number of countermeasures against predators. This suggests that a comparison of *carolinus* coding with that found in other members of the *consimilis* complex might provide insights into the *Photinus* nervous system. Note that *carolinus* also occurs in small populations, as along damp roadside ditches, and in such sites the "old" system works.



Fireflies in the text, and except for that of the "pocket of moonlight glower" from the Andes Mountains, are of archived specimens, and show data on the locality labels. Note that the *P. obsoleta* specimen is not from the studied coastal population, but from the highlands, some distance from the coast. Though in the tray it was similar enough for an extrordinariy talented and energetic taxonomist (Les Ballantyne) to pragmatically recognize as the same species, populations so disposed for the present may not have exchanged genes for centuries. Expectations?; see the brief discussion at the end of Chapter 6.

Chapter 36

Photuris forresti n. sp.

This firefly was found at a single site, a roadside, culvert-centered marsh in northwestern Pickens County, South Carolina, at the southern end of the Appalachian Mountains (**Figs. 1-3**). It is indistinguishable from *Photuris tremulans* in appearance and can only be identified by its FP, a series of 4-11 pulses (**Fig. 4**); this FP bears close resemblance to the FPs of members of the *Photinus ardens* group, noteworthy because *Photinus carolinus*, a member of the group, occurs widely and sometimes abundantly in the Appalachians; but note, *forresti* emits green and *carolinus* and kin, yellow or orange-yellow luminescence. These *Photinus* and *Ph. forresti* are marsh and low grassland inhabitants. Unexpectedly, when answered with an appropriately-flashed LED *forresti* males did **not** default but instead continued to emit the pulsing FP as they approached and landed—that is, their pulsing FP **was** their ID FP!, not merely an adjunct (s.s.) FP. This site was demolished by bulldozer three days after discovery (**Fig. 8**). On a subsequent visit to the region no *forresti* were seen where the marsh had been and no other population was found in the area. This loss was unfortunate not only because it harbored the only known population of this firefly, but because a few individuals of another extremely rare firefly, *Photinus acuminatus*, were found within 100 feet of the marsh (**Fig. 9**), perhaps indicating that this site might have had something further, ecologically, historically significant or unusual to reveal. The golf tee that replaced the site looks pretty much like tees seen elsewhere (**Fig. 13**).

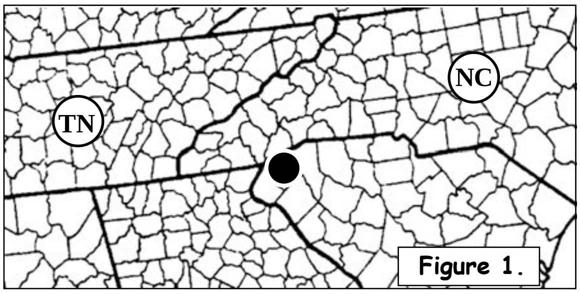


Figure 1.

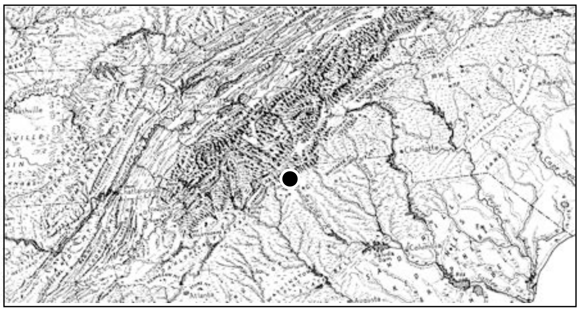


Figure 2. Physiographic perspective.

Figure 3. Site early in demolition; FPs hovering in columns sketched in.

Flashing behavior, ecology. Males began flashing from perches low within the marsh vegetation as early as 25 minutes after sunset (0.86 creps), and flying and flashing 41-52 minutes after sunset (1.4-1.8 creps, n=3). Flashing activity continued about 2.5 hours (n=2), ending before midnight. The FP was 4 to 11 flashes, emitted while males flew just above the marsh vegetation. While flashing they flew/hovered primarily in vertical columns, that is, up and down without appreciable lateral movement—obviously an adaptation for transmitting down into tall marsh grass—and then they probably wait a moment, to see responses back (up) through the same open space. Between FPs they moved laterally 6-8 feet. FPs were emitted at relatively long intervals, and a few counted *pauses* between them were 12-26 sec in duration (21°/70°). Males occasionally flew out of the marsh and over the adjacent dry land, but soon returned or flew and flashed along its margin.

PM-records of 8 patterns from 7 males show the following (**Fig. 4**): though flash (pulse) periods in each FP averaged 0.53 sec (1.9 Hz), the periods within an FP, period by period, were rather variable though generally trending shorter—that is, pulse rate tended to increase (**Fig. 5**). Note the simultaneous beginning of the terminal crescendo pulse following the OFF of the penultimate pulse (**Fig. 4B** arrow. Average pulse rate as measured from PM-recordings and train-timed (e. g., phrase duration/n periods) with a stopwatch, was similar to that of *Photinus carolinus*.

The form and duration of flashes within a pattern are also variable in most recorded patterns, as readily observed in clean recordings (**Fig. 4A**). At the beginning of the FP flashes are short (120-140 mSec) and more nearly symmetrical (**Fig. 4D**), but they gradually become longer with terminal (ultimate)

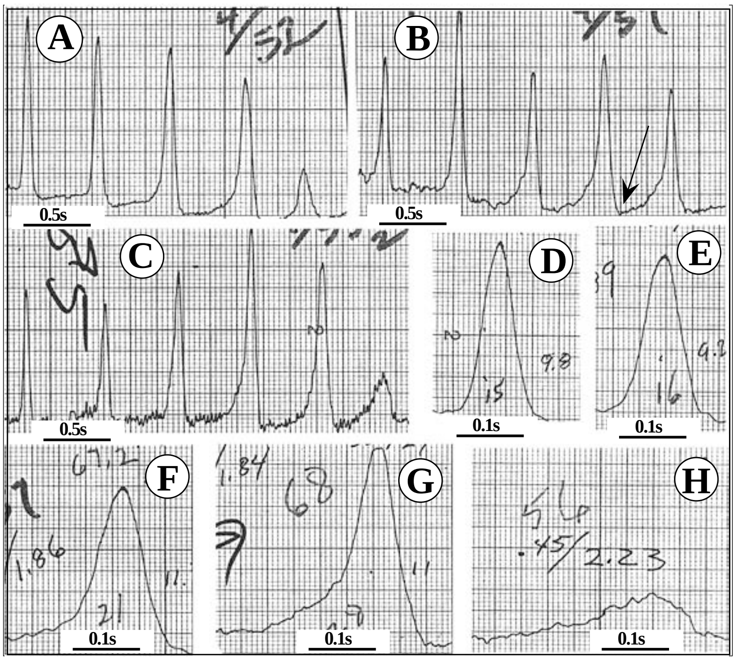


Figure 4. FPs and flashes; note changing shapes and acceleration.

flashes 280 mSec or longer, and distinctly a crescendo in form (**Figs. 4A, C**); the transition is somewhat gradual (**Figs. 4A**, **D-H**), and have a sharp OFF transient—perhaps suggesting a countermeasure connection? In the field the last flash is visibly different from the others, and notes, made before PM analysis, say that it appears longer, with a tail, and "not as sharp."

The unusual variation in pulse rate and duration may indicate the presence of an unknown and yet unimagined information coding system, with perhaps a different evolutionary origin of the neural mechanism that generates multiple-pulse FPs in this firefly—say, that it has evolved from an A-flicker, pulsed-glow mechanism rather than from the rapid repetition of independent, tightly-controlled single flashes (see below, **Fig. 7**). Perhaps, such a change was prologue and precursor to the sequence on the left side of the figure?

Decoying. Males were attracted to an answering LED that approximated the responses of female *Photinus carolinus*, and they did not switch (default) to another pattern in numerous experimental LED attractions. While the pulsing FP would appear to be this firefly’s identification FP, it is reasonable to expect variation among local isolates—and in doing so look for evidence that it has evolved from a what was once an *adjunct* FP, and specifically the A-flicker as used in *tremulans* (male mimicry FP).

When the flashpole LED emitted a short flash about one second after the last flash of a male's pattern, no response was observed and males continued their flight. When the LED was delayed about 4 seconds after the last flash of the FP, and then emitted 3 short flashes at about same rate of male FPs, males approached and landed within a few inches of the LED—this experimental response was suggested by the responses of females of the *Photinus consimilis*-group, and would seem a reasonable prediction of what to expect of *P. forresti* females—I think it doubtful that these males were drawn to such LED flashes from the ground because cruising males identified (i.e. neurally processed) them as female-approaching males, hence interloping opportunities.

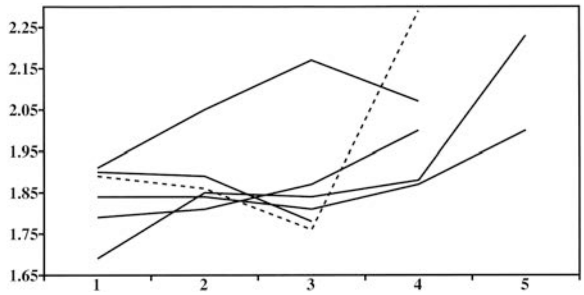


Figure 5. FPs in sequence accelerate (AX: Hz/position within FP sequence); see augmented legend.

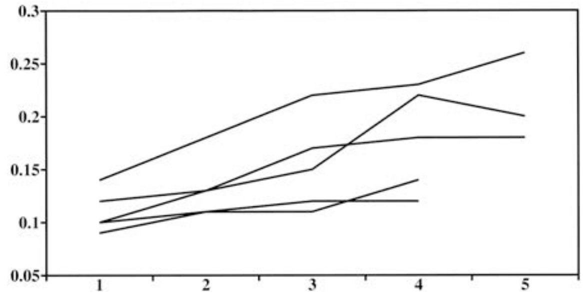


Figure 6. Durations of FPs in sequence—they get longer (seconds/position within in FP sequence; see augmented legend.

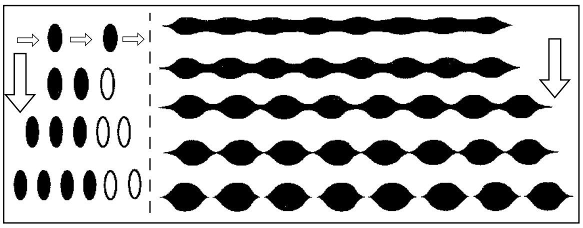


Figure 7. Evolutionry sequences to pulsed FPs from different beginnings; see augmented legend.

Phylogenetic considerations. It is important to emphasize that not once in LED-attraction experiments did males default *from* their pulsing FP (seeming a mimicry of the *Photinus carolinus* FP) to another (i.e., ID, own, default) FP, but instead they used this pulsing FP as their own and only FP. As a sketchy working notion: (**1**) perhaps *forresti* was separated from a *tremulans* ancestor in an isolated edge or cove of these mountains; (**2**) over long contact with and female predation on *carolinus* male pre-*forresti* evolved a mimicking pulsing FP from the A-flicker (**Fig. 7**); but (at first) continued to use the single short (ancestral *tremulans*-like) default FP when their *carolinus*-approaching, adjunct, mate-seeking FP was answered; then (**3**) upon subsequent contact with an abundant, wide-ranging, signal-competitor and/or predator, e. g. *"tremulans"* the pre-*forresti* abandoned their short-flash (default) FP and co-opted the pulsing FP as their own, avoiding contact, sexual or as prey, with *tremulans* females.

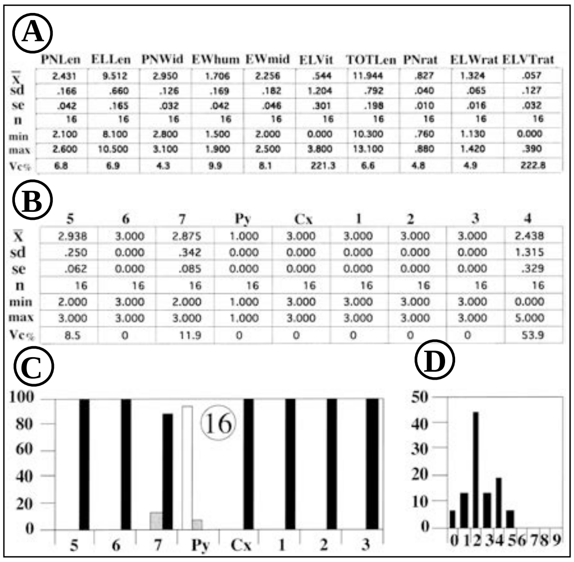
Barber's *Photuris tremulans* was active around one end of the marsh and across the road from the *forresti* site. On several/all LED-testing occasions, A-flickering (adjunct FP) *tremulans* defaulted to short flashes when answered by the LED decoy.

Morphological data; (FigTable. 10). General morphological means are (n=16): PNL 2.4, ELL 9.5, PNW 3.0, EWhum 1.7, EWmid 2.3, ELVit 0.54, TOTLen 11.9, PNrat 0.83, ELWrate 1.32, ELVTrat 0.06 (FigTab 10A, with other stats). Data for sclerite and other colors are shown in **Figure 10B-C**, and pre-lantern ventrite splash in **10D** (see **Fig. 12**). **Figure 12** is key to sclerites and splashing on ventrite 4. A range of vittagrams of *forresti* vouchers is shown in **Figure 11**.

Holotype Description. male, voucher 86165, collected 13 June 1986, Pickens County, South Carolina, Near JCT Rts. 11 and 175, by present golf course tee, at roadside culvert; site now obliterated. FB page 52: "KB 70 86165 pulsing 15' away over marsh. I counted [delayed] 4 sec and gave 3 pulses, and he came over, his next phrase was over the LED. I ans again and he again over @ few inches I netted. he gave 7-8 … his pause shorter when being attracted". Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.4, ELLen 8.8, PNWid 2.9, ELWhum 1.6, ELWmid 2.3, LELVit 0.0, TotLen 11.1, PnRat 0.83, ElRat 1.38, VitRat 0.0; Colors: T 333, Py 1, Cx 3, V 333, Edg 3. Types will be deposited in the USNM.

Figure 8. Site soon after bulldozing.

Figure 9. Site viewed from *Pn. acuminatus* locus.



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.431	9.512	2.950	1.706	2.256	.544	11.944	.827	1.324	.057
sd	.166	.660	.126	.169	.182	1.204	.792	.040	.065	.127
se	.042	.165	.032	.042	.046	.301	.198	.010	.016	.032
n	16	16	16	16	16	16	16	16	16	16
min	2.100	8.100	2.800	1.500	2.000	0.000	10.300	.760	1.130	0.000
max	2.600	10.500	3.100	1.900	2.500	3.800	13.100	.880	1.420	.390
Vc%	6.8	6.9	4.3	9.9	8.1	221.3	6.6	4.8	4.9	222.8

B

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	2.938	3.000	2.875	1.000	3.000	3.000	3.000	3.000	2.438
sd	.250	0.000	.342	0.000	0.000	0.000	0.000	0.000	1.315
se	.062	0.000	.085	0.000	0.000	0.000	0.000	0.000	.329
n	16	16	16	16	16	16	16	16	16
min	2.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	0.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	8.5	0	11.9	0	0	0	0	0	53.9

FigTable 10. Morphology, measurements, ratios, color.

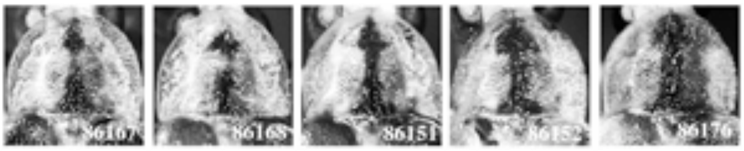


Figure 11. Array of selected vittagrams.

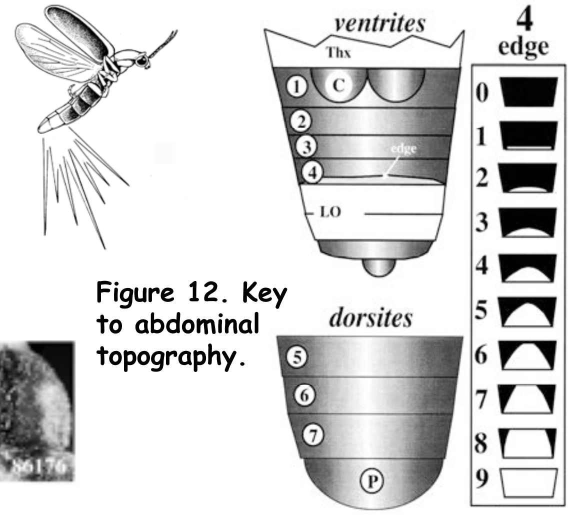


Figure 12. Key to abdominal topography.

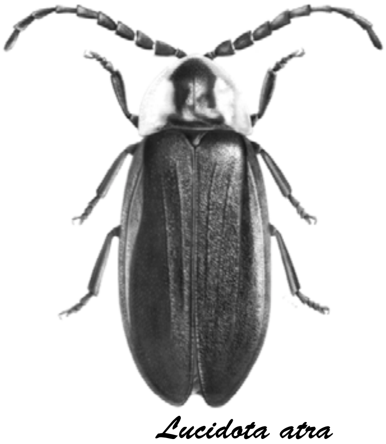
Figure 13. Site, May 2000, no fireflies.

Taxonomic notes. This site was near Table Rock State Park, which identified the area as the Sahkanaga region, which was said to mean the *Great Blue Hills of God*—I do not document nor test this assertion, but it is a grand place to look for a recently-discarded firefly.

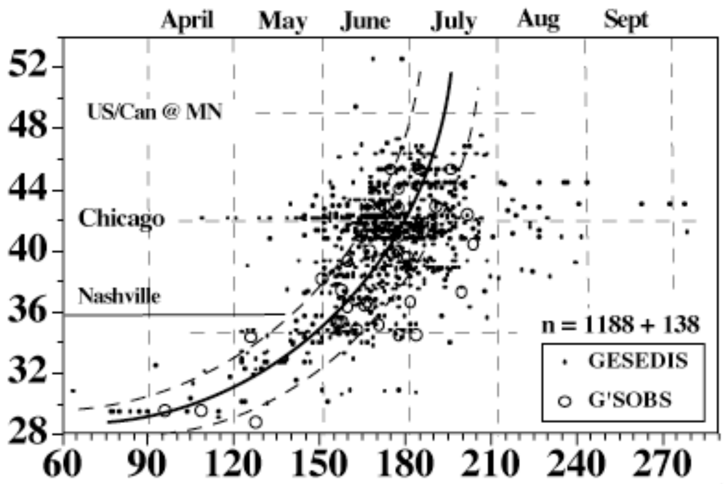
The scientific name of this firefly recognizes Timothy Forrest, long ago a UF PhD graduate, firefly enthusiast, acoustic insect naturalist and engineer, teacher, and department chairman; this patronymy intends to pressure him and his students in UNC at Asheville to rediscover and then examine the nature and evolutionary origin of the signals of *Photuris forresti*.

Augmented figure legends. 3. The *forresti* site near the intersection of Rts. 11 and 178. This photo was taken shortly after bulldozing had begun; a pile of pushed up stumps and habitat is at the lower right. **4**. PM-traces: (**A-C**) The terminal several flashes of three FPs showing duration variation among intervals and flash-forms within each FP, and the relatively larger change occurring in the ultimate and penultimate flashes; note that the OFF-time (pause) between pulses trends shorter through each FP, and that the ultimate pulse begins immediately at the end of the penultimate pulse (B arrow). **D-H**. Individual flashes selected from different FPs, showing the duration and form change that occurs through each FP. **5**. Rate changes during pulse sequences in FPs trend generally in an upward (faster) direction. X-axis numbers indicate the pulse sequence through the patterns of five males, beginning with the first *recorded* pulse, which is not necessarily the first pulse the male emitted—probably the second or third—only after I saw his first pulse and then could aim the PM. For instance, probably the line (dashed) for male 3 should end at pulse 5 not 4 (X-axis, pulse sequence; Y-axis, pulse rate). **6**. Pulse-duration generally increases through pulse sequences in FPs though reverses occur. **7**. Individual flashes in the multiple-pulse patterns of *Photinus* and *Photuris* are generally rather sharply defined. The FPs of species groups are easily compared and arranged in reasonable evolutionary sequences beginning with repeated 1-flash FPs and combining short series of them into multi-pulse patterns—e. g. the *Photinus consimilis* and *Photuris versicolor* groups (as left of dashed line). The sequence at the right suggests a different transition to a multi-pulse FP, arising from a different neural control mechanism, beginning with a modulated glow and then ever-increasing modulation separation, say with continued selection for distinct pulse-rate matching in the context of prey-FP mimicry. This of course probably does not explain in itself the crescendo flash-form of *forresti*, the fact that the pulses of this species are skewed and have rather sharp OFF transients. **8**. A poster for species loss? The remaining marsh at the moment this photo was taken is near the center. Though raucous the previous night, *Hyla crucifer* and *versicolor* were silent thereafter. **9**. Viewing the marsh site past the tree and herbs (left) where the rare *Photinus acuminatus* was active then gone.

Seasonal appearance of adult *Lucidota atra*, a daytime-dark firefly, showing an eye-fitted Lat/DOY curve rather than a 2-segmented line breaking at about 36° north latitude, as discussed on page 174.



Lucidota atra
by Laura Line



Chapter 37

Photuris frontalis LeConte 1852

Flashing of this firefly appears similar to that *Ph. congener*, with two notable differences: males are seen higher into the foliage of trees, especially later in the evening; and they apparently synchronize their flashes more commonly/readily than *congener*. David Lee described synchronizing (1990). LeConte named both fireflies but later considered them under one name; Barber correctly recognized both. Distributions of the two are contiguous along/near the Florida-Georgia border and perhaps they hybridize there (**Fig. 1**); but FP periods are different with those of *frontalis* being longer (**Fig. 2**). Rates are compared in **Figure 3**. Note in **Figure 5** that the exponential model fits the *frontalis* data slightly better than the linear model as would be expected from experience with other species. Field notes are few but data are several and the following deals almost exclusively with these data and their figures. Seasonal distribution of *frontalis* is shown in **Figures 4**, and shown with that of *congener* in **Figure 6.** **Figure 7** shows a *frontalis* flash train and variation among individual flashes of the train. For **Figures 9-12** see legends.

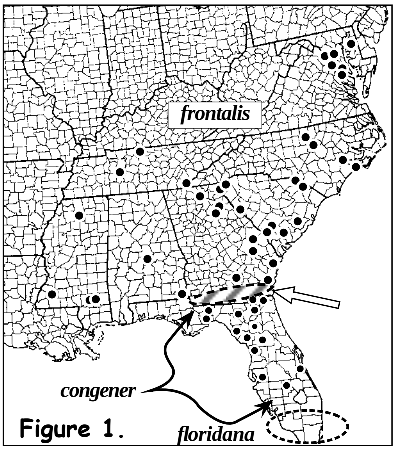


Figure 1.


Carbon dust by Laura Line.

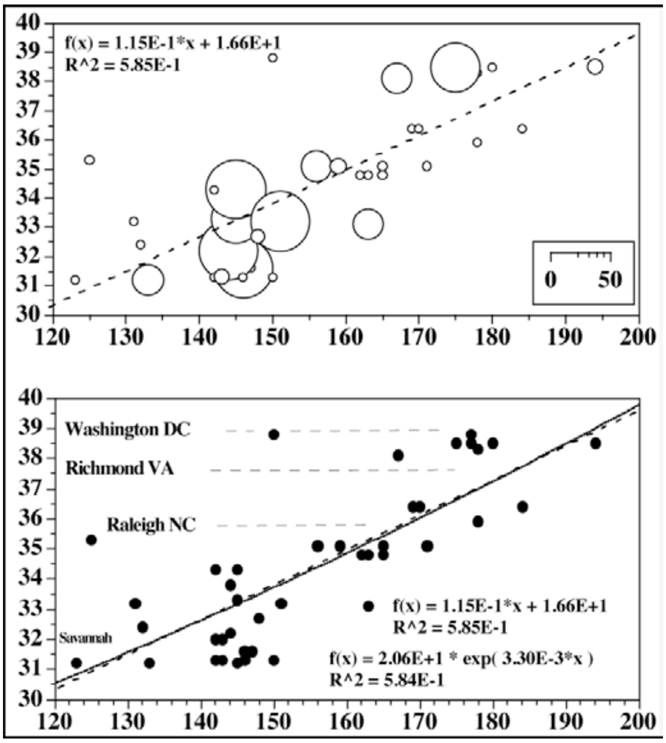


Figure 4. Seasonal distribution, G'SOBS, GESEDIS (AX: Lat/DOY).

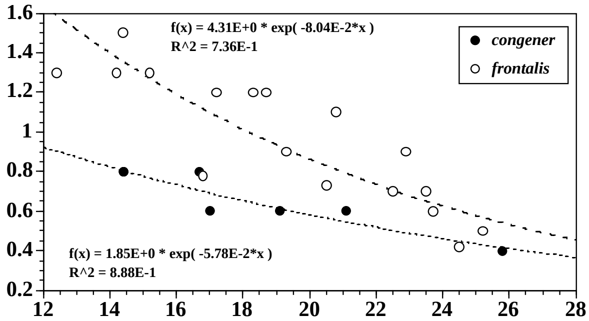


Figure 2. FP periods compared (AX: sec/temp).

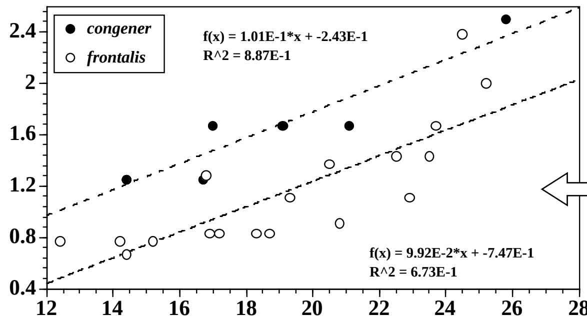
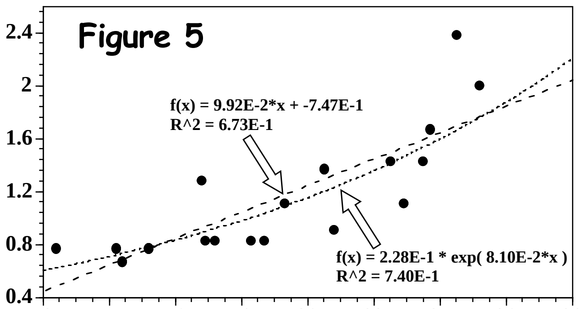


Figure 3. FP rates compared (AX: Hz/temp).



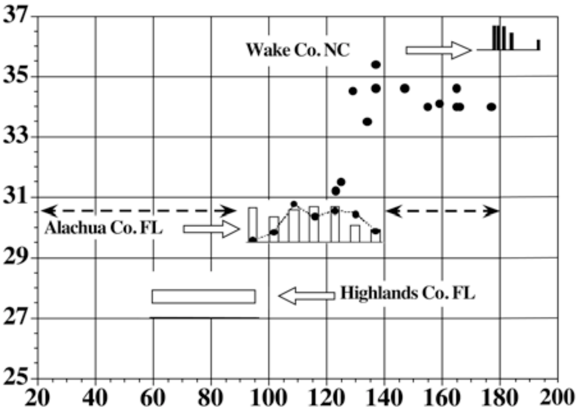


Figure 6. Three-way combination: SESOBS and GESEDIS: *frontalis* above dashed arrows (FL/GA border), *congener* below. NC SESOBS from David Lee (AX: Lat/DOY).

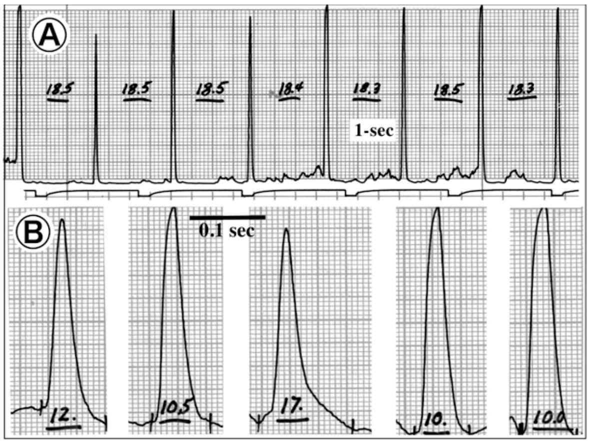


Figure 7. PM, (A) train, (B) variation among flashes in train, 19.4°/ 67° (AX: rel. int./time).

	$\bar{x}$	@ half max's	n
angustata	552	529-601	3/14*
ecostata	558	533-602	1/6*
eureka	555	521-598	1/6*
other *Pyrac.*	573.8	546-613	8/13/69**
most *Photur.*	554.6	528.4-597.1	±29/55/318**
Ph. frontalis	570	539-619	3/13*

Figure 8 .Comparison of bioluminescence spectra.

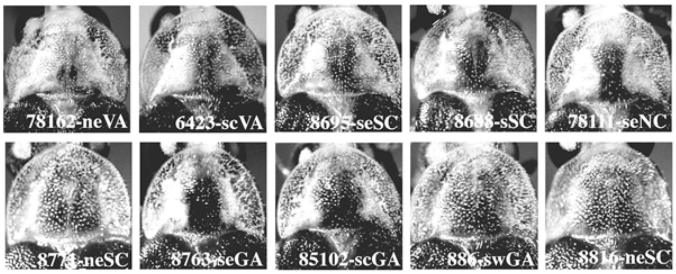
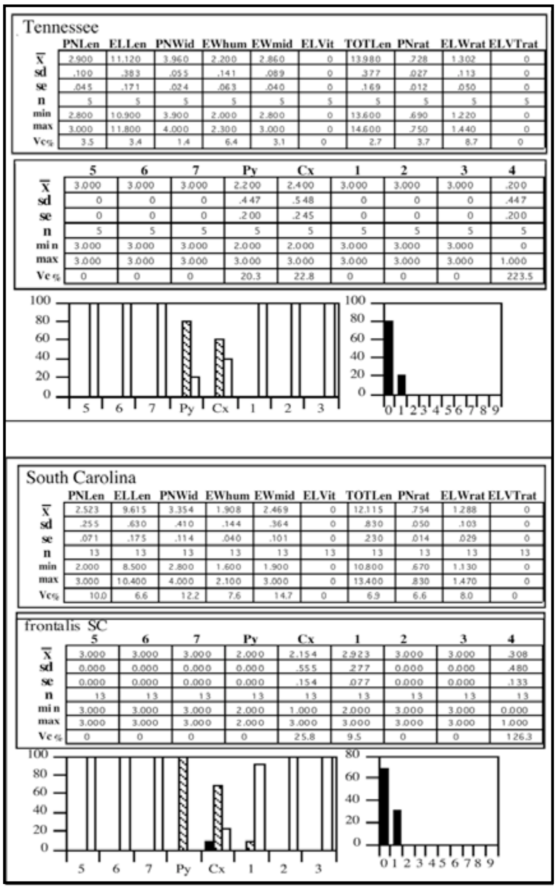


Figure 9. Pronota of *frontalis* from various regions, as noted on PN.

Figure 10. *Ph. frontalis* flashes in NC woodland; B&W conversion from color by David Lee (1990).

Figure 11. LeConte "type"; Barber's 2X voucher.



Tennessee

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.900	11.120	3.960	2.200	2.860	0	13.980	.728	1.302	0
sd	.100	.383	.055	.141	.089	0	.377	.027	.113	0
se	.045	.171	.024	.063	.040	0	.169	.012	.050	0
n	5	5	5	5	5	5	5	5	5	5
min	2.800	10.900	3.900	2.000	2.800	0	13.600	.690	1.220	0
max	3.000	11.800	4.000	2.300	3.000	0	14.600	.750	1.440	0
Vc%	3.5	3.4	1.4	6.4	3.1	0	2.7	3.7	8.7	0

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	3.000	2.200	2.400	3.000	3.000	3.000	.200
sd	0	0	0	.447	.548	0	0	0	.447
se	0	0	0	.200	.245	0	0	0	.200
n	5	5	5	5	5	5	5	5	5
min	3.000	3.000	3.000	2.000	2.000	3.000	3.000	3.000	0
max	3.000	3.000	3.000	3.000	3.000	3.000	3.000	3.000	1.000
Vc%	0	0	0	20.3	22.8	0	0	0	223.5

South Carolina

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.523	9.615	3.354	1.908	2.469	0	12.115	.754	1.288	0
sd	.255	.630	.410	.144	.364	0	.830	.050	.103	0
se	.071	.175	.114	.040	.101	0	.230	.014	.029	0
n	13	13	13	13	13	13	13	13	13	13
min	2.000	8.500	2.800	1.600	1.900	0	10.800	.670	1.130	0
max	3.000	10.400	4.000	2.100	3.000	0	13.400	.830	1.470	0
Vc%	10.0	6.6	12.2	7.6	14.7	0	6.9	6.6	8.0	0

frontalis SC

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	3.000	2.000	2.154	2.923	3.000	3.000	.308
sd	0.000	0.000	0.000	0.000	.555	.277	0.000	0.000	.480
se	0.000	0.000	0.000	0.000	.154	.077	0.000	0.000	.133
n	13	13	13	13	13	13	13	13	13
min	3.000	3.000	3.000	2.000	1.000	2.000	3.000	3.000	0.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	1.000
Vc%	0	0	0	0	25.8	9.5	0	0	126.3

FigTable 12 . Comparative measurements: SC, Berkeley, Dillon, Pickens; TN, Dixson, Polk, Sumner.

Chapter 38

Photuris gentrae n. sp.

Lesser Texas-Red Firefly

This description is based on few observations and data. *P. gentrae* can be recognized in its range by its apparent rather long “short” flash delivered continuously at about two second intervals, which may resemble that of Texas’ *Photinus stellaris* and Florida’s *collustrans*, though males flew higher. It may occur only in a limited area of Texas, and perhaps only along or near water (**Fig. 1**); in hand it is most easily confused with the much larger Texas-Red, *katrinae*.

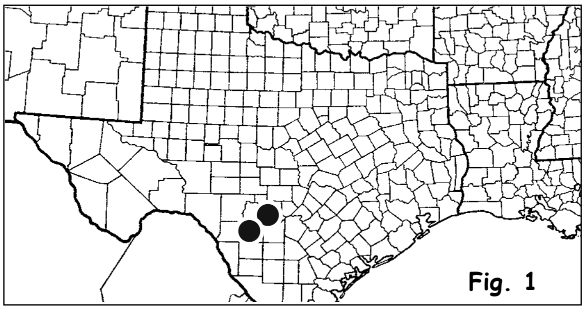


Fig. 1

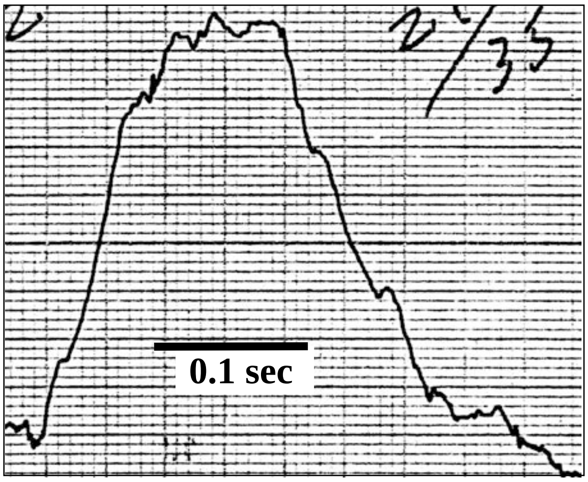


Fig. 2. One of four PM recorded.

This firefly was observed along the Nueces and Sabinal Rivers in the hill country of Texas, and as with other lampyrids in the region, it could be exclusively riparian, or at least confined to the immediate vicinity of water. Two males were seen flying at grass-top in a field just above the Nueces River at a bridge north of Uvalde, only briefly, moments before they were blown into the tall grass by a stiff breeze. Another was seen cruising downstream over the Sabinal River at an altitude of about 10 feet, and two others as they passed around the crown of a tree on this river at about 12 feet altitude, as they apparently followed it downstream.

The observed FP was a single ≈0.3-sec flash emitted during rapid and level flight. In one instance a slight twinkle or blink was noted. Flash pattern period ranged 1.8-2.8 sec, n=2 males, 5 FPs; ≈26°/79°). Four flashes of one male were recorded (male not captured) under difficult moonlit conditions, and were shorter than visual appearance had suggested. The two best PM-records, not vouchered, show an asymmetrical flash with a more rapid rise which then slows, and after peaking decays gradually to termination (**Fig. 2**). Base duration is about 280 mSec, and half-max ≈166. Main season of adult appearance may be June, since the few individuals observed in July appeared to have been stragglers(?).

Holotype description male, voucher number 9290, collected 6 July 1992, Uvalde County, Texas, 22 miles north of Uvalde, 3 miles south Montell at Nueces River bridge. FB page 79: One of two, collected after emitting arced FP (like *collustrans*), only saw two consecutive flashes as wind seems to have blown down into grass. Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.8, ELLen 10.3, PNWid 3.5, ELWhum 1.6, ELWmid 2.4, LELVit 6.5, TotLen 13.0, PnRat 0.79, ElRat 1.46, VitRat 0.63; Colors: T 332, Py 2, Cx 2, V 333, Edg 4. The Holotype will be deposited in the USNM.

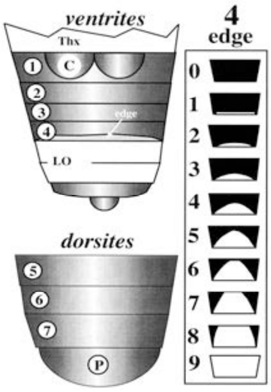
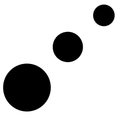


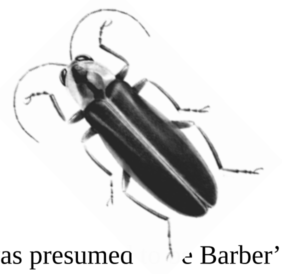
Figure 3. Topography and splash key.

Miscellaneous notes. The specific epithet recognizes my former student Erin Gentry, who now teaches in England, for her extensive and outstanding Masters research on *Pyractomena borealis*, which was equivalent to and indeed worthy of a PhD degree. The suggested common name notes the brick-red trim-color found in others of the working Red-Group, and size, relative to that of Texas Red (*katrinae*). A second specimen, a designated Paratype, voucher number 9289, was collected with the Holotype.

Aggressive mimicry by firefly femme fatales at the old UF Med Garden, Page 1. *Photuris* females prey on other fireflies. These females are the JAWS of Western Hemisphere firefly ecology: (1) They mimic the mating signals of females of other species, attract males of these other species, and eat them; (2) they attack light-emitting fireflies in the air, using their prey's emitted light as a target, like a sidewinder missile using the engine heat of an aircraft or a sidewinder snake using the heat of a mouse to focus and attack; (3) they may even remain near females of prey species and attack males that are attracted to them; females of large species perhaps exploit or attack the predaceous females of smaller species; and so on. Many years ago a UF undergraduate entomology student, Mike Sipe, placed several blinking LEDs in a large cube of clear (bio)plastic, with batteries—for art and philosophical reasons—in the field and it attracted *Photuris*. These females are even known to enter the webs of spiders to steal prey (Barber, 1951; Faust et al, 2013). That *Photuris* females eat firefly males has been known since early in the 20th century, but it was Barber who first was suspicious that aggressive signal mimicry might occur. Once it was discovered by Tom Eisner and colleagues that these females obtain protective chemicals from *Photinus* prey it was generally assumed that these chemicals were the primary explanation for this predation, though it was easily determined that in the lab they would even each a cockroach. It is now obvious from the fireflies these females have been found eating in the field, that more than protective lucibufagens feed this practice, and that other nutritional elements are also important. Aggressive signal mimicry in known to occur in the three described genera of the Subfamily Photurinae: *Bicellonycha*, *Crematogaster*, and *Photuris*. In addition, a ~wasp-colored female of an undescribed genus in the Colombian Andies was observed attracting a *Photinus* male of an undescribed species—he had a *Photinus macdermotti*-like FP, but is unrelated. In the photos here, together comprising a picture book for the morbidly curious, females of at least three *Photuris* species in the Med Garden (*harrannorum*, *lamarcki*, *stanleyi*) are shown eating males of three genera, *Photinus*, *Pyractomena*, and *Photuris*; some were certainly captured by signal mimicry, but others were probably from incidental ground stalking and the exploitation of flashers in other contexts. (see also special index in Table Of Contents, page viii)


Incidental Encounters





Chapter 39

Photuris harrannorum n. sp.

Florida Versi (J-3-4)

This firefly is known to occur only in Florida (**Fig. 1**). During early years of study it was presumed e Barber's *versicolor* because its FP repertoire appeared to closely match that described and illustrated by him and McDermott (see discussion in *Ph. quadrifulgens*). However, after some experience and extended field work in the Potomac/Chesapeake region (Barber's bailiwick), and elsewhere on the North American continent, it was clear that the repertoires of Florida and continental *versicolor* differed significantly. Florida Versi is most often seen singly, emitting a "jagged flicker" of 3-4 pulses of decreasing intensity (**Fig. 2A**), though when several males occur together, say above woodland canopies (**Fig. 3**), 4-6 pulse FPs are emitted. Florida Versi virtually never emits FPs with pulses of equal intensity (**Fig. 2B)**—seen only on one or two occasions in more than 40 years of field work. But such FPs are frequently emitted by *versicolor* on the continent and are a conspicuous element of its repertoire (**Fig. 4**). The significance of this particular configuration is unknown. Geographic connection between the two variads was sought briefly. FPs characteristic of the continental *versicolor* were observed in Leon Co. in Florida, and in Thomas Co., Georgia, just north of the Florida/ Georgia line (**Fig. 1**, circles). This species pair is one of several that seems for the moment to "match-up" across a FL/GA frontier. Perhaps it was a barrier that according to some geologists and paleontologists was a broad stream of running sea water (Suwannee Straits) between the Gulf and the Atlantic (Webb, 1990). Unlike *versicolor*, *harrannorum* was never seen flying in numbers over grassy meadows and fields; instead, it was always one or few in number and associated with tree-dominated habitats, mesic forests, groves, and "gallery" treetops along roads and power-lines (**Figs. below**)—perhaps where more moist soil conditions exist.

Florida Versi has spring and late-summer broods—lab-reared eggs from spring females matured to adults in late summer (pers. comm., D. Minnick, ca. 1970).

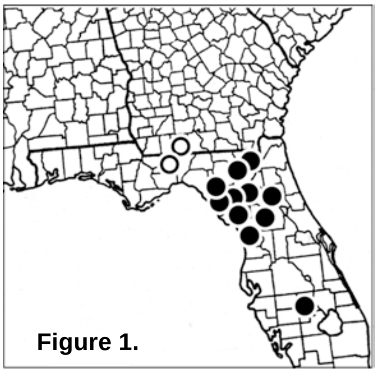


Figure 1.

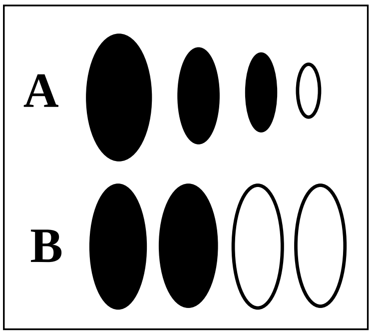


Figure 2. (A) step-down pulses(J-3-4); (B) even-intensity.

Figure 3. Wooded site with J-4-6 FPs (ellipse).

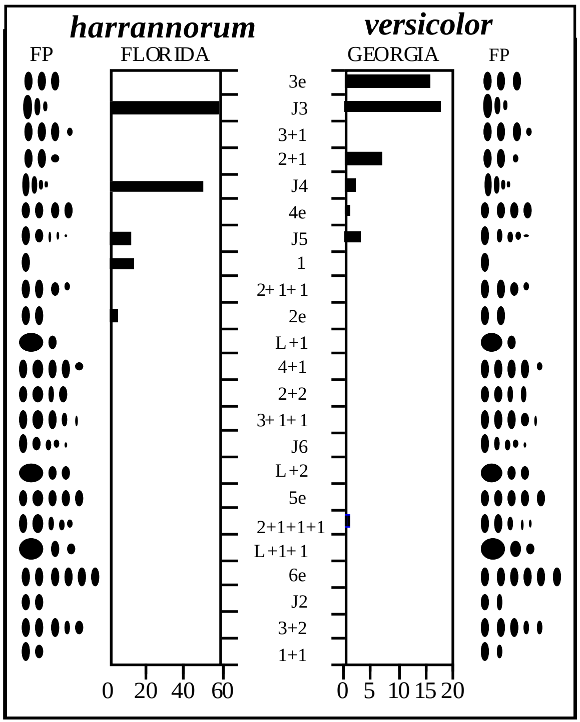


Figure 4. FP frequency comparison, based on non-systematic scattered notes in fieldbooks.

Males of the spring brood emit an adjunct FP, a single short flash which matches the FP of co-active *Pyractomena limbicollis*, except for color (**Fig. 5). Figure 15** shows a site where adults of both occurred—a preserved *Scenic* roadway. **Figure 6** juxtaposes SESOBS records of the two, and their spring coexistence—*limbicollis* adults appear only in spring; late-summer Versi have never been seen to use a short flash. However, more thorough observations on this firefly may reveal other adjunct FPs: experiments with free *harrannorum* females and observed prey are indicative (several jel refs). Other J-3-4 SESOBS records in **Figure 29**.

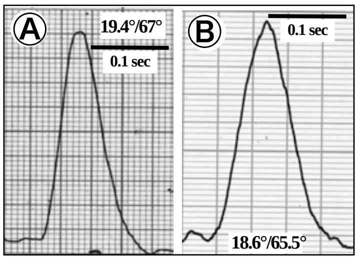


Fig. 5. Single flashes of (A) *harrannorum* and (B) *limbicollis* (probable) (AX: ri/time).

When answered with a decoy, short-flashing males of *harrannorum* default to their J-3-4 FP—a behavior discovered in this species on the same evening at a different site by Tim and Susan Forrest. [Curiously, "distractingly?," *limbicollis* "might almost" appear to promote the seasonal co-existence. Unlike *Py. borealis*, which in the same habitat pupates "high" on the southern (sunny) exposure of large trees, which will accelerate development (**Fig. 7**), *limbicollis* pupates near the ground (a "cold sink") on the north-facing perimeters of small shrubs and trees (jel, 1997). *Py. borealis* adults appear earlier in the spring than do *harrannorum*, which pupates in the cold, post-winter, woodland soil. For *limbicollis*, perhaps, the avoidance of larval competition for prey with those of *borealis* trumps adult security?]

Individual *harrannorum* females, so it would appear, range widely, and hunt, mate, and distribute eggs among several suitable larva-nurturing and hunting sites. Such scattered habitats are presumably the targets of the often-seen roving males as they seek females, those ready to mate, via the default FP, and those found via prey FP mimicry.

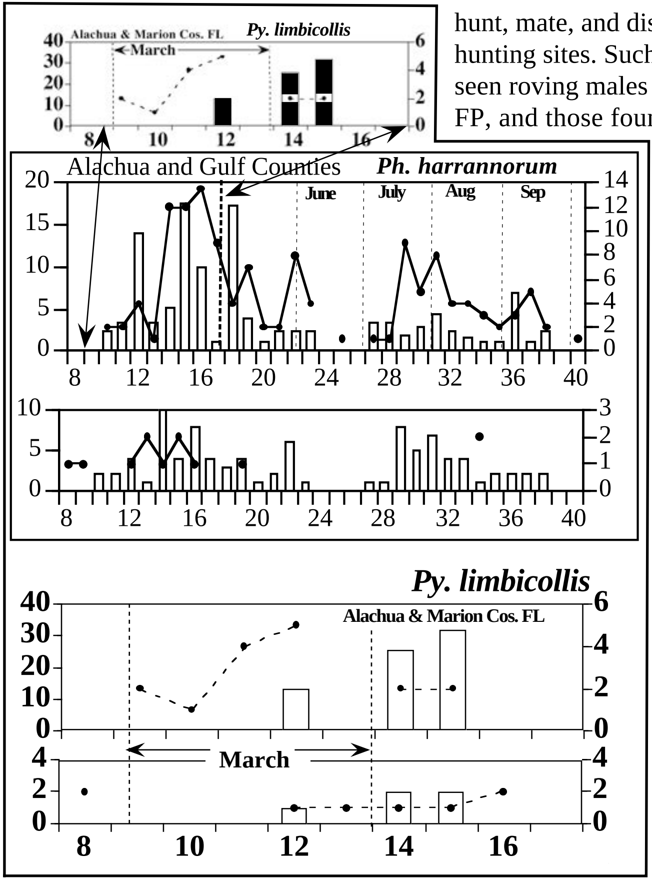


Figure 6. SESOBS for *harrannorum* and *Py. limbicollis* as indicated. Note WOY scale, and miniature with allignment arrows (at top).

The FP of *harrannorum* (**Fig. 8**) will not be confused with that of any other firefly on the Florida peninsula. At warm temperatures this down-stepped FP has a ragged/ jagged appearance (hence the original nickname (Jagged-3-4), with pulses presented too rapidly to be counted or seen distinctly. To the eye, they sometimes *appear in space* to run backwards, and to begin with a dim flash and increase in intensity, but no PM-record ever demonstrated this to actually occur. Although FPs often appear to have four pulses, as noted in fieldbooks, PM-records reveal only three, with one exception (**Fig. 9**).

A sample of PM flash widths at base and half max for 3-pulse FPs at 17°, measured roughly 140/80, 100/60, and 70/50 mSec. Luminescence spectrum measurements averaged 554 mm at peak with 527.5 and 597 at half max, in two samples of 1 and 7 specimens, June 1967 and April 1978 (B. Biggley and H. Seliger, at Johns Hopkins).

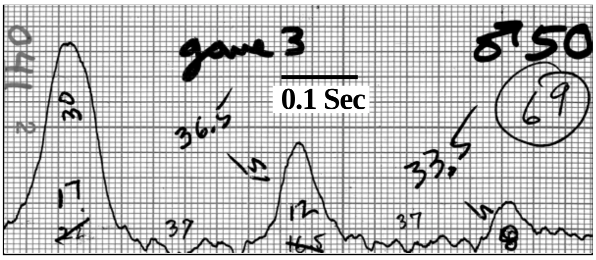


Figure 8. Jagged-3-4 FP at 16.7°/62° (AX:rel inten/time).

Figure 7. Understory of a hardwood swamp forest, the Possum Creek site in Gainesville, where *Py. borealis* and *limbicollis* pupated on tree-trunks, *borealis* adults appearing earlier in spring before those of *Ph. harrannorum*—position matters? See text, ref..

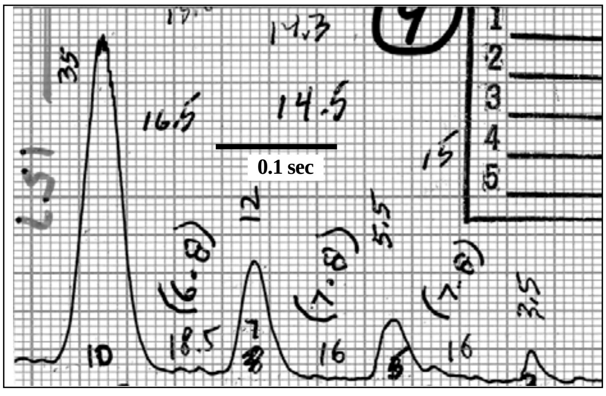


Figure 9. A rare(?) 4-pulse FP, at 24.4°/76° (AX:rel inten/time).

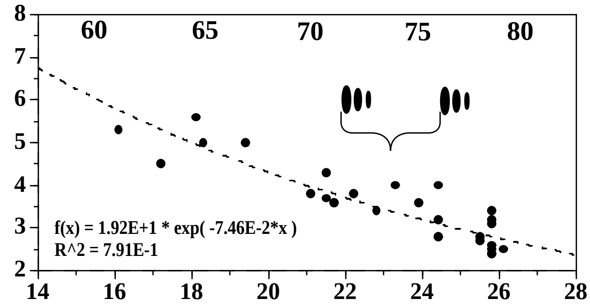


Figure 10. J-3-4-flicker FP period (AX: sec/temp).

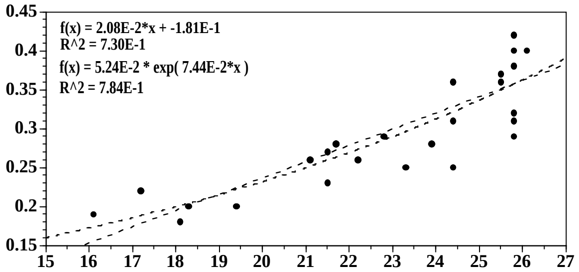


Figure 11. J-3-4-flicker FP rate (1/period ; AX: Hz/temp).

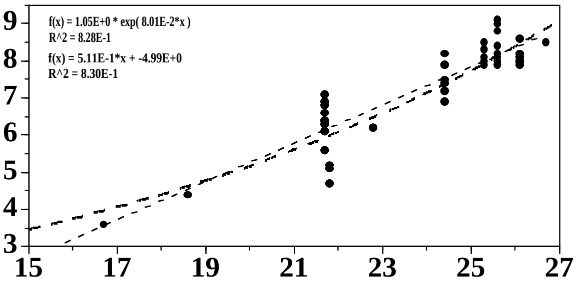


Figure 12. J-3-4-flicker pulse rate (AX: Hz/temp).

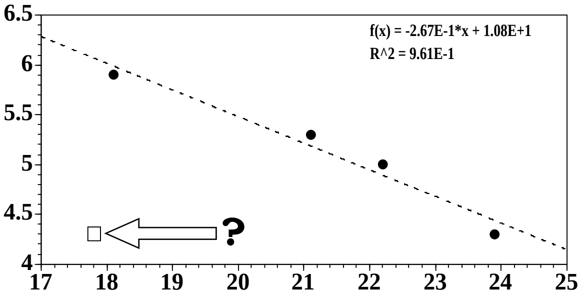


Figure 13. Short-flash FP period (AX: sec/temp).

The FP period of the diagnostic J-3-4 averages about 4 sec at 21°/70° (**Fig. 10**), rate in **Fig. 11**). Pulse rate in the J-3-4 FP is about 6 Hertz at 22°/71.6° a common spring viewing temperature (**Fig. 12)**. The short flash (spring adjunct FP) period is perhaps as plotted in **Figure 13**, but possibly other periods are used, say ≈2 sec, when seeking *macdermotti*-hunting females; note the non-conforming measurement in the figure.

Mate-seeking males of many species detect the approaches of other/rival males to FP-answering flashes, including simulations by decoys. Observe **Figure 14**: A *harrannorum* male detected the approach of a flashing prey-species (*Pn. macdermotti*) male to an answering flash, and approached the responding decoy. He then emitted his default J-3-4 FP (**H**); an "attempt" (s.l.) to switch a hunting female (the decoy) to a mating mode. Barber perhaps unknowingly witnessed the same thing (page 275 E). Observations of such interactions may provide clues to the initiation/beginnings and evolution of some of the complex signals and sequences observed in *Photuris*.

Incidental notes on ecology, flashes, hunting. Observations were made along highways less traveled (**Fig. 15**), a woodland drive (**Fig. 16**), a small second-growth mesic hammock next to a pine woods and a power-line right-of-way (**Fig. 17),** and a tiny woodland remnant (**Fig. 18**). Males could easily be attracted to a penlight or flashpole decoy from distances approaching 100 feet, but sometimes inexplicably were totally unresponsive. Decoy attraction made PM-recording simple, because the PM-tube had direct light from (normal to) the lantern; there was never evidence that these FPs were different from recordings of roving (not being attracted) males.

As to actual pulse numbers in the J-flicker FPs, as a case in point, the FP of this firefly was referred to as the Jagged-3-4 for decades because it often appeared to have four step-down pulses. In going through more than 100 PM-records of more than 50 individuals, only one 4-pulse FP was found (**Fig. 9**), the rest being 3-pulsers. Likewise, it must be presumed that visual observations of 4-5-6-pulse FPs, so far only noted when several males were seen together (competing for signal time) at the treetops, may also be off the mark.

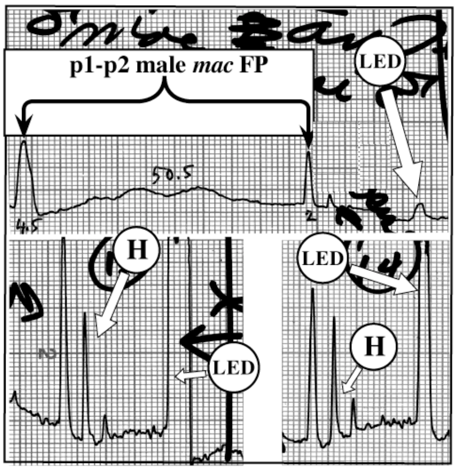


Figure 14. Male intruding on a setup, (AX:ri/time; see text.

Among the recognizable flashes seen at a *harrannorum* site were those emitted by females. First, they are the source of distinctive landing and take-off flashes seen along roadsides—those of *Ph. douglasae* are shown (**Fig. 19**). On some evenings a dozen or more Versi J-3-4 could be seen as they approached the ground, beginning about a half-hour after male flashing flight began, as they descended from treetops, presumably having just mated there. Second, female *harrannorum* were commonly found hunting, via aggressive mimicry, from low vegetation along roadsides, into fields along tree rows, in groves and woodland glades, and at sites with active populations of various species. They are often most responsive to penlight simulations of the *Photinus macdermotti* FP, two short flashes with an interval of about two seconds.

The first really conclusive evidence of aggressive mimicry in fireflies began with *harrannorum* by a little stream in a low mesic woods in northern Gainesville (**Fig. 20**). (It was 1964, and the concept of aggressive mimicry in any organism other than humans was being discounted by some, including a professor of personal consequence.) A few years later, in the Med Garden on the UF campus another *harrannorum* female demonstrated the presumptive origin of different attack tactic of her kin, the hawking strike, that is so highly developed in *Ph. lamarcki* and *beanii*. A perched *harrannorum* female was being filmed by John Paling as she answered a flashpole decoy being "flown" in front of her; apparently, "impatience got the better of her" (s.l.), and she attacked the LED in the air! Barber would have truly been amazed at what some UF Entomology graduate students (W. Prince, T. Forrest, J. Sivinski, S. Wing) discovered long ago just east of Ocala—*lamarcki* males flashed their FPs from tall perches and their females attacked "anything" that flew! How can a deme escape?

Individual *Ph. harranni* females are able to mimic the flashes of females of more than one *Photinus* species, and their hunting behavior suggests the existence of at least four (by old-fashion characterization/ classification) types of learning; it has also been responsible for the evolution of a *Lady and the Tiger* lekking system in *Pn. macdermotti* (s.s.) where rivals compete simultaneously, lie about everything, winners find a conspecific mate or escape(?), and losers get eaten—if not by getting too close to a green-flashing respondent, by a J-3-4 tiger or others prowling darkly in false security amongst the arena's herbs and grasses (jel 1981).

Figure 15. Newnans Lake Drive (Lake Shore Drive), a preserved Scenic roadway east of Gainesville. A site where *harrannorum* occurs with *Py limbicollis,* and one month later *Pn. collustrans* flies at twilight.

Figure 16. YMCA Camp, J-3-4 hunting site—with a place for luminous earthworms in the middle.

Figure 17. The gunclub site near the Regional Airport.

Female *Ph. harrannorum* with male *Pn. tanytoxus*.

Figure 18. A tiny woodland remnant, with hunters.

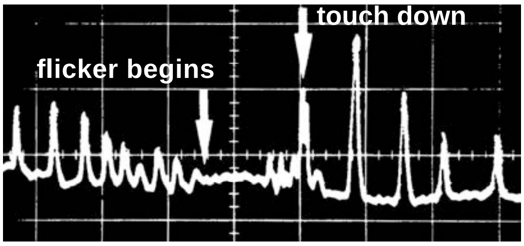


Figure 19. Flashes and flicker-flashes of a landing *douglasae* female. After landing, a few bright pulses—then dark.

Figure 20. Tiny woodland sand-bottom creek in northwest Gainesville where the first complete sequence of aggressive mimicry and hunting success was seen, 1964. The arrow marks the spot. The female attracted and ate a male *Pn. macdermotti.*

Figure 21. Campfire clearing where during the firefly-class camping weekend occasionally a roving J-3-4 male passed overhead or circled around the surrounding treetops.

Figure 22. Med Garden site on UF campus, looking north through the grove where J-3-4 females hunted. The arrow marks the location of the photo of female and prey shown above..

❊ ❊ ❊

Morphology. *Ph. harrannorum* specimens are, with some uncertainty, distinguishable from other Florida *Photuris* by a combination of characters: black elytra; completely dark, glossy (piceous) hind coxae; somewhat characteristic pronotal vittagram; yellowish rather than rufus-tawny base/trim-coloration; and rather large size (11-14 mm). Though *harrannorum* is sometimes completely without elytral vittae, on average these end posteriorly (from humerus) about one-third the length of its elytron. This firefly is morphologically perhaps most likely to be confused with species in the *Ph. lineaticollis* Group, and in particular with Giant Red (*lineaticollis* s.s.), which is larger (a sometimes "imposing" often robust 12.3-15.8 mm), with a rufus-tawny base-coloration ("trim"), and generally without elytral vittae. *Ph. stanleyi* is slightly smaller, more "delicate," and has pale hind coxae; *P. eureka* occurs along the nw peninsular Gulf coast and the Mallory Swamp area, is larger and is seasonally much earlier, and rare/gone since 1990.

harranni MG

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.727	9.853	3.433	1.947	2.460	2.853	12.567	.801	1.267	.293
sd	.162	.487	.191	.106	.176	1.940	.572	.020	.082	.201
se	.042	.126	.049	.027	.046	.501	.148	5.207E-3	.021	.052
n	15	15	15	15	15	15	15	15	15	15
min	2.500	9.000	3.100	1.800	2.100	0	11.600	.770	1.130	0
max	3.000	10.600	3.800	2.100	2.800	5.000	13.500	.840	1.430	.530
Vc%	5.9	4.9	5.6	5.4	7.2	68.0	4.6	2.5	6.5	68.6

FigTable 23. Measurements and ratios.

harranni MG

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	2.933	1.600	1.067	1.000	3.000	2.533	2.933	3.000	5.867
sd	.258	.507	.258	0	0	.516	.258	0	1.642
se	.067	.131	.067	0	0	.133	.067	0	.424
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	3.000	2.000	2.000	3.000	3.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc %	8.8	31.7	24.2	0	0	20.4	8.8	0	28.0

FigTable 24. Sclerite color and splash..

Morphological summary for Med Garden voucher series. Means (n=15): PNL 2.7, ELL 9.9, PNW 3.4, EWhum 2.0, EWmid 2.5, ELVit 2.9, TOTLen 12.6, PNrat 0.80, ELWrate 1.27, ELVTrat 0.29 (**FigTable. 23**, with other stats); sclerite colors and prelantern- ventrite splash in **FigTable 24** and **Figure 25**, **Figure 26** is a key for anatomical elements and splashing on ventrite 4. **Figure 27** show an array of vittagram diversity; **Figure 28** shows an analysis of vittagrams as illustrated in the reference array Figure 201.2 elsewhere in

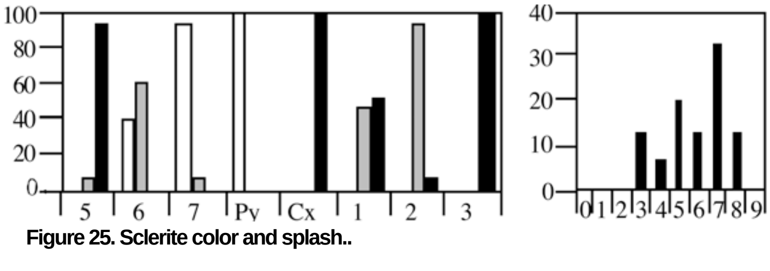


Figure 25. Sclerite color and splash..

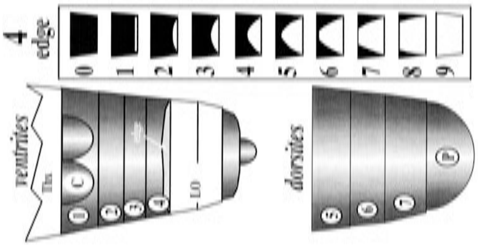


Figure 26. Topographic and splash keys.

elsewhere in this paper, and a feeble contingency table. The Appendix has morphological data from several regions

Holotype description. male, voucher number 6849. Collected 4 April 1968, Alachua County, Florida, Med. Plant. Gard., UF campus. (From FB, 1968 page 21: "2 jagged 3-4 attracted both—no others seen \6849, 6850" Morphological data: genitalia partially extruded; from spread sheet—PNLen 2.8, ELLen 9.9, PNWid 3.4, ELWhum 1.9, ELWmid 2.5, LELVit 5.0, TotLen 12.6, PnRat 0.81, ElRat 1.33, VitRat 0.51; Colors: T 322, Py 1, Cx 3,V 333, Edg 7. Types will be deposited in the USNM.

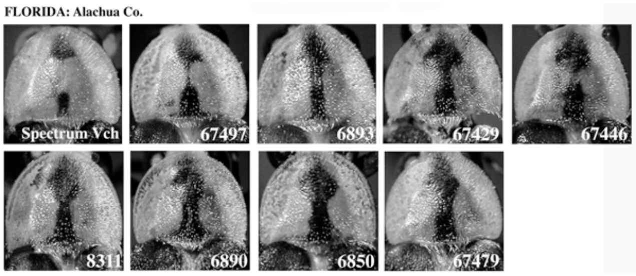
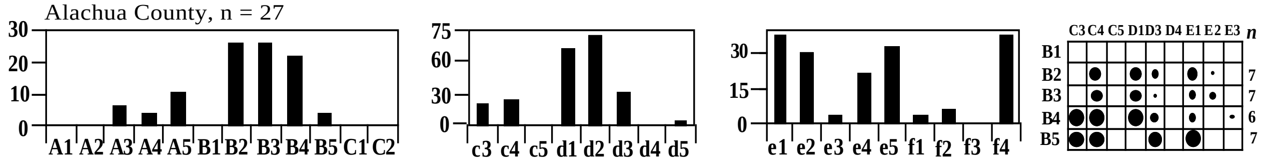
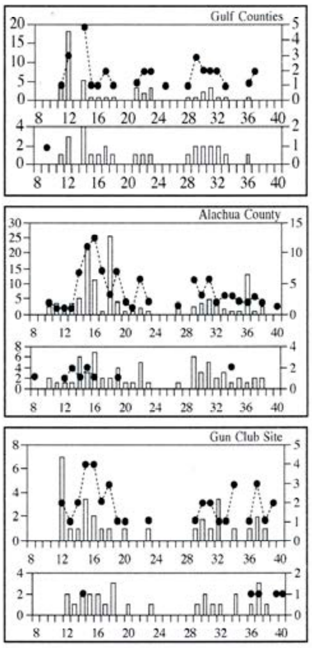


Fig. 27. Array of vittagram development in Alachua County.

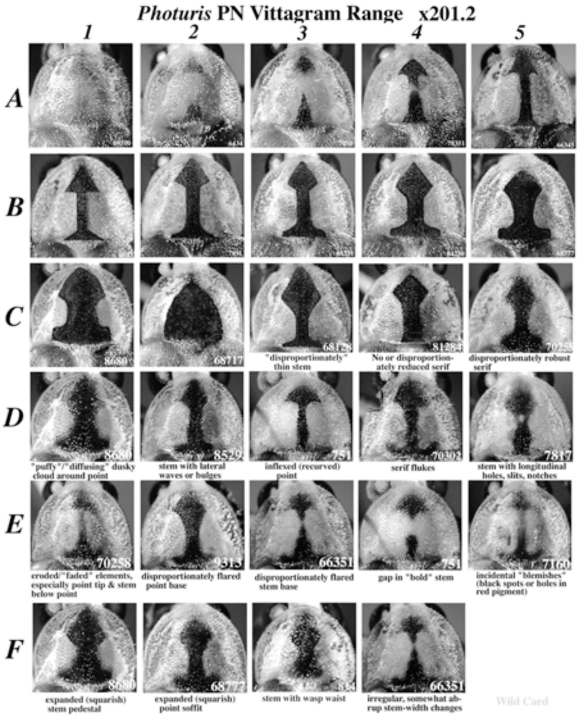
Taxonomic Notes. This firefly is the Florida *Ph. versicolor* of many early jel publications, and was observed extensively around Gainesville; one useful teaching site was along Lake Shore Drive (Road 329B), on the west shore of Newnan's Lake, just east of the city (**Fig. 15**). An earlier name for this lake was Pithlachoco, which may have meant Fish Eagle Place in Timucuan, and appears as a once-considered epithet for this species in some notes and manuscripts. The chosen epithet is in memory of my incredible parents, who, in their retirement, lived near the lake shore site, saw their firefly overhead, and harbored femmes fatales in their little woods (**Fig. 18**)—where Brits came to film—just as they had other fireflies on their lawns and in carefully tended oldfields at home in upstate New York (see Chapter 26).

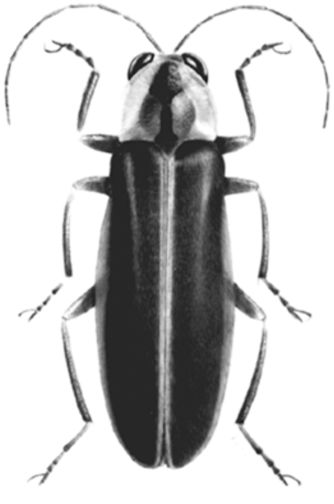


28. Pronotal Vittagram-Character Appraisal and Contingencies (201.2)



29. SESOBS records for several *harrannorum* sites/regions.





***Ph. harrannorum*, carbon dust, by Laura Line.**

Appendix

Gulf Counties

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2. 950	10.275	3.550	1.925	2.600	2.325	13. 225	.822	1.362	.223
sd	.238	.640	.265	.126	.141	1.550	.866	.028	.064	.149
se	.119	.320	.132	.063	.071	.775	.433	.014	.032	.074
n	4	4	4	4	4	4	4	4	4	4
min	2. 800	9.600	3.300	1.800	2.500	0.000	12. 400	.790	1.290	0.000
max	3. 300	11.100	3.900	2.100	2.800	3.100	14. 400	.850	1.430	.310
Vc%	8.1	6. 2	7. 5	6.6	5.4	66.7	6.6	3.5	4. 7	66. 8

Med Garden

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2. 727	9. 853	3.433	1.947	2.460	2.853	12.567	.801	1. 267	.293
sd	.162	.487	.191	.106	.176	1.940	.572	.020	.082	.201
se	.042	.126	.049	.027	.046	.501	.148	5. 207E-3	.021	.052
n	15	15	15	15	15	15	15	15	15	15
min	2. 500	9. 000	3.100	1.800	2.100	0	11.600	.770	1. 130	0
max	3. 000	10. 600	3.800	2.100	2.800	5.000	13.500	.840	1. 430	.530
Vc%	5.9	4.9	5.6	5.4	7.2	68.0	4.6	2. 5	6. 5	68.6

Pine Top

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	3. 133	11.650	3.700	2.150	2.683	3.783	14.767	.847	1.255	.322
sd	.273	.432	.200	.164	.204	3.152	.650	.050	.023	.268
se	.112	.177	.082	.067	.083	1.287	.265	.020	9. 220E-3	.110
n	6	6	6	6	6	6	6	6	6	6
min	2. 800	11.300	3.500	2.000	2.500	0	14. 100	.790	1.220	0
max	3. 500	12.300	4.000	2.300	2.900	6.900	15. 800	.930	1.280	.560
Vc%	8.7	3.7	5.4	7. 6	7. 6	83.3	4.4	5.9	1.8	83. 2

Gainesville misc. sites

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.782	10. 473	3. 382	1. 982	2.455	1.936	13.236	.823	1. 251	.176
sd	.296	.871	.223	.154	.121	2.010	1.039	.045	.113	.183
se	.089	.263	.067	.046	.037	.606	.313	.013	.034	.055
n	11	11	11	11	11	11	11	11	11	11
min	2.100	9. 100	2. 900	1. 800	2.300	0	11.300	.740	1. 060	0
max	3.300	11. 900	3. 800	2. 300	2.600	5.600	14.600	.880	1. 400	.500
Vc%	10. 6	8.3	6.6	7.8	4.9	103.8	7. 9	5. 5	9.0	104.0

Alachua County, initial misc. combination from sites above

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2. 720	10. 200	3.400	2.020	2.480	2.480	12.895	.803	1. 238	.245
sd	.209	.780	.210	.226	.177	1.966	.883	.032	.118	.198
se	.047	.174	.047	.051	.039	.440	.197	7. 250E-3	.026	.044
n	20	20	20	20	20	20	20	20	20	20
min	2. 100	9. 000	2.900	1.800	2.100	0	11. 300	.740	1. 000	0
max	3. 000	11. 900	3.800	2.800	2.800	5.000	14. 600	.880	1. 430	.530
Vc%	7.7	7.6	6.2	11.2	7. 1	79. 0	6.9	4.0	9.5	80.8

Gulf Counties

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.750	1.250	1.250	3.000	3.000	3.000	3.000	3.750
sd	0.000	.500	.500	.500	0.000	0.000	0.000	0.000	.500
se	0.000	.250	.250	.250	0.000	0.000	0.000	0.000	.250
n	4	4	4	4	4	4	4	4	4
min	3.000	1. 000	1. 000	1. 000	3.000	3.000	3.000	3.000	3. 000
max	3.000	2. 000	2. 000	2. 000	3.000	3.000	3.000	3.000	4. 000
Vc%	0	28.6	40. 0	40. 0	0	0	0	0	13.3

Med Garden

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	2.933	1.600	1.067	1.000	3. 000	2. 533	2. 983	3.000	5.867
sd	.258	.507	.258	0	0	.516	.258	0	1.642
se	.067	.131	.067	0	0	.133	.067	0	.424
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	3. 000	2. 000	2. 000	3.000	3.000
max	3.000	2.000	2.000	1.000	3. 000	3. 000	3. 000	3.000	8.000
Vc%	8.8	31.7	24. 2	0	0	20.4	8.8	0	28.0

Pine Top

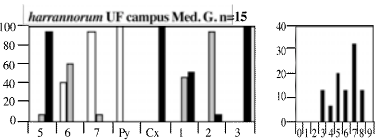
	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3. 000	1. 667	1.000	1.000	3.000	2.833	3.000	3. 000	4. 833
sd	0. 000	.516	0.000	0.000	0.000	.408	0.000	0. 000	1. 329
se	0. 000	.211	0.000	0.000	0.000	.167	0.000	0. 000	.543
n	6	6	6	6	6	6	6	6	6
min	3. 000	1. 000	1.000	1.000	3.000	2.000	3.000	3. 000	3. 000
max	3. 000	2. 000	1.000	1.000	3.000	3.000	3.000	3. 000	7. 000
Vc%	0	31. 0	0	0	0	14.4	0	0	27. 5

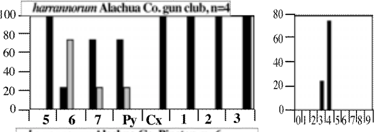
Gainesville misc. sites

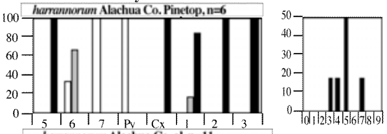
	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	2.818	1.727	1.091	1. 091	2. 727	2. 727	2.909	2.909	6.182
sd	.405	.467	.302	.302	.647	.467	.302	.302	1.722
se	.122	.141	.091	.091	.195	.141	.091	.091	.519
n	11	11	11	11	11	11	11	11	11
min	2.000	1.000	1.000	1. 000	1. 000	2. 000	2.000	2.000	3.000
max	3.000	2.000	2.000	2. 000	3. 000	3. 000	3.000	3.000	8.000
Vc%	14.4	27.0	27. 7	27. 7	23.7	17.1	10.4	10.4	27.9

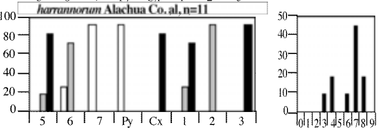
Alachua Co., initial misc. comb. from sites above

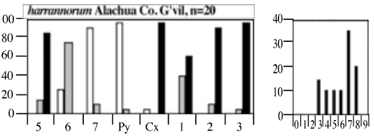
	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	2.850	1.750	1.100	1. 050	2. 900	2. 600	2.900	2.950	6.000
sd	.366	.444	.308	.224	.447	.503	.308	.224	1.777
se	.082	.099	.069	.050	.100	.112	.069	.050	.397
n	20	20	20	20	20	20	20	20	20
min	2.000	1.000	1.000	1. 000	1. 000	2. 000	2.000	2.000	3.000
max	3.000	2.000	2.000	2. 000	3. 000	3. 000	3.000	3.000	8.000
Vc%	12.8	25.4	28.0	21. 3	15. 4	19.4	10.6	7.6	29.6







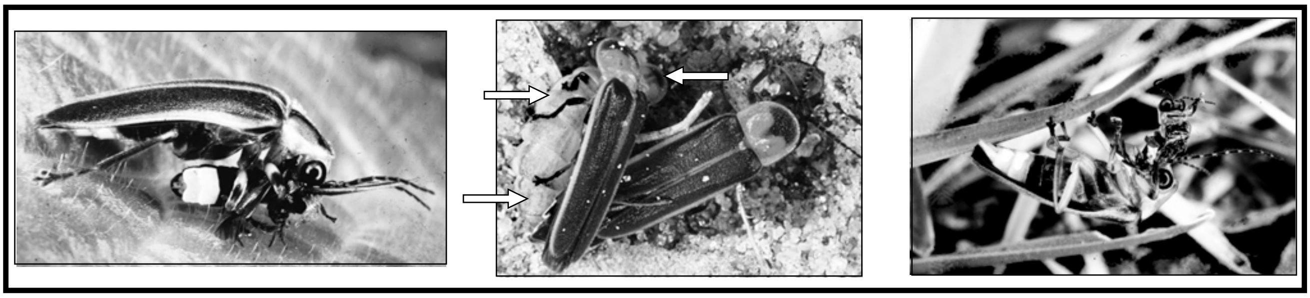




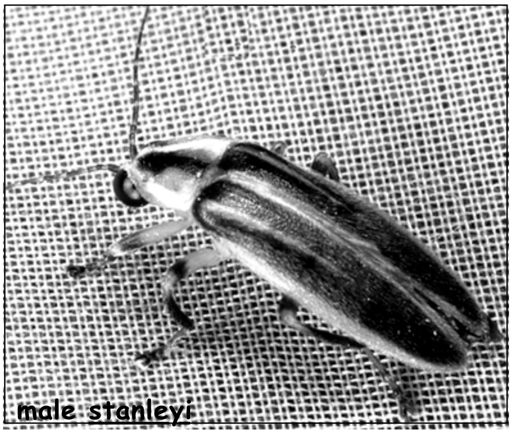
In early years of this study, 1966-80, the stream that flows through the Med Garden had vegetation that had developed over a number of years and harbored snails and other organisms that are prey of firefly larvae. This breeding ground for *Photuris* was then destroyed, and never recovered. Just upstream a cleared "reflecting pool" became a mud hole.

At the left is a view through the Med Garden grove, south toward the small lawn where *Ph. douglasae* were most active, and the shruby backdrop where *Ph. lamarcki* once flew in numbers.

Aggressive mimicry at the old UF Med Garden, page 2. The largest and presumably top predator among the *Photuris* females in Florida is probably *Photuris harrannorum*, shown immediately below at the left with a male *Photinus tanytoxus*. This was a strange encounter because for the male to approach the female he climbed several inches up the herb's stem, while she waited and then pounced. But *tanytoxus* females are brachypterous, clumsy, burrowing, and grub-like (center, arrows), and usually on or near the ground and their burrow's entrance. One would expect that natural selection would have long since removed such "foolish climbing genes" from access to male genotypes? But perhaps the photo itself answers the question: one male is plugged in and the other interfering, and competition keen, hence rare females are worth a gamble in the long-term calculus of gene (allele) frequency. At the right, a captured male *tanytoxus* with a *lamarcki* female (right) has raised his forelegs as though beseeching outside assistance in escaping his predicament. The second and third tiers of photos show a sequence in the mastication of a *Pyractomena angulata* male, identifiable by the color of his abdomen, and a female *Photuris stanleyi*—her males mimic the flicker of *angulata* males, indicating that theirs has been a long-continuing interaction in the evolutionary lineages of these two species.



male angulata



male stanleyi

First in a sequence of 7 exposures: a female stanleyi chewing on a male angulata.

Chapter 40

Photuris hebes Barber 1951

Slow-Hitch (SH)

Because the identification of this firefly requires very close observation of the FP and examination of the specimen in hand, the county-based distribution (**Fig. 1**) is but a sketchy and tentative outline. In some places such as goldenrod-dominated oldfields in the Mohawk Valley of upstate New York (**Figs. 2, 3**) there can be no doubt of ID—hundreds or even thousands are seen flying low over the herbs at a temperature low enough to make their shouldered (bimodal, hitched) flash easily discernible (**Fig. 4A**). At other times when only a scattered one or two are flying, say at the edge of a weedy ditch by a mowed hayfield and at a warm temperature, special attention is required (**Fig. 4C** vs **4A; Fig. 5**). Seasonal distribution is primarily during June and July across a broad range of latitudes (**Fig. 6**); **Figure 7** gives limited SESOBS records for the Madison Co., NY region. This firefly often physically appears as a small *Photuris lucicrescens*, with pale coxae, *luci*-group vittagrams and typically, but not always with well-marked lateral elytral vittae.

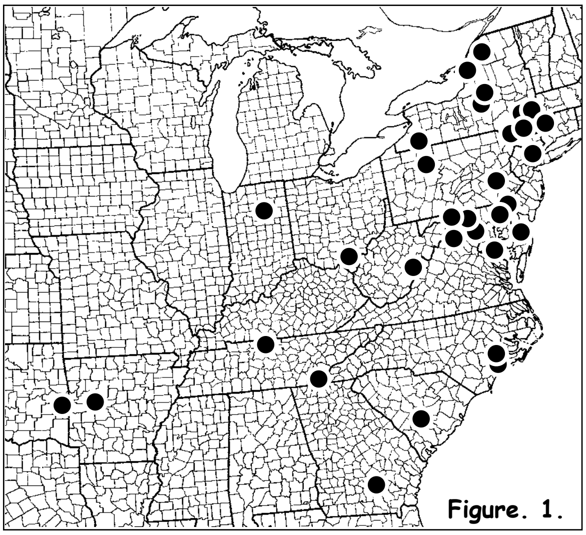


Figure. 1.

Flashes and associated behavior. The hitched FP (**Fig. 4**) is emitted in long continued sequences (**Fig. 8**) as males fly at herb- and grass-tops of oldfields and other grassland, occasionally up to altitudes of 10 feet and lower amongst the tips of taller herbs. In the oldfield shown in **Figures 2** and **3** a few males flew up around the branches of the vase-shaped (now-defunct) American Elm seen in the distance.

In addition to the more than 100 SWAT FP-period measurements made on 15 evenings, nearly 1000 periods of the flashes of 194 males were PM-recorded because of questions raised by the curious hitched FPs, ease of recording, and the occurrence of another but rare/adjunct FP(?) in the repertoire of this firefly. FP period ranges 1-2 seconds at typical field temperatures (**Fig. 9**); rates are shown in **Figure 10**.

Typically in cruising flashers such as *hebes* there is significant variation among consecutive FPs of individual males

Figure 2. Oldfield site with elm, Wampsville, NY.

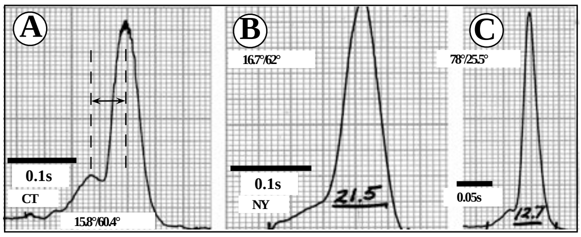


Figure 4. PM-records of *hebes* slow-hitch.

Figure 3. Oldfield herbs closeup, Wampsville.

Figure 5. Ditch, hay, and oldfield in West Virginia.

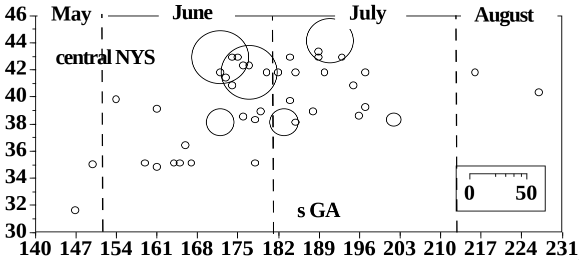


Figure 6. GESEDISOBS records (AX: Lat/DOY/n).

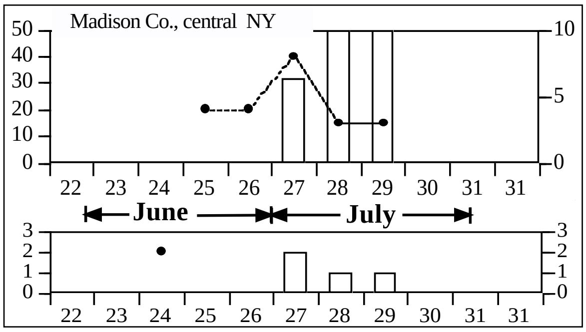


Figure 7. SESOBS records (AX: see M&T).

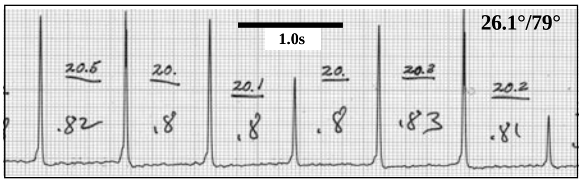


Figure 8. FP sequence, MD, southern Potomac River (AX:ri/time).

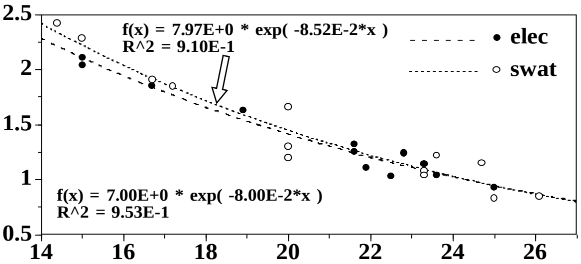


Figure 9. FP period means, see text (AX: sec/temp).

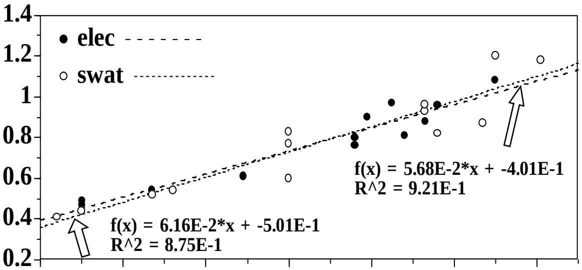


Figure 10. FP period rate means, see text (AX: Hz/temp).

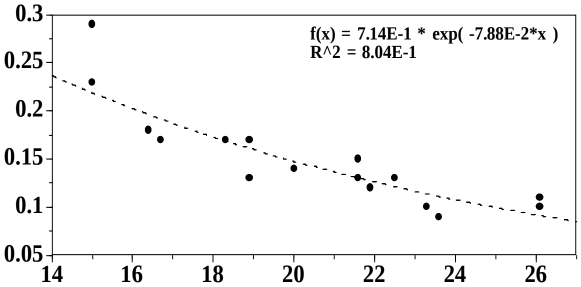


Figure 10. Hitched FP duration (AX: sec/temp).

as they monitor habitat structure and the behavior of competitors. In this firefly FP-period variation is slight. The coefficients of variation (standard deviation/mean, to "correct for" temperature differences) for the sequences of FPs from six males (n = 5-15 FPs) were: 0.045, 0.018, 0.01, 0.059, 0.009, and 0.062. In more obvious and understandable terms, a representative PM-recorded sample is the following from the FP sequence of a male (in seconds, 21.9°/71.5°): 1.15, 1.13, 1.12, 1.14, 1.14, 1.18, 1.2, 1.12; his coefficient of variation was 0.026. Such regularity might suggest that FP rhythm (rate) is part of signal coding, as is *only suspected* to occur in "true" train-flashing species such as *frontalis* and *potomaca*, and not merely efficient broadcasting in a highly competitive arena or one with dense vegetation. One difference between *potomaca* and *hebes* FPs is that those of *frontalis* and *potomaca* (and *missouriensis* and *chenangoa*) are simple unmodulated pulses. (see Figure 18 and text).

A large number of recorded FPs made possible and convenient a quick calculation and survey of flash duration across a broad range of temperatures—mindful that duration data have serious flaws because the breadth of a PM trace is influenced by the distance from the target. Measured across the base, as the trace leaves the (often irregular) base-line, rises and then falls, the duration of *hebes* shouldered flashes ranged 100-250 mSec at temperatures 14°-26° (57°-78.8°) as seen in **Figure 10**.

The structure of the hitched FP is interesting, and unlikely to be confused in the field with the FP of any other species except that of *bridgeniensis*—the Hitched-Single firefly—which apparently has a limited and northern distribution. PM records of *hebes* usually show merely a shoulder on the ON transient of the flash (**Fig. 4B, 4C**) but occasional records have a distinct preliminary peak (**Fig. 4A**). The visual situation becomes interesting when two observers follow and closely view the flashes of individual flying males: viewed from behind the flash of a flying male appears as a short crescendo; flashes simultaneously viewed (and announced) from the side are seen as distinctly bimodal. The hitch that is so often characteristic of *hebes'* may appear because observers often view the flasher at an angle. As for explanation, perhaps the crescendo/shouldered flashes as typically PM-recorded are produced by asynchronous emissions of the two segments of the lantern, with one segment peaking just slightly before the other, but when viewed from the side the asynchronous segments are seen separated in space by the fantastic human eye/brain?

Figure 11. A *hebes* without elytral vittae.

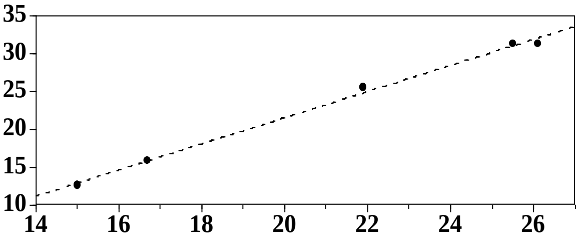


Figure 12. FP modulation (hitch) rate (AX: Hz/temp).

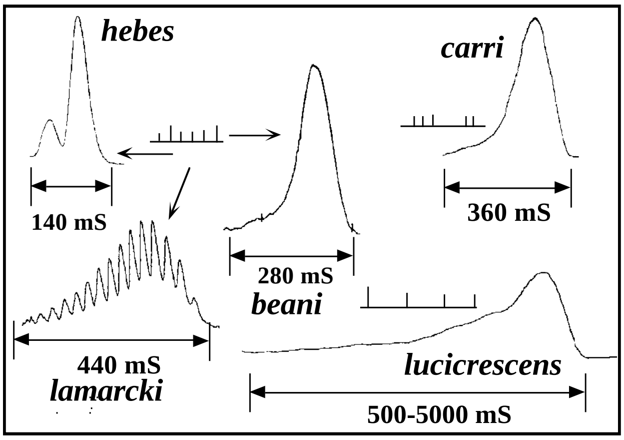


Figure 13. Flashes of a (working) *luci* Group.

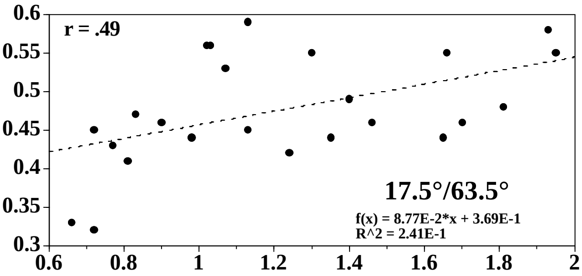


Figure 14. AX: Flash-rate/flight-speed; constant temp!

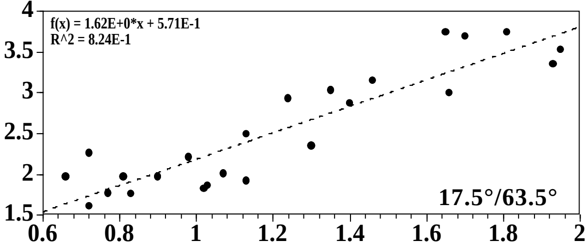


Figure 15. Wheel data: AX: ft/FP//flight speed.

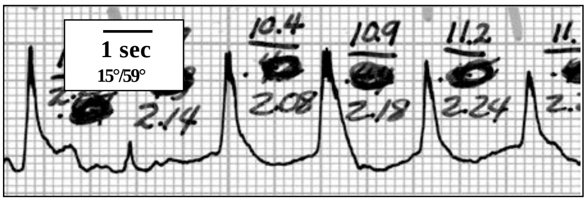


Figure 16. Series of decrescendo FPs (AX: rel. int./time).

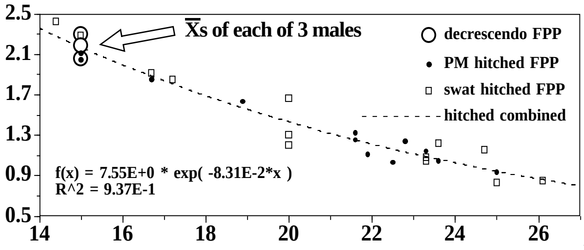


Figure 17. Decrescendo FPPer agreement (AX: sec/temp).

A pulse-rate for the distinctive peaks seen in some FP-records was determined by dividing the chart speed (125 mm/sec) by the measured distance between the peaks, and indicated in **Figure 4A**. A small sample of several males and 26 FPs across a range of five temperatures was made; this revealed, as expected, that modulation rate increases with temperature (**Fig. 12**). What was not expected—given the uncertainty sometimes experienced in determining the exact peak of the preliminary pulse—was that the plotted means of the small sample would fall so tightly along a regression line! (Sample numbers at temperature ranged 4-6, and standard deviations, 0.9-2.8.) Rate might have been calculated from half-max positions on the slopes of the two peaks, but this could introduce other uncertainties, though a few comparisons of the two methods did not suggest that there was an appreciable difference. Note that the shouldered flash of *hebes* suggests how the crescendo flashes seen in species such as *lucicrescens* and *moorei* are produced, or may have been during their evolution—and perhaps the asynchronous peaking of the two segments of lanterns are responsible for flash twinkles and modulations rarely seen in other species —such as those occasionally noted in the flashes of a western (Missouri) variad of ***Photinus*** *macdermotti*. **Figure 13** shows traces of flashes of species in a (working) *lucicrescens* Group (spiked lines show phrasing).

Bioluminescent spectra of living *hebes* (n=12) from four shipments were measured; means and half-max measurements in millimicrons are: 557, 529-597, n=4, se MD, 1968 (Biggley et al, 1967); 554, 529-597, n=1, cNYS, 1968; 556, 528-598, n=3, 1970, cNYS; 558, 530-602, n=4, 1978, wMD.

Search-flight characteristics were sampled in the goldenrod oldfield. Ground surface was furrowed, having been plowed but not harrowed—a source of error in linear measurement by a wheel rolled over the ground. Stats: 24 males, ∑ = 1343.2 ft.; speed: x=1.22 ft/sec (0.83 mph), range 0.66-1.95; ft/FP: x=2.54, range 1.61-3.74; FP/sec: x= 0.48, range 0.32-0.59. Note in **Figure 14** that FP rate tends to increase slightly with flight speed (r=0.49) at the ≈same temperature (other variables?). Searching males of various species are known to adjust to vegetation beneath them—skip flashes over roads, aim flashes at dark spots on leaves—perhaps the data are showing male response to changing vegetation structure. **Figure 15** illustrates what might be expected, that the slower males fly the closer together their FPs are delivered through space.

Perhaps *hebes* males have a repertoire of two (or three?) distinctive FPs. On first sighting one of them was thought to be emitted by a male with a faulty lantern, but then several males were seen emitting the same FP, and this FP was seen again on the next evening. These appeared at a site near and similar to that shown in Figure 2, in central New York. This FP is a decrescendo flash: **Figure 16** shows a train of these

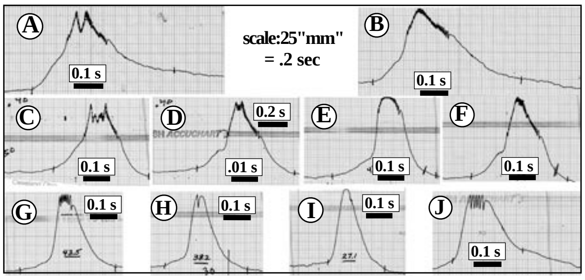


Figure 18. Decrescendo FPs, and transition (AX: rel. int./time).

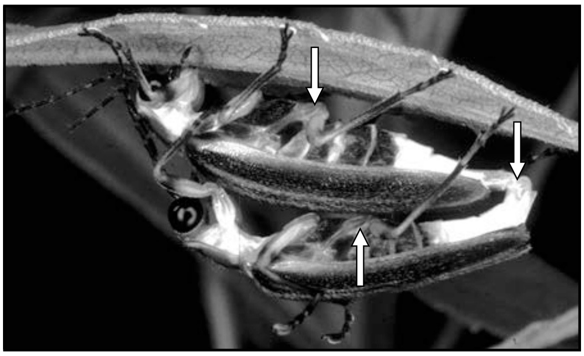


Figure 19. Note pale hind coxae; defensive posture!

Barber's specimens

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.400	8.700	2.825	1.500	1.975	5.675	11.100	.845	1.310	.648
sd	.115	.183	.150	0	.050	.741	.294	.044	.040	.075
se	.058	.091	.075	0	.025	.371	.147	.022	.020	.037
n	4	4	4	4	4	4	4	4	4	4
min	2.300	8.500	2.600	1.500	1.900	4.600	10.800	.780	1.250	.540
max	2.500	8.900	2.900	1.500	2.000	6.300	11.400	.870	1.330	.710
Vc%	4.8	2.1	5.3	0	2.5	13.1	2.6	5.2	3.1	11.6

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.250	1.000	1.000	1.000	1.000	1.500	1.750	2.500	6.250
sd	.500	0.000	0.000	0.000	0.000	.577	.957	.577	.957
se	.250	0.000	0.000	0.000	0.000	.289	.479	.289	.479
n	4	4	4	4	4	4	4	4	4
min	2.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	5.000
max	3.000	1.000	1.000	1.000	1.000	2.000	3.000	3.000	7.000
Vc%	22.2	0	0	0	0	38.5	54.7	23.1	15.3

Voucher specimens

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.530	9.580	3.150	1.820	2.410	6.550	12.120	.802	1.344	.683
sd	.116	.290	.108	.092	.129	.707	.385	.032	.082	.076
se	.037	.092	.034	.029	.041	.224	.122	.010	.026	.024
n	10	10	10	10	10	10	10	10	10	10
min	2.400	9.100	3.000	1.600	2.100	4.900	11.500	.760	1.210	.500
max	2.800	10.000	3.300	1.900	2.500	7.500	12.800	.850	1.540	.760
Vc%	4.6	3.0	3.4	5.1	5.4	10.8	3.2	4.0	6.1	11.1

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.444	1.000	1.000	1.222	1.333	2.222	2.778	7.889
sd	0	.726	0	0	.441	.500	.441	.441	1.167
se	0	.242	0	0	.147	.167	.147	.147	.389
n	9	9	9	9	9	9	9	9	9
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	6.000
max	3.000	3.000	1.000	1.000	2.000	2.000	3.000	3.000	9.000
Vc%	0	50.3	0	0	36.1	37.5	19.9	15.9	14.8

Figure 20. Morphological measurements, ratios, and sclerite color.

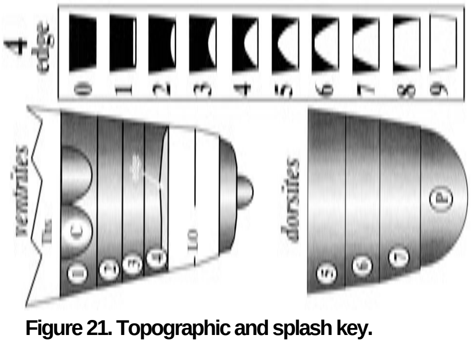


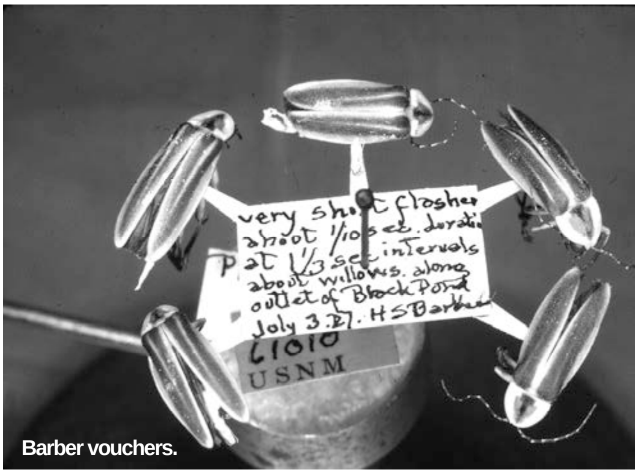
Figure 21. Topographic and splash key.

flashes and **Figure 17** places the FP period on the *hebes* (slow hitch) FP regression. **Figure 18** spreads out several traces (A, B, G-J) of decrescendo flashes; and C-J, flashes of one of these males that are confusing, and perhaps indicating a transition between flash types. In another curious *hebes* (variad) observation (Le Flore Co. OK) two short-flashing males being attracted individually to a decoy began emitting a slow-hitch flash when near the decoy—the only and questionable suggestion of defaulting seen in demes of this nominal species.

The approach of a male to a responding female was "observed" in Wampsville, New York, but happened so quickly that it allowed no description except that the male zipped in after one or possibly two flash-responses. When reached, they were coupled and hanging beneath a goldenrod leaf (**Fig. 19**). In the figure note the raised (lowered) mid-legs of the male, perhaps a defensive posture; his aedeagal filaments are placed outside and along the female abdomen. This photo was used in a *Scientific American* article, and this was used in the film *The Applegates* as insect porn by an insect-like, human-mimicking space traveler—so reported to this author long ago by a graduate student.

Morphology. **Figure 20** gives morphological details of a few Barber's voucher specimens and a sample of flash vouchers from Madison County, New York; the Appendix gives separate morphological data for several demes; **Figure 21** is a guide to anatomy. **Figure 22** shows an array of vittagrams from various localities.

Taxonomic Notes. The significance of the specific epithet is puzzling. Borror (1971) gives possible translations of *blunt*, *youth*, and *puberty*, which are not clearly applicable, and neither Barber nor McDermott mentions the derivation. The *Encyclopoedia Britannica* gives "Hebe (from Greek hebe, 'young maturity,' 'bloom of youth'), daughter of Zeus . . . ." and illustrate her with a winged female carrying nectar and ambrosia, from an Italian vase. If Barber's epithet has such an origin it was rather unusual for him I believe. The suggested common name is the nickname I used for this species for several years, from the hitch-along appearance conspicuous at the lower temperatures in the oldfields of home in upstate New York.



Barber vouchers.

APPENDIX: *Ph. hebes*
Regional Morphological Data

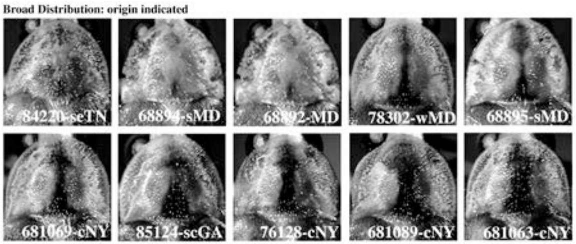


Figure 22. Array of vittagrams, various localities.

Barber specimens

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.400	8.700	2.825	1.500	1.975	5.675	11.100	.845	1.310	.648
sd	.115	.183	.150	0	.050	.741	.294	.044	.040	.075
se	.058	.091	.075	0	.025	.371	.147	.022	.020	.037
n	4	4	4	4	4	4	4	4	4	4
min	2.300	8.500	2.600	1.500	1.900	4.600	10.800	.780	1.250	.540
max	2.500	8.900	2.900	1.500	2.000	6.300	11.400	.870	1.330	.710
Vc%	4.8	2.1	5.3	0	2.5	13.1	2.6	5.2	3.1	11.6

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.250	1.000	1.000	1.000	1.000	1.500	1.750	2.500	6.250
sd	.500	0.000	0.000	0.000	0.000	.577	.957	.577	.957
se	.250	0.000	0.000	0.000	0.000	.289	.479	.289	.479
n	4	4	4	4	4	4	4	4	4
min	2.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	5.000
max	3.000	1.000	1.000	1.000	1.000	2.000	3.000	3.000	7.000
Vc%	22.2	0	0	0	0	38.5	54.7	23.1	15.3

NY Madison Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.530	9.580	3.150	1.820	2.410	6.550	12.120	.802	1.344	.683
sd	.116	.290	.108	.092	.129	.707	.385	.032	.082	.076
se	.037	.092	.034	.029	.041	.224	.122	.010	.026	.024
n	10	10	10	10	10	10	10	10	10	10
min	2.400	9.100	3.000	1.600	2.100	4.900	11.500	.760	1.210	.500
max	2.800	10.000	3.300	1.900	2.500	7.500	12.800	.850	1.540	.760
Vc%	4.6	3.0	3.4	5.1	5.4	10.8	3.2	4.0	6.1	11.1

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.444	1.000	1.000	1.222	1.333	2.222	2.778	7.889
sd	0	.726	0	0	.441	.500	.441	.441	1.167
se	0	.242	0	0	.147	.167	.147	.147	.389
n	9	9	9	9	9	9	9	9	9
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	6.000
max	3.000	3.000	1.000	1.000	2.000	2.000	3.000	3.000	9.000
Vc%	0	50.3	0	0	36.1	37.5	19.9	15.9	14.8

se MD

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.346	8.823	2.954	1.608	2.100	4.177	11.162	.795	1.315	.465
sd	.181	.650	.304	.185	.204	2.124	.813	.048	.076	.222
se	.050	.180	.084	.051	.057	.589	.225	.013	.021	.062
n	13	13	13	13	13	13	13	13	13	13
min	2.000	7.800	2.600	1.400	1.900	0	9.800	.660	1.210	0
max	2.600	10.000	3.600	1.900	2.500	7.800	12.600	.860	1.450	.850
Vc%	7.7	7.4	10.3	11.5	9.7	50.8	7.3	6.0	5.8	47.7

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.769	1.692	1.385	1.154	1.000	1.154	2.077	2.308	8.077
sd	.439	.855	.768	.555	0.000	.376	.641	.480	.862
se	.122	.237	.213	.154	0.000	.104	.178	.133	.239
n	13	13	13	13	13	13	13	13	13
min	2.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	6.000
max	3.000	3.000	3.000	3.000	1.000	2.000	3.000	3.000	9.000
Vc%	15.9	50.5	55.5	48.1	0	32.6	30.9	20.8	10.7

DEL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.510	8.930	3.050	1.650	2.090	3.520	11.430	.819	1.268	.396
sd	.120	.226	.127	.143	.137	2.711	.316	.018	.066	.303
se	.038	.072	.040	.045	.043	.857	.100	5.667E-3	.021	.096
n	10	10	10	10	10	10	10	10	10	10
min	2.300	8.500	2.800	1.400	1.900	0.000	10.800	.800	1.150	0.000
max	2.800	9.400	3.300	1.900	2.300	6.900	12.100	.850	1.360	.760
Vc%	4.3	2.5	4.2	8.7	6.6	77.0	2.8	2.2	5.2	76.5

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.100	1.000	1.000	1.000	1.300	2.100	2.500	8.600
sd	0.000	.316	0.000	0.000	0.000	.483	.568	.527	.699
se	0.000	.100	0.000	0.000	0.000	.153	.180	.167	.221
n	10	10	10	10	10	10	10	10	10
min	3.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	7.000
max	3.000	2.000	1.000	1.000	1.000	2.000	3.000	3.000	9.000
Vc%	0	28.7	0	0	0	37.2	27.1	21.1	8.1

NJ Bergen Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.483	9.033	3.017	1.750	2.317	5.850	11.500	.828	1.335	.648
sd	.117	.427	.232	.197	.133	1.638	.551	.035	.109	.184
se	.048	.174	.095	.081	.054	.669	.225	.014	.044	.075
n	6	6	6	6	6	6	6	6	6	6
min	2.300	8.300	2.800	1.500	2.100	2.800	10.500	.780	1.200	.300
max	2.600	9.500	3.400	1.900	2.500	7.500	12.100	.870	1.500	.790
Vc%	4.7	4.7	7.7	11.3	5.7	28.0	4.8	4.6	8.2	28.4

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.500	1.000	1.000	1.000	1.333	2.333	2.667	7.500
sd	0.000	.548	0.000	0.000	0.000	.516	.516	.516	.837
se	0.000	.224	0.000	0.000	0.000	.211	.211	.211	.342
n	6	6	6	6	6	6	6	6	6
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	7.000
max	3.000	2.000	1.000	1.000	1.000	2.000	3.000	3.000	9.000
Vc%	0	36.5	0	0	0	38.7	22.2	19.4	11.2

GA

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.540	9.140	3.060	1.700	2.280	4.360	11.680	.838	1.348	.478
sd	.055	.288	.167	.141	.110	.974	.342	.033	.108	.111
se	.024	.129	.075	.063	.049	.435	.153	.015	.048	.050
n	5	5	5	5	5	5	5	5	5	5
min	2.500	8.900	2.900	1.500	2.100	3.400	11.400	.800	1.210	.360
max	2.600	9.500	3.300	1.800	2.400	5.600	12.100	.870	1.500	.630
Vc%	2.2	3.2	5.5	8.3	4.8	22.3	2.9	3.9	8.0	23.2

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.400	1.000	1.000	1.000	2.000	2.600	3.000	6.600
sd	0	.548	0	0	0	0	.548	0	.894
se	0	.245	0	0	0	0	.245	0	.400
n	5	5	5	5	5	5	5	5	5
min	3.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000	5.000
max	3.000	2.000	1.000	1.000	1.000	2.000	3.000	3.000	7.000
Vc%	0	39.1	0	0	0	0	21.1	0	13.6

NC

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.450	8.800	2.975	1.625	2.125	1.300	11.250	.820	1.312	.140
sd	.129	.432	.150	.189	.189	1.510	.545	.037	.083	.162
se	.065	.216	.075	.095	.095	.755	.272	.018	.041	.081
n	4	4	4	4	4	4	4	4	4	4
min	2.300	8.400	2.800	1.500	2.000	0	10.800	.780	1.230	0
max	2.600	9.400	3.100	1.900	2.400	2.800	12.000	.860	1.420	.290
Vc%	5.3	4.9	1.7	11.6	8.9	116.2	4.8	4.5	6.3	115.7

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.000	1.500	1.000	1.000	1.500	2.250	2.750	5.750
sd	0	0	.577	0	0	.577	.957	.500	3.862
se	0	0	.289	0	0	.289	.479	.250	1.931
n	4	4	4	4	4	4	4	4	4
min	3.000	2.000	1.000	1.000	1.000	1.000	1.000	2.000	0
max	3.000	2.000	2.000	1.000	1.000	2.000	3.000	3.000	8.000
Vc%	0	0	38.5	0	0	38.5	34.8	18.2	67.2

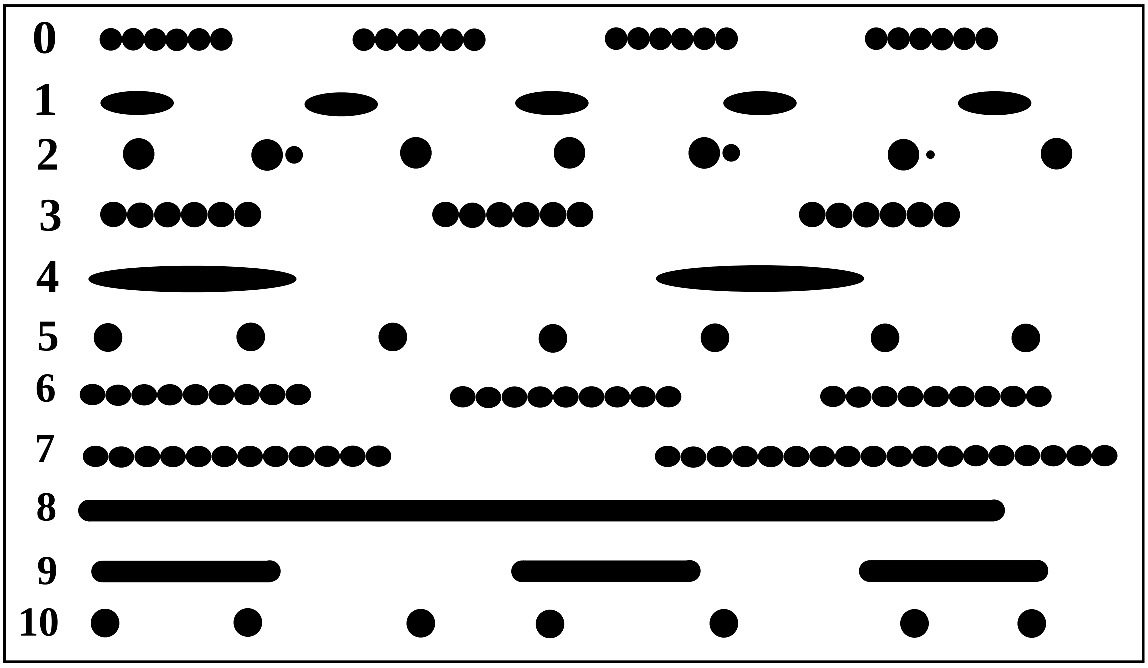
TN

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.460	9.080	3.020	1.700	2.240	4.220	11.540	.820	1.318	.462
sd	.207	.550	.259	.200	.195	1.424	.709	.042	.074	.146
se	.093	.246	.116	.089	.087	.637	.317	.019	.033	.065
n	5	5	5	5	5	5	5	5	5	5
min	2.100	8.300	2.600	1.400	1.900	1.900	10.400	.770	1.200	.230
max	2.600	9.800	3.300	1.900	2.400	5.300	12.300	.880	1.380	.590
Vc%	8.4	6.1	8.6	11.8	8.7	33.7	6.1	5.1	5.6	31.6

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.600	1.600	1.200	1.400	1.800	2.400	2.600	7.400
sd	0	.894	.894	.447	.894	.837	.548	.548	2.608
se	0	.400	.400	.200	.400	.374	.245	.245	1.166
n	5	5	5	5	5	5	5	5	5
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	9.000
Vc%	0	55.9	55.9	37.3	63.9	46.5	22.8	21.1	35.2

Generalized *Pyractomena* FPs, Their Presentation In Time

see also pages 363-364



0 amber flickers of 5-8 pulses, low over wet areas, at shrub-, treetops
1 "longish" short flashes as dipping low, marsh or damp meadows
2 short flashes with occasional dimmer after-flash, damp woodlands
3 series of 4-6 distinct pulses, but flicker-like at warmer temperatures
4 flaring long flashes, high flight, long intervals
5 single short flashes emitted with somewhat "mechanical regularity"
6 series of rapid pulses, flicker-like at warmer temperatures (or glow?)
7 continuous long green glow, indefinite length, occasional short breaks
8 series of short glows— OFFs and ONs of similar duration?
9 short flashes of rather short, variable intervals, southern Texas, Mexico

0 *angulata, barberi, floridana.*   pages: 371-377; 385-386; 411-413
1 *linearis, lucifera, palustris.*   pages: 403-404; 407-408; 405-407
2 *borealis, limbicollis, marginalis.*   pages: 387-388; 401-402; 409-410
3 *dispersa, floridana.*   pages: 389-393; 411-413 (late summer, rare)
4 *ecostata, punctiventris.*   pages: 395-396; not treated (Texas)
5 *similis.*   pages: 415-416
6 *sinuata.*   pages: 417-420
7 *angustata*.   pages: 379-384
8 HUDSON.   page: 400
9 *vexillaria.*   pages: 421-422

Chapter 41

Photuris hiawasseensis n. sp.

The apparent geographic distribution of this firefly includes the western slope, coves and valleys of the Appalachians and extends westward to north-central Tennessee (**Figs. 1, 2**). Its (default?) FP is a distinctive, truncated flash-OFF-glow (dot-dash) pattern of classic *pennsylvanica*, but the dash is short, only three to four times longer than the dot (**Fig. 3**). The modulation rate, as established by the dot then dash ON *transients*, is about 9 Hertz at 20°/68° (**Fig. 4**). FP period is 2.5 sec at 20°/68° and a comparison of Polk and Sumner County, TN measurements revealed no difference (**Fig. 5,** rate in **6**). Males usually appeared singly or were few in number, along and around the crowns of tall gallery trees by small streams and ravines and near sloughs (**Fig. 7, 8**). With its slow and steady flight and "electronic" FP, the appearance is that of a cruising starship flashing an alpha (A=dot-dash) recognition signal. This FP is required for ID.

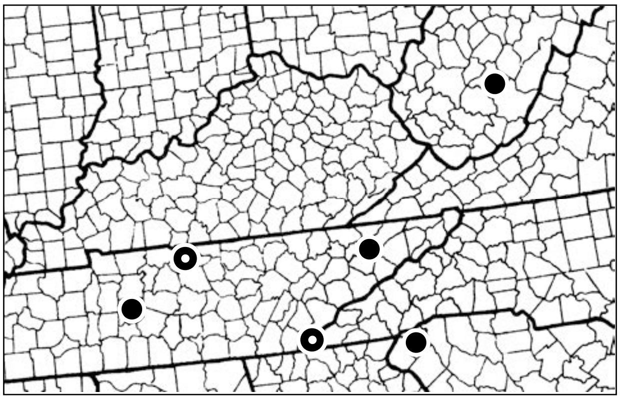


Figure 1. Vouchered localities with dots.

Figure 2. Overview of *hiawasseensis* Appalachian landscape.

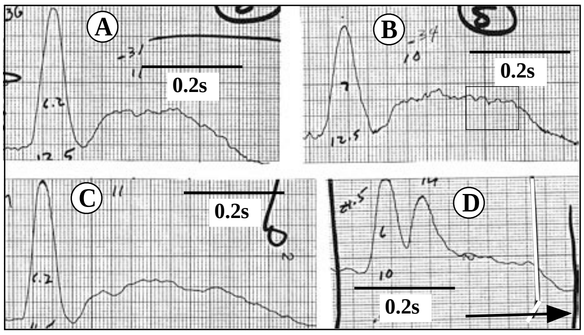


Fig. 3. PM-scans of *hiawasseensis* FPs, temperature as indicated: (A-C) apparent typical dot-short-dash FPs; note lack of a crescendo and clear break between the dot and dash; (D) an unusual FP that appeared in a train of (normal) FPs as seen in A-C, and was apparent to the eye during recording (AX: rel. int. /time)..

Ecology, flashing behavior. The observed adult season of this firefly in Sumner and Polk Counties TN was mid to late June. Males flew singly or in small numbers (only once were numbers recorded as “many”) at the crowns of taller trees, sometimes patrolling back and forth and around the crowns, sometimes following the gallery and moving along the water-course for some distance. When flying across open spaces between crowns they usually stopped flashing.

The dot-dash FP is conspicuously reminiscent of the Morse Code "A" (**Fig. 3**), but at a distance the break may not be visible and the FP appear as a square wave. There are descriptive parameters to be noted in PM recordings though they are not apparent or useful to the eye. The values given are from a sample of the FPs of three males that were recorded in Polk County TN, near the Hiawassee River at Wetmore, TN, at 19.4°/66.9°. All parameters are not usable in all recorded patterns. Overall mean duration, 421/487 mSec (duration at half max/duration at base); short flash (dot) mean duration, 58/92 mSec; long flash (dash) mean duration, 319/388 mSec.

There is also a difference in the maximum intensity reached by the two flashes in an FP, with the dash flash usually being slightly more than one-third the brightness of the dot flash: average for two males, in a sample of 10 FPs, dash intensity/dot intensity = 0.38.

One recorded FP is conspicuously different from others, and its deviation would not seem to be entirely accounted for by assuming the male's light organ was rapidly turned away from the PM, or partially occluded by vegetation. In this FP, one of a sequence of six, with the other five being "normal," the modulation rate is more rapid, at 12.5 Hz, and the dash-flash is initiated by a bright peak that is about 83 percent the intensity of that of the dot-flash—then dash intensity drops and is sustained at a typical comparative dash intensity for the duration of a normal dash-flash (**Fig. 3D**).

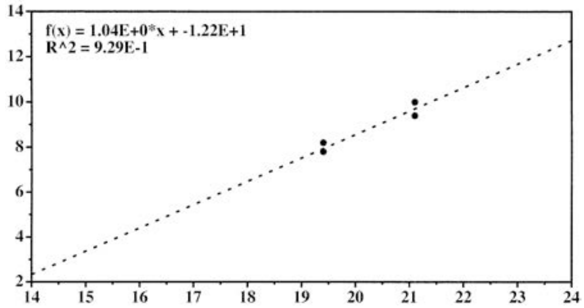


Figure 4. FP (dot-to-dash) pulse rate (AX: Hz/temp).

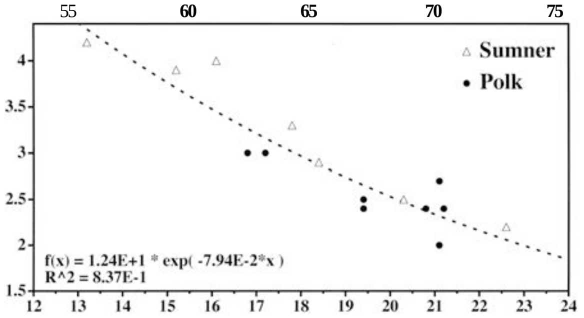


Figure 5. FP period (AX: sec/temp).

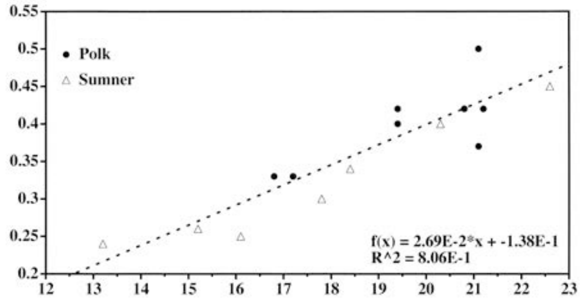


Figure 6. FP interval (period) as rate (AX: Hz/temp).

Figure 7. Creek and slough, Polk Co. TN; sketched FPs.

Figure 8. Bledsoe Creek (foreground) Sumner Co., TN.

At the Polk County, TN and Nicholas County, WV sites short crescendo flashes were noted. At the Polk Co. site pumping-crescendo flashes as used by *whistlerae* and *beanii* in Florida were seen. Once—related here with some uncertainty—a dot-dash flasher switched to a crescendo and a short flasher to a crescendo. When attracting males to the penlight, at times presumptive dot-dash flashers appeared to emit a crescendo with a "twinkle" or a break. These notes suggest that this firefly may emit more than one FP. However, fireflies that *swoop* through space while emitting bright flashes sometimes appear to emit crescendo flashes, and this may explain some of these observations.

Attractions. Sometimes males were easily attracted to a penlight with a one-third-sec flash presented about one-sec after their FP; they approached directly ("bee line") from as high as 60'. As they closely approached they sometimes swooped upward, leaving a crescendo-appearing stripe, which often appeared to "hitch" or twinkle. After approaching to 3-6', males usually paused and would not continue although a few reached the decoy. At times males could not be induced to approach, even when the LED on the flashpole was placed high in a shrub.

Mimicry/hawking? In one especially interesting observation, an attracted, electric dot-dash flasher was grabbed in the hand immediately after it flashed close-by; it was a *Photuris lucicrescens* female!

Miscellaneous recognition notes. The dot-dash FP of this species gives rise to many associations and descriptive similes, especially when viewed from different angles, and at different distances and temperatures. The following terms and phrases, some of which were mentioned above because they may aid in field identification, appear in field notes: twinkle, blink, hitch; almost a *versicolor* twinkle, snap on front; spike at the front; hardly perceptible break; quivers, looks electric, like a square wave with a positive certainty about it, robust assurance, nothing tentative, very sharp transients; looks like the start of a *versicolor* pattern but the second pulse is held; flies slowly, stately, almost regal like a starship, circles crown like an airship, across the top slowly and deliberately; at a distance cannot see break.

* * *

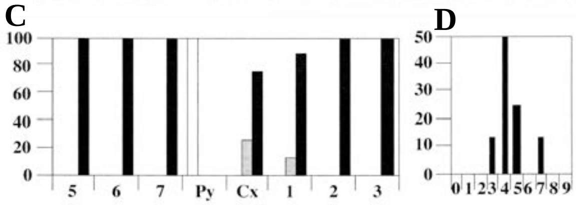
Morphological data. General morphological data means are (n=7, **FigTable 9A**): PNL 2.5, ELL 3, PNW 3.3, EWhum 1.8, EWmid 2.2, ELVit 2.1, TOTLen 11.8, PNrat 0.83, ELWrat 1.25, ELVTrat 0.22). Data for the colors of various abdominal plates and hind coxae are shown in **FigTable 9B-C**, and the pale splashing on the posterior margin of the pre-lantern ventrite-4 in **9D**. **Figure 10** a guide to exoskeletal elements and numbers for degrees of splashing on ventrite 4. A array of vittagrams (pronotal vittae) of *hiawaseensis* is shown in **Figure 11**.

A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.486	9.343	3.000	1.800	2.186	2.057	11.814	.830	1.246	.221
sd	.146	.683	.216	.252	.195	.947	.863	.048	.151	.102
se	.055	.258	.082	.095	.074	.358	.326	.018	.057	.038
n	7	7	7	7	7	7	7	7	7	7
min	2.300	8.400	2.600	1.500	1.900	0	10.600	.760	.940	0
max	2.600	10.300	3.300	2.300	2.500	2.800	12.900	.880	1.430	.290
Vc%	5.9	7.3	7.2	14.0	8.9	46.0	7.3	5.8	12.1	46.2

B

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	3.000	1.000	2.500	2.875	3.000	3.000	4.250
sd	0.000	0.000	0.000	0.000	.926	.354	0.000	0.000	1.282
se	0.000	0.000	0.000	0.000	.327	.125	0.000	0.000	.453
n	8	8	8	8	8	8	8	8	8
min	3.000	3.000	3.000	1.000	1.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	0	0	0	37.0	12.3	0	0	30.2



FigTable 9. Measurements and ratios..

Holotype Description. male, voucher number 84221, collected 16 June 1984, Polk County, Tennessee. Across highway U. S. 441 from entrance to Gee Creek Camp-ground (near Wetmore), and down country road 1/4 mile to low spot. FB page 75: "KB 36 84221 another attr[acted], & netted—flash each 2 to 3 sec—spike on front in appears [appearance] then a flash after w[with] break, but hardly perceptible, between. over all 0.3-0.35 dur." Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.6, ELLen 10.0, PNWid 3.0, ELWhum 1.8, ELWmid 2.1, LELVit 0.0, TotLen 12.6, PnRat 0.88, ElRat 1.21, VitRat 0.0; Colors: T 333, Py 1, Cx 3, V 333, Edg 4. Types will be deposited in the USNM.

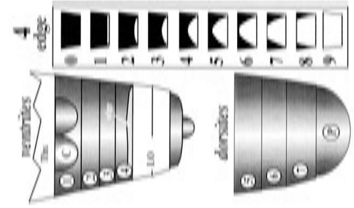


Figure 10. Guide to anatomical elements.

Taxonomic Notes. This species is named for the Hiawassee River, which is a few hundred yards from the type locality, near Gee Creek campground. It is formally named as a species but as with many other *Photuris* noteworthy entities, we are far from understanding what the true nature of this variad is, or how versatile it is in its flashing and communication.

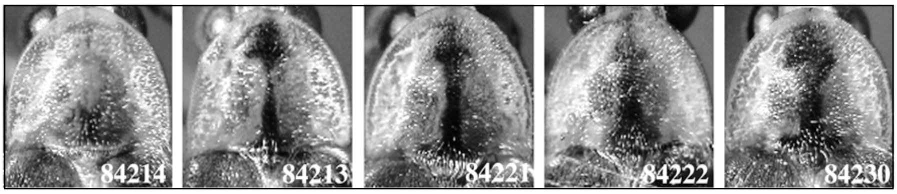
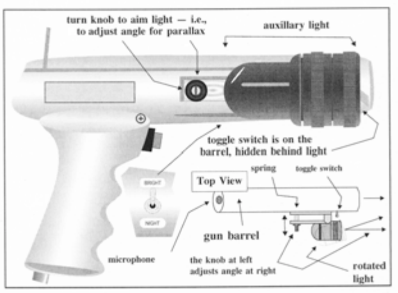
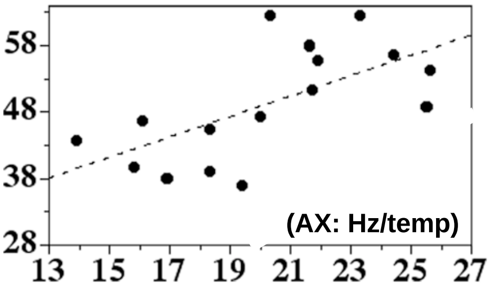


Figure 11. Range of pronotal vittagrams.

Wingbeats and temperature independence? As introduced in the Chapter 75 (*Py. angustata*), what appeared to be temperature independence was noted in the WBs of fireflies, as they were first observed in PM-records of light emissions. If so, this would be in contrast with the strong relationship between flash characteri-stics and temperature. The initial impression was that WBs were roughly about the same ≈35 Hertz (cycles per second), regardless of ambient temperature. Comparison of flash records of several species, and especially of samples made along a continuous recording of a glow suggested another view. This was disappointing in one specific instance: the high rate of flicker of *Photuris lamarcki's* FP at the light organ is strongly temperature dependent; hence, if its WB were independent and the neural control was in the same ganglion …?!! Some WB measurements were made as described (pp. 381-382). In another method, an optical tachometer shone a light on a flying firefly to measure the pulsing light reflected from beating wings. It failed: apparently the wings are "unusually non–reflective." I suspect now, as certainly I should have, that wingbeat rate is varied with circumstances of flight just as airplane pilots vary the pitch and rpms of their props and engines. There have been a number of studies on the ability of insects to maneuver and control their beating wings. Here are sketches of Alton Higgons' tachometer and a summary of species' PM records.

Figure 1. The Higgin's wingbeat tachometer detects reflections of light from an insect's beating wings, converts the reflections to an electrical signal which is then recorded on tape (see text).





Incidental camera encounters, at the old UF Med Garden, 1974-75, Page 3.

Chapter 42

Photuris katrinae n. sp.

Texas Red

This large ($\bar{x}$=15 mm), tawny firefly is the only "big/giant red" presently known to occur in Texas. "It" was found along south-central rivers including the Frio, Sabinal, Nueces, Guadeloupe, and Concho, and also Live Oak Creek in Gillispie Count; in late May and early July in 1992 and 1999 (**Figs. 1, 2**). Its continuous "trains" (series) of flashes emitted at a short period of less than a second (**Fig. 3**; rate 1.2-1.3/sec, **Fig. 4**), will only be confused with momentary fast-flashing by a *Photuris billbrowni*. The latter has a conspicuous hitch in its FP; in *katrinae* a subtle, inconspicuous hitch only occasionally *appears* to be present but was not confirmed in PM records. This firefly's large size, tawny color, and feeble vittagram, or its complete absence, should make identification certain. Populations along the mentioned rivers may have had no contact and been separated a long time. The dry uplands between rivers in the region may effectively isolate many populations and provide an interesting assemblage for genetic diversity/divergence studies, and comparison with certain river-associated Division 1 *Photinus* species that may have less between-rivers movement.

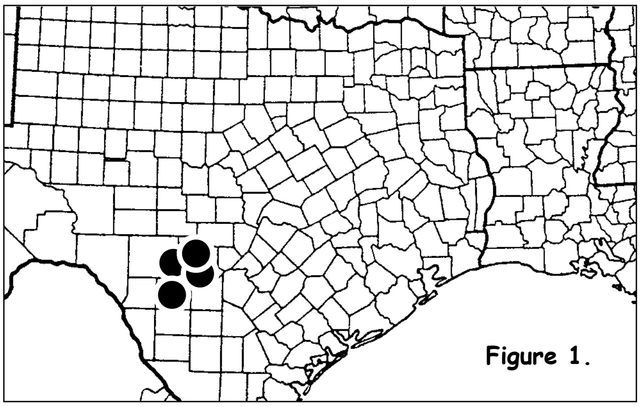


Figure 1.

Figure 2. Texas Red site off the Concho River, 1999.

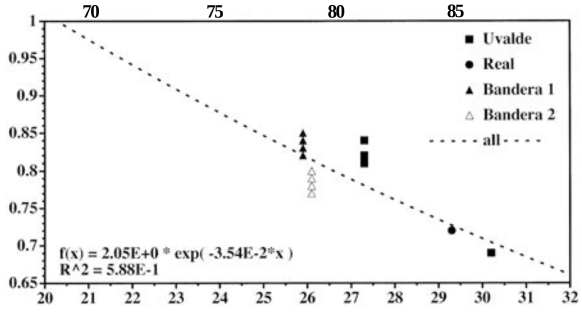


Figure 3. FP period (AX: sec/temp).

Ecology, flashing behavior. Limited observations suggest that flashing populations of this species occur only along rivers and creeks, though they may also occur near lakes and ponds. I found localized adult flashing in patches of herbaceous vegetation immediately adjacent to the water, in woody scrubs along natural levees, and in small woods 100 yards from the water (**Fig. 2**). Males began activity early, at 0.5 creps in deep shade, and 0.7 creps in the open (n=1). Later they flew low over herbaceous vegetation and up over and along the crowns of low and tall trees. Flashing was noted at 6 creps, and probably continued much later into the night. Single individuals occasionally flew though the activity space of *Photinus sabinalensis* (below).

Though the flashes are emitted somewhat train-like, flash rate itself may not be of coding significance. SWAT timings were made with 10 periods per sample per male and together with PM records give a mean flash period of ca 1.2 Hz at 26°/ 78.8° (**Fig. 4**). Flash rate sometimes appeared to be mechanically constant, but from time-to-time varied in momentary accelerations; no tendency to synchronize flashes was noted (**Fig. 5D-E**).

Flashes occasionally appeared (to the eye) to be bimodal, through either a "hitched" appearance or the presence of a small "image/shape" of light in space when viewed from beneath. However, PM-records do not show any shoulders or bimodality (**Fig. 5A-C**). In a few records there is the suggestion of such a mode in the correct position, but this probably was noise in the PM system (under heat stress?).

The flash is very short and nearly symmetrical, with a slightly faster rise- than fall-time, the asymmetry being due to tailing-off during the last one-third of the fall (**Fig. 5A-C**). The base duration is about 48 mSec, and half-max about 22, with ranges of 40-56 and 20-28 mSec respectively, based on inspection of 100 recorded flashes from 11 males. (26.1°-27.3°).

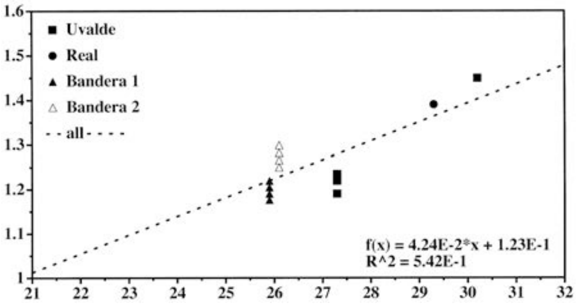


Figure 4. FP rate (AX: Hz/temp).

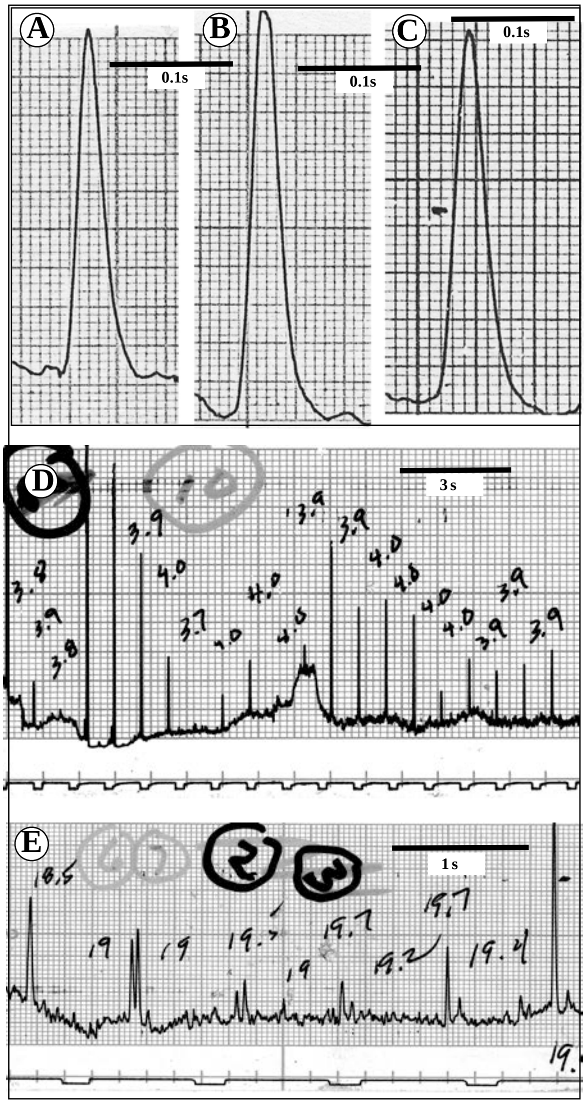


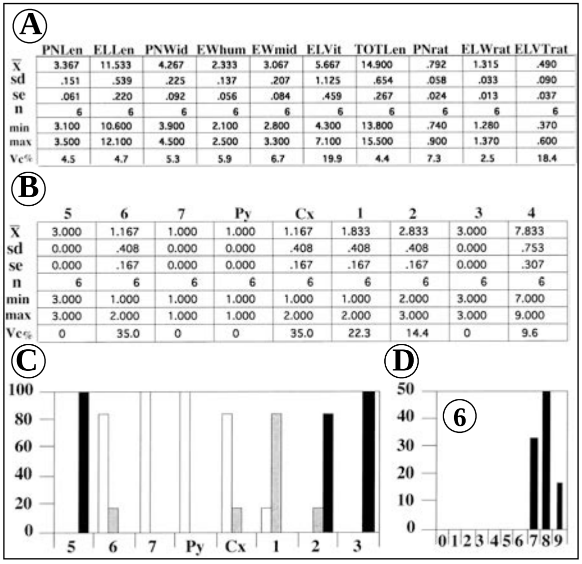
Figure 5. PM traces (AX: ri/time).

Decoy Experiments. Four (Sabinal River) males were attracted by presenting a snappy flash (flashpole) immediately after each of their flashes, continuously during their aerial and walking approaches: (**1**) The male was flashing from a perch in tall grass. He directly approached the decoy from two feet, until he reached and stood upon it. (**2**) The male landed one foot from the LED and approach through grass until he was about 3 inches from the decoy. Then, about 5 inches from the LED a group of three closely-spaced (<2 inches) fireflies began flashing rapidly and asynchronously, their combined flashing resembling a roadside fireworks advertisement. The attracted male was lost in the confusion. (**3**) The male landed 15 inches from the LED, approached quickly through the grass toward the decoy to 5 inches, where he stopped approaching and flashing. After 15 sec, a short flash of the decoy appeared to stimulate him to flash, and he then continued flashing and approached until he stood on the LED. (**4**) The male landed at six feet, and approached to 15 inches and stopped. At 15 sec he answered a flash of the decoy and continued approaching, then stopped. After several flashes of the decoy he "finally answered" and continued approaching until he stood on the LED. Perhaps the hesitating approach behavior in 3 and 4 relates to predation by their own or other females?

Aggressive Mimicry. A female T-Red was observed flash-answering and attracting males of *Photinus sabinalensis* (Bandera Co.). She perhaps flew into this prey site from the active mating population of her species across the River, about 100 feet away. Joe Cicero (pers. comm.) previously noted hunting females of a large red Texas (conspecific?) firefly in a *Photinus dimissus* site, that flew in from their adjacent mating space. I observed another T-Red female to attract two *Photinus pyralis* males to within a three feet, and a few minutes later, with an entirely different response she attracted a conspecific male to within an inch. She was perched on the ground by a "marshy swale" immediately by the Frio River (Uvalde Co.). The flash response to the *pyralis* males was a single ca 0.4 sec-long flash at ca 1 sec delay (wrong?). In response to the T-Red male she emitted short flashes continuously at a rate that appeared to be about twice that in the male's train. However, when this response was simulated with an LED, passing males (n=2) were not even briefly attracted.

* * *

Morphological data. General morphological means are (n=6, Bandera Co.): PNL 3.4, ELL 11.5, PNW 4.3, EWhum 2.3, EWmid 3.1, ELVit 5.7, TOTLen 14.9, PNrat 0.79, ELWrat 1.32, ELVTrat 0.49 (**FigTable. 6A**, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **FigTable 6B-C**, and the color of the pre-lantern ventrite in **6D**. **Figure 7** is a key for skeletal plates and degree of splashing on ventrite 4. An array of T-Reds pronota and vittagrams is shown in **Figure 8**. The histograms in **6C** and **6D** are shown with those of other "Red Group" species/variads for comparison in the Appendix.



Ⓐ

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	3.367	11.533	4.267	2.333	3.067	5.667	14.900	.792	1.315	.490
sd	.151	.539	.225	.137	.207	1.125	.654	.058	.033	.090
se	.061	.220	.092	.056	.084	.459	.267	.024	.013	.037
n	6	6	6	6	6	6	6	6	6	6
min	3.100	10.600	3.900	2.100	2.800	4.300	13.800	.740	1.280	.370
max	3.500	12.100	4.500	2.500	3.300	7.100	15.500	.900	1.370	.600
Vc%	4.5	4.7	5.3	5.9	6.7	19.9	4.4	7.3	2.5	18.4

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.167	1.000	1.000	1.167	1.833	2.833	3.000	7.833
sd	0.000	.408	0.000	0.000	.408	.408	.408	0.000	.753
se	0.000	.167	0.000	0.000	.167	.167	.167	0.000	.307
n	6	6	6	6	6	6	6	6	6
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	3.000	7.000
max	3.000	2.000	1.000	1.000	2.000	2.000	3.000	3.000	9.000
Vc%	0	35.0	0	0	35.0	22.3	14.4	0	9.6

Figure 6. Morphology measurements.

Holotype description: male, voucher number 92112, collected 8 July 1992, Bandera County, Texas, Lost Maples State Park. (FB page 87: "KB 7 {∧red 92112}—1/2 sec male flying by, I ans each of his. He land 6’ away from LED. I kept ans, he appr to 2’ and stopped flashing. I wait 15s. I flashed, he seemed to ans, I attr by ans a little further [toward LED]. He stop, I wait ca 15 sec, I flashed and had to 4-5 times at 10 sec intervals, then he “ans” or begin flashing I ans, etc he started [approaching] to LED again. He got to LED.” Morphological data: genitalia not extruded; from spread sheet—PNLen 3.4, ELLen 12.1, PNWid 4.5, ELWhum 2.4, ELWmid 3.3, LELVit 6.3, TotLen 15.5, PnRat 0.75, ElRat 1.38, VitRat 0.52; Colors: T 311, Py 1, Cx 2,V 233, Edg 8. Types will be deposited in the USNM.

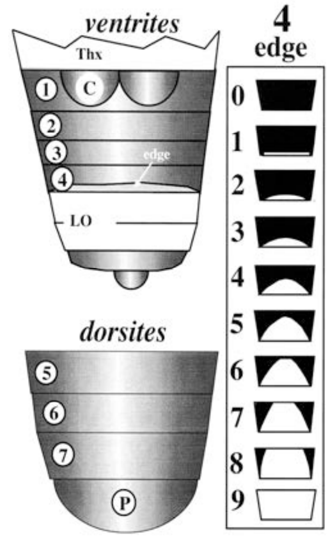


Figure 7. Topographic and splash key.

Taxonomic Note. The specific epithet recognizes Kathrin Stanger-Hall, an inspiring research associate who began work on Madagascar lemurs until she saw the light, and began to chase fireflies all across North America and do some interesting and instructive research on them. The suggested common name informally classifies this species with certain "Red" species that occur in Florida.

Augmented figure legends. 4. FP rate may not be as constant as even this line would indicate. The dot for Real County was based on trains of 10 flashes from each of four males, two from one site falling above the line, two from the other falling below. Suspecting the difference was due to pilot error I averaged the four sets. Still, I am not convinced. **5**. PM-traces. (**A-C**) Typical flash forms, with near symmetry except for slight tailing-off in last one-third of fall, and a duration at base of 56 mSec and at half-max about 22 mSec. (**D**) A metronomic series of flashes almost as regular as the 1-sec markers on the chart-channel just below. (**E**) Flash trains from two or three fireflies that were in the view of the PM-tube; note that they don’t fall into close synchrony but perhaps the tall spike at the right suggests that by chance some flashed together. In E the chart speed was 25mm/sec. Recordings A and B from Bandera Co., 26.1°C; C, Uvalde Co., 27.3°C, D and E .

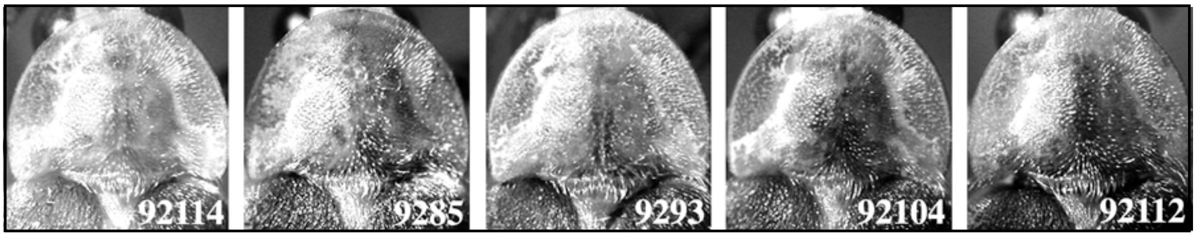
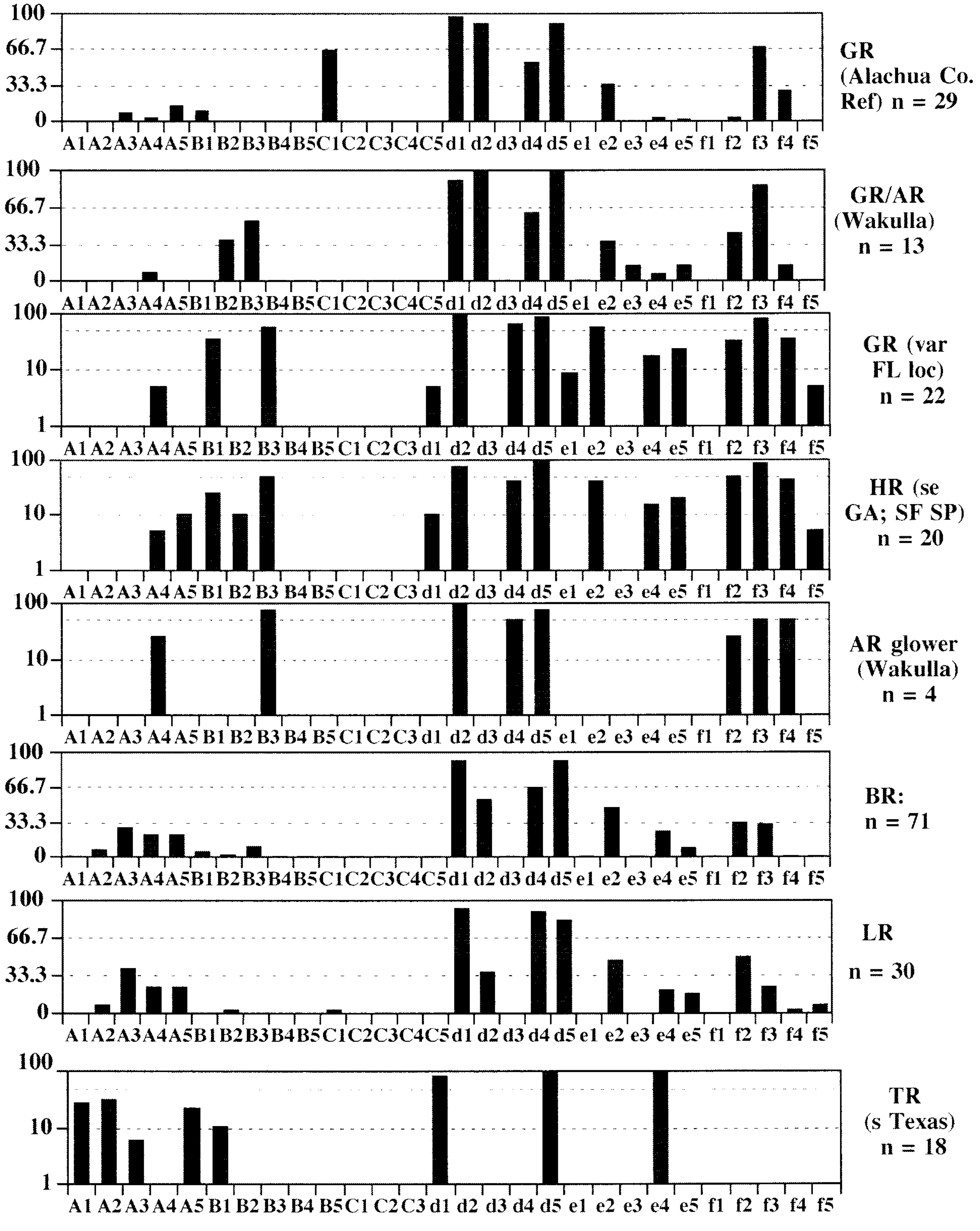


Figure 8. Voucher PN array.

Appendix

Red Group Vittagram Comparison



Chapter 43

Photuris lamarcki n. sp.

Sidewinder Firefly, *Photuris* D

This species is known from several localities in southeastern North America (**Figs. 1, 2**), and is one of an operational species-group characterized by crescendo flashes; however, with remarkable finesse, this species modulates its crescendos producing a rapidly-pulsed envelope (**Fig. 3**). Body color is often pale but not necessarily diffuse (**Fig. 4**), with pale hind coxae, and variously reduced PN vittigrams (**Fig. 32**). FPs typically are emitted while males course closely around and amongst the outer leafy boughs of bushes and low trees, in particular those edging forests near low, wet areas and streams (**Figs. 5, 6**). Specific identification depends upon detecting the rapid (nearly subliminal) modulations (**Figs. 3, 7, 8**). At temperatures below 20°/68° this flicker is seen in fast-flying emitters as a string of short dashes or points of light. **Figure 13** is a hand-held, open-shutter photo apparently showing 11± pulses of an FP. With transduction to an audible signal, the flicker is an easily recognized as a 25-50 Hz buzz. At higher temperatures, when the modulations are less likely to be visually detected, field clues are "soft" lime-green and weak crescendo flashes, that are emitted in *continuous* series at periods of 1.5-3.5-sec (18°/64°-25°/77°, **Fig. 9**). This firefly was not seen emitting an adjunct FP in any of the variads observed. Adult season in Florida begins in early May and sometimes continues to the end of September, but the prime season appears to be from mid May through July (**Figs. 10, 11, 33**). This is perhaps the *most* inviting and potentially rewarding N.A. firefly for behavioral, evolutionary, and neurological studies—in other words, as with its namesake, there is more than meets the eye in a superficial glance. To pick but one, it is the favorite.

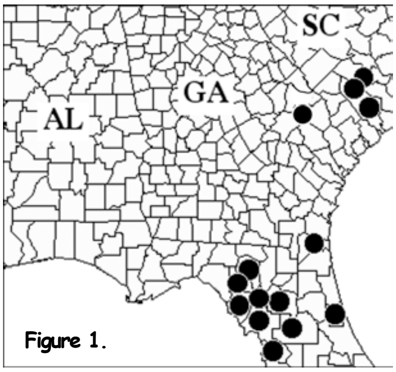


Figure 1.

Flashing behavior, ecology. This discussion develops around the *lamarcki* of Alachua County FL, the "Alachua Reference Population (**ARP**): the combined local demes (sites) were those of the Med Garden (Holotype locality, UF campus, **Figs. 12**); Gun Club and Airport Pond (**Fig. 34**) —the last two are probably

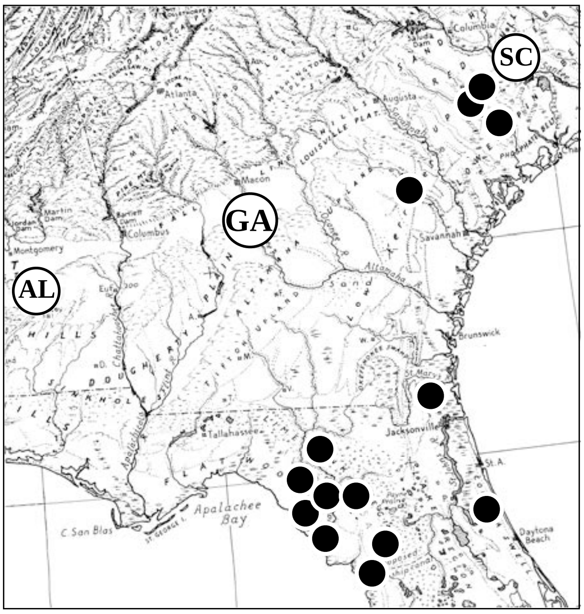


Figure 2. Physiographic perspective.

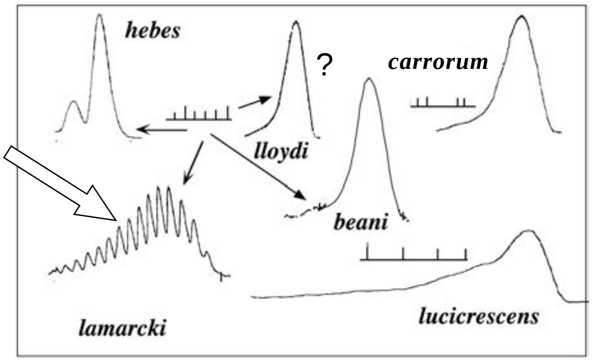


Figure 3. FPs of the "*lucicrescens* group."


Figure 4. Male with a single pseudoscorpion hitchhiker.

Figure 5. Forest Creek site, Gainesville.

Figure 6. Rivers Bridge site, SC.

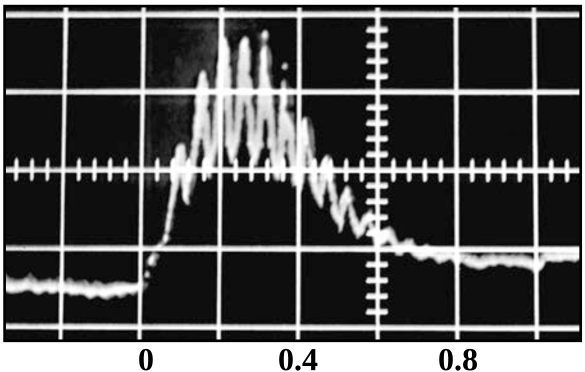


Figure 7. PM recording of FP on oscilloscope (AX: rel. int./sec).

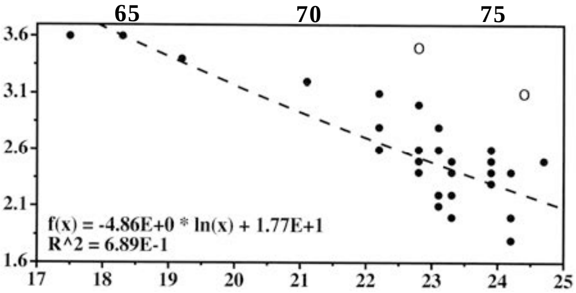


Figure 9. FP period (sec/temp)

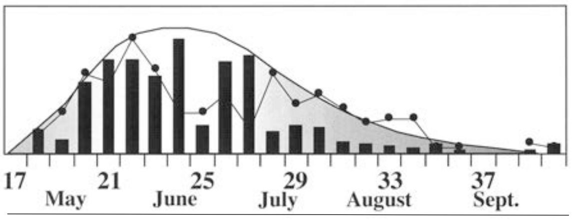


Figure 10. SESOBS ARP/FL (#/WOY; see Fig. 35).

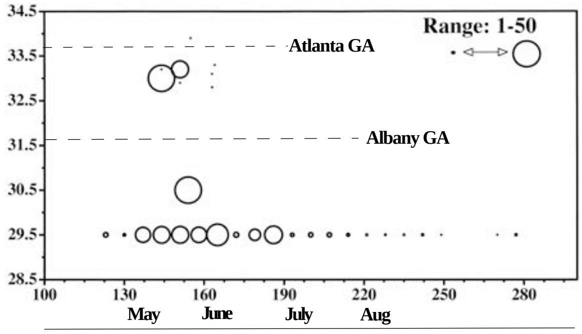


Figure 11. GESEDISOBS (AX: Lat/DOY/number)

Figure 12. SW corner of Med Garden, *lamarcki* site.

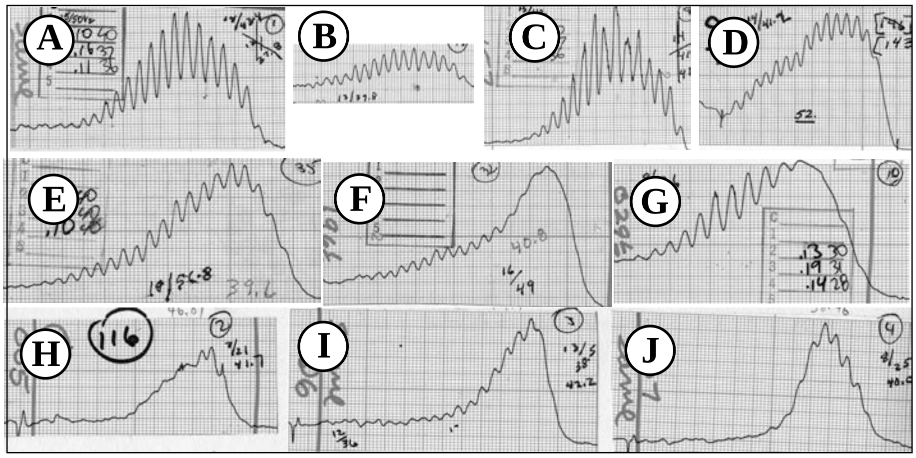


Figure 8. PM-records via chart recorder (AX: rel.int./time); see adjunct legends.

Figure 13. Field, photographic exposure: hand-held, open shutter, f1.4, ISO 400 (Med Garden, UF).

Figure 14. Cannibalism.

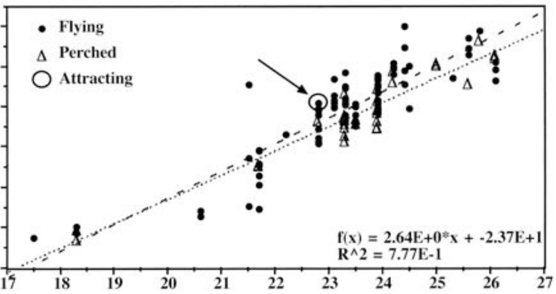


Figure 15. ARP FP modulation rate (AX: Hz/temp).

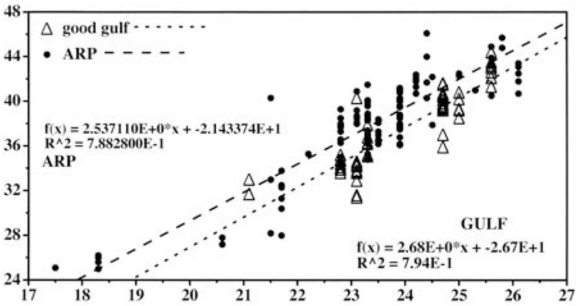


Figure 16. FP Hz. comparisons (AX: Hz/temp).

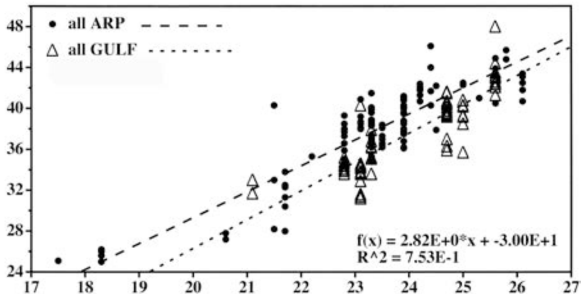


Figure 17. Compare FP Hz. (AX: Hz/temp).

part of the same extended local population and within a few hundred yards of each other.

Evening flight began about 1.9 Creps (n=7, r=1.5-2.5; C=26-28 min), slowly increased over several minutes, then continued for three or more hours. Males first flew low within forests and over herbs and grass under ecotonal boughs. As darkness deepened they flew higher, and out into the open. The FP often appeared as a short, soft, jade-green glow, with a weak crescendo, and occasionally its extremely rapid and virtually subliminal modulations were visible. Males emitted these flickers continuously, as they moved steadily and continuously, not in phrases/groups—without poising or pumping— around and over leafy boughs. They sometimes slowed their flight and curved or hooked at the end of an FP, and when landing emitted FPs in closer succession, presumably using them to illuminate a touchdown spot.

FPs are emitted at periods of 2-3 seconds (22°/71.5°-24°/ 75·; **Fig. 9**). FP base-duration in PM-records is variable: in Alachua County males it is about 700 mSec at 18°C and at 26°C, 400 mSec; it appears to be slightly shorter in Levy and Dixie Counties, and may perhaps be somewhat longer in Bamberg Co. SC.

Many PM-recordings do not show a well-formed crescendo *envelope,* and in the field, to the eye, the crescendo form may scarcely be noticed at first. The FP in **Figure 8B** would probably appear to be a short steady glow. Recordings such as **8C** perhaps result from males flying behind twig, with the two occlusions each perhaps being less than 8 milliseconds in duration. Perched males probably aim their lanterns to signal in different directions. Examination of hundreds of recorded FPs also suggests that there may be more than merely incidental emitter-detector misalignments involved in certain intensity variations.

Perhaps males conditionally vary the shape of the envelope and its modulations, and modify portions of each envelope according to circumstances? **Figures 8E and F** were emitted by the same male a few seconds apart; note the clear, strong crescendo in both, but a substantial difference in modulation depth and OFF slopes. Compare these with **8A**, emitted by a male in the same population.

Perhaps *lamarcki* males modify FPs not only to enhance signaling effectiveness and avoid rival intrusions, but to confuse illegitimate(?) receivers, chief among them being their own cannibalistic females (**Fig. 14**). Such predator-prey interactions may have a bearing on some FP differences that are noted between the ARP and other *lamarcki* populations. Though most FPs recorded in Alachua County were modulated from beginning to end with 15-20 modulations, the situation is different in the two Florida Gulf counties and Jenkins County GA. As a very rough estimate, 14 percent (9/64) of Gulf males, and 20 percent (2/10) of Jenkins County males emitted FPs that partially or completely lacked modulations. In most examples the “atypical” FPs were modulated only in the beginning.

Figures 8H-J were emitted by the same Georgia male a few seconds apart, and figure **8G** by a Gulf male. Sometimes it appears that the loss of modulation at the end of an FP was because the OFF transient was very abrupt, but that is not the case in the Gulf male pattern **8G**. **Figure 8D** is from a male from a "special" population/situation about 30 miles south of the ARP, east of Ocala on Rt. 40. This is discussed below. To completely resolve the question may require two PM-detectors and operators simultaneously recording the same emitter.

FP modulation *rate* averages range from ca 25 Hz at 18°C to ca 45 Hz at 26°C (**Fig. 15**). There are no apparent differences in modulation rate among the flickers of perched males, males being attracted to a decoy, and free-flying males, although there is a slight difference in the slopes plotted from present data, the flying slope appearing slightly steeper, but this probably not significant. The flickers of four males as they were being attracted to a decoy averaged 38.0 Hz and those of nine *flying* males at the same temperature averaged 36.2 Hz (**Fig. 15**, circle).

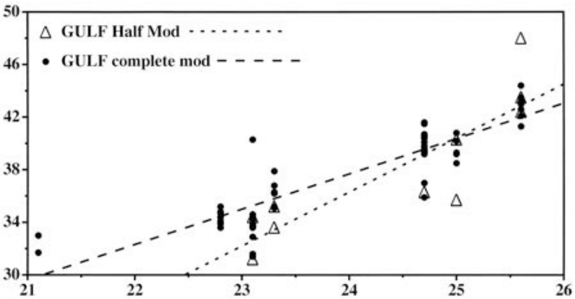


Figure 18. Compare Gulf FP mods (AX: Hz/temp).

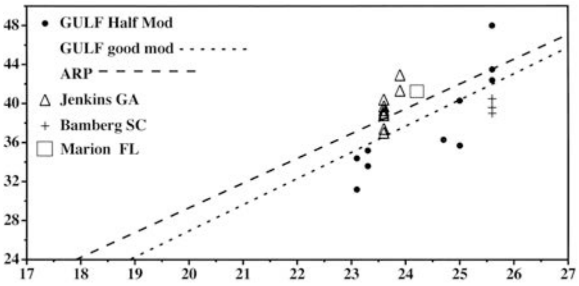


Figure 19. Compare FP modulation rates (AX: Hz/temp).

Figure 16 shows the slopes of ARP males and those of Gulf males emitting *only* (as could be known only from the limited PM-record sample) well-modulated FPs. Note the similarity, near identity of slopes but slightly different positions—Gulf males being about 2 Hertz slower at a given temperature. Note the similarity of correlation coefficients. **Figure 17** also compares the slopes of ARP and Gulf males, with the modulation rates of males with poorly modulated FPs are included—only slightly lowering "r". **Figure 18** compares the rate slopes of the two forms of FPs found in Gulf males, the difference perhaps/probably being accounted for by a small sample size.

Finally, **Figure 19** combines all these and data from other localities: showing regression *slopes* for the well-modulated FPs of ARP and Gulf males, and *symbols* for the FPs in Jenkins County GA, Bamberg County SC, Marion County FL, and the half- or poorly-modulated Gulf males. Two of the Jenkins County males emitted both modulated and poorly-modulated FPs; in the chart both place in the closely-tied vertical cluster. Marion County males came under heavy aerial attack from their females (see below). Modulation rates of flying and perched ARP and Marion County male modulation stats are virtually identical: $\bar{x}$, 41.4, 41.1 Hz; s, 1.7, 1.5; se, 0.39, 0.40; n, 18, 14; min, 36.8, 39; max, 43.3, 44.1.

Modulation rates may vary slightly within flickers. In 34 FPs from 13 ARP males, the average rate of four modulations measured at beginning, middle, and end dropped 5.5 percent from the beginning to the end, and from the middle to the end it increased 0.6 percent.

Bioluminescence color of *lamarcki* from three shipments (1967-68): peak: 557.5 (557-558.5); half max 531.3-598.3; width at half max 67. The color seems to compare with *Roscolux*® number 3304, "Tough Plusgreen". (Biggley, Lloyd, Seliger)

Technical Note. One method of observing *lamarcki's* rapid flicker modulations for field identification and collecting voucher specimens, would be to transduce them to audio pulses with a photo-detector coupled to a mini-speaker. An audio buzz of 25-50 Hz (depending upon temperature) would be immediately diagnostic of the presence of a high but unknown rate. A more expensive solution for rate evaluation in the field would be a flicker detector that displayed output on a time-calibrated LCD screen.

Predation. Female *lamarcki* are aggressive-mimic predators (**Fig. 20**), and responded to simulated 2-flash *macdermotti* patterns using both female answer and male

Figure 20. Aggressive mimic *lamarcki* and victim (*Pn. tanytoxus*).

competitive flash-injection timing (jel 1983). Males possibly also hunt via aggressive mimicry, based on female-like flash-response mimicry observed in two instances; however, mitigating against such a conclusion is the fact that never has a male *Photuris* of any species been found eating a firefly in the field though females have been found with male prey since the early 20th century (Hess, 1920; Williams, 1917).

Females are especially aggressive hawkers (aerial attackers) of light-emitting targets as demonstrated experimentally through the use of decoys, and were the main subjects of a study made on this phenomenon (Lloyd and Wing, 1982). First, an LED decoy was placed at the tips of three bamboo poles rotating around a hub (**Fig. 21A, B**). A variable-speed, low-voltage, high-torque DC motor powered the hub (**Fig. 22**). One LED blinked, one glowed, one remained unlit; all were covered with insect-sticking paste. Only the glowing target was struck by attackers (**Figs. 23A, B**)—whose feet were then wiped clean and the attackers released. Next, LEDs inside 8 mm translucent beads suspended from flashpoles were trolled along the bushes at the side of a sandy utility road (**Fig. 25**). Attackers struck flashing targets that also emitted dim (4%) glows a few seconds faster than flashing-only targets **Fig. 23C**). Next, a male prey was strung on a slippery, crooked wire below an LED target; the attacking female grasping the male slid down and off the wire, carrying the male to the ground where she began to eat him (**Fig. 24A-C**). On one occasion two attackers struck simultaneously, sparred, and one killed the other (**Figs. 25, 26**). See also pages 461, 462.

Figure 21. Aerial targets on orbiting poles.

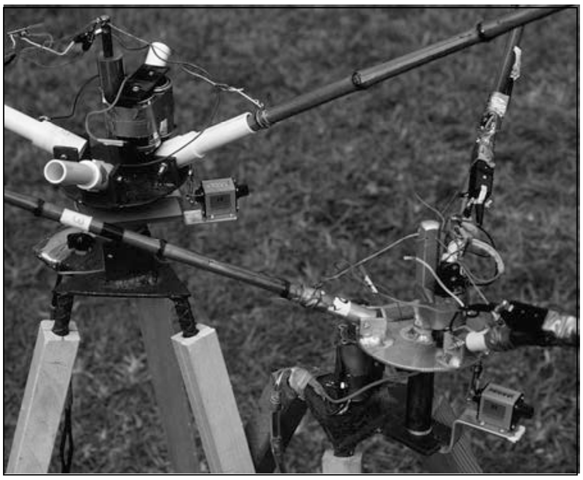


Figure 22. Tripods, pole-socket platforms, motors.

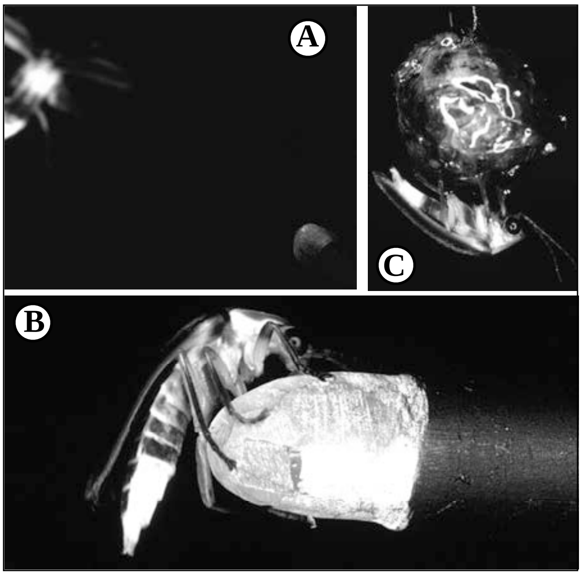


Figure 23. Decoys, attackers.

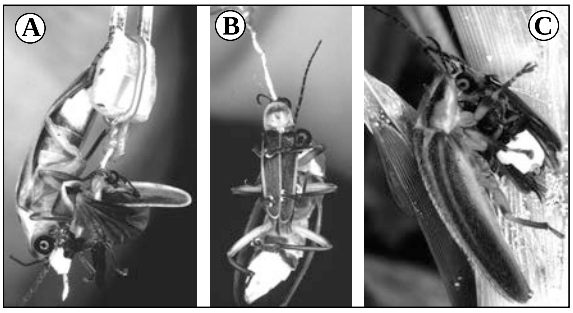


Figure 24. Decoy-attacking female finds male, eats.

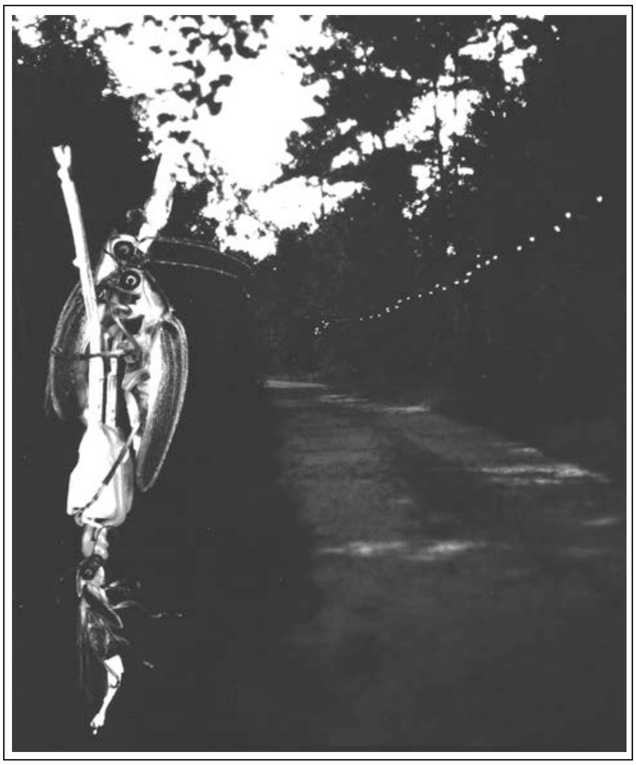


Figure 25. A composite illustration: macro- and time exposures: target LED/reward, a hooked male below, and two attackers fighting.

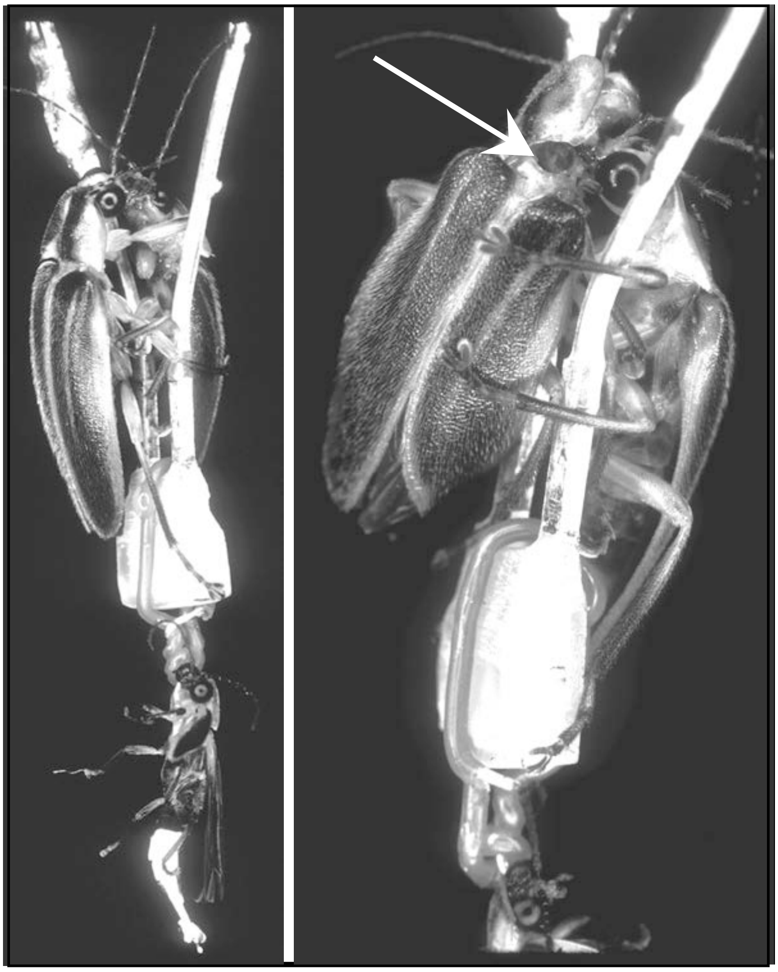


Figure 26. Sparring and decapitation; note torn cervical membane.

Of special interest, with respect to hawking predation, is the common occurrence of perched signaling in *lamarcki* males, and the possible counter-measure (CM) significance of the males' rapidly modulated signal. At a site on US. 40, east of Silver Springs (Ocala National Forest, Marion County, FL), at the Oklawaha bridge, Warren Prince (unpub.) found that males in one copse of shrubs seldom flew, though many were present. They signaled virtually exclusively from perches. When sticky flashpole targets were used they were struck quickly by hawking females. Enigmatically, at shrubs 75 yards away, on the north side of the bridge's western approach, males flew in apparent more typical fashion.

The rapid modulations of the FP resemble modulations produced by wing shuttering of luminescence emitted by flying fireflies. The appearance of a wingbeat flicker might indicate to an attacker that a beeline attack straight (in) from their preparatory hovering position must be through the arc of beating wings, which could knock the two apart reducing attack success and/or cause self-damage—when attackers approached a target they paused briefly a few inches away before striking. The presence of a flicker might cause a hawker to delay and benefit the target firefly. In other words, a false wingbeat (FP flicker) might evolve as mimicry of beating wings, and be seen from all angles of approach. This provides an alternative explanation for something observed many years ago. Observations had suggested that lampyrid wingbeat frequency might be temperature independent. In using a detector-recording system that would detect reflected light from their beating wings it was found that little light was reflected. It was assumed that this reduced reflection of their own emitted light for visual or defensive reasons. Perhaps firefly wings are opaque to enhance wingbeat shuttering as a CM against aerial-attacking *Photuris* or others? The possible connection between the FP-flicker and aerial attack holds taxonomic interest. The occurrence of partially-flickered or non-flickered FPs in Dixie and Levy County *lamarcki* males may indicate that predation is different or less common there. What information might an attacker receive from the air-pulses of beating wings was not examine—but such pulses are felt on the hand when males are decoyed to a penlight.

One additional thought on the origin of the high flicker rate: The similarity of the lantern flicker and wingbeat frequency raises the question whether the same neural oscillator could be involved. Flicker modulation rates found in other American

Figure 27. Hitchhiking arachnids.

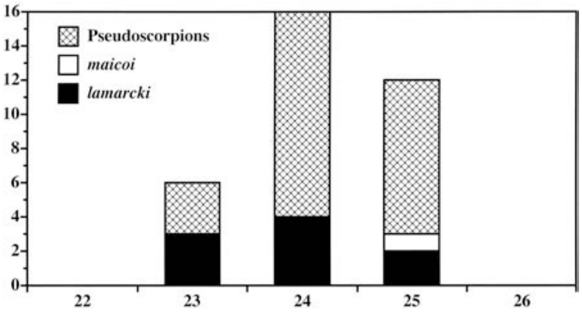
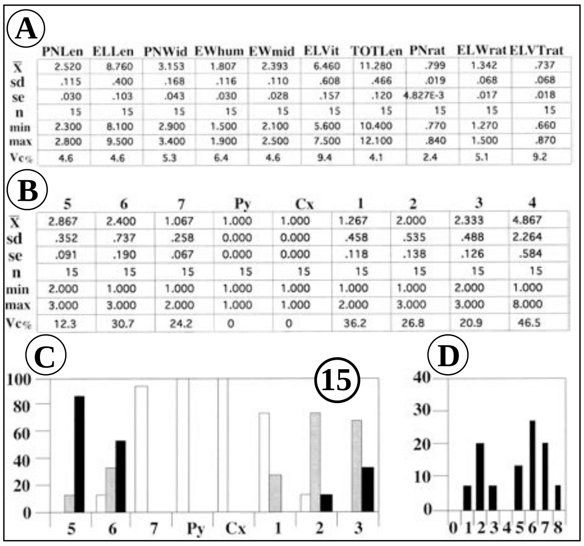


Figure 28. *Paratemnus* phoresy (AX: n/WOY).

Figure 29. *Paratemnus* female with young; photo by Rich Gary.



	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.520	8.760	3.153	1.807	2.393	6.460	11.280	.799	1.342	.737
sd	.115	.400	.168	.116	.110	.608	.466	.019	.068	.068
se	.030	.103	.043	.030	.028	.157	.120	4.827E-3	.017	.018
n	15	15	15	15	15	15	15	15	15	15
min	2.300	8.100	2.900	1.500	2.100	5.600	10.400	.770	1.270	.660
max	2.800	9.500	3.400	1.900	2.500	7.500	12.100	.840	1.500	.870
Vc%	4.6	4.6	5.3	6.4	4.6	9.4	4.1	2.4	5.1	9.2

	5	6	7	Py	Cx	1	2	3	4
X̄	2.867	2.400	1.067	1.000	1.000	1.267	2.000	2.333	4.867
sd	.352	.737	.258	0.000	0.000	.458	.535	.488	2.264
se	.091	.190	.067	0.000	0.000	.118	.138	.126	.584
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	1.000
max	3.000	3.000	2.000	1.000	1.000	2.000	3.000	3.000	8.000
Vc%	12.3	30.7	24.2	0	0	36.2	26.8	20.9	46.5

FigTable 30. Morphology data: Holotype locality.

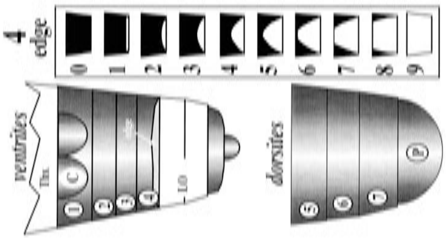


Fig. 31. Topographic and splash key.

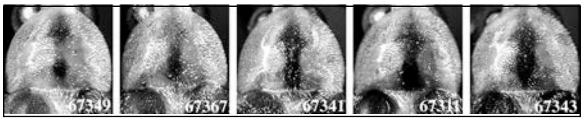


Figure 32. Array of voucher vittigrams from Med Garden.

Taxonomic, other notes. The specific epithet pays tribute to the French naturalist Jean Baptiste Lamarck, whose work, now 200 years in the past, like the flashing of this firefly, cannot be properly appreciated by the ill informed, or with merely a passing glance. His most oft-cited contribution was, in his time, the only scientific alternative to the hopeful hallucinations and corrupted intellects of lordly contemporaries. The suggested common name refers to the hawking tactic that is so well-developed in *lamarcki* females, by which they "home in" on energy emitted by their targets, like the sidewinder rattlesnake and aircraft attack missile.

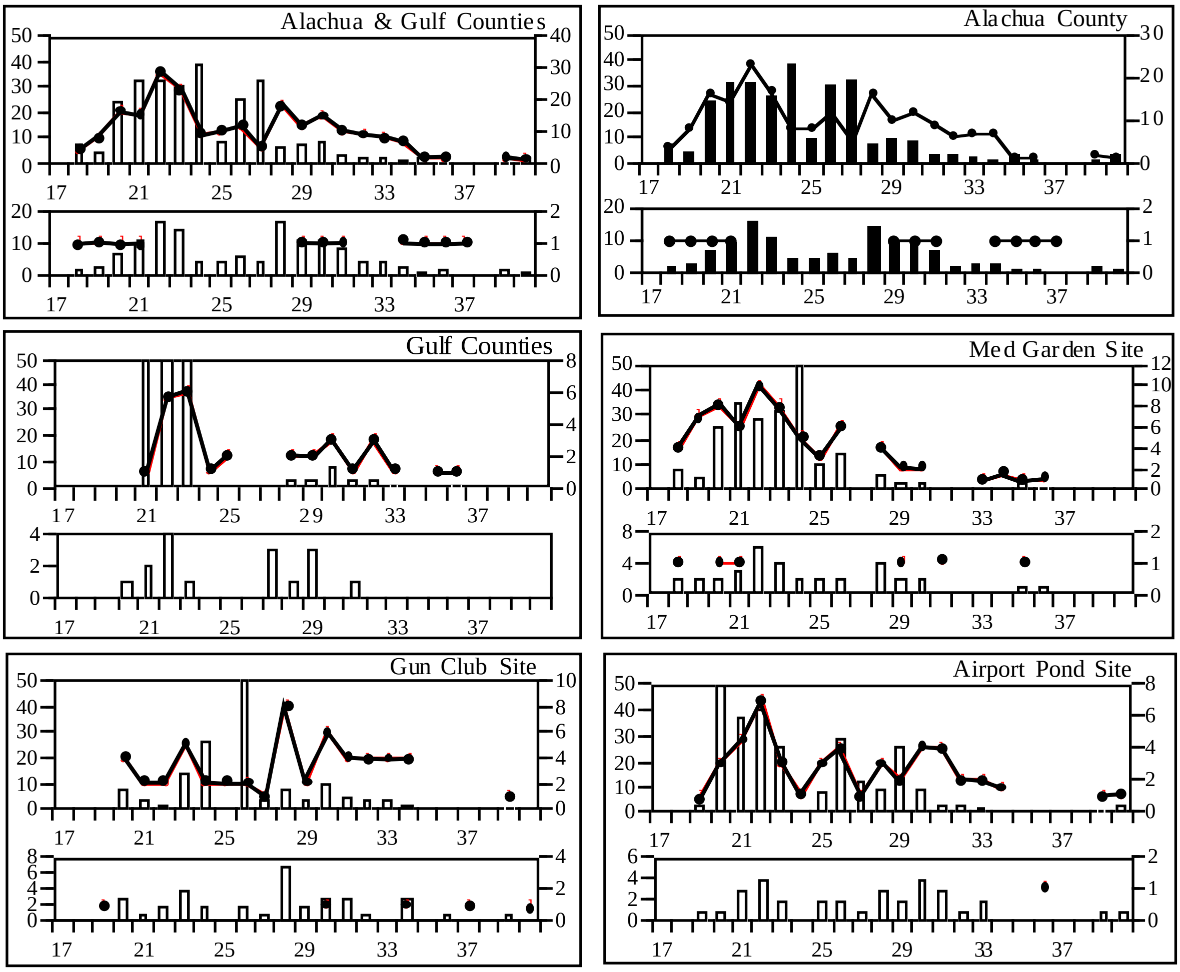
Photuris are much lower, around 12 Hz; that is, there are yet no known species to examine as possible evolutionary examples or models of *intermediate* rates and their ecological circumstances. Might *lamarcki* ancestors have made the leap in one step by coupling to or duplicating a neural wingbeat-oscillator circuit?

Phoresy. *P. lamarcki* at the UF campus Med Garden site was the most common host of the phoretic pseudoscorpion *Paratemnus elongatus* (Banks) (**Figs. 4, 27**). These arachnids preferentially attach to lampyrids, and to date all hitchhikers have been females (Lloyd and Muchmore 1974; Lloyd et al 1975; jel unpub.). Up to five were found attached to a single firefly, and in a measured example their collective weight was 29 percent that of their host. A firefly with two riders is barely able to fly and one with five has difficulty walking. The known seasonal window for attachment in Gainesville is about three weeks, 4-24 June (**Fig. 28**). These arachnids are social, with extended maternal care, and it has been suggested that phoresy in this species is family migration (**Fig. 29**).

Morphological data. General morphological means are (n=15): PNL 2.5, ELL 8.8, PNW 3.2, EWhum 1.8, EWmid 2.4, ELVit 6.5, TOTLen 11.3, PNrat 0.80, ELWrate 1.34, ELVTrat 0.74 (**FigTable 30A**, with related stats). Data for the colors of abdominal plates and hind coxae in **FigTable 30B-C**, and splash-color of the pre-lantern ventrite in **30D**. **Figure 31** is key to skeletal plates and splashing on ventrite 4. Such data for other populations are given in **FigTable 36**. An array of vittagrams is in **Figure 32**.

Holotype Description. male, voucher number 67341, collected 28 May 1967, Alachua County, Florida, Univ. Florida campus, Medicinal Plant Garden. FB page 64: One of a series of six, collected after emitting their crescendo-flicker FP; series voucher numbers 67341-67346. Morphological data: from spread sheet—PNLen 2.5, ELLen 9.0, PNWid 3.1, ELWhum 1.8, ELWmid 2.4, LELVit 6.5, RELVit 6.6 , TotLen 11.5, PnRat 0.80, ElRat 1.36, VitRat 0.73; Colors: T 112, Py 1, Cx 1, V 122, Edg 8. Types will be deposited in the USNM.

The FP flicker is often not discernible visually, though its measured rate would place it within the limit of experimental values given for human flicker fusion. Perhaps the flicker is "subliminal" (for humans) because the modulations differ from those used for testing human vision—fireflies do not emit square waves of light, with troughs between modes falling to zero. Rather, Sidewinder modulations are roughly sinusoidal, and often maintain a 30-50 percent intensity level in troughs, though there is variation, and trough drops range 20-90 percent.



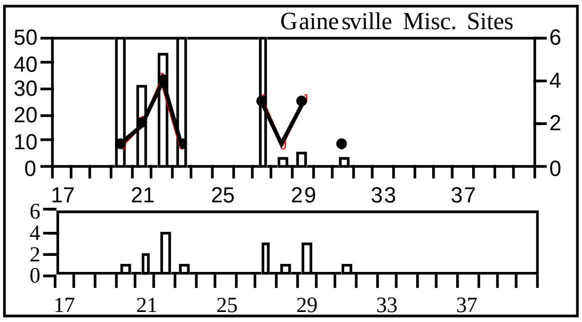


Figure 33. SESOBS from various ARP and other sites.

Figure 34. Airport Pond locality, 1965; stream in front of tree row.

A Problem In "Group" Selection?, Just For Thinking: Aerial Attack On Males By Their Own Females

Females of *Photuris lamarcki* attack aerial/flown LED targets that emitted flashes and dim glows; when an immobilized *Photinus* male was attached to the LED, the attacker carried it to the ground and began to eat it (Lloyd and Wing, 1983). When two attackers struck the LED at the same time, one began to eat the other. The FP emitted by males of *lamarcki* is a jade-colored crescendo that is modulated at the lantern at 35-45 Hertz, frequency depending upon ambient temperature. This rate is similar to the wing-beat frequency of fireflies—and may suggest to a physiologist the neural/cellular origin of the FP's oscillator? The following consideration connects these two behaviors, female aerial attack and male FP modulation rate.

When an attacker strikes a flying male, the beating wings of the male target would be expected knock the two apart, spoiling the attack, and perhaps damaging the wings of the attacker. Females would be expected to maneuver to achieve an angle of attack that avoided flapping wings—which angle they would determine by FP-shuttering by the wings. Hence, selection would favor an FP modulation rate similar to that of wing-beats once it occurred because females would detect modulations from all angles, delaying attack. As a possibly relevant aside, a wing-modulation detector that was expected to bounce light off flapping wings for later oscilloscope analysis, failed to work as expected and after brief testing it was put aside: perhaps firefly wings are non-reflective and opaque … defensive countermeasures?

Many years ago an Entomology graduate student at UF, Warren Prince, discovered an unusual population of *lamarcki* at the northwest end of the Oklawaha River bridge east of Ocala (route 40). The activity site was across the tops of 7-12’ shrubs (wax myrtle?), about 150’ from the River. Females attacked their own flying males and some males emitted their FPs from perches atop the shrubs. On the night following Warren’s discovery several of us, including Tim Forrest, John Sivinski, and Steve Wing, visited the site with Warren and saw what he had described.

The flow diagram arranges several steps in an evolutionary development of this behavior, and “logical” consequences; it illustrates the conundrum imagined here. We ask, how would it be possible for natural selection bring aerial, conspecific cannibalism in a local population to a halt, because as soon as an attack (allele) occurs it will be favored in individuals that do it, and ultimately all deme-members will be disadvantaged equally. Individuals that emigrate will carry eggs or sperm with this poison and plant it in other demes—females with loaded spermathecae may found demes with it.

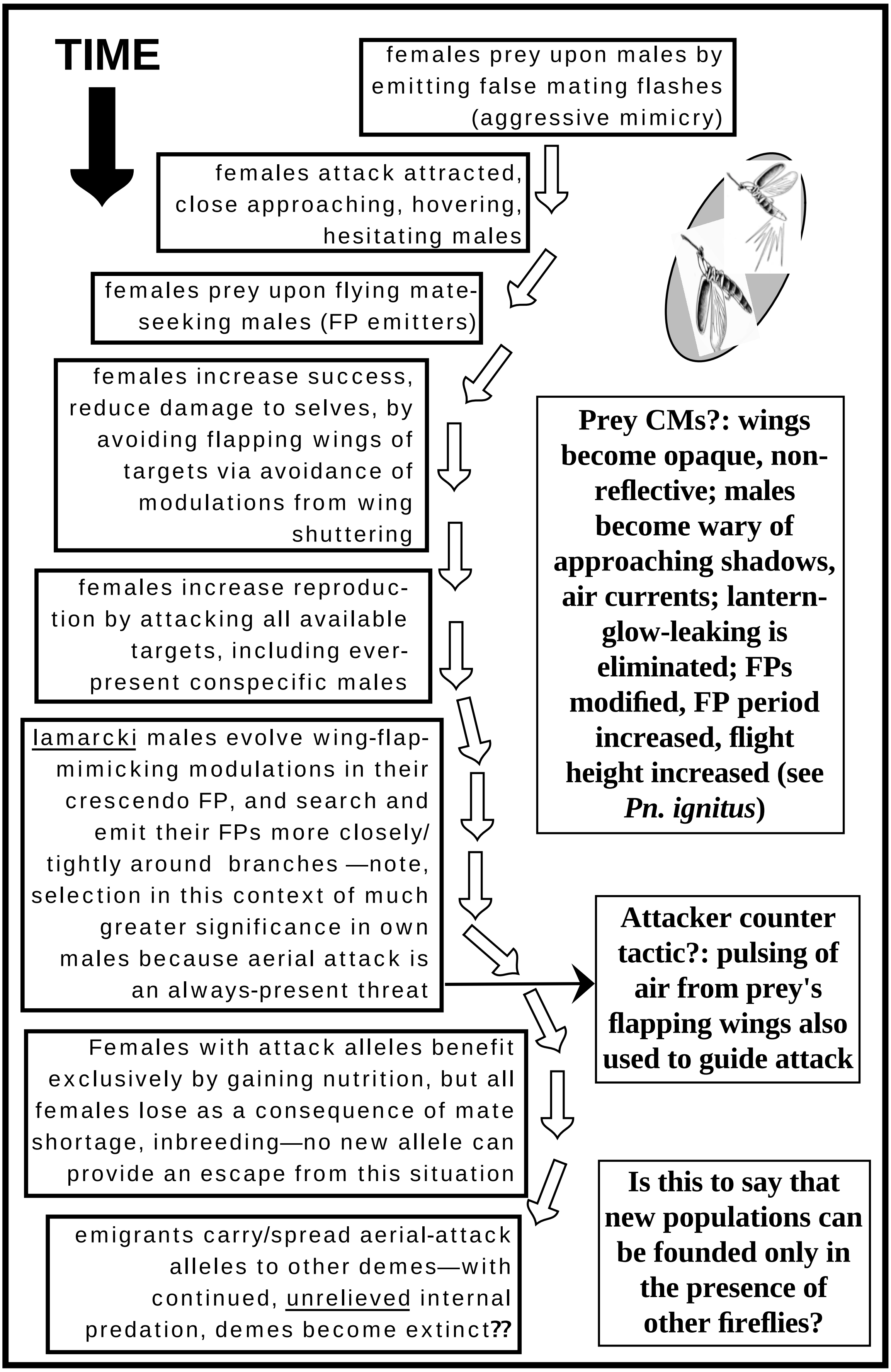
Will not local populations eventually become extinct once the allele for such aerial attack is established, and continues to increase in frequency? What can stop it? This is to say, the deme, the *Group* will vanish? Though individual countermeasures occurred as deterrents—the unusually high-frequency FP flicker, as example—it would make little difference. The Ocala bridge population apparently revealed this to be ineffective, sometimes? Curiously, females could even favor flickering males, in the context of sexual selection, for the usually-suggested reasons! (This concept having replaced Providence as the ultimate confusion in understanding adaptation/selection.)

Somewhere in this dismal equation the presence and number of males of other resident flashing (prey) species must be entered—for those old enough to remember, ancient discussions and conclusions concerning *prudent* predators flicker across the mind. A sample of geographically disbursed *lamarcki* demes will certainly reveal clues to reality, to demise, delay, or escape. and experimentation with populations of LEDs is a possibility. Can it possibly be that ultimately, in the end, this self-serving cannibalism will end each lineage that evolves it? Photo-multiplier recordings of a *lamarcki* variad in Dixie County (Gulf region) was modulated over only half of its crescendo FP; on the other hand, recordings from a South Carolina deme were, apparently, like those seen in Alachua County populations (north central Florida)—this is not to say that the two are in contact, only on borrowed time?

Figure 35. Flow chart suggesting an evolutionary sequence for the rise, escapes, and eventual demise of local populations of *Photuris lamarcki*. See them while they last.

Augmented figure legends. **8**. Chart records of photomultiplier recordings of *lamarcki* FPs: (**A**) Almost an idealized ARP FP (23.9°C; 25 June 1967); (**B**) A weak glow-appearing ARP FP (24.2°C; 26 June 1967); (**C**) An ARP FP with two abruptly reduced modulations, perhaps partial twig occlusions (24.4°C; 26 June 1967); (**D**) FP from a Marion Co. male perched in the copse with hawking females (24.4°C; 21 July 1981); (**E, F**) FPs emitted by the same ARP male a few seconds apart; 23.9°C; 19 June 1969); (**G**) FP of Gulf male, Levy County (23.1°C; 7 June 1968); (**H-J**) Three FPs emitted by a Jenkins Co. GA male, near Magnolia Springs SP (12 June 1978; 23.9°C). **12**. Med Garden site on the UF campus, the Holotype locality. From 1960 to about 1980 *lamarcki* was abundant. Since then the bushes and woods have become less dense and an adjacent stream has been stripped bare of its vegetation and a reflecting mud-hole added; the water table does not seem to have changed. Lake Alice is beyond the tree line about 75 yards. **13**. Photograph with a hand-held 35 mm camera aimed a passing male (f1.4 Auto-Nikor, Kodak ISO 400 slide film). Note the doubled, slightly out-of-phase illuminations in the pulses of light—perhaps the two lantern ventrites do not fire together (see *hebes* section). **16**.Temperature regressions of FP modulation rates of ARP males compared with

(cont. p. 219.)



TIME

females prey upon males by emitting false mating flashes (aggressive mimicry)

females attack attracted, close approaching, hovering, hesitating males

females prey upon flying mate-seeking males (FP emitters)

females increase success, reduce damage to selves, by avoiding flapping wings of targets via avoidance of modulations from wing shuttering

females increase reproduction by attacking all available targets, including ever-present conspecific males

lamarcki males evolve wing-flap-mimicking modulations in their crescendo FP, and search and emit their FPs more closely/ tightly around branches —note, selection in this context of much greater significance in own males because aerial attack is an always-present threat

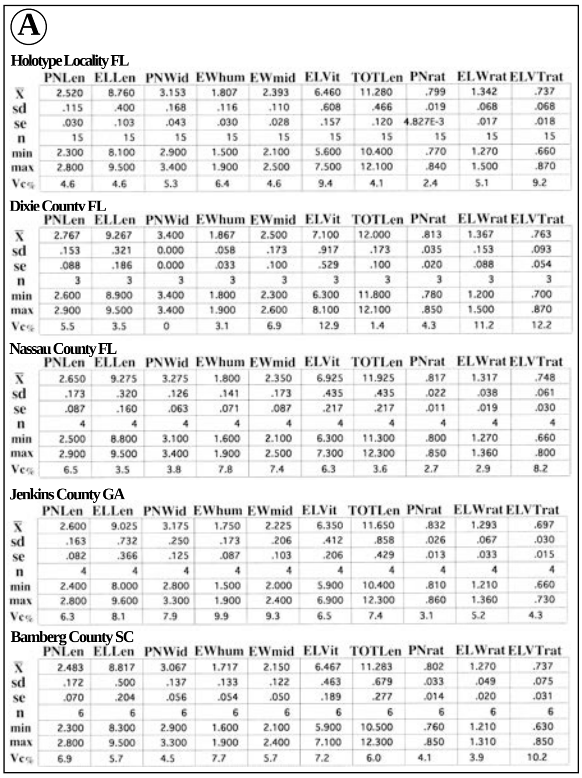
Females with attack alleles benefit exclusively by gaining nutrition, but all females lose as a consequence of mate shortage, inbreeding—no new allele can provide an escape from this situation

emigrants carry/spread aerial-attack alleles to other demes—with continued, unrelieved internal predation, demes become extinct**??**

Prey CMs?: wings become opaque, non-reflective; males become wary of approaching shadows, air currents; lantern-glow-leaking is eliminated; FPs modified, FP period increased, flight height increased (see *Pn. ignitus*)

Attacker counter tactic?: pulsing of air from prey's flapping wings also used to guide attack

Is this to say that new populations can be founded only in the presence of other fireflies?



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Holotype Locality FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.520	8.760	3.153	1.807	2.393	6.460	11.280	.799	1.342	.737
sd	.115	.400	.168	.116	.110	.608	.466	.019	.068	.068
se	.030	.103	.043	.030	.028	.157	.120	4.827E-3	.017	.018
n	15	15	15	15	15	15	15	15	15	15
min	2.300	8.100	2.900	1.500	2.100	5.600	10.400	.770	1.270	.660
max	2.800	9.500	3.400	1.900	2.500	7.500	12.100	.840	1.500	.870
Vc%	4.6	4.6	5.3	6.4	4.6	9.4	4.1	2.4	5.1	9.2

Dixie County FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.767	9.267	3.400	1.867	2.500	7.100	12.000	.813	1.367	.763
sd	.153	.321	0.000	.058	.173	.917	.173	.035	.153	.093
se	.088	.186	0.000	.033	.100	.529	.100	.020	.088	.054
n	3	3	3	3	3	3	3	3	3	3
min	2.600	8.900	3.400	1.800	2.300	6.300	11.800	.780	1.200	.700
max	2.900	9.500	3.400	1.900	2.600	8.100	12.100	.850	1.500	.870
Vc%	5.5	3.5	0	3.1	6.9	12.9	1.4	4.3	11.2	12.2

Nassau County FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.650	9.275	3.275	1.800	2.350	6.925	11.925	.817	1.317	.748
sd	.173	.320	.126	.141	.173	.435	.435	.022	.038	.061
se	.087	.160	.063	.071	.087	.217	.217	.011	.019	.030
n	4	4	4	4	4	4	4	4	4	4
min	2.500	8.800	3.100	1.600	2.100	6.300	11.300	.800	1.270	.660
max	2.900	9.500	3.400	1.900	2.500	7.300	12.300	.850	1.360	.800
Vc%	6.5	3.5	3.8	7.8	7.4	6.3	3.6	2.7	2.9	8.2

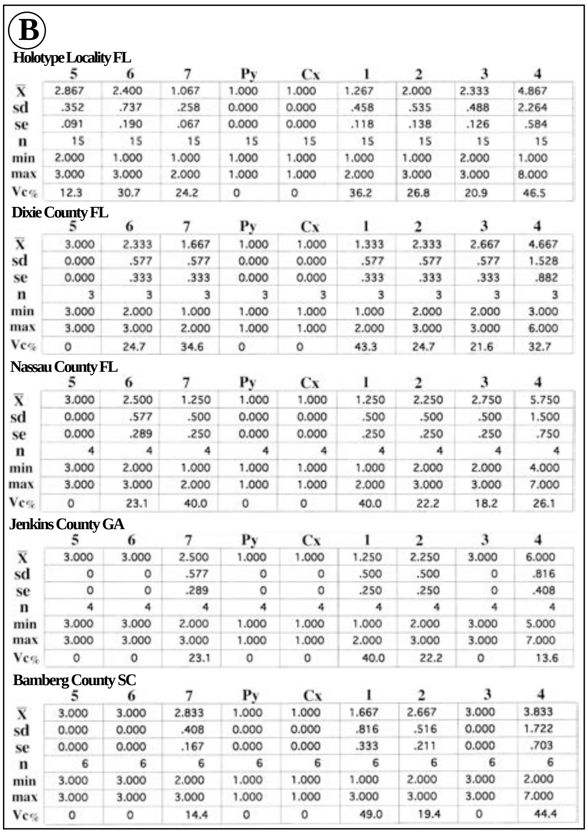
Jenkins County GA

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.600	9.025	3.175	1.750	2.225	6.350	11.650	.832	1.293	.697
sd	.163	.732	.250	.173	.206	.412	.858	.026	.067	.030
se	.082	.366	.125	.087	.103	.206	.429	.013	.033	.015
n	4	4	4	4	4	4	4	4	4	4
min	2.400	8.000	2.800	1.500	2.000	5.900	10.400	.810	1.210	.660
max	2.800	9.600	3.300	1.900	2.400	6.900	12.300	.860	1.360	.730
Vc%	6.3	8.1	7.9	9.9	9.3	6.5	7.4	3.1	5.2	4.3

Bamberg County SC

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.483	8.817	3.067	1.717	2.150	6.467	11.283	.802	1.270	.737
sd	.172	.500	.137	.133	.122	.463	.679	.033	.049	.075
se	.070	.204	.056	.054	.050	.189	.277	.014	.020	.031
n	6	6	6	6	6	6	6	6	6	6
min	2.300	8.300	2.900	1.600	2.100	5.900	10.500	.760	1.210	.630
max	2.800	9.500	3.300	1.900	2.400	7.100	12.300	.850	1.310	.850
Vc%	6.9	5.7	4.5	7.7	5.7	7.2	6.0	4.1	3.9	10.2

FigTable 36A. ARP and other variads(?).



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Holotype Locality FL

	5	6	7	Py	Cx	1	2	3	4
X̄	2.867	2.400	1.067	1.000	1.000	1.267	2.000	2.333	4.867
sd	.352	.737	.258	0.000	0.000	.458	.535	.488	2.264
se	.091	.190	.067	0.000	0.000	.118	.138	.126	.584
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	1.000
max	3.000	3.000	2.000	1.000	1.000	2.000	3.000	3.000	8.000
Vc%	12.3	30.7	24.2	0	0	36.2	26.8	20.9	46.5

Dixie County FL

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.333	1.667	1.000	1.000	1.333	2.333	2.667	4.667
sd	0.000	.577	.577	0.000	0.000	.577	.577	.577	1.528
se	0.000	.333	.333	0.000	0.000	.333	.333	.333	.882
n	3	3	3	3	3	3	3	3	3
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000
max	3.000	3.000	2.000	1.000	1.000	2.000	3.000	3.000	6.000
Vc%	0	24.7	34.6	0	0	43.3	24.7	21.6	32.7

Nassau County FL

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.500	1.250	1.000	1.000	1.250	2.250	2.750	5.750
sd	0.000	.577	.500	0.000	0.000	.500	.500	.500	1.500
se	0.000	.289	.250	0.000	0.000	.250	.250	.250	.750
n	4	4	4	4	4	4	4	4	4
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	4.000
max	3.000	3.000	2.000	1.000	1.000	2.000	3.000	3.000	7.000
Vc%	0	23.1	40.0	0	0	40.0	22.2	18.2	26.1

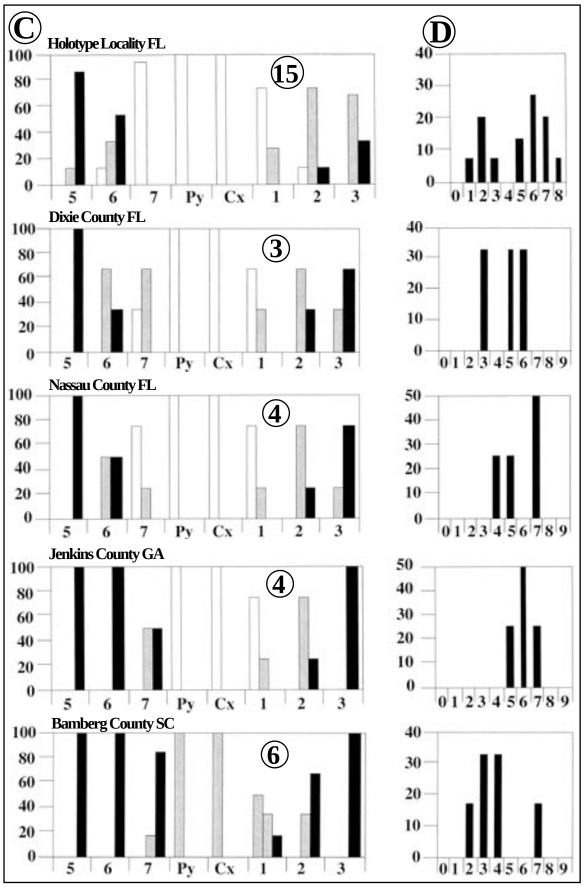
Jenkins County GA

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	2.500	1.000	1.000	1.250	2.250	3.000	6.000
sd	0	0	.577	0	0	.500	.500	0	.816
se	0	0	.289	0	0	.250	.250	0	.408
n	4	4	4	4	4	4	4	4	4
min	3.000	3.000	2.000	1.000	1.000	1.000	2.000	3.000	5.000
max	3.000	3.000	3.000	1.000	1.000	2.000	3.000	3.000	7.000
Vc%	0	0	23.1	0	0	40.0	22.2	0	13.6

Bamberg County SC

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	2.833	1.000	1.000	1.667	2.667	3.000	3.833
sd	0.000	0.000	.408	0.000	0.000	.816	.516	0.000	1.722
se	0.000	0.000	.167	0.000	0.000	.333	.211	0.000	.703
n	6	6	6	6	6	6	6	6	6
min	3.000	3.000	2.000	1.000	1.000	1.000	2.000	3.000	2.000
max	3.000	3.000	3.000	1.000	1.000	3.000	3.000	3.000	7.000
Vc%	0	0	14.4	0	0	49.0	19.4	0	44.4

FigTable 36B. ARP and other variads(?).



FigTable 36C, D. ARP and other variads(?).

Gulf males whose FPs were completely modulated—i. e., like those of ARP males. **17**. The same as Figure 16 except that Gulf males with half-modulated FPs are *included*, lowering the correlation coefficient only slightly. **18**. A comparison of modulations rates of two FP forms occurring in Gulf males, half (partially)- and fully-modulated. (A third FP form recorded is unmodulated.) **19**. A summary of all FP classes, including data from South Carolina and Georgia localities, as indicated. **20**. A *lamarcki* female with a *Photinus tanytoxus* male she has attracted with false mating signals. She hangs beneath the leaf with the male's feet away from a substrate that he could grab. His abdomen is already chewed and mangled. His females live in burrows and have not been found more than a few inches from the entrance, but this (ill-adapted) male climbed up this grass blade to reach the predator. **21**. Tripod setup for flying LED targets. A high-torque, variable speed, battery-operated DC motor flew three targets at the same elevation (here separated for the photo in **21B**). On an evening, after a few captures all of the active neighborhood hunters seemed have been removed, though they were released immediately after they had the sticking paste wiped off their feet. Note the skyglow over Gainesville in the background; skyglow is an important conderation for experiments because it provides a background to silhouette/ observe attacks. **22**. Poles in their holder which are attached to the circular platform atop the DC motor (dark cylinder below aluminum disk). Trip-counters count the number of rotations, a meaningless datum. **23**. Attackers and LED targets: (**A**) The female (upper left) approaches the target at lower right as it orbits the tripod hub; the bright flare is the reflection of the camera flash from her pale thorax. (**B**) The female has landed and her feet have become stuck in the paste. (**C**) A spherical target flown from a hand-carried flashpole has captured an attacker. The flat LED was inside the bead—this provided a more equal emission of light in all directions. **24**. (**A**) A flashpole-flown target with a naked LED and a male impaled on a slightly-bendy, slippery wire below; the LED attracted an attacker, and she has male in her grasp, (**B**) is sliding down the wire, drops to the ground, and (**C**) begins eating him. **25**. A composite photo with sparring females superimposed on a time exposed photo of the flashing target being carried along the shrubs at the edge of the sandy utility road. Gainesville skyglow provided the back-lighting needed to see attacks. **26**. Two *lamarcki* females have attacked the flashpole target simultaneously and fight. **26**. The female at the right has severed the neck/thorax of her rival. The arrow points to the gaping space between the pronotum (with head inside) and the elytra and mesonotum. **27**. A *lamarcki* with three pseudoscorpions, two on a leg and one clamping an elytron. They persist indefinitely leaving such fireflies with no further reproduction options. **28**. Phenology of *Paratemnus elongatus* phoresy at the Med Garden, UF campus (4-24 June). One species was an abundant resident and the other a passing rover. The significance of riding is not known. Hosts are not eaten, nor scavanged after death and all *riders* have been females (n=24). They usually attach to the legs, holding on by one or both chelae (pincers), with as many as five riding one firefly. These arachnids are found between the paper-thin laminations of pine bark and perhaps the fireflies had landed on their trees. A clue to this situation is the continuous emission of single, erratic flashes on the ground. In this small sample the ratio of passengers to *lamarcki* increased with each week: 1:1, 3:1, 4.5:1—during week 25 the two *lamarcki* had four and five riders. **29**. Before hatching these juveniles appeared as elongate kernels of corn poking out around the posterior margin of this mother's abdomen. Discovery and photo by Rich Gary.

"Lamarck is remembered primarily as a pre-Darwinian evolutionist who proposed [the first mechanism]—the inheritance of acquired characteristics—to explain evolutionary change. But this view of Lamarck does not do justice to Lamarck's own conception of organic change, nor does it indicate how Lamarck's views on organic change related to the rest of his biological thinking or his scientific and philosophical work as a whole."

"Lamarck's problem was that he was unable to relate his broad hypotheses to factual evidence in such a way as to cause his contemporaries to treat his hypotheses as profound insights rather than unfounded speculation. To say this does not deny the great profundity of Lamarck's idea that the diversity of living beings was the product of natural causes operating over immense periods of time."

Richard W. Burkhardt, Jr., 1984, in H. Elliot translation of Lamarck's 1809 "Zoological Philosophy"; Chicago)

"As Burkhardt explains in his contribution to this volume, Lamarck's acceptance of the inheritance of acquired characteristics was not in the least unusual for his time. Nor was the inheritance of acquired characteristic central to his transmutation theory. According to Lamarck, evolutionary change had a direction, but this direction was produced by a tendency toward increasing complexity or perfection that Lamarck thought was inherent in all living creatures, not by the inheritance of acquired characteristics."

"Substantial evidence indicates that Darwin was a special creationist when he read the second volume of Lyell's principles and remained a special creationist for a good long time thereafter. … In science, posing the right question in a tractable way is often half the battle. … Lyell's rejection of Lamarck's theory did more to further the cause of evolutionism than did the advocacy of all previous evolutionists combined (Corsi 1978)." David L. Hull. 1984, in H. Elliot translation of Lamarck's 1809 "Zoological Philosophy"; Chicago)

With appropriate reservations and understanding regarding the meaning of the word "perfection," dear reader, how capable are you of debating both sides of Lamarck's "complexity/perfection" question, considering the infinite layering and fine-tuning occurring over long periods of time that is found in much adaptation, and also, perhaps even the complexity in the DNA of, say, parasitic organisms that have secondarily greatly simplified and reduced their anatomical structure? jl

Chevalier de Lamarck
Jean Baptiste Pierre Antoine de Monet

Chapter 44

Photuris lineaticollis (Motschulsky) 1854

Giant Red, GR

Several *Photuris* species have a distinctive, rufus (brick red) trim/ground color, where other *Photuris* usually are trimmed in yellowish to dusky. "Reds" are placed in a “Red Group” and nicknames used for them reflected this: Giant Red (**Fig. 5**), Big Red, Hitched Red, Long Red, Little Red, Texas Red, and Lesser Texas Red. They differ in their FPs and some are recognized with confidence only by their FPs. Geographic occurrence is useful for diagnosis but with further field study it may become less so. To a small degree, morphological characters may be useful, though analyses of vittagrams and body color were not found useful. Which of these fireflies Victor Motschulsky actually collected on his journey through Florida, if any, is unknown; no specimen has been identified as his “holotype” but it could have been one of those discussed here (Notes below). From among these, a variad with a simple flash at about four seconds, and that occurs in Alachua County is selected as Motschulsky's *lineaticollis* s. s. for reference; it may occur more widely. Other of these forms have been given formal names, including *dorothae*, *gentrae*, *lynfaustae*, *katrinae*, *maicoi*, and *walkeri*. A red-tinted, notched-dash *Photuris* also occurs in Texas (*campestra*). All but two members of the operational Red Group are known only from deep southeastern United States (**Figs. 1**, **2**).

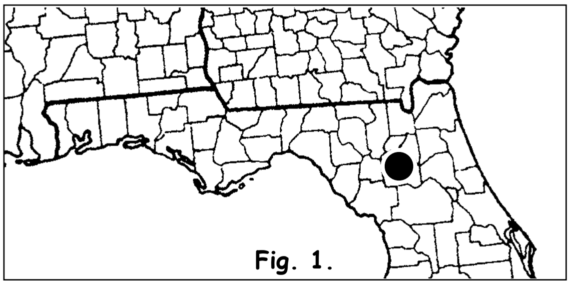


Fig. 1.

Ecology, Flashing Behavior. In Alachua County, Giant Red males flew among the tops of tall pines of a thinned plantation in the UF teaching forest (ACF; **Fig. 3**), over tall pines adjacent to a mixed, second-growth mesic woods (**Fig. 4**), and along second-growth, scrubby hardwoods and bushes by a stream; from mid March to late May (**Fig. 8**). They emitted 1-flash FPs (**Fig. 2A**) at long and somewhat- (though not conspicuously) rhythmic intervals (5 sec/18°/64.4°, **Fig. 6,** rate in **Fig. 7**). High-flying males could often be attracted from 100' or more with a penlight decoy, and often several, even a dozen would join and slowly approach, always flashing out of synchrony. **Figure 9A** shows the FP sequence of a single male and 9**B** those of two approaching males.

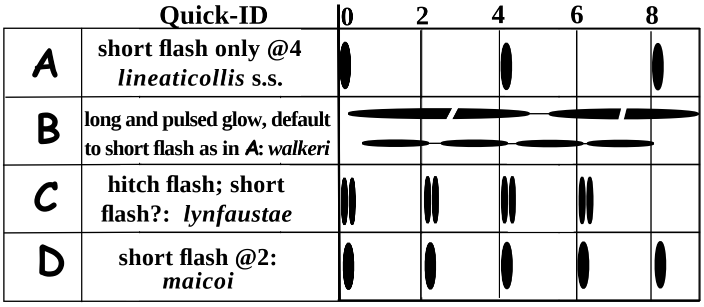


Fig. 2. Some red-group FPs, names, forms, ≈ period timings.

Fig. 3. UF's Austin Cary Forest site.

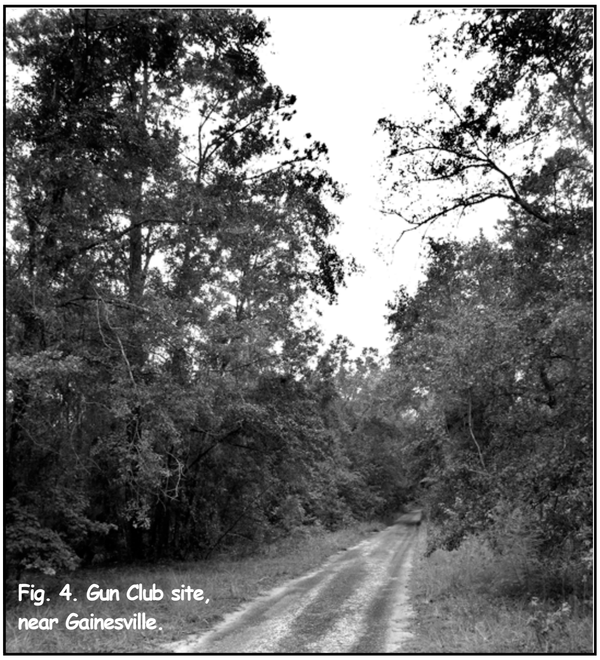


Fig. 4. Gun Club site, near Gainesville.

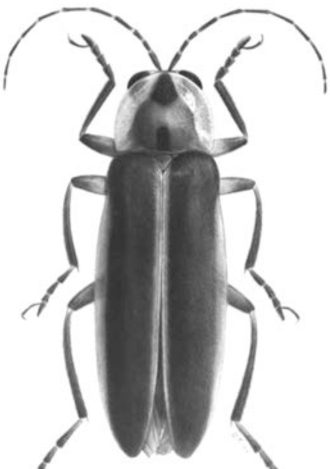


Fig. 5. *P. lineaticollis*.

Flashes of approaching males sometimes visually appear as a tear-drop, and in PM-records flash form typically shows a slightly slower rise- than fall-time (**Fig. 9D, F**); PM-records of other forms (e. g., **9C**, **E**, **G**) may be artifacts of simultaneous spatial movement—turns, twisting swoops. Flash duration at 21.1°/70° is about 160 mSec and at half max about 100. Color spectra of two samples examined were: peak 553 millimicrons, half max at 526 and 593, n=6, 23 April 1968, Austin Cary Forest.

No long-glowing or short-glowing emissions (Long Red "FPs", *walkeri*) were ever seen in Alachua County, where hundreds of nights were spent in the field in season. In a brief experiment, one evening when several GRs were active at the Austin Cary Forest (**Fig. 3**), two students and I "flew" green-glowing LEDs on wands by hand for several minutes throughout the grassy area where males were often attracted to decoy flashes (foreground **Figure 3**). No males were converted to glowing during this exposure. The naming of *walkeri* (Long Red) is based on the conclusion that local nearly-contiguous demes may diverge dramatically given strong selection pressure, as discussed by Erlich and Raven (1967), and the Reds and some other *Photuris* seem to be examples of this (see *walkeri* for further discussion). Whether the formal separation of species made here in the Red group is correct is a question that has been considered continuously: perhaps HR is BR?—they have identical FP periods (**Fig. 10**; or was the BR FP seen on the Florida panhandle merely competing GR males with shortened periods, or HR? Such things are known to happen in *Photuris*.

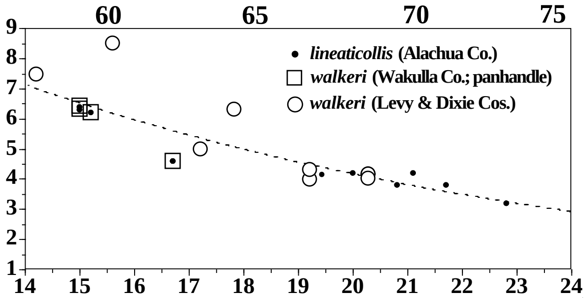


Figure 2. FP Period (sec/temp). Regression and FP means for variads in the *lineaticollis* section (AX: sec/temp).

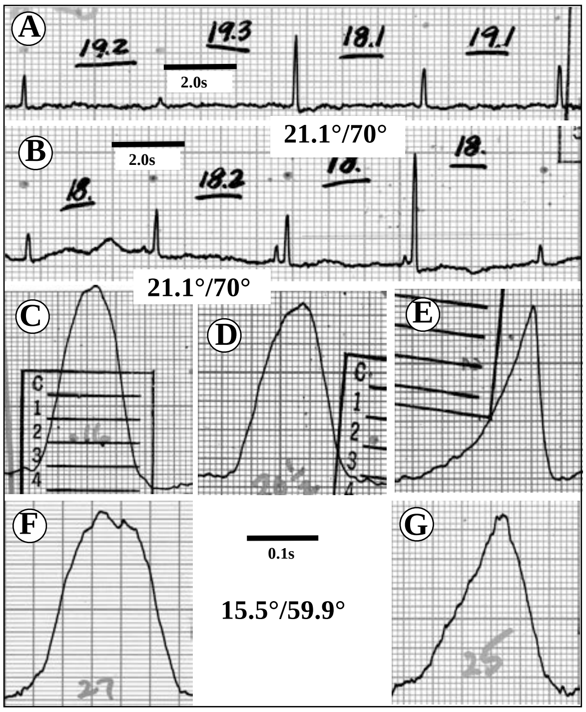


Fig. 9. PM traces (AX: rel int/time).

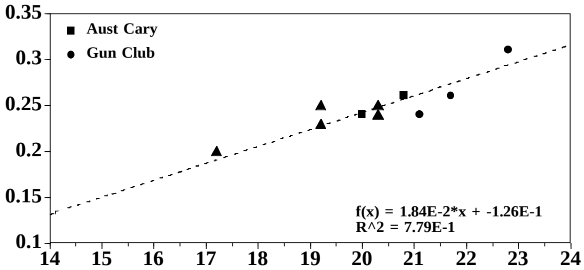


Fig. 7. FP Period rate (1/period; AX: sec/temp).

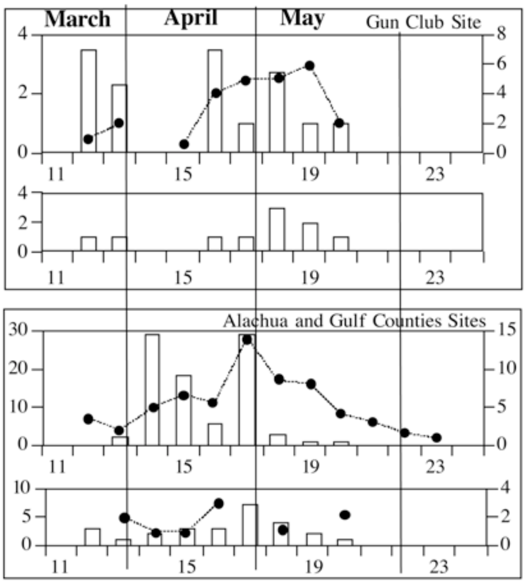


Fig. 8. SESOBS *lineaticollis* (AX: quant/WOY).

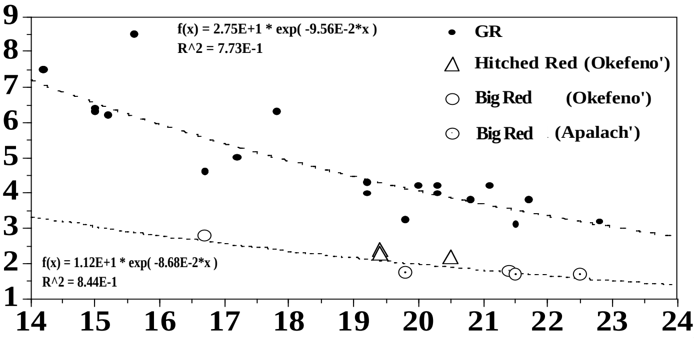
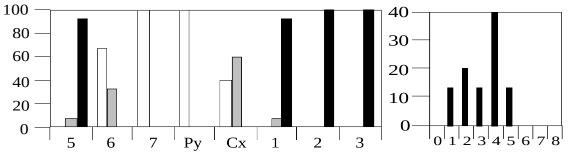


Fig. 10. All FP period means; n ≈ 155 (AX: sec/temp).

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	3.113	11.213	3.893	2.107	2.700	0.000	14.340	.801	1.284	0.000
sd	.370	.673	.246	.175	.207	0.000	.846	.096	.070	0.000
se	.096	.174	.064	.045	.053	0.000	.218	.025	.018	0.000
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.900	3.500	1.900	2.300	0.000	12.300	.660	1.130	0.000
max	3.600	12.500	4.400	2.400	2.900	0.000	15.800	1.000	1.350	0.000
Vc%	11.9	6.0	6.3	8.3	7.7	0	5.9	12.0	5.5	0

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	2.933	1.333	1.000	1.000	2.600	2.933	3.000	3.000	3.200
sd	.258	.488	0.000	0.000	.507	.258	0.000	0.000	1.320
se	.067	.126	0.000	0.000	.131	.067	0.000	0.000	.341
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	1.000
max	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	8.8	36.6	0	0	19.5	8.8	0	0	41.3



FigTable. 11. Measurement, ratio, color data ACF.

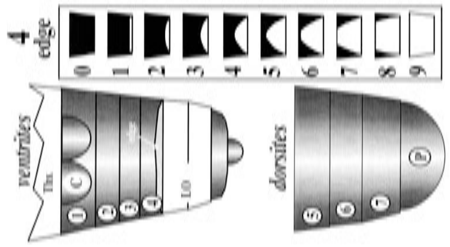


Figure 12. Topographic and splash key.

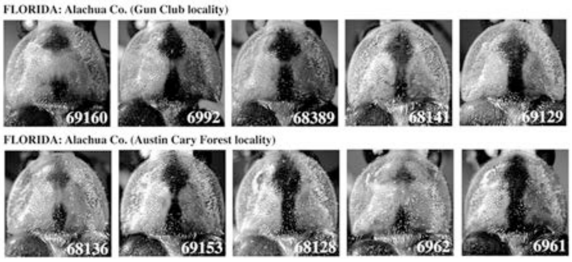


Fig. 13. PN arrays, to Alachua County sites.

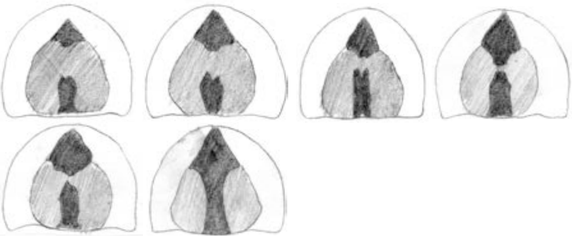


Fig. 14. Alachua Co. GR vittagram sketches.

Fig. 15. USNM *lineaticollis*, 2013.

Morphology. **FigTable 11** has measurements, ratio, and color data for a GR series from Austin Cary Forest; **Fig. 12**, the anatomical and splash key. **Figures 13** and **14** are arrays of vittagrams from Alachua County vouchers. **Figures 20** and **21** show vittagrams and vittagram analyses for some Red Group (working) species. and **FigTables 22-25** present various data from Red-Group species for comparison and reference.

Taxonomic Notes. In the LeConte collection at the MCZ (Harvard, October 1992) were three large specimens that might be candidates for *lineaticollis*—this "*pennsylvanica*" assortment certainly is not as LeConte left it. With respect to the six specimens that Barber mentioned in the U.S. National Collection, in August 2013 there were only three in the *lineaticollis* tray, all of which could appear to be *lineaticollis* as recognized in this paper (**Fig. 15**). They were from Duval and Polk Counties, Florida. **Figure 17** shows the pronota of these three specimens, **Figure 18**, the Duval Co. (Jacksonville) specimen and Figure **19**, Polk County. There are specimens in the Florida DPI collection not examined.

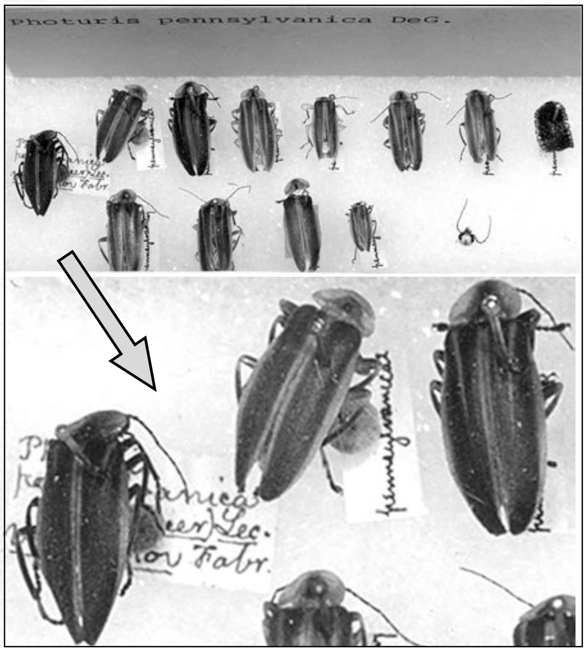


Fig. 16. Harvard's MCZ "LeConte" "*pennsylvanica*" tray.

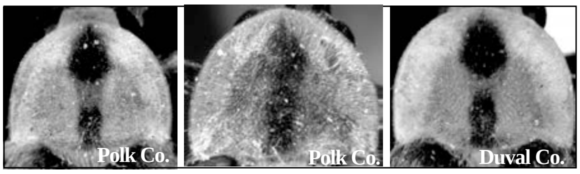


Fig. 17. Pronota of Barber-noted USNM specimens.

Victor Ivanovich Motschulsky (1810-1871), from Essig.

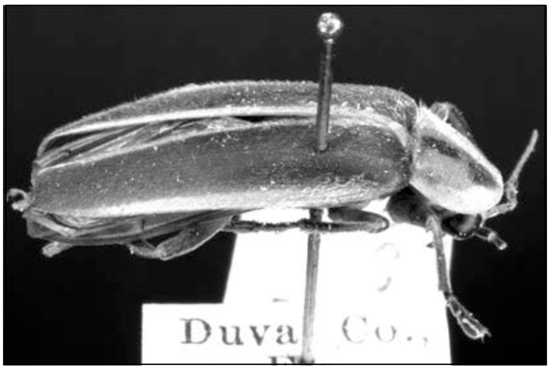


Fig. 18. USNC Duval Co., FL specimen.

Fig. 19. USNC Polk Co., FL specimen.

Red Group Pronotal Vittagram Comparison

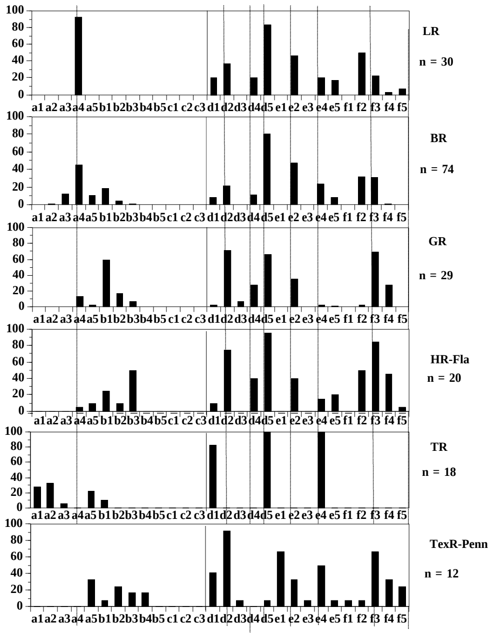


Fig. 20. Vittagram comparison.

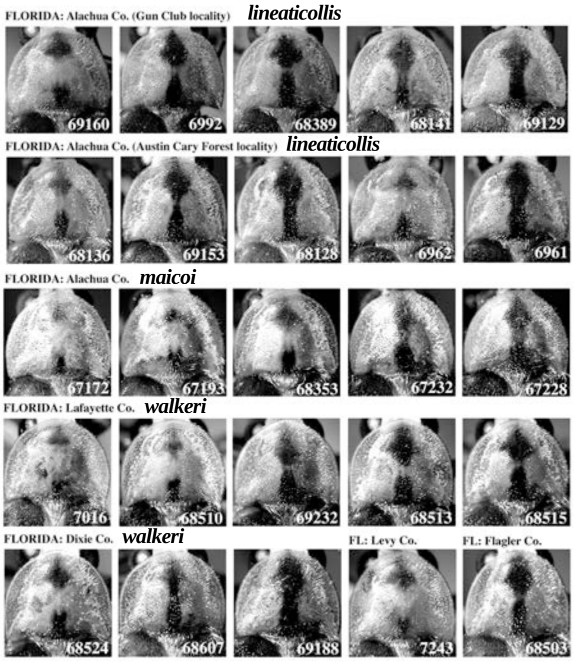


Fig. 21. PN arrays of vouchers in Red Group.

Giant Red (*lineaticollis*), Vouse Branch, Wakulla Co. FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.150	11.517	3.850	2.250	2.767	0.000	14.683	.822	1.233	0.000
sd	.122	.366	.138	.122	.151	0.000	.458	.023	.041	0.000
se	.050	.149	.056	.050	.061	0.000	.187	9.458E-3	.017	0.000
n	6	6	6	6	6	6	6	6	6	6
min	3.000	11.000	3.600	2.100	2.600	0.000	14.000	.780	1.170	0.000
max	3.300	12.100	4.000	2.400	3.000	0.000	15.400	.840	1.290	0.000
Vc%	3.9	3.2	3.6	5.4	5.5	0	3.1	2.8	3.3	0

Long Red (*walkeri*), Vouse Branch, Wakulla Co. FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.775	11.200	3.700	2.100	2.700	0.000	13.975	.758	1.287	0.000
sd	.320	.200	.115	.141	.115	0.000	.465	.102	.073	0.000
se	.160	.100	.058	.071	.058	0.000	.232	.051	.036	0.000
n	4	4	4	4	4	4	4	4	4	4
min	2.500	10.900	3.600	2.000	2.600	0.000	13.400	.670	1.220	0.000
max	3.100	11.300	3.800	2.300	2.800	0.000	14.400	.860	1.380	0.000
Vc%	11.5	1.8	3.1	6.7	4.3	0	3.3	13.5	5.7	0

Long Red (*walkeri*), Ellzey Rd., Levy Co. FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.223	11.550	3.950	2.175	2.750	1.375	14.750	.817	1.283	.117
sd	.119	.624	.289	.222	.173	1.592	.676	.043	.083	.136
se	.060	.312	.144	.111	.087	.796	.338	.022	.042	.068
n	4	4	4	4	4	4	4	4	4	4
min	3.130	10.900	3.600	1.900	2.600	0.000	14.000	.760	1.210	0.000
max	3.380	12.400	4.300	2.400	2.900	2.900	15.600	.860	1.400	.240
Vc%	3.7	5.4	7.3	10.2	6.3	115.6	4.6	5.3	6.5	116.2

Big Red (*maicoi*), Vouse Branch, Wakulla Co. FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.400	11.933	4.200	2.400	2.933	5.100	15.333	.820	1.210	.427
sd	.265	.058	.265	.265	.153	4.419	.208	.026	.072	.370
se	.153	.033	.153	.153	.088	2.551	.120	.015	.042	.213
n	3	3	3	3	3	3	3	3	3	3
min	3.100	11.900	3.900	2.100	2.800	0.000	15.100	.800	1.150	0.000
max	3.600	12.000	4.400	2.600	3.100	7.800	15.500	.850	1.290	.650
Vc%	7.8	0.5	6.3	11.0	5.2	86.5	1.4	3.2	6.0	86.7

Fig. 22. Measurements and ratios of vouchers in Red Group.

Giant Red (*lineaticollis*), Vouse Branch, Wakulla Co.FL

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	2.667
sd	0.000	.632	0.000	0.000	0.000	0.000	0.000	0.000	1.033
se	0.000	.258	0.000	0.000	0.000	0.000	0.000	0.000	.422
n	6	6	6	6	6	6	6	6	6
min	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	1.000
max	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	4.000
Vc%	0	31.6	0	0	0	0	0	0	38.7

Long Red (*walkeri*), Vouse Branch, Wakulla Co. FL

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.750	1.250	1.250	2.500	2.750	3.000	3.000	3.750
sd	0.000	.500	.500	.500	.577	.500	0.000	0.000	2.217
se	0.000	.250	.250	.250	.289	.250	0.000	0.000	1.109
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	2.000
max	3.000	2.000	2.000	2.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	28.6	40.0	40.0	23.1	18.2	0	0	59.1

Long Red (walkeri), Ellzey Rd., Levy Co. FL

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.000	1.000	1.000	2.500	2.500	3.000	3.000	2.000
sd	0.000	0.000	0.000	0.000	.577	.577	0.000	0.000	2.160
se	0.000	0.000	0.000	0.000	.289	.289	0.000	0.000	1.080
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	0.000
max	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	0	0	23.1	23.1	0	0	108.0

Big Red (*maicoi*), Vouse Branch, Wakulla Co. FL

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.000	1.667	1.000	2.333	2.667	3.000	3.000	4.667
sd	0.000	0.000	.577	0.000	.577	.577	0.000	0.000	1.155
se	0.000	0.000	.333	0.000	.333	.333	0.000	0.000	.667
n	3	3	3	3	3	3	3	3	3
min	3.000	2.000	1.000	1.000	2.000	2.000	3.000	3.000	4.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	0	34.6	0	24.7	21.6	0	0	24.8

Fig. 23. Color data of vouchers in Red Group.

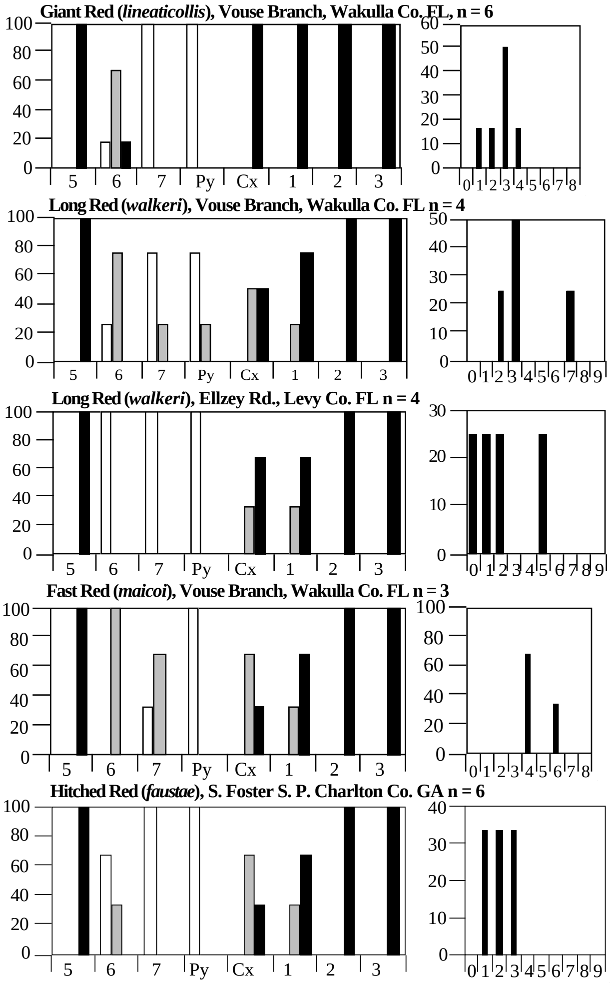
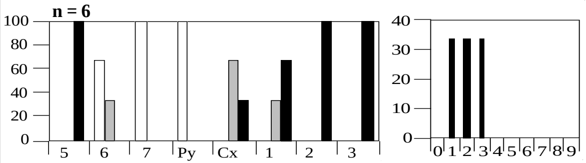


Fig. 24. Color histograms of some vouchers of Red Group.

Hitched Red, S. Foster S. P. Charlton Co. GA (*faustae*)

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.233	11.667	3.940	2.188	2.792	0.000	14.753	.820	1.277	0.000
sd	.123	.816	.233	.105	.151	0.000	.916	.030	.069	0.000
se	.050	.333	.095	.043	.062	0.000	.374	.012	.028	0.000
n	6	6	6	6	6	6	6	6	6	6
min	3.130	11.000	3.630	2.125	2.625	0.000	13.880	.780	1.170	0.000
max	3.380	13.000	4.250	2.375	3.000	0.000	16.380	.860	1.350	0.000
Vc%	3.8	7.0	5.9	4.8	5.4	0	6.2	3.7	5.4	0

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.333	1.000	1.000	2.333	2.667	3.000	3.000	2.000
sd	0.000	.516	0.000	0.000	.516	.516	0.000	0.000	.894
se	0.000	.211	0.000	0.000	.211	.211	0.000	0.000	.365
n	6	6	6	6	6	6	6	6	6
min	3.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	1.000
max	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
Vc%	0	38.7	0	0	22.1	19.4	0	0	44.7



Giant Red, Austin Cary For., Alachua Co. FL (*lineaticollis*)

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.113	11.213	3.893	2.107	2.700	0.000	14.340	.801	1.284	0.000
sd	.370	.673	.246	.175	.207	0.000	.846	.096	.070	0.000
se	.096	.174	.064	.045	.053	0.000	.218	.025	.018	0.000
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.900	3.500	1.900	2.300	0.000	12.300	.660	1.130	0.000
max	3.600	12.500	4.400	2.400	2.900	0.000	15.800	1.000	1.350	0.000
Vc%	11.9	6.0	6.3	8.3	7.7	0	5.9	12.0	5.5	0

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.933	1.333	1.000	1.000	2.600	2.933	3.000	3.000	3.200
sd	.258	.488	0.000	0.000	.507	.258	0.000	0.000	1.320
se	.067	.126	0.000	0.000	.131	.067	0.000	0.000	.341
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	1.000
max	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	8.8	36.6	0	0	19.5	8.8	0	0	41.3

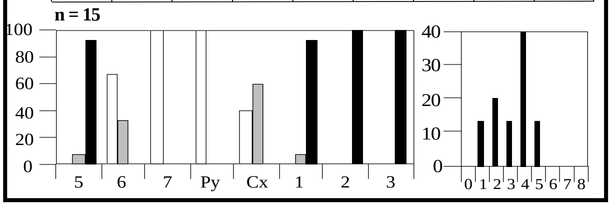


Fig. 25. Data comparisons of two members of Red Group.

As a final note of caution while making comparisons with data from the Vouse Branch site, there were several species/FPs present and though care was taken in collecting vouchers, there is less confidence associated with these; the "Big Red" there, *maicoi* in particularly should be carefully observed.

Incidental camera encounters, at the old UF Med Garden, 1974-75, Page 4.

Chapter 45

Photuris lloydi McDermott 1967

Highlands Hammock Crescendo

This species is known to occur only in Florida (**Fig. 1**). It sometimes is seen in numbers in set-back coastal lowlands and other damp habitats, and along streams. At the Holotype locality (Highlands Co.) it was seen from late February through April (**Fig. 2**) and in north-central FL, about five weeks later, from mid April to early June (**Fig. 3**). Habitus in **Figures 4**. Males flew from a few feet above ground, round palmettos in the Hammock at the type locality and up to 30 or more feet (**Figs. 5A, B**). Males traced over, around, in back of leafy boughs of shrubs and trees. At stream-sides males cruised along and against gallery walls, and at times flew high up into and around the crowns and through spaces between them (**Fig. 15**). They delivered short crescendo FPs in continuous sequence—not in phrases or groups of a few crescendos as observed in certain other crescendo species. Nor were they ever seen to gesture, to pump up and down during crescendos, but instead sometimes swooped slightly, which made their crescendo easier to see through space, or turned or curled in a shallow arc, or flew straight along their established route. Because this crescendo is short/ fast it takes a rather experienced eye to discern it on warm nights. FP period ranged 2-4 seconds @24°/75°—14°/57° (**Fig. 6**); FP rate in **Figure 7**.

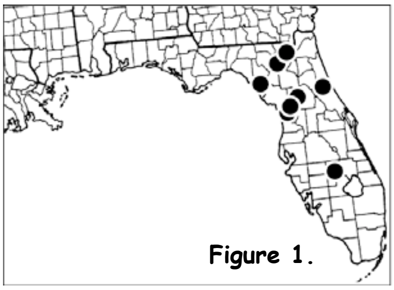


Figure 1.

In hand this firefly has little of note to distinguish it, being of average appearance and size (9.3-11.8 mm), and with a broad range of vittigram development (**Figs. 12, 14**). However, whereas the hind coxae of other crescendo flashers are nearly always pale, in *lloydi* they range from pale to dark (**FigTable. 13B, C**).

Flashes, flashing behavior. The short crescendo of this firefly is emitted continuously (**Fig. 9A**). Many PM-records show an idealized crescendo form with a smooth rise and fall (**Fig. 9B-D)**, but others are not so simple, and show a sinusoidal wave atop the crescendo that is presumably caused by lantern-shuttering of their beating hind- beating wings. These ripples are sometimes seen as weak waves on the rising

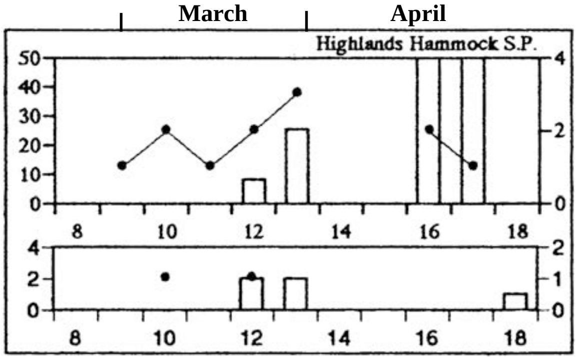


Figure 2. SESOBS, Holotype locality, Highlands County.

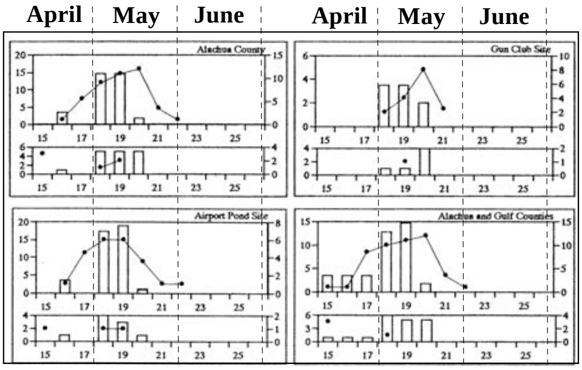


Figure 3. SESOBS in north central Florida.

Figures 4.

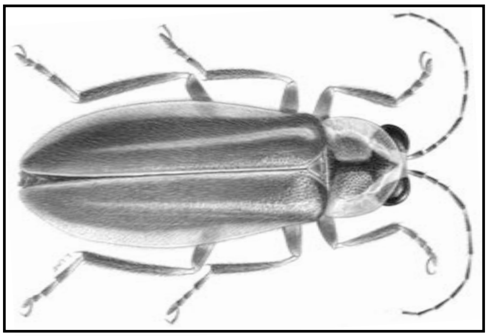


Figure 5. Holotype locality: A, loop road, B. activity spaces.

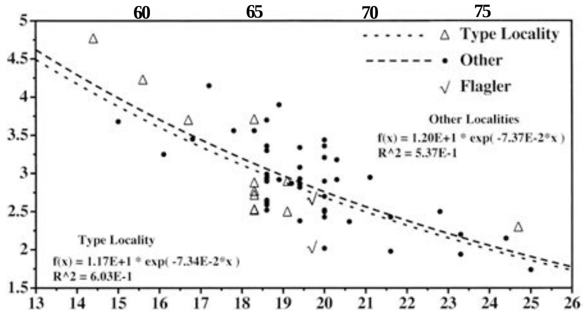


Figure 6. FP period (AX: sec/temp).

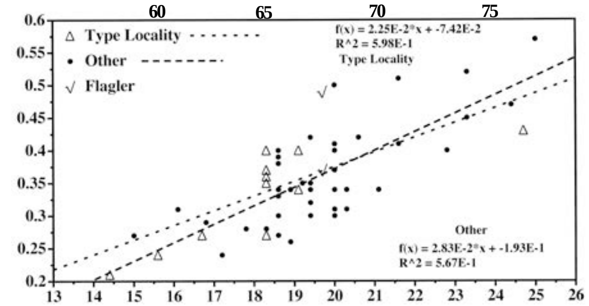


Figure 7. FP rate (AX: Hz/temp).

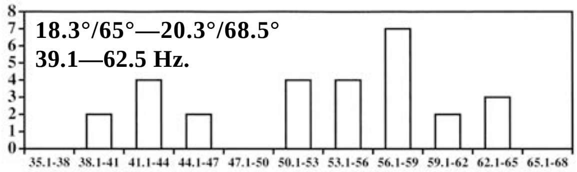


Figure 8. FP ripples—wingbeats (AX: #/Hz).

ramp or decay (**Figs. 9E, F**), but sometimes are distinct ripples at the peak of the flash as well (**Fig. 9G**). Across the rather narrow temperature range for which there are records (18.3°-20.3°C), their frequency (rate) apparently ranged considerably more broadly than expected, from 39.1 to 62.5 Hz (**Fig. 8**).

These ripples, and their intermittent showing, attract special attention here because: (**1**) another crescendo species (*lamarcki*), possibly a close relative/clade-mate, a flicker in this frequency range *at the lantern* in its FP; (**2**) females of *lamarcki* species are important aerial attackers, and the flicker in *lloydi* males perhaps(?) is a condition-activated counter-measure against such attacks, not by activating a flicker at the lantern but by manipulation of their wings.

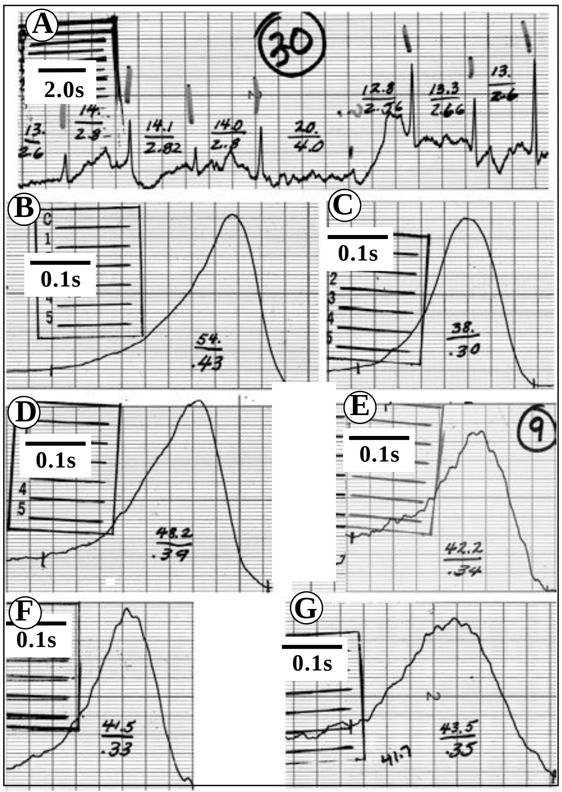


Figure 9. PM records (AX: rel. int./time).

Among the parameters of flashing known and expected to have a direct and predictable relationship with ambient temperature is flash duration. One of the problems in measuring flash duration accurately is that records vary with PM-to-emitter distance, and when photo-multiplier sensitivity is increased to compensate, the peak flash intensity saturates the system and blocks-out for seconds. For this reason only an estimate based on the inspection of a number of recordings is usually given. Further, with PM-recording of crescendo flashes where the onset is low and slow there is even more uncertainty and more of the dim onset will pass undetected. It is obvious in *lucicrescens*, a species with long crescendo, at a given time and place and temperature, crescendo durations do vary conditionally.

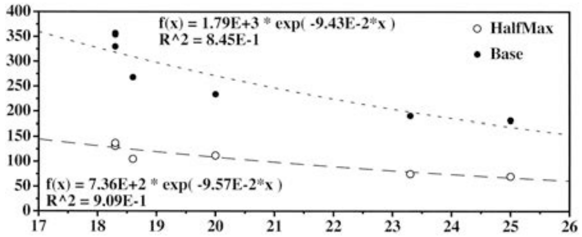


Figure 10. Flash duration/temperature (AX: mSec/temp).

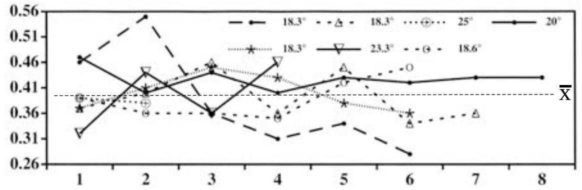


Figure 11. Flash ratio (AX: ratio/postion in FP sequence).

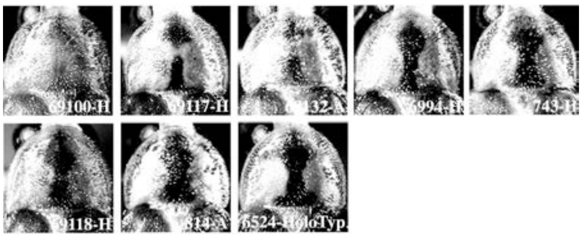
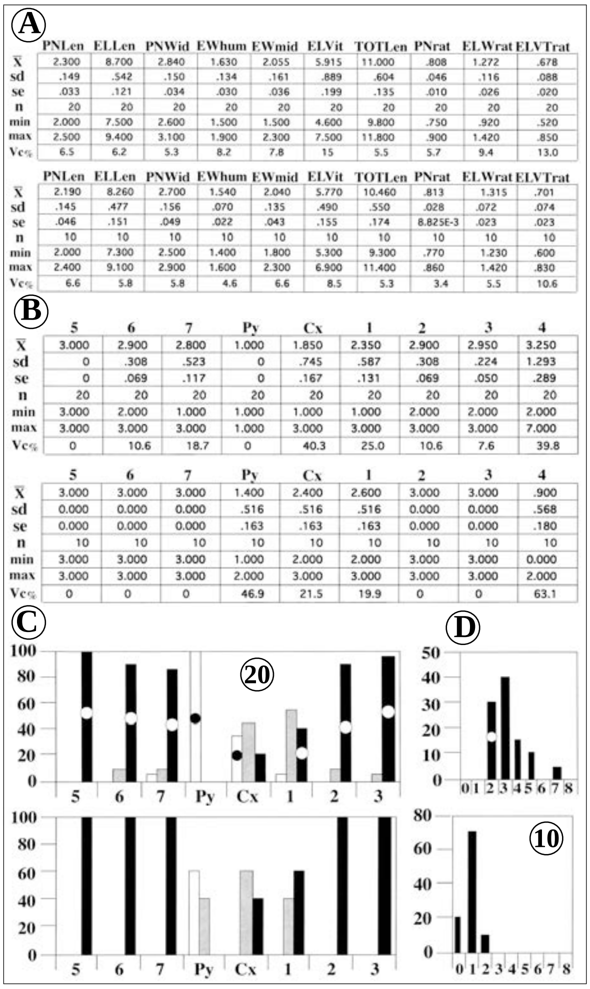


Figure 12. Holotype and other vouchers.



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	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.300	8.700	2.840	1.630	2.055	5.915	11.000	.808	1.272	.678
sd	.149	.542	.150	.134	.161	.889	.604	.046	.116	.088
se	.033	.121	.034	.030	.036	.199	.135	.010	.026	.020
n	20	20	20	20	20	20	20	20	20	20
min	2.000	7.500	2.600	1.500	1.500	4.600	9.800	.750	.920	.520
max	2.500	9.400	3.100	1.900	2.300	7.500	11.800	.900	1.420	.850
Vc%	6.5	6.2	5.3	8.2	7.8	15	5.5	5.7	9.4	13.0

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.190	8.260	2.700	1.540	2.040	5.770	10.460	.813	1.315	.701
sd	.145	.477	.156	.070	.135	.490	.550	.028	.072	.074
se	.046	.151	.049	.022	.043	.155	.174	8.825E-3	.023	.023
n	10	10	10	10	10	10	10	10	10	10
min	2.000	7.300	2.500	1.400	1.800	5.300	9.300	.770	1.230	.600
max	2.400	9.100	2.900	1.600	2.300	6.900	11.400	.860	1.420	.830
Vc%	6.6	5.8	5.8	4.6	6.6	8.5	5.3	3.4	5.5	10.6

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.900	2.800	1.000	1.850	2.350	2.900	2.950	3.250
sd	0	.308	.523	0	.745	.587	.308	.224	1.293
se	0	.069	.117	0	.167	.131	.069	.050	.289
n	20	20	20	20	20	20	20	20	20
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	10.6	18.7	0	40.3	25.0	10.6	7.6	39.8

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	3.000	1.400	2.400	2.600	3.000	3.000	.900
sd	0.000	0.000	0.000	.516	.516	.516	0.000	0.000	.568
se	0.000	0.000	0.000	.163	.163	.163	0.000	0.000	.180
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	3.000	1.000	2.000	2.000	3.000	3.000	0.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	2.000
Vc%	0	0	0	46.9	21.5	19.9	0	0	63.1

FigTable 13. Morphological data (Highlands and Alachua Cos.). Dots show positions of Holotype.

With the above as background: After examining and measuring several *lloydi* FPs with respect to duration at base and half-maximum intensities, only a very general statements can be made because of the considerable variability. When duration *means* of FPs in different temperature sets were compared they suggested a clear influence of temperature (**Fig. 10**).

The mean duration ratios (flash width at half max/flash width at base) of these sets appear crudely constant across a moderate temperature range (18.3°-25.0°C): x=0.39, s=0.01, r=0.38-0.40, n=7 sets, 39 flashes (**Fig. 11**).

Signal interaction? Very rarely was signaling between a male and a female observed in *Photuris* species across decades and thousands of nights (3001+). Those few "seen" were unexpected and passed so quickly as to be over over before full attention could be directed toward them. An exception, almost, to this occurred with this firefly, though not much was learned, and that uncertain. Abstracted notes from the fieldbook: <PM-recording— male got answer from leaf seven feet up—crescendo with little delay and dimmer than the males—happened three or four times, then followed three or four dim crescendos in faster sequence—think female gave these. Looked with the headlamp, found KB-80 male on leaf 6 inches from female [locus of "her" light]—the male in KB-80 probably the male recorded> …

The luminescence spectrum peak is 553 millimicrons, with half max at 526.0 and 594.0, and half max width 68.0; this spectrum subjectively may most closely or somewhat match *Roscolux* filter #87, *pale yellow green.*

* * *

Morphology. General morphological means for a series from the Holotype locality are (n=20): PNL 2.3, ELL 8.7, PNW 2.8, EWhum 1.6, EWmid 2.1, ELVit 5.9, TOTLen 11.0, PNrat 0.81, ELWrate 1.27, ELVTrat 0.68 (**FigTable 13A**, with other stats). Data for sclerite and hind coxae color in **FigTable 13B-C**, and the color (splashing) of the pre-lantern ventrite in **13D**. **Figure 14** is a key to skeletal components and splashing on ventrite 4. A range of vittagrams is shown in **Figures 12** and **14:** those in **Figure 14** are pencil sketches made by a non-taxonomist, but instead a professional and especially sharp-eyed artist—as we sought an inexpensive way to illustrate a range of pronotal vittagrams in the days before CoolPic cameras. As a result there is large sample of vittagram illustrations for comparison.

Taxonomic note. On the evening of 4 March 1965 Glenn Morris and I, grad students at Cornell at the time, were on a collecting trip to Highlands Hammock State Park at Sebring, Florida. Back on the loop road behind the "Girl Scout gate" and nearly to the turn (see **Fig. 5**), we found some fireflies flashing over the palmettos and up into the low branches of the canopy overhead. I measured FP periods, estimated duration, noted that they flew up and arced in flight sometimes, and flew slowly, but completely missed seeing their crescendo. I collected two specimens, and one of them, voucher number 6524, was sent to Frank McDermott in a Schmidt box along with many other *Photuris* specimens. To my surprise he put my name on it. He may have been pleased to have someone with whom to correspond about fireflies after Barber so recently had ended his fireflying.

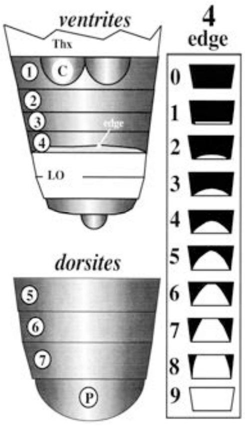


Figure 13. Topographic and splash keys.

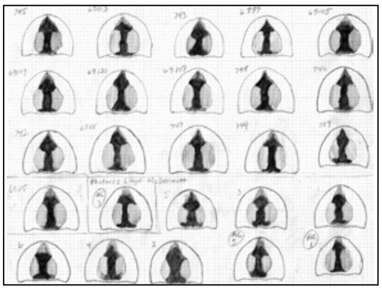


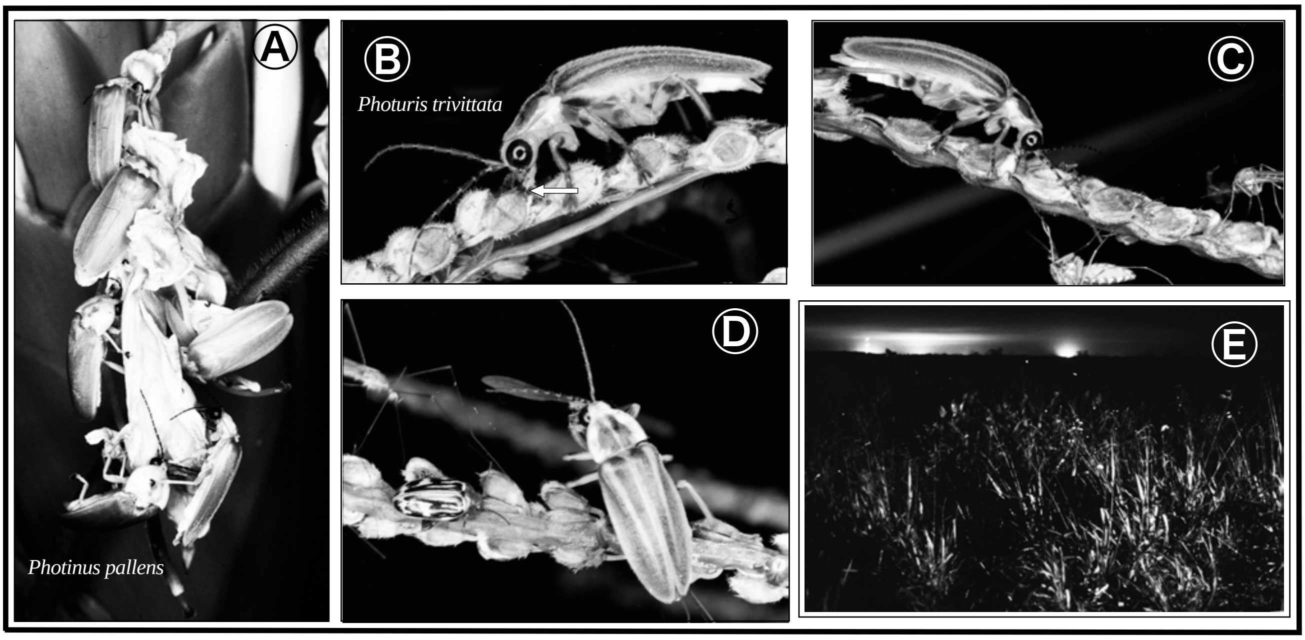
Figure 14. Pencil sketches, type locality

Figure 15. This tree-wall is over a culvert where Little Hatchet Creek passes under the road. The road beyond the gate once led to the Airport Pond locality. The last time this was visited, circa 1990, the site had been worked over by bulldozer and no longer rich in fireflies. The road to the left at this corner, travels 150 yards to the heart of the gunclub firefly locality—still intack but silent, having lost most of its resident fireflies, nighthawks, and screech owls.

ON THE EVOLUTION OF AGGRESSIVE MIMICRY (part 1 of 2)

Photurine firefly phagy: Though not much is known about photurine genera other than *Photuris*, and what we eventually learn from them will provide important clues as to the evolution of predation in this subfamily, this is a place to broach this question and make a sweeping outline of possible recognizable steps on a ramp up to the femmes fatales, and beyond, if it turns out that tropical genera do it "better."

In building a model for this evolution each step must provide a smooth transition from the previous—in reality there would be no steps, but continua, "progress" that moved along among “advancing” and phylogenetically, and sometimes reticulating demes. The outline suggested here came from thoughts forced to consciousness after *Photuris trivittata* was seen feeding on grass seeds (**B**, **C**) and feeding on (predating) other insects (**D**) that were at the same time licking/chewing/sucking the seeds. The site was along a large ditch between the college at Cardenas, Mexico, and an oil field (**E**). The model must begin—if not with *Photuris*, a progenitor—with fireflies feeding on vegetation, perhaps flowers as seen in Jamaican *Photinu pallens* on ginger lily (**A**), and many other reported examples, including *Pteroptyx valida* in mangrove estuaries in Thailand. Continued on page 268.

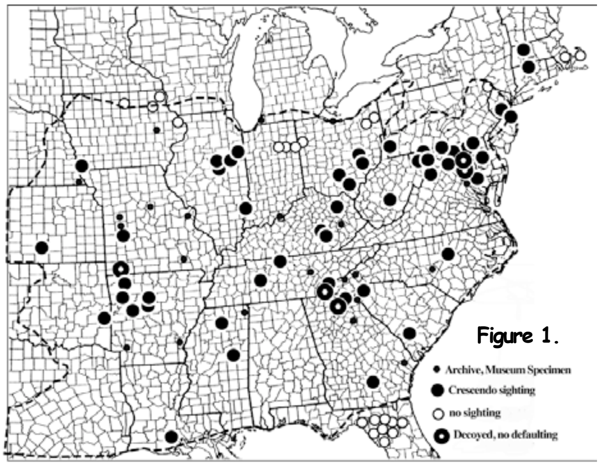


Chapter 46

Photuris lucicrescens Barber 1951

Big-Lucy

For the bench taxonomist this is perhaps the only common Division II *Photuris* species that can be recognized in a potpourri-tray of cabinet specimens. It is for this reason that its ranges of geographic and seasonal occurrence are better understood/suggested than those of any other species in the old "pennsylvanica" section, Division II (**Figs. 1**, **2**). Its extensive geographic distribution and mid-summer adult season are similar to those of *Photinus pyralis* (**Fig. 1**, dashed line), which perhaps is (obligately?) preyed upon by *lucicrescens* females. Perhaps Big Lucy's curious non-default FP repertoire has a connection to this?



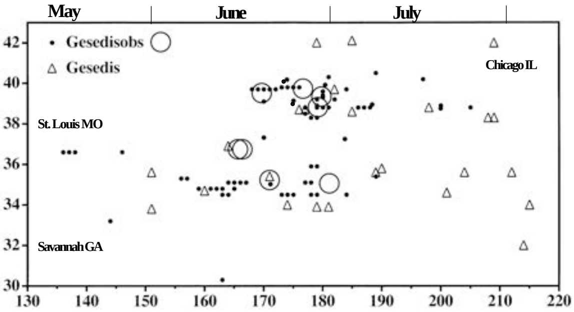


Figure 2. GESEDIS-GESEDISOBS (AX: Lat/DOY)

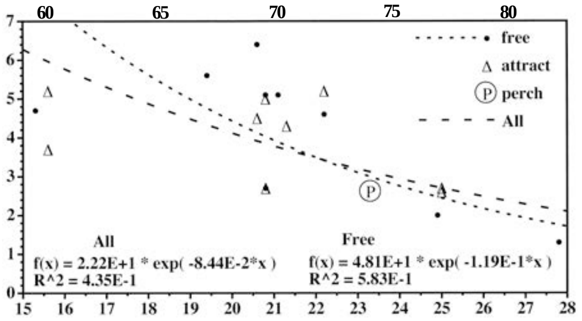


Figure 3. Short-flash FP period (AX: sec/temp).

In the field *lucicrescens'* long crescendo FP is unmistakable, but its short-flash FP is easily confused with those of other *Photuris* species. It has never been found to *default* from one FP to the other (see **Fig. 1** index; page 475 I). If the variable interval of *lucicrescens* short flashes is involved in prey-FP mimicry, this was not recognized nor even come under suspicion until many other species were observed to emit prey-resembling adjunct FPs. The short flash was once described as having a flash-bulb appearance in its exceeding brilliance; curiously, to the eye these bright flashes appear white, not green, though it would be expected that such apparent intensity should stimulate human color vision elements (cones). The average period of the short-flash FP ranges from about 6 sec at 15°/59° to 2 sec at 27°/81° (**Fig. 3**).

Crescendo duration ranges from about a half-second to 2 or more seconds, and varies with temperature, perhaps male vigor, and probably environmental elements, including the presence of rivals, and phenology. On rare occasions and evenings of marginal temperature (≈10°/50°) crescendos near 4 seconds in duration were measured. Though hardly needed or as added benefit for field identification, the period of the long crescendo FP ranges from about 8 seconds at 14°/57° to about 3 seconds at 27°/81° (**Fig. 4**); crescendo FP rate is shown in **Figure 5**. The intensity reached in the crescendo varies from only a slight increase from a moderate onset to an extremely bright, explosive peak (**Figs. 7G, I—6B**, **E**, **F**)—which, at close range, especially when standing in water or on a precarious perch, can literally upset an observer's equilibrium—as experienced within an intense chorus of certain frogs.

This firefly's large size, pale and sometimes "washed-out" appearance, pale or only slightly fuscous (dingy) hind coxae, and somewhat characteristic vittagrams, are not generally found together in other known North American species (**Figs. 8, 9, 18**). Smaller specimens of *lucicrescens* cannot be distinguished unless collected outside the range of (presumptive) clade-mates; large examples of *hebes*, a wide-ranging species, are presently confused with smaller *lucicrescens*. In several areas, such as southeastern Ohio, *lucicrescens* specimens have dusky or darker hind coxae. **Figure 2** shows several outlying GESEDIS points that may be misidentifications, or specimens that arrived from other latitudes, or were mislabeled and retained from student collections, or, unless too extreme, longer-lived females whose sex was not recorded in the GESEDIS record.

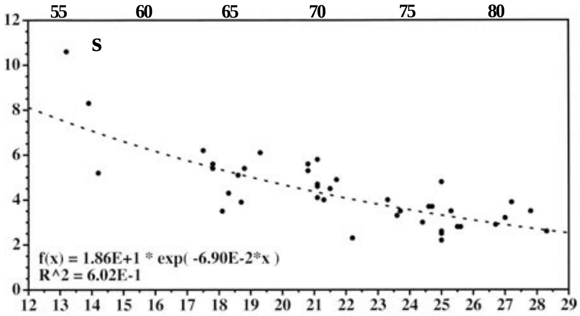


Figure 4. Crescendo-flash FP period (AX: sec/temp).

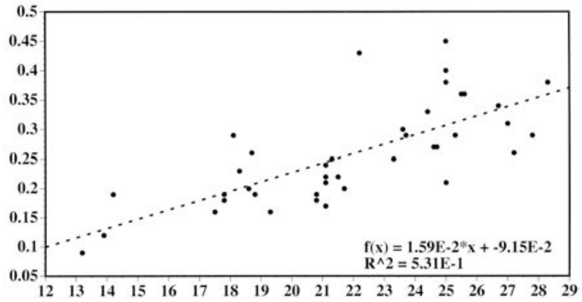


Figure 5. Crescendo FP rate (AX: Hz/temp).

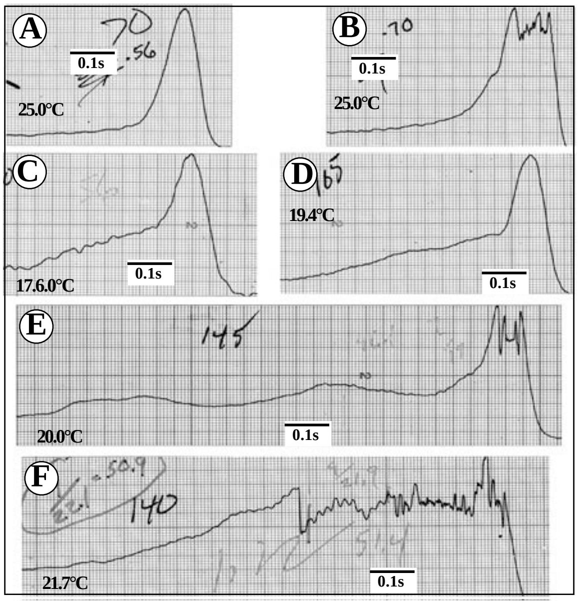


Figure 6. PM-records (AX: rel. int./time).

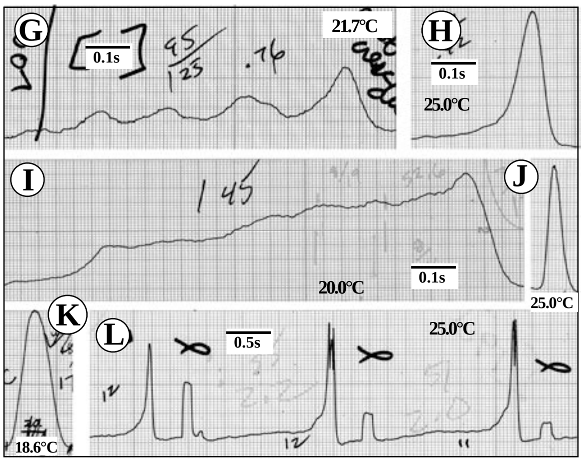


Figure 7. Pm records (AX: rel. int./time).

Barber found *lucicrescens* at several of the sites he monitored somewhat regularly in his bailiwick in the lower Potomac/Chesapeake region—Sherwood Forest, Black Pond, Breton Bay, Hunting Creek, and others. One of them especially attracted interest because it was located not far from the Naval Air Station where this author stationed for three years in the early 1950s, and was at a bridge often crossed on US 301. This site, the *lucicrescens* Holotype locality, was Priest's Bridge across the Patuxent River, where there remained densely wooded low shores just as Barber had described (**Figs. 10, 11**).

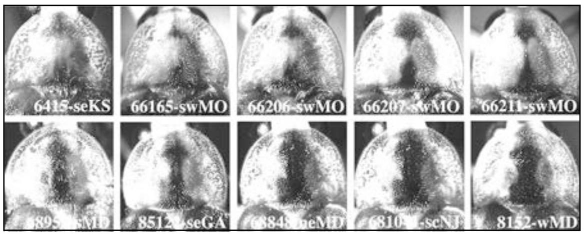


Figure 8. Pronotal vittigram variation.

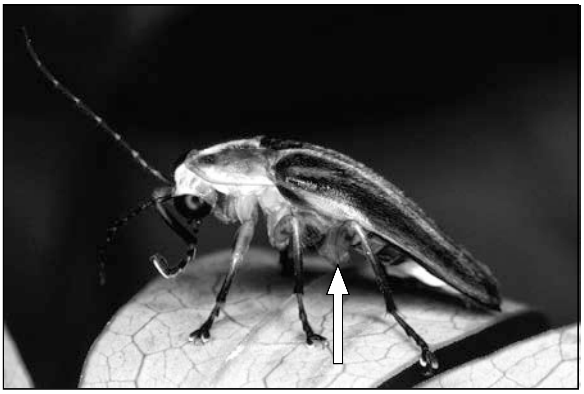


Figure 9. Note PN and pale hind coxa.

Figure 10. Bridge over the Patuxent, at/near old Priest's Bridge site.

Figure 11. Holotype locality region.

Figure 12. Roaring River site, River indicated.

Figure 13. Shoreline at RRSP MO.

Figure 14. Dot-marked Big Lucy.

A focused study site was in Barry County, MO, which can be seen in **Figure 12** as the illuminated clearing up the bridle path from the shoreline from Roaring River, but *lucicrescens* occurred all along the wooded shoreline (**Fig. 13**). Evening flashing began about the end of Civil Twilight (x=0.95 Crep, s=0.30, n=17), based upon observations of crescendo-flashing, not short-flashing males, which certainly missed an important aspect of *lucicrescens* mate-seeking behavior. Perched males began flashing deep in grass and herbs as early as 0.1 Crep. Early flying-male values of 0.6-0.7 Crep were observed in shaded sites.

Males searched over understory herbs during early evening, and after complete darkness they flew and flashed up against the faces of stream-side foliage. These generalizations are largely based on field observations of the crescendo flash; it is not yet possible to recognize high-flying short flashers with confidence unless they are attracted to a decoy flash and viewed. Possibly *only* short-flashing occurs in some upland habitats (e.g. mixed-oak forests in Maryland, northern Georgia.

When Barber formally named his flasher of long crescendos he indicated in his table and flash chart, and discussed in text, that he was not completely satisfied that it also emitted a short flash; he asked:

> *Why were none of these* [short] *flashes seen at Priest's Bridge or at two other stations? Why do both types of flash occur here and at some other places? Various answers will satisfy various persons, but no one knows. Envy the bats their wings. With them we might follow single specimens through their evening's activities and see if they change their flashes.*

Barber selected his Holotype from his crescendo-only site, Priest’s Bridge.

2-FP repertoire confirmed. At the Roaring River site many crescendo and short flashing *lucicrescens* flew over the narrow bridle path and up each face of the closely appressing forest (**Fig. 12**), and, in early evening, low over the herb understory. Many flew where single individuals could be watched closely, and within reach of the hand, or as last resort the net, a critical consideration. On several occasions a change of FPs was seen within "very isolated" flight space, that seemed was probably the result of a single male changing patterns—that is, not from a second firefly quickly entering the air space of the first.

Twenty-one crescendo-flashing males were marked with a tiny dot of airplane-dope on an elytron (**Fig. 14**), and the next night 19 short-flashing males were marked with a different color. There were 6 short-to-crescendo change-overs the night they were marked. At 24 hours, recaptures were: 2 crescendo-to-short change-overs and 6 crescendo-to-crescendo flashers. Barber’s suspicions were confirmed, assuming that Missouri and Maryland *lucicrescens* demes behave similarly in this respect. Whether actual circumstances are more complex, say, with some individuals not changing or changing more often, or changing with age, or whether males of more than one (“sibling”) species were present, cannot be answered. Although data are few, one tentative explanation, based on what has been observed in other *Photuris,* will fit the observations: some individuals seek hunting females via FPs simulating those of prey species, and though complicated by elements of sexual selection, the short flash FP in *lucicrescens* may be common early in low herby situations where and when certain *Photinus* species are active. Such species include *Photinus marginellus* and *sabulosus* in the east, and *australis, curtatus, macdermotti (s. l.), punctulatus,* and *tenuicinctus* variously in the east, south, and west.

Crescendo FP notes. The long crescendo of Big Lucy is one of the most distinctive, quickly-recognized FPs found in North American *Photuris*. When McDermott (1910) first reported that each of the species he had observed "appears to emit its light in a different and characteristic way", he made a special exception for *Photuris pensylvanica* (in the antiquated, pre-Barber 1951 sense), because it had several distinctive "ways", and one of these ways was the crescendo flash of *lucicrescens*:

> *probably the most common mode of light-emission of this insect* [i. e. old "pennsylvanica"], *consists of a single prolonged flash . . . It begins as a faint glow, rapidly increasing in brilliancy, until it attains an intensity obviously much greater than that of the illumination of* [pyralis]. *It then ends suddenly, leaving an impression on the retina similar to, but of course much less intense than that produced by a sudden flash of lightning observed at night …* [sometimes] *the flash is not ended suddenly, but allowed to fade out more gradually* (ibid:359):

The crescendo FP is highly variable in some parameters, though some variation noted among PM recorded flashes is probably due to flight movements of the male, such as the slow modulations in **Figures 6E** and **7G**, which presumably are caused by fishtailing, broadcasting flight. The crescendo sometimes appears to the eye to have a high-frequency modulation. McDermott noted that it often appeared to be "vibratory," to flicker at about 50 Hz. (McDermott, 1917). The PM-recorded wingbeat flicker was 51.4 Hz. (**Fig. 6F**). McDermott's estimate, may have been based on his experience with flickering 50 and/or 60 Hz. house lights. However, there may be more to it. Only one PM-recording shows such a flicker.

Perhaps the "vibrancy" seen when the crescendo is observed at very close range is an illusion, involving human perception; or so faint that the PM does not usually detect it (doubtful); or a scintillation over the surface of the light-organ that averages out as detected by the PM; or rapid alternation of firing between the two lantern segments that averages out (see *Photuris hebes*)?

Short-flash FP notes. Recorded short flashes are nearly symmetrical; inspection of two dozen PM-records suggests durations of 68 mSec half max and 126 mSec base @19.4°/67° and 36/88 mSec at 25°/77°. Clearly the short-flash period varies with temperature, and at first was thought to occur at two distinct modes because of the considerable spread (**Fig. 3**). Note that the period of free-flying males is about 2 sec at 21°C/70°F and that of males approaching a flash-answering decoy about 5 sec at this temperature. However, from observations on other species there is another view: perhaps the variation seen occurs because males mimic the intervals of certain prey species to which their females are attuned, or males are chumming. Possibly this change in period is functionally equivalent to pattern-sequencing (in defaulting) observed in other *Photuris*, although note that the figure is based on observations of periods of different males, and in no single case is based on the change occurring in a sample of free-flying *then* approaching single individuals.

Bioluminescence spectra were measured by Biggley et al. from specimens from three localities at three different dates and only minor variation was found; mean values in milli-microns are: peak=553.3, half max=527.7 and 597.0, width at half max= 70.3. Simple visual comparison with *Rosculux* filters and their frequency/ transmission curves suggest their *Lime* and *Gaslight Green* may approximate *lucicrescens* luminescence.

Copulation. **Figure 15** shows a *lucicrescens* site near the Hiawassee River in Polk County, TN. A crescendo-flashing male received an answer from a perched female and within moments he reached and mounted her. They quickly moved under the leaf on which she had been perched (**Fig. 15).** leg position may be important for rapid bail-out should the female turn to grab and eat him.

Figure 15. Gee Creek site, River at left 150'.

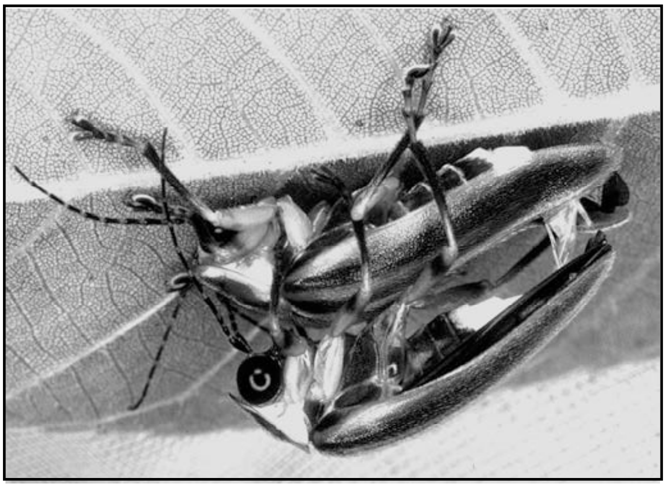


Figure 16. Note coital connection, slender, fish-bone-like aedeagal filaments that are extensions of the basal piece, and males mid-legs.

In **Figure 17** the photo in Figure 16 as been flipped vertically. The male is above and female below with the tip of her abdomen pushed upward between her elytra. In **Figure 18** aedeagal elements are labelled. Consider the notion that she may "intend" to turn, grab, and eat him, and he is preparing to bail out.

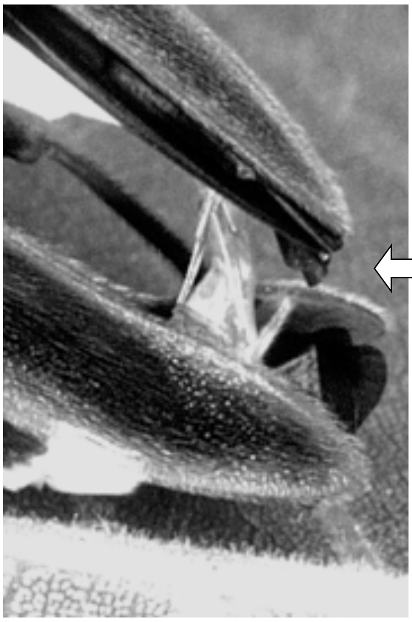


Figure 17. Enlargement and vertical flip of Figure 16, to ID elements in Fig. 24.

f filament
d dorsum of bent-up female tail
v ventral sclerite of female
ae male aedeagal shaft
p female pygidium

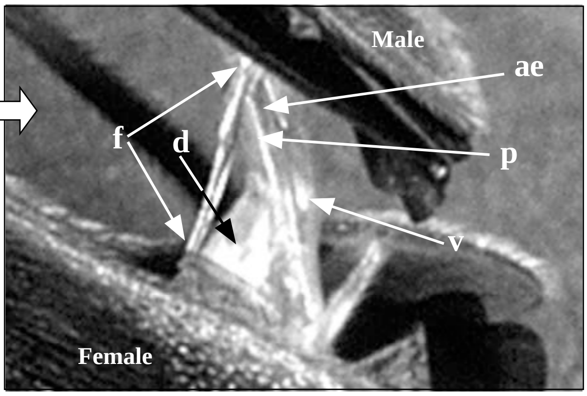
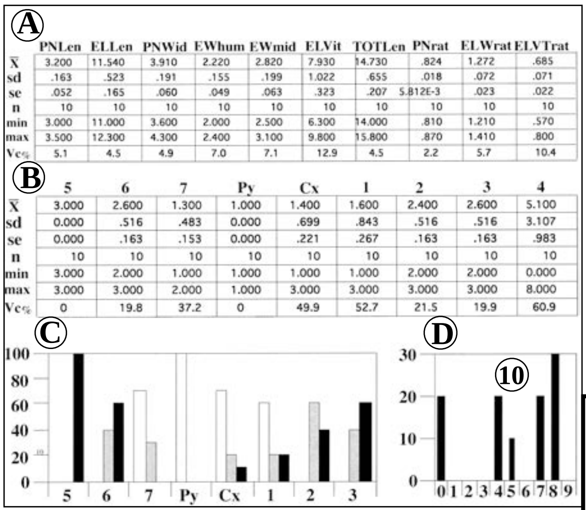


Figure 18. Coital connection explained.

* * *

Morphological data and notes. Morphological means of vouchers from Cedarville State Forest not far from Barber's Type locality: PNL 3.2, ELL 11.5, PNW 3.9, EWhum 2.2, EWmid 2.8, ELVit 7.9, TOTLen 14.7, PNrat 0.82, ELWrat 1.27, ELVTrat 0.69, n=10 (**FigTable 19A**, with other general stats). Color of abdominal plates and hind coxae of the Cedarville S. F. series in **FigTable 19B-C**; splashing on the pre-lantern ventrite in 1**9D**. **Figure 20** a key to anatomy and splashing on ventrite 4. Data in **FigTable 19A-C** and the histogram in **19D** are repeated and compared with those of presumptive variad populations in **FigTables 22A-D**.



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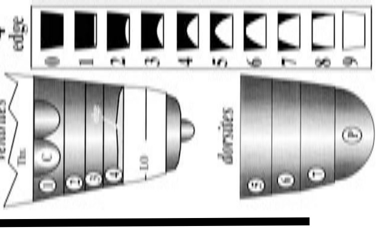
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.200	11.540	3.910	2.220	2.820	7.930	14.730	.824	1.272	.685
sd	.163	.523	.191	.155	.199	1.022	.655	.018	.072	.071
se	.052	.165	.060	.049	.063	.323	.207	5.812E-3	.023	.022
n	10	10	10	10	10	10	10	10	10	10
min	3.000	11.000	3.600	2.000	2.500	6.300	14.000	.810	1.210	.570
max	3.500	12.300	4.300	2.400	3.100	9.800	15.800	.870	1.410	.800
Vc%	5.1	4.5	4.9	7.0	7.1	12.9	4.5	2.2	5.7	10.4

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.600	1.300	1.000	1.400	1.600	2.400	2.600	5.100
sd	0.000	.516	.483	0.000	.699	.843	.516	.516	3.107
se	0.000	.163	.153	0.000	.221	.267	.163	.163	.983
n	10	10	10	10	10	10	10	10	10
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	0.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	19.8	37.2	0	49.9	52.7	21.5	19.9	60.9

FigTable 19. Cedarville SF, near Priests Bridge, Maryland.

Figure 20. Topographic and splash keys.



Augmented figure legends. **1**. Though *pyralis* is a firefly of grassy or herby patches and fields and *lucicrescens* occurs at forest edges and along tree rows near water, *pyralis* may be important prey of *lucicrescens*. **4**. Crescendo flash period as a function of ambient temperature. An exponential curve was fitted by the graphing program. The "deviant" point "s" at the upper left may be closer to factual than the curve; it was taken at the SC site and another that was measured at this site and

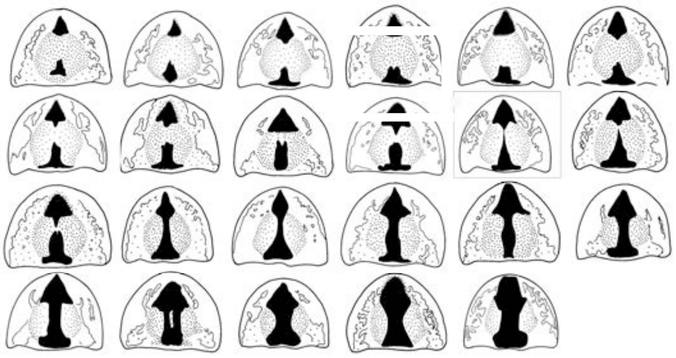
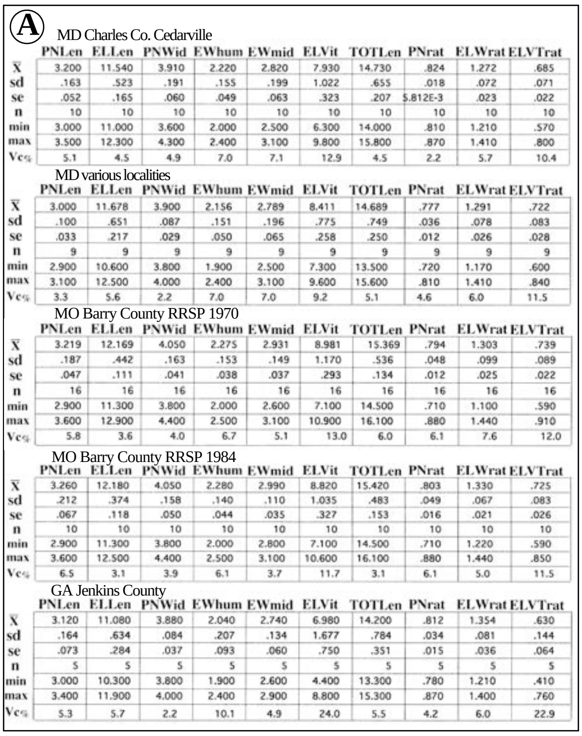


Figure 21. Array of pronotal drawings.

A range of vittagram photographs of *lucicrescens* is shown in **Figure 8**. **Figure 21** shows an array of (professional) drawings of *lucicrescens* pronota ranging from the most reduced observed in *lucicrescens* vouchers to the most expansive. Note that no pronotum in this *lucicrescens* series is totally lacking a vittagram, nor is any totally black; the male in **Figure 9** is missing a stem and serif. PNs in the **Figure 21** series are from vouchers from various localities.

made at a lower temperature fits with other measurements. Flash data included are from several populations: MD, VA, KY, SC, OH, CT, & NY. **7**. PM-traces of flashes of flying *lucicrescens* males. Temperatures as indicated: **A-E, G, I**, Crescendos of varying forms, some due to aerial maneuvers but perhaps there are modulations at the LO; **B, E, F**, show overload of PM-system with resulting grass from the distortion alarm; **E**, slightly oscillating intensity, perhaps from fish-tailing flight; **F**, Overloaded PM crescendo termination but apparently showing wingbeat modulations before the overload was reached because on enhanced sensitivity during the ramp, and showing a rate of about 50 Hz—the sharp down-step resulted from an unsuccessful attempt to reduce sensitivity so that the full length of the flash could be recorded; **G**, same as **E**; **J, K**, average short flashes at different temperatures; **L**, three flashes of a male being attracted to an LED decoy—note different chart speed, and any indication of the beginning of the crescendo FPs.



Ⓐ MD Charles Co. Cedarville

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.200	11.540	3.910	2.220	2.820	7.930	14.730	.824	1.272	.685
sd	.163	.523	.191	.155	.199	1.022	.655	.018	.072	.071
se	.052	.165	.060	.049	.063	.323	.207	5.812E-3	.023	.022
n	10	10	10	10	10	10	10	10	10	10
min	3.000	11.000	3.600	2.000	2.500	6.300	14.000	.810	1.210	.570
max	3.500	12.300	4.300	2.400	3.100	9.800	15.800	.870	1.410	.800
Vc%	5.1	4.5	4.9	7.0	7.1	12.9	4.5	2.2	5.7	10.4

MD various localities

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.000	11.678	3.900	2.156	2.789	8.411	14.689	.777	1.291	.722
sd	.100	.651	.087	.151	.196	.775	.749	.036	.078	.083
se	.033	.217	.029	.050	.065	.258	.250	.012	.026	.028
n	9	9	9	9	9	9	9	9	9	9
min	2.900	10.600	3.800	1.900	2.500	7.300	13.500	.720	1.170	.600
max	3.100	12.500	4.000	2.400	3.100	9.600	15.600	.810	1.410	.840
Vc%	3.3	5.6	2.2	7.0	7.0	9.2	5.1	4.6	6.0	11.5

MO Barry County RRSP 1970

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.219	12.169	4.050	2.275	2.931	8.981	15.369	.794	1.303	.739
sd	.187	.442	.163	.153	.149	1.170	.536	.048	.099	.089
se	.047	.111	.041	.038	.037	.293	.134	.012	.025	.022
n	16	16	16	16	16	16	16	16	16	16
min	2.900	11.300	3.800	2.000	2.600	7.100	14.500	.710	1.100	.590
max	3.600	12.900	4.400	2.500	3.100	10.900	16.100	.880	1.440	.910
Vc%	5.8	3.6	4.0	6.7	5.1	13.0	6.0	6.1	7.6	12.0

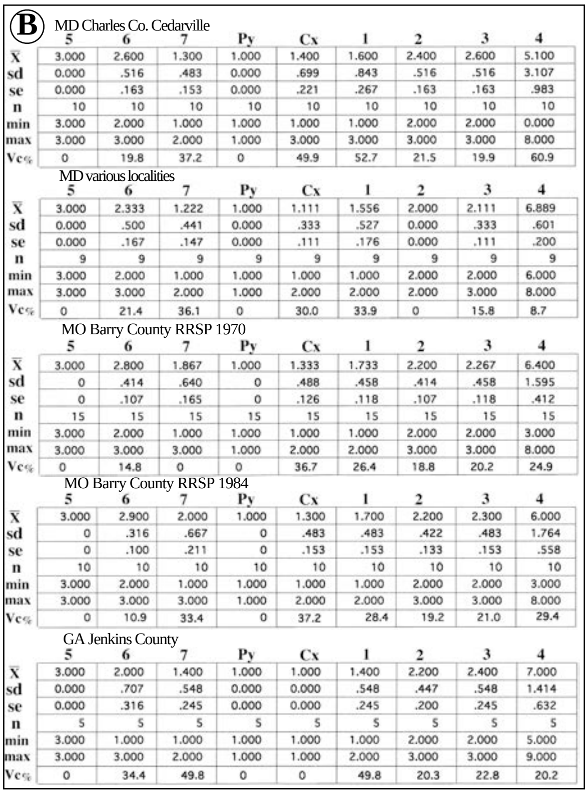
MO Barry County RRSP 1984

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.260	12.180	4.050	2.280	2.990	8.820	15.420	.803	1.330	.725
sd	.212	.374	.158	.140	.110	1.035	.483	.049	.067	.083
se	.067	.118	.050	.044	.035	.327	.153	.016	.021	.026
n	10	10	10	10	10	10	10	10	10	10
min	2.900	11.300	3.800	2.000	2.800	7.100	14.500	.710	1.220	.590
max	3.600	12.500	4.400	2.500	3.100	10.600	16.100	.880	1.440	.850
Vc%	6.5	3.1	3.9	6.1	3.7	11.7	3.1	6.1	5.0	11.5

GA Jenkins County

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.120	11.080	3.880	2.040	2.740	6.980	14.200	.812	1.354	.630
sd	.164	.634	.084	.207	.134	1.677	.784	.034	.081	.144
se	.073	.284	.037	.093	.060	.750	.351	.015	.036	.064
n	5	5	5	5	5	5	5	5	5	5
min	3.000	10.300	3.800	1.900	2.600	4.400	13.300	.780	1.210	.410
max	3.400	11.900	4.000	2.400	2.900	8.800	15.300	.870	1.400	.760
Vc%	5.3	5.7	2.2	10.1	4.9	24.0	5.5	4.2	6.0	22.9

FigTable 22A. Variad data compared.



Ⓑ MD Charles Co. Cedarville

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.600	1.300	1.000	1.400	1.600	2.400	2.600	5.100
sd	0.000	.516	.483	0.000	.699	.843	.516	.516	3.107
se	0.000	.163	.153	0.000	.221	.267	.163	.163	.983
n	10	10	10	10	10	10	10	10	10
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	0.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	19.8	37.2	0	49.9	52.7	21.5	19.9	60.9

MD various localities

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.333	1.222	1.000	1.111	1.556	2.000	2.111	6.889
sd	0.000	.500	.441	0.000	.333	.527	0.000	.333	.601
se	0.000	.167	.147	0.000	.111	.176	0.000	.111	.200
n	9	9	9	9	9	9	9	9	9
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	6.000
max	3.000	3.000	2.000	1.000	2.000	2.000	2.000	3.000	8.000
Vc%	0	21.4	36.1	0	30.0	33.9	0	15.8	8.7

MO Barry County RRSP 1970

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.800	1.867	1.000	1.333	1.733	2.200	2.267	6.400
sd	0	.414	.640	0	.488	.458	.414	.458	1.595
se	0	.107	.165	0	.126	.118	.107	.118	.412
n	15	15	15	15	15	15	15	15	15
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000
max	3.000	3.000	3.000	1.000	2.000	2.000	3.000	3.000	8.000
Vc%	0	14.8	0	0	36.7	26.4	18.8	20.2	24.9

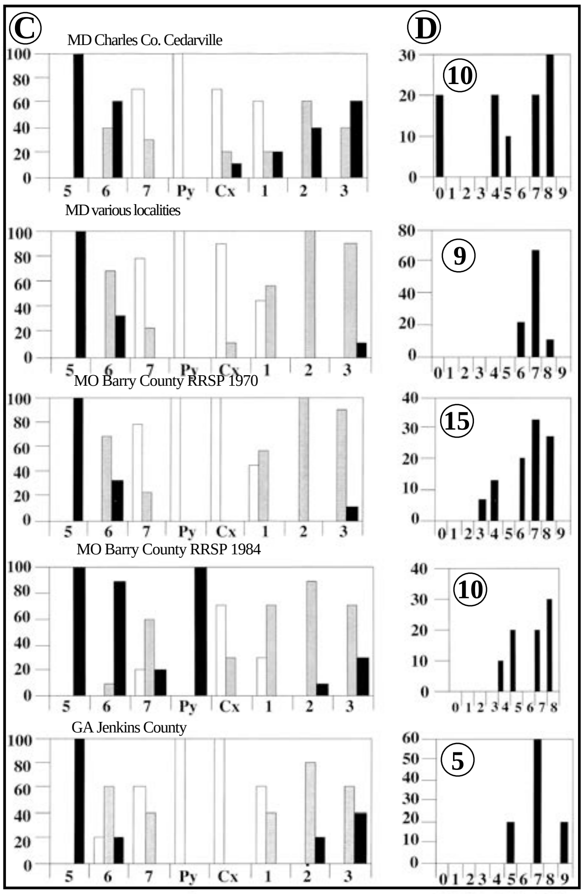
MO Barry County RRSP 1984

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.900	2.000	1.000	1.300	1.700	2.200	2.300	6.000
sd	0	.316	.667	0	.483	.483	.422	.483	1.764
se	0	.100	.211	0	.153	.153	.133	.153	.558
n	10	10	10	10	10	10	10	10	10
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000
max	3.000	3.000	3.000	1.000	2.000	2.000	3.000	3.000	8.000
Vc%	0	10.9	33.4	0	37.2	28.4	19.2	21.0	29.4

GA Jenkins County

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.000	1.400	1.000	1.000	1.400	2.200	2.400	7.000
sd	0.000	.707	.548	0.000	0.000	.548	.447	.548	1.414
se	0.000	.316	.245	0.000	0.000	.245	.200	.245	.632
n	5	5	5	5	5	5	5	5	5
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	5.000
max	3.000	3.000	2.000	1.000	1.000	2.000	3.000	3.000	9.000
Vc%	0	34.4	49.8	0	0	49.8	20.3	22.8	20.2

FigTable 22B. Variad data compared.



FigTable 22CD. Variad data compared.

Chapter 47

Photuris lynfaustae n. sp.

Hitched Red (HR)

This firefly is presently known only from the Holotype locality in Okefenokee Swamp in southeastern Georgia (**Fig. 1**). It is morphologically indistinguishable from *maicoi*. The distinguishing FP is the apparent (to the eye) hitch/ crescendo. HR was found in a pine forest (plantation) within the Okefenokee Swamp (Okefenokee National Wildlife Refuge) near the entrance gate of the Steven Foster State Park, Georgia, on Route 177. As with other *Photuris* "Red-Group" species, males are often high-flyers at 10-50 feet above the ground. HR emits single flashes at 2-3 sec intervals (**Fig. 2,** rate in **Figs. 3** and **4**). At close range flashes can be seen to twinkle, hitch, or ramp, probably depending upon the angle viewed and light-organ movement/speed relative to the observer's eye (see also *hebes*). Flashes with three *apparent* peaks were observed. The red (tawny) color of various species nicknamed "Red" may have no higher taxonomic significance beyond being a temporary organizing/sorting convenience. Seasonal record is shown against that of its apparent "sibling" species *maicoi* in **Figure 5**. It is becoming evident that *Photuris* females prey upon *Photuris* males and probably those of their own species. **Figure 13** shows the pronotum of a crescendo flashing male with punctures in the pronotum as might be made by those of a *Photuris* female. It is one of the six that has been found on close examination of vouchers of many species. Puncture dimensions are appropriate. As noted elsewhere in this paper, males have been found flashing and dragging their genitalia as though they had pulled free from a mate. A connection already has been noted between hitched FPs and crescendo flashing in this and other species.

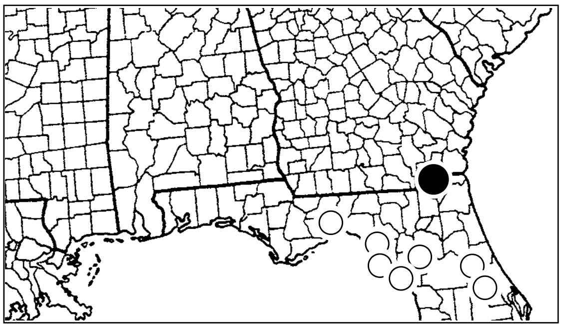


Figure 1. Only record of *lynfaustae* occurrence, with records for *maicoi* (circles).

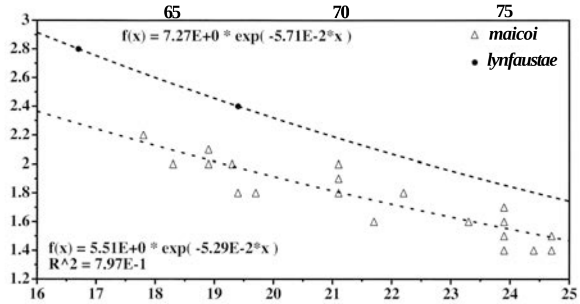


Figure 2. FP Period (AX: sec/temp).

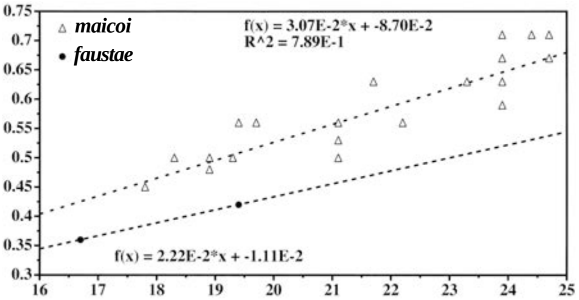


Figure 3. FP rate (AX: Hz./temp).

Morphological summary for one voucher series. Means (n=6): PNL 3.2, ELL 11.7, PNW 3.9, EWhum 2.2, EWmid 2.8, ELVit 0.0, TOTLen 14.8, PNrat 0.82, ELWrat 1.28, ELVTrat 0.0 (**FigTable 6);** sclerite colors and prelantern ventrite splash (**Fig-Table 7** and **Fig. 8,** see also **Fig. 11); Figure 12** is a key to anatomical elements and splashing on ventrite 4. **Figures 9** shows an photo array of voucher pronota, and **Figure 10**, the analysis of some Red species based on the vittagrams illustrated in the PN vitta reference "201.2" elsewhere in this paper.

Vouchers. 7215, 7217, 7220, 7226, 7229, 7232, 7233, 7234, 7237, 7238. (probably also 7235, 7236).

Holotype description. male, voucher number 7238, collected 13 May 1972, Charlton County [mislabeled Ware Co.], GA. Okefenokee Swamp, SC Foster Pk, near gate. [above on page:"new sp, ca 2 sec int, def twinkle." (From FB, 1972 page 21: "HR — recorder won't work." Morphological data: genitalia extruded remain attached; from spread sheet—PNLen 3.3, ELLen 12.4, PNWid 4.3, ELWhum 2.4, ELWmid 2.9, LELVit 2.9, TotLen 15.6, PnRat 0.76, ElRat 1.21, VitRat 0.23; Colors: T 311, Py 1, Cx 3,V 333, Edg 2. Types will be deposited in the USNM.

Taxonomic Notes. Voucher specimens are labelled as from Ware County, Georgia. This is incorrect, and should read Charlton County. The specific epithet recognizes Lynn Faust, amateur fireflyer in name only, whose work would do credit to an academic biology department—as appreciated of Frank McDermott only after his passing.

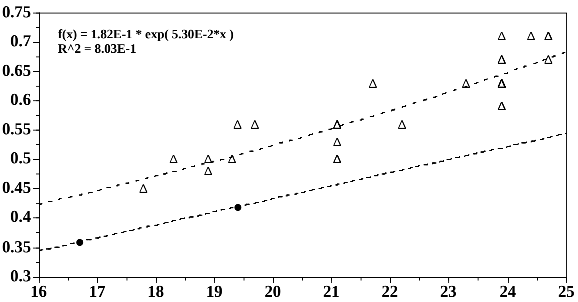


Figure 4. FP rate, exponential model (AX: Hz./temp).

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.233	11.667	3.940	2.188	2.792	0.000	14.753	.820	1.277	0.000
sd	.123	.816	.233	.105	.151	0.000	.916	.030	.069	0.000
se	.050	.333	.095	.043	.062	0.000	.374	.012	.028	0.000
n	6	6	6	6	6	6	6	6	6	6
min	3.130	11.000	3.630	2.125	2.625	0.000	13.880	.780	1.170	0.000
max	3.380	13.000	4.250	2.375	3.000	0.000	16.380	.860	1.350	0.000
Vc%	3.8	7.0	5.9	4.8	5.4	0	6.2	3.7	5.4	0

FigTable 6. Morphological measurements and ratios of HR vouchers.

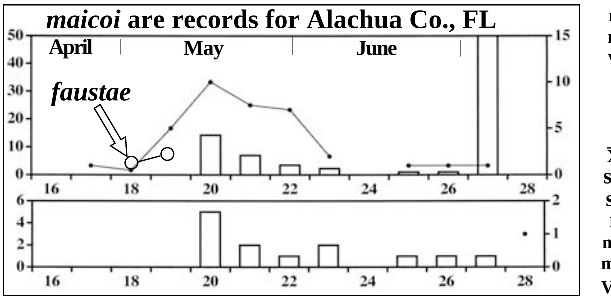


Figure 5. SESOBS: lyn*faustae* (HR) with background of *maicoi* (BR).

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.333	1.000	1.000	2.333	2.667	3.000	3.000	2.000
sd	0.000	.516	0.000	0.000	.516	.516	0.000	0.000	.894
se	0.000	.211	0.000	0.000	.211	.211	0.000	0.000	.365
n	6	6	6	6	6	6	6	6	6
min	3.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	1.000
max	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
Vc%	0	38.7	0	0	22.1	19.4	0	0	44.7

FigTable 7. Sclerite colors and splash of HR vouchers.

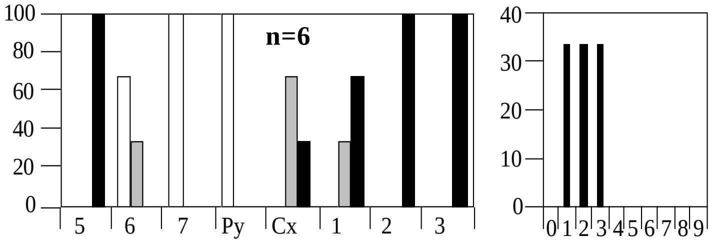


Figure 8. Sclerite colors and splash of HR vouchers.

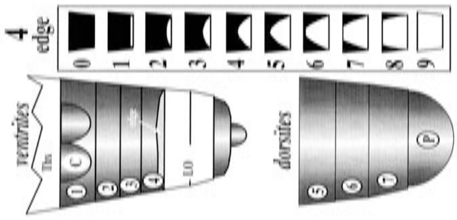


Figure 12. Topographic and splash key.

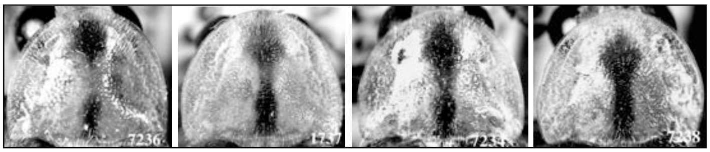


Figure 9. Array of vouchers vittagrams.

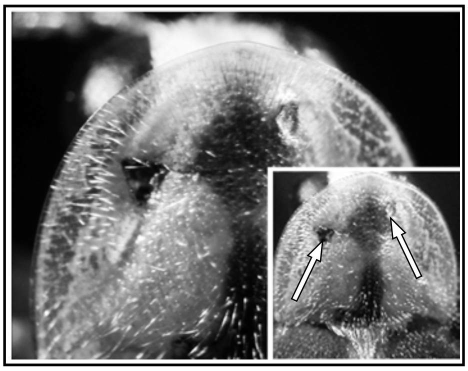


Figure 13 . Punctures in PN of a crescendo-flashing *Photuris* in the Okefenokee Swamp. HR?

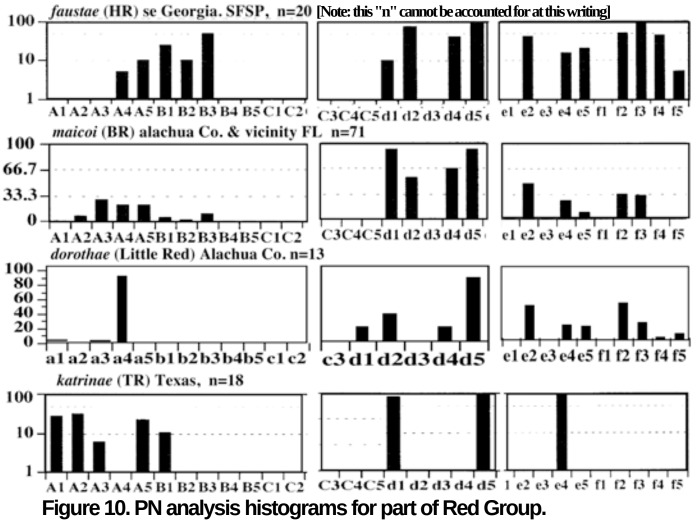


Figure 10. PN analysis histograms for part of Red Group.

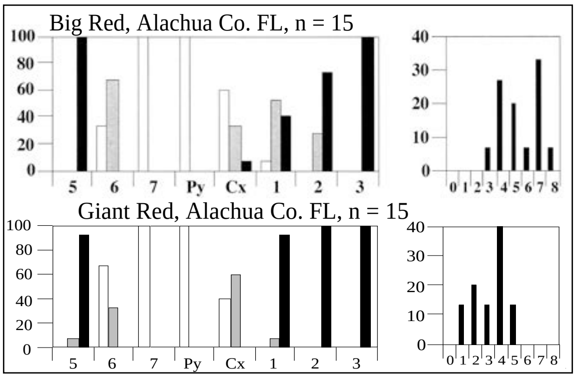


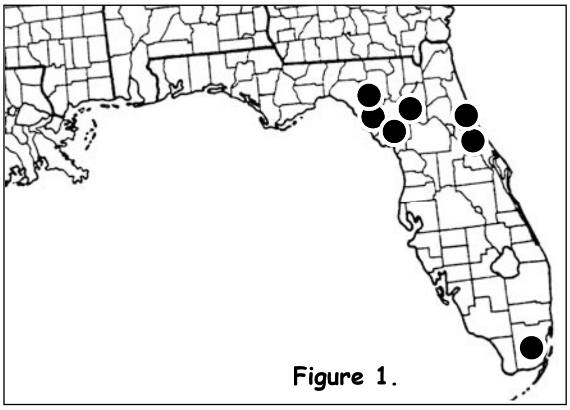
Figure 11. Comparison of colors and splash of vouchers.

Chapter 48

Photuris maicoi n. sp.

Big Red (BR)

This is an uncommon firefly, rarely seen in the field and never recognized with confidence among thousands of archived specimens examined. The known range of *maicoi* is restricted to peninsular Florida (**Fig. 1**), but an apparent sister species (or two?), was found in the Okefenokee swamp. Big Red's large size (13-15 mm), tawny ground color, and often broken vittagram make it somewhat distinctive. In Florida *maicoi* specimens are most likely to be confused with *Photuris lineaticollis* and *harrannorum*: they have dark/black hind coxae (vs tawny in BR) and fly earlier in spring. FP period in *maicoi* ranges from 1.5 to 2.2 seconds @25°/77°—18°/65.5° (**Fig. 2**); FP rate is shown in **Figure 3**.



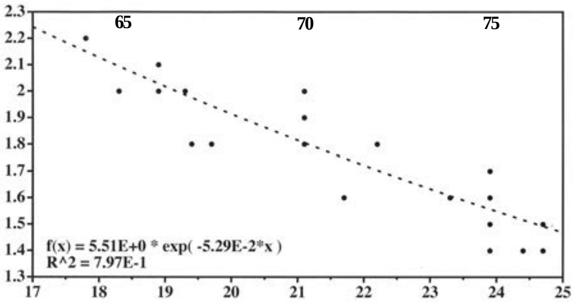


Figure 2. FP period (AX: sec/temp).

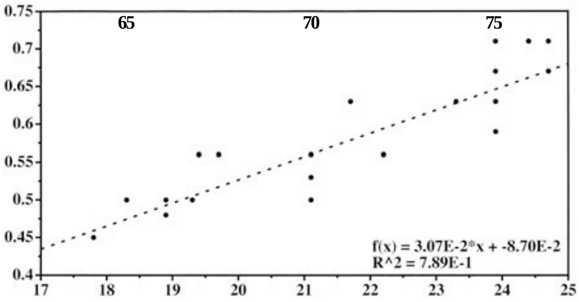


Figure 3. FP rate (AX: Hz/temp).

Ecology, flashing behavior, phenology. On all but one occasion only few or a single male of *maicoi* was seen and they were flying high along roadsides or over adjacent fields, pine plantations, and regrowth (successional) pine situations, searching at the tree tops (**Fig. 4**). The exception was large numbers flying low over a pasture and meadow a few miles inland from the coast in Volusia County, FL.

Figure 4. BR's own view of the world and activity space.

The single, short flash approaches crescendo form, with rise-time being longer than the fall (**Fig. 5 B-I**). This slight crescendo, which in a few recordings appears as a shoulder (**Fig. 5 I**)—as seen in many PM-records of *hebes*, a species that shows a range of flash forms that suggest an evolutionary sequence in crescendo development—possibly indicates a phylogenetic connection with *lucicrescens*-Group fireflies (**Fig. 6**). The duration of flashes PM-recorded at temperatures between 23.9°/75° and 24.7°/76.5° averaged 46 mSec at half max and 113 mSec at base (n=58 flashes, 15 males). The bioluminescence spectrum peak was 552 millimicrons, with half max at 526.5 and 594.0, and half max width 67.5 (Biggley et al); this spectrum subjectively may somewhat match *Roscolux*® filter #87, *pale yellow green*.

Through virtually all of the several specimens collected were attracted to the penlight from distances as far as 150 feet, and often came readily without hesitation, occasionally they either could not be attracted more than a short distance or would only approach when the delay or duration of the decoy flash was lengthened. This appeared to be more than merely an adjustment for a temperature differential. One grounded blinking *maicoi* carried a phoretic, social pseudoscorpion (**Figs. 7-8, 10**; *Paratemnus elongatus*).

The recorded seasonal (SESOBS) profiles for the Gulf and north-central region of peninsular Florida are shown in **Figure 9**—an adult season from late April to July.

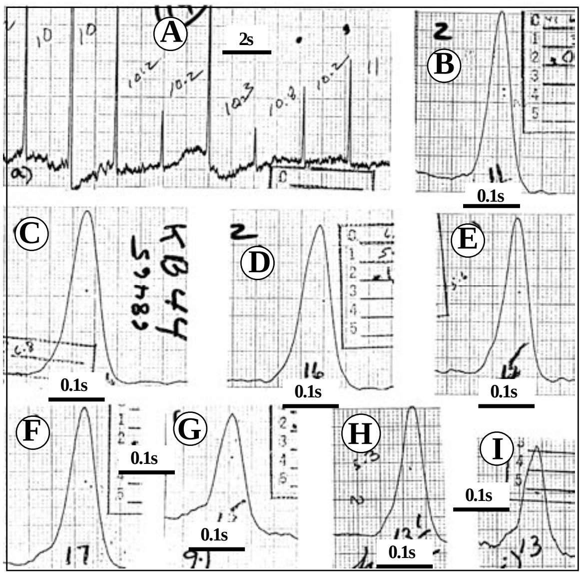


Figure 5. PM-chart-records of flashes of flying males. Temperatures as indicated: (A) Series of FPs from a single male; (B-I) flashes at a faster chart speed; note the gradual onset of each crescendo and the initial shoulders in some (AX: rel. int./time); scale shown..

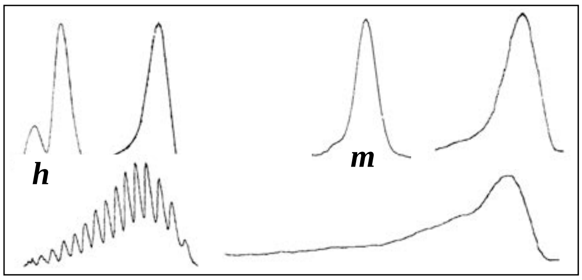


Figure 6. Some Luci-group reps: h, *hebes*; and m, *maicoi*.

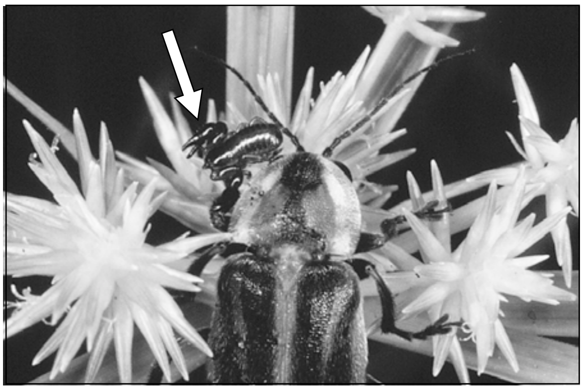


Figure 7. *Ph. maicoi* with *Paratemnus* grabbing foreleg.

Figure 8. Pioneering/colonizing *Paratemnus* family on *lamarcki*.

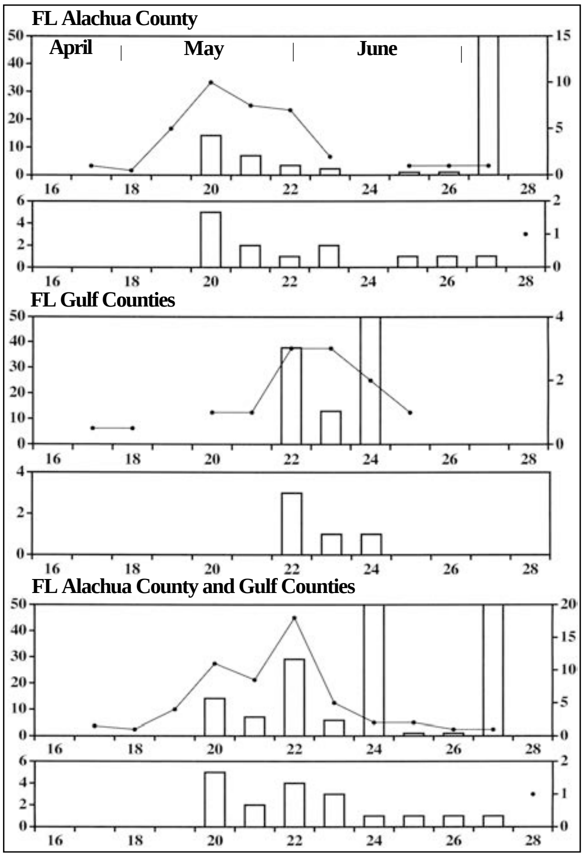


Figure 9. SESOBS (AX: number/WOY, see M&T).

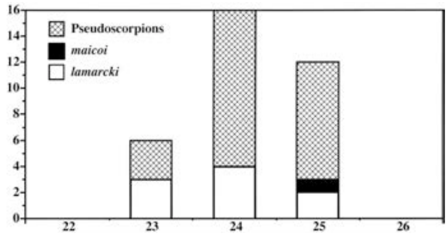
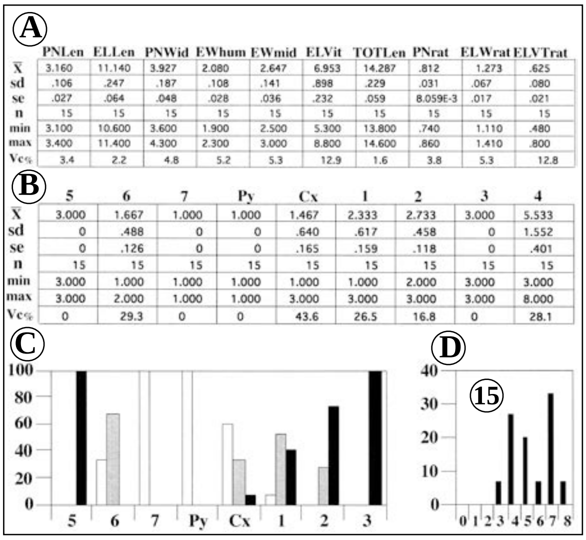


Figure 10. *Paratemnus* phoresy (AX: n/ WOY).



	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	3.160	11.140	3.927	2.080	2.647	6.953	14.287	.812	1.273	.625
sd	.106	.247	.187	.108	.141	.898	.229	.031	.067	.080
se	.027	.064	.048	.028	.036	.232	.059	8.059E-3	.017	.021
n	15	15	15	15	15	15	15	15	15	15
min	3.100	10.600	3.600	1.900	2.500	5.300	13.800	.740	1.110	.480
max	3.400	11.400	4.300	2.300	3.000	8.800	14.600	.860	1.410	.800
Vc%	3.4	2.2	4.8	5.2	5.3	12.9	1.6	3.8	5.3	12.8

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.667	1.000	1.000	1.467	2.333	2.733	3.000	5.533
sd	0	.488	0	0	.640	.617	.458	0	1.552
se	0	.126	0	0	.165	.159	.118	0	.401
n	15	15	15	15	15	15	15	15	15
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	3.000	3.000
max	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	29.3	0	0	43.6	26.5	16.8	0	28.1

Figure 11. Gainesville, Alachia County, FL.

Morphology. General morphological means are (n=15): PNL 3.2, ELL 11.1, PNW 3.9, EWhum 2.1, EWmid 2.7, ELVit 7.0, TOTLen 14.3, PNrat 0.81, ELWrate 1.27, ELVTrat 0.63 (**Fig. 11A**, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **Figure 11B-C**, and the splash of the pre-lantern ventrite in **11D**. (**Figure 12** is a guide to the numbers used for various skeletal plates and for degrees of splashing on ventrite 4.)

Holotype description: Male, voucher number 67198, collected 4 May 1967, Alachua County, Florida, Univ. Florida campus, Medicinal Plant Garden FB page 46: Two attracted, collected, voucher numbers 67193, 67198. FB note: "attracted two broken vitta male[s] from 40'. they gave single sharp at 2 sec. [penlight] Answered 0 delay." Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.4, ELLen 10.9, PNWid 4.0, ELWhum 2.0, ELWmid 2.6, LELVit 6.9, RELVit 6.3, TotLen 14.1, PnRat 0.81, ElRat 1.32, VitRat 0.603; Colors: T 31, Py 1, Cx 1, V 333, Edg 5. Types will be deposited in the USNM.

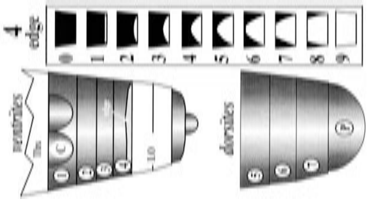


Figure 12. Topographic and splash keys.

Figure 13 shows an array of (Laura Line) drawings of *maicoi* pronota ranging from the most reduced seen in vouchers to the most expansive. Note that no pronotum in the array is totally lacking a vittagram, nor is any PN totally black; the individual in **Figure 7** has a rather robust vittagram and the one in **Figure 14** has a broken stem and like all others, lacks a serif. Finally. **Figure 15** shows BR's PNV arrays from three regions of Florida.

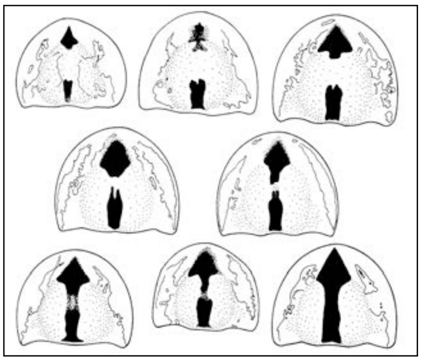


Figure 13. PNV array, artist sketches.

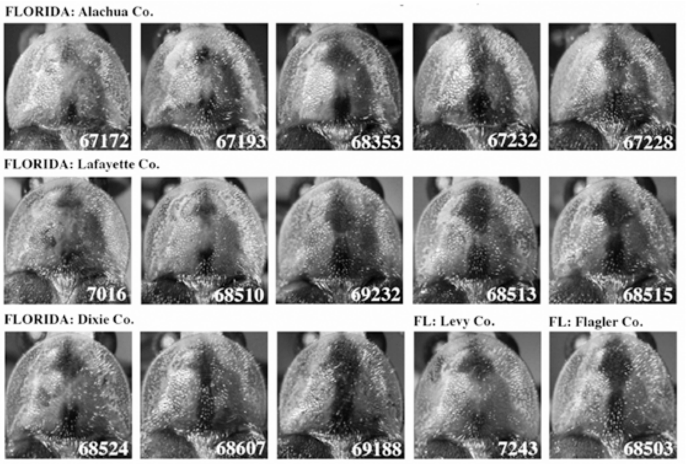


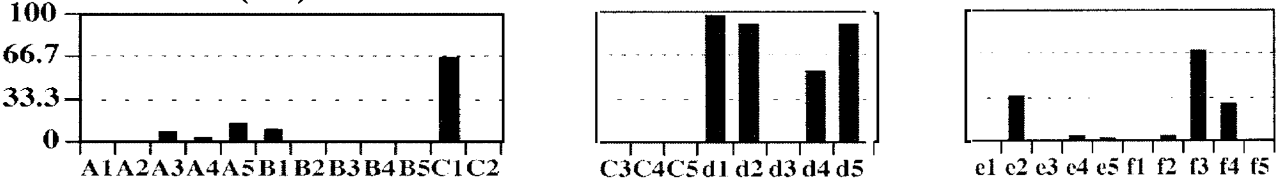
Figure 15. PNV photo-arrays from five regions in Florida.

Figure 14. Female at the Med Garden, UF.

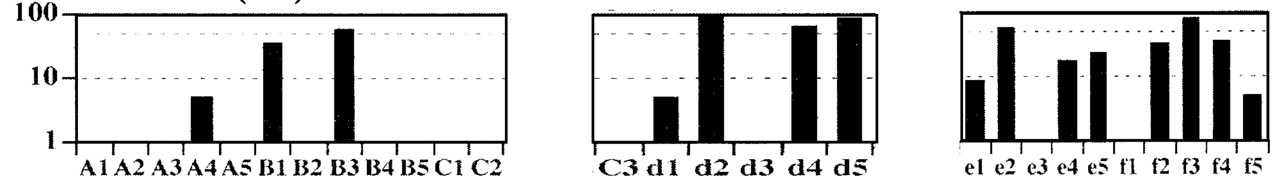
Taxonomic and other notes. The scientific name of this firefly gives thanks and pays tribute to Dan Maico, a naturalist, photographer, friend, and the physician whose skills twice made it possible for me to continue the chase, and on many other regularly scheduled occasions kept me ahead of growing concerns.

PN Comparisons: lineaticollis & maicoi Red GROUPS

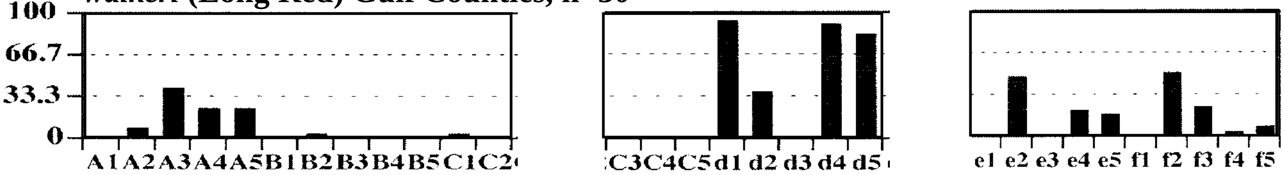
lineaticollis (GR) Alachua Co. n=29



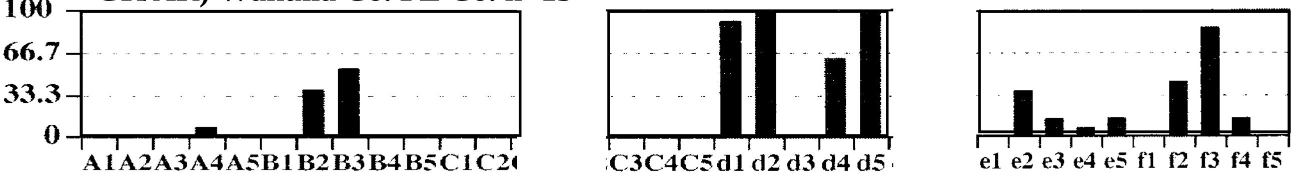
lineaticollis (GR) various FL localities. n=22



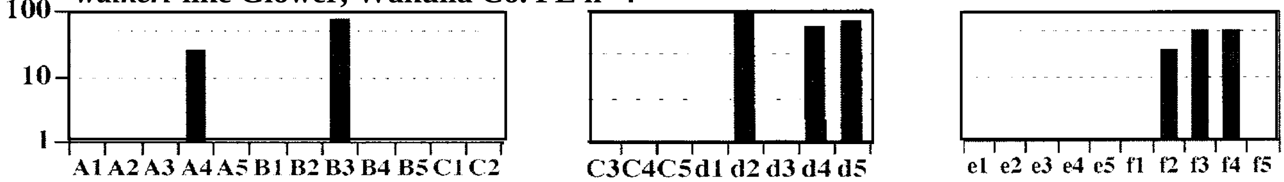
walkeri (Long Red) Gulf Counties, n=30



GR/AR) Wakulla Co. FL Co. n=13



walkeri-like Glower, Wakulla Co. FL n=4



Chapter 49

Photuris margotooleae n. sp.

Integrity Firefly

This firefly "is clearly" a peripherally isolated variad of continental *Photuris tremulans*, and its primary and only known FP is a single, short flash. That is, unlike *tremulans* it does not have, has not yet shown a recognizable adjunct FP—though it *does not* emit an A-flicker, it may have unrecognized coded timing differences in its short-flash signaling, as discussed for *tremulans*. I recognized/found *margotooleae* only in northeastern US (**Fig. 1**), where it occurred in ecological situations similar to those of *tremulans* though more commonly over grassland than noted for *tremulans*. **Figures 2** and **3** show an aging oldfield site near Avon, CT, and a shrub-tree-line site near a highway overpass at Walhalla, NY. All observations were made during June variously between 1988 and 2003.

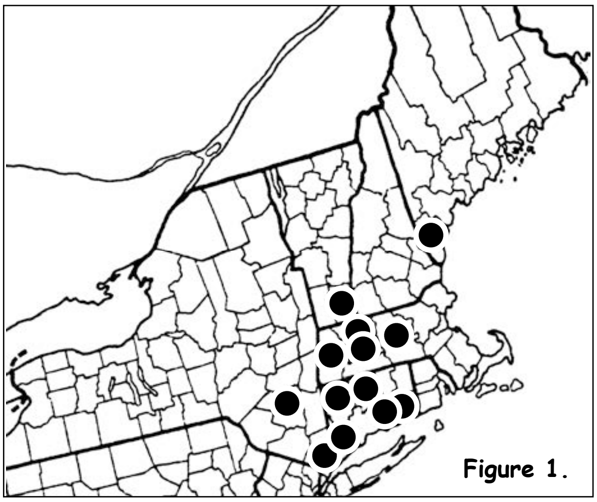


Figure 1.


Figure 2. Oldfield on Old Farm Road near Avon, CT.


Figure 3. Overpass site, Walhalla, NY.

This firefly can be identified with certainty only by its short-flash FP, but the presence of *Ph. stevensae* will be disconcerting to fireflyers familiar with *tremulans* because the ubiquitous A-flickering males observed in *margotooleae's* range will be those of *stevensae*. Flickering *stevensae* default to a pulsing FP. A free-ranging and similar *Photuris* in the area is *fairchildi* which sometimes and under unknown circumstances elsewhere has been seen emitting short flashes; in northeastern *fairchildi* only the rapidly-repeated, and many-pulsed FPs were seen, but Buschman observed the short flash in Nova Scotia..

Figure 4 shows sequences of short flashes and individual flashes at two different temperatures, **Figure 5** shows the regression of FP interval on temperature, and **Figure 6** the rate regression. Field observation is necessary for identification, and in hand this firefly resembles *fairchildi* and *stevensae* though is somewhat smaller, averaging 13.8 mm versus 15.1 and 14.3 mm respectively.

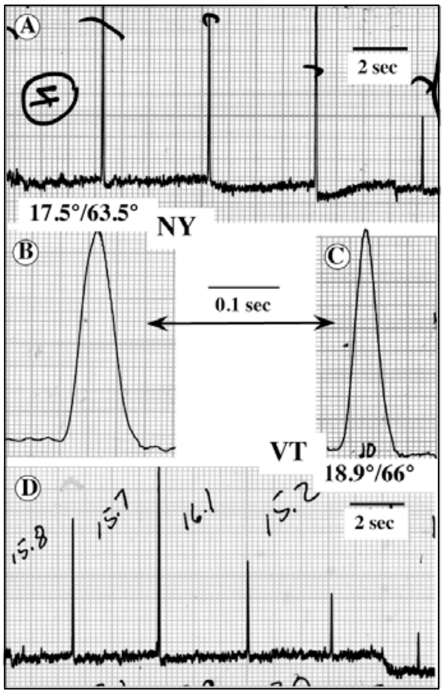


Figure 4. Flashes at two temps (AX: rel. int./time).

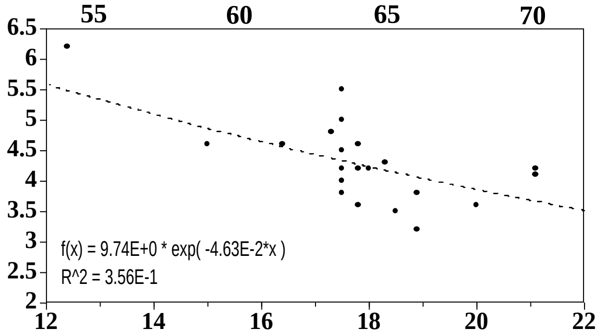


Figure 5. FP period (AX: sec/temp).

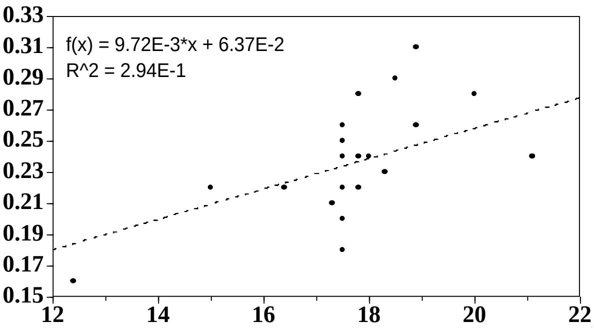


Figure 6. FP rate (AX:Hz/temp).

* * *

Ⓐ	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.650	11.108	3.250	1.842	2.450	7.017	13.783	.824	1.346	.632
sd	.168	.450	.193	.124	.151	1.341	.556	.038	.095	.119
se	.048	.130	.056	.036	.044	.387	.160	.011	.027	.034
n	12	12	12	12	12	12	12	12	12	12
min	2.400	10.100	2.800	1.600	2.100	4.000	12.500	.780	1.190	.400
max	3.000	11.600	3.500	2.000	2.600	9.000	14.500	.890	1.500	.810
Vc%	6.3	4.1	5.9	11.9	6.2	19.1	4.0	4.6	7.1	18.8

Ⓑ	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.923	1.846	1.000	3.000	2.769	3.000	3.000	4.308
sd	0.000	.277	.689	0.000	0.000	.439	0.000	0.000	.855
se	0.000	.077	.191	0.000	0.000	.122	0.000	0.000	.237
n	13	13	13	13	13	13	13	13	13
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	9.5	37.3	0	0	15.9	0	0	19.9

FigTable 7. Measurements, colors, and ratios from combination New England sample; see below for data by locality and histograms.

Morphology. General morphological means are (n=12): PNL 2.7, ELL 11.1, PNW 3.3, EWhum 1.8, EWmid 2.5, ELVit 7.0, TOTLen 13.8, PNrat 0.82, ELWrate 1.35, ELVTrat 0.63 (**Fig. 7A**, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **Figure 7B. Figure 8** is a guide anatomical plates and degrees of splashing on ventrite 4.) **Figure 9** shows an array of PN vittagrams from CT and NY. FigTable 10 gives measurement, color, and splash data and histograms for individual New England sites.

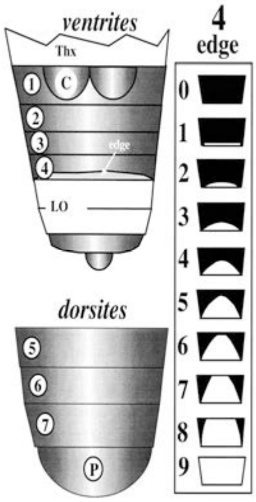


Figure 8. Topographic and splash keys.

Holotype description. male; voucher number 9019; collected 20 June1990, as it flew over the oldfield on Old Farm Road (Fig. 2), near Avon, Connecticut: it was noted as emitting single bright flashes, tandem SWAT measurements of 4.4 and 4.1 sec at 18.3°/65° in Field Book 1989-90, p 220. Measurements and ratios: PNLen 2.6 mm, ELLen 11.3 mm, PNWid 3.4 mm, ELWhum 1.9 mm, ELMid 2.6 mm, LELVit 6.3 mm, TotLen 13.9 mm, PnRat 0.78, ElRat 1.40, VitRat 0.56. Pigmentation and splash: T5-3. T6-3, T7-2, Py-1, C-3; V1-3, V2-3, V3-3, V4-splash-4. Pronotal Vittigram in Figure 6 (arrow). Paratype numbers listed under Voucher heading below. Types will be deposited in the USNM.

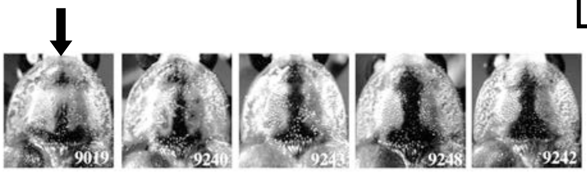


Figure 9. Vittagram array, New Eng. & NY; arrow indicates Holotype.

Note: This firefly is named in honor of Dr. Margot O'toole, a scientist of uncommon and uncompromising courage who personally and virtually alone confronted post-modern man's race to the bottom in scientific integrity, and provided an example for the rest of us.

Ⓐ

margotooleae NEng

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.650	11.108	3.250	1.842	2.450	7.017	13.783	.824	1.346	.632
sd	.168	.450	.193	.124	.151	1.341	.556	.038	.095	.119
se	.048	.130	.056	.036	.044	.387	.160	.011	.027	.034
n	12	12	12	12	12	12	12	12	12	12
min	2.400	10.100	2.800	1.600	2.100	4.000	12.500	.780	1.190	.400
max	3.000	11.600	3.500	2.000	2.600	9.000	14.500	.890	1.500	.810
Vc%	6.3	4.1	5.9	11.9	6.2	19.1	4.0	4.6	7.1	18.8

margotoolae ny

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.600	10.833	3.267	1.767	2.433	7.300	13.500	.810	1.387	.677
sd	0.000	.404	.153	.153	.153	.889	.346	.030	.163	.102
se	0.000	.233	.088	.088	.088	.513	.200	.017	.094	.059
n	3	3	3	3	3	3	3	3	3	3
min	2.600	10.600	3.100	1.600	2.300	6.300	13.300	.780	1.200	.560
max	2.600	11.300	3.400	1.900	2.600	8.000	13.900	.840	1.500	.750
Vc%	0	3.7	4.7	8.7	6.3	12.2	2.6	3.7	11.8	15.1

margotoolae avon

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.657	11.171	3.257	1.857	2.429	6.686	13.843	.826	1.323	.597
sd	.190	.499	.237	.127	.170	1.595	.643	.040	.075	.134
se	.072	.189	.090	.048	.064	.603	.243	.015	.028	.051
n	7	7	7	7	7	7	7	7	7	7
min	2.400	10.100	2.800	1.600	2.100	4.000	12.500	.780	1.190	.400
max	3.000	11.600	3.500	2.000	2.600	9.000	14.500	.890	1.400	.810
Vc%	7.2	4.5	7.3	6.8	7.0	23.9	4.7	4.8	5.7	22.5

margotoolae midd

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.667	11.133	3.267	1.967	2.533	7.933	13.800	.820	1.303	.713
sd	.208	.351	.153	.115	.058	.723	.529	.053	.112	.081
se	.120	.203	.088	.067	.033	.418	.306	.031	.065	.047
n	3	3	3	3	3	3	3	3	3	3
min	2.500	10.800	3.100	1.900	2.500	7.100	13.400	.780	1.180	.620
max	2.900	11.500	3.400	2.100	2.600	8.400	14.400	.880	1.400	.770
Vc%	7.8	3.2	4.7	5.9	2.3	9.1	3.8	6.5	8.6	11.4

Ⓑ

margotooleae New Eng

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.923	1.846	1.000	3.000	2.769	3.000	3.000	4.308
sd	0.000	.277	.689	0.000	0.000	.439	0.000	0.000	.855
se	0.000	.077	.191	0.000	0.000	.122	0.000	0.000	.237
n	13	13	13	13	13	13	13	13	13
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	9.5	37.3	0	0	15.9	0	0	19.9

margotoolae ny

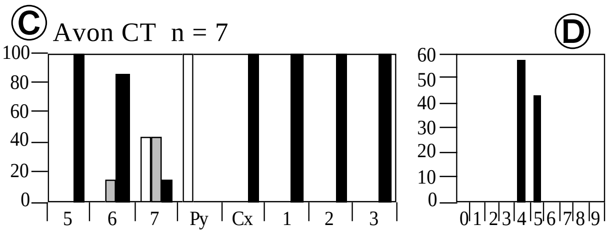
	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	1.667	1.000	3.000	2.333	3.000	3.000	4.333
sd	0.000	0.000	.577	0.000	0.000	.577	0.000	0.000	.577
se	0.000	0.000	.333	0.000	0.000	.333	0.000	0.000	.333
n	3	3	3	3	3	3	3	3	3
min	3.000	3.000	1.000	1.000	3.000	2.000	3.000	3.000	4.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	34.6	0	0	24.7	0	0	13.3

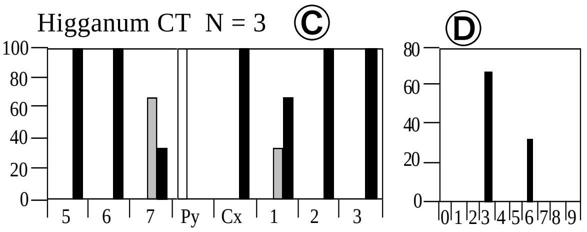
margotoolae avon

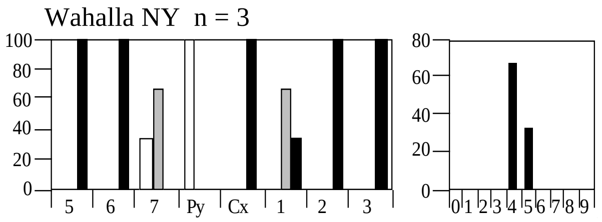
	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.857	1.714	1.000	3.000	3.000	3.000	3.000	4.429
sd	0	.378	.756	0	0	0	0	0	.535
se	0	.143	.286	0	0	0	0	0	.202
n	7	7	7	7	7	7	7	7	7
min	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	4.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	13.2	44.1	0	0	0	0	0	12.1

margotoolae midd

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	2.333	1.000	3.000	2.667	3.000	3.000	4.000
sd	0.000	0.000	.577	0.000	0.000	.577	0.000	0.000	1.732
se	0.000	0.000	.333	0.000	0.000	.333	0.000	0.000	1.000
n	3	3	3	3	3	3	3	3	3
min	3.000	3.000	2.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	0	24.7	0	0	21.6	0	0	43.3







FigTable. 10. Measurements, ratios, and sclerite/Cx color of FP vouchers from various New England sites.

The Naturalist

Nature and nurture conspire to form a naturalist. Predisposition, an opportune period, and a happy series of events ... [67]

Among the greatest men of all time are the creative naturalists, from Aristotle to Darwin, whose enduring work and self-effacing lives are our most precious possessions. I prefer the naturalist to the scientist, because there is less of the ego in him. In the truly creative naturalist the ego entirely disappears, and through his impersonal vision we see nature with the least human aberration. [3]

Henry Fairfield Osborn, 1928, pages 3, 67. *Impressions of Great Naturalists*, Charles Scribner's Sons, New York, pp. 294.

Photo by E. L. Fowler

Chapter 50

Photuris missouriensis McDermott 1962

Prairie Train Firefly, Missouriensis

This firefly may occur over a much greater range and acreage than suggested by the few localities shown on the map **(Fig. 1**), and at times in parts of its range be the most common *Photuris*. Its known distribution is within the Mississippi River drainage, across grassland, hilly and low-mountain regions (**Fig. 2**). In the figure, probably the Kansas records are legitimate but some uncertainty exists; a museum series from Colorado without flashing notes may also be conspecific (coll. Hugh Leech, CAS). In the field, *missouriensis* presents much like *potomaca* and *chenangoa* in key diagnostic characters, occurring over "damp and swampy" ground (**Fig. 3, 4**), near and along water courses, and emitting its short flashes in trains. Flashing flight began at full darkness and continued at a high level for an hour or so, and then gradually diminished, with some males continuing to fly and flash until midnight. Adult seasonal occurrence is noted to be from late May to mid July (**Fig. 5**). *Missouriensis* has the slowest flash rate of the *Photuris* train-flashing species and note that its temperature regression is interesting, as discussed below (**Figs. 9, 10**).

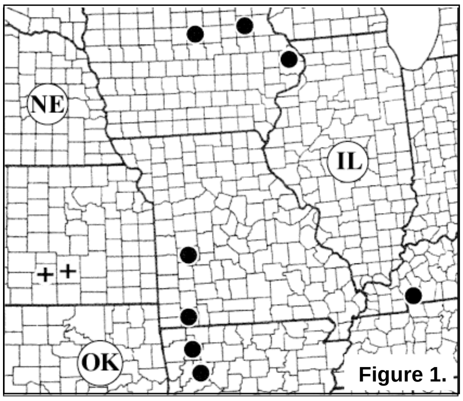


Figure 1.

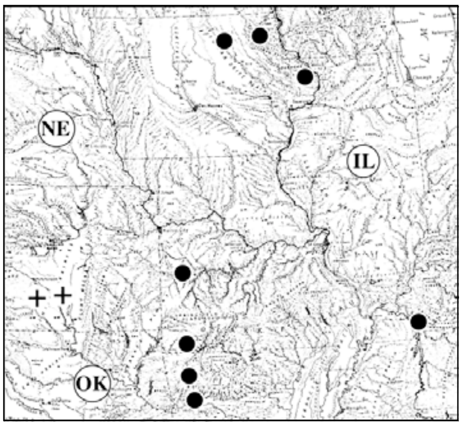


Figure 2. Physiographic perspective.

In Jackson and Franklin Counties, Iowa, in mid June, this firefly was exceedingly abundant, flying low over fields, meadows, roadsides, and marshes, and up into shrubs and tall trees (**Figs. 6, 7**). “Fast flashers here by the millions—low, med, high, over fields, marshes, everywhere … over cattails, fields, up in willows” (FB 1987: 5-6). At the same week/year at Volga River S. P. in Fayette County, only a few, were seen and those were along a stream. So also, at the same time, though specifically sought in the vicinity of Yellow River S. P. in northeastern Iowa, Allamakee County. In Barry County (RRSP), Missouri, *missouriensis* occurred in numbers along a low-lying, willow-lined creek; two sites noted in Arkansas were along a tree-lined stream, and a dry stream-bed and narrowly over adjacent mowed-herbaceous areas.

Flashing. Males emitted long-continued, intermittently broken trains of short flashes at a temperature-dependent periods and rates that ranged from ca 2.5 sec/0.4 Hz at 14°/57° to ca 0.8 sec/1.25 Hz at 25°/77° (**Figs. 6, 7**). Unbroken train lengths of 4-16 consecutive flashes were noted. This is the only train-flashing *Photuris* within its range, so far as known. Males in close proximity were not seen to synchronize their flashes.

PM-recordings show near symmetry in flash form (**Fig. 8**), with a very fast rise and slightly slower fall (r/f ca 0.65). Records of 18 flashes emitted by five males in Jackson County, IA (18-VI-87, 22.6°C), show a base duration of ca 56 mSec, and a halfmax duration of about 22 mSec. PM-records of 78 flashes emitted by 13 males in Barry County, MO (23-VI-70, 18.9°C), show a base duration of ca 60 mSec, and a halfmax duration of about 26 mSec.


Figure 3. Iowa marsh.


Figure 4. Low wet grassland, Iowa.

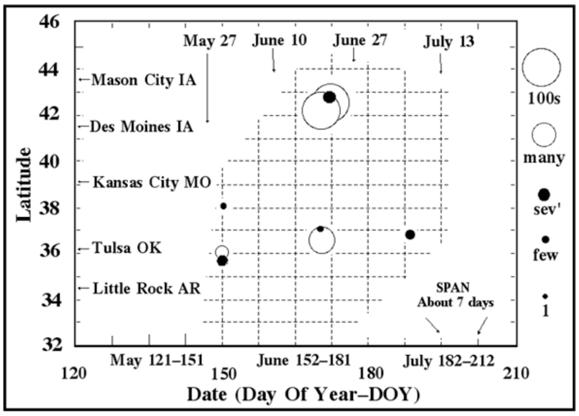


Figure 5. GESEDISOBS (AX: Lat/DOY).

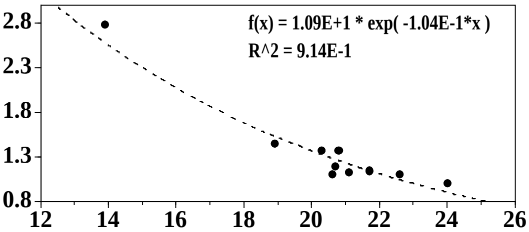


Figure 6. FP period (AX: sec/temp).

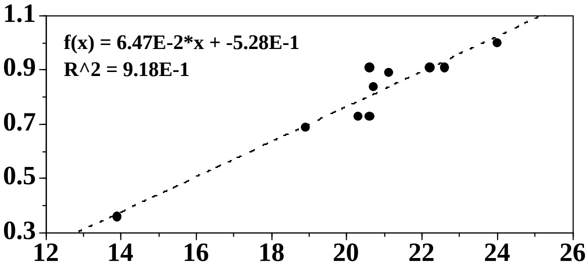
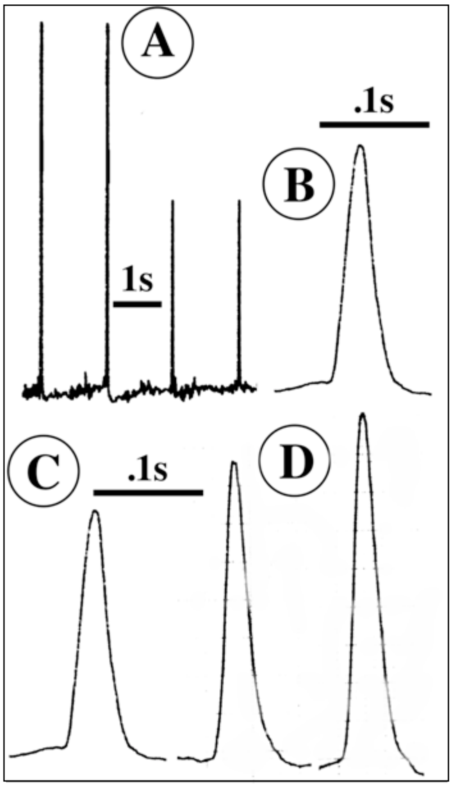


Figure 7. FP rate (AX: Hz./temp).



FP rate/temperature slope "anomaly"? More must be said of the rate/temperature slope of *missouriensis* flashes: The observed rate/temp slope shown in **Figure 4** differs from the slopes of other ("related?") train-flashing species, *potomaca* and *chenangoa.* **Figure 9** shows the regression slopes of these two species with that of *missouriensis*; if we apply a similar slope at a point where ambient temperatures often occur during the adult *missouriensis* season, and a straight-line relationship is maintained, then at ≈16.5°C the line intersects zero Hz. (**Fig. 10**). This temperature would not preclude search flight.

Though the regressions for *missouriensis* and *chenangoa* do cross, that is, at ≈16°C they have identical flash rates, the two are geographically widely separated. See also **Figure 10** legend.

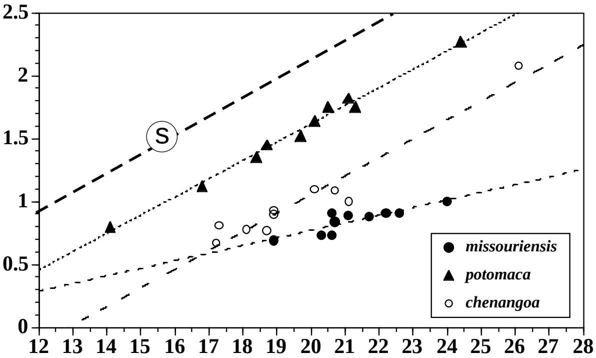


Figure 9. A deviant slope? If these three species are closely related one might expect the slopes to be parallel (AX: Hz/temp).

f(x) = 6.04E-2*x + -4.36E-1 *missouriensis*
R^2 = 7.31E-1
f(x) = 1.45E-1*x + -1.28E+0 *potomaca*
R^2 = 9.89E-1
f(x) = 1.48E-1*x + -1.91E+0 *chenangoa*
R^2 = 9.29E-1

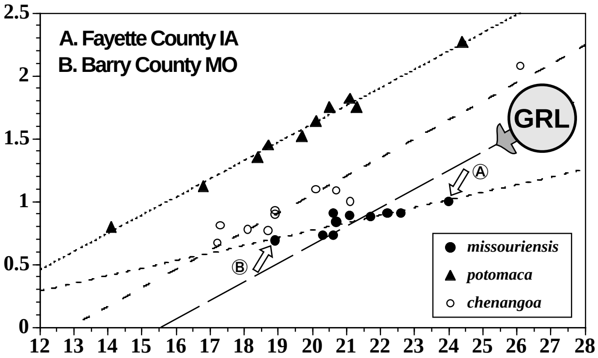


Figure 10. The GRL line might be predicted if these three species are closely related. Could the *missouriensis* line (as also shown in Figs. 9 and 4) be rotated here by chance, from two "deviant" measurements in power positions, as shown at points A and B? A temperature error of 1 degree could account for such "deviance" —that is, put these two dots near the "proper" line …

Figure 8. Note the near symmetry, with a rapid rise and slightly slower fall. **(A)** Train of a male recorded at the Holotype locality, Roaring River S.P., Barry Co. MO, 23-VI-70, 18.9°C; **(B, C)** Two flashes from this train. **(D)** 2 flashes recorded in Jackson Co. IA, 18-VI-87, 22.6°C. **9.** Comparison of the flash rates of train-flashing NA species, and note of "Sullivan," a voucher-less northeastern observation in Sullivan County, NY.

Decoying. A short flash with the flashpole-LED on the ground, emitted immediately after each flash of flying males sometimes attracted them to a foot or so. Decoy flashes after alternate male flashes sometimes caused them to land closer to the LED. When males broke off an approach they apparently departed rapidly and darkly.

Miscellaneous Notes: McDermott named this firefly from 20 specimens sent to him by J. W. Green that did “not conform to any of Barber’s (1951) species … Type locality, Roaring River State Park, Missouri; collected on June 15, 1954, by J. W. Green … Habitat Conditions: ‘In grassy field, with few trees near river, some swampy ground.’ … Holotype male in collection of California Academy of Sciences. … Flashing Conduct: ‘Flying low just at top of vegetation; flash single, repeated contiuously while flying at two or three second intervals.’ (J. W. Green).” Specimens were deposited at the CAS and USNM.

A series I collected in Sedgwick and Butler Counties KS in 1964 have label tags with flash sketches and numbers that indicate they were train flashing fireflies; the timing noted is slightly different from what found at the Holotype locality. These Kansas fireflies may have been probably *missouriensis*.

Only belatedly (2008), after 42 years, was it decided that a 1966 series collected and recorded at the type locality was probably McDermott's *missouriensis*—note that the flash rate associated with the type series (i.e. Green/McDermott) was slower than observed during this study. In the absence of accurate flashing measurements and associated temperature for the type series, but with agreement in general ecological and morphological features, a tentative association/identification was made here.

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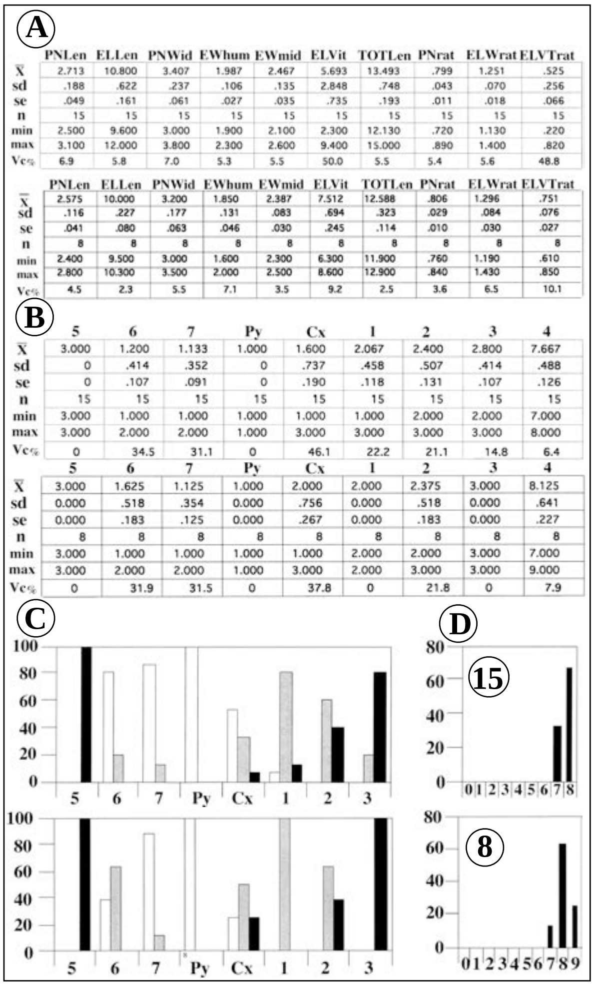


A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.713	10.800	3.407	1.987	2.467	5.693	13.493	.799	1.251	.525
sd	.188	.622	.237	.106	.135	2.848	.748	.043	.070	.256
se	.049	.161	.061	.027	.035	.735	.193	.011	.018	.066
n	15	15	15	15	15	15	15	15	15	15
min	2.500	9.600	3.000	1.900	2.100	2.300	12.130	.720	1.130	.220
max	3.100	12.000	3.800	2.300	2.600	9.400	15.000	.890	1.400	.820
Vc%	6.9	5.8	7.0	5.3	5.5	50.0	5.5	5.4	5.6	48.8

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.575	10.000	3.200	1.850	2.387	7.512	12.588	.806	1.296	.751
sd	.116	.227	.177	.131	.083	.694	.323	.029	.084	.076
se	.041	.080	.063	.046	.030	.245	.114	.010	.030	.027
n	8	8	8	8	8	8	8	8	8	8
min	2.400	9.500	3.000	1.600	2.300	6.300	11.900	.760	1.190	.610
max	2.800	10.300	3.500	2.000	2.500	8.600	12.900	.840	1.430	.850
Vc%	4.5	2.3	5.5	7.1	3.5	9.2	2.5	3.6	6.5	10.1

B

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.200	1.133	1.000	1.600	2.067	2.400	2.800	7.667
sd	0	.414	.352	0	.737	.458	.507	.414	.488
se	0	.107	.091	0	.190	.118	.131	.107	.126
n	15	15	15	15	15	15	15	15	15
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	7.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	34.5	31.1	0	46.1	22.2	21.1	14.8	6.4

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.625	1.125	1.000	2.000	2.000	2.375	3.000	8.125
sd	0.000	.518	.354	0.000	.756	0.000	.518	0.000	.641
se	0.000	.183	.125	0.000	.267	0.000	.183	0.000	.227
n	8	8	8	8	8	8	8	8	8
min	3.000	1.000	1.000	1.000	1.000	2.000	2.000	3.000	7.000
max	3.000	2.000	2.000	1.000	3.000	2.000	3.000	3.000	9.000
Vc%	0	31.9	31.5	0	37.8	0	21.8	0	7.9

FigTable 11. Morphological data.

Morphological data. General morphological means for two separate data sets from RRSP (n=15, 8; 1966, 1970), are shown in **FigTable 11.** Set 1: n=15, PNL 2.7, ELL 10.8, PNW 3.4, EWhum 2.0, EWmid 2.5, ELVit 5.7, TOTLen 13.5, PNrat 0.80, ELWrate 1.25, ELVTrat 0.53 (**FigTable 10A**, with related stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **FigTable 10B-C**, and the splash-color of the pre-lantern ventrite in **10D**. **Figure 11.** Key to skeletal plates and degrees of splashing on ventrite 4. A range of vittagrams of *missouriensis* is shown in **Figure 12**. Data for four other populations of *missouriensis* are given below in **Figure 13**; vittagrams from several populations are in **Figure 14**.

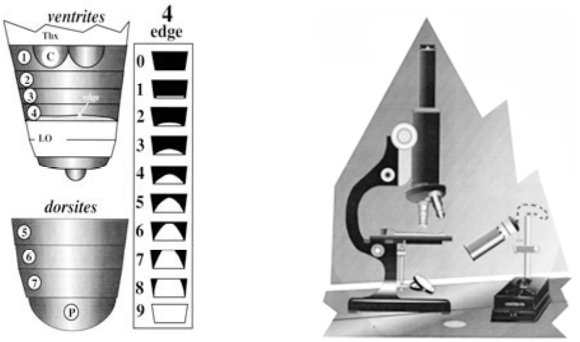


Figure 11.

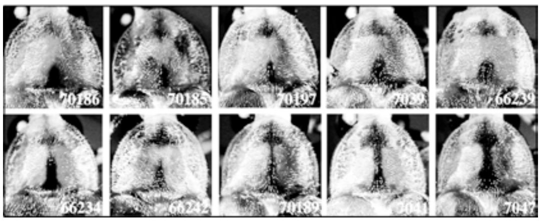


Figure12. Array of "topotype"-voucher PNs, from RRSP.

FigTable 13. Part A.

missouriensis RRSP

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.713	10.800	3.407	1.987	2.467	5.693	13.493	.799	1.251	.525
sd	.188	.622	.237	.106	.135	2.848	.748	.043	.070	.256
se	.049	.161	.061	.027	.035	.735	.193	.011	.018	.066
n	15	15	15	15	15	15	15	15	15	15
min	2.500	9.600	3.000	1.900	2.100	2.300	12.130	.720	1.130	.220
max	3.100	12.000	3.800	2.300	2.600	9.400	15.000	.890	1.400	.820
Vc%	6.9	5.8	7.0	5.3	5.5	50.0	5.5	5.4	5.6	48.8

missouriensis KS butler

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.686	9.986	3.200	1.829	2.557	7.586	12.686	.840	1.431	.759
sd	.107	.445	.163	.049	.399	.644	.511	.036	.232	.038
se	.040	.168	.062	.018	.151	.243	.193	.014	.088	.014
n	7	7	7	7	7	7	7	7	7	7
min	2.600	9.400	3.000	1.800	2.100	6.600	12.000	.780	1.210	.710
max	2.800	10.600	3.400	1.900	3.400	8.100	13.400	.880	1.930	.810
Vc%	4.0	4.5	5.1	2.7	15.6	8.5	4.0	4.3	16.2	5.0

missouriensis KS sedg.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.600	9.720	3.140	1.830	2.330	6.580	12.290	.829	1.277	.673
sd	.205	.588	.222	.142	.200	1.180	.732	.042	.071	.093
se	.065	.186	.070	.045	.063	.373	.232	.013	.023	.029
n	10	10	10	10	10	10	10	10	10	10
min	2.300	8.500	2.900	1.600	2.000	4.000	11.000	.780	1.190	.470
max	2.900	10.600	3.500	2.000	2.600	8.000	13.500	.920	1.430	.780
Vc%	7.9	6.1	7.1	7.8	8.6	17.9	6.0	5.1	5.6	13.8

missouriensis KY

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.520	10.480	3.180	1.840	2.320	4.640	13.000	.802	1.280	.448
sd	.130	.622	.179	.055	.130	1.716	.800	.028	.054	.181
se	.058	.278	.080	.024	.058	.767	.358	.012	.024	.081
n	5	5	5	5	5	5	5	5	5	5
min	2.300	9.400	2.900	1.800	2.100	3.100	11.600	.770	1.210	.290
max	2.600	10.900	3.300	1.900	2.400	7.000	13.500	.840	1.360	.660
Vc%	5.2	5.9	5.6	3.0	5.6	37.0	6.2	3.5	4.2	40.4

missouriensis NE

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.700	10.400	3.450	1.950	2.400	6.100	13.050	.780	1.235	.590
sd	.283	.566	.212	.212	.141	.707	.778	.014	.078	.042
se	.200	.400	.150	.150	.100	.500	.550	.010	.055	.030
n	2	2	2	2	2	2	2	2	2	2
min	2.500	10.000	3.300	1.800	2.300	5.600	12.500	.770	1.180	.560
max	2.900	10.800	3.600	2.100	2.500	6.600	13.600	.790	1.290	.620
Vc%	10.5	5.4	6.2	10.9	5.9	11.6	6.0	1.8	6.3	7.1

leachi COL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.686	10.414	3.429	1.914	2.457	6.586	13.086	.786	1.291	.633
sd	.146	.667	.243	.107	.215	.308	.797	.030	.048	.046
se	.055	.252	.092	.040	.081	.116	.301	.011	.018	.017
n	7	7	7	7	7	7	7	7	7	7
min	2.500	9.500	3.100	1.800	2.100	6.100	12.000	.740	1.210	.560
max	2.900	11.400	3.900	2.100	2.800	6.900	14.300	.810	1.360	.710
Vc%	5.4	6.4	7.1	5.6	8.8	4.7	6.1	3.8	3.7	7.3

FigTable 13. Part B.

missouriensis RRSP

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.200	1.133	1.000	1.600	2.067	2.400	2.800	7.667
sd	0	.414	.352	0	.737	.458	.507	.414	.488
se	0	.107	.091	0	.190	.118	.131	.107	.126
n	15	15	15	15	15	15	15	15	15
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	7.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	34.5	31.1	0	46.1	22.2	21.1	14.8	6.4

missouriensis KS Butler Co.

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.429	1.143	1.000	2.571	2.286	2.857	3.000	6.857
sd	0.000	.787	.378	0.000	.535	.488	.378	0.000	1.773
se	0.000	.297	.143	0.000	.202	.184	.143	0.000	.670
n	7	7	7	7	7	7	7	7	7
min	3.000	1.000	1.000	1.000	2.000	2.000	2.000	3.000	3.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	55.1	33.1	0	20.8	21.3	13.2	0	25.9

missouriensis KS sedgewick Co.

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	2.857	1.143	1.000	1.000	1.857	1.714	2.571	2.714	6.429
sd	.378	.378	0.000	0.000	.690	.488	.535	.488	1.272
se	.143	.143	0.000	0.000	.261	.184	.202	.184	.481
n	7	7	7	7	7	7	7	7	7
min	2.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	4.000
max	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	8.000
Vc%	13.2	33.1	0	0	37.2	28.5	20.8	18.0	19.8

missouriensis KY Trigg Co.

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.200	1.000	1.000	3.000	2.600	3.000	2.800	7.000
sd	0.000	.447	0.000	0.000	0.000	.548	0.000	.447	0.000
se	0.000	.200	0.000	0.000	0.000	.245	0.000	.200	0.000
n	5	5	5	5	5	5	5	5	5
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	2.000	7.000
max	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	37.3	0	0	0	21.1	0	16.0	0

missouriensis NE

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	2.500	1.000	1.000	3.000	3.000	3.000	3.000	4.500
sd	0	.707	0	0	0	0	0	0	3.536
se	0	.500	0	0	0	0	0	0	2.500
n	2	2	2	2	2	2	2	2	2
min	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	2.000
max	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	28.3	0	0	0	0	0	0	78.6

missouriensis CO.

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	2.000	1.429	2.714	2.286	3.000	3.000	1.714
sd	0.000	0.000	.577	.535	.488	.488	0.000	0.000	1.254
se	0.000	0.000	.218	.202	.184	.184	0.000	0.000	.474
n	7	7	7	7	7	7	7	7	7
min	3.000	3.000	1.000	1.000	2.000	2.000	3.000	3.000	0.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	3.000
Vc%	0	0	28.9	37.4	18.0	21.3	0	0	73.2

FigTable 13. Parts C, D.

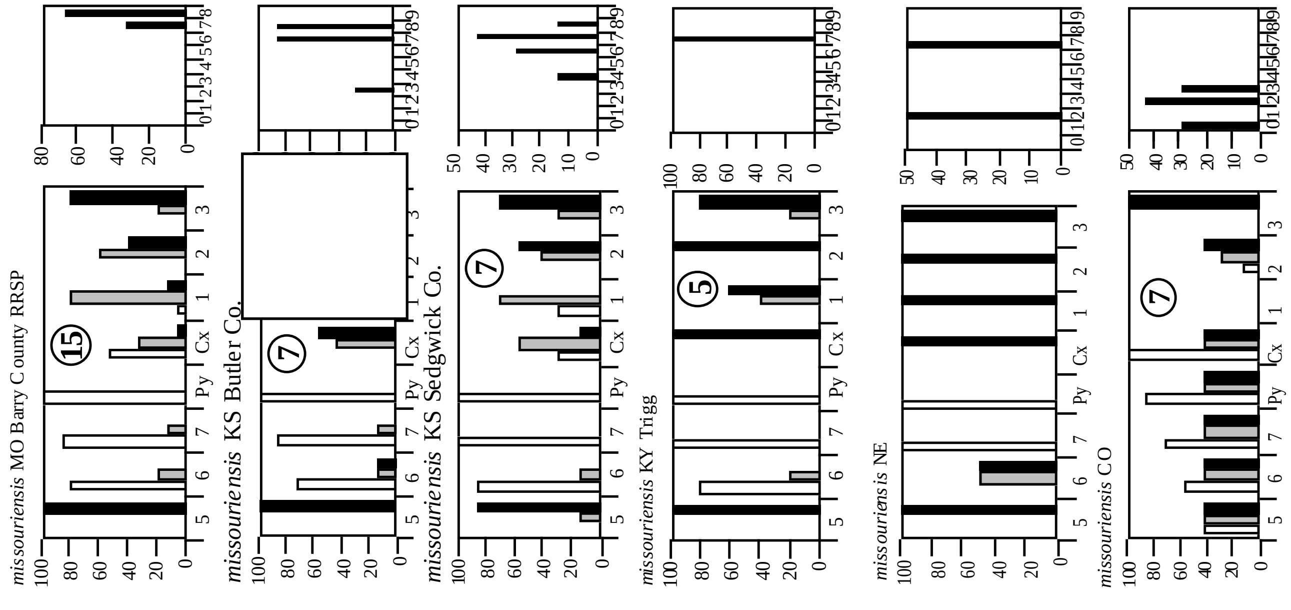
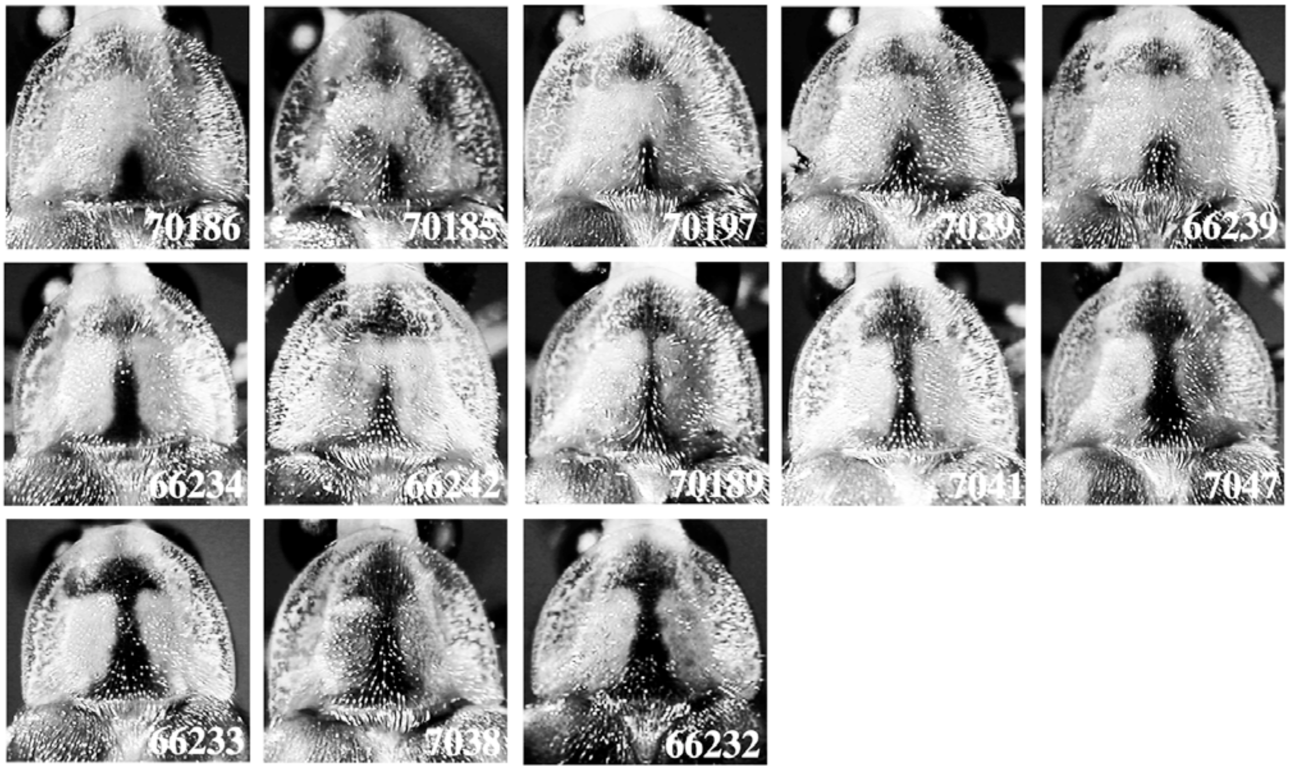


Figure 14. Vittagram arrays of *missouriensis* vouchers from several localities.

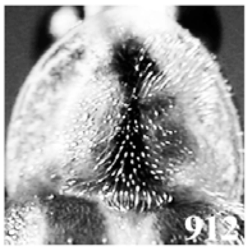
MISSOURI: Barry Co. RRSP. Type Locality



IOWA: Franklin Co. IOWA: Fayette Co. IOWA: Jackson Co.

ARKANSAS: Conway Co.

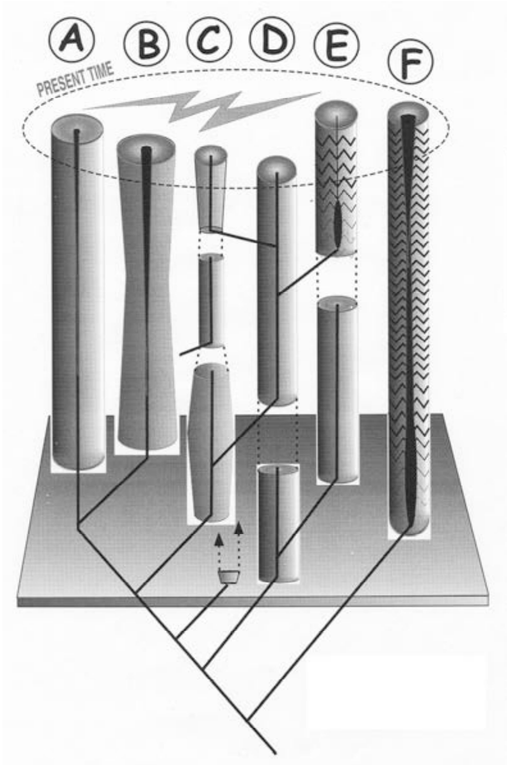
ARKANSAS: Madison Co.

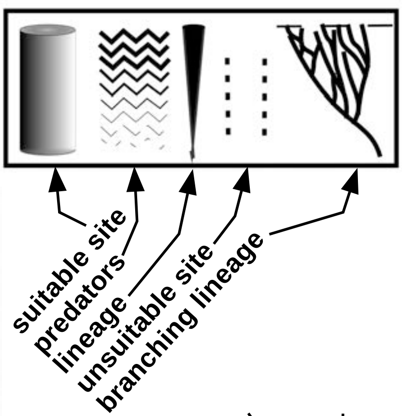


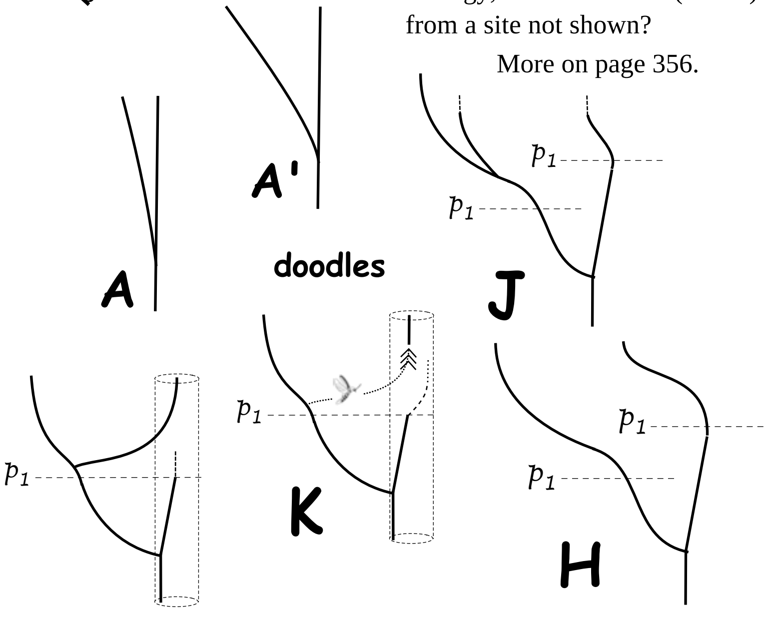
Thinking about species and speciation, a smaller scale: “Human beings are storytelling creatures. We structure reality in terms of narratives. In other words, we start at Point A and get to Point B, and everything in between is called hope. If you’re a human, you’re a storyteller, a story believer, and that’s just the way it is” (Cline, 2009). In this paper you are being asked to pivot in your thinking from the BSC to a D(eme)SC, and imagine species stories at a different and hopefully more operational scale. Historically, the primary model for the extrinsic separation of species that could lead to genetic divergence has been the geographic separation/isolation model. In experimenting with deme-thinking many of the same ideas apply, just on a smaller scale, and interdemic shuffling is a phenomon and active principle to be viewed as something to focus on. In former times the idea of reticulate evolution—the interconnection of working branches of a conceptual tree—was a heresy, well beyond heterodoxy. In a seminar given at a job-interview, 50 years ago, I was challanged as to the bifurcation and rejoining of a lineage in the evolution of flashing behavior—the diagram in question was merely showing that there were two possible ways to get from point A to point B. But, the crusty old fossil ornithologist, being sharply tuned to anti-reticulation, saw the diamond diagram in a flow chart and pounced, in a kindly way. At this working level, while knowing virtually nothing about the reality of deme sizes or shapes, or their conformation to weather or geographic or drainage patterns, or even whether fireflies might fly between them or are carried by other forces, we seek to find and understand the biogeography of demes, and reticulation.

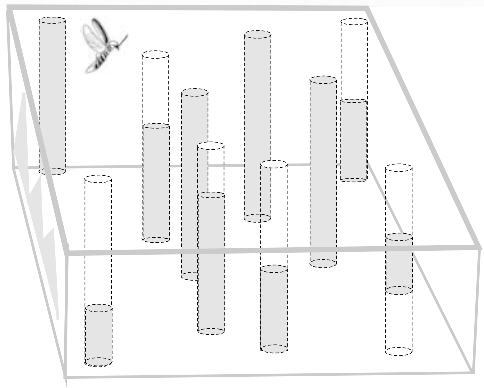
The diagrams are to visualize some of the basic elements involved in evolutionary, deme story-telling, including branching lineages, suitable habitats across space that disappear and reappear, the changing sizes of firefly populations, interconnections among them that shuffle, accept and discard genes, and the appearance of a strong selection force, predator fireflies. Six sites are indicated by letters A-F—a seventh barely started but ended almost immediately; site suitability by column diameter and changed ecology by a break in the column; the dotted oval is the present time horizon; tree diameter indicates population size changes; and the variable chevrons, the occurrence and pressure intensity of signal-mimicking predators. Note in **F** that the prey population decreased with the appearance of predators, but eventually recovered, an imagined successful countermeasure to predation? Both **C** and **D** indicate that colonist/founders arrived soon upon the return of suitable ecology, and in one case (mid-**C**) from a site not shown?

More on page 356.









Chapter 51

Photuris moorei n. sp.

Fast Crescendo

Populations of this firefly were seen at RRSP, Missouri, and in Coffee County, Georgia. At four other localities passing individuals tentatively identified as this species were seen moving along riparian tree-lines and over streams (**Fig. 1**). Vouchers of *moorei* are distinctive and should be recognizable in a museum insect tray, but since I have never found one in many examined collections it may be rare and not likely to be encountered in the field by usual collecting techniques. This firefly resembles a large (<12 mm) *cinctipennis*, but the hind coxae are dusky, not an "unblemished" ivory or white. The flash pattern is a continuous and sometimes somewhat mechanical train of short crescendo flashes with a 2 second period at 18°/64.5° (**Figs. 2-4**). Both observed populations were adjacent to streams as were the incidental sightings.

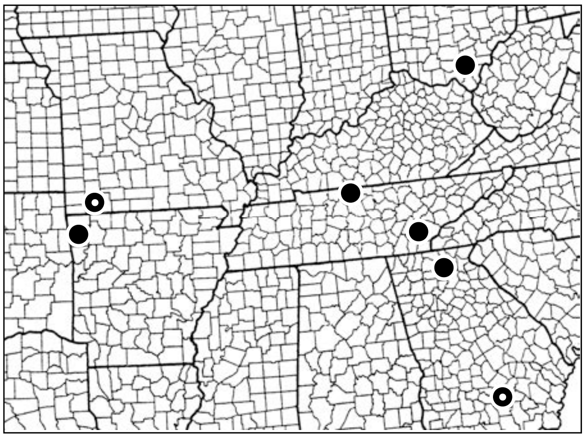


Figure 1.

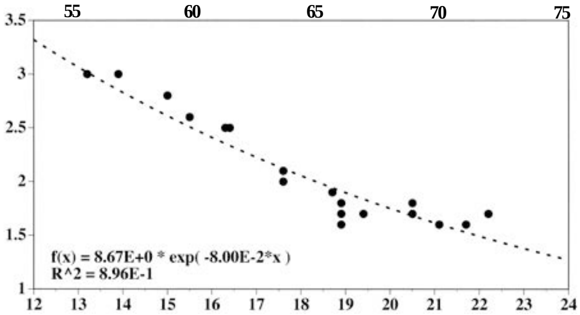


Figure 2. FP Period (AX: sec/temp).

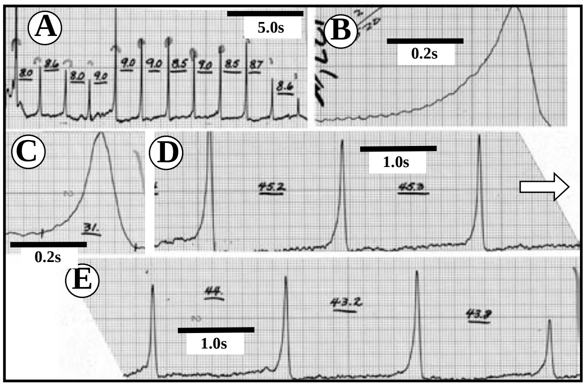


Figure 3. PM traces (AX: rel. int./time).

Flashing behavior. At the Roaring River, MO site *moorei* flew within a widened space along a bridle trail passing through a mixed forest less than 150 feet from a stream. At the Otter Creek site in southern Georgia they flew around the foliage of shrubs and trees along the wide and low roadside berm that probably was constructed as a sluiceway, to drain extensive runoff to the nearby creek during heavy rain. Males outlined foliage primarily above eight feet, and generally emitted their crescendo flashes continuously in straight flight without pumping or other emphasizing flight gestures. Occasionally they swooped a long down- and then slightly upward arc, ending as flight speed slowed and flash intensity reached maximum. Though flight was usually fast and direct they changed flight speed so that at times they flew a few inches during a flash and at other times covered two or more feet. Only once was a male seen to make the scallop-shaped swoops around foliage similar that which seems the hallmark of *whistlerae*. Though flash trains are typically very regular and continuous, when males crossed spaces between trees or clumps of foliage they sometimes stopped flashing, and terminal flashes at such breaks appeared dimmer and shorter than those preceding. It occasionally appeared that flash duration was varied, but *appearance* of flash duration is greatly influenced by flight speed, and crescendo flashes make judgment and estimation more difficult.

Observations at other sites were of single or few males that were flying high, directly and rapidly along water courses, though occasionally they slowed and coursed around tree boughs to deliver a few flashes before flying on. **Figures 2** and **4** show FP-period and rate temperature regressions, and **Figure 3** shows crescendo trains from two males, each at a different charting rate. In PM-records of many crescendo flashers variation in the slope is seen but in quality *moorei* traces nearly all show a very sharp exponential rise. Measurements of 11 well-formed crescendos from two males recorded at 20.5°/69° gave the following means for base and half max durations, in milliseconds: male 1: 70/277; male 2: 69/247; combined averages, 69.5/262. Bioluminescent spectrum from a sample of 6 males peaked at 556 millimicrons, with half-max points at 527.0 and 600.5, and width at half-max 73.5 (Biggley et al).

Morphological Data. General morphological means are (n=20, MO): PNL 2.5, ELL 9.3, PNW 3.0, EWhum 1.7, EWmid 2.2, ELVit .364, TOTLen 11.8, PNrat 0.84, ELWrat 1.26, ELVTrat 0.038 (**Fig. 5A**, with other stats and those from GA). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae and splashing on ventrite 4 are in **Figure 5B, 5C**, and **D**. **Figure 6** shows numbers used for various skeletal plates degrees of splashing on ventrite 4. A range of vittagrams (pronotal vittae) of *moorei* from two study sites is shown in **Figure 7**. A comparison of *moorei* deme PN-histograms with those of others of the presumptive *whistleri* (*cinctipennis*) group is on page ____ (Ref: Fig. 201.2, page 446).

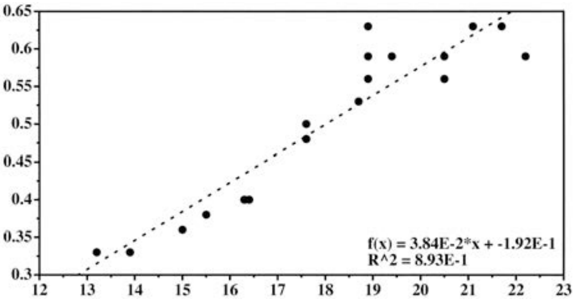
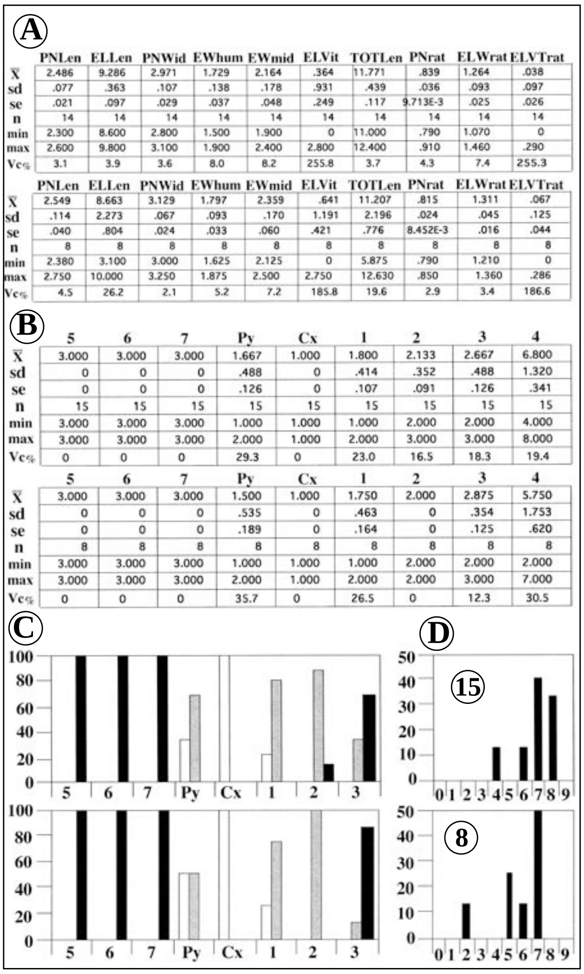


Figure 4. FP rate (AX: Hz./temp).



	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.486	9.286	2.971	1.729	2.164	.364	11.771	.839	1.264	.038
sd	.077	.363	.107	.138	.178	.931	.439	.036	.093	.097
se	.021	.097	.029	.037	.048	.249	.117	9.713E-3	.025	.026
n	14	14	14	14	14	14	14	14	14	14
min	2.300	8.600	2.800	1.500	1.900	0	11.000	.790	1.070	0
max	2.600	9.800	3.100	1.900	2.400	2.800	12.400	.910	1.460	.290
Vc%	3.1	3.9	3.6	8.0	8.2	255.8	3.7	4.3	7.4	255.3

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.549	8.663	3.129	1.797	2.359	.641	11.207	.815	1.311	.067
sd	.114	2.273	.067	.093	.170	1.191	2.196	.024	.045	.125
se	.040	.804	.024	.033	.060	.421	.776	8.452E-3	.016	.044
n	8	8	8	8	8	8	8	8	8	8
min	2.380	3.100	3.000	1.625	2.125	0	5.875	.790	1.210	0
max	2.750	10.000	3.250	1.875	2.500	2.750	12.630	.850	1.360	.286
Vc%	4.5	26.2	2.1	5.2	7.2	185.8	19.6	2.9	3.4	186.6

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	3.000	1.667	1.000	1.800	2.133	2.667	6.800
sd	0	0	0	.488	0	.414	.352	.488	1.320
se	0	0	0	.126	0	.107	.091	.126	.341
n	15	15	15	15	15	15	15	15	15
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	4.000
max	3.000	3.000	3.000	2.000	1.000	2.000	3.000	3.000	8.000
Vc%	0	0	0	29.3	0	23.0	16.5	18.3	19.4

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	3.000	3.000	1.500	1.000	1.750	2.000	2.875	5.750
sd	0	0	0	.535	0	.463	0	.354	1.753
se	0	0	0	.189	0	.164	0	.125	.620
n	8	8	8	8	8	8	8	8	8
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	2.000
max	3.000	3.000	3.000	2.000	1.000	2.000	2.000	3.000	7.000
Vc%	0	0	0	35.7	0	26.5	0	12.3	30.5

Figure 5. Morphology data (MO/GA).

Holotype Description. male, voucher number 66201, collected 17 June 1966, Barry County, Missouri, Roaring River State Park. One of a series of eight, collected after emitting their crescendo FP; FB page 21: "taken along road on bridle path between highway and stream … short .5 sec crescendo flash each 2 sec [sketch] 64° vouchers 66197-66204 all males all taken in flight giving flash." Morphological data: genitalia extruded, remain attached; from spread sheet—PNLen 2.5, ELLen 9.4, PNWid 2.9, ELWhum 1.5, ELWmid 2.0, LELVit 0.0, TotLen 11.9, PnRat 0.87, ElRat 1.33, VitRat 0.00; Colors: D 333, Py 1, Cx 1, V 222, Edg 6. Types will be deposited in the USNM.

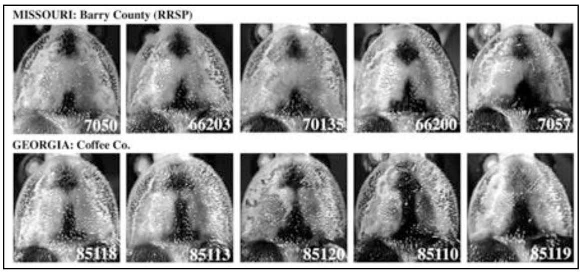


Figure 7. PN vittagrams two sites.

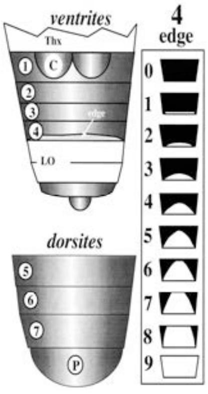


Figure 5. Anatomical and splash key.

Taxonomic Notes. The specific epithet salutes Dr. Thomas E. Moore, a long-time professor at the University of Michigan Museum of Zoology (UMMZ), and special friend when I was there for the MA and on a postdoc. Tom showed me the Ypsilanti marsh where I made my first study on fireflies—a life-changer—and bent the wire around the ON/OFF button on the first penlight.

Augmented figure legend. **3**. PM-traces of flashes of flying *moorei* males. (**A**) A train of crescendos shown at 5mm/sec chart speed, recorded at RRSP Barry Co. MO), 23 June 1970, @20.5°/69°; (**B**) Crescendo recorded in Coffee Co. GA, 27 May 1985, @17.6°/63.7°; (**C**) Crescendo recorded in Barry Co. MO, 23 June 1970, @20.5°/69°; (**D**) A train of crescendos shown at 25mm/sec chart speed, recorded at RRSP Barry Co. MO), 23 June 1970, @20.5°/69°; (**E**) the continuation of D as indicated by diagonal slash.

Chapter 52

Photuris mysticalampas Heckscher 2013

This firefly is known only from certain forested wetlands in southern Delaware (**Fig. 1**), and is the only *Photuris* species to be described from North America since those of Barber and McDermott a half century ago. It may be unique among our *Photuris* in that it has a morphological feature that clearly distinguishes it from congeners, an oval outline when viewed from above (**Fig. 2**). Heckscher describes the FP as "a single flash consisting of a slight crescendo of 0.4-0.8 sec., usually with a 3-7 sec interval (intervals can be much longer). Occasional signals may last more than 1.0 sec. … Females have been observed giving short multiple weak flashes from vegetation when signaling to males. On rare occasions, males have been observed giving a momentary trembling green flash when moving rapidly through vegetation toward a signaling female. … Females usually remain on low vegetation at <1m while signaling to approaching males."

Figure 3 is Heckscher's Figure 5. Extreme dates of occurrence given by him are 28 June (2011) and 22 July (2010).

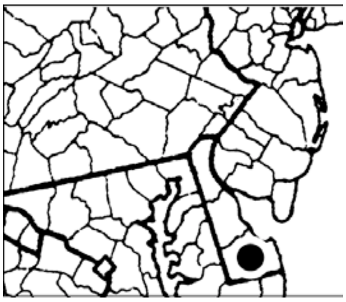


Figure 1. DE, s NJ, n VA, ne MD, se PA.

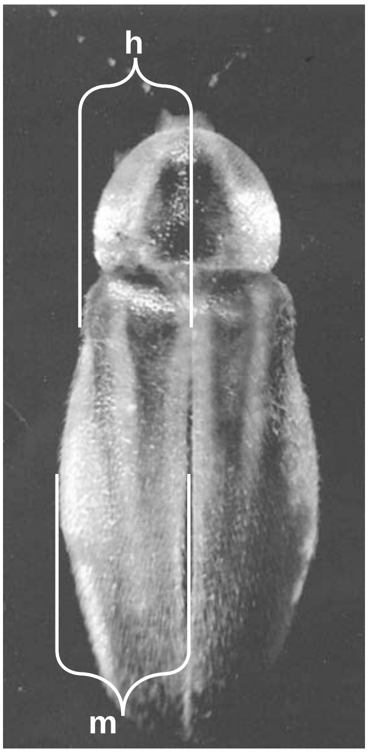
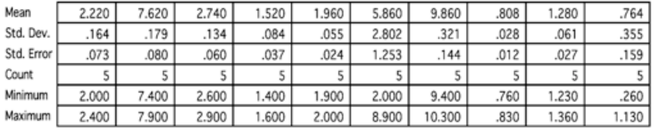


Figure 2. Habitus, showing breadth of elytra at mid-point (compare with width at humerus) (after Heckscher's Fig. 1).

Figure 3. Site photo of the type locality: "forested peatland floodplain with dense understory … a mix of hardwood species co-dominated by *Chamaccyparis thyoides* … interspersed with sphagnum hummocks."

Morphology. Measurements and PN-photos of specimens that Heckscher deposited in the jelc collection are shown. The vittagram extremes noted by Heckscher are placed at each end of the photo-array (**Figs. 4, 5**). The oval body shape is of some interest and is discussed elsewhere; note, the brackets indicate elytral width measurements at the humerus and mid-elytral positions. **Figure 6** is a specimen in the jelc .



	PNLen	ELLen	PNWid	ELWhum	ELWmid	LVitLen	TotLen	PNRat	ELRat	VitRat
Mean	2.220	7.620	2.740	1.520	1.960	5.860	9.860	.808	1.280	.764
Std. Dev.	.164	.179	.134	.084	.055	2.802	.321	.028	.061	.355
Std. Error	.073	.080	.060	.037	.024	1.253	.144	.012	.027	.159
Count	5	5	5	5	5	5	5	5	5	5
Minimum	2.000	7.400	2.600	1.400	1.900	2.000	9.400	.760	1.230	.260
Maximum	2.400	7.900	2.900	1.600	2.000	8.900	10.300	.830	1.360	1.130

FigTable 4. Measurements and ratios of jelc specimens.

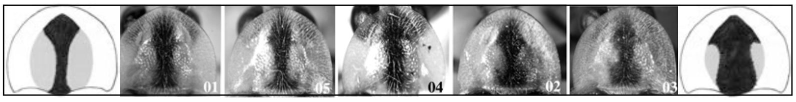
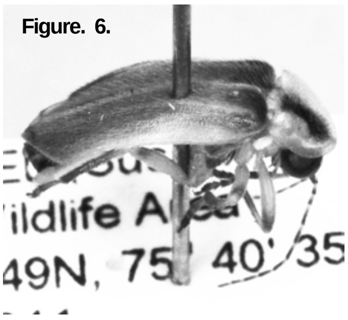


Figure. 5. Pronota of specimens in jel (➨USNM) collection.

Figure. 6.



Brief Reflections On A Table of Means: Aerodynamics

Two spread sheets below show mean values for morphological features of most Division II *Photuris* sampled in this study. In the table at the left demes are arranged alphabetically by epithet (column 1), and in the table at the right they are arranged by total body length (column 8). It is interesting that the two largest species would be considered closely related on the basis of flashing behavior. They are among the pairs of "species" that might have diverged, become distinct when the land mass that is now Florida was separated from the continent long ago. Going on in exploration, by regressing a character on another, clues into hidden aspects of adaptation and ecology may appear, or ideas tested. The reason that measurements of elytral width at the humeral angle and at the midpoint were made was because it was reasoned that during flight when the wing-covers are held aloft they must, in addition to being sails in the wind, influence flight dynamics, such as stability and lift—beating wings perhaps send drafts of air over them. Perhaps broader wings (higher ratios, hum/mid in **Fig. 1**; col. 5/col. 6) also have greater camber, that is, have deeper airfoil arching, and are better for some flight modes than narrow wings. For example, for hovering flight during slow, hovering search or when setting up an attack on a flying luminescing target, perhaps broader wings provide stability. The regression in **Figure 2** reveals outliers for further attention in this context. Note that there is considerable scatter, that body length is a lousy predictor of elytral width ratio, but—(by quadrant, box in **Fig. 2**)—that larger males would appear to have narrower elytra (lower ratios), and smaller males tend to have broader elytra—perhaps they tend to search for mates in more sheltered places. The ellipses in the figure enclose extreme outlyers named in the list. Points mark quadrents.

SPECIES	PNLen	ELLen	PNWid	EWhum	Ewmid	ELVit	TOTLen	Pnrat	ELWrat	ELVTrat
alexanderi	2.57	10.29	3.17	1.94	2.51	6.9	12.85	0.81	1.31	0.67
alleganiensis	2.48	10.5	3.13	1.9	2.45	7.7	13	0.79	1.3	0.73
appalachian	2.61	10.83	3.29	1.88	2.45	7.71	13.44	0.8	1.32	0.71
aureolucens	2.55	10.31	3.19	1.85	2.39	6.75	12.86	0.8	1.3	0.65
branhami	2.3	8.15	2.81	1.57	2.1	0	10.45	0.82	1.33	0
campestris	2.83	10.6	3.53	2	2.45	8.1	13.4	0.81	1.22	0.76
carrorum	2.44	9	3.09	1.76	2.29	6.46	11.41	0.78	1.32	0.72
chenangoa	2.7	10.63	3.23	2.01	2.51	7	13.3	0.81	1.26	0.66
cinctipennis	2.43	9.13	2.94	1.65	2.24	1.3	11.53	0.82	1.34	0.14
darwini	2.68	10.93	3.29	1.97	2.48	2.49	13.59	0.82	1.27	0.23
dorothy	2.31	7.99	2.71	1.51	2	0.39	10.21	0.82	1.32	0.05
douglasae	2.78	10.47	3.38	1.98	2.46	1.94	13.24	0.82	1.25	0.18
eureka	3.18	12.57	3.89	2.29	2.87	2.72	15.72	0.82	1.26	0.22
fairchildi MN	2.93	11.44	3.62	2.06	2.69	8.05	14.44	0.81	1.32	0.7
faustae	3.23	11.67	3.94	2.19	2.79	0	14.75	0.82	1.28	0
forresti	2.43	9.51	2.95	1.71	2.26	0.54	11.94	0.83	1.32	0.06
hebes	2.53	9.58	3.15	1.82	2.41	6.55	12.12	0.8	1.34	0.68
hiawassee	2.49	9.34	3	1.8	2.19	2.06	11.81	0.83	1.25	0.221
harrannorum	2.73	9.85	3.43	1.95	2.46	2.85	12.57	0.8	1.27	0.29
katrinae	3.37	11.53	4.27	2.33	3.07	5.67	14.9	0.79	1.32	0.49
lamarcki	2.5	8.76	3.15	1.81	2.39	3.46	11.28	0.8	1.34	0.74
lineaticol alach	3.11	11.21	3.89	2.11	2.7	0	14.3	0.8	1.28	0
lloydi	2.3	8.7	2.84	1.63	2.06	5.92	11	0.81	1.27	0.68
lucicrescens md	3.2	11.54	3.91	2.22	2.82	7.93	14.73	0.82	1.27	0.69
mad dotdash	2.51	10.39	3.09	1.83	2.41	5.21	12.89	0.81	1.33	0.5
maicoi	3.16	11.14	3.93	2.08	2.65	6.95	14.29	0.81	1.27	0.63
margotoole	2.65	11.11	3.25	1.84	2.45	7.02	13.78	0.82	1.35	0.63
missouriensis	2.71	10.8	3.41	1.99	2.47	5.69	13.49	0.8	1.25	0.53
moorei	2.49	9.29	2.97	1.73	2.16	0.36	11.77	0.84	1.27	0.04
paludivulpes	2.3	8.83	2.79	1.55	2.09	2.91	11.11	0.83	1.35	0.32
potomaca	2.61	10.37	3.32	2	2.52	3.15	12.98	0.79	1.29	0.31
quadrifulgens	2.96	12.02	3.64	2.09	2.66	6.5	14.97	0.81	1.28	0.54
sivinskii	2.23	8.49	2.67	1.48	2.02	2.66	10.72	0.83	1.37	0.31
stanleyi	2.4	9	2.95	1.75	2.26	4.55	11.35	0.81	1.31	0.5
stevensae	2.97	11.31	3.68	2.17	2.77	8.19	14.28	0.81	1.27	0.73
tasunkowitcoi	2.76	11.12	3.36	1.92	2.42	7.2	13.84	0.82	1.28	0.65
tremulans md	2.45	9.75	2.98	1.8	2.29	4.58	12.21	0.82	1.29	0.47
versicolor md	2.88	10.86	3.53	2.13	2.73	6.45	13.74	0.82	1.28	0.59
walkeri	2.78	11.2	3.7	2.1	2.7	0	14	0.76	1.29	0
whistlerae	2.43	8.7	3	1.66	2.24	0.13	11.12	0.81	1.36	0.01

SPECIES	PNLen	ELLen	PNWid	EWhum	Ewmid	ELVit	TOTLen	Pnrat	ELWrat	ELVTrat
eureka	3.18	12.57	3.89	2.29	2.87	2.72	15.72	0.82	1.26	0.22
quadrifulgens	2.96	12.02	3.64	2.09	2.66	6.5	14.97	0.81	1.28	0.54
katrinae	3.37	11.53	4.27	2.33	3.07	5.67	14.9	0.79	1.32	0.49
faustae	3.23	11.67	3.94	2.19	2.79	0	14.75	0.82	1.28	0
lucicrescens md	3.2	11.54	3.91	2.22	2.82	7.93	14.73	0.82	1.27	0.69
fairchildi MN	2.93	11.44	3.62	2.06	2.69	8.05	14.44	0.81	1.32	0.7
lineaticol alach	3.11	11.21	3.89	2.11	2.7	0	14.3	0.8	1.28	0
maicoi	3.16	11.14	3.93	2.08	2.65	6.95	14.29	0.81	1.27	0.63
stevensae	2.97	11.31	3.68	2.17	2.77	8.19	14.28	0.81	1.27	0.73
walkeri	2.78	11.2	3.7	2.1	2.7	0	14	0.76	1.29	0
tasunkowitcoi	2.76	11.12	3.36	1.92	2.42	7.2	13.84	0.82	1.28	0.65
margotoole	2.65	11.11	3.25	1.84	2.45	7.02	13.78	0.82	1.35	0.63
versicolor md	2.88	10.86	3.53	2.13	2.73	6.45	13.74	0.82	1.28	0.59
darwini	2.68	10.93	3.29	1.97	2.48	2.49	13.59	0.82	1.27	0.23
missouriensis	2.71	10.8	3.41	1.99	2.47	5.69	13.49	0.8	1.25	0.53
appalachian	2.61	10.83	3.29	1.88	2.45	7.71	13.44	0.8	1.32	0.71
campestris	2.83	10.6	3.53	2	2.45	8.1	13.4	0.81	1.22	0.76
chenangoa	2.7	10.63	3.23	2.01	2.51	7	13.3	0.81	1.26	0.66
douglasae	2.78	10.47	3.38	1.98	2.46	1.94	13.24	0.82	1.25	0.18
alleganiensis	2.48	10.5	3.13	1.9	2.45	7.7	13	0.79	1.3	0.73
potomaca	2.61	10.37	3.32	2	2.52	3.15	12.98	0.79	1.29	0.31
mad dotdash	2.51	10.39	3.09	1.83	2.41	5.21	12.89	0.81	1.33	0.5
aureolucens	2.55	10.31	3.19	1.85	2.39	6.75	12.86	0.8	1.3	0.65
alexanderi	2.57	10.29	3.17	1.94	2.51	6.9	12.85	0.81	1.31	0.67
harrannorum	2.73	9.85	3.43	1.95	2.46	2.85	12.57	0.8	1.27	0.29
tremulans md	2.45	9.75	2.98	1.8	2.29	4.58	12.21	0.82	1.29	0.47
hebes	2.53	9.58	3.15	1.82	2.41	6.55	12.12	0.8	1.34	0.68
forresti	2.43	9.51	2.95	1.71	2.26	0.54	11.94	0.83	1.32	0.06
hiawassee	2.49	9.34	3	1.8	2.19	2.06	11.81	0.83	1.25	0.221
moorei	2.49	9.29	2.97	1.73	2.16	0.36	11.77	0.84	1.27	0.04
cinctipennis	2.43	9.13	2.94	1.65	2.24	1.3	11.53	0.82	1.34	0.14
carrorum	2.44	9	3.09	1.76	2.29	6.46	11.41	0.78	1.32	0.72
stanleyi	2.4	9	2.95	1.75	2.26	4.55	11.35	0.81	1.31	0.5
lamarcki	2.5	8.76	3.15	1.81	2.39	3.46	11.28	0.8	1.34	0.74
whistlerae	2.43	8.7	3	1.66	2.24	0.13	11.12	0.81	1.36	0.01
paludivulpes	2.3	8.83	2.79	1.55	2.09	2.91	11.11	0.83	1.35	0.32
lloydi	2.3	8.7	2.84	1.63	2.06	5.92	11	0.81	1.27	0.68
sivinskii	2.23	8.49	2.67	1.48	2.02	2.66	10.72	0.83	1.37	0.31
branhami	2.3	8.15	2.81	1.57	2.1	0	10.45	0.82	1.33	0
dorothy	2.31	7.99	2.71	1.51	2	0.39	10.21	0.82	1.32	0.05

Figure 1.

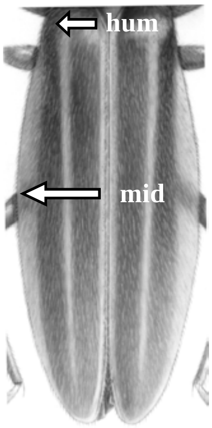
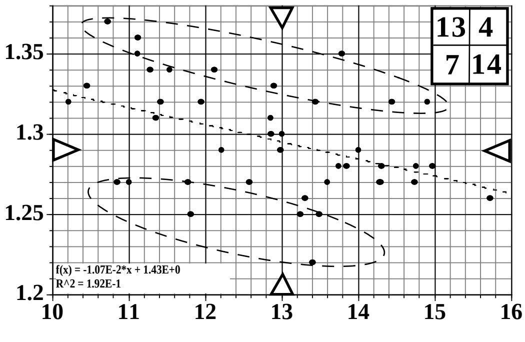


Figure 2.



Lower left
billbrowni
lloydi
moorei
hiawassee
harrannorum

Upper right
appalachianensis
fairchildi MD
katrinae
margotooleae

Upper left
stanleyi
alexanderi
dorothae
carrorum
forresti
branhami
potomaca
penn NY
aureolucens
hebes
cinctipennis
lamarcki
paludivulpes
whistlerae
sivinski

Lower right
campestris
douglasae
missouriensis
chenangoa
darwini
maicoi
lucicrescens MD
versicolor MD
tasunkowitcoi
lineaticollis Alachua
faustae
quadrifulgens

Chapter 53

Ozark Enigma

Flashes like those emitted by this firefly were seen only in southwestern Missouri on the Ozark Plateau (**Figs. 1, 2**). Perhaps it separated in peripheral isolation from *quadrifulgens*, which occurs with it now in sw Missouri. The primary (default) FP was pulsed like that of *quadrifulgens* but at about half the rate (**Figs. 3-5**). Its adjunct FP, from which it defaulted to the slow-pulse FP, was the A-flicker. This ghost must remain Anonymous here as a taxonomic/nomenclatural curiosity for the record: No voucher specimens were collected, and without a Holotype specimen for name-holding, this firefly cannot by the *Rules* be given a formal name. This makes sense. The reality: *Photuris* species cannot be recognized by their morphology, only by the their flashing behavior; this firefly is represented only by an electronic record of its mating signal (**Fig. 5**), a specimen alone would be on no value—there may have been specimens in museums for decades—but the FP must remain unnamed. Interesting, like a 5-legged calf on a farm, but of little real consequence, except for the calf.

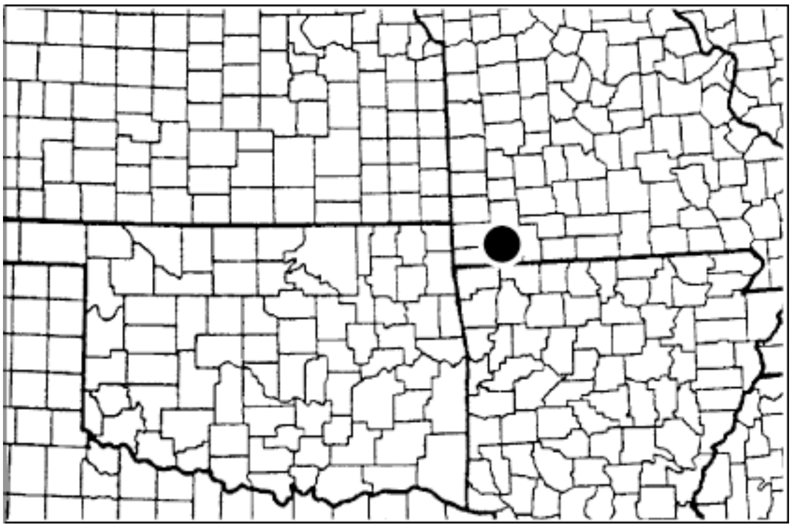


Figure 1.

Ecology, flashing. The site was a small pasture with mixed hardwoods around and scattered within, and a willow bordered gully and stream along one side (RRSP Barry County, MO, 25 June 1970). A short penlight response was flashed after a flying male's 7-9-pulse flickers; he was cruising at 25', and as he slowly approached the decoy his FP was PM-recorded (**Fig. 5B, C, E**). After the second recorded flicker, at 15' and about five flickers into his approach, he switched to a pulsing FP similar to that of *Ph. quadrifulgens* and Florida *Ph. eureka*, but his pulse intervals were much longer (1.2 sec vs 0.7 sec at 19.7°/67.5°, **Fig. 5A**).

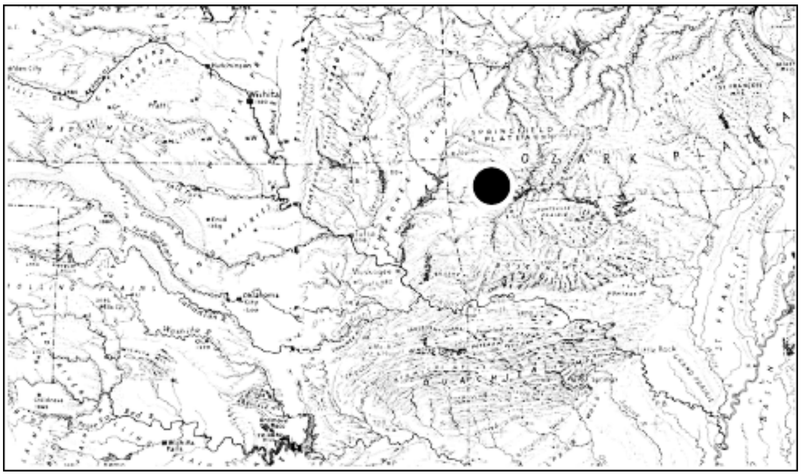


Figure 2. Physiographic perspective.

Pulses in the pulsing FP were short crescendos, with a measured base duration of about 280 mSec, and 88 mSec at half-max (only one record was suitable for "precise" measurement, see **Fig. 5D, F**). The single pulsing FP period measured was 6.2 sec (19.7°C/67.5°F). These data points are plotted with various regressions of *quadrifulgens* (**Figs. 3, 4**)

Flicker modulation was roughly sinusoidal, and its rate was about the same as one of the adjunct FPs of certain other *Photuris*, including *quadrifulgens*—that of *Pyractomena angulata* (9.7 Hz, at 19.7°/67.5°). The single flicker period measured was 3.1 sec.

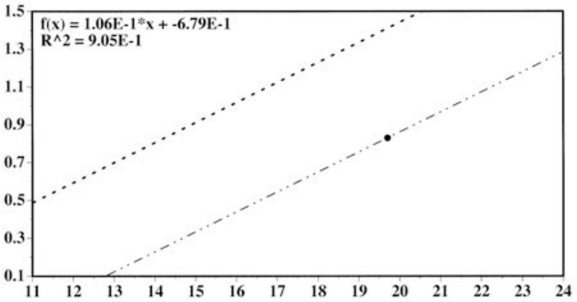


Figure 3. FP pulse rate prediction (AX: Hz/temp).

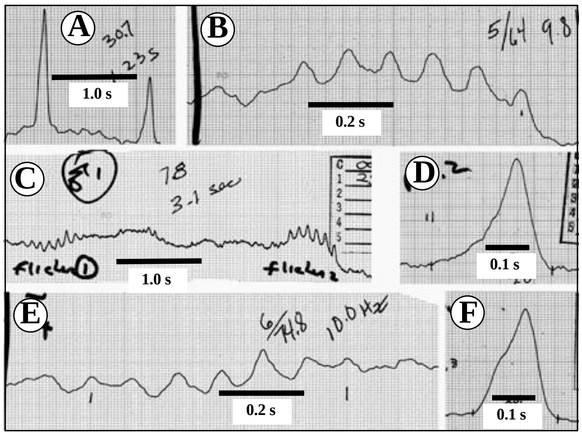


Figure 5. PM traces (AX: rel. int./time).

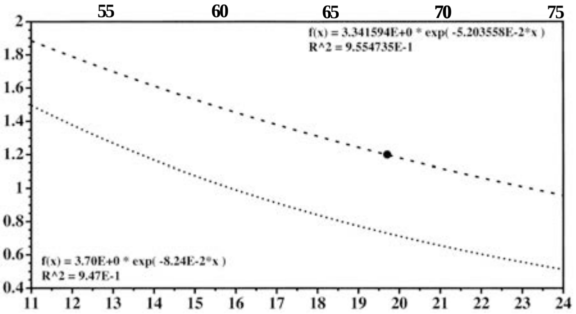


Figure 4. Pulse period, and prediction (AX: sec/temp).

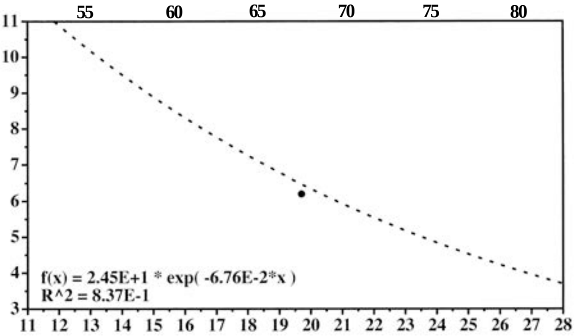


Figure 6. Pulsing FP period prediction (AX: sec/temp).

On the evolution of smart fireflies? In general it makes sense that offspring of certain kinds of organisms should be like their parents when their ecology doesn't change very much from generation to generation. Surprising differences are observed among local *Photuris* populations. These differences are in adjunct FPs, in signal-mimicking behavior. The development of local differences must relate to the mimicry and hunting of their females. But, if arms races between *Photuris* predator and *Photinus* prey were responsible, why do the signals of *Photinus* not show such local variation, as they respond to selection with countermeasure leading to ever more complex flash patterns and codes? How is it that the signals of *Photinus* appear to be so simple? Have they been skipped over too quickly and important details missed? Perhaps the pressures to change that drives *Photuris* is not related to the predation of *Photinus* by their females. (**1**) Possibly it is the varied predations and interactions within "smart" *Photuris* species and the conflicts and arms races between and among them, as they compete with each other for prey, and prey upon each other, in different combinations. But also, (**2**) attention must be given to the importance of versatility in the hunting of different prey with different signal codes, by the females, and a quickness of wit, to use the right code at the right time, as they shift among prey depending upon varying circumstances. Chapter 7 lists found and expected patterns of behavior, and it will be noted that certain of the complex behaviors seem only to be explained by a somewhat higher level of "intellectual activity" than hitherto would have been ascribed to a beetle brained-organism—these are in the context of learning (>four kinds?). So the genetic question specified is, what was it in the DNA of now-smart *Photuris* that let them break free of the intellectual doldrums found in other fireflies?—except maybe some few other photurines. One of the positive consequences of sexual reproduction is that the genetic reshuffling will result in a few super individuals. In a stabile population these will tend to be the survivors, and in some *Photuris*, such super smart hunters will quickly raise the IQ. Because *Photuris* females may have an "unlimited" source of food, not having to rely upon stores provided by larval feeding, they may have developed the ability to produce an "unlimited" number of eggs, resulting in great fecondity. Couple this with a developing "intellect" and hunting proficiency, it may be imagined that rapid changes may occur.

If we could take smart fireflies out of the mix, would we be able to write a morphological key to the rest of them? I suspect not, but we might do a little better.

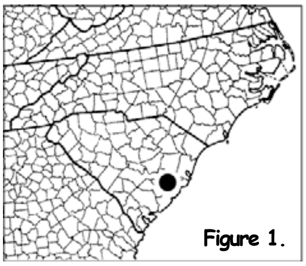
Chapter 54

Photuris paludivulpes new species

Swamp-Fox Firefly

This *cinctipennis*-like firefly, if indeed it is but a single population as treated here, was observed one evening at two stops near the Huger area of the Francis Marion National Forest, Berkeley County, South Carolina, 13 June 1978 (**Fig. 1**). Males flew in a shrubby clearing in a second-growth woods and in a flatwoods near a stream. They searched up to 12', low around shrubs and quickly across open spaces—the bright moonlight perhaps kept them at lower shaded altitudes. The similarity of the sites to an Austin Cary Forest area in Gainesville was noted, and indeed the rare *Photuris sivinskii*, known from the ACF, was flying with *paludivulpes* at one.

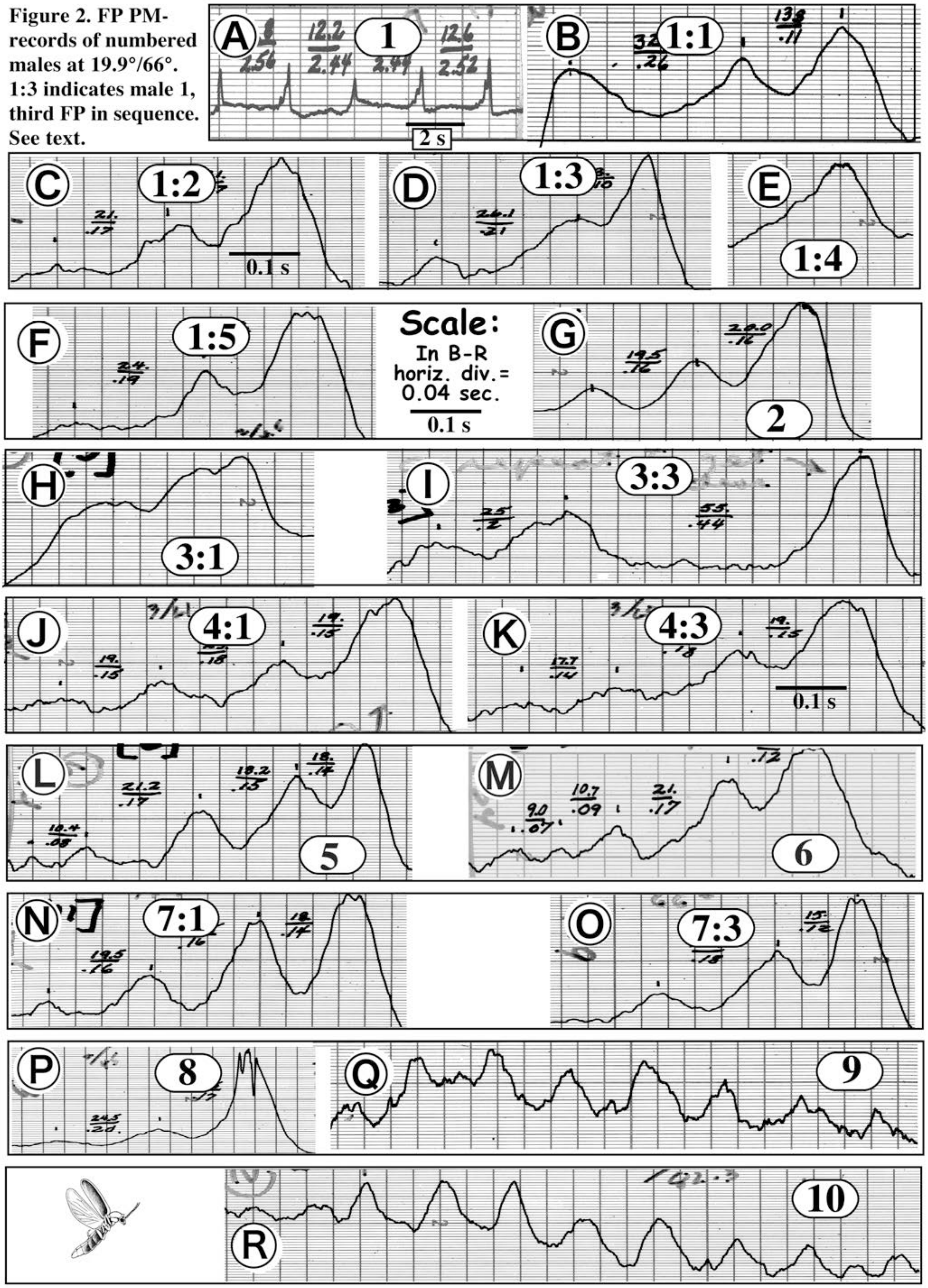
Three different FPs were visibly apparent but at the analysis of PM-records (detailed below and in the next section) it was revealed that usually what had appeared to be simple crescendo flashes were often strongly modulated—although when PM-recording it was noted on one occasion that pulsing was heard in the side-tone monitor (the Holotype specimen). From these data and morphological comparisons, and with yet some reservation, all FP forms are finally considered to be the emissions of males of a pair of conspecific demes. First, a brief synoptic overview of the visual appearance of flashes and FPs emitted by this firefly: (**1**) a flicker like that of *Py. angulata*—an FP used as an adjunct FP by several *Photuris*; (**2**) short swooping "crescendos," sometimes emitted in short series (of 2-9) while poising/pumping near the foliage of low shrubs; and (**3**) indeterminate? sequences of short crescendos while flying laterally. In addition, PM-records indicate the presence of a fourth type—(**4**) crescendos modulated at the *Py. dispersa* rate (≈6 Hz., 18.9C°/66F°). Possibly all crescendos are modulated, and the single example used here to illustrate otherwise is actual an error, another species perhaps (**Fig. 2 E**). Finally, (**5**) a few PM-traces appear to show elements and variations of the above, irregular rhythms, pauses. Together these FPs appear almost as a collection of FPs emitted by *Photuris beani*, *carrorum*, *stanleyi*, and *whistlerae*, all working species found in Florida. With respect to the modulated crescendo FP, which is by far the most common among recordings, not only were modulations not usually apparent, field notes rarely mention there being even hitch or twitch among them. It was noted on one occasion that when viewed from one angle a crescendo was seen and from another the emission appeared to be a bright, symmetrical flash. Impressions/illusions are occasionally seen in other *Photuris*. For example, viewed from the side a flying *Ph. hebes* appears to emit a hitched flash, and from the rear, a crescendo—these are seen in simultaneously viewings with a co-viewer. Perhaps this appearance is from an asynchrony of the two segments of the lantern and the human eye/brain detects this in space when a flying firefly **crosses** the line of vision.



At the time this firefly was observed (June 1978) the ubiquity of multiple FPs in *Photuris* and defaulting, though suspected was not fully appreciated, and although field notes question whether these FPs were emitted by the same species, this was not pursued. However, flickering males were attracted to the penlight and interactions between crescendo-emitters and responding females were noted, but no mention was made of FP changing/defaulting.

PM-record analysis, insights?; Note Fig. 2, others. An illustrated enumeration of observations is simplest: (**1**) The A-flicker closely matches that of *Py. angulata* in rate, in both the Florida/Georgia and combined-continental regressions (**Fig. 2: Q, R**; **Fig. 3**). (**2**) The crescendo FP is emitted in obvious sequences (**Fig. 2A**), and seen in groups of from 2 to 9 with pumping as in *Ph. whistlerae*, and also in what apparently is a searching mode when the sequence is of indefinite length. (**3**) The crescendo FP appears to be simple in form, but in all but one PM-recording (**Fig. 2E**) the crescendos are modulated (**Fig. 2C, D, F-P)**. Perhaps 2:E was another species passing through, or indicates that such FPs are used only rarely or in special conditions. Note that in **2E** the duration at 240 mSec is considerably shorter than in modulated crescendos (e. g., 480-680 mSec)., and in **Figure 2P** two initial modulations are weak. (**4**) Modulation rates of most but not all crescendos fall on the rate regression for *Py dispersa* (**Fig. 4**). Note that the figure shows the mean modulation rate of all readable crescendos, but one—the positions of all individuals are indicated with a vertical oval. (**5**). Crescendos in **Figures 2L** and **M** appear to have feeble peaks or shoulders in positions that would, if actually were modulations, raise the rate in one case to that of *Py. angulata*, as seen in the flicker FP (8.9 Hz. at 18.9°/66°).

Figure 2. FP PM-records of numbered males at 19.9°/66°. 1:3 indicates male 1, third FP in sequence. See text.



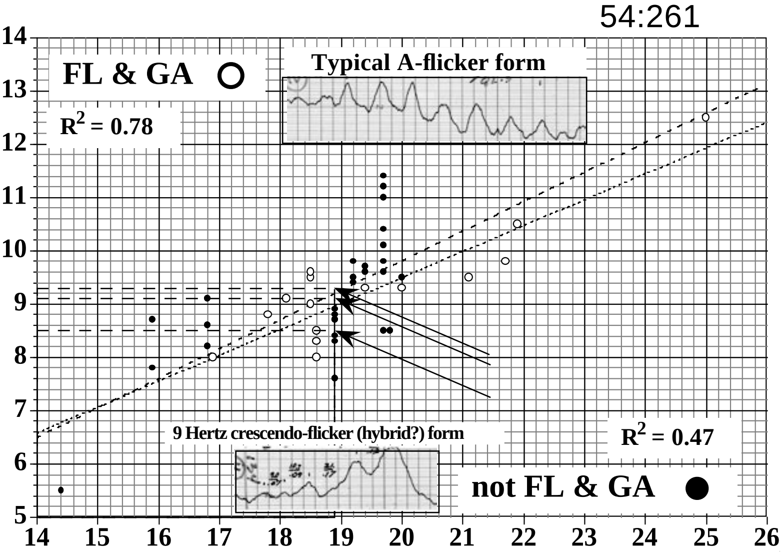


Figure 3. *Py angulata* rate regression with *paludivulpes* values indicated (AX: Hz/temp).

(**6**) Several FPs have distortions as though the control system were "confused," with odd timing and narrow and broad peaks. Probably some of this can be attributed to flasher orientation and momentary occlusion by vegetation.

Morphological summary. Means (n=15): PNL 2.3, ELL 8.8, PNWid 2.8, EWhum 1.6, EWmid 2.1, ELVit 2.9, TOTLen 11.1, PNrat 0.83, ELWrat 1.4, ELVTrat 0.32 (**FigTable 5**)**;** sclerite colors and prelantern ventrite splash (**Fig-Table 6** and **Fig. 7**)**; Figure 8** is a key to anatomical elements and splashing on ventrite 4. **Figure 9** shows photo arrays of crescendo and flicker voucher pronota.

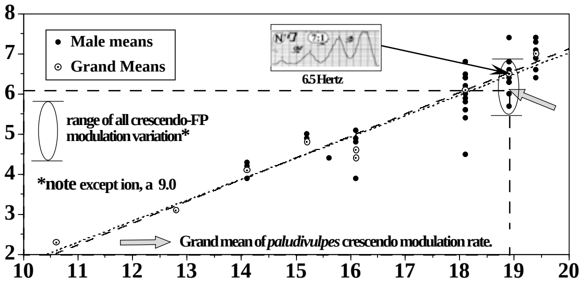


Figure 4. Comparison of *paludivulpes* crescendo modulation rate and *Py. dispersa* flicker modulation rate (AX: Hz/temp).

Holotype description. male, voucher number 78103, collected 13 June 1978, Berkeley, SC. (From FB, 1978 page 144: "KB 14 Recorded "cresc", sound like it had modulations in it". Morphological data: a tiny *Photuris*. genitalia extruded remain attached; from spread sheet—PNLen 2.1, ELLen 8.8, PNWid 2.8, ELWhum 1.5, ELWmid 2.0, LELVit 2.5, TotLen 10.9, PnRat 0.77, ElRat 1.33, VitRat 0.29; Colors: T 333, Py 1, Cx 3,V 233, Edg 4. Types will be deposited in the USNM.

Taxonomic and nomenclatural notes. Fieldbook notes confusingly (for readers) refer to different FP types observed with reference to Florida species—"B" and "C" for example. This firefly pays tribute to the Swamp Fox of the Revolutionary War, Francis Marion, for whom the National Forest is named; a hero of the region as well as nationally for his heroic and harassing actions against the British, though many of his financially motivated neighbors were Tories.

paludivulpes all

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.300	8.833	2.793	1.553	2.087	2.907	11.113	.827	1.350	.321
sd	.185	.631	.249	.155	.210	1.986	.795	.040	.069	.205
se	.048	.163	.064	.040	.054	.513	.205	.010	.018	.053
n	15	15	15	15	15	15	15	15	15	15
min	2.000	7.800	2.500	1.400	1.800	0	9.800	.770	1.230	0
max	2.600	9.800	3.300	1.900	2.600	6.900	12.400	.900	1.450	.710
Vc%	8.0	7.1	8.9	10.0	10.1	68.5	7.2	4.8	5.1	63.9

FigTable 5. Measurements, ratios.

paludivulpes all

	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	2.933	3.000	2.867	1.600	2.733	2.667	2.867	3.000	3.133
sd	.258	0	.352	.507	.704	.617	.352	0	1.246
se	.067	0	.091	.131	.182	.159	.091	0	.322
n	15	15	15	15	15	15	15	15	15
min	2.000	3.000	2.000	1.000	1.000	1.000	2.000	3.000	0
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000
Vc %	8.8	0	12.3	31.7	25.8	23.1	12.3	0	39.8

FigTable 6. Sclerite colors, splash.

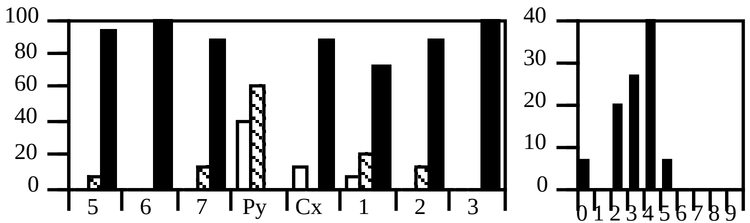


Figure 7. Sclerite colors, and splash.

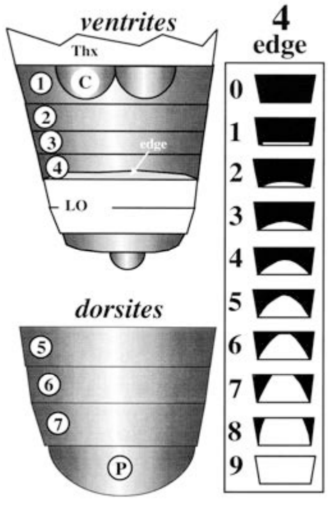


Figure 8. Topographic and splash keys.

Crescendo Flashers, South Carolina: Berkeley Co.

Flicker Flashers, South Carolina: Berkeley Co.

Figure 9. Arrrays of PN vittagrams of two FP types oserved.

FP data etc: 13 June 1978. Berkeley Co. t-78-4, 20.5°/69°. Crescendo periods. (ELEC): [male 1] 2.4 [2] 2.4 2.6 2.4 2.4 2.5; n=5, x=2.5, s=0.1 [3] 2.3 2.4; n=2, x=2.4, s=0.1 [4] 2.2 [5] 2.2 2.3 2.3 2.5; n=4, x=2.3, s=0.1 [7] 2.6 2.4; n=2, x=2.5, s=0.1 [8] 2.8 2.8; n=2, x=2.8, s=0 [9] 2.5 2.4 2.5; n=3, x=2.5, s=0.1 **Grand**: n=8 males, x=2.5, s=0.2. (SWAT) 18.9°/66°: 1.9 2.2 2.0 1.8 2.2; n=5, x=2.0, s=0.2. **Flicker periods**. 18.9°/66°: 3.2 4 3.8 4.6 5.4 4 3.2 4; n=8, x=4.0, s=0.7.

Modulation rates. Crescendo flicker: [1] 6.3 6.8 x=6.6 s= 0 [2] 5.5 5.5 5.7 6 5.8 x=5.7 s=0 [3] 6.3 6.3 x=6.3 [4] 9.0 [5] 5.9 6.1 6.3 6.6 x=6.2 s=0.3 [6] 5.6 [7] 5.8 5.7 5.6 x=5.7 s=0.1 [8] 5.9 5.6 5.2 x=5.6 s=0.4 [9] 5.8 [10] 6.5 [11] 6.3 6.9 6.7 x=6.6 s=0.31. Grand n=11 males, 27 FPs, x=6.1, s=0.4. A-flicker: [12] 8.6 8.6 8.7 8.5 x=8.6 s=0.1. [13] 9.1. [14] 9.3. Grand n=3 males, 6 FPs, x=9.0. s=0.4. **Vouchers.** crescendo 7893 7894 7895 7897 7898 7899 78101 78102R 78103R **A-flicker** 7888 7891 7896 **Fieldbook**. 1978: 143 144 145.

Records Of Vouchered *Photuris* Predation Behavior. These references/notes are in addition to observations mentioned in chapters and those associated with specimen photos on pages 455-56. Vouchers are archived together in the collection. **1**. 1963p16, If7. *Photuris* sp. ♀ answered penlight with delay like that of *Pn. ignitus* (5.5-6.3 sec, @57°), Goochland Co. VA. **2**. 1963p22, IIc4. *Ph. versicolor*?♀ ans. penlight when flying, landed, ans. penlight again, Green Co. **3**. 1963p97,VIId9. *Ph. lucicrescens* ♀, ans. penlight @ 2.2 sec., 71°, Lawrence Co. IL. **4**. 1963p98, VIIe4. *Ph. lucicrescens* ♀ ans. penlight w quick short flash, in *Pn. australis* site, Lawrence Co. IL. **5**. 1963p103, VIIIb9. *Ph.* ♀ ans. penlight in *Pn. punctulatus* site, IL. VA. **6**. 1964p28, f17. *Ph. cinctipennis* Gp. ♀ ans. penlight in *Pn. tanytoxus/umbratus* area Alach. Co. **7**. 1964p33, h1. *Ph. versi/lineaticol)* ♀ clasping glowing *Pn. tanytoxus* ♂, Alach. Co. **8**. 1964p48, L12. *Ph.* ♀ ans. penlight in *Pn. tanytoxus* site, Alach. Co. **9** 1965p103, no-numb. *Ph.* ♀ long delay, *Pn. ignitus* site, Tompk. Co. NY. **10**. 1965p102, no-numb. *Ph.* ♀ ans. penlight in *Pn. ignitus* site (4.0-5.0 sec, @ 71°), Tompkins Co. NY. **11**. 1965p24, 65184. *Ph. lamarcki* , ans. penlight *Pn.* SP *consimilis* simulation, after last pulse @ 5.2, 5.4, 5.8 sec @ 72°, airport pond. **12**. 1966p32, 66395. *Ph.* ♀, Ann Arbor dipper?, eating *Py. linearis* ♂, Warren Rd marsh, MI. **13**. 1967p74, 67431. *Ph. harrannorum* ♀, ans. *Ph. douglasae* ♂ and penlight @ 1 sec delay, MedGard. **14**. 1967p80, 67486. *Ph. harrannorum* ♀ (autumn, small), ans. PM recorded, MedGard. **15**. 1967p90, 67517. *Ph. lamarcki* ♀ ans. penlight *Pn. consanguineus* FP, airport pond. **16**. 1968p31, 68106. *Ph. harrannorum* ♀, ans. *Pn. macdermotti* ♂, fm perch 9’ up, Alach. Co. FL. **17**. 1968p61, 68233. *Ph. versicolor* Gp. ♀, *Pn. collustrans* site, ans. penlight wo after glow, Leon Co. FL. **18**. 1968p219, 681447. *Ph. harrannorum* ♀ (fall) ans. short flash @1.5-2 sec, in *Ph. douglasae* site, MedGard. **19**. 1968p220, 681449–*Ph. harrannorum* ♀, small!, ans. penlight w peculiar flash, PM-record, MedGard. **20**. 1973p65, 7312. *Ph. lamarcki* ♀, PM recorded, ans. *mac* simulat., after both P1 and p2 sometimes, MedGard. **21**. 1973p65, 7313. *Ph. lamarcki* ♀, PM recorded, MedGard. **22**. 1978p41, 78284. *Ph. versicolor*? ♀, in *Ph. salina* site, ans. ♂, he flash a few times, moved away, St. Mary’s Co. MD. **23**. 1981p163, 8115. *Ph. beanii* ♀, ans. *Pn. floridanus* ♂♂ w short sharp flash, Levy Co. FL. **24**. 1981p4, 8122. *Ph. versicolor*? ♀, ans. *Pn. marginellus* ♂♂ , in dense woods, w double pulse (*forma castus*, see McDermott early ref.!?), DeSota Falls Camp, Lumpkin Co. GA. **25**. 1982p142, 8230. *Ph. lamarcki* ♀, ans. *mac.* simulat., in woods, gun club. **26**. 1982p145, 8231. *Ph. lamarcki* ♀, ans. *mac.* simulat., not inject. between P1&P2, airport pond. **27**. 1983p6, 83210. *Ph. quad.* ♀ prob., a hawker?, hit penlight when I simulat. *Pn.* ♂, in *Pn. australis* site, @10$ bridge, Lumpkin Co. GA. **28**. 1983p10, 83222. *Ph. quad.* ♀ prob., ans. ♂ *Pn. pyralis*-like stim. precisely @1.5 sec. 3X @71°,@Gee Cr., Polk Co. TN.

Chapter 55

Photuris patriei n. sp.

Oklawaha

This firefly is the smallest *Photuris* in North America, based on the single voucher at hand. This male was seen flying in mid-summer—a season generally of diminished firefly activity in north-central Florida—along a small (Eaton) creek in the Ocala National Forest east of Ocala (**Figs. 1, 2, 6-8**). Brief notes were made of its simple FP and flight behavior.

Figure 1. Ocala National Forest, Marion Co., FL.

This species could have broad distribution in the watershed of the Oklawaha River, an extensive region of swamps, marshes and lakes. Though Eaton Creek itself flows sse into Eaton Lake, judging from DeLorme maps for Florida (1989:72; 2012:84), this Creek connects north through Mason Bay (a marsh) and variously to Mud Creek, more wetlands and then nominally reappears to flow into the Oklawaha River.

From the fieldbook (74/75/76), 19 July 1975, page 71: "KB 26 New sp of Photuris 7514 single flash, ca. 0.25-.3 sec long, each 3 sec, fly 6'-10'-12' up [20°/ 68°]. Locality at a bridge on rt ~~88~~ [\in pencil "no. rt 314] as we head S to jct of rt 40 [—] when fly [they] cover 10-15' between flash[es] and makes 6" stripe during flash. coll. at 10:25 PM [—] this bridge was 8.8 [7.9] miles [east] ~~north~~ of JCT 40[.] saw fast fast consim [*consimilis*] here at bridge also a D-like [*lamarcki*] female [.] left stream and crossed JCT 314A immediately, 0.4 mi later."

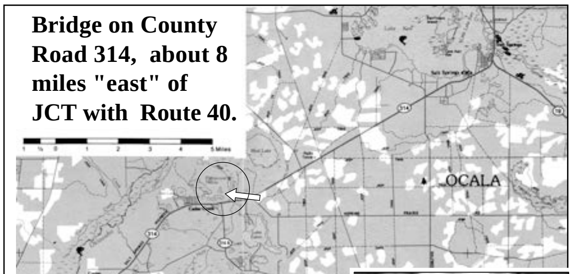


Figure 2. Location of Eaton Creek bridge (after DeLorme, 1989).

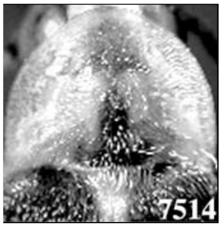


Figure 3. Holotype pronotum.

The site was visited again in 2016 for photographs, and the mileage recorded then was 7.9 miles east of route 40. From the wetlands indicated on DeLorme maps this firefly could be very abundant but very localized; it was never recognized elsewhere in Florida. When seeking sites along paved highways, culvert markers and the presence of cabbage palms and water-loving hardwoods could be indicators (**Fig. 6**).

Fig. 4. Holotype.

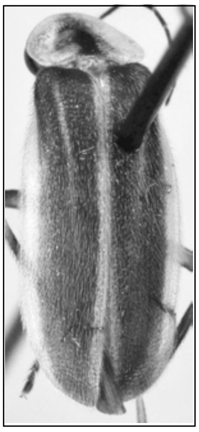


Fig. 5. View of elytron.

Morphology. With a length of 8.9 inches this is the smallest *Photuris* yet encountered. A comparison with the minimum lengths given in the statistics tables of other small *Photuris*, revealed that none yet was this diminutive. PNV of the Holotype is shown in **Figure 3**. Two ratios of this firefly are extreme: it shares the PN ratio of 0.79 with *walkeri*, and is sole possessor of an elytral ratio of 1.5. The latter is discussed elsewhere.

Figure 6 . Wet spot, not Eaton Creek, on Rt 314.

Holotype: male (**Figs. 3-5**), voucher number 7514, collected 19 July 1975, Marion County, Florida, Ocala National Forest, at Eaton Creek bridge on County Road 314, about 8 miles north of JCT Route 40 (see text). Only specimen of this species seen or collected. FB page 71: "KB 26 New sp of *Photuris* 7574 single flash, ca .25-.3 sec long, each 3 sec, fly 6'-10'-12' up." Morphological data: from spread sheet—PNLen 1.9, ELLen 7.0, PNWid 2.5, ELWhum 1.3, ELWmid 1.9, LELVit 3.1, RELVit 2.9, TotLen 8.9, PnRat 0.76, ElRat 1.5, VitRat 0.44; Colors: T 333, Py 1, Cx 2, V 333, Edg 2. The type will be deposited in the USNM.

Figure 7. Unlabeled Eaton Creek site from highway.

Figure 8. Fisherman's trail along Eaton Creek, fireflyer access?

Larry Patrie, Fredonia College of Ed, professor of chemistry, geology, and physics. The best teacher I ever had, anywhere.

Chapter 56

Photuris pensylvanica (DeGeer) 1774

Barber's Penn

(Dot-Dash Icon)

There is no better way to start this Chapter than with a direct quotation from Barber (1951; an example of descriptive, taxonomic natural history at its best?), cuing us to a broad range of topics in simple everyday terms. It was this text that opened up, made defensible to this writer, an informal style of science writing that can appeal to the uninitiated as well as provide professionals with necessary details. Here we travel, wearing our boots, with Barber to the tidal marshland of the Anacostia River at Washington, DC, not far from the Patuxent River Naval Air Station:

> *… over the level tops of the tall, rank grass another very different flash greets us—an instantaneous explosion of light followed immediately after an extremely short, dark interruption by a protracted brilliant light lasting 1 to 2 seconds, with the end perceptibly diminished in intensity. We wade into the deep grass and ooze and catch samples. They are not half so large as the crescendo species on shore, and some have wing covers pale except basal remnants of their brown vittae. Certainly it is the only species seen tonight to which the original habit notes and description of pensylvanica (original spelling of the specific name* [epithet]*, published by DeGeer more than a century and a half ago, can be applied. While emitting this double flash the male (for no females are visible to us) poises in his flight over the grass tops, dips slightly and rises describing little* U*-shaped curves of light, the finish a little higher than the first flash. He must watch for his bride's answer straight beneath, since marsh grass stands vertical at this season and cannot be seen through obliquely. But his behavior is the result of instinct instead of reason and reflects an immensely old specific adaptation to this particular ecologic environment. No females can be found while we walk forward, but if we turn and force our way backward through the grass their annoyed flashes deep in the disturbed grass or on the surface of the ooze permit their capture in numbers. In the vial used to preserve these females I find a minute fish (*Umbra*). Was a female eating a fish when caught? No other debris is in the vial.*


H. S. Barber, 1910?

In the taxonomic section Barber (p. 26) notes that this species "appears in great abundance over the tall grass of the Potomac and Patuxent tide marshes," and he makes observations concerning the morphological differentiation and identification of this firefly. He also makes comments that have a significant bearing on the ecology and geographic location of the "type" (name-bearing) specimen's origin: "… it appears likely that the type locality is within the present city of Wilmington, Del., the southern part of which was until a few years ago a *fresh water-marsh* [jel emphasis] and might have been called a prairie. Ecologically it must have been practically identical with the marshes near Washington, over which vast numbers of this little firefly may be observed." (page 27) He refers to a note by Jones (1930), which mentions an unpublished manuscript by Hesselius (ca >1713, 80 pp.) on the natural history of the region.

❊ ❊ ❊

During this study a firefly flashing in the manner described by Barber was seen within what would have been the range of Barber's historical view of *pensylvanica* (**Fig. 1**), in marshes in Charles County, Maryland, one within sight of the Potomac River Bridge (H. W. Nice Mem. Br.), and one near Welcome, west of LaPlata, on Mill Swamp Road—perhaps the "swamp" recognized in the road's name? Dates ranged 25 May-25 June (**Fig. 2**). They flew as Barber had noted, sometimes making Us and sometimes down-sliding; no twilight short flashes were seen though sought. Across from the Mill Road marsh dot-dashers flashed up the face of the forest and over road-side and forest shrubs. The dot of the FP sometimes snapped as though electric at the Mill Road site, but at the Bridge some FPs appeared to have neither a dot nor even a dash-initiating "pip." Dashes at both sites ended abruptly, without a noticeable taper. FP period was much longer than in other *penn*-Group demes (**Fig. 3, rate in Fig. 4**), excepting at a northern Long Island deme along a stream in Smithtown running to the Sound, Suffolk County, NY.

Morphology. McDermott examined Barber's specimens and provided detailed measurements and notes (Barber, 1951:45); most notably, length 9-10 mm, the remainder detailing features that may become useful for later comparisons when more is known about the genus in the region. Voucher measurements, ratios, and colors from the present study are in **FigTable 5** with the key to anatomy in **Figure 6. Figure 7** is vitta ref:4D from the all-*Photuris* 201.2-PNV array (page 423), illustrating serifs with flukes, as also illustrated in the "*pensylvanica*" from another locality in **Figure 8**; serifs occur on nearly half of the vouchers from Charles County, MD.

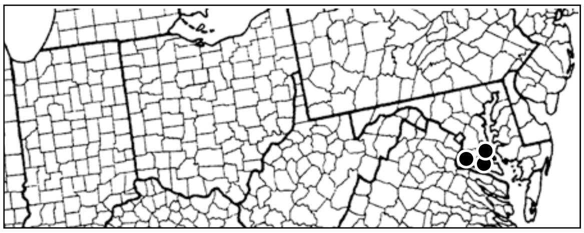


Figure 1. Counties for Barber's name-referencing *Penn*.

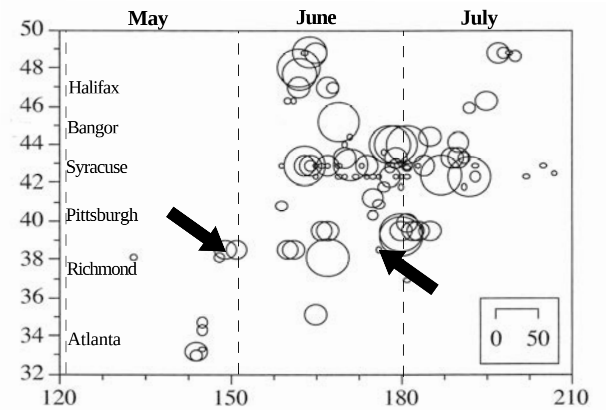


Figure 2. Dot-dash FP occurrence, arrows mark jel Chesapeake-*Penn* observation dates (AX: Lat/DOY).

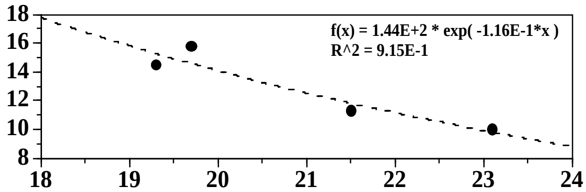


Figure 3. Dot-dash FP period (AX: sec/temp).

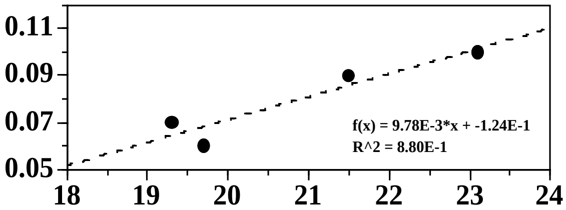
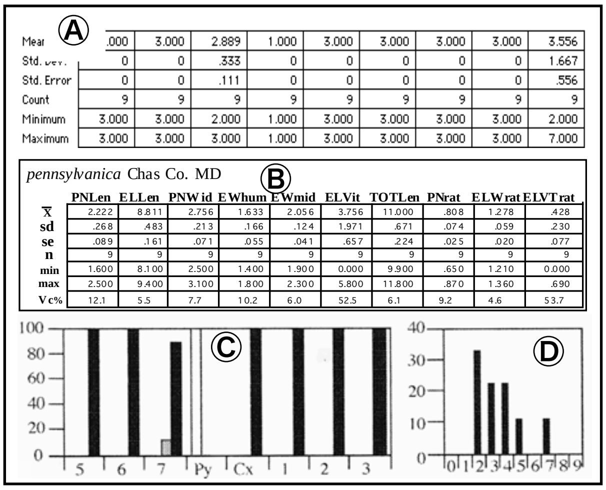


Figure 4. Dot-dash FP rate (AX: sec/temp).



Mear	.000	3.000	2.889	1.000	3.000	3.000	3.000	3.000	3.556
Std. Dev.	0	0	.333	0	0	0	0	0	1.667
Std. Error	0	0	.111	0	0	0	0	0	.556
Count	9	9	9	9	9	9	9	9	9
Minimum	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	2.000
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000

pennsylvanica Chas Co. MD

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.222	8.811	2.756	1.633	2.056	3.756	11.000	.808	1.278	.428
sd	.268	.483	.213	.166	.124	1.971	.671	.074	.059	.230
se	.089	.161	.071	.055	.041	.657	.224	.025	.020	.077
n	9	9	9	9	9	9	9	9	9	9
min	1.600	8.100	2.500	1.400	1.900	0.000	9.900	.650	1.210	0.000
max	2.500	9.400	3.100	1.800	2.300	5.800	11.800	.870	1.360	.690
Vc%	12.1	5.5	7.7	10.2	6.0	52.5	6.1	9.2	4.6	53.7

Figure 5. Morphological data for vouchers from DeGeer's general "Holotype" region as determined by Barber (1951).

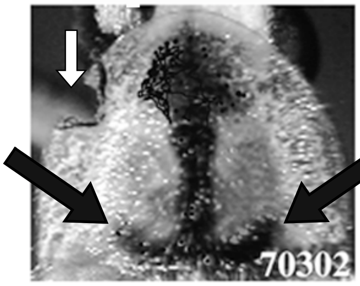


Figure 7. Pronotum of a *aureolucens* voucher from WI locality, to illustrate the serif flukes (black arrows) common in the se MD *pensylvanica* voucher series. In this specimen note the torn section (white arrow), possibly removed by the mandibles of a just-mated female; others have punctures the size and spacing to have been made by mandibles.

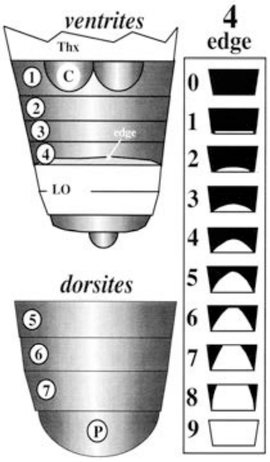


Figure 6. Key to morphological elements.

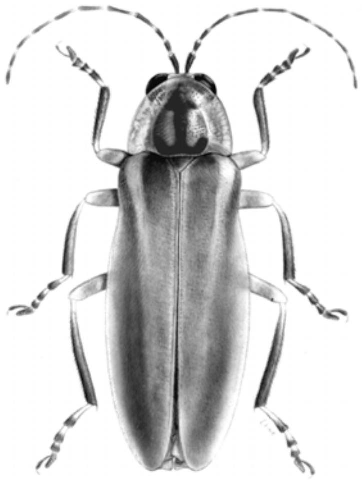


Figure 8. Carbon dust illustration of a dot-dash flashing *Photuris* clearly showing a vittagram serif with flukes (a Laura Line carbon dust).

Chapter 57

Photuris polacekae n. sp.

A single specimen was collected on 25 May 1999, in Gillispie County, TX (**Figs. 1, 2**), on route 16 near Lady Bird Municipal Park, Fredericksburg, at the Live Oak Creek bridge. A *Photuris* Division I firefly, morphologically it appears much like *Ph. congener* and *Ph. billbrowni*, but the FP did not agree with either, nor with that of *Ph. divisa* to the north. A pronotal vitta is only slightly indicated, with the posterior median line being a bit darker (**Fig. 3**). Fieldbook notes are brief (pages 109-10): "gave a little single /KB 60 /9935 each ≈2.5 sec. from bridge I thought it was a Div. I [*Photinus*]."

Holotype: male (**Fig. 4**), voucher number 9935, collected 25 May 1999, Gillispie County, Texas, route 16 near Lady Bird Municipal Park, Fredericksberg, at Live Oak Creek bridge. FB page 109-10: "gave a little single \KB 60 \9935 each ≈2.5 sec. from bridge I thought it was a Div. I [*Photinus*]." Morphological data: from spread sheet—PNLen 2.8, ELLen 9.5, PNWid 3.5, ELWhum 1.9, ELWmid 2.4, LELVit 0.0, TotLen 12.3, PnRat 0.79, ElRat 1.27, VitRat 0.0; Colors: T 331, Py 1, Cx 3, V 333, Edg 2. Will be deposited in the USNC

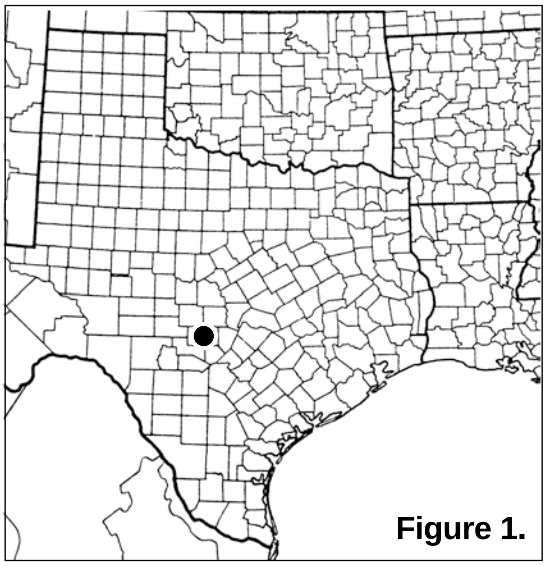


Figure 1.

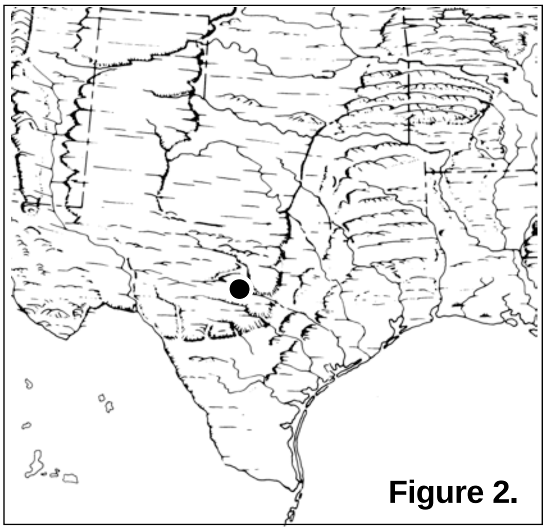


Figure 2.

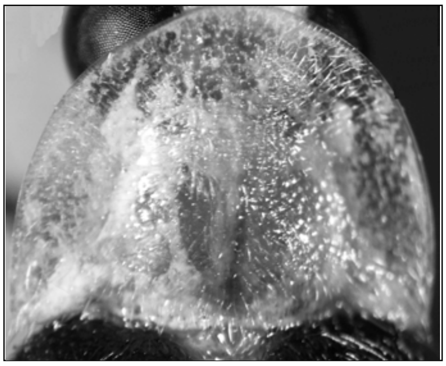


Figure 3. Holotype PN.

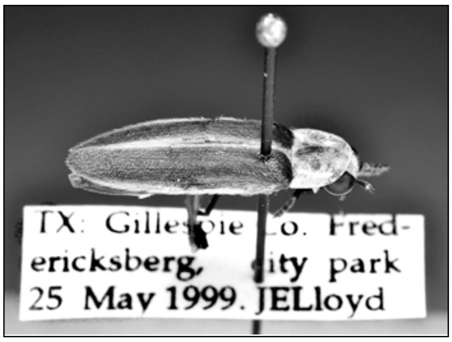
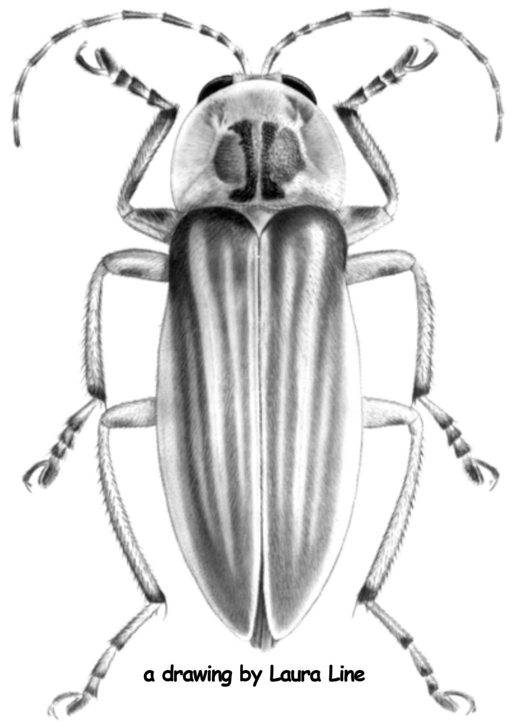


Figure 4. Holotype.

Nomenclatural note. The epithet recognizes Barbara Polacek, an algologist and professor at Fredonia (now SUNY) who taught the first course I ever took in biology, and started it all; and then encouraged me to go to her alma mater, where, at the museum at the Univ. of Mich. I met Darwin and others like him—curators of insects, and an evolutionary anthropologist … and at Nat. Sci. great and unforgettable botanists—Sparrow and Wagner! This and other professor photos are from Fredonia year-books.

EVOLUTION OF AGGRESSIVE MIMICRY (part 2; from p. 230)

Toward a model. Sliding beyond a mere vegan diet to include a meat supplement is easily seen in the behavior of this *Photuris*, but a transition from plant juice to aphid juice, meaning licking then eating the aphids too is also imaginable, seems easier and shorter, and might metabolically be a simpler move. A next slide-along needs more field observation: *Photuris* fireflies blink when perched, but other fireflies in North America are not (generally) known to; perhaps some in the tropical Americas once did, initially an aposematic signal, but eventually as an invitation to other fireflies, potential mates. Sedentary mating swarms would seem to be a logical development too, but then they would come under attack by an evolving firefly predator seeking blinks on vegetation. This is to say, that when one asks why was it that mass aggregating, synchronizing fireflies evolved in Asia but not in the Americas, the answer is that they probably once did, they started and they were eaten up by a co-evolving predator—an important development ("step," transition) perhaps in the evolution of photurine fireflies. In North America we also have rich, localized sites that grow hundreds of fireflies, as witnessed by the flying clouds of some species —*Photinus carolinus*—where males synchronize competitively with those near them, but they probably remain in the air (no anthropomorphism should be inferred) lest a *Photuris* catch up with them. But it must be anticipated that there may be specializing *Photuris* in these swarms exploiting them. Some readers may recognize the name change of this striped *Photuris*. This is explained and illustrated below.



Photuris trivittata **Lloyd and Ballantyne**
(formerly presumed *Photuris trilineata* (Say))

Toward A Model For the Evolution of Firefly-Phagy

1. flower sipping **(water, sugar, etc.)**
2. plant nibbling **(enhancing nutrient accessibility)**
3. aphid/scale nibbling, chewing
(animal nutrients obtained)
4. bugs, plant feeders added
(additional, richer nutrients, defensive compounds)
5. feeders/fireflies attracted to ego's blinking
6. seek feeding prey via flashing on plants
7. seek prey in evolving perched mating swarms (leks)
8. predate flashers attracted near ego’s flashes
in feeding swarms and breeding leks
9. predate flashers attracted to ego’s solitary flashes
(away from swarm)
10. eat mate after sex (sexual selection aspect also)
11. attract and eat flashers via own sexual response flashes
12. vary response flashes facultatively
13. attack approaching hesitating males
(walking/flying)

The firefly "type specimens" of Thomas Say, *Py. angulata* for example, have long been known to have disappeared through neglect or other means, an old academic bone of contention. Three Schmidt boxes of his specimens were found in storage a decade or so ago at the MCZ by the Curator, coleopterist David Furth. Most or all were tropicals, and one of them was the specimen Say named *Lampyris trilineata* (now *Aspisoma trilineata*). This meant that the 3-striped *Photuris* that a European taxonomist had presumed to be Say's specimen, was not. This was discovered by Lesley Ballantyne as she was searching through old specimens in European collections as part of her studies on Asian and Indonesian fireflies. Thus, the American (Mexican) 3-striped *Photuris* jel had studied in Cardenas, Mexico was unnamed and needed to be. Hence, *Photuris trivittata*, the grass-haunting predator featured here.

Chapter 58

Portage Crescendo-Flasher

This Penn-Group variad was found in northeastern OH, Portage and Trumbull Counties (**Fig. 1)**. Its repertoire and timeline of evening occurrence is similar to that of Iowa's *asacoa.* Short-flash FP period measurements of individual males are shown with those of *asacoa* in **Figure 2**, and average about 2.5 sec at 20°/68°. Whether it defaults from its twilight short to a crescendo FP is uncertain or possibly optional(?). Crescendo FP period measurements and prediction are shown in **Figure 3**. Like others of the Group, this is a grass- and wetland firefly and was found in a perennial (maintained) old field near an artificial lake, and later in the same evening in an adjacent county at a marsh and along the adjacent grassy roadside ditch. Its dark hind coxae, vittigram, and slightly smaller size (14 mm) will distinguish it from *lucicrescens*, whose known range closely approaches; note also, *lucicrescens* is a forest and edge firefly, and not known to occur in numbers over grassland; the crescendo of the Portage firefly is not dramatic, merely a gentle ramp, without the exponential explosion often seen in *lucicrescens.*

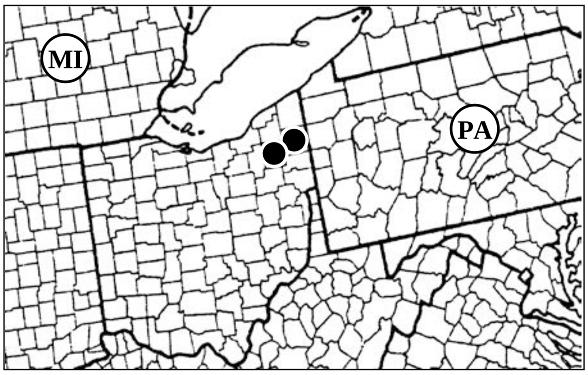


Figure 1. County-based occurrence of provonshai.

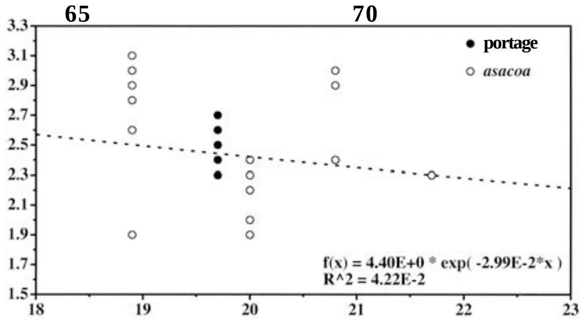


Figure 2. Individual short FP periods (sec/temp).

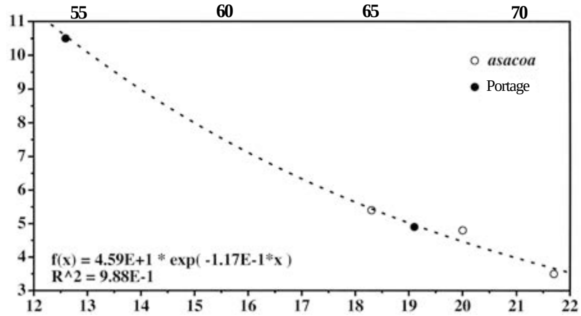


Figure 3. Crescendo FP period agreement (sec/temp).

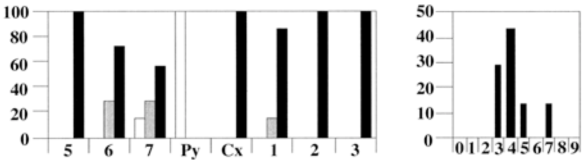
Flashing behavior. This firefly was observed only briefly on one evening. Males began flying and emitting short flashes about 30 min after sunset and a few minutes later crescendo flashing began. Though none were marked and defaulting was not elicited, there is some confidence that both FP types were emitted by males of the same population. They flew over low herbs and shrubs, rarely higher than 10' around bordering trees. Though none were seen, the presumptive prey of Portage females is *Photinus curtatus,* a twilight, short-flashing species. It is often abundant in such habitats in this region (Lloyd 1967). Flight of Portage was slow and poising. During their crescendo flash they sometimes flew amongst the branches and foliage of low bushes, and lower, in slowly winding courses below the tips of grasses and herbs. The crescendo began dimly not abruptly, and rose slowly in an apparent simple, linear ramp. The incline sometimes was followed by a sustained maximum briefly before the FP ended. Occasionally a "wink" appeared about three-fourths through the flash. SWAT-measured crescendo flash duration averaged 1500 mSec (r=1.0-2.0) @19.1°/66.4°), and 2800 (r=2.0-3.0) @12.6°/54.7°.

Decoy experiments. The LED was placed below several flying, crescendo-flashing males at distances <6'. All approached and flashed successive 4-13 FPs; apparently none switched to another FP. Two did not land near the decoy, and after 4 crescendos were not seen to flash again in the vicinity. Males that landed near the decoy had emitted up to 6 airborne crescendos before alighting, and then landed <1' from the decoy. Several dimmed their flashes during approach.

The FP period of approaching males did not change appreciably, but after males landed, and two or three more crescendos had been emitted, the period conspicuously leng-

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.800	11.283	3.500	2.000	2.600	7.733	14.083	.798	1.307	.685
sd	.219	.479	.261	.089	.110	.671	.659	.033	.073	.050
se	.089	.196	.106	.037	.045	.274	.269	.013	.030	.020
n	6	6	6	6	6	6	6	6	6	6
min	2.500	10.900	3.100	1.900	2.500	7.000	13.400	.750	1.240	.630
max	3.100	11.900	3.900	2.100	2.800	8.900	15.000	.850	1.400	.750
Vc%	7.8	4.3	7.5	4.5	4.2	8.7	4.7	4.1	5.6	7.3

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.714	2.429	1.000	3.000	2.857	3.000	3.000	4.286
sd	0.000	.488	.787	0.000	0.000	.378	0.000	0.000	1.380
se	0.000	.184	.297	0.000	0.000	.143	0.000	0.000	.522
n	7	7	7	7	7	7	7	7	7
min	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	18.0	32.4	0	0	13.2	0	0	32.2



FigTable 4. Morphological data of Portage.

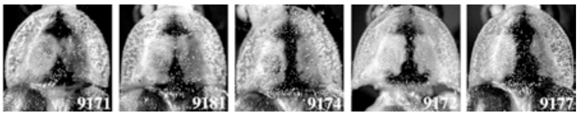


Figure 5. PNV of Portage.

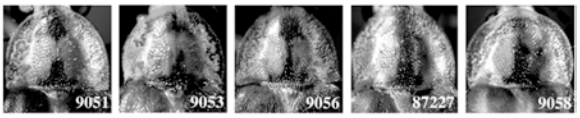
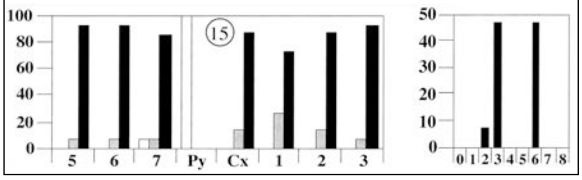


Figure 6. PNV of *asacoa*.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNRat	ELWrat	ELVTrat
$\bar{X}$	2.860	11.327	3.467	2.087	2.619	7.780	14.160	.833	1.260	.685
sd	.199	.578	.172	.151	.100	1.296	.735	.072	.091	.098
se	.051	.149	.044	.039	.026	.335	.190	.019	.024	.025
n	15	15	15	15	15	15	15	15	15	15
min	2.500	10.600	3.100	1.900	2.500	5.000	13.250	.700	1.100	.470
max	3.100	12.500	3.900	2.400	2.750	9.800	15.500	.900	1.500	.810
Vc%	7.0	5.1	5.0	7.2	3.8	16.7	5.2	8.6	7.2	14.3

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.933	2.933	2.800	1.000	2.867	2.733	2.867	2.933	4.333
sd	.258	.258	.561	0.000	.352	.458	.352	.258	1.633
se	.067	.067	.145	0.000	.091	.118	.091	.067	.422
n	15	15	15	15	15	15	15	15	15
min	2.000	2.000	1.000	1.000	2.000	2.000	2.000	2.000	2.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	8.8	8.8	20.1	0	12.3	16.8	12.3	8.8	37.7



FigTable 7. Morphological data of asacoa.

thened. When one attracted male landed 5” from the decoy, a previously unnoticed male zipped in, landed, and flashed 1” from the LED. Males walked and flew short hops as they approached the LED after initial landing. The LED flash was usually a 200-300 mSec answer, and those presented after and during crescendos seemed equally attractive. While attracting a crescendo flasher, a short-flashing male (species?) flew close and hovered ca 2’ from the decoy, paused and flashed once or twice, and then flew away. LED-responses (200-300mSec) were given to four short-flashing and presumably Portage males, as described; all continued to emit short flashes—that is, none switched/defaulted to a crescendo, but were attracted to the LED. There remains uncertainty, serious doubt, as to the results of these decoy experiments, in particular because defaulting is recalled to have been observed in Trumbull County an hour or so later in the evening though this "fact" was not recorded in the field book. Otherwise, in some respects Portage appears to be similar to *asacoa* in northeastern Iowa.

Morphological data. Data are shown in **FigTable 4; Figure 7** shows those of *asaco* for comparison. An array of PN vittagrams for Portage are in **Figure 5** and those of *asacoa* in **Figure 6**. Anatomical references are in **Figure 8**. Specimens will be deposited in the USNM.

Miscellaneous notes. It was originally intended that this firefly would be named to recognize Arwin Provonsha, Curator and taxonomist at the Purdue University Museum who made a number of field observations on it or one much like it. He sent his records to me, recognizing that there was more to the problem than first appeared. His data are not included here but will be kept for reference. The nickname Portage recognizes the area where this firefly was first seen, which is said to be on the water route from Lake Erie to the south and where the overland transport of canoes was made by traveling Amerindians.

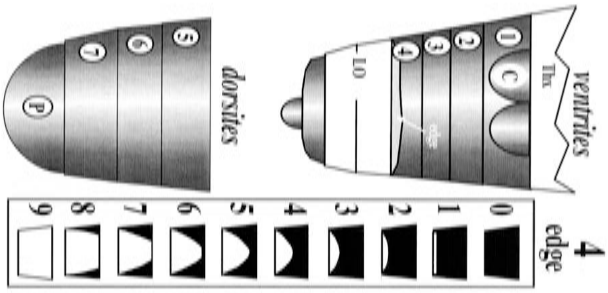


Figure 8. Topographic and splash keys.

Chapter 59

Photuris potomaca Barber 1951

Potomac River Firefly

On either side the River lie
Strands of grass where sparks do fly
Tennyson (var)

Barber described *potomaca* from along the Potomac River in the vicinity of Washington, DC, and noted its close association with the river. This study found what is operationally referred to his species further upstream along the Potomac and also along streams and rivers elsewhere (**Figs. 3-7**). As understood here, working (FP-period defined) *potomaca* occurs in eastern river systems from New York, and possibly Connecticut, to South Carolina, and west of the Appalachian Mountains into the Ohio River drainage **(Figs. 1, 2**). It was not seen along the remote uppermost reaches of the Potomac (**Fig. 8**). Barber noted that its larvae occurred in masses of drift (river flotsam) deposited by the river in flood (**Figs. 9, 10**). Whether such deposits, with accumulations of decaying vegetation (with a framework of sticks, logs, broken camp-stools etc.), are important in the ecology of *potomaca* is not known, but they are the most remarkable and memorable aspect of Potomac River ecology.

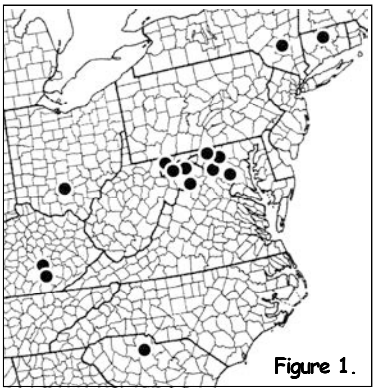


Figure 1.

This firefly is easily recognized in the field throughout its known distribution by its river and stream association and its very short flashes emitted in rapid, rhythmic, seldom-broken sequences (i. e, trains; **Fig. 11**). Only flash period is diagnostic, and ranges 0.5-0.9 sec @21°/70°-17°/66° (**Figs. 12, 13**). **Figure 8** in the *chenangoa* Chapter 23 compares the flash rates of the three "known" train-flashing species in this “working species group.” The possibgility of a fourth is also indicated in the figure. In southern New York State and southwestern New England three of the four noted will cause confusion without accurate temperature measurements made in the *actual* activity space.

In much of its known distribution *potomaca’s* (green) flash trains could only be confused with those of *Photuris frontalis*: the two species are morphologically distinct in hand (**Fig. 14**).

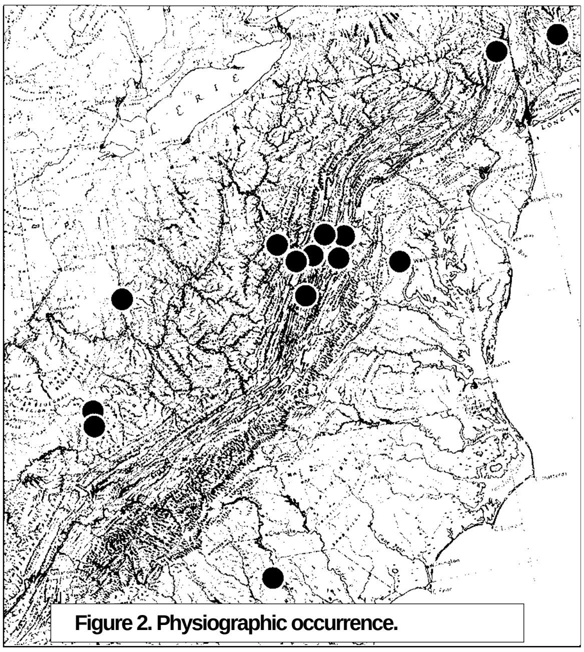


Figure 2. Physiographic occurrence.


Figure 4. Shoreline habitat, Potomac River.


Figure 3. Shoreline habitat, Potomac River.


Figure 5. Shoreline habitat, Potomac River.

Contrast: rapid flash trains more than 100 feet from rivers and streams, concentrations of train-flashers often but not exclusively within a meter or so of the ground, and occurrence of precise flash synchrony by neighboring flying males, will usually (so far as now known) be diagnostic of *frontalis*. Seasonal occurrence of *potomaca* around the Potomac River latitudes is from early June to early July (**Fig. 15**).

Flashing Behavior and Ecology. On islands in the Potomac males first flashed in deep shade amongst nettles, poison-ivy, poke, mints, maple seedlings and prostrate grape vines. They began as early as one minute *before* sunset; on two occasions they appeared to start at about the end of civil twilight (0.97 and 1.15 crep), that is, at full darkness, though special effort had not been made to detect first flashing. As darkness deepened they gradually moved out to flash low over herbaceous strands along the shore, over such bars and points extending from shore, and up around willows and maples along the banks. They flew slowly, poising a few inches out from leafy branches or over herbs to flash, then moved a few inches to their next flashing position. I also observed males flying around a pile of drift as Barber described (**Figs. 9-10**).

The center of activity at the SC site, a stream-bed by a bridge, was a large aspen (**Fig. 6**). Males also flashed over herbs and shrubs beneath the tree and along the adjacent sward in both directions for several yards. Though most arboreal-flashing males

Fig. 6. Too-wide bridge tree by the Little Sandy, SC.

Figure 9. River flotsam of a sort; larval habitat?, MD.

Fig. 7. Creek-side meadow near the Rockcastle, KY.

Figure 8. Upper Potomac River, MD.

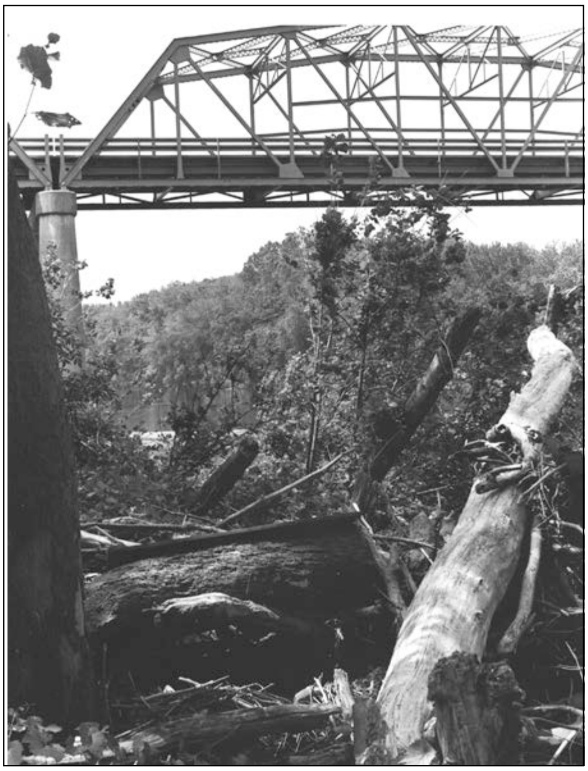


Figure 10. Potomac shore, WV.

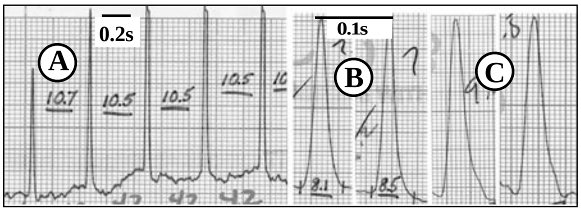


Figure 11. PM traces (AX: rel. int./time). (Augmented legend below)

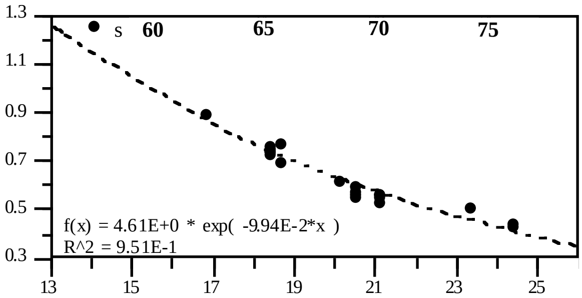


Figure 12. FP period (AX: sec/temp).

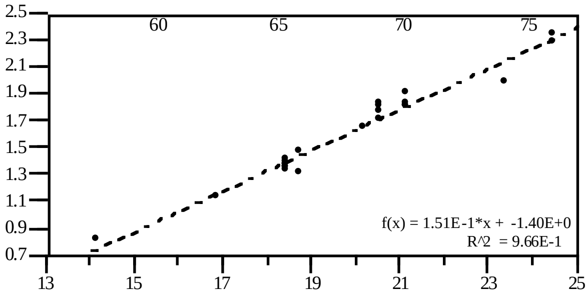


Figure 13. FP period rate (AX: Hz/temp).

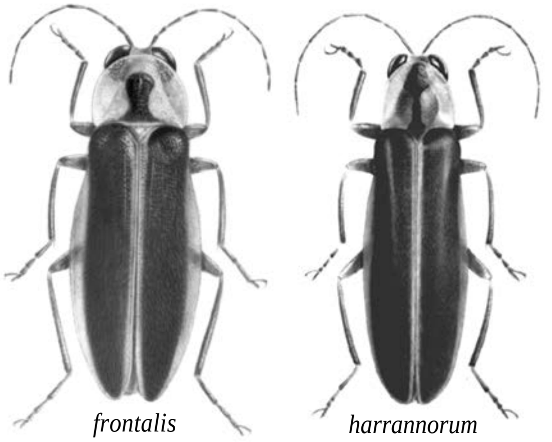

frontalis *harrannorum*

Figure 14. *Ph. potomaca* resembles *harrannorum*.

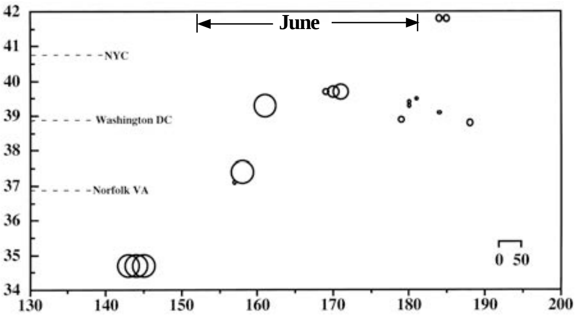


Figure 15. GESEDISOBS (AX: Lat/DOY)

flew closely about the tree a few flashed from perches and at full darkness males flew and flashed halfway up the tree 40 feet above ground. The combination of short, bright and nearly stationary flashes, short flash period, tight activity space about the tree, and proximity to the stream produced a scene as seen in Thailand and New Guinea with aggregating Luciolinae fireflies, except that *potomaca* lacked any semblance of flash synchrony. At the Rockcastle River site in Kentucky *potomaca* was active around shrubs and trees at stream-side and for a few yards into the adjacent oldfield -hayfield (**Fig. 7**).

The flash period of *potomaca* ranges from 0.44 sec (rate=2.3 Hz) at 24.4°/76° to 1.25/0.8 at 14.1°/57.5° (**Fig. 12,** rate regression in **Fig. 13**). Although the flashing of *potomaca* is machine-like and continuous, trains are sometimes broken and not rigidly constant in rate. An unbroken series of electronic flash recordings included (incomplete) counts of 15, 21, 22, 23, 24, 25, and 25 flashes. When flash trains were broken, usually it was with the omission of but one or two flashes. Extensive PM records reveal a period constancy in trains, with long sequences of low variance only occasionally broken at irregular intervals. Once an Ohio male was seen to begin flashing at half the typical rate, then abruptly switch back to the usual/described rate.

Flash Configuration and Color. Recorded flashes of *potomaca* reveal a slightly slower fall- than rise-time, that is, a moderate asymmetry. Flash duration is among the shortest PM-recorded: ca 32 mSec half-max and 70 mSec base at 17.9°, and ca 20 mSec half-max and 56 mSec base at 24.4°: 130 PM-recorded flashes from 20 males examined. In the field in/or adjacent to their known range, the flashes of *potomaca* might also be mistaken for those of *Photuris hebes*, *bridgeniensis*, and *chenangoa* because of flight, flash period and ecological similarities. Note that *potomaca* has unimodal flashes whereas those of *hebes* are usually shouldered or nearly bimodal, and those of *bridgeniensis* are bimodal— embellishments that often give the flashes of these last-mentioned species a hitched, jerky appearance. Only rarely does a flash of *potomaca* appear to hitch.

Sexual Interaction. Fragmentary observations suggest that flash synchrony could possibly be involved in courtship: On one occasion an individual (lower Potomac) flying a few inches from the end of a bough of a small tree and emitting the male FP, attracted attention because he was flashing in synchrony with a perched firefly adjacent to him on the foliage. Upon approaching (the same?) two synchronizers were found perched about a 1 inch apart, both flashing a male-like pattern in synchrony.

On another occasion, a flying flashing "male" (MD) approached a firefly that was on the ground flashing at male-like intervals, and they flashed in synchrony. Then, one flew up emitting a series of longer arhythmic flashes, and flew off emitting the flashes characteristic of flying *Photuris* females. On another occasion, a flying male (SC) approached a female (subsequently captured) that was flashing on the ground, and that may have been flashing at a slower rate. The impression was that they had briefly synchronized their flashes (a flash or two) before he flew off. In none of these three brief observations was a flash-answer sequence seen.

Female flashing, predation. Barber noted that flying *potomaca* females emit flashes similar to those emitted by males, though longer in duration. This was easily seen one evening on an island near Point of Rocks, MD. There were more females flying and flashing, landing and taking off in a damp area of low vegetation by the shore (**Figs. 3-5**), than there were flashing males present. Probably they were ovipositing; males did not pursue them.

If females of this species are aggressive mimics of other fireflies, along the Potomac River *Photinus scintillans* is one likely prey, since it too is abundant along the shoreline. Measurements of *potomaca's* green bioluminescence in millimicrons are: peak, 559; half-max, 533/599, and breadth at half max, 66; note, *scintillans* flashes are conspicuously orange-yellow, a color associated with twilight activity in NA *Photinus* (Biggley et al.).

Notes on ecology, geography, collecting. Barber's Potomac River habitat is unique. On its islands huge vagrant logs are piled like jackstraws and flotsam includes broken camp stools, branches, twigs, straw, boards, clothing, and broken boats. There are gravel banks cut through with freshet channels, silty impatiens depressions, and an overgrowth of sapling maples thatched with grape-vines.—*Three major streams—the North and South Branches and the Shenandoah—converge to form the single river and tidal estuary now known as the Potomac. Bounded on the north by the watershed of the Susquehanna, on the west by that of the Ohio, on the south by the James and Rappahanock, and on the east by Chesapeake Bay, into which it flows, the Potomac River and basin cover an area of over one hundred thousand square miles—4 percent of the continental United States. Parts of Pennsylvania, Maryland, Virginia, and West Virginia, and the entire District of Colombia, are included in this area* (Metcalf l982).

In the Potomac River watershed *potomaca* was found on the main river at: Point of Rocks (Frederick Co.) MD, about 25 miles (measuring directly) above Washington, on islands and the Virginia and Maryland shores; at Fort Frederick State Park (Frederick Co.) MD, about 60 miles above Washington, on islands and the Virginia and Maryland shores; at Fort Frederick St. Park (Frederick Co.), MD, about 60 miles above Washington, 25 miles above the confluence of the Shenandoah; at Old Town (Allegheny Co.), MD, about 100 miles above Washington on the North Branch of the Potomac, less than 5 miles above the South Branch fork, on a presque island and both the Maryland and West Virginia shores; at Romney (Hampshire Co.), WV, on the South Branch about 15 miles above the confluence; at Burlington (Mineral Co.), WV on Patterson Creek, about 7 miles west of Romney; and possibly at the Potomac State Forest near Oakland (Garrett Co.), MD, about 45 miles above the fork, on Lost Land Run, a small tributary of the North Branch, although it was not found on the North Branch proper near there; and finally, on the Shenandoah near Strasbourg (Shenandoah Co.), VA, about 30 miles above its confluence with the Potomac River.

Beyond this river system the Potomac River firefly was found in the watershed of the Ohio River, near Chillicothe (Ross Co.), OH, on Hickory Run, a small tributary of the Scioto River; and near Mount Vernon (Rockcastle Co.), KY on the middle fork of Rockcastle River, a tributary of the Cumberland River which joins the Ohio River just above its confluence with the Tennessee. The latter then flows into the Mississippi. Thus, this firefly and apparent variads, though named for the Potomac River, may be found along many rivers and streams, and in an arborescent distribution could possibly occur widely in the Mississippi's huge drainage basin—a total area of 1.2 million square miles.

A few flashes of a *potomaca*-like firefly was seen near Farmington (Hartford Co.), CT., at a forest-oldfield ecotone, though perhaps it was not resident there. This site is not near a stream, but the Farmington River is not far. Thus, the Connecticut River and its drainage, and to its west the Housatonic River and its drainage, could have a *potomaca*-firefly. I tentatively include the Farmington train-flash firefly in *potomaca* for simplicity, but note that some other *Photuris* species in the New England "firefly province" seem to be distinct isolates from populations to the southwest, across a frontier at or near the Hudson River.

Two problematic observations were made in southeastern New York State: In Sullivan County, a mile south of the Ulster County line on Rt. 209, a too-fast flash period/rate of 0.67/1.5 at 15.9°C (n=6, 26 June) was measured, but the temperature was measured at the ground and the fireflies were in the treetops (no vouchers). About six miles west of New Paltz in Ulster County a single measured specimen fell on the *potomaca* regression (0.77/1.3, 18.7°C, 26 June, no voucher). Note, on the Raisz-topographical **(Fig. 2**) a a possible connection from these two New York localities through the Great Valley to the Potomac River drainage.

In the deep south, near Chester, SC, a *potomaca*-like flasher occurred on the Little Sandy River, a tributary of the Broad River, which joins the Santee and goes to the Atlantic Ocean. This firefly's range may therefore also extend through minor river systems east of the Appalachians, from the Potomac River south, including, for example the James, Roanoke, Cape Fear and Savannah Rivers. It was not found on Florida's Apalachicola or Suwannee Rivers, both of which drain to the Gulf of Mexico. The Apalachicola, which becomes the Chatahoochee north of Florida, the only Florida river to originate in the piedmont, might permit *potomaca* to reach Florida. Note that except for Barber's original localities near Washington DC, there are presently no known localities on the coastal plain, a sampling bias perhaps.

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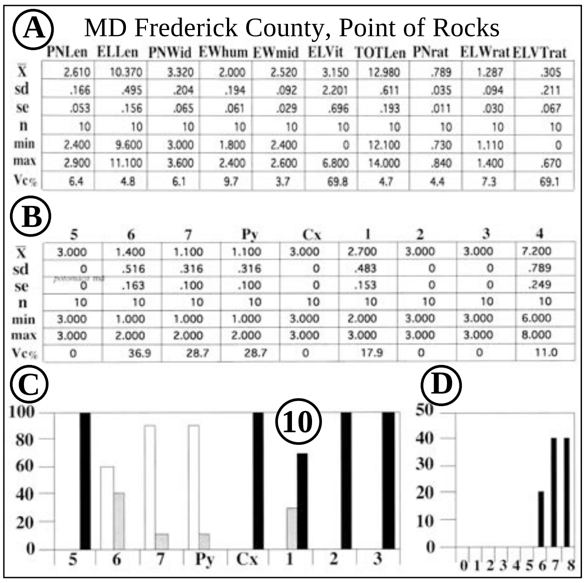


Ⓐ MD Frederick County, Point of Rocks

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.610	10.370	3.320	2.000	2.520	3.150	12.980	.789	1.287	.305
sd	.166	.495	.204	.194	.092	2.201	.611	.035	.094	.211
se	.053	.156	.065	.061	.029	.696	.193	.011	.030	.067
n	10	10	10	10	10	10	10	10	10	10
min	2.400	9.600	3.000	1.800	2.400	0	12.100	.730	1.110	0
max	2.900	11.100	3.600	2.400	2.600	6.800	14.000	.840	1.400	.670
Vc%	6.4	4.8	6.1	9.7	3.7	69.8	4.7	4.4	7.3	69.1

Ⓑ

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.400	1.100	1.100	3.000	2.700	3.000	3.000	7.200
sd	0	.516	.316	.316	0	.483	0	0	.789
se	0	.163	.100	.100	0	.153	0	0	.249
n	10	10	10	10	10	10	10	10	10
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	6.000
max	3.000	2.000	2.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	36.9	28.7	28.7	0	17.9	0	0	11.0

Figure 16. Morph stats: measurements, ratios.

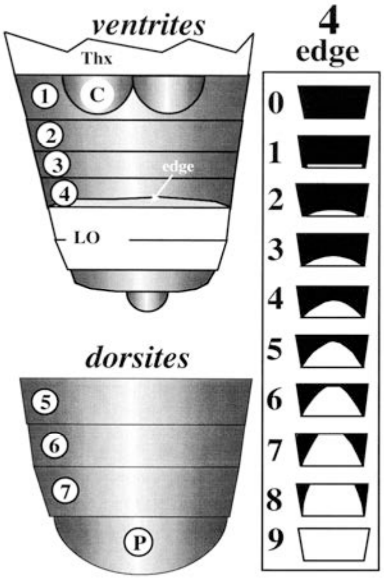


Figure 17. Topographic and splash key.

Morphological data. General morphological means from Potomac River vouchers are (n=10): PNL 2.6, ELL 10.4, PNW 3.3, EWhum 2.0, EWmid 2.5, ELVit 3.2, TOTLen 13.0, PNrat 0.79, ELWrate 1.29, ELVTrat 0.31 (**Fig 16A**, with other general stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae of the Potomac River series are shown in **Figure 16B-C**, and the pale splashing on the pre-lantern ventrite in **16D**. **Figure 17** is the key to skeletal plates and extent of splashing on ventrite 4. The data in **Figure 16A** and **B** and the histograms in **16C** and **D** with those of working variad populations for comparison in **Figure 19A-D,** next page. A range of vittagrams (pronotal vittae) of *potomaca* is in **Figure 18**.

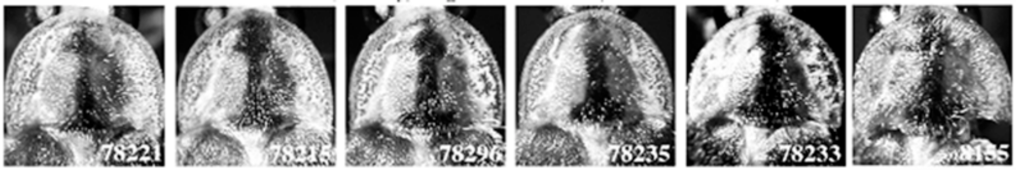
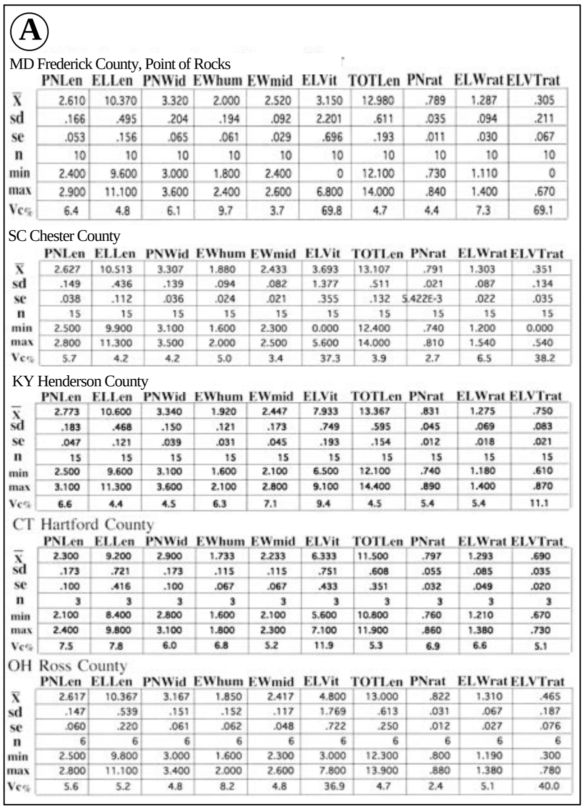


Figure 18. From sites MD & VA: variously along Potomac River, west to Pt. of Rocks, MD.



MD Frederick County, Point of Rocks

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.610	10.370	3.320	2.000	2.520	3.150	12.980	.789	1.287	.305
sd	.166	.495	.204	.194	.092	2.201	.611	.035	.094	.211
se	.053	.156	.065	.061	.029	.696	.193	.011	.030	.067
n	10	10	10	10	10	10	10	10	10	10
min	2.400	9.600	3.000	1.800	2.400	0	12.100	.730	1.110	0
max	2.900	11.100	3.600	2.400	2.600	6.800	14.000	.840	1.400	.670
Vc%	6.4	4.8	6.1	9.7	3.7	69.8	4.7	4.4	7.3	69.1

SC Chester County

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.627	10.513	3.307	1.880	2.433	3.693	13.107	.791	1.303	.351
sd	.149	.436	.139	.094	.082	1.377	.511	.021	.087	.134
se	.038	.112	.036	.024	.021	.355	.132	5.422E-3	.022	.035
n	15	15	15	15	15	15	15	15	15	15
min	2.500	9.900	3.100	1.600	2.300	0.000	12.400	.740	1.200	0.000
max	2.800	11.300	3.500	2.000	2.500	5.600	14.000	.810	1.540	.540
Vc%	5.7	4.2	4.2	5.0	3.4	37.3	3.9	2.7	6.5	38.2

KY Henderson County

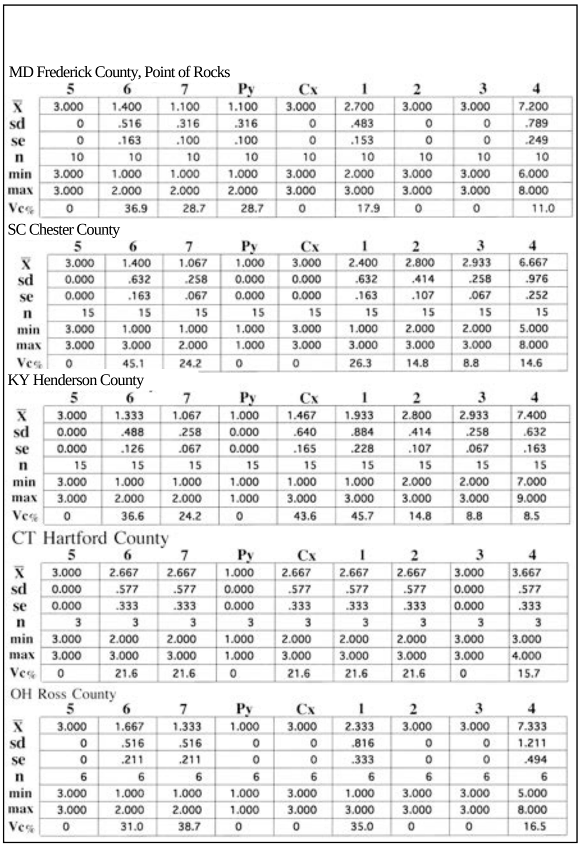
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.773	10.600	3.340	1.920	2.447	7.933	13.367	.831	1.275	.750
sd	.183	.468	.150	.121	.173	.749	.595	.045	.069	.083
se	.047	.121	.039	.031	.045	.193	.154	.012	.018	.021
n	15	15	15	15	15	15	15	15	15	15
min	2.500	9.600	3.100	1.600	2.100	6.500	12.100	.740	1.180	.610
max	3.100	11.300	3.600	2.100	2.800	9.100	14.400	.890	1.400	.870
Vc%	6.6	4.4	4.5	6.3	7.1	9.4	4.5	5.4	5.4	11.1

CT Hartford County

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.300	9.200	2.900	1.733	2.233	6.333	11.500	.797	1.293	.690
sd	.173	.721	.173	.115	.115	.751	.608	.055	.085	.035
se	.100	.416	.100	.067	.067	.433	.351	.032	.049	.020
n	3	3	3	3	3	3	3	3	3	3
min	2.100	8.400	2.800	1.600	2.100	5.600	10.800	.760	1.210	.670
max	2.400	9.800	3.100	1.800	2.300	7.100	11.900	.860	1.380	.730
Vc%	7.5	7.8	6.0	6.8	5.2	11.9	5.3	6.9	6.6	5.1

OH Ross County

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.617	10.367	3.167	1.850	2.417	4.800	13.000	.822	1.310	.465
sd	.147	.539	.151	.152	.117	1.769	.613	.031	.067	.187
se	.060	.220	.061	.062	.048	.722	.250	.012	.027	.076
n	6	6	6	6	6	6	6	6	6	6
min	2.500	9.800	3.000	1.600	2.300	3.000	12.300	.800	1.190	.300
max	2.800	11.100	3.400	2.000	2.600	7.800	13.900	.880	1.380	.780
Vc%	5.6	5.2	4.8	8.2	4.8	36.9	4.7	2.4	5.1	40.0



MD Frederick County, Point of Rocks

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.400	1.100	1.100	3.000	2.700	3.000	3.000	7.200
sd	0	.516	.316	.316	0	.483	0	0	.789
se	0	.163	.100	.100	0	.153	0	0	.249
n	10	10	10	10	10	10	10	10	10
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	6.000
max	3.000	2.000	2.000	2.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	36.9	28.7	28.7	0	17.9	0	0	11.0

SC Chester County

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.400	1.067	1.000	3.000	2.400	2.800	2.933	6.667
sd	0.000	.632	.258	0.000	0.000	.632	.414	.258	.976
se	0.000	.163	.067	0.000	0.000	.163	.107	.067	.252
n	15	15	15	15	15	15	15	15	15
min	3.000	1.000	1.000	1.000	3.000	1.000	2.000	2.000	5.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	45.1	24.2	0	0	26.3	14.8	8.8	14.6

KY Henderson County

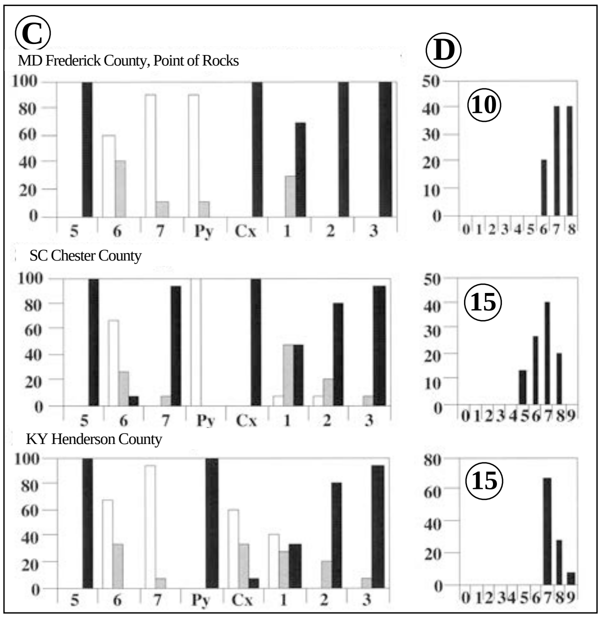
	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.333	1.067	1.000	1.467	1.933	2.800	2.933	7.400
sd	0.000	.488	.258	0.000	.640	.884	.414	.258	.632
se	0.000	.126	.067	0.000	.165	.228	.107	.067	.163
n	15	15	15	15	15	15	15	15	15
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	2.000	7.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	9.000
Vc%	0	36.6	24.2	0	43.6	45.7	14.8	8.8	8.5

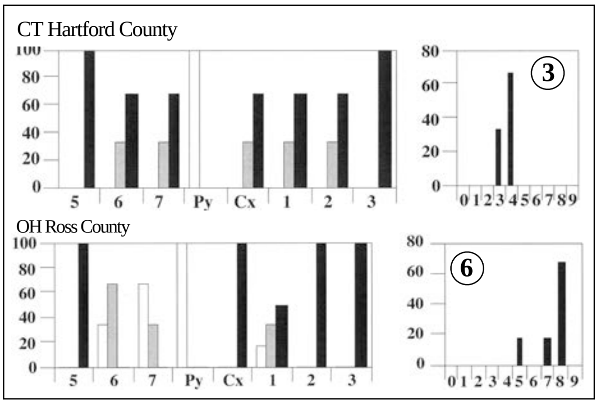
CT Hartford County

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	2.667	2.667	1.000	2.667	2.667	2.667	3.000	3.667
sd	0.000	.577	.577	0.000	.577	.577	.577	0.000	.577
se	0.000	.333	.333	0.000	.333	.333	.333	0.000	.333
n	3	3	3	3	3	3	3	3	3
min	3.000	2.000	2.000	1.000	2.000	2.000	2.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	4.000
Vc%	0	21.6	21.6	0	21.6	21.6	21.6	0	15.7

OH Ross County

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	1.667	1.333	1.000	3.000	2.333	3.000	3.000	7.333
sd	0	.516	.516	0	0	.816	0	0	1.211
se	0	.211	.211	0	0	.333	0	0	.494
n	6	6	6	6	6	6	6	6	6
min	3.000	1.000	1.000	1.000	3.000	1.000	3.000	3.000	5.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	31.0	38.7	0	0	35.0	0	0	16.5





FigTable 19. Morph stats: measurements, ratios, note localities.

Augmented figure legends. 11. PM-traces of flashes of flying *potomaca* males. (**A**) A train recorded at Point of Rocks MD, 18 June 1978, @24.4°/76°; (**B**) Two flashes from the train in A; (**C**) Two flashes recorded in Chester County SC, @18.4°/65.1°. Bars indicate time in sec. **12**. Flash period as a function of ambient temperature. An exponential curve was fitted by the graphing program. The “deviant” point “s” at the upper left may be closer to factual than the curve; it was taken at the SC site and another that was measured at this site and made at a lower temperature fits with other measurements. Flash data included are from several populations: MD, VA, KY, SC, OH, CT, & NY. **15**. Seasonal occurrence (GESEDISOBS) of *potomaca* adult flashing activity. **16**. Morphological data/information, from Barber’s bailiwick.

Chapter 60

Photuris quadrifulgens Barber 1951

SRSP-*Versi*

(slow-repeating-slow-pulsing)

Photuris quadrifugens is known to occur in grassland from the mid-Atlantic coast southwest to Missouri and Arkansas, with possible outliers/variads (**Fig. 1**). Its repertoire includes slow-pulsing (default) FPs and adjunct flickers which in the field resemble those seen in *tremulans*, other *Photuris*, and certain *Pyractomena* (except for color). Males most commonly—in "most" places and most often—emit 4-pulse- and sometimes to a lesser extent 3-pulse-FPs, with an FP-pulse rate that is the slowest seen among all members of the *Versi* Group (**Fig. 2**)—excepting an enigmatic firefly ("Ozark") that was PM-recorded in Barry County, MO. Ozark defaulted from a flicker and emitted very slow pulses at 0.59 *quadifulgens'* rate (i. e., a pulse period ca.1.7 times longer; **Fig. 2D,** cf. **A).** FP pulse number in *quadrifulgens'* slow-pulse FPs actually varies considerably around 4: lower numbers sometimes occur early in the season and evening, when single flashes are sometimes seen (**Fig. 3**). Six- and 7-pulse FPs, as observed in the related *Ph. eureka* in Florida, have also been noted, rarely. There may be deme/regional differences in pulse-repertoires? A study by Forrest and Eubanks (1995) clarified and quantified some of this variability for an Oxford deme in northern Mississippi.

Identification of *quadrifulgens* is certain only via the 4-pulse, slow-pulse FP; fortunately, a sample of SWAT-measured pulse-intervals for comparison with the diagnostic pulse-period/temperature regression (**Fig. 4**), is usually not necessary because its slow, green pulses are distinctive (FP **pulse** period in **Fig. 4;** rate in **Figs. 5 and 6**). A pulsed-FP period regression is in **Figure 7**, its rate with two models/charts in **Figures 8 and 9**.

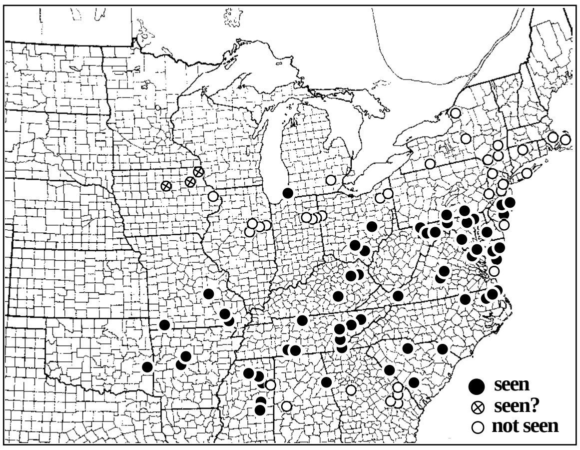


Figure 1.

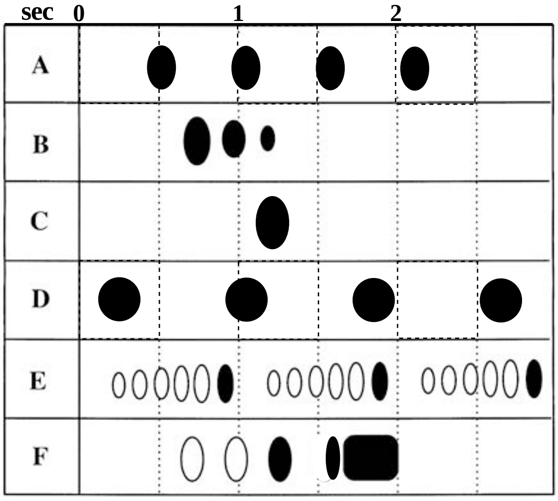


Figure 2. Much-abbreviated sampler *Versi*-group FPs.

Figure 3. Early-evening FPs with fewer pulses, near Nashville, TN.

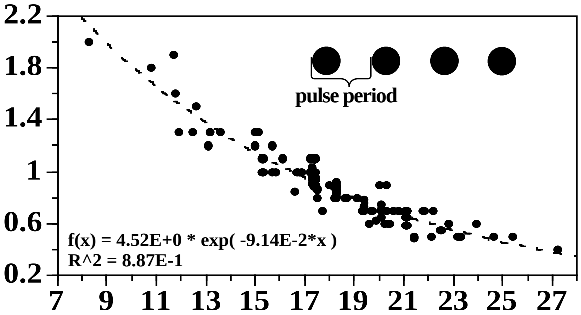


Figure 4. Pulse periods of pulse FPs (AX: sec/temp).

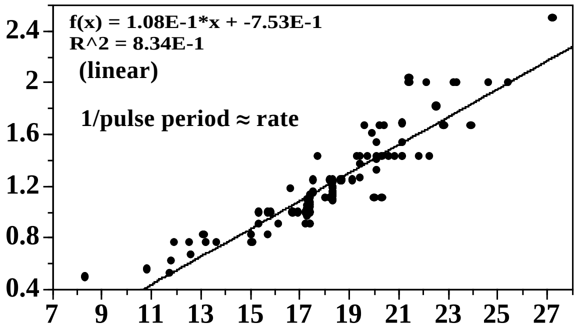


Figure 5. FP pulse rate , linear model; exponential in Figure 6 (AX: Hz/temp).

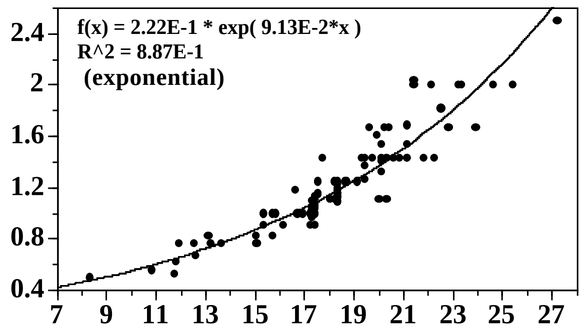


Figure 6. FP pulse rate, , exponential model (AX: Hz/temp).

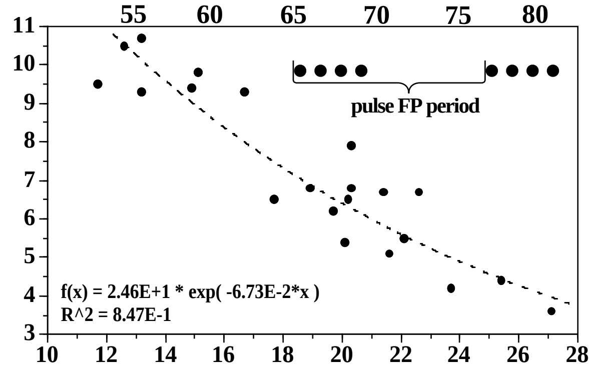


Figure 7. Pulsed-FP period (AX: sec/temp).

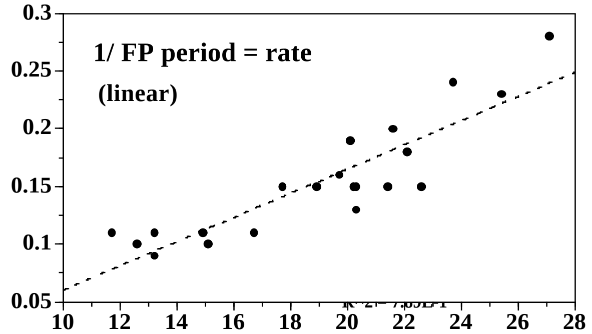


Figure 8. Pulsed FP rate, linear model (AX: Hz/temp).

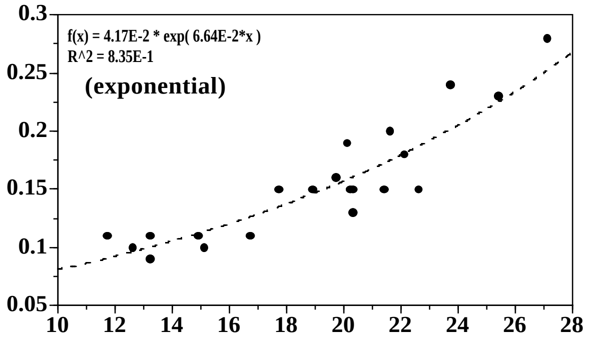


Figure 9. Pulsed FP rate, regressed on temperature via Deltagraph® program, exponential model (AX: Hz/temp).

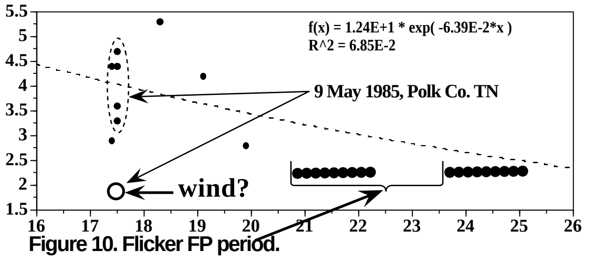


Figure 10. Flicker FP period.

A data-limited temperature regression for the flicker FP period is in **Figure 10**, rate in **Figure 11**. The flicker modulation "rate" of *quadrifulgens* is unlike those PM-recorded from other *Photuris*, which typically are very near the rates of one or another of their co-regional and sometimes co-active *Pyractomena*. In the limited, temperature-fragmented sample at hand, those of *quadrifulgens* are variable and would *appear* to be concentrated along the two (eye-drawn) lines shown (**Fig. 12**). But, these lines **do not** match those of the measured regression lines of the two presumptive *Pyractomena* models (**Fig. 13**)—which are *dispersa*, occurring a bit earlier in spring, and *angulata*, the usual/expected model. Both are sometimes seen in damp fields with *quadrifulgens*.

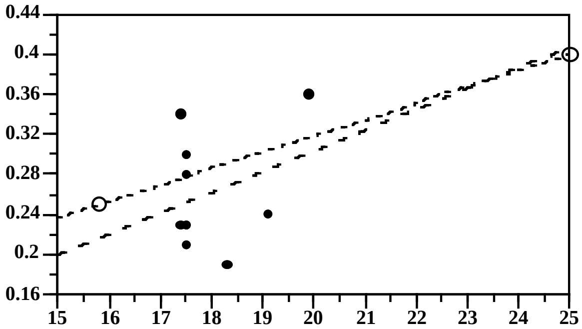


Figure 11. Flicker FP rate, dots are observations, circles are conversiosn from period regression line (AX: Hz/temp).

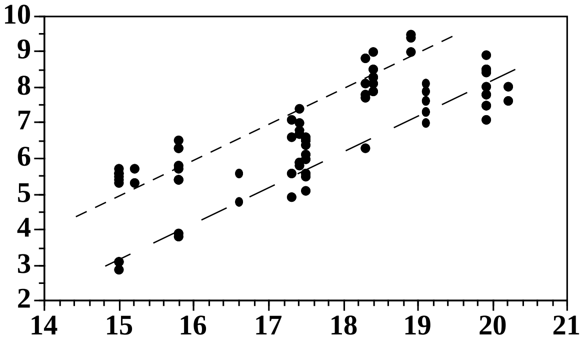


Figure 12. Flicker pulse rates (means) for all males (PM-records): number of flickers (n) for each dot ranges 1-to 14. Note the false(?) suggestion/indication of two regression lines (as drawn here by eye; AX: sec/temp).

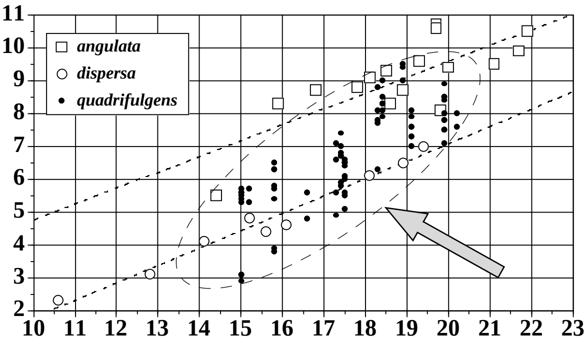


Figure 13. Pulse-rate/temperature regressions for the flickers of two *Pyractomena* with the pulse rate means of *quadrifulgens* flickers (AX: Hz/temp). Note contrary axis rotation of *quadrifulgens* recordings (dashed elipse, arrow).

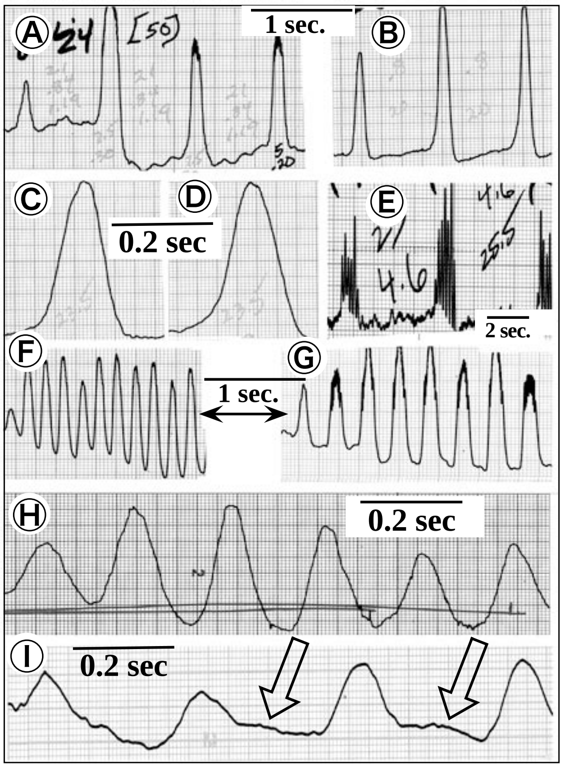


Figure 14. PM records: (A) Four-pulse FP, Appomattox Co. VA, 18.3°/65°; (B) three-pulse FP, Giles Co. TN, 18.3°/65°; (C, D) pulses from FP in B; (E) fast-flicker FPs, Polk Co. TN, 17.5°/ 63.5°; (F) part of a fast flicker FP, Appomattox Co. VA, 15°/59°; (G) part of a slow flicker FP, data as in (F); (H) part of a fast flicker FP, data as in (F); (I) part of a slow flicker FP, data as in (F). Note: compare pulse separation in (H) and (I), troughs in (I)'s are virtually flat, but apparently not completely OFFs—a clue to pulse/flicker-generation machinery (note arrows)?

This coexistence, as well as that with flickering *Ph. tremulans* is addressed in a little more detail below, as they may provide some insight in circumstances previously unappreciated. Photo-multiplier (PM) records of *quadrifulgens'* FPs, pulses, and flicker variations are shown in **Figure 14**.

When flicker-emitting *quadrifulgens* males are answered with a decoy flash they default to a pulsing FP—note that flicker-emitting males of *tremulans*, sometimes occurring in the field with *quadrifulgens*, default to a single, short flash. Decoy experiments with *quadrifulgens* gives variable defaulting results —possibly by chance, or related to its variable flicker modulation rates, or as counter-measures against hunting females of other *Photuris*, or regional differences, and/or other? For example, sometimes males responded to rapidly (erratic/twittery) decoy flicker responses, and sometimes to short flashes; sometimes they quickly approached the LED to within a few inches, but sometimes landed a foot or more from it, or left darkly. (Such experiments were few, brief, and not systematic.)

Ecology/habitat. G'SOBS records of seasonal occurrence are shown in **Figure 15**. This firefly occurs in very large numbers in agricultural and successional grassland, including hayfields, meadows, pastures, and oldfields (**Figs. 16-18**). Sites are easily spotted in season by slow-pulsing males flying a yard or so above the vegetation (**Fig. 19,** see also **Fig. 3**). Males also search around and over tree-line crowns and copses, especially within and adjacent to active grassland. Activity space and time partially overlaps that of *P. tremulans* and *P. versicolor*, presumably closely related species. Females are known predators of *Pyractomena dispersa* and probably they hunt others, certainly including *Py. angulata*, and possibly *Py. palustris*.

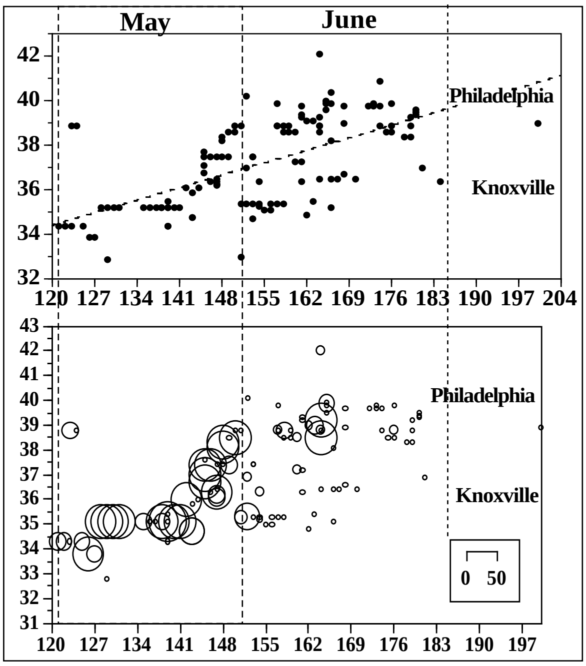


Figure 15. G'SOBS: above, all records (count); below, those quantified (amount) (<u>AX: Lat/DOY</u>).

Flicker-flashing behavior: problems—with a lagniappe? This rambling section considers questions on flashing behavior raised by the limited data at hand, and is intended to encourage focused, multi-year, regional studies of this remarkable and enigmatic firefly.

Because of its FP variability and confusing multi-pulsed FPs and flickers of green-flashing species flying with it—*Ph. versicolor* in particular, but also *tremulans* and occasionally *fairchildi* (**Fig. 20**)—it is important to be cautious in making SRSP identification. Also, because of mutual female predation, signals and signal interactions may be expected to be confusing. However, such ID difficulties are only the beginning. The really interesting and confusing *quadrifulgens* questions may actually center upon its adjunct flicker FP: Whereas adjunct FPs of other *Photuris* have been found to match fairly closely or be rather similar to FPs of other species—those often known to be prey of their females—the flickers of *quadrifulgens* have modulation rates that range broadly in frequency, and do not consistently and clearly match those of any single model, though as noted above, they overlap the modulation rates of two (please review **Figs**. **12**, **13**). Guided by the limited data at hand, and imagination, the following is an attempt to answer to some questions of interest, to encourage further examination of the situation.

Figure 16. Twilight hayfields and meadows, the real Americana; as rich in prey and predators as an African savanna, at a different scale. V. & M. Smith farm, Fairfax Co., VA, 1980s; with their passing, sacrificed to development $$$$. BMWs.

Figure 17. Hayfield site near Delano (a Gee Creek site), Polk Co., TN, in the 1980s—now only houses. Pal Bean and Guinea fowl.

Figure 18. Fields at Appomattox Civil War site, Virginia.

Figure 19. *Ph. quadrifulgens* flashes over bottomland near a stream; an oldfield a hoot 'n' holler north of Nashville, TN.

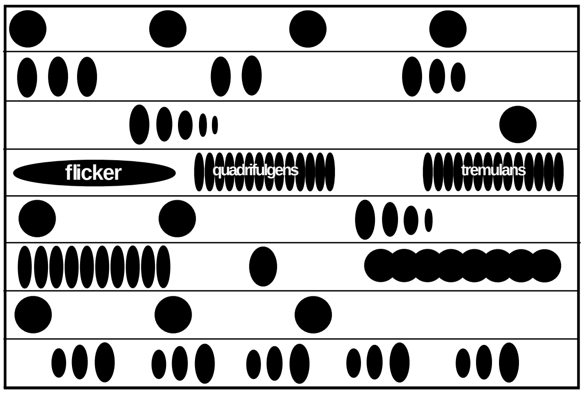


Figure 20. Array of *Photuris* FPs sometimes seen together over fields of Polk and Appomattox Counties in 1983, being emitted by males that in morphological appearance all looked to be "pretty much" the same (AX: rel. int./time).

The basic assumption on the avenue of reasoning traveled here, is that *quadrifulgens* is tuned in some way to satisfy the discrimination "circuitry"of their own hunting females, these females "being programmed" to accept the flickers of both *Py. dispersa* and *angulata*, given certain *conditions*. This argument follows from the nature of adjunct-FP tuning observed in other *Photuris* (which tuning also occurs with respect to habitat spaces, diurnal-times active, and phenology). Also, and in particular, this expectation follows from the situation observed in *quadrifulgens'* closest relative, *eureka* in Florida, which also uses "two" adjunct FPs, one being finely tuned to the FP of a *Pyractomena* species that occurs in its space and time (*Py. angustata*), and the other(s) presenting confusion apparently similar/parallel to that discussed here (see *Ph. eureka*, Chap. 312).

G'SOBS records indicate that with respect to season, *dispersa* precedes *angulata* by a little more than two weeks, but there is an overlap, increasingly so in the north (**Fig. 21**). Given the working premise that *quadrifulgens* emits flicker modulation rates that are ultimately tuned to the rates of its co-active *Pyractomena* the tactic might be: (**1**) match *dispersa's* slower rate first/early in the spring, and *angulata's* later, with individual males making the adjustment (gradual or jump?) during their lives; or (**2**) because there is not a sharp seasonal boundary separating the occurrence of the two *Pyractomena*, emit both FP rates conditionally, alternately, or according to some randomized or other program; or (**3**) use a combination of

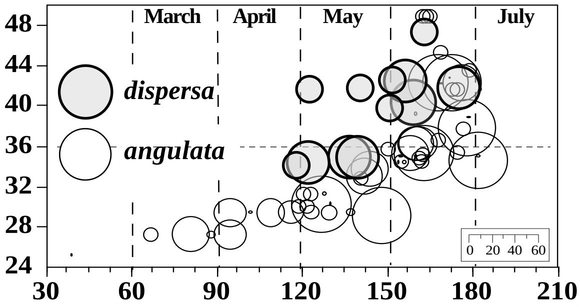


Figure 21. 3-D G'SOBS records, *dispersa* symbols atop/ over *angulata's* (AX: Lat/DOY).

these, perhaps changing the balance/ratio of the two as the season progresses. This does not exhaust the possibilities, which might include a genetic or conditional polymorphism? Or, for example, (**4**) note the regressions angles of the three species in **Figure 13;** might the steeper slope of SRSP have significance? However, given the fine-tuning of some adjunct FPs in *Photuris*, the potential abilities of monitoring/selecting females in fine discrimination cannot be doubted—nor dismissed without consideration.

The horizontal (zig-zag) lines in **Figure 22** show pulse rate variations of flickers in continuous PM-recorded sequences emitted by individual males. What can be seen in the figure is that males sometimes emit sequences with only slight rate-variation among successive FPs (a 0.5 Hz. range is indicated for one n=14 FP sequence), and sometimes rate variations are seen sufficient to jump the *Pyractomena* flicker gap (ranges of 1.4, 1.6, and 1.9 in the figure, are examples). Brackets in **Figure 23** show spans of the mentioned rate jumps for direct comparison with the *quadrifulgens* records (dots) and *Pyractomena* regressions (long dash lines). The gray "swath" has a span of 1.9 Hertz as recorded for a male in the zig-zag sample (**Fig. 22**), but greater spans, including those reaching and beyond regression lines, might be expected?

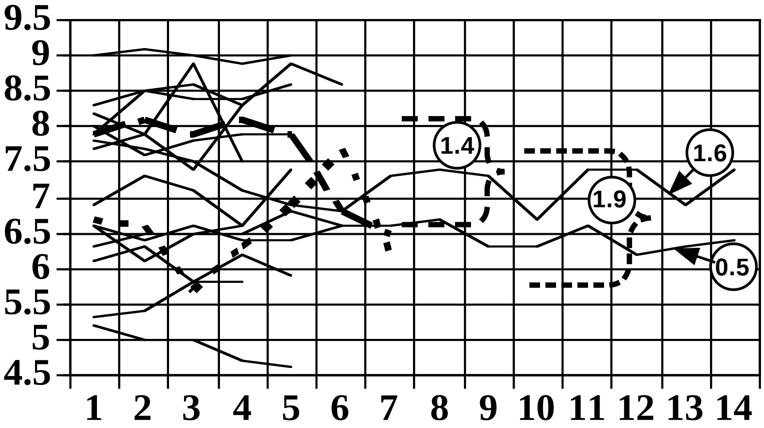


Figure 22. Lines trace consecutive flicker FPs of individual males showing FP to FP rate variation. Circled numbers show rate spans of individual males. The rate span <u>between</u> mean *angulata* and *dispersa* flickers is about 2.7 Hz across all temperatures (<u>AX: Hz/position in FP sequence</u>).

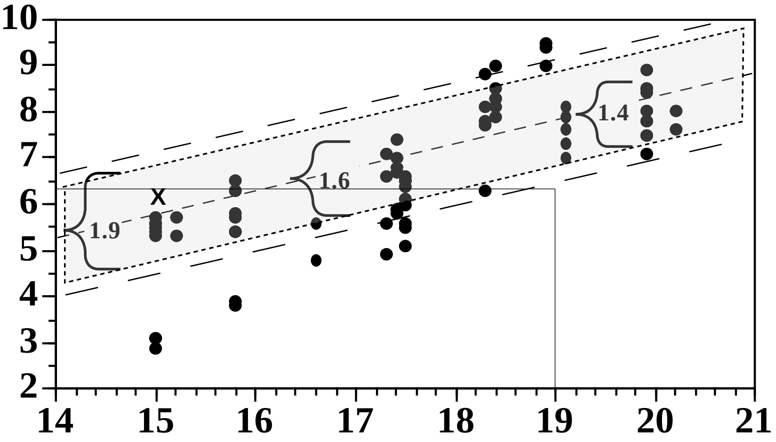


Figure 23. Flicker modulation rates (means) for all males (PM-records): number of flicker FPs (n) for each dot ranges 1 to 14 (<u>AX: Hz/temp</u>).

The dots seen well below the swath and regression lines at lower temperatures in **Figure 23** are puzzling but suggestive, maybe! *Pyractomena* species are uncommon, seemingly an archaic and vanishing group and it would seem are poorly adapted to certain intellectual/versatile *Photuris* in their midst—Neanderthal meeting Cro-Magnon? Might these dots on the chart suggest the FP of an undiscovered or recently extinct species of *Pyractomena*? Alternatively, perhaps they open another can of worms, because at 3.2 Hz/15° they find a position along the pulse-rate regression of *Photuris versicolor* FPs (**Fig. 24**). That this is a mis-ID, a recording mistake is doubtful: **Figure 25** shows that these enigmatic FPs were clearly those of *quadrifulgens* and not *versicolor*. Further, the minute' intercalated pulses in the recording would double the modulation rate to about 6.2 Hertz, a rate clearly in the *dispersa-angulata* range ("X" in **Figure 23**). There is one more point to note: In **Figure 12**, these too-low data points fall on the initial hand-drawn regression line. Pehaps by having a single, rotated slope, SRSP maximizes FP matching of the two species/rates across the temperature range and was the solution genetically available to *quadrifulgens*?

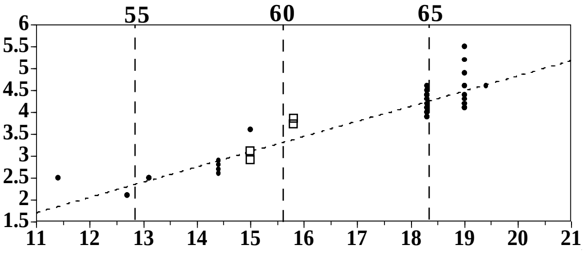


Figure 24. Modulation rate of *versicolor's* pulsed FP (dots and regression line) with unexplained PM-records of *quadrifulgens* flicker FP (squares) (<u>AX: Hz/temp</u>).

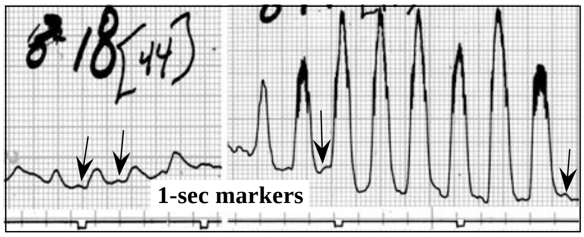


Figure 25. Very slow modulations? Note arrows, see text. Modulation rate about 3.2 Hertz (<u>AX: rel. int./time</u>). (Recorded at Appomattox River, 26 May 1983,15°/59°)

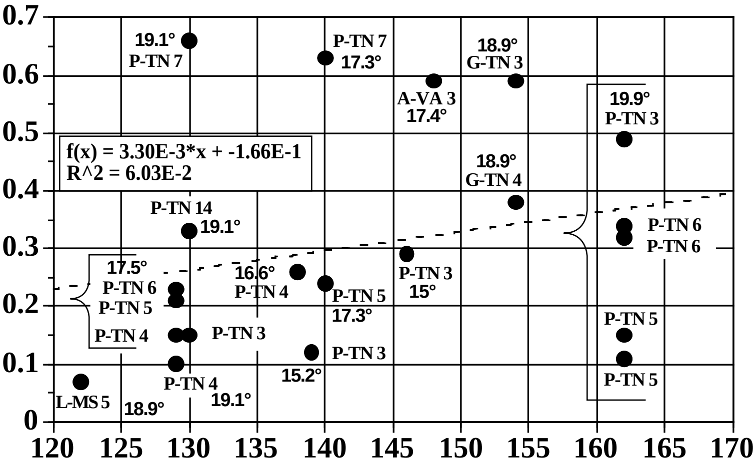


Figure 26. Rate variation among consecutive FPs (AX: sd/DOY). Dot tags show locality, number of flickers in each sample, and recording temperature: P-TN, Polk C. TN; A-VA, Appomattox C. VA; G-TN, Giles C. TN; L-MS, Lafayette C. MS.

To explore another view, if male *quadrifulgens* match the rate of *dispersa* early in the season and only later begin jumping between the rates of both *Pyractomena*, the variances of male sequences should increase through the season. When standard deviation is plotted against DOY there is scarcely/hardly a suggestion of this (**Fig. 26**), but clearly the samples at hand to answer such questions are inadequate and results perhaps biased by temperature. Instead of regressing s.d. on DOY, the coefficient of variation should have been used to eliminate temperature considerations.

Finally, the flicker modulation rate of *Py. angulata* is matched or somewhat matched by several *Photuris*, including *tremulans*. Since both *quadrifulgens* and *tremulans*, which are sometimes seen together, both use an adjunct flicker FP, what is the nature and mutual/reciprocal influence of their relationship? That question cannot now be answered directly, but G'SOBS records suggest that their seasonal peaks of activity may differ by about two weeks, decreasing toward the north (**Fig. 27**).

Taxonomic/Nomenclatural Notes. Barber's epithet recognized what he presumed the most common pattern of *quadrifulgens.* He noted a 3-flash pattern observed by McDermott in Delaware, which was certainly was that of *fairchildi* and not that of a 3-pulsing *quadrifulgens*. Barber's mention of a 3-pulse FP may indicate that he was familiar with *quadrifulgen's* variation? The suggested common name was used from early in this study; *quadrifulgens* was elevated to species rank in 1993, Barber having originally given it varietal (subspecies) status (**Fig. 29**).

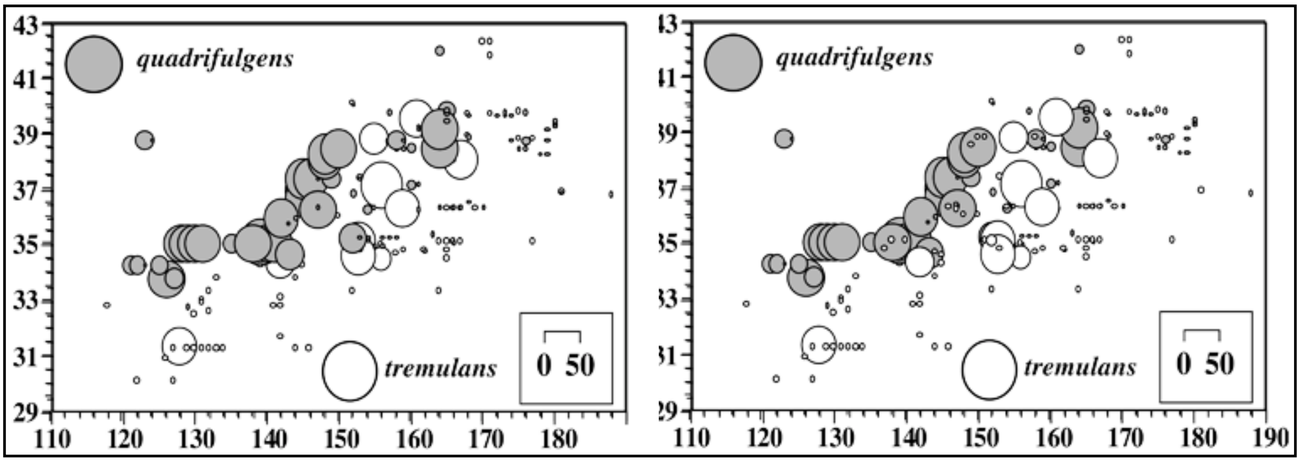


Figure 27. Overlapping G'SOBS records of *quadrifulgens* (on top at left) and *tremulans* (on top at right) showing that peak occurrence of the two (that is, the aggregate phenological peaks of demes so identified as these two species) differ by two weeks or more at southern latitudes but appear to overlap in the north (latitude/DOY).

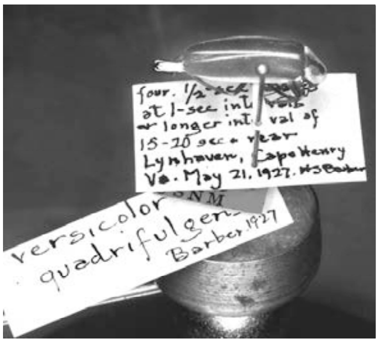


Figure 28. Barber's subspecies voucher/ type specimen.

Morphology. Size, ratios, and sclerite colors are in the Appendix; pronotal vittae of species in the Group are arranged for comparison.

❄ ❄ ❄

Appendix: Ph. quadrifulgens voucher data

quadrifulgens VA

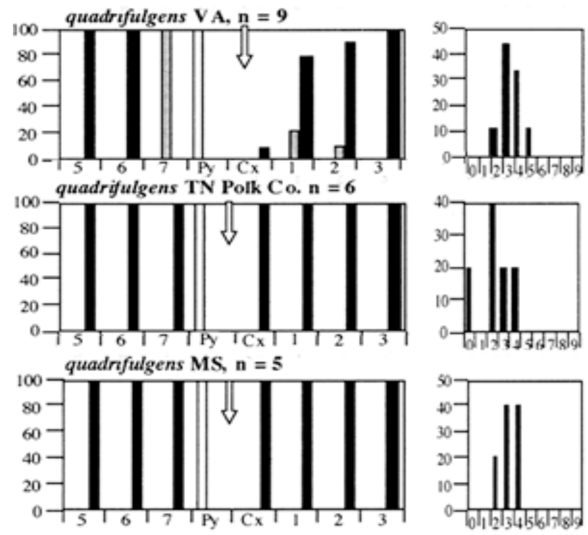
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.956	12.022	3.644	2.089	2.656	6.511	14.967	.813	1.276	.538
sd	.073	.563	.167	.136	.113	2.280	.587	.043	.066	.189
se	.024	.188	.056	.045	.038	.760	.196	.014	.022	.063
n	9	9	9	9	9	9	9	9	9	9
min	2.900	11.300	3.400	1.900	2.500	2.300	14.100	.770	1.170	.180
max	3.100	12.900	3.800	2.300	2.800	9.300	15.800	.890	1.400	.770
Vc%	2.5	4.7	4.6	6.5	4.3	35.0	3.9	5.3	5.2	35.1

quadrifulgens MS

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	3.220	12.760	4.020	2.180	2.860	8.980	15.940	.800	1.298	.690
sd	.356	.207	.164	.110	.055	1.301	.477	.075	.029	.092
se	.159	.093	.073	.049	.024	.582	.214	.034	.013	.041
n	5	5	5	5	5	5	5	5	5	5
min	2.600	12.500	3.900	2.100	2.800	7.500	15.100	.680	1.280	.580
max	3.500	13.000	4.300	2.300	2.900	10.600	16.300	.880	1.350	.790
Vc%	11.0	1.6	4.1	5.0	1.9	14.5	3.0	9.4	2.2	13.3

quadrifulgens TN

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.840	11.660	3.500	2.020	2.580	6.160	14.480	.814	1.274	.522
sd	.167	.619	.200	.110	.130	1.959	.683	.027	.064	.228
se	.075	.277	.089	.049	.058	.876	.306	.012	.029	.102
n	5	5	5	5	5	5	5	5	5	5
min	2.600	10.900	3.300	1.900	2.500	3.100	13.600	.780	1.180	.130
max	3.000	12.500	3.800	2.100	2.800	8.100	15.500	.850	1.330	.680
Vc%	5.9	5.3	5.7	5.5	5.0	31.8	4.7	3.3	5.0	43.7



Appomattox Co., VA

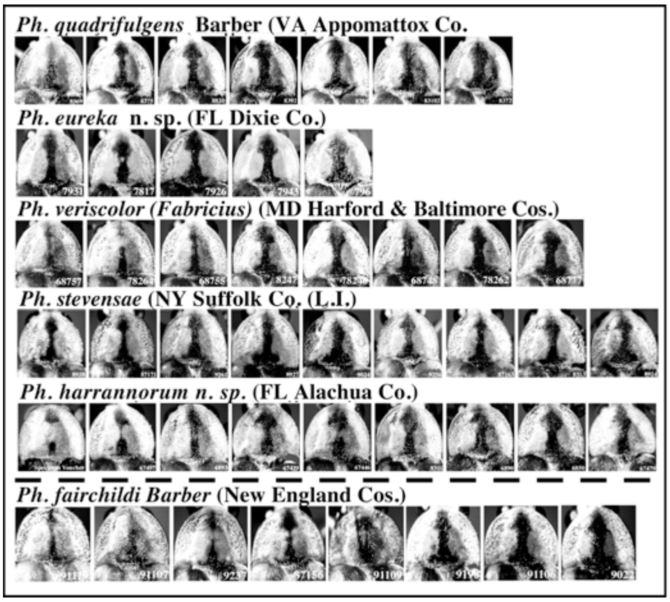
Mean	3.000	3.000	2.500	1.000	3.000	2.900	2.950	3.000	3.000
Std. Dev.	0.000	0.000	.513	0.000	0.000	.308	.224	0.000	1.124
Std. Error	0.000	0.000	.115	0.000	0.000	.069	.050	0.000	.251
Count	20	20	20	20	20	20	20	20	20
Minimum	3.000	3.000	2.000	1.000	3.000	2.000	2.000	3.000	0.000
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	5.000

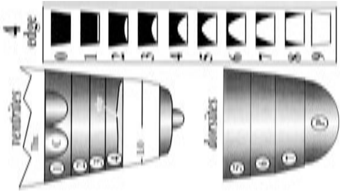
Polk Co., TN

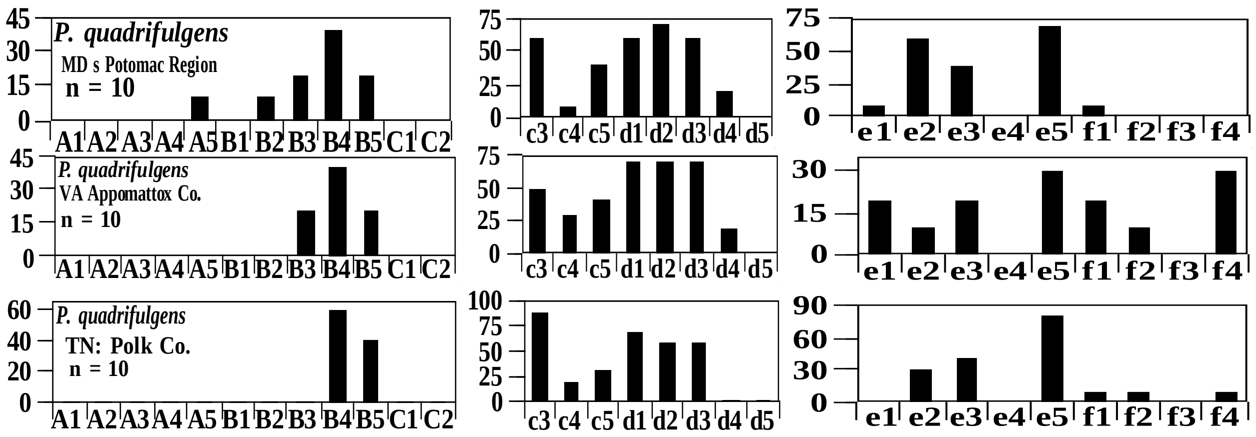
	5	6	7	Py	Cx	1	2	3	Edge
Mean	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	2.200
Std. Dev.	0	0	0	0	0	0	0	0	1.483
Std. Error	0	0	0	0	0	0	0	0	.663
Count	5	5	5	5	5	5	5	5	5
Minimum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	0
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	4.000

Lafayette Co. MS

	5	6	7	Py	Cx	1	2	3	Edge
Mean	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.200	
Std. Dev.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.837	
Std. Error	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.374	
Count	5	5	5	5	5	5	5	5	
Minimum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	2.000	
Maximum	3.000	3.000	3.000	1.000	3.000	3.000	3.000	4.000	





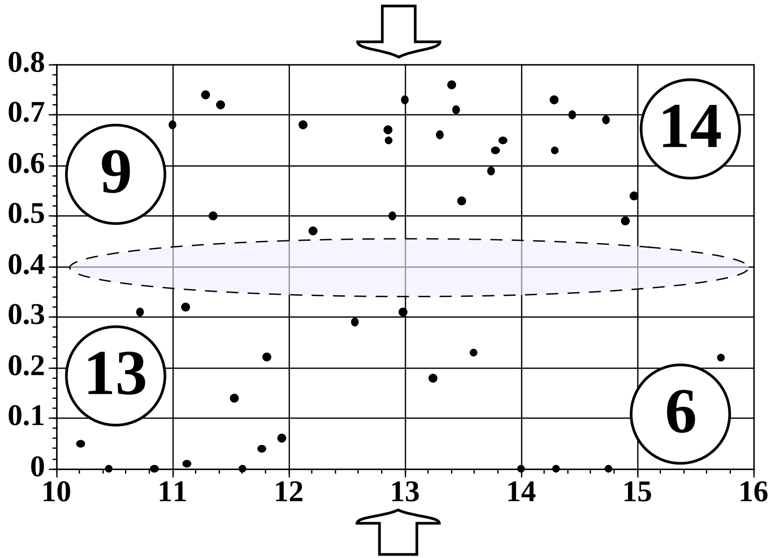


Brief Reflection On A Table of Means: Elytral Vittae

Some *Photuris* have stripes in the middle of their elytra; these are typically somewhat variable in length among members of a population. In some "species" they are much reduced or not present. Though long examined as possibly useful in taxonomy they are disappointing. The length of these "lateral vittae" was measured in hundreds of vouchers; mean ratios for several "species" are in the far right column of the table (the ratio is vitta length divided by elytral length). A general tendency seems apparent, though was not tested statistically: males of larger "species" have proportionally longer vittae than males of smaller "species," and males of larger "species" are more likely to be endowed with short or no vittae than those of smaller "species." In smaller "species" the difference noted may not be significant.

Perhaps vittae give larger insects, ones more likely to be recognized as prey, a more plant-like appearance. Experience of the past makes the suggestion that such differences are mere pleiotropy much less attractive.

alexanderi, appalachianensis, aureolucens, campestris, carrorum, chenangoa, fairchildi, hebes, katrinae, lamarcki, lloydi, lucicrescens, maicoi, margotooleae, missouriensis, penn (Mad NY), *quadrifulgens, stanleyi, stevensae, tasunkowitcoi, tremulans, versicolor*



barberi, branhami, cinctipennis, darwini, dorothae, douglasae, eureka, faustae, forresti, harrannorum, hiawassee, lineaticollis, moorei, paludivulpes, potomaca, sivinskii, walkeri, whistlerae.

SPECIES	PNLen	ELLen	PNWid	EWhum	Ewmid	ELVit	TOTLen	Pnrat	ELWrat	ELVTrat
campestris	2.83	10.6	3.53	2	2.45	8.1	13.4	0.81	1.22	0.76
lamarcki	2.5	8.76	3.15	1.81	2.39	3.46	11.28	0.8	1.34	0.74
stevensae	2.97	11.31	3.68	2.17	2.77	8.19	14.28	0.81	1.27	0.73
alleganiensis	2.48	10.5	3.13	1.9	2.45	7.7	13	0.79	1.3	0.73
carrorum	2.44	9	3.09	1.76	2.29	6.46	11.41	0.78	1.32	0.72
appalachian	2.61	10.83	3.29	1.88	2.45	7.71	13.44	0.8	1.32	0.71
fairchildi MN	2.93	11.44	3.62	2.06	2.69	8.05	14.44	0.81	1.32	0.7
lucicrescens md	3.2	11.54	3.91	2.22	2.82	7.93	14.73	0.82	1.27	0.69
hebes	2.53	9.58	3.15	1.82	2.41	6.55	12.12	0.8	1.34	0.68
lloydi	2.3	8.7	2.84	1.63	2.06	5.92	11	0.81	1.27	0.68
alexanderi	2.57	10.29	3.17	1.94	2.51	6.9	12.85	0.81	1.31	0.67
chenangoa	2.7	10.63	3.23	2.01	2.51	7	13.3	0.81	1.26	0.66
tasunkowitcoi	2.76	11.12	3.36	1.92	2.42	7.2	13.84	0.82	1.28	0.65
aureolucens	2.55	10.31	3.19	1.85	2.39	6.75	12.86	0.8	1.3	0.65
maicoi	3.16	11.14	3.93	2.08	2.65	6.95	14.29	0.81	1.27	0.63
margotoole	2.65	11.11	3.25	1.84	2.45	7.02	13.78	0.82	1.35	0.63
versicolor md	2.88	10.86	3.53	2.13	2.73	6.45	13.74	0.82	1.28	0.59
quadrifulgens	2.96	12.02	3.64	2.09	2.66	6.5	14.97	0.81	1.28	0.54
missouriensis	2.71	10.8	3.41	1.99	2.47	5.69	13.49	0.8	1.25	0.53
mad dotdash	2.51	10.39	3.09	1.83	2.41	5.21	12.89	0.81	1.33	0.5
stanleyi	2.4	9	2.95	1.75	2.26	4.55	11.35	0.81	1.31	0.5
katrinae	3.37	11.53	4.27	2.33	3.07	5.67	14.9	0.79	1.32	0.49
tremulans md	2.45	9.75	2.98	1.8	2.29	4.58	12.21	0.82	1.29	0.47
paludivulpes	2.3	8.83	2.79	1.55	2.09	2.91	11.11	0.83	1.35	0.32
potomaca	2.61	10.37	3.32	2	2.52	3.15	12.98	0.79	1.29	0.31
sivinskii	2.23	8.49	2.67	1.48	2.02	2.66	10.72	0.83	1.37	0.31
darwini	2.68	10.93	3.29	1.97	2.48	2.49	13.59	0.82	1.27	0.23
hiawassee	2.49	9.34	3	1.8	2.19	2.06	11.81	0.83	1.25	0.22
eureka	3.18	12.57	3.89	2.29	2.87	2.72	15.72	0.82	1.26	0.22
douglasae	2.78	10.47	3.38	1.98	2.46	1.94	13.24	0.82	1.25	0.18
cinctipennis	2.43	9.13	2.94	1.65	2.24	1.3	11.53	0.82	1.34	0.14
forresti	2.43	9.51	2.95	1.71	2.26	0.54	11.94	0.83	1.32	0.06
dorothy	2.31	7.99	2.71	1.51	2	0.39	10.21	0.82	1.32	0.05
moorei	2.49	9.29	2.97	1.73	2.16	0.36	11.77	0.84	1.27	0.04
whistlerae	2.43	8.7	3	1.66	2.24	0.13	11.12	0.81	1.36	0.01
faustae	3.23	11.67	3.94	2.19	2.79	0	14.75	0.82	1.28	0
lineaticol alach	3.11	11.21	3.89	2.11	2.7	0	14.3	0.8	1.28	0
walkeri	2.78	11.2	3.7	2.1	2.7	0	14	0.76	1.29	0
barberi	2.5	9.1	3	1.6	2.4	0	11.6	0.83	1.46	0
billbrowni	2.49	8.34	3.26	1.7	2.16	0	10.84	0.78	1.27	0
branhami	2.3	8.15	2.81	1.57	2.1	0	10.45	0.82	1.33	0

Figure above. "Proportional length" of elytral vittae relative to body length. Those above the hiatus (ellipse) have longer stripes. Some below have none (AX: vitta length/elytron length /// body length—i. e., ratio/total length).

A second-generation streetlight with a shield to block stray street light from entering the firefly study space across the street (to the left) beyond a hedge. UF administration said no, but in a meeting with the Plants and Grounds chief—on another matter—when the problem came to light he had better sense and got some action in a couple of days! Originally put in place in 1969 it was replaced two times over the years and served its purpose, providing dark space for fireflies, photos and study until about 1995.

Chapter 61

Photuris salina Barber 1951, and others—

Atlantic and Gulf Near-Coast Single-Flashers

Barber described *Photuris salina* from salt marshes near the mouth of the Potomac, described its habitat and flight characteristics suited to the windy coastal environment, and archived voucher specimens. A number of demes of fireflies that might easily be presumed to be *salina* were found during this study near Barber's and similar sites at various locations along the coast from New Jersey to Volusia County, Florida; then west, jumping over the peninsula to Crystal River and Cedar Key; thence north to the panhandle at a slightly more inland site in Bay County **(Fig. 1)**. Data on these populations are limited, but all emitted single, short flashes similar to those described by Barber for *salina*—an FP one would assume to be adapted to the habitat, often a damp/wet grass- and rush-shrub land with wind. Sometimes flashes were emitted at variable, searching/examining-type intervals as emitted by many grass- and herb-searching males of inland species, but at others they appeared as rhythmic trains, and a "peculiar" near synchrony of flashes was sometimes noted but not explored further. Some but not all sites were obviously brackish, while others were less clearly so. It is expected that some details in this summary may be inaccurate; voucher numbers should be cross-referenced with fieldbooks and specimens when possible. None of the demes discussed are given scientific binomens, merely informal designations.

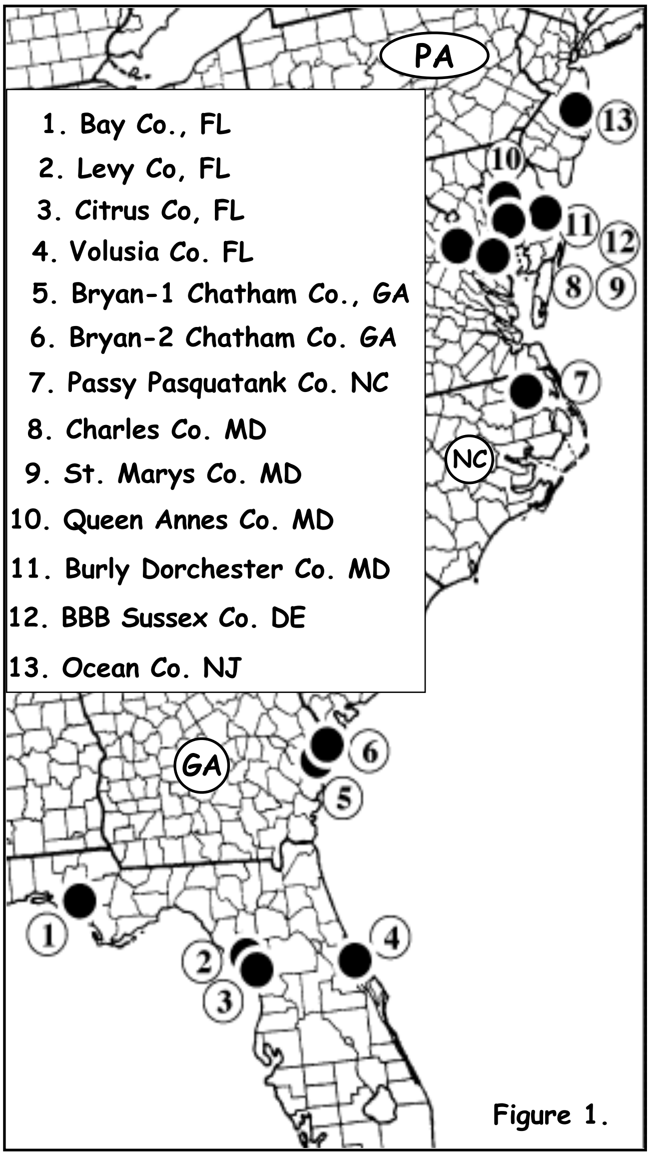


Figure 1.

When FP-period means of these demes are plotted on X/Y (period/temp.) coordinates it is seen that they might fit along three regression lines, with but few serious outliers **(Fig. 2;** see also **14, 15)**, but reality must be more complicated than this. Because of the nature of the locations of these demes, generally along thin coastal ribbons with occasional habitat breaks of varying lengths and unsuitability, sections of them may have long been independent of others. Also, some may have been derived not from a neighboring coastline, salt-marsh source, but independently from inland forms, and then become convergently adapted to local, coastal habitat conditions. At the least, one cannot be satisfied with judging as conspecific those demes that are well-separated along the coast merely because their FP intervals fall along the same or a similar temperature regression. Given the historical record of taxonomic disappointments of *Photuris* morphology, and the FPs as understood *now* being merely single, simple flashes, these coastline *Photuris* present a different kind of taxonomic problem when seeking actual *lineages*—or realistic, formal, taxonomic resolution. What follows is a sketch from fieldbooks of what was observed in this study. Closer behavioral scrutiny than reported here, and data from other methods will be required to confirm these notes and reveal genetic connections and relationships among the demes on this coastal necklace.

Ecology. First, from Barber (1951), on his *salina*: "… a small salt meadow near the mouth of the Potomac River in front of pines, hollies, oaks, *Myrica*, *Baccharis*, and *Iva* bushes, in successively more frequently inundated tidal shore line than the wetter salt marsh.—Among these bushes and straying among the nearby grass tops appear short, slightly orange [sic] flashes at 2- to 3- second intervals, but the insects keep well down where the shore breezes do not blow them away from their native habitat, thus strongly contrasting with other species visible in the woods.[p.6] … Type locality, a *Baccharis* thicket on sand spit at Sherwood Forest, 7 miles northwest of Annapolis, Md. [p. 35]" Barber vouchers, **Figure 16**.

Flashing Behavior. Barber's description generally fits that of demes mentioned here; under each there are occasional notes. These are not necessarily pertinent only to the deme being discussed. However, two features that Barber did not mention that should be noted, and remain the puzzle they were when first observed: (**1**) sometimes FPs are emitted in trains with **almost** mechanical rhythmicity; (**2**) males flying near each other sometimes emit their flashes in **near** synchrony. This is described as seen and recorded for the Crystal River deme. Subsequent examination of PM records for other sites revealed that though males flashed in "near synchrony" none were clearly "in synchrony." Rather it might be that precise synchrony was being avoided. A brief "experiment" was performed on males of the Cedar Key deme: after PM-recording a few flashes a bright light was sharply flashed to see whether males would adjust their subsequent phase to synchronize on the next cycle—a technique T. J. Walker developed in his studies of tree cricket synchrony (later adopted by others via extensive tutelage by Walker for their publications on synchronizing Asian fireflies. All that was noted here was that males delayed their next FP (**Figs. 3, 9D**), or did not flash again. Further experimentation on such male interactions on this "simple" system will be interesting as they related to mate competition. (In a New Guinea katydid males interfere with broadcasts of other males by emitting noisy (raspberry-like) pulses simultaneously with their rivals' songs; Lloyd, 1981). A detailed theoretical paper regarding flash synchrony and competition in fireflies was published by Otte and Smiley (1977).

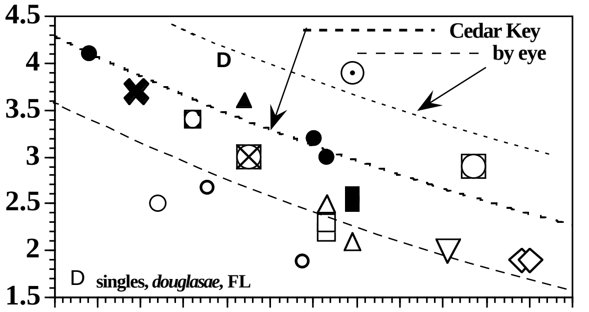
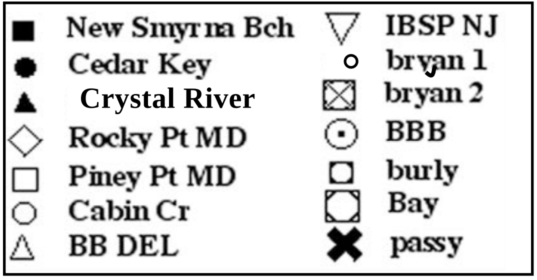


Figure 2. Mean FP periods noted.



Key to Figure 2.

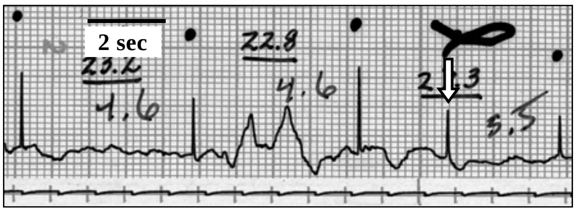


Figure 3. Male flash-train (dots above); after penlight flash (arrow) the next FP was delayed but apparently not reset to the "phase" of the intrusive flash. (3 May 1976, Cedar Key, 17.8°/64°).

Figure 4. *Ph. salina* site in southern Maryland.

Lower Potomac/Chesapeake area: Figure 4, a presumptive *salina* s. s. site on the Chesapeake; **Figure 5**, PM-records from Piney Point, MD. Measurements and various other morphological data and illustrations are in the Appendix. **Bioluminescence color**: peak: 557 millimicrons; half max. 530-598 (n=12). se Maryland, 27 May 1968 (Coll. W. Biggley). **Piney Point, MD.** (27 June 1968) FP period: x=2.2 sec, range 1.7-2.7, n=18, 23.3°/74°. Windy, fly low over marsh grass, many perched. **Rock Point, MD.** (26 June 1968) FP period: x=1.9 sec, range 1.4-2.8, n=22, 27.8°/82°. Habitat as above. Fly 1-6' over ground, just below tips of *Iva* but a

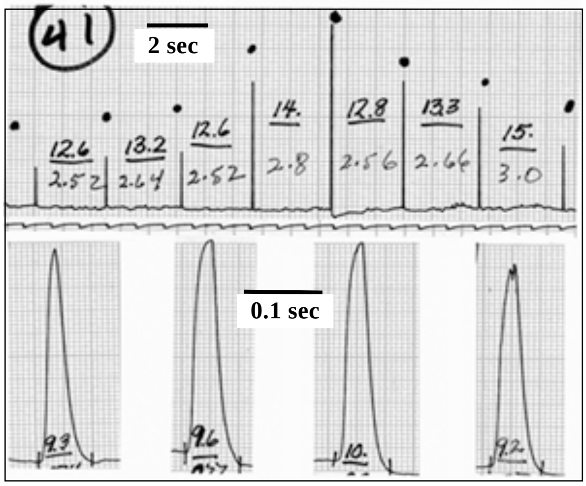
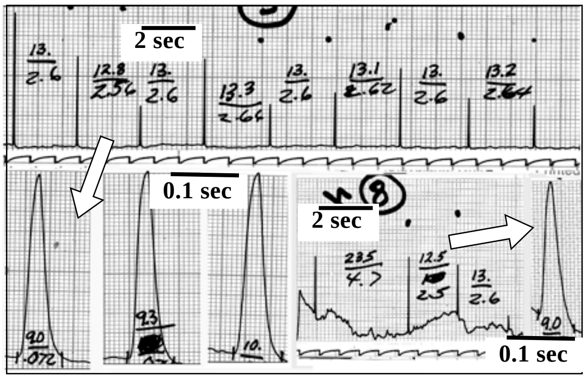


Figure 5. Piney Point MD, 27 June 1968, 23.3°/74°.

few in the open. **Cabin Creek MD.** (28 June 1968) Grasonville site; similar to above. FP period: $\bar{x}$=2.5 sec, range 2.1-3.0, n=11, 19.4°/67°. **Bethany Beach DE** (near). Two different data sets (see **Fig. 2**). Set 2 may possibly have been *P. bethaniensis*, though only single flashes were noted at the site. Florida's *douglasae* is perhaps a distant variad of this species; its single-flash FP period is **D** on the chart. The specific mileages and directions from the Bethany Beach municipality given in the fieldbook are not clear, but were within two miles, and now, five decades later, all have disappeared. **Set 1.** (29 June 1968). Wind, males fly below vegetation in short flights. Not over dunes; along moist ditches. FP period: $\bar{x}$=2.5 sec, range 2.1-3.0, n=11, 23.3°/74°. 15 July 1968. x=2.1 sec, range 1.8-2.4, n=4, ca 24°/75°. **Set 2. 15 July 1968.** Lagoon side of road, wax myrtle, *Baccharis*, ferns, damp with lush growth, grass. Fly 1-10' above 2-4' vegetation. Many but not abundant. FP period: $\bar{x}$=3.9, range 3.4-4.1, n=10, 23.9°/75°.

Figures 6. Sites at Richmond Hill, Chatham Co. Georgia.



Figures 7. On sand spit, Volusia Co., New Smyrna Beach, above perched, below right flying (23.9°75°).

Dorchester County, Maryland, (**Burly**): (13 June 1992) Rt. 335, 1 mile off Rt. 16, at small bridge with tree row, agriculture fields, thicket, and old field. . FP period: 3.5 3.1 3.5 3.0, $\bar{x}$=3.4, s=0.2, range 3.0-3.5, n=4 (20.2°/68.3°)

Ocean County, New Jersey (Island Beach St. Pk.): (30 June 1968) Route 35, 8.4 miles south of Park entrance, on a sand spit, lagoon side, about 35' from the water; emitting a single short flash, 1.8-2 seconds noted (26.1°/79°.

Pasquatank Co, North Carolina, (**Passy**): (27 May 1987) Rt. 34, one-half mile from JCT 158/34. Over ditch with cattails, between road and agriculture field. Flew at tip of cattails; near coast with coastal breezes. Not see multipulse FPs. The regression slope used here to view data points in **Figure 2** is from the slope from Cedar Key-Crystal River data and may not be appropriate for east-coast or more northern demes? FP period: $\bar{x}$=3.7, range 3.3-4.0, n=10 (18.9°/66°).

Chatham County, Georgia, two sites, Figs. 6. (**Byron 1**): Evening flashing activity began about 9 pm (22-23 May 1986). Males emitted a short, single flash each 2-3 sec of flight (nr 20°/68°), low over the vegetation, at and along the edge of a salt marsh, and up into adjacent shrubs and trees, near Richmond Hill, GA. FP period: $\bar{x}$=2.7, s=0.3, range 2.2-3.3, n=9 (20.8°/69.4°); $\bar{x}$=1.9, s=0.1, range 1.7-2.2, n=5 (22.7°/72.8°). (**Byron 2**) Flew over and amongst grasstops, 7 feet up. FP period: $\bar{x}$=3.0, s=0.4, range 2.6-3.3, n=18, (21.5°/70.7°).

Bay County, Florida (**Bay**): A small population in a low marshy area between two small rises (dunes) about one mile north of Lynn Haven, Bay County, FL, east off SR 77 (8 July 1987). Observations were made 9:45-10:15 pm. FP a very snappy flash emitted at 3 sec intervals at 26.6°/80°, while flying at 8' over the marsh and up to 10-15' in the adjacent low trees and shrubs, flashers covering 3-10' between flashes. Flight "erratic," and it was difficult to predict where the next flash would be emitted. In hand they remain motionless, did not scramble and flash as do many *Photuris*. A possible sexual attraction: male FP 15' up off tree branch 5'; FR a double flash from branch; quickly, one flash from branch (male?). FP period: $\bar{x}$=2.9, $s=0.\bar{3}$, range 2.5-3.2, n=6 (26.7°/80°.

Volusia County, Florida (New Smyrna Beach): 11 May 1967. On a spit of land 7.8 miles south of JCT Atlantic and Flagler Aves., along the road for some distance, on Indian River (lagoon) side. Single sharp flash at about 2-sec intervals, low over vegetation (25°/77°). **25 May 1968**. FP period: $\bar{x}$=2.5, range 2.1-2.7, n=13. PM-records in **Figure 7**. Males fly up to 10' but most above grass tops (4-5'); usually 2' between flashes but range 5-8'. Gusty. Males appear to synchronize flashes when within 10'; strongly phototactic. Females use landing light as seen in other species. These occur for 1-2 miles on lagoon side of road. **Morph**: Note curious longitudinal "slit/crease" in PN vitta with red from beneath visible. **Bioluminescence color**: peak: 558 millimicrons; half max. 530-599 mm (n=10).

Citrus County, Florida (Crystal Riv. Preserve St. Pk.). Along north side of Route 44 just west of Crystal Isle Campground (DeLorme© Gazetteer), >3 miles west of the municipality of Crystal River (as crow flies, not by road): 30 April 1976. Various sites along Rt. 44 across marsh with palm islands. Short flash at 2± second intervals at tips of vegetation (24.4°/76°). Males extremely phototactic and rapidly flew toward the headlamp. Though not a dense population, spaced at 10-15 feet, there seemed a tendency to synchronize, and most of the flashes occurred within a quarter-second within the 2-second FP interval. When a small portion of the population was viewed through a "peep-hole" synchrony was even tighter. This loose synchrony could easily be disrupted by waving a light rapidly, briefly back and forth over the marsh.

Levy County. Florida (Cedar Key). Site a large flat marsh near the junction of routes US-24 and C-347 a few hundred yards from open tidal areas (**Figs. 8**). Males flew low and slowly 1-3' above the top of vegetation emitting a single flash each 2-3 seconds, each 1-4', but sometimes remained motionless. A flash response from the top of a spike answered a male 2 or 3 times at ca 1-sec delay; respondent not found. FP period like that of Crystal River in Citrus County to the south (**Fig. 10**); rate in **Figure 11**. Flash form and duration regression shown in **Figures 9, 12**. SESOBS records in **Figure 13**. **Bioluminescence color (**Biggley et al**)**: peak:557 millimicrons; half max. 530-599 (n=12); Levy County, Florida, 12 May 1968.

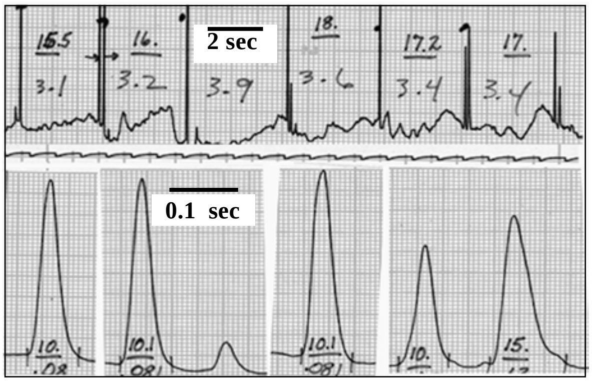


Figure 7. Crystal River, FL, 1 May 1976, 21.4°/70.5°,

Figure 8. Cedar Key site, below with flashes added.

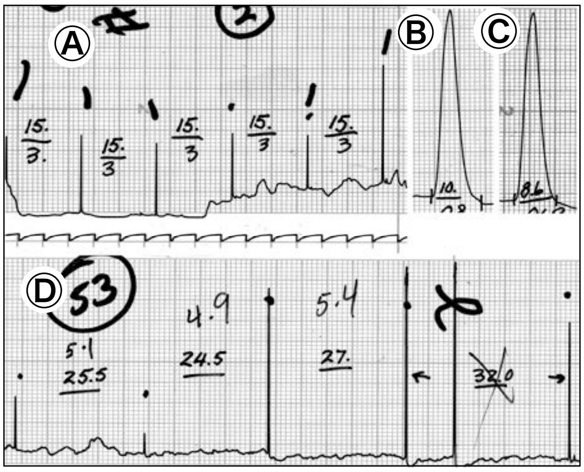


Figure 9. PM records: A-C, 23.3°/74°; D (exp.), 17.8°/64°.

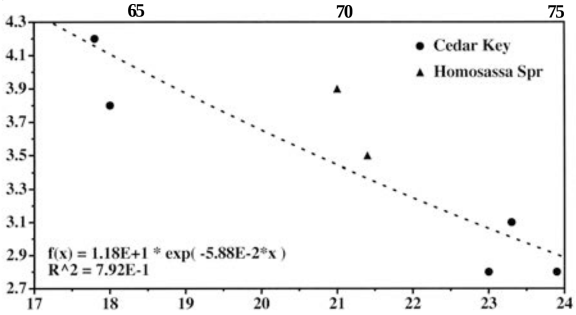


Figure 10. FP period (<u>AX: sec/temp</u>).

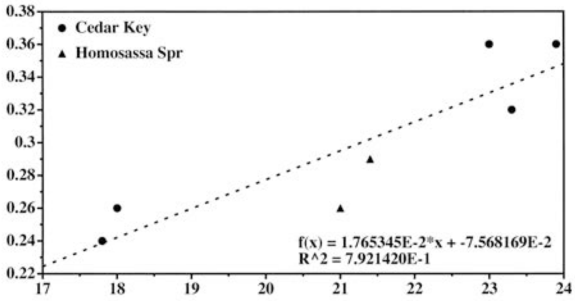


Figure 11. FP rate, individual means (<u>AX: Hz/temp</u>).

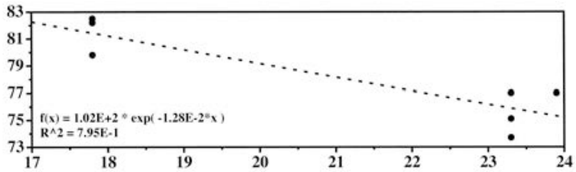


Figure 12. Flash duration (AX: mSec/temp).

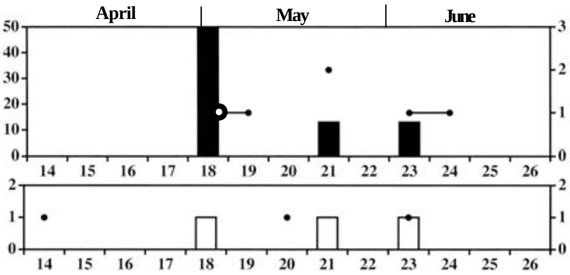


Figure 13 . SESOBS Cedar Key (AX: #/WOY).

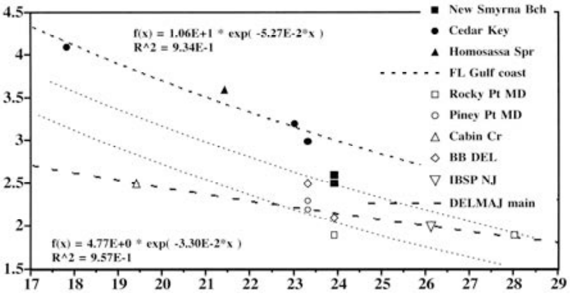


Figure 14. FP period, a different view (AX: time/temp)..

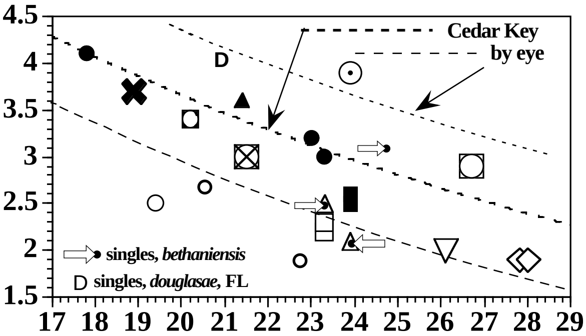


Figure 15. FP period, with similar and confusing *bethaniensis* periods shown (AX: time/temp).

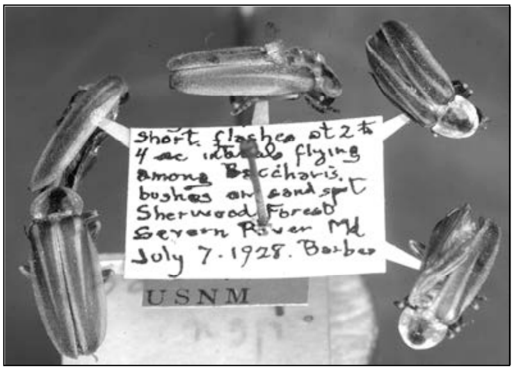


Figure 16. Barber's *salina* vouchers.

* * *

BAY

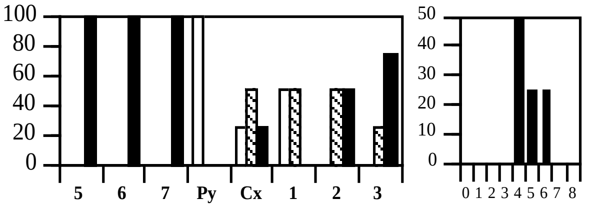
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.675	9.125	3.150	1.875	2.450	5.700	11.775	.852	1.328	.627
sd	.150	.330	.191	.096	.100	.200	.427	.031	.094	.013
se	.075	.165	.096	.048	.050	.100	.214	.015	.047	6.292E-3
n	4	4	4	4	4	4	4	4	4	4
min	2.500	8.800	2.900	1.800	2.400	5.600	11.300	.810	1.190	.610
max	2.800	9.500	3.300	2.000	2.600	6.000	12.300	.880	1.400	.640
Vc%	5.6	3.6	6.1	5.1	4.1	35	3.6	3.6	7.1	2.1

	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	3.000	3.000	3.000	1.000	2.000	1.500	2.500	2.750	4.750
sd	0.000	0.000	0.000	0.000	.816	.577	.577	.500	.957
se	0.000	0.000	0.000	0.000	.408	.289	.289	.250	.479
n	4	4	4	4	4	4	4	4	4
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	4.000
max	3.000	3.000	3.000	1.000	3.000	2.000	3.000	3.000	6.000
Vc%									

salina MD **Rock Point**

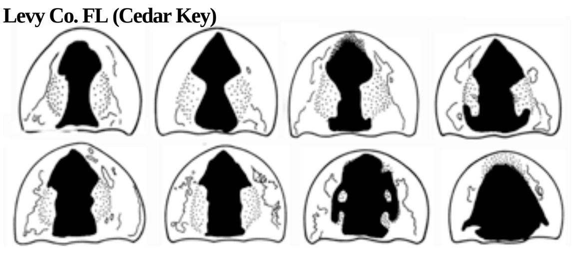
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.267	8.193	2.820	1.613	1.967	5.660	10.460	.800	1.214	.691
sd	.226	.684	.186	.160	.123	.702	.840	.055	.059	.077
se	.058	.177	.048	.041	.032	.181	.217	.014	.015	.020
n	15	15	15	15	15	15	15	15	15	15
min	1.900	6.900	2.500	1.400	1.800	4.300	9.100	.710	1.130	.530
max	2.500	9.500	3.100	1.900	2.300	6.900	12.000	.910	1.330	.850
Vc%	10.0	8.3	6.6	9.9	6.3	12.4	8.0	6.9	4.9	11.1

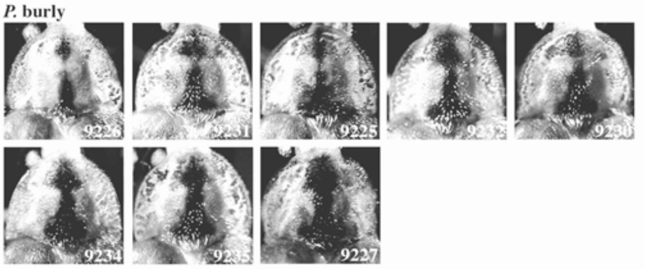
	5	6	7	Py	Cx	1	2	3	4
$\bar{X}$	2.733	2.200	1.333	1.000	1.400	1.400	1.867	2.267	5.533
sd	.458	.561	.488	0	.507	.507	.352	.458	.990
se	.118	.145	.126	0	.131	.131	.091	.118	.256
n	15	15	15	15	15	15	15	15	15
min	2.000	1.000	1.000	1.000	1.000	1.000	1.000	2.000	4.000
max	3.000	3.000	2.000	1.000	2.000	2.000	2.000	3.000	7.000
Vc%									

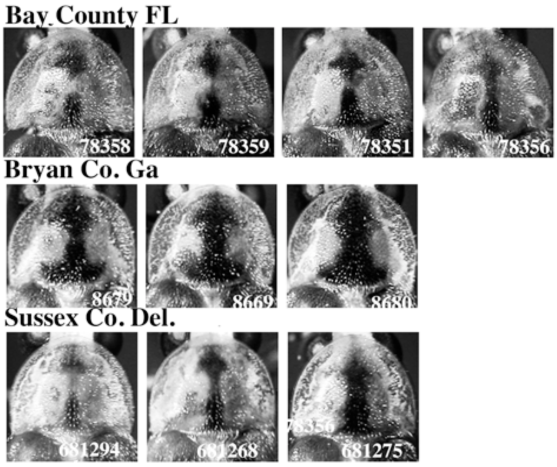


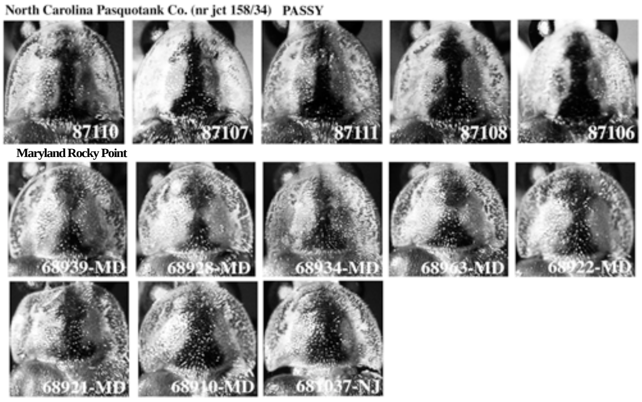
Volusia Co., FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.400	8.550	3.233	1.717	2.050	6.383	10.900	.737	1.193	.747
sd	0	.251	.288	.133	.138	.299	.276	.061	.039	.044
se	0	.102	.117	.054	.056	.122	.113	.025	.016	.018
n	6	6	6	6	6	6	6	6	6	6
min	2.400	8.300	3.000	1.600	1.900	6.000	10.600	.660	1.140	.700
max	2.400	8.900	3.600	1.900	2.300	6.900	11.300	.790	1.230	.830
Vc%	0	2.9	8.9	7.7	6.7	4.7	2.5	8.3	3.3	5.9

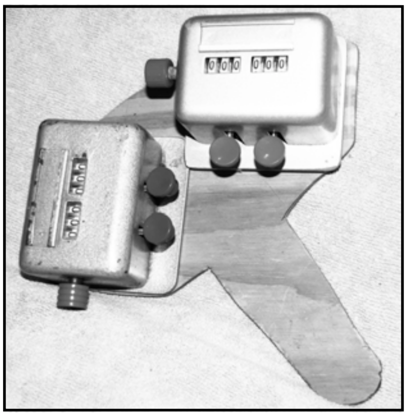

Levy Co. FL (Cedar Key)

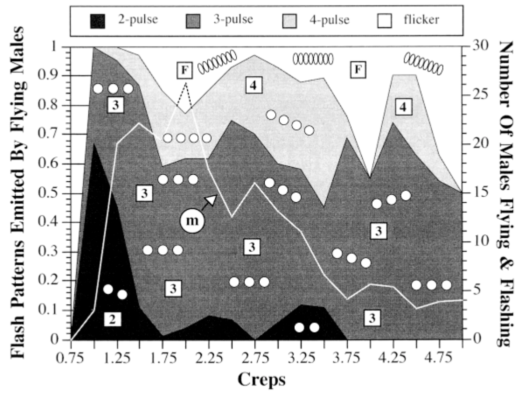

P. burly





Scan Sampling. Several *Photuris* species use different flash patterns from their repertoires at various times through an evening. This is most notable and regular in *Ph. stevensae*, and inscrutable in *Ph. tremulans*. Several species use *Photinus*-like, single, short flashes at twilight during the window of *Photinus* Division I species, and gradually switch to another FP. When studying these fireflies, scan-sampling is used to record the times of occurrence of the different FPs. Two 2-channel cell counters were mounted on a plywood "paddle" such that the thumb could reach and easily identify each separate channel in the dark (**Fig. 1**). **Figure 2** shows a two-hour sample of *Ph. stevensae* at a narrow roadside site in Putnam County, New York; the chart tracks the frequency of occurrence of four FPs and gives the total number of males flashing at each sampling moment. In sampling, each sample: (**1**) is made from the same position; (**2**) is begun with the pointing arm/hand with the paddle and eyes aimed at one edge of the area to be sampled; (**3**) is made as the body and aim is gradually rotated to view across the area to be sampled; and (**4**) counts made of the flashes in a continuing "line" of view during the rotation. Rotation rate is easily adjusted to avoid duplicating counts of individuals. Sampling intervals during an evening depended upon the situation and other projects in progress.





Chapter 62

Photuris sivinskii n. sp.

Quick 1-2

This firefly was recognized only from southeastern United States and a single locality in southwestern Missouri (**Fig. 1**). The main observation site was along a row of shrubs adjacent to a damp occasional soggy pine plantation near Waldo, FL (UF Austin Cary Forest), and elsewhere near small creeks; seemingly, demes/variads are of rare and geographically widespread occurrence (**Fig. 2**). Diagnosis requires the step-up 3-pulse FP: a series of three short and distinctly-separated flashes, always of increasing intensity (**Fig. 3, 4**), but single- and double-flash FPs are usually more common, the double being the most common, hence the suggested vernacular name. Seasonal adult flashing activity in Alachua County began in late April and ended by late June, the peak occurring in mid May (**Fig. 5**).

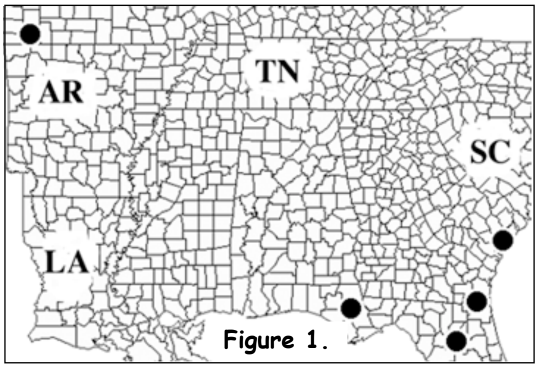


Figure 1.

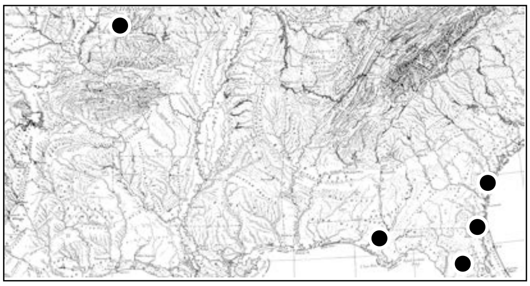


Figure 2. Physiographic perspective.

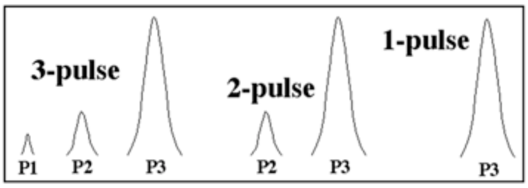


Figure 3. FP array and nomenclature.

Figure 4. Austin Cary Forest site (ACF); flash dots added.

Ecology and Flashing behavior. The primary observation site was in the UF Austin Cary Forest (ACF), near Waldo, Alachua County, at the edge of the sawmill and utility building area (**Fig. 4**), a few hundred yards inside the main entrance on SR-24. This site is northeast of Gainesville and about 5 miles northeast of the Gun Club site where *sivinskii* was seen only once —this site was surveyed hundreds of times during its season, on research visits and class field trips over a span of 40 years. For many years this site would have seemed to have been suitable, though over the past decades its damp spot with rivulet and small creek have all but disappeared.

At the ACF males flew and flashed a few to several feet above ground around wax myrtle and other shrubs separating a raised sawmill area from adjacent, lower, and often-damp pine-palmetto flatwoods; over a low and damp lawn along the shrubby border; 5–10' over palmettos in the near flatwoods (**Fig. 4**); and around and into two nearby mesic copses. At other sites, at Vouse Branch (creek) about 6 miles north of Sopchoppy FL on Rt–375, and at Roaring River State Park Missouri, males flew around trees and shrubs near small streams. Occasionally 1-flash FPs predominated; undoubtedly the presence of this species was not noted at various times and localities when males were emitting only 1-flash FPs.

Late-summer flashing was never recognized, suggesting one generation per year. Noted onsets of evening activity (n=2) were after full darkness, 72 and 83 minutes after sunset (i.e., at 2.8–3.3 creps). Activity continued for more than 3 hours, gradually diminishing, and ending after midnight (n=2). Though the key diagnotic FP consists of three step-up pulses, termed P1, P2, P3 (**Figs. 3, 6A**), early evening FPs may be mostly 2-pulse (**Fig. 6B-D**), with the 1- and 3-pulse patterns and switching among the three types perhaps occurring primarily a half-hour or so after flashing onset. At a site in Nassau Co. FL, 70 percent of the FPs counted were 3-pulsed.

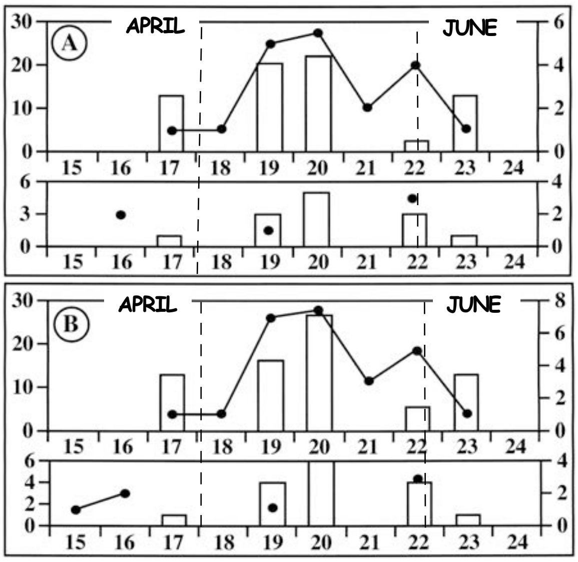


Figure 5. SESOBS: A. Alacha Co. 3 sites; B. ACF.

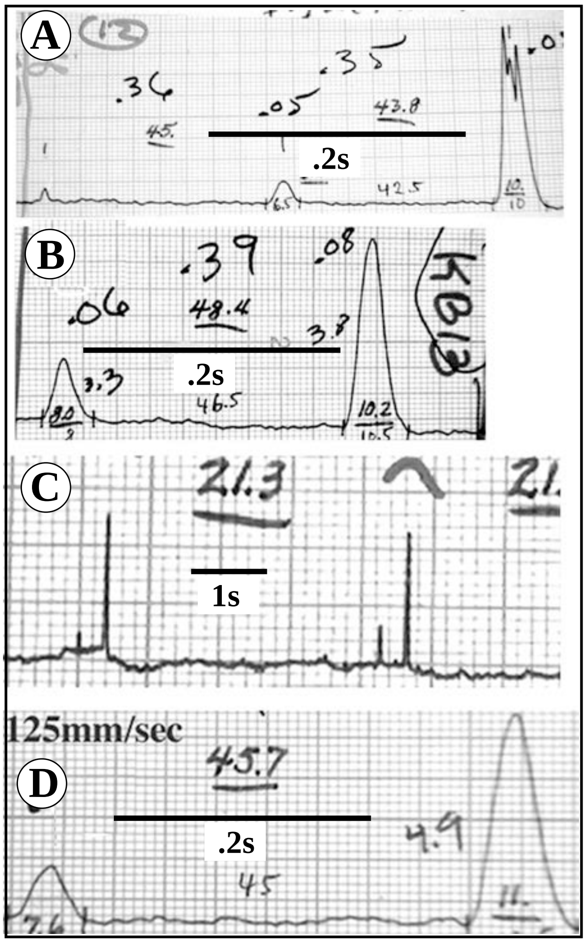


Figure 6. PM traces (A) a 3-pulse FP; (B-D) 2-pulse FPs. Note symmetry of the flashes, fall-time nearly a mirror image of rise-time. (AX: rel. int./time).

Male flash patterns (combining 1-, 2-, and-3-pulse FPs) are emitted at about 5 sec intervals at temperatures near 16.5°/61.7°, and 4 sec near 20°/68 (**Fig. 7**). The two pulse periods within 3-pulse patterns appear similar in duration, and may be identical, though one poor and questionable recording shows the first period only 61 percent that of the second: measured P1–P2 periods at 19.4°/66.9° averaged 0.35 sec (n=2), and P2–P3, 0.37 sec, s = 0.03 (n=12, **Fig. 8**). Perhaps males change pulse periods as inducement of predator error (countermeasure). A male FP with a pulse period of 0.57 sec was recorded one evening, though the periods of several others recorded at the time were about 0.43 sec.

The flash configurations of PM-recordings of 39 males were examined and measured—these data and conclusions are tentative approximations: On the single occasion when a P1 was clearly PM-detected (**Fig. 6A**) the amplitude was weak and form quality too poor to be compared reliably with P2, and P3 overloaded the PM-system—in this example, the P1/P2 amplitude ratio is 0.56). Data here are for P2 and P3 flashes—note that as convention/definition, a 2-pulse FP is composed of a P2 and P3 flash, and a 1-pulse FP is the P3.

P3 pulses averaged 3.1 times brighter than their previous P2 pulse (n = 33 patterns, of 19 males, @16.7°–19.4°), with only a weak suggestion that the increase might average slightly less at higher temperatures.

Flashes are virtually symmetrical except for the OFF-tail, where the slope appears to decrease slightly to termination, perhaps an artifact of the PM-system circuitry which, by design, slightly overrides certain amplitude changes to deal with background ambient light variation when panning. This mechanism is responsible for the tail dipping slightly below the established baseline in PM traces.

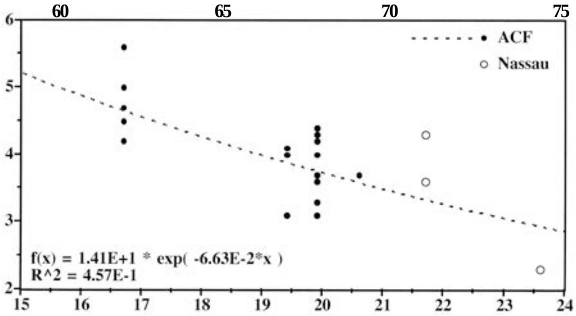


Figure 7. FP periods, various forms.

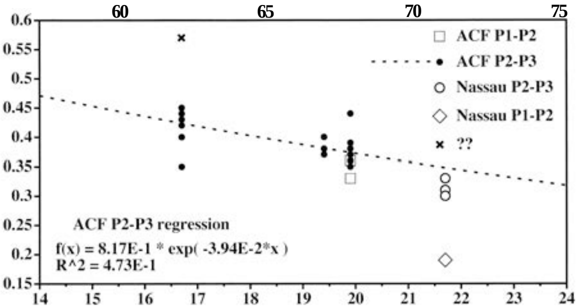
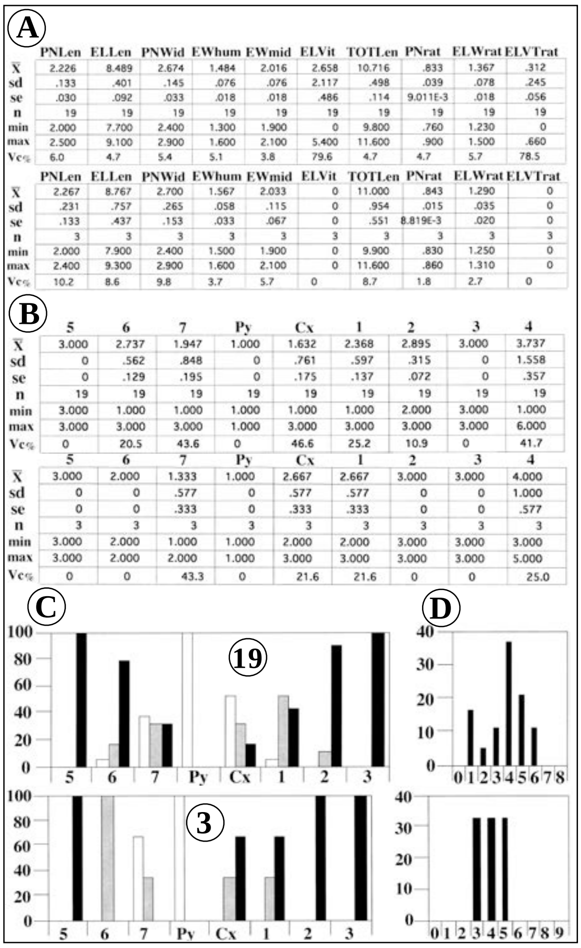


Figure 8. Pulse periods, various localities.

Flash width of both P2 and P3 measures 2.2-2.6 times greater at the base than at half max intensity (16.6°-19.7°). The P3 flash ranges 1.1–1.3 longer than P2 at both half-max and base, in the temperature range 16.7°-19.4°), with no indication that temperature effects this ratio. As example, at 16.7° mean duration of P2 at half max was 28 mSec and at base 71 mSec,



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.226	8.489	2.674	1.484	2.016	2.658	10.716	.833	1.367	.312
sd	.133	.401	.145	.076	.076	2.117	.498	.039	.078	.245
se	.030	.092	.033	.018	.018	.486	.114	9.011E-3	.018	.056
n	19	19	19	19	19	19	19	19	19	19
min	2.000	7.700	2.400	1.300	1.900	0	9.800	.760	1.230	0
max	2.500	9.100	2.900	1.600	2.100	5.400	11.600	.900	1.500	.660
Vc%	6.0	4.7	5.4	5.1	3.8	79.6	4.7	4.7	5.7	78.5

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.267	8.767	2.700	1.567	2.033	0	11.000	.843	1.290	0
sd	.231	.757	.265	.058	.115	0	.954	.015	.035	0
se	.133	.437	.153	.033	.067	0	.551	8.819E-3	.020	0
n	3	3	3	3	3	3	3	3	3	3
min	2.000	7.900	2.400	1.500	1.900	0	9.900	.830	1.250	0
max	2.400	9.300	2.900	1.600	2.100	0	11.600	.860	1.310	0
Vc%	10.2	8.6	9.8	3.7	5.7	0	8.7	1.8	2.7	0

B

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.737	1.947	1.000	1.632	2.368	2.895	3.000	3.737
sd	0	.562	.848	0	.761	.597	.315	0	1.558
se	0	.129	.195	0	.175	.137	.072	0	.357
n	19	19	19	19	19	19	19	19	19
min	3.000	1.000	1.000	1.000	1.000	1.000	2.000	3.000	1.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	20.5	43.6	0	46.6	25.2	10.9	0	41.7

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.000	1.333	1.000	2.667	2.667	3.000	3.000	4.000
sd	0	0	.577	0	.577	.577	0	0	1.000
se	0	0	.333	0	.333	.333	0	0	.577
n	3	3	3	3	3	3	3	3	3
min	3.000	2.000	1.000	1.000	2.000	2.000	3.000	3.000	3.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	43.3	0	21.6	21.6	0	0	25.0

FigTable 9. Morphological measurements, ratios, etc.

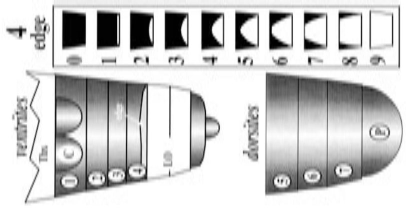


Figure 10. Key to anatomical elements, splash.

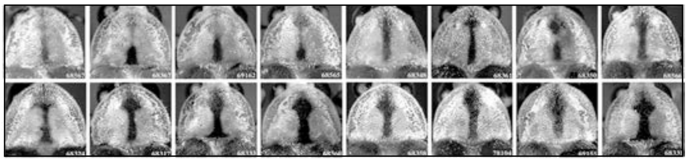


Figure 11. Array of vittagrams.

and for P3 these measurements were 34 and 90 mSec; at 19.4°C these elements measured 30 and 67 mSec and 34 and 83 mSec respectively. These comparisons and generalizations, based on measurements of only 22 flash patterns emitted by 18 males, are tentative. Recordings described were made at the ACF Holotype locality; others, from Nassau Co. FL are comparable.

Bioluminescence wavelength (color) peaks at 555, with half maxima at 529 and 595; spectrum width at half maximum is 66 mm. These data are based on measurements of the spectra of 11 males (Biggley/Seliger).

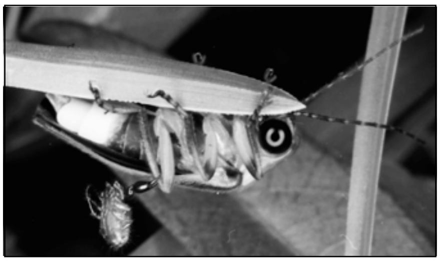
Morphological data. General morphological means are (n=19): PNL 2.2, ELL 8.5, PNW 2.7, EWhum 1.5, EWmid 2.0, ELVit 2.7, TOTLen 10.7, PNrat 0.83, ELWrate 1.37, ELVTrat 0.31 (**FigTable. 9A**-top, with other stats). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **FigTable 9B-C**-top, and the color of the pre-lantern ventrite in **9D**-top. **Figure 10** a key to skeletal plates and degree of splashing on ventrite 4. A range of pronotal vittagrams (pronotal vittae) of *sivinski* is shown in **Figure 11**

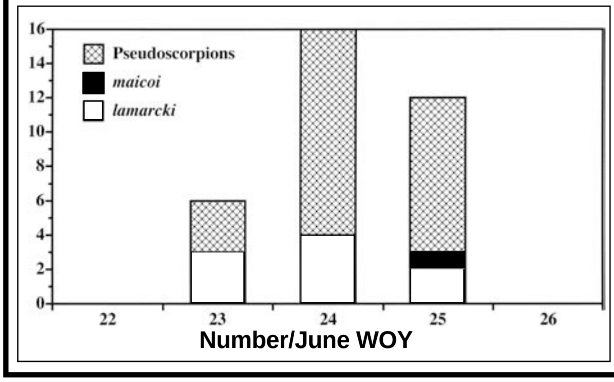
Holotype: male, voucher number 68327, collected 20 May 1968, Alachua County, Florida, Univ. Florida Austin Cary Forest, near sawmill. FB page 52: One of a series of eight, collected after emitting 2- or 3-pulse FPs; measured-series voucher numbers 68324-68329, 68332, 68333. FB note: "KB 33 a 2 and 3 flasher." Morphological data: genitalia not extruded; from spread sheet—PNLen 2.3, ELLen 8.7, PNWid 2.6, ELWhum 1.5, ELWmid 2.0, LELVit 0.0, TotLen 11.0, PnRat 0.86, ElRat 1.33, VitRat 0.0; Colors: T 321, Py 1, Cx 2, V 333, Edg 5. Types will be deposited in the USNM.

Nomenclatural note. The specific epithet recognizes one of my former PhD students, a scholar from whom I learned far more than I ever could have taught. More than this, a long-time friend, fishing buddy, co-editor on several symposia, and bright spirit at hard times.

***Paratemnus elongatus* phoresy on *Photuris*, UF Med Garden**. Among reasons that grounded *Photuris* fireflies were found blinking is that they were in the grasps of pseudoscorpions that had attached themselves, singly or in numbers, variously to firefly legs, antennae, and elytral tips. This behavior was observed only during a three-week span in June, and not noted during weeks before or after. With a single rider a firefly was able to fly; with more, flight was reduced/precluded, depending on rider number. Obviously mate-competitive ability of hosts is diminished. These arachnids live in social/family groups between the very thin sheets/layers comprising bark slabs on pine tree trunks.

Mothers care for offspring, which remain attached to them by an umbilicus (see *lamarcki*). Parasitized fireflies probably in most cases became “infected” by landing on trees with them. Perhaps the arachnids expose themselves on tree-trunks, moving from between their sheltering sheets, during the flight time of (certain) *Photuris* species? In tests with various insects confined with *elongatus*, they selectively attached to (“preferred”) fireflies. At the Med Garden the two firefly hosts were *lamarcki* and *maicoi*. Experts suggest that multiple attachments are emigrating family groups.





Chapter 63

Photuris stanleyi n. sp

Florida Tremulans

This firefly appears to be a scion of continental *Photuris tremulans* with the geographic separation between them occurring near the Florida-Georgia border (**Fig. 1**). Whether there is a zone of intergradation or region of mutual exclusion remains to be determined, but one must suspect that the same geographic/geologic events that separated certain other Florida species, such as *harrannorum* and *congener* from their apparent continental counterparts was involved. *Ph. stanleyi* is found in, along, and over woodlands and tree rows (**Fig. 2**). Its flicker FP is similar to that of continental *tremulans*, and certain other *Photuris*, both in PM-measurements and in general appearance: in flight it traces (often rapid) pulsing, bright, <one-second trails around leafy boughs of shrubs and trees. Unlike *tremulans* this firefly does not emit bright, short flashes while cruising in mate-seeking flight; instead, single, short flashes occur only inconsistently (?), when attracted males approach a decoy or responding female, that is, in a seeming or pseudo-default situation, and then were usually/sometimes of low intensity, merely weak “uncertain” blinks—at (counted) periods of 1.5-2.5 sec. Recall that continental *tremulans* more typically emits its bright short default FP, rather than the flicker for which Barber named it, as he noted. PM-records of two *stanleyi* flickers are shown in **Figure 3**. In a PM-recorded sample of 29 flickers from 19 males the mean modulation rate was 11.8 Hz. at 23.3°/73.9°; PM data in **FigTable 19**. **Figure 4** regresses the pulse-rates of *stanleyi*/*angulata* flicker FPs across temperatures; **Figures 17** "dissects(?)" these with additional computer regressions. FP period averages about 2.8 seconds at 21°/70° **(Fig. 5)**; FP period (=interval) **rate** is shown in **Figure 6**. In **Figure 7** the FP period rates of *stanleyi* and *angulata* are compared, though the biological significance of this similarity, if any, is not known.

Note that the matching (mimicry) of *angulata's* FP modulation rate by *stanleyi*—which occurs also with several continental *Photuris*, and

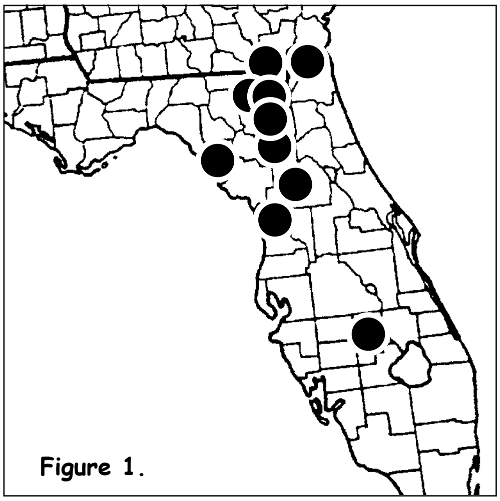


Figure 1.

Figure 2. Lake Shore Drive, Gainesville.

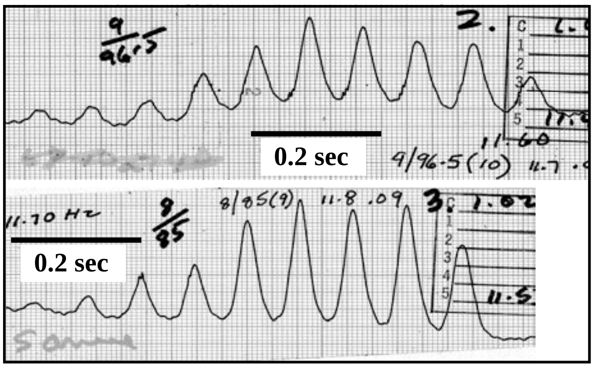


Figure 3. Flicker FP pm-records (rel. int.(AX: rel.int./time).

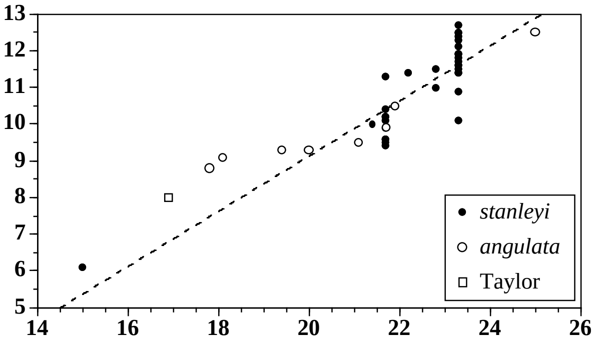


Figure 4. Modulation (pulse) rates (AX: Hz/temp).

which plays a significant role in their biology—is quite precise, compared with similar matchings (match-ups) recognized on the continent. This is because in Florida the compared PM-records are from the same region, sites in some cases, that is, where where the two occur together. In various continental matches PM data from different localities/regions must be used and *angulata's* modulation rate varies somewhat geographically.

In north-central Florida *stanleyi'*s short adult season begins in late April and extends into early June (**Fig. 8, FigTable 19**), and overlaps completely with that of *Pyractomena angulata* (**Fig. 9**); *stanleyi* females attract and eat *angulata* males (**Fig. 10; page 55**).

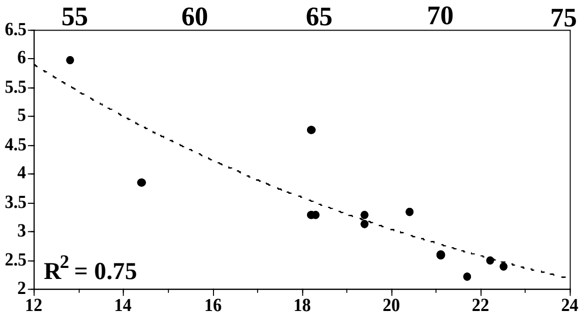


Figure 5. Flicker FP period (AX: sec/temp).

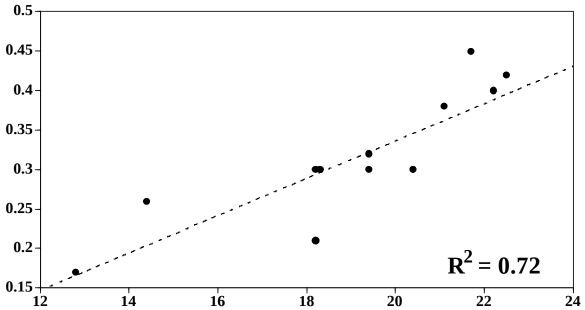


Figure 6. FP interval (period) rate (AX: Hz/temp).

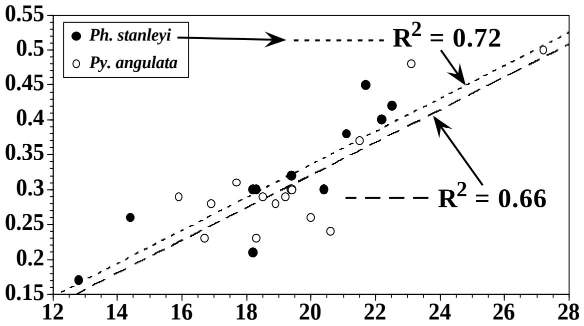


Figure 7. FP rates (i.e., periods) compared (AX: Hz/temp).

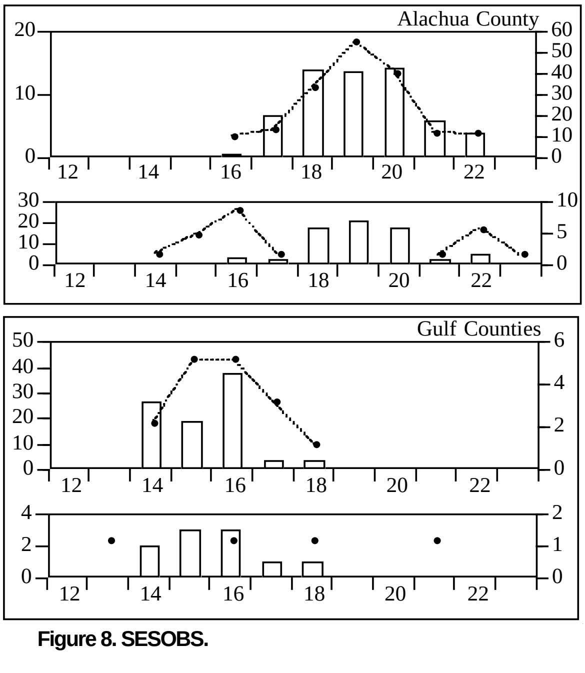


Figure 8. SESOBS.

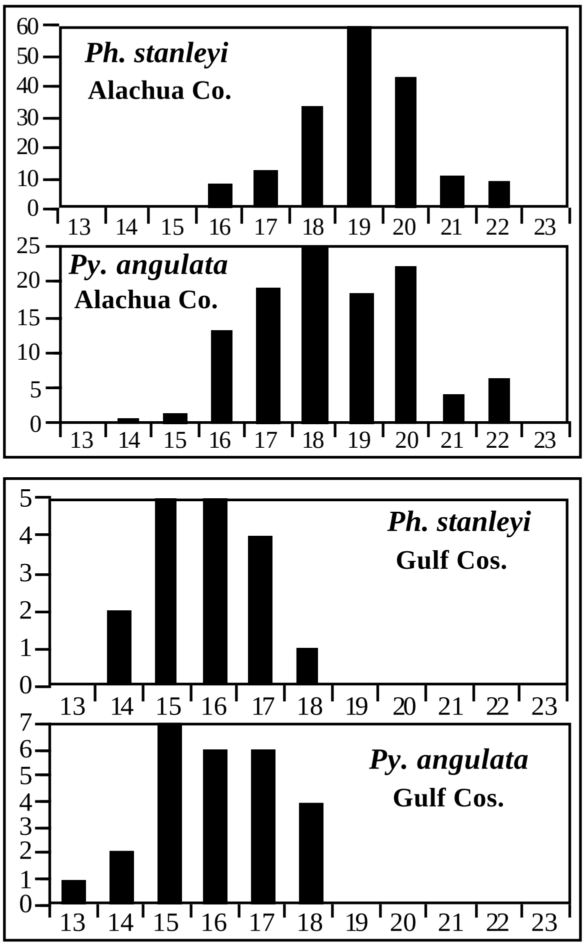
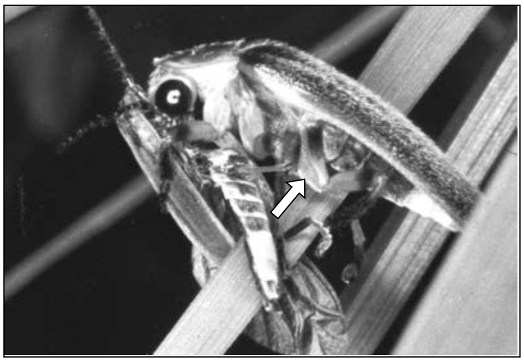


Figure 9. Comparing phenologies (SESOBS).



Figures 10. *Ph. stanleyi* female; note pale hind coxa. *Py. angulata* male;. *angulata* venter diagnostic.

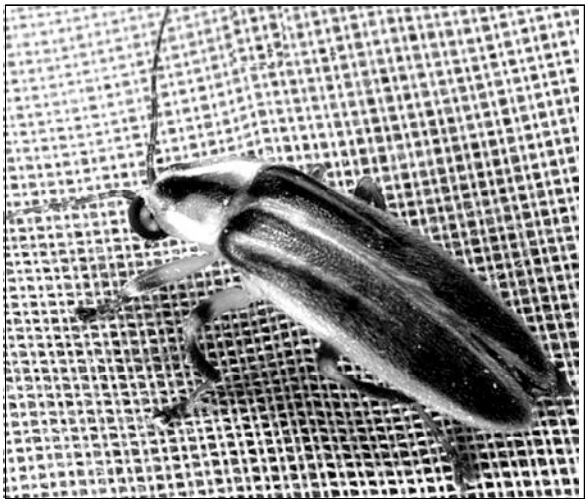


Figure 11. *Ph. stanleyi*.

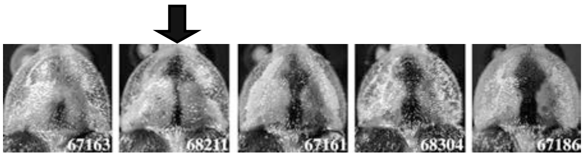


Figure 12. Array of vittagrams noted.

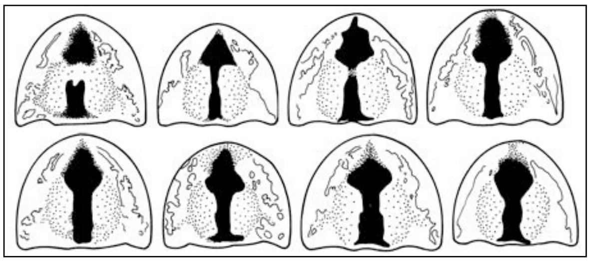
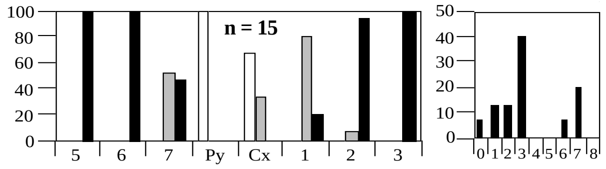


Figure 13. PN pen and ink array.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.400	8.973	2.953	1.747	2.260	4.547	11.347	.807	1.308	.503
sd	.085	.395	.099	.130	.155	1.034	.478	.028	.076	.108
se	.022	.102	.026	.034	.040	.267	.123	7.281E-3	.020	.028
n	15	15	15	15	15	15	15	15	15	15
min	2.300	8.300	2.800	1.500	2.000	2.000	10.600	.760	1.130	.240
max	2.500	9.500	3.100	1.900	2.400	5.600	12.000	.860	1.420	.640
Vc%	3.5	4.4	3.4	7.4	6.9	22.7	4.2	3.5	5.8	21.5

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	2.467	1.000	1.333	2.200	2.933	3.000	3.400
sd	0	0	.516	0	.488	.414	.258	0	2.293
se	0	0	.133	0	.126	.107	.067	0	.592
n	15	15	15	15	15	15	15	15	15
min	3.000	3.000	2.000	1.000	1.000	2.000	2.000	3.000	0
max	3.000	3.000	3.000	1.000	2.000	3.000	3.000	3.000	7.000
Vc%	0	0	20.9	0	36.6	18.8	8.8	0	67.4



FigTable. 14. Measurements, ratios, color, Alachua Co.

Figure 15.

Stan, collecting at Bear Lake outlet, 1959.

In general physical appearance *stanleyi* is much like *tremulans* and Florida's *Ph. harrannorum* (**Fig. 11**), save one distinctive character—*stanleyi's* hind coxae are pale or dusky rather than dark brown or black (**Fig. 10, arrow**)—a character that is convenient to distinguish certain working species groups in *Photuris*. Specimens are, with expected uncertainty, distinguishable from other Florida *Photuris* by a combination of characters: black elytra; pale or slightly dusky hind coxae; characteristic pronotal vittagram (**Figs. 12-13**; yellowish rather than rufus-tawny base-(trim)-coloration; and moderate size (10-12.5 mm; **FigTables 14, 20**). **Figure 21** is an anatomical and splash key. Elytral vittae, on average, terminate posteriorly from the humerus (elytral shoulder) about half the length of its elytron and range from one-quarter to three-quarters. In **Figure 11** the vitta on the left elytron ends at about 0.57, and the right vitta is somewhat shorter.

Holotype description. male; voucher number 68211; collected 9 May 1968, as it flew and emitted its flickering FP—Florida, Alachua County, Univ. Fla. campus, Medicinal Plant Garden, Field Book 1968 #1, p 56. Measurements and ratios: PNLen 2.3mm, ELLen 8.8mm, PNWid 2.8mm, ELWhum 2.3mm, ELMid 2.3mm, LELVit 4.3mm, TotLen 11.0mm, PnRat 0.82, ElRat 1.50, VitRat 0.49. Pigmentation and splash: T5-3. T6-3, T7-2, Py-1, C-1; V1-2, V2-3, V3-3, edge splash-1. Pronotal Vittigram Figure 12, arrow. Types will be deposited in the USNM.

Note: This firefly is named in honor of the late Professor Willard F. Stanley (**Figure 15**), undergraduate advisor, teacher, mentor, and friend, and Chairman of a group of outstanding and memorable teachers on the science faculty at Fredonia State College (now SUNY) during my years of attendance from September 1955 to January 1960. Others were Barbara Polacek, an algologist who persuaded me to go next to the University of Michigan, one of the best decisions of my life; Lawrence Patrie, friend, the best teacher I ever had, who taught me chemistry and geology, and shared my interest in target shooting; George Zimmer, who gave me a new perspective on science education, and Robert Boenig, friend, advisor and inspiration during my campus-school teaching, and long afterward.

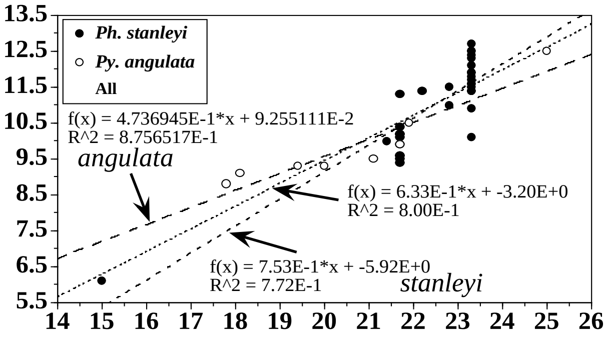


Figure 16. Modulation rate comparison, linear model (AX: sec/temp).

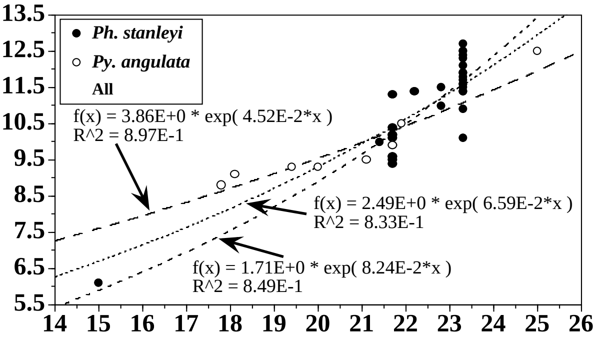


Figure 17. Modulation rates, exponential model (AX: sec/temp).

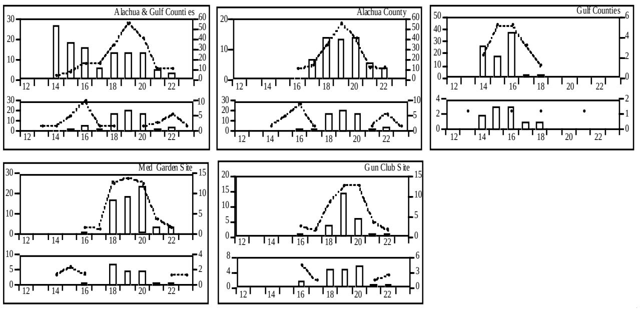


Figure 18. Regional SESOBS.

FigTable 19. FLICKER MODULATION RATE. FL Alachua Co. 1-V-68, t68-9, 21.7˚C: [1] 10.3|6 10.7|4 10.2|6; n=3, x=10.4, s=.3. [2] 10.2|5 10.2|5 10.1|5; n=3, x=10.2, s=.1. [3] 10.1. [4] 9.6|4 9.6|3 9.7|6; n=3, x=9.6, s=.1. [5] 9.8|4 10.0|3 9.9|6; n=3, x=9.9, s=.1. [6] 9.3|3 9.6|2; n=2, x=9.4, s=.3. [7] 9.6|6. [8] 9.5|4. **Grand** n=8/17, x=9.8, s=.4. **2-V-68**, 22.8˚C: [9] 11.5|6. [10] 10.9|4 11.1|4; n=2, x=11.0, s=.1. **Grand** n=2/3, x=11.3, s=.4. **22.2˚C**: [11] 11.1|7 11.7|7 11.5|7; n=3, x=11.4, s=.3. **21.4˚C**: [12] 10.0|2. **21.7˚C**: [13] 10.1|4 10.5|6 10.2|6 10.2|6 10.2|7; n=5, x=10.2, s=.2. **t68-10, 23.3˚C**: [14] 11.7|3. [15] 12.1|4. [16] 11.6|4. [17] 12.7|4. [18] 12.3|7 12.4|10; n=2, x=12.4, s=.1. [19] 11.7|6 12.0|7; n=2, x=11.9, s=.2. [20] 11.8|5 11.4|3; n=2, x=11.6, s=.3. [21] 12.5|7. [22] 119|6. [23] 12.5|3. [24] (KB42) 11.4|9. [25] 11.5|9. [26] 12.3|7. [27] 12.0|8 11.7|4 11.8|8 11.8|7 11.7|7; n=5, x=11.8, s=.1. [28] 11.8|5 11.9|8; n=2, x=11.9, s=.1. [29] 11.4|6. [30] 10.9|3. [31] 10.2|6 10.0|5 10.1|5; n=3, x=10.1, s=.1. [32] 11.4|3. **Grand 23.3˚C**, n=19/29, x=11.8, s=.6. **21-V-68**, t68-11, 15.0˚C: [33] 6.2|4 6.0|3; n=2, x=6.1, s=.1. **23-V-68**, t68-11, 21.7˚C: [34] 11.5|3.

stanleyi Alachua Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.400	8.973	2.953	1.747	2.260	4.547	11.347	.807	1.308	.503
sd	.085	.395	.099	.130	.155	1.034	.478	.028	.076	.108
se	.022	.102	.026	.034	.040	.267	.123	7.281E-3	.020	.028
n	15	15	15	15	15	15	15	15	15	15
min	2.300	8.300	2.800	1.500	2.000	2.000	10.600	.760	1.130	.240
max	2.500	9.500	3.100	1.900	2.400	5.600	12.000	.860	1.420	.640
Vc%	3.5	4.4	3.4	7.4	6.9	22.7	4.2	3.5	5.8	21.5

Alachua Co.

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	2.467	1.000	1.333	2.200	2.933	3.000	3.400
sd	0	0	.516	0	.488	.414	.258	0	2.293
se	0	0	.133	0	.126	.107	.067	0	.592
n	15	15	15	15	15	15	15	15	15
min	3.000	3.000	2.000	1.000	1.000	2.000	2.000	3.000	0
max	3.000	3.000	3.000	1.000	2.000	3.000	3.000	3.000	7.000
Vc%	0	0	20.9	0	36.6	18.8	8.8	0	67.4

Highlands Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.492	8.925	2.900	1.750	2.225	5.392	11.417	.859	1.287	.604
sd	.131	.469	.154	.138	.136	.807	.539	.051	.072	.095
se	.038	.135	.044	.040	.039	.233	.156	.015	.021	.027
n	12	12	12	12	12	12	12	12	12	12
min	2.300	8.100	2.600	1.500	2.100	3.900	10.500	.780	1.200	.440
max	2.800	9.800	3.100	1.900	2.400	6.500	12.500	.950	1.420	.720
Vc%	5.3	5.3	5.3	7.9	6.1	15.0	4.7	5.9	5.6	15.7

Highlands Co.

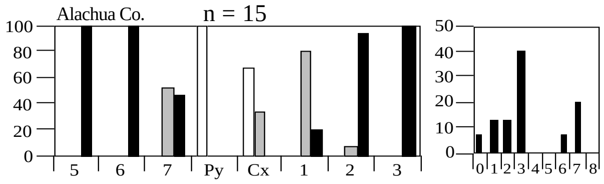
	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	2.667	2.167	1.000	1.417	1.750	2.500	3.000	3.750
sd	0	.492	.718	0	.515	.754	.522	0	.965
se	0	.142	.207	0	.149	.218	.151	0	.279
n	12	12	12	12	12	12	12	12	12
min	3.000	2.000	1.000	1.000	1.000	1.000	2.000	3.000	2.000
max	3.000	3.000	3.000	1.000	2.000	3.000	3.000	3.000	5.000
Vc%	0	18.5	33.1	0	36.3	43.1	20.9	0	25.7

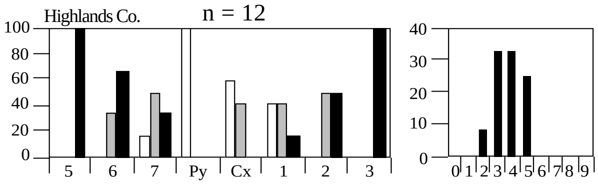
Med Garden, UF campus

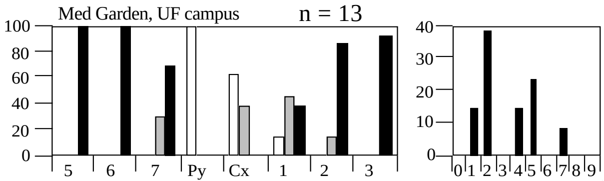
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.438	8.892	2.931	1.731	2.262	4.623	11.315	.834	1.321	.519
sd	.119	.608	.118	.132	.189	1.031	.689	.035	.119	.122
se	.033	.169	.033	.036	.053	.286	.191	9.841E-3	.033	.034
n	13	13	13	13	13	13	13	13	13	13
min	2.100	7.900	2.800	1.500	1.900	2.000	10.000	.770	1.210	.240
max	2.500	9.800	3.100	1.900	2.600	6.100	12.300	.910	1.620	.770
Vc%	4.9	6.8	4.0	7.6	8.4	22.3	6.1	4.2	9.0	23.5

Med Garden, UF campus

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	2.308	1.000	1.385	2.231	2.846	2.923	3.231
sd	0	0	.480	0	.506	.725	.376	.277	1.878
se	0	0	.133	0	.140	.201	.104	.077	.521
n	13	13	13	13	13	13	13	13	13
min	3.000	3.000	2.000	1.000	1.000	1.000	2.000	2.000	1.000
max	3.000	3.000	3.000	1.000	2.000	3.000	3.000	3.000	7.000
Vc%	0	0	20.8	0	36.5	32.5	13.2	9.5	58.1







FigTable 20. Regional morphological stats.

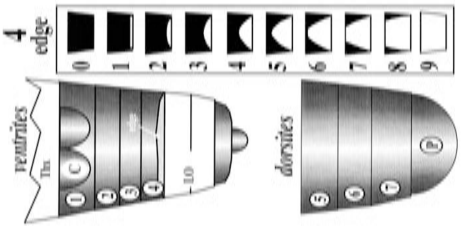


Figure 21. Key to anatomical elements, splash.

Chapter 64

Photuris stevensae n. sp.

Nettie's Firefly

This is one of two *Photuris* species in New England known to emit FPs of several pulses, and the only one known to occur on Long Island—though a dot-dasher (*pensylvanica group)* occurs in both regions. The *stevensae* range extends from the Bronx (NYC) northward along the east side of the Hudson River to Putnam County, east across central Massachusetts, and south to New London, CT; it was not found west of the Hudson nor on Cape Cod, but occurs just west of the Canal in Plymouth County, MA **(Figs. 1, 2**). This firefly flew over oldfields, hayfields, and moist grassland, but, and not surprisingly, was not seen over acres of sod farms. Long Island presents the more difficult firefly situation, with high human density and high levels of skyglow illumination (**Fig. 10**). Historically, the grassland and successional nature of Long Island east of Queens/Nassau Counties (Spinzia et al. 1991, Cronon 1991), probably produced large numbers of this firefly. Both the ocean-side of the island and the northern half, the latter once with firefly-friendly family-farm agriculture, have lost much habitat. Islands of green space along the length of the island, the LIE Archipelago (below), could if appropriately tended could perhaps provide an enduring chain of suitable habitat.

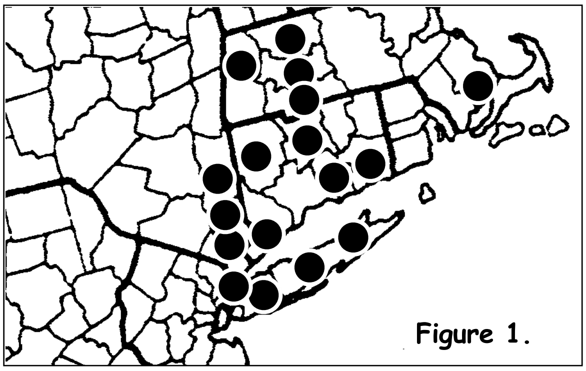


Figure 1.

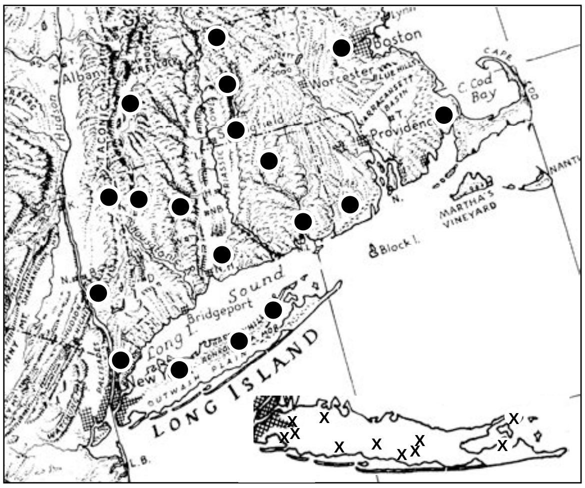


Figure 2. Physiographic distribution (see Adjunct Legends).

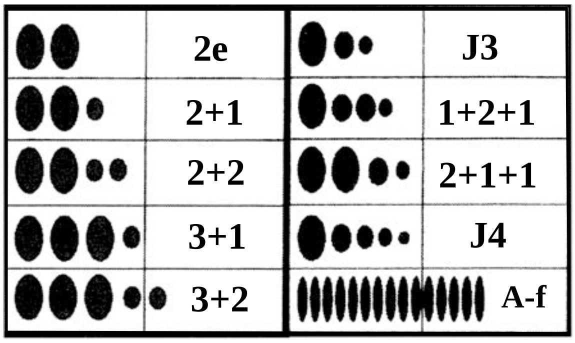


Figure 3. An abbreviated array.

Males emit an array of pulsed FPs (**Figs. 3, 21**) and an "≈A-flicker" with a pulse rate that sometimes approaches the slower rate of *Py. dispersa* (D-flicker). SESOBS records are from visits to L.I. and N.E. during six summers, from early June to early July (**Figs 4, 48**). Pulsing-FP periods and flicker-FP periods are temperature dependent and similar if not identical (**Figs. 5**, **6**). For positive diagnosis a multi-pulsed FP is necessary (**Figs. 3, 21**), and no other fast-flickering species with green luminescence is known to occur within *stevensae's* range—males of *fairchildi,* a similar species, were never observed to emit a flicker FP, from MN to AR, and VA to Nova Scotia. When emitting this flicker *stevensae* males will always default to a pulsing FP when answered with a female-like decoy flash. In continental (N.E.) populations some FPs of *fairchildi* may be confusing; the two species may be distinguished in the field by the following: (**1**) *stevensae* FPs are separated by a rather distinctive *pause*, whereas FPs of *fairchildi* are presented in hurried (*eye-catching*) succession; (**2**) *stevensae* FPs only rarely consist of more than 5 pulses, where-as the FPs of *fairchildi* sometimes, say in large open-field populations, may have 7 or more pulses (<18). (**3**) Finally, but less useful for identification, the pulses of *fairchildi* commonly appear to be of equal intensity (though actually intensity *increases* during each FP), but those of *stevensae* often have various *decreasing* intensity configurations (**Figs. 3, 21**). Note also, populations of *stevensae* nearly always have some proportion of males emitting a flicker (*tremulans*-like) FP (see below). No flashing distinction between L.I. and New England *stevensae* was noted, except perhaps on L.I. the J3 (1+1+1) FP may be less common (**Figs. 3, 21**).

Ecology. Because of the continued and considerable loss of natural and pastoral space on Long Island, it is important to record the firefly situation there as it existed in the late 1980s-early 1990s. These notes are not suggesting that these populations were all that remained, but rather as examples of places they were found. In Nettie Marie Stevens' time—early 1900s, when she worked on firefly genetics at Cold Spring Harbor

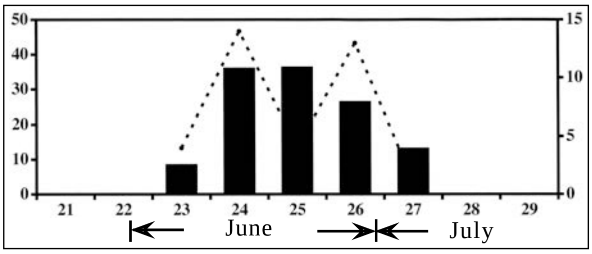


Figure 4. Synopsized SESOBS record (AX:no/WOY).

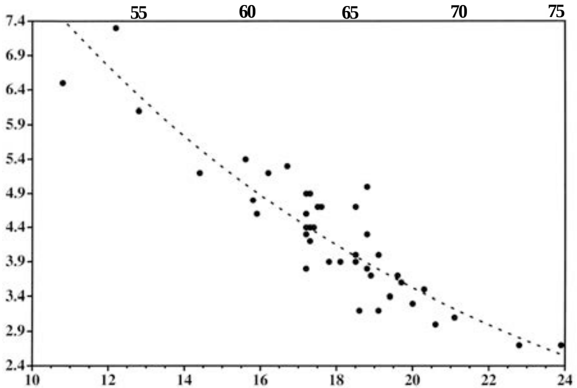


Figure 5. Pulsing FP period (AX: sec/temp).

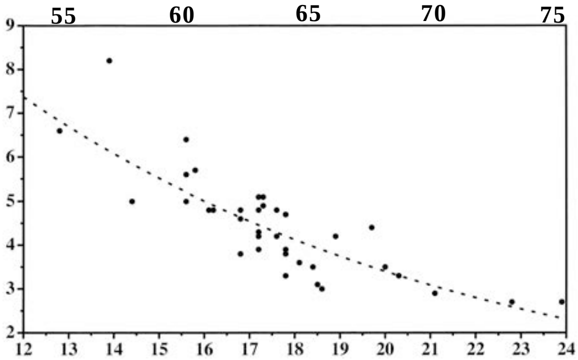


Figure 6. Flicker FP period (AX: sec/temp).

Harbor—*stevensae* must have been present in uncountable millions—it and others then went by the name "*pennsylvanica*." In this study, large populations were found in Suffolk County in old fields at Peconic, north of Route 48 at Mill Lane (**Fig. 7**), and on the then-developing Shoreham Nuclear Plant site, immediately north of Route 25A, near Wading River (**Figs. 8-10**). Small populations flew over the wooded lawn of an old farmhouse on Old Country Road and roadside areas on Old North Road (**Figs. 11**, **12**.), over an active farm pasture on Moriches Road, over a coastal "scrubby and marsh" area at the junction of Moriches and River Roads—where flicker modulation frequency approached that of *Py. dispersa* (**Fig. 13**), and at Greenport, in a early-shrub-stage oldfield and at the edge of a woods by a pond. Few FPs were seen in a scrubby re-growth area adjacent to Smithhaven Mall just east of Centereach, and high along tree-lined highways at various locations along the Sound, west of Sound Beach. In Nassau County it occurred near East Norwich over mowed grass and adjacent trees and shrubs at a horse training area in a wildlife refuge, and near Upper Brookfield where it flew at the edge of an unkempt lawn and over adjacent hedgerows and conifers of an abandoned mansion.

In the Bronx it flew in trees at the edge of the Pelham Bay Golf Course parking lot; it was not seen during an overnight

Figure 7. Peconic site.

Figure 8. Shoreham site.

Figure 9. Shoreham site.

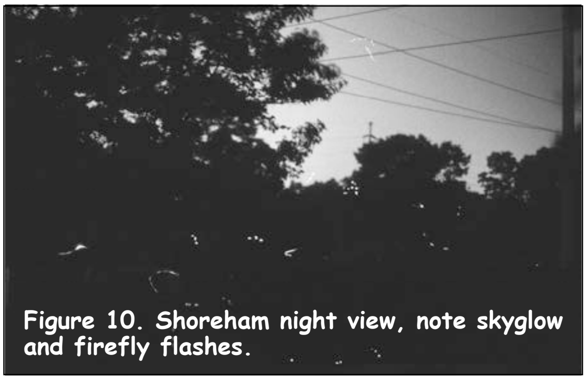


Figure 10. Shoreham night view, note skyglow and firefly flashes.

Figure 11. Old North Road site.

Figure 12. Farmhouse dooryard, as Nettie Stevens might remember it.

Figure 13. Moriches and River Roads site.

Figure 14. Near Avon CT, Old Farm Road.

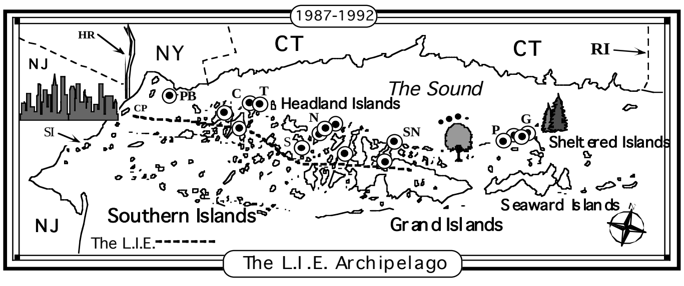
Figure 15. Norwich CT site.

stay in an enclosed natural area on Staten Island at the Museum. In Putnam County, NY a small population occurred along route 301 across from Canopus Lake in a narrow scrub area just below the road. Near Avon, CT, on Old Farm Road observations were made in a shrubby old-field on a hillside sloping down to scrubby woods (**Fig. 14**). West of Norwich, CT (near I-395 exit 80), a large population was observed and photographed (**Figs. 15-16**). PM-recordings were made at several of the mentioned sites. Certainly there must be populations west of the Hudson River and *stevensae* traffic westward across the Hudson River but in brief searches none were found.

Figure 16. Norwich, CT site.

Figure 17. Smithtown bridge, looking upstream.

Figure 18. Smithtown bridge view, looking downstream.



Noted green spaces forming the remaining LIE Arechepelago.

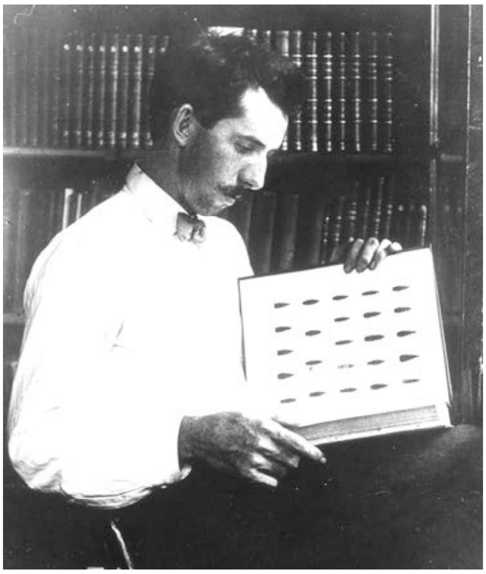


Figure 19. H. S. Barber, circa 1911.

Flashing Behavior. The signaling of *stevensae* incorporates several features that made the genus difficult for H. S. Barber (**Fig. 19**) to understand, as well as the beginning of a solution to the problems/adventure he uncovered. He mused (1951:11): "Imagining the ideal opportunity for observation, we might wish for two adjacent pure colonies [demes] which could be observed and contrasted at leisure." On Long Island at Smithtown, not far from the Nassau–Suffolk County line, there is a bridge where a stream runs under the road and then down to the Sound; this is Barber's bridge now, for there a resident population of *stevensae* flashed around the parking area to the south (**Fig. 17**), and a population of dot-dashers ("*pennsylvanica"*) flashed to the north, not 100 yards downstream (**Fig. 18**). Smithtown would have been *the* place for Barber to have spent a summer chasing his *Photuris*, and fishing, for he could have seen before him, moment to moment, fireflies switching their FPs and they would default to his "torch" (flashlight) decoys—though he would have been too late to meet firefly geneticist Nettie Stevens.

Male *stevensae* began flashing at field edges in shadier places, along tree rows 27-54 min after sunset ($\bar{x}$=38, s=8.2; crep range=0.8-1.6, $\bar{x}$=1.1, s=0.2.). This considerable variation may in part be due to variations in skyglow intensity, which was considerable on nights of dense high fog and cloud cover, and perhaps also in part—and historically—to population density and phenology as it relates to high-value female availability.

At the two main oldfield study sites, Peconic and Shoreham (**Figs. 7-8**), males flew 2-10' above the herby/grassy vegetation, and up the fronts and over, along, and among the crowns of adjacent tree rows. At the beginning of activity for a few minutes males emitted only their pulsing FPs (**Figs. 3, 21**); at this time, 2-pulse patterns were occasionally and briefly noted. This variation may occur more frequently near field edges? At a site in Putnam County NY a higher proportion of males emitted the 2-pulse FP, and seemed to do so longer into the evening than noted elsewhere (**Fig. 20**). The shrubby or narrowness (edge/area increase) of this site perhaps was connected with this.

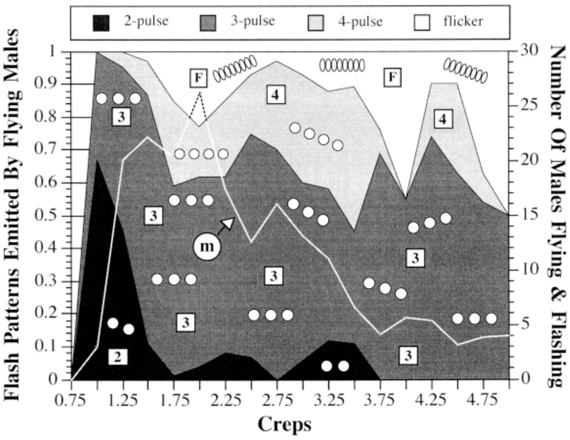


Figure 20. Putnam Co. scan sample.

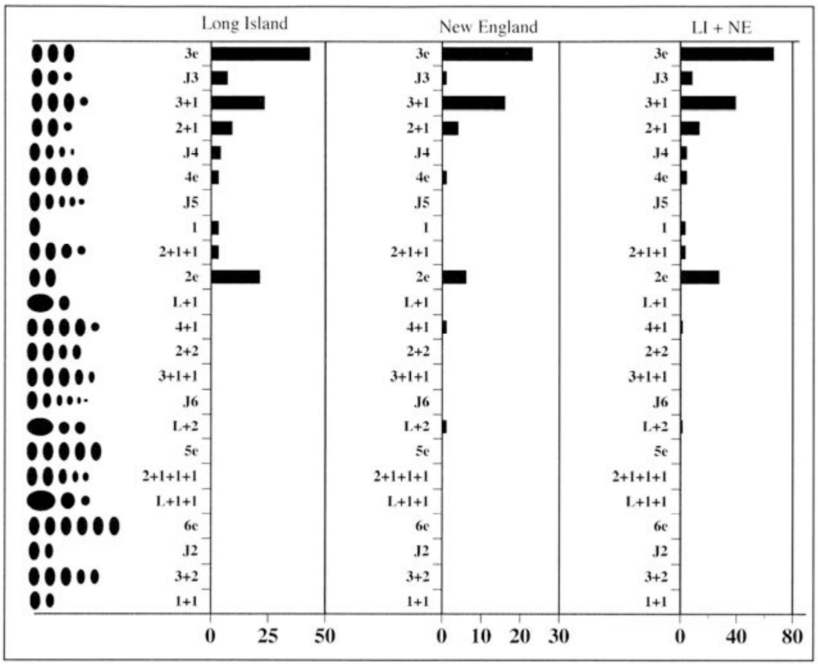


Figure 21. FPs noted in FB.

Pulsing FPs, configurations. The pulsing FP repertoire has several distinctive configurations: Each FP is comprised of 2-5 pulses with up to three *apparent* levels of intensity. FPs seen were noted from time to time as incidental (i. e., not systematic) records in the fieldbook (**Fig. 21**). The discerned (relative) intensity-level and pulse-number configurations can be categorized as follows: (**1**) all flashes of *apparently* equal (even) or nearly equal (relative) intensity (e.g., 2e, 3e, 4e); (**2**) two apparent intensities, always step-down (e.g., 2+1, 3+1, 3+2; (**3**) three apparent intensities, always step-down (e.g. J3 =1+1+1; 2+1+1). Step-up intensity changes were not

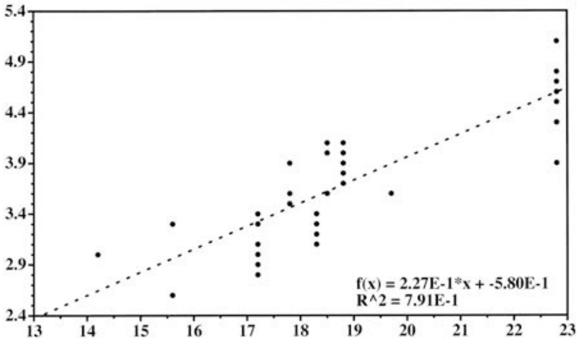


Figure 22. Pulsing FP pulse rate Hz/Temp.

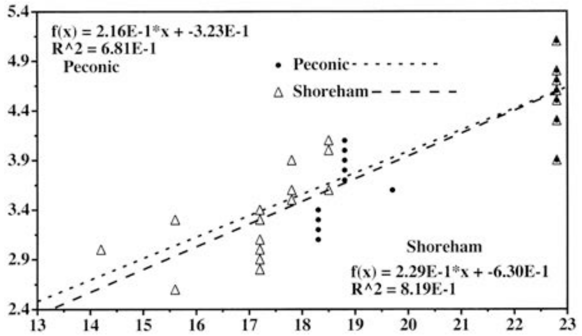


Figure 23. Pulsing FP rate, sites separated.

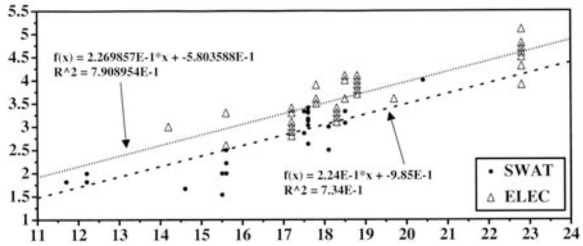


Figure 24. Comparing techniques.

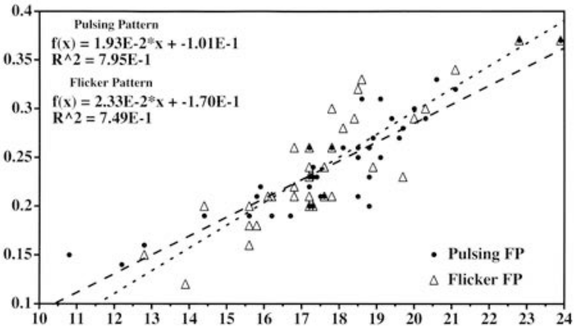


Figure 25. FP-period rate comparison Hz/Temp.

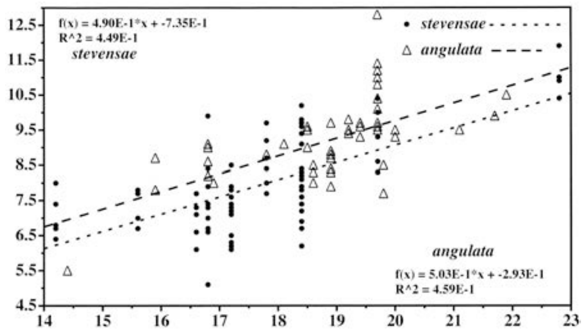


Figure 26. Flicker modulations (Hz/Temp.)

visually noted, but occasionally occurred in PM-records, probably due to changes in lantern-PM orientation and not as emitted at the lantern. The significance of *stepped* intensity differences is perhaps important. The fact that sometimes an intensity step has two pulses, perhaps indicates that the steps are sometimes important and are repeated (made redundant) to ensure that the distinction is transmitted? FP selection by individual males may also be influenced by vegetation type and level of competition, and thus *conditional* options.

Occasionally FP configuration *transitions* were noted. Such data when viewed with site and population considerations may with study provide insight into the adaptive significance of the variation and cues (releasers) that elicit the various configurations. Observed: 3e>3+1, 2e>3e, 1>2e, 1>2e>3e, 2>1, 1+1+1>3e, 1>2e>3e>2e, 2e>3e>2e>3e>2e, 2e>1>1, 3e>2e.

Pulse rate in pulsing FPs ranges from 2.4-5 Hz, 13°-23° (**Fig. 22**). Only rarely did the pulses within a pulsing FP appear to the eye to be connected, and then perhaps was the result of flashing-organ malfunction. Occasionally the rate changed slightly within a single FP, as detected with certainty only in PM-records; also, occasionally the first pulse of an FP appeared somewhat longer than those following. **Figure 23** separates the rate-temperature regressions for the two major LI study sites. More importantly, for practical reasons, **Figure 24** is a valuable comparison for observers without PM-recorders; it shows the consistent error made with SWAT measurements—averaging about 0.5 Hz too slow.

Flashes in pulsing FPs are nearly symmetrical and vary in duration in connection with their intensity variations, i.e., their position in the FP. Finally, as afterthought, when *rate* plots of pulsing FP and flicker F*P periods* are plotted together their similarity, or perhaps identity is more easily seen (**Fig. 25**).

Flicker FPs. Modulations in the flicker FP appear sinusoidal and 7-12 in number (**Fig. 29G**). At low temperatures intensity may decrease to zero (go "flat") in intensity troughs, but in most PM-recordings the trough is rounded, without indication that the light is completely shut OFF (**Fig. 29G**). The flicker modulation rate averages range 6-10 Hz. in recordings made at temperatures ranging 14-23° (**Fig. 26**), and is slightly more than twice the pulse rate in pulsing patterns. This chart also shows the values for the flickers of *Py. angulata (*recorded at various locations around the U.S.—the/one presumptive (historical) model for the flickers of *stevensae* and several other North American *Photuris*. Note that modulation rates of both *angulata* and *stevensae* have broad variation though their means are similar, differing by about 0.7 Hz. Judging from museum specimens and field observation, rarely if ever do Long Island *stevensae* males (now) see the flickers of male *angulata*—or that they could differentiate between them and flickering *stevensae.* The only near-Long Island record I have found is a specimen from the Staten Island Museum that

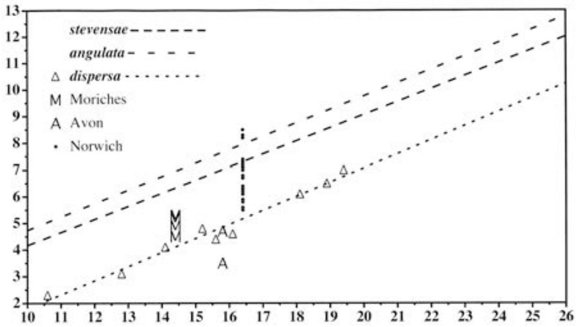


Figure 27. Flicker modulations (AX: Hz/temp.)

Figure 28. Peconic Mill Lane hedge.

was collected many years ago. Some of the flicker moduation rates in *stevensae* fall to the rate of *Py. dispersa* (**Fig. 27**).

PM-records from near Avon, CT, are especially interesting: Mean aggregate rate of two males was 4.6 Hz (n=5, r=4.3-4.8, s=0.2, 15.8°/60.5°). Two somewhat clear, unambiguous flickers from a third male were both 3.7 Hz. The nine patterns in a train from the fourth male are difficult to interpret; his patterns included one clear pulsing FP (2.2 Hz); 4 apparent *dispersa*-matching FPs (x=4.2 Hz, r=4.0-4.6, s=0.3); and other FPs which appeared to be combinations of pulsing and flicker modulations, with the one having a combination and irregular rate of 5.8 Hz—with apparent superimposed wingbeats. Mixed-FP periods in this male averaged 5.4 sec (n=8, r=5.0-5.8, s=0.2). The date of recording (19 June) does not in itself suggest that there might be a change-over in FP models, from *dispersa* to *angulata*, as seems might *possibly* occur in southern NA with A and D-flickering *quadrifulgens*. **Figures 29H, J-L** illustrate some of these FPs.

There is no known record of *Py. dispersa* for Long Island but it is not rare on the continent. As suggested and discussed elsewhere, perhaps there is an historical mimicry connection among these FPs, and that *Pyractomena* model species have become rare or lost since a super abundance that occurred after the Wisconsin glacier. Sexual selection has perhaps become a confusing factor when trying to unravel the secrets of the signals we seek to unravel today.

With respect to the form of flicker FPs in *stevensae*, there appears to be no consistent intensity envelope such as seen in Florida *lamarcki*, and the symmetrical rise and fall that is sometimes seen probably results from chance changing of background illumination when the PM is panned across light-variable horizons when aiming the PM at passing fireflies.

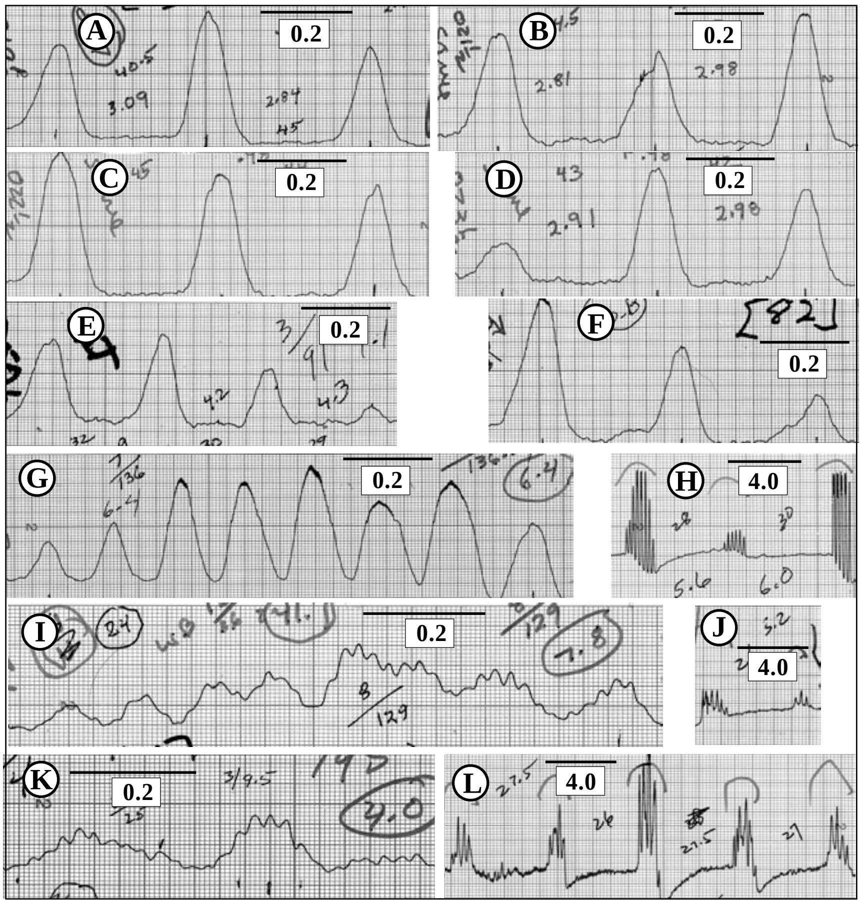


Figure 29. PM traces; see also augmented figure legends: (**A-D**) A sequence of FPs emitted consecutively by the same male. (**E**) The form is 2+1+1 based on intensity alone, but pulse duration suggests J4—the truncated first pulse may have been accidental or from a PM overload. (**F**) A J3 (1+1+1). (**G**) Flickering male from below, some pulses showing the non-linear-amp alarm's grass atop the peaks. (**H**) A short train of Py. dispersa-matching 4.6 Hz flickers. (**I**) Wingbeats of 41.7 Hz from wing-shuttering, riding atop a flicker. (**J**) A dispersa-like pulse rate. (**K**) Wingbeats of 40.0 Hz atop a flicker. (**L**) Sequence from the one male has a jumbled mix of flickers and pulse-like FPs.

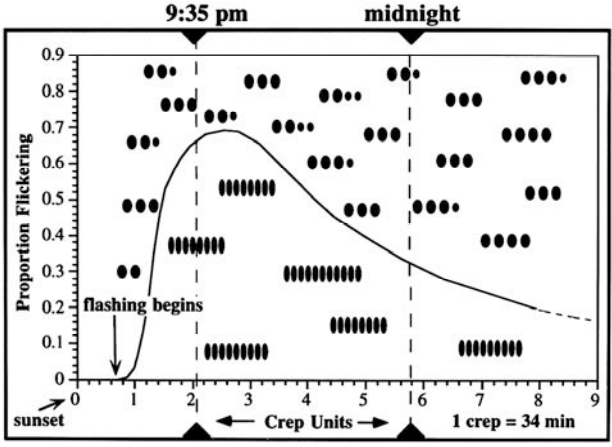


Figure 30. Evening FP profile model for *stevensae*.

Early-flight, other FPs. For several minutes at the beginning of evening activity 2-pulse and 1-pulse FPs were occasionally emitted, possibly mostly near edges, shrubs and other coarse vegetation, but the 3-pulse, pulsing FP soon became the most common. The pulse interval in 2-pulse FPs was about the same as seen in 3-5-pulse FPs (ca 0.5 sec), that is, with the *enlightening* 2-second exception noted in next section, in which 2-pulse FPs matched the FP of an expected prey species, *Photinus macdermotti*-complex/variad. Though this FP was not seen as part of *stevensae's* evening repertoire, it is of more than passing interest (see below). Finally, 6-pulse FPs were never seen emitted by *stevensae*, as sometimes occur in *versicolor* in east-central US, and *harrannorum* in Florida.

A through-evening increase in the pulse number in pulsing FPs has been noted in another species of the *versicolor-quadrifulgens* group by T. and S. Forrest (pers. com.); Forrest and Eubanks, (1995); and during this study. Scan-samples were not made of this progression in *stevensae* in large open-field populations where appropriate (but note **Fig. 20**), though it was subjectively noted that such a transition occurred and began with occasional 1- and 2-pulse FPs amongst 3 pulse patterns; it continued through a phase dominated by 3-pulse patterns, until finally 4-pulse FPs became the most common, about 2 hours after sunset. But, this synopsis excludes the most noteworthy aspect of FP transition in *stevensae*, which is the gradual and ubiquitous increase in the number of males emitting the flicker FP, and the subsequent gradual decrease of this FP through the night (**Fig. 30**).

Defaulting; evening FP transition. When *Photuris* males of several species that are emitting their adjunct FPs receive a decoy's response-flash they switch (default) to their species' own ID pattern. When *P. stevensae* males default from their flicker FP they switch to a 3- or 4-pulse configuration. A "natural" default transition was seen across the road from the field at Peconic: While intent on watching *Photinus macdermotti*-var. males (FP: 2 flashes 2 sec apart (21°/70°) flying near the hedge (**Fig. 28**), "one of them" less than three feet from me received an answer from a female in the hedge about three feet in front of me. A few moments later the male emitted another 2-flash FP from the same airborne position, and another flash response followed from the hedge. Then, in less than 4 sec, from the same aerial space, a 1+1+1 -*stevensae* FP was flashed, but was not answered; another such FP again received no answer, and the male emitted another as he slowly flew away. The respondent was a female *mac*-variad which certainly had been deceived as I had been (though the flash color is distinctively different) by the 2-sec flash-pairs emitted by the *stevensae* male. This was a surprising observation because unlike other *Photuris* that emit FPs that sometimes closely match pulsed FPs of other genera—for example, Gulf *Ph. branhami*—*stevensae* males had not been noted to emit *mac*-like flash pairs, either, as described, or as a routine part of their evening programme, or even as an occasional passing event. Perhaps *mac*-flashing *stevensae* males only occur near active *mac* populations, and fly-by *stevensae* males observe and then adopt this specific 2-sec 2-pulse timing. (Finally!, here maybe is in a clue to a possible evolutionary origin of this mimicry behavior in *Photuris* males!; biological *mimicry* sensu Wickler and Pasteur having become ad hoc, less simple).

Defaulting *stevensae* males switch to a simple pulsing FP—the 3e, 3+1, and J3 configurations were noted but others may be used—there may be some subtle refinement as to when or in what sequence particular pulsing configurations are used. Between the first decoy response and the emission of the default pattern, one and sometimes two subsequent flicker FPs were emitted, and then a dark pause of 3 sec to 2 min occurred ($\bar{x}$=42 sec, s=35 sec, n=18—durations estimated/counted). Usually the male landed before he emitted the default FP, and occasionally after landing another flicker FP was emitted before defaulting occurred. Males could be attracted to the LED and would stand on it if flash responses to their pulse-FPs were continued. **None** of several males decoy-tested reverse-switched, from a pulsed FP (3e, 2+1 etc) **to** the flicker. Male behavior in this situation suggests that males are preyed upon by their own females. (This default experiment is about as simple as putting iodine on a raw potato to test for starch, but requires more patience and finesse.)

On three occasions flickering males over a field were seen "spontaneously" to begin emitting a pulse pattern and approach the ground, and occasionally males that were flying toward the edge of the open field and approaching the tree-line, or flying up toward the foliage of trees, *changed* from the flicker to a pulsed FP. These are perhaps important changes to note, for eventually determining the cues males monitor to determine which

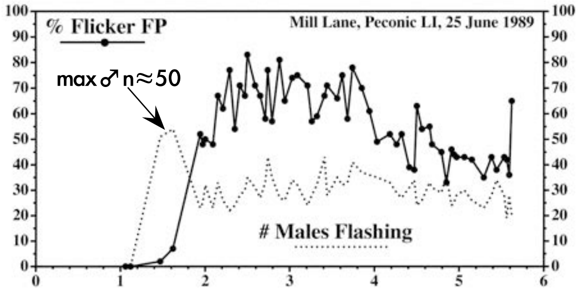


Figure 31. Model-matching profile (flick/flick+pulses; (AX: % flicker/creps).

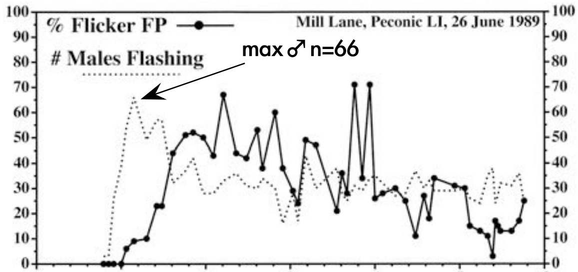


Figure 32. Model-matching profile.

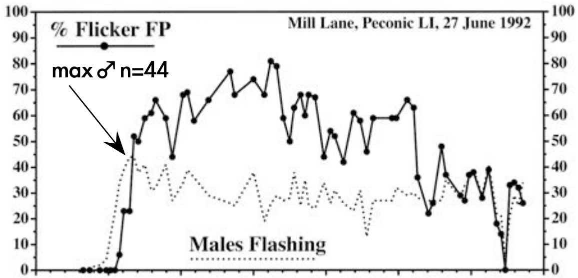


Figure 33. Model-matching profile.

FP to use from their repertoires. In *defaulting*, the identifiable proximate stimulus to the male change is a female flash-response to an adjunct pattern; the male defaults to the *identifying* FP of his species. In the "spontaneous" changes described above males were entering a different ecological situation and perhaps the realms of females with different reproductive histories.

Systematic observations of males flashing near the center of the Peconic site at a time when the flicker ratio (see below) ranged around 0.50 (1.0-5.8 Crep, **Fig. 30**) revealed the tendency for males then and there to remain with the flicker FP. In counted successions of 10 FPs for each of 18 males, none emitted a pulsing FPs; another male gave 4, another 6 and another 7 flickers, and then were lost among other flashing males.

FP change-overs. The flicker FP is sometimes very common, with 80% or more of flashing males over an oldfield emitting it. The proportion of flickering versus pulsing varies through the evening, often as illustrated in **Figure 30**. The level of flickering reached is suspected to be influenced by population density, that is, the level of competition (male-male contact), and phenology, as this relates to female reproductive condition—virgin (high-value) vs mated (with sperm and perhaps a greater tendency to be predatory), and previous oviposition and hunting success. (Note that *number flashing* is a “quick and dirty” method to quantify male *density*—it presumably was adequate in these samples because sampled areas were usually about of the same size.)

In a standard *reference* model (**Fig. 30**), which was derived from scan-sampling, as illustrated in **Figures 31-36**: (**1**) the flicker ratio begins at zero; (**2**) quickly rises to a maximum 50-80 percent and remains there for a few, sometimes 10 minutes, and

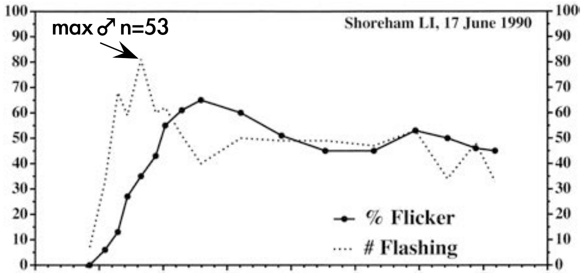


Figure 34. Slight deviation from model.

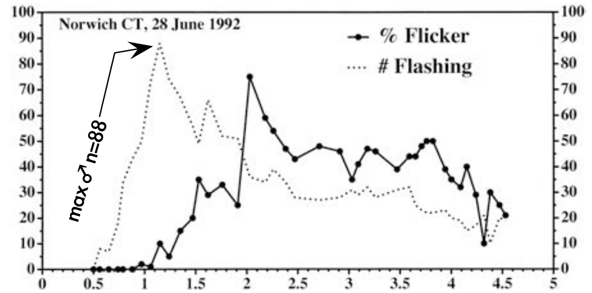


Figure 36. Deviation from model profile.

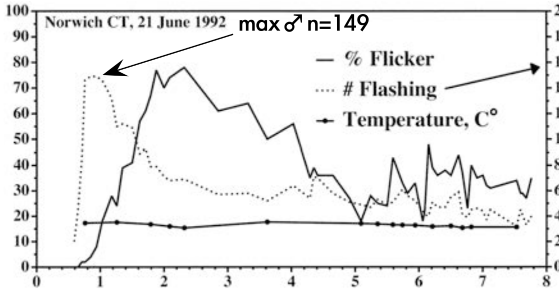


Figure 35. Model-matching profile.

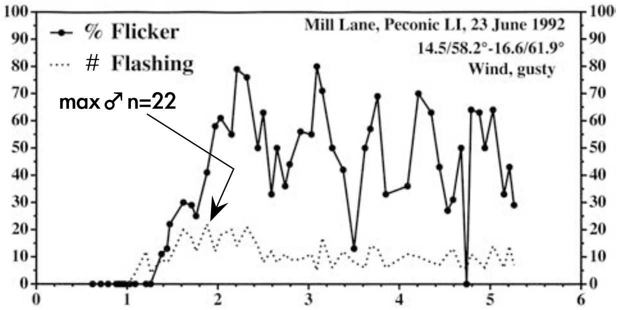


Figure 37. Deviation: windy.

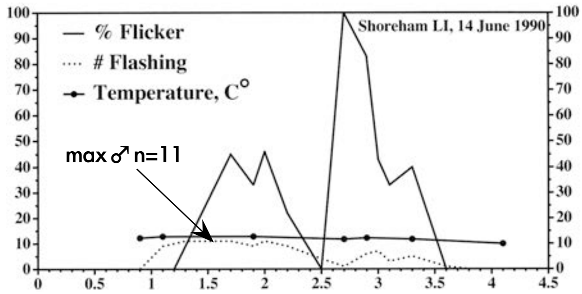


Figure 38. Deviation: low temperature.

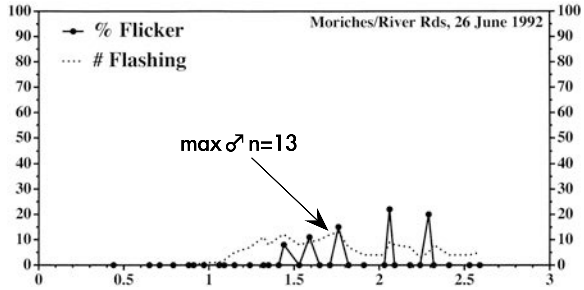


Figure 39. Model not fit: low encounter rate?

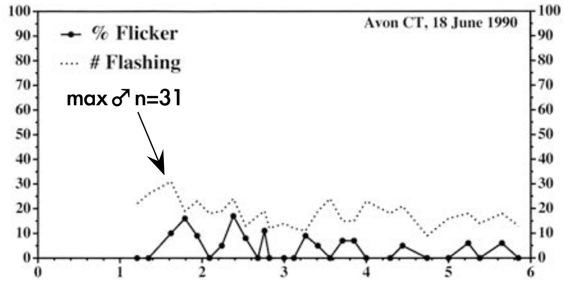


Figure 40. Model not fit: low encounter rate?

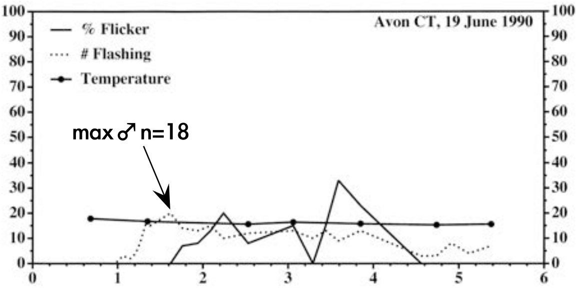


Figure 41. Model not fit: low encounter rate?

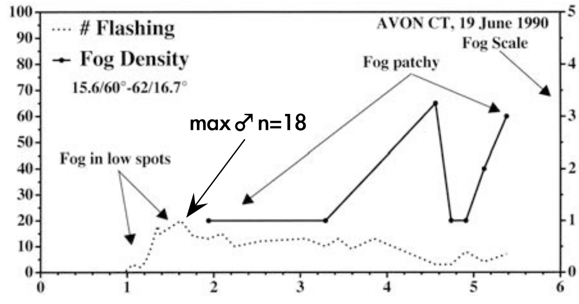


Figure 42. Model not fit: low encounter rate.

(**3**) then drops to about 50% of the peak (r=35-65), and from there slowly decreases for several hours—perhaps until dawn under certain circumstances.

Though scan-samples were originally made only to quantify the level and nightly timing of flicker use by males (points 1-3), scan-samples revealed/suggested other interesting aspects of mate search, and additional considerations: (**4**) On many nights there were more males flashing "momentarily" at the beginning of activity than *at any other* time of the night (dotted lines in **Figs. 31-36,** peak n# on chart), and indeed, this number profile becomes an important element of the model. As explanation, (**i**) perhaps most males are active at flight onset because unmated (high-value) females that eclosed during the previous hours, or immigrating females from other local populations are briefly more available then; (**ii**) Perhaps the total number of flying flashing males drops because, say, through the activity period individuals switch between flying and perching bouts, or fly darkly, parasitizing the FPs of males flying near them or seeking attractions in progress (see pages 82, 98, 146, 156).

Working from the model, other factors of significance to male search behavior are recognized and quantified: (**5**) Note that many fewer males were active on 23 June 1992 (**Fig. 37**) than on either 21 June or 28 June 1992 (**Figs. 35, 36**) though the temperature was not limiting—the FB says it was gusty and windy the 23rd; it is not surprising that wind would be significant. On 14 June 1990 (**Fig. 38**) male numbers reached a maximum of ten at the prolific Shoreham site, though on June 13th and 17th of that year the maxima were 40 and 80 respectively—on the 14th temperature scarcely edged above 10°/50°.

In small populations, that is, at low densities the model's profiles are not observed and the proportion of males emitting the flicker FP erratically spikes and falls. For example, the Moriches site was an open marsh area bordered by shrubs on one side and numbers counted peaked at 13; the percent-flickering rose and fell sharply (**Figs. 13, 39**). The same can be said of the Avon, CT scans shown in **Figures 40, 41**. It would appear, after comparing the several scan-samples, that when male numbers in these samples were around 30 or below ("controlling" for density) the percent-flickering became erratic and a percent-flicker profile was not observed. This should be easy to explore experimentally with LEDs manipulating/controlling apparent male density (male-male contacts). This deserves a little more consideration::

A beetle may or may not be inferior to a man
—the matter awaits demonstration; but if he
were inferior to a man by 10,000 fathoms,
the fact remains that there is probably a
beetle view of things of which a man is
entirely ignorant. Chesterton, 1901

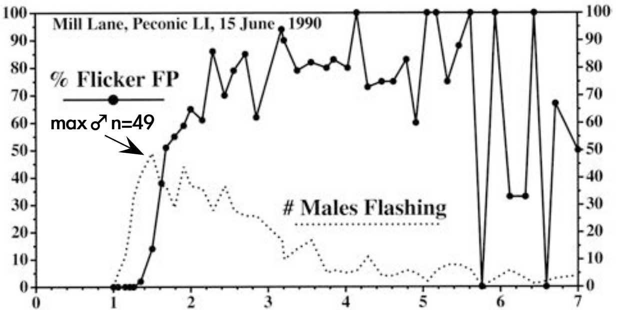


Figure 43A. Model not fit.

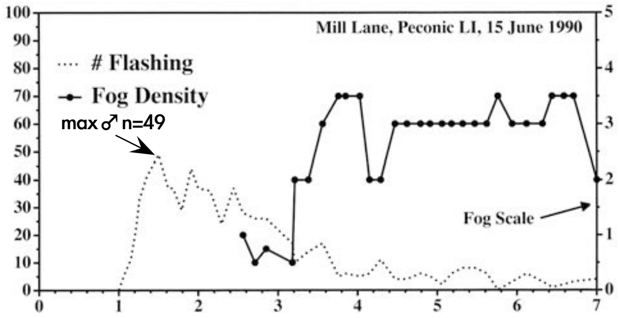


Figure 43B. Model not fit: fog, light breeze.

Figure 43. Model not fit: low encounter rate?.

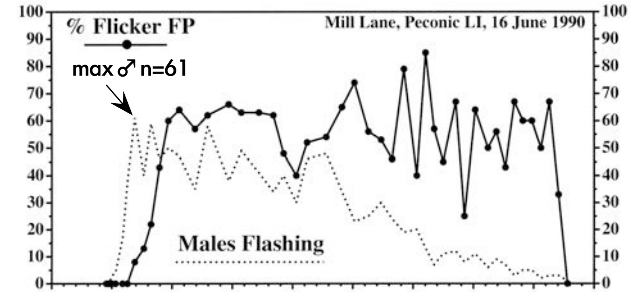


Figure 44A. Model not fit.

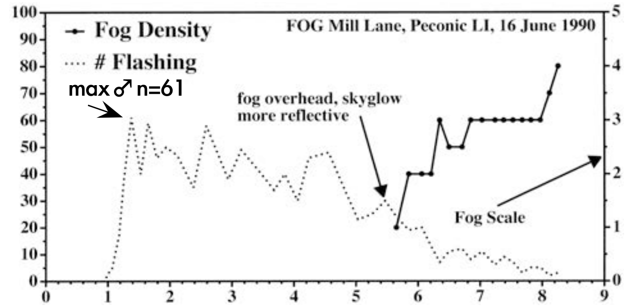


Figure 44B. Model not fit: fog, low encounter rate.

Figure 44. Model not fit:fewer fly, low encounter rate.

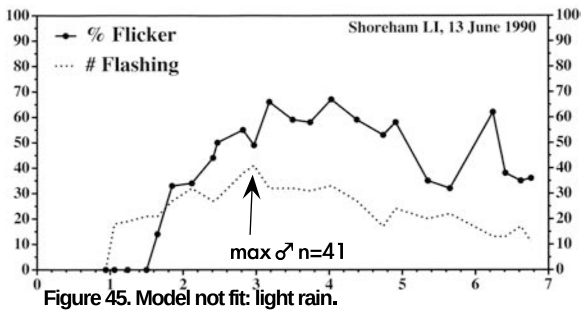


Figure 45. Model not fit: light rain.

A focus on the information that is available to individual males that enters into their data ("Boolean") stream and logic, and that will determine what FP a male uses at a given moment, brings attention to the fact that male numbers and density are not *specifically* the data that need consideration. Rather, it must actually be male-male encounter rates, which males can assess/count. This involves the frequency of and distances at which they pass/meet rivals in their flights. Male-male contact can be influenced by environmental elements. The Avon population was in a maturing old-field *broken* by shrubs of various sizes, thus flicker profiles from this site may be erratic not from low spatial density but from low beetle-apparent density, because male-male contact was reduced by occluding shrubbery. To achieve the model percent-flicker profile there is probably a minimum level of male-male encounters per unit of time required. This is amenable to experimental manipulation, say with appropriately flashing LEDs scattered throughout an activity space, or artificial shrubs, perhaps in mathematically-determined designs?

Other scan-samples seemed to make it clear that meteorological elements can lower effective population size, thus, male-male encounter rate. They may become suspect when inexplicable or anomalous observations are recorded. On 19 June 1990 the Avon population (**Fig. 42**) received further insult when patches of fog appeared at the bottom of the site and later, a patchy cloud moved invasively up the slope (**Figs. 14, 42**). The influence of fog on flying beetles and other insects can be predicted to also entail additional flight costs because of the retarding impact of water (fog) droplets on beating wings, and perhaps also the cooling effect on *warmed* wing-muscles by saturated air and the high specific heat of water vapor—some insects are known to use metabolic heat to keep their wing muscles at an efficient operating temperature.

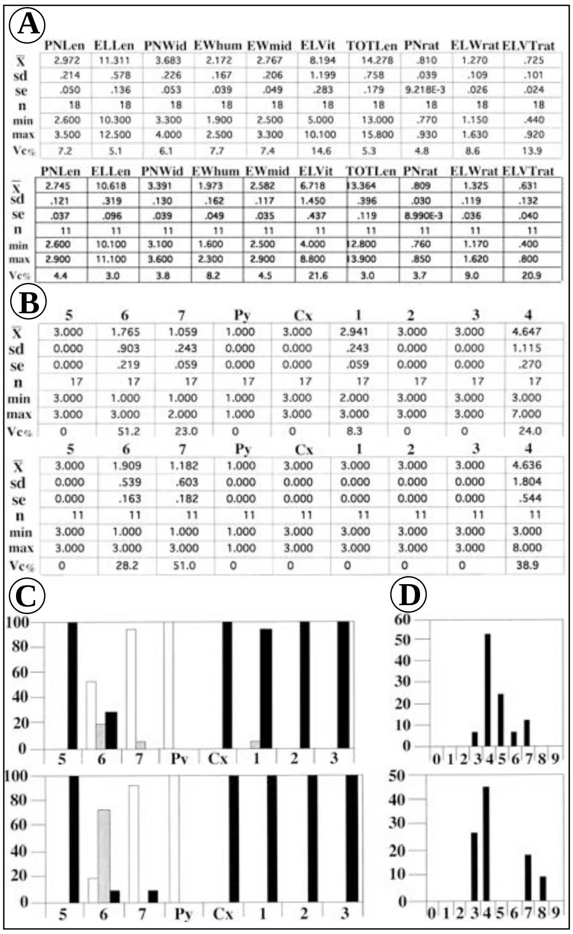
Scanned profile **pairs** may suggest the influence of fog (fog estimated densities, right Y-axis, arrow), on evening flashing activity: Charts in **Figures 43A** and **44B** show number flashing and percent flicker profiles that begin in the form of the general model but then numbers drop off sooner than would be expected. Charts in **Figures 43B** and **44B** show similar number profiles with the estimated fog density—estimated/calibrated via the distance that the shrub-border was visible across the activity space. The maritime environment of Long Island with its many nights of fog make it an ideal place for such fog research. The profile in **Figure 45** is from an evening of light rain (sprinkle), also deviates from the model—male flashing numbers rose slowly, without an early peak, and reached a low peak (at 3.6 creps, vs x=1.2, s=0.18, r=1-1.5, n=5); this endures about 1 crep (vs x=0.2, s=0.11, r=0.1-0.4, n=5), and then slowly declines. The FB notes that a light sprinkle began at 3 creps, but the number-rise even before then was already lagging. Perhaps some males that otherwise would have started mate-search did not; the FB also noted that before flight began, more than the usual number of males were flashing in low herbs. If the observation is significant, is the proximate cause meteorological, and the ultimate explanation that certain males avoid marginal search and flight conditions? If so, is it younger males with more reproductive potential (search nights) before them, or older males garnering their few remaining resources to use them under better circumstances.

Curiously, though one might expect that an important influence on use of the flicker FP would be the availability of prey males and their signals, but on Long Island *stevensae's* flicker seems to have become totally divorced from this, in total absence(?) of the prey species Py. *angulata* or its FP. Archive records indicate there have been few or no *Py. angulata* or *dispersa* present for 100 or more years on Long Island, though both occur across the Sound. Finally, it should be emphasized that change-overs should be viewed and approached as individual adaptation, even though the quantifying focus is on a population-level phenomena.

Wingbeats. Apparent wingbeats modulations were detected by the PM-system as they were superimposed upon 7 luminescent flickers of 5 males at the Avon site (**Fig. 29 I, K**). Wingbeats on the flicker in trace-I measures 41.7 Hz and in trace-K, 40.0 Hz. In aggregate they averaged 39.8 Hz (r=39.1-41.7, s= 0.9) at 15.8°/60.5°).

❄ ❄ ❄

Morphological data. General morphological means for *stevensae* males from Long Island (n=18) and Connecticut (n=11) are shown in **FigTable 46**, A-D, top vs bottom; for LI they are: PNL 3.0, ELL 11.3, PNW 3.7, EWhum 2.2, EWmid 2.8, ELVit 8.2, TOTLen 14.3, PNrat 0.81, ELWrate 1.27, ELVTrat 0.73 (**FigTable 46A**-top, with other stats.). Data for the colors of various abdominal plates (sclerite combinations) and hind coxae are shown in **FigTable 46B-C**, and the color of the pre-lantern ventrite in **46D**. **Figure 47** is an anatomical key for various skeletal plates and numbers for degrees of splashing on ventrite 4. A range of vittagrams of *stevensae* is shown in **Figure 48**.



A

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.972	11.311	3.683	2.172	2.767	8.194	14.278	.810	1.270	.725
sd	.214	.578	.226	.167	.206	1.199	.758	.039	.109	.101
se	.050	.136	.053	.039	.049	.283	.179	9.218E-3	.026	.024
n	18	18	18	18	18	18	18	18	18	18
min	2.600	10.300	3.300	1.900	2.500	5.000	13.000	.770	1.150	.440
max	3.500	12.500	4.000	2.500	3.300	10.100	15.800	.930	1.630	.920
Vc%	7.2	5.1	6.1	7.7	7.4	14.6	5.3	4.8	8.6	13.9

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.745	10.618	3.391	1.973	2.582	6.718	13.364	.809	1.325	.631
sd	.121	.319	.130	.162	.117	1.450	.396	.030	.119	.132
se	.037	.096	.039	.049	.035	.437	.119	8.990E-3	.036	.040
n	11	11	11	11	11	11	11	11	11	11
min	2.600	10.100	3.100	1.600	2.500	4.000	12.800	.760	1.170	.400
max	2.900	11.100	3.600	2.300	2.900	8.800	13.900	.850	1.620	.800
Vc%	4.4	3.0	3.8	8.2	4.5	21.6	3.0	3.7	9.0	20.9

B

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.765	1.059	1.000	3.000	2.941	3.000	3.000	4.647
sd	0.000	.903	.243	0.000	0.000	.243	0.000	0.000	1.115
se	0.000	.219	.059	0.000	0.000	.059	0.000	0.000	.270
n	17	17	17	17	17	17	17	17	17
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	3.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	51.2	23.0	0	0	8.3	0	0	24.0

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.909	1.182	1.000	3.000	3.000	3.000	3.000	4.636
sd	0.000	.539	.603	0.000	0.000	0.000	0.000	0.000	1.804
se	0.000	.163	.182	0.000	0.000	0.000	0.000	0.000	.544
n	11	11	11	11	11	11	11	11	11
min	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	28.2	51.0	0	0	0	0	0	38.9

Figure 46. Morphology data: Peconic/Shoreham.

Holotype: male, voucher number 8924, collected 10 June 1989, Suffolk County, Long Island, New York. At the Shoreham Nuclear Power Plant site, route 25A, behind the sign. FB page 130: One of several collected after they defaulted from flicker FP to pulsing FP; from FB: "1st flicker [of evening] 6-7 pulses [modulations], at 9:34 [pm]. I ans[wer], he circle and gave another. then dark. ≈1 min later he gave versi [J] pattern [FP]. KB 63. *8924*. he had landed in hay about 6" fm [from] light [LED]. then he gave versi [J] patt at ≈3-4 sec period. 3 pul patt." Morphological data: from spread sheet—PNLen 3.0, ELLen 10.9, PNWid 3.6, ELWhum 2.4, ELWmid 2.9, LELVit 8.9, RELVit 9.4, TotLen 13.9, PnRat 0.83, ElRat 1.21, VitRat 0.84; Colors: T 331, Py 1, Cx 3, V 233, Edg 5. Types will be deposited in the USNM.

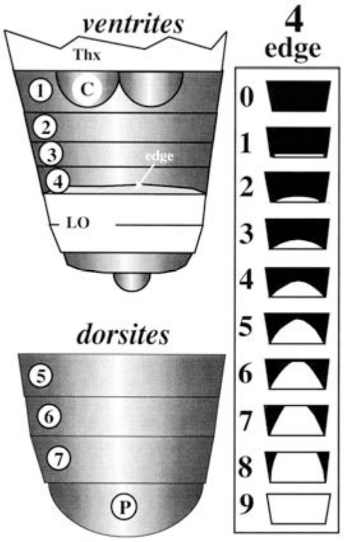


Figure 47. Key to anatomical areas and splash.

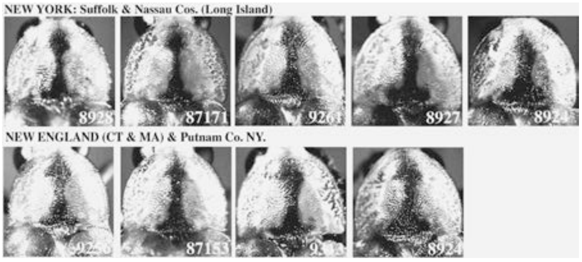


Figure 49. PN vittagram arrays.

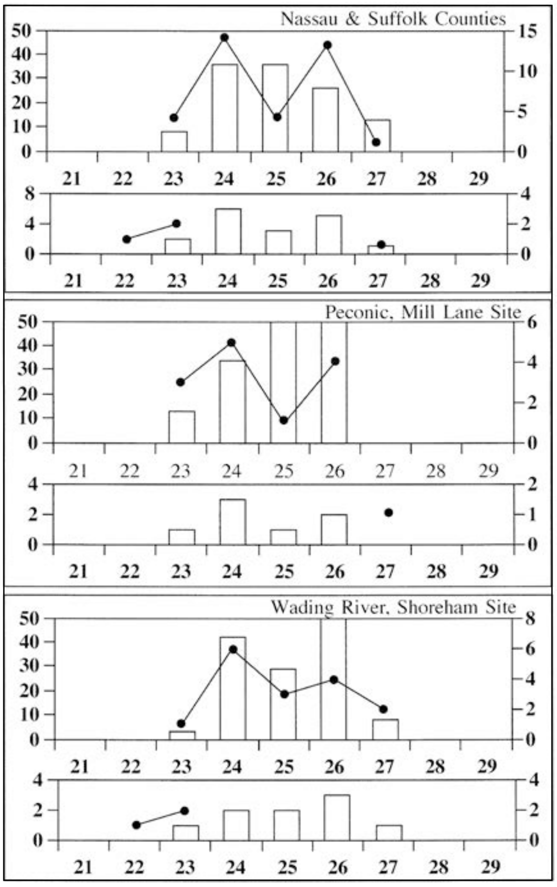


Figure 48. SESOBS, Long Island.

* * *

Sympatric and parapatric *Photuris*. The apparent closest relative of *stevensae*, *Photuris versicolor*, occurs in New Jersey. Where the two might now come into contact was not determined but diagnostic confusion will be avoided if the flicker FP is noted, and queried for default. *Photuris tremulans* occurs in New Jersey and emits flicker FPs, but will default to a single flash. I found neither in an overnight stay in a natural area on Staten Island, nor in Westchester or Ulster Counties, NY, but found *stevensae* in Putnam County. Perhaps neither *stevensae* nor *versicolor* occur west of the Hudson River north of the Palisades. Contact between continental and Long Island *stevensae* populations must now be virtually nonexistent, from habitat loss in urbanized greater New York City and the expanse of Long Island Sound. It could possibly occur in Central Park in Manhattan. In New England there are at least four resident *Photuris* in addition to *stevensae*: a dot-dash *"pennsylvanica," fairchildi*, *hebes*, and *margotooleae*.

Museum specimens from the early 1900s indicate that at least four other *Photuris* species may once have occurred on western Long Island—*P. hebes, P. pensylvanica, P. lucicrescens, and P. fairchildi.* Some or all of these are presently in New England and in adjacent continental New York. *Photuris salina* and/or *P. bethaniensis*, both smaller species, may possibly occur along the south-western coast of Long Island in marshes behind dunes or in lagoon-bordering halophytic vegetation. Of all of these species, only a dot-dash "*pensylvanica"* was found on Long Island, at one, possibly two sites: at Smithtown, about 3.5 miles southwest of Stony Brook Harbor, and at the junction of Moriches and River Roads (**Figs. 13, 18**). Before extensive land modification this *pensylvanica* may have occurred along and near the northwestern shore of the Island, throughout the Necks region.

Taxonomic and other notes. The scientific name of this firefly pays a belated tribute to Nettie Maria Stevens, PhD, a pioneering geneticist who studied firefly genetics at Cold Spring Harbor early in the 20th Century, and according to some historians did not receive the credit she deserved for her work on *Drosophila*—this was the era of the "Lords of the Fly," not Ladies of the Fly.

Nettie Maria Stevens: photo ref. in Bibliography.

Photuris research specimens collected in New England early in the 20th century and identified as *versicolor* may have been *stevensae, fairchildi* or *margotooleae*. When research specimens were identified as "*pennsylvanica"* it was usually in the pre-Barber sense, and not what we now understand as *pensylvanica*. *Photuris* collected at Woods Hole or elsewhere on Cape Cod, Barnsytable County, MA, for example Williams (1917), was probably *fairchildi* rather than *margotooleae* or *pensylvanica* sensu Barber.

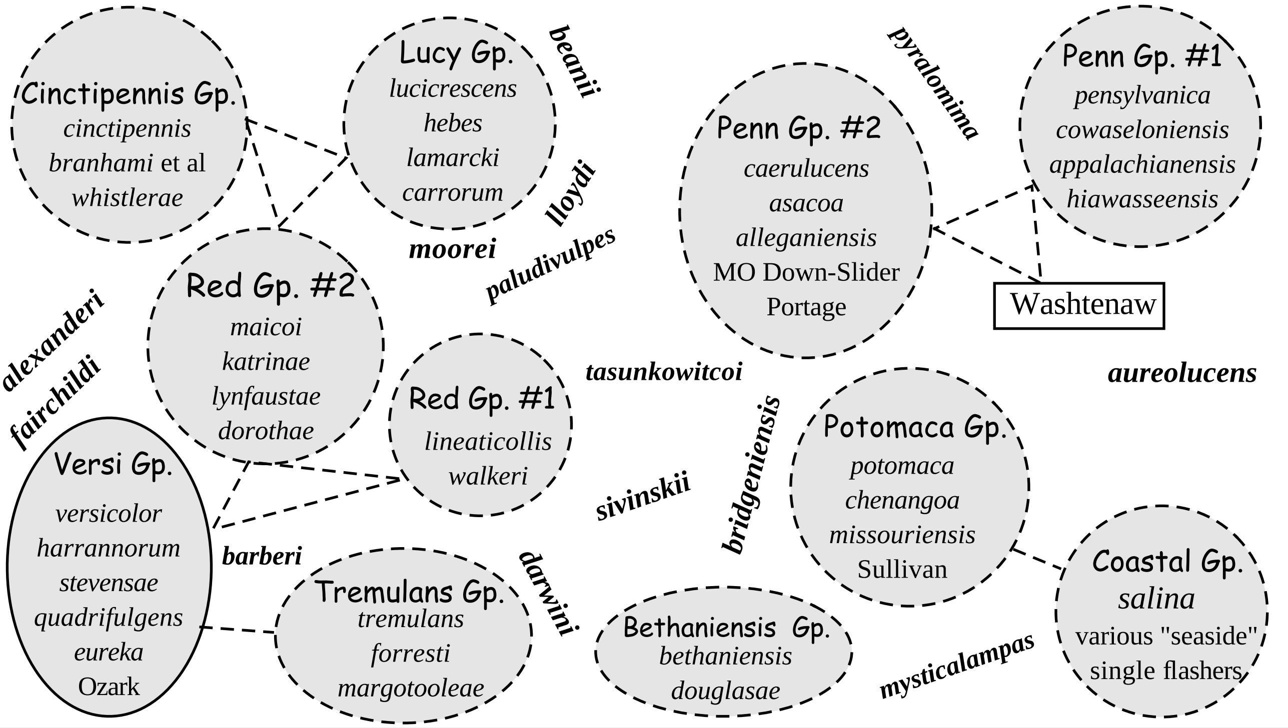
At both major L.I. study sites the other common lampyrid species was in the *Photinus consanguineus* Group (a variad of *macdermotti*; nominal population in Florida), which was numerous in tree and shrub rows and copses at the margins of fields. After full darkness occasionally males of this species were seen briefly over the open fields. A small population of *Photinus marginellus* was present at the Peconic site. Adults of this latter species emerge a little later in the year, and if female *stevensae* are firefly predators, which they probably are, late-season and long-lived females probably hunt *marginellus* males.

Augmented figure legends. **2**. Physiographic distribution. That a sharp western barrier should exist at the Hudson River and eastern one at the Cape Cod Canal remains inexplicable but not unusual. Xs on LI are presumptive museum records. **3**. An abbreviated short sampler of FPs emitted by *stevensae* with terms that have been used to refer to them. **4**. Synopsized SESOBS record for Long Island based upon observations made there during six summers (cf **Fig. 48**). **8**. View across a large old field on the property of the Shoreham Nuclear Power Station near Wading River; several years after this study Station construction was terminated. This area supported a large population of *stevensae.* **9**. A view north on the Shoreham property toward an electrical facility. Fireflies flew at all levels including high up as they crossed between treetops. A "substation" of some kind is at the right beyond the tree row. **10**. A composite night view with a perspective similar to that in figure 9; the bottom and top portions are from two separate exposures made a few minutes apart on the same night. Note the skyglow though exposure was reduced and less than that of the bottom half. FPs are visible. **13**. Moriches and River Road site where flicker modulation frequencies were somewhat lower than recorded elsewhere on the Island. **14**. The maturing old field with an ever-increasing number of shrubs on Old Farm Road near Avon, CT. **15**. When at an early oldfield stage this site near Norwich, CT had hundreds of *stevensae* but a few years later, in its middle age, shrubs had increased in number and size and the fireflies were much fewer in number. **16**. The Norwich site during its firefly heyday, probably only a few years after the site had been retired as a hayfield. **17**. The population of *stevensae* over the grassy area and trees behind the parking area would have given Barber what he needed to see individual fireflies changing their FPs, and perhaps experimentally, with a leaf over his "torch" (flash light), cause flickering males to default to a pulsing FP. **18**. The dot-dash "*pensylvanica"* site seen from the Smithtown bridge might have given Barber the chance to further experiment with defaulting. Also, both populations at this bridge locality could have led him to discover FP change through the evening, though I did not note that the dot-dasher used a short 1-flash, early-evening FP at this site. The two populations would have provided Barber's "ideal … two adjacent pure colonies." **20**. Scan sample at the Canopus Lake site showing an "atypical" high level of early-evening 2-pulse FPs. The white line (n) indicates the number of males flashing, as read from the right Y axis. The density of flashing males, that is, level of competition, may also influence the FP being used. A crep unit (length of Civil Twilight) was about 34 minutes in duration at this latitude and longitude on this date. **21**. FPs in *stevensae* repertoire, in the proportion anecdotally noted in the FB. **26**. Flicker modulation rate of *stevensae* showing the broad variation (see text), and for comparison the rates of *Py. angulata* flickers from recordings made at sites across its broad U.S. distribution. **29**. PM flashes of flying male *stevensae,* data as noted. (**A-D**) A sequence of FPs emitted consecutively by the same male. Probably all were of the 3e form and pulse intensity variation seen here was due to lantern-PM alignment; C would be expected by chance alone, but could be trending toward J3 (1+1+1). Simultaneous multiple PM-recording angles will be necessary to resolve such questions (Shoreham , 17 June 1990 @17.2°/63°). (**E**) The form is 2+1+1 based on intensity alone, but pulse duration suggests J4—the truncated first pulse may have been accidental or from a PM overload (Shoreham, 12 June 1989 @19.4°/67°). (**F**) The form is J3 (1+1+1) (data as in A-D). (**G**) A flickering male recorded from below, with some pulses showing the non-linear-amp alarm's grass atop the peaks—from tuning the amplifier for maximum signal. Note rounded troughs indicating that the light does not reach OFF (data as in A-D). (**H**) A short train of *Py. dispersa*-matching 4.6 Hz flickers (Avon CT, 19 June 1990, 15.8°/60.5°). (**I**) Wingbeats of 41.7 Hz from wing-shuttering, riding atop a flicker—note slower chart speed (data as in A-D). (**J**) An FP with a *dispersa*-like pulse rate (data as in H). (**K**) Wingbeats of 40.0 Hz atop a flicker. (**L**) This sequence from the same male has a jumbled mix of flickers and pulse-like FPs of 5.3, 3.3, 4.2, and 6.6 Hz (data as in H). **30**. A generalized model of the nightly FP change in *stevensae*, with double-pulses early, then triple, to 4-pulsers, while at the same time, after a slow start, the flicker FPs rise to dominate and then they taper off over the next several hours. **48**. SESOBS (quantified seasonal observation records) of *stevensae* for combined major LI sites and for each separately.

Acknowledgments. I must make special mention and give considerable thanks to the Greenport Campground, Durland Fish and staff, Alan and Julia Moutron, the Wading River parking area, and the grounds crew at the Shoreham Nuclear site, who closed the gate to a work area too soon—Bean and I could have used just a few more safe nights there.

Note of academic concern. There have been scientific papers as well as a public letter of criticism published by one who claims to have done similar *Photuris* research on Long Island fireflies. From the present extensive field study, evidence of such research is lacking, and should arouse administrative interest in Albany; the situation could be examined by students, at several grade levels. It will be revisited.

Grouping *Photuris* Species Using Flash Patterns and Superficial Appearance. The relationship of the various operational species and variads placed in Division II in this paper, as interpreted from the most general of features—without the benefit of DNA as being developed today— may eventually be mildly interesting and instructional for comparison. This because, at the least, this grouping might reveal what would have been the best available organization toward a working model in the days before DNA. In the grouping shown, those that seem more reasonable are in shaded orbs, and at the margins or further adrift are those that are, variably, somewhat less than "maybe."



Chapter 65

Photuris tasunkowitcoi n. sp.

Crazy Horse Firefly (CH)

This firefly was found in a deep valley/depression in northeastern North Dakota upslope from a bridge across the Pembina River near Walhalla (14 June 1991; **Figs. 1, 2**). Males flew along the herbaceous, shrubby and tree-lined banks of the River and over an adjacent field for about 100 yards, a few feet above the coarse grassy vegetation (**Fig. 3**). A short flash was common until about 10:30 local time but was not noted later in the evening (**Fig. 4G**). Long flashes were 1+ sec in duration (69.2°/20.7°), and visually *appeared* to be of several forms: (**1**) with little change in overall intensity; (**2**) with a slow decrease in intensity; (**3**) with a rapid decrease in intensity; (**4**) and with a slight increase in intensity. Airborne long flashes sometimes appeared to have "beads" or “dips” in them, possibly merely from flight movements. One long flash was clearly and strikingly modulated only in the middle. In another a flicker was clearly imposed on a crescendo. Simultaneous carefully-observed and PM-records revealed that there often are weak modulations that are not visually apparent in some long flashes (**Fig. 4D, E**); and some flashes that appeared only slightly modulated actually had very strong modulations (**Fig, 4F**). The most distinctive FP in this "repertoire" was the A-flicker (**Fig. 4A-C, F**). As recognized here, *tasunkowitcoi* (CH) is distinguished from the dot-dasher ("*pensylvanica"*) of surrounding areas by its flashing versatility and variability, but especially by its A-flicker FP which was never seen in nearby dot-dash populations—though a dot-dasher (*appalachianensis*) at a Garrett County site in the mountains of western Maryland emits it. This interesting variant in the *pensylvanica* group, like its clansmate *asacoa* that is known as tucked away in an isolated Iowa river valley, may provide interesting information on population divergence when its DNA is examined. CH is a moderately large firefly (13-14 mm) and similar in physical appearance to *pensylvanica* and *asacoa*, and aspects of its flashing find homologies (analogies) in FPs of these species.

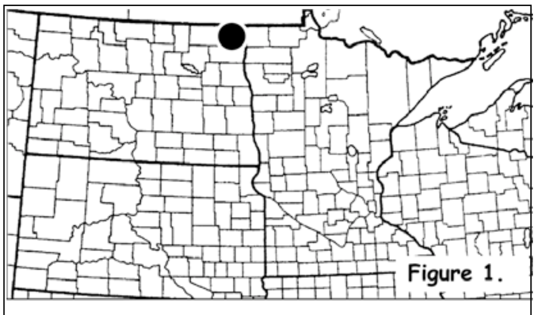


Figure 1.

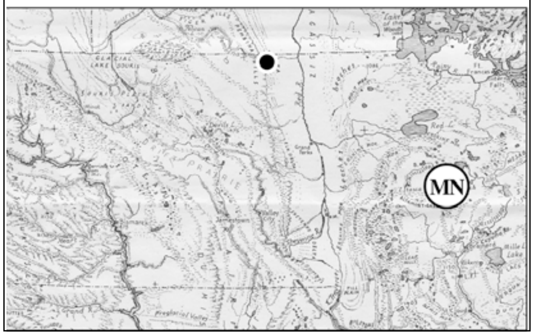


Figure 2. Physiographic location.

Ecology, flashing behavior. This firefly perhaps occurs only along the deep channel of the Pembina River, which is a special situation in a prairie setting. The ecology is a complete surprise for a high-plains traveler expecting flat or rolling infinity with occasional marshes and monotonously grand and expansive vistas, where at night you see no lights and know that you are indeed alone. According to a campsite brochure, about 8000 years ago glacier meltwater broke out of ice-impounded lakes and gouged deep channels and pockets which have since become permanently damp and wooded retreats—providing downhill skiing for prairie dwellers and an ecologically different and isolated firefly habitat. *Ph. tasunkowitcoi* near Walhalla, surrounded by the expansive habitat of a close relative, is seemingly a laboratory for study of isolation and divergence.

Several *Pyractomena angulata*, the presumptive current and/or historical species-group model for *tasunkowitcoi’s* flicker FP, flew at the same time and in the same activity space; it is probably preyed upon by CH females. The modulation frequency of the CH flicker falls tightly within the range of *angulata* measurements for north-central North America (**Fig. 5**). No other firefly species was seen at the site during the single evening of observation.

The short flash of CR appeared to be similar in duration to early short flashes of other *Photuris* and was emitted continuously at short (ca 1-2 sec) intervals; it was common until about 10:30 local time. In the figure I used a recording of *asacoa* to illustrate CH’s short flash, my best guess as to its nature (**Fig. 4G**, @20°/68). The short flash was not noted later in the evening.

A predicted long flash FP-period temperature regression is in **Figure 6**. As noted, CH's flicker modulation rate is in the range of *Py. angulata* (**Fig. 5**), with 7-12 modulations per flicker. Flicker FP periods averaged 3.3 sec (n=6 periods, 3 males; 20.3°/68.5°; **Fig. 7**). The figure shows the CH mean on a temperature regression of all *angulata*; measurements

Figure 3. Pembina site.

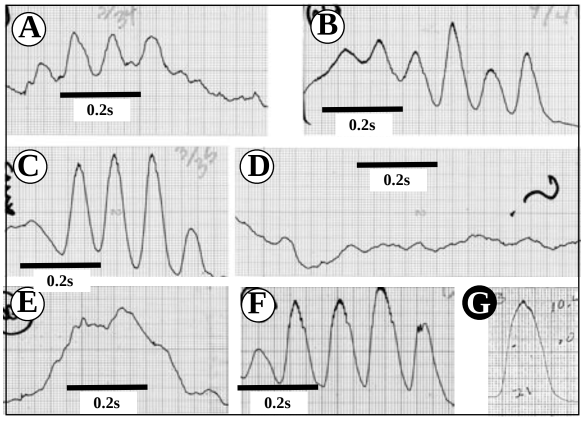


Figure 4. PM-traces (AX: rel. int./time). (see Aug. Leg.)

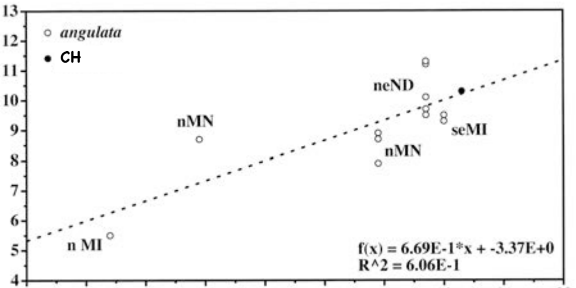


Figure 5. Flicker modulation rate (AX: Hz/temp).

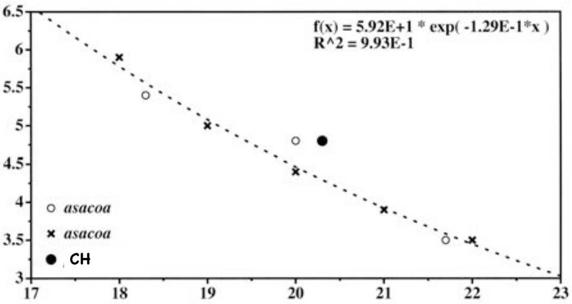


Figure 6. Prediction, long flash period (AX: sec/temp).

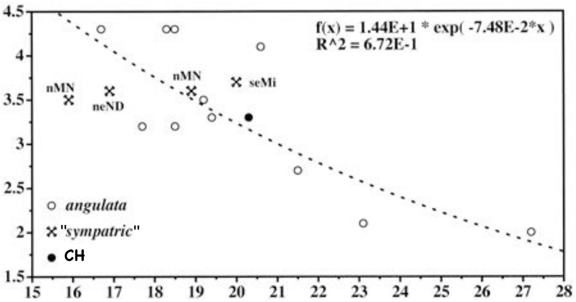


Figure 7. Flicker FP period (AX: sec/temp).

of *angulata* from the northern, mid-western region are also indicated—the extreme northern Minnesota data point is based on one interval from one male.

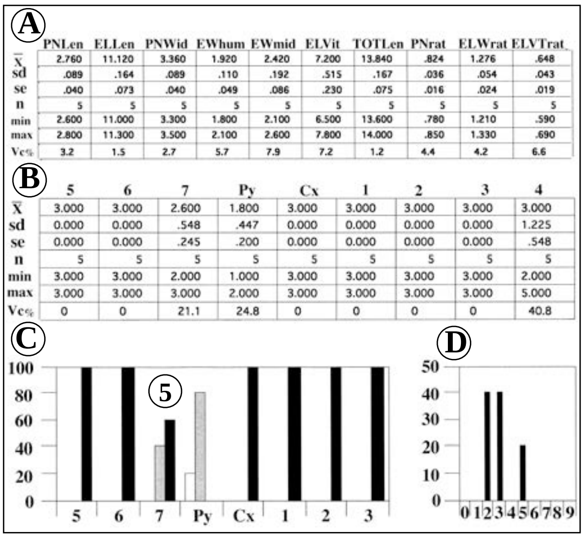
Modulations in the *angulata*-flickers of some *Photuris* species (e.g. *tremulans*, *quadrifulgens*), are occasionally not apparent (to some eyes), at least at some angles to the lantern. This fact is known by simultaneous eye-observation and PM-detection/recording. Without extensive comparison and dual recording detectors an absolute statement cannot be made about the reality of non-modulated long patterns. That is, though CH emits non-flickered long flashes of various apparent forms (**Fig. 4D, E**), in specific instances of non-flickering, an unseen flicker may actually be present. For example, the strongly modulated emission in **Figure 4F** was not apparent at recording, as noted on the PM-tape, though a strongly "warbled" side-tone of the frequency-modulated transduction was clear. From other such experiences, the eye is sometimes deceived. In all instances there appeared to the eye to be a sharp ON-transient in all long patterns, including those that are clearly *angulata*-modulated, though the PM-charts do not show this.

When a 1-2 sec moderate crescendo was LED-answered with a short flash from the hay below, the male landed a few inches from the decoy and emitted another moderate crescendo. A flying male that had given three flickers changed spontaneously to a moderate crescendo; when the LED-answered his crescendo he approached and landed, and emitted another (apparent) moderate crescendo.

Pattern switching & defaulting. Males perhaps emit short flashes primarily (or only) during the first several minutes of flashing activity and then switch to another FP. When the LED-answered short-flashing CH males (n=2) they defaulted to a long pattern: they approached the decoy, flashing the short flash <3 times, with answers, and landed in the tall grass a few inches from the decoy. Both then emitted an apparent sharp-ON moderate crescendo. With little else to draw conclusions from, CH default FP would seem to be crescendo, and the short flash and flicker FPs occur as adjunct FPs.

Morphological data. General morphological means are (n=5): PNL 2.8, ELL 11.1, PNW 3.4, EWhum 1.9, EWmid 2.4, ELVit .648, TOTLen 13.8, PNrat 0.82, ELWrate 1.28, ELVTrat 0.23 (**Fig. 8A**, with other stats). Sclerite colors and hind coxae are in **Figure 8B-C**, and edge splash on ventrite 4 in **8D**. **Figure 9** is key to skeletal plates splashing on ventrite 4. A range of pronotal vittagrams is in **Figure 10**.

Nomenclatural note. The names are those of a spiritual leader of the Sioux Nation who perhaps camped in the region in the 1800s, saw and reflected on this firefly when he considered his role and destiny in a new and significantly changing world.



A	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.760	11.120	3.360	1.920	2.420	7.200	13.840	.824	1.276	.648
sd	.089	.164	.089	.110	.192	.515	.167	.036	.054	.043
se	.040	.073	.040	.049	.086	.230	.075	.016	.024	.019
n	5	5	5	5	5	5	5	5	5	5
min	2.600	11.000	3.300	1.800	2.100	6.500	13.600	.780	1.210	.590
max	2.800	11.300	3.500	2.100	2.600	7.800	14.000	.850	1.330	.690
Vc%	3.2	1.5	2.7	5.7	7.9	7.2	1.2	4.4	4.2	6.6

B	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	2.600	1.800	3.000	3.000	3.000	3.000	3.000
sd	0.000	0.000	.548	.447	0.000	0.000	0.000	0.000	1.225
se	0.000	0.000	.245	.200	0.000	0.000	0.000	0.000	.548
n	5	5	5	5	5	5	5	5	5
min	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	2.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	21.1	24.8	0	0	0	0	40.8

FigTable 8. Morphological data.

Holotype description. male, voucher 9142, collected 14 June 1991, Pembina County, North Dakota, 6 miles w Walhalla, rt 55 at bridge. (FB page124: "KB 20 —red 9142 —slight chance for error, gave several cresc, thern gave flicker by himself [i.e. switch not default]. I ans and he approached." (FB page 46). Morphological data: genitalia not extruded; from spread sheet—PNLen 3.0, ELLen 11.0, PNWid 3.3, ELWhum 1.8, ELWmid 2.1, LELVit 7.0, TotLen 13.8, PnRat 0.85, ElRat 1.21, VitRat 0.64; Colors: T 333, Py 1, Cx 3,V 333, Edg 2. Types will be deposited in the USNM.

Augmented figure legends. 4. PM-traces of CH emissions, @20.3°/68.5°): (**A-C**) flickers emitted by the same male; (**D-E**) emissions that appeared steady to the eye but PM-records suggest the presence of subliminal modulations; (**F**) a strongly-modulated flicker that to the eye appeared to have only weak modulation strength; (**G**) a PM-trace of the short flash of *asacoa*, perhaps similar to that of CH. **5**. Modulation rate of CH flicker (dot) with means of *Py. angulata* flickers from various north-central US localities. The northern Michigan locality was at the tip of the southern peninsula, at Cheboygan, near Burt Lake. **6**. Long-flash(es) FP period of CH (dot) plotted on the calculated temperature regression data from *asacoa* crescendo FP. The three FP period means for *asacoa* were converted to rates (circles); a straight (linear regression) line through them constructed (graphed); and points along the line were (re)converted to interval (in sec) values; which were then graphed (X's); to serve as a prediction for both species. **7**. Flicker FP period of CH (dot) plotted on the regression of *Py. angulata* with measurements of *angulata* from north-central US localities indicated. The extreme measure for northern Minnesota is based on a single recorded flicker. **10.** PN vittigrams (vittae) of a short and probably not adequate as a representative array of voucher specimens of CH from the site near Walhalla.

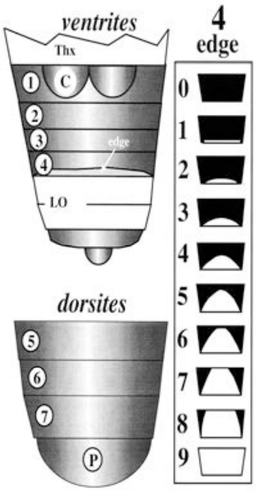


Figure 9. Topographic key.

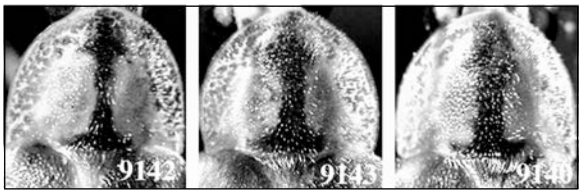
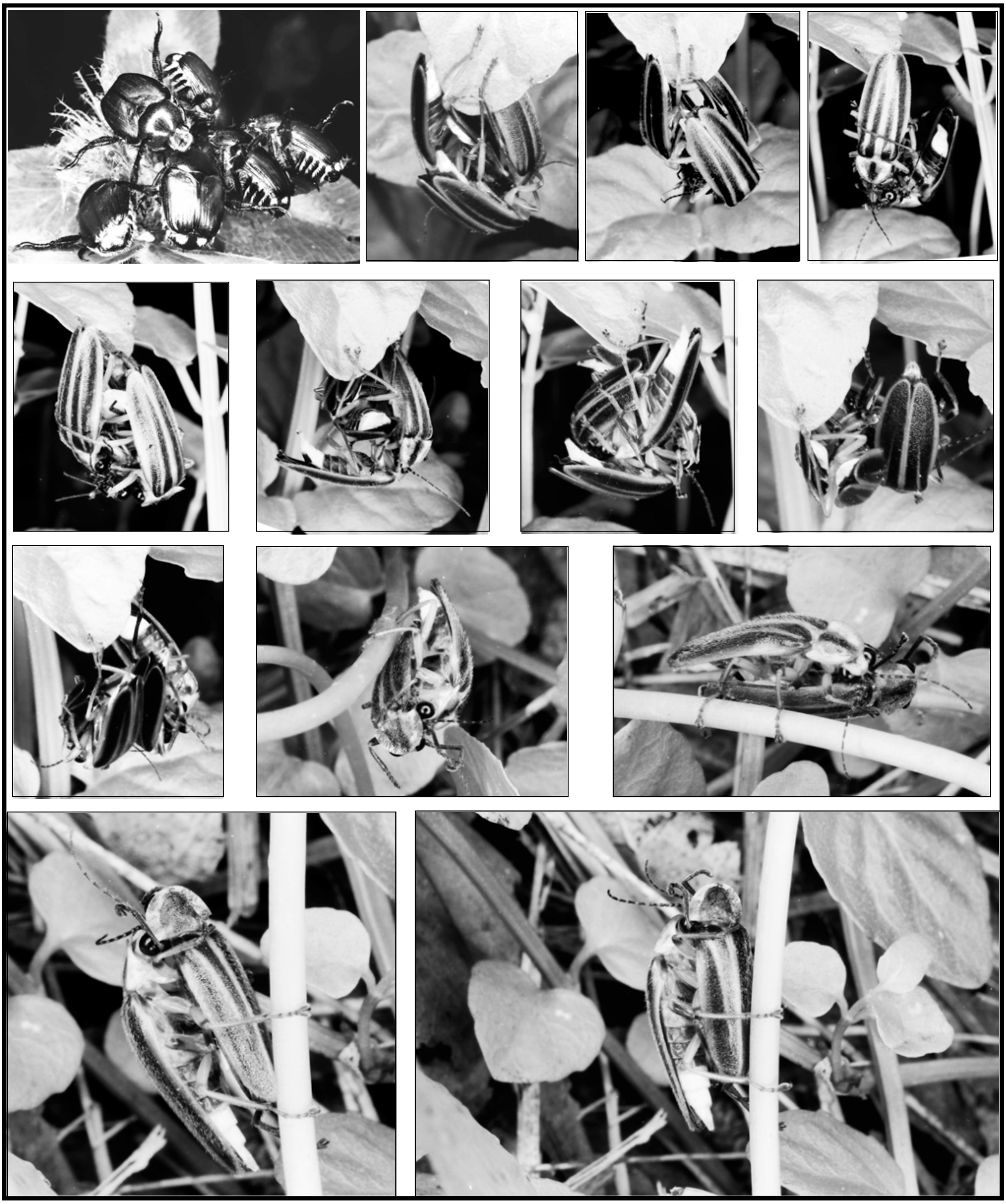


Figure 10. Voucher PN array.

Balling at the UF Medicinal Plant Garden. When a mate-worthy female Japanese beetle is available males gather and form a clump, a ball around her, competing to couple with her (photo from Madison Co. NY). Such balling also occurs when drone bumble bees (*Bombus fervidus*) compete for gynes as they emerge from nest entrances in the fall. Balling in fireflies, as observed in the Med Garden, is more complicated than "mere" sexual coupling, and probably occurs when a predaceous *Photuris* female intrudes upon a courtship in progress, say, when two competing males are in close approach to a responding potential mate. Over the years this was only observed twice and though both balls were photographed in part, specimens and data were not taken such that a proper interpretation could be made. Two photos are from one balling and the remainder, in sequence, are from the second ball—the last few revealing the outcome in a subsequent "pairing" of two participants. The predator(s) was probably *P. lamarcki*, and prey, *P. douglasae*. These ballings could have developed from the approach of competing males to the false responses of an aggressive mimic and not a conspecific female—and a contested female might also become prey?



Chapter 66

Photuris tremulans Barber 1951

Confusing Firefly

So quickly simple things come to confusion.
≈Shakespeare

This nominal species may present as many obstacles for accurate identification, that is, biological understanding and taxonomic resolution, as any *Photuris* on the North American continent. This, in spite of the fact that its FPs are *merely,* or so it might appear, a short flash (default) and the A-flicker (adjunct)—almost ultimate simplicity itself, for *Photuris*. The distribution in **Figure 1** is based entirely upon field sightings, but there are reasons to suspect that such IDs may be much too inclusive, with respect to detecting lineages/variads of biodiversity. The difficulty is not only because: (**1**) among observed populations there are unresolved inconsistencies; or (**2**) within individual populations there occur unresolved—but not unanticipated—timing differences in FP intervals; or (**3**) within populations there is an inexplicable *use* versus *non-use* of "its" two FPs; or (**4**) because its single-flash default and most commonly-used FP is, under some conditions, not readily (easily) distinguished from those of sympatric *Photuris*. It seems rather fitting that Barber should have named this firefly *tremulans* for its even-then-acknowledged “infrequently” displayed FP (flicker). This flicker (**5**) also appears as an adjunct FP among the repertoires of several other *Photuris* species; and which (**6**) *only* sometimes and in some places never(?) puts in an appearance, and there is no readily apparent trigger or ecological association to provide a clue as to why this is so—save one evening’s FP transition (scan sample) that may offer some small insight (**Fig. 3**). Lastly, as encouragement for further suspicion, (**7**) *tremulans* has what at this moment *appear* to be isolated, distinctive, diverged variads, two of which have travelled in opposite directions in FP usage. And a third, in the most southern of the Appalachians, may have lost both of these FPs, and instead—in a suggested working interpretation—uses an FP that had previously been an adjunct FP. All three are given species status in this paper. This might suggest that hidden flashing complexity and evolutionary lability exists in the various populations of *tremulans.* But, these suggestions will serve as DNA-testable suggestions to those who will begin an incautious life with *Photuris*. Perhaps my uncertainty and confusion arise from *tremulans* only because of the reputation of *Photuris* which leads one to expect complexity if not a duplicity in even the simplest of actions.

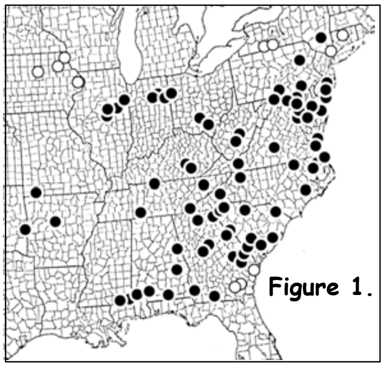


Figure 1.

Recognized here is a single, continental/operational *tremulans,* keying/ referenced on Barber’s Chesapeake-Potomac variad (**Fig. 2**), with three named variads. Fireflies identified and presently placed in this working/operational species were found over and along tree and shrub rows and gallery forests along streams, and over adjacent grasslands, meadows and hayfields (**Figs. 4-7**). The largest populations were over the canopies of Appalachian forests where thousands or millions flashed their short flash FP (**Fig. 6**), though sometimes such unreachable displays could have been those of *Ph. lucicrescens.* Among observation sites were: a small hollow below a parking lot in Davy Crocket S. P., TN (**Fig. 4**); along the berm and over low trees and shrubs at the entrance of Cedarville State Forest, MD (**Fig. 5**); over the forest canopy fronted by a hayfield along the entrance road of Gee Creek (Whitewater) Campground, Polk Co., TN (**Fig. 6,** see also **23**), and at a site that had everything—a stream, meadow, and forest, in southern Ohio (**Fig. 7**). Dates of *tremulans* observations provide data for expectations of phenology (G’SOBS), and are shown in **Figure 8**—these data are influenced by the times of annual travels northward during several spring seasons, as well as ID uncertainties already noted.

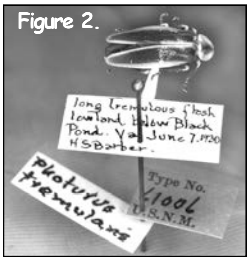


Figure 2.

Flashes, behavior, uncertainty. Short flashes are emitted during slow sometimes hovering flight, but flickering males fly rapidly, almost recklessly, emitting luminescent, beaded strands around boughs and along edges, and race around boughs high along tree rows. They also flicker at lower altitudes, over shrubs, grass, and herbs. Observed flicker pulse number ranged 9-14, and flicker durations as long as 1.5 seconds were SWAT-timed. Both FPs must be observed and defaulting from the flicker to the short flash elicited for definite ID. The short flash sometimes appears to be a snappy (flashbulb) burst. In mate-seeking males it is emitted at intervals of 2-6 seconds, depending upon temperature and other factors (**Figs. 9, 10A, C, E**; rate in **Fig. 11**). The considerable variation noted in **Figure 9** is discussed below and is based on 425 individual data points, most being

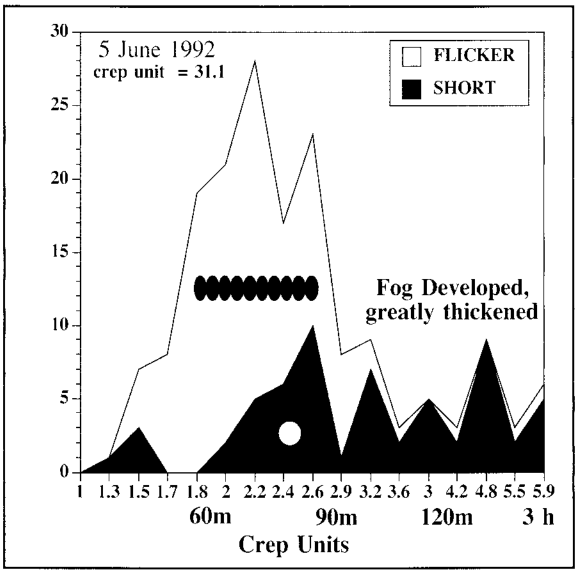


Figure 3. Scan sample, Halifax Co. NC (AX: n/creps-min).

Figure 4. A Tennessee hollow.

Figure 5. Cedarville, MD site.

Figure 6. Gee Creek forest, entrance drive before "development.".

Figure 7. Ohio site with everything.

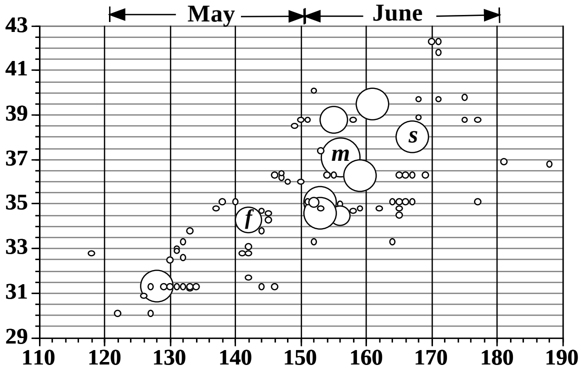


Figure 8. G'Sobs records (AX: Lat/DOY); noted < many.

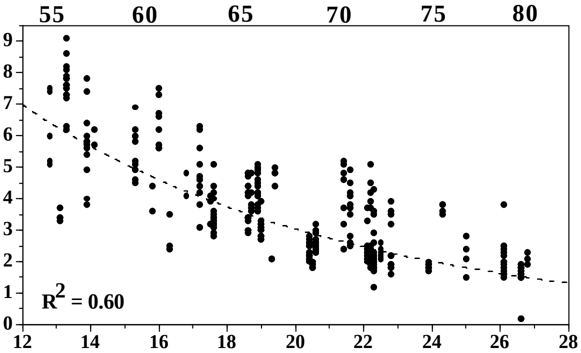


Figure 9. FP period, short flash (AX:sec/temp).

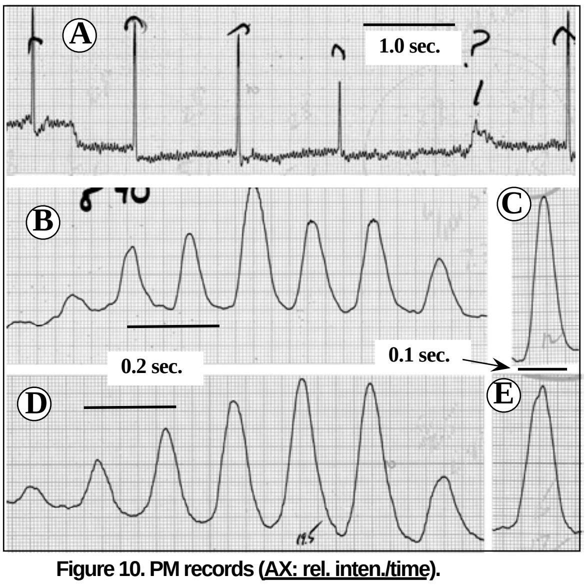


Figure 10. PM records (AX: rel. inten./time).

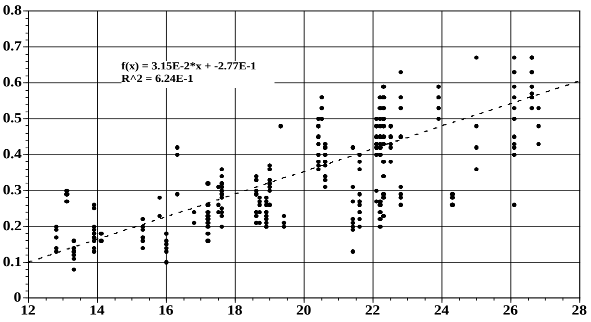


Figure 11. FP (short flash) rate (AX: Hz/temp).

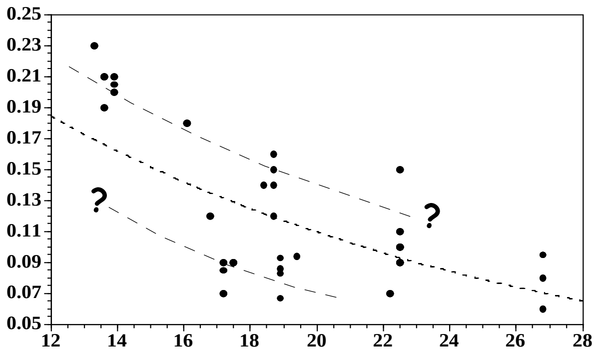


Figure 12. Duration of single flashes (AX: sec/temp).

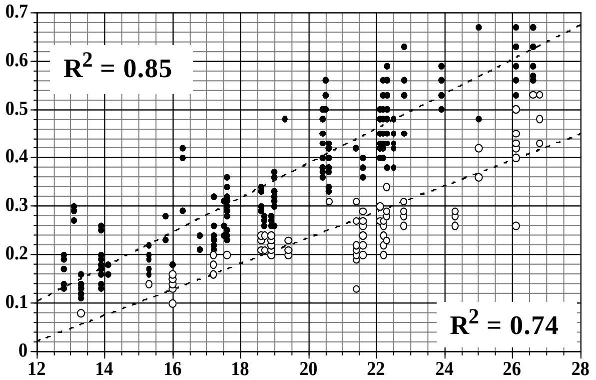


Figure 13. Rate separation "by eye" (AX: sec/temp).

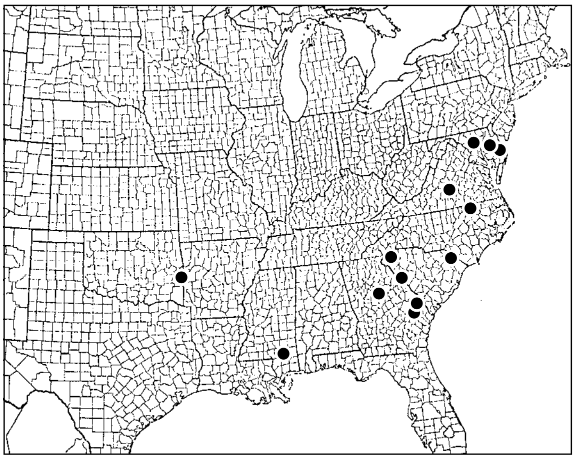


Figure 14. County records of observed defaults.

SWAT-measured intervals of individuals, but a few mean intervals from PM-recorded sequences of individuals were included. When being attracted to a decoy males typically began to emit their short flashes more rhythmically and at intervals shorter than those used by cruising males (discussed below). Defaulting (previously-flickering) males seem to immediately enter this short-interval, rhythmic mode.

PM-recordings of flashes suggest that short-flash FP duration may fall into two or three modes (**Fig. 12,** ?-lines added by eye). Bioluminescence spectrum was measured in three samples from near Barber's bailiwick (Biggley et al):

	peak	half-max		n	locality
23 Jun '68	552	527.5	597	9	Baltimore Co. MD
24 Jun '68	553	528	595	2	Harford Co. MD
24 Jun '78	558	531	602	6	Washington Co. MD

Short-flash period modes? When short-flash periods are plotted as a function of temperature (**Fig. 9**), there appears to be a tight clustering along and just below the regression line; on the other hand above the line (the slower side of the FP intervals), the points are dispersed, appear to be more variable. Sampling bias can produce this, but there may something else to note. When short-flashing *tremulans* males were attracted to a decoy it often appeared that their FP intervals became shorter and more regular, even rhythmic. Perhaps there are two modes in the timing of short flash FPs. Data for the two situations were not identified as to this distinction, so they were reviewed/eyed to see whether there were any suggestion of this. In **Figure 11** all short FP intervals are plotted as rates (1/period) to arrange them along a (nearly?) straight line regression—FP-timing is more easily visualized. Then a separation of the two speculated modes was made **by eye**, and a rate/temperature regression was made for each imaginary set (**Fig. 13)**. This should be easily tested with a SWAT and penlight without complication.

Two explanations for such a difference, should it be real, come to mind: (**1**) If searching males aim their flashes at specific points in the boughs and herbs over which they search—such targets being those more likely to be locations of females—and such targets occur at varying flight distances along the flight path—then variability should be expected to decrease when males receive an answer from a specific location, and begin to move directly toward a specific, immobile target in space. When higher ambient light permits searching males to see details of their search area more clearly—say, the first minutes of evening activity—short-flash FP periods may be longer than they will a few minutes later/darker.

(**2**) Flash period may be connected with coding for species recognition and/or predator avoidance/tricking in a CM con-

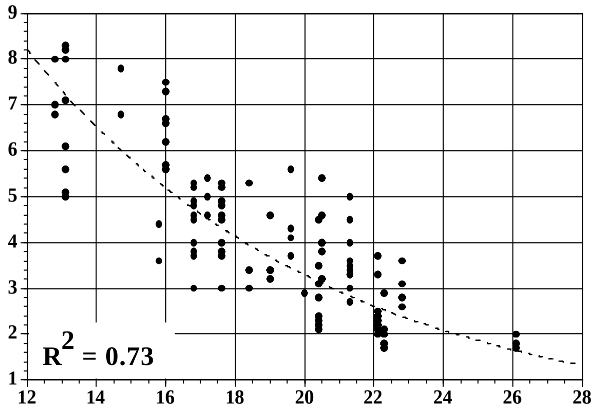


Figure 15. Flicker FP period (AX: sec/temp).

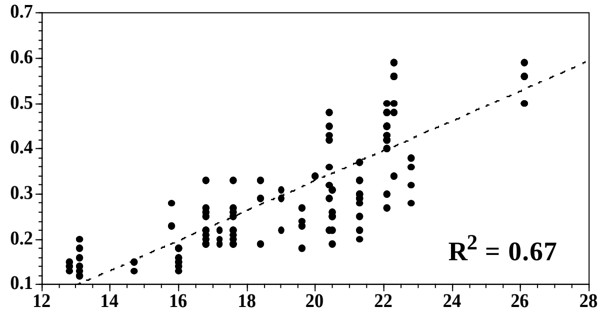


Figure 16. Flicker FP interval rate (AX: Hz/temp).

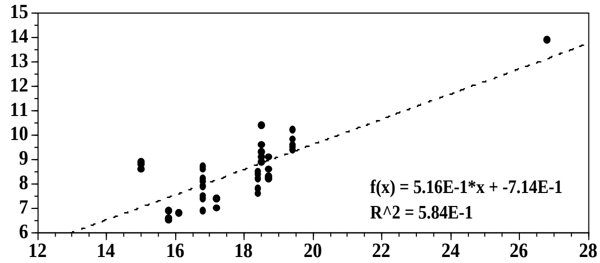


Figure 17. Flicker modulation rate (AX: Hz/temp).

text. Unlike species with multipulse or other complex FPs, a species with but a single short-flash FP may use subtle variations in pulse timing or flash durations, easily overlooked or dismissed unless flash interactions are closely examined.

Some populations diagnosed as *tremulans* were observed to emit only short flashes, and one, in South Carolina, only flickers; others emitted both. Possibly over several evenings in any of these demes, both would have appeared, but perhaps some populations are losing or have already lost either the short or flicker FP. This possibility in mentioned because of behaviors observed on suspected variads from *tremulans*: *Photuris margotooleae* on Long Island, NY, and *Photuris stanleyi* in Florida; see also *forresti*. **Figure 14** shows counties where decoyed and female-answered flickering males were seen to default to the short FP.

A-Flicker FP. The adjunct FP is the A-flicker (**Fig. 10B, D;** period in **Fig. 15,** rate in **Fig. 16**), which, as Barber noted is the much less common of *tremulans* FPs. On rare occasions it was used exclusively for an entire evening or part of an evening; in other presumed *tremulans* demes it did not appear (during observations). At the Cedarville site (**Fig. 5**) a flicker was not seen for the first three evenings of observation, but on the fourth it was used exclusively for much of the evening. With one exception there were no clues or suggestions as to what conditions result in the emission of this FP: By chance, in the only scan-sample made of this species (Halifax Co., NC, **Fig. 3**), the simultaneous presence of two variables, time-of-night and fog, prevents definitive insight—but **note** that the **number** of males emitting the short flash **after** fog onset does not suggest that flicker emitters began emitting short flashes!

Flicker modulation rate is near that of *Pyractomena angulata* (A-flicker) and may be rather precise if the flickers from the same geographic area are compared.

Figure 18.

A similar flicker FP is used in several other *Photuris*, but only that of *quadrifulgens* was seen and possibly common in the same area at the same time as *tremulans*. Note in **Figure 19** that the two are seasonally separated in the south and less so in the north (see also Chap. 59, Fig. 27). Perhaps at such times *quadrifulgens* emits the D-flicker (*Py. dispersa* rate)? The two *Photuris* species may be somewhat spatially separated, field versus forest edge. Unfortunately their flickers were not PM-recorded when they were together and flickering.

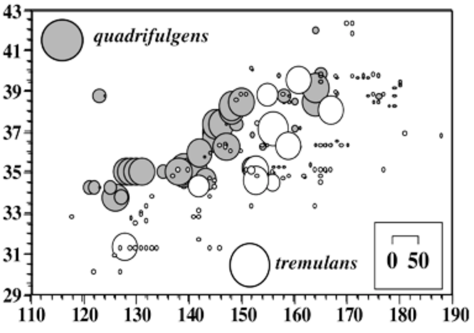


Figure 19. See also Figure 27 in Chapter 59.

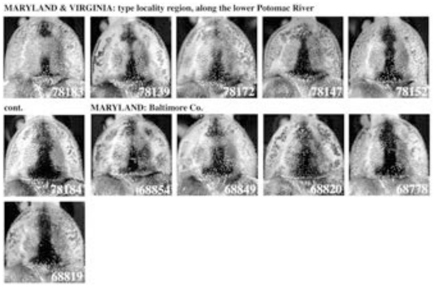


Figure 20. Vittagrams from two localities.

❊ ❊ ❊

Morphology. In hand *tremulans* is a dark firefly, similar to *versicolor* and *quadrifulgens* in appearance, with dark hind coxae, usually with short elytral vittae and rarely with none (**Figs. 18, 23**, **FigTable 21, key in Fig. 22**; it is somewhat smaller than *versicolor* and *quadrifulgens*, and one would suspect males to be preyed upon by females of both of these, and any CMs employed, adapted to counter the tactics of them in particular. A PN vittagram array is in **Figure 20**.

FigTable 21. Morphology: Voucher measurement & Pigmentation.

tremulans MD cv

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.450	9.750	2.975	1.800	2.288	4.575	12.213	.820	1.286	.469
sd	.093	.239	.104	.093	.125	1.723	.242	.027	.042	.179
se	.033	.085	.037	.033	.044	.609	.085	9.636E-3	.015	.063
n	8	8	8	8	8	8	8	8	8	8
min	2.300	9.400	2.800	1.600	2.100	2.300	11.800	.780	1.210	.230
max	2.600	10.100	3.100	1.900	2.400	7.500	12.600	.860	1.360	.780
Vc%	3.8	2.5	3.5	5.2	5.5	37.7	2.0	3.3	3.3	38.1

tremulans TN

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.530	9.550	3.030	1.740	2.290	1.900	12.070	.840	1.324	.202
sd	.125	.922	.170	.171	.256	1.413	1.003	.032	.128	.153
se	.040	.291	.054	.054	.081	.447	.317	.010	.040	.048
n	10	10	10	10	10	10	10	10	10	10
min	2.300	7.600	2.800	1.500	2.000	0	9.900	.800	1.200	0
max	2.800	10.800	3.300	1.900	2.900	3.800	13.300	.880	1.640	.410
Vc%	4.9	9.7	5.7	9.8	11.2	74.4	8.3	3.8	9.7	75.7

tremulans MD blt

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.510	9.740	3.050	1.860	2.310	4.990	12.250	.828	1.257	.518
sd	.099	.566	.172	.237	.145	1.197	.667	.026	.100	.146
se	.031	.179	.054	.075	.046	.378	.211	8.273E-3	.032	.046
n	10	10	10	10	10	10	10	10	10	10
min	2.300	8.800	2.800	1.500	2.000	3.500	11.100	.800	1.000	.350
max	2.600	10.400	3.300	2.400	2.400	7.100	12.900	.880	1.360	.790
Vc%	3.9	5.8	5.6	12.7	6.3	24.0	5.4	3.1	8.0	28.2

tremulans GA 10$

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.400	9.525	2.838	1.675	2.225	1.163	11.900	.845	1.336	.117
sd	.177	.565	.220	.149	.139	1.257	.735	.028	.074	.127
se	.063	.200	.078	.053	.049	.444	.260	1.000E-2	.026	.045
n	8	8	8	8	8	8	8	8	8	8
min	2.000	8.400	2.400	1.400	2.000	0	10.400	.790	1.290	0
max	2.500	10.300	3.000	1.800	2.400	2.500	12.800	.870	1.460	.250
Vc%	7.4	5.9	7.8	8.9	6.3	108.1	6.2	3.3	5.5	108.5

tremulans GA 10$ 4 sec

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.480	10.060	2.990	1.900	2.340	2.970	12.560	.833	1.234	.292
sd	.103	.448	.213	.067	.117	1.617	.527	.025	.058	.155
se	.033	.142	.067	.021	.037	.511	.167	8.035E-3	.018	.049
n	10	10	10	10	10	10	10	10	10	10
min	2.300	9.000	2.600	1.800	2.100	0.000	11.500	.790	1.190	0.000
max	2.600	10.600	3.300	2.000	2.500	6.000	13.300	.870	1.330	.590
Vc%	4.2	4.5	7.1	3.5	5.0	54.4	4.2	3.0	4.7	53.1

tremulans cedarv

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	2.500	1.125	3.000	3.000	3.000	3.000	3.125
sd	0	0	.535	.354	0	0	0	0	1.959
se	0	0	.189	.125	0	0	0	0	.693
n	8	8	8	8	8	8	8	8	8
min	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	0
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	0	21.4	31.5	0	0	0	0	62.7

tremulans tn

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	2.700	1.000	3.000	3.000	3.000	3.000	3.500
sd	0	0	.483	0	0	0	0	0	1.900
se	0	0	.153	0	0	0	0	0	.601
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	0
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	0	17.9	0	0	0	0	0	54.3

tremulans balto

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	2.600	1.000	3.000	2.800	3.000	3.000	3.200
sd	0	0	.516	0	0	.422	0	0	1.874
se	0	0	.163	0	0	.133	0	0	.593
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	2.000	1.000	3.000	2.000	3.000	3.000	1.000
max	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	0	19.9	0	0	15.1	0	0	58.6

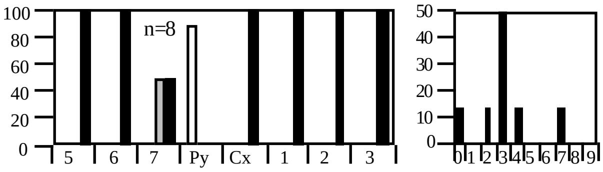
tremulans 10$

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	3.000	1.143	3.000	3.000	3.000	3.000	2.571
sd	0	0	0	.378	0	0	0	0	1.397
se	0	0	0	.143	0	0	0	0	.528
n	7	7	7	7	7	7	7	7	7
min	3.000	3.000	3.000	1.000	3.000	3.000	3.000	3.000	1.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	0	33.1	0	0	0	0	54.3

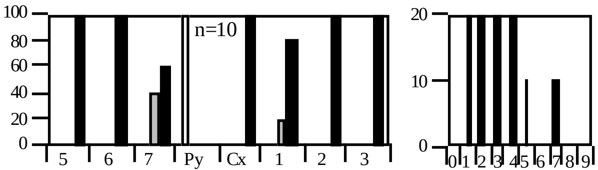
tremulans 10$ 4 sec

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	3.000	2.900	1.300	3.000	3.000	3.000	3.000	2.500
sd	0.000	0.000	.316	.483	0.000	0.000	0.000	0.000	1.509
se	0.000	0.000	.100	.153	0.000	0.000	0.000	0.000	.477
n	10	10	10	10	10	10	10	10	10
min	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	1.000
max	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	6.000
Vc%	0	0	10.9	37.2	0	0	0	0	60.4

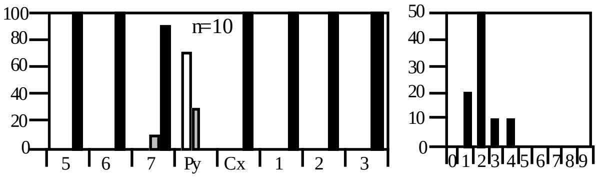
tremulans MD cdv



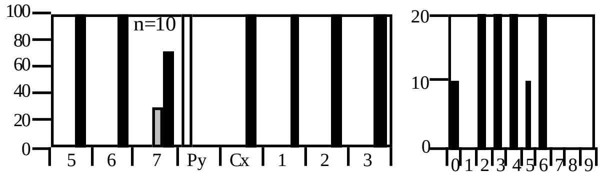
tremulans MD balt



tremulans GA 4-$



tremulans TN



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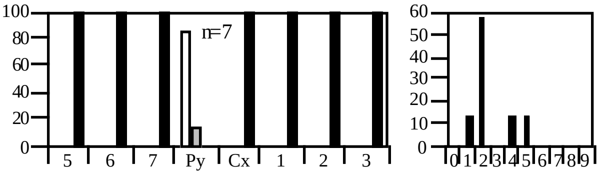


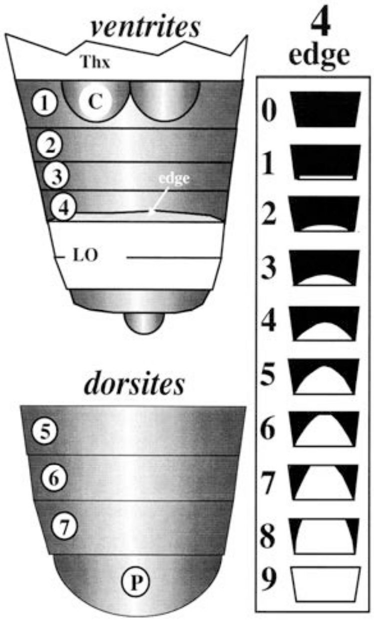


Figure 22. Key to anatomical elements.

Adjunct figure legends. 3. Scan-sample, Halifax Co. NC site, showing number of males emitting the two FPs, and then a drop in activity as fog developed, as also recorded in *Ph. stevensae*. Time of evening may be one factor that determines the use of the default versus the adjunct flicker FP. **4**. Study site at Davy Crocket State Park, Sumner Co. Tennessee, where *Py. angulata* and P*h. tremulans* flew together. **5**. Study site along the entrance road at Cedarville State Forest in Maryland, just east of Washington, D. C. **7**. This site in southeastern Ohio combined many features associated with *tremulan*. **10**. Photo-multiplier (PM) traces of short flashes and flickers: (**A**) Cedarville MD site, 13.8°; (**B**) Davy Crocket TN site, 16.8°; (**C**) Pot Spring (Baltimore Co.) MD, 20.6°; (**D**) Cedarville MD site, 13.8°; (**E**) Cedarville MD site, 15.8°. **12**. Regression of short-flash duration on temperature, from PM-records. The considerable variation may be partially connected to actual differences in male behavior, but other factors, such as distance between flash and PM-detector, are involved. These data are shown for this species because of the possible involvement in flash-communication coding. **13**. The data points in Figure 12 separated (by eye) into two possible sets, reflecting differences in target-approaching versus cruising male emissions.

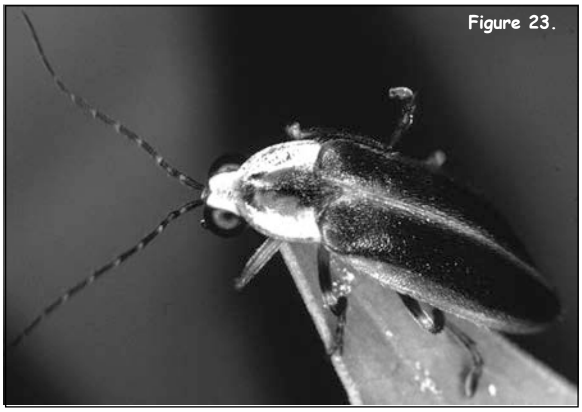


Figure 23.

Fig. 24. Gee Creek TN site, near river.

Chapter 67

Photuris versicolor (Fabricius) 1798

SRFP-*Versi* (slow repeating, fast pusing)

Photuris versicolor s.s. is known to occur in a narrow triangle in eastern North America (**Fig. 1**), with its apex in northern New Jersey. At its northeastern and southeastern limits it yields to contiguous variads: in the southeast to *harrannorum* on the Florida peninsula, and in the northeast, in New England and on Long Island, to *stevensae.* Its FPs are seen in a variety of habitats including grassland—in large, sparkling populations (**Fig. 2**), and open glades, sometimes flying from ground level to the crowns of trees. Males are often seen flying singly, in roving mode, high along woods edges as observed in *fairchildi* (**Fig. 3**). Hunting females and roving males pass through many ecological situations where other species are active. Females hunt and lay eggs where prey is abundant, presumably for both adult females and their omnivorous larvae. Males emit a variety of diagnostic FP variations which are crudely illustrated in **Figure 4** (described more fully below); the figure shows regional differences that may provide useful clues for recognizing diversity beyond the present 3-species (nominal) level (data from FB anecdotal mentions, not systematic counts).

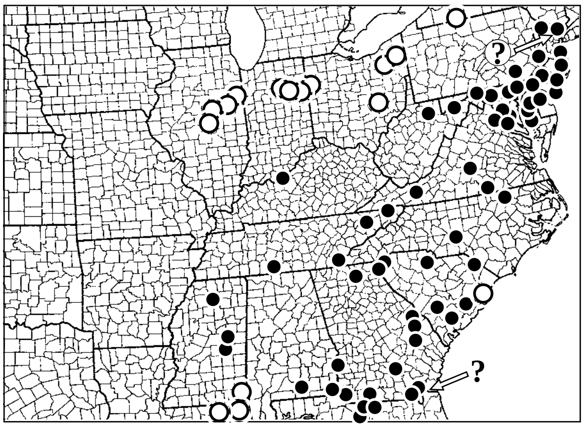


Figure 1. Dots, continental *versicolor*; circles, not sighted.

Figure 2. Hayfields and meadows, V. & M. Smith farm, Fairfax Co., VA—all gone now.

Figure 3. Forest edge flight-way, Madonna, northern MD.

Some FPs are shared with both *harrannorum* and *stevensae.* **Figures 5** and **6** compare the repertoires of these two with the that of *versicolor* from adjacent regions. Though not seen in these charts, in the field the actual frequency (profiles) of occurrence at a site differs conspicuously among these OTUs: in Florida's *harrannorum* the J3-4 is nearly always the FP observed, except when several are seen together in the treetops, when J5-6 is common. In demes of *stevensae* a variety of FPs is seen at a site on most evenings, and the "≈A-flicker," an FP not occurring in *versicolor's* repertoire, is virtually always presented in numbers. Possibly a graded continuum of pulsing FPs is significant in *stevensae* communication (e. g. **Fig. 6**). Especially note that the repertoire of Florida's *harrannorum* is in better agreement with Barber's original description of *versicolor's* repertoire, and that *versicolor* actually emits a broad range of FPs.

Although locality is presently definitive for diagnosis, as presented here, *versicolor* can be distinguished from Florida's *harrannorum* by the occurrence of 3e and 4e FPs (**Figs. 4, 9E**) —i.e., FPs with 3 or 4 pulses that are of even/equal, i. e. not diminishing intensity—such are of exceedingly rare occurrence in *harrannorum.* No clear evidence of intergrading was noted in the few evenings spent in the presumed region of contact of the two. In the northeast, *stevensae* populations will always include —except for a very brief initial early-evening moment—males emitting the <1-sec-long rapidly-pulsed flicker (≈8Hz, A-flicker), which in *versicolor's* range is emitted by *tremulans* and *quadrifulgens*, and perhaps (though less commonly?) by *cinctipennis.* (To identify emitters of flicker FPs, a decoy response will usually induce defaulting to a diagnostic FP.) The geographic line of separation between *versicolor* and *stevensae* may be the Hudson River—Manhathattan Island, and Central Park may have resident populations of *stevensae,* which

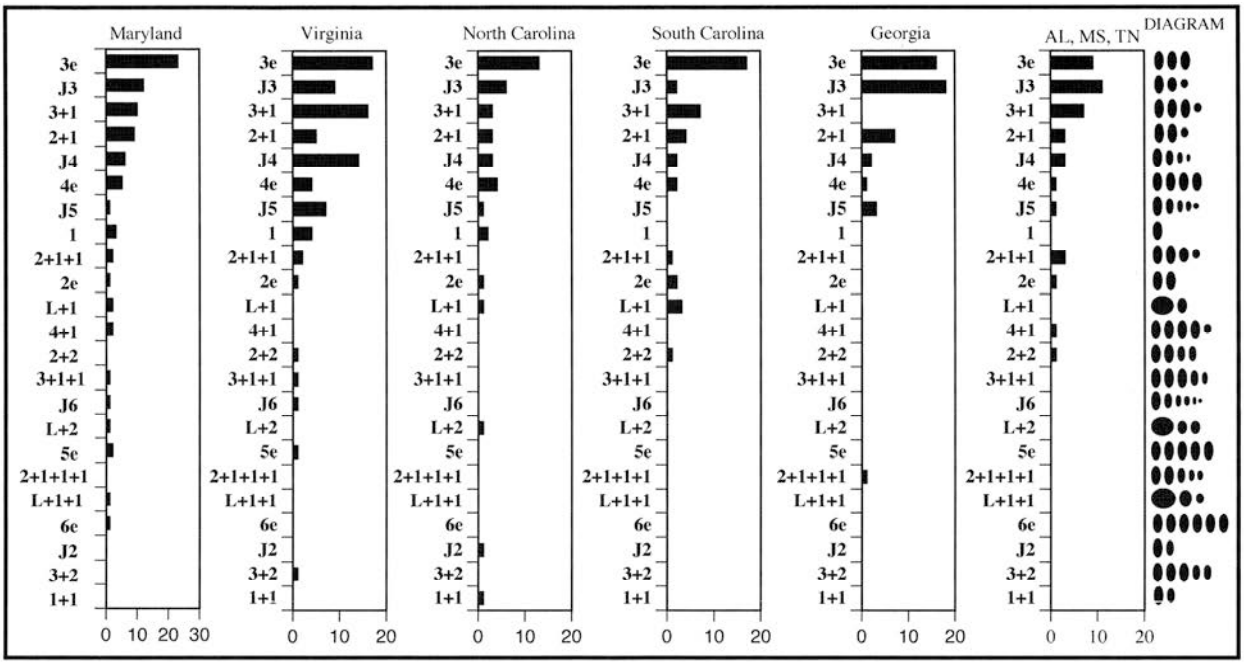


Figure 4. Vertical axis: array of FPs emitted by *versicolor*, by "code designation" at left, and symbol at far right.

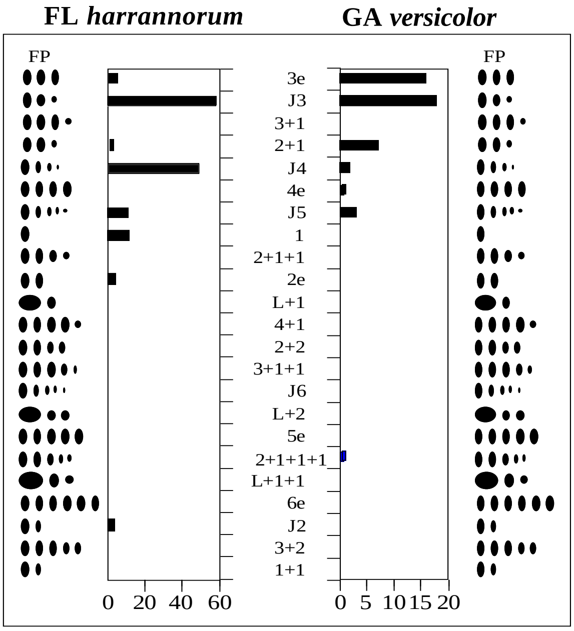


Figure 5. FP repertoires of *harrannorum* and GA *versicolor*.

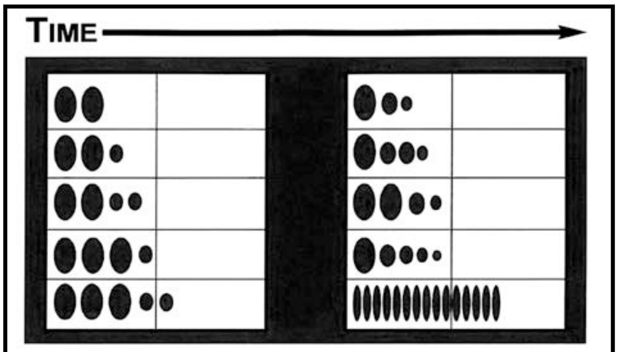


Figure 6. Using the fieldbook sample of FP configuations as guide, perhaps FPs were drawn (sampled) from a continuum such as shown here that quantifies some aspect of male quality or history?

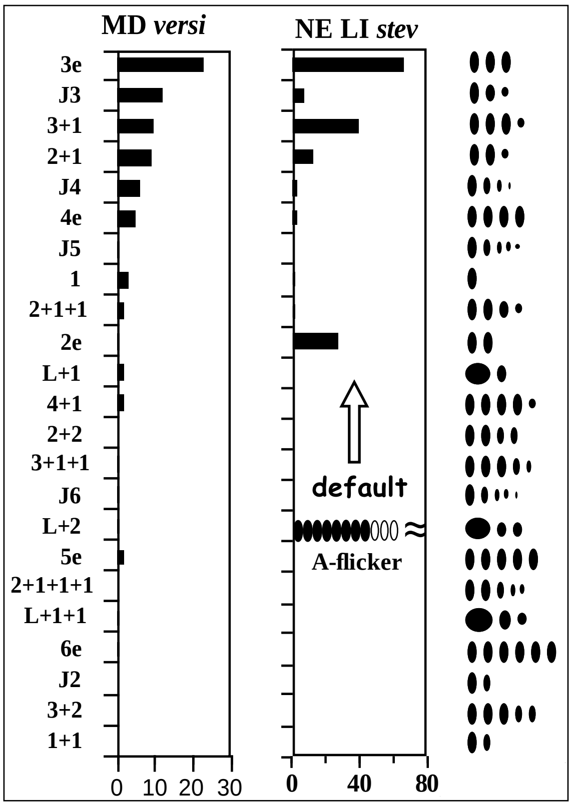


Figure 7. Repertoire comparisons.

was found in the Bronx in the Pelham Bay region along a tree row by the golf course parking lot (thanks to Durland Fish), and further north in Putnam County. It was not seen on a brief overnight camp on Staten Island but the night was early seasonally, and "cool."

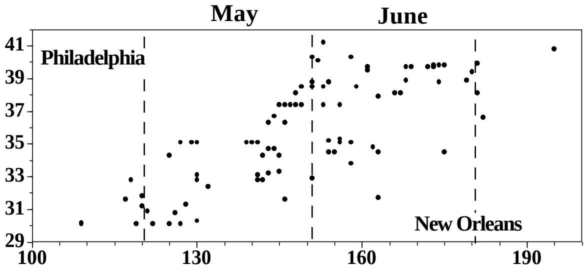


Figure 8. G'SOBS records of seasonal occurrence (AX: Lat/DOY).

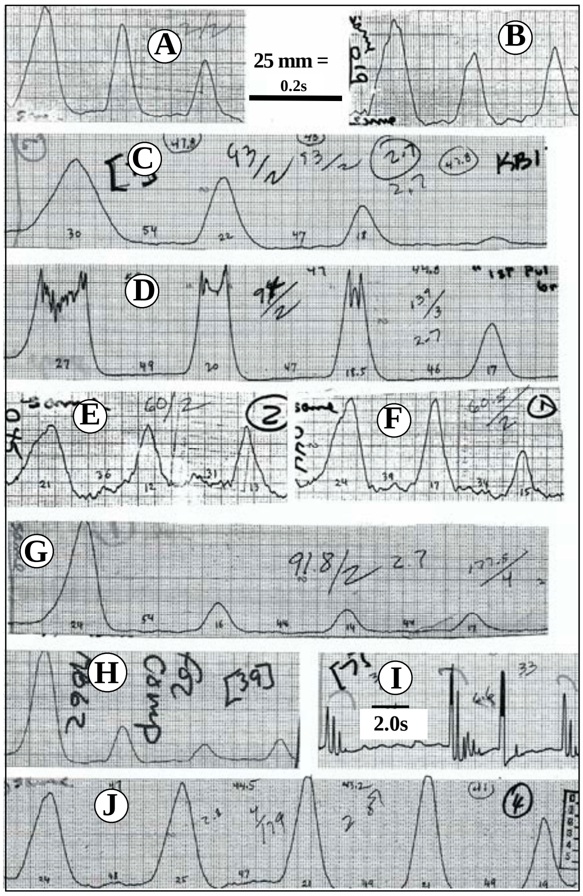


Figure 9. PM FPs from *versicolor* repertoire (AX: Rel. Int./time).

Nomenclature of these FPs is discussed in the text, but in particular, note the coding potential possible in E and F, where pulse intensity and duration seem to be "mismatched" compared with "here-recognized" FP types/modes.

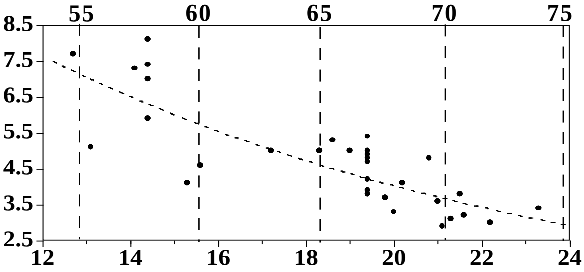


Figure 10. Pulsing FP period (AX: sec/temp).

It would be surprising if *versicolor* as constituted here were not found to have regional genetic and FP repertoire differences within the working distribution shown in **Figure 1**—though it might be argued that these fireflies are more vagile/mobile and apt to be less regional because females roam broadly to hunt and lay eggs, and males rove broadly to find them. FP subtleties and variations of *versicolor's* FPs are numerous and complex—to the eye/brain and the PM-detector—and regional difference may be tedious to distinguish. **Figure 1** shows open circles where no *versicolor* FPs were seen but might have been expected—shown here to anticipate geographic limits of *versicolor* occurrence.

Season of occurrence across a range of latitudes is late-spring and early summer, May-June (**Fig. 8**).

Flashing details. The diagnostic FP for *versicolor* is the group of 3-4-6 fast pulses, most commonly 3-4 (except in dense populations(?); these often have various step-down but **never step-up** intensity changes (**Fig. 9A, C, D, F, I**). FPs are emitted at 3-5 sec intervals (**Fig. 10**; rate in **Fig. 11**). That step-down FPs of several forms (**Fig. 4**) actually occur and are not merely an optical illusion is confirmed in PM-recording, but some occur that are not perceived and the eye/brain often misses or is uncertain of flash-duration and intensity differences. Thus, the charts in **Figures 4, 5, 7**—based on counts of incidental **not** systematic notations in field books—are preliminary and estimates. These may guide DNA and other analyses probing the nature of "intraspecific" diversity in this operational *versicolor*. Pulse rate within pulsing FPs ranges 2-5 Hertz (11°/52°-20°/68°; **Fig. 12**).

As specific examples of nomenclature used here for diagnostic, step-down FPs: 2+1 (=2 bright, 1 dimmer, **Fig. 9F**); 1+2 (= 1 bright, 2 dimmer, **Fig. 9B**); 1+1+1 or J3 (3 all step down, **Fig. 9A**) and 1+1+1+1 or J4 (4 all step down, **Figs. 9C** and **D**). Especially note: FPs in Figure **9C** and **9D** were emitted by the same male, but the PM sensitivity was turned up for **9D** to get a good record of pulse 4, which resulted in the brighter first three overloading the system; second, the eye/brain will not correctly diagnose the FP in Figure **9G,** nor is it clear from the PM trace—it could be a 1+1+2, or a 1+3, or emitted/programmed as seen. Simultaneous PM-detection from two directions would presumably resolve many such ambiguities. The FP in Figure **9J** was one in a series of six emitted by a single male which included normal and unusual configurations. As examples and crude flash duration estimations from PM-records: at 15°/59°, pulse #1, base 220 mSec, half max 110 mSec; #2, 190, 72; #3, 144, 64.; and at 18.9°/66°, #1, 144, 88; #2, 104, 56; #3, 96, 60.

Single, short-flash FPs were occasionally observed and PM-recorded in *versicolor* populations. Some resemble individual pulses seen in pulsing FPs, and some could have been from intruding *tremulans* or possible *fairchildi*. Barber noted the occurrence of unattributable single flashes and referred some to "primitive unnamed." He notes, "The … simple flash is given

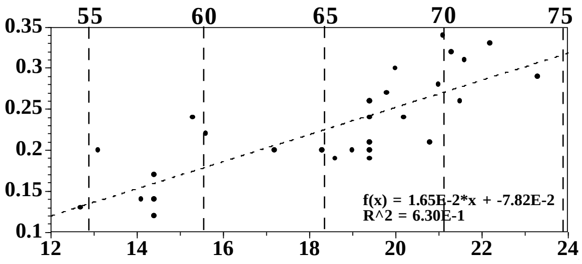


Fig. 11. Pulsing FP interval rate (AX: Hz/temp).

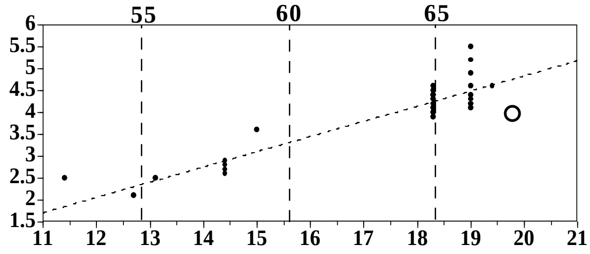


Fig. 12. Modulation rate of pulsing FP (AX: Hz/temp).

in such diverse colonies, varying so in size, color, localities, and dates of appearance, that no well-defined single species is discernible at this time, and no specific name is here attached to samples." In **Figure 13A** is what appears to be the transition of a J3-flashing (1+1+1) changing to a single flash. **Figure 13B** and **D** show sequences of single-flash FPs at different rates, and **Figure 13C**, example flashes from these sequences. Perhaps some of these mimic a particular prey species of their females, as found in spring populations of *harrannorum* in Florida—which emits single flash FPs in association with the FP of the spring-only firefly *Pyractomena limbicollis*—such short flashes have not been observed to be emitted by fall *harrannorum*, the offspring of the spring generation (D. Minnick, unpub.). **Figure 14** shows the FP intervals of single flashes in Maryland, possibly emitted by *versicolor*.

The bioluminescent spectrum data of Maryland *versicolor*, are: mean 555 millimicrons, half max 529.0 and 599.0, n = 5 (Biggley et al).

❄ ❄ ❄

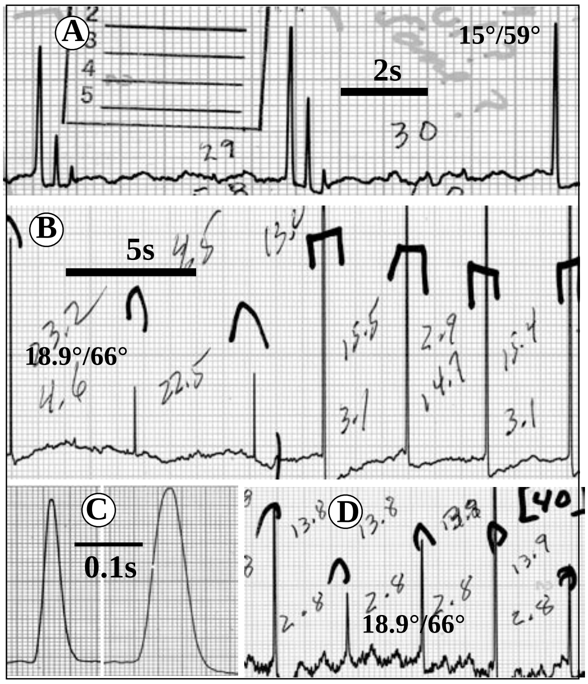


Fig. 13. Unidentified singles in a SRFP-versi deme.

***Ph. versicolor* FP confusion: historical, clerical, nomenclatural.** Biologically the “*versicolor* problem” is tentatively reduced to three identifiable OTUs: (**1**) continental SRFP*versi* (*versicolor* s.s.), with additional regional distinctions possibly yet to be made in a bottom-up pursuit of deme distinctions; (**2**) Florida *harrannorum*; (**3**) New England-L.I. *stevensae.*

Barber’s FP figure and notes were assembled by others for publication after his death and errors occurred which are of some importance and are reviewed here: **Figure 15** shows his three *versicolor* lines, 6, 7, 8, as scanned from his Figure 1. **Line 6** shows a 6-pulse down-stepped FP (J-6, or 1+1+1+1+1+1), and is but one of several FPs for *versicolor* that Barber notes in his text; it is the only illustration of the three that agrees with the text, and that is not in error with respect to actual field observation. **Line 7** is identified in Barber’s chart as “var. *quadrifulgens*.” Though the Line 7 pulse rate matches that of an FP that is actually emitted by *versicolor* (that is, the 3e/3-even), the actual FP of *quadrifulgens*, as verbally described by Barber and since observed during this study and by others (e. g., Forrest and Eubanks, 1995), is composed of longer pulses emitted at a much slower rate, as shown at the bottom right of **Figure 16** (see "var. *quadri*-"). From Barber’s Key: “male coruscations consisting of four slow flashes. Cape Henry VA,” and from his text, page 30, “… greenish, bright, perhaps one-half second flashes in series of four, with short intervals [pulse

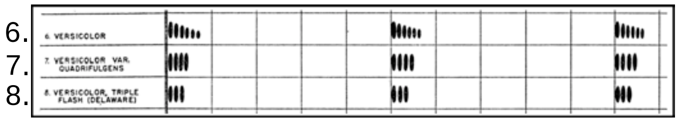


Figure 15. From Barber's Figure 1.

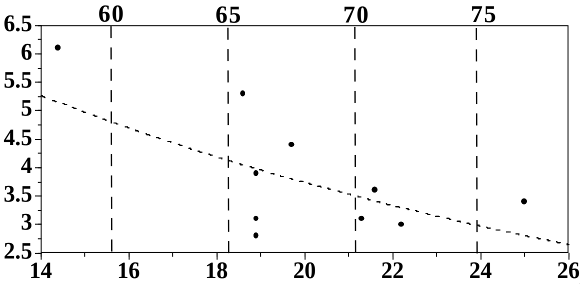


Fig. 14. Short-flash FP period (sec/temp).

periods] of about a second and longer intervals [FP periods] at a quarter to a half a minute ….” (note bracketed inserts). **Line 8**, a triple flash, as emitted by *versicolor*, and in actuality, in various pulse-intensity configurations (see Figures above). **However**, the triple flash observed by McDermott, which was Barber’s reference, was described by McDermott as pulses **increasing** in intensity **(bottom of Fig. 16, 1&1&1)**, which step-**up** form does not occur in *versicolor*. McDermott probably observed one FP of *fairchildi*. Barber’s text reads: "… flew 3 to 10 feet above the grass, emitting three rapid **successively brighter** flashes at 2- or 3-second intervals." [jel emphasis]

Taxonomically, and speculatively, that Barber, an experienced and competent taxonomist, would name *quadrifulgens* as a subspecies is curious, but perhaps he did it as a solution to an unsolvable problem he had encountered. Taxonomists that formally describe “sub-species,” correctly do so only for allopatric populations. Barber’s *quadrifulgens* locality was near Cape Henry, VA, and possibly he thought that this was out of the range of *versicolor*. This is doubtful because *quadrifulgens* occurs in Maryland and Virginia, and it seems unlikely that he had not seen the two in sympatry in his bailiwick. Perhaps he saw that his slow pulsing "versi" (*quadrifulgens*) as well as his *tremulans* and *cinctipennis* all emitted the "≈A-flicker" and this was a source of uncertainty? This remains for consideration another time.

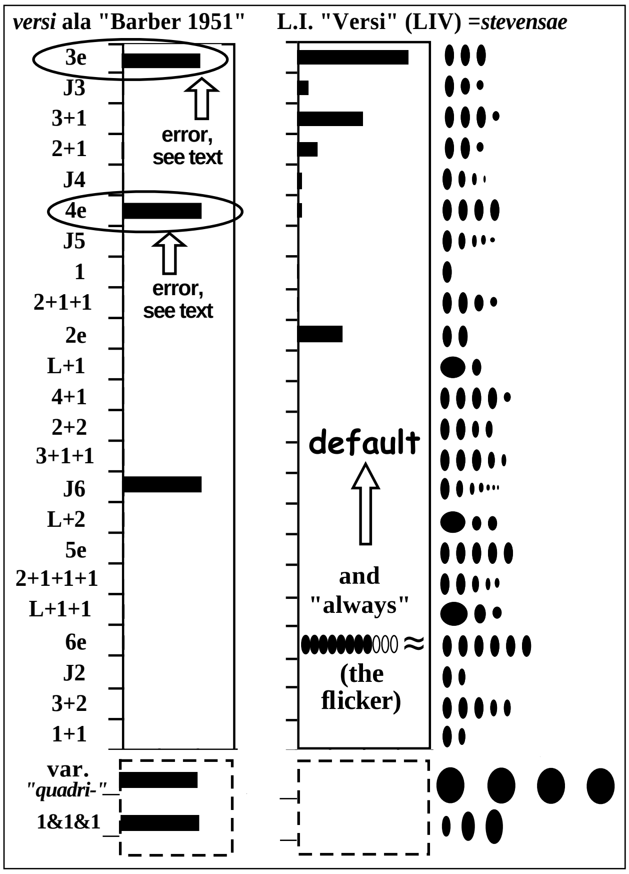


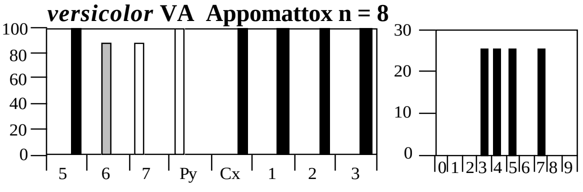
Figure 16. Repertoire comparisons, Long Island (at right)versus Barber's Figure 1 and text at left. Barber's 1951 paper and Mcdermott's supplement (1967) were the only ID references for *Photuris* for several decades.

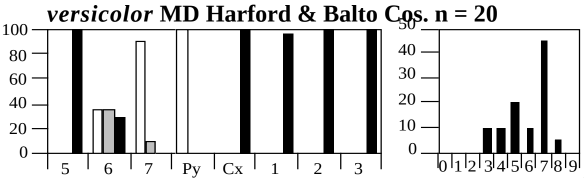
VA Appomattox Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.022	11.722	3.778	2.222	2.722	6.100	14.700	.797	1.233	.523
sd	.282	.653	.228	.179	.239	1.641	.795	.065	.047	.154
se	.094	.218	.076	.060	.080	.547	.265	.022	.016	.051
n	9	9	9	9	9	9	9	9	9	9
min	2.600	10.600	3.400	2.000	2.400	2.900	13.400	.660	1.170	.230
max	3.400	12.400	4.000	2.500	3.100	7.500	15.600	.870	1.310	.680
Vc%	9.3	5.6	6.0	8.1	8.8	26.9	5.4	8.2	3.8	29.5

MD Baltimore Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.882	10.855	3.527	2.127	2.727	6.445	13.736	.816	1.284	.592
sd	.178	.543	.162	.190	.261	1.223	.655	.025	.049	.104
se	.054	.164	.049	.057	.079	.369	.197	7.419E-3	.015	.031
n	11	11	11	11	11	11	11	11	11	11
min	2.600	9.800	3.300	1.900	2.400	3.100	12.400	.790	1.180	.310
max	3.100	11.500	3.900	2.400	3.100	7.500	14.600	.860	1.350	.670
Vc%	6.2	5.0	4.6	8.9	9.6	19.0	4.8	3.1	3.8	17.6





FigTable. 17. Measurements from near Barber's bailiwick and further south toward Herschel's' presumptive N.A. collection site.

❊ ❊ ❊

Morphological notes. Specimens from several geographic regions were measured, certain ratios calculated, and colors of anatomical elements graded/scored (**FigTable 17,** Appendix). The Appendix shows color histograms of *harrannorum* and *stevensae* for comparison. Body measurements in the Figures are for FP-voucher males; females, such as Fabrician syntypes, would average somewhat larger. **Figure 18** is a key to anatomical elements. Arrays of PN vittagrams are shown in **Figures 19** (photographs including those of syntypes), and **20** (vittagram sketches); syntype pronota in **Figure 21** are carbon dust drawings by Laura Line.

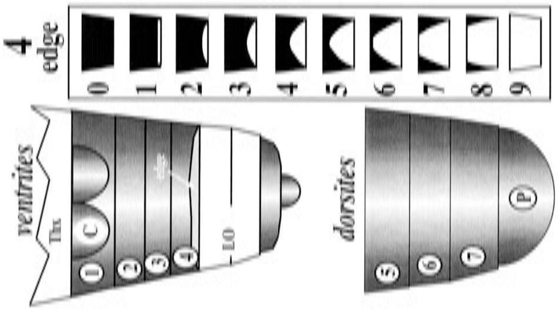


Figure 18. Topographic and splash keys.

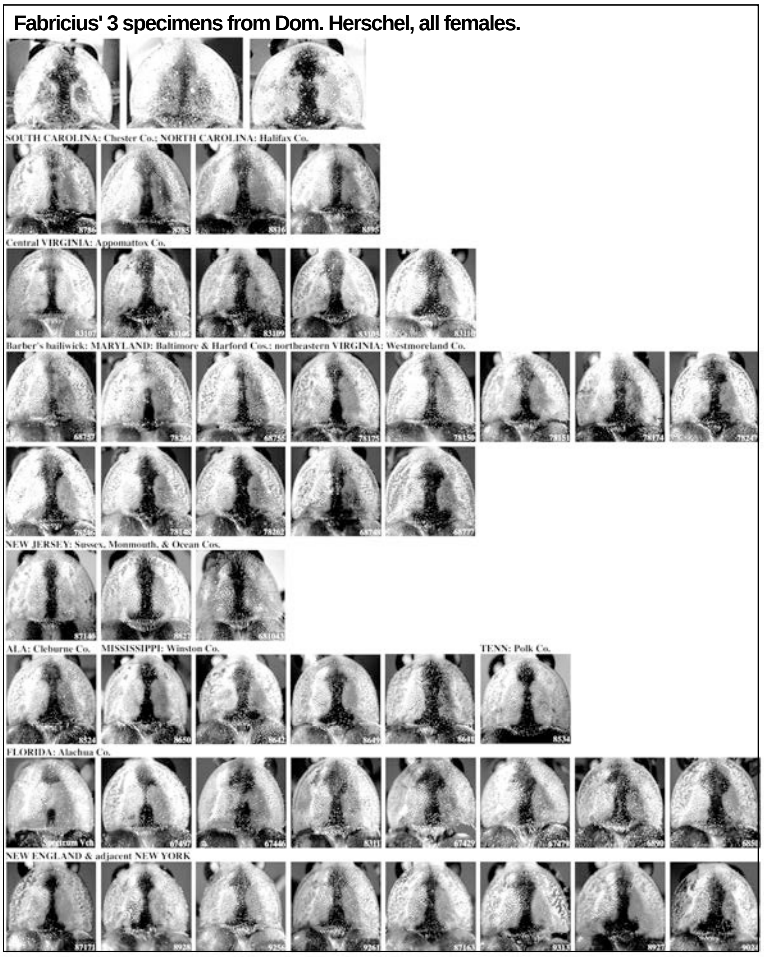


Figure 19. Syntype PNs and arrays of deme vouchers.

Historical and taxonomic notes. *P. versicolor* remained in junior synonomy for many decades following the conclusion that there were few *Photuris* species in North America and because the name *pensylvanica* had seniority. Leng (1920) catalogued only three. Barber's field work brought him to conclude that there actually were many *Photuris* species, and that the name *versicolor* belonged to the species that he observed to emit the 3-6 pulse FP (his "flicker flash") with pulse intensity gradually diminishing through each pattern (**Fig. 15**, **pattern 6**). Although McDermott believed that the decision to associate the Fabrician name with this particular FP was incorrect (:54-56, in Barber, 1951), he had no way of resolving the matter and followed Barber. Neither were able examine Fabricius' specimens, which were in Denmark, and all that was said of them was that there were three (syntypes) and that they came from North America (directly or indirectly) to Fabricius via "Dom. Herschel" before 1798.

Dr. Ole Martin of the Copenhagen Zoology Museum, where the Fabrician specimens are archived, understood that Fabricius received material from Herschel (letter 1988), a collector that apparently lived in Hanover (Germany; Horn and Schenkling 1928:548), but had no further information on the specimens' origin. Whether Herschel collected them or received them from a traveler was unknown, and because this identifier, “Dom. Herschel,” actually appeared on labels of many American species, many coleopterists were puzzled/affected. This mystery was partially resolved by R. B. Madge, and discussed in his “Who was Herschel?” (1994). Dom. Herschel was Johann Dietrich Herschel, a musician, published entomologist, and a younger brother of astronomer William Herschel. Knowing this, we can suspect that the North American origin of Fabricius’ *Photuris* (nee *Lampyris*) *versicolor* specimens was probably either Charleston, South Carolina, where Herschel’s son Dietrich died of yellow fever (Madge, ‘94:544); or Savannah, Georgia, where Herschel had an entomological contact named Oemler, whom Madge suggests was Augustus Oemler, a pharmacist, botanist, and entomologist (‘94:545).

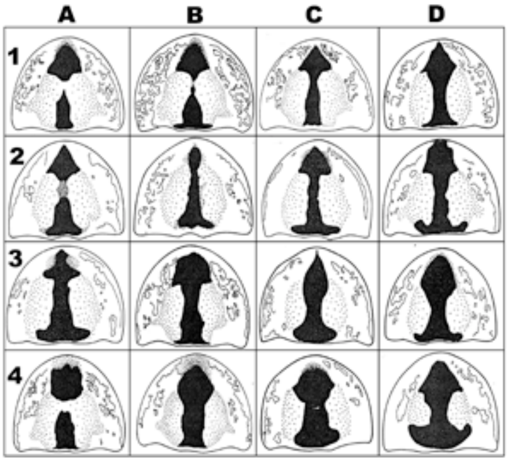


Figure 20. Combined array of *versicolor* PN vittae.

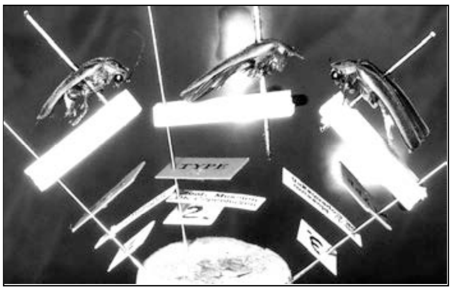


Figure 21. Fabricius' three specimens.

Fabricius' three syntypes were borrowed through the generous accomodation of Dr. Martin (**Fig. 21**). All were females and certainly belong to what Barber would have identified as near *versicolor* or in the "*versicolor* complex." The collector probably picked them from the ground as they were ovipositing, guided by their flashing (and light from a candle or oil-lamp?). **Figure 22** shows the pronotal vittae. The three are missing various parts of their anatomy. It is possible that they could actually be *P. quadrifulgens*. Perhaps DNA can answer the question, but whether nomenclature should be "adjusted" is another matter, not unexpected in the long adventure that has been *Photuris* species taxonomy.

One specimen had a small scrap of paper, with "La" (i.e. *Lampyris*) written on one side and "*versicolor"* on the other. Label handwriting compares with that of a Fabrician label illustrated in Zimsen (1964:10), who observed that Fabricius used "… usually only a small scrap of paper on which was written the name of the species …" (**Fig. 23**).

The actual identification (i.e. association with contemporary names) of the syntypes may always remain equivocal. They perhaps resemble current voucher specimens of Barber's *quadrifulgens* more than they resemble current vouchers of Barber's *versicolor*. But, given the possibility of DNA making even fragments identifiable, the nomenclatural matter should perhaps be revisited and then brought to a conclusion. Were a decision to be made here and a single specimen selected, it would be female #3 (**Fig. 24**), with pronotum as shown in **Figures 19 and 22**.

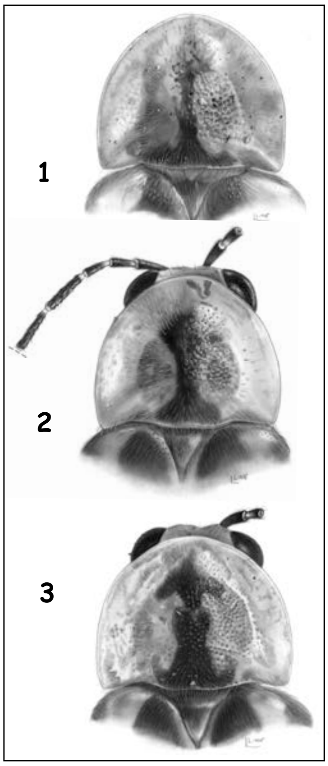


Figure 22. PNs of Fabrician syntypes as numbered. Carbon-dust by Laura Line.

Fig. 23. Fabricius' "*La[ampyris]*") and "*versicolor*" labels, with reference label from Zimsen at right for comparison.

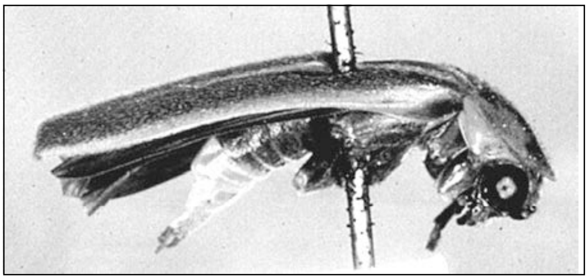


Figure 24. *versicolor* Syntype, the Fabrician specimen #3.

Johann Christian Fabricius, January 1745–March 1808, Danish: Described *Lampyris (Photuris) versicolor*

Fabricius, from the Osborn collection.

Historical and recent misidentification, misattribution. (**1**) For several decades, until Barber removed it from synonomy, and on several occasions thereafter, *versicolor* s.s. fireflies would have been identified as "pennsylvanica," and because *versicolor* is common and sometimes occurs in large populations this may have happened often in certain regions. (**2**) Cape Cod, MA references to *versicolor* should be tentatively attributed to *fairchildi*. *Ph. versicolor* was not found on the Cape and *stevensae* was found immediately west of the canal on the mainland in Plymouth County. (**3**) Upstate New York references west of the Hudson River could be attributed to any of several *Photuris* species, but apparently not *versicolor*. (**4**) Early jel publications (1964-1985) on Florida *versicolor* should be referred to *harrannorum*. (**5**) Data and behavior published by a L.I. university lab under the name *versicolor* should be closely compared/examined with reference to information in this study. After this lab (and associates) made very public and conspicuously flawed criticisms of lengthy, comprehensive, and detailed studies by the present author, many nights of observation were spent over several summers on Long Island, including a site a short distance from the mentioned lab. *Ph. versicolor* as would be recognized by the only identification references <u>of the time</u> (Barber, 1951; McDermott, 1967; see above, Figs. 15, 16, and text) does not occur on Long Island. The *versicolor*-Group-member that does is distinctive, and has an FP repertoire unlike any described by Barber. This firefly was found in great abundance and presented the same flashing behavior on all years of study there (see *stevensae*). Its repertoire **includes** an "≈A-flicker" (similar to that described in detail for other species in the present paper). A brief visit to a field of flashing *stevensae* by the critics would have revealed this flicker, and from Barber's Figure 1, Key, and description, such emitters would only for a moment have been identified as *Ph. tremulans*. Then, by decoying the emitters of this flicker—as theorized in the criticized study—defaulting to a pulsing FP (not the *tremulans* short, single-flash, default FP) would have been elicited/observed. The cited criticism denied both the existence/occurrence of such a flicker (by inference even that described by Barber), and the possibility of FP switching (defaulting) as suggested in the criticized paper. It is puzzling: (**1**) that the critics could have denied the flicker and defaulting when they are so easily observed, even by a fifth-grade class; and (**2**), that across a span of 30+ years apparently no students or faculty member, or reporter, ever brought this to the attention of anyone, as an invitation to make proper "corrections" in the literature. Entomology students that I have known certainly would been have been in touch, with someone. There is a great deal more to this incident—but, such matters will become ever more common in the practice of science, as economics and top-down, business-micro-management impose an ever-greater influence on academic conduct, and especially, *integrity* …

APPENDIX: *versicolor* & Group Measurements, Colors, Ratios, Comparisons

VA Appomattox Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.022	11.722	3.778	2.222	2.722	6.100	14.700	.797	1.233	.523
sd	.282	.653	.228	.179	.239	1.641	.795	.065	.047	.154
se	.094	.218	.076	.060	.080	.547	.265	.022	.016	.051
n	9	9	9	9	9	9	9	9	9	9
min	2.600	10.600	3.400	2.000	2.400	2.900	13.400	.660	1.170	.230
max	3.400	12.400	4.000	2.500	3.100	7.500	15.600	.870	1.310	.680
Vc%	9.3	5.6	6.0	8.1	8.8	26.9	5.4	8.2	3.8	29.5

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.875	1.125	1.000	3.000	3.000	3.000	3.000	4.750
sd	0	.354	.354	0	0	0	0	0	1.581
se	0	.125	.125	0	0	0	0	0	.559
n	8	8	8	8	8	8	8	8	8
min	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
max	3.000	2.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	18.9	31.5	0	0	0	0	0	33.3

MD Harford Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.767	10.633	3.411	2.078	2.611	6.056	13.367	.806	1.258	.569
sd	.132	.768	.190	.148	.190	1.546	.879	.033	.084	.136
se	.044	.256	.063	.049	.063	.515	.293	.011	.028	.045
n	9	9	9	9	9	9	9	9	9	9
min	2.500	9.100	3.000	1.900	2.300	4.100	11.600	.750	1.110	.400
max	2.900	11.900	3.600	2.300	2.900	8.100	14.800	.850	1.380	.780
Vc%	4.8	7.2	5.6	7.1	7.3	25.5	6.6	4.1	6.7	23.9

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.111	1.111	1.000	3.000	3.000	3.000	3.000	5.333
sd	0	.928	.333	0	0	0	0	0	1.658
se	0	.309	.111	0	0	0	0	0	.553
n	9	9	9	9	9	9	9	9	9
min	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	3.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	8.000
Vc%	0	44.0	33.3	0	0	0	0	0	31.1

MD Baltimore Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.882	10.855	3.527	2.127	2.727	6.445	13.736	.816	1.284	.592
sd	.178	.543	.162	.190	.261	1.223	.655	.025	.049	.104
se	.054	.164	.049	.057	.079	.369	.197	7.419E-3	.015	.031
n	11	11	11	11	11	11	11	11	11	11
min	2.600	9.800	3.300	1.900	2.400	3.100	12.400	.790	1.180	.310
max	3.100	11.500	3.900	2.400	3.100	7.500	14.600	.860	1.350	.670
Vc%	6.2	5.0	4.6	8.9	9.6	19.0	4.8	3.1	3.8	17.6

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.818	1.091	1.000	3.000	2.909	3.000	3.000	6.273
sd	0.000	.751	.302	0.000	0.000	.302	0.000	0.000	1.272
se	0.000	.226	.091	0.000	0.000	.091	0.000	0.000	.384
n	11	11	11	11	11	11	11	11	11
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	4.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	41.3	27.7	0	0	10.4	0	0	20.3

NJ Bergen Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	2.967	11.033	3.600	2.067	2.700	7.267	13.967	.823	1.310	.660
sd	.115	.252	.173	.208	.173	.462	.404	5.774E-3	.082	.026
se	.067	.145	.100	.120	.100	.267	.233	3.333E-3	.047	.015
n	3	3	3	3	3	3	3	3	3	3
min	2.900	10.800	3.500	1.900	2.500	7.000	13.600	.820	1.220	.640
max	3.100	11.300	3.800	2.300	2.800	7.800	14.400	.830	1.380	.690
Vc%	3.9	2.3	4.8	10.1	6.4	6.4	2.9	0.7	6.3	3.9

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	1.667	1.000	1.000	3.000	3.000	3.000	3.000	6.000
sd	0	1.155	0	0	0	0	0	0	1.732
se	0	.667	0	0	0	0	0	0	1.000
n	3	3	3	3	3	3	3	3	3
min	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	4.000
max	3.000	3.000	1.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	69.3	0	0	0	0	0	0	28.9

MS Neshoba Co.

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.075	12.200	3.875	2.350	2.800	5.400	15.275	.805	1.202	.445
sd	.050	.200	.096	.058	.141	2.099	.250	.021	.022	.171
se	.025	.100	.048	.029	.071	1.050	.125	.010	.011	.086
n	4	4	4	4	4	4	4	4	4	4
min	3.000	11.900	3.800	2.300	2.600	3.400	14.900	.780	1.170	.280
max	3.100	12.300	4.000	2.400	2.900	7.800	15.400	.830	1.220	.630
Vc%	1.6	1.6	2.5	2.5	5.0	38.9	1.6	2.5	1.8	38.4

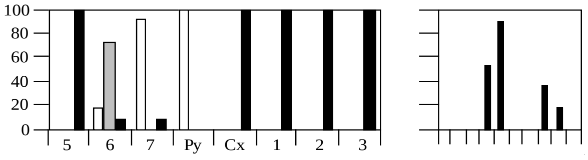
	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.750	1.250	1.000	3.000	3.000	3.000	3.000	5.250
sd	0	.500	.500	0	0	0	0	0	1.258
se	0	.250	.250	0	0	0	0	0	.629
n	4	4	4	4	4	4	4	4	4
min	3.000	2.000	1.000	1.000	3.000	3.000	3.000	3.000	4.000
max	3.000	3.000	2.000	1.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	18.2	40.0	0	0	0	0	0	24.0

TN Polk Co.

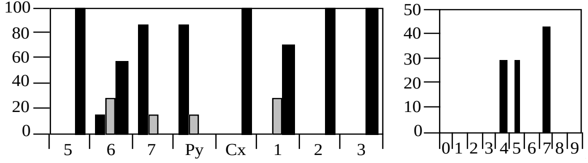
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
X̄	3.214	12.114	3.900	2.357	2.829	7.114	15.286	.826	1.201	.590
sd	.107	.406	.082	.053	.049	1.079	.410	.023	.045	.099
se	.040	.153	.031	.020	.018	.408	.155	8.690E-3	.017	.037
n	7	7	7	7	7	7	7	7	7	7
min	3.100	11.600	3.800	2.300	2.800	5.400	14.800	.810	1.160	.420
max	3.300	12.800	4.000	2.400	2.900	8.400	16.000	.870	1.280	.710
Vc%	3.3	3.4	2.1	2.3	1.7	15.2	2.7	2.8	3.8	16.8

	5	6	7	Py	Cx	1	2	3	4
X̄	3.000	2.429	1.143	1.143	3.000	2.714	3.000	3.000	5.571
sd	0	.787	.378	.378	0	.488	0	0	1.397
se	0	.297	.143	.143	0	.184	0	0	.528
n	7	7	7	7	7	7	7	7	7
min	3.000	1.000	1.000	1.000	3.000	2.000	3.000	3.000	4.000
max	3.000	3.000	2.000	2.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	32.4	33.1	33.1	0	18.0	0	0	25.1

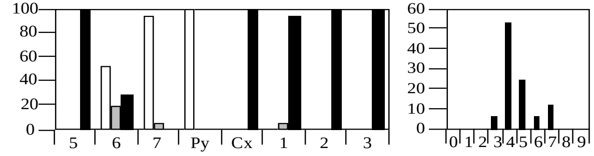
stevensae CT Hartford Co. n = 11



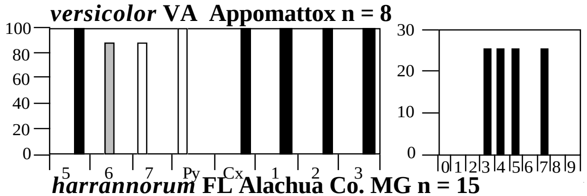
versicolor TN Polk Co. n = 7



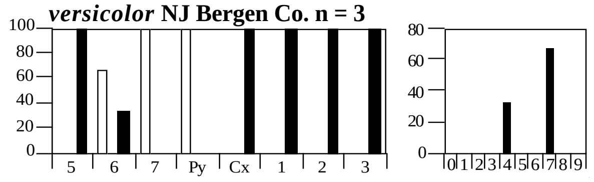
stevensae NY LI Suffolk Co. n = 17



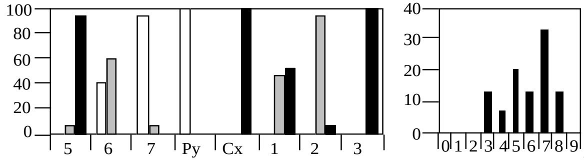
versicolor VA Appomattox n = 8



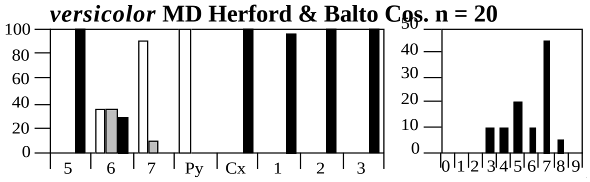
versicolor NJ Bergen Co. n = 3



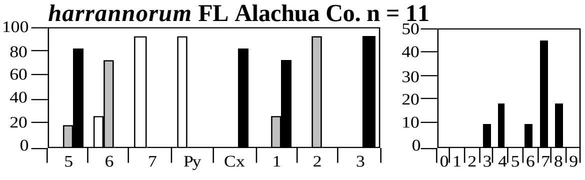
harrannorum FL Alachua Co. MG n = 15



versicolor MD Herford & Balto Cos. n = 20



harrannorum FL Alachua Co. n = 11



Chapter 68

Photuris walkeri n. sp.

Long Red

This firefly “clearly” is a western peripheral isolate of Alachua County’s *lineaticollis*, and "finely tuned" ecologically to the region—it emits an adjunct "FP" that belongs to *Pyractomena angustata*, which occurs there but not inland in Alachua County. *Ph. lineaticollis* is not known to have an adjunct FP, thus is revealed a phylogenetic mystery/enigma. *Py. angustata's* signal ("FP") is a remarkable, long-continued green(!) glow, and certainly the target of glow-hunting *Photuris*, *walkeri* probably included. Among questions of lesser importance that might be raised is whether *walkeri* should receive formal species recognition based on this "minor" FP difference. Because *lineaticollis*-**like** demes (variads) are what we seek when taxonomic species are pushed to the next level of reality—toward understanding biodiversity and its evolutionary development—it is important to recognize example variads when they are distinctive and attractive subjects for genetic examination by taxonomist/naturalists with such interests and skills.

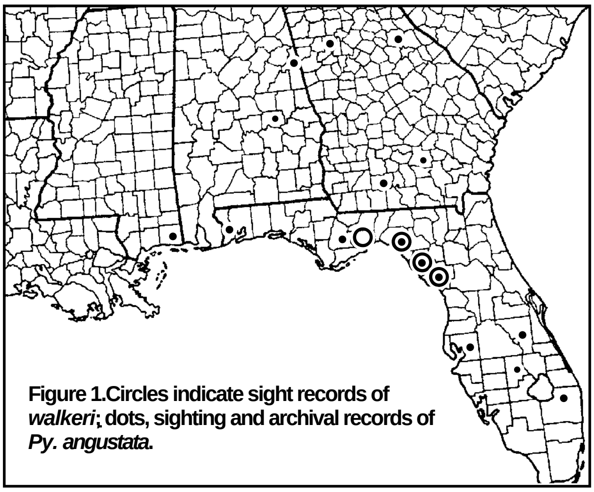


Figure 1.Circles indicate sight records of *walkeri*; dots, sighting and archival records of *Py. angustata.*

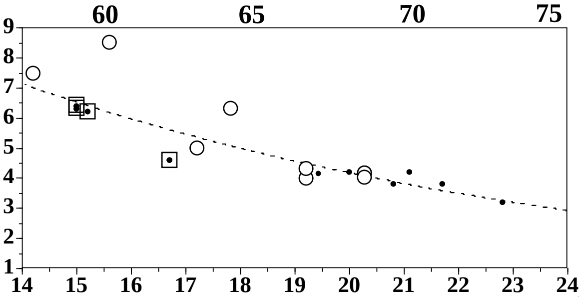


Figure 2. FP Period. This is the regression of FP means for variads in the *lineaticollis* section. Circles are means of *walkeri* from Levy and Dixie Co., squares are for Wakulla Co.; dots are *lineaticollis* records (AX: sec/temp).

Figure 3. Cypress dome near Ellzey, Levy Co., FL.

In the map (**Fig. 1),** dots indicate the known occurrence of *angustata* demes and the circles, those of *walkeri*. In many respects *walkeri* appears to behave as described for *lineaticollis* just to the east. Its species-recognition short flash is emitted at about four second intervals at 20°/68° (**Fig. 2**). At sites near Otter Creek, Florida (**Figs. 3, 4)**, both short flashing and long-glowing males flew along the highway berm and over adjacent areas with cypress, pine, and scrubby hardwoods.

Figure 4. Site near Ellzey, Levy Co., FL.

The FP period chart is that from the *lineaticollis* section, except that *walkeri* periods are indicated. The adjunct glow signal is emitted as males fly winding courses 3-8' above ground, in the usual space of *angustata*. As noted for *angustata*, these glows are occasionally observed higher, sweeping around and over shrubs and sometimes near the tops of spring-leafless trees.

Because the *walkeri* glow is usually indistinguishable from glows of *Photuris eureka* and *Pyractomena angustata*, positive identification, even to genus, requires the capture and physical examination of the emitter. However, the glows of *walkeri* were sometimes emitted in short pulse-like glows, with these separated by continuing dimmer glows (**Fig. 5B**).

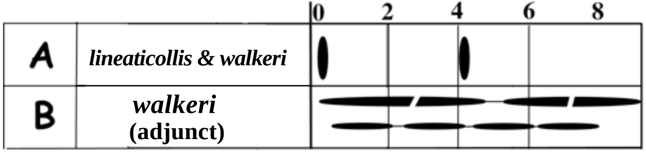


Figure 5. FP forms, period timings (near 20°/68°).

Figure 6. Area at Austin Cary Forest where *angustata*-like glows were presented to *lineaticollis* without visible effect.

Alachua County’s *lineaticollis* were **never** seen to emit long- or short-glow FPs during hundreds of nights spent in the field in season. In a brief experiment, one evening at the Austin Cary Forest in Alachua County when several *lineaticollis* were active, three of us flew/carried "green"-glowing LEDs on hand-held wands for several minutes throughout the grassy area and along sandy roadways where *lineaticollis* males were often attracted to decoy flashes (**Fig. 6**). No males were converted to glowing during this exposure.

When glowing males at the Ellzey and Wakulla, (and Okefenokee?) sites were presented with a short glow-response via LEDs, some defaulted to a short flash, some disappeared, and some emitted a few short, wavering glows before disappearing—hovering or slow-flying lights are easy targets for aerial attack.

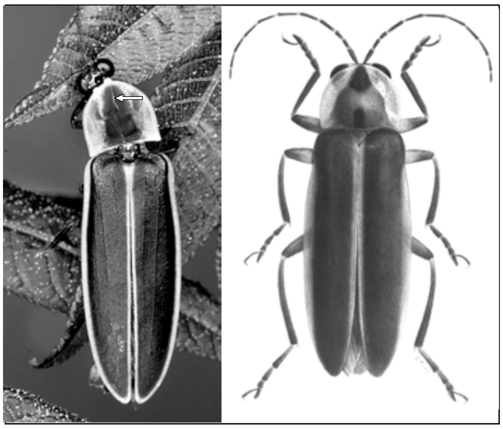


Figure 7. *Py. angustata* at left, *Ph. lineaticollis* at right.

Ph. walkeri has a reddish/tawny "ground-color" contrasting with the yellowish trim/borders as seen in *eureka*, and usually lacks elytral vittae. All *Pyractomena* have a longitudinal, median ridge on the pronotum. **Figure 7** shows the habiti of *angustata* and the *walkeri* look-alike *lineaticollis*; **Figure 8** is a time-exposure of the flying glow of an *angustata* male; **Figure 9** is the SESOBS record for *walkeri*.

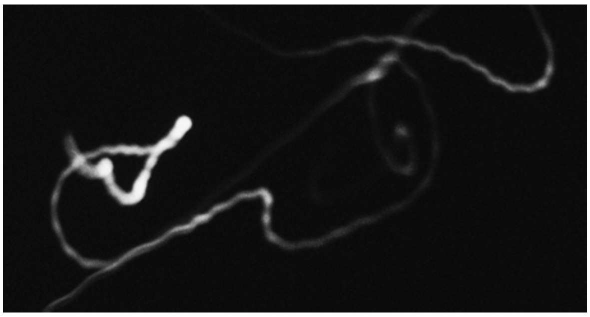


Figure 8. Hand-held on-the-run, open-shutter (film-camera) exposure of a flying *angustata* male's glow. The apparent pulsing remains unexplained and is not seen in PM-records though wing-shottering, a much faster modulation, is seen. Perhaps the pulsing seen in this photo is from the asynchronous emissions of the two lantern segments, which together produce a steady beam of light, but the camera separated them in space?

Morphological summary for Ellzey voucher series. Means (n=4): PNL 3.2, ELL 11.6, PNW 4.0, EWhum 2.2, EWmid 2.8, ELVit 1.4, TOTLen 14.8, PNrat 0.82, ELWrate 1.28, ELVTrat 0.12

FigTable. 10 has measurements, sclerite colors, ratios and prelantern ventrite splash for Levy Co. vouchers; **FigTable. 11** for Wakulla Co. vouchers; **Figure 12** is key for anatomical elements and splashing on ventrite 4. **Figure 13** shows photos of pronota from several localities and **Figure 14**, the analysis of some based on the vittagrams illustrated in the reference Figure 201.2 elsewhere in this paper.

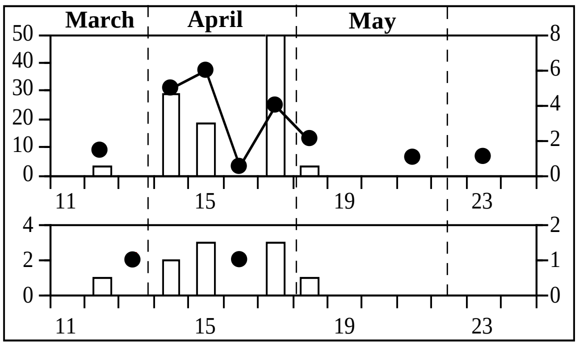


Figure 9. SESOBS for *walkeri*.

Holotype description. male, voucher number 724, photo below. Collected 14 April 1972, Levy County, Florida, 4.5 miles w of Ellzey, a JCT sw Otter Creek). (From FB, 1972 page 2: "collected 4 long-green-red 721-724 fly high, at least 15' up and higher, slow drifting flight." Morphological data: genitalia extruded remain attached; from spread sheet—PNLen 3.3, ELLen 12.4, PNWid 4.3, ELWhum 2.4, ELWmid 2.9, LELVit 2.9, TotLen 15.6, PnRat 0.76, ElRat 1.21, VitRat 0.23; Colors: T 311, Py 1, Cx 3,V 333, Edg 2. Types will be deposited in the USNM.

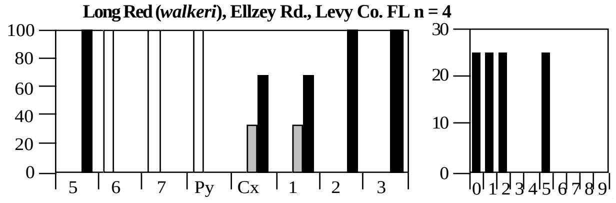
Holotype specimen, *Ph. walkeri*.

Long Red (*walkeri*), Ellzey Rd., Levy Co. FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	3.223	11.550	3.950	2.175	2.750	1.375	14.750	.817	1.283	.117
sd	.119	.624	.289	.222	.173	1.592	.676	.043	.083	.136
se	.060	.312	.144	.111	.087	.796	.338	.022	.042	.068
n	4	4	4	4	4	4	4	4	4	4
min	3.130	10.900	3.600	1.900	2.600	0.000	14.000	.760	1.210	0.000
max	3.380	12.400	4.300	2.400	2.900	2.900	15.600	.860	1.400	.240
Vc%	3.7	5.4	7.3	10.2	6.3	115.6	4.6	5.3	6.5	116.2

Long Red (walkeri), Ellzey Rd., Levy Co. FL

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.000	1.000	1.000	2.500	2.500	3.000	3.000	2.000
sd	0.000	0.000	0.000	0.000	.577	.577	0.000	0.000	2.160
se	0.000	0.000	0.000	0.000	.289	.289	0.000	0.000	1.080
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	0.000
max	3.000	1.000	1.000	1.000	3.000	3.000	3.000	3.000	5.000
Vc%	0	0	0	0	23.1	23.1	0	0	108.0



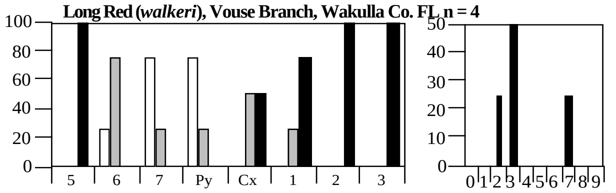
FigTable 10. Measurements, colors, and ratios of *walkeri* Levy Co. vouchers.

Long Red (*walkeri*), Vouse Branch, Wakulla Co. FL

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{X}$	2.775	11.200	3.700	2.100	2.700	0.000	13.975	.758	1.287	0.000
sd	.320	.200	.115	.141	.115	0.000	.465	.102	.073	0.000
se	.160	.100	.058	.071	.058	0.000	.232	.051	.036	0.000
n	4	4	4	4	4	4	4	4	4	4
min	2.500	10.900	3.600	2.000	2.600	0.000	13.400	.670	1.220	0.000
max	3.100	11.300	3.800	2.300	2.800	0.000	14.400	.860	1.380	0.000
Vc%	11.5	1.8	3.1	6.7	4.3	0	3.3	13.5	5.7	0

Long Red (*walkeri*), Vouse Branch, Wakulla Co. FL

	5	6	7	Py	Cx	1	2	3	4
$\overline{X}$	3.000	1.750	1.250	1.250	2.500	2.750	3.000	3.000	3.750
sd	0.000	.500	.500	.500	.577	.500	0.000	0.000	2.217
se	0.000	.250	.250	.250	.289	.250	0.000	0.000	1.109
n	4	4	4	4	4	4	4	4	4
min	3.000	1.000	1.000	1.000	2.000	2.000	3.000	3.000	2.000
max	3.000	2.000	2.000	2.000	3.000	3.000	3.000	3.000	7.000
Vc%	0	28.6	40.0	40.0	23.1	18.2	0	0	59.1



FigTable 11. Measurements, colors, and ratios of *walkeri* Wakulla Co. vouchers.

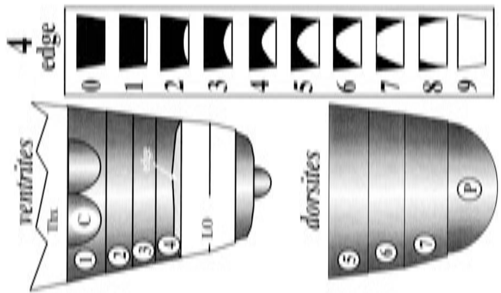


Figure 12. Topographic and splash keys.

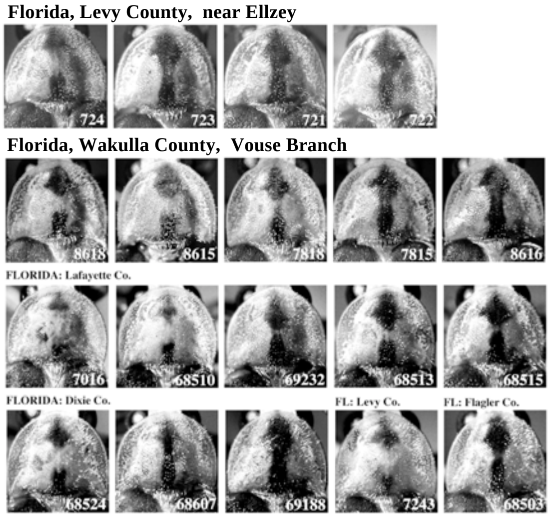


Figure 13. Pronotal vittae, source as indicated.

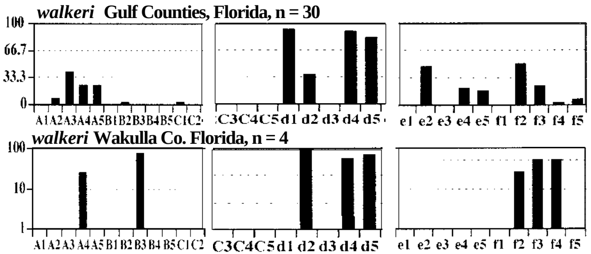


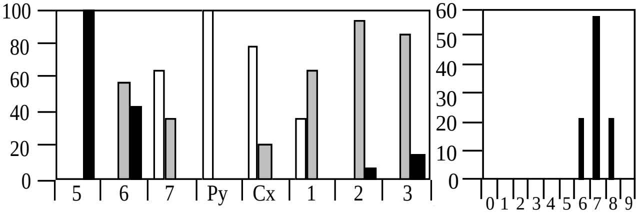
Figure 14. Pronotal vittae, source as indicated.

“They are never fearful in the Night, nor do the Thoughts of Spirits ever trouble them; such as the many Hobgoblns and Bugbears that we suck in with our Milk, and Foolery of our Nurses and Servants suggest to us; who by their idle tales of Fairies, and Witches, make such Impressions on our tender Years, that at Maturity, we carry Pigmies Souls, in Giants Bodies and ever after, are thereby so much dpriv’d of Reason, and unman’d, as never to be Masters of half the Bravery Nature design’d for us.”

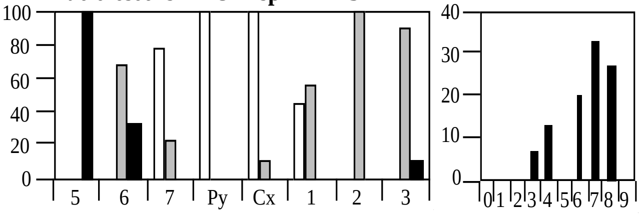
(From 1709, “A New Voyage To Carolina, ...” John Lawson, p. 210-211: in reference to the English bias towards fear of the dark, as compared with beliefs of Indians. From a note sent to jel in 2008 by Wes Taucheray)

Compared Color Histos: Luci and Hebes, Lucy and Versi

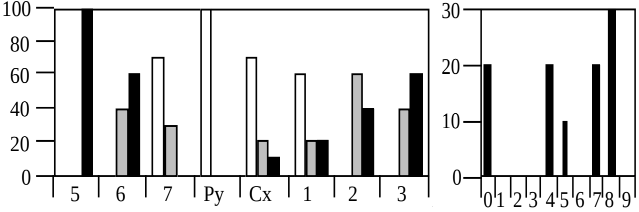
lucicrescens **MD n = 15**



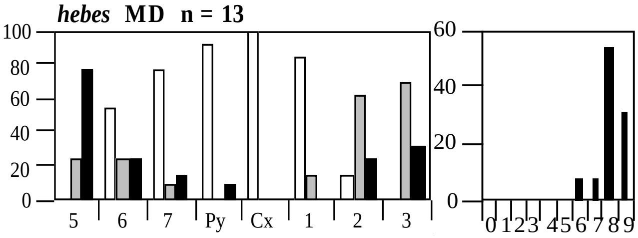
lucicrescens **MO rrsp n = 15**



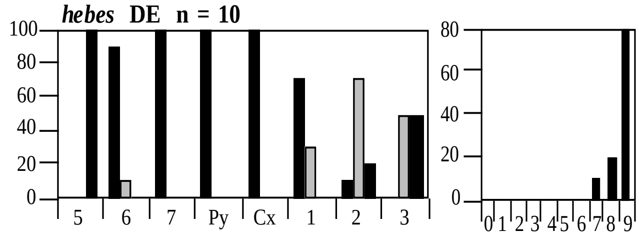
lucicrescens **MD cv n = 10**



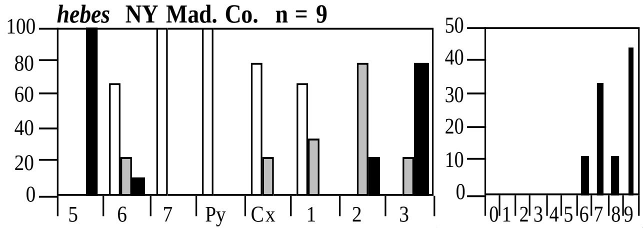
hebes **MD n = 13**



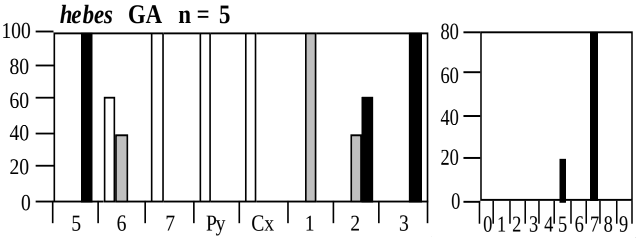
hebes **DE n = 10**



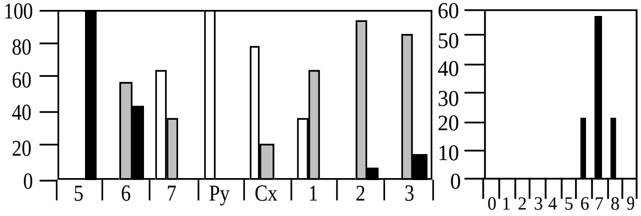
hebes **NY Mad. Co. n = 9**



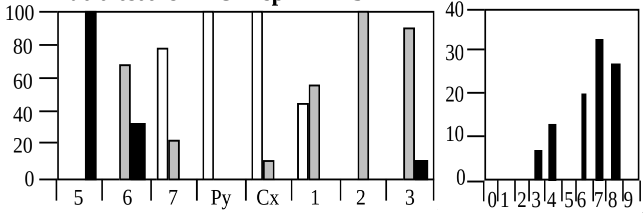
hebes **GA n = 5**



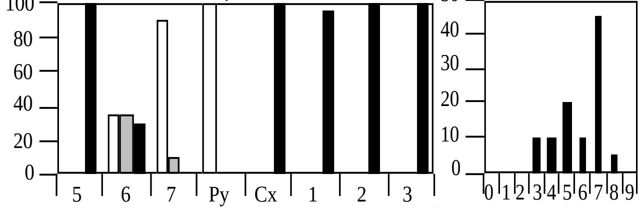
lucicrescens **MD n = 15**



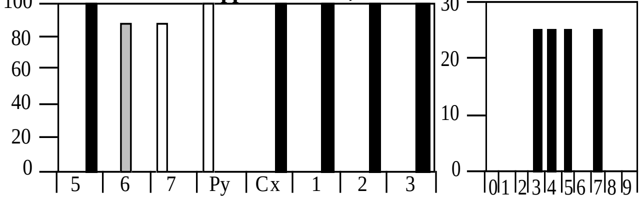
lucicrescens **MO rrsp n = 15**



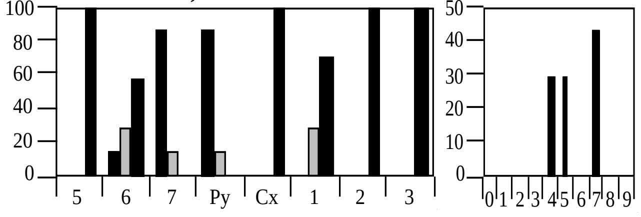
versicolor **ne MD, n = 20**



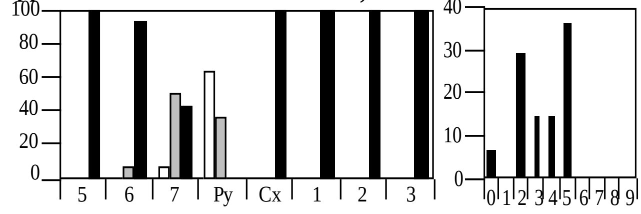
versicolor **VA Appomat. CO., n = 8**



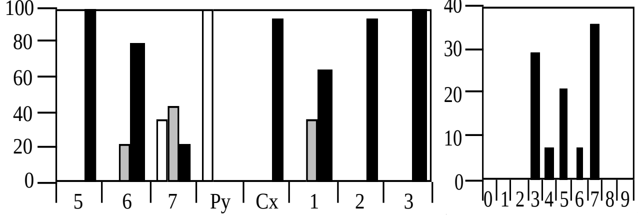
versicolor **TN, n = 7**



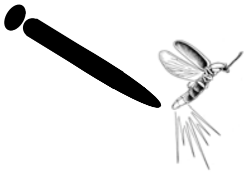
appalachianensis **MD Garrett Co., n = 14**



cowaseloniensis **NY Mad. Co. n = 14**

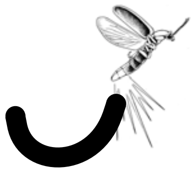


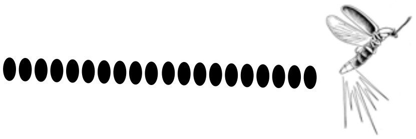
Chapter 69



Marshes of Washtenaw County MI

(with three *pensylvanica* connections?)





In marshes along Warren Road on the outskirts of Ann Arbor, Michigan, and other marshes in Washtenaw County (**Fig. 1**), is another of the interesting and perhaps complex evolutionary *Photuris* problems that this long walk in the field encountered, and left unanswered. It was in these marshes in 1966 that studies were begun on *Photuris*, almost to the complete exclusion of all others. Unfortunately after this beginning these marshes were visited only twice or thrice more and then only briefly. In 1966 three distinctive *Photuris* FPs were noted, and it was presumed then that they belonged to three species, these three being among FPs that were discussed and illustrated in Barber's 1951 chart (**Fig. 2, arrows**): *pensylvanica, pyralomima,* and *tremulans*.

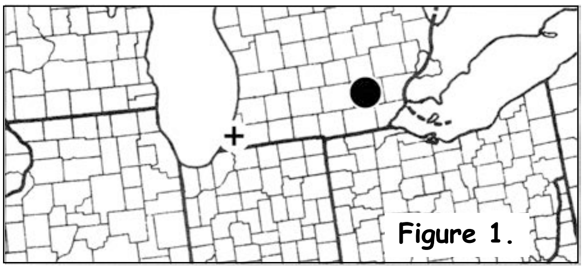


Figure 1.

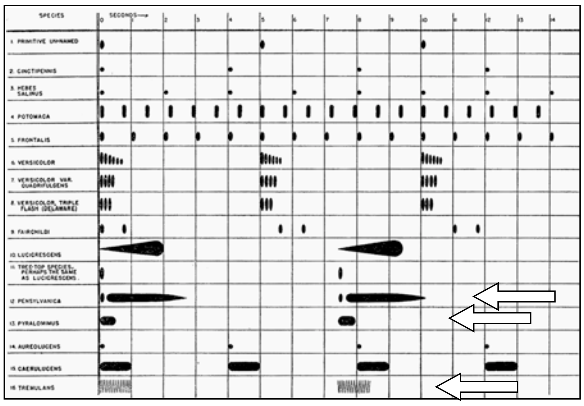


Figure 2. Barber's chart. Note arrows, and that two of Barber's epithet spellings have had their inflections changed from from -us to -a, including pyralimima.

Today, 2015, it is clear from broad geographic experience, including Barber's Chesapeake/Potomac bailiwick, that none of the flashers in Washtenaw County is what it was initially presumed to be; that the novice explorer who examined them in 1966 did not know the *Photuris* questions that should be asked, but that in accordance with signaling patterns found in *Photuris* demes elsewhere, there could be one, two, or three genetic populations present. Further, one or two additional discrete and functional FPs might be involved, and were overlooked. A case will not be made here for any of these possibilities; instead a sketch of the situation, with descriptions of each of the three FP-types, based on field notes, PM-records, and close voucher examination is presented, with the suggestion that there may also be present: (**1**) twilight short flashes with defaulting, (**2**) that one of these three FPs may ("could") default to another of them, or (**3**) like *lucicrescens,* there may be no defaulting at all. As a final introductory note, though a detailed *Photinus* study in 1966 had just been completed, involving the movement of a western species eastward along the prairie peninsula and into the steppe corridor in New York where it hybridized with an eastern species (jel, 1967), it was only long after discovery of this Washtenaw marsh that the possibility that recent gene exchanges could have taken place in *Photuris*, and should at least be considered—and that the situation in Washtenaw County perhaps remains a dynamic one.

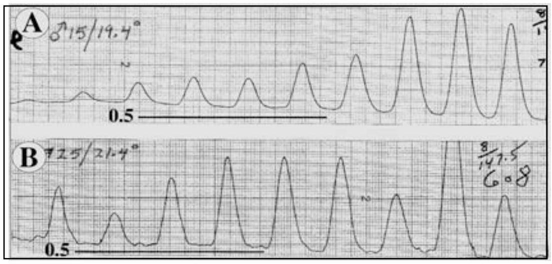


Figure 3. Segments of two long FPs (AX:r.i./time).

Incidentally, note that curious vittagrams occur only in Michigan *Lucidota atra*, a daytime dark species of broad occurrence (**Fig. 12**).

The AA-Flicker. Males flew low over marsh and adjacent field vegetation and emitted rapidly-pulsed FPs of 5-19 but most commonly 10-15 green pulses (**Fig. 3**). Flight was usually horizontal or on a slightly downward-sloping course. FP period was 7-9 sec at 20°/68° (**Fig. 4**). The long, bright, fast-pulsing, green emissions of this AA-flicker can only be confused with long FPs of *fairchildi*, though a short 5-pulse AA flicker may be confusing.

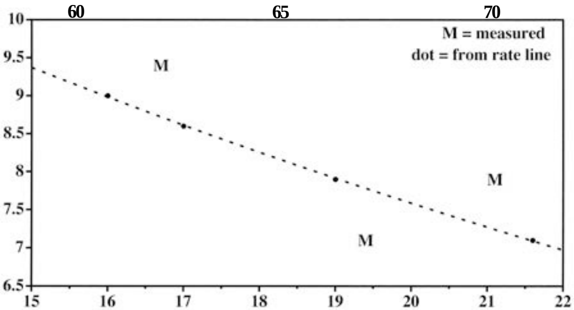


Figure 4. FP period, variable FP durations (AX: sec/temp).

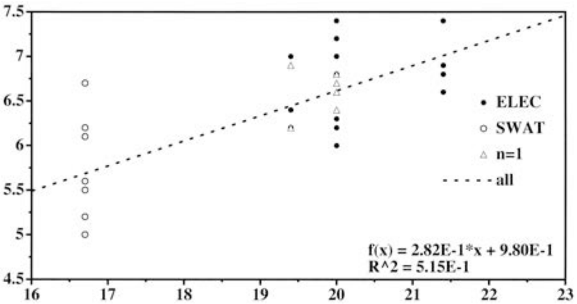


Figure 5. FP pulse rate (AX: Hz/temp).

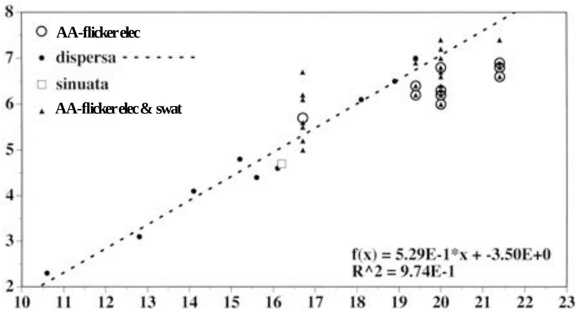


Figure 6. FP pulse rate of AA-flicker and presumptive *Pyractomena* models (AX: Hz/temp).

Figure 7. Abandoned flooded gravel pit in Washtenaw County that supported a *Pyractomena dispersa* population in 1962.

Presently this OTU is known only from Washtenaw County; a map record for Berrien County cannot presently be verified from specimens or field notes. FP period varies with varying FP lengths, thus the figure only gives a crude, estimated mean line based on the PCE (period-conversion-extrapolation) method. Stats from a sample of SWAT **pulse**-period measurements at 16.7°/62.1° gave a pulse rate of 5.7 Hz (duration/pulse-number: x=2.8/16 (sec/n), sd=0.9/5.3, range 1.3-4.0/8-22, n=9; hence 1/.175=5.7 Hz). At 20°/68° pulse rate is about 6.6 Hz (**Fig. 5**). Pulse rate was similar to that recorded for *Py. dispersa* and a single and very poor recording of *Py. sinuata*. Compared with PM and SWAT measurements made of flickers of other fireflies those in Figure 5 perhaps unusually variable.

Pulse duration at 19.4°/66.9°, from an examined PM sample of 8 males, 20 FPs and 162 pulses was: base 114 mSec and at half-max 53 mSec; a sample at 21.4°/70.5° of 4 males, 18 FPs and 136 pulses had a base of 98 mSec and at half-max of 43 mSec. The last pulse of an FP sometimes appears slightly longer than previous pulses, showing a slightly longer fall-time; other FP modulations are not perfectly symmetrical, i.e. sinusoidal, but have a slightly longer fall- than rise-time. At 19.4°/66.9° some pulses appear to reach zero, and the emission cease briefly. However, from most records it is impossible to determine whether the light is totally extinguished, because it “roundly bottoms out” in the trough between pulses (**Fig. 3A & B**). In the field the visual impression is clearly that the light goes OFF between pulses at temperatures below 20°/68°. This same visual impression is noted in the pattern of *Py. dispersa*, one presumptive model species for this flickering/fast-pulsing *Photuris*.

Although in a few recordings pulse intensity gradually increases through the FP (e.g. **Fig. 3A**; see trains of *P. fairchildi*), this probably results from chance—say from flight toward the PM, or the gradual increase (adjustment) in PM-system sensitivity as the PM-system was tuned (peaked) to obtain a maximum but undistorted recording level. There is no certain evidence of a species-typical envelope of gradual intensity increase as seen in *fairchildi*. In many recordings dim flashes occur "randomly" during the pulse-train, perhaps due to male wagging or twisting in flight or momentary partial occlusion by a blade of vegetation (**Fig. 2B**). On several occasions the decay of the last flash appeared in the field to be a slow, tapering OFF.

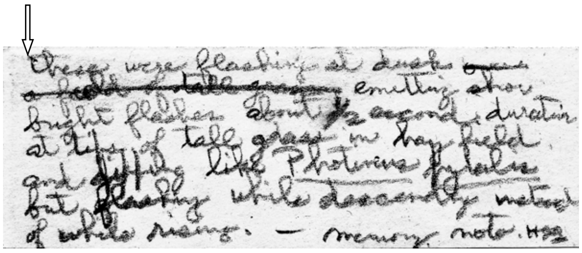
The FP of this species may be a mimicry of the FPs of *Pyractomena dispersa* and/or *sinuata* (**Figs. 6, 7**), though it typically is much longer than that of *dispersa* and much more strongly modulated than that seen in the single recording of *sinuata* or that field observations indicate for this species. Also, *sinuata* may only recently have occurred in Michigan, having moved eastward into the area and beyond as far as New England after the last glacier. In **Figure 6** pulse rate data for all three OTUs, the models and mimic, are shown. Data for *dispersa*, at hand across a broad range of temperature, was used for the regression in the figure—note that significant geographic variation also occurs in the flickers of *Pyractomena angulata*, another "old and out-of-date?" firefly.

Spectral analysis: luminescence peaks at 554 millimicrons, with halfmax at 527 and 597, half-max width 70, n=9, in two samples, different dates (Biggley, et al).

Morphology. General morphological data means are (n=15): PNL 2.5, ELL 9.7, PNW 3, EWhum 1.8, EWmid 2.2, ELVit 5.4, TOTLen 12.2, PNrat 0.83, ELWrate 1.25, ELVTrat 0.57. FigTables of data are in the Appendix where they can be compared with data from Dipper and Dot-dash vouchers from the marshes.

Augmented figure legends. 3. PM-recorded FPs of flying males. Bar is 0.5 sec. **A**, at 19.4°/;66.9°; **B**, at 20.0°/ 68.0°. **3**. Periods are variable because FP durations are variable. Data from 23 males at 3 temperatures. **5**. SWAT pulse-period mean (1 FP each) from 8 males; dots ELEC means, 17 males from which 2 or more FPs were recorded; deltas are ELEC means from 9 males from which only one FP was recorded—single-FP samples were representative.

* * *



These were flashing at dusk ~~over~~ ~~a field of tall grass~~ emitting short bright flashes about ½ second duration at tips of tall grass in hay field and dipping like Photinus pyralis but flashing while descending instead of while rising. — memory note. HSB

Figure 8. Barber's note to himself on pyralomima FP.

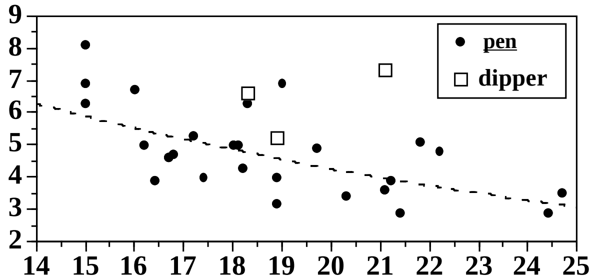


Figure 9. AA-dipper FP periods positioned in the penn dot-dash regression for all US demes (AX: sec/temp).

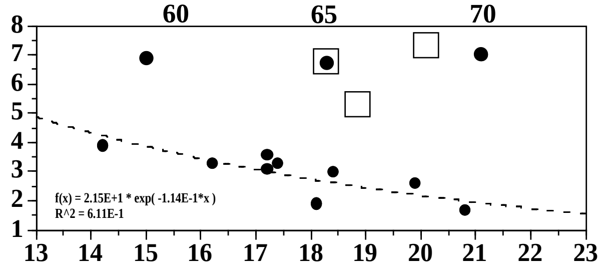


Figure 10. AA-dipper FP periods positioned in the Penn short-flash (adjunct) regression for all US demes (AX:sec/temp).

AA-Dipper. Males flew low over marshes in small "hops" at grass tips and emitted simple, unmodulated flashes of about 0.4 second duration in dipping Us, at intervals of 5-8 seconds. This FP resembles those of marsh dippers *Pyractomena linearis* and *lucifera*, both of which have have records of occurrence in Washtenaw County. This FP presentation has been assumed to be what Barber observed and attributed to his new species *pyralomima* (translation: appearing like *Pn. pyralis*), from Selkirk, New York. Such an FP has been observed rather often and regularly by fireflyers in the MD/DE area. During this study such a dipping FP was seen only on two other occasions, and emitted by only one or two specimens on each occasion. Perhaps this *Py. linearis*-like FP is an adjunct FP in some demes, but in others, say in Washtenaw County and those in the Maryland-Delaware area, has become the prime FP? Barber's original note to himself (**Fig. 8**) as to *pyralomima's* flashing behavior was attached to one of his pinned specimens (arrow marks pinhole), and from the wording appears to have been a "note from memory" and not necessarily contemporaneous with collection, and originally placed in a bottle of preservative with more than one voucher. It describes the flash as "about 1/2 second long" (i. e. not short), and emitted on the down slope of a dipping presentation, contrary to that of its name-reference.

The phyletic connection would seem to be with the *pensylvanica* Group, considering ecology and morphology, especially the PNV fluke (**Appendix no. 66384**). In **Figure 9** the mean FP periods of this firefly at three temperatures is placed in the dot-dash regression for US demes, and in **Figure 10**, in the short (twilight) regression. Field notes from Ann Arbor only mention the Dipper early in evening observations, perhaps indicative of a brief window of activity?

Morphology. General morphological data means are (n=15): PNL 2.6, ELL 9.7, PNW 3.0, EWhum 1.8, EWmid 2.2, ELVit 6.4, TOTLen 12.3, PNrat 0.86, ELWrate 1.25, ELVTrat 0.66. Figures and Tables of data are in the Appendix where they can be compared with data from Dipper and Dot-dash vouchers from the AA marshes.

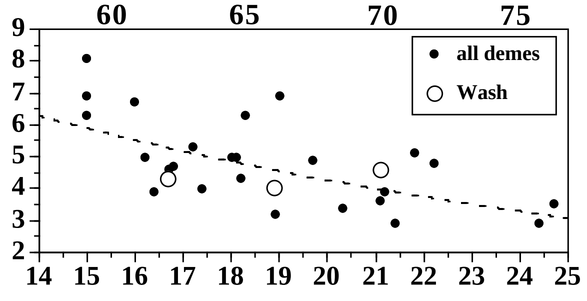


Figure 11. AA-dot-dash FP mean periods positioned in the penn dot-dash regression for all US demes (AX:sec/temp).

AA-Dot-Dash (penn). Flight and flashing were as described elsewhere in this paper, with variations among individuals in the duration of the dot-to-dash break, relative intensity of the dot and dash, and the beginning of the diminution-tapering of the dash. **Figure 11** shows the FP period means measured against those of all US demes, excepting the eastern Maryland and Long Island populations.

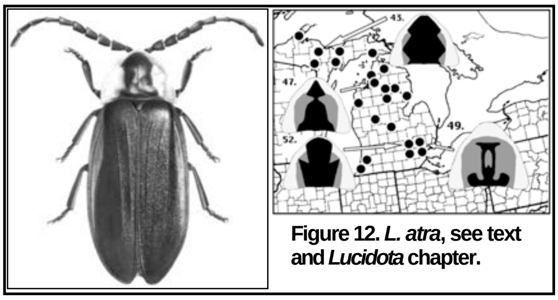


Figure 12. *L. atra*, see text and *Lucidota* chapter.

Morphology. General morphological data means are (n=15): PNL 2.7, ELL 10.3, PNW 3.2, EWhum 1.9, EWmid 2.5, ELVit 6.1, TOTLen 13.0, PNrat 0.82, ELWrate 1.31, ELVTrat 0.60. FigTables of data are in the Appendix where they can be compared with data from Flicker and Dipper vouchers from the marshes. FP Vouchers will be deposited in the USNM.

Comparisons of morphological features of the three series of specimens—flickerer, dipper, dot-dasher. A visual comparison of both sclerite-color histograms and pronotal vitta (vittagram) histograms revealed no distinctive contrasts, nor did a visual comparison of photographic arrays of the vittagrams (**Appendix**). A cladistic analysis of some of these characters might be made from these data. Statistical comparisons performed are not necessarily clear-cut, and probably amateurish, as follows: Mean total length of the dot-dasher exceeds that of the other two, 13.0 mm versus 12.2 and 12.3. A cautionary and confusing consideration of this statistic is that the FP that a male uses might be selected from his repertoire, based upon the individual's physical characteristics, such as age since emergence as an adult, or physical size. That is, if smaller males have a tendency to use one or the other of the compared FP-selected samples, they could comprise a statistically different but not genetically separate population. With respect to total length, dot-dashers (x=13.0) are significantly longer than flickerers (x=12.2): t = 3.54, df = 28, @ 0.14% level, 2-tailed, as calculated with both equal and unequal variances. Likewise, dot-dashers are significantly longer than dippers (x=12.3): t = 3.04, df = 28, @ 0.51% level, 2-tailed, as calculated with both equal and unequal variances. And finally, also with respect to total length, flickerers and dippers are not significantly different: t = 0.48, df = 28, 65.1%. Other characters: Pronotal length/width ratios are "no difference"; elytral humeral/mid-length ratios are not-. near-, and barely significant, as are comparisons of elytral-vitta/elytral-length ratios, but the latter are not concordant with the former. The similarity of the last three mentioned general characters might be expected among species adapted to a similar environment.

Ⓐ

Appendix

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Flickerer

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.480	9.700	2.967	1.780	2.207	5.407	12.167	.833	1.254	.565
sd	.174	.463	.135	.152	.175	1.233	.565	.054	.092	.135
se	.045	.120	.035	.039	.045	.318	.146	.014	.024	.035
n	15	15	15	15	15	15	15	15	15	15
min	2.100	8.800	2.600	1.500	1.900	3.100	10.900	.760	1.130	.290
max	2.800	10.600	3.100	1.900	2.500	7.000	13.100	.960	1.420	.750
Vc%	7.0	4.7	4.6	8.5	7.9	22.8	4.6	6.5	7.3	23.9

	5	6	7	Py	Cx	1	2	3	4
Mean	3.000	2.733	1.867	1.133	2.933	2.533	2.867	2.867	4.600
Std. Dev.	0	.458	.640	.352	.258	.640	.352	.352	1.298
Std. Error	0	.118	.165	.091	.067	.165	.091	.091	.335
Count	15	15	15	15	15	15	15	15	15
Minimum	3.000	2.000	1.000	1.000	2.000	1.000	2.000	2.000	3.000
Maximum	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	7.000

Dipper

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.587	9.687	3.007	1.800	2.220	6.420	12.273	.862	1.247	.663
sd	.177	.558	.144	.136	.142	.976	.590	.058	.089	.094
se	.046	.144	.037	.035	.037	.252	.152	.015	.023	.024
n	15	15	15	15	15	15	15	15	15	15
min	2.400	8.900	2.800	1.600	2.100	4.400	11.300	.800	1.130	.460
max	3.000	10.900	3.300	2.000	2.500	8.100	13.500	.960	1.380	.760
Vc%	6.8	5.8	4.8	7.6	6.4	15.2	4.8	6.7	7.1	14.2

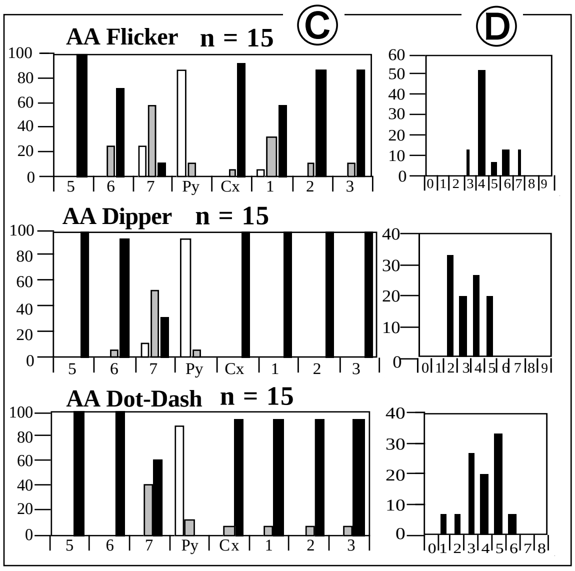
Mean	3.000	2.933	2.200	1.067	3.000	2.933	3.000	3.000	3.333
Std. Dev.	0.000	.258	.676	.258	0.000	.258	0.000	0.000	1.175
Std. Error	0.000	.067	.175	.067	0.000	.067	0.000	0.000	.303
Count	15	15	15	15	15	15	15	15	15
Minimum	3.000	2.000	1.000	1.000	3.000	2.000	3.000	3.000	2.000
Maximum	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	5.000

Dot-dasher

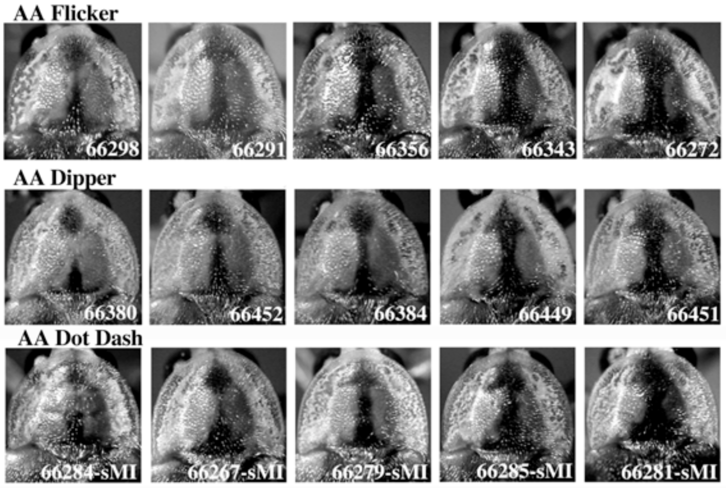
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{X}$	2.647	10.307	3.220	1.933	2.507	6.140	12.953	.823	1.305	.595
sd	.188	.578	.193	.062	.103	1.049	.649	.060	.057	.104
se	.049	.149	.050	.016	.027	.271	.168	.015	.015	.027
n	15	15	15	15	15	15	15	15	15	15
min	2.400	9.100	2.900	1.900	2.400	3.100	12.000	.750	1.190	.320
max	3.000	11.300	3.500	2.100	2.800	7.300	14.300	.920	1.400	.710
Vc%	7.1	5.6	6.0	3.2	4.1	17.0	5.0	7.3	4.4	17.5

Mean	3.000	3.000	2.600	1.133	2.933	2.933	2.933	2.933	3.867
Std. Dev.	0.000	0.000	.507	.352	.258	.258	.258	.258	1.356
Std. Error	0.000	0.000	.131	.091	.067	.067	.067	.067	.350
Count	15	15	15	15	15	15	15	15	15
Minimum	3.000	3.000	2.000	1.000	2.000	2.000	2.000	2.000	1.000
Maximum	3.000	3.000	3.000	2.000	3.000	3.000	3.000	3.000	6.000

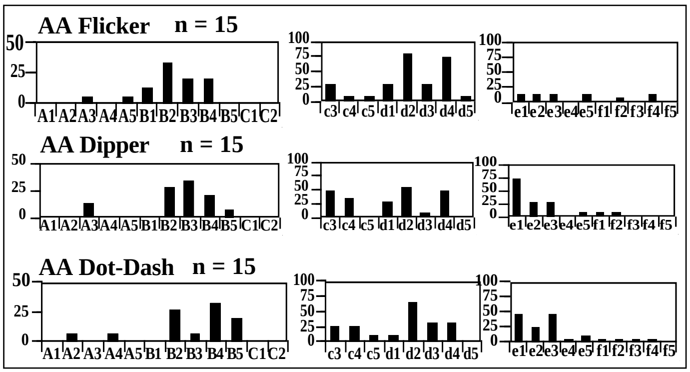
(**A**) Basic voucher measurements and ratios (rat); (**B**) Colors of abdominal ventrites and dorsites, 3-color discrimination: 1=pale, 3=dark), except ventrite 4 which indicates pale splash on posterior margin. (**C**) Histogram of sclerites (5-3, not 4) numerically quantified in B (n=8): bar position (l-c-r) and bar color indicate sclerite color (1-3); bar height indicates percentage in sample—note percents for each sclerite total is 100. (**D**) Histogram showing degree of pale splash on hind margin of visible ventrite 4, represented in array (0-9) at right in Figure 9. Circled number is n. **9**. Anatomical key to color-coded elements on abdomen and splash on 4, which is much generalized, and actually is very irregular or fragmented with strands and splotches. **10**. PN vittigrams (vittae) of a representative array of vouchers.



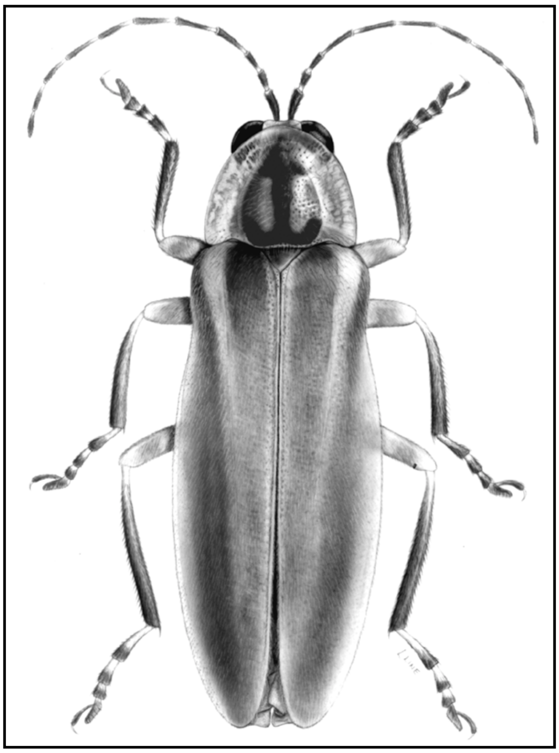
Abdomen color comparisons.



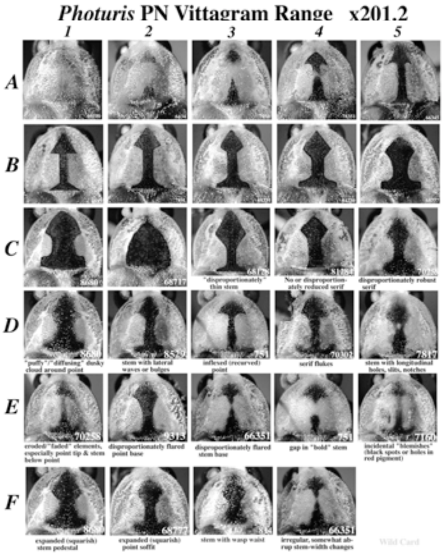
Vittagrams of the three AA marsh FP types.



Pronotal Vitta Comparisons



General drab appearance of penn-Group, but some more vividly marked; note flukes at ends of serif.



Note serifs with flukes at 4D

Seeking behavior of an extinct firefly: A fossil flex? Female delay in *Photinus ignitus* is rather long (**Fig. 1C**), and in experiments with female *macdermotti* it was demonstrated that *ignitus*' delay could have reasonably evolved from an ancestor like *macdermotti* (**Fig. 1A**), with the omission of the second flash (P2) of the *macdermotti* FP (**Fig. 1B**) (jel, 1984c). Such an evolutionary step was placed in context by considering male *macdermotti* behavior and the problems of signaling with beams of light in an environment where leaves and other obstructions may often interfere with transmission, blocking P2 from reaching the female once she has already seen, identified and responded to one or more antecedent (just-previous), properly-timed, 2-pulse FPs (**Fig. 1A**). That fireflies have solutions to such

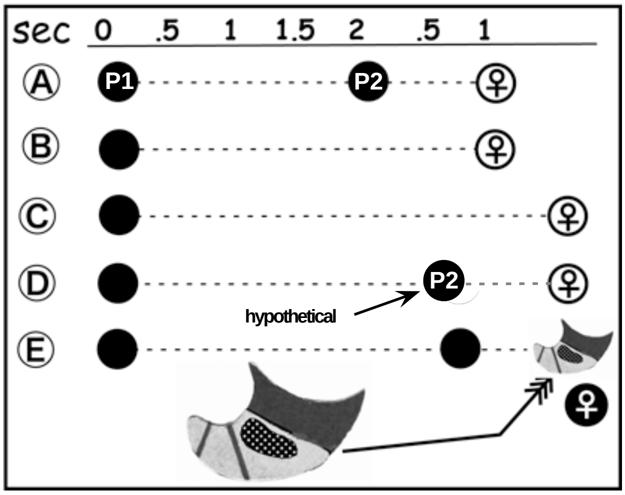


Figure 1.

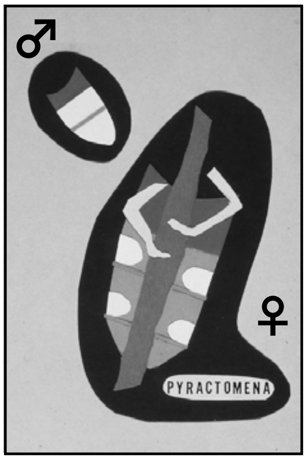


Figure 2.

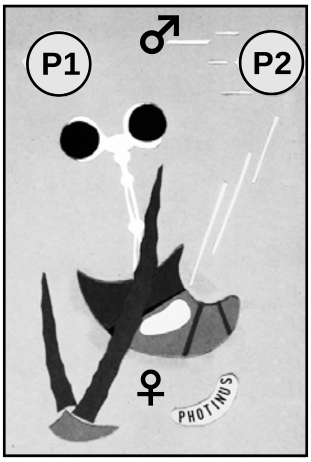


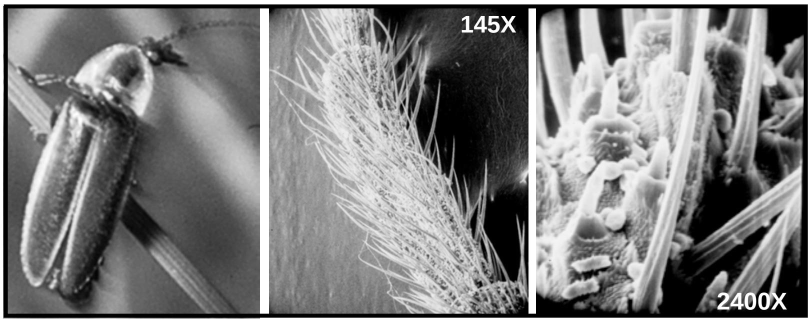
Figure 3.

visual problems is seen in females: When perched on stems or blades of vegetation, light from their lanterns can be obstructed by their perch. The four lanterns of ***Pyractomena*** females are positioned at the sides of the abdomen and usually avoid complete blockage (**Fig. 2**); and when ***Photinus*** females flash-respond to males, they flex their abdomens such that their lantern is aimed toward the male's flash—*macdermotti* females aim toward P2 (**Fig. 3**). *Photuris* females standing horizontally on a perch, roll their abdomens so that their venter aims toward the FP. The selection pressure/context for *ignitus*' ancestors to permanently lose the P2 flash could have been to trick predaceous females into disclosing themselves.

Another member of this species group, *Pn. indictus,* may have responded to such predator pressure, aggressive-mimicry-predation in their signaling system, in a more drastic way. *Pn. indictus* has lost its lantern, flies during the day, and uses pheromones. That is, it got out of the luminescent signal system entirely. Perhaps *indictus*' behavior can suggest something about its ancestors signaling. It is observed that sometimes *Photinus* females flex their abdomen **without** flashing—perhaps when their "motivation" to flash is low, in a manner of speaking. This indicates that flexing and flashing are separate operations and are not inextricably, tightly linked. Might some "variant" (atavistic) *indictus* females (still) flex their abdomen when a pair of pulses of the ancient timing was flashed at them?

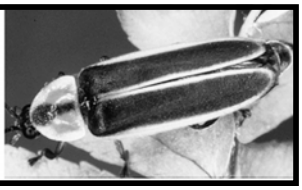
Reasoning from the *ignitus* experiment: (**1**) the P2 flash of the 2-pulse ancestor of *ignitus* occurred about 1 second before the female flash (**Fig. 1D (**a 1-second delay in females of this group is common, "standard"); (**2**) The ancestor of *ignitus* therefore might have spaced the 2 pulses of its FPs slightly more than *macdermotti's* "2 seconds" as shown in **D** (compare **Fig. 1A-C**, and reach **D** as a predicted timing of the female flash-response. (**3**) If *ignitus* and *indictus* came from the same 2-pulse FP ancestor, then the first experimental 2-flash FP to show to *indictus* females could be that predicted by *ignitus* ancestral behavior, and then variations on it (**Fig. 1E**), anticipating a properly-timed flex not a flash.

Interesting in a different way, a 1-pulse experiment with females of the non-luminescent *Pn. cookii* might also induce abdomen flexing. With this species another dimension can be examined: In part of their range *cookii* males have more extensive pale color under the tail, perhaps indicating they are genetically more similar to their flashing ancestor than *cookii* from other parts of their range, and thus more likely to flex? Though notes were not made at the time archived specimens were identified, from a center near southern Alabama, the darker specimens are recalled to have occurred in the northeastern part of the range toward eastern Tennessee, and the paler specimens toward the northwest, toward Missouri.



***Photinus indictus*: In the field at the Bug Camp, UMMZ Biological Station at Pellston, , a mate-seeking male in daytime; antennal closeups, by Pat Carlysle, at 145X and 2400X.**

At the right is a male of the nonluminescent *Pn. cookii*. In an amazing stroke of luck a firefly almost identical in appearance to it, but with a lantern, was found near the Gulf.



Chapter 70

Photuris whistlerae n. sp.

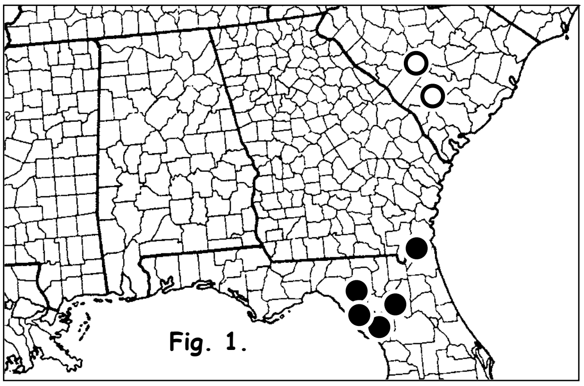
Whistler's Mother

If eyes were made for seeing, then
whistlerae is its own excuse for being!
(reflection ala Emerson)

This will-o-the-wisp is one of the most beautiful fireflies in North America, not only for the delicacy of its morphological appearance (**Fig. 2**)—which, except for certain minor details is like that of *P. branhami* (and variads)—but especially for the eye-catching presentation of its FP around the crowns of trees. Its laterally pumping dips are as embroidery … lacy, luminescent loops (**Fig. 3**). **Figure 1** shows geographic sightings, and **Figure 4**, adult seasonal occurrence in Alachua County—for counties west toward the Gulf the SESOBS records for *branhami* may be indicative. With one notable exception only one or a few WMs were seen at one time, emitting their short, sharp crescendo flashes around the crowns of bushes or hardwood trees along tree rows (**Fig. 5**). The single exception was an incredible display of a very large number around low bushes and over thick herby vegetation of a damp and once-dynamic firefly marshland that was gradually losing its water source (later abruptly lost, bulldozer) —a creek at the old "Airport Pond" locality **(Fig. 6**). In Florida the only firefly emitting a confusing, pumping or looping, aimed crescendo is the default FP of *beanii*, presently known to occur only along Rt. 24 southwest of Otter Creek in Levy County.

Males emit phrases/trains of short crescendos (**Fig. 7A**), with a few to several flashes (3-12) in each phrase—one evening in Dixie Co. FL 3-4 were predominant. Phrase periods are highly variable (a consequence of phrase length variability—though phrase *pauses* (breaks between them) might reveal a somewhat predictable relationship if regressed on temperature). Crescendo periods within pauses are rhythmic, highly regular, with individual PM-recorded phrases often showing standard deviations of zero at the 0.1-sec level. However, PM recordings show variation among mean periods of individuals though they were recorded at the same time and in the "same" activity space; **Figure 9** shows crescendo mean periods regressed on temperature, and **Figure 10**, the rate regression.

As noted above, the distinctive FP presentation close around the crowns of woody vegetation is diagnostic: crescendos are emitted during narrow and deep (8-12"?) dips (pumps) in flight



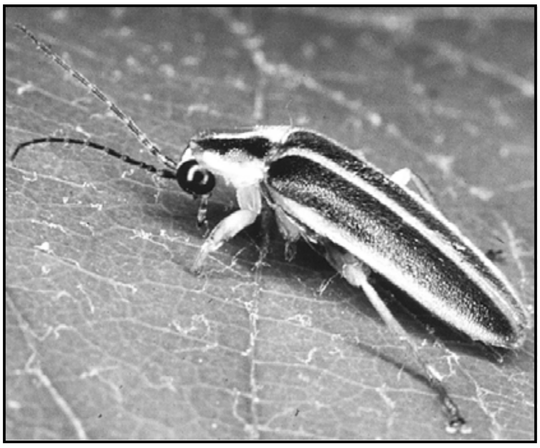


Fig. 2. *Ph. branhami*, a *whistlerae* look-alike.

Fig. 3. A tree addressed with pumps and lace.

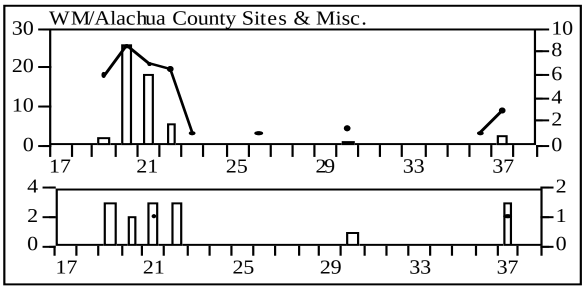


Fig. 4. SESOBS.

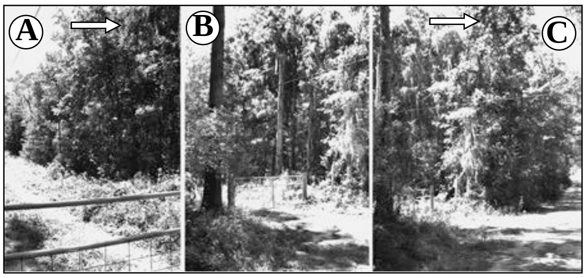


Fig 5. Powerline site at Pinetop; from C turn left into B.

Fig. 6. Airport Pond site, 1965.

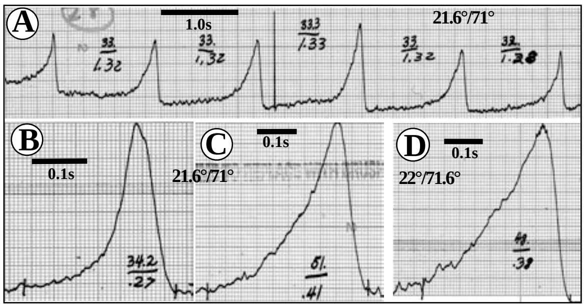


Fig. 7. WM at Airport Pond, 10/9/67 (AX: rel. int./time).

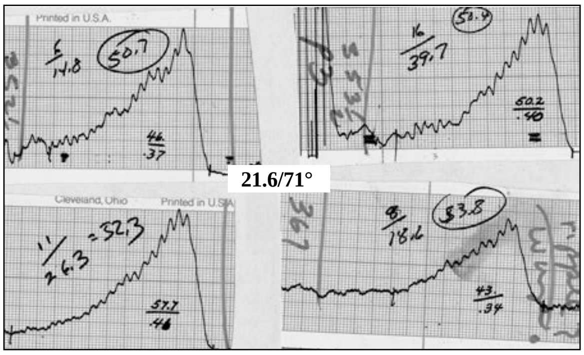


Fig. 8. Wingbeats atop FP scans (rel-int/time).

as emitters fly slowly, laterally, or up and down in the same place as though directing their message to a specific point. Rarely, instead of dips, flashing-movements were humping up-then-down traces or *pyralis*-like "Js". More common was a flattened/shallow stripe of light when males flew more rapidly around crowns; this was the only form seen in the few observed at South Carolina sites, and may lead to an incorrect diagnosis or uncertainty—note the open circles in **Figure 1**. The first and last crescendos of a phrase may be somewhat shorter than others, and the last often "leads off" (points) in the direction of the next phrase and flashing space.

At 23.9°/75° "typical" crescendos (**Fig. 7C**) are about 440 mS in duration at base and 120 at half max, from examination of 100+ PM records. Occasional variations noted in crescendo forms (e. g., **Fig. 7B-D**) are probably due to a changed orientation of swooping/pumping flyers with respect to the PM axis; in **Figure 7**, both **B** and **C** are from the phrase of a single male—but proficiency and versatility of intensity change cannot be excluded as an element of intersexual selection. With respect to the color of luminescence, this firefly exhibits the same enigmatic appearance seen in the flashes of many other *Photuris*: though all of the many measured are green and nearly and all appear very bright to the eye, to some observers, including me, WM flashes appear bright white. When colored objects or lights appear white ("at night all cats are gray"), so it is said, it is because rods and not cones of the eye are responding to dim light. In contrast, the flashes of related species *branhami* (DM) do appear green—perhaps it is the difference in flash form? Spectral measurements of six specimens averaged 555 millimicrons, with 528.0 and 598.0 at half max (27/5/68, Biggley et al).

The crescendos of only one of the more than 40 males PM-recorded showed rippling produced by wing shuttering (**Fig. 8**). Curiously, six of the eight crescendos in this recorded phrase showed the modulations—the other two were too dim for modulations to have registered. Average modulation rate was 51.8 Hertz.

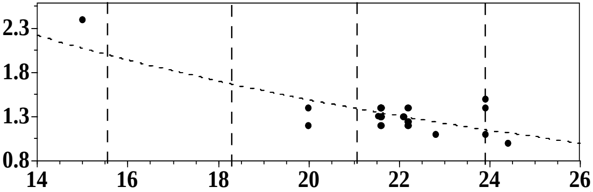


Fig. 9. FP period (AX: sec/temp).

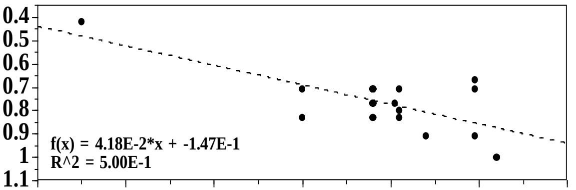


Fig. 10. FP interval rate (AX: Hz/temp).

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\overline{x}$	2.432	8.700	3.000	1.658	2.237	.126	11.116	.810	1.361	.014
sd	.120	.462	.197	.143	.171	.551	.561	.031	.090	.060
se	.028	.106	.045	.033	.039	.126	.129	7.092E-3	.021	.014
n	19	19	19	19	19	19	19	19	19	19
min	2.100	7.800	2.600	1.500	2.000	0	10.000	.760	1.210	0
max	2.600	9.500	3.300	1.900	2.600	2.400	12.000	.870	1.500	.260
Vc%	4.9	5.3	6.6	8.6	7.6	437.3	5.1	3.8	6.6	428.6

	5	6	7	Py	Cx	1	2	3	4
$\overline{x}$	3.000	3.000	3.000	1.526	1.053	1.684	2.421	2.684	3.316
sd	0.000	0.000	0.000	.513	.229	.582	.507	.478	1.108
se	0.000	0.000	0.000	.118	.053	.134	.116	.110	.254
n	19	19	19	19	19	19	19	19	19
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	1.000
max	3.000	3.000	3.000	2.000	2.000	3.000	3.000	3.000	5.000
Vc%	0	0	0	33.6	21.7	34.6	20.9	17.8	33.4

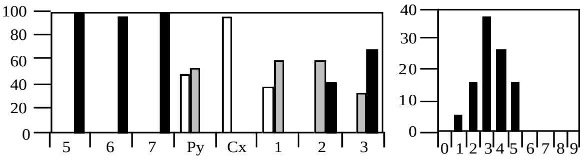


Fig. 11. WM morph: meas, ratios, color.

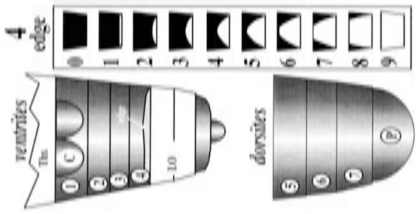


Figure 12. Topographic and splash guide.

Fig. 13. WM—gun club/airport pond localities

Morphology. **Figure 11** gives the basic morphological measurements, ratios, and colors of a sample of specimens from Alachua County; **Figure 12**, a guide to anatomical elements; **Figures 13 and 14**, show a representative array of PN vittagrams and an analysis.

Taxonomic Note. From the very beginning the working epithet for this species was Whistler's Mother, from the common name given to a James (A.) M. Whistler painting (1871-72) featuring shades of black and gray, and formally entitled "Arrangement in Grey and Black, No. 1: The Artists Mother." The distinctive color, delicacy, and "charm" of this firefly deserve similar recognition.

The **Appendix** gives SESOBS charts; additional numerical morphological data; numerical values for colors illustrated in histograms; a PN vittagram analysis histogram; and allows comparison of WM histograms with those of *branhami* (DM) and other sampled demes (variads/cognates).

Holotype: male, voucher number 68276, collected 18 May 1968, Alachua County, Florida, near airport ("Airport-Pond" Site), FB page 66: One of several collected after emitting crescendo FPs. Morphological data: from spread sheet—PNLen 2.3, ELLen 8.1, PNWid 2.6, ELWhum 1.5, ELWmid 2.0, LELVit 0.0, TotLen 10.4, PnRat 0.86, ElRat 1.33, VitRat 0.0; Colors: T 333, Py 1, Cx 1, V 233, Edg 4. Types will be deposited in the USNM.

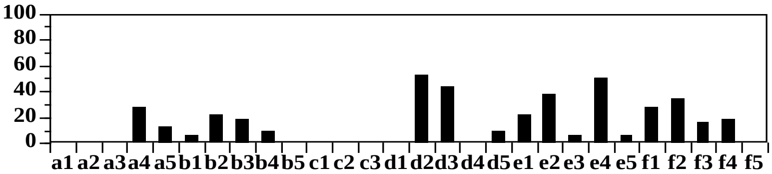
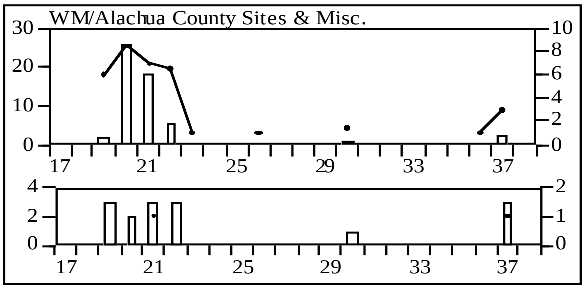
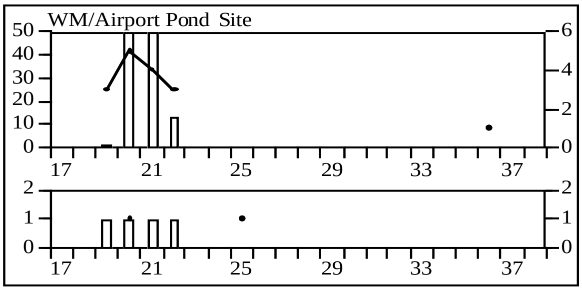
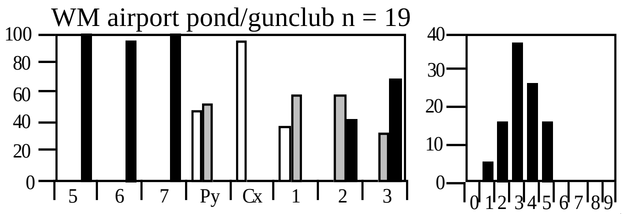


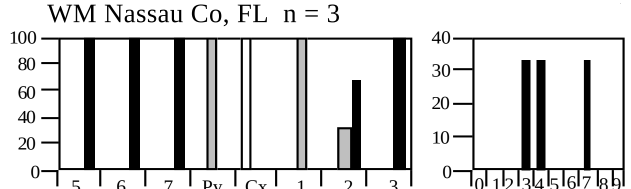
Fig. 14. WM PN analysis, n=32; —gun club/airport pond localities.

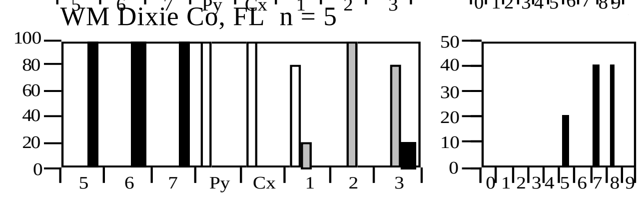
Appendix

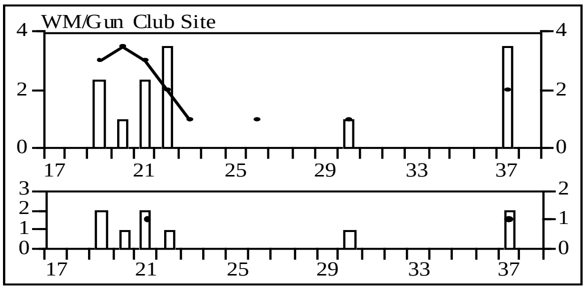


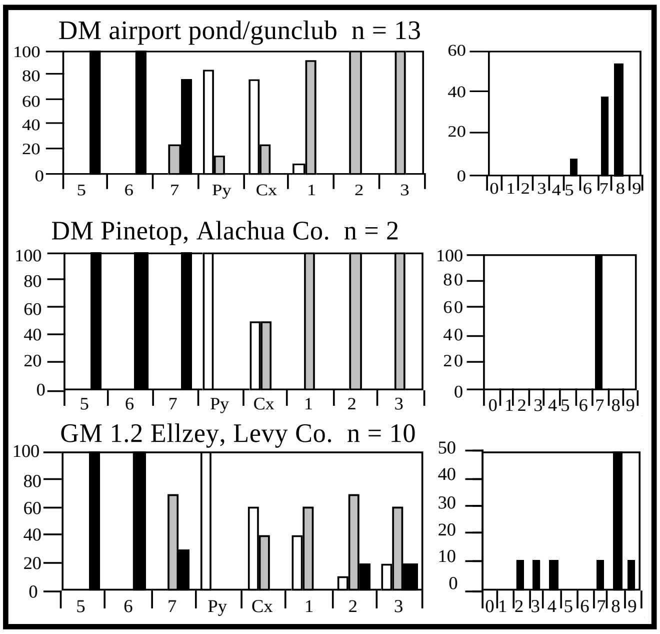












WM gun club/airport pond

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.432	8.700	3.000	1.658	2.237	.126	11.116	.810	1.361	.014
sd	.120	.462	.197	.143	.171	.551	.561	.031	.090	.060
se	.028	.106	.045	.033	.039	.126	.129	7.092E-3	.021	.014
n	19	19	19	19	19	19	19	19	19	19
min	2.100	7.800	2.600	1.500	2.000	0	10.000	.760	1.210	0
max	2.600	9.500	3.300	1.900	2.600	2.400	12.000	.870	1.500	.260
Vc%	4.9	5.3	6.6	8.6	7.6	437.3	5.1	3.8	6.6	428.6

WM gun club/airport pond Alachua Co. FL

	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	3.000	1.526	1.053	1.684	2.421	2.684	3.316
sd	0.000	0.000	0.000	.513	.229	.582	.507	.478	1.108
se	0.000	0.000	0.000	.118	.053	.134	.116	.110	.254
n	19	19	19	19	19	19	19	19	19
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	1.000
max	3.000	3.000	3.000	2.000	2.000	3.000	3.000	3.000	5.000
Vc%	0	0	0	33.6	21.7	34.6	20.9	17.8	33.4

WM Dix/LaF

	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.433	8.550	2.933	1.567	2.233	0.000	10.967	.827	1.392	0.000
sd	.082	.543	.103	.052	.151	0.000	.609	.023	.044	0.000
se	.033	.222	.042	.021	.061	0.000	.249	9.189E-3	.018	0.000
n	6	6	6	6	6	6	6	6	6	6
min	2.300	7.600	2.800	1.500	2.000	0.000	10.000	.790	1.330	0.000
max	2.500	9.000	3.000	1.600	2.400	0.000	11.500	.860	1.460	0.000
Vc%	3.4	6.4	3.5	3.3	6.8	0	5.6	2.8	3.2	0

WM Dixie Co. FL

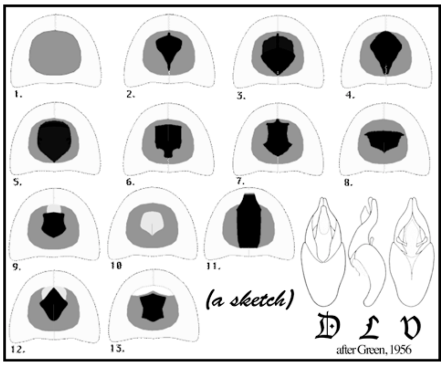
	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	3.000	1.000	1.000	1.200	2.000	2.200	7.000
sd	0	0	0	0	0	.447	0	.447	1.225
se	0	0	0	0	0	.200	0	.200	.548
n	5	5	5	5	5	5	5	5	5
min	3.000	3.000	3.000	1.000	1.000	1.000	2.000	2.000	5.000
max	3.000	3.000	3.000	1.000	1.000	2.000	2.000	3.000	8.000
Vc%	0	0	0	0	0	37.3	0	20.3	17.5

WM Nassau Co. FL

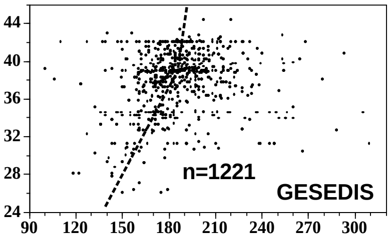
	PNLen	ELLen	PNWid	EWhum	EWmid	ELVit	TOTLen	PNrat	ELWrat	ELVTrat
$\bar{x}$	2.467	9.300	3.000	1.733	2.233	0.000	11.767	.820	1.297	0.000
sd	.058	.346	.100	.115	.115	0.000	.321	.017	.012	0.000
se	.033	.200	.058	.067	.067	0.000	.186	1.000E-2	6.667E-3	0.000
n	3	3	3	3	3	3	3	3	3	3
min	2.400	8.900	2.900	1.600	2.100	0.000	11.400	.800	1.290	0.000
max	2.500	9.500	3.100	1.800	2.300	0.000	12.000	.830	1.310	0.000
Vc%	2.4	3.7	3.3	6.6	5.2	0	2.7	2.1	0.9	0

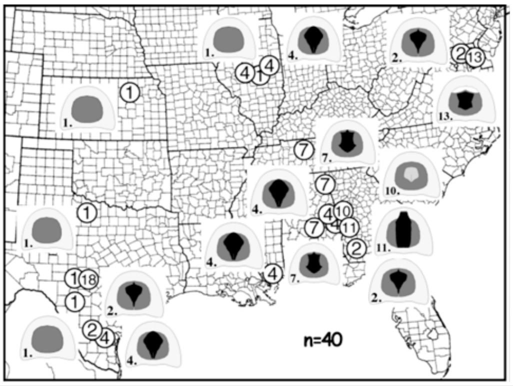
WM Nassau Co. FL

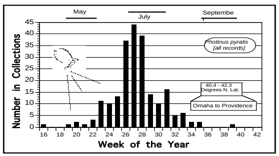
	5	6	7	Py	Cx	1	2	3	4
$\bar{x}$	3.000	3.000	3.000	2.000	1.000	2.000	2.667	3.000	4.667
sd	0	0	0	0	0	0	.577	0	2.082
se	0	0	0	0	0	0	.333	0	1.202
n	3	3	3	3	3	3	3	3	3
min	3.000	3.000	3.000	2.000	1.000	2.000	2.000	3.000	3.000
max	3.000	3.000	3.000	2.000	1.000	2.000	3.000	3.000	7.000
Vc%	0	0	0	0	0	0	21.6	0	44.6

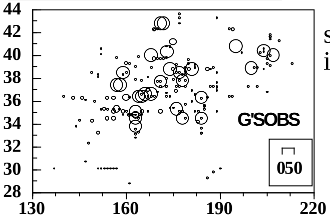


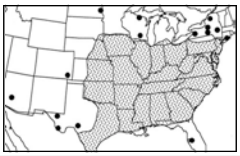
Notes On *Photinus pyralis* (L.). The Big Dipper is the most common, well known, easy to study, widely distributed, available firefly in North America, and important to mention in certain distinctive respects: (**1**) A Lat/Doy line shows less if any bend at 36°N; (**2**) Its extensive distribution, large size, abundance—even in disturbed grassland habitats—may make it prey for many *Photuris* unless its distinctive flash code is difficult to break … if so, why? Perhaps it is a promising subject for the study of counter-measures; (**3**) Variation noted in its PNV and abundance of archived specimens make it a good subject for the recognition of local populations to guide DNA investigation. (**4**). Its physical distinctiveness, and FP that in situ is unmistakable, are unlikely to be mistaken for any other. (**5**) The above suggest also that this firefly is perhaps ideal for initiating studies on vagility and interdemic travel.

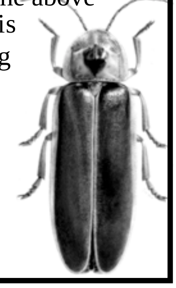












Chapter 71

Queries As To Countermeasures To Photurinae Predation:

Toward Deciphering Firefly Signal Milieux In the Americas

Earth, Air, Fire, Water … **Jaws!**

> *… if ever a master defined the unknown and pointed*
> *the way of investigation, certainly it was Darwin.*
> Henry Fairfield Osborn, 1928

A half-century and a thousand demes of watching *Photuris*, yet still not enough to understand the signals that it was long hoped would finally clarify their taxonomy and relationships. This chapter is a very dim candle on a path toward understanding what must be the quintessence of all American firefly signaling: deceptive flashes and their manipulative interplay, arms races, predator versus prey in lights. Only close and lengthy scrutiny of them, and experimentation in the field, will discover satisfying facts and proofs of this assertion. As for here and now, as with many other aspects of firefly study, expectations and imagination must serve as introduction. What we can know is this: compared with the Eastern Hemisphere, the Western, wherever photurines occur, is as the Wild West, and as counterpart to Samuel Colt's *Peacemaker*—his large-caliber, 6-shot revolver—in firefly life it is the Jaws of photurines that have made the rules (**Fig. 1**). At this point a distinction must be made between deceptive/misleading flash signal elements that serve to confuse, misinform, misdirect, and deter predator fireflies, and those that have evolved in the context of misleading rivals that compete for mates. Though some tactics may serve both ends, distinguishing between these two will be necessary for understanding signal adaptation, exaptation ("pre-adaptation"), and the eternal conflicts of measure and countermeasure.

Figure 1. Jaws: major authors of American firefly signaling ecology and evolution?

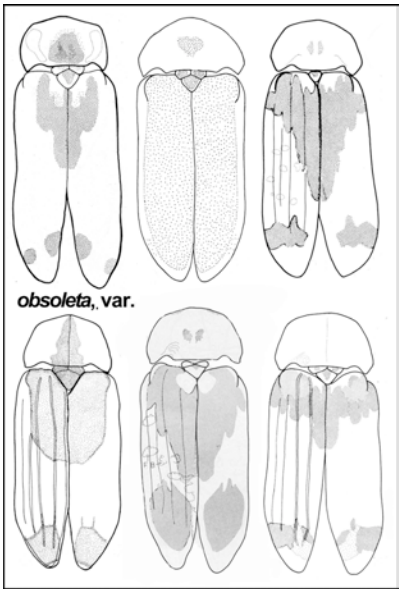
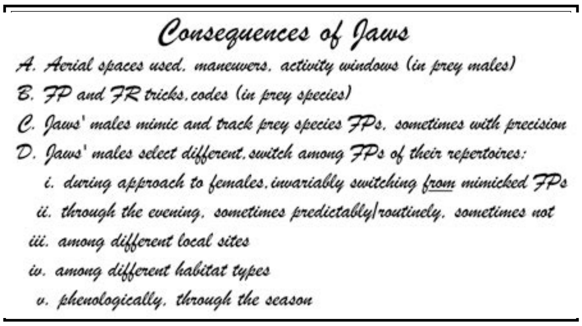


Figure 2. A few species of a New Guinea group in which sexual selection may have been a major selective agent (drawings from Ballantyne, 1968).

Fifty years ago when one thought about the adaptive significance and evolution of firefly signals, the notion of reproductive isolation was in play, and hidden ("cryptic") "Biological Species" that were sympatric and synchronic, and morphologically "identical," but had different and testable mating signals, were inspiration and encouragement. In Florida fireflies, for example, *Photinus consanguineus* versus *macdermotti*, focused attention and were reassuring (jel, 1966ab). Not a decade later sexual selection was rediscovered, grabbed significant attention, and was invoked to explain enigmatic mating behavior and other puzzling phenotypes. For example, consider *Pygatyphella* (nee *Luciola) obsoleta* variads in New Guinea (jel, 1972; see Ballantyne, 1968, for taxonomy). In the *obsoleta* of the Madang/ Sek-Harbor region, long bouts of sedentary, solitary, luminescent soliloquies, aerial chases and bumps, dogfights between and among female-chasing males, and leaf-top dances are prelude to copulation (**Figs. 32, 34**; jel, 1972). In this group of fireflies, including congeners and nominal conspecifics, which have the general appearance of bird-droppings loaded with uric acid against daylight predators (**Fig. 2)**, try to guess what strange courtships remain to be discovered. Today, it is clear, there can be no question, that both reproductive isolation and sexual selection are important frameworks for contemplation, and either may be expected to have been a/the dominant theme in individual cases, but … in the Americas, the role of Jaws can be overlooked no longer. It should have been taken more seriously long ago, received more than the passing comment that it did (jel, 1965). Now it must be expected, at least suspected, that anti-predator codes and countermeasures could be the single most important influence on flashed signals. A natural experiment is available in a comparison of signals found in American species with those of non-aggregating, "**site**-patrolling" (not roving) species of Asia and Africa, if there are any? Maybe such behavior itself is an unrecognized consequence of *Jaws*?

Full appreciation will require detailed knowledge of signaling-*interaction* subtleties which presently are mostly lacking. This elusive element will become important not only for understanding hidden codes, but, as indicated here and there in FP descriptions of many *Photuris* species sketched in this paper, what could be more important for field ID than understanding the reasons for signal use or non use at any particular moment of nocturnal or seasonal activity (**Fig. 3)**?



Consequences of Jaws

A. Aerial spaces used, maneuvers, activity windows (in prey males)
B. FP and FR tricks, codes (in prey species)
C. Jaws' males mimic and track prey species FPs, sometimes with precision
D. Jaws' males select different, switch among FPs of their repertoires:
  i. during approach to females, invariably switching from mimicked FPs
  ii. through the evening, sometimes predictably/routinely, sometimes not
  iii. among different local sites
  iv. among different habitat types
  v. phenologically, through the season

Figure 3. Flashing-behavior features known or expected to be among the consequences of jaws.

Details of the general structure of flashed signals, their differences, geographic occurrence, and sets that appear among them may suggest evolutionary pathways and specific selection pressures that produced them (**Figs. 4, 5**). We may now be better able to make informed guesses as to which species-type might be better suited to explore specific problems. For example, *Photuris chenangoa*, *missouriensis*, and *potomaca*, the “river fireflies,” **appear** to have simple FPs, mere trains of flashes, and may be non-predators and intellectually bereft, not among the best choices for experimentation on matters of neural/molecular finesse and flash trickery. On the other hand, the *Photuris cinctipennis* complex in Florida—a seeming species swarm in the *cinctipennis* Group centered on *Ph. branhami*—seems to have developed out of specific mimicries of the pulse-timings of various of members of the *Photinus consanguineus* Group (and/or vice-versa?), in a multi-pronged evolutionary game of tag, and a difficult place to begin—perhaps DNA will at the least, be a necessary adjunct at the beginning to rein in its many confusions.

The procedure here is first to review and synopsize some elementary known and *suspected/possible* modes of *Photuris* attack, and then, based upon field observations and a few field and desktop experiments, suggest a some possible aspects of firefly ecology and of their signals and signaling that may have arisen in the context of avoiding rendezvous with *Jaws*.

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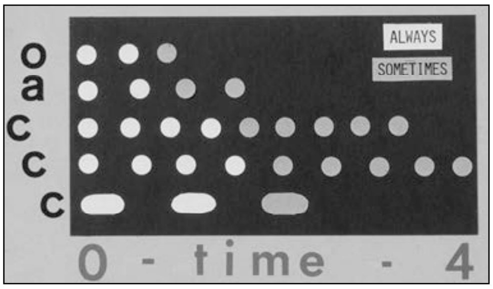


Figure 4. Pulsed FPs of the *Photinus ardens* Group, in 1972: *obscurellus*, *ardens*, FFP-*consimilis* (and *carolinus*?), SFP-*consimilis*, SP-*consimilis*,

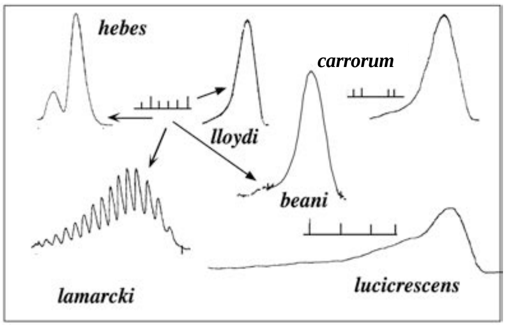
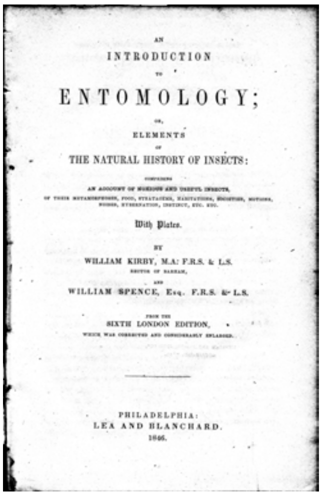


Figure. 5. *Photuris lucicrescens* Group, unified operationally on the basis of the crescendo shape or envelope of their FP, non-reddish trim/ground color—and in most, pale hind coxae.



AN
INTRODUCTION
TO
ENTOMOLOGY;
OR,
ELEMENTS
OF
THE NATURAL HISTORY OF INSECTS:

With Plates.

BY
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AND
WILLIAM SPENCE, Esq. F.R.S. & L.S.

FROM THE
SIXTH LONDON EDITION,

PHILADELPHIA:
LEA AND BLANCHARD.
1846.

Figure 6. Kirby & Spence *Entomology*, 1846.

❄ ❄ ❄

Modes Of Attack

(**1**) **Aggressive mimicry** (an imprecise, but long-established term). In his lengthy analysis of *biological mimicry* Wolfgang Wickler (1968) considered "Peckhammian mimicry" to be an alternative name, recognizing E. G. and G. W. Peckham papers from the late 19th Century as being early recognition of ≈*deceptive appearance enabling exploitation of the flesh*, that is, a mimicry being used for more than escaping exploitation by others (i.e. Batesian). Georges Pasteur (1982) explained that "aggressive mimicry was known and understood as such long before the Peckham publications" and cited an early textbook, *An Introduction to Entomology* (Kirby and Spence, 1826). The 6th edition from 1846 is at hand (**Fig. 6**): This edition also precedes Darwin and recognition and explication of natural selection; it attributes such adaptation, for example, to "the Author of nature," but uses the suggestive term *mimicry* (p. 440) as well as other expressions—*imitating*, *look alike*. To avoid a layman's misunderstanding of the term mimicry, Pasteur begins his analysis, "Unconscious biological mimicry, hereafter 'biological mimicry' …" If nothing more, Pasteur's detailed, skilled dissection reveals that a convenient, useful taxonomy of the intricate ways organisms deceive and exploit each other is probably not possible. For the foreseeable future we non-specialists are stuck with using simple adjectives for an operational mimicry taxonomy: say, "Batesian, "Mullerian," and "aggressive."

In North American fireflies, *Photuris* females of some species take perched positions in grasses, herbs, and bushes in the activity spaces of other species, from which they flash attractive, appropriate/adequate, prey-specific sexual response flashes (RFs) to the FPs of passing males, which they attract and eat (see photo-fillers: 4 parts, pages186, 194, 204, 226; 2 parts, pages 230, 268; photos, pages 461-462, 470, 471). It is not known whether these femmes fatales: (**A**) orient to specific prey FPs when selecting hunting sites; (**B**) return to fruitful sites they had used previously or remain at sites where they grew up—where they and some sibs had been placed as eggs by their mother; or (**C**) return to remembered sites during the activity-windows of specific prey that had been learned from previous experience.

Nor is it known whether they (**D**) use experience from previous hunts when emitting response flashes, and/or (**E**) adjust their RFs ad hoc, trial and error, by keying on approach rates and other movements of responding males. That females of some species have at least crude templates for FP characteristics of particular prey species, or sets of prey species—e. g. 2-pulse *consanguineus*-Group FPs—and for RFs, is clearly indicated/demonstrated. Such templates provide an Achilles heel for exploitation by countermeasures (CMs), and a starting place for students pursuing CMs.

Certain prey (*Photinus*, *Pyractomena*) provide chemicals that are used in the predators' own defenses (Eisner, et al, 1997; Eisner, 2003 and refs.); others *perhaps* do not (conspecific males, insects grazing on plant substances; see photo fillers, 230, 268). Life-time predation by *Photuris* females may be expected to increase their reproduction/fecundity well beyond what could be achieved through nutrition gained only during their larval stage. Thus hunting success (neural-lantern competence) by such females would seem a counterpart to mating success in highly attractive, polygamous males, be strongly favored by selection, and perhaps shift somewhat a balance-point in Richard Dawkins' life vs. dinner considerations. Comparisons of female ovaries and relative longevity should reveal consequences of such selection.

Figure 7. Site of 25 or more late-season, perched, flash-responsive, mate-eager *Photinus ignitus* females, July 1962.

(**2**) **Aerial attack, hawking**. *Photuris* females approach small airborne lights and attack them (jel and Wing, 1983; photo-filler, 2 parts, pages 91-92; photos pages 461, 462). Experimentally they attacked glowing targets in shorter time than they did flashing LEDs. When a freshly killed male was attached to a decoy light the female ate it. That a seized free-flying male will be taken to a perch and eaten is assumed since experimentally a male attached to an LED via a curvy, slippery wire slid down and free with the added weight of the female, and was taken/accompanied to an herb stem and eaten.

Attacking females use the dim glow of light-leaking lanterns (4% amps in LED experiments) of flying males to guide attacks after approaching bright flashes. Females probably detect and evade lantern-shuttering by beating wings to avoid attacking a flying target through beating wings, (see *lamarcki*). Females may possibly detect/orient via the rapid (40± Hertz), air-compressions from beating wings—as felt softly on the hand when attracting males to a penlight—and be able to attack a darkened, hovering male at close range in the pause between his FPs.

(**3**) **Aerial attack option**. Females hunting by aggressive mimicry leave their perches and attack hesitating, partially-attracted males. While filming with nature-photographer John Paling, and stimulating (on camera and at length) FRs from a perched *Photuris harrannorum* female via a dangling LED, the female left her perch and attacked the LED. This tactic perhaps is also used in situations where a self-landing prey male would be more difficult to locate or reach—as in foliage high above ground?

(**4**) **Attack flash-responding females**. Females of prey species would be rich prey, bearing eggs and other nutritional stores, and stationary and vulnerable. At phenological end-times responsive females may be abundant, though typically scarce in early and mid-season. A predator might emit FP-like emissions and prey upon responding females. As many as 25 extremely flash-responsive *Photinus ignitus* females were seen in a small area of a stream-side, farm-house herby-lawn in Madison County, central New York, in July, 1962 (**Fig. 7**, arrows).

(**5**) **Aggressive mimicry by proxy**. (**A**) A female *harrannorum* landed and remained within inches of a *Photinus macdermotti* female that was answering an approaching *macdermotti* male. The outcome was not seen with certainty, but an attack on the approaching male seemed possible. (**B**) On several occasions female *harrannorum* have been seen to land near other aggressive mimics, in one example, landing near a female *Photuris stanleyi*, a smaller predator, and possibly a specialist on *Pyractomena angulata*. Such a tactic might be expected to occur with larger/"dominant?" (regional) species, when they lack the code of prey species, or where smaller predators might become prey.

(**6**) **Lek-like scrambles, melees**. In Florida, males of *Photinus macdermotti* sometimes approach answering FRs slowly and land amongst grass and herbs at distances of <3’ from an answering light, such that that several males may be perched in close proximity, peering around grass-blades with necks stretched out, walking, and emitting coded FPs and in particular an assortment of code-intruding/disrupting and predator-mimicking flashes. Aggressive mimicry predation is certainly the *root* cause of this situation, and any stalking/ ambulating predator "sneaking darkly" within the group has ready access to prey. Multi-channel recording and computer analysis will be necessary to understand the variety and specific effects of deceptive and other flashes that are emitted as males compete with each other to mate and avoid being eaten by potentially lurking predators (jel, 1981)—a multidimensional lady or tiger situation.

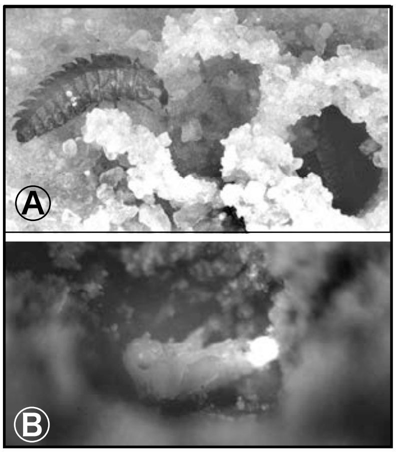


Figure 8. *Photuris* larvae (A) digging, constructing; (B) pupal chamber uncovered, pupa tickled, glows.

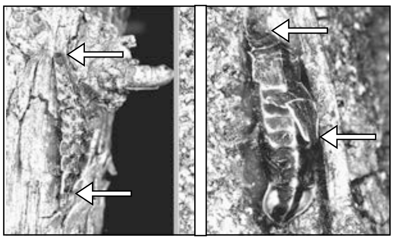


Figure 9. Hanging *Py. borealis* prepupa (left), and a pupa hanging out of its cast-off larval skin (arrows), on swamp forest trees.

Predation Avoidance In Time and Space & Color

The avoidance of high-risk situations and places—seasons, times of night, and activity spaces—is a first level of defense against attack. Escape in season occurs in *Pyractomena borealis* in Florida, but its congener, *limbicollis*, introduces a caution against complete satisfaction in this explanation. *Photuris* fireflies pupate underground; such chambers in Florida will remain cool into early spring (**Fig. 8AB;** see also photo-filler page 86). *Py. borealis* pupates on the sunny, southern periphery of trees (**Figs. 9, 10A**; jel, 1997), where sunlight and sun-warmed tree-water overnight will accelerate development and eclosion (**Fig. 11, 12**). *Py. limbicollis* pupation stands in sharp contrast: Adults appear few weeks later than *borealis* and in overlapping sites; *limbicollis* pupates nearer the cold ground and on the north-facing periphery of smaller trees (**Fig. 10B**). *Py. limbicollis* adults emerge with the spring generation of the predator *Photuris harrannorum*, which has as adjunct FP like the FP of *limbicollis* and flies with it (jel, 1980)—late-summer *harrannorum* males do not use this FP. Spring *harrannorum* males switch to their default J3-4 FP when answered with a female-simulating decoy (see *harrannorum*, this paper). This seasonal window for *limbicollis* obviously places it in harm’s way from predation by *harrannorum* females. Why does *limbicollis* appear to tune (via pupation temperature control) its adult activity to its predator’s active season?; perhaps it is unable to escape?—say, countervailing selection from larval competition between *borealis* and *limbicollis* for minute' snails/eggs, which otherwise would occur during simultaneous, tiny, first-instar stages? Or, their short flash FP actually warns against hawking by *harrannorum* females that avoid their own, larger and more dangerous males?

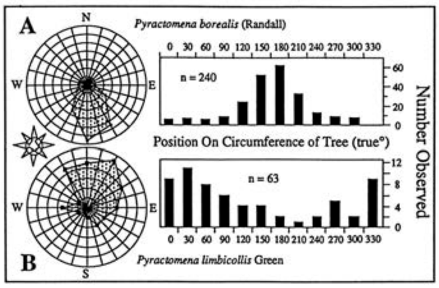


Figure 10. Pupation azimuths on north-central Florida swamp-forest trees.

Figure 11. Experimental model of firefly thermo-regulation: clay balls and wet sand, wires and thermocouples.

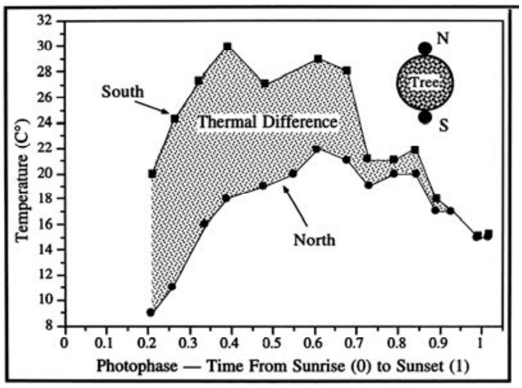


Figure 12. Thermocouple measurements of modeling-clay fireflies on north versus south side of a free-hanging, sunlit, wet-sand-filled jug (model tree).

Evening activity of some *Photinus* species precedes the onset of *Photuris* flight, though toward the end of their window the situation gets difficult. Such *Photinus* species as *marginellus*, *floridanus* and *curtatus* of Division I and *australis*, *collustrans*, *pyralis* and *scintillans* of Division II, have the airways and signal channels predator free, at least for a few minutes, though I am less certain of this generalization with *collustrans*. These early *Photinus* have red-shifted light and some

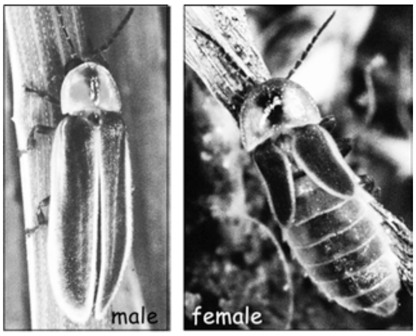
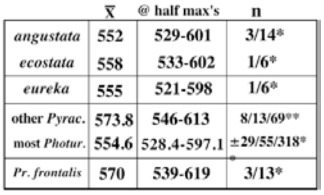


Figure 13. Div. II: *Photinus scintillans*;_spectrum peak 579 mm, half-max 533-"625" (yellowist in N.A.!).



	$\bar{x}$	@ half max's	n
angustata	552	529-601	3/14*
ecostata	558	533-602	1/6*
eureka	555	521-598	1/6*
other *Pyrac.*	573.8	546-613	8/13/69**
most *Photur.*	554.6	528.4-597.1	±29/55/318*
Pr. frontalis	570	539-619	3/13*

FigTable. 14. Luminescence color from master list (Appendix 3).

are known to have eye-filtering, which results in greater contrast for flash-detection when green reflected light (monochromatic noise) from vegetation is at a high level (see also page **414**). The most red-shifted *Photinus* measured so far is *Photinus scintillans*, whose males were been seen sneaking through twisting cracks of airspace beneath ground-draped layers of vines in Rock Creek Park (DC, jel 1966), more than an hour before dark. It was their own twilight zone, a *Photuris*-free time-warp (**Fig. 13**). Why do *Photuris* females not pursue these prey and *Photuris* males not begin activity earlier? Perhaps females do hunt at this time—but none have ever been noted this early. Perhaps *Photinus* males can identify hunting females in high ambient light and avoid them. As for *Photuris* males, if their females are not hunting there is no reproductive benefit. Perhaps twilight insect hunters —certain dragonflies Twilight and Phantom Darners in Florida (Beaton, 2007)—would attack. When male mate search in a (certain few) *Photuris* does begin, late in the twilight-*Photinus* window, males of these species emit short, *Photinus*-like flashes in *Photinus* spaces for a brief period, and then, as the twilight *Photinus* window closes, these *Photuris* males gradually change to their default and/or other adjunct FPs (see *appalachiensis, asacoa* and other *penn*-complex species, and *douglasae*). With respect to the luminescence color question in fireflies, it is not yet resolved, for there are red-shifted species that are not active at twilight. This is mentioned briefly on page **414**.

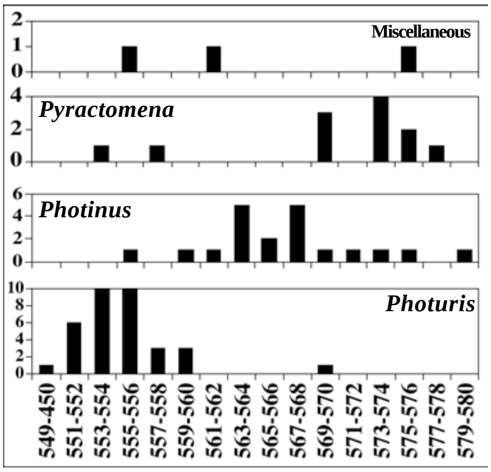


Fig. 15. Luminescence color comparisons. See page 412 for discussion.

Flight speed, color mimicry? Slow-flying glows are easy targets as demonstrated in the merry-go-round attack study. The lanterns of many *Pyractomena* males, apparently inescapably, leak dim glows between FPs. Males of *Pyractomenas angulata, barberi, dispersa, palustris* and probably others drop to the substrate when answered and remain dark without flashing again for a few minutes (jel 1964, 1966b). This is obviously one way to avoid a hawking respondent. Such dropping behavior was not seen in Florida *borealis* which flies in very early spring before *Photuris* are active. An unnamed *Pyractomena* (near *sinuata*?) in the Hudson Valley *apparently* (n=2) emits a few short glows separated by dark moments of about the same duration before landing briefly, waits a short time, and then repeats this program, and then again, and so on.

Two *Pyractomena* that emit distinctive, attack-inviting glows occur with *Photuris* in coastal Florida. They are *angustata*, which emits seconds-long, bright green "FP" glows, and slow-flying *ecostata*, that emits its dimmer green glows between bright flash-flares that are emitted at >8 seconds-long intervals. Only these two of all *Pyractomena* seen so far emit green bioluminescence, this as determined by specific and independent lab measurement. See page 414 for details. Other *Pyractomena* emit yellow, yellow-orange, or amber luminescence (**FigTable 14, Fig. 15, Appendix 3**). On several occasions green glows of presumptive *Photuris eureka*—judged from agility of flight—were seen closely following (<6 inches), flying/tailing green glows, as though inspecting them. Note in its dedicated text that one of *eureka's* "two adjunct" FPs is a green glow that is indistinguishable from that of *angustata*. This close following suggests the possibility of a hawking connection that may have been responsible for the noted green color shift in these two *Pyractomena*, and further, that rather discriminating color vision may actually occur in *Photuris eureka*, at least at very close range. Note here, however, that the tailing green glow would seem to have been that of a male *eureka*, though males are not known to be hawkers. Something important is clearly amiss, and remains to be explained. Unfortunately, *eureka* and *angustata* in Florida are on the "now gone?" list.

In *Photinus*, glowing between FPs is not common, but does occur in a few species, especially in Green's (1956) *punctulatus* Group, including *collustrans, stellaris,* and *tanytoxus*, all fast-flying, arcing fireflies that travel rapidly over grassland and would be difficult if not impossible targets for an aerial set-up and attack.

Moving toward deception in signal codes, this example involves escape into the dark with a code change. When a *Pn. macdermotti* flashes the first pulse of his 2-pulse FP, a *mac*-tuned predator hunting/watching from below can start toward his space and be there ready to strike when pulse 2 is emitted (**Fig. 16B**)—a target is not painted on his back but around his broadcasting space. Such a predator, say a specialist like *lamarcki*, might pressure such prey to shorten the time between the P1 and P2 (**Fig. 16A**). Obviously a male cannot move far from the space where he emitted his first pulse to emit his second because both need to travel through open space, the open path that will allow the female response to reach him (**Fig. 17**). This might influence vegetation types or perches taken by females or rejected by males.

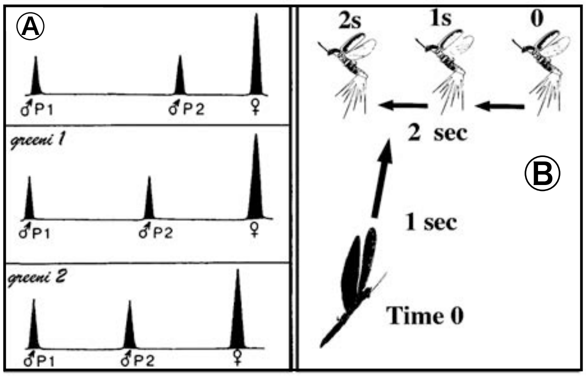


Figure 16. One possible reason that a 2-sec pulse period might be shortened.

Deceptions and escapes in FP configurations. In the examples that follow, flash form, timing, and seeming potential for manipulation are the focus. First, as an introduction to CM discovery—the application of suspicion and intuition perhaps—are two stand-out FP types, one emitted by North American *Photuris* and the other by a Jamaican *Photinus*, though possible examples are suggested by *Photuris* the have FPs with combinations of different elements—*barberi* and *dorothae*.

Crescendo FPs: One experiment and casual observations lead to the expectation that firefly females generally time their response flashes from the sharp onset (ON transient) of a male's flash, and in particular, when this delay is an important part of the code (as demonstrated experimentally in *Photinus australis* (**Fig. 18**, jel-1966). With this in mind, consider this: the FPs of some *Photuris* are crescendos, flashes that begin dimly **without** a sharp transient, and gradually become brighter. Those of some species are easily seen to vary in duration and the intensity that is finally reached. Crescendos usually end abruptly (**Fig. 21A-C**). Such variation is commonly seen in the FPs of *Photuris lucicrescens*, especialy on cool evenings when crescendos average longer. A crescendo flash could be used to trick a potential predator into making a timing mistake as illustrated (**Fig. 21B-C**). Should a prey species time its critical mate-recognizing delay from the OFF transient not the ON (as in **21A)**, the ON, lacking a conspicuous transient and instead having a sloping intensity rise, might induce a predator into delaying variably. Or, if manipulated by the crescendo-emitting male using a variable slope, caused to make controlled mistakes (**21B, C**). Crescendo flashes may also be confusing to aerial attackers, or rival males, for locating emitters in 3D space—and of course there are other possibilities in the nebulous realm of sexual selection—neural finesse …?

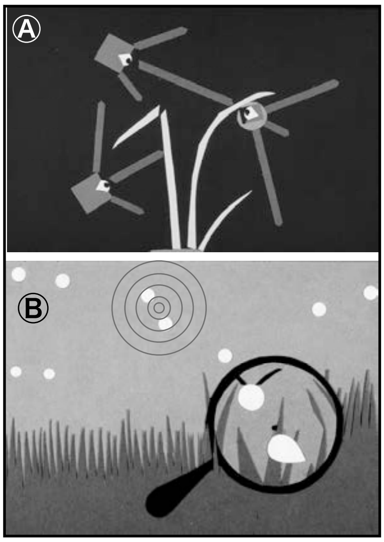


Figure 17. In consideration of light propogation.

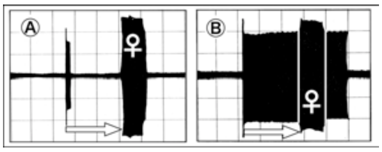


Figure 18. Female *australis* response to a normal short flash then an experimental long flash, with the same response delay from ON transient (jel, 1966; oscilloscope traces).

FP bait and switch: *Photuris jamaicensis* apparently preys upon several *Photinus* in Jamaica (Farnworth, 1969). The FP of one begins with a few short flashes and ends with a flicker (**Fig. 21D,** PM-flicker in **20-8**). The initial pulses might cause predators to emit an inappropriate response flash or otherwise disclose their identity. With the large number of species in Jamaica, and the variety of FPs known from there (short sample in **Fig. 20**), perhaps this would be an alchemist's brew for CMs, and the ideal place to study details of aggressive mimicry as it occurs in *jamaicensis*. This nominal species may actually be a complex of unrecognized "cryptic/sibling" species, which in turn historically was in part responsible for the development of the seemingly large numer of *Photinus* species described from this tiny island—though recent studies on Caribbean islands indicates that Jamaica may not be a disproportionately speciose as previously thought (M. Bramham, pers. com.). Note that some Jamaican *Photinus* have perhaps escaped in time, for they become active as late as midnight and one an hour or so later later. Tropical but not temperate climates may allow such escapes (jel-1969).

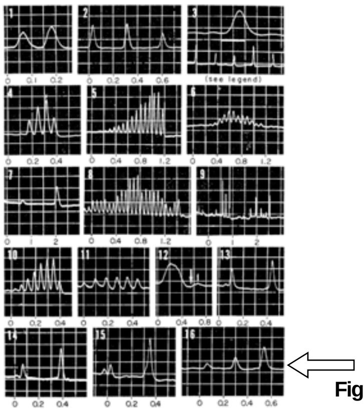


Figure 20. Oscilloscope traces of FPs in Jamaica.

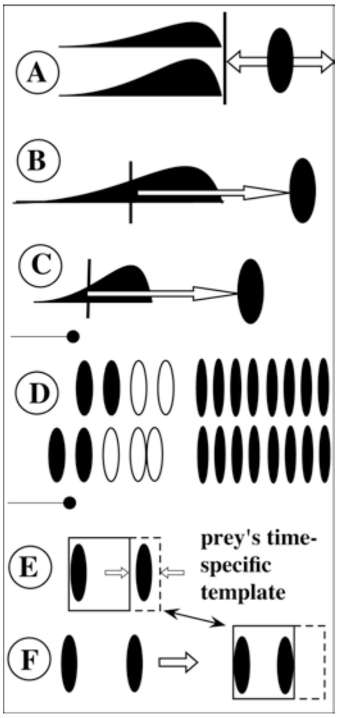


Figure 21. Deception in FP configuration. Note crescendo variations in A.

On FPs, FRs, and CMs of Green's remarkable *Photinus consanguineus* Group. This taxonomic association of fireflies might be considered the white rats for study of firefly signals, and in particular, the historical development of FPs as CMs and other means of escape from predators. FP variation among members of the Group (**Fig. 22**) suggests experiments, and one particular FP timing, that originally was known from Florida *macdermotti* (**Fig. 21B**), occurs broadly across eastern North America. Demes using this basic form provide innumerable natural experiments because they confront different *Photuris* predators, each of which in turn is expected to be tuned to a different array of prey, as well as different and sometimes larger and dangerous competitors. Among these many prey and predator demes one would expect to find different "*macdermotti"* CM solutions resulting from their varying histories of confrontation, a kaleidoscope of signal "colour" in time and space. Noted variations include a "short-*mac*" deme in the mountains of northern Georgia and a "long-*mac*" deme in southern Georgia.

The following is a brief sketch of the *consanguineus* Group, some of its FPs with CM-related thoughts. Members of this Group are morphologically easily distinguished from all other North American *Photinus* by male aedeagi (**Fig. 23**).

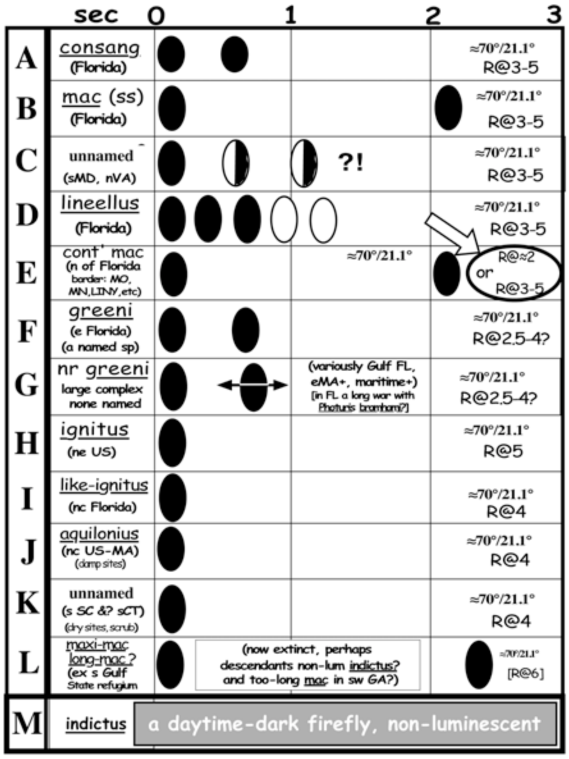


Figure 22. FPs of Green's *Photinus consanguineus* Group.

Taxonomically, *Photinus consanguineus* itself, as presently defined for operational purposes, was described by LeConte in 1851, but the specimens of "his specimen series" (in an MCZ tray at Harvard) were numbered and reshuffled in the century following such that the specimen numbered "1" (I) was probably (most certainly) not LeConte's "prime/only" reference (note: the *type* specimen concept had not yet come into use). As a temporary fix, under the guidance of wise committee member Prof. Bill Brown, this specimen was informally considered to be the temporary *consanguineus* name bearer (jel, 1965); its physical appearance was similar to, that is, most resembled that of the Florida species with the FP as in **Figure 22A.** The other Florida species, the one that hitherto had not been recognized/distinguished on morphological grounds, flashed as in **22B**, and was then named *Photinus macdermotti.*

One place to begin a discussion of CMs, would be to note that there seems to be something very curious about the timing code(s) used by Florida versus continental *macdermotti* (**Fig. 22B, E**), such that it is "broken into" by several predators—in Florida, *branhami*, *carrorum*, *harrannorum*, and *lamarcki*, these belonging to three different operational species groups of *Photuris*—as though striking a primal template deep in a flashing firefly's nervous system? (There is also a *Photinus* with such an FP and FR that occurs in the Andes Mountains near Cali, Colombia, South America (**Fig. 24A**), and with it a hunter (**24B**), a Photurinae of an unnamed/unknown genus that flashes correctly-timed answers to

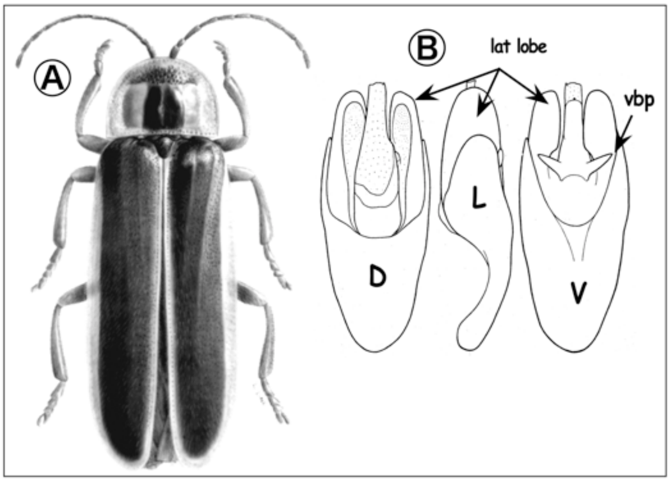


Figure 23. ID *consanguineus* Group: lateral lobe rounded, simple ; slightly variable but simple vbp; A, *macdermotti*, B, *consanguineus.*

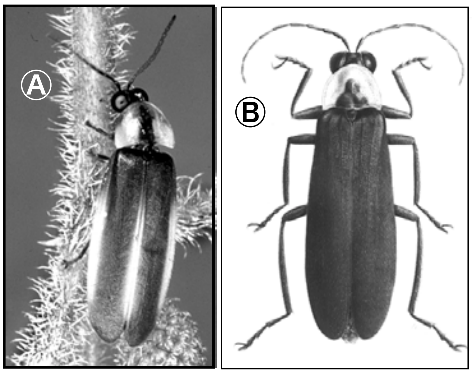


Figure 24. Andean *Photinus* with a *mac*-like FP and its Photurine predator.

passing males, and certainly must prey upon them—aggressive mimicry has also been reported in other genera of the photurine subfamily, *Bicellonycha* and *Crematogaster*.

On templates. Consider, that should the predator's template accept a variable pair of pulses, as may be the case with *Photuris harrannorum*, and the prey code is a fairly precise 2-second interval (≈70°) between the two pulses (**Figs. 22B, 24A**), as it is in Florida *macdermotti*, a male can test a respondent by emitting a pulse-pair at an interval outside the *mac* bracket (**Figs. 21E, F**). This of course suggests experiments as to the precise nature of the mimicry of any hunters of *macdermotti* and their template differences and weaknesses.

Bait and switch. Another way to confuse, short-circuit or block a template is to initiate a specific FP-FR interaction (**Fig. 24B**) and then change to another FP. That is, after a male *macdermotti* had received answers to a couple of his 2-pulse FPs, if he then emitted only single-flash FPs (at 4 or 5 seconds; **Fig. 24C**), a predator might at first not answer at all, and then after seeing two or more such spaced single flashes, use a different template, one used on a single-flash species. In experiments in nature, *Ph. harrannorum* females are tricked this way; they emitted single long, jagged flashes with little delay. *Pn. macdermotti* females answered in a most interesting way: in extensive experiments with females of both spring and late-summer generations, when first shown one or two normal *mac*-FPs (**Fig. 24A**), and next only single flashes, they answered the experimental singles as though they had seen the second (P2) pulse (**Fig. 24D**).

This opened up a new line of thought. This FP-FR interaction was like the FP-FR of a relative, *Photinus ignitus* (**Figs. 21H, 24E**), except that the delay of *ignitus* females is a little longer than the experimentally-induced delay of *macdermotti* females (**Fig. 24,** compare **D and E**). These experiments suggested that there *might* already have existed in the neural circuitry of females of a 2-pulsing pre-*ignitus* ancestor, the variation that later became the substrate for selection that led to a fixed 1-pulse FP with a long female delay. The significance of this in the context of CMs in the evolution of mating signals is obvious. As precursor in nature to this—i.e., female acceptance of a 1-pulse FP in a 2-pulse species, note that the P2 of FPs of males approaching females, as amongst grasses or bush foliage, must often be obscured (**Fig. 17A**).

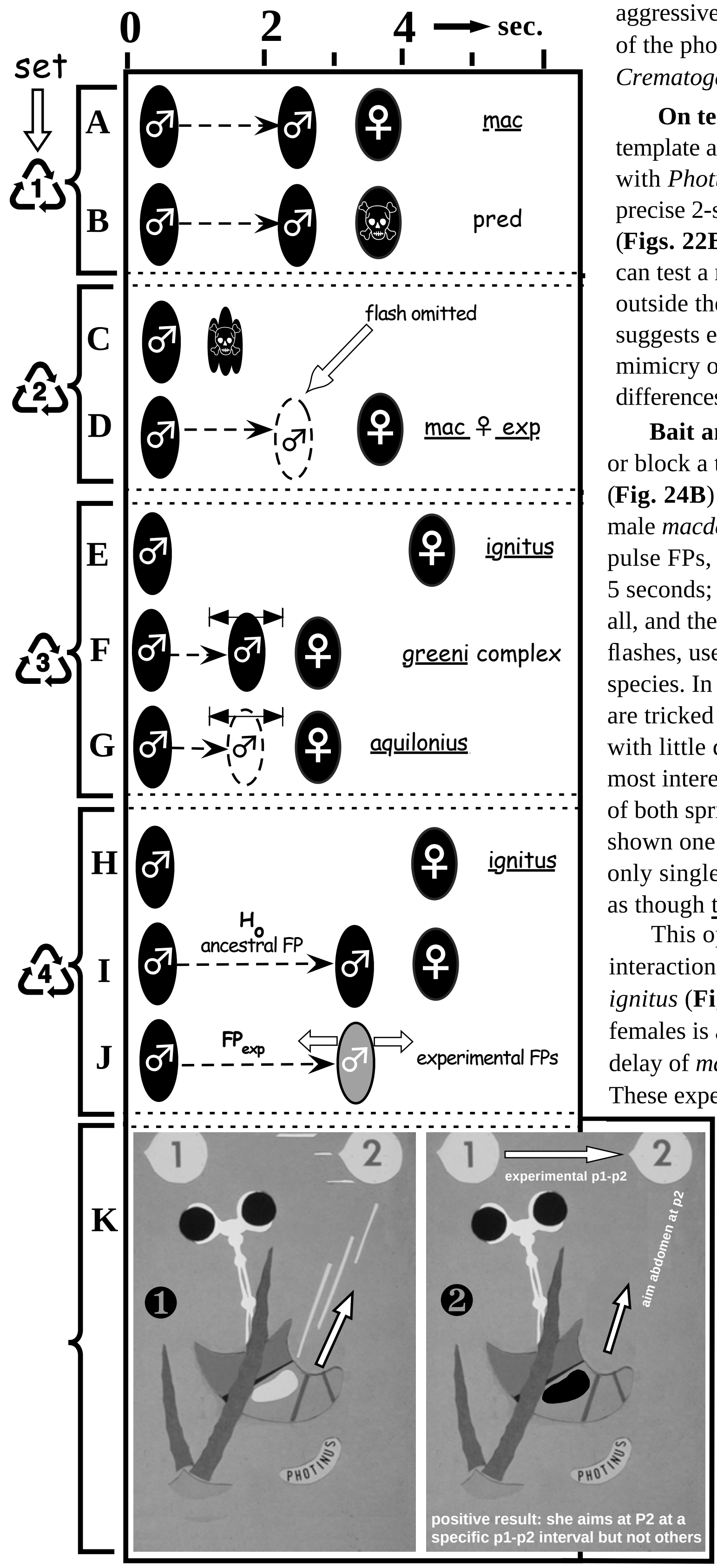


Figure 24. Evolutionary considerations of FPs in the *consanguineus* Group.

Now consider other FPs in **Figure 24**: reflect on **24F** and **24G**, **24H** and **24I, 24J** and **24K**. A similar explanation may apply and examination of other 1-flashers in the Group shed further or different light on the *macdermotti* model. (see page 340, and below)

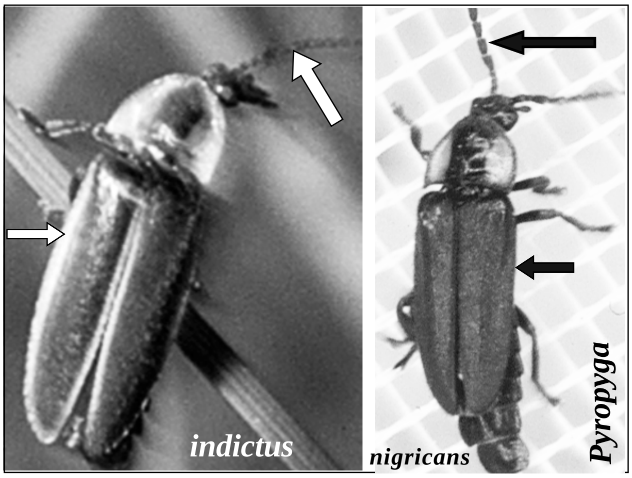


Figure 25. *Pn. indictus* has simple antennae and pale elytral margins; *Pyropyga* species have slightly serrate (saw-toothed) antennal elements ("segments") and dark elytral margins.

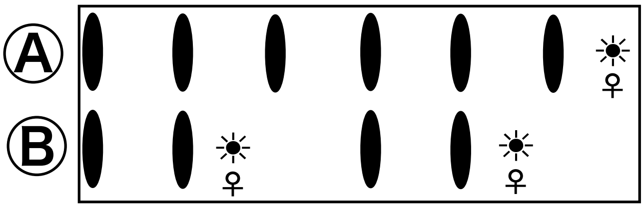


Figure 26. A CM origin for the 2-pulse *macdermotti* FP.

A thorough examination of the FPs, codes, CMs, and other communication in the *consanguineus* Group demands reflection upon the the black sheep among them. Most surprisingly, and happily, one of the Group has lost its fire, is active in daylight hours, and uses pheromones—*Pn. indictus* (**Fig. 25**). Viewed in the context of the FPs of its group mates, and the imagined predator-induced CM explanations being sought here, might the *indictus* lineage have escaped predation by gradually relying less and less upon flashed signals and, say, depending more and more upon reflected light clues or wafting chemical clues in ever-earlier twilight? Suppose, as a thought experiment, that *indictus* evolved from a 2-pulse ancestor; might *indictus* yet retain any of the behavior package that was connected with using such a flashed signal? For example: females of *Photinus*, and also some *Photuris*, aim their response flashes at the flashes they answer. Maybe females of *indictus*, if tested at dusk, would aim—say, via a lingering atavistic gene, a throw-back—their abdomen at a 2-pulse FP (**Fig. 24K**). Would it be too much to expect that they would demonstrate a preference for the timing of one particular timing, perhaps that of the presumably lost *ignitus* ancestor (**Fig. 24I, J**). This would be one of those throw-away experiments that takes little time, has little expectation of success, but what if worked!—a *T. rex* without all the problems, and an invitation for DNA comparisons. Note that a 2-pulse FP "retrodicted" to have been used by *ignitus*' ancestor should be a little longer than that of most contemporary, measured *mac*, except for a population found at a dam in southern Georgia. *Pn. indictus* has an extensive occurrence, is found in damp meadows and can be collected with a sweep net. *Pyrogyga* spp. occur with it; *indictus* can be distinguished as shown in **Figure 25**.

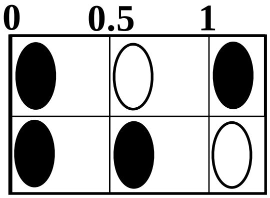


Figure 27.

A final note on CMs of *macdermotti*: Continental FPs differ from those of Florida in that they often are "trains" of single flashes (2sec-≈2sec-2sec) as shown in **Figure 26A**—only twice observed over decades in Florida, and then by single individuals. (**1**) When 2-2-2- continental males are answered with a decoy they begin emitting the 2-pulse pair (2-4-2-4-) we recognize as the Florida species-typical FP (**Fig. 26B**). While 2-2-2- can easily be explained as more efficient for mate search, because in trains every pair of flashes (moving) along the sequence is an FP, it is also an easier target for hawking predators. In Arkansas, Maryland, Minnesota, and elsewhere, continental males were usually seen flying low over the ground in woodlands; on the other hand, Florida *mac* flies in open space above palmettos in pinelands and around shrubs at mesic woods edges. Low-flying males are less likely to be targets of attack. **Figure 27** shows a mysterious FP variation of a member of the *consanguineus* Group from southern Maryland and just across the Potomac in northern Virginia. It was occasionally seen high above ground searching at the tree-tops. From fleeting glimpses it seemed to emit a 3-pulse FP and to omit pulses as shown (see **Fig. 22C**).

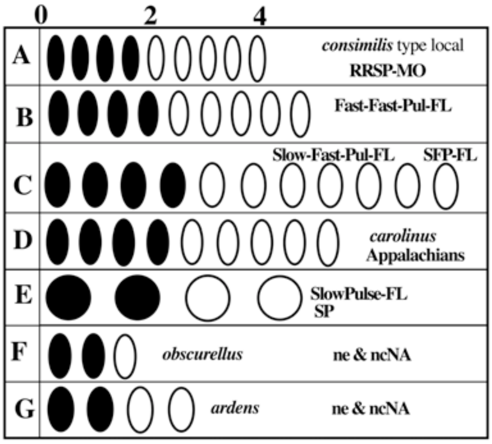


Figure 28. *Photinus ardens* Group, timings are crude approximations, for perspective and generalizing only.

The *ardens* Group, the simplicity of counting and timing pulses, or is there more to it than encountered elsewhere in North American *Photinus*?

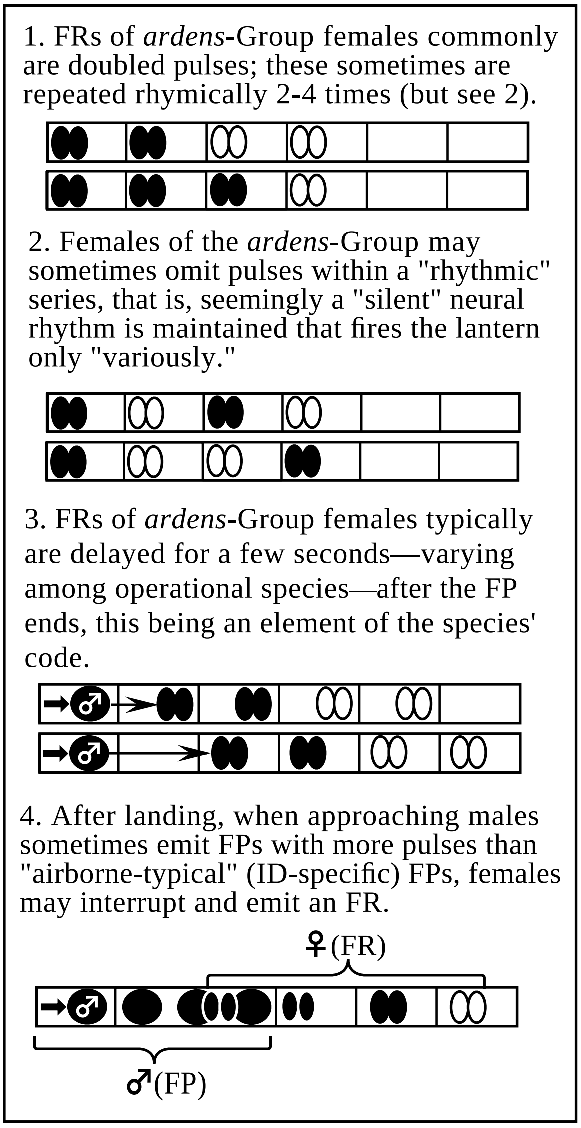
If members of the *consanguineus* Group are as white rats and appropriate for initiating masters-level studies on the workings of firefly signals, suspicions must arise that the signals of Mr. Green's *ardens* Group could possibly be more suitable for a PhD, and then post-doc, or a life. **Figure 28** gives a crude synopsis of the FPs of the Group, and **Figure 29** notes fragments of female FRs, as anecdotally noted in fieldbooks, supplemented with a few SWAT measurements (1966). From the standpoint of coding potential, certain members of this group exhibit an extreme for North American *Photinus*, with FP, FR, response delay, and the interplay of all these being imaginable if not possible. Only a simple aspect of the signals of this *ardens*-Group is possible, and brings back a subject discussed above, exposure to aerial predation.

Duty Cycles and risk. The FPs of some of the *ardens*-Group species are very long, one having as many as many eleven pulses, and such would seem to provide easy targets for hawking predators. At the UF Med. Garden where a large population of the hawking ace *Ph. lamarcki* occurred, there were three *consimilis* species present, Fast-Fast (FFP), Slow-Fast (SFP), and Slow (SP) pulsers (**Fig. 28 B, C, E**). Pulse number is variable and males might adjust their FPs according to circumstances they monitored. The three mention species were seen in somewhat different habitats at the MG, and this is connected with risk: SP flew primarily over open water and off-shore emergent and floating-plant regions; SFP flew over shoreline vegetation and only slightly inland, and FFP flew over a lawn area further inland, immediately adjacent to the hawker population flying over lawn-side shrubs.

Relevant to this discussion, it would be surprising if FP duration (pulse number) and FP period were not interrelated in some way in connection with the risk of aerial predation. **Figure 30** shows a method of quantifying FP exposure to risk: The duration of an FP is divided by the duration of the FP period, and the quotient is the exposure measurement. Following engineering, machinery operation and the like, this is termed the duty cycle. In the FP example (A/B), the exposure is 28%.

The pulse rates of the different species are different and the temperature regressions for them fall along different slopes (**Fig. 31**). Whether duty cycles are similar among species, or are constant for a given species remains to be determined. Duty cycles can be varied with circumstances by emitting FPs with different numbers of pulses and varying the lengths of FP periods. The measurements in **FigTable 32** are based on the few data available in an earlier paper (jel-1966).

From the standpoint of coding information, probably what is seen in North American *Photinus*, falls far short of what is to be expected south of the Rio Grande. The Colombian *Photinus* in **Figure 33** adds another dimension of complexity, with its subliminal modulations of 26.8 Hertz. Pooled mean modulation rate averages 24.5 Hz. (s=1.0, r=22.1-26.8, nr 23°/73.5°).



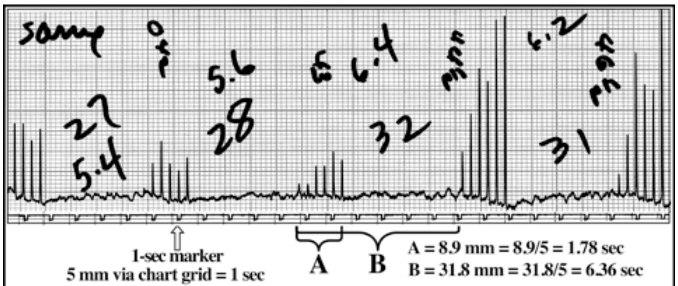
1. FRs of *ardens*-Group females commonly are doubled pulses; these sometimes are repeated rhymically 2-4 times (but see 2).

2. Females of the *ardens*-Group may sometimes omit pulses within a "rhythmic" series, that is, seemingly a "silent" neural rhythm is maintained that fires the lantern only "variously."

3. FRs of *ardens*-Group females typically are delayed for a few seconds—varying among operational species—after the FP ends, this being an element of the species' code.

4. After landing, when approaching males sometimes emit FPs with more pulses than "airborne-typical" (ID-specific) FPs, females may interrupt and emit an FR.

Figure 29. Notes on FRs of *Photinus ardens* Group females. Timings approximate; use for perspective and generalizing.

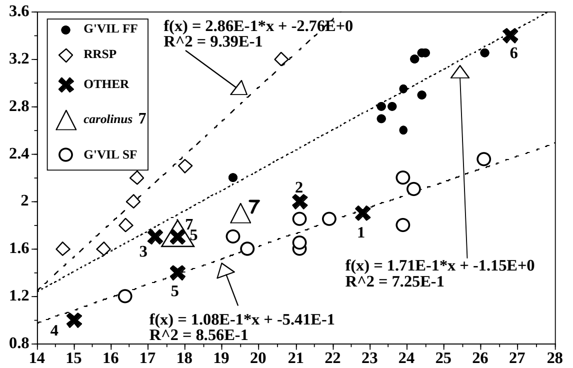


A = 8.9 mm = 8.9/5 = 1.78 sec
B = 31.8 mm = 31.8/5 = 6.36 sec

duty cycle = A/B = 1.78/6.36 = 0.28

As a working/thinking estimate, at 24.1°/75.5°, male FFP-*consimilis* (FL) are illuminated targets to aerial predators 28% (0.28) of their flying-flashing time. How does this compare with with the target-time (duty-cycle) of SFP-*consimilis* FP.

Figure 30. FP duty cycles, definition, measurement.



1. Chambersburg, Frankllin Co., PA
2. Highlands Hammock S. P., Highlands Co. FL
3. Vernon, Oneida Co. NY
4. Allegany S. P., Cattaraugus Co. NY
5. Babcock S. P., Franklin Co. WV
   also carolinus, Rowan Co. KY
6. Shell Mound Rd., Levy Co. FL
7. Gatlinburg, Sevier Co. TN (carolinus)

Figure 31. Regressions for members of the *ardens* Group.

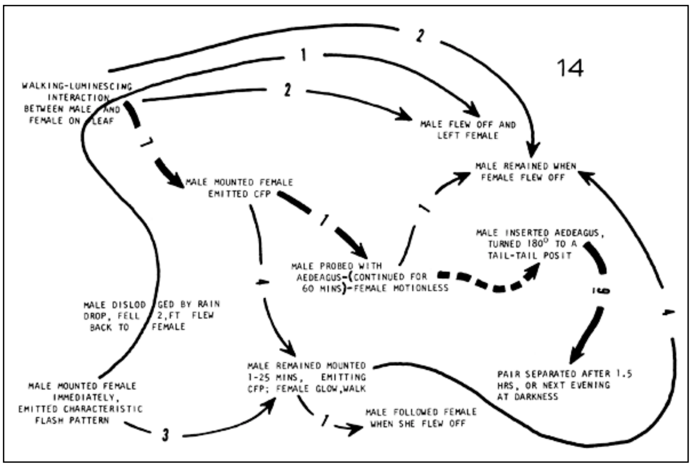


Figure 32. Schematic for the mating protocol of the New Guinea lucioline *Pygatyphella* [*Luciola) obsoleta (f*rom jel, 1972*)*.

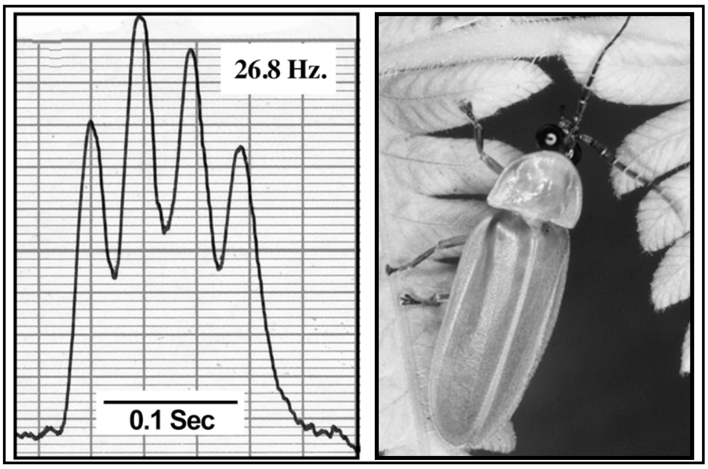
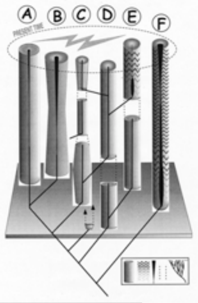


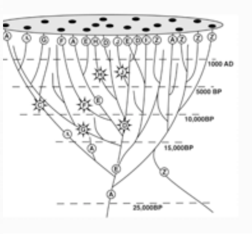
Figure 33. A Colombian *Photinus* and its subliminal (to the human eye) rapidly-pulsed FP, as recorded in the Andes Mountains near Cali.

Figure 34. Plantation worker quarters, Sek Harbor, 1969, where obsoleta courtship was in a woods just up the road.

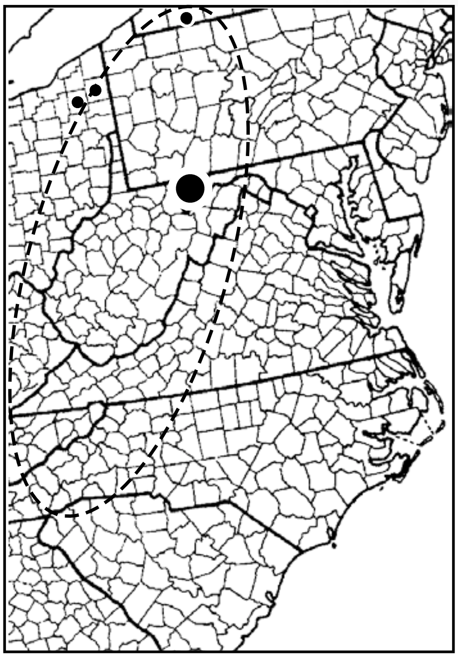
> *"There is then left the third class, which possess experimental philosophy. These indeed derive the causes of all things from the most simple principles possible; but then they assume nothing as principle, that is not proved by phenomena. They frame no hypotheses, nor receive them into philosophy otherwise than as questions whose truth may be disputed. They proceed therefore in a twofold method, synthetical and analytical. From some select phenomena they deduce by analysis the forces of Nature and the more simple laws of forces; and from thence by synthesis show the construction of the rest."* From Roger Cote's Preface to the Second Edition of Newton's *Principia*, 1713.

Reflections on species and those who would understand them. There is madness in trying to understand what we would wish to call species—to see numbers of populations of similar organisms spread over a region each reacting to local circumstances, and obsessing on how or why they could or would not become different. People possessed with this affliction make doodles, sketches to aid their thinking, diagrams of scattered ecologically fit then deteriorating sites, branches of lineages, combinations with alleles appearing and spreading, then disappearing with extinctions—they imagine how extreme forces such as multifaceted aggressive mimicry might drive things. Some thoughts cannot be rushed. It is time to go back to the field, re-examine what has been learned, and pursue opportunities left there, explore and experiment.



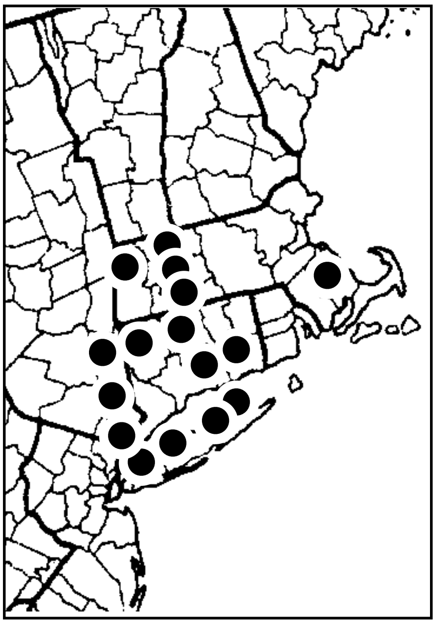


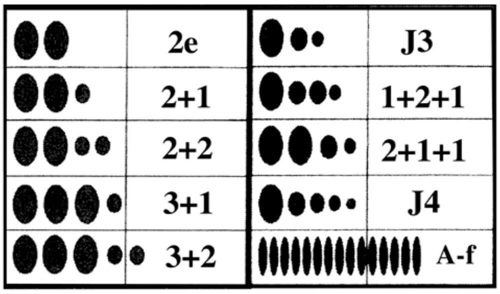
One puzzle that lies at the center of questions is presented by a population of dot-dash flashers in western Maryland, *Photuris appalachianensis* (Chap. 11). At twilight it emits short flashes over deep grass at the edge of a clearing and then moves out into the clearing to short-flash for a few more minutes. It presents like a *Photinus marginellus*, which is native to the area, and presumable prey of its females. Then, on the nights watched, almost all gradually began emitting their dot-dash signature/default FP. The exceptions were those that began emitting a flicker FP like that of *Photuris tremulans*. When short-flashers were answered with a female-like decoy flash, and later when flickerers were so answered, all defaulted to the dot-dash FP—decoy-answered dot-dash flashers continued to emit the dot-dash. and approached as the others had (page 472C; Chap. 11, Figs. 6, 7).



Here is the question: dot-dash flashers with certain long flashers appear—but without DNA examination—to form a natural group, centered more or less around Barber's *pensylvanica* and *caerulucens*. None are *angulata*-flicker mimics, one would suppose, based on the several variads observed! *Photuris* that emit such a flicker appear to be in or near the *versicolor* group. In the mountains with *appalachiensis* this would be *P. tremulans*. Did *appalachianensis* observe then copy the flicker to acquire it, remember it for days, or were genes exchanged? I did not seek other populations of *appalachianensis* in these mountains, but perhaps there are variads to be found that could provide some clues, including populations sampled in northeastern Ohio and southwestern New York that emit long and crescendo FPs as well as dot-dash FPs as defaults. Do such twilight short flashes straggle latter as in *asacoa*, or end rather abruptly. Do they always default or only under certain circumstances. (Chaps. 10, 12, 58)

In northeastern United States is a *Photuris* that emits perhaps the most extensive repertoire of all Chap. 64). *Ph. stevensae* emits phrases of even-intensity pulses and down-step pulses, sometimes doubling at steps as though to "be certain" the step down was not overlooked, and a flicker. Though at some sites 2-flash FPs were seen, in many sites and on many evenings the 2-flash timing of the local *consanguineus*-Group *Photinus* was never seen, except on one *significant* occasion, when a *stevensae* male was observed courting a *Photinus* female. See Chapter 7, numbers 36-38 for details. Did this male initiate and use the correct 2-flash timing because he observed several *Photinus* males using it?; or, because he saw a flashed answer to this FP and his "neural program computed 'a hunting conspecific female'"? Experiments of several kinds can be imagined to explore the nature of the male copying, tuning (learning) template.





Chapter 72

On Imagination In Science, With Certain *Photuris* "penns" In Mind …

Things in themselves are wrapped
in such a veil that not a few philosophers,
and those of no mean caliber,
have come to the conclusion that
they are absolutely unknowable.
Marcus Aurelius *Meditations* V.10 (121-180 C. E.)

* * *

O for a muse of fire, that would ascend
The brightest of invention:
A kingdom for a stage, princes to act,
And monarchs to behold the swelling scene.
Shakespeare, *King Henry the Fifth*

There is always an easy solution to
every human problem—neat, plausible,
and wrong. H. L. Mencken

It is his intuition, his mystical insight into
the nature of things, rather than his
reasoning which makes a great scientist.
Karl R. Popper

We ask here, *how can the incredibly variable and complex behavior of certain North American* Photuris*—the apparent key to untangling the connections and sinuous entwining pathways of their genealogies on a long-abused and ever-changing continent—be explored and then explained in mere words and still-life illustration?* From what I have seen, the first problem is that few entomologists will readily accept or even imagine that insects are capable of such complex behavior as suggested to exist from this study. Further, the complexities of their behavioral variations in time and space will challenge long-held simple beliefs and concepts of species and "the" units of selection and evolution. This brief chapter will focus on, make the case for the importance of creative thinking, for "thinking outside the box."

Imagination, as Monsieur J. B. Lamarck said so long ago, and quoted at length below—along with agreement from other notables—is a necessary component of science. The mind's eye, when instructed by careful description, is the sine qua non for addressing the inscrutable and indescribable. Unlike patrons of the Globe Theatre, to some extent knowledgeable of courtly intrigue and maybe beheadings as entertainment, the uneasy nocturnal explorer has little in experience to draw upon, to guide his observation, to rein or loosen his imagination; and, he will be concerned lest he upset the sensibilities of the comfortable. Nevertheless, he must practice, work at it, spend solitary dark hours watching flying, flickering, blinking, changing crescendos of animated chemical light, recognizing clues, and interpreting fleeting images, those ghostly-silent libretti that conceal coded themes of love, deceit, and betrayal, and then, tragedy—all this in liberal translation of course. And I … I am not completely certain of that of which I write, seen as it were over long fading decades and even then through a prism only darkly.

Shakespeare used an introducing Chorus, a single individual perhaps, to ask how a larger than life drama and panorama can possibly be presented on the confines of a small stage, and successfully tell such a story. His answer? Imagination! So also is Darwin's solution in presenting his theory; from his *Origin*: "In order to make it clear how, as I believe, natural selection acts, I must beg permission to give one or two imaginary illustrations." A half-century before Darwin, in 1809, Jean Baptiste Lamarck, in his "Zoological Philosophy," expounded on his view of the importance of imagination in science, and to give this remarkable naturalist some well-deserved time in the sun, his view of imagination is quoted extensively, from a translation by Hugh Elliot, Chicago Press:

> "Chapter VIII. Of the Principle Acts Of Understanding, Or Those Of the First Order From Which All the Rest are Derived. / … IMAGINATION." (The third of Lamarck's principle faculties of the intellect—following (1) Attention and (2) Thought.)

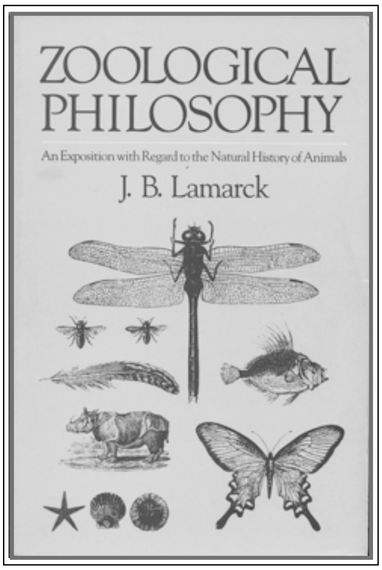
"The imagination is that faculty for creating new ideas that the organ of intelligence acquires by means of its thoughts. It is dependent on the presence of many ideas, out of which new complex ideas are constantly being formed. / The intellectual operations, which give rise to acts of imagination, are excited by the individual's inner feeling, carried out like other acts of thought by the movements of his nervous fluid, and controlled by judgments.


from Ency. Brit.

"Acts of imagination consist in creating new ideas by comparisons and judgments of previous ideas, these being taken either as models or as contrasts; so that with this material the individual can form for himself a number of new ideas which are impressed on his organ, and out of these many more again, with no limit to this infinite creation beyond that suggested by his endowment of reason. …

"Imagination is one of the finest faculties of man: it ennobles and elevates his thoughts and relieves him from the domination of minute details; and when it reaches a very high development, it makes him superior to the great majority of other people. / What would literature be without imagination? / … Since literature arouses, animates, and charms every man who is able to appreciate it, science is to that extent inferior; for she teaches coldly and stiffly: but science is superior in this, that not only does she serve all the arts and furnish us with the best means of providing for all our physical needs, but that she also greatly broadens our thoughts by showing us everywhere what is really there and not what we want to find there.

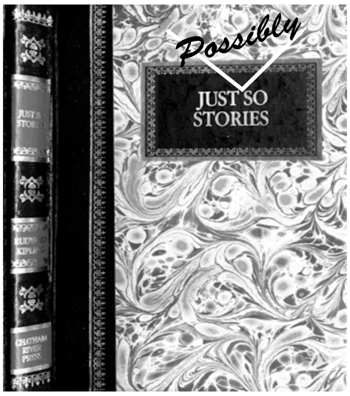
"The purpose of the former is to give pleasure; that of the latter is to collect all practicable positive knowledge. / This being so, imagination is as much to be feared in the sciences as it is indispensable in literature; for its aberrations in the latter are merely a lack of taste and reason, whereas it aberrations in the former are errors; for the imagination nearly always gives rise to errors, when it is not controlled and limited by learning and reason; and if these errors are captivating, they inflict upon science an injury which is often very difficult to repair. / Yet without imagination there is no genius, and without genius there is no possibility of discovering anything but facts, without drawing any satisfying inferences. Now since every science is a body of principles and inferences carefully deduced from observed facts, genius is absolutely necessary for stating these principles and drawing their inferences; but it has to be guided by a sound judgment, and kept within the limits imposed by a high degree of enlightenment.



"Thus, although it is true that imagination is to be feared in the sciences, this only holds good when it is not controlled by a lofty and enlightened reason; when it is so controlled, it is one of the essential factors in the progress of science."

Steven J. Gould acknowledged the importance of imagination in more scientific terms when recognizing and appreciating certain prescient perceptions of Lamarck: “We cannot comprehend nature’s complexity—particularly for such comprehensive subjects as evolution and the taxonomic structure of nature’s diversity—unless we impose our mental theories of order upon the overt chaos that greets our senses” (1999). Nobel Laureate P. B. Medawar, in his “Advice to a Young Scientist” (1979), promised that, “Science will dry up only if scientists lose or fail to exercise the power or incentive to imagine what the truth might be. One can envisage an end of science no more readily than one can envisage an end of imaginative literature or the fine arts.”

"Imagination is more important than knowledge." Albert Einstein, 1929

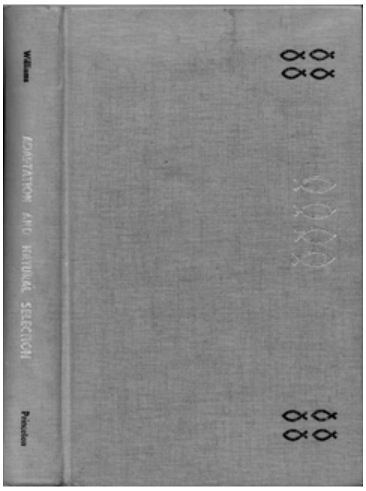


And semifinally, two more notable quotables on creativity:

Bold ideas, unjustifiable anticipations, and speculative thought, are our only means for interpreting nature: our only organon, our only instrument, for grasping her. Karl Popper, in Beveridge, 1980.

The creative mind is able, as Schopenhauer has stated it, ‘to think something that nobody has thought yet, while looking at something that everybody sees.’ Imagination, thus, is ultimately the most important prerequisite of scientific progress. Ernst Mayr, 1982.

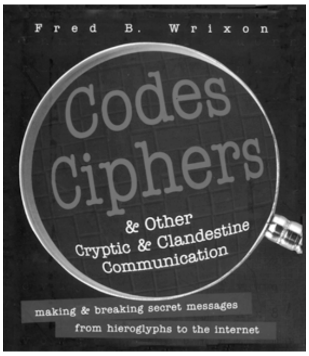
For teachers, imaginative perspectives have a value beyond problem solving: The only specific detail that I am able to recall from Prof. Bill Brown’s evolution course at Cornell, more than 50 years ago, was his adaptation model, which was based on functional variation and the evolutionary development of U. S. Mail trucks.



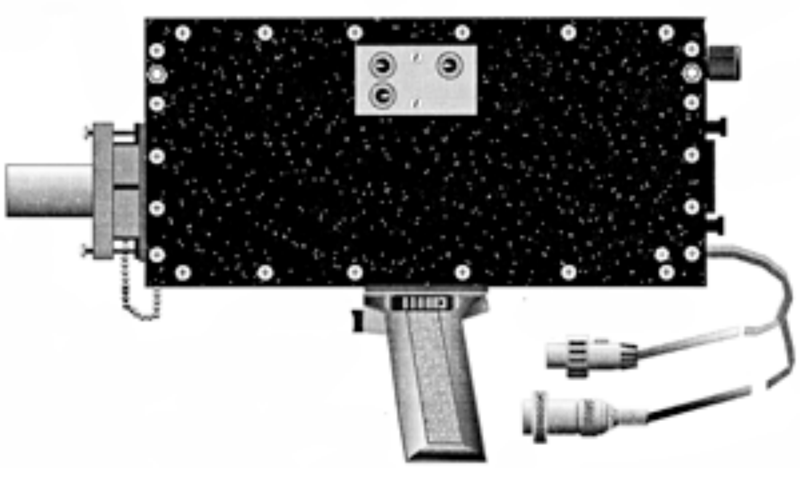
To conclude this protracted argument for the only approach to understandng *Photuris*, as I see it from 50 years of experience, here is one last expression of the importance of imaginative thinking when confronted with intractable problems. It is by the author of a book that I cited in the Preface to this study as being an extremely important clarifying and reassuring influence in my education. In the decades preceding the publication of George Williams book in 1966 even Darwin had been trashed by many who would call themselves biologists. Thier arguments often were merely blind assertions. A professor at Cornell informed me in no uncertain terms that there was no such thing as aggressive mimicry, and demanded that I withdraw my 1964 paper on the subject. On a New Guinea expedition in 1969 I met a number of American "fireflyers" who could not be reached by genetic reasoning, one influential elder (by default and seniority) stated that he had been "in biology long enough to know that was nothing to 'that' simple minded nonsense of evolution and natural selection."

Williams asked not that we blindly accept natural selection, but merely that we entertain the idea of it in our research imaginations to see if would fly, could carry us further—say, like the longer-finned fish he features on pages 2-3 of his first chapter.

I believe that modern opposition, both overt and cryptic, to natural selection, still derives from the same sources that led to the now discredited theories of the nineteenth century. The opposition arises, as Darwin himself observed, not from what reason dictates but from the limits of what the imagination can accept. Williams, 1966.



The reason for much bad science is not that talent is rare, not at all, what is rare is character.
Sigmund Freud

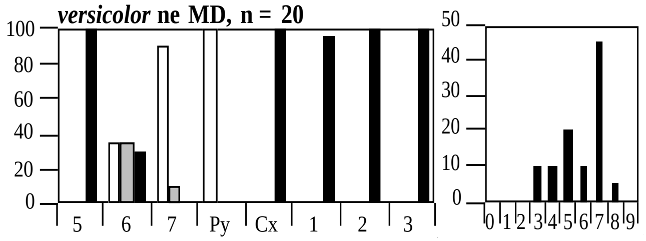


Organismic diversity is not chaotic but patterned, revealing all sorts of regularities … These regularities have various causes, and it is one of the major tasks of systematics to discover the nature of the causation of these patterns. Ernst Mayr, 1991

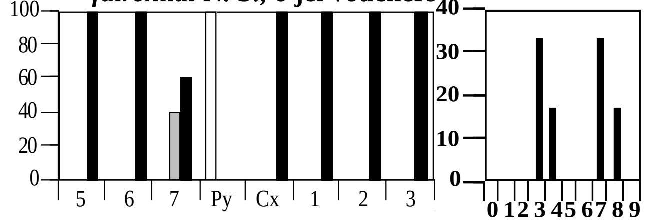
… the destiny of speculation is less the tangent than the maze—the maze of innumerable lesser principles … if ever a master defined the unknown and pointed the way of investigation, certainly it was Darwin. Osborn, p-63.

Compared Color Histos: Versi and FRFV, FRFV and others

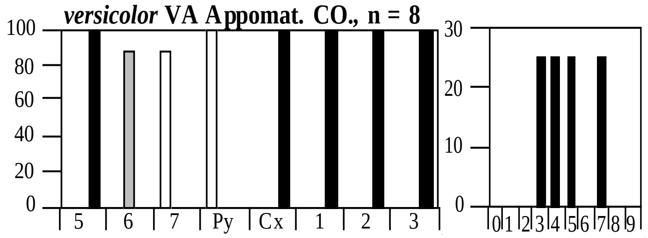
versicolor **ne MD, n = 20**



fairchildi **N. S., 6 jel vouchers**



versicolor **VA Appomat. CO., n = 8**



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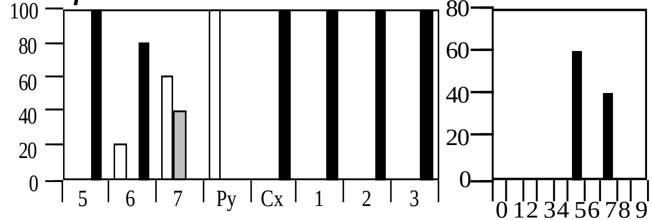

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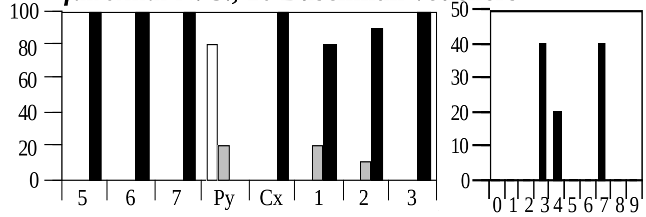
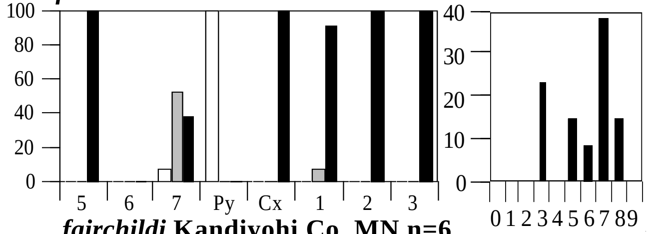
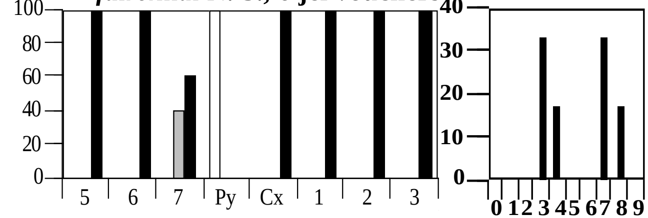


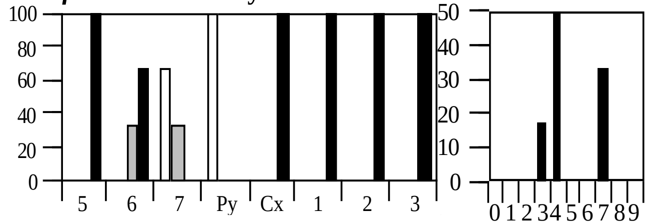
fairchildi **Winona Co. MN n=13**



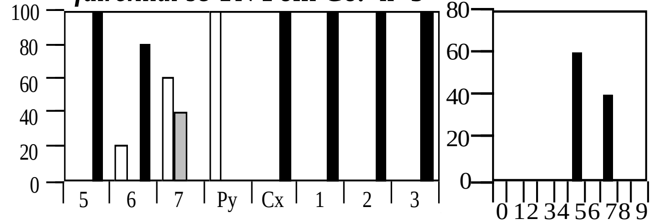
fairchildi **N. S., 6 jel vouchers**



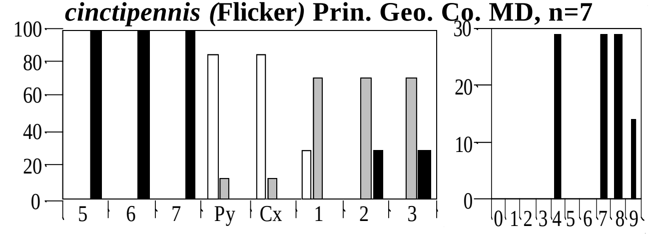
fairchildi **Kandiyohi Co. MN n=6**



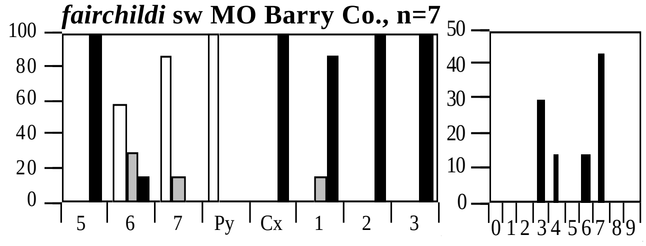
fairchildi **se TN Polk Co. n=5**



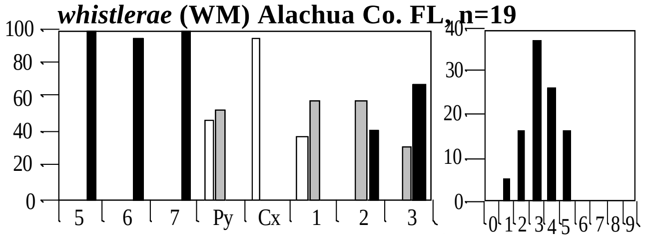
cinctipennis (**Flicker*****)* Prin. Geo. Co. MD, n=7**



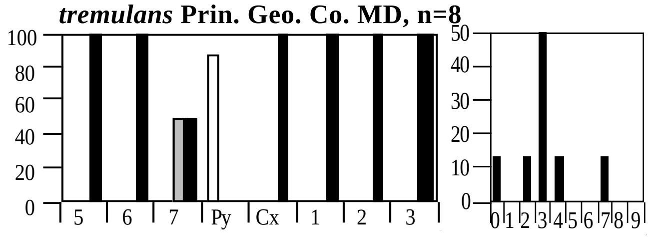
fairchildi **sw MO Barry Co., n=7**



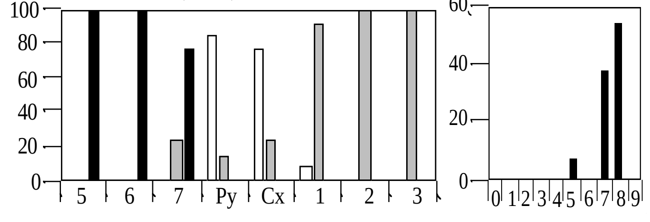
whistlerae **(WM) Alachua Co. FL, n=19**

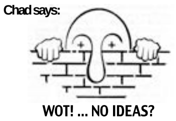


tremulans **Prin. Geo. Co. MD, n=8**



branhami **(DM) Alachua Co. FL, n=13**



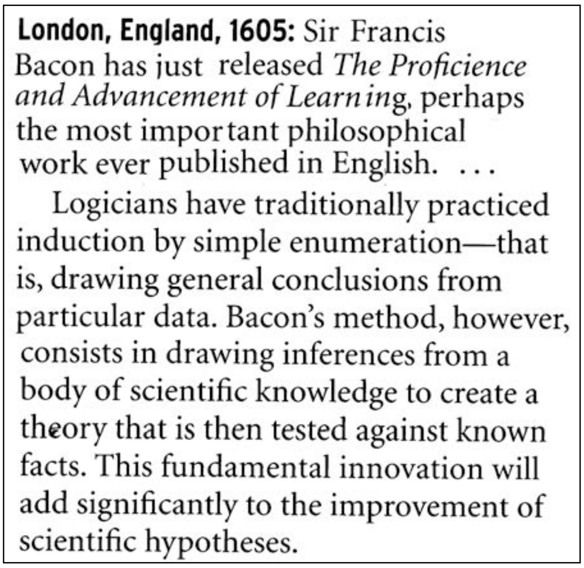


(I. H. Evans, 1981, var.)

Chapter 73

Advice To Young Fireflyers: Two Examples Of Pushing Selection & Imagination

Part 1. On several occasions I have emphasized the necessity for making liberal use of using one's fact-oriented imagination when trying to approach firefly questions … thinking of *Photuris* puzzles in particular. People who have made discoveries in science, or have studied and written about those who have done so, have made a particular point of this "our only *organon*" in science. And, they have suggested ways to aid, to stimulate the imagination—say, a visit a hardware store to find mechanical gadgets as guides as to how insect aedeagi might subvert female sperm control, hence control egg fertilization (jel, 1984). It is obvious that discoveries are found off the path of normal practice ("outside the box" in Madison Ave. parlance). By definition must they not be? The question remains as to why in the fairly-recent past was there such resistance to theorizing, to making educated guesses and generalizations about function, especially about adaptation and function. One writer on marine bioluminescence suggested that an area he researched was, to paraphrase, 'a minefield for those who would speculate'; why should he have been fearful of ideas to share and toss around, of cross-fertilizations? Another, one who wielded a club of ignorance and errant authority for decades in "his" field when refereeing manuscripts, argued that science should **only** be the gathering of facts. As a point of fact, I finally, perhaps somewhat exasperated but very politely, asked him how one could know what facts to gather? As I waited, looking into his eyes to learn and then address *his* reasoned view, it appeared as though there was no one "in there," and no answer was forthcoming. Fact-guided imagination *is* the Darwinian method, *is* the scientific method. Imagine, if you can, sitting with Charles Darwin, Sir Francis Bacon, and Sir Isaac Newton under an apple tree in a "Hyde Park," watching apples fall, discussing the acquisition of knowledge, scientific how-to, *The Inductive Method*! (I once read that imagination fell into disrepute over unguided speculation—ants with funerals, carrying corpses two by two!)



London, England, 1605: Sir Francis Bacon has just released *The Proficience and Advancement of Learning*, perhaps the most important philosophical work ever published in English. …

Logicians have traditionally practiced induction by simple enumeration—that is, drawing general conclusions from particular data. Bacon's method, however, consists in drawing inferences from a body of scientific knowledge to create a theory that is then tested against known facts. This fundamental innovation will add significantly to the improvement of scientific hypotheses.

Figure 1. An imaginary newspaper item, from the time of Bacon!

At some point after Darwin biology seems to have taken a wrong turn, and resisted, even misrepresented *induction* as specified by Francis Bacon—it seems that way to me, as I recall "classroom lectures" and readings over the years … Fortunately, in a sweeping revolution that began in the 1960s, chauffeured by several notables, and in particular G. C. Williams and W. D. Hamilton, and for me personally, R. D. Alexander, a real and improved Darwinian logic was vigorously introduced. This was the *inductive* method Bacon himself had promoted, though perhaps not invented, and that he had defended from the very beginning (**Fig. 1**): (**A**) induce (*imagine*) explanations from facts—observation or experimentation; (**B**) construct testable hypotheses (formally stated expectations); (**C**) test these hypotheses. **Figure 1** shows a hot item from "Historica," an elegant, rather elephant-sized book that presents events of history as they might appear in modern newspapers—but if you are disposed of an extremely patient disposition, Bacon's original is in Encyclopedia Britannica's "Great Books" collection, Vol. 30.

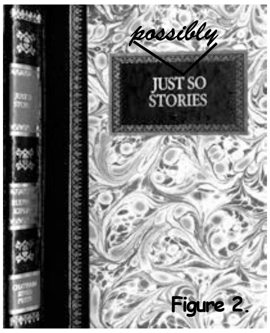


Figure 2.

Imagination, and the simple but apparently elusive, common-sense method of Bacon and Darwin really have all that is needed for the naturalist to embark on a road to discovery, and it amazes me that Darwin's method and ideas about natural selection and species could "fall out of favor and use" for decades with zoologists and others. Darwin, in one of his writings, comments that once he had gotten onto this approach, *everything* he observed was addressed from this perspective. A grand view it was. What was really surprising was that when Darwinism was vigorously revived and honed in the middle of the last century it received the same-ol'-same-ol' resistance from some quarters, its utility and application thoroughly misunderstood even by those with contemporary august credentials as evolution experts—egos finally finally relegated to the dust-bin of scientific natural history.

> *Among the greatest men of all time are the creative naturalists, from Aristotle to Darwin, whose enduring work and self-effacing lives are our most precious possessions. I prefer the naturalist to the scientist, because there is less of the ego in him. In the truly creative naturalist the ego entirely disappears, and through his impersonal vision we see nature with the least human aberration.*
>
> Henry Fairfield Osborn, 1928, page 3, *Impressions of Great Naturalists*

What is under discussion here is not explanation for explanation's sake, not explanation for the sake of having one, nor didactic "just so stories" (**Fig. 2**), but rather "just ***possibly*** so stories," reasonable explanations for inscrutables, such stories being part of the scientific method, a critical component of an informed ***methodology*** of science.

Once upon a time, a very long time ago, I kept company with bumblebees at the entrance of a vacated woodchuck hole (**Figs. 3-11**). Their nest was underground, and for several days I remained seated or lying near the hole in New York pasture grass—no ticks nor chiggers—and took photographs and meals there. Males from various independently-queened nests in the vicinity had gathered around the hole waiting and contesting for virgin females (gynes), the nest's production of next-year's queens, to emerge to be seized and ridden away on nuptial flights by single winners. Males fanned their wings over the hole, *maybe* sending a pheromone signature down the shaft?, and bumped into each other, *maybe* smearing something, feces or pheromones?, on their genetically-sworn enemies? Sometimes it appeared that males paired off as they waited at the entrance?, and pairs fought, stripping setae ("hairs") from cuticles, which made them look somewhat like carpenter bees! They became entangled in deadly

Figure 3. A heifer pasture, last-year's woodchuck hole, and an arena where gynes and fertilizations are gained in fierce jousting and deadly combat among rival males (drones).

Figure 4. *Marmota monax rufescens*, (Millie) woodchuck.

Figure 5. *Bombus fervidus*; drones don't have stings, and workers were mostly "gentle."

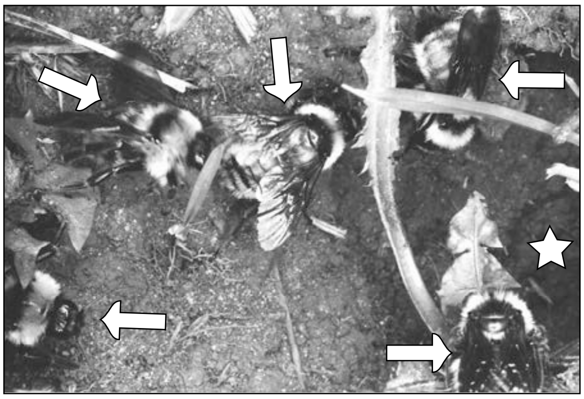


Figure 6. Drones (males, 5 arrows) waiting at nest entrance (star).

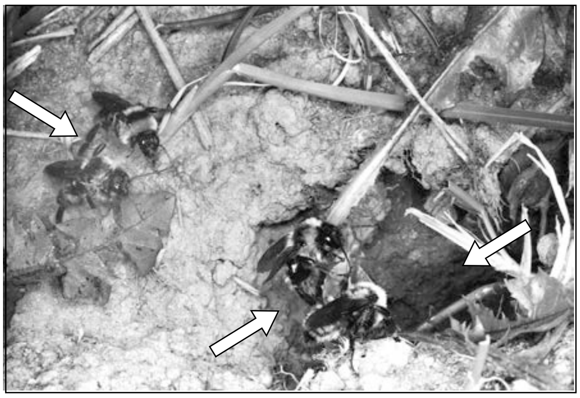


Figure 7. Pairs of males at the nest entrance. Arrows mark pairs and the entrance.

Figure 8. Setae scraped off and wings ripped off, yet waiting at the nest entrance. Arrow points near bases of stubs of detached wings.

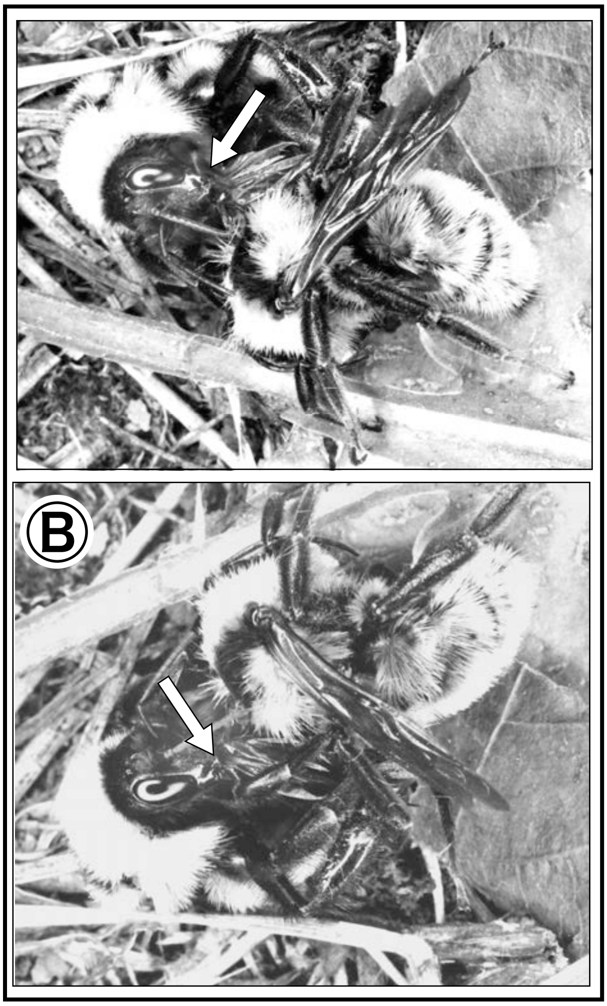


Figure 9. Wing pulling in a fight: (A) mandibles gripping wing near tip, wing bent, but base still attached; (B) wing detached from rival's body, base apparently in puller's mandibles (arrow).

Figure 10. Cricket eats at wing-removal wound of a recently killed bee.

> ***If in the relatively small part of his life that he devoted to speculation and or hypothesis his contributions are less permanent, it is because after all, Nature is unreasonable and irrational in her methods.***
>
> **Henry Fairfield Osborn, writing of Darwin in his *Impressions Of Great Naturalists*.**

fights that tumbled away from the nest entrance. Wings were grasped in mandibles, pulled, and torn off; once a cricket was found sipping at the wounds of a dead loser. Obviously, much was in need of explanation, re genes and queens (*alma mater*—bounteous mothers) and fitness (W).

Why would selfish individual males leave their ultimate goal, gynes, to fight a *single* rival, and leave several "rivals" with free reign at the entrance? Was there some asymmetry among males, prior knowledge guiding gynes to choose an endurable male whose signature they had smelled at the entrance-hole high above for several days? Toward explanation I made a case for individual selection involving individual scent-recognition by long-monitoring gynes (note: stripped setae would remove evaporating surfaces?); but at the time felt that there *could* be something involving kin, brothers, as reported in lion and turkey sexual rivalry. Bee brothers might gather at the same entrance and as a *team* take on teams from rival nests. Maybe the pairs of males seen at the entrance were not rivals but brothers working together; maybe one was a fighter and the other the gyne-grabber/rider? If drones were as teams, would they play man-to-man (bee-to-bee) or zone, depending upon team sizes? Or, maybe, could the genetics of bee brothers have some odd twist to it?, such a circumstance having been found significant in the evolution of social behavior and “non-reproductive” workers in such (aculeate) hymenoptera.

Oh well. When asked about bee-brother relationships, two bee genetics researchers were of no help. I sent my question to a lab that was renown for decades as a center of bee study. They replied that *they* had kept drones together in cages for years and they had never had seen a fight! But what species?; from rival nests?; and what prizes, were gynes present? Naturalists written about by Osborn (1928) to say nothing of properly-educated bee scientists on the prowl for new insights, might have jumped at the possibilities for discovery in this instance—or so I had expected. Premier universities, departments and research specialists, don't necessarily mean adequate education and preparation! In fact,

Figure 11. Balling of the queen (large, head down at left), with rivals struggling to climb aboard her thorax, with but one ride to the mating site. Whether she guides the decision, has a role in mate selection during the "scramble" may be recorded in the literature … but then, maybe not.

study at a tiny, isolated college of education may be the start—check-out its bio-curriculum and field-bio profs first.

To close **Part 1**, review Chapter 72, with thoughts from experienced, thinking scientists, concerning imagination and creativity, and the need for such things, whether questioning worm-holes or super-strings, or horny, combative, murderous drones at a woodchuck hole.

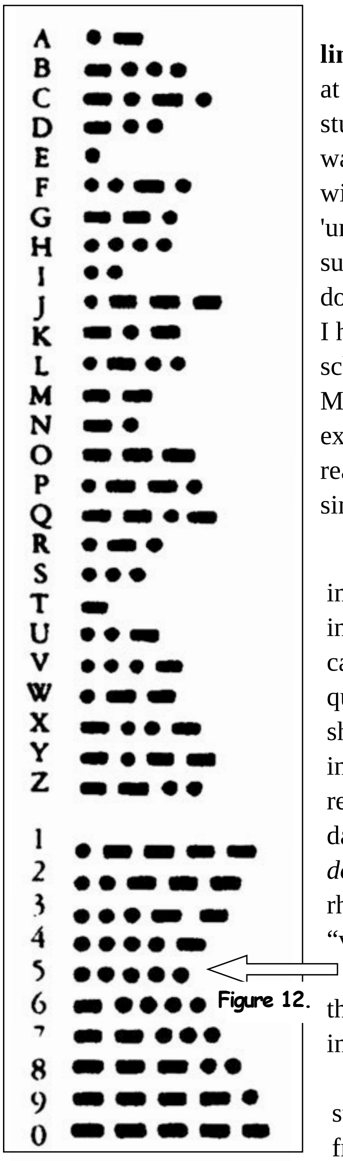


Figure 12.

Part 2. **Firefly language, a too-wild ride with lessons from archaeology and linguistics?** Almost within moments of reporting for duty, graduate school in Entomology at Cornell, my committee chairman Tom Eisner tersely averred, as he raced through his students' lab, that since I was studying fireflies I needed to look at the Morse Code*. Tom was not usually recognized as a proactive theorist—when he read my 1964 paper he averred with special emphasis that there was "no such thing as aggressive mimicry," and that 'unlike man, animals didn't lie to members of their own species.' But pragmatically, his suggestion was correct, an especially sound and productive directive to compare and contrast dots and dashes—one must consider and extract/adopt working ideas wherever, everywhere. I had once studied Morse code, i.e., learned to send/receive eight words a minute in a USN school for aviation electronics. I knew that the ecology of and selection pressures on the Morse Code were different from those on firefly signals. For example, it's not difficult to explain 5-character codes for numbers (**Figs. 12, 13;** think DNA and 3**)**. But what was the reason, say, that the dot was selected to code for "e"?—was it because the dot is the simplest, and "e" the most commonly-used letter in English? Why a dash for "t"?

Perhaps the English spelling of words was a consideration when coding other letters in dots and dashes (dits and dahs), with commonly-occurring *sequences* of letters taken into consideration? Or, maybe it was easily recognized and remembered *rhythms* in some cases—di-di-dah-dit, "get a haircut" (" f, fox"), or dah-dah-di-dah, "no balls at all" ("q, queen")? But maybe it was the sound of a clicking telegraph key and not tones as heard on shortwave radios, that first-guided choices. Similar considerations must have been involved in the ancestral placement of letters on typewriter keyboards? All of this will be recorded somewhere, in "Encyclopedia Britannica"? But, specific knowledge of such di-dah details themselves would not be expected to provide a clue, say, as to why *Ph. dorothae* males flying at the pinetops in Florida flatwoods sometimes sign with the rhythm of the introductory notes of Beethoven's Fifth Symphony?—dot-dot-dot-dash?, "v, victor" in Morse Code.

Note that the now archaic and forgotten terms *fox*, *queen*, and *victor*, were used above; they have since been replaced. Perhaps the reason for this substitution would provide insight into function/adaptation, the topic of this discussion?

Pushing Eisner's methodological suggestion further, archaeology of ancient texts in stone and papyrus also have an occasional concept to consider. Among remembered fragments from "Extinct Languages," by Johannes Friedrich (1957; **Fig. 14**): "the decipherment of any unknown script or language presupposes the availability of some clue or reference; nothing can be deciphered out of nothing" (p.151). Also from Friedrich, in deciphering such texts, the figures ("letters") themselves may be pictograms or abstractions of them as ideograms, spoken sounds, syllables, consonants or vowels, or even mixtures of these. Sometimes, many of the subjects being written about can be known, predicted/expected. This is because archaeologists are educated social humans and will understand and are able to guess at *contexts* and specifics of the written concerns of ancient cultures: deities, names of kings, lengths of reigns, laws, social positions, trading partners, marriages, trade items, quantities/amounts, goods, transport methods, dates, catastrophes, wars, battles won, heroes, adventures, etc. Levels of difficulty arise in reading ancient texts because, for example "there are cases involving an unknown

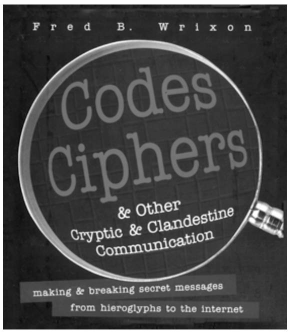


Figure 13.

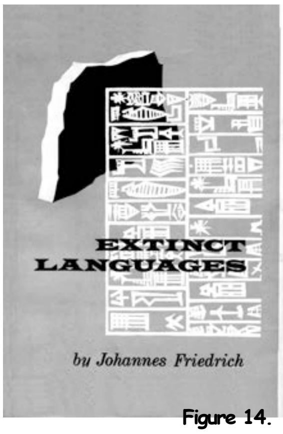


Figure 14.

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*Note, the Morse code is considered/defined a cipher not a code: *codes* substitute whole words whereas *ciphers* transpose or substitute letters or digraphs— a digraph is an encipherment in which the plaintext is written using letter pairs (ref. Wrixon, 1992, **Fig. 13**) language written in a likewise unknown script" (p. 152). To begin deciphering, "be on the lookout for names of persons, cities, countries . . ." (153). Thus it is not surprising that among the earliest successes in the translation of Egyptian hieroglyphics were the *names* of pharaohs—nor was it surprising that the greatest advancement in understanding hieroglyphics was made by someone who at age 11 determined to decipher them, and over several years "obtained reproductions of every accessible Egyptian inscription and papyrus … compiled from them all the forms of hieroglyphic signs … did all this without yet daring proceed to the reading of one single character" (this was Jean Francois Champollion-1790-1832).

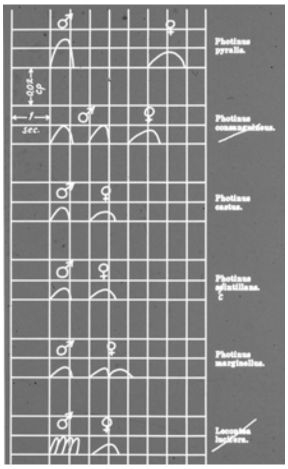


Figure 15. Early McDermott firefly "cartouche."

Contrariwise. While archeologists pursue extinct and now silent languages that reach back millennia in fragmented stone and papyrus texts, fireflyers pursue firefly languages written in transient light pulses and chemistry, but never in stone, maybe eventually in amber, and guess about those that could reach back eons. They learn of them only through the behavior and DNA of extant but yet "primitive" types. As to the complexities of firefly communication, one really cannot expect very much to be there(?), but should be aware, judging from experience, that we are now most likely to err by expecting too little, scientific "Taoism," and under-reach in our theorizing. As with Egyptologists, the first words we (that is, Frank McDermott, 1908-9s) learned were names, not the Latin, but flash patterns (FPs), some imperfectly but a break-through and on the right track (**Fig. 15**). Archaeologists recognize names of pharaohs in cartouches, round-cornered rectangles with a vertical line at one end, Firefly pioneers recognized firefly names as light pulses isolated in moments of time and appearing in long sequences. What else can be expected?, how can we know what to look for?, especially considering that our commonality with them in many respects ends millennia, nay, eons ago, all the way back to a protostome/deuterostome (worm/mesodermic) embryonic divide?—we do share the very basic needs of life.

Figure 16. *Pteroptyx valida* male in Thailand atop a female with his tail spread open, putting it over her face, for her to smell or taste his previous successes—and fitness as a father for her sons—, or lack of recent copulations —thus having a supply of accessory-gland material to provide—or some other unknown?

Firefly message content. We can predict what information is exchanged between fireflies by knowing their social and ecological interactions, and from inferences from other insects. Our two firefly pioneers only would have been certain of mate attraction and identification, but suspicious of aggressive mimicry and warning. Since then we have learned of the prevalence of aggressive mimicry and the mimicked signals of *Photuris* males, the potential variety of messages in competing Florida *Pn. macdermotti*, and become aware of the potential widespread occurrence and significance of countermeasures in signals of prey species. We are also suspicious that there is possibly much more to learn, such as subtle information on individual fitness and mating history/success —both of which are easily invoked and very difficult or virtually impossible to demonstrate, or prove with confidence (**Fig. 16**).

The next section seeks new ideas to be considered when analyzing firefly signals by taking a brief glimpse into human linguistics for comparisons and contrasts and then trying to apply some of the ideas seen there.

01. underlying properties
02. universals
03. disparity among groups
04. disparity among group members
05. dialects among group members
06. variations within demes
07. features all hard-wired
08. any parameters tunable
09. are any patterns adoptable
10. how comparisons to be measured

FigTable 17. Thinking, but not yet exhaustively nor exclusively. Which have relevance for fireflies? Can any be excluded as too complex for a beetle?

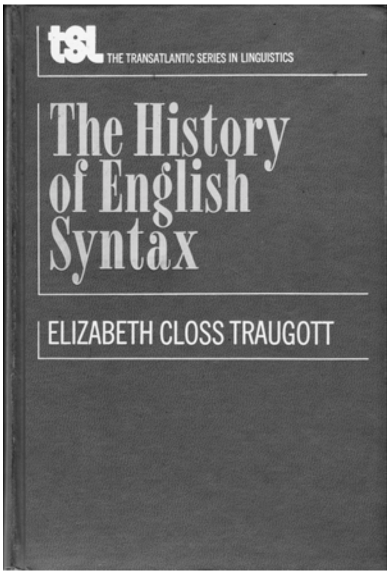


Figure 18. A new paradigm (source) perhaps?

Identifying Patterns, Toward Cross-Referencing Systems; Thinking Forward To Cladistic Analysis Of Firefly Communications and Linguistics

Several decades ago a book title turned up on a mail-order list that sounded intriguing though esoteric, but meshed with word/writing self-help references being accumulated. As it happened, merely a nodding acquaintance with a tiny part of this text stimulated different perspectives and insight into firefly language, and encouraged reflections of a different sort than might have been expected—it resulted in the construction of the "checklist" in **FigTable 17**—merely a memo to be noted before moving on. The book was “The History of English Syntax,” by Elizabeth Closs Traugott (1972; **FIg. 18**). Quoting from Chapter 1, *Patterns of Language*:

> *What kinds of patterns occur in all languages?* [genera, subfamilies?] … *What are the particular patterns available in any one language?* [immediately her questions can be seen to hold promise for fireflies, for species and species groups; and then she goes on, in a manner of speaking, to talk about firefly demes and variads] *Over a period of time one can usually detect marked changes in the patterns of a particular language; in the span of twenty-five years these changes may not seem very significant, but, over a hundred years and especially over several hundred, the cumulative effect of the changes is often such that the patterns seem markedly different.* [in such matters of time and space, isolation and vagility, fireflies are at a different scale, but the concepts seem to be pretty much the same!] … *Why do linguistic patterns change?, In what kinds of ways can linguistic patterns change?, and What kinds of changes have the patterns of any one language undergone?* … [here we] *will be making an investigation into … the changes these particular patterns underwent, and into the causes of these changes, wherever it is possible to speculate* [!] *about them. … refer to the universal patterns of which* English [e.g. Penn-Group demes] *provides just a small sample …* .) (jel emphases)

Human language has complexity and variation, as easily seen in word position in sentences and inflection (endings on words: -ed, 's, -ite, -ent). It evolves and has traceable changes linearly (chronologically) and branches laterally (geographically). Very smart people have worked long and hard to explain some of the same kinds of events and details that fireflyers have only begun to address—though Barber (1951) obviously reflected on the phylogeny of flashed signals from his small sample. Now, we ask of human linguistics, what are the elements and patterns of firefly language that would provide the parallel answers fireflyers might seek? **Figure 17** is a "preliminary" list of general areas, a checklist for stimulating thought.

Found and suspected patterns in firefly communication were listed in Chapter 7, and exist at different levels of organization. Many were at the at the bottom of a hierarchy, at a structure and configuration level:

Level 1: Bioluminescent signals are composed of pulses of light. At a higher level: no FPs are known in which exactly/only three pulses, no more nor fewer, form the species-specific (male) signal. At a higher level: the timing of these elements, their rates and durations, is used to encode information. Jumping to a higher level: adjunct FPs are often (phylogenetically always?) copies/simulations of prey species FPs. But has this one jumped to a different track by connecting with function, ecology and adaptation? These levels were used merely for illustration, to distinguish levels in first thoughts on the matter. But what are examples of higher-level patterns to be looked for, those that will give access to a deeper understanding of firefly communication, its complexity and phylogenetic history?

Time does not permit an examination of what is now at hand in these regards—there must occur many false starts in the process—and much of the available data are merely preliminary sketches, for no detailed longitudinal (seasonal/ phenological) study was made of any species—in fact it would seem that more time was spent with *Photuris stevensae* in the northeast than with any single Florida species because of what it seemed to offer. Traugott’s introduction to the study of human language can provide a broader and different perspective from that which could be gained by looking only within and among the languages of arthropods—though I must emphasize that recollections and reflections from Lindauer’s book on the evolution of bee language has served this author well for many decades (**Fig. 19**).

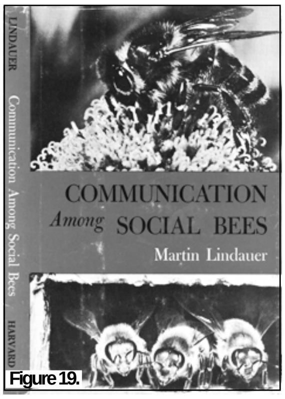
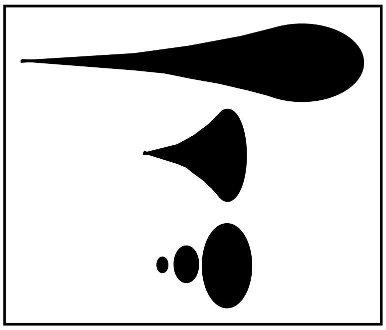


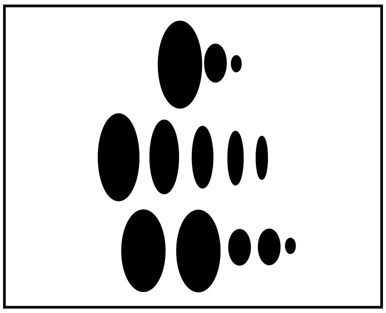
Figure19.

Very preliminary notes/sketches, scanning for ideas, photo-linguistic elements.

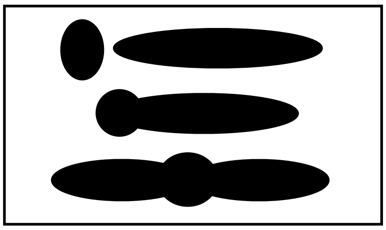
Firefly "Language" Groups?



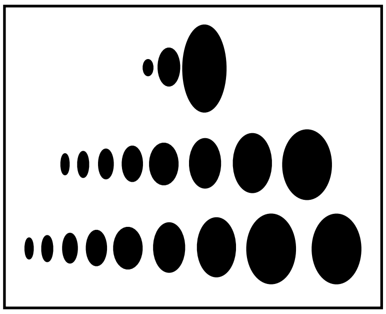
Photuris lucicrescens **language Group?**



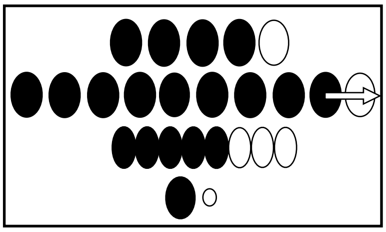
Photuris versicolor **language Group?**



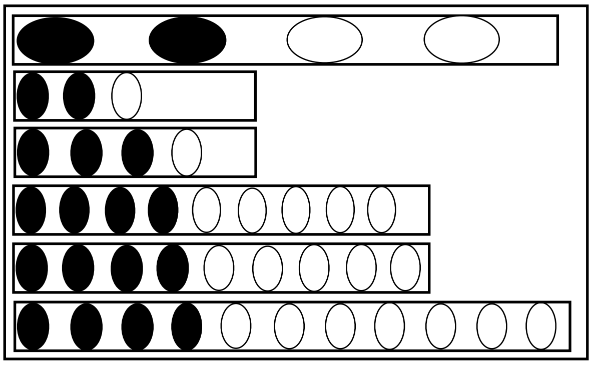
Photuris pensylvanica **language Group?**



Photuris fairchildi **language Group?**



Pyractomena angulata **language Group?**



Photinus ardens **language Group?**

1. **Pulse characteristics of lightningbug firefly signals.**
   - A. Signals are composed of pulses of light that appear against a darker background.
   - B. Light pulses are composed of electromagnetic wavelengths within a certain band of frequencies—to which receptors are tuned.
   - C. Certain parameters (e. g., rates, durations) of pulses are influenced in a predictable manner by ambient temperature.
   - D. Pulses may be short to long in duration (40-2000< milliseconds), but most are in the range 60-400 . . . 1000mS. Stretching the definition to include the long-glow "FPs" of the lightningbug fireflies *Pyractomena angustata*, *Photuris eureka*, and *Photuris walkeri*, duration reaches 30 seconds and more (1.8 million milliseconds and counting).
   - E. Pulse intensity-form may be virtually-symmetrical, skewed, or modulated through the duration.
   - F. Crescendo pulses may be lengthened or the intensity-rise-rate varied.
   - G. …

2. **Apparent signal units (FPs) may consist of single pulses or pulses combined to form multi-pulse FPs.**
   - A. Single pulses may be separated by intervals of varying length and be FPs themselves, or be emitted in trains, separated from each other by relatively short intervals, emitted at near-metronomic (constant) rhythmic intervals.
   - B. Single pulses emitted in trains—separated from each other by relatively short and nearly-equal intervals—may present FP-coding via moving sequences of two or more pulses, these establishing a pulse rate.
   - C. Pulses occur in discrete, species-typical groupings of 2 to 11 (e.g. 2-3. 3-4. 4-9, 4-11, etc.). (False grouping of varying numbers of pulses are formed by broken trains seen when emitters respond conditionally to their environment and skip/omit pulses.)
   - D. Pulses in FPs may occur in groups of exactly/only two, but no FPs are known in which exactly/only-three or exactly/only-four . . . . exactly/ only-N form a species-specific code.
   - E. Pulses in multi-pulse FPs may all be of equal intensity, or increase or decrease in intensity stepwise in even progression, or with a pair of pulses of equal intensity at some steps. (no step-intensity *reversals* are known?)
   - F. Multi-pulse FPs of decreasing intensity do not occur in repertoires with multi-pulse FPs of increasing intensity. (a major historic divide?)
   - G. …

3. **Routine flash pattern (FP) adjustments, ecological, other.**
   - A. FP periods are typically less variable at low ambient light when males have fewer environmental clues to guide their flight and signal presentations. **(continued)**

3. (continued) Routine flash pattern (FP) adjustments, ecological, other.

B. The FP presented (selected) by a male from his species-typical repertoire of FPs may be influenced by time of night and/or other ambient conditions: at twilight the emission of short flashes in certain Penn-group species; presentation of an A-flicker in the presence of other males emitting the A-flicker; with the passage of time through an evening, a week, among sites, other unknown factors.

C. A male may select alternative FPs from his repertoire when he switches from a within-site search mode to a roaming search mode (across, through scattered habitat patches). (*versicolor*, *fairchildi*)

D. …

4. Flash pattern (FP) ad hoc "of-the-moment," conditional adjustments.

A. FPs may be omitted, that is, FP periods lengthened, when males enter spaces providing fewer clues to female locations, such as when crossing highways or between the crowns of well-spaced tall trees along a row.

B. FP periods may be lengthened when males approach a responding female and a potential rival has flashed nearby.

C. Pulse interval within a presented FP may be other than (varied away from) a species-specific, critically-timed, pulse-interval, as a countermeasure to predation—a hunting *Photuris* female would answer incorrectly timed pulses but a conspecific females would not.

D. Pulse number within an FP may be increased to enhance the likelihood that a male's signal will be seen as he emits his FP over/among blades of tall vegetation.

E. Pulse number within an FP may be decreased to reduce the likely-hood of attack by an aerial predator.

F A male may adjust his FP pulsing to synchronize with pulses of nearby flashing rival males, in the context of competing—for the aim of a female's answer, for recognizing a specifically timed answer of a female.

G. A male may adjust his FP pulsing to synchronize with pulses of nearby flashing rival males to make it more difficult for aerially-attacking predators to aim—becoming part of local synchronizing selfish herd?

H. A male may increase the number of pulses in his FP in a greater rival density (more frequent encounter) of conspecific males.

I. A male will change from the adjunct FP of his repertoire to the default FP when answered by a female (or decoy) flash.

J. …

5. New FPs derived from modification (evolution) of pulses within an FP.

A. Complex FP of *Ph. dorothae* repertoire concludes with one or more rapidly doubled (paired, fused) pulses.

B. Crescendo FPs produced by asynchronous flashing of two lantern segments (*hebes*). (visual evidence only)

C. Rapidly modulated crescendo FPs produced from "innervation" of lantern by "wing-beat neurological oscillator" (*lamarcki*). (no experimental or anatomical evidence for this explanation)

D. …

6. FPs derived from different contexts.

A. An adjunct FP becomes a default FP (*forresti*).

B. FP repertoires become simplified, reduced to a single FPs. (coastal and other marginalized OTUs (coastal singles (*aureolucens*). (wild guess?, DNA will help)

C. FP within a repertoire combined with another in the repertoire resulting in a combination (joined tandem) FP (*barberi*).

D. A landing/illumination emission become a default FP; no examples, idea seems inescapable, historic?

E. …

7. New FPs derived from hard-wiring of FPs that began as *ad hoc* copies?

A. Initial/historic occurrence of close matching of *Photuris* FPs with various *Pyractomena* FPs, flickers of *Ph. versicolor* Group with those of *Py. angulata* and *dispersa*. This seems a "certainty" as a source of such FP matching.

B. …

8. New FPs derived from hybridization between diverged demes

A. Variads with different FPs recontact, interbreed (*cowaseloniensis*?)

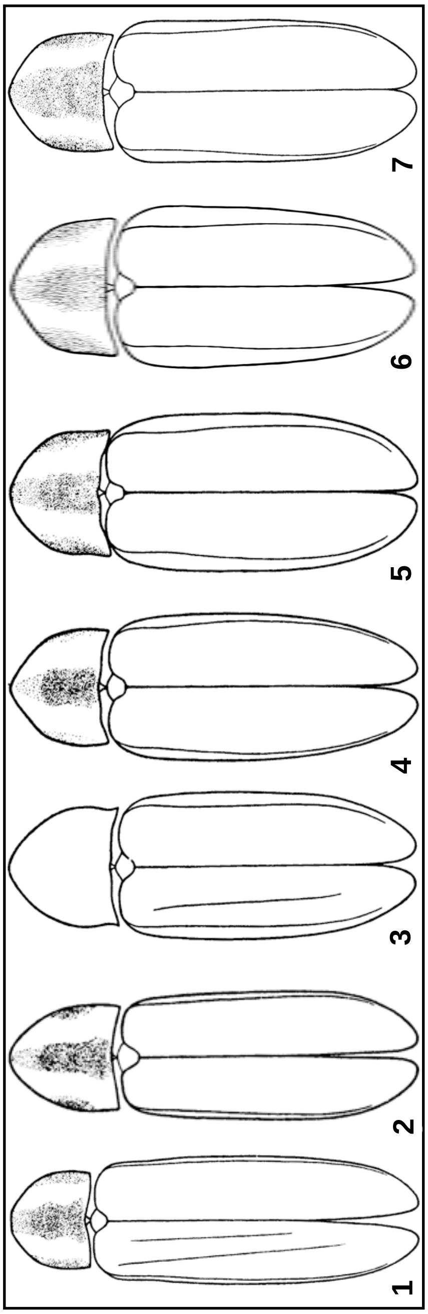
Surely this organization, while it has gone off track with respect to what should have been inferred from Traugott's linguistics model, has something to teach, and may give an insightful fireflyer a start toward important discoveries.

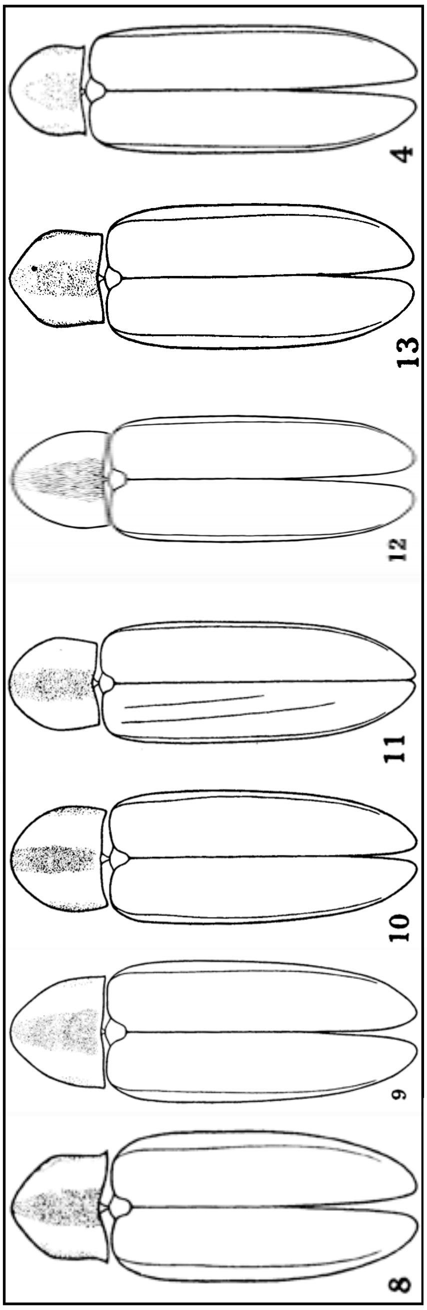
"Shadow" in the title of this outline survived repeated reflection, editing and vetting, and consultation with Funk and Wagnall, Thorndike-Barnhart, Webster's and Merriam-Webster's, Oxford and others. Taxonomically it is first an allusion to Plato's cave allegory, but there are many other definitions working here: (1) a delusive image of semblance; (2) the dark image thus produced on a surface and representing the approximate shape of the intercepting body; (3) a faint representation or indication; (4) a symbol; (5) a phantom; (6) a comparative darkness within an illuminated area; (7) a remnant; (8) a vestige; (9) an insignificant trace or portion; and finally … (10) an inseparable companion.

Pyractomena Fireflies With Relevance To *Photuris* Signaling

Key and illustrations from J. W. Green, 1957.

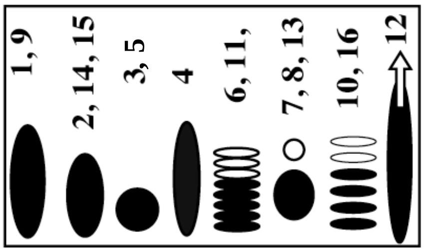
The flash patterns (FPs) of a few species of *Pyractomena* are similar and sometimes identical to the adjunct FPs of certain *Photuris* species. Some are known to be the prey of the females of the FP-matching *Photuris* males; the significance of this matching is discussed elsewhere in this paper. This is to say that the few *Pyractomena* outlined in the chapters that follow here are known to be or suspected of being historical and perhaps present-day models for *Photuris* FPs. This introduction provides information for identifying these *Pyractomena*. The known models are those that emit flicker or rapid-pulsing FPs, the long-glower, *Py. angustata*, and the single-short sometimes paired flasher *limbicollis*. The relation between these two genera may have a very long history, even millennia, and it would be surprising if there were not other model-matcher connections with other *Pyractomena* to be discovered. Of major importance in J. W. Green's key which appears below, are male genitalia and the distribution of the secondary pubescence over the surface of the elytra—which, viewed under the dissecting microscope, is most easily seen with incident illumination shining across the elytra at a low angle, as instructed by Green. (See page 136 for simple aids to distinguishing flashing genera.)

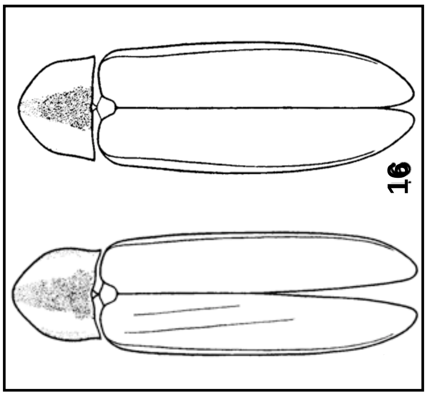




Lengths in mm., from Green, 1957.

1. *ecostata* 11.5-16	9. *punctiventris* 12-16.3
2. *lucifera* 7.5-12	10. *floridana* 9-11.5
3. *vexillaria* 11.5-13	11. *barberi* 11-12.8
4. *sinuata* 8-11	12 *angustata* 11-14.5
5. *similis* 9-12.8	13. *limbicollis* 7-12
6. *angulata* 7.5-13	14. *linearis* 8.3-11
7. *borealis* 11-19	15. *palustris* 10-13.5
8. *marginalis* 6.3-11	16. *dispersa* 9-12.5





KEY TO MALES OF NEARCTIC PYRACTOMENA

1. Viewed ventrally, aedeagus with inner margins of lateral lobes strongly diverging and sinuate distally, apices abruptly much narrowed ...... *P. lucifera* group 2

— Viewed ventrally, aedeagus with inner margins of lateral lobes not strongly divergent, apices not abruptly narrowed..*P. borealis* group 7

P. lucifera Group

2. Elytra subglabrous, primary pubescence very minute and sparse, secondary pubescence confined to lateral explanate margins ...... (1) *P. ecostata* (LeConte)

— Elytral pubescence distinct 3

3. Secondary pubescence covering definitely more than half of elytral surface 4

— Secondary pubescence distal, covering less than half of elytral surface ...... (4) *P. sinuata* Green, new species

4. Form narrowly elongate, lateral explanate margin of elytra narrow throughout; pronotum distinctly pubescent ...... (2) *P. lucifera* (Melsheimer)

— Form broader, lateral explanate margin of elytra wide basally, gradually narrowing to apex; pronotum subglabrous, hairs minute and inconspicuous 5

5. Primary elytral pubescence longer and denser, very conspicuous; discal costa of elytra narrowly fulvous....(3) *P. vexillaria* (Gorham)

— Primary elytral pubescence short and of normal density, not notably conspicuous; discal costa of elytra concolorous 6

6. Secondary pubescence densely covering most of elytral surface, absent or less dense near basal margin, never involving humeral callus. Genitalia as in figure 19. Habitus very similar to *P. angulata* ...... (5) *P. similis* Green, new species

— Secondary pubescence covering entire elytral surface, equally dense to extreme base. Genitalia as in figure 20........(6) *P. angulata* (Say)

P. borealis Group

7. Secondary pubescence covering definitely more than half of elytral surface 8

— Secondary pubescence distal, covering less than half of elytral surface 10

8. Form broader, lateral explanate margin of elytra wide, gradually narrowing to apex 9

— Form narrow, lateral explanate margin of elytra narrow throughout, only very slightly wider basally 17

9. Large species, 11–19 mm. in length; pale borders of elytra very narrow, often nearly obliterated; epipleurae fuscous basally ...... (7) *P. borealis* (Randall)

— Small species, rarely as long as 12 mm.; lateral pale border of elytra wide, epipleurae pale......(8) *P. marginalis* Green, new species

10. Species of the Southern States, Georgia and Florida to Texas........11

— Species of more northern distribution 16

11. Scutellum and mesonotal areas flavate or fulvous, sometimes partly infuscate 12

— Scutellum and mesonotal areas dark piceous or black, rarely tip of scutellum narrowly pale 13

12. Larger species, 12–16 mm. in length; pronotal vitta normally subtriangular, widest at base. Habitat Texas and Mexico ...... (9) *P. punctiventris* (LeConte)

— Smaller species, 9–11.5 mm. in length; pronotal vitta of nearly uniform width throughout, widest near middle, thence narrowing somewhat in basal half. Habitat Southeastern States ...... (10) *P. floridana Green*, new species

13. Pronotal vitta narrow, subparallel-sided; smaller species................14

— Pronotal vitta subtriangular, widest near base; larger species......15

14. Elytra piceous brown, discal costa pale; pronotum without lateral maculation ...... (11) *P. barberi* Green, new species

— Elytra piceous black, discal costa concolorous; pronotum with distinct narrow lateral maculation ...... (13) *P. limbicollis* Green, new species

15. Form narrow, lateral explanate margin of elytra narrow throughout; pronotum nearly as long as wide......(12) *P. angustata* LeConte

— Form broader, lateral explanate margin of elytra wider, gradually narrowing to apex; pronotum distinctly transverse ...... tentatively referred to (16) *P. dispersa* Green, new species

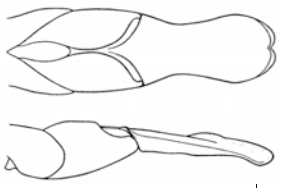
16. Primary elytral pubescence conspicuous, longer and denser, of nearly equal length throughout; secondary pubescence covering nearly apical half of elytra, sometimes more extensive. Pronotum usually with lateral maculation 17

— Primary elytral pubescence short, sparse, and inconspicuous basally, somewhat longer distally; secondary pubescence covering about apical third or fourth of elytra. Pronotum usually without lateral maculation ...... (16) *P. dispersa* Green, new species

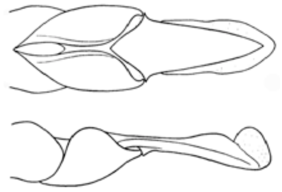
17. Smaller species, 8–11 mm. in length. Median vitta of pronotum usually subparallel in basal half, usually obscure in apical half and often not reaching apex ...... (14) *P. linearis* LeConte, and *P. linearis* complex

— Larger species, 10–13.5 mm. in length. Median vitta of pronotum entire, subtriangular, somewhat expanded and widest near base, thence regularly narrowing to apex ...... (15) *P. palustris* Green, new species

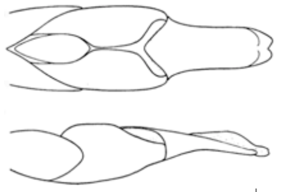
17. *ecostata*



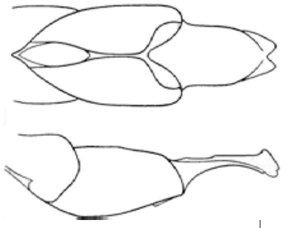
18. *lucifera*



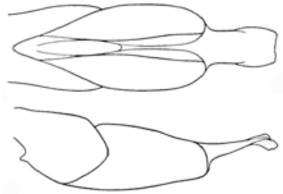
19. *similis*



20. *angulata*



21. *borealis*



Chapter 74

Pyractomena angulata (Say) 1825

Candle Firefly

Pyractomena angulata has one of the most extensive distributions presently known for North American flashing fireflies, extending west from the Atlantic beyond the Mississippi and to the northwest beyond North Dakota **(Fig. 1)**. It probably ranges further north in Canada than shown, perhaps more than 100 miles. It is the only commonly-occurring *Pyractomena*, and is a lightningbug likely to be identified correctly by a casual observer. Its history, population structure, and variations in signaling behavior across its range of occurrence are of considerable interest because of the intimate connection it has or historically had with certain *Photuris* species, as prey and because its FP (lineage) apparently was a model for *Photuris* species' adjunct FPs. Occasional archived specimens suggest the possible existence of isolated populations—as in New Mexico and Colorado—but such outlying records could be from mislabeling or student collections. Probably *angulata* and *Py. dispersa* occur in valley marshes and wet meadows in the Rocky Mountains. A graph of *angulata's* museum specimens perhaps indicates the level of insect study and collecting activity over several decades **(Fig. 2**).

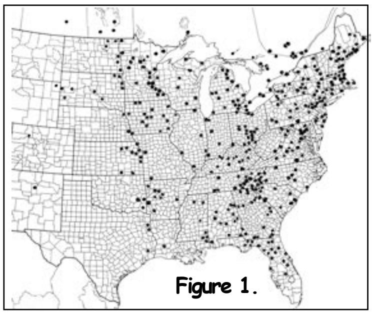


Figure 1.

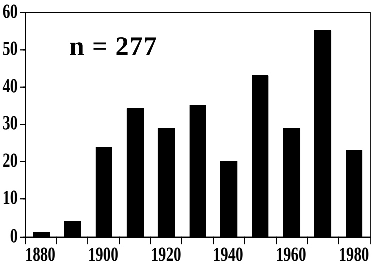


Figure 2. Museum archives (specimens).

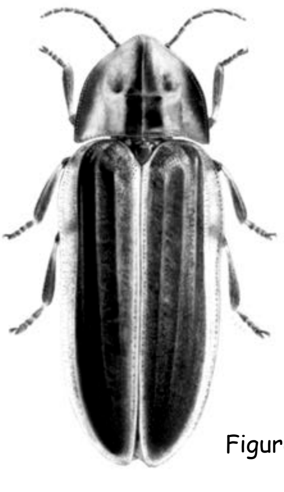


Figure 3.

The Candle's 9-13-pulse *amber* flicker can be mistaken for no others except those of: (**1**) *Py. barberi,* which occurs only in very early spring in the Big Bend Gulf region of southeastern United States, and (**2**) the 5-7-pulse FP of *Py. dispersa* at **warm** temperatures, when its slower pulses are no longer seen as distinct entities but meld into a short flicker. *Py. barberi* and *dispersa* nearly always fly/flicker within eight feet of the ground. In hand, *angulata's* distinctive appearance (**Figs. 3 & 24; pages 453**), with its usually/typically colorful broad form, keeled, angular and rather 5-sided pronotum, and wide, pale, lateral elytral margins will distinguish it from all others, with the possible exception of *Py. similis*—which is of restricted geographic occurrence, is less colorful (**page 456**), and has a slightly different genitalic form (**Fig. 25;** see also **Figs. 23-24**, **26-27**). FPs are diagnostic, that of *similis* being a single flash.

This species may be seen in almost any mesic or tree-lined or creek-side site in eastern North America during their adult season (**Fig. 4**), where they weave and flicker jaggedly at tree tops. Often none were seen for several minutes, then, seemingly, a *squadron* of two or three would pass through—actually, perhaps perched, watching individuals were stimulated to fly when a roving male passed or something else triggered a short neighborhood *spree* (a useful term, courtesy T. J. Walker). In treetops, the FP presents as a 1-2-foot trail of several sharp, amber flashlets that jerk around and amongst the tips of boughs. In wetlands they fly in greater numbers low over herbs and grasses. Although inspection of PM-records indicates that the FP at the lantern is a phrase of about a dozen evenly-spaced pulses of nearly equal or slightly rising then falling intensity (**Fig. 5A**), the appearance in the field and in some PM records is quite different (**Fig. 5B**), probably due to the twisting, turning (aiming) flight of emitters, hence its changing orientation to the PM-tube. Individual pulses may appear bright or dim, or do so alternately, or be skipped, leading sometimes to an erratic, jagged flicker. FP period is about 3 sec at 21°/70° (**Fig. 6**; rate regression in **Fig. 7**).

Though *angulata* and other *Pyractomena* typically occur in mesic and damp situations, male *angulata* were occasionally seen over xerophytic sites. A population was found at the dry crest of Sea Horse Key, off the village of Cedar Key (near the light house, Univ. Fla. Biol. Sta.), and occasional individuals were seen in upland oak forests in the midwest. The site shown in **Figure 28** was a dry hillside in Virginia but had an active population of *angulata*. Large active populations were also seen, as examples: in a marsh and adjacent old field in Ann Arbor, MI (22-24 June 1966, n=<35); by an earthen dam site in Pembina Co., ND, over a marsh and

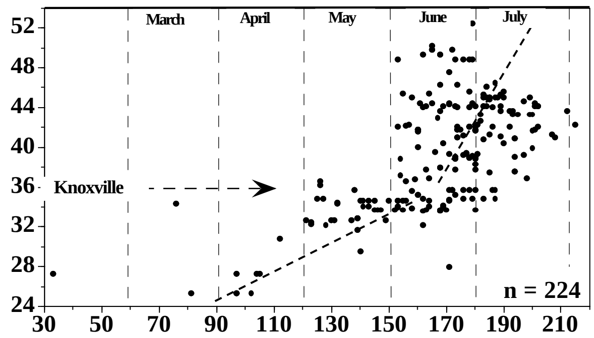


Figure 4. GESEDIS (archives; (AX: Lat/DOY).

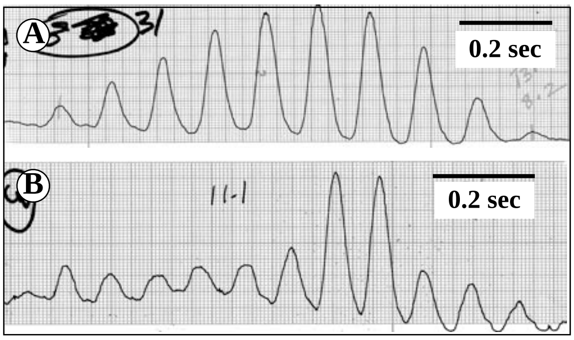


Figure 5. TN & ND (AX: rel. int./time).

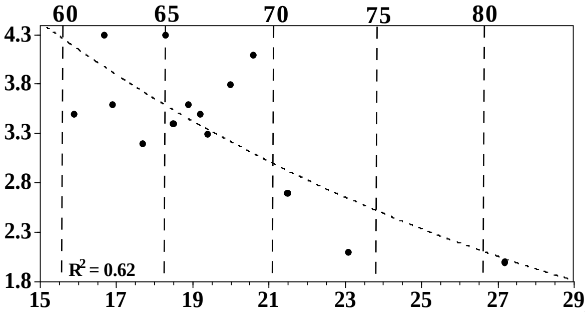


Figure 6. FP period (AX: sec/temp).

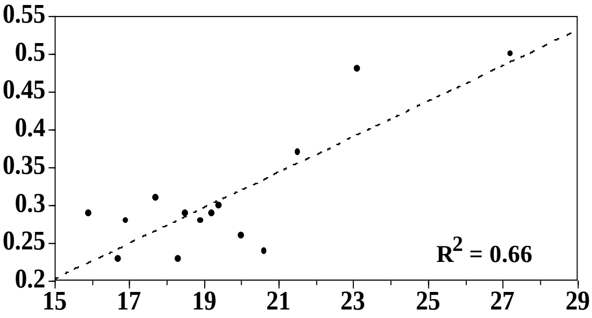


Figure 7. FP interval as rate (1/period; AX: Hz/temp).

oldfield (**Fig. 8**, 12 July 1991); in a tiny "wet prairie" by a tiny creek or seep at the Archbold Biological Station in FL (7-9 April 1967, n=<20); over a low roadside near Lake Itasca, Clearwater Co., MN (2-3 July 1980, n=<20); and around low trees in a gully in a hay field at David Crocket St. Pk., TN (1-3 June 1984, <20 (see *Ph. tremulans*, Fig. 4). A few decades ago at the Gun Club site in Gainesville (**Fig. 10**), they occasionally occurred in large numbers (n=25-35). **Figures 9A** and **B** (next page) give seasonal distribution, in overview and detail for north central Florida.

Because the FP of this ("keystone") firefly (that of its ancestors) figures significantly in the signaling and focused predation (and sexual selection?) of several *Photuris* species, it is important to know in detail *angulata's* seasonal occurrence (phenology), and factors that influence it. Such records will also be of use with respect to the changes that will occur with developing climate changes. *Py. angulata's* adult activity begins in south Florida in February but not until early June north of the 39th parallel (Baltimore, e.g. **Figs. 11 and 12**). Note, in the figures that slopes are somewhat flat near Miami until late March, then rise ca 7.5 days per degree latitude to 36° (Winston-Salem-Knoxville-Nashville-Fayetteville-Tulsa), then, by bending/breaking the rise into two linear segments, the slope rises at ca 2.5 days per degree to 44° Lat. (Burlington VT). A similar upturn is noted in data for some other fireflies.

The duration of the adult season, taken from the figures and excluding isolated outliers (see M&T), is as much as two months at some latitudes. Such (misleading) broad spans are from records for all years in aggregate. Individual years may be only half this.

The large number of identified *angulata* specimens associated with localities allows a speculative glimpse into another phenological question—do adults emerge (does spring arrive) earlier in the western region of a distribution. A “strip” sample of specimen data from east to west between latitudes 31.1° and 41.1° N was used (the shape of the US/NA required this); this strip was divided into east and west sections: eastern 81.1°-85.8° W Long.; western 86.2°-96.9° W Long.). Specimen *numbers* in the sample were graphed by WOY (Week Of the Year) in **Figure 13**, and in **Figure 14** as the *accumulated* fraction of adults “active” in the region through the season. Hardly definitive, the graph suggests that adult appearance is a bit earlier in the west, and that gradually the curves join. **Figure 29** illustrates a questionable attempt to quantify *angulata's* phenological difference, comparing east and west data, though perhaps it is the seasonality of collectors that is suggested. If conditions are suitable earlier in the west and stay suitable there as late as they do in the east, would selection favor greater longevity in the west—or diminish the degree of protandry?

Figure 8. ND oldfield and marsh behind a dam.

SESOBS records for Florida (**Figs. 9A and B**) show Highlands County activity beginning in early March, that in the Gulf Region in late

Table 1: SESOBS.

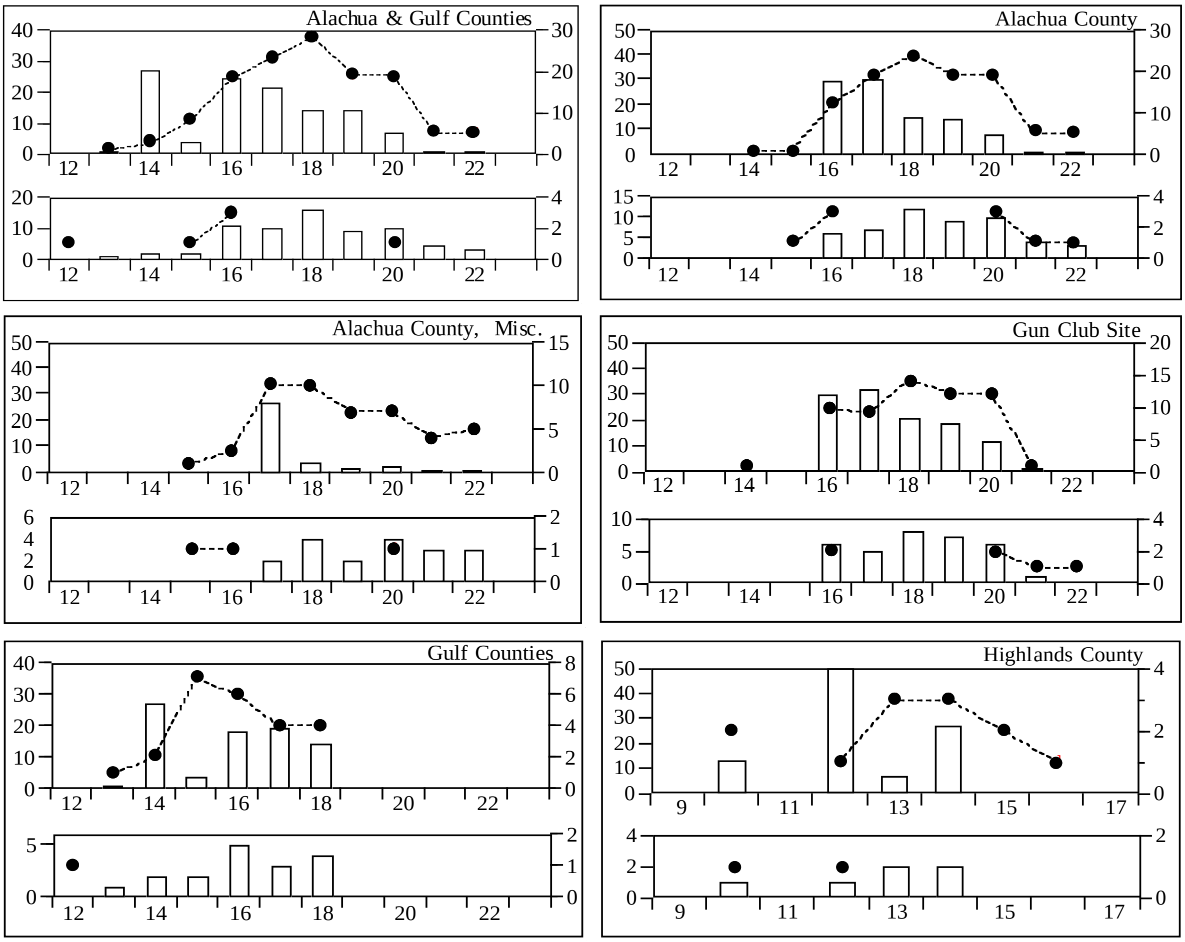


Figure 9A. SESOBS summary for Alachua County (AX: Number/WOY).

Month	March	April	May
DOY - Span	60 - 90	91-120	121-151
WOY:DOW - Span	9:4 - 13:6	13:7-18:1	18:2-22:4

Synoptic Guide; see M&T, Chapter 3: In the upper chart of each pair (set) columns show weekly Mean Amount (left Y axis); dots show weekly Total Count (right Y axis). In the lower chart of each pair columns show N(umber)(left Y axis) of weekly amount estimates contributing to the Mean Amount value for that week of the year (shown below on the X axis); dots show total N(umber) (right Y axis) of Zero activity nights (casually) noted during the week of the year indicated. Horizontal axes of all charts show Week Of the Year (WOY). Observe Date Bar for month, week, and day equivalents, and M&T for detailed explanations of methods and limitations of data.

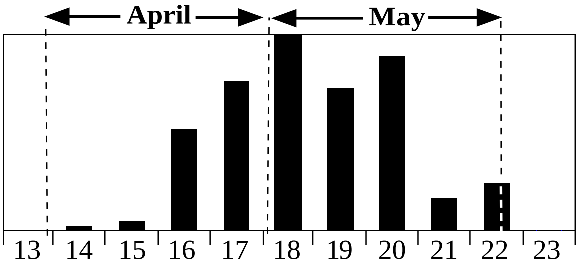


Figure 9B. SESOBS summary for Alachua County (AX: Number/WOY).

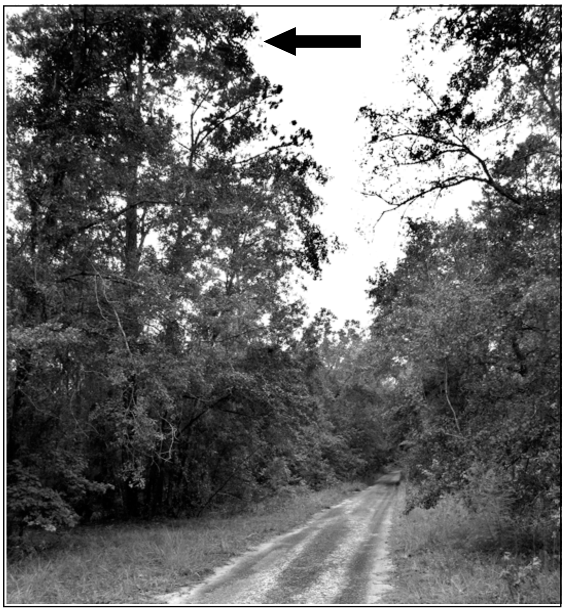


Figure 10. Gun Club site; arrow, site of flickering males.

March, and in Alachua County in mid April. Note that the Gulf County region is about the same latitude as Alachua County but the firefly seasons are earlier. Inconsistent (random), idiosyncratic pockets (areas), and chaotic (*sensu* deterministic disorder) pockets must occur, and perhaps explain the breadth of seasonal distribution seen in such graphs.

Finally, the season of *angulata* coincides with that of its flickering presumptive mimic *Photuris stanleyi*, in the Gulf Counties and the Alachua County Regions where seasonal data are extensive (**Fig. 15**). Such concordance may be expected to be the case wherever these two species occur and in other cases of A-flickering *Photuris* species—though in others, for example *Ph. quadrifulgens*, it appears to be “confused” as well as confusing by the earlier presence of *Py. dispersa* with its “flicker” of a different Hertz (also fewer pulses and slower rate). This situation becomes even more confusing and perhaps unresolvable in Florida's vanishing or now gone *Ph. eureka*.

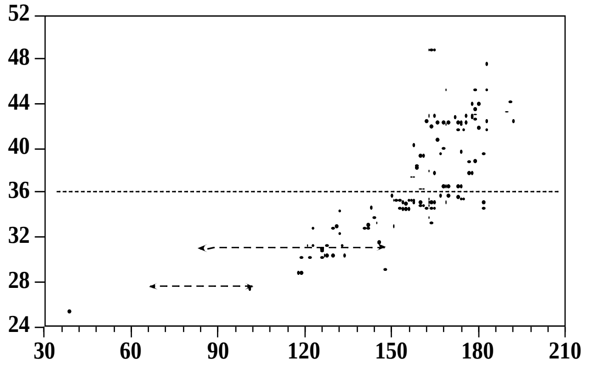


Figure 11. G'SOBS (sightings; AX: Lat/DOY).

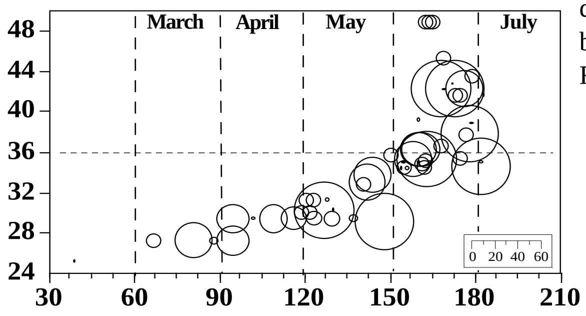


Figure 12. G'SOBS: Quant. records (m, s, f, 1; AX: Lat/DOY).

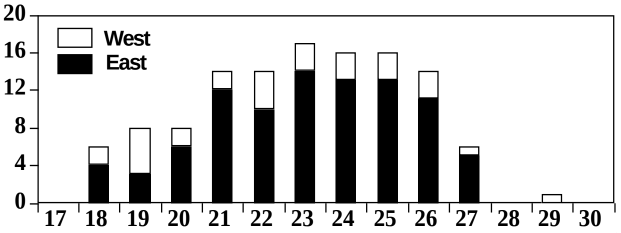


Figure 13. Phenology comparison 1 (AX: number/WOY).

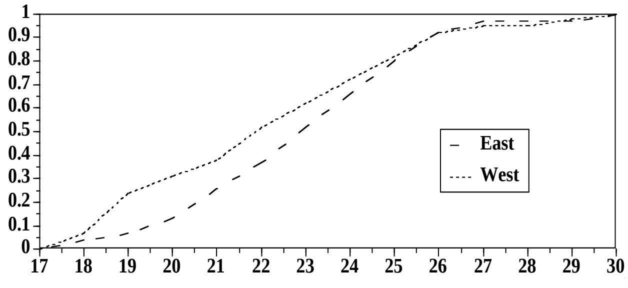


Figure 14. Phenology comparison 2 (AX: fraction/WOY). See also Figure 29 for further examination.

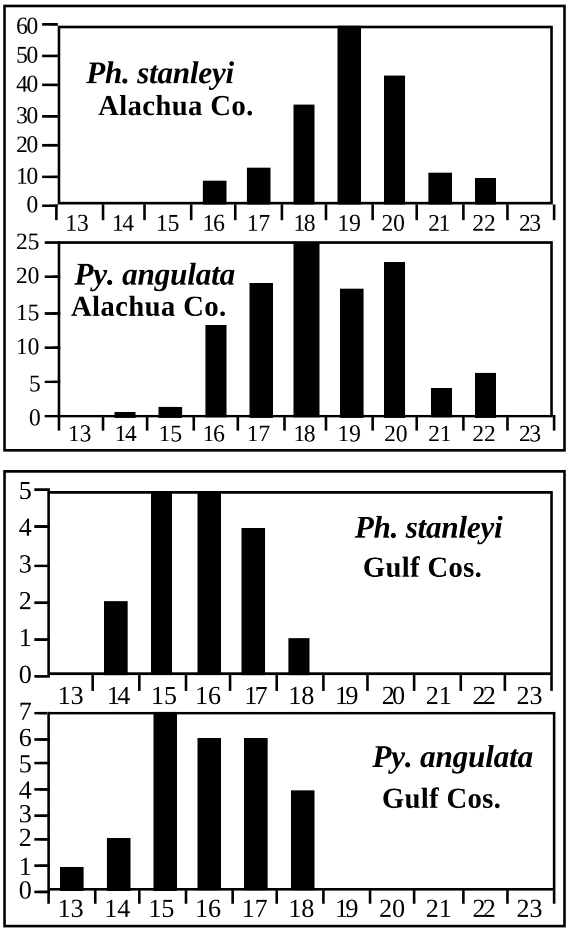


Figure 15. Comparing phenologies (SESOBS).

Additional and incidental details of flashing behavior: Male flashing flight begins after dusk, at full darkness. At sites in Michigan and North Dakota, between 1.0 and 1.1 creps; in Florida and Tennessee, between 1.4 and 2.0 creps (x=1.7, n=8). Activity sometimes continued until after midnight, with diminishing numbers (seen at 5.6 and 8.5 creps, but finished at 4.7 on another occasion. Mate-seeking, flickering males fly twisting, winding and often "twitchy" paths among and around leafy branches of trees and shrubs. When low over the ground they twist and turn along winding courses even low among grass/herb tops. Males searching trees and shrubs usually fly a few inches out from the foliage and, for example, may move on an angle up-up-up, then straight across an open space and down-down-down, winding

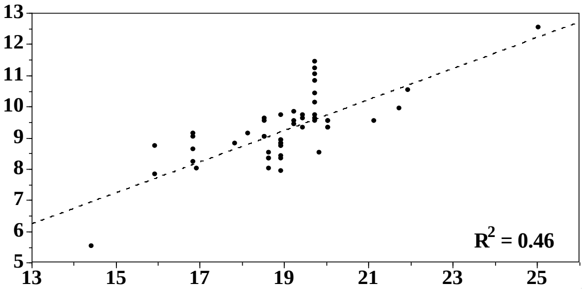


Figure 16. Mean modulation rates (AX: Hz/temp).

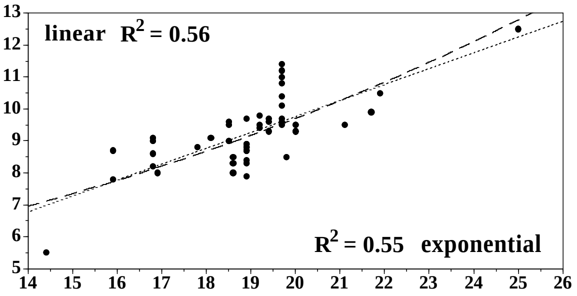


Figure 17. All means, all localities (*angulata*; AX: Hz/temp).

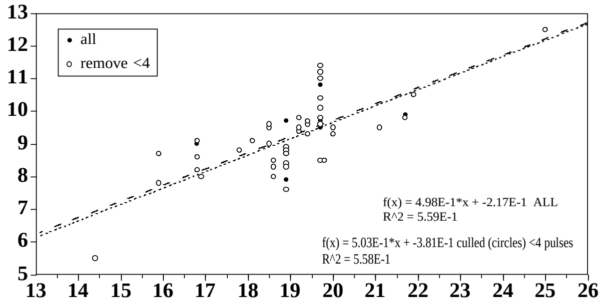


Figure 18. Comparison of culled set.

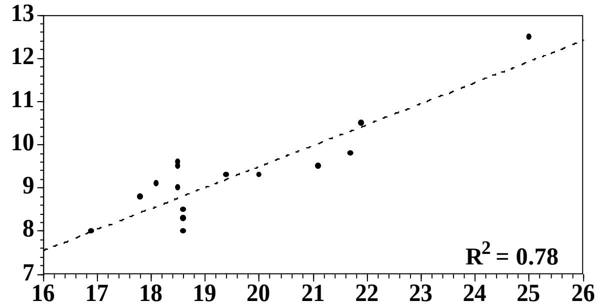


Figure 19. FL and GA with 4 or more pulses.

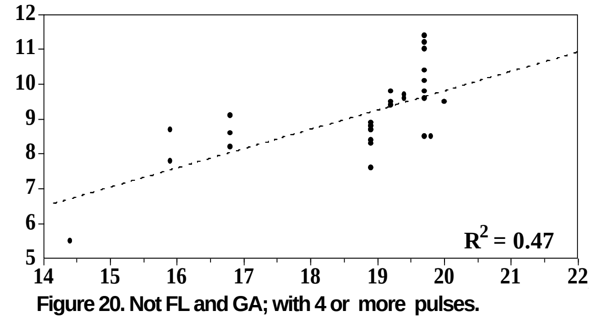


Figure 20. Not FL and GA; with 4 or more pulses.

in and out as to stimulate/examine each dark niche they pass. At other times they fly straight and quickly, arcing around treetops, seemingly giving them only a passing look.

The FP of *angulata* is one of the most easily recognized fireflies in North America. Flicker color distinguishes it from those of all *Photuris* species, all of which have green luminescence—but when viewed near sources of artificial illumination the human eye/brain will often misjudge color. Perhaps this explains why McDermott once described this firefly's FP as "greenish, twinkling." *Py angulata's* flicker is a rusty-orange (peak 577 nm, half-max 551-610 nm) of variable duration (700-1200 mSec), and of 7-15 (usually 10-13) modulations (**Fig. 5**). McDermott associated this flicker with a specific taxon but because of the rudimentary/crude taxonomic circumstances of *Pyractomena* at the time (early 1900s), he incorrectly associated the FP with another name.

At 20°C/68°F flicker modulation frequency is about (roughly) 10 Hz (i.e., pulses/sec; **Fig. 16**); note the considerable variation among PM-measurements from across *angulata's* broad geographic occurrence. This modulation rate averages about the same as that of *Py. barberi*, and also that of *several Photuris* species. Because this ***A-flicker*** is so important for understanding the sexual biology and predation of several *Photuris* it is especially important to measure this parameter as it occurs (variously) in/among ***local*** populations of *Py. angulata* as accurately as possible—and to understand the (natural and observational) origins of the variations that are so obvious in **Figure 16**—and especially the disparity sometimes observed between *angulata* and presumptive *Photuris* mimics—and the implications of variations in these phenomena for understanding sexual selection and predation avoidance.

The following is a sketchy overview of *angulata's* flicker records: **(1) Figure 17** compares the linear with the exponential regression model (*Deltagraph®Pro3*), and finds little difference; the linear model is used in the following. **(2)** In **Figure 18** measurements of flickers with fewer than four detected pulses (those when PM aim was slow to reach target) were excluded, and the resulting regression is compared: fit, slope equation, and nearly parallel lines are shown; the culled set is used in the following. **(3) Figure 19**: the regression for Florida/Georgia *angulata* measurements (0.78). **(4) Figure 20**: the regression for not-Florida/Georgia *angulata* (0.47). **(5) Figure 21**: the two previous regressions on the same chart. **(6) Figure 22** compares the regressions of FL/GA *angulata* and Florida's *Ph. stanleyi*.

(7) Field temperatures in a study site vary, often sensibly and sometimes appreciably with each zephyr that wafts through, with local air masses by marsh versus that 10 steps away up a rise, between ground and treetop levels, and with a passing sunset and clearing skies. As males take flight their muscles may warm and alter FP Hz somewhat, there are genetic differences among males, and males at isolated localities may have drifted or have been selected away from some archetypal frequency. These alone and in combination certainly were responsible for some of the variation seen in sampling, as was human error.

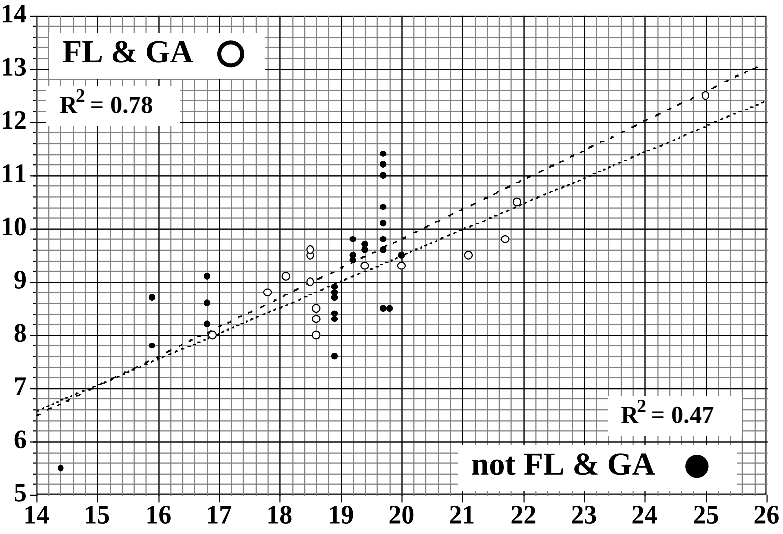


Figure 21. Comparison of two data sets (AX: Hz/temp).

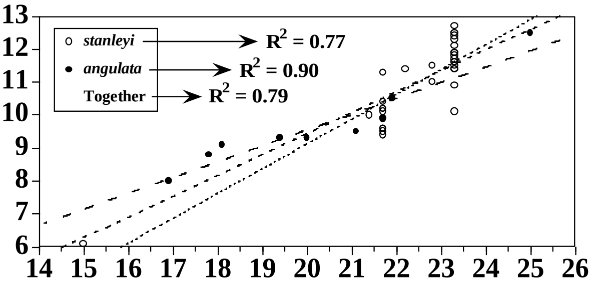


Figure 22. Species comparison with fits (AX: Hz/temp).

Females, Juveniles: Females look much like males though they may average slightly smaller (see note below). The topography of the lanterns of females is characteristic of the genus. I have often unsuccessfully looked for hanging pupae in sites where I had previously seen many adults. Once a larva was collected with several *Py limbicollis* larvae. They were found by their glows as they walked along the twigs of understory shrubs on a wet evening in a mesic hammock (Gun Club site) in Florida. The *angulata* larva was broader and paler than the *limbicollis*; these were identified after eclosion. Green (:256-7) described a larva and pupae that may belong to this species, and quoted a note of larval occurrence on trees (:257). Response flashes of a bottled Ann Arbor female that attracted males were about 1 sec in duration, amber, and not visibly modulated, and began immediately after the male flicker ended (17°C/63°F). Males responded to simulations of female flash responses by dropping (or quickly flying down?), occasionally with lantern glowing, to the vegetation or ground a few feet from the answering light. After 1-4+ min they flickered again, and if answered, approached with short flights and walking, and continued long pauses between signals. Perhaps males drop in controlled falls as noted by Schwalb (1961) in *Lampyris noctiluca* in Germany, but unlike the north-European glowworm, *angulata* males may aim to avoid landing "too" near. When answered with a penlight sometimes males are found in the hair or on the shoulders of the penlight operator. An indirect and long approach may be a counter-measure against aggressive-mimicry and aerial hunting/hawking by *Photuris* females of several species.

Morphological Notes. No significant departures from or additions to Green's descriptions are noted. A geographical assortment of specimens was measured: males, n=22: mean length=11.0 mm, s=1.0, v=0.1, range=8.6-12.3; mean pronotal l/w ratio=0.77, s=.05, v=.07, range=0.68-0.89 mm. Females, n=14: mean length 10.8 mm, s=0.8, v=0.1, range=10.0-12.5 mm; mean pronotal l/w ratio=0.77, s=0.06, v=0.08, range=0.67-0.92.

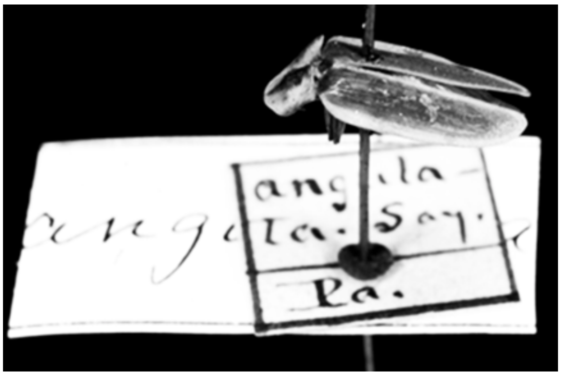


Figure 23. Melsheimer's specimen.

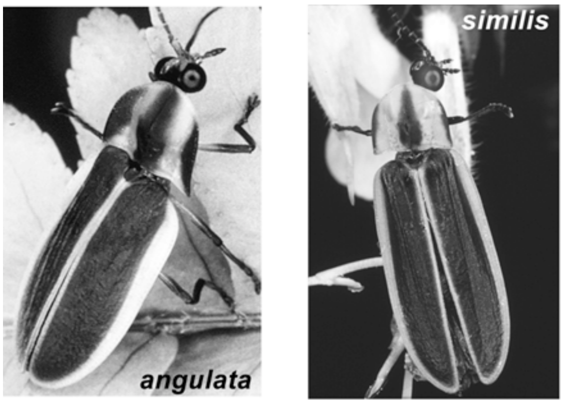


Figure 24. Compared habiti.

Miscellaneous notes. This was among the earliest of North American fireflies to be recognized. The Holotype is certainly gone, with most or all of Say's North American collection, and I am not aware of any Neotype designation. Say's choice of epithet may have been derived from the angular shape of the pronotum. No mention of the source locality of Say's original ("type") specimen for this species has been found, but there may be clues to permit an educated guess. As with all fireflies named between 1767 and 1833, *angulata* was originally placed in the genus *Lampyris*. Frederick Ernst Melsheimer was a correspondent of Say and probably compared his specimens with those of Say: a *Py. angulata* in the Melsheimer collection at the MCZ in shown in **Figure 23.** Green (1957:259) noted that "This is our most abundant and most widely distributed species, accounting for about 40 percent of the total number of Nearctic specimens of *Pyractomena* now in collections. The flashing of males is recorded by Barber as follows: Sebago Lake, Maine, 'A flickering half-second flash each one and one-half seconds over marsh on cold night'; and Sherwood Forest, Maryland, 'Orange flicker ascending'". Perhaps these labels caused Green to look carefully at the flash contrast noted on labels attached to *Py. similis* and were responsible for the latter's discovery?

In reading about American naturalists, a now-forgotten reference led to the suspicion that Say may have gotten his *angulata* specimen from his friend— another member of the Philadelphia Academy—botanist Thomas Nuttall, who had collected Say's "type" of *Phausis reticulata* near Fort Smith, Arkansas. Going on Nuttall's itinerary and notes, it was surmised the *angulata* type came from the region of Dardanelle, Arkansas, a little east of Fort Smith, and *angulata* was sought there without success. A dam across the River and other human activities have changed the region a great deal since the early 19th century.

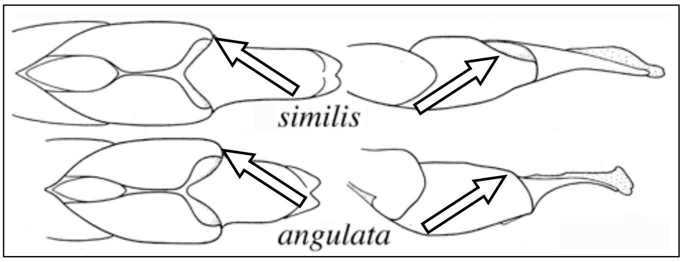


Figure 25. Comparison of aedeagi of *angulata* and *similis*, from Green, 1957. Note narrower LL apex in *similis*..

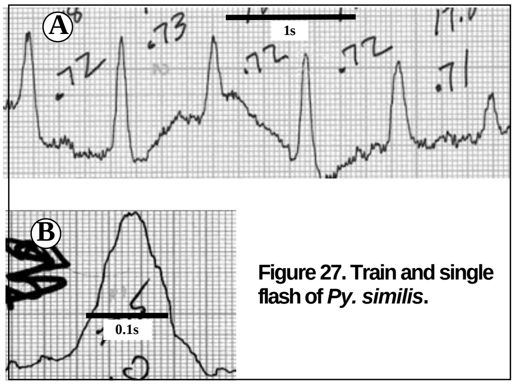


Figure 27. Train and single flash of *Py. similis*.

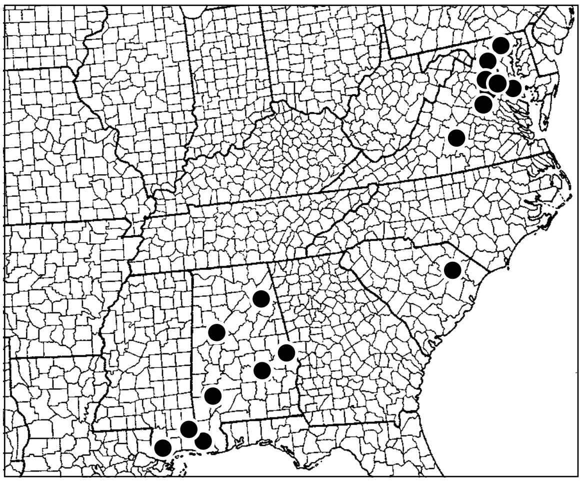


Figure 26. *Py. similis* counties of recorded occurrence.

Figure 28. *Py. angulata* site in Goochland County, Virginia, 1963.

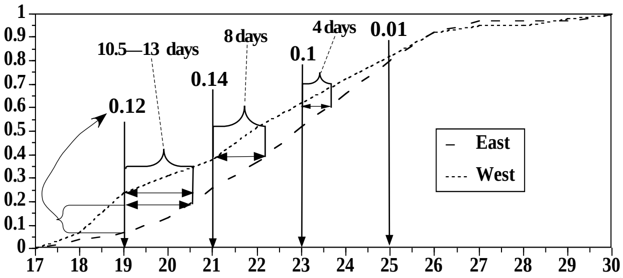
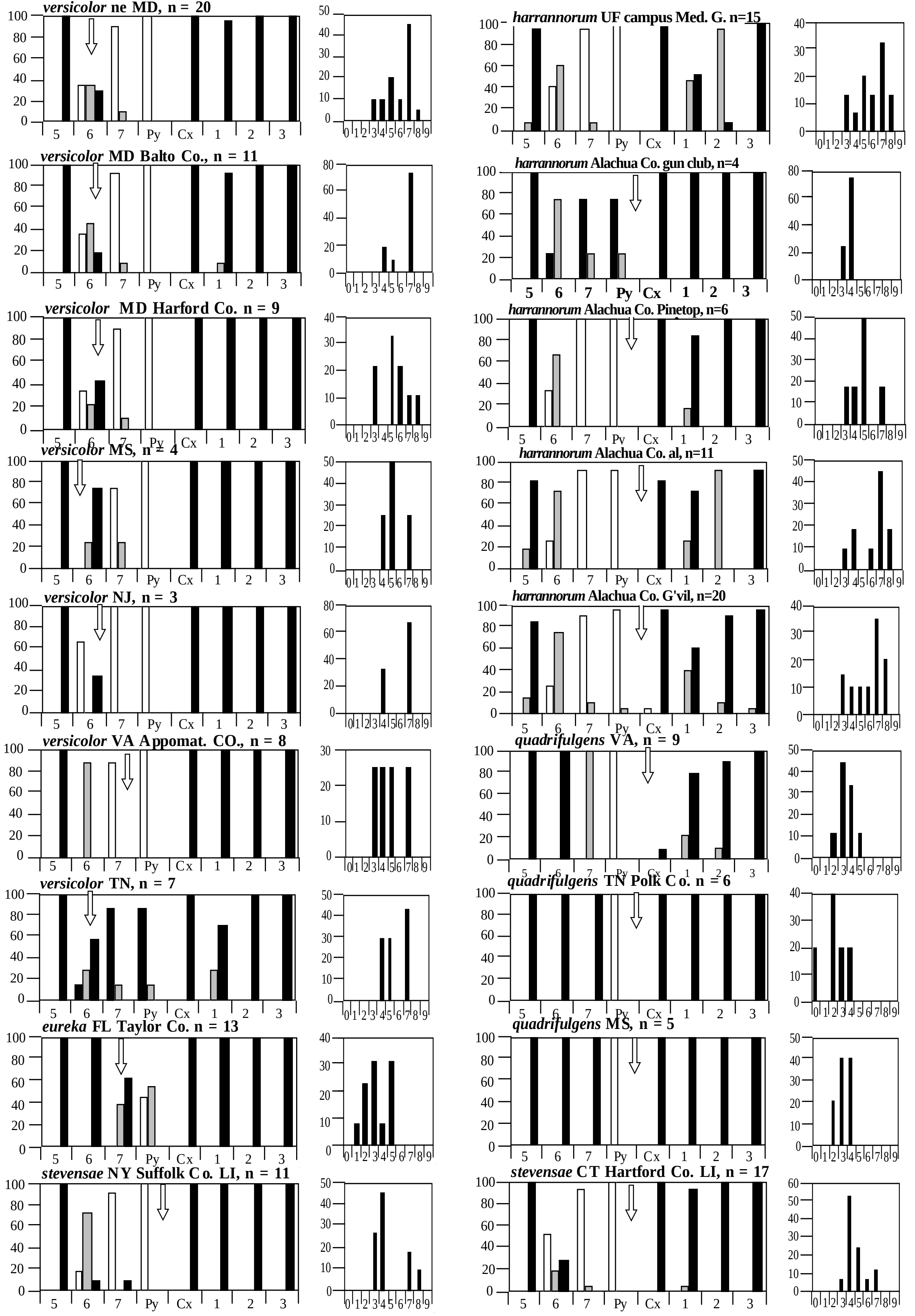


Figure 29. As after-thought, as an attempt to quantify in units/terms of days, the difference in east versus west in phenological development: on average, perhaps, about a week± difference until 21 May, with convergence at 21 June.

VERSI Group


versicolor ne MD, n = 20
versicolor MD Balto Co., n = 11
versicolor MD Harford Co. n = 9
versicolor MS, n = 4
versicolor NJ, n = 3
versicolor VA Appomat. CO., n = 8
versicolor TN, n = 7
eureka FL Taylor Co. n = 13
stevensae NY Suffolk Co. LI, n = 11
harrannorum UF campus Med. G. n=15
harrannorum Alachua Co. gun club, n=4
harrannorum Alachua Co. Pinetop, n=6
harrannorum Alachua Co. al, n=11
harrannorum Alachua Co. G'vil, n=20
quadrifulgens VA, n = 9
quadrifulgens TN Polk Co. n = 6
quadrifulgens MS, n = 5
stevensae CT Hartford Co. LI, n = 17
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Py
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Chapter 75

Pyractomena angustata LeConte 1851

Flash-Back Firefly

> *… By night or day,*
> *The things which I have seen*
> *I now can see no more.*
> Wordsworth

This **glowing** lightningbug is a real and probably slowly disappearing enigma; scientifically it is radically exciting. Here are but two reasons: (**1**) Its “FP” is a glow of indefinite duration, like that found in males of a few *Phausis* **glowworm** fireflies; and (**2**) its glow is **green**, rather than orange-yellow or amber as found in all but one other of the known *Pyractomena.* Geographically it occurs in a wide arc around the apex of the Big Bend and further south in peninsular Florida (**Figs. 1-2**); it was one of three very rare, spatially limited, very early spring fireflies known to occur around the "armpit" of this region, and like *Photuris eureka,* has not been seen for several years. In the Big Bay region *angustata’s* season begins (began) only slightly later than that of *Py. borealis,* in mid to late February (**Figs. 3, 4**). In Florida, *angustata's* habitat is damp grassland, the wet prairies and pond margins included in the Gulf Hammock region (**Figs. 5-6**). In Alabama I found a single male glowing over a hayfield in a river bottom near Coleman Lake State Park (Cleburne Co.), and in Georgia it flew over a roadside marsh near Baggley State Park. *Py. angustata* probably pupates either in low shrubs or low on woody trunks and stems, and as a result local populations may sometimes be eradicated by unnatural late-winter burning in commercial and pastured pinelands. With the arid conditions predicted to develop in Florida in the coming decades this glowing lightningbug must certainly pass into a dark and all but forgotten history.

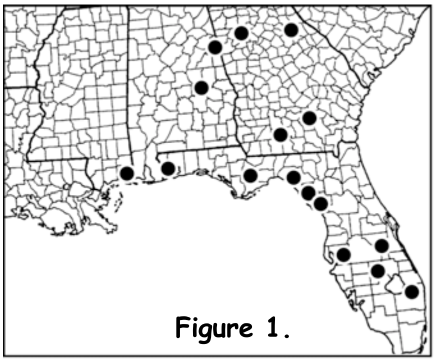


Figure 1.

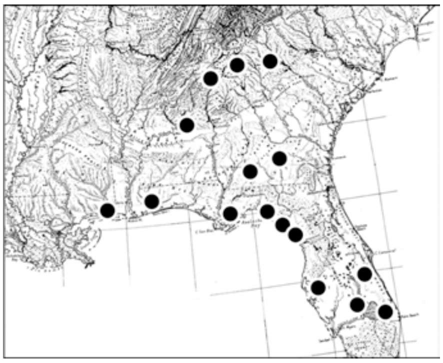


Fig. 2. Physiographic perspective.

Identification is simple, and should not require consultation of Green’s key: a southeastern locality (**Figs. 1, 2**); a very early collection date (Feb.-Mar.; **Figs. 3, 4**); body elongate, 11-14.5 mm in length (ex Green), shiny black elytra, without lateral pronotal vittae (**Fig. 7**). It cannot be confused with any species except possibly *Py. borealis* which is conspicuously broader, more robust, and averages longer (11-19 mm (ex Green). **Figure 7** allows some comparison of the two, though size difference is exaggerated in the Figure. The glow-FP will easily be confused with two known Florida sympatric and synchronic *Photuris* species, which are apparent mimics of *angustata*: *P. walkeri* and *P. eureka*. There are localities in Georgia and Florida where the green (and blue?) glows of males of *Phausis reticulata* (and *luminosa*?) might also be encountered: flying *Phausis* males typically appear as tiny and spark-like, sometimes "wandering" (rather than large and drifting), usually low over forest floors; *Phausis* probably occurs only rarely in *angustata's* range, with adults occurring later in spring. *Phausis* males often cast a defined patch of light on the ground beneath them, probably because they fly lower. Other and seasonally later thus less-likely to be confused glowers are males and females of flashing species whose light-organs "leak" dim continuous light—several *Pyractomena* species, especially *ecostata*.

Glowing behavior, ecology. Male glow-flight activity begins on average at about 1.9 creps, about 45 minutes after sunset, and continues for 2 or more hours. Observations may suggest a seasonal change in starting time of about 15-20 minutes, with late February populations beginning at about 1.7 creps and those in early April averaging 2.1 (**Fig. 8**). This is not presently attributable to temperature or moon-phase, and, if characteristic, may be related to phenological circumstances, that is, population size and number/quality of available females, or possibly a seasonal delay in post-twilight falling temperatures.

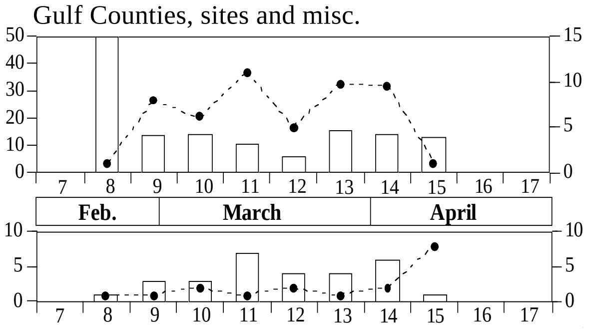


Fig. 3. SESOBS (Sight/Amt/WOY(see adjunct legend).

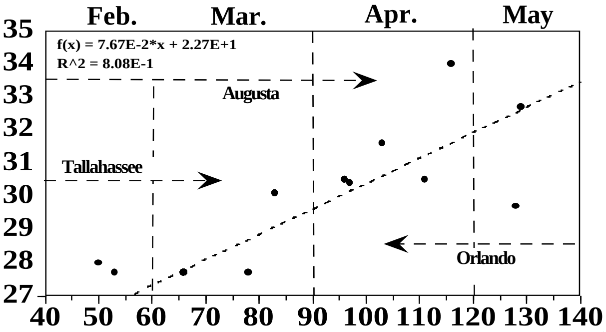
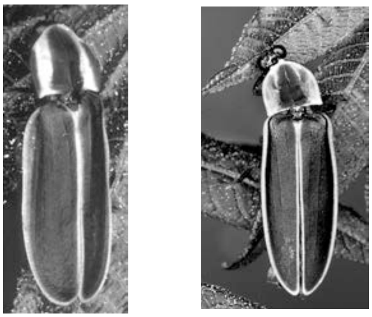


Fig. 4. GESEDIS (AX: Lat/DOY).

Figure 5. Hines FL site—at seasonal flooding.

Figure 6. Roadside berm at Hines FL; males "drift" and meander along the road edge and over the trees.



Py. borealis

Py. angustata

Figure 7. Note absence of lateral PN vittae in angustata.

Mate-seeking glows of males are from a few seconds to a minute or more in duration, depending upon immediate conditions—that is, are to some extent condition-determined. They douse their lights after landing near a glow-responding female or decoy, sometimes when flying across open spaces between the crowns of trees, and after a close-passing insect net. At ground level, they fly "drifting," winding courses a yard or so above vegetation. The glow in **Figure 9** (camera hand-held, open shutter while following) suggests body-twisting, with the lantern alternately and rapidly aimed left and right, or lantern segments not synchronized(?). Male flight speeds were measured (**Fig. 10**; stop-watch/measuring wheel), and showed a slight increase with temperature (1.9'/s@13.3°–3.1'/s@18.3°; n=18, dots are means). The super-fast male in Figure 10 (X) was not included in calculations.

Sometimes males fly around the boughs of trees, which are often tall pines in their habitat, and when only a few are active in an area all may fly there. An uncertain impression is that high flight occurs more often toward the end of the season, but because *angustata's* glow is green, like the glows of *Ph. eureka* males, glowing fireflies must be captured for positive identification—glowing males in treetops sometimes eventually fly lower while continuing to glow, and they can be reached with a (tropical) net and identified. Glowing high-flying *eureka* will often switch to their more pulsing, short glow FP as they approach the crown of a tree.

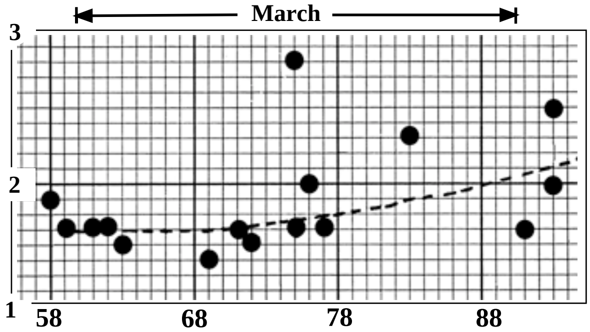


Figure 8. Evening activity start (AX: creps/DOY).

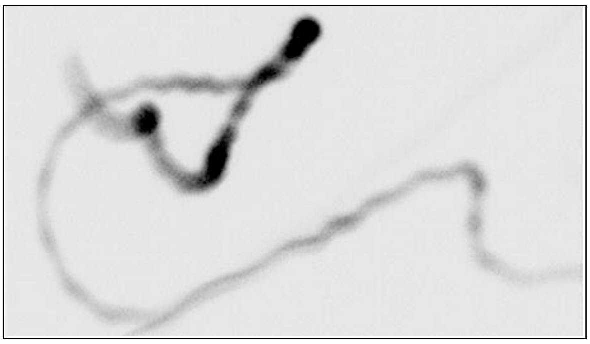


Figure 9. Flying glow on film, hand-held (color to B&W, inverted).

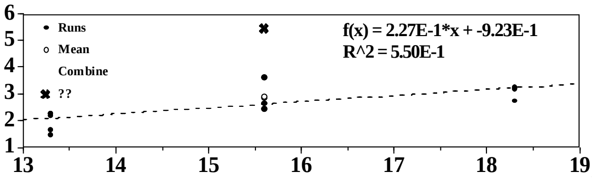


Figure 10. Flight speed (AX: ft per sec/temp).

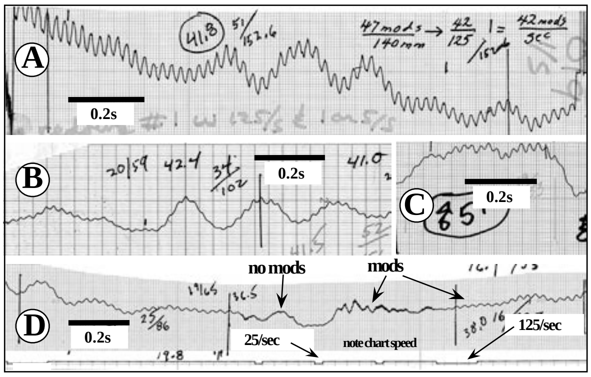


Figure 11. 35-45 Hz; PM-recorded shuttered modulations of glows (AX: rel. int./time).

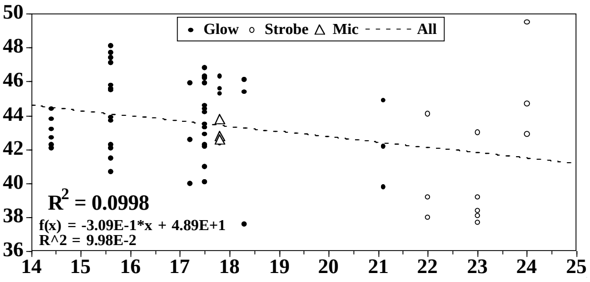


Figure 12. Wingbeats (AX: Hz/temp; linear regress.).

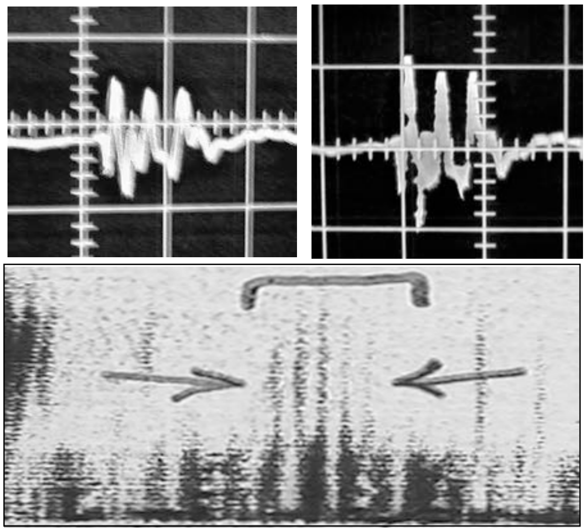


Figure 13. Wingbeat microphone bumps, see text and augmented legend. Oscilloscope display (20mS/small Div); audiospectrograph chart (AX: sond freq./time/, with intensity via darkness of image).

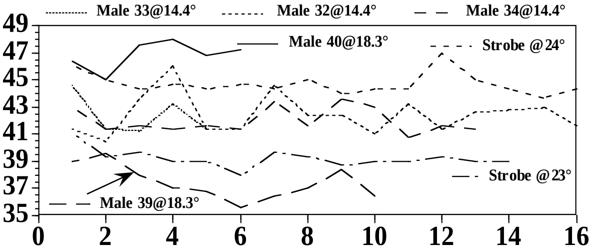


Figure 14. Hertz tracks (AX: Hz/position in sequence).

Sexual interaction, decoys. A female on a palmetto frond about three' above the ground glowed brightly for about 2 seconds at/after the glow of a flying, passing male about six' from her. After she doused her light there were no more glows for about 10 minutes. Then, a male emitted a 2-sec glow from a perch about a foot above her, and she then again glowed for about 2 sec. At this point both were captured—to determine species and sex.

Decoys placed on the ground beneath flying males were attractive (<12 feet, n=19). All but two approached and landed near the light (x=6.4 inches, s=3.4, r=2-14, n=17). All doused their light within a few seconds of landing, and one immediately before landing. After landing and dousing, males remained dark for several minutes, a pattern observed in other but not all *Pyractomena*.

Notes on *angustata's* glow modulations. These notes are presented as invitational and suggestive, and not necessarily critically evidentiary, though care was used in their pursuit. To the human eye *angustata's* glow usually appears to be a steady green light, although, as McDermott noted in the long flash (crescendo) of *Photuris lucicrescens*, *angustata's* glow sometimes appears to have an "electric vibrancy." This appearance is certainly due to wing shuttering, as beating wings rapidly pass between the observer and the lantern. PM-recordings of *angustata's* glow frequently show a high-frequency modulation of 35-50 Hz that also gives the appearance—suggesting cautiously—of having some independence from ambient temperature (**Figs. 11-12**). This flicker varies in amplitude, sometimes fades in and out, seems to be more often recorded from the side of the insect than from below, and is roughly sinusoidal (**Fig. 11, cf. A-D**). It was noted only in flying males, and not in glowing captives in spiderwebs or the killing bottle. Note: (**1**) the frequency is within the wingbeat range observed for other fireflies; (**2**) it is matched by samples made of *angustata's* wingbeat frequency by two other techniques (**Figs. 13, 16**); (**3**) it "seems somewhat" independent of ambient-temperature, as apparently the case in some insect wingbeat frequencies—whereas the rates of light-emission phenomena are strongly temperature dependent.

Figure 14 shows considerable second-by-second modulation variation at temperature (among momentary means of several males (with varying n's). The modulation-rate spread of male #32 was 40.8–47.2 Hz at 14.4°, and nearly that of male means observed in **Figure 12** at 15.5° and 17.5°. This comparison is of samples at different temperatures, and the cold temperature for male 32 may have been a contributing factor in thoracic (wing muscle) thermoregulation(?)—should it exist. Such variation might be expected for a number of reasons to occur in wingbeat frequency, though perhaps not if modulation rate were an important element for sexual recognition/evaluation. **Figure 13** shows oscilloscope traces and an audiospectro-graphic record of microphone bumps of beating wings (see Augmented Figure Legends below).

Wingbeat frequency of tethered fireflies was measured with a strobe-light by Alan Gale, an undergrad, out of interest not course-connected. His base results are shown as circles in

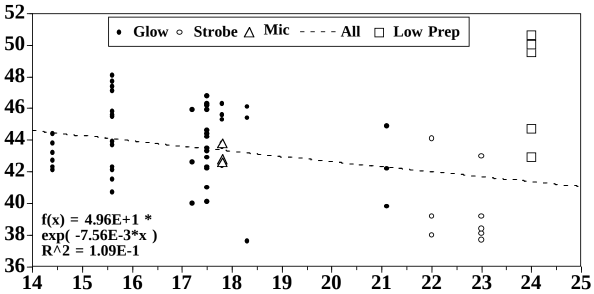


Figure 15. Same as Fig. 13 but with "cold prep." data shown (squares); same regression data but line here exponential.

Figures 12 and 15, and fall with measurements made by other methods. In addition, Gale also conducted temperature experiments which exposed subjects to various temperatures before measurement at room temperature. Nothing of significance was indicated after brief, minutes-long exposure, however, when he maintained subjects for an unspecified (hours-long) period at 15C°, and then measured wingbeat at 24C° their rates were all faster than previously observed (**Fig. 15**, squares; n=3 males, 47 samples (see also page 203 for wingbeats).

Systematic notes. Two compound evolutionary questions "come to mind." The first (**A**) concerns *angustata's* glow "FP", a "primitive" signal type requiring relatively simple light-organ structure and found in glowworm fireflies; the second, (**B**) speculates on *angustata's* green (versus yellow/orange) bioluminescence, which is unusual in the genus *Pyractomena.* Considering **A** first: (**A1**) Is the primitive-appearing glow ("FP") the ancestral (plesiomorphic, "primitive") condition, and relatively *unchanged* from a hypothetical glowing ancestor of its genus, indicating that a flashing light-organ evolved independently in this genus?; or (**A2**), alternatively, is its glow derivative (apomorphic), a secondary development derived anew from a short flash or flicker FP of a flash-capable ancestor; and might it (**A3**) be an amplification of the "leaking" of light that is so commonly seen among its congeners?; or might (**A4**) the glow be a "throw-back," ("flash-back"), an atavism, from a previously adaptive genetic program that was subsequently turned OFF by an over-riding "control gene," but then, "as chance would have it," when it was switched ON, it was fortuitously adaptive in new ecological/sociobiological circumstances, and favored/re-established in a population?

There prresently are a few clues to advise/consider in the selection of favorite working notions from among these, for the origin of *angustata's* glowing: We know that *angustata's* light-organ has certain fine-structure features that are found in a flashing organ, as presently understood (H. Ghiradella, pers. com.). If *angustata* came from a flashing ancestor (**A2**) we might imagine that its light-organ has retained features of a flashing-typical construction as found in ancestors because, say, emissions with rapid time-intensity control, are still important in a context that is unknown at present; or the flashing-type organ is also a better glowing organ, say, for energetic efficiency; or a lantern flicker that will augment the wing-beat at certain times—say, as a hawking deterrent; or for some other proximate or "genetic inertial" reason; or, unsatisfyingly, they are merely remnants, as suggested for certain (misunderstood?) features of other organisms (male nipples in certain mammals?).

Is it possible that *angustata's* glow might actually be primitive (plesiomorphic in its genus/clade), as in **A1**?, with the evolution of the "flashing-type" organ in the *Pyractomena* lineage brought about by selection in the context of modulating the light, say, to make it more visible? As unlikely as it may seem, that *angustata's* signal could be primitive, it is difficult to simply set aside the fact *angustata's* <u>green glowing</u> signal comprises <u>two</u> unique primitive features! Probabilities? I await the DNA report.

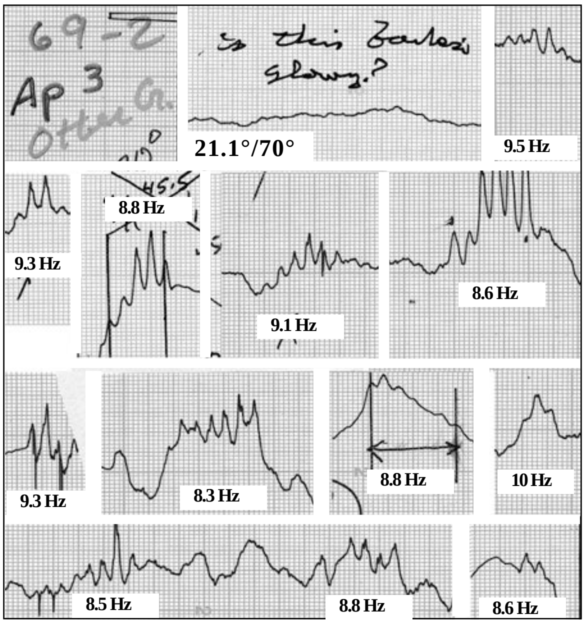
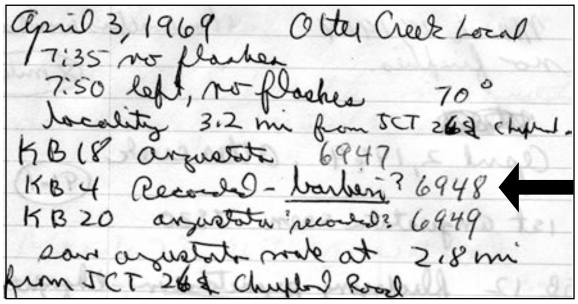


Figure 16. Incoherant ($x=\bar{8}.97$ Hz) flickers found (embedded) in a long bright glow; a *barberi*!

Providing a suspicious glimmer toward the real explanation, is the peculiar PM-recording of a *Py. barberi*: at the moment of interest the presumed target was the flying bright glow of an "*angustata*," though the 35-50 Hertz side-tone (ear-phone) buzz that often accompanies an *angustata* glow was not heard. When this lengthy 56–sec recording was charted there appeared irregularly spaced, totally unsuspected, and poorly constructed ("twitchy") short flickers (**Fig. 16**). This male's glow was bright enough to have been confused with that of co-active *angustata*—and upon revisiting the recording tape no voice note of uncertainty followed this specimens glow-recording, which was made when *angustata* males were also being recorded. Upon curating it was obvious that the specimen was *barberi*—note fieldbook entry (**Figs. 17**). This might support a flashing-to-glowing evolutionary direction—analogously reasonable, showing such transitional intermediates (**A3**) are possible and occur in nature, but **not** suggesting



April 3, 1969 Otter Creek Local
7:35 no flashes
7:50 left, no flashes 70°
locality 3.2 mi from JCT 24 & Chfld.
KB18 angustata 6947
KB 4 Recorded - <u>barberi</u>? 6948
KB 20 angustata ?recorded? 6949
saw angustata male at 2.8 mi
from JCT 24 & Chiefland Road

Figure 17. FB entry: 1969, page 12. Note arrow; written at curating, morning of 4 April 1969).

barberi as a taxonomic candidate! Male KB-4 (6948) raggedy-flickers' have a mean modulation rate of 9.0 Hz, which is normal for *barberi*; his flicker stats were: std. dev. 0.49; std. err. 0.14; min. 8.3; max. 10.0; co. var. 0.05, n=12. That a note was **not** made that his luminescence color was amber not green is somewhat puzzling—but then, maybe it wasn't amber!

As to (**B**), considerations and speculations about green versus yellow/orange bioluminescence: Is its green luminescence: (**B**1) primitive (plesiomorphic), and unchanged from the ancestral green color of fireflies as seen in several other lampyrid genera—and once, and originally, tuned to the spectral sensitivity of the typical, daytime, insectan, superposition eye (Seliger, et al, 1982ab)?; or (**B**2) is it a secondary redevelopment (apomorphism) having orange-yellow-lit ancestors in its direct lineage? A model can be imagined for each of these histories—which might encourage search and recognition of evidence, pro and con. The selection **B**2 is favored here:

Figure 18. Striped *Py. ecostata*.

First, the green of *angustata's* "FP" does not merely appear to the eye to be green and indistinguishable from the glows of its two *Photuris* mimics (*Photuris eureka* and *barberi*)—human eye/brain judgments notoriously misinform. Laboratory spectro-photometric measurement of *angustata's* glows are virtually identical to those of the two glow-mimicking *Photuris*: 4 *angustata* males, a total of 10 scans in two shipments revealed an average peak and high and low half-maximum values in millimicrons: 552.0, 526.0 and 594.0; 555.0, 529.0 and 601.0. And for the *Photuris*, n=6 each: *eureka*-555.0, 529.0, 598.0; *walkeri*-554.0, 528.0, 598.0. Because all but one other *Pyractomena* species have yellow or amber luminescence, the question arises whether *angustata's* color has converged upon the color of the luminescence of *Photuris* species, say, those that mimic its glow. *Photuris* are not distasteful (to known predators) unless they have eaten members of a distasteful species (Eisner et al., 1997). More than this, if *angustata* has converged on *Photuris* green, what/who is the targeted (targeting) viewer—a hawking *Photuris*? Further, the colors are so similar, could an attacker be expected to be **that** finely discriminating—but perhaps there are only certain and very similar emitter molecules and emission systems available in lampyrid genomic repertoires?

The other *Pyractomena* species that has green luminescence, *ecostata*, is a huge firefly that also occurs in coastal Florida. *Py. ecostata's* glow is less green than that of *angustata*: $\bar{x}$ peak 558mm versus 553.5. Though *ecostata's* season partly overlaps that of *angustata*, it begins later in the spring, and is seen late into summer. "Suspiciously," *ecostata's* FPs, bright, <1+ sec long, "crude" ("transient-lacking") flares, which are emitted at unusually long intervals (<15 sec), are separated by glows that are sometimes strong enough to be seen at considerable distance. (Surely of no significance (?) in the present context is the occurrence of *Photuris*-like lateral, elytral vittae, such that archived *ecostata* specimens are occasionally misidentified and in archived collections are sometimes labeled *Photuris* [**Fig. 18**].)

Here is perhaps a clue toward a color-convergence explanation?: On several occasions an unidentified green glower was flew within inches of and closely followed behind another green glower (*angustata* site), then swerveed away, as one might closely examine a tail-light's color? Abner Lall, who probes firefly vision with incredibly tiny electrodes, suggested at the time that fireflies are "color blind," however, at very close range, hence viewing more intense light, perhaps it is possible that green would be distinguished from orange-yellow? But why would a male glower inspect another such glower, and what would be the potential disadvantage of the "inspectee"?—though *eureka* females were never collected flying and glowing, a sample was never made. That these briefly-chasing followers were *eureka* females inspecting potential prey for hawking one explanation, or that *eureka* males were seeking their own females? This could also explain the one other *Pyractomena* with a color shift to green, the sympatric, slow-flying, flaring and glowing *ecostata* mentioned above. However, rising salt water and lowered water tables and their consequences will eventually put this puzzle beyond the reach of exploration, if not already.

Historical notes of glowing *Pyractomena*. Several species of *Pyractomena* fireflies glow dimly from their lanterns between FPs and some males can easily be followed from a distance. When Willis Blatchley noted such a glow and identified the firefly as *borealis* perhaps what he actually observed was an *angustata*, *Pyractomena* taxonomy and keys

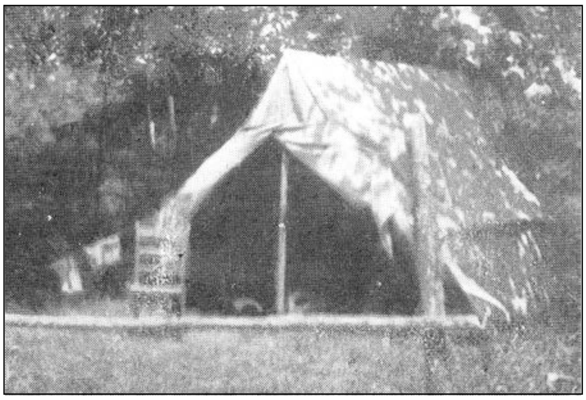


Figure 19. A Blatchley "June-Time Home" (1912).

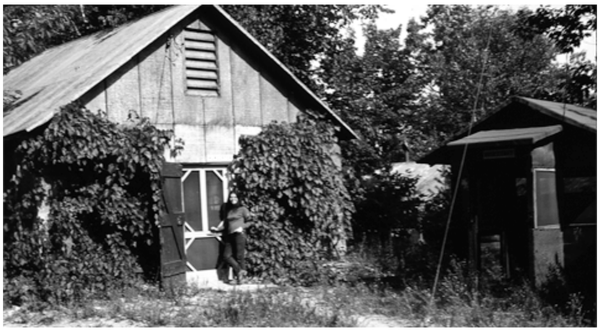


Figure 20. Dr. Ann Pace at a UMBS classroom (1971).

being woefully inadequate in his time, that is, before J. W. Green (1957). The following is Blatchley's note:

> *On the evening of Feb 19* [1913], *while at our second camp, which was on an island in Kissimmee Lake* [Osceola Co. FL], *I noted a firefly or two over a damp meadow near the tent* [e.g., **Fig. 19**]. *Getting my net, I sallied forth, eager for prey. The only specimen which I was able to capture was one which, instead of flashing its light intermittently, turned it on apparently to stay and flew in a wide half circle out over the lake and back within twenty feet of where I stood. I traced its entire flight by the steady constant light.*

Fifty-four years later, while studying leopard frogs (Rana pipiens s. l.) near Otter Creek (Levy Co. FL, March 1967), Univ. Mich. graduate student Ann Pace saw *angustata's* bright glow high in pines and soon thereafter brought it to my attention. I, like Blatchley presumed it to have been a *borealis* with a brightly-leaking lantern—who would have guessed, or at the time could have presumed what the fine-structure of the lantern might reveal, or what stories it might have to tell, or what interest it could create?

Augmented Figure Legends: 5. Seasonal flooding in Mallory Swamp sometimes, more so in the past, filled up low areas. It was in such areas that *angustata* seemed to be more common. **6.** Causeways built through the Swamp to gain access to woodland probably provided additional pond-margin and shrubby areas for firefly life, and along these roadways in the 1960s-80s three uncommon to rare species could be found. This site is a few mile north of Hines, a once-active (1900) railroad access point for the timber industry—now the railroad tracks and even a building once used by a poacher acquaintance are gone. This firefly road was interesting, and served not only loggers and poachers, but rustlers, drug traffickers and other mysterious traffic, that, as I did, drove it with their lights out. **8.** Post-twilight starting time in creps by date (DOY). At this date and place a crep was/is about 24 minutes in duration. Late-season activity appears to begin about 0.4 creps later than early-season activity. **9.** Glow of a flying *angustata* male recorded on color film (ASA 400) with a hand-held camera positioned beneath him, shutter open. The green image was converted to white on black and this "inverted," in the term of *Photoshop*®, to black on white. Note the rhythmic weaving(?), and that a 44 Hz. flicker is not apparent. **10.** Flight-speed data from measuring-wheel. Speed seems to increase slightly with temperature: from 1.9'/sec at 13.3°C to 3.1'/sec at 18.3°C; n=18 males. The super-fast male (X at 15.6°C) was not included in calculations; it might have been *Ph. eureka,* though protocol should have excluded this possibility. **12.** Mean modulation rates of several PM-recorded males and strobe-measured and microscope bumped wing-beat measurements. Note the apparent or virtual temperature independence (but see filler page on wingbeats, p. 203). The strobe analysis was done by an undergraduate Alan Gale, many years ago (1970-80s), as a project of interest rather than an assignment. Note the near-negligible correlation coefficient. **15.** "Hertz tracks," sequences of modulation-rate samples of the PM-recorded glows of individual males; each sample was one-half second long, and samples were taken at approximately one-second intervals. **16.** The same data as Figure 12 except: (1) the regression line (and equation) generated by the charting program is exponential; (2) additional data are shown but not used in the regression; these data are for specimens that were maintained at a cold temperature (15°C) and measured at a higher temperature 24°C. These results suggest that perhaps there had occurred some physiological change (physiological adaptation) that had taken place. Note the near-negligible correlation coefficient. **17.** Some clippings from the 56-sec-long, bright, *angustata*-like glow of a *Py. barberi* male, showing various poorly-formed flickers, and also the reference on the chart-record (scrapbook) that provided access to the specimen in the cabinet to triple-check the remarkable ID, to assuage the forever-arising doubts of a field researcher. **18**. Fieldbook entry written the morning after, showing killing bottle number (KB 4) and the then-assigned cabinet-accession number (6948) that was placed on the specimen for future associations—as in this case, to confirm, once again, identification and data association.

Chapter 76

Pyractomena barberi Green 1957

Florida-Candle Firefly

By the gray woods,—by the swamp
Where the toad and newt encamp ...
Poe

In the northern section of its apparent range (**Figs. 1, 2**), *Py. barberi* occurs in wet prairies and pine flatwoods of the Gulf Hammock region, and is most easily found along grassy roadsides in Dixie, Lafayette, and Levy Counties (**Fig. 3**). With its congeners *Py. borealis* and *Py. angustata*, *barberi* introduces firefly spring, late in February or early March (**Fig. 4**). Though sometimes locally abundant, the Florida Candle is not likely to be seen unless it is specifically sought, and was a will-o-the-wisp for several seasons, existing only as fleeting, uncertain sightings of a low, jagged, orange flicker, hopeful expectation and a rare capture. Many nightly quests to its range, 50 miles west of Gainesville, ended with the unusually rapid onset of sub-firefly temperatures (<9°C/≈52°F) common to its season of adult activity.

Preserved specimens of this rare firefly can be identified with certainty by Green's Key (**pages 369-370**). In the field, the jerky amber flicker, typically emitted within a yard or so of the ground, very early spring (late winter) activity, and the geographic occurrence of this species suffice for diagnostic certainty. The single source of error is that occasionally a late season will cause overlap with *Py. angulata*. The hiatus indicated on the map between coastal Levy and Dade Counties, Florida, may be real—such a break in distribution along that strip of Gulf coast is also known also for tiger beetles, and perhaps is associated with a break in required habitat type (P. Choate pers. comm.).

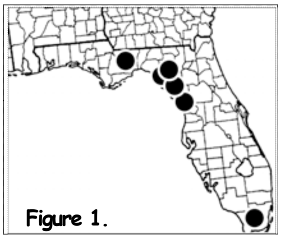


Figure 1.


Figure 2.

Flashing behavior. Male flight begins after full darkness at 1.5-1.8 creps (n=7; roughly ss+42 min) though sometimes it appears to be delayed 4 creps or more; a few intermediate values were noted (2.1-2.5 crep, n=5).

The FP is an orange-yellow flicker; the spectra of two samples were: 1978: 576, 549.0-616.0, n=2; 576, 548.0- 614.0, n=4, in millimicrons. The flicker is composed of 5-9 not-bright modulations of about 9.3 Hz at 18.5°/65° (**Figs. 5-6**). This signal is emitted each 2 seconds at this temperature (**Figs. 5A, 6**; FP rate, **Fig. 7**). Flickers sometimes appear erratic or dis-connected because males waggle their abdomens when flashing (**Fig. 5A, C, D**). Recordings of *barberi* flickers typically show sinusoidal modulations, thus the light is not or only barely turned OFF between pulses (**Fig. 5B-D**).


Figure 3. Hines, Dixie County, FL roadside.

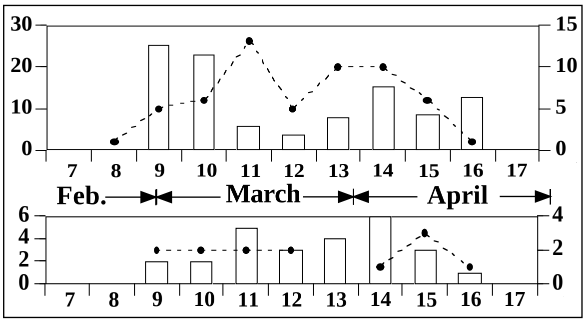


Figure 4. SESOBS. Gulf Region (AX: Amt-Cnt/WQY).

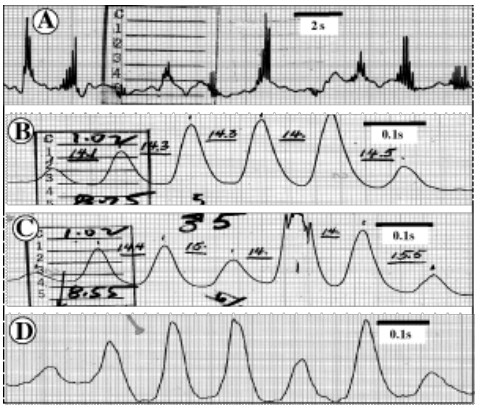


Figure 5. PM-scans: A@16.1°, B-D@18.3° (AX: rel int/time).

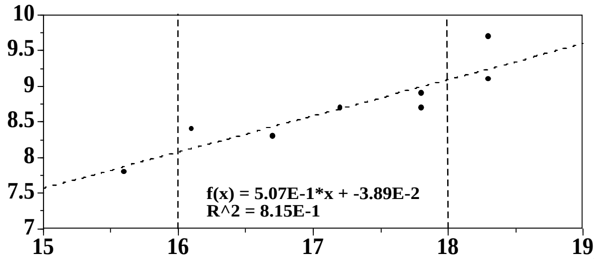


Figure 6. Flicker modulation rate (AX: Hz/temp).

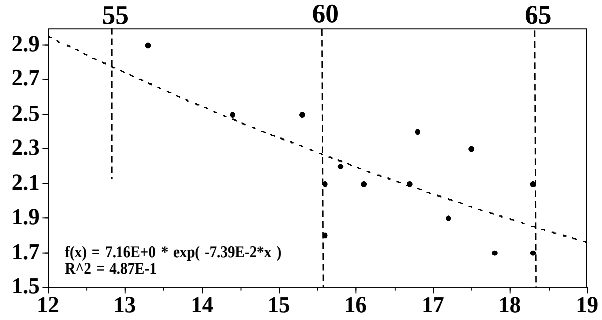


Figure 7. FP period, exp. (AX: sec/temp).

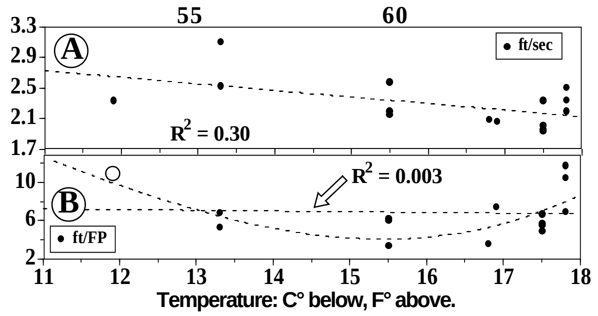


Figure 8. (A) Flight speed (AX: ft/sec/temp); (B) linear coverage (AX: ft/FPper) across a range of temperatures. Each dot is a male mean.

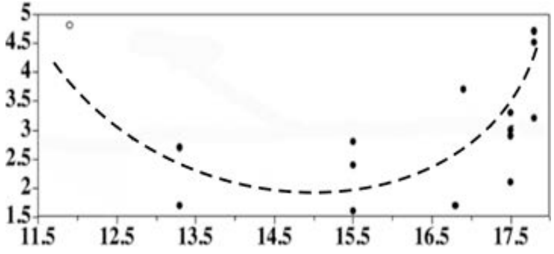


Figure 9. (AX: ft/sec)/(ft/FPper) // regressed on temperature.

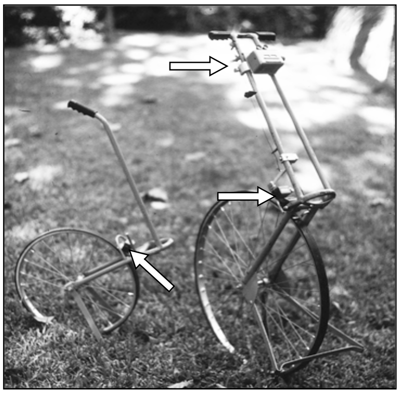


Figure 10. Measuring wheels; the bigger the better. Arrows at counters: mileage and event.

Males rarely fly more than 6-8 feet in altitude over their grassland or sward ($\bar{x}$=4.3 ft, s=1.60, r=1-14, n=306. When over taller vegetation such as shrubs, where they could be viewed from beneath, their flickers were impossible to distinguish from those of *Py. angulata*; the restricted geographic and seasonal overlap of these two species will make this a rare confusion.

Decoy attraction. Males were attracted to an LED decoy that was flashed immediately after their flicker. Unmodulated 1-sec flashes were less attractive than pulsed ones (thumbing of penlight switch; 1/6 vs 5/6). Males either dropped immediately to the ground or vegetation within a yard of the decoy, or paused, flickered again and then dropped. After dropping, males waited up to 4 minutes before signaling again, and then emitted bouts of up to 4 closely-spaced flickers. They continued to approach decoys that answered at least one flicker in each bout.

Flight of searching males. Several males were followed with the measuring wheel (**Figs. 8, 10**); possibly this simple behavior is more complex than might be assumed, but data are few—each dot (in **8**) is the mean of a male followed/measured, with each sample having 30 FPs as minimum. At temperatures near 18°/64° males travelled about 2.2 feet per second and 8' per FP period (**Fig. 8, A and B respectively**): with increasing temperature, distance traveled per second may decrease slightly (**8A**); in contrast, distance flown per FP may decrease and then rise (**8B**). The dipping line was fitted by eye, suggesting a decrease and then an upturn with further increase in temperature. **Figure 9** regresses the ratio of the two quotients in Figure 8 (that is, FP distance flown per second [speed] divided by feet flown per FP [unit coverage]), regressed on ambient temperature. The line was fitted "by eye." Perhaps this suggests that at mid-temperatures search is more "deliberate," but interpretation is difficult (mind bending). It may help to consider flight speed (**8A**) unchanged across temperature, and then consider the slope.

Notes. The practice of burning grass and scrubby understory in plantation flatwoods of the Gulf and Mallory Swamp region during late winter may destroy many local populations of this rare species from time to time, along with those of *Py. angustata*, because, presumably, they pupate in low vegetation or low on woody trunks—however, they were not found there in several hours of searching a fortnight before the adult season began. The water table in the area has dropped over the past several years and may also be responsible for the observed reduction in population size.

Py. barberi was originally described from four specimens collected in what is now the Everglades National Park, by H.S. Barber and E.A. Schwarz in 1919 (20 Feb-9 Mar.), while on one of their several expeditions. The actual collecting site may have more recently been known as Royal Palm Hammock, a hundred yards or so from what was Anhinga Trail in the 1960s.

Chapter 77

Pyractomena borealis (Randall) 1828

The natural history of this firefly has been studied more than that of any other in Florida, partly because it is the first to appear each year, and even on cool late January evenings it flies alone among the leafless branches of swamp forests. More than this, it attracts attention because of its peculiar pupation behavior, behavior that makes its late-winter, adult season possible. Nominal *borealis* occurs broadly across eastern North America (**Fig. 1**) but whether this behavior occurs in populations further north, or is limited to its sympatry with *Py. limbicollis,* is unknown. This behavior is sum-marized below, and has been published in some detail (Lloyd, 1997 ; Gentry, 2003; see Letters, Firefly Life, on line).

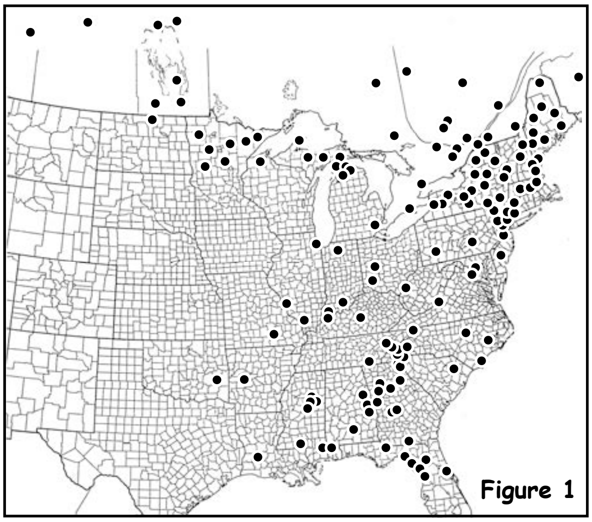


Figure 1

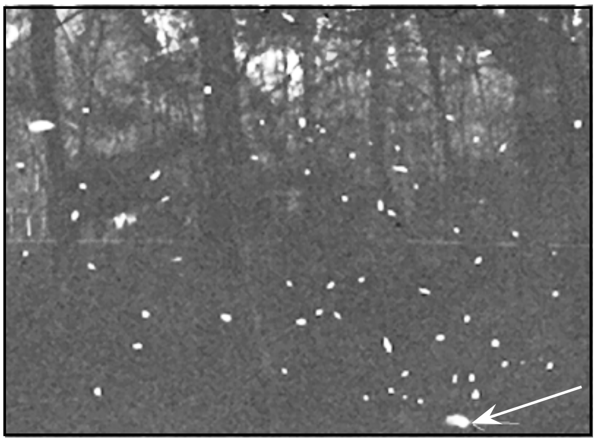


Figure 2. Males approaching a decoy (arrow).

The FP is most commonly a single, moderately short flash, but for unknown reasons, a 2-flash FP is sometimes seen, the second pulse being variably less bright than the first. Female flash response is similar to that of male flashes, emitted at a moderately short delay. Perhaps the second flash of the male is a remnant from an ancestral FP and disappearing, or a deception to mislead nearby rivals. This second explanation would seem a possibility in view of male interloping behavior shown in **Figure 2:** a decoy response flasher that repeatedly answered only the flashes of the same individual male, was approached by several others, seen funneling toward the decoy. In treeless late-winter forests such interactions can be seen for some distance; note that no 2-flash FPs are apparent. This photo was taken in Dr. Skip Choate's back yard, which borders on a low forest. (The horizontal line is the top rail of a low border fence.)

Flash-pattern period regression on temperature is shown in **Figure 3** and rate, in **Figure 4**. No measurements were made of pulse period in 2-flash FPs but it appeared to be somewhat variable.

Adult season may begin as early as late January in north-central Florida, and in some years adults may be seen in April: **Figure 4** shows these data points; **Figure 7** shows combined data for Alachua and adjacent Gulf counties. **Figure 5** shows the GESEDIS record summary. Note that acceleration, an inflection "point," occurs near 36° north latitude. Other examples of this are noted and discussed on page 174.

Figure 6. Male on a darkly-colored, spring hickory leaf.

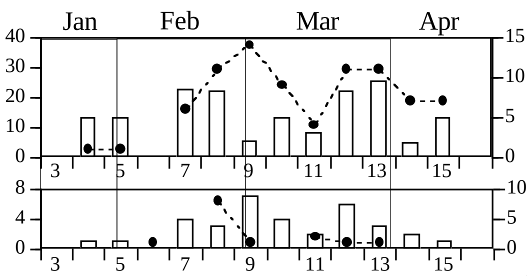


Figure 4. SESOBS record for Alachua County.

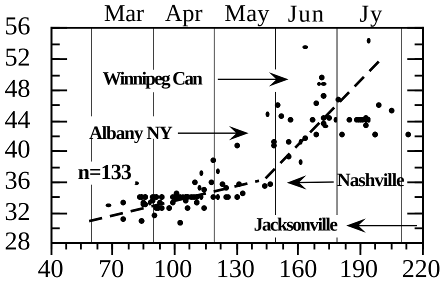


Figure 5. GESEDIS: note the apparent upturn near the Nashville latutude (see page 168; AX: Lat/DOY).

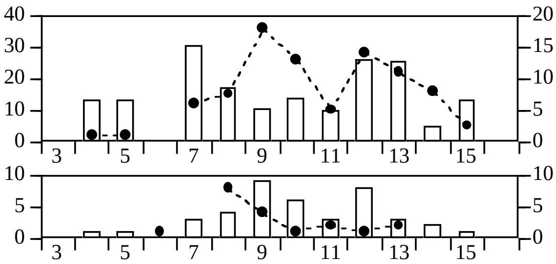


Figure 7. SESOBS: combined data for Alachua and near-Gulf counties.

Thermal ecology in *Py. borealis*! As seen in other members of the Subfamily Cratomorphinae, *borealis* does not pupate underground but on vegetation, swamp-forest tree trunks in this case. Larvae may be seen glowing on trees on rainy nights, apparently throughout the year, hunting snails (**Fig. 8**). For pupation, larvae often select a semi-sheltered site—next to another, an enation, or a vine (**Fig. 9**)—and glue their tails to the bark. They shed their larval skin and about two weeks later adults emerge. Males tend to emerge before females (protandry) and are occasionally found clinging to pupae (**Fig. 10**); this earlier emergence is enhanced by a difference in the pupation orientation of males and females (Gentry, 2003, see also 2001 for other interesting research ideas).

Figure 8. A lab larva attacking, "kissing" a snail—injecting anesthesia to immobilize them to eat.

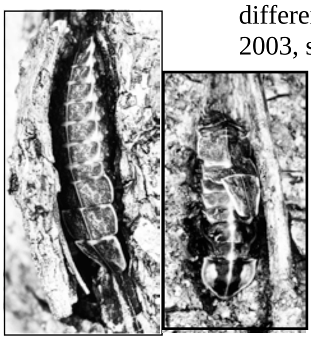


Figure 9. Larva under a sheltering "flap" on bark, and a pupa by a vine.

When wandering through the Possum Creek wetland forest in Gainesville to photograph *borealis* juveniles (**Fig. 17**), it was noticed that pupae were generally on the southern face of larger trees and 1-2 yards above ground. Various data were taken; mentioned here are those that concern thermoregulation, and accelerating metabolism and emergence as adults. Later, larvae of *Py. limbicollis* were found on the north side of smaller trees (**Fig. 11**), near the ground; they appeared as adults a few weeks after *borealis* adults.

Figure 10.

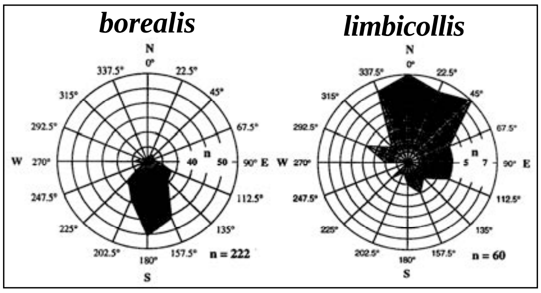


Figure 11. Azimuths of pupae on trees.

Sand-filled jugs, wet and dry, large and small, with clay balls with inserted thermocouples as fireflies, were used to measure heat gain on a south versus north exposure (**Figs. 12-16**). After sunset, warmed tree-water would further contribute to thermal economics.

Why hurry their adult season? To beat *Photuris* predators? Or so their 1st instar larvae don't compete with those of *limbicollis* . . . and north of *limbicollis* . . . ?

Figure 12-15. Jugs, clay balls with thermocouples in sunshine.

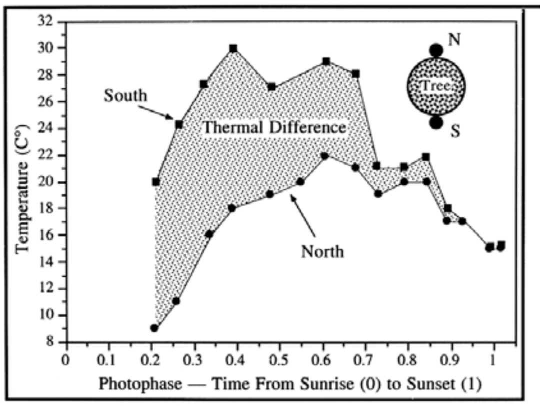


Figure 16. Thermal difference in azimuth.

Figure 17. Views of Possum Creek and its woods.

Portrait of a Possum.
(an Opossum)

Algonquain, *op* (white) + *assom* (dog)

Chapter 78

Pyractomena dispersa Green 1957

Dispersa

I never met a firefly I didn't like; and this one introduced me to them all (jel,).

This one of the most widely-occurring lightningbugs in North America (**Fig. 1**), but though it has been found from near the Florida border northwest to Idaho and further north into Canada, thus spanning a broad physiographic domain (**Fig. 2**), the paucity of archived records would suggest that it is not common. **Figure 3** shows its seasonal/latitudinal occurrence based on archived specimens, and **Figure 4**, on quantified field sightings. (One can almost see an inflection in the seasonal trajectory near 36° N latitude.) Like a few other *Pyractomena*, such as *palustris* and *angulata*, it is found in a variety of damp-grass and wetlands: **Figure 5** shows the marshy gravel pit where years earlier developers had dug out a glacial moraine for road fill, and where the first firefly observations of this writer were made (1962). In the northeast, *dispersa* sites are often low wet pastures where the water table has prevented other agriculture (**Figs. 6, 19-20**). It was also found in poorly-drained areas by impoundments at beaver dams and causeway constructions (**Fig. 7**). **Figure 17** shows the sweeping meadowland of a small farm in Halifax County, northern Virginia, that harbors many firefly species—at the creek bottom is a small stream, Little Difficult Run, that feeds into Difficult Run, and eventually into the Potomac River; at the far left is where one should seek *dispersa*. This beautiful old family farm and firefly paradise at this writing is destined become another housing development. The site in **Figure 18** is somewhat upland, though damp, perhaps above a perched water table, but below it in the background it is very low and soggy, and has one of the few known populations of the rare *Py. palustris*.

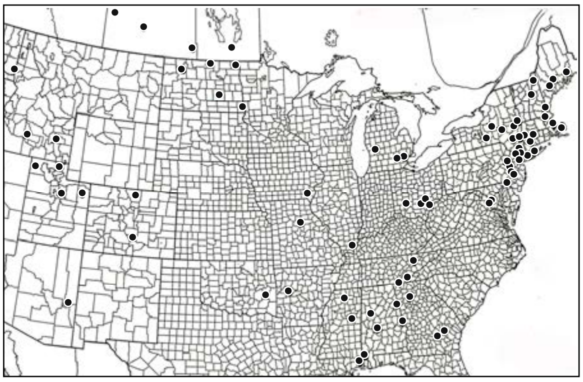


Figure 1. Archival and field-observed records.

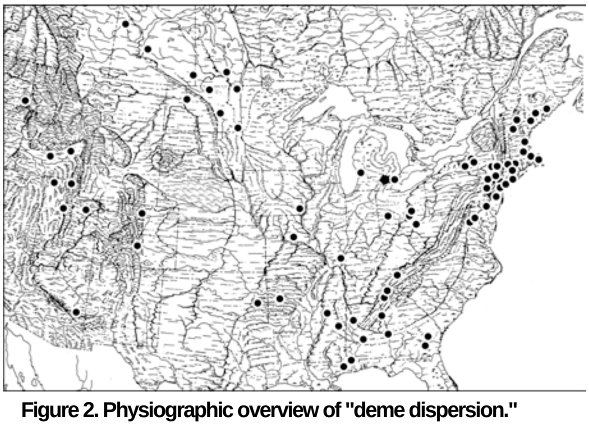


Figure 2. Physiographic overview of "deme dispersion."

Py. dispersa's FP is an yellow-orange 5-8-pulsed phrase that is usually emitted low over the grass and herb tops as the male jerks along, casting his light to the right and left (**Fig. 8**). This usually makes the actual signal difficult to fully appreciate and PM-records subject to interpretation; perhaps pulses gradually increase and then decrease in intensity through each short phrase. At warm temperatures the FP appears as a flicker rather than a pulsing FP; recordings do suggest that at lower temperatures intensity drops to near zero between pulses. FP period is about 3 seconds at 21°/70° (**Figs. 8A-C, 9**; FP rate in **Fig. 10**). Modulation rate of flicker pulses varies from 2 Hz at 10.5°/56° to about 7 Hz at 20°/68° (**Figs. 8E, F, 11**); **Figure 11** compares the temperature regressions of the means of the flickers of individual males with the collective means of all males recorded at the same time and temperature (Grand means), and includes data from the 1964 study. In the field from FP alone it will often be difficult to distinguish *dispersa* from *Py. angulata* though their pulse rates are quite different; their FP periods/rates are probably identical (**Fig. 12)**—*dispersa* was never seen flying up around the boughs of shrubs and trees. This confusion is more likely to occur at warm temperatures, when the then-rapid pulsing of *dispersa* especially has the appearance of *Py. angulata's* flicker. In the hand the two are unmistakable. Although the *dispersa-linearis* complex and *dispersa* wide-ranging broken occurrence remains unresolved, *Py. dispersa's* pulsing flash pattern in the east is easily distinguished from the single, diminutive, dim, and dipping flash of *linearis*, but see below.

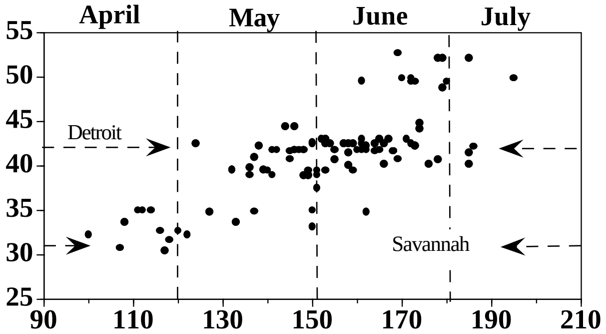


Figure 3. GESEDIS records (AX: Lat/DOY).

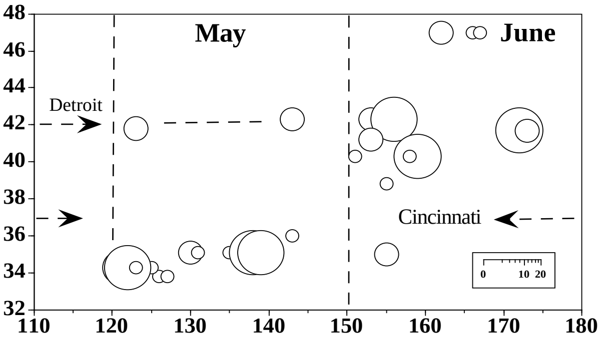


Figure 4. G'SOBS records (AX: Lat/DOY, Quant).

Figure 5. Ypsilanti MI gravel pit, 1962.

Figure 6. Creek Road, Merrillsville, Madison Co. NY.

Figure 7. Iowa roadside marsh.

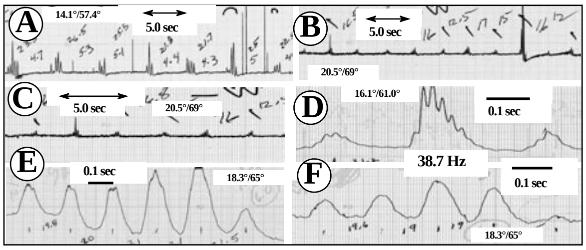


Figure 8. PM-records (AX: rel. int./time).

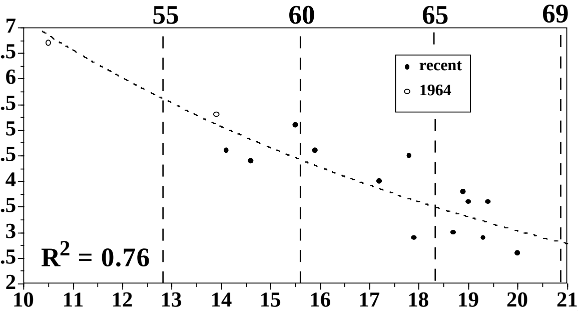


Figure 9. FP period (AX: sec/temp).

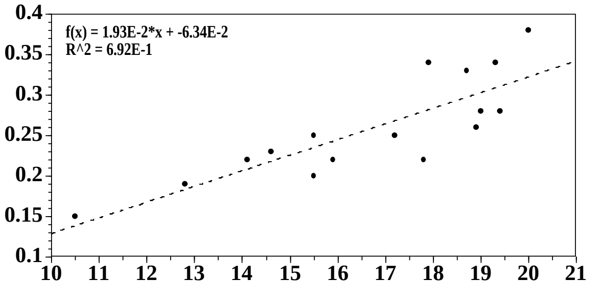


Figure 10. FP interval (period) rate (AX: Hz/temp).

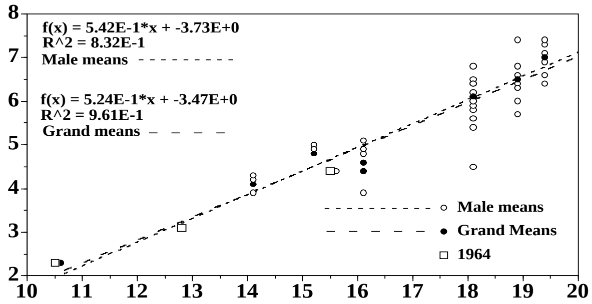


Figure 11. Flicker-pulsing pulse rate: a comparison of means (AX: Hz/temp).

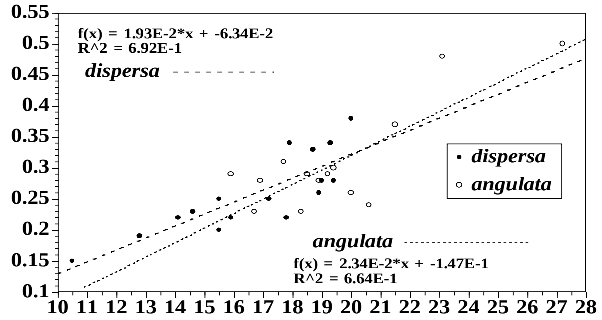


Figure 12. FP-period comparison (AX: Hz/temp).

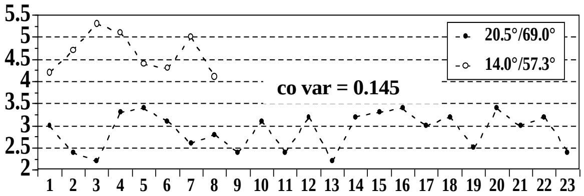


Fig. 13. FP intervals for FP sequences of two males (AX: sec/FP position in sequence).

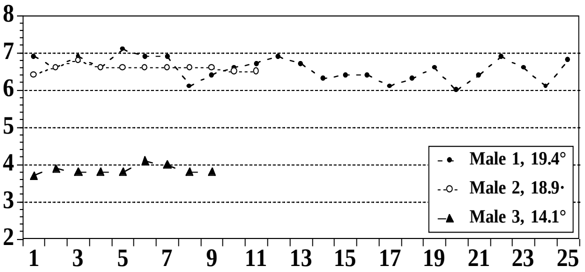


Figure 14. FP sequences (AX: Hz/position in FP series).

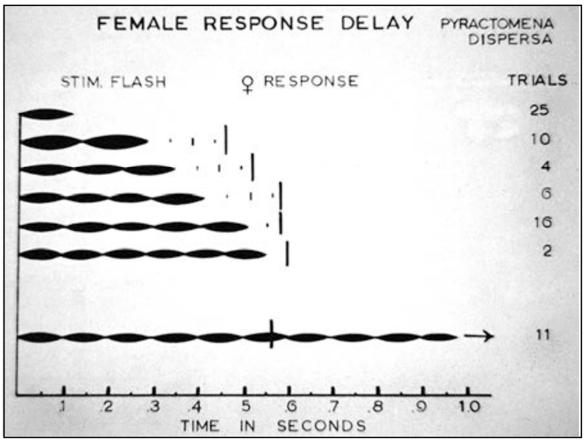


Figure 15. Female response (SWAT).

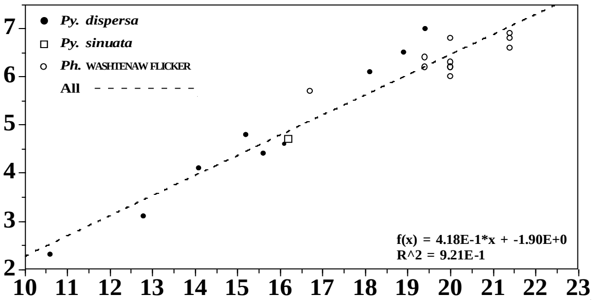


Figure 16. Mod. frequency comparisons (AX: Hz/temp).

Figure 17. Lost *Py. dispersa* habitat, Fairfax Co. VA.

Longer PM-recorded sequences make it possible to see timing variations in the emissions of individual males. **Figure 13** shows the FP intervals (periods) in continuous sequences of FPs emitted by two males, and **Figure 14** shows the modulation rates of pulsed FPs in continuous sequences (see also **Fig. 8A-C**). The variation among consecutive emissions of the FP suggests that the firefly is able to see well enough to adjust the intervals of his advertisements to vegetation or competition conditions he observes; the coefficient of variation (sd/x) in the lower sequence is 0.145, about 2.5 times that of the same statistic of the modulation rates of this male (0.057, **Fig. 14**, male 1). This is to be expected when the modulation rate of the FP is of coding significance and FP repetition (advertisement) is not, and instead tuned to advertising conditions of the moment.

Female flash response. Several details of *dispersa's* adult behavior connected with flash communication were reported previously (jel 1964). Worthy of further note here are observations that can be interpreted in light of more recent information about firefly behavior: (**1**) The observed indirect approach of males to responding females, by dropping nearby instead of flying in, now can be interpreted as an anti-predator tactic, and has been noted in certain other *Pyractomena* species. (**2**) Lab experiments in 1962 using a push-button flashlight to elicit response flashes from females had suggested that females timed (delayed) their flashes responses from the (a) fourth pulse of the male pattern, with a delay of 0.15-0.2 sec (24°-26.6°). The flashlight pulses (clicks) and female responses (voice marked) were tape recorded and later timed with a stopwatch. **Figure 15** shows the results of these experiments, and was prepared at the time on a drawing board with pen and ink and the standard plastic penning-templates of the era—a tedious and often messy process. I incorrectly decided not to use the figure in the 1964 publication because I had doubts about the general significance of precision female delays (reasoning that escapes me now)—not appreciating that the timing was interesting in its own right, perhaps relating to mechanisms and neural systems. Here finally I give belated thanks to my long-time mentor R. D. Alexander for making the drawing, now a relic of times agone!

Wingbeat note. An interesting and confusing feature of PM-recordings is the comparatively common appearance of high-frequency modulations, in the range typical of firefly wing beats (30-45 Hz; **Fig. 8D**, 38.7 Hz @16.1°). Such modulations appear occasionally upon the recorded flashes of other fireflies but in *dispersa* may appear more often, and are more pronounced. Certainly they are from wing-shuttering of the emitted light. A brief, and for the moment failed experiment suggests an explanation: after noting in a photograph the ladder-like reflections of the wings of hovering flies, a sensor-system that would detect reflections of a small beam of light from the wings of fireflies was devised (by A. Higgins, the engineer who designed and built the PM-detector system in 1967). Apparently the wings of fireflies are non-reflective. This would not only

Figure 18. Near Delano, Polk Co. in se TN.

Figure 19. Otsego Co. NY low pasture, 1963.

Figure 20. McLean Bog, damp pasture with standing water (cow-step puddles) and hummocks, Cortland Co. NY, 1963.

reduce their visibility to an aerial-attacking predator (*Photuris* female), it would prevent reflections from reaching the eyes of the emitter himself. A quotation from an article by Richard Waller, Esq., Fellow of the Royal Academy in 1685 on firefly light is interesting in this regard: *Possibly the use of this light is to be a Lantern to the Insect in catching its prey, and to direct its course by in the Night, which is made probable by the Position of it on the under part of the Tail, so that by bending the same downward (as I always observed it to do,) it gives a light forward upon the Prey, or object: the Luminous Rayes in the meantime not being at all incommodious to its flight, as they would have bin, if this Torch had been carried before it. This conjecture is also favoured by the position of the eyes …* (**Fig. 21**, from Waller, 1685, in Harvey, 1957).

Taxonomic note. This species (this taxonomic complex), would appear to be the most interesting of all *Pyractomena* from an taxonomic/evolutionary standpoint, and this study has done little to clarify the situation beyond what Green indicated (1957). It can be recognized at the bench, in a broad sense (s. l.), with Green's key, and his text points out the confusion that exists between "*dispersa*" and *linearis*. Further, he noted variation within his *dispersa* that was worthy of note. He named this species, we only presume, from the wide distribution of his working-*dispersa*; **Figures 1** and **2** somewhat suggest broad geographic subsets, but taxonomic complexity may be much greater than that indicated. As a general note, *dispersa* (s. l.) is easily distinguished from all others within its range except *Py. linearis*: *Py. lucifera* is much rarer and has an elongate and distinctive pronotum; *Py. sinuata* apparently is rare (except in certain areas of the plains, e. g., western NE); *Py. dispersa* and *linearis* are commonly found together in marshes and low grassland, within the more restricted (and northern) geographic range of *linearis*. Both have the same broad range of elytral color variation, from dark, black in *dispersa*, to tan, though perhaps within single demes coloration is fairly uniform. Distribution of secondary elytral pubescence now seems to be the most reliable morphological feature to distinguish them on the pin—but these clues are simply a place to start. DNA analyses must be accompanied by very careful field observation and voucher collection, and bench taxonomy!

Models for mimics. The mimicry of *Photuris* of the FPs of other species often involve *Pyractomena* models—except for those copying twilight *Photinus* and of the *Photuris cinctipennis* Group whose signals match those of the *Photinus consanguineus* Group. It was thus no surprise when a long-flickering *Photuris* PM-recorded in a marsh (Washtenaw) near Ann Arbor, MI was later determined to modulate its FP at a rate like that of *dispersa*. Observations on this firefly were made too early in studies to know or understand this, to have asked the important questions, or to have made appropriate experiments. Not only does this modulation rate fit that of *dispersa*, but the single and barely readable PM-record I have of *Py. sinuata*—whose emission is much longer than that of *dispersa*—falls along the same regression (**Fig. 16**).

Variads and the *dispersa/linearis* situation. As noted, observations on populations belonging in this complex arouse suspicion but are not sufficient to draw conclusions. I previously noted three "*linearis*-related" populations, one of which pulsed like *dispersa* (jel 1966); I have since observed two individuals in Putnam County, NY ("HUDSON") emitting an FP that resembles that of *Py. sinuata*—though pulsing was not observed—morphologically they do **not**

belong to this complex. The three “suspicious variads” were: (**1**) long-pulsed *linearis*, whose FP seemed to be appreciably longer than *linearis* FPs observed elsewhere, in Madison Co. (**Fig. 6**, and Otsego County, NY (**Fig. 19**); (**2**) a 4-pulsed *linearis* whose behavior was much like if not identical to that of *dispersa* (1964) was seen at McLean Bog near Cortland NY (**Fig. 20**), but morphologically drew my suspicions at the time; (**3**) delayed-*linearis* was observed later in the season at the McLean Bog site (**Fig. 20**), emitted an FP as described for the long-pulsed *linearis* and females emitted their flashes at a longer average delay of 1.4 sec (14.4°/58°). Though this genus gives the impression of being stagnated and millennia beyond creeping divergence, perhaps there is something of theoretical significance to be learned here.

Adjunct figure legends. **2**. Physiographic view suggesting regional differences for possible significant subsets/variads of *dispersa*. **8**. PM-records of *dispersa* flashing including FP successions from single males at 5mm/sec (A-C), 125mm/sec traces (E, F), and wing-shuttering superimposed on flashed pulses (D). **9**. FP-period regression of male means on temperature with measurements from an earlier study (1964). Note the variation, as would be expected if males aim their FPs at likely female-holding vegetation. **20**. A low pasture site near Cortland, Cortland County, NY, where a so-called pulsed “*linearis*“ was noted. This site adjoined the field site of Cornell University (Ithaca) known as “The Shack.” Perhaps this firefly, in spite of the seeming antiquity and stability (indolence) of its genus, has something to teach about Darwin’s understanding of speciation.

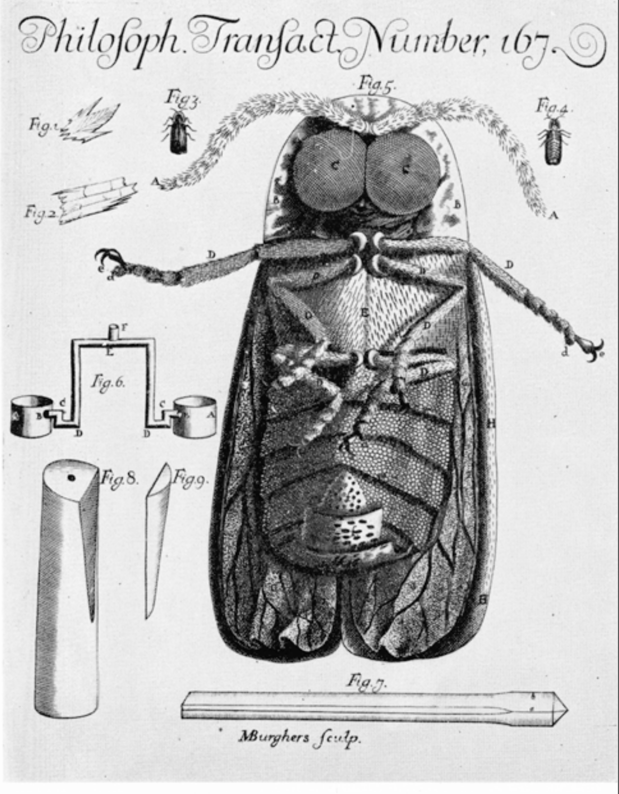
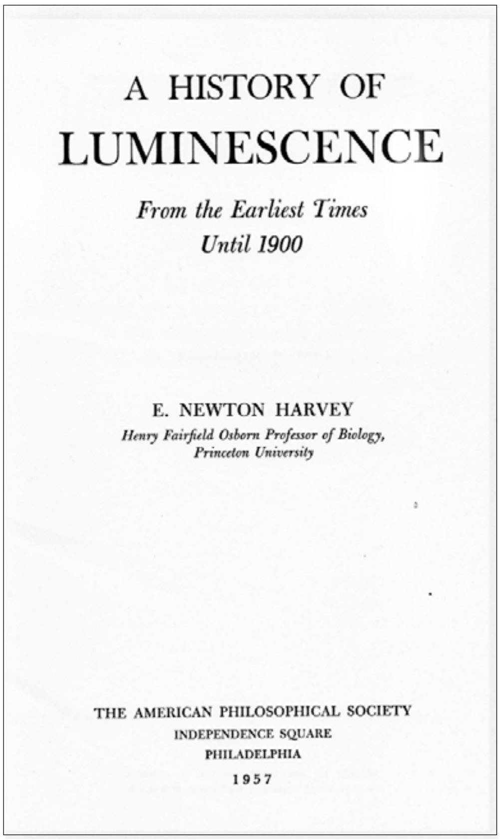


Fig. 41. A handsome drawing of a flying glowworm, reproduced as a plate to the paper of Richard Waller, " Observations on the Cicindela volans " in the *Phil. Trans.* for 1685.



A HISTORY OF
LUMINESCENCE
From the Earliest Times
Until 1900

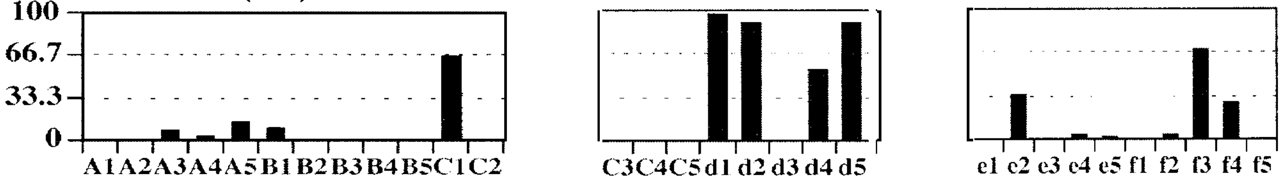
E. NEWTON HARVEY
Henry Fairfield Osborn Professor of Biology,
Princeton University

THE AMERICAN PHILOSOPHICAL SOCIETY
INDEPENDENCE SQUARE
PHILADELPHIA
1957

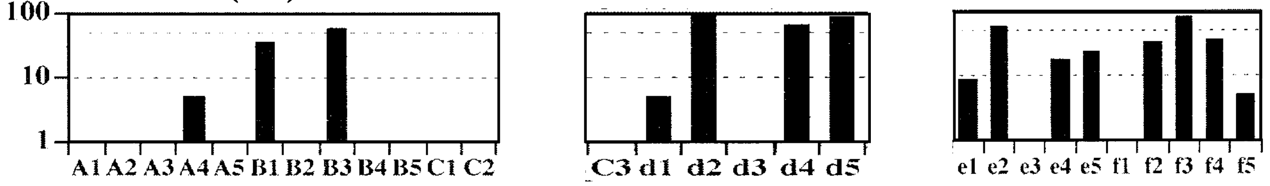
Figure 21. Illustration from Waller's 1685 article and Harvey's 1957 book.

PN Comparisons: lineaticollis & maicoi Red GROUPS

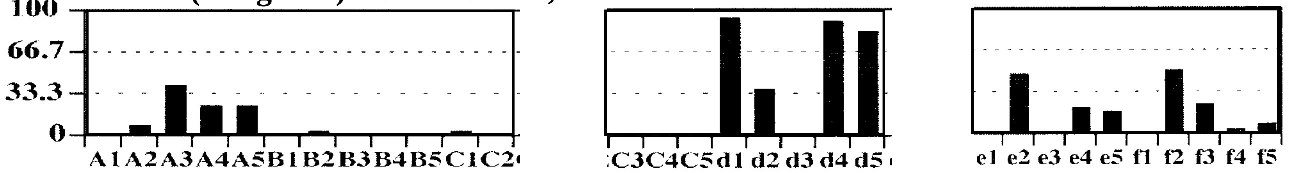
lineaticollis (GR) Alachua Co. n=29



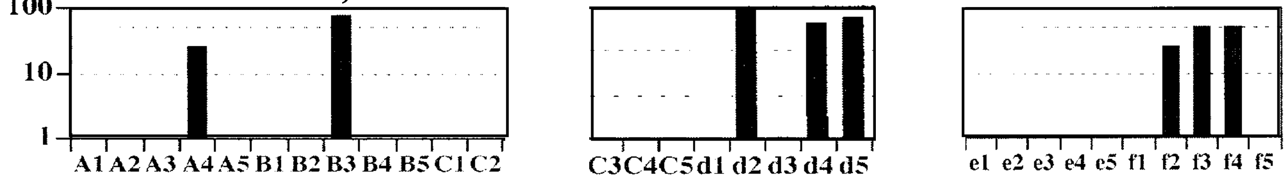
lineaticollis (GR) various FL localities. n=22



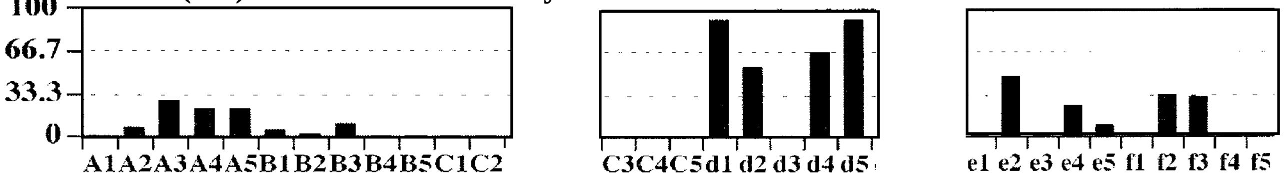
walkeri (Long Red) Gulf Counties, n=30



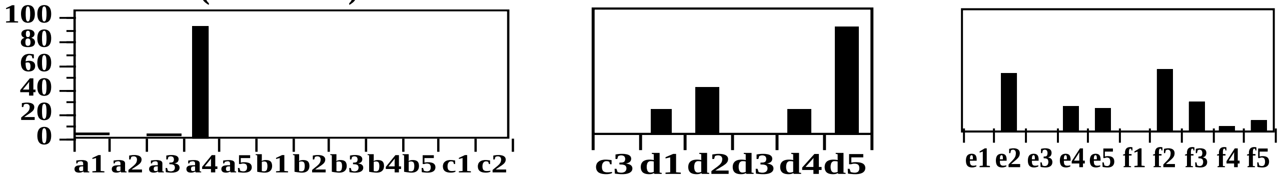
walkeri-like Glower, Wakulla Co. FL n=4



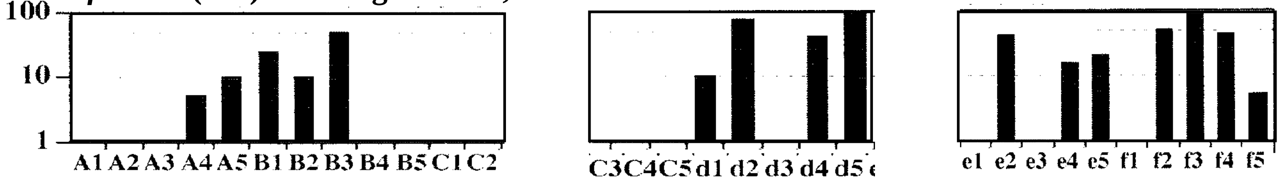
maicoi (BR) alachua Co. & vicinity FL n=71



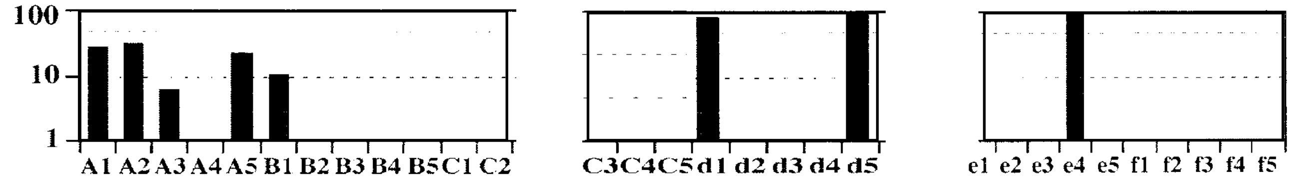
dorothae (Little Red) Alachua Co. n=13



faustae (HR) se Georgia. SFSP, n=20



katrinae (TR) Texas, n=18



Chapter 79

Pyractomena ecostata LeConte 1878

This keel-necked firefly has an interesting and segmented coastal occurrence, as presently documented, continuous but with breaks from Alabama around Florida, but then a long hiatus north to coastal marshes in Delaware and New Jersey (**Fig. 1**). In Florida sites are within a few miles of the Gulf or Atlantic Ocean. Though sometimes seen around halophytic marshland, such as those of black-needle-rush in Florida (**Fig. 2**), and at the margins of sea meadows of southern New Jersey (**Fig. 3**), further inland it was seen in abundance in low wet pastures and along highway swards, presumably too far inland to have saltwater intrusion/ecology (**Figs. 4, 5**). During glacier times *ecostata's* range may have extended along the Atlantic in brackish marshes of the now-submerged continental shelf—if it occurs today between Delaware and Florida it has long escaped being archived or reported, and that's remarkable given its appearance.

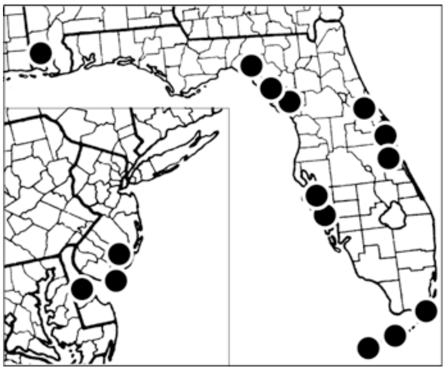


Figure 1. Florida, Alabama, New Jersey, Delaware.

This species is easily distinguished from all other *Pyractomena* species by its median elytral stripes (**Fig. 6**)—which give it a superficial *Photuris*-like appearance—, and large size (11.5 -16 mm). In the field its flaring FP is distinctive, and though it is green by measurement (n=6, 9/1967, Levy Co. FL: 558, 533.0-602.0 millimicrons), it often appears yellow—there is no evidence of color-switching ability in fireflies. A curious color "change" was also noted in another (somewhat) flaring, marsh-inhabiting *Pyractomena, palustris*, though in the latter its yellow luminescence *appeared* to be metallic/coppery.

Flashing behavior. The flaring FP is easily recognizable—after a 10-20-second wait for a repeat—as a solitary male moves slowly, silently/eerily along the edges of a country road, at an altitude of 8-15 feet. The bright, swooping flare, with indistinct/gentle transients (**Fig. 7**)—and sometimes with "lumps" in luminosity apparently from twisting flight—is often strung on a continuous dim glow as the male "drifts" slowly along. SWAT measurements indicate flash durations ranging 0.5-1-sec and PM-recordings of three males (n=4) at 23.3°/74° averaged 0.42 sec (s = 0.18, r = 0.39-0.44, **Fig. 7)**. This FP is characteristically emitted at unexpectedly long intervals of 8 seconds or more (**Fig. 8**), perhaps a counter-measure to aerial attack, and at high altitudes over open areas is like no others—except perhaps that of *Py. punctiventris* in Texas. In populations of several individuals the FP gesture takes different forms: J-upward-swoops like those of *Pn. pyralis*, horizontal dashes, upward slants, or as sparks blown in the wind. One fieldbook note records a rapid flight that slows and slides into the flash, then stops, hovers, and then starts up again. The FP period regression shown in **Figure 8** is only a rough estimate made from counted (not SWAT) period values, except for the x=5.6@27.8°C (arrow). The FP period is not necessary for identification but will be of interest when hawking studies of *Photuris* females upon these males are pursued—their almost-unique green bioluminescence certainly has some connection with this.


Figure 2.Black needle-rush, Cedar Key, FL


Fig. 3. Causeway, Sea Isle, New Jersey.

In Florida *ecostata* is perhaps a continuous breeder, i. e., without distinct broods—as was found for its congener *Py. lucifera* (var.) through careful studies by Larry Buschman, (1984a)—adults have been observed from February to September in northwestern peninsular Florida (**Figs. 9, 10**).

Fig. 4 . Roadside site for roving *ecostata* near Cedar Key FL; the most-inland specimen record, Bronson, FL.

In one PM recording of a flare (FP) an obvious wingbeat flicker is seen (**Fig. 7C,** arrow); this registers 50.8 Hertz (13:32=X:125mm.).

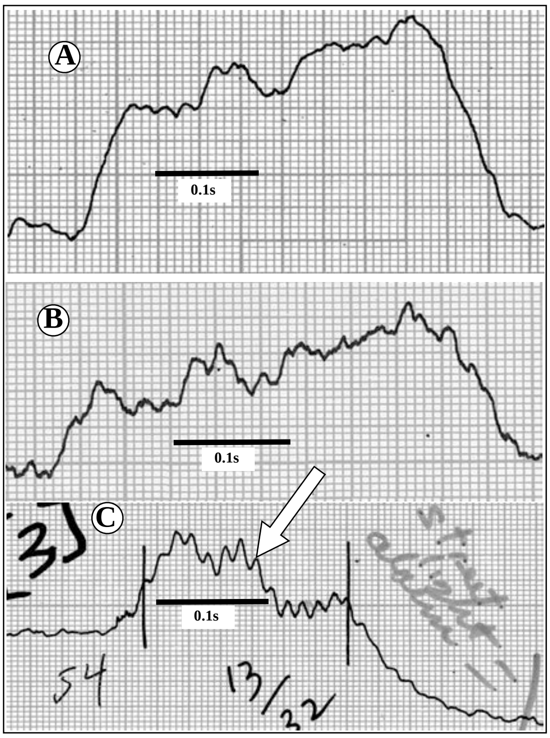


Figure 7. PM-records (AX: rel. int./time).

Fig. 5. Roadside for roving *ecostata,* nr Ellzey, FL (nr Otter Creek).

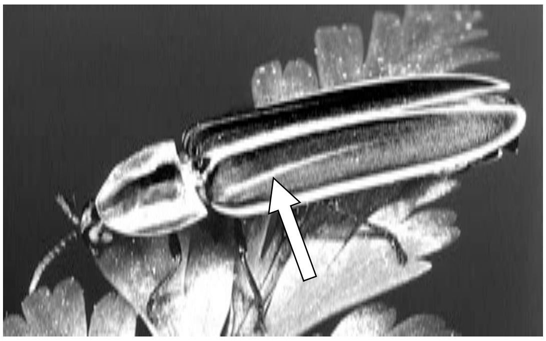


Fig. 6. Habitus, showing lateral elytral vitta

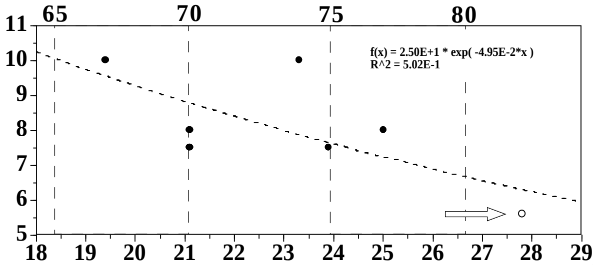


Figure 8. Est. FP period regression (AX: sec/temp).

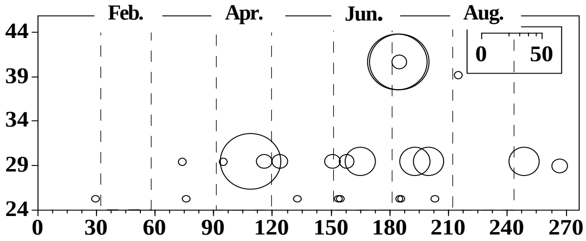


Figure 9. G'SOBS + SESOBS (AX: Lat/Doy and Amt).

Augmented Figure Legends: Figure 7. PM-records from 25 May 1968, near Cedar Key, Levy County, Florida, at 23.3°/74°. Ragged records, especially in (**B**) may be the result of high humidity affecting the electronics, or spurious light from distant houses or even a street light (60 Hz) as noted on the chart. **Figure 10.** The charting model was exponential. The apparent simplicity of this species' (lazy) signal periodicity led me to neglect making several FP period samples(?).

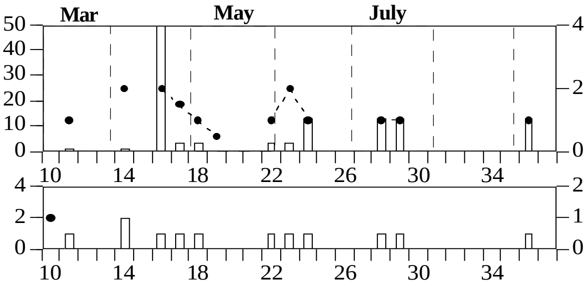


Figure 10. SESOBS, Gulf Counties.

Chapter 80

Pyractomena floridana Green 1957

Hurricane Firefly

Pyractomena floridana is of rather rare and restricted occurrence, until now found only within miles of the coastline around the Gulf from the tip of Florida to Mississippi. Records are few and a gap occurs between southern Alabama and northwest peninsular Florida, and again between Tampa and Miami **(Fig. 1**). A single female collected in the Austin Cary Forest in Alachua County, northeast of Gainesville near Waldo (1968, light-trap), perhaps was carried there by winds, mislabeled, or represent a now extinct inland population: This site was observed and collected extensively during the present study and none were seen—also, there have been many insect-collecting entomologists and students in Gainesville and Alachua County for decades. In Dixie County, FL this firefly occurs along elevated rural roadsides through Gulf Hammock flatwoods with wetland areas (**Fig. 2**). It is the only known *Pyractomena* species whose adults are active *only* during the late summer and early fall (**Figs. 3, 4**).

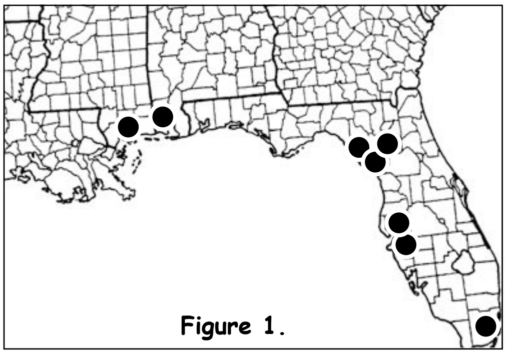


Figure 1.

Fig. 2. Mallory Swamp, near Hines, Dixie County, FL.

The combination of genus (note PN keel), late summer season, fulvous (tawny) rather than pink or red pronotal discal color, and locality, will positively identify *Py. floridana*. The only other Keel–Collar known to be active during its season is *Pyractomena ecostata*, a larger (11.5-16 versus 9-11.5 mm, ex Green, 1957), and a morphologically distinct firefly that appears almost *Photuris*-like with its olive elytra and distinctive elytral stripes (vittae); *floridana* has raised elytral costae (ridges) but no noted vittae (**Fig. 5)**. Aedeagal form sharply contrasts with that of *ecostata*. FPs of the two are easily recognized: *Py. floridana* emits 7-14 pulse, orange–yellow flickers each 3-7 seconds while flying rather quickly, typically waist high over the ground; *ecostata* emits bright and "huge" green flare-flashes at long intervals, often several feet above the ground.

Flashing behavior. The FP of *Py. floridana* is a 1-2 second-long, yellow-orange, sometimes-jerky, flicker (**Fig. 6**) that is emitted each 3-7 sec of flight at 24.4°/76°—as projected/anticipated in **Figure 7**. Males flew along roadside berms and ditches through pine flatwood and plantations, 6-15 feet above the ground. During flickers they traversed <5 feet, and between them as much as 15 feet. As noted for several other species, at times of low abundance, males sometimes seemed to travel in squadrons; none would be seen for several minutes, then two or three would appear, moving along together in the same direction—though perhaps this is due to spreeing, as noted in the singing of frogs and insects (Walker, 1983). Amplitude variation among recorded pulses of flickering fireflies is certainly not significant in communication, and when amplitude appears to be erratically uneven in PM-records, as in *floridana's*, it is probably due to changes in flight attitudes (lantern orientation), with respect to the PM-detector (**Figs. 6A, C-E; 7**).

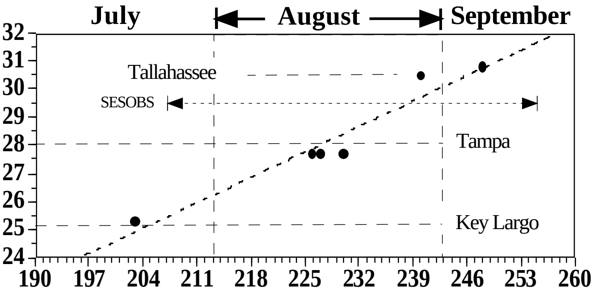


Fig. 3. GESEDIS—the archives (AX: Lat/DOY).

The term *flicker* is problematic: though at Florida's too-warm, late-summer temperatures the emission appears as a flicker, at somewhat lower temperatures FPs will be seen as series of discrete pulses. Pulse number in each flicker ranged 7-14, with 10 being most common in PM-records; modulation frequency is 5.5 Hz (180mSec period) at 24.4°/76°. Each pulse is nearly symmetrical, with the decay being slightly slower than rise; each is 100-150 mSec in duration, and the intensity of each may fall to full OFF before the next begins; note pulse elongations in **Figure 6B, E**.

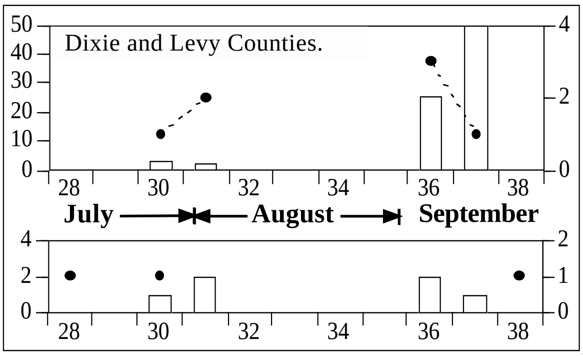


Fig. 4. SESOBS—observations (AX: Cnt-amt/WQY).

Fig. 5. Habitus; note keel.

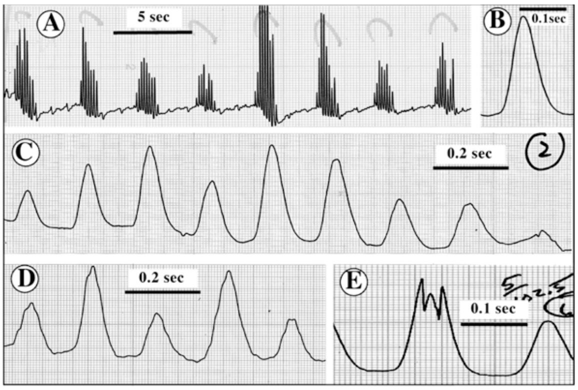


Figure 6. PM-records (AX: rel-int/time); see supplement).

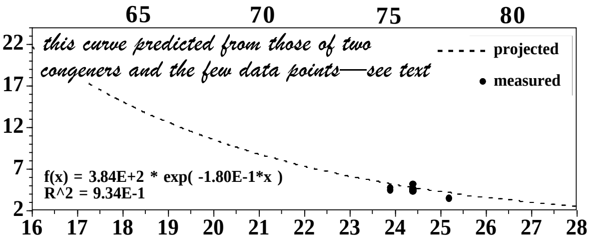


Fig. 7. Projected FP period regression (AX: sec/temp).

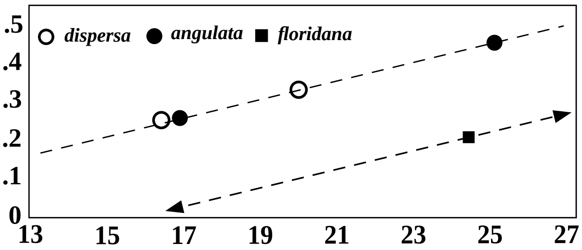


Fig. 8. Projecting *floridana* FP rate (rate/temp).

Other FP considerations. SWAT-measuring and recording temperatures were too similar (23.9°-24.4°) to provide regression charts for FP period and modulation rates. Therefore, the FP-period regression slopes of *Py. angulata* and *dispersa*—congeneric flickering species that differ in their FP modulation rates—were applied through the (too-few) *floridana* data points to suggest and tentatively project an FP-period-rate regression (**Fig. 8**), and from points along this slope, a FP-*period* regression as used for field identifications (**Fig. 7**).

Likewise, a parallel regression slope for modulation rate was borrowed from two parallel congener slopes (**Fig. 9**); and these extended for temperatures even below, say 19°, should they ever be encountered with *floridana*, and for other curious considerations there is **Figure 10.**

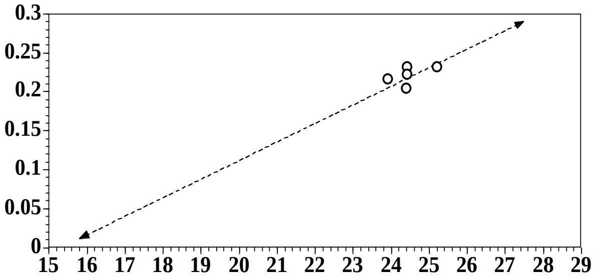


Figure 9. FP-period projected rate (AX: Hz/temp).

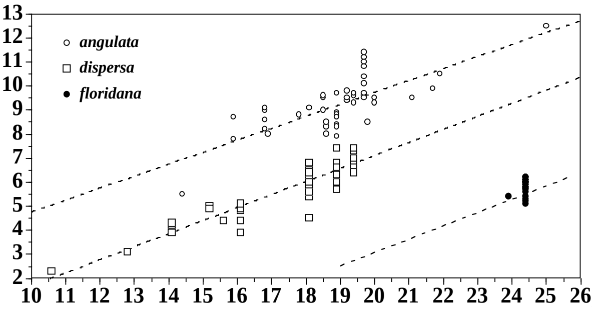


Figure 10. Projected pulse modulation rate (AX: Hz/temp).

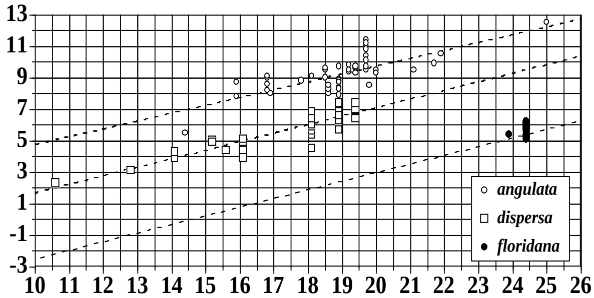


Figure 11. Note "projected" curious low-temperature rates! ? AX: (Hz/temp)!

Miscellaneous notes. *Py. floridana* is unusual in having a fall adult season; all other Keel-Collared fireflies, except *Py. ecostata*, have their adult seasons in early spring or summer. There are late-season *Photinus* and *Photuris* fireflies that occur with *Py. floridana*, including the predaceous though smaller and single-brooded (univoltine) *Photuris dorothae*. Possibly connected with *floridana's* seasonal occurrence and dryer habitat is the tawny color of the pronotum. In other *Pyractomena* the colorful pigment around the head and pronotum, and internally around the testes, is pink. This is from pterodine compounds, which are fluorescent, and may be of taxonomic use since they are fairly easily seen (Wilkerson and Lloyd, 1972). A similar pronotal color shift is seen in several *Photinus*, including *Pn. pyralis*, when specimens from southwestern localities are compared with those of the eastern North America.

A glance at the “predicted” FP and modulation rates would encourage a fireflyer to make every effort to see this species in the field at unseasonably low temperature snear 13°/55°—Asian philosophers, it is said, consider the sound of one hand clapping?; here we can ponder the appearance of flickers with *minus* rates; perhaps they disappear? A reasonable question is what would evolutionarily happen to such a flicker in a cooling climate—the slope would rotate could such a situation play a role in the evolution of an FP with only one or two pulses—such as found in *Py. borealis*, *limbicollis*, and *marginalis*. At reasonable near-glacier temperatures *floridana’s* pulse rate could be near those of this trios occasional 2-pulse FPs, and they share the same aedeagal form.

Females. Two females were found perched about a foot above ground on herbs. They answered decoy flash pattern simulations (crude, penlight) with single, unmodulated flashes that began shortly after the stimulus ended, that is, with a delay of about 1.5 sec. At onset female flashes were bright for 0.5-1 sec, then gradually dimmed to a final OFF in 2-3 sec. A rapidly-flashing female flew into pines and switched to a glow. This is my single observation of a flying *Pyractomena* female. Flight luminescence is common in females of certain *Photuris* species, and has been seen in females of the *Photinus consimilis* complex. Its function is probably illumination.

Figure Legend Augmentations. Figure 7: PM-scans: (**A**) a sequence of FPs; (**B**, **E**) stretched pulses to show apparent (flat) OFF; (**C**, **D**) flickers showing occasional reduced pulse intensity, probably from lantern being aimed away from PM. **Figures 7-12:** Because few FP data are available and these are from similar temperatures, a crude FP period prediction is made by drawing the *rate* slope found in two related species through the few *rate* data points available for *floridana* (**Fig. 8**). Then, points from along this line are converted to the (reciprocal) interval/period data points (=1/rate), and plotted on a dedicated chart (**Fig. 9**). To produce a rate slope for **pulse** modulation rate in *floridana's* flicker, because rates are involved in both sets, the slopes from congeners was drawn through the data points available for *floridana* (**Fig. 10**). **Figure 11** simply extends the line toward the colder temperature end to raise interesting questions. This regression illustrates why the *floridana* slope may actually be flatter than that inferred from congeneric relatives, and if nothing else, be an inspiration, as noted above, to the consideration of an evolutionary model for a transition between a *floridana*-like slow-pulse flicker to an abbreviated FP, most notably such as that found in *borealis*, a species happily in the same genitalic group. If a chilling atmosphere reduced flight opportunities, would 2-pulse FPs work better from perches in a wet grass- and herb-land?

Chapter 81

Hudson River Firefly

This firefly is presently known from a single site near the Hudson River, in Putnam County, New York (**Figs. 1, 2**). It is in the confusing *Py. dispersa-linearis* complex that J. W. Green drew attention to, and can presently be diagnosed only by observing male light-emitting behavior. Its emission pattern is similar to that of *Py. sinuata*, based on limited observations made of both species—a 1-2.5 sec glow with OFFs between glows of a similar or somewhat longer duration, <5 sec(?). Its short flights may be a defense against aerial attack by a *Photuris*?

The site was a low, somewhat-damp, oldfield between the highway (US-9, at JCT 301) and a shrubby hillside rising to 75'. Over a combined observation period of about 4 hours over 3 evenings, only five males were seen. All arose glowing from the grass and flew a few yards and up to 3' altitude above the ground before alighting. During these arcing-sinuate flights they emitted 2-3 short, orange-yellow glows. Short flights may be characteristic of this firefly, because the temperature was not a limiting, and the dates of observations (11-16 June) were not seasonally late.

A few *Photuris stevensae* were active. Considering the apparent close relationship of this firefly and *dispersa*, its short glow may be weakly modulated at a similar rate (ca 5 Hz @ 16.5°—curiously, seemingly the same rate as that of *sinuata* which is of a different genitalic type distinguished by Green (**Fig. 3**). Morphological measurements and PN ratio are in **FigTable 4,** and habiti in **Figure 5.**

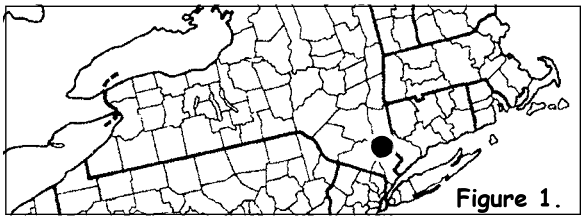


Figure 1.

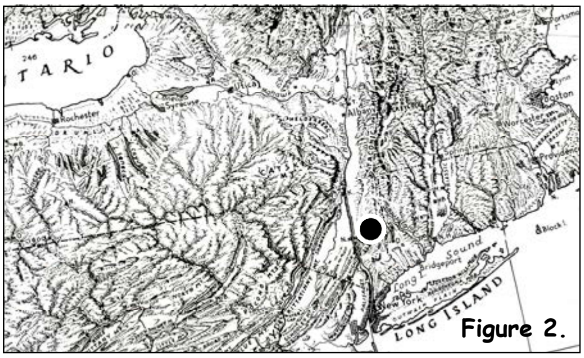


Figure 2.

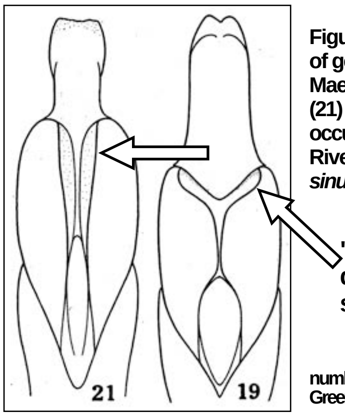


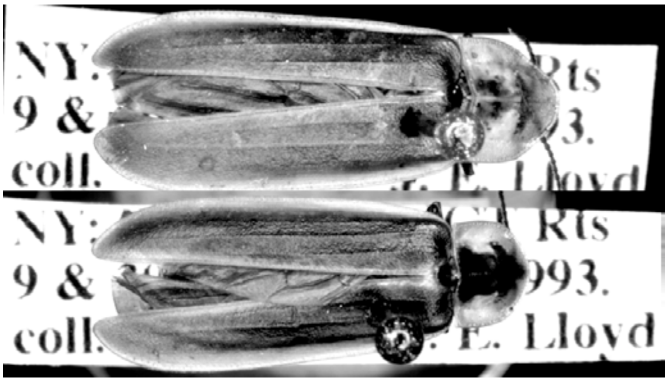
Figure 3

Figure 3. Ventral views of genitalia, from Maestro Green, 1957: (21) *dispersa*-like, as occurs in the Hudson River firefly; (19) *sinuata*-like.

numbers as in Green, 1957)

	PNL	ELL	PNW	TLEN	PNrat
Mean	2.500	9.250	2.950	11.750	.850
Std. Dev.	.141	.212	.212	.354	.014
Std. Error	.100	.150	.150	.250	1.000E-2
Count	2	2	2	2	2
Minimum	2.400	9.100	2.800	11.500	.840
Maximum	2.600	9.400	3.100	12.000	.860

FigTable 4



FigTable 5. Vouchers, 9310 above, 9316 below.

Chapter 82

Pyractomena limbicollis Green 1957

This firefly makes its appearance every once in a while, not because it is rare or reclusive, but because a fireflyer won't notice it though several males are silently and discretely flying and flashing only 70 feet away, in the upper reaches of tall trees, while attention is focused elsewhere. Then, when prompted to think "*limbicollis*" it is difficult to place confidence in identifications made largely through the process of elimination—color at a distance is often difficult to determine and the diagnostic asymmetrical 2-pulse FP is typically emitted by only a few or an occasional male. All but one record is from Florida (**Fig. 1**), the South Carolina exception is an archived specimen I identified for a State List many years ago, perhaps incorrectly. I found this species in pine flatwoods, a swamp forest (**Fig. 2**), a hydric hammock, gallery pines along highways, in a gallery of hardwoods paralleling pond cypress along a lake (**Fig.3**), and at the edge of a mesic hammock adjacent to an open glade. *Limbicollis* is a spring firefly, in Gainesville adults appearing with *Ph. harrannorum*—which mimics its FP—and has a single generation each year (**Figs. 4, 5**). In Gainesville larvae pupate low on the north side (**Figs. 6-8**) of trees of small diameter, in contrast to those of *Py. borealis*, that pupate on the south side and much higher on larger trees—perhaps this avoids competition for tiny molluscan prey during early instars by separating their hatching dates. Adults are smaller, seemingly more delicate, and sharply marked than other *Pyractomena*, and have dark or black elytra and vivid red coloration on the pronotum (**Fig. 9**). Green gives size range as 7-12 mm. Bioluminescence data in millimicrons are: 774, 546.0-614.0 (April 1978, n=6).

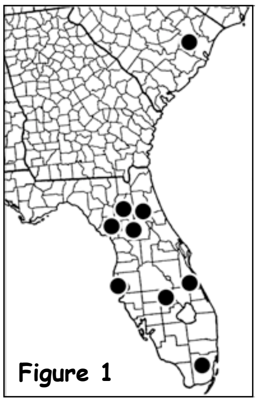


Figure 1

The FP is similar to that of both *Py. borealis*, an earlier species sometimes found with it, and *Py. marginalis*, a species of more northern occurrence. In all three the most common FP is a single short flash, and in all three, for undetermined reasons, a second flash is emitted shortly after the first. It is usually uncommon, and is variably dimmer than the first, though rarely of similar intensity. Also, the pulse interval is variable, but typically less than a half second. Only single flash FPs of *limbicollis* were recorded (**Fig. 10**); duration of one at 16.7°/62° was about 250 mSec and another at 18.6°/65.5° about 150 mSec. FP period is an interesting puzzle: in north central Florida (Alachua and Marion Counties) it is shorter than in Highlands County, 200 miles to the south (**Fig. 11**; rates in **Fig. 12**).

Figure 2. Possum Creek runs through a swamp forest.

Figure 3. Gallery adjoining pond cypress by lake.

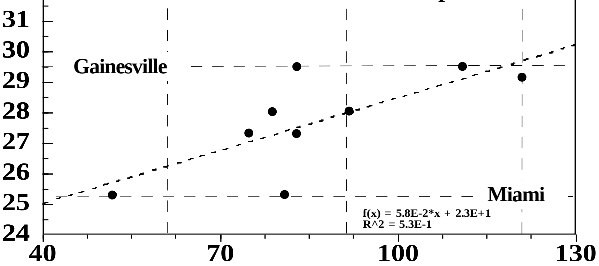


Figure 4. GESEDIS (AX: Lat/DOY; intervals ca 1 week).

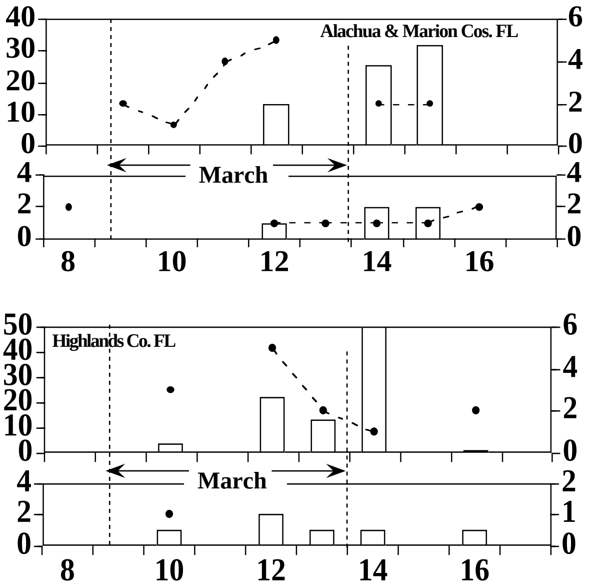


Figure 5. SESOBS (AX: Cnt-Amt/WOY).

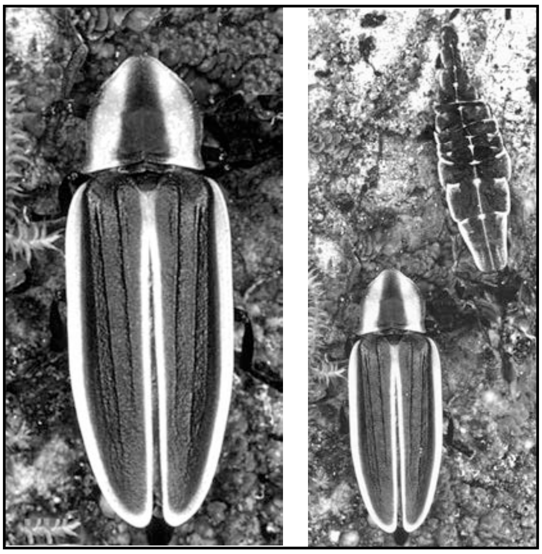


Figure 9. *Py. limbicollis* male, larval and pupal skins.

Figure 6. *Pyractomena* larva sucking out anesthetized prey.

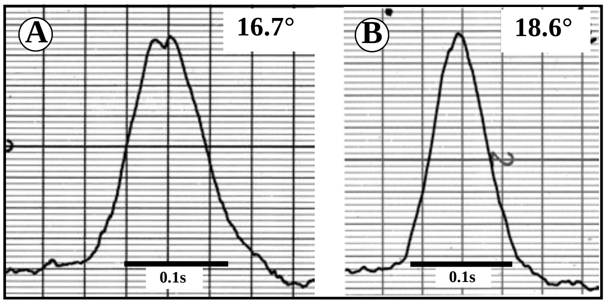


Figure 10. PM-scans (AX: rel-int/time).

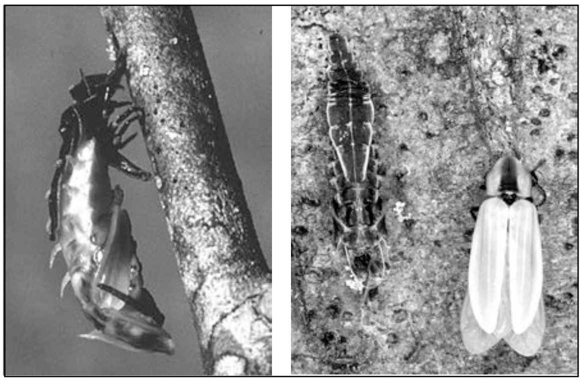


Figure 7. *Pyractomena* pupa; larval & pupal skins, teneral adult.

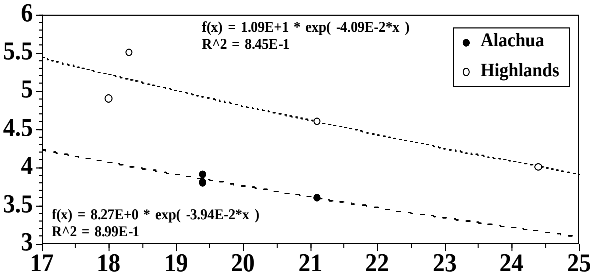


Figure. 11. FP period (AX: sec/temp).

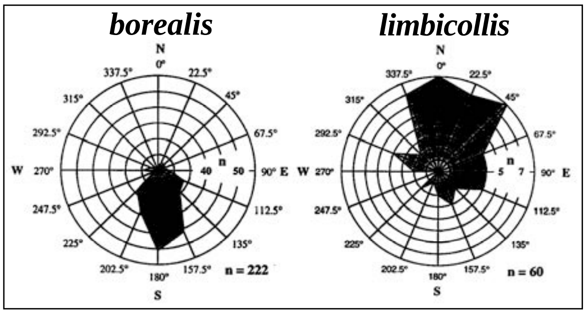


Figure. 8. Contrast in orientation.

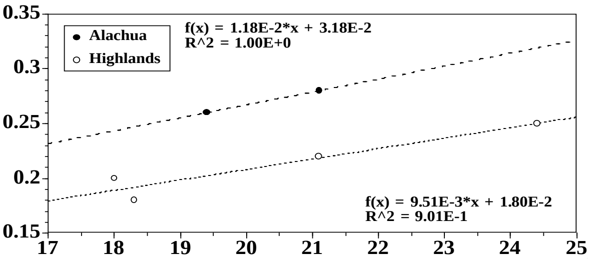


Figure. 12. FP rate (AX: Hz/temp).

Chapter 83

Pyractomena linearis LeConte 1852

The fault, my dear Misters Barber and Lloyd,
most certainly, is not in nor among the fireflies,
but what you may have expected of them.

This firefly's middle name is *confusion*: for simplifying "openers" *linearis* (sensu lato) can be said to occur in various wetland types in a narrow band along and generally below the US-Canada border from the Atlantic to the Midwest (**Figs. 1-5**). Its FP will be confused with that of *Py. lucifera*, which occurs in the the same habitats. The two are morphologically distinct, and in separate "sections?" of the genus via genitalic form. Archived label records and observations perhaps suggest that possibly/cautiously *linearis*' season is primarily in June—which might provide some seasonal separation from *Py. lucifera*—seasonality of field work would not seem to explain the noted phenological distinction. That of *linearis* is shown in the figure but an occasional *lucifera* record may have been included (**Fig. 6**). Focused study may reveal several variads/species sharing those morphological features presently used for recognition of LeConte's *linearis*: as examples, see below under (**1**) long-pulsed *linearis*, (**2**) delayed *linearis,* and (**3**) pulsing *linearis.*" Further, *linearis* and *Py. dispersa*, with noted variations (Green, 1957), together form an unresolved complex. The following sketchy summary should be presumed to incorrectly combine and confuse details belonging to long-flashing and also perhaps pulsed-flashing (*dispersa*), presumably distinct evolutionary entities.

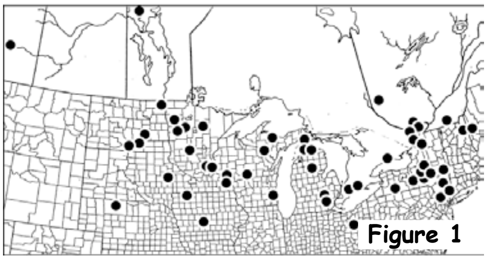


Figure 1

Figure 2. McLean Bog, damp pasture with water puddles between hummocks, Cortland Co., NY, 1963.

In hand *Py. linearis* s. l. is a relative small and pale firefly (**Fig. 7**), with body length ranging 8-10.5 mm (**FigTable 8**), in agreement with that given by Green (8.25-11 mm. It is readily distinguished from all others within its range except *Py. dispersa*: *Py. lucifera* has a conspicuously more elongate pronotum (**Fig. 9**), with a pronotal/elytral ratio (PNL/ELL) of 0.32 versus 0.30 in *linearis* (**Fig. 8**). *Py. linearis* and *dispersa* are commonly found together in their shared wetland habitats and though usually seem easily separable, are sometimes confusing; their FPs are very different except in the unresolved possibility of a "pulsing *linearis*." Both may have the same broad range of elytral color variation, from black to tan, though perhaps within single demes coloration is uniform—FP-observed *linearis* were never as dark/black as seen in some *dispersa*.

Flashing behavior; noted variads? The FP of "base" (long-pulsed) *linearis* is a 0.4±-sec-long (**Fig. 10A, B**) dipping or down-sliding, yellow flash emitted just above or amongst vegetation tips, and

Figure 3. Soggy Ed Moon's pasture in the Cowaselon Valley, Madison Co., NY, 1963.

Figure 4. Wet pasture, Otsego Co., NY, 1963.

one that was confused with that of *lucifera*—even collecting a series of four specimens via FP only to find that the voucher series included two of each. Also, the FP period of *linearis* is confusing: at times it is very long, for example, 17 seconds at low temperatures, and sometimes about half this, with both periods being observed in the same deme at the same time (**Fig. 11**). This difference may be connected with reproductive isolation (contra *lucifera*) or used as an anti-predator tactic (contra "*Ph. pyralomima*" females?). The spectral measurements of an 8-specimen sample collected in Madison County NY, 18 June 1968 was: 570, 541.0-610.0 millimicrons.

Figure 5. Expansive marsh near Verona, Oneida Co., NY.

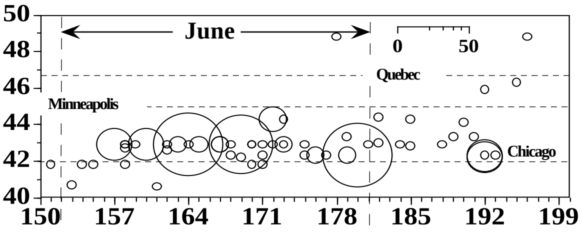


Figure 6. GESEDISOBS (AX: Lat/DOY).

Figure 7. *Py. linearis*.

	Vouch #	PNLen	ELLen	PNWid	BodyLeng	Pn/PwRat	Pn/ElLRat
MI	66364	2.0	7.0	2.0	9.0	1.00	0.29
MI	66366	2.5	7.9	2.5	10.4	1.00	0.32
MI	66387	2.2	7.8	2.2	10.0	1.00	0.28
MI	66368	2.3	7.8	2.5	10.1	0.90	0.29
MI	66413	2.4	7.8	2.4	10.2	1.00	0.31

Mean	2.280	7.660	2.320	9.940	.980	.298
Std. Dev.	.192	.371	.217	.546	.045	.016
Minimum	2.000	7.000	2.000	9.000	.900	.280
Maximum	2.500	7.900	2.500	10.400	1.000	.320

	Vouch #	PNLen	ELLen	PNWid	bodyLeng	PNRat	Pn/ElLRat
NY	66470	2.2	7.8	2.4	10.0	0.90	0.28
NY	66471	1.9	7.0	2.2	8.9	0.89	0.28
NY	66472	1.9	6.8	2.0	8.8	0.94	0.28
NY	66473	2.3	7.4	2.5	9.7	0.90	0.31
NY	66475	1.9	6.1	2.2	8.0	0.89	0.31

Mean	2.040	7.020	2.260	9.080	.904	.292
Std. Dev.	.195	.642	.195	.792	.021	.016
Minimum	1.900	6.100	2.000	8.000	.890	.280
Maximum	2.300	7.800	2.500	10.000	.940	.310

FigTable 8. Sample voucher measurements, and stats.

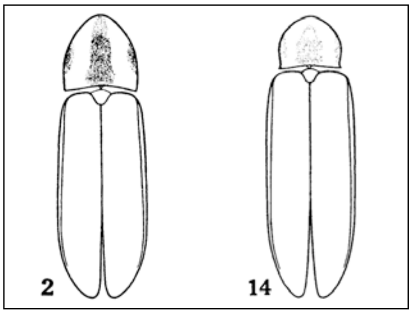


Figure 9. Note relatively elongate PN of *lucifera*, #2, as compared with *linearis*, #14, drawings from Green, 1957.

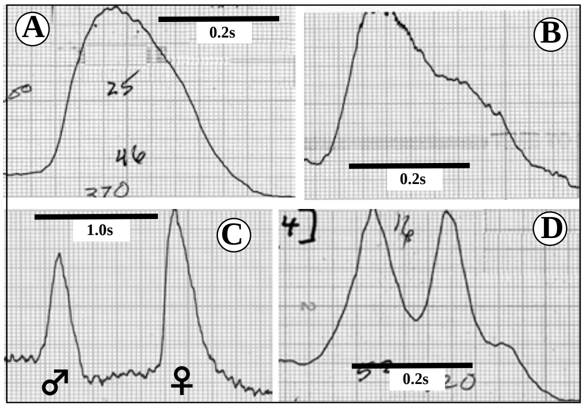


Figure 10. FPs etc., (see Augmented Figure Legends below).

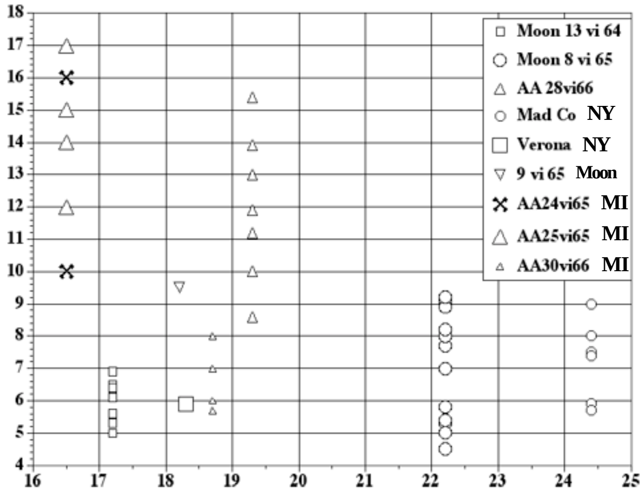


Figure 11. FP periods for *linearis;* see Figure 12 for known *lucifera* records. However, further comparison of specimens and data taken with vouchers are necessary, see text. "Moon" records are Madison Co., NY; Verona, Oneida Co., NY; and AA are Washtenaw Co., MI (AX: sec/temp).

The following accounts are of variads described previously (jel, 1966): "*Long-pulsed linearis*: This species [speculated variad] was observed at Oneida and Milford Center, New York [Figs. 3, 4]. Activity began 40-50 minutes after sunset and continued for about an hour. Males flashed while flying slightly downward 1-2 meters above the ground; 20-50 centimeters were traversed during their flash-pattern, a steady emission estimated to be 0.5 seconds in duration at 66°. Mean flash-pattern interval at 63° was 5.9 seconds. Flight paths of some males consisted of a series of angularly displaced segments. During each flash-pattern they flew in straight lines; between flashes they moved laterally 1-2 meters and rotated a few degrees. As a result during the next flash-pattern they scanned a different area.

"Several females were found in the grass within 1 [yard] of the ground. They responded to male and flashlight flashes with single flashes 1 second or less in duration, at short time delays.

"Attractions of males to free and caged females and to the flashlight were similar. After receiving response flashes from in front of or below them, males dropped immediately to the ground, usually within 1 meter of responding lights.

"*4-pulsed linearis*: This species was observed at McLean Bog, McLean, New York [Fig. 2]. Activity began about 50 minutes after sunset. Male flight paths, including angular displacement, were similar to those described for long-pulsed *linearis*. Male flash patterns were similar to those described for *P. dispersa* (jel, 1964). Flash-pattern interval at 60° averaged 5.1 seconds.

"Females were found on grass stems within 1 meter of the ground; they answered male and flashlight flashes with 4- or 5-pulsed emissions, similar to those of males, at short time delays.

"Male approaches were similar to those described from long-pulsed *linearis* and *dispersa*, in contrast to those described for *borealis* and *Photinus* species.

"*Delayed-linearis*: "On July 12, 1963, considerably later than the season for the previously discussed members of this complex, three males emitting flashes similar to those described for long-pulsed *linearis* were seen at the 4-pulsed *linearis* site at McLean, New York. One responsive female was found in the grass. She emitted single-pulses responses approximately 1 second in duration at an average delay of 1.4 seconds (stop-watch) at 58°. This is possibly a third species in the *linearis* complex, considering that (1) female delay was much longer than that of long-pulsed *linearis*, and (2) long-pulses *linearis* had never been observed in this site during several nights of early summer observations" (jel, 1966)."

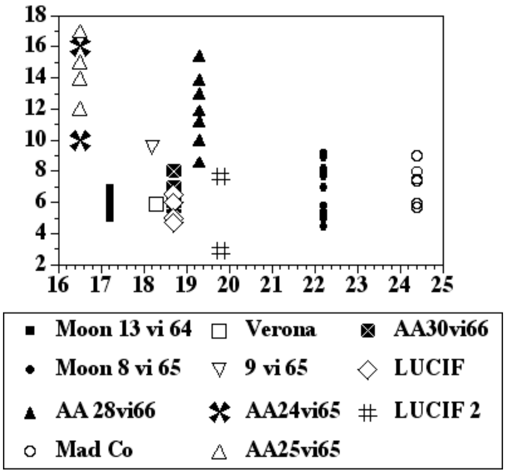
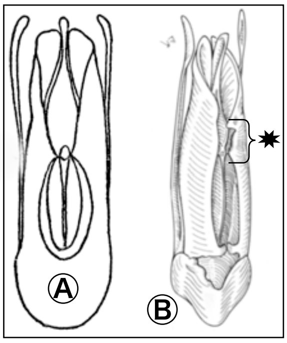


Figure 12. FP periods for *linearis* and *lucifera;* further comparison of specimens and data taken with vouchers may resolve, see text (AX: sec/temp).

Augmented Figure Legends. Figure 10. (**A-D**) PM-recordings of flashes of *Pyractomena linearis* (s. l.): (**A**) FP over the low, wet corner of pasture in Figure 3, near Merrillsville NY, 21.7°/71.1°, 21 June 1976; (**B**) FP over a marsh near Ann Arbor, Washtenaw Co. MI, 20°/68°, 17 June 1967; (**C**) Male FP-female response flash in a cattail marsh (Fig. 5, near Vernon NY, 18.3°/, 8 July 1968; (**D**) Male "FP" showing intriguing modulation pattern. The morphologically and ecologically similar species *P. dispersa* has a modulated pattern, though at this temperature it would be about 5 Hz, not ≈8.9 as seen here. Too much should not be made of this pattern, but kept in mind for future reference—an ancestral circuit switched on, a hybrid, passed behind a couple of (fortuitously-positioned) twigs during the by-chance PM-recording … Same data as in "A".

Taxonomic promise for *Photuris* aedeagi from modern light microscopes and SEMs. John W. Green's taxonomic success with the genitalia of *Photinus* and other genera gave hope that the aedeagi of *Photuris* would be useful for resolving the century-long taxonomic impasse encountered with specimens at the bench, thus making the label-data of hundreds of archived specimens available/useful. Though initially *Photuris* aedeagi were presumed to reveal little variation (**Fig. 1A**), the sharp eye of an artist/biologist (Laura Line) recorded something in the 1970s (**Fig. 1B**), but it passed without attention. Much later, with better microscopes and stained and cleared preparations, it was found that there were several potentially useful points that needed closer examination (**Fig. 2**). Though further study was delayed until pressing studies were completed, the aedeagi of vouchers of several "noteworthy demes" have been removed and prepared for scrutiny. Recently, several but not all scanning electron micrographs (Polaroid® prints) from work done with Pat Carlysle at the USDA in Gainesville in 1972, were rediscovered. Missing SEMs —it was then remembered—had revealed minute points ("teeth") and other distintive structures within the circle in **Figure 3A**, shown here in a cleared specimen photographed through a light microscope and enlarged in **Figure 3B**. This detail is not present in the genitalia of at least some Division I *Photuris*: *congener, frontalis*; **Fig. 4**). Though the recovered SEMs of *Ph. lamarcki* show virtually nothing of the area that looked most promising because of the orientation of the specimen, they will be instructional for the uninitiated—especially, that single individual of/for the next half-century that will continue an eccentric naturalist's obsessive, proprietary study of the genus. The unnumbered figures below are of two *Ph. lamarcki*.



Figs. 1A. Barber/ McDermott figure; (B) L. Line drawing with early unappreciated clue.

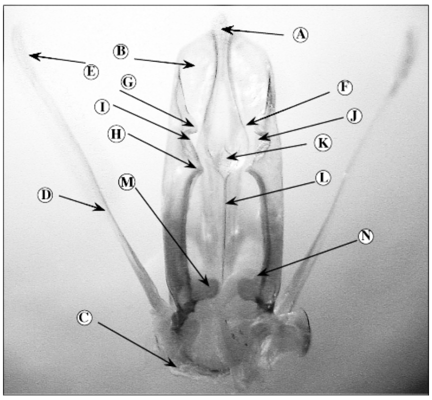
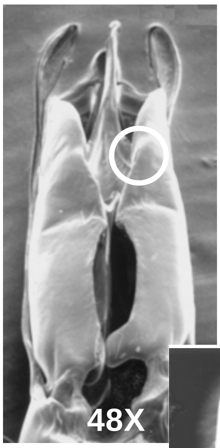


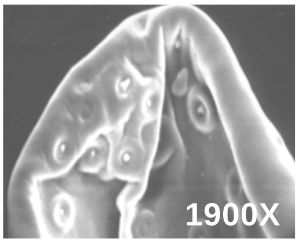
Fig. 2. Anatomical details with points for comparative examination. Note I-L.

A. median lobe
B. lateral lobe(s)
C. basal piece remnants
D. shaft of filament
E. paddle of filament
F. sinuate mesal edge of lateral lobe
G. distal cusp of LL armature
H. proximal cusp of LL armature
I. loop of LL armature
J. veil of LL armature
K. spermatic pore
L. medial septum
M. ventro-basal LL process(es)
N. epilobe of VB LL process

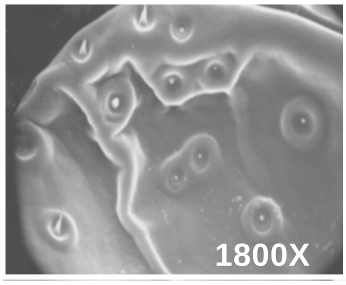
Figs. 3. (A) Cleared, light microscope; (B) enlarged area of interest..

Fig. 4. Stained, cleared: *Ph. congener*.

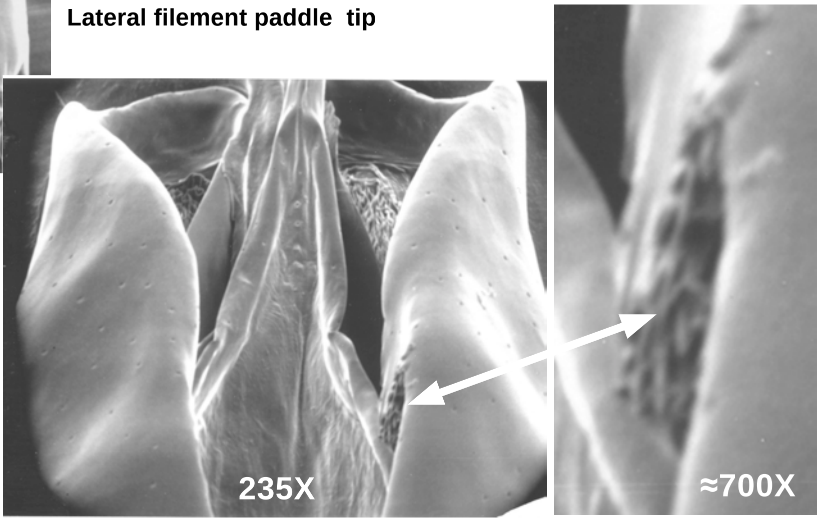




Lateral filement paddle tip



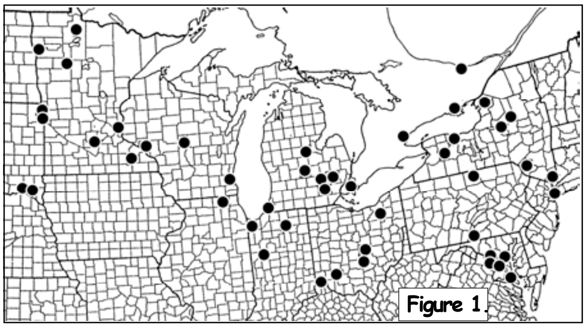
Lateral filement paddle tip



Chapter 84

*Pyractomena lucifera (*Melsheimer) 1845

This firefly remains mostly unknown, a mystery, and a taxonomic uncertainty. With one exception only one or two males were seen active at the same time. This is a sketchy overview of what previously had been the northern section of *lucifera*, the southern section here will be recognized later as a new species. Flashing behavior notes for this species and for *linearis* are similar for specimens observed at the same time and place. They are morphologically distinct (genitalia) and certainly are legitimate species; something has been overlooked—see *linearis* Chapter 79 for more.



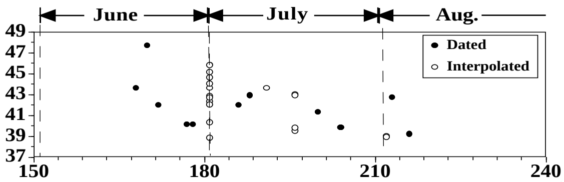


Figure 2. GESEDIS. Py. *lucifera* (AX: Lat/Doy).

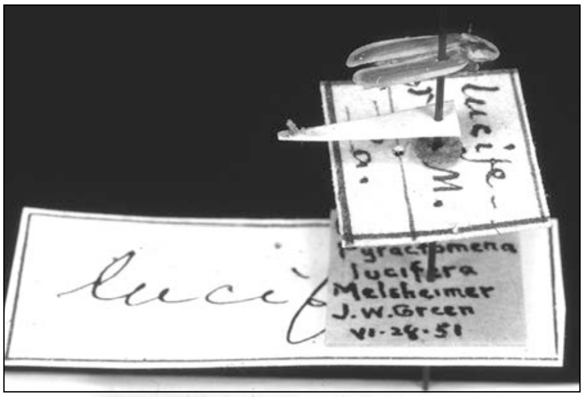


Figure 3. A Melsheimer specimen.; aedeagus pointed by J. W. Green..

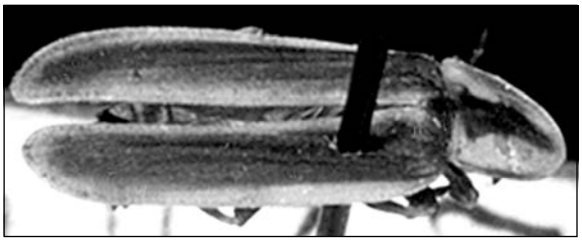


Figure 4. Melsheimer's specimen, from Figure 3.

Py. lucifera (s. s.) occurs through the Great Lakes region from New York to Minnesota and southward to Maryland, Ohio, and northeastern Nebraska (**Fig.1**); adult season of occurrence is from mid-June to early August (**Fig. 2**). Green examined Melsheimer's specimens, none of which had locality data, and designated one of the three as lectotype (nomenclatural name-bearing specimen; **Figs. 3, 4**). We can probably be somewhat confident that it was collected in Pennsylvania, the State of Melsheimer's residence, and within the region indicated in **Figure 1**. Green also included in *lucifera* many virtually identical specimens of more southern origin (**Fig. 5**); these will later receive new-species recognition. Though there no notable morphological differences, more importantly, their known ranges of occurrence suggest that all of the comprising local populations will have been out of contact for a long time, with no point of interaction (cf. **Figs. 1 and 5**).

Py. lucifera was observed in large numbers at a marsh north of Ann Arbor MI (23-29-VI-1966) and elsewhere at marshes and adjacent grassland as a single or a few individuals (**Fig. 6**). Green (:249) noted that "Barber has recorded the flashing of a male specimen, collected at Annapolis, Maryland, as a 'short sharp flash at irregular intervals.'" I observed the FP to be a single orange-yellow flash emitted as the male flies small "Us"/ dips over vegetation tips; it was estimated 0.3-0.4 seconds in duration, and FP period 5.4 sec at 18.7°/66° (**Fig. 7**). And therein lies a rub—this is similar in duration and period to that observed for *Py. linearis*, a far more common firefly that occurs in the same habitat and region, and is morphologically distinctive (different "section?" of the genus). I previously noted that in one *linearis* population females delayed their flash-responses for what seemed to be an unexpected long time (jel, 1965); perhaps this has a bearing on the present *lucifera-linearis* confusion. The two seem to overlap in the range of their FP periods (**Fig. 10**), but this leaves the question unanswered. There is also a continuing confusion in the *linearis-dispersa* distinction, where morphology is in the mix. Note that the seasons of adult occurrence of these two species *possibly* only narrowly overlaps (cf. **Figures 2 and 8**)?

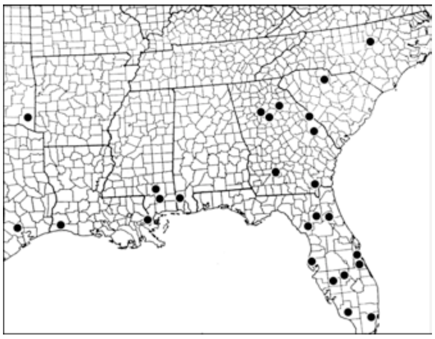


Figure 5. Southern *lucifera* records of occurrence.

In hand. *Py. lucifera* differs from other *Pyractomena* (except southern form) by the proportions of its pronotum (**Fig. 9**); *lucifera* and *linearis* are morphologically distinct and uncertainty will quickly be resolved on the pin via genitalia and pronotum (but a *linearis-dispersa* confusion will remain). Green's measurements of the length of 148 specimens (*lucifera*, northern and southern combined) was 7.5-12 mm; those here for *lucifera* (s. s.) are in agreement (**FigTable 11**).

Extinction?: Perhaps (northern) *lucifera* is being overwhelmed by *linearis*, or has only "recently" spread northward and is marginally successful, or cannot survive in the presence of some smart *Photuris* that is ahead of it in an arms race? We may never know?

Figure 6. *Py. lucifera* site near Vernon, in central NY.

Nomenclatural note. Melsheimer's Latin epithet is one of several used in older literature that is translated as "having light."

Augmented figure legends. Fig. 2. For this species Green only provided months—perhaps all that specimen labels actually provided. For these records I have used the mid-month DOY, as indicated by open circles. **5.** Note the thinning then lack of records north of Georgia and the southern-most records for *lucifera* (compare **Figs. 1 and 5**. **7.** The open circles are FP periods for the southern form, used here as the best indication of what the *lucifera* FP period *might* be. (FP *period* as an adaptation resulting in reproductive isolation has not been demonstrated.)

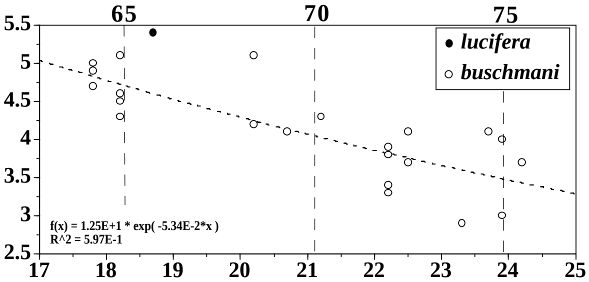


Figure 7. FP period possibility (AX: sec/temp).

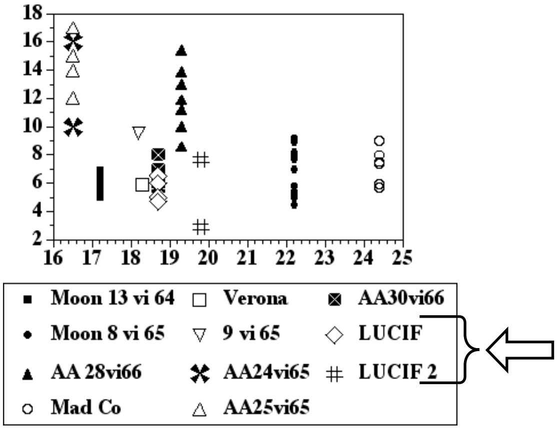


Figure 10. FP periods for *linearis* and *lucifera;* further comparison of specimens and data taken with vouchers may resolve, see texts (AX: sec/temp).

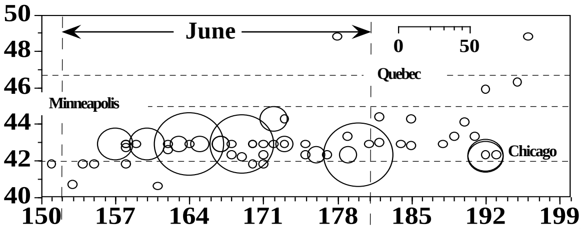


Figure 8. G'SOBS of *Py. linearis* (AX: Lat/DOY/number).

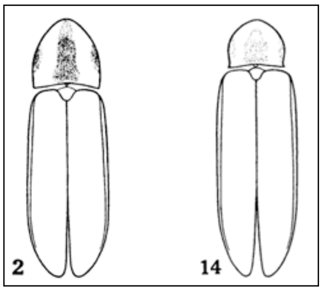


Figure 9. Note relatively elongate PN of *lucifera*, #2, as compared with *linearis*, #14, drawings from Green, 1957.

	Vchr #	PNLen	ELLen	PNWid	TotLen	Pn/PwRat	PN/ElRat
MI	66365	2.5	7.2	2.8	9.7	0.91	0.35
MI	66426	2.5	7.6	2.4	10.1	1.05	0.33
MI	66538	2.2	6	2.3	8.2	0.95	0.37
MI	66420	2.3	9	2.4	11.3	0.95	0.26
MI	66371	2.5	7	2.5	9.5	1	0.36
MI	66372	2.3	6.8	2.3	9.1	1	0.34
MI	66408	2.3	7.4	2.4	9.7	0.95	0.31
MI	66409	2.4	7	2.4	9.4	1	0.34
MI	66410	2.3	7.4	2.5	9.7	0.9	0.31
	Mean	2.367	7.267	2.444	9.633	.968	.330
	Std. Dev.	.112	.800	.151	.823	.048	.033
	Minimum	2.200	6.000	2.300	8.200	.900	.260
	Maximum	2.500	9.000	2.800	11.300	1.050	.370

	Vchr #	PNLen	ELLen	PNWid	TotLen	Pn/PwRat	PN/ElRat
NY	no #	1.8	6	2	7.8	0.88	0.30
NY	68115	2.6	8	2.5	10.7	1.05	0.33
NY	68118	2.6	8.3	3	10.9	0.88	0.31
NY	76173	2.2	7.4	2.4	9.6	0.9	0.30
	Mean	2.300	7.425	2.475	9.750	.928	.310
	Std. Dev.	.383	1.021	.411	1.420	.082	.014
	Minimum	1.800	6.000	2.000	7.800	.880	.300
	Maximum	2.600	8.300	3.000	10.900	1.050	.330

FigTable 11. Morphological measurement stats and ratios.

Chapter 85

Pyractomena marginalis Green 1957

Pyractomena marginalis is a medium to small and dark *Pyractomena*. The occasional presence of a dimmer flashlet immediately after the single *Photinus*-like yellow flash is diagnostic, when season and geographic location are taken into consideration (see below). A flashlet is sometimes emitted by *Pyractomena borealis*, which occurs earlier in the season and is typically restricted to damp woods and swamp forests—its flash also appears "bigger" and longer. Although nominal *marginalis* occurs across a broad span of eastern United States from New England to Texas (**Fig. 1**), active populations were seen only in the Appalachians, and in one curious example, over a hillside heavily draped with the introduced and nuisance Kudsu vine. *Marginalis* occurred in a shrubby hedge row along a wet ditch in a hayfield, and at stream-side woods' edges and groves. Usually only one or a few scattered individuals were seen. Its season extends from mid-May in the southwest to July in the northeast (**Fig. 2**).

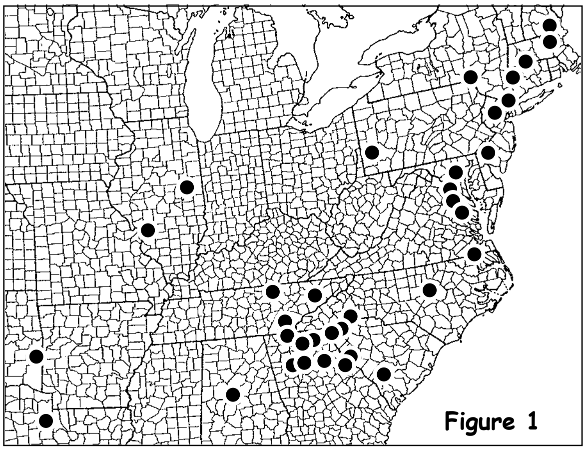


Figure 1

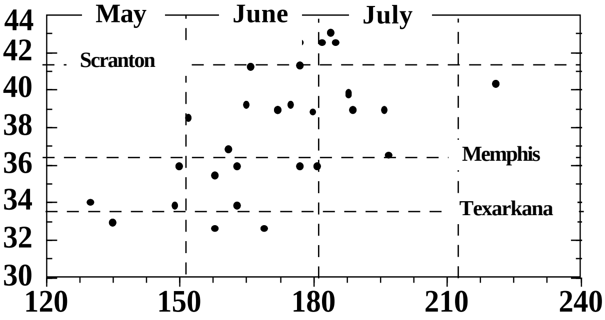


Figure 2. GESEDIS (AX: Lat/DOY).

In the field *marginalis'* FP could be confused with *Pyractomena limbicollis*, a more southern and mainly Florida Keel-Neck firefly with a similar if not an identical FP. The two possibly occur together in Georgia. *Py. limbicollis* is of more delicate appearance with more narrow elytral margins and sharp rather than diffuse margins of the median PN vitta (**Fig. 3**). Couplet 7 of Green's key must nearly always be consulted for certain identification.

Flashing behavior. Males were seen flying up to 10 feet above ground, and seldom far from woody vegetation. They emitted nondescript short, yellowish flashes that could be easily dismissed as solitary, late-active *Photinus*. The clue that attracts attention and instant recognition is the second and nearly always dimmer flash (flashlet) that

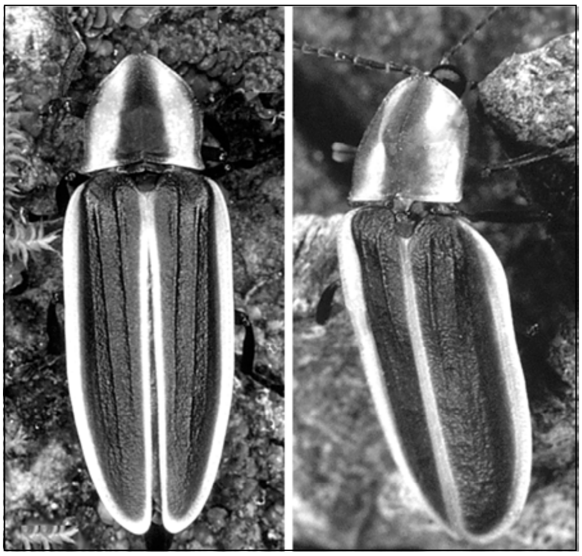


Figure 3 . ***Py. limbicollis* 7-12 mm; *marginalis* 6.2-11 mm.**

occasionally occurs immediately quickly after the bright single flash. This flashlet was never observed to be common. Whether some individuals are more likely to emit it than others, or that all individuals emit it under specific circumstances (age, phenology, level of local predation pressure, competition), or if its occurrence is geographically variable, is unknown.

The flash is estimated to be 150-200mSec in duration (20.8°/69.5°). The flashlet is less than half the apparent brightness of the first. Also, though many *Pyractomena* males glow dimly between FPs, an un-elaborated field note indicated that *marginalis* males do not glow following the flashlet(?). FP period in the sample is irregular, and 3-4 sec in duration at temperatures near 23°/ 73.5° (**Fig. 4**; rate in **Fig. 5**).

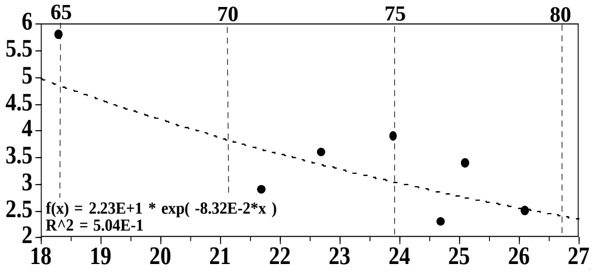


Figure 4. FP period, expon. (AX: sec/temp).

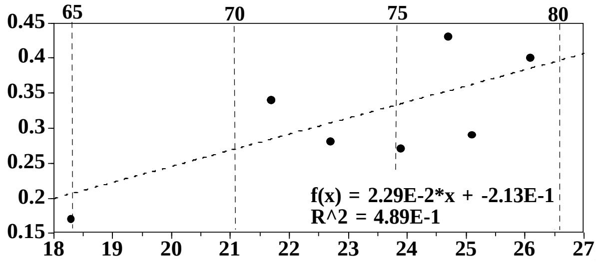


Figure 5. FP period/interval rate, linear (AX: Hz/temp).

Red-shifted *consimilis*-complex puzzle. Some *Photinus* species have orange-yellow luminescence. This extreme shift lines up with what is seen in most *Pyractomena* species, and of course has invited speculation as to adaptive significance. For a visual comparison of the spectra of these groups and further introduction to this note, see page 412. There is an ecological factor that these species share: they are associated with damp, standing water habitats—marshes and pond edges. One early thought was that perhaps being in habitats that had open sky above, the red-shift was an adaptation to enhance vision against a visible-light, noisy background, as suggested for other *Photinus*, or perhaps other electromagnetic raditions from the sky interfered with firefly photoreceptors. I think the answer is simpler, and requires the same thinking that automobile manufacturers discovered a long time ago when they put a set of yellow- or orange-filtered lights on front bumpers.

It seems possible, even likely that the less-extreme yellows seen in many *Photinus* is connected with enhancing vision against twilight green backgrounds. It was one particular exception to the general rule <*Photinus* fireflies emit yellow light> that birthed the color-shift, twilight model: The luminescence of *Pn. tanytoxus* (#8 in **Figure 3**) a dark-active sibling species of the twilight *P. collustrans* is shifted (back?) toward the green! (Curiously, *collustrans'* luminescence is less yellow than that of most other *Photinus*.)

Fog lights. Marsh-inhabiting species of *Pyractomena* and *Photinus* usually have orange-yellow or amber luminescence and are not twilight flyers (**Fig. 3**, bracket 11, and directly above). The suggestion here is not as wild as it might at first appear to those who have not stood in a dark marsh in the Great Lakes region in late May, as the temperature approaches 50° and a cold fog chills in. "Orange" light penetrates fog for a greater distance than does green with its shorter wave-lengths—the latter is reflected back at the emitter from water (fog) droplets, fogging the view, and diffusing the light of communicating fireflies, thus shortening the viewing range. On foggy, marginally cold evenings that inhibit sustained flight (<≈51°F), the marsh and lowland fireflies of Green's *Ph. consimilis* Group—as noticed especially in *Photinus obscurellus*—will often be seen flashing from perches, and coupled pairs are surprisingly rather common. Apparently they make visual contact from their perches and males are able to walk and fly-hop toward females —and vice versa? Those who would test this in a northern marsh, with precision filters over their test lights (not dirty LEDs), and choirs of *Pseudacris (*nee *Hyla) crucifer* and *Pseudacris nigrita triceriata*, are to be envied.

Chapter 86

Pyractomena palustris Green 1957

Closely-related demes (variads) of this firefly would appear to only occur in a narrow lane southward from Washington DC along the eastern edge of the Appalachians, then through the Cumberland Gap to the western side of these old Mountains, and then southward, gradually turning westward toward Mississippi and Arkansas (**Figs. 1, 2**)—with much of this track a long arc within a specific climatic zone (**Fig. 3**), and curiously, as it happens, with FP-known localities twice neatly fitting neatly into little marginal irregularities of that zone! Impossible. Surely, this cannot really be correct, though in one view of the available taxonomic-geographic data, it could be. Another view is that *palustris* has been found at localities outside the zone (**Fig. 4**), a view that is not as interesting, nor intriguing. Support for the second view is that there are archived specimens that could be *palustris* but differ in some respects, and in such as way to have caused Maestro Green to have considered them a less-than-resolved subset of *Py. dispersa*. Their position in his Key is the consequence of a couplet that separates species of "Southern States" versus "more northern distribution"—a reasonable solution, and he probably had other finer details such as elytral pubescence complicating matters. So it is that for the moment *palustris* is but one of a *Pyractomena* quartet of taxonomic confusion—*dispersa*, *linearis*, *palustris*, Hudson—that will not be resolved here, nor easily thereafter. But, that there are at least three legitimate species-worthy entities cannot be denied: one a little U-dipper in northern marshes (*linearis*); one a flare-flashing, wetland firefly from DC south to and across southern States via a narrow belt (*palustris*); the third, a widespread, pulsing, damp-meadow inhabitant, that is broadly sympatric with the others (*dispersa*)., and finally, a species with a signal similar to that of *sinuata*, a species of another genitalic group.

FPs of these four are diagnostic—the yellow FPs of *P. lucifera* in the north and its southern form may be confusing—and separation from *palustris* require in-hand examination. Useful characters are the basally-broadened, sub-triangular median PN vitta and diffuse lateral vittae of the *palustris* PN; its dark piceous mesonotal plates and scutellum; and somewhat larger size (10-13.5 mm). Green observed pale grayish brown elytra and narrowly paler discal costae, but TN specimens have totally dark elytra (**Fig. 5**). The yellow FPs of some *Photinus* species will be confused, but *Photinus* generally appear later in the season, and in hand they are quickly distinguished by their non-keeled, semi-circular pronota.

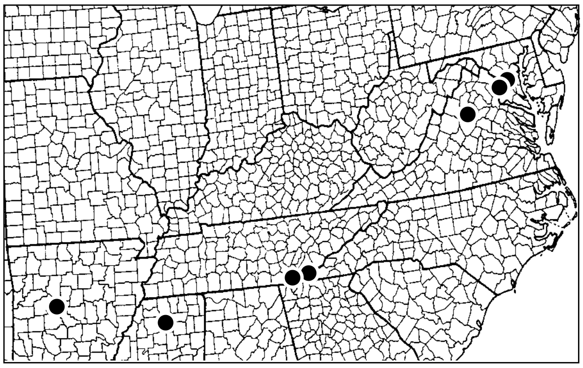


Figure 1. FP-associated counties of occurrence.

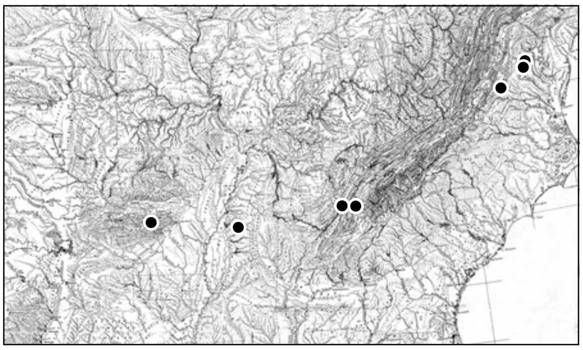


Figure 2. Physiographic perspectives.

Ecology, flashing behavior. *Py. palustris*—the epithet meaning marsh or swamp—was found in damp meadows in Tennessee and Arkansas (**Fig. 6**), a young/early oldfield near Oxford, Mississippi; and a Perry County, Arkansas site, which was a grassy roadside. Seasonal occurrence based on archived specimens and personal observations is within May at all latitudes, but extended into June in the often-visited Gee Creek site in Polk County, southeastern Tennessee (**Fig. 7**). Observations on flashing behavior and ecology are in general agreement with those of Barber. The FP typically appears as a metallic-yellow (coppery) flare that is emitted on average at 4-second intervals at temperatures near 21°/70° (**Fig. 8**; rate in **Fig. 9**), as the insect glides, dives, or dips down into or just at the top of grassy/herby vegetation. Green (1957:279) reported a label on a Barber flash-voucher: "Barber recorded the flashing of a male as 'three-fourths second crescendo flash diving into grass of marsh at three second intervals'". The duration of the male flare-like flash as estimated and measured with a stopwatch varies from 0.5-0.75 sec at temperatures near 16°/61°, to 1.5-1.75 sec at 12°/53 °. PM recordings show similar

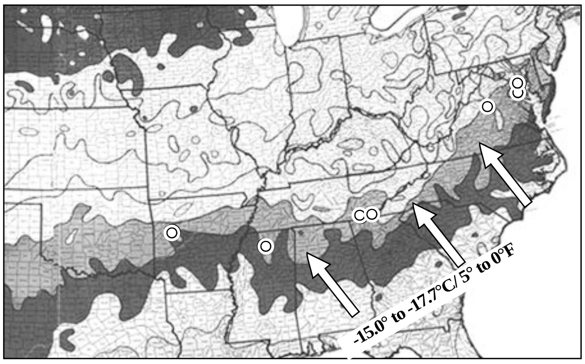


Figure 3. Records within a specific zone of mean winter low temps? USDA Plant Hardiness Zone Map, H. M. Cathey, Misc. Pub. 1475.

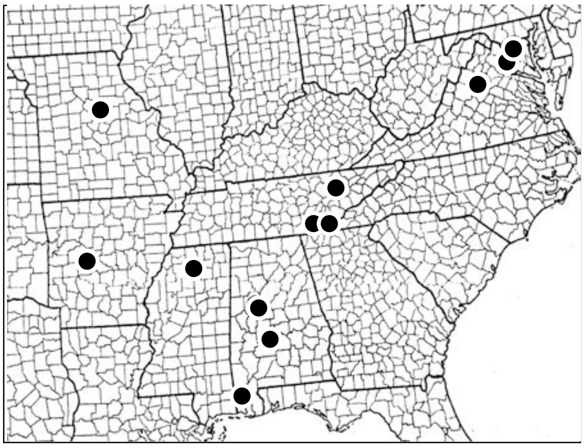


Figure 4. Another (total) view of *palustris* problem.

Figure 5. *Py. palustris*.

Figure 6. Wet meadow site in se TN.

durations, and at 15.5°/60° they also show a wingbeat frequency of 43.7 Hz (n=3 flutters on flashes, s=1.9 Hz; **Fig. 10E-H**). Inexplicably, occasionally the flaring FPs of this species appeared to be a bright metallic green!, and sometimes appeared to glide or slide in a "liquid" trajectory, as though carried on a sled. Occasionally the flash is emitted during rising flight, and then its resemblance to the flash of *Photinus pyralis* is notable. During emission 1-3 feet are flown. There are no sharp transients in the flash, and the light-organ typically glows dimly between flashes, at which time 1-3 yards are flown. Because of their bright, flaring, yellowish flash, an interesting illusion is created when a glowing male approaches, stops, and remains stationary during his flare—he appears to slowly ignite and burn up, incinerate

Some PM-recordings in southeastern Tennessee show Barber's crescendo (**Fig. 10A, B**), but flashes also appear or are recorded as having other forms: including bimodal crescendos (**Fig. 10C**), modulated decrescendos (**Fig. 10D, I**), and near-symmetrical flickers (**Fig. 10E**). One commonly seen form was a bimodal flash that flared then dimmed then brightened again briefly, as caught by the PM in **Figure 10I**. Limited observations of flares emitted by perched males suggest that at the lantern (i.e. the actual photic emission) it is not modulated; if so, always, the flash is a simple, slow-rising, slow-falling bright surge. However, on two occasions from a view under the tails of a flying, flaring male, the flash appeared to be bimodal—perhaps segment asynchrony?

If flashes are emitted at the lantern as unmodulated flares, then the modulation patterns seen, result from males wagging their abdomens or twisting in flight (or a view of segment asynchrony). Such movement has been noted in flickering *Pyractomena* species, such as *angulata* and *barberi*, and possible is coordinated with light-organ modulation. Because *palustris* is apparently closely related to *Py. dispersa*, a species that has a well-developed and consistent flicker for its flash pattern, a close comparative study of the two might tell something of the evolutionary relationship between flare and flicker flashes—and the physical beginnings of the flicker with tail wagging. A sample of the crude but apparent modulation patterns from PM-recordings in **Figure 10** (**D, E**) gives a mean frequency of 5.1 Hertz (15.5°C/60°F), whereas *dispersa* has a frequency of 4.7 Hertz at this temperature. Barber collected more than 50 *palustris* males from three localities near Washington DC, and apparently noted only a crescendo flash.

Females. Females perch in the grass during evening flashing activity, sometimes climbing all the way to the extreme tips. They answer males with a nondescript, yellow flare that is emitted about 1 sec after the male flash begins (16°C/61°F). When answered, males do not flare again from the air, but fly or drop to the substrate and pause a long time before flashing (e.g. 2+ min), as noted in many other but not all *Pyractomena* species.

Notes. As with certain other Keel-Collared fireflies, *palustris'* absence from collections may be due in part to its early-spring adult season, but it is not of common occurrence. It was absent from collections that seem generally to have good lampyrid representation. It would seem curious that the range of this species is through a gap in the Appalachians and not south along the coastal plain and then westward around the mountains as indicated for *Py. similis.*

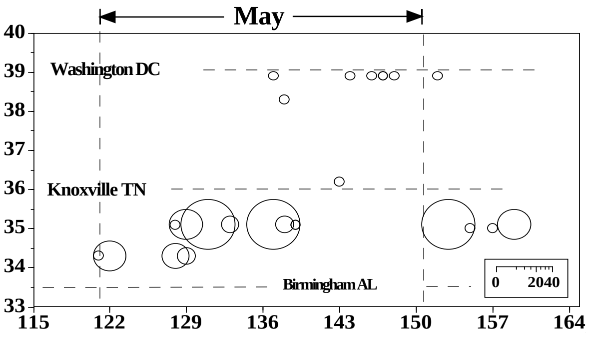


Figure 7. GESEDISOBS (AX: Lat/DOY & Number).

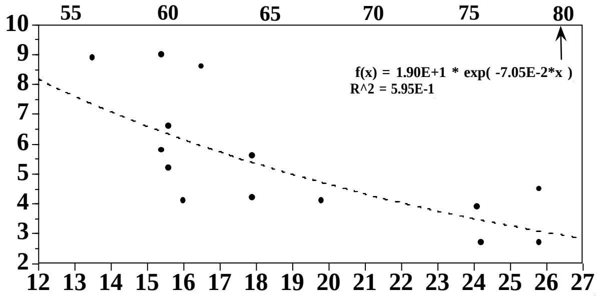


Figure 8. FP exponential regression (AX: sec/temp).

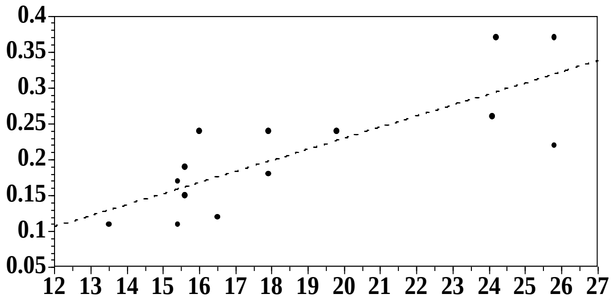


Figure 9. FP period rate regression (AX: Hz/temp).

Augmented figure legends. **3**. This is the Dept. of Agriculture's "Plant Hardiness Zone Map" (Misc. Pub. 1475), a huge (plastic coated?) colored wall map. It shows the lowest temperatures that can be expected. **4**. This map includes label data of specimens that may be *dispersa* variants, in AL and MO, from Green (1957). Suspicions that additional hitherto unrecognized, name-worthy species may be involved must be kept in mind. **7**. GESEDISOBS (combined archives and personal observations) are included; the smallest circles are "noted present" or archival records, and others according to the *number*-quantifying scale shown—in the chart, 20 and 40 are "squeezed/run" together.

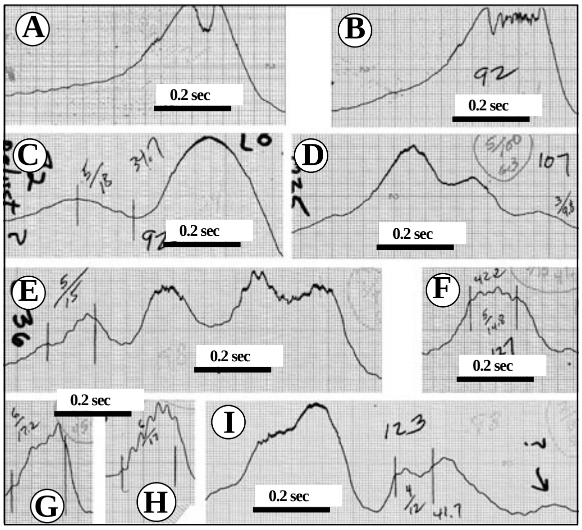


Figure 10. PM-recordings (AX: rel. int./time; see FLS).

"... all those who are much occupied with the study of natural history, know that naturalists now find it extremely difficult to decide what objects should be regarded as species. / They are in fact not aware that species have really only a constancy relative to the duration of the conditions in which are placed the individuals composing it; nor that some of these individuals have varied, and constitute races which shade gradually into some other neighbouring species. Hence, naturalists come to arbitrary decisions about individuals observed in various countries [counties] and diverse conditions, sometimes calling them varieties and sometimes species. The work connected with determination of species therefore becomes daily more defective, that is to say, more complicated and confused." J. B. Lamarck, 1809

Luminescence color considerations/speculations. Hundreds of specimens were mailed alive in canisters to William Biggley and Howard Seliger at The Johns Hopkins University for spectral measurement beginning in 1964. A few early results were published (Biggley et al, 1967). For several years the spectra of additional species were analyzed. All results, including peak wavelengths and wavelengths at half-maxima are listed in Appendix 3, with techniques then used for mailing specimens (pages **432-4**). From the beginning the color of firefly luminescence was considered as an adaptation to be considered from an evolutionary standpoint. This note offers a brief comparative look at these spectra, asks some questions and raises some considerations. Portable spectrum analyzers are available for use in the field today. Human color perception can err greatly (amber even appearing green sometimes to some eyes!) when evaluating color. For use as crude reference colors, transparent color films in swatch-books, which are accompained by spectral measurement charts, are produced by Vincent Lighting Systems. (Such filters are used in commerciial lighting and stage lighting in theaters. A few in particular would be useful references to prevent the worst of errors in the absence of a spectrum analyzer (606-344-1900; 800-356-5356*; **Figs. 1, 2**)

Figure 1. Swatch book. The transparent films appear black in this photo (arrow).

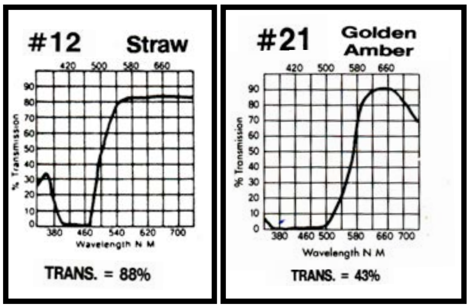


Figure 2. Charts accompanying and behind two color films.

Figure 3 shows the arrays for peak wavelengths of the emissions of species of three flashing genera and three additional species. The following is a list of generali-zations and observations in reference to these arrays. Following the list is a suggested explanation for some of the extreme long wavelengths measured in the lab and often conspicuous in the field.

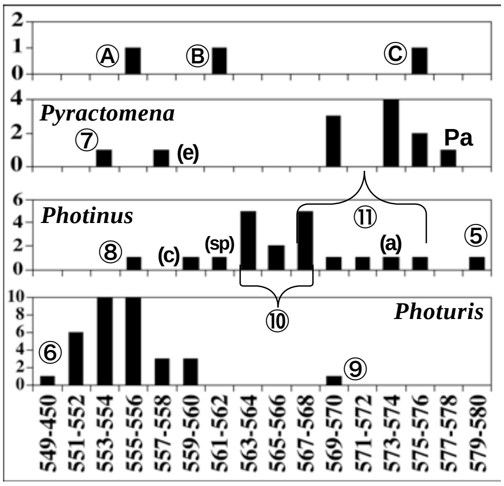


Figure 3. Arrays for three lightningbug genera and others: In top array, (A) Ellychnia corrusca larva. (B) Lucidota luteicollis. (C) Micronaspis floridana. For numbers and lower-case letters in other arrays, see list and text. (AX: No. of species/peak wavelength in mmicrons).

1. Mean wavelength of all in sample: 561.8.
2. Peaks range from 549 (green) to 579 (orange-yellow, amber).
3. Half-max spectrum width for the three main genera is about the same.
4. Peaks of *Pyractomena* average longer, those of *Photinus* are in the middle, and those of *Photuris* shorter and more compact as a group.
5. *Pn. scintillans* has the longest wavelength at 579. I find this puzzling, since in the field its flash appeared orangish-yellow but that of *Py. angulata* (**Pa**) always appeared a more red-shifted amber!
6. *Ph. douglasae* has the shortest peak wavelength at 549
7. The peak of *Py. angustata is* the most green-shifted of the two green *Pyractomena*, perhaps because its glow is an advertising signal, and that of *Py. ecostata* (**e**) is not to stimulate female responses at maximum distance possible, but is a much dimmer glow as though leaking from a malfunctioning or more primitive(?) lantern.
8. The most green-shifted of *Photinus* is *tanytoxus*, the post-twilight sibling of twilight *collustrans* (**c**) which surprisingly emits luminescence that is "greener" than that of all other *Photinus*(!?).
9. The luminescence of *Ph. frontalis* is significantly red-shifted from the other *Photuris* which clump at short wavelengths. *Frontalis* begins flight earlier than other *Photuris* and also synchronizes its flashes more extensively than noted in other *Photuris* Division I species.

   Either of these behaviors, both potentially benefitting from enhanced vision in a green environment, may explain the color difference.
10. Twilight *Photinus* mostly clump together except for *acuminatus* (**a**) which is a special case and more red-shifted. This rare species flies earlier than other Division I, has a very short, sharp, bright flash, and to guess, it has escaped predation by flying ever-earlier with a flash that is very conspicuous—but is losing the battle with extinction.
11. Most members of the *Pn. consimilis* complex clump at the red-shifted end of the spectrum, positioned with most *Pyractomena* species seen in the histogram above theirs. An exception Slow-Pulse *consimilis* (**sp**) which flies over floating/emergent vegetation in ponds in north Florida and southern Georgia. No *consimis* (complex) are twilight flyers. The (an) explanation is not complex but will give the marine biologist I mentioned elsewhere in this paper with respect to speculation, terminal fits. See page 408.

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Chapter 87

Pyractomena similis Green 1957

> *Full many a flower is born to blush unseen,*
> *And waste its sweetness on the desert air.*
> Thomas Gray

The geographic occurrence of this firefly could well extend from the Mason and Dixon Line nearly to the Mississippi delta, via the coastal plane and piedmont, and then south around the Appalachians (**Fig. 1**). Except for one record, in South Carolina, there would be a considerable hiatus extending from central Virginia, to central Alabama. Insufficient collecting is a commonly invoked and a legitimate explanation for such appearances and other fireflies have similar disjunct collection records—*Photinus marginellus* and *sabulosus* as examples—but after decades of focused collecting including many nights in the region in question without sighting *similis* it is reasonable to suspect that the break might be real. If so, it could be of long duration, since the Wisconsian glacier-age, or perhaps the result of 200-300 years of abusive unrelenting agriculture which obliterated natural habitats.

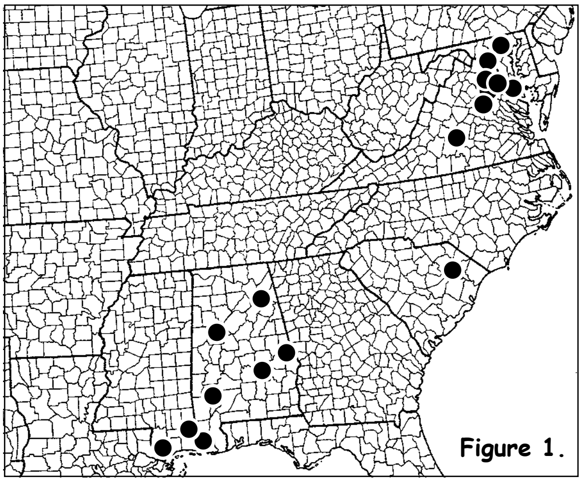


Figure 1.

Py. similis was seen on an oldfield slope about 50 yards east of the Appomattox River, at Appomattox Courthouse, Virginia, a half mile below the Courthouse and a dozen yards from the spot that tradition says General Robert E. Lee waited under an apple tree for word from General Grant regarding plans for ending the Civil War (**Figs. 2, 3**). It also occurred near the Confederate cemetery a quarter of a mile above the Courthouse, in a mowed field next to the Raine monument (**Fig. 4**).

Figure 2. Early-oldfield sloping toward a damp area.

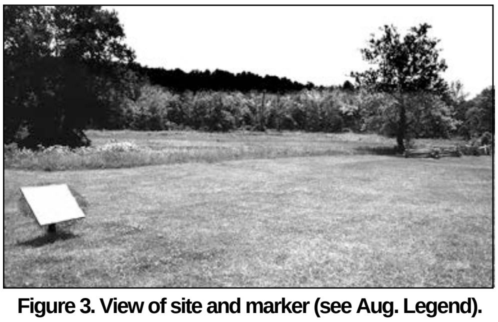


Figure 3. View of site and marker (see Aug. Legend).

Adult activity begins in mid-April and extends through May in the south and through May into June in the north (**Fig. 5**).

Flashing behavior. The FP is a continuous, occasionally broken train of short but not sharp, amber (or rosy) flashes that are emitted at short intervals (May 1983, n=5: 573, 546.0-613.0 millimicrons). Flash interval varies with temperature and ranges from about 1 sec at 11°C/ 52°F, to 0.5 sec at 17°C/62.5° (Figs. 6. 7). Trains of flashes were sometimes broken briefly, and sample counts for unbroken series were 8, 15, 20, and 27 flashes. A total of 8 recorded flashes from two males were examined. They are nearly symmetrical in form, and 160(90)-180 (110)mSec in duration (nr 14°C/57°F; Fig. 6). Barber's flash notes on specimen labels were as follows (Green 1957:255): "3 flashes at 1 second intervals, flying"; "6 flashes at 1 second intervals, on twig, cold"; "11 flashes at about 1 second intervals, long rest, not flying, cold." In Lee's weedy old-field (**Fig. 3**), males flew at the weed-tops; over the mowed area they flew at 3-6’. Their flight was straight and moderately fast.

For identification, when only a preserved or pickled specimen is available, this firefly is most likely to be confused with *Py. angulata* (**Fig. 9**). Male genitalia are distinctive and diagnostic, and the setal condition on the basal, humeral regions of the elytra (absent or thinning in *similis*) is useful but less reliable. Body length is 8-12.75 mm, ex Green. In the field, the flash patterns of the two *Pyractomena* are definitive, and not likely to be confused with those of any other North American *Pyractomena* fireflies (but see under *Py. angulata* and *Py. barberi*). The color and timing of the flashes, taken with the early season of activity, will usually enable the experienced observer to identify *similis* in flight from flashes alone, but late in its season the yellow-amber-appearing flashes of certain *Photinus* species, such as those of *P. brimleyi* could cause confusion. Note also that green-train-flashing *Photuris* occur in part of the *similis* range.

Figure 4. Confederate Monument site.

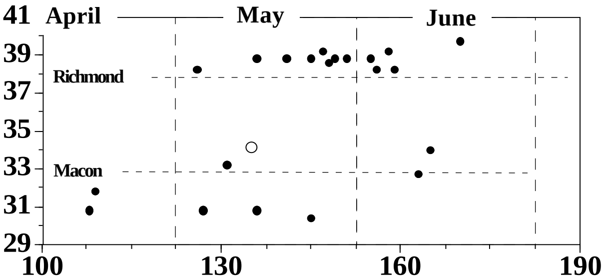


Figure 5. GESEDIS (AX: Lat/DOY).

Augmented figure legends. 3. The marker at this site provided the following: "Near this spot stood the apple tree under which General Robert E. Lee rested while waiting the return of a flag of truce sent by him to General U. S. Grant on the morning of April 9 1865." **5**. The open circle marks a record that reported only the month and locality. Because of the significance of this record, it is included, placed on May 15. **10**. One of the many camping shelters used from 1963 to 2013: a small pickup backed slightly under a large canvas fly supported by a center-pole.

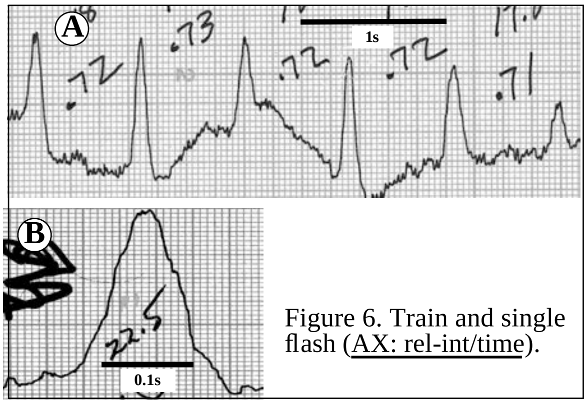


Figure 6. Flash train and single flash.

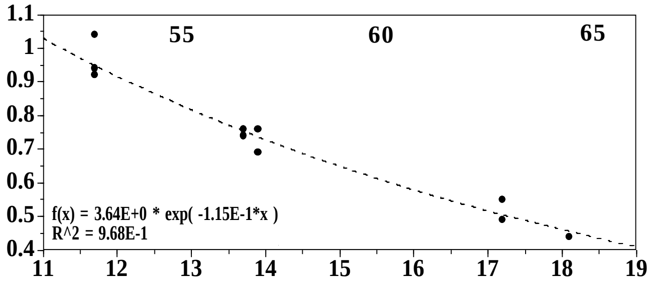


Figure 7. FP period, expon. (AX: sec/temp).

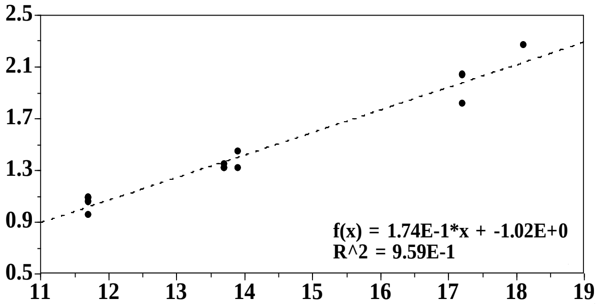


Figure 8. FP period rate, linear reg. (AX: Hertz/temp).

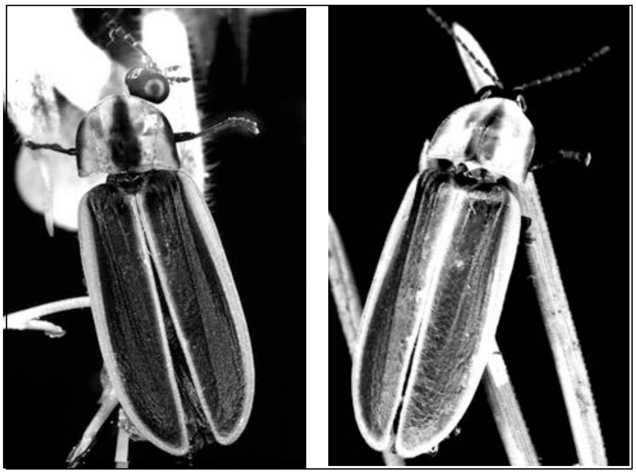


Figure 9. Note pronotal carinula (little keel) along the mid-line.

Figure 10. Campsite at Appomattox, 1983.

Chapter 88

Pyractomena sinuata Green 1957

To be able to concentrate on the same matter
for a considerable time is essential to difficult
achievement, and even to the understanding
of any complicated or abstruse subject.
Bertrand Russell, 1927

Based on early decades of field experience and review of archived records in Green (1957), it was concluded that *Pyractomena sinuata* had become an uncommon firefly of reduced geographic and seasonal distribution, that had disappeared from the eastern portion of its range and was now rare elsewhere in North America north of the Rio Grande (**Fig. 1**). However, at the western limits of its known U. S. occurrence, North Dakota and Nebraska, it was found in numbers, and later was finally found in isolated sites in the east, in Vermont and Connecticut. This almost-lightningbug (see below) appears to have a rather short, mostly June appearance throughout its mostly-northern range (**Fig. 2**), and there is one small indication that eastern and western populations may differ in one potentially significant detail. As the case with other members of its genus, *sinuata* seems to be a firefly of wetlands and damp or adjacent grasslands.

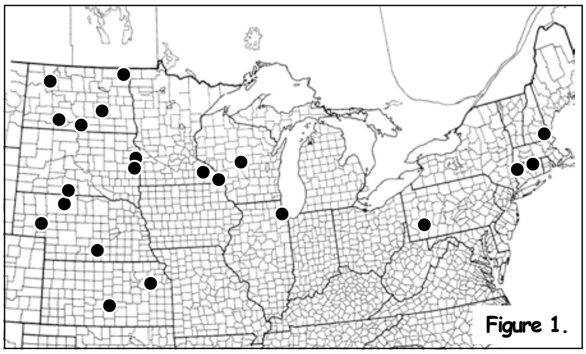


Figure 1.

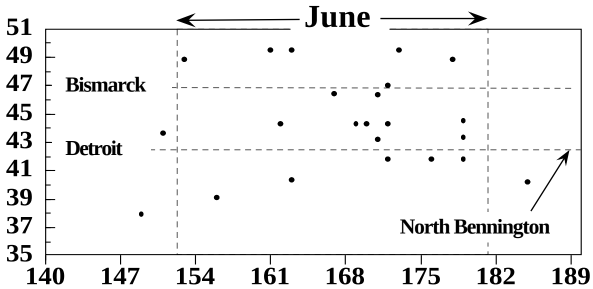


Figure 2. GESEDIS (AX: Lat/DOY).

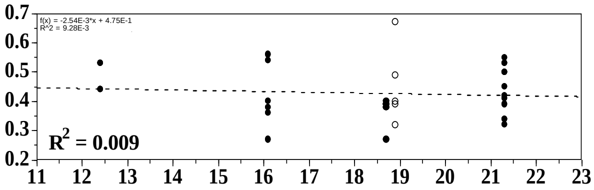


Figure 3. Duty cycle regression (AX: ratio/temp).

Py. sinuata is easily identified in the field, within its known range, by its coppery “FP” which usually appears as a short glow, one that is about half as long as its “FP” period: its ON-time (glow duration) averages almost as long as OFF-time —expressed another way, it has a *duty cycle* of about 0.4 (ON/ON+OFF; **Fig. 3**). Note in the figure that the duty cycle is temperature independent. The duty cycle of *sinuata* is longer than that of most other firefly species belonging to "typically flashing" genera. Though the glow generally appears to be unmodulated PM-records and an occasional glimpse/impression in the field, reveal moderately slow pulsing, and also occasional wingbeat shuttering (**Fig. 4**).

Emissions of sympatric, congeneric flashing species found in the same habitat are distinctly modulated (*Py. angulata*, *dispersa*) and have much shorter duty cycles. Glowing *Phausis* species may occur in the southern part of *sinuata's* range, but are rare, will probably occur in a woodland habitat, and in hand are easily recognized. They and *Photuris* species have green luminescence, *sinuata's* is yellow. In hand, note *sinuata’s* keeled PN (**Fig. 5**).

Ecology. Populations were found near marshes, river backsets, damp swards and ditches, and other flooded grassland: in Nebraska: over low portions of agriculture fields and ditches on Route 44, 2.3 miles south of the Platte River bridge at Kearny (**Fig. 6**); at the Route 26 bridge across the North Platte River near Lewellen (Ash Hollow), where a few scattered males flew over the ditch, sward and hayfield that were adjacent to the river's marshes; in the Sand Hills at several sites over meadows, hay, swards and wet ditches (**Fig. 7**). In North Dakota it was not found at sites where specimens had been collected a dozen years earlier by Paul Lago—along Beaver Creek near Linton on Route 13—nor in promising wetland where this creek joins the Missouri River (**Figs. 8, 9**).

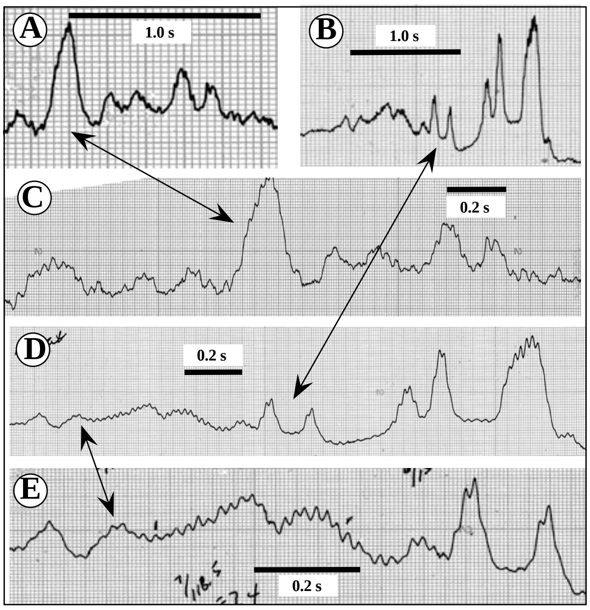


Figure 4. CT (A, C) & VT (B, D, E); note chart speed.

Figure 7. A Nebraska Sandhills wetland.

Figure 5. Note keel, elytral costae.

Figure 8. Beaver Creek at Missouri River: top, the Missouri in the distance; bottom, view of Beaver Creek upstream.

Figure 6. Nebraska roadside near Kearny.

Figure 9. Overview of Beaver Creek at the Missouri River.

Figure 10. Bridge at Stuttsman Wildlife Refuge, ND.

Figure 11. Farm Road oldfield site, Avon, CT.

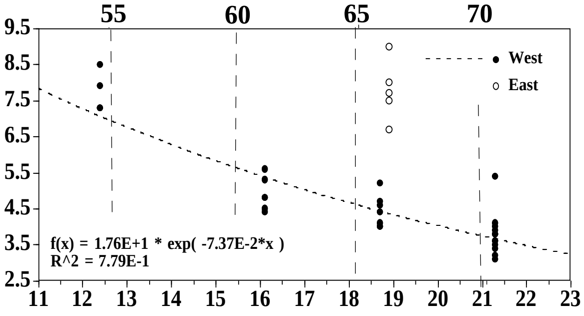


Figure 12. "F(glow)P" period (AX: sec/temp).

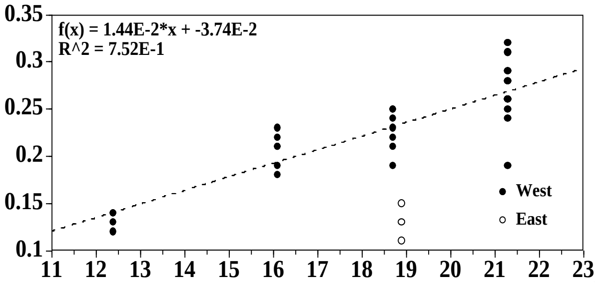


Figure 13. FP period rate (AX: Hz/temp).

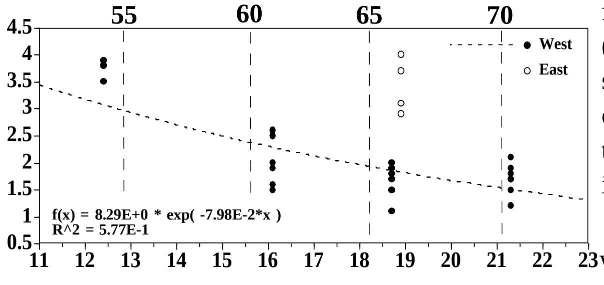


Figure 14. FP duration, exp. regression (AX: sec/temp).

It was abundant in early June at the Arrowwood National Wildlife Refuge, Stutsman County, at the main bridge near Headquarters, where males flew over the sward and herbage adjacent to a marsh (**Fig.10**). Curiously, though several were active at the Arrowwood site on 11 June 1991, four and five days later only one male was seen in a long and careful search; the seasonal window of adult activity at a given site may be brief. In the east, the Vermont site was a hayfield, and the Connecticut site, a maturing oldfield (**Fig. 11**).

Luminescent behavior. Males fly at moderate speeds in winding sometimes twisting flight near the tops of hay and other herbage, and usually emit their glow-like "FPs" with a regular periodicity comparable to the periodicity of the FPs of other lightningbugs. Glow periods varied, in most cases, with temperature (**Fig. 12**; rate in **Figure 13**); note the difference between western and eastern observations. (It seems too large to be an error in temperature or time measurement?)

On most occasions the duration of glows ranged from about 1 sec to 4 sec, and was without apparent transients or visually distinct/certain modulations, but the two PM-records clearly show crude modulations at rates seemingly too high to be from tail-wagging (**Fig. 4**). The duration of “normal” glows varied with temperature from less than 2 sec near 70°/21°) to nearly 4 sec at (12°/53.6°; **Fig. 14**). Rarely glow duration was more than 10 sec, then interrupted by a brief <1 sec OFF, and this was followed by another lengthy glow. This was observed on two occasions, late in the evening (3+ creps), in rain and wind on both occasions.

Three different modulation rates were calculated from the two FPs; the two most reliable are plotted in **Figure 15** (the third is also shown in **Figure 16**); extrapolation provides a working prediction across a broader temperature range. As noted in Chapter on *Py. dispersa* and the Ann Arbor flickerer, there is an unexpected agreement among the modulation rates of these three demes/species, this in spite of the erratic and crude nature of *sinuata’s* flicker (**Fig. 16**).

Miscellaneous notes. To get another view of the duty cycle, ON and OFF durations were plotted as axes of a Cartesian chart—OFF-time of each cycle was regressed on the ON-time (**Fig. 17**). If the duty-cycle were 0.5 measurements would fall along the dashed line with arrowheads at each end, as shown in the 3/3 intersection (white arrow). In actuality it fell very loosely, on average, along the computer-generated (heavy dashed) line—maybe future comparisons will suggest something. The eastern and a very few of the western observations fall to the right perhaps indicating a mode shift that has become more common in the east . . . Another view is in the 3-D graph **Figure 18**.

The two PM-records clearly show erratic modulations that would seem too rapid to be body movements (**Fig. 4**). Is a flicker coming and/or going—such uncertainties are enjoyed

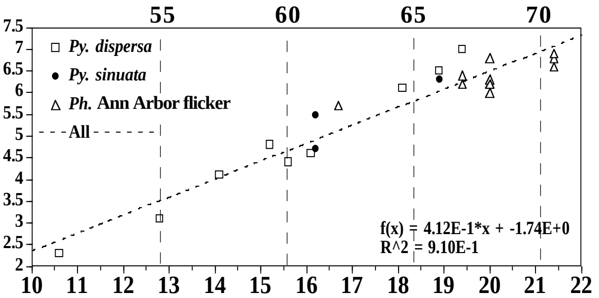


Figure 16. Comparison of mod-rates (AX: Hz/temp).

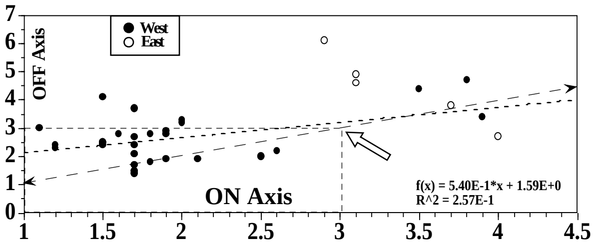


Figure 17. OFF/ON regression (AX:On sec/Off sec).

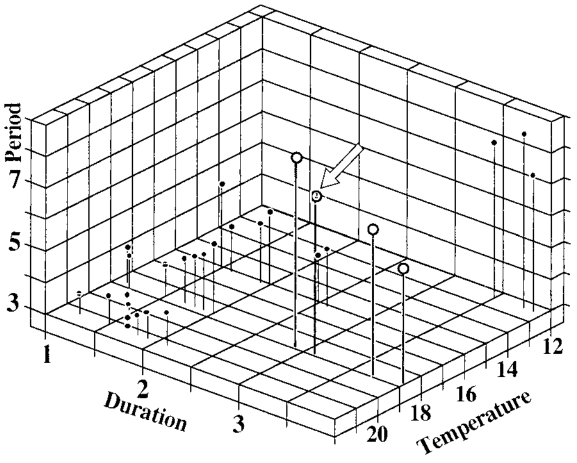


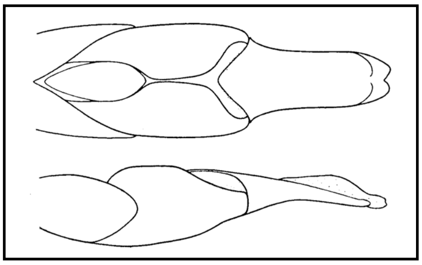
Figure 19. Eastern outlyers are white balls (AX: duration/ temp/period).

because perhaps we see often-elusive intermediate stages in the evolution of FPs?

High-frequency modulations appear in both PM-records, but only in the Vermont trace is it possible to get a clear reading (**Fig. 4B, D, E**): 18/45 = 50.0 Hz; 6/15 = 50.0 Hertz, at 18.9°/66°. The Avon CT trace (Fig. 4A, C), is somewhat/ questionably readable at one high point: 5/11 = 56.8 Hertz, at 16.2°/61.2°. Note: chart speed 125 mm/sec. Therefore, 18mods:45mm=X:125 = 2250/45 = 50.0 Hz.

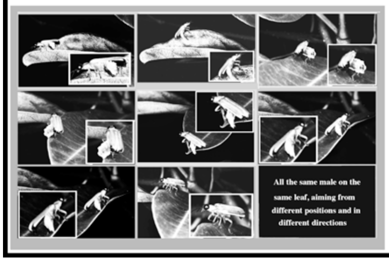
Green's species epithet probably refers to the strongly *sinuate* (S-shaped) ventral, inner margins of the lateral lobes of the male aedeagus.

Augmented figure legends. **1**. Perhaps *sinuata* originated in the southern midwest during Wisconsian glacial time and moved eastward through scattered wetlands in the prairie peninsula during the xerothermic period—having since largely disappeared from what is now northern Indiana and Ohio where there has been extensive agricultural and urban development. **4**. **A** and **C** the same record at 25 mm and 125 mm per second, at 16.2°/61.2°, Avon CT, 18 June 1992. **B, D, E** the same record, at 25 mm and 125 mm per second, at 18.9°/66°, near West Halifax, VT, 19 June 1993. **9**. Empty campground, Lewis and Clark paddling upstream in the distant fog, and solitude.



***similis:* similar to *sinuata* (Green, 1957)**

In firefly trees of southeast Asia how do approaching females select a place to land? As a base for answering this, what do males on their perches do that might suggest how they make their leaf competitve, the one to land on? Do males hold territories and threaten males that approach? The photos below may suggest what to do when you get to a firefly tree. The composite at the left are all of the same male as he aims in different directions—aiming at females, or threatening neighbor males? To research, how are different individuals to be identified, recognized, if they change leaves? Bee tags are too big.



All the same male on the same leaf, aiming from different positions and in different directions

Does he look non-confrontational?

To other fireflies …

Get to know several individuals on a "personal" level!

Synchronized flashing results in an epiphenomenal* magnet; a firefly tree is composed of spatially integrated local arenas.

***epiphenomenon*: a secondary effect arising from but not causally influencing**

Chapter 89

Pyractomena vexillaria (Gorham) 1881

Every firefly has an interesting story for a fireflyer—for a moment. I missed *vexillaria* on trips to Texas, and much later while seeking taxonomic relationships, applied Green's 1957 key to a *Pyractomena* series I had collected in southern Mexico—it "keyed out"! The literature (Green, 157: 250 and Gorham, 1881: 3(2):50), provides as much confirmation as presently possible: *Py. vexillaria* originally was based on a single specimen from Veracruz, Mexico—Green found 5 archived Texas specimens in collections of three American institutions—only finally in southern Mexico did our paths, apparently, accidentally cross (map, **Fig. 1**) …

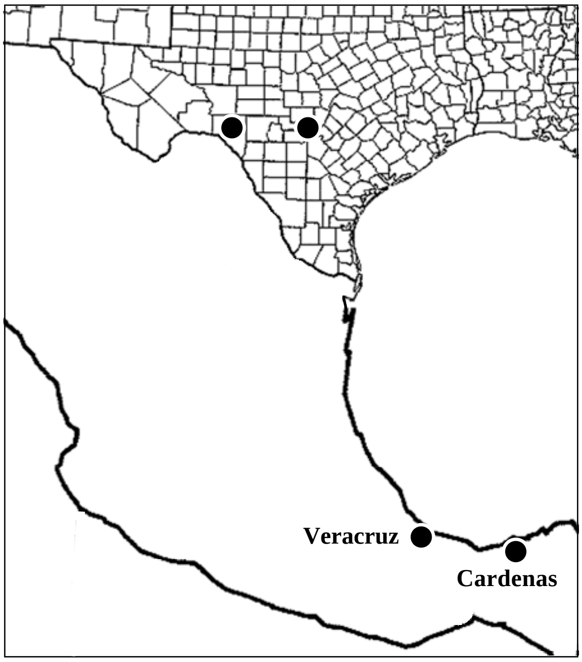


Figure 1. Localities noted in text.

Figure 2. Site at Cardenas, Mexico.

Males flew low over and immediately adjacent to a marsh at Cardenas, Tabasco. **Figure 2** shows the habitat type and possibly the specific site, though photographic notes are unclear. Flashing activity began about sunset+30 minutes (1.4 crep, n=2), and lasted 30-45 min (n=2). Males flew <4' over and amongst the tops of vegetation—an emergent-standing, arrow-leaf, in standing water—and moved about 10 inches between flashes. The FP was a single, short/sharp (est. 100-150 mSec duration), yellow flash, and was emitted rather mechanically at 1.8 sec intervals (s=0.1, r=1.6-1.9, nr 25°/77°, in a slow but somewhat train-like fashion. In its timing and flying *vexillaria* resembles patrolling *Photinus macdermotti* (variad) from continental United States. Known dates of occurrence are shown in **Figure 3**.

Gorham's illustration bears some resemblance to Cardenas vouchers (**Fig. 4**). Vouchers had more extensive median pronotal vittae than noted by Green, and in his illustration the pronotum is immaculate. The pale/yellow color of the elytral bead did not border the scutellum and connect with that of the elytral margin in any vouchers, as noted in some of Green's specimens. Body length ex Green: 11.5-13 mm; vouchers average 10.8 and range 9.6-11.9 mm (**FigTable 6**).

Special acknowledgments. My enthusiastic and special thanks to Awinash Bhatkar for the invitation to lecture at the Agricultural College at Cardenas, and to Awinash and Helga Sitta-Bhatkar and students Juan Morales and Hector Blanco for their hospitality, guidance, transportation, and assistance chasing fireflies and visiting local archeological sites—at one I saw several flying *Tenaspis angulata*.

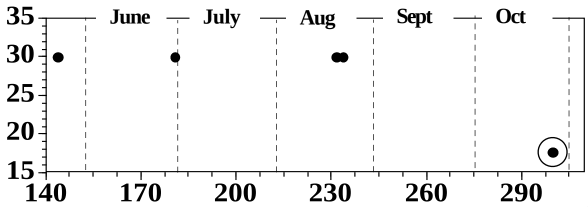


Figure 3. GESEDIS+OBS (Lat/DOY).

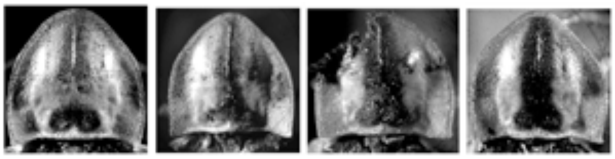


Figure 5. Above: PN array from Cardenas *vexillaria* vouchers. At right: PN from Gorham's illustration. Note that it easily fits at the left end of the voucher array.

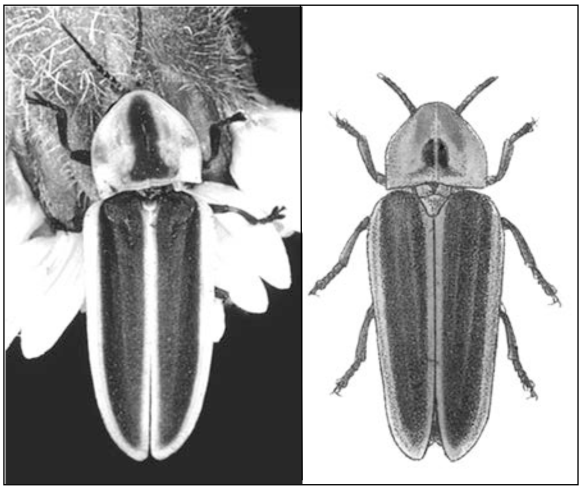
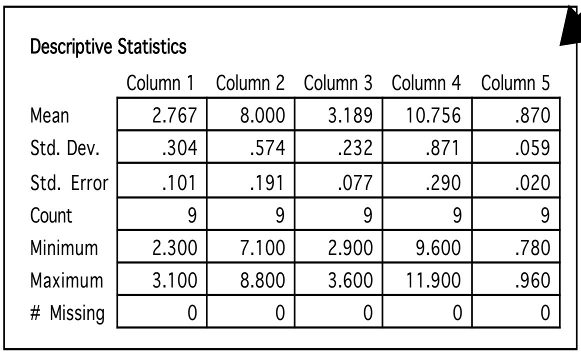


Figure 4. *Py. vexillaria,* Voucher and Gorham (1880-86).

LOCALity	Vcher#	PNLen	ELLen	PNWid	TotLen	PnRat
MEX	m8097	3.1	8.8	3.3	11.9	0.96
MEX	m8098	2.5	7.1	3.0	9.6	0.83
MEX	m8092	3.1	8.8	3.6	11.9	0.86
MEX	m8091	2.8	8.1	3.3	10.9	0.85
MEX	m8090	3.1	8.3	3.3	11.4	0.96
MEX	m8096	2.3	7.4	2.9	9.6	0.78
MEX	m8089	2.9	7.9	3.3	10.8	0.88
MEX	m8068	2.6	7.8	3.1	10.4	0.84
MEX	m8078	2.5	7.8	2.9	10.3	0.87



Descriptive Statistics

	Column 1	Column 2	Column 3	Column 4	Column 5
Mean	2.767	8.000	3.189	10.756	.870
Std. Dev.	.304	.574	.232	.871	.059
Std. Error	.101	.191	.077	.290	.020
Count	9	9	9	9	9
Minimum	2.300	7.100	2.900	9.600	.780
Maximum	3.100	8.800	3.600	11.900	.960
# Missing	0	0	0	0	0

FigTable 6. Measurements, ratios, statistics.

Chapter 90

Micronaspis floridana Green 1948

Fiddlercrab Firefly

The genus *Micronaspis* comprises a single named species. It is distinctive both in form and ecology and has been found only in coastal marshes around the margin of Florida but probably occurs in the keys (**Map 1**). A *Micronaspis* has also been found in the Bahamas by Lynn Faust; this isolated population is certainly now on its own separate evolutionary trajectory. *M. floridana* was described only in 1948 though it occurs in an oft-observed/collected habitat—one that will disappear with a rising sea level. Males are easily distinguished by their unmistakable habitus (**Figs. 2, 9**); their forked, anterior, tarsal claws on the anterior and middle legs are definitive (**Fig. 3**).The earliest collection record found in archives was dated 1925, but after this few were collected until the 1960s. *Micronaspis* has been placed in the tribe Cratomor-phini, and considered to be related to *Pyractomena* and the tropical genera *Cratomorphus* and *Aspisoma*, which it somewhat resembles.

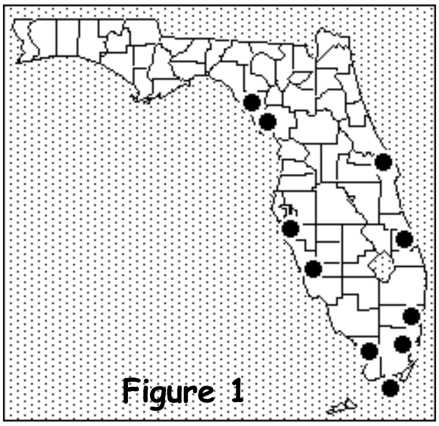


Figure 1

Ecology, flashing behavior. Larvae of this firefly were found by their glows at the fringe of a tidal salt marsh amongst grasses and rushes (**Fig. 4**, arrows). In captivity they ate/preyed upon snails that were collected in their habitat; they are perhaps preyed upon by the fiddler crabs in whose habitat they occur. At latitudes near that of Cedar Key adults have been seen flashing from late April to early October, but they may be more common in May (**Figs. 5, 6**). A *Photuris* (see *salina* Chapter 60) is sometimes found with *floridana* and may have similar larval ecology, though probably *floridana* larvae are specialized predators of gastropods and those of the *Photuris,* omnivoreous and scavangers. *Photuris douglasae* is found in adjacent, landward grassy sites, often along roadside swards of causeways that cross coastal marshland.

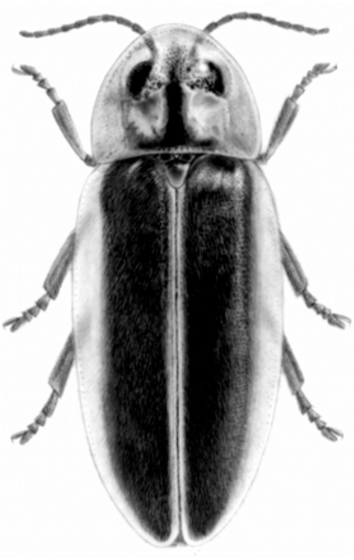


Figure 2, carbon dust by L. Line..

Evening flashing activity begins at 1.7-1.9 creps (n=2) and continues for at least three hours (<7.5 creps). Both males and females flash while flying and perched, and their signal system may be a combination of systems I and II. A typical flash-answer dialogue may be used when males approach females, but perhaps more often, glowing and sometimes spontaneously soliloquy-flashing females attract males to approach near them. Then a simple flash-answer dialogue may occur. Systematic behavior studies have not been made and there is much uncertainty. The flashing flight of males does not seem to be an evening marathon, but instead males —and perhaps females too— make short "hopping" flights of 4-20 flashes covering from a few to several feet with each hop. Actually, this may occur to some extent in *Photinus* and *Photuris* but has not been fully appreciated, and perhaps is well-suited to the often-windy conditions in *Micronaspis* habitats, but there may be more involved. During their short flights males probably look for female glows and spontaneous flashes, and as well as female flashing elicited by their flight flashes.

The male flash pattern is a single, yellow, short, unmodulated flash of about 140 mSec duration, which is emitted at irregular intervals ranging from 1.5 to 4 sec in duration (**Fig. 7A, B**). The flashes of perched males are emitted at less regular and longer intervals than those of flying males. The flash responses of females are simple long-tailed flashes, with high intensity for less than one-half second, and then gradually diminish to a dim glow that sometimes continues until the next male flash. Female response delay is about 400 mSec (25°C/77°F; **Fig. 7C, D**). Three PM-recorded spontaneous female flashes show chart profiles that are the reverse of most response flashes, with a slow onset and faster decay. Spontaneous flashes are also of longer duration than response flashes.

Two male approaches were observed, the first to a hand-held, caged female that flashed in response to the flashes of a passing male. This approach was straight-forward and photinus-like. In the second approach, the female's cage was placed in the rushes near a perched flashing male. During his approach, from about 30 cm distance, the male made short hops. When he reached her cage she stopped answering and he withdrew several inches. She attracted and "rejected" him four times.

Larvae are readily identifiable by four dorsal rows of tubercles/ spines (**Fig. 8**; McDermott 1954). Females are similar to males in appearance (**Fig. 9**), but have light-organs similar to those of *Photinus* spp. females **Figure 10**; none of their tarsal claws is bifid.

In an experimental biogeographic study near Sugarloaf Key, in which four small mangrove islands were fumigated, one specimen of *M. floridana* was collected three years after fumigation. None occurred in samples made at 0, 1, and 2 years (Simberloff 1976).

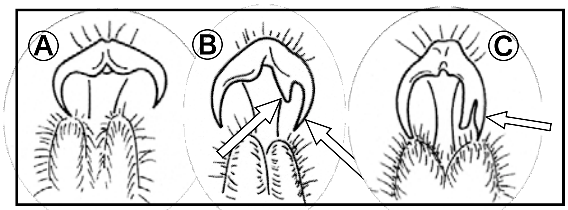


Figure 3. Tarsal configurations to distinguish: (A) *Photinus* and *Pyractomena*; (B) *Micronaspis* [note asymmetry]; (C) *Photuris*.

Figure 4. Coastal marsh at the Shell Mound site just north of Cedar Key, FL. Larvae a found along landward margin among oyster shells and other debris under shrubs. Occasionally, after tide goes out glowing comb-jellies are found clinging/caught on stems of black needle-rushes. When seeking in the needle-rush wear goggles!

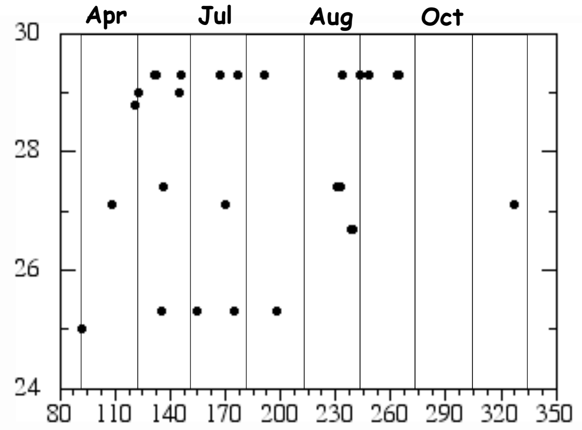


Figure 5. GESEDIS 1967-1993 (AX: Lat/DOY).

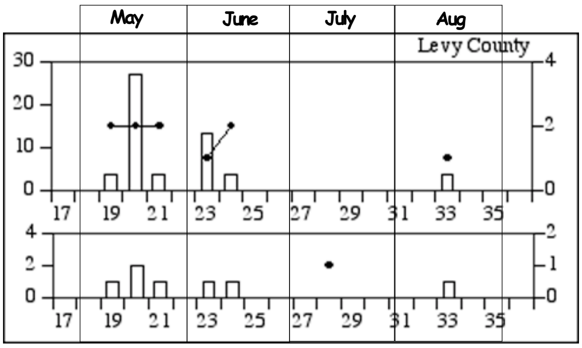


Figure 6. SESOBS 1967-1993 (AX: #/WOY).

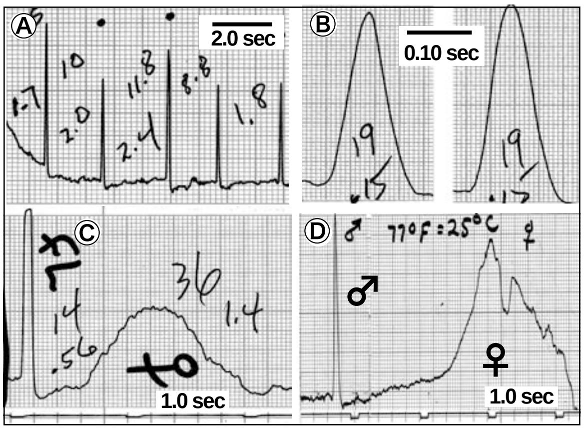


Figure 7. (A) Sequece of single flashes; (B) Two flashes from the sequence in A; (C) Female flash response to a penlight flash; (D) PM record of male flash pasted over a penlight flash that was answered by a female; all recorded at 25°/77° AX: rel.Int./time.

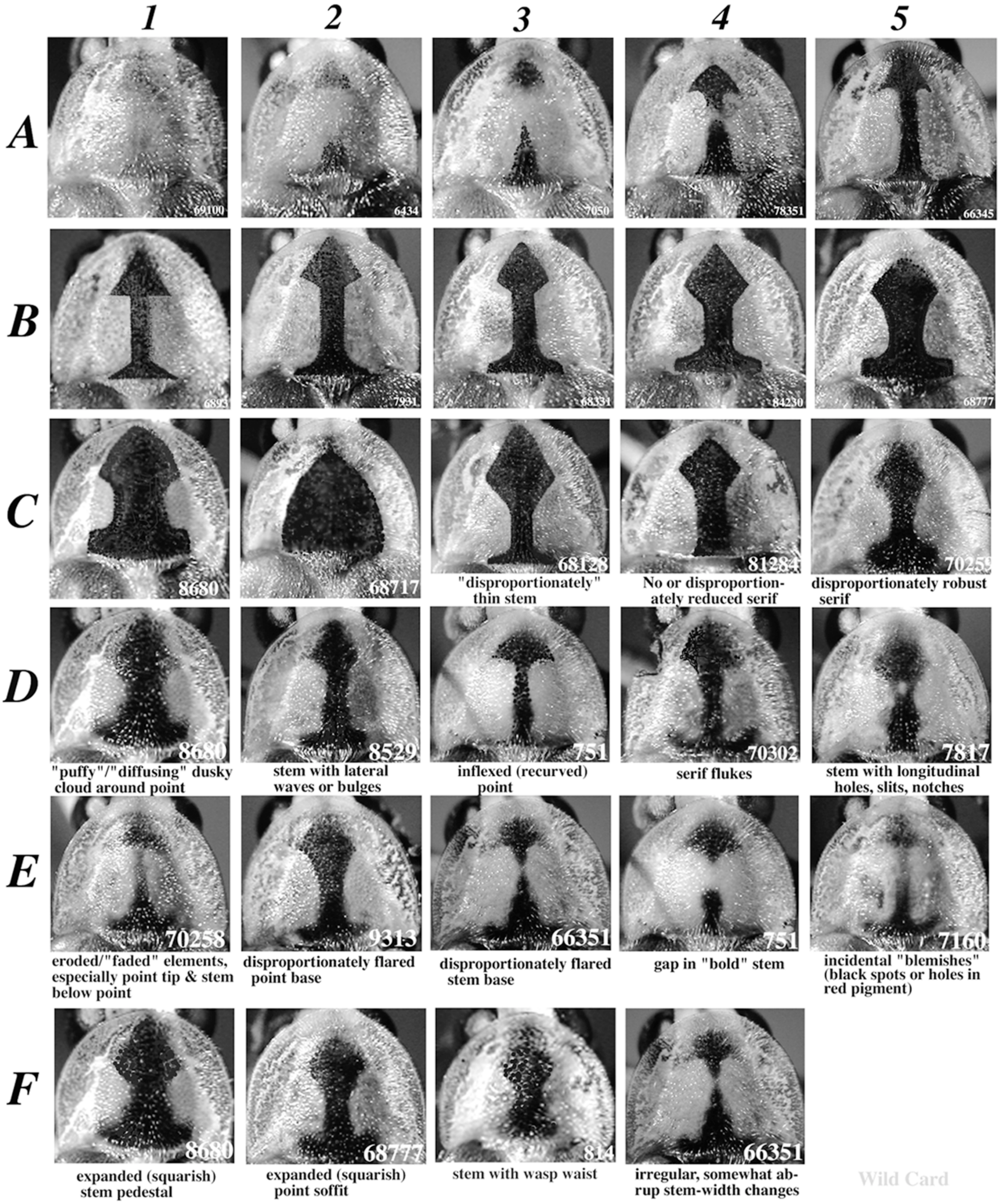
Figure 8.

Figure 9. Male.

Figure 10. Female.

PNV RANGE 201.2

See page 446 for color



C3: "disproportionately" thin stem

C4: No or disproportionately reduced serif

C5: disproportionately robust serif

D1: "puffy"/"diffusing" dusky cloud around point

D2: stem with lateral waves or bulges

D3: inflexed (recurved) point

D4: serif flukes

D5: stem with longitudinal holes, slits, notches

E1: eroded/"faded" elements, especially point tip & stem below point

E2: disproportionately flared point base

E3: disproportionately flared stem base

E4: gap in "bold" stem

E5: incidental "blemishes" (black spots or holes in red pigment)

F1: expanded (squarish) stem pedestal

F2: expanded (squarish) point soffit

F3: stem with wasp waist

F4: irregular, somewhat ab-rup stem-width changes

F5: Wild Card

Appendix 2. Flash Pole
from *Firefly Life* (on line)

Field, Lab, & Bench XXV

Firefly Fishing & Cane Poles

SYNOPSIS of OBJECTIVES. Learn something of the origin and evolution of long-handled firefly decoy lights and make one, including constructing its electronic circuits and attaching it to a cane pole.

Introduction

In a study of the aerial attacks of *Photuris* females on flying flashing male fireflies, artificial targets were mechanically moved through the air. A rig with three cane fishing poles was rotated on a hub that was driven by a small and slow motor. There was a tiny light (LED) at the tip of each pole, one glowing, one flashing, and one dark. The LEDs were painted with a sticky substance to catch the feet of fireflies that grabbed them. It was found that after this merry-go-round had been in operation for a few minutes at a site it seemed to have caught most of the available females — possibly *Photuris* females hunt from perches in hunting territories and after the local hunters have been caught it takes a few days for other females to move into the area. Next, we hand-carried similar poles along the hedges beside a sandy roadway. This meant putting flash controls on the fish poles, and suddenly we had (re) invented the firefly fish-pole. In the decoys that were used on these poles to capture hawking females, the LED was embedded in an 8-mm plastic bead so that the target would offer the same target shadow and light size for females attacking from any direction (figure).

Many years ago (circa 1964) when I visited pioneer fireflyer Frank McDermott at his home in Wilmington he showed me a flashlight with a 16" flexible stem on the end that held a "germ-of-wheat" (tiny) incandescent bulb. He showed me how he could hold this against the ground as a decoy (pseudo-female) and flash answers with it to attract males, and, as I recall, he explained its advantages over a penlight. He may have seen such a light used for a trouble light when a repair-man illuminated a dark crevice or tight corner in a dead engine, under the sink, or behind the water heater. Though this "McLight" helped in getting the fireflyer back away from the bulb a bit and out of the action space, giving the male firefly more room to circle around during his approach, it needed a longer stem. McDermott's light was the ancestor of the flash pole.

Since its origin the firefly fish pole has evolved considerably in general improvement and it has adaptively radiated into several forms with different uses. Today's pole has interchangeable control boxes that "snap" quickly in and out of a carrier, each with different specializations; it has poles of different lengths including one that has a telescoping stem that was made from a golf ball retriever (water-holes); and it has interchangeable LEDs that plug into a micro mini jack at the end of the pole. The LED can be made to flash or glow with different intensities, and it can flash and glow simultaneously, superimposing bright flashes over dim glows. One control box not only has controls for making thumb—driven flashes, but also has a receptacle that accepts complex flashing information (electronic input) from a solid-state flash generator.

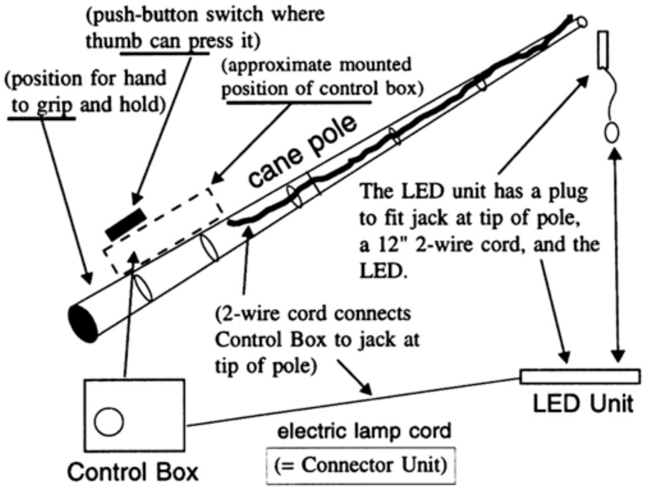
Attacking female stuck to LED–bead.

Constructing A Firefly ~~Fish~~ Flash Pole

The manufacture of a firefly fish pole requires: (1) component parts, which can be purchased from *Radio Shack®*, (2) schematic instructions for connecting them correctly, (3) planning and instructions(?) for compartmentalizing the components correctly, and (4) technical and mechanical practice and skill. Thus, should you decide to make a flash pole you must purchase the components that are itemized on the parts list, read a block diagram and a schematic diagram, practice soldering and drilling, and spend some time in the lab to get personal instructions and assistance.

In equipment design and manufacture a block diagram shows the separate physical electrical-holding units of a project. For the firefly flash pole the units are the *control box* that is placed on the handle, the *cane pole,* and the *phone jack* (receptacle) that is put at the tip end of the pole, and the LED + phone-plug unit that plugs into the jack at the tip of the pole.

On the other hand, a schematic diagram shows electrical components, their names or code numbers, and electrical connections, in a clear uncluttered layout without concern for actual physical size, component positions, wire lengths, or visual appearance. It identifies the specific electrical components and how they are electrically linked together, without regard for space-saving, wire separation, economy, positioning for access, or other convenience or necessity.



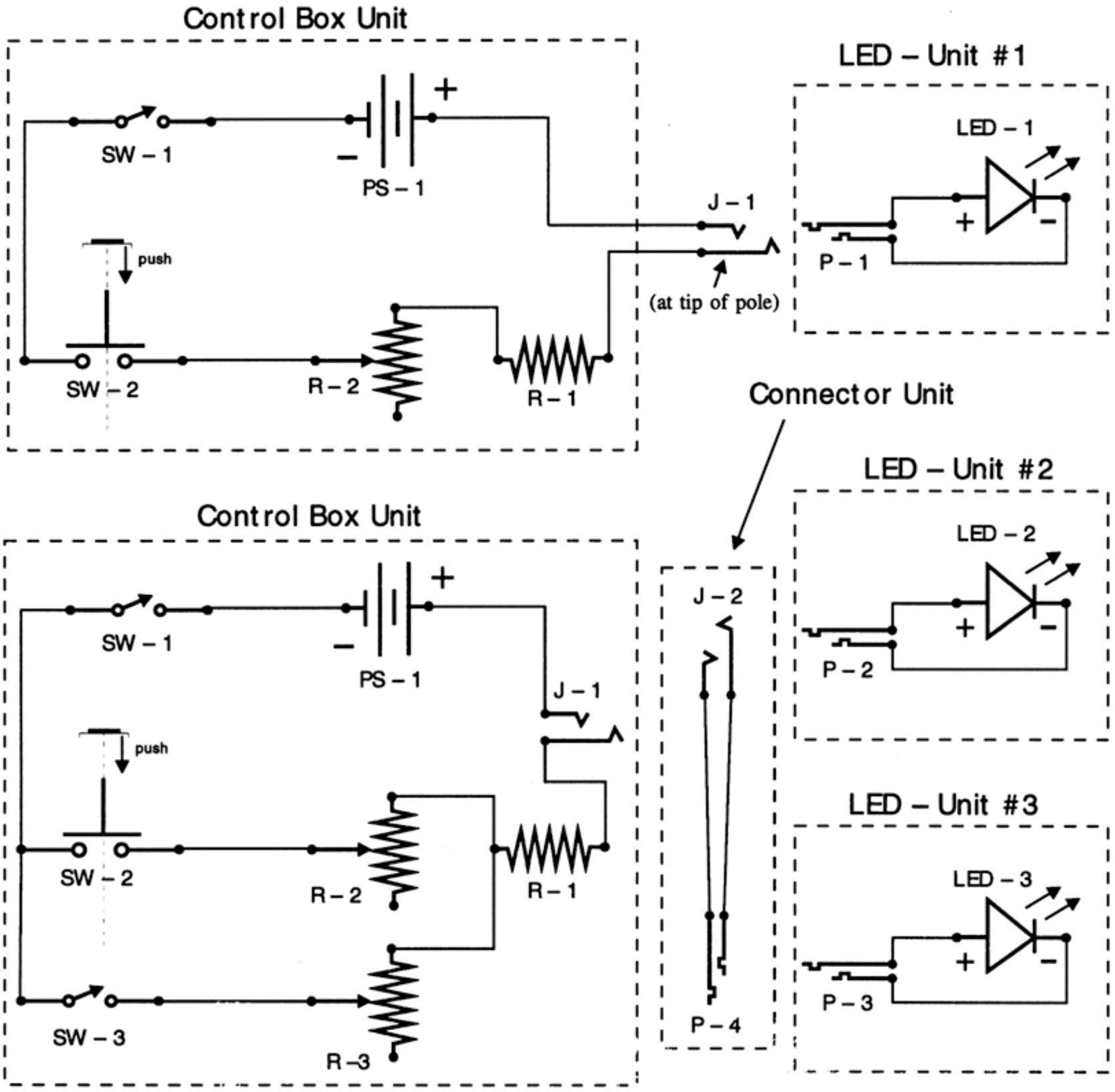
Block diagram for a firefly flash pole.

Procedure

(Follow the steps closely)

1. Purchase electronic components at a Radio Shack® or other electronic supply store. Some components are sold with two or more in a package. In such cases you may wish to split costs with a classmate. See relevant notes on the Parts List.
2. Patch electronic components together with patch-cords so that you can get polarities and connections correct and see how the components work together, before you begin soldering and permanently assembling them.
3. Carefully draw the outline of the control box on a sheet of paper, tracing around the box, and then carefully draw the controls in the proper position on the box-sketch outline. Mark the points for drilling holes, and show drill size for each hole.
4. Measure the diameter of each threaded shaft that requires a hole in the control box (2 switches, 1 variable resistor). Use a ruler or outside caliper to make these measurements. Note these measurements on your drawing. Also, mark a position on your drawing for drilling a 3/16' hole on the end of the control box that will face the pole tip. Through this hole will pass the lamp cord (double) wire that connects the control box to the mini phone jack at the end of the pole. (Into this jack you will plug the mini phone plug that is attached to the LED unit).
5. Observe the made-boxes on the poles in the lab, but note that these made-boxes have a phone jack on the side that you will not put in your box.. Hold a made-pole and see whether the thumb operated push-button is in a convenient place on the box for your hand and thumb size, or whether you need to individualize your fish pole.
6. Put a 1" X 1" piece of tape (masking or Time) over drilling points and carefully mark the exact position that the center point of each drill bit will be placed for drilling, as per your measured drawing (you may wish to remove the box-top from the box when pricking and drilling it, and "back-up" the box where you will apply pressure, with a wooden block). With precision, and using a prick-punch, scribe, or sharpened nail, press or tap a sharp impression (dimple) into the tape at the bit penetration point — this sharp dimple will keep the bit tip from skittering to the side when you apply pressure to drill the hole in the (hard and slippery) box.
7. With the drill press, while wearing eye-protective goggles, drill the holes in the control box, as per your measured drawing. Have a goggle-wearing observer stand by while you drill, and get final instructions for drilling, and a check of your preparations and setup from the instructor.
8. Cut off the tip of your cane pole at the place where its diameter is about that of the demonstration made-pole, and at a node of the cane (bamboo stem). To do this, hold your pole in the vise, cut it off with the hack saw, and file and sand the rough corners and edges.
9. Mount the two switches, variable resistor, and mini phone jack in the control box or on the top-plate of the control box, as per your drawing. Tighten the nut of each component carefully with gas-pliers or with the long-nose pliers because a wrench will probably not fit into the available working space. Be certain to use the lock-washer between the box and nut on each shaft.
10. Measure the length that each wire connector in your control box must be, and, allowing for about 1/8" extra at each end for bending through holes or around soldering posts, and allowing additional length for shaping and turning each wire's path through the box to reduce confusion, congestion, and mutual interference, cut the necessary wires. Strip about 1/4" of the insulation from each end of each wire. But **NOTE**: connecting wires between components fastened to the removable cover and those fastened in the control box must be cut longer so that when the cover is removed to replace the batteries, the cover can be pushed to the side far enough to accommodate the complete removal.

Schematic Diagrams for Firefly Fish-Pole Controls, Lights, & Connections



Component code for schematic diagrams: SW–1, SPST toggle switch; SW—2, normally OFF push-button switch; SW—3, same as SW—1; PS—1, power supply consisting of 2 AA batteries connected in series as in battery clip, giving a total of 3 volts; R—1, 47 ohm fixed dropping resister; R—2, 1000 ohm — 5000 ohm variable resister; R—3, same as R—2; J—1, miniature or micro-miniature phone jack; J—2, same as J—1; P—1, miniature or micro-miniature phone plug (to fit J—1 and J—2;); P—2, P—3, and P—4, same as P—1; LED—1, yellow light emitting diode; LED—2, green light emitting diode; LED—3, amber light emitting diode — all LEDs should be of the non-flashing type.

11. After measuring the distance from the control box to the end of the pole where the phone jack will be mounted, allowing 2 extra inches for error, cut a length of lamp cord of this length. Tie a simple overhand knot in the lamp cord near one end, such that when the knot is inside the box and against the hole through which the long tail passes, it will not pass through the hole and the wires of the short end (inside the box) will reach their appropriate terminals.
12. Place each connecting wire in position, after tinning the bare wire (see Appendix, item 1), bend and pinch (with miniature long-nose pliers) the stripped ends around (or through holes in) the posts where they will be soldered. Bend and arrange the wires conveniently into their box position, making certain that you will have enough room to insert the tip of the soldering iron to the terminals and posts that will be soldered, without burning insulation or your fingers in the process. Check the schematic diagram and then, patching as necessary, make a final check to see whether the hookup works before you solder components together. Check for electrical continuity, isolation, and polarity.
13. Practice these aspects of soldering: cleaning and tinning the soldering iron tip if it needs it, tinning the tips of stripped wire, tinning of soldering posts (terminals), joining tinned wire to tinned posts.
14. Solder all connections, after you have practiced soldering a few connections as per instructions given in the Appendix.
15. Tape the box to the butt of the cane pole and at intervals of 6-8" wrap a short (2") piece of 1/2" -wide duct tape around the twisted wires and the pole.
16. Assemble the LED unit, with the LED, 12" connecting wires, and the mini phone plug. Check for continuity and polarity of the LED before soldering. The plus (+) side of the electrical circuit is wired to the center (tip) contact of the phone jacks and plugs. After soldering the wires, wrap a small piece of electrical tape around the LED connections, first passing a piece of this insulating (black plastic) tape between the LED legs to be certain they do not touch together when both are wrapped with tape for strength and protection and to avoid snagging on vegetation when the pole tip and LED is put in trees and herbs for attracting male fireflies.
17. Tape the control box to the butt end of the cane pole. Note that for now you are using tape to hold the box to the pole, and that when you need to change the batteries you must unwrap the tape. Later you can mount the box in a frame, as on the made-box demonstrator, or fasten the control box to the pole with screws through the box floor into the cane.

Parts List (*Radio Shack®* Cat. Numbers shown)

• 1 @ 7-8-foot cane pole (can buy at tackle store)	
• 1 @ Project Case	Cat. No. 270-1802
• 1 @ Momentary Push-Button Switch	Cat. No. 275-618A
• 1 @ Snap Battery Holder 2AA	Cat. No. 270-382
• 1 @ 9V Battery Clip* (need 1, come in 5-pack)	Cat. No. 270-325
• 1 @ 47 ohm Resistor* (need 1, come in 2-pack)	Cat. No. 271-1105
• 1 @ Submini SPST (toggle) Switch)	Cat. No. 275-612
• 1 @ 2-Conductor 1/8" Phone Jack (come in 2-pack)	Cat. No. 274-248A
• 1 @ Variable Resistor, 1000 Ω (1k ohm)	Cat. No. 271-1714
• 1 @ 1/8" Phone Plug (2 in pack)	Cat. No. 274-286A
• 1 @ Green LED (non flashing, 2 in pack)	Cat. No. 276-022
• 1 @ Knob for shaft of variable resistor. Are several kinds, but get one with brass insert and set-screw; ask for help from fd and ask questions, work carefully, and safely. Do not burn fd.	

Soldering Instructions. [using low-wattage iron of 20-40 watts, and small-diameter resin core solder]

Hot soldering irons will burn fingers and clothes; resin spatters, use goggles; unplug unused soldering irons; do not breathe resin fumes from melting solder; ask for help from jel and ask questions, work carefully and safely. Do not burn the professor.

Practice the following steps on a few connections between the tips of some scraps of wire. **(1)** Touch solder to the tip of the soldering iron lightly, to put a thin coat of solder on it — this is called *tinning.* **(2)** Heat the connection to be joined first (by somewhat-broadly touching the tip of the soldering iron to it), then, after a moment, touch the tip of the solder to the connection, briefly, and the solder's tip will melt and run into the union and bond with the hot tinning there. Do not apply too much solder; do not let the connected pieces move until the joint has cooled or you will produce a brittle *cold solder joint,* recognized by its gray and dull rather than silvery-shiny surface. **(3)** Clean and keep clean, the tip of the iron — wipe resin remnants, burnt insulation, dead solder etc. from it with the damp towel, and retin the tip. **(4)** To separate (desolder) a connection, touch the connection with the iron's tip until the soldered joint melts, then gently pull the wires free with the miniature long-nose pliers.

Notes On Prep & Construction of "Flashpole"

1. You may prefer to do the electronic work now and postpone the fish pole prep and mounting of the electronic box on a pole until later, rather than doing the project illustrated in **Appendix 2** or making some simpler substitute rig.

2. Although the instructions in the HO are for the use of a bamboo fishing pole, you might prefer to use the two basal sections of an inexpensive telescoping pole (about $10.00 from a department store such as Walmart®); see the example on the front table.

3. The parts list in the FLB includes part numbers, but note that RadioShack® sometimes changes their product-line, so shop with an eye to a better or more appropriate substitution.

4. Before buying electronic supplies note these two points: (1) fd has a surplus of some items and may be able to supply you with some items, such as the battery clip and 47Ω resistor; (2) some items are sold with two or more in a pack so find a class mate or two and purchase the pack together.

5. When shopping for a p-box or project-box, or whatever they may now call the little box that contains such circuits, do not get one that is too small to hold two AA batteries in the bottom as well as the large bases of the variable resistor, ON/OFF switch, and the Push-button switch.

6. You may wish to use two AAA batteries, and use the appropriate AAA battery holder instead of the one listed on the parts list. This would let you use a somewhat smaller p-box, but make certain that the holders and battery clips are available too. (there are several RadioShack® retailers in Gainesville)

7. Be certain that the push-button switch is one that allows current to flow when the button is pushed — there are some that are ON **<u>except</u>** when the button is pushed.

8. We have solder, soldering irons, drills, and other tools for construction, so don't purchase such things unless you think it would be nice to make a donation to the shop's tool chest!

A Control-box Holder For the Firefly Fishpole

The control–box can be held on the fish pole with a wooden frame made of 1/2 inch quarter–round molding and 1/4" plywood (Fig. 1). The frame is fastened to the bamboo pole with two small bolts that pass down through the floor of the frame (Fig. 7), through the cane, and held with the nuts, each with a washer so that the small nuts will not pull through the bamboo. The box sets down inside the frame and can be held in place with a large rubber band. Drill the anterior hole on the front of the box for the wire high enough on the box so that you won't have to notch the 1/4–round at that point.

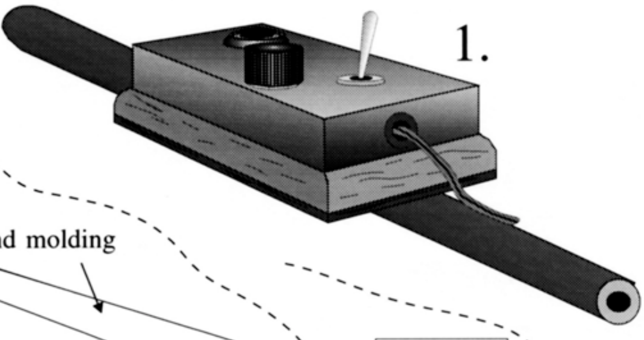
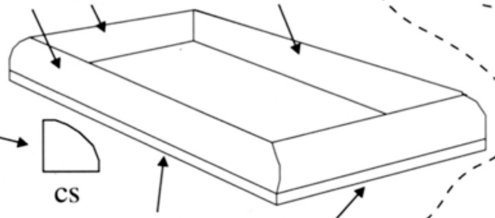
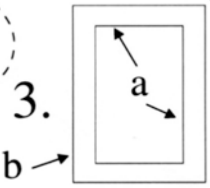


Figure 2 shows the frame without the box. Note, the 1/4–round meets at the corners at angles of 45°.

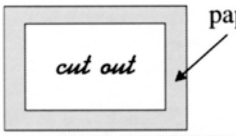


Cross–section of quarter–round, showing where this type of molding gets its name.



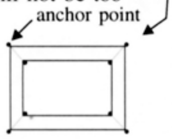
To mark the plywood and the molding for cutting, first trace around your control–box (Fig. 3a) with a pencil, on a scrap sheet of paper (8.5"X11"). Then measure out 1/2" on each side of the rectangle you drew, and draw another rectangle (Fig. 3b). Put your box on the drawing to make certain you measured and traced correctly.

4.



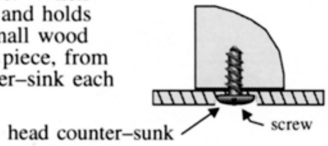
Carefully cut out the 1/2" paper frame (Fig. 4), and place and trace it on the sheet of plywood adjacent to other so–marked floor–pieces, for cutting.

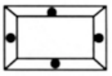
5. Mark the quarter–round stock for cutting the 4 pieces that will make the holder frame. Use your paper frame as a template and carefully mark the 45° angles, using inner and outer corner points to anchor cutting lines along the stock stick. No need for haste! Leave the lines when you measure and cut so that your frame pieces will not be too short.

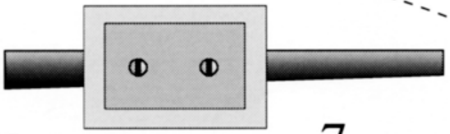


Note that 1/2 inch molding really measures 15/32 inches so the floor will "over–hang" the molding. This edge will be filed and sanded down (off) when you dress up your frame.

6. After checking the fit of the frame pieces with the contol box in position, glue them there. When the glue dries and holds them, put a small wood screw in each piece, from below. Counter–sink each screw.



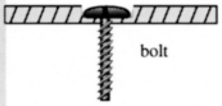




7.

Then bolt the frame on the pole, and you are ready to flash.

The last step, after the sanding and spar–varnishing, is to fasten the frame to the pole. Holes for the bolts must be drilled and the heads of the nuts must be recessed (counter–sunk) into the plywood — carefully so as not to make a too–large hole completely through the floor.

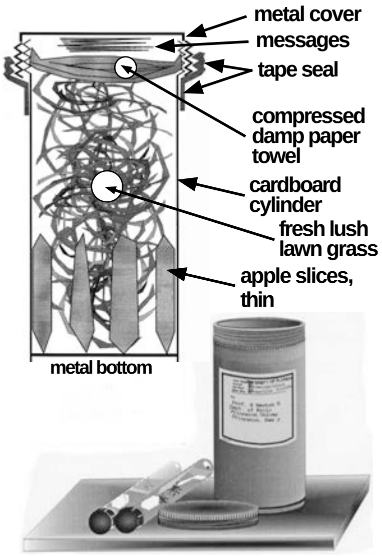


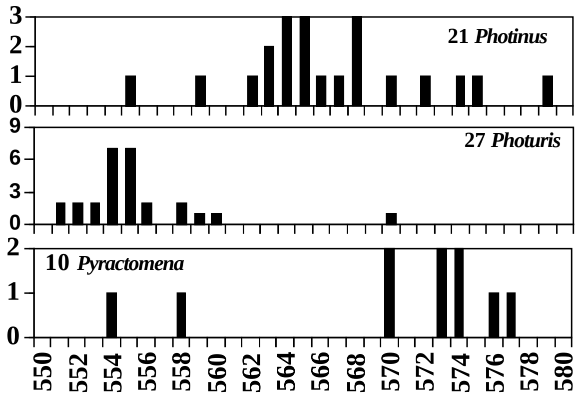
APPENDIX 3: Color Of Bioluminescence Of Some North American Fireflies

Beginning in 1964, during field studies of fireflies of the genus *Photinus,* this author began sending living fireflies to biologists at The Johns Hopkins University who were studying luminescence in lampyrids and click beetles and had made extensive studies in Jamaica. This began a collaboration with Bill Biggley and Howard Seliger that lasted for more than 20 years. Though some early shipment records have been misplaced and are not included in the total count, more than 300 shipments and 1000 fireflies representing more than 60 operational taxonomic units (flash pattern vouchers) were analyzed. Many vouchers were returned after their spectra had been recorded and are now maintained with other FP vouchers in the USNM collection at UF, and carry both voucher and spectrum scan numbers.

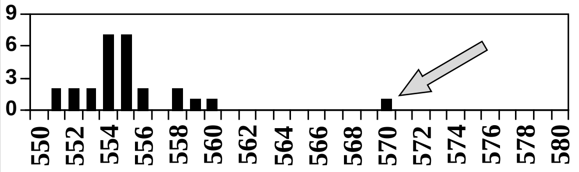
For shipping, fireflies were placed in metal-reinforced, hard cardboard canisters with: a loose gathering of fresh, damp grass, 3 thin slices of apple slid down and around the grass, a pad of damp paper-towel placed over the top of the grass, and a folded note above the towel with the identification of the specimens enclosed. The metal cover was ringed with string-reinforced, clear, shipping tape. Shipments were made via US Mail on early weekdays so that specimens would spend a weekend in a hot mailroom or truck.

In the charts wavelengths are given in millimicrons.

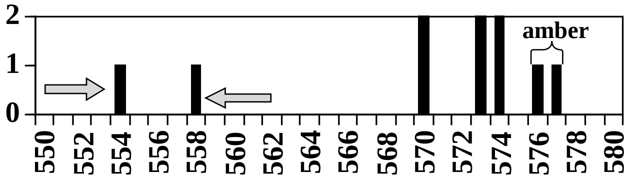




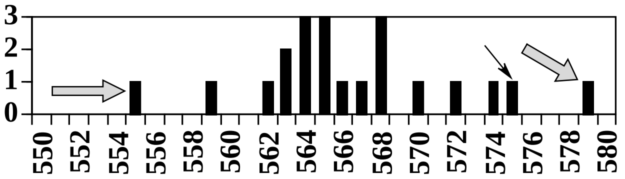
Arrays for comparison.



Photuris frontalis is **shifted toward yellow; it flies earlier in the evening than other measured *Photuris*, strengthening the suggestion that twilight activity favors such a shift (<u>AX: number of species/peak wavelength in millimicrons</u>).**



Two *Pyractomena, angustata* and *ecostata,* have shifted toward the green, now matching the green of *Photuris*. Incidental observations suggest that aerial attack by *Photuris* may be the selective agent involved. The two amber fireflies are the flickering *angulata* and *barberi* (<u>AX: number of species/peak wavelength in millimicrons</u>).



Two *Photinus,* the too-green *tanytoxus* and too-orange *scintillans* have shifted away from the yellow spectra observed in most sampled congeners. The former, a close relative of *collustrans,* a twilight flyer, flies at full darkness after *collustrans* finishes; *scintillans* flies well before sunset in deep shade. Though emitters above 570 were, as expected, wetland species, finding *acuminatus* at 575 was a surprise. This rare firefly was once seen in what was assumed to be natural habitat in numbers, a low woodland. Not found since, perhaps it also is a victim of lowered water tables (<u>AX: number of species/peak wavelength in millimicrons</u>).

Genus	Species	coll Date	n	Locality	Peak	000.0	50%	Half W
Ellychnia	*corrusca*	8 viii 71	?	n MI	555	529.0	600.0	71.0
Lucidota	*luteicolis*	13 v 81	5	Marion C FL	562	535.0	606.0	71.0
Micronaspis	*floridana*	26 v 68	4	Levy C FL	571	544.0	608.0	64.0
Micronaspis	*floridana*	26 v 67	2	Levy C FL	575	549.0	611.5	62.5
Photinus	*acuminatus*	4 vi 78	2	Levy C FL	575	546.0	611.0	65.0
Photinus	*acuminatus*	4 vi 79	2	Levy C FL	574	547.0	611.0	64.0
Photinus	*curtXmarg* hybrid	8 vii 68	6	c NYS	563	539.0	606.0	67.0

Genus	Species	coll Date	n	Locality	Peak	000.0	50%	Half W
Photinus	*floridanus*	10 ix 78	5	nc FL	571	544.0	609.0	65.0
Photinus	*floridanus*	2 v 65		nc FL	565	538.0	605.0	67.0
Photinus	*marginellus*	14 vii 65		Tompkins C NY	565	536.0	602.0	66.0
Photinus	*sabulosus*	21 vii 68	3	c MD	570	543.0	606.0	63.0
Photinus	*sabulosus*	14 vii 65		Tompkins C NY	566	530.0	608.0	69.0
Photinus	*ardens s.s.*	8 vii 68	6	c NYS	565	540.0	605.0	65.0
Photinus	*consimilis* cplx FFP	10 ix 78	6	nc FL	575	548.0	612.0	64.0
Photinus	*consimilis* cplx FFP	2 v 65		nc FL	568	542.0	606.0	64.0
Photinus	*consimilis* cplx SFP	10 ix 78	6	nc FL	574	547.0	611.0	64.0
Photinus	*consimilis* cplx SP	3 v 65		nc FL	562	535.0	602.0	67.0
Photinus	*obscurellus*	8 vii 68	2	c NYS	570	543.0	608.0	65.0
Photinus	*obscurellus*	8 vi 65		c NYS	566	539.0	607.0	68.0
Photinus	*consanguineus*	3 v 65		nc FL	563	537.0	603.0	66.0
Photinus	*consanguineus* cplx	7 vi 83		e MD	566	540.0	602.0	62.0
Photinus	*ignitus*	18 vi 68	3	c NYS	568			
Photinus	*macdermotti* cpx	23 vi 68	4	e MD	567	540.0	601.0	61.0
Photinus	*macdermotti* cpx	11 vi 67		Murray C GA	563	540.0	605.0	64.0
Photinus	*macdermotti* cpx	24 vi 78	6	ne MD	570	542.0	607.0	65.0
Photinus	*scintillans*	5 vii 79	3	Biggley collect	579			
Photinus	*pyralis*	29 vi 71		ne MD	564	537.0	604.5	67.5
Photinus	*pyralis*	29 vi 71		ne MD	563	537.0	607.0	70.0
Photinus	*brimleyi*	1 vii 78	4	ne TN	564	538.0	611.0	73.0
Photinus	*collustrans*	28 iv 68	10	nc FL	560	544.0	601.0	57.0
Photinus	*collustrans*	25 iv 78	6	nc FL	560	536.0	605.0	69.0
Photinus	*collustrans*	3 v 65		nc FL	558	531.0	603.0	72.0
Photinus	*tanytoxus*	2 v 65		nc FL	555	529.0	596.0	67.0
Photinus	*tenuicinctus*	23 vi 70	6	sw MO	570	543.0	608.5	65.5
Photinus	*umbratus*	13 v 68	12	nc FL	565	540.5	602.0	61.5
Photinus	*umbratus*	2 v 65		nc FL	562	535.0	599.0	64.0
Photuris	nr lineaticollis (AGR)	14 iv 78	3	Wakulla C FL	555	528.0	598.0	70.0
Photuris	nr walkeri	14 iv 78	3	Wakulla C FL	554	528.0	598.0	70.0
Photuris	*dorothae*	10 ix 67	14	nc FL	551	524.0	593.0	69.0
Photuris	*lineaticollis*	23 iv 68	6	nc FL	553	526.0	593.0	67.0
Photuris	*maicoi*	17 v 67	5	nc FL	552	526.5	594.0	67.5
Photuris	*carrorum*	17 v 67	4	nc FL	554	528.0	598.0	70.0
Photuris	*carrorum*	20 v 68	5	nc FL	553.5	526.0	594.0	68.0
Photuris	*carrorum*	27 v 68	6	nc FL	554	528.0	594.0	66.0
Photuris	*carrorum*	23 v 78	5	nc FL	557	529.0	600.0	71.0
Photuris	*lamarcki*	28 v 68	6	nc FL	558.5	532.0	599.0	67.0
Photuris	*lamarcki*	5 vi 67	7	nc FL	557	531.0	598.0	67.0
Photuris	*lamarcki*	22 v 67	4	nc FL	557	531.0	598.0	67.0
Photuris	*beanii*	4 vi 78	2	Dixie Co FL	559	532.0	604.0	72.0
Photuris	*hebes*	27 vi 68	4	se MD	557	529.0	597.0	68.0
Photuris	*hebes*	2 vii 68	1	c NYS	554	529.0	597.0	68.0
Photuris	*hebes*	19 vii 70	3	c NYS	556	528.0	598.0	70.0
Photuris	*hebes*	20 vi 78	4	w MD	558	530.0	602.0	72.0
Photuris	*lucicrescens*	23 vi 68	9	e MD	552	526.0	596.0	70.0
Photuris	*lucicrescens*	22 vi 70	6	sw MO	550	524.5	592.0	67.5
Photuris	*lucicrescens*	23 vi 78	4	ne MD	554	528.0	601.0	73.0
Photuris	*lloydi*	7 v 68	11	nc FL	553	526.0	594.0	68.0

Genus	Species	coll Date	n	Locality	Peak	000.0	50%	Half W
Photuris	*lloydi*	29 iv 78	6	Citrus C FL	554	528.0	597.0	69.0
Photuris	*lloydi*	31 iii 78	6	Highlands C FL	555	528.0	598.0	70.0
Photuris	*frontalis*	11 vi 67	5	Murray C. GA	568	539.0	611.0	72.0
Photuris	*frontalis*	26 vi 78	4	e MD	571	540.0	619.0	79.0
Photuris	*frontalis*	30 vi 81	4	e MD	571	540.0	616.0	76.0
Photuris	*congener*	2 v 67	5	nc FL	554	528.0	602.0	74.0
Photuris	*congener*	22 iv 68	10	nc FL	551	527.0	602.0	75.0
Photuris	*congener*	31 iii 78	6	Highlands C FL	558	530.0	602.0	72.0
Photuris	*eureka*	3 iv 78	6	Dixie C FL	555	529.0	598.0	69.0
Photuris	*tremulans*	23 vi 68	9	e MD	552	527.5	597.0	69.5
Photuris	*tremulans*	24 vi 68	2	e MD	553	528.0	595.0	67.0
Photuris	*tremulans*	24 vi 78	6	ne MD	558	531.0	602.0	71.0
Photuris	*cowaselonensis*	18 vi 68	7	c NYS	553	527.0	579.0	52.0
Photuris	*harrannorum*	1 vi 67	1	nc FL	552	527.0	595.0	68.0
Photuris	*harrannorum*	12 iv 78	7	nc FL	556	528.0	599.0	71.0
Photuris	*versicolor*	24 vi 78	5	ne MD	555	529.0	599.0	70.0
Photuris	*alexanderi*	28 vi 71	9	n MI	554	528.0	599.0	71.0
Photuris	*stanleyi*	13 v 68	12	nc FL	554	527.0	598.0	71.0
Photuris	*whistleri*	27 v 68	6	nc FL	555	528.0	598.0	70.0
Photuris	*cinctipennis* cpx	26 vi 78	6	e MD	555	520.0	598.0	76.0
Photuris	*missouriensis*	22 vi 70	6	sw MO	555	528.5	599.0	70.5
Photuris	*potomaca*	3 vii 81	1	w MD	559	533.0	599.0	66.0
Photuris	*potomaca*	19 vi 78	6	w MD	560	531.0	603.0	72.0
Photuris	*sivinskii*	28 v 68	7	nc FL	555	529.0	595.0	66.0
Photuris	*sivinskii*	23 v 78	4	nc FL	557	529.0	600.0	71.0
Photuris	coastal single	12 v 68	12	Levy C FL	557	530.0	599.0	69.0
Photuris	coastal single	25 v 68	10	ec FL	558	530.0	599.0	69.0
Photuris	*salina*	27 vi 68	8	se MD	557.5	530.0	598.0	68.0
Photuris	*caerulucens*	7 vii 70	3	sw WI	551	551.0	595.0	44.0
Photuris	*douglasae*	10 v 65		nc FL	549	523.0	590.0	67.0
Photuris	*douglasae*	6 v 68	9	nc FL	551	525.0	592.0	67.0
Photuris	*douglasae*	3 v 67	4	nc FL	550	524.0	591.0	67.0
Photuris	*douglasae*	24 iv 78	5	nc FL	553	526.0	596.0	70.0
Photuris	AA flicker	13 vii 70	7	s MI	554	527.0	597.0	70.0
Photuris	AA flicker	16 vi 67	4	s MI	553	528.5	598.0	69.5
Pyractomena	*angustata*	2 iv 68	10	Levy C FL	552	526.0	594.0	68.0
Pyractomena	*angustata*	3 iv 78	4	Dixie C FL	555	529.0	601.0	72.0
Pyractomena	*barberi*	20 iii 78	2	Levy C FL	576	549.0	616.0	67.0
Pyractomena	*barberi*	3 iv 78	4	Dixie C FL	576	548.0	614.0	66.0
Pyractomena	*borealis*	31 iii 68	11	nc FL	570	542.0	611.0	69.0
Pyractomena	*borealis*	20 iii 78	7	Levy C FL	575	545.0	614.0	69.0
Pyractomena	*floridana*	5 ix 78	5	Dixie C FL	574	546.0	612.0	66.0
Pyractomena	*limbicollis*	1 iv 78	6	Highlands C FL	574	546.0	614.0	68.0
Pyractomena	*linearis*	18 vi 68	8	c NYS	570	541.0	610.0	69.0
Pyractomena	*angulata*	25 iv 78	3	nc FL	578	550.0	618.0	68.0
Pyractomena	*angulata*	6 v 78	4	Levy C FL	577	550.0	614.0	64.0
Pyractomena	*angulata*	14 vi 67	4	s MI	577	551.0	610.0	59.0
Pyractomena	*lucifera*	9 v 67	5	nc FL	568	540.5	611.5	71.0
Pyractomena	*lucifera*	24 iv 78	5	nc FL	571	543.0	611.0	68.0
Pyractomena	*ecostata*	18 ix 67	6	Levy C FL	558	533.0	602.0	69.0
Pyractomena	*similis*	27-29 v 83	5	c VA	573	546.0	613.0	67.0

Notes On Taxa Recognized by Barber and McDermott

aureolucens Barber: no change, but confusing as to legitimacy, origin, and connections with other populations

bethaniensis McDermott: no change

brunnipennis flavicollis Barber: elevated herein to species status—***flavicollis*** **Fall**

brunnipennis floridanus Barber: elevated herein to species status—***floridanus*** **Barber**

caerulucens Barber: no change, but recognized (via seniority, in company with *pensylvanica* sensu Barber) as being central to a wide-ranging diversity of FPs and variably connecting long-flash and dot-dash FPs—their demes—and involving twilight short-flash adjunct FPs, and others

cinctipennis Barber: no change, but tentatively recognized as possibly emitting two FPs in Barber's bailiwick and having connections with southeastern species, one/some with complex flashing match-ups with *Photinus consanguineus*-Group species—*branhami, whistlerae*, and others, named and unnamed

congener LeConte: no change, but connection/fusion with *frontalis* at/near FL/GA seems unlikely?

divisa LeConte: no change

fairchildi Barber: recognized operationally here via distinctive FPs—their variation and continuity—as broadly occurring from the type locality in Nova Scotia to Minnesota and south to Arkansas and South Carolina

frontalis LeConte: no change, but connection/fusion with *congener* at/near FL/GA line unlikely?

lineaticollis Motschulsky: name-bearing specimen ("holotype") of Motschulsky apparently lost (in Russia?); recognition here based on Barber's understanding sharpened to apply to a species occurring in nc FL, and informally attached to an operational name-bearer

lloydi McDermott: no change

lucicrescens Barber: no change

missouriensis McDermott: no change, and recognized as one of few to several such "train-flashing" and "river-associated(?)" entities with different geographic occurrence and FP (flash) period intervals—*chenangoa, potomaca*, unnamed

pensylvanica **(**DeGeer**)**: recognized as one (se MD) of several dot-dash flashing entities/variads having significant variation in adjunct FPs, and seemingly with ties with Barber's *caerulucens*

potomaca Barber: no change, and recognized as one of few to several such "train-flashing" and often "river-associated" entities with different geographic occurrence and FP (flash) period intervals—*chenangoa, missouriensis*, unnamed.

pyralomima Barber: suffix corrected; never encountered as described by Barber and more recent observers, though the FP as described may have been observed as an adjunct FP; see especially the Washtenaw "trispecta": AA dipper, AA dot-dash, AA flicker

quadrifulgens Barber: no change, but possibly/actually the species named by Fabricius from 3 females

salina Barber: suffix corrected; recognized as one of several coastal entities/variad demes, with similar FPs; will require genetic analysis—an interesting project!

versicolor Fabricius: continental form of a complex, herein recognized as one of at least three geographic entities—*harrannorum* (FL), *stevensae* (NE, eastern NY including L.I.)

GLOSSARY

Some of the terms in this collection have different or more restricted meanings from what is found in a general or entomological dictionary; some were invented here because none found elsewhere seemed to fit the intention here.

accuracy n. the correctness or truthfulness of something, that is, its degree of closeness to a known referent such as a specific value or statement (contrast with precision)—quality of being very close to some specific "standard"—e. g. (a measurement)

active space n. the three dimensional area (space/volume) where the concentration of a chemical substance is high enough to be detected by the receiver-organism under consideration (a function of molecular dispersal from a source and detector sensitivity)

activity space n. the three dimensional area (volume/space) in the habitat in which a (site patrolling) firefly species carries out the flight and signaling associated with its sexual communication; i.e., where males fly and emit their flash patterns, and typically within or just at the bottom edge of which females perch to observe and answer males; it may change during a species period of activity—e.g. move up into the canopy later in the evening

adjunct flash pattern n. the mate-seeking/advertising flash pattern(s) of a *Photuris* species other than its primary (species identification) flash pattern (see primary/default flash pattern)

aedeagus n. male genitalia, singular; pl. aedeagi)

A-flicker n. *Photuris* flicker modulation rate that closely matches the rate of the flicker of *Pyractomena angulata*; *angulata's* rate is now known to vary somewhat geographically—an initial conclusion of similarity/identity was based on small sample comparison via nonparametric statistics. With increased data across temperature ranges, adjunct FPs of some *Photuris* are now known to have rates matching/crossing both that of *Py. dispersa* (D-flicker) and rates ranging in between these two models. See discussions in *Ph. quadrifulgens*, *eureka*. The flicker of Florida's *Ph. stanleyi* is a good match of *angulata's* (see page 295); no other flickering species is present in their season.

aggressive mimicry n. a case of mimicry in which the exploitation of the dupe by the mimic involves direct physical harm/ exploitation of a specific/single individual, such as predation

Airport Pond a firefly study site in Gainesville FL, near the airport on City Industrial Park property, where extensive observations were made 1964-1985

allochronic adj. active at different times, not overlapping in time

allopatric adj. living in geographically different (i.e. separate) places, not overlapping in distribution

altitude n. the height of flight above the ground; notes of distance above other substrates such as woody canopy or grass-tops is stated specifically

antennomere n. the individual unit of an antenna, i.e. a section, segment s.l., article, element

approximate adj. near to; as when body parts, such as the two eyes, are close together they are said to be approximate

article n. a joint, a unit section of any jointed or (apparently) “segmented” structure

attitude n. flight orientation of flying insects in three dimensions (pitch, yaw, roll) critical and partially responsible in the detection of the firefly flash by the receiver

aurora borealis n. (traditional; northern lights)—luminous bands or streamers of light sometimes visible in the night skies of northern latitudes, caused by the ejection of charged particles into the magnetic field of the earth

bailiwick n. special domain; here, geographic region of focus, expertise

basal piece n. the basal sclerite of male genitalia, from and within which the projecting three lobes arise; the element of male genitalia that is nearest to the body

bifid adj. (contrast with *simple*) a forked, two-pronged, two-pointed or cleft claw or projection

biological species n. ". . . groups of interbreeding natural populations that are reproductively isolated from other such groups" [a temporarily useful but a theoretically/operationally unsatisfying "concept"].

bioluminescence n. chemiluminescence produced by living organism—see chemiluminescence

bipectinate adj. (contrast with *pectinate*) having two branches (“tines”) on a joint, e.g., as on each of several antennal antennomeres

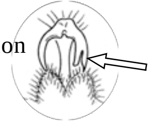
carina (pl., carinae) n. an elevated ridge that is somewhat sharp at its crest

carinula (pl., carinulae) n., the diminutive of carina, a little elevated ridge

chemiluminescence n. emission of light (photons) by a chemical reaction in which a substrate molecule (in fireflies generically termed luciferin) is oxidized in the presence of an enzyme (generic term, luciferase), and a coenzyme (manganese, magnesium)

clasper n. the small apparent terminal ventrite of males of some genera, that closely encapsulates the aedeagus

claw n. a sharp prong or structure at end of insect tarsi, usually paired, sometimes bifid or modified in some fashion



clypeus n. the lower part of the face of an insect below the frons and above the labrum (“upper lip”)

concolorous adj. of the same color

connate adj. fused or otherwise firmly united; e.g., the labrum is said to be connate with the frons on the face of *Photuris*

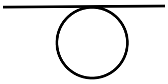
constituted. adj. term used in speaking of the way working-taxa are viewed and constructed/assembled/defined to exist, based on an *assemblage* of characters that is taken to be indicative and representative of relationships of uncertain depth

constitution n. how the named taxon under discussion is presently viewed and defined with its inclusive (morpho/typo) parts and populations, for working and discussion purposes. A term used in headings of species discussions, this indicates the section where a summary statement is made, relative to systematic progress toward understanding and locating the actual and incipient isolated evolutionary entities, i.e. species and variads within the nominate taxon.

continuous adj. (contrast *discontinuous*) gradual/smooth versus with an abrupt variation, say, in the direction along the sweep of an arc

costa (-ae) n. a ridge that is rounded at its crest

crep, crep unit n. the duration of Civil Twilight (CT) in minutes; the duration of time, in minutes, that is required for the setting sun to pass from tangency of the upper limb (top arc) of the sun with the horizon, to a point where the upper limb is 6° below the horizon; the unit of measurement of elapsed time that is used just before and after sunset that gives a comparable measure of ambient light intensity among localities at different geographic localities with respect to latitude and longitude—but not weather conditions, which are variable.



crepuscle n. twilight, see crep.

crescendo adj., n. a flash of light with a slow, drawn out onset, i.e. rise-time, as in *Photuris lucicrescens*

cucujo n. a click beetle, family Elateridae.

Day-Glo® n. a trademark name used for fluorescent coloring agents and materials—higher energy wavelengths are re-radiated at the lower and a dominant color wavelength.

daytime dark firefly n. a member of the family Lampyridae that is sexually active in the daytime and is without light organs as an adult (e.g. *Ellychnia*, *Pyropyga*, some *Lucidota*)—with one known U. S. exception, *Lucidota luteicollis* adult males are luminescent

decay n. decrease in intensity of luminescent emission, say, at the end of a flash, contrast with increase; see rise (rise-time)

default (flash pattern) adj. the flash pattern that males begin emitting after receiving a flash response to one of the other FPs in their repertoire; it is recognized as the species own, species-typical flash pattern

deflexed adj. (contrast with *horizontal*) bent downward abruptly, as in angular position or attachment of a body part. e.g., a deflexed head

D-flicker n. a *Photuris* flicker modulation rate that matches that of the flicker of *Pyractomena dispersa* (and *sinuata*?). (see A-flicker)

delay n. the time elapsed after a male flash pattern to the beginning of the females flashed response, as measured from the beginning of the male's flash

deme n. the local breeding population of a nominal or working/operational species, which size depends upon the vagility and size of the organism and its movement and occurrence within the grain-structure of its own and interspersed habitat (type)—a fundamental/key, tangible, presumably recognizable, operational unit of evolution

determination n. term used by taxonomists to mean identification

diagnosis n. as used in heading of texts, indicating the quickest, simplest, and most reliable features for distinguishing the taxon being considered from the most likely equivalent taxa to be confused with it

diapause n. a period of suspended development or growth in insects, sometimes triggered or terminated by seasonal changes

disk n. the central raised part of coleopteran pronotum or elytron

dorsite n. the dorsal sclerotized plate of a segment, i.e., tergite plus fused collateral sclerites from adjacent pleura

duty cycle n. time fraction occupied by the emission in the signaling of a male: calculated, FP duration/FP period

eclose v. to emerge from the egg chorion (shell) by a first instar larva; to emerge from pupal skin, by an adult

electroluminescence n. the light emitted when layers of substances are separated and electrical charges from the separated surfaces stimulate molecules in the air between the surfaces; as in blue light seen when adhesive tape is sharply peeled from a spool of library tape or a peppermint "Lifesaver" is crushed between the teeth, and the nitrogen molecules in the air are stimulated by electrical discharge—see also triboluminescence

epipleural fold n. the raised lower edge of an epipleuron

epipleuron (pl., epipleura) n. the deflexed or inflexed lateral margin of an elytron

explanate adj. flattened out, as in the flange-like, out-turn of a pronotal or elytral margin, lateral to the pronotum’s central disk

fabric n. think of the physical existence of a “species” across its geographic distribution, and the forces and elements that maintain it and those that cause it to be broken up into demes/variads (sub-parts); think of this "spread" as a carpet, with the ties (gene-flow, genic inertia) holding two selected places together as the longitudinal threads in a carpet, the *warp*; and the phenomena that cause the two selected places in the distribution to be and become more isolated, as the *woof*, the cross-threads of the fabric.

filiform adj. long and narrow, thread-like, e.g., a thin (fine) antenna comprised of not-robust cylindrical, nor spherical joints

firebeetle n. a luminescent beetle of the family Elateridae; this usage is occasionally found in the older literature and is favored here; among other terms that have been or are used for these beetles are: glowfly, cucujo, pyrophore, firefly, night-lighting elater and peeny wally

firefly n. a beetle of the family Lampyridae, not necessarily luminescent; in older literature this term was used for luminescent click-beetles (Elateridae) to distinguish them from Lampyridae, then termed lightning bugs. See firebeetles.

flash n. a single emission of light of short duration

flash pattern n. (**FP**) rather strictly speaking, that unit of light emission by male fireflies that is repeated at somewhat regular intervals and which stimulates a female of his species to emit a flash response—note that these two definitive features are not always the same structural unit of the flashing; for working purposes, the flash pattern is that obvious repeated unit of light emission of flying male fireflies that can be distinguished by a competent field naturalist; it is the species-typical unit of light emission of "lightningbug" fireflies that is repeated at somewhat regular time intervals by advertising, mate-seeking males; commonly, the flashed entity that stimulates the female response flash

flashing-type (light organ, lantern) adj. a firefly light organ so constructed that it is capable of rapidly turning bioluminescence emission ON and OFF, as contrasted with light organs that glow all of the time, or can only be turned ON and OFF slowly.

flicker n. an emission of light in which the intensity is rapidly varied, usually in firefly flash patterns, regularly, rhythmically; sometimes intensity falls to OFF, but not always; this meaning at some variance with H. S. Barber's original use; see also tremulating.

fluorescence n. the emission of light from a substance when it is exposed to radiation; emission occurs **only** during the actual time of radiation exposure and virtually not afterward ($<10^{-8}$ sec; see phosphorescence), as seen in certain white shirts under UV lights at dances

folded completely adj. an epipleuron is said to be completely folded if it turns back on itself abruptly, forming a (“sharp”) crease, e.g., as in the sharply creased trouser legs of a military uniform

FP n. in capital letters, used for the phrase *flash pattern* especially when a different type of emission might be confused; FP means more than the physical phenomenon itself, but also any male luminescent sexual-advertising emission; the signaling *glow* signal of *Py. angustata* is referred to as the FP of this species, usually with a clarifying note

gesture n. the move in space executed during the emission of the flash pattern (FP) by a mate-seeking male; such movements presumably make FP emitters more likely to be seen by females

glabrous adj. without setae (i.e. without insectan “hair”—by definition and ancestry insects don't have hair)

glow n. a steady emission of light; the term by itself does not indicate intensity level

glowworm n. (**1**) a luminescent larva or larviform female, usually of the family Lampyridae but also a few other beetle families; in older literature this term commonly referred to species of Lampyridae that had, as it was said then, "imperfect" adult females, especially the well-known European *Lampyris noctiluca.* (**2**) luminescent larva of Mycetophilidae (Diptera)

glowworm firefly n. a "primitive" member of the family Lampyridae that uses glow signals for sexual communication, typically with glowing females attracting nonluminescent males (e.g. *Microphotus, Pleotomus*)

glowworm fly n. adult fly of family Mycetophilidae whose larva is luminescent

grain (fine versus coarse) n. the density of demes/variads in geographic space; various other concentrations/dispersions of interest—food plants, prey, etc.

Group n. ala J. W. Green (1956), a working grouping of species sharing several features and consequently thought to be phylogenetically closely related

Gun-Club n. a study site near the airport in Gainesville FL, on City's Industrial Park Property, where observations were made extensively 1964-1985

habitat n. the ecological:botanical/hydrological type or class of living space of an organism; a kind of environmental structure/system: for example, mesic hammock, pine flatwoods, cattail marsh—not the same as site

hard-wired adj. behavior understood to be “built into” the nervous-system, as in *near* automatic, instinctive, and other weighty and difficult ethological understandings

Hertz n. unit of modulation rate, equal to cycles per second, CPS, the latter being the designation that Hertz replaced in many usages/contexts; abbreviated Hz or HZ.

heuristic adj. having predictive ability, as in a(n) heuristic ('small' t) theory.

hitch n. the apparent rapid twinkle or sparkle in the short flash of a firefly that usually indicates that a rapid submodulation occurs before, after or as part of the major flash; sometimes apparently/perhaps due to the asynchrony of light bursts from the two (spatially separate/adjacent) segments of a lantern that is detected by the spacially-acute human eye (e. g. see *Photuris hebes*)

hypomeron (pl., hypomera) n. inflexed edge of a pronotum, reminiscent of side-blinders on horse’s halter; said to be closed when reaches the anterior margin of the pronotum (and forms/meets a corner angle there); is open when does not reach the margin

ignis fatuus n. (traditional) a light source that hovers or flits over swampy ground at night, possibly caused by spontaneous combustion of methane or other gases from rotting organic matter; also called Friar’s Lantern, Will-O’-the-Wisp

inspection-dialogue n. variable phase of the male approach flight that occurs when the male is responding to the female signal and hovers and signals near her

interval n. time between the beginning of an event (flash pattern, pulse) and the beginning of the next such event—PERIOD is undoubtedly a better term in some but not all situations (when RATE (1/period) is involved in discussion

jagged adj. descriptive term for multiple-pulse flash patterns, indicating a ragged, jerky appearance; is caused by firefly flagging (waving) abdomen during emission of a rhythmical flicker (e.g. *Pyractomena barberi*), or from changing pulse intensity and duration within a flicker (esp. Florida *Photuris harrannorum*).

keel-necked (firefly) adj. referring to species of the genus *Pyractomena*, as named for the distinctive longitudinal keel (carina, carinula) at the center mid-line of the *Pyractomena* pronotum

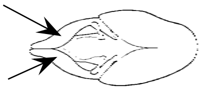
labrum n. the fore (upper) lip of an insect which covers the bases of the mandibles, someimes membraneous

lanternfly n. *Fulgora laternaria.* tropical New World hemipteran of the family Fulgoridae that was once thought to be luminescent; also other similar insects and myths (?) in Africa and Asia

latency n. see response delay.

lek n. gathering of members of a breeding population, resulting in/enabling/setting up mate competition among males, comparison and selection by females

lateral lobe n. one of two lateral processes of lampyrid male genitalia; sometimes termed *paramere*



lightningbug (lightningbug-firefly) a member of the family Lampyridae whose adults use flashes, flickers, or other rapidly controlled bioluminescent emissions for sexual signaling (e.g. *Photinus, Photuris* (compare: glowworm firefly, daytime dark firefly)

local species n. traditional—the species found/known in nature by the local naturalist in his bailiwick

luciferase n. generic name given to certain biological catalysts of bioluminescence; enzymes that facilitate a light-emitting reaction

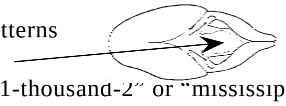
luciferin n. generic name given to photon-emitting molecules that are oxidized in many light-emitting reactions

luminescence n. emission of light energy by molecules involving the shifting of sub-atomic particles; contrasting with incandescence; examples: chemiluminescence (e.g. the bioluminescence of organisms); phosphorescence (toys with sustained light emission after being illuminated with an electric light), fluorescence (light emission only during stimulation by high-energy radiation, e.g. office lighting).

male mimicry n. flashing behavior of male *Photuris* fireflies of certain species, in which, during their own mate search flight, they emit adjunct flash patterns that are similar or identical to the flash patterns of the males of other species, which the *Photuris* males' own females prey upon (through aggressive signal mimicry); and which are (or historically were), according to the hypothesis, indistinguishable by the *Photuris* females; also in leks of Florida *Photinus macdermotti* when males mimic FRs of their females and predators

match n. to be similar to, be like with respect to specified qualities—e.g. flash patterns

median lobe n. central/middle process/finger of male genitalia



mentally-timed v. measuring a period of time by counting as in “1-thousand-1-1-thousand-2” or “mississippi-1-mississippi-2” … (i.e, timing without a stopwatch)

mesepimeron n. the ventral plate of the midthoracic segment that is adjacent to the mesepipleuron; their suture provides a distinction between certain cantharoid/elateroid families

mimicry n. The presentation of false signals or other information by an organism (the mimic) that are mistakenly interpreted by another organism (the dupe) to belong to a different organism or object (the model), with the result that the dupe is deceived/exploited by the mimic (mimicry is an *ultra-complex* phenomenon (see Wickler, 1956; Pasteur, 1982)

modulation rate n. frequency of intensity changes per second, Hertz, cps

morpheme n. unit of a signal that conveys species or other information that cannot be divided into smaller, independently functional, communicative units.

OFF n. referring to the luminescent emission of a firefly light to indicate that the light has stopped showing, or abruptly dropped to or nearly to zero level/lux; if rate of decay of intensity is thought to be important, this will be stated.

ON n. referring to the luminescent emission of a firefly light to indicate that the light has begun to show or to be emitted, usually abruptly; if rate of onset is thought to be important, this will be stated.

parapatric n. inhabiting abutting geographic regions, not sympatric and not clearly allopatric, but beside, next to each other; used in connection with species, but as considered at a much finer scale as with demes, recognized as of considerable/major research interest and importance

patrolling adj. searching flight throughout a specific, firefly-rich, ecological site by advertising (flashing) males for mates (contrast with roving); this may occur only in the Western Hemisphere, where sedentary mating protocols are not possible

pause n. time lapse in seconds between the end/OFF of a last pulse in an FP to the beginning/ONSET of the next FP

pectinate adj. comb-like, i.e., with a single branch on many antennal articles

period n. elapsed time between the beginning of a periodically recurring element through time (e.g. male's flash pattern) to the beginning of the next consecutive element—

peenywally see firebeetle.

phenology n. the study, knowledge, or information about the seasonal appearance of a biological phenomenon such as adult activity or flowering of plants

phrase n. see flash pattern (FP).

PM-recorder PM-gun. n. The photo-multiplier system used to record luminescent emissions of fireflies and the artificial lights used to experiment with fireflies, for accurate information of their timing and relative intensity (profile) through time

precision n. (see, compare with *accuracy*) quality of repeatability, achieving the same result, say, in making repeated measurements of the same item—instead of matching an established reference (accuracy), repetitions of the observational system reach "the same" result—though it may not be accurate with reference to an established referent

primary flash pattern n. (default FP) the mate-seeking/advertising flash pattern of a *Photuris* species that is understood to be the species-distinctive recognition pattern; in some species it is the pattern that males **default** to when they receive a flashed response to one of their other patterns (see adjunct flash pattern)

pronotum n. the dorsal sclerite of a the prothorax; in Lampyridae the pronotum forms the roof- or sunshade-like cover over the head; in many genera—most North American species—unless the neck is stretched out the eyes are also covered, sometimes excepting *Photuris*; contrast with many Luciolinae

protocol n. the behavior complex preliminary to and including mating—courtship and the behavior elements leading to sperm transfer; originally used when it was apparent from a study on the New Guinea firefly *Pygatyphella* (nee *Luciola*) *obsoleta* that enumerating systems (as in I and II) would not adequately permit classification of mating procedures (Lloyd, 1966, 1972)

pulse n. term used for a flash/flashlet or modulation within a pattern of two or more flashes or intensity increases, usually used when confusion might result from use of the term "flash"

pulse rate n. (same as modulation rate)

pygidium (pl., pygidia) n. the last dorsal plate of the adult abdomen, the tail piece ("telson")

pygopodium n. eversible rubber-glove-like structure at the tail-end of a/ lampyrid larva used in locomotion, for grooming after eating, for clinging to vegetation during pupation in *Pyractomena*

ramp adj., n. flash with a slow intensity onset phase (same as crescendo), or the slow onset phase itself

recital n. portion of a *Photuris* repertoire that is displayed in a population over a designated period of time, e. g. an evening

release v., **releaser** n. from classical ethology: to trigger a behavioral response in another individual; the element that stimulates the action in the observer

response interval n. see **delay**

rise n. same as **ramp**, increase in intensity of a luminescent emission, say, at the beginning of a flash (rise-time, duration in mSec during which increase occurs)

robust adj. sturdy, rugged, i.e. not frail or delicate

roving adj.

Saint Elmo's Fire n. (traditional) luminescence from the electrical discharge on a pointed object, such as the mast of a ship or airplane wing, during an electrical storm

segment n. individual unit of a larger structure (antenna, leg, abdomen) that is recognzed by the presence of individual/ independent musculature—evolutionary origin and history enter into formal understanding and recognition

semiosystematics n. taxonomic/systematic approach that focuses attention, not exclusively but superlatively cautiously and perspicaciously, on the mating signals of sexual organisms, for clues to gamete transfer, hence to gene flow, sexual choice and common gene pools; and clues to evolutionary relationship, patterns, pathways and mechanisms

semiosystematic voucher specimen n. a curated and labeled firefly specimen that was captured immediately after it emitted a taxon-diagnostic signal, a male flash pattern usually, but also a female signal flashed in response to a conspecific male's flash pattern

serrate adj. a structure with a serially pointed edge, i.e. with a saw-toothed outline on one side

variad n. a distinctive species-level group which may or may not be deserving of formal/nominal species recognognition, and often/typically cannot be distinguished from other regional variads with confidence except by behavioral-ecological data, especially in *Photuris*—this is at the "shoreline" of exploring and understanding "diverse" in biodiversity

shouldered adj. a flash with a partial rise, then pause or slight dip followed by a full rise, as in *Photuris hebes*

site n. locality, location, "spot" where fireflies are studied, such as a stream-bank by a bridge, a specific meadow, or woods; compare/contrast with "habitat"

sky-glow n. light reflection from clouds illuminated by artificial sources such as street, residence, and industrial lighting; transmission through clouds back-lighted by the moon is often bright, but will occur in the natural moon phase to which organisms may be tuned if it is significant.

smooth-necked (firefly) adj. referring to smooth pronotal disk surface found in many fireflies; term is used here specifically for *Photinus* to contrast with the pronotal ridge of *Pyractomena; Photinus* have a smooth or slightly grooved pronotal disc

species swarm n. a group of similar species living in close geographic proximity but not necessarily sympatric, the component species of which are thought to be closely related and generated approximately in the region in which they are presently found—i.e., endemic

spree n. the time-limited/momentary occurrence of signaling or other "group" activity by several individuals in somewhat close proximity, after a period of no or very little activity, and after which another period of little or no activity follows

squadron n. a group (flight) of two or three male fireflies that suddenly appears in an area where for several minutes previously there had been none of their species active, flying and flashing—either they move into the area together, or were there but inactive and abruptly became active, say, after a roving conspecific male flew by

sub- pref. almost, nearly, approximately, roughly, as in almost-trapezoidal and almost-triangular, i.e., sub-trapezoidal and sub-triangular

swarm n. (**1**) a group of insects congregated or aggregated in a limited space, sometimes in reference to a marker (chimney, bough, sunlit patch, bush, cowpie); nearly always with males in exceedingly greater number, and in which a species' mating occurs, exclusively, or under certain circumstances exclusively; note: a single individual behaving in a swarming manner, as in reference to a swarm marker, may be said to be swarming; (**2**) a group of social insects belonging to the same nest, moving, or remaining in mass between bouts of actual movement, as to a new nest site.

swarm marker n. the physical referent used by unrelated (non kin), conspecific insects to pilot ("navigate") and orient their position in space, during sexual gathering (see swarm)

SWAT n. abbreviation for stopwatch

sympatric adj. having overlapping geographic distributions, living in the same geographic area

System n. the method, arrangement, order of signaling or signal exchanging between communicating individuals; System I: one individual (sex) broadcasts a signal, the other receives and approaches; System II, one individual broadcasts a signal, the other receives and responds with a signal, the first individual moves toward the respondent; several additional "systems" have been recognized in Asian fireflies.

teneral adj., n. the soft, unscleratized, often pale-colored appearance of an insect that has just eclosed/emerged, its cuticle has not hardened (tanned); n. the insect itself,

terminal adj. the last unit of a series, of antennal joints or body segments, i.e., the terminal antennal article is the joint at the apical end

thermoluminescence n. emission of light by minerals and some rocks as a result of gentle heating or warming (warmth stimulates electrons in a metastable [= unstable, transient] state back to a transition state and then there may be a subsequent return to ground level with emission of photons)

train n. a long-continued series of flashes emitted with rhythmic rather constant (near metronomic) regularity and only occasionally interrupted, say by transient local environmental conditions; characterstic of certain species such as those in the *Photuris frontalis* and *potomaca* groups.

train-flashing adj. emitting flashes in trains (see train).

train-timing v. a method of measuring average flash period (rate) by timing (stopwatch) several (counted) periods and determining the mean by [timed-interval/no. periods]

transient n. the change in intensity (value), as at the beginning and end of a flash; the transition from being OFF to ON and vice versa

tremulating adj. Barber's term for rapid modulations seen in *Photuris tremulans;* see flicker

triboluminescence n. The emission of light by the grinding of certain crystalline substances, such as cane sugar; positive and negative charges are produced by separation of surfaces and glows are from the excitation of molecule fragments or excitation of atmospheric gasses

tridentate adj. three-toothed, with three cusps projecting

truncate adj. with a sharply cut-off apex and somewhat spatulate in form, perhaps broadening toward the apex

twinkle n. short, sharp, rapid, irregular pulses

typological (species) adj. descriptive and indicative of a species, emphasizing that the usage of the term "species" is utilitarian and pragmatic and based on various morphological, behavioral, ecological etc. identities or similarities; that is, not based on knowledge that could directly be taken as evidence of the species members sharing a "proximate/local/integrated" common gene pool

variad n. a regional form of a "species complex" showing some variation from a reference population within the complex—a term apparently originating in the early 20th century

ventrite n. a ventral sclerotized plate of the abdomen, that cannot be termed a sternite because it is formed of two fused pleurites and a sternite

ventro-basal-process n. two tiny projections arising ventrally at the base of the median lobe of the male aedeagus (genitalia) in certain fireflies, such as some *Photinus*; used for identification and classification, and their form has been found useful for distinguishing species and species groups

vitreous n. glass-like, clear or translucent, shiny (see ultimate/distal antenna element of *Phausis*, *Microphotus*)

voucher (specimen) adj. see semiosystematic voucher specimen; a representative specimen linked to specific behavior

warp and woof n. referring to the “forces and elements” of genetic connection and isolation in the fabric of a spatially dispersed collection of populations, with gene flow on the one hand and physical separation on the other contributing to continuity and the reduction or lack of connection/"cohesion" (see fabric)

working species/taxon n. an operational recognition of pragmatic convenience, recognized especially at preliminary (alpha) stages of taxonomic work, but probably always the situation in taxonomic recognition; the opinion given here is that most named firefly species, with possible mentioned exceptions, are probably and should be assumed to be "merely"bookkeeping entities for organization and communication

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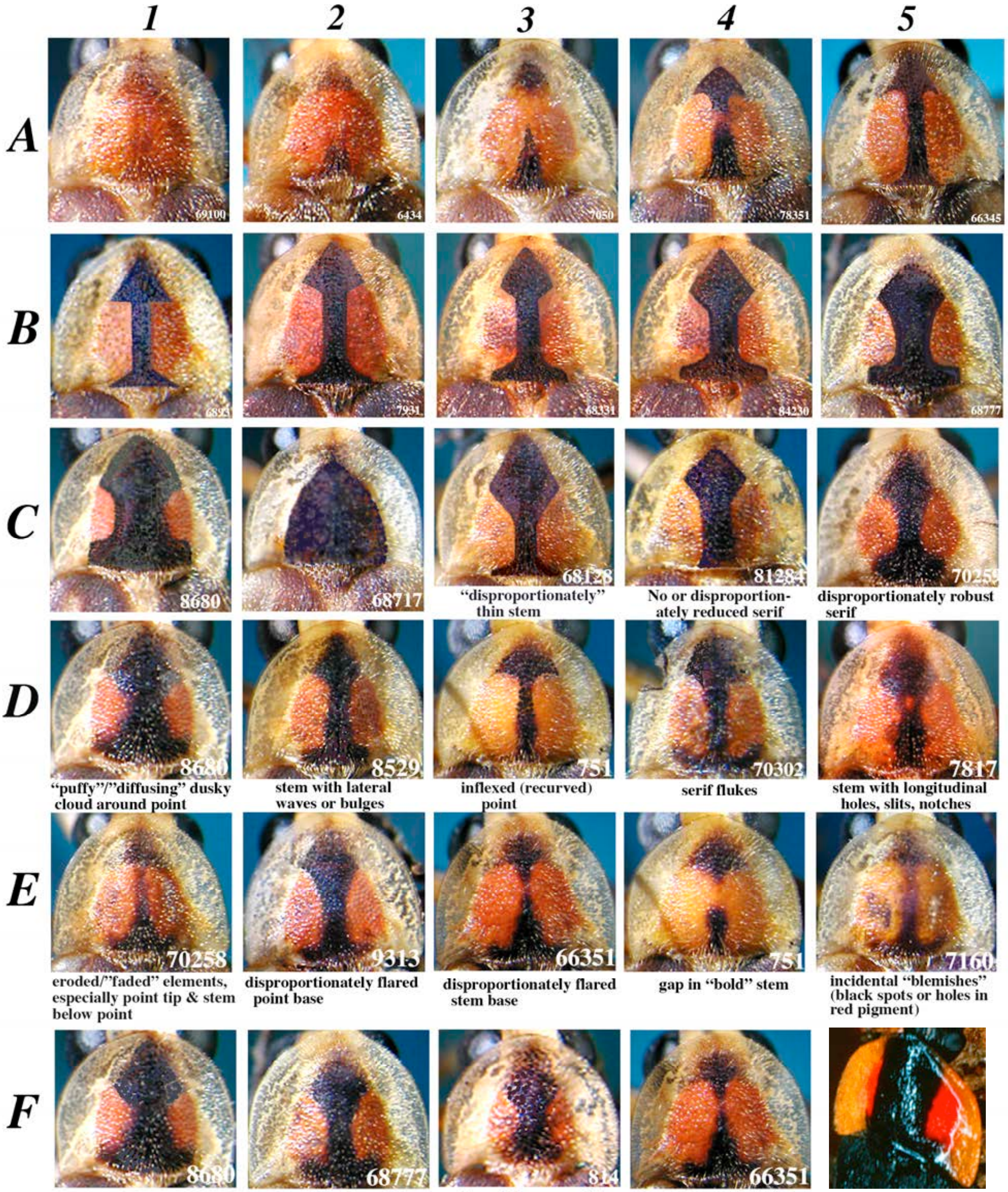
PNV ARRAY 201.2



C3: "disproportionately" thin stem

C4: No or disproportionately reduced serif

C5: disproportionately robust serif

D1: "puffy"/"diffusing" dusky cloud around point

D2: stem with lateral waves or bulges

D3: inflexed (recurved) point

D4: serif flukes

D5: stem with longitudinal holes, slits, notches

E1: eroded/"faded" elements, especially point tip & stem below point

E2: disproportionately flared point base

E3: disproportionately flared stem base

E4: gap in "bold" stem

E5: incidental "blemishes" (black spots or holes in red pigment)

F1: expanded (squarish) stem pedestal

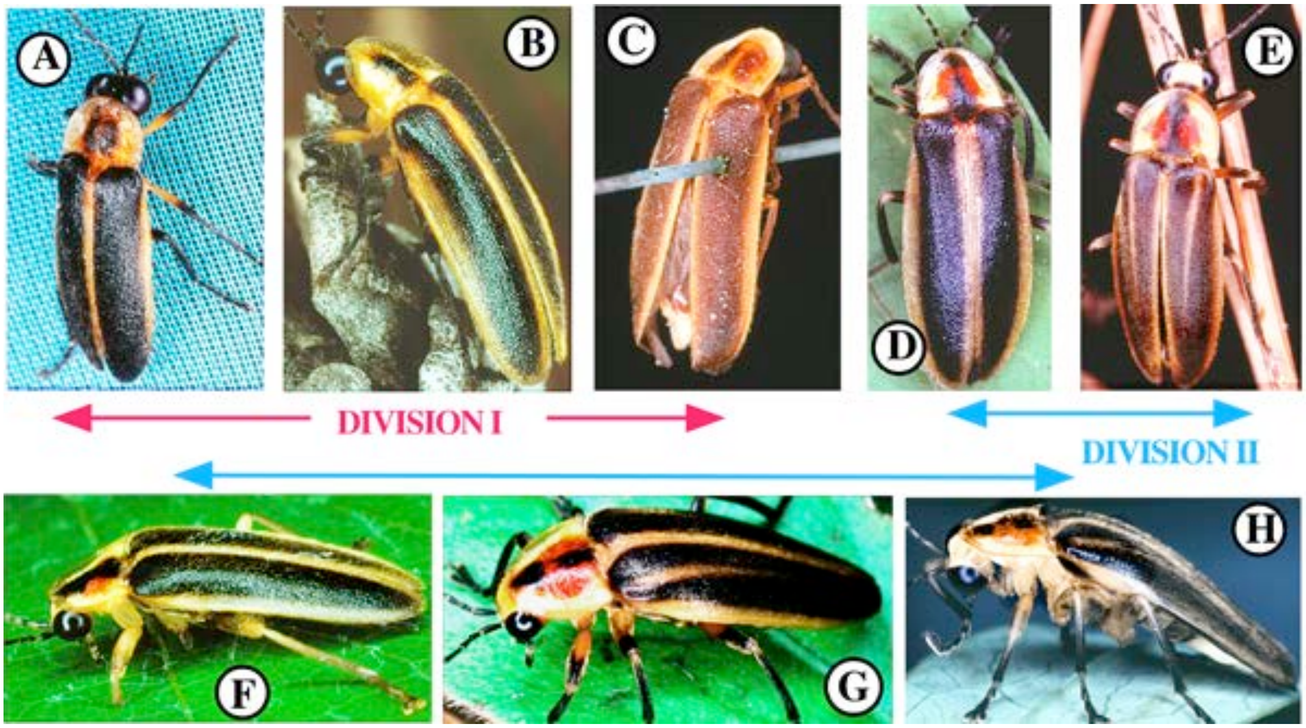
F2: expanded (squarish) point soffit

F3: stem with wasp waist

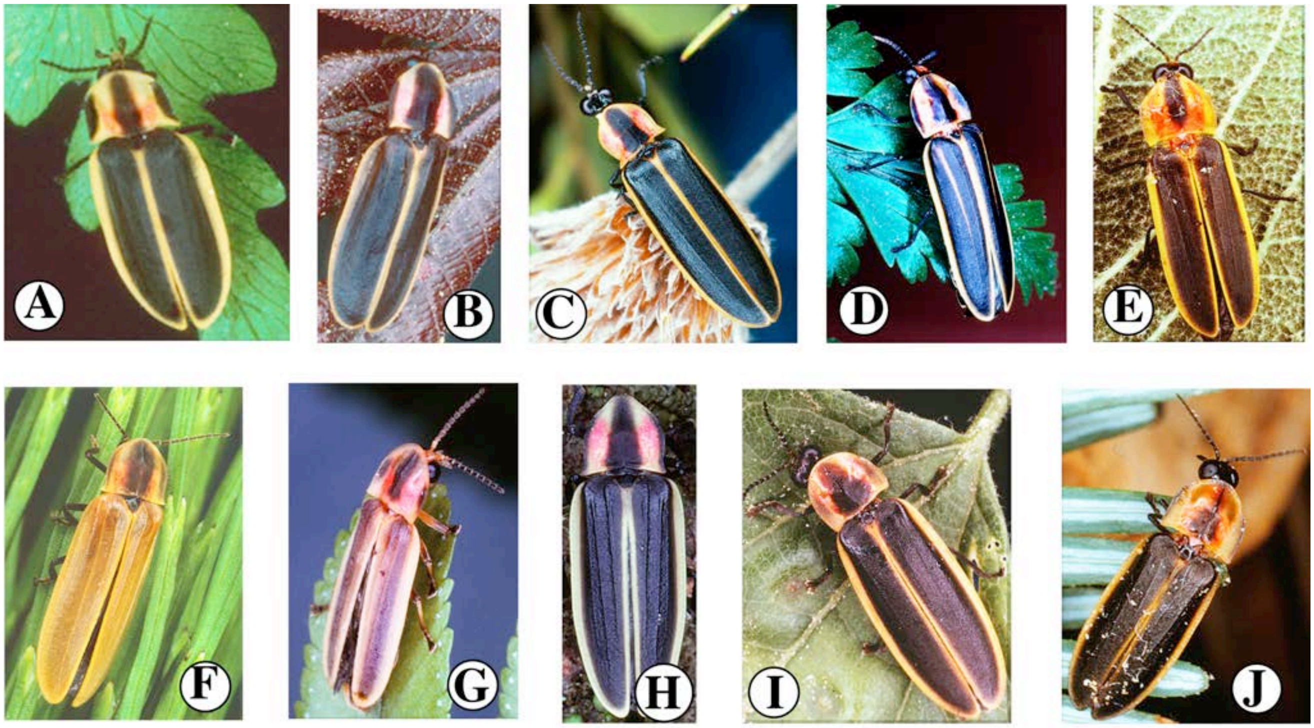
F4: irregular, somewhat abrup stem-width changes

F5: score this one

Firefly Sampler: Photuris and Pyractomena

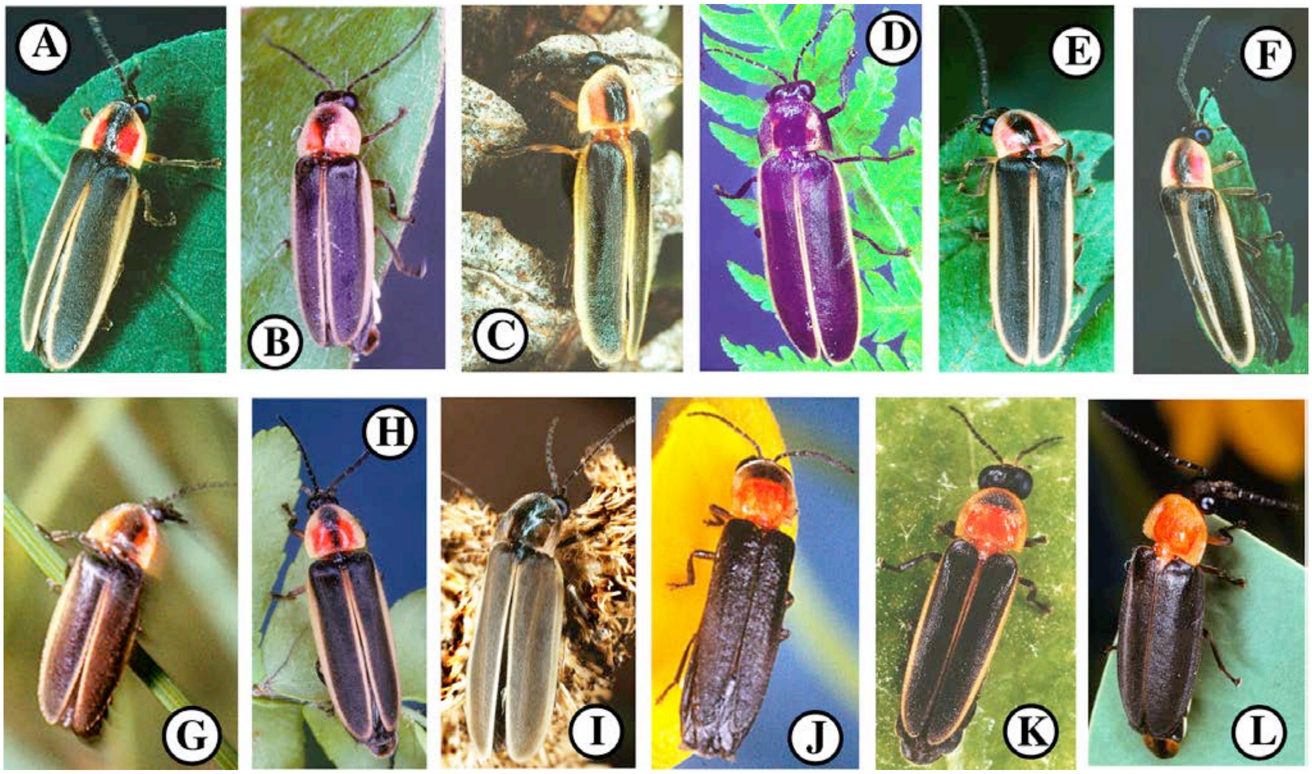


Photuris (A) *congener*, (B) *frontalis*, (C) *divisa*. Division II, (D) *tremulans* Group, (E) *versicolor* Group, (F) *cinctipennis* Group, (G) *lineaticollis* Group, (H) *lucicrescens* Group.



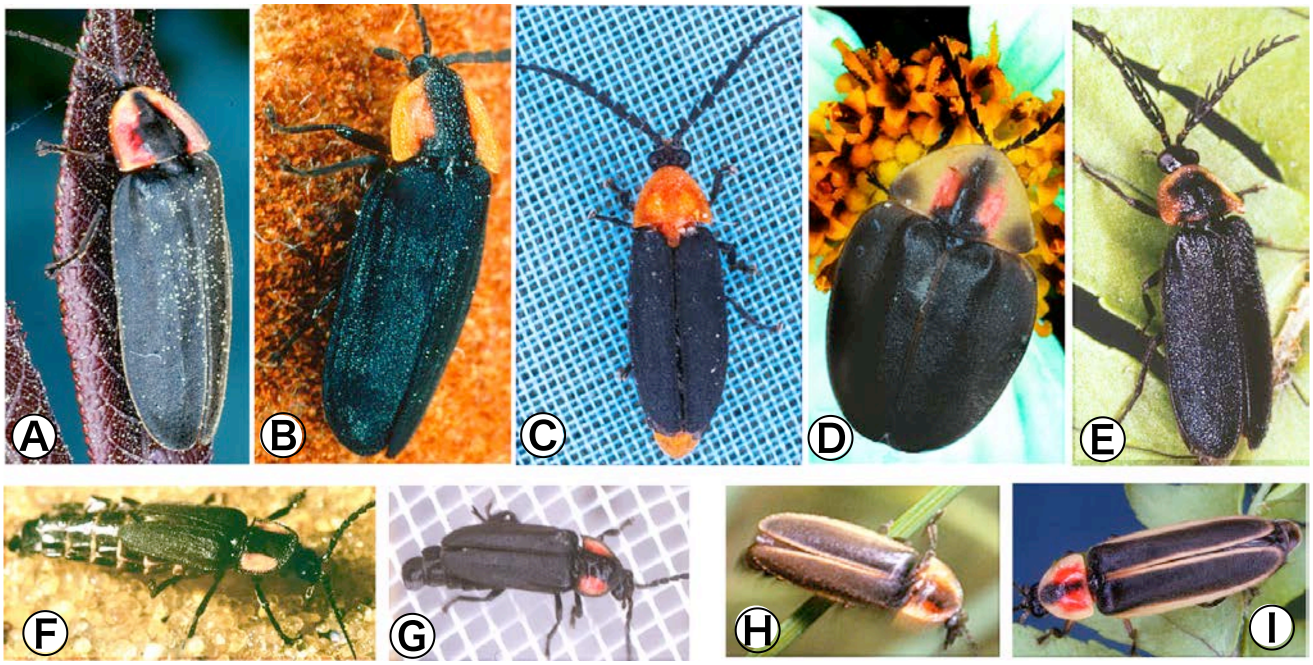
Pyractomena (A) *Py. angulata*, (B) *Py. borealis*, (C) *Py. angustata*, (D) *Py. ecostata*, (E) *Py. floridana*, (F) *Py. linearis*, (G) *Py. lucifera*, (H) *Py. limbicollis*, (I) *Py. palustris*, (J) *Py. sinuata*. For *Py. vexillaria* see portraits

Firefly Sampler: Photinus and Daytime Dark



Photinus

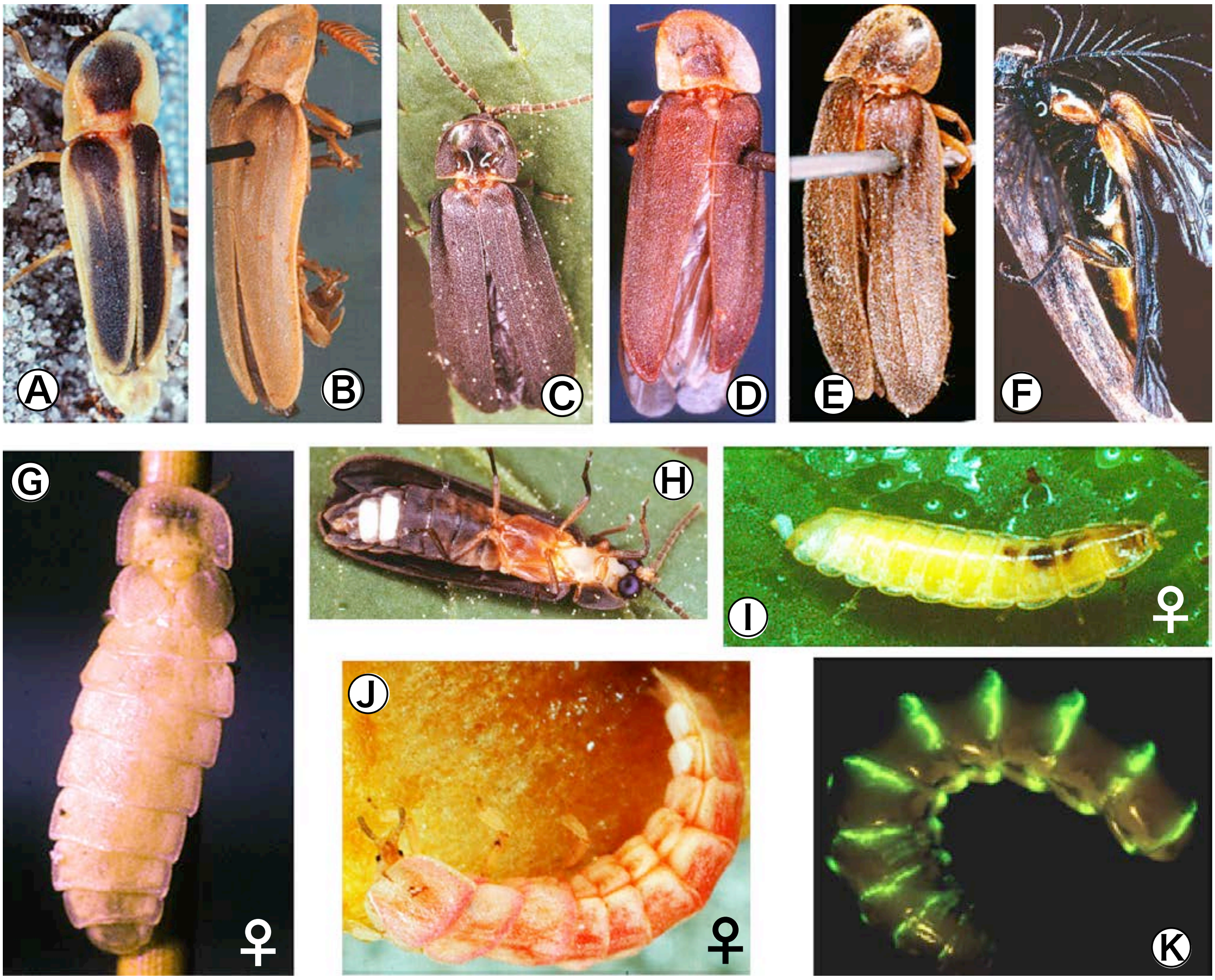
(A) *acuminatus*, (B) *australis*, (C) *brimleyi*, (D) *carolinus* (darker than typical), (E) *consanguineus*, (F) *ignitus*, (G) *indictus*, (H) LUM, (I) *obscurellus*, (J) *stellaris*, (K), *tanytoxus*, (L) WLS.



Dark FFs

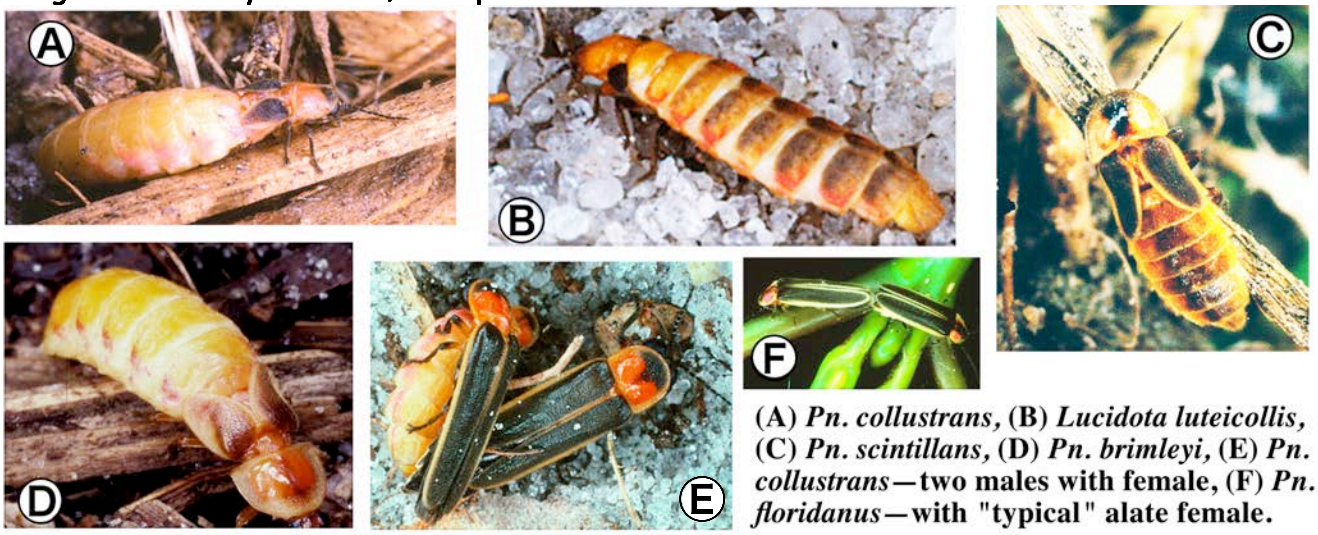
(A) *Ellychnia corrusca complex*, (B) *Lucidota atra*, (C) *Lucidota luteicollis*, (D) *Tenaspis angularis*, (E) *Pollaclasis bifaria*, (F) *Pyropyga nigricans* (wetland/beach form), (G) *Pyropyga nigricans* (typical form), (H) *Photinus indictus* (see above also), (I), *Photinus cookii*.

Firefly Sampler: Glowworm Fireflies, Larvae



Glowworm FFs+ (A) *Pleotomodes knulli*, (B) *Pleotomus pallens*, (C) *Phausis reticulata*, (D) *Microphotus angustus* male, (E) *Lamprohiza splendidula male* (European, 2 very old records, not established in NA), (F) *Phengodes* male (not Lampyridae), (G) *Pleotomodes knulli* female, (H) *Phausis reticulata* male, (I) *Phausis reticulata* female, (J) *Microphotus angustus* female, (K) *Phengodes* female or larva.

Flightless Firefly Females, except 1



(A) *Pn. collustrans*, (B) *Lucidota luteicollis*, (C) *Pn. scintillans*, (D) *Pn. brimleyi*, (E) *Pn. collustrans*—two males with female, (F) *Pn. floridanus*—with "typical" alate female.

Firefly Sampler: Juveniles: Larvae, Pupae—ID & Life

(A) *El. corrusca* cmplx, (B) *Pn. pyralis*, (C) *Py. borealis* larva, (D) *Py. borealis* prepupa (sheltered under enation), (E) *Photuris* larva, (F) *Photuris* larva with one latern visible, (G) *Photuris* larva, (H) *Photuris larva* (digging a chamber), (I), *El. corrusca* larva, (J) *Py. borealis* pupa, (K), *Micronaspis floridana* larva, (L) *Py. borealis larva* ("kissing" snail), (M) *Pleotomodes needhami* larvae, (N) *Py. ecostata* pupa, (O) *Py. borealis* teneral adult with its larval and pupal skins, (P) *Py. borealis* larva and teneral adult, (Q) *Py. borealis* larvae, (R) *Py. borealis* larva, (S) *Photuris* pupa, (T) *Photuris* pupa with its larval light turned on.


Ph. hebes

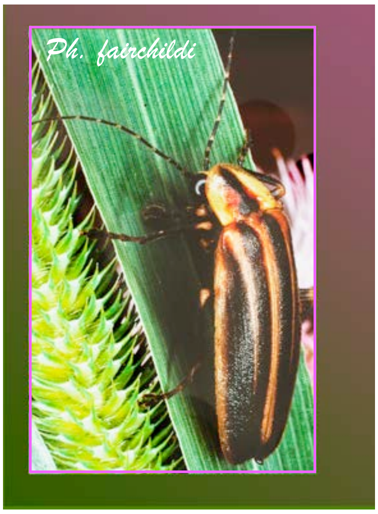

Ph. lucicrescens


Ph. branhami


Ph. douglasae


Ph. tremulans


Ph. quadrifulgens


Ph. fairchildi


Ph. quadrifulgens


Ph. harrannorum


Ph. lamarcki


Ph. maicoi


Ph. douglasae


Ph. frontalis


Ph. caerulucens


Ph. quadrifulgens


Ph. congener


Ph. stanleyi

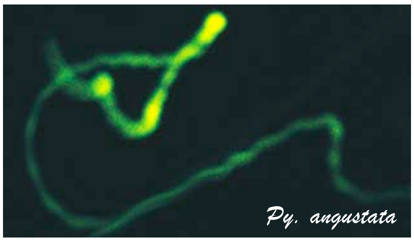

Py. angulata


Py. angulata


Py. angulata


Py. angulata


Py. angustata


Py. angustata


Py. angustata


Py. angustata


Py. angustata


Py. angustata


Py. barberi


Pyractomena barberi


Py. barberi


Py. barberi


Py. barberi, Hines spring roadside


Py. borealis


Py. borealis, swamp forest habitat


Py. borealis, swamp forest habitat


Py. borealis


Py. borealis


Py. floridana


Py. floridana

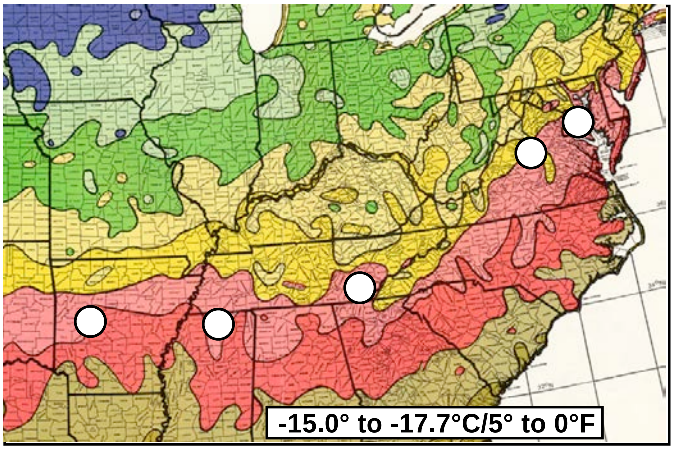

Py. limbicollis


Py. lucifera


An incredibly firefly-rich marsh near Verona, NY


Py. linearis


Py. marginalis



Pink zone?: average mean low in range shown. Why *palustris there*? Lost in the history of the moutains or post-glacial advance from a localized ice-age refugium? Surely must merely be chance?

Pyractomena palustris site in eastern Tennessee.

Pyractomena sinuata

Pyractomena sinuata

Pyractomena sinuata

Pyractomena vexillaria

John Wagoner Green


Photinus australis


Photinus acuminatus

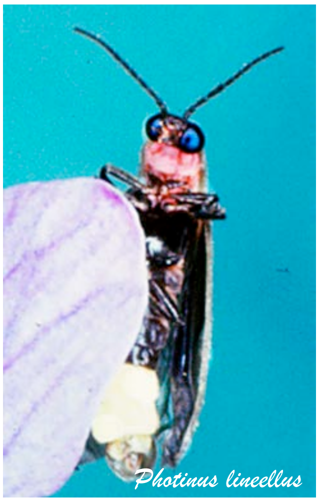

Photinus acuminatus


Photinus floridanus


Photinus umbratus


Photinus LUM


Photinus lineellus


Photinus lineellus


Photinus ignitus


Photinus obscurellus


Photinus macdermotti


Photinus marginellus


Photinus curtatus X marginellus


Photinus carolinus

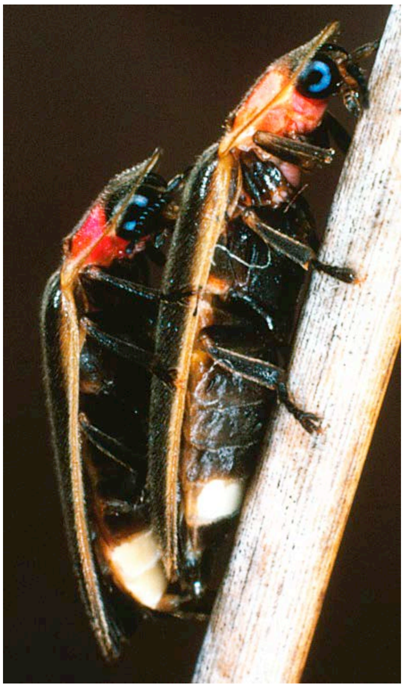

Photinus pyralis

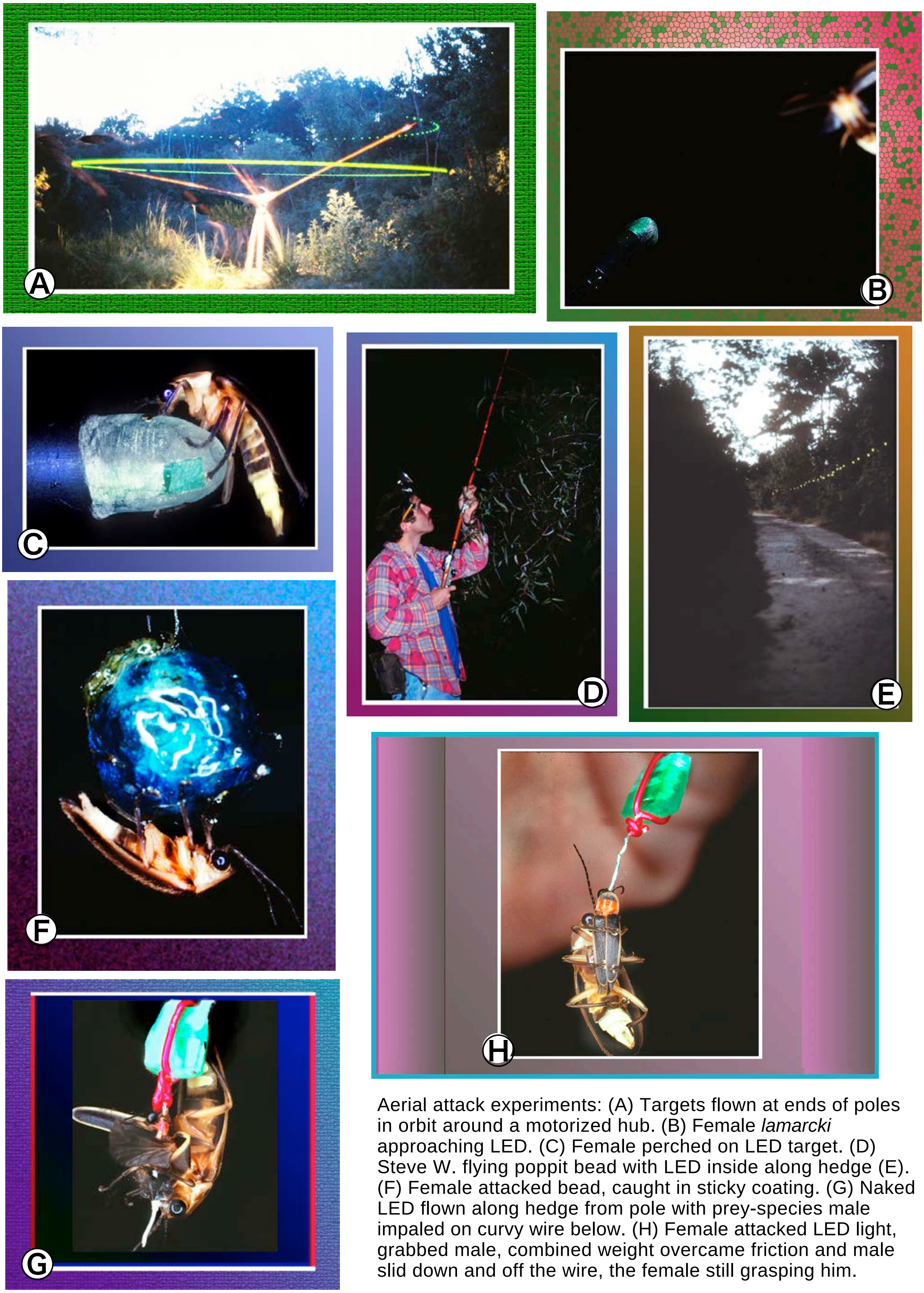

Photinus scintillans


Photinus indictus

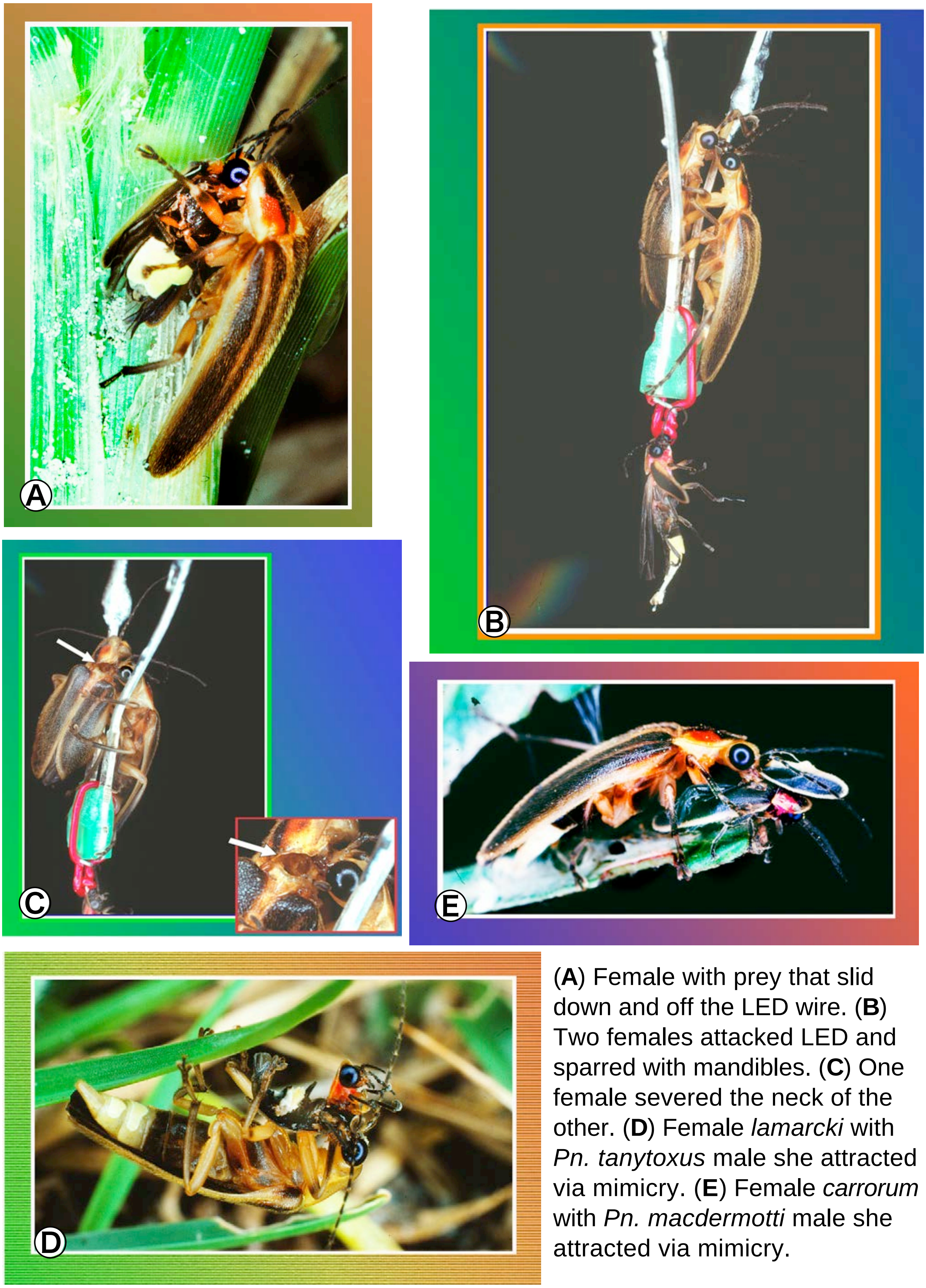

Photinus consimilis

A page of Micronaspis floridana





Aerial attack experiments: (A) Targets flown at ends of poles in orbit around a motorized hub. (B) Female *lamarcki* approaching LED. (C) Female perched on LED target. (D) Steve W. flying poppit bead with LED inside along hedge (E). (F) Female attacked bead, caught in sticky coating. (G) Naked LED flown along hedge from pole with prey-species male impaled on curvy wire below. (H) Female attacked LED light, grabbed male, combined weight overcame friction and male slid down and off the wire, the female still grasping him.



(**A**) Female with prey that slid down and off the LED wire. (**B**) Two females attacked LED and sparred with mandibles. (**C**) One female severed the neck of the other. (**D**) Female *lamarcki* with *Pn. tanytoxus* male she attracted via mimicry. (**E**) Female *carrorum* with *Pn. macdermotti* male she attracted via mimicry.

(A) *Py. limbicollis* with hiding buprestid, (B) *El. corrusca* on spring hickory, (C) *Pg. nigricans* with ticks, (D) *Pn. scintillans* female on station, (E) *El. corrusca* pupa as never seen, (F) *Lucidota luteicollis* male and seldom seen female above the sand.

Ⓐ

Ph. fairchildi

Ⓑ

Ph. stevensae

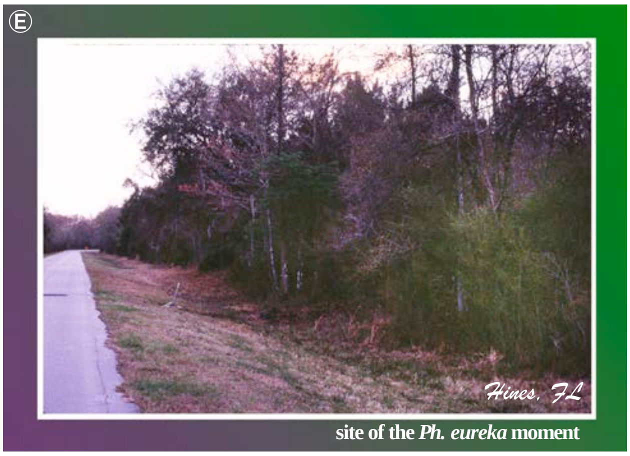
Ⓒ

Ph. bridgeniensis, Ph. hebes

Ⓓ

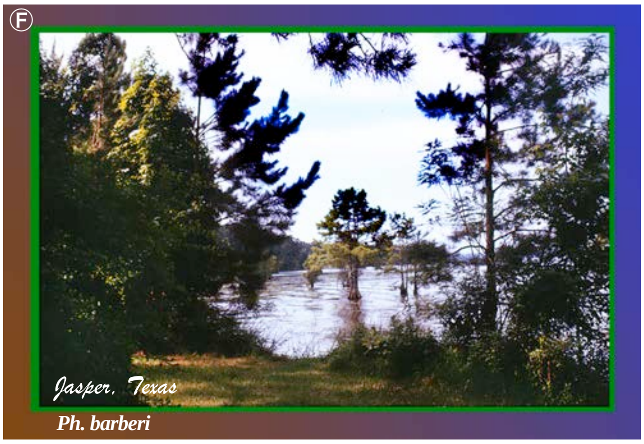
Py. sinuata

Ⓔ



site of the *Ph. eureka* moment

Ⓕ



Ph. barberi

Ⓖ

Py. borealis, Py. limbicollis

Ⓗ

Phosphaenus hemipterus

Ⓐ

Ph. "pensylvanica"

Ⓑ

Py. dispersa, Py. palustris

Ⓒ

Ph. maicoi

Ⓓ

Ph. quadrifulgens, Pn. pyralis

Ⓔ

Ph. tasunkowitcoi

Ⓕ

Py. ecostata

Ⓖ

Ph. potomaca

Ⓗ

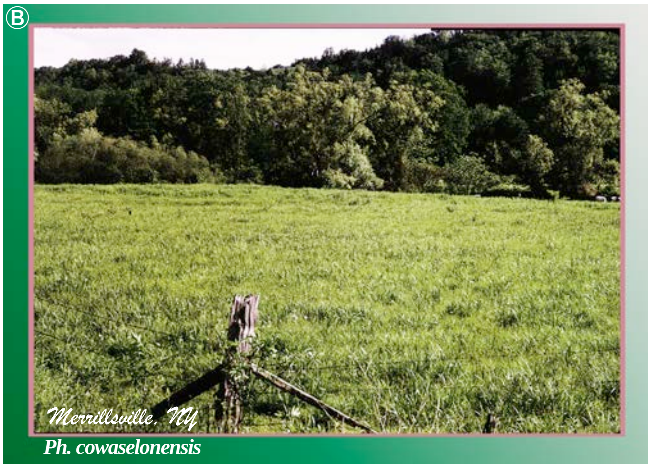
Py. barberi, Py. angustata

Ⓐ

Shell Mound, FL

M. floridana

Ⓑ



Merrillsville, NY

Ph. cowaselonensis

Ⓒ

Stockton, MN

Ph. caerulucens

Ⓓ

Newnans Lake, FL

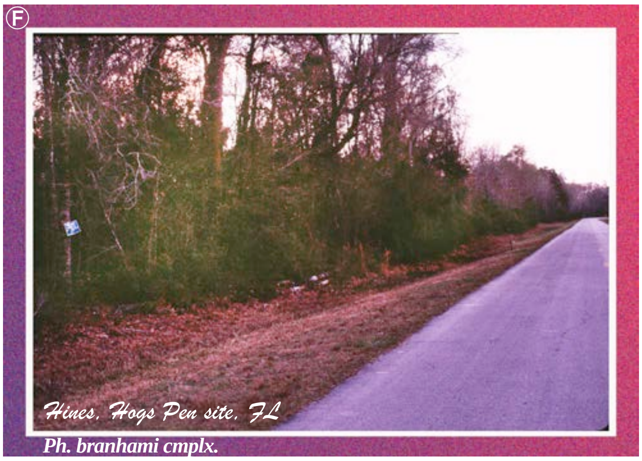
Pn. consimilis, Pn. umbratus, Ph. douglasae

Ⓔ

Cedar Key, FL

Ph. "salina"

Ⓕ



Hines, Hogs Pen site, FL

Ph. branhami cmplx.

Ⓖ

Chao Phraya R. Bangkok

Ⓗ

Chao Phraya R. Bangkok

Pteroptyx spp.

Ⓐ

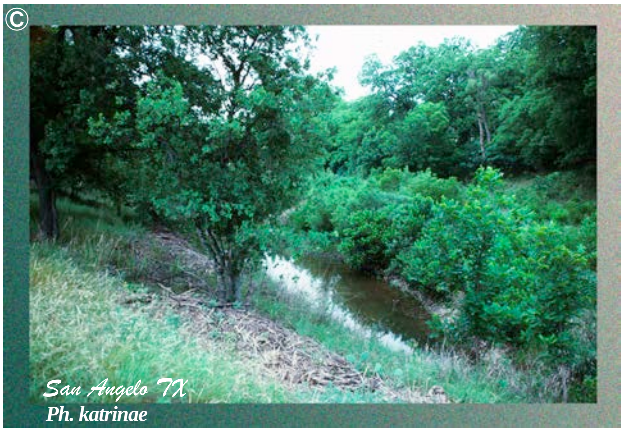
Potomac island, MD-WV

Ph. potomaca

Ⓑ

Ellzey, FL

Ph. beanii



Ⓒ

San Angelo TX

Ph. katrinae

Ⓓ

Cedarville S. F., MD

Ph. tremulans

Ⓔ

Wampsville, NY

Ph. cowaselonniensis, Ph. hebes

Ⓕ

Ypsilanti, MI

Py. dispersa

Ⓖ

Goochland, VA

Py. angulata

Ⓐ

Bluff Siding, WI

Ph. aureolucens, caerulucens, Pn. aquilonius

Ⓑ

Frio River shore site, TX

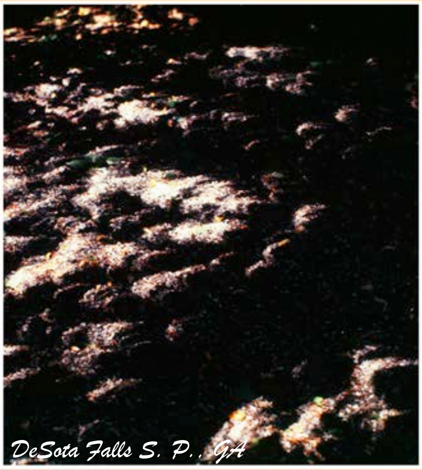
Pn. texanus, walshi, Py. punctiventris

Ⓒ

Bluff Siding, WI

Ph. aureolucens, caerulucens, Pn. aquilonius

Ⓓ



DeSota Falls S. P., GA

solar eclipse crescents

Ⓔ

Chesapeake Bay, MD

Ph. salina

Ⓕ

Douglas Lake, MI

Pyg. nigricans?

Ⓖ

Douglas Lake, MI

Pyg. nigricans

Ⓗ

Frio River, TX

Pn. texanus, walshi, Py. punctiventris

Off-season *Ph. bridgeniensis site:* conservation area maintained by Harry A. Lloyd at the Bridgen. The flowering oldfield shown in autumn 1967 in the upper photo is the area at the right, in front of the evergreens along the millstream dike in the lower, from 1961. Photos by Ann L. Lloyd.

Photo-Morgue Of Assassins and Victims, page 1

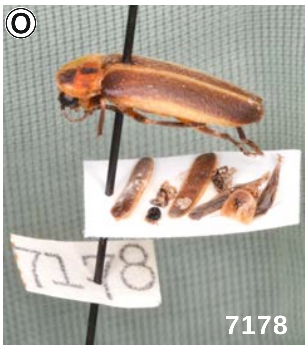
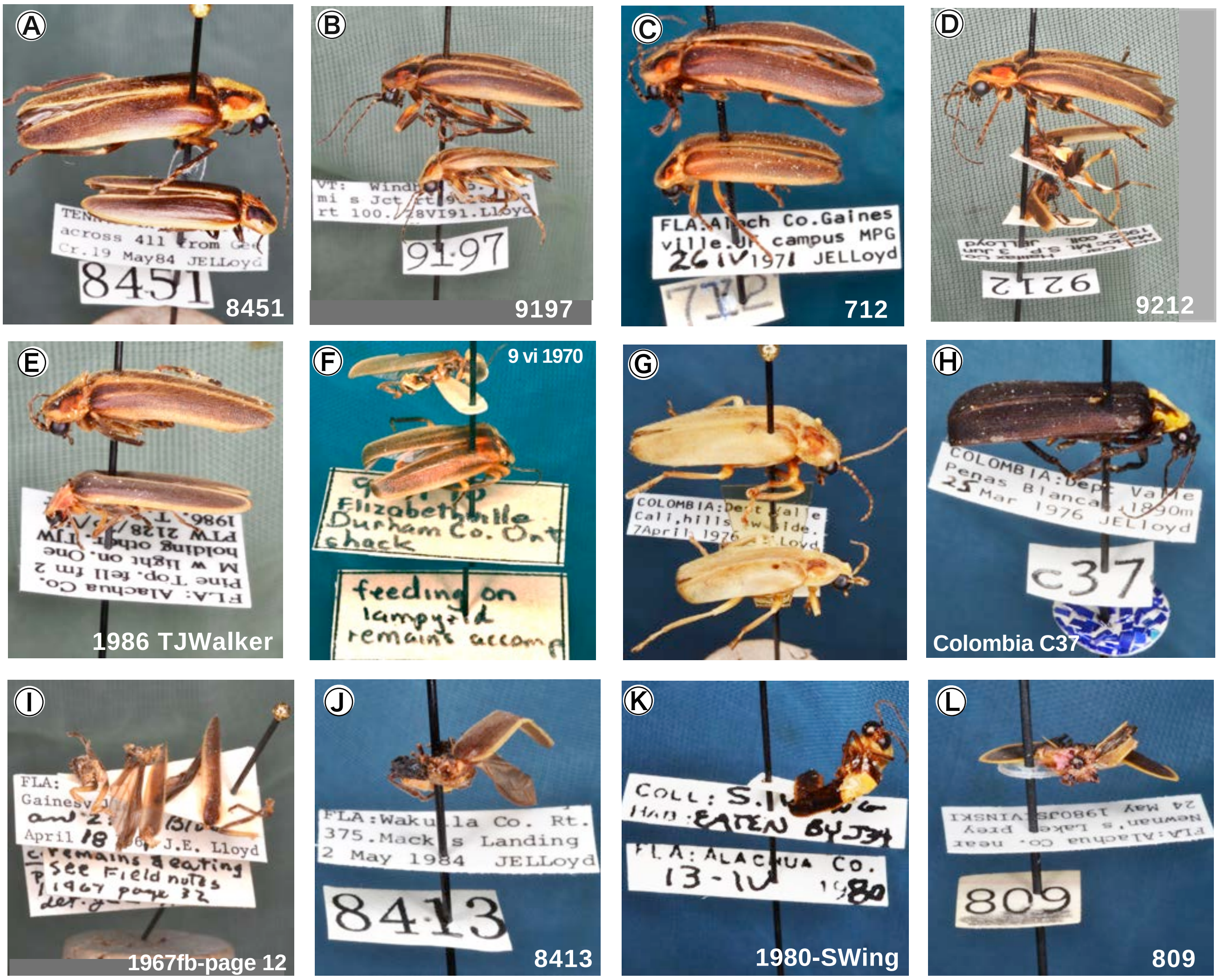


Photo-Morgue Of Assassins and Victims, page 2



Chipping away; the tangled web. Predation by *Photuris* females —and perhaps also by males of *cinctipennis* Group—on signaling males has been an important influence on the evolution of the signals and signaling behavior of fireflies occurring with them. Because these females mimic mating signals to attract prey and some use the mating signals of advertising aerial prey as targets, they may exert broad influence—leading to countermeasures. More than this, females of large species may prey upon those of small species, and both may exploit prey-species' signals by using them as proxies. Briefly said, the system is probably too complex to understand—but we must pick at it, filament by filament, gathering and speculating as we go. The following is a collection of fragments of observations and illustrations, prey species and captors, as a start. Unfortunately, in many/most cases the predators can not be identified with certainty. Sometimes their males may be active at a site and an educated guess may made; at other times the females may be visitors in the site and no *Photuris* males are active, nor even seen passing through in search of hunting females. ID of females, without DNA, will almost always be problematic.

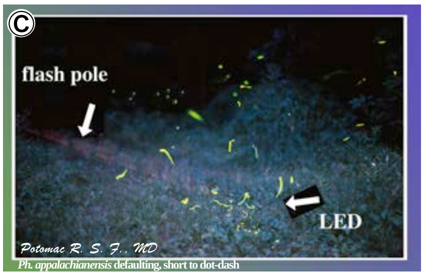
Page 1: **A**, If4–A first experience, *Photuris* sp. ♀, continental *Photinus macdermotti* ♂, after both placed in same collecting bottle. **B**, *Ph. harrannorum* ♀, *Ph. congener* ♂. **C**, *Ph. lineaticollis* ♀, *Ph. douglasae* ♂. **D**, *Ph. lineaticollis* ♀, *Ph. douglasae* ♂. **E**, *Ph. harrannorum* ♀, *Ph. douglasae* ♂. **F**, original obs. *Ph. harrannorum*, *Pn. macdermotti* s.s..**G**, 67132–*Ph. lineaticollis* ♀, *Ph. congener* ♂. **H**, 67145–*Ph. douglasae* ♀, *Pn. tanytoxus* ♂, female glowed like *tanytoxus* ♀, ans. 6♂♂. **I**, 68450–*Ph. harrannorum* ♀, *Pn. tanytoxus* ♂. **J**, 68692–mated *Ph. cowaseloniensis* ♂♀, kept in jar overnight. **K**, 68368–*Ph. lucicrescens* ♀, *Pn. sabulosus* ♂. **L**, 69125–*Ph. lineaticollis* ♀, *Ph. congener* ♂. **M**, 69168–*Ph. lamarcki* ♀, *Ph. douglasae* ♂. **N**, 7161–*Ph. alexanderi* ♀, *Ph. alexanderi* ♂. **O**, 7178–*P. dorothae* ♀, *Pn. umbratus* ♂. **P**, 76184–*Ph. hebes* ♀, *Pn. curtatus*X*marginellus* ♂. **Q**, 78167–*Photuris* ♀, *Photuris* ♂, female ans 3 *Ph. pensylvanica* (dot-dash) ♂♂ while eating this one. **R**, 7969–*P. lamarcki* ♀, *Pn.* SloPul. *consimilis* ♂. **S**, 83197–*Ph. versicolor*? ♀, *Pn. marginellus* ♂. **PAGE 2. A**, 8451–*Ph. quadrifulgens* ♀, *Py.dispersa* ♂. **B**, 9197–*Ph. fairchildi* ♀, *Ph. hebes* ♂. **C**, 712–*Ph. harrannorum* ♀, *Ph. douglasae* ♂, ♀ ans 3X, ♂ land, ♀ grab, hang/hold as suspended under grass blade. **D**, 9212–*Ph. versicolor* ♀, *Ph. tremulans* ♂. **E,** –*Ph. harrannorum* ♀, *Pn. macdermotti* ♂. **F**, –*Photuris* sp. ♀, *Py. linearis*? ♂. **G**, c155– *Photuris* sp. ♂♀, Cali, Colombia, S.A. **H**, unknown/new Photurinae genus ♀, ans 2-pulse *Photinus* ♂♂, Penas Blancas, Colombia, S.A.. **I**, –pred. *Ph. harrannorum* or *lineaticollis* ♀, *Ph. congener* ♂. **J**, 8413–*Photuris* sp. ♀ (Red Group, *lineaticollis?*, *walkeri*?), *Pn. frosti* ♂. **K**, –*Ph. harrannorum* pred. ♀, *Pn. collustrans* ♂. **L**, 809–*Py. angulata* ♀ taken from a blue dragonfly (daytime flying, =ovipositing?).

Shoreham, L.I., N. Y.

Ph. stevensae

Norwich, CT

Ph. stevensae



Potomac R. S. F., MD

Ph. appalachianensis defaulting, short to dot-dash

Gainesville, FL

Pn. collustrans

Py. borealis

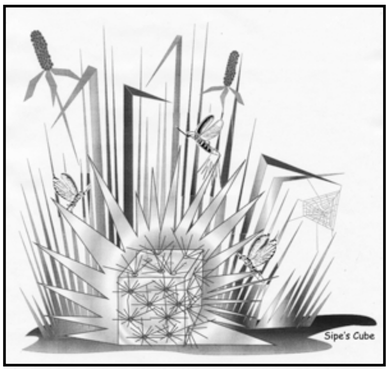
Gainesville, FL

Nashville, TN

Ph. quadrifulgens

A Natural Experiment: Comparing Asian and American Firefly Mating Protocols

A major difference in the firefly fauna of the Americas and that of Asia is that in Asia there are many species that have a sedentary mating system in which individuals flash at each other from perches. This continues night after night. The most dramatic are those that occur in the coastal mangrove swamps of Thailand (Siam in historical reports), and in particular, those that synchronize their flashes en masse (by the trees-full). The species of most reports and history is *Pteroptyx malaccae*. Perched *Pteroptyx* (bent-wing) flashers of several species occur in Malaysia, the Philippines, and Burma/Myanmar. Related swarmers occur in New Guinea (Genus *Medeopteryx*). Perched swarmers also occur in the Genus *Luciola*, especially the New Guinea and aerial dog-fighter *Pygatyphela* (nee *Luciola*) *obsoleta*. The ecological factors that may have led to and have allowed such sedentary behavior to evolve are discussed on pages 176 and 178.



An artistic bioplastic cube with blinking LEDs and batteries, attracted fireflies—no codes, just targets? (by Mike Sipe)

A major difference in the firefly ecology of the Americas and that of Asia is that in the Americas, predaceous fireflies, guided by their preys' flashes, attack and eat other fireflies—obviously sedentary flashers are vulnerable, are sitting ducks. Sedentary swarms must once have occurred in North and South America, such leks being a logical development in rich habitats that produced high densities of fireflies. Such early swarmers would have been devoured in the early evolution of predatory fireflies, and might/could have been a key and fascilitating factor in the evolution of this behavior. *Photinus knulli*, a sedentary swarmer of sorts, occurs in Arizona where *Photuris* does not occur (Cicero, 1983).

Predation is only one of the two most interesting focal points to emerge from contrasting the two "faunas". The other is that of sexual selection, with questions arising from observations that Steve Wing and I made on *Pteroptyx valida* in the four-river area at Bangkok, along the Chao Phraya and others, and inland near canals—and actually, next door to a mushroom-raising "barn." While aggressive mimicry seems to have been the driving force in the evolution of signaling in American fireflies, and the mating signals of fireflies in the Western Hemisphere will have evolved tricks and codes, and neurological-flashing finesse that certainly must play a role in mate choice, we ask here what are the driving forces of Asian species that are not not under such predator pressures?—the species that perch in swarms and flash "at each other" for hours? Certainly male rivalry (intrasexual selection), and female choice (intersexual selection) play an important role—perhaps the latter has been turned loose and "run amok?" We found some clues toward seeking answers to this question. Here are some photos and suggestions for avenues of research that might be pursued.

Each male is competing with every other male perched near him. First, to attract incoming females to land near him, and second—once females are near and watching, whether he sees that they are present or not?—to "out-perform" or "outshine" his rivals. Photos of one individual show that he moved to various positions on his leaf, and aimed his light in different directions. Whether there is physical combat and intimidation as the red-lined photo might suggest, remains to be determned; this male's aggressive look is frozen into his exoskeleton, and a human interpretation. At this point there


Does he look non-confrontational?

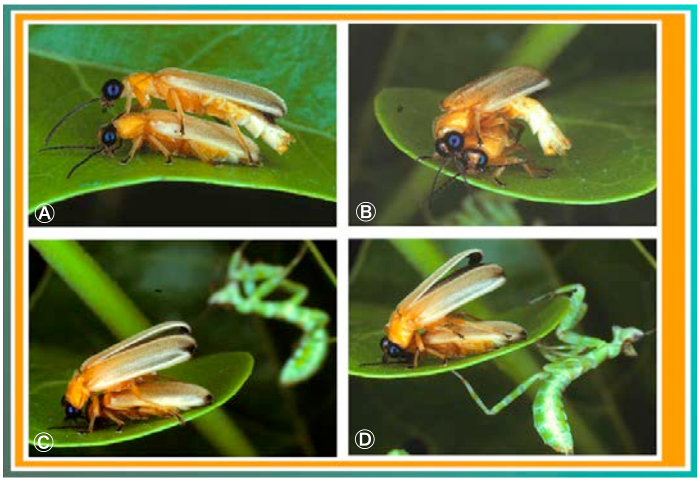
All the same male on the same leaf, aiming from different positions and in different directions


Learn to recognize several or many individuals by "name."

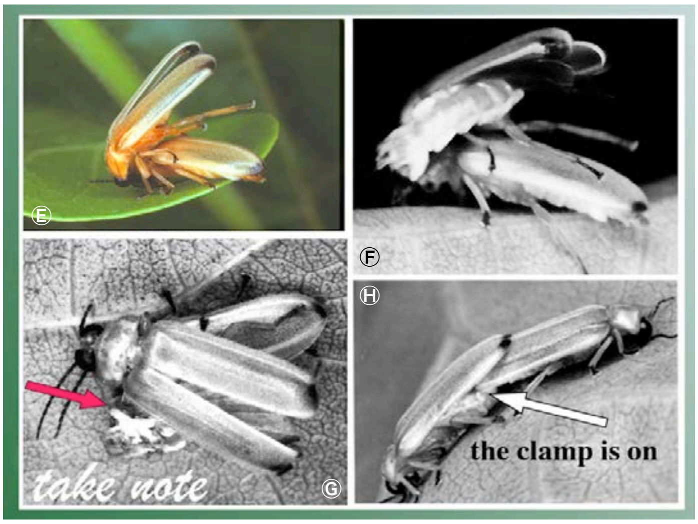
is a difference to be noted between males of species that flash in synchrony and those that don't, such as the *P. valida* shown in these photos. A comparison in these regards may provide clues to questions asked. Though males of synchronizing species are rivals, maybe even unto death, they must cooperate with those around them, even as they compete with them, in order to maintain the flash rhythym/rate that incoming females of their species will seek. Hence these males may behave differently than the *valida* male shown above, aiming this way and that, continuously?, successively? *P. valida* males may be totally independent and rather than cooperate, exploit or deceive rivals?

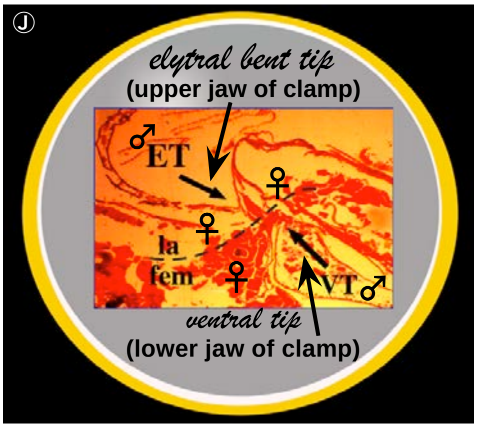
Individual males must be followed over time, as to their continuing successes with females and interactions with rivals. This means that males must be marked for continuing recognition—obviously the numbered plaques once used in bee studies are too large, but tiny dots of paint could work. Bar codes that are minute' and can be recieved and translated electronically at a distance would be suitable.

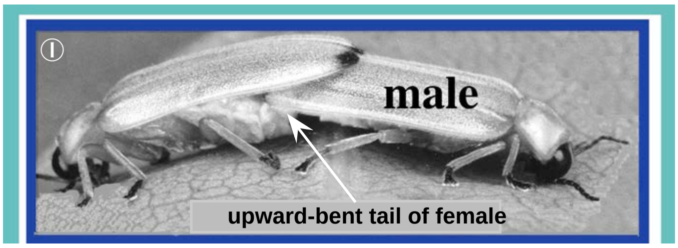
The initial point of sexual contact was never caught, but a moment following, with the male atop the female was photographed (**A**), as was the following sequence of a male's display: he bent his tail around (**A-F**), lifting his elytra upward, and placed his pygidium with spread lateral edges over the female's face (**G**). (The mantid was not noted until the photos were examined much later, in an interesting element for comment, since mantid matings are known for ending in mate cannibalism by females.) The male then, in unknown order: inserted, rotated, and clamped the female's abdomen.



Whatever females may determine about the characteristics or quality of her suitor through his flashing is no more obscure than what she may learn by the presence of his tail over her face. I strongly suspect that it is of a chemical nature, and the two contexts that come to mind have to do with (1) his genetic characteristics, and (2) his previous sexual experience. With respect to the second, she may be able to determine something of his previous success, and number of copulations and/or how recently he has coupled. A male with "multiple" mates indicates that he has features that females select, and would be a good sire for her sons. A recent mating might indicate that he has exhausted nutritional contributions from his accessory glands and is less suitable as a mate.





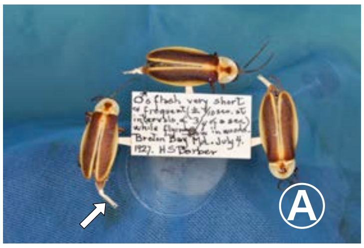


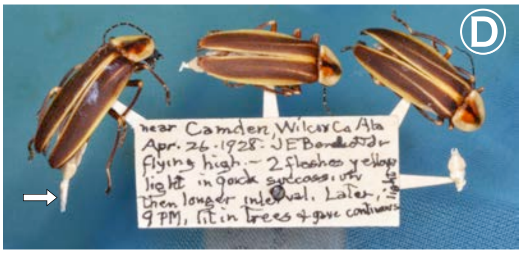
Steve Wing, as seen in a long-tailed boat on the "Chao Phraya."

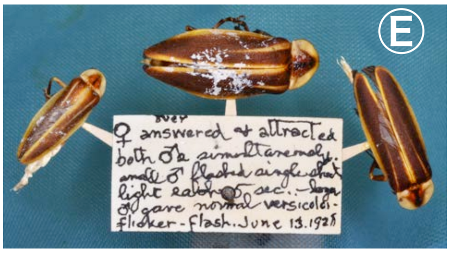
The slide preparation shown in (J) is a sagital section through the coital connection, expertly preserved, prepared, sliced, stained, and mounted by Steve Wing, a partner in the work described here.

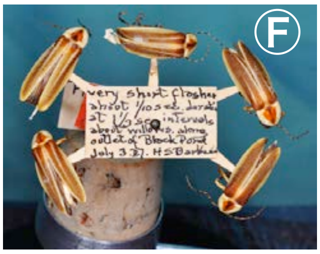
Archived Notes On HSB's Voucher Labels—with One of McDermott's

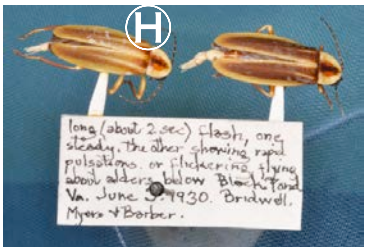
Labels on insect specimens in university and museum collections are compact records of someone's escape into the field with his thoughts, for a day or evening. While we might suspect that there are more records for 4 July or Labor Day, or Saturdays, to my knowledge no one has looked into this. What interesting stories might be hidden, or unknown facts that the collector's themselves could not appreciate in their the time? As a break from spell-checking, as this *Photuris* outline was coming to an end, I went through the USNM collection and examined labels on Herbert Barber's FP-voucher *Photuris*—to see what they might teach: For example, I had previously learned that Eunice Myers had been Barber's technician at the museum, but the labels told me more, that she had collected FP-vouchers in the field with him, had field experience with the master—this might be important to know because she and her student Bernard Boland had sent specimens to Barber from Minnesota and Wisconsin (see page v). Here are *Photuris* labels and an occasional comment; note that some have extruded aedeagi, and that (**A**) is the only Division I species, *Ph. frontalis*.











(A) This label as all others lacks temperature and stopwatch measurements—but was collected on 4 July. (**B**) McDermott's *Ph. lucicrescens* voucher label records the flash "vibration" that he mentions in one of his papers. (**C**) This voucher has an interesting and personal association: its collector was from Peterboro, NY, a few miles from where I grew up and collected; and, years before carbon-14 dating identified Piltdown Man as a hoax, Miller had "blown the whistle on it." ID is probably *Ph. cowaseloniensis*. (**D**) The noted FP suggests that this could possible be *Ph. darwini*; if correct this would extend the known range of this species. (**E**) The data recorded with this triad suggests that the *Ph. versicolor* female was attracting prey, the smaller male, a *Ph. hebes*, and the *Ph. versicolor* male recognized the interaction, approached and emitted the *Versi* ID FP. (**F**) Probably *Ph. hebes*. (**G**) The female appears to have a damaged elytron, perhaps bumped in the wind before it had hardened following eclosion; the label refers to notes that may still be on file somewhere. (**H**) Note Myers name. (**I**) These vouchers were part of the puzzle Barber mentions in his 1951 text—why *lucicrscens* emits only the crescendo FP at this site but at another not far down the road they used both crescendo and short. (**J**) Faust et al reported examples of *Photuris* females robbing spider webs, but this one apparently got caught. (K) *Ph. quadrifulgens*. (**L**) *Ph. tremulans*. (**M**) *Ph. potomaca*. (**N**) *Ph. salina*.

Photos Of Taxonomic Interest To Fireflyers

Carl von Linne' (1707-1778) described the first North American fireflies in 1758, and as strange as it might seem now, he put them in the Genus *Cantharis*—among the soldier beetles. Taxonomists share a fondness for Linnaeus, a naturalist who really knew flowers and with a special talent for organization. In 1999 I had the chance to visit Sweden and long-time good friend and fellow naturalist Bo Svenssen. He took me see Linnaeus' summer home, and the mansion of Carl DeGeer, the author of *Photuris* (nee Lampyris) *pensylvanica*. Because I was there in the off season our points of interest were not crowded with tourists in modern clothes, though the buildings were closed. Hence, the photo of the bench Linnaeus lectured from was photographed through his lab's windows. These are some of the photos of from this visit.


Linnaeus' summer home, which then overlooked an arm of the sea, but since then the land has risen from post-glacial lift, and the view is dry land.


The building seen at the right in the other photo.


Linnaeus' lab on a little hill behind the house.


Spring flowers on the lab's hillside


Linnaeus' teaching lectern/bench combo, with sunshine . . . as Linnaeus would have greeted
on teaching days . . .


Prof. Bo Svenssen

From Chapter 7, Appendix II

Suggested Procedures/Rules for Field Identification

First (after hanging out a thermometer):

1. The identification of solitary flashing individuals is problematic without experience. Seek populations of a dozen of more flying, flashing males, all emitting identical or very similar FPs (flash patterns).

2. Without local experience, do not rely upon (use the charts in the preceding chapter) to identify the flashes of perched or stressed individuals—those trapped in spider webs, water, spanish moss.

3. Observe flashing individuals in the population for a few minutes, noting the area of the site they are using, height of flight, flight speed, interactions of males as they fly near each other or behavior as they near the edges of the activity space.

4. Do not be distracted, lose focus, by the flashes of perched individuals unless they follow quickly (<2 seconds) after the FP of a male—if so, watch again before intruding, to be certain that the proximity in time was not fortuitous. Note whether any change their FP to a different type.

Then (with SWAT [a split-timer stopwatch] in hand):

5. Turn attention to the travels of an individual male. With eyes on him only, note the unit of flashing that he repeats—is it a single flash, a pair of flashes, a group/phrase of several flashes/pulses—then, watching his presumptive path for him to repeat after a few moments or seconds, see him repeat the same unit/phrase/group—that is, his same advertising flash pattern (FP). Practice this.

6. With stopwatch, time the duration/interval from the beginning of a FP to the beginning of the next consecutive FP (FP period), and record its duration in seconds on a pocket tape-recorder (TR).

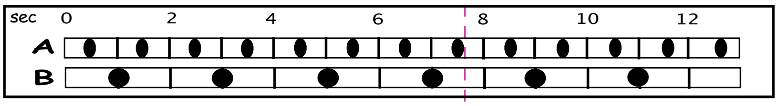
7. If the FP has more than one flash, with the stopwatch time the duration/interval between the flashes/pulses within the FP, and record.

8. Check the TR to be certain that it recorded. Record temperature on the TR following the FP measurements.

9. Take a larger sample of FP measurements.

10. At 8 am record notes and data in a fieldbook.

AA



AA Page 61

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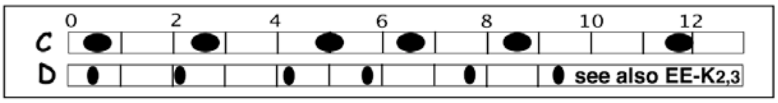

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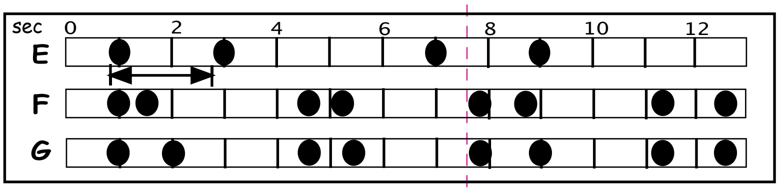

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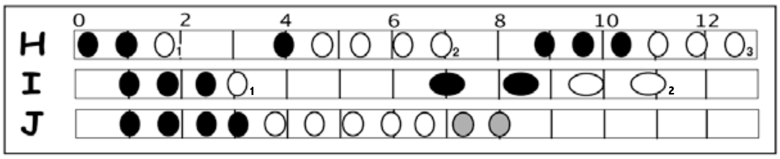

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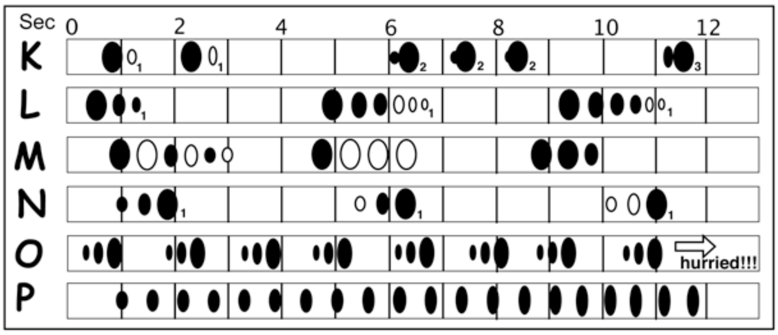

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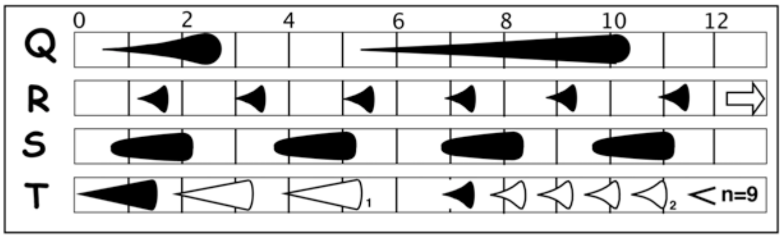

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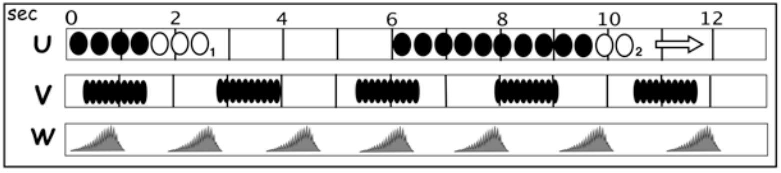

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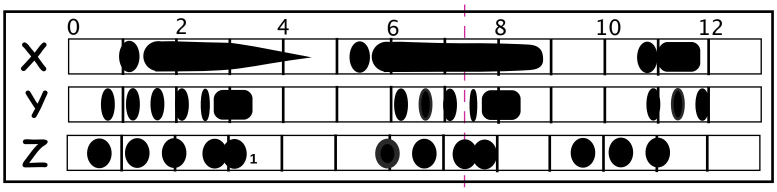
HH



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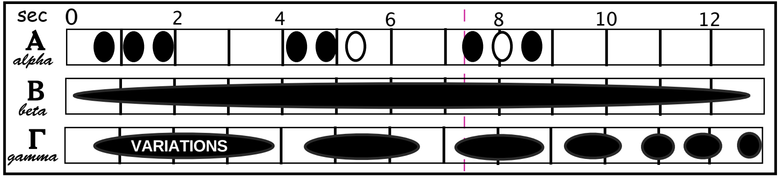
II



II Page 62

Shadows

From these remarks it will be seen that I look at the species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake. (Chapter 2, p 108; C. Darwin, The Origin Of Species, 1859).

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in [illegible] almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and [illegible]; a Ratio of Increase so high as [illegible] Life, and [illegible] Selection, [illegible] Divergence of Character and the Extinction if less-improved forms. Thus, from the war of nature, from famine and death, the most exalted which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed laws of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved. (Chapter 14, p 459; C. Darwin, The Origin Of Species, 1859).