GRYLLUS OVISOPIS N. SP.[1]: A TACITURN CRICKET WITH A LIFE CYCLE SUGGESTING ALLOCHRONIC SPECIATION[2]

THOMAS J. WALKER[3]

Department of Entomology and Nematology
University of Florida, Gainesville 32611

ABSTRACT

G. ovisopis, common in north Florida woods, is the first *Gryllus* known to lack a calling song. Its courtship song is similar to that of other *Gryllus,* but its aggressive song is dominated by frequencies of 12-16 kHz rather than 4-5 kHz. Indoor and outdoor rearing experiments and periodic collecting showed *ovisopis* to be strictly univoltine with all individuals becoming adult in September and early October. Similar studies indicated that *G. fultoni* (Alexander), a close relative, has both univoltine and bivoltine cycles; and even within one week's progeny of a single female, individuals may become adult over a period of seven months. Attempts to hybridize *ovisopis* and *fultoni* failed. Seasonal rather than geographical isolation may have initiated speciation in the ancestral population that became *ovisopis* and *fultoni.*

Rehn and Hebard's (1915) conclusion that U. S. *Gryllus* represented a single species was generally accepted until Fulton (1952) published convincing evidence that 4 species occurred in North Carolina. Alexander (1957), unlike Fulton, used binominal nomenclature for *Gryllus* species in eastern United States, recognizing 4 previously described species and describing a fifth species as *Gryllus fultoni.* Subsequently Alexander and Bigelow (1960) described *G. veletis,* and Alexander and Walker (1962) reported the occurrence of *G. assimilis* (Fabricius) in Florida.

This paper describes a previously unrecognized species of *Gryllus* from eastern United States. *G. ovisopis* is the only *Gryllus* known to lack a calling song. It is the only southeastern *Gryllus* that is strictly univoltine. Unlike *fultoni,* a species with which it was confused, it diapauses in the egg stage, and the name *ovisopis* (*ovi-,* egg; *sopis,* sleep) refers to this characteristic. Morphologically *ovisopis* can be distinguished from other eastern *Gryllus* by its short tegmina, long ovipositor, and closely-spaced file teeth (Nickle and Walker 1974).

Gryllus ovisopis, n. sp.
Taciturn Woods Cricket

Holotype.—Male, FLORIDA: Alachua Co., NW 1/4, Sec. 31, T9S, R19E, collected as juvenile, 7 June 1972, in deep leaf litter in mesic hammock, reared

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[1]Orthoptera: Gryllidae.

[2]Florida Agricultural Experiment Station Journal Series No. 5059. This study was aided by NSF Grant GB 20749. I thank Dr. J. J. Whitesell for aid in the field and review of the manuscript, Mr. D. L. Mays for living specimens from several locations in north Florida, and Dr. J. E. Lloyd for help with the manuscript.

[3]Research Associate, Florida State Collection of Arthropods.

outdoors, adult 10 Sept. 1972, T. J. Walker; deposited in (U. S.) National Museum of Natural History. Black except for lighter areas on proximal portions of femora and costal margins of tegmina. Length of body, 26 mm; pronotal length × width, 5.6 × 7.5; length of tegmen, 10.0; length of hind femur, 16.2. Length of wings less than half length of tegmina. Stridulatory file 3.13 mm with 147 teeth.

Allotype.—Female, same locality as holotype, 15 Oct. 1967, T. J. Walker; deposited in (U. S.) National Museum of Natural History. Similar to holotype. Length of body, 28 mm; pronotal length × width, 6.3 × 7.9; length of tegmen, 11.0; length of hind femur, 16.6; length of ovipositor, 23.

Paratypes.—41 males, 50 females, Florida State Collection of Arthropods. FLORIDA: Alachua Co., 5 females, collected as adults at 5 sites near Gainesville, 10 Oct. 1971, J. J. Whitesell and D. L. Mays, 12 Oct. 1971, J. J. Whitesell, 20 Oct. 1971, D. Baker, 6 Nov. 1971, T. J. Walker, 20 Oct. 1972, J. E. Lloyd; 34 males, 38 females, reared from juveniles or from eggs laid by females collected at 4 sites near Gainesville, 1967, 1971, 1972, T. J. Walker and J. J. Whitesell. Baker Co., 1 male, 1 female, reared from juveniles collected 1 mi. s. Georgia line, Fla. 121, 18 Aug. 1970, D. L. Mays. Leon Co., 5 males, 2 females, reared from juveniles collected Tall Timbers Research Station, 2 July 1970, D. L. Mays. Wakulla Co., 1 female, Ochlockonee River State Park, 3 Oct. 1970, D. L. Mays; 1 male, 3 females, progeny of above female.

HABITAT AND SEASONAL LIFE CYCLE

G. ovisopis occurs in the broadleaf forests known as mesic hammock and xeric hammock (Laessle 1942) and in late secondary successional stages leading to these. It occurs on and in leaf litter and under objects such as logs and discarded pieces of plywood. When confined in jars partially filled with sand, larger juveniles and adults sometimes conceal themselves, as do other *Gryllus* spp., in shallow burrows. *G. ovisopis* often occurs with *G. fultoni*; however, *fultoni* sites include wetter and drier, more-often-burned woods. *G. ovisopis* is most abundant at sites that are buffered from extremes of moisture and have deep leaf litter.

I long confused *ovisopis* with *fultoni* because they often occurred together and *ovisopis* had no identifying calling song. Their distinctness became apparent during studies of seasonal life histories (Fig. 1). These studies included systematic field observations of adults and laboratory and field rearing of progeny of field-collected, field-fertilized females. In 1970-71 such females were individually confined in screen-capped gallon jars with substrate for oviposition (800 ml moistened sterilized sand), food (Purina dog chow in a vial cap), and water (15-dram vial with a stopper penetrated by a dental cotton wick). The jars were kept on the ground in a wooded area. A sheet of plywood supported by 4 posts protected the jars from rain and direct sun but allowed natural photoperiod; temperatures were within the range encountered at ground level elsewhere in the woods. Each week the females were transferred to new jars. The jars with 1-week's oviposition were alternately left under the shelter in the woods or transferred to a rearing room held at 25 ± 3°C and a photoperiod of 16 L: 8 D.

The jars in the laboratory and in the woods were tended weekly and the crickets censused. Four weeks after initial hatch, all juveniles were transferred from the oviposition jar to a new gallon jar similarly equipped with sand, food,

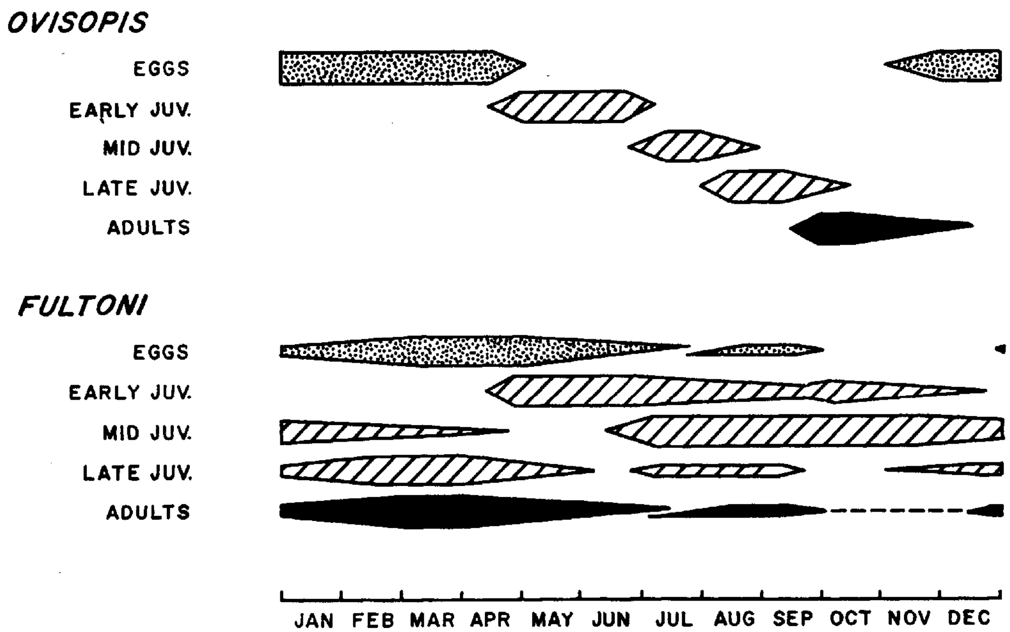

Fig. 1. Seasonal life cycles of *G. ovisopis* and *G. fultoni* at Gainesville, Florida, largely based on periodic collection of individuals and subsequent outdoor rearing of juveniles and of the progeny of adult females. The occurrence of adults of *fultoni* is based on records of calling males except that the dotted line indicates a period when no calling songs were heard but when outdoor rearing records suggested adults were present.

and water. A 13 × 5-cm cylinder (ht × diam) made of a 13 × 18-cm card was added to the juvenile jars to increase the standing room. The oviposition jar was watched for further hatch for several weeks. If none occurred, first a sample and then the entire 800 ml of sand was examined for unhatched, viable eggs by a washing technique. As F_1 adults appeared, they were removed weekly from the juvenile jars and preserved for morphological studies.

Females that eventually proved to be *fultoni* (n = 7), were collected in the spring and laid eggs that hatched in 3 to 7 weeks indoors or out. The juveniles of *fultoni* in a single jar often had 2 modes of development: some developed rapidly and became adults in late summer or fall; others stopped developing in the middle instars, and did not resume development for a month or more in the laboratory or until the following spring outdoors. Some that matured outdoors in late summer and fall were transferred to new jars outdoors with the aim of monitoring the development of their offspring. Eggs were obtained from early September through November. Those laid in September hatched in about 4 weeks and produced early mid-stage juveniles by December. These individuals (F_2) did not survive, but slightly larger *fultoni* juveniles (F_1) in other jars survived and produced adults the following spring. Most eggs laid in October and November hatched in 5 to 7 weeks and died as early-stage juveniles the following spring. In 1 jar with eggs laid 9 Oct.-27 Nov., 40 hatched between 27 Nov. and 26 Dec. These died by 5 Mar. Two additional hatchlings were found on 30 Apr., and these died by 14 May. If only the above data are considered, one would have to conclude that *fultoni* adults maturing in late summer and early fall contribute nothing to future gene pools. However, many uncaged *fultoni* mature during this period as evidenced by a resurgence of male calling activity during August and September (Fig. 1). Calling then ceases until mid December, although adults should occur on the basis of outdoor rearing data. Perhaps the most reasonable hypothesis compatible with the present data is that adults maturing in late summer and early fall lay eggs that soon hatch and sometimes contribute to the adult population of the following spring. Those maturing later in the fall (if such occur outside of jars) do not begin mating and egg laying until winter, at which time the likelihood of the hatchlings surviving is improved. One further hypothesis: the occurrence of 2 April hatchlings from Oct.-Nov. eggs suggests that variation exists in *fultoni* eggs that, if selected for, could lead to an *ovisopis*-type life cycle (Fig. 1).

Females that eventually proved to be *ovisopis* (n = 4) were collected in October and November. They were morphologically distinct from those collected in the spring and laid eggs that required 10-16 weeks to hatch at 25 ± 3°C and 20-30 weeks to hatch outdoors. Juveniles in a single jar, whether kept indoors or out, were nearly synchronous in their development. In the laboratory (25 ± 3°C, 16 L: 8 D) development time from egg laying to eclosion of the adult varied from 34-41 weeks (n = 13). In the jars in the woods, all last instars molted to adults (n = 17) within a 4-week period (Table 1, first line).

TABLE 1. DATES OF FINAL MOLTS FOR *G. ovisopis* REARED OUTDOORS IN JARS, 17 OCT. 1971 TO 4 OCT. 1972.

Origins of individuals	n		Date of final molt of median individual*		Range of dates of final molts (wks)*
	♂	♀	♂	♀	
Eggs laid 17 Oct.-6 Dec. 1971 by 2 females collected from separate demes	7	10	20 Sept.	20 Sept.	4
Juveniles collected from 3 demes 25 Apr.-27 July 1972	17	7	14 Sept.	20 Sept.	4
Juveniles collected from 2 demes 14 Aug.-25 Sept. 1972	7	6	14 Sept.	28 Sept.	3
TOTAL	31	23	14 Sept.	20 Sept.	5

*Since jars were censused weekly, the best estimate of median date of molt is 3 1/2 days prior to the census date of the median adult of the appropriate sex. Adults found on a particular census date might have molted at any time during a 7-day period. It is assumed that the first final molt occurred 3 1/2 days prior to its census date and that the last final molt did likewise.

In 1972 the life histories studies were expanded to compare speed of development in wild crickets with those confined outdoors with a surfeit of food and water. Woods crickets of all stages that could be found were collected at biweekly to triweekly intervals in 3 areas several miles apart, and the juveniles were allowed to mature outdoors in sheltered gallon jars. The crickets in the jars apparently developed at the same rate as those loose in the woods: the field-collected juveniles continued to match in size and stage of development those being reared in the jars outdoors. Juveniles collected in late August and September matured within a few days of those collected earlier as juveniles or reared from eggs laid in jars the previous year (Table 1). No wild adults were seen while searching 4 Sept., but 3 males were caught 24 Sept.

All available evidence indicates that *ovisopis* is strictly univoltine with an obligatory egg diapause. A higher degree of synchronism of final molts outdoors than in laboratory rearing suggests that an environmental cue such as photoperiod may be involved in timing some phase of juvenile development. In contrast to *ovisopis, fultoni* at Gainesville shows no egg diapause and has a partial second generation each year. It calls, and presumably mates, at all times of the year except when *ovisopis* is mating (Fig. 1).

Hybridization Experiment

Most biologists agree that the ultimate criterion of species status for a population of sexually reproducing animals is that no significant genetic exchange occurs under natural conditions between it and other such populations. For populations that occur together this is a practical criterion.

Populations of *G. ovisopis* occur intermingled with those of *G. fultoni* and to a lesser but noteworthy extent with those of *G. rubens* Scudder and *G. firmus* Scudder. I have found no individuals intermediate in morphological characters (Nickle and Walker 1974) between *ovisopis* and any of the 3 other *Gryllus* species living with it and consequently consider it a species.

TABLE 2. Results of laboratory crosses between *Gryllus ovisopis* and *G. fultoni*.

♂	X	♀	Number of Replicates		
			Total	Producing eggs	Producing progeny
ovisopis	X	*ovisopis*	4	4	4
ovisopis	X	*fultoni**	2	2	0
fultoni	X	*ovisopis***	4	3	0
fultoni	X	*fultoni*	4	4	4

*The female in 1 replicate was taken out of the hybridization experiment after 6 weeks and placed with a *fultoni* male. Eggs laid during the first 6 weeks did not hatch; subsequent ones produced normal *fultoni* progeny.

**Transfer of spermatophores with no abnormal delay observed in 2 replicates.

The experimental crosses described below were not designed to test the specific status of *ovisopis* as much as to produce hybrids between a *Gryllus* with a calling song and one without. The closest relative of *ovisopis* is probably *fultoni* (see below), but their mating seasons barely overlap outdoors. By rearing *ovisopis* and *fultoni* in the laboratory, I obtained virgin adults of both species at the same time. Pairs of crickets were held at 25 $\pm$ 3°C and 16 L: 8 D in gallon jars equipped and tended weekly as described above under seasonal life cycles. Each of the 4 possible crossings was made a minimum of 2 times. Results are shown in Table 2. Interspecific matings occurred and 13 of 14 females laid eggs; however, only conspecific pairs produced offspring.

These results agree with previous studies of interfertility of *Gryllus* spp. (Alexander 1968). Many species will hybridize, but so far no egg-diapausing species has been successfully crossed with a juvenile-diapausing species.

Acoustic Behavior

The most peculiar feature of *ovisopis* is its lack of a calling song. Males of other *Gryllus* (including 5 Florida species) are easily recognized in the field by their persistent, distinctive calling songs. The absence of such a song in *ovisopis* was responsible for my not recognizing this species earlier.

Several sets of evidence support the contention that *ovisopis* has no calling song. The first is that in 15 years of field studies of north Florida cricket calls I have failed to detect one. During this period I lived within 50 ft. of populations of *ovisopis*. For more than 2 years I made weekly censuses of all calling crickets in 2 habitats that had vigorous populations of *ovisopis*. Yet I have detected *ovisopis* only 3 times in the field by its sound: twice by courtship and once by aggressive sounds. Another set of evidence is that in more than 2 years of laboratory rearing of *ovisopis* I never heard a calling song. A third set is that I kept 15 individually caged adult males in my bedroom for 1-3 weeks and never heard a song. In similar tests with other *Gryllus*, 12 or more of the 15 individuals called within the first week.

The possibility that *ovisopis* produces an ultrasonic calling song can be discounted for these reasons: (1) the frequencies produced during courtship and fighting are similar to the frequencies in the acoustic repertoires of other *Gryllus* (see below), (2) the stridulatory apparatus is similar to that of other *Gryllus* (Nickle and Walker 1974), and (3) no "silent" stridulatory movements were noticed.

Courtship songs are produced by *ovisopis* males in the same circumstances and with the same readiness as such songs are produced by other *Gryllus* spp. Furthermore the songs (Fig. 2) have the same composition, consisting of a somewhat regular alternation of short, sharp "ticks" and sequences of less intense pulses (Alexander 1961). The frequency spectra of the 2 types of pulses are dramatically different—the dominant frequencies of the ticks are about 14 kHz, and those of the less intense pulses are about 4 kHz. Nocke (1972) found similarly contrasting frequency spectra for courtship singing in *Gryllus campestris* Linné.

G. ovisopis males also produce aggressive songs. The circumstances under which such songs are produced are the same as for other *Gryllus* spp. However, the frequency spectrum of the aggressive song (Fig. 3) contrasts with those of other species. In *ovisopis*, aggressive stridulation consists of pulses similar to the ticks of courtship stridulation, with the most intense frequencies near 14

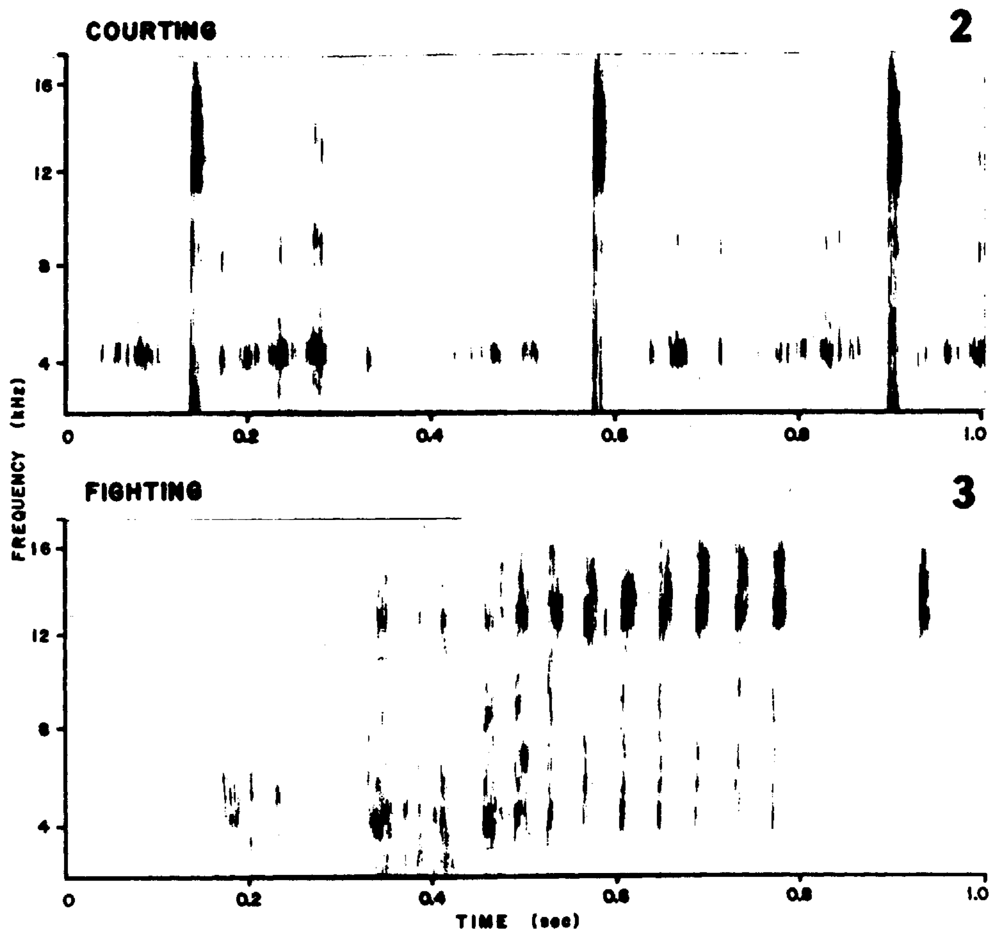

Fig. 2-3. Audiospectrograms of songs of *G. ovisopis*. Fig. 2. Courtship song. Male placed in jar with virgin female. Song began upon contact and continued for 20 sec. Female then mounted and received spermatophore. Fig. 3. Aggressive song. One of 2 field-collected males just placed in jar. Aggressive interaction related to feeding on a piece of dog chow.

kHz. Aggressive songs of other *Gryllus* spp. are composed of pulses similar to those of calling and have the bulk of the sound energy at frequencies near 4 kHz (Alexander 1961, Nocke 1972). To the human ear the aggressive song of *ovisopis* is much less intense than the aggressive song of other *Gryllus*; however, the human ear is much less sensitive to 14 kHz than to 4 kHz. Nocke (1972) has demonstrated that the tympanic organs of *G. campestris* are most sensitive to frequencies near 4 and 14 kHz. The tympanic organs of *ovisopis* may have lost the 4 kHz optimum.

Loss of calling song has occurred independently in crickets of many phyletic lines. Even if only Florida examples are considered, there are species representing mute genera in otherwise noisy subfamilies (*Oligacanthropus prograptus* Rehn and Hebard, Mogoplistinae; *Tafalisca lurida* Walker, Eneopterinae; *Falcicula hebardi* Rehn, Trigonidiinae), there are mute species in otherwise noisy genera (*Scapteriscus abbreviatus* Scudder vs. *S. vicinus*

Scudder and *S. acletus* Rehn and Hebard, Gryllotalpinae; *Hapithus brevipennis* Saussure vs. *H. agitator* Uhler and *H.* undescribed sp., Eneopterinae), and there are mute demes of otherwise noisy species (northern populations of *H. agitator* lack a calling song—Alexander and Otte 1967; the population of *Gryllus fultoni* on Key Largo apparently lacks a functional calling song—Walker, unpublished).

With so many examples, one would hope to find a common circumstance to which to attribute loss of long-range acoustically assisted pair formation. The principal one apparent to me is that such species are sedentary. Of the 8 mute or partially mute species named above, all but *T. lurida* have lost the ability to fly. Sedentary populations characteristically occupy relatively permanent habitats (because such populations can evolve only in such habitats) and are not subject to the extreme fluctuations in density of breeding adults characteristic of temporary habitats. Consequently chance encounters or short-range signals become more dependable pair-forming techniques.

Two other circumstances may have contributed to loss of song in *ovisopis*: (1) Relatively few species call in October and November in sites supporting *ovisopis*. Consequently acoustically orienting predators might destroy a higher proportion of calling crickets than at other seasons (Walker 1964). (2) The calling song of the earliest *ovisopis* may have been confusingly similar to that of *fultoni*. If *fultoni* was more numerous than *ovisopis*, *ovisopis* may have changed in both song and mating season in response to interference from *fultoni*. The mating season of *ovisopis* now scarcely overlaps that of *fultoni* (Fig. 1).

A circumstance that should often correlate with loss of calling song is restricted breeding season. If individuals find mates only through chance encounters, selection will more strongly favor those that time their readiness to mate to coincide with maximum density of mate-ready adults of the opposite sex. Breeding adults of mute crickets are difficult to census, but the data on *ovisopis* and other north Florida *Gryllus* are adequate to demonstrate that *ovisopis* is much more highly restricted in its breeding season than the other 3 species. Of the 54 *ovisopis* juveniles reared to maturity in sheltered jars outdoors in 1972 (Table 1), all became adult during a 5-week period, and 34 matured in the median 2 weeks (10-24 Sept.). Although there are peaks of adult emergence in *G. fultoni, firmus,* and *rubens,* in each of these species some emergence occurs during at least 7 months (unpublished data).

Geography and Phylogeny

The geographical distribution of *ovisopis* may prove to be much more extensive than presently known (see list of paratypes). However, its southern limits are unlikely to change because mesic broadleaf woods are sparse south of Gainesville. Northward it is probably restricted to the southeastern coastal plain, but except for Fulton's failure to find it in North Carolina the evidence is inadequate.

G. fultoni is probably the nearest relative of *ovisopis*. *G. ovisopis* was confused with *fultoni* rather than with some other species largely because of similar habitats. However, 2 other similarities support the hypothesis of *fultoni* and *ovisopis* having a recent common ancestor: (1) both are 100% micropterous (except for a few jar-reared *fultoni*), and (2) *fultoni* is a less persistent singer than most other *Gryllus* spp. (but not *ovisopis*). However, both of these similarities could stem from woods being a relatively permanent habitat capable of continually supporting dense populations of *Gryllus* spp.

Gryllus firmus may prove to be a closer relative of *ovisopis* than *fultoni.* It has egg diapause (as well as mid-juvenile diapause), some individuals are as large as those of *ovisopis,* and the spacing of the file teeth is similarly close (Nickle and Walker 1974, Fig. 10).

Reconstructing the evolutionary history of *ovisopis* is made difficult by not knowing whether it shares a more recent common ancestry with *firmus* or with *fultoni.* If it be *firmus,* speciation is more easily attributed to geographical than to seasonal isolation. Both *ovisopis* and *firmus* are egg overwinterers, but *firmus* has its principal distribution to the south of *ovisopis.* Its adaptations to the sandy, burning-prone habitats of south Florida instead of the more equitable hammocks to the north agree with the geographical hypothesis.

On the other hand, if *ovisopis* proves closer to *fultoni,* the circumstances are reversed and speciation is more easily attributed to seasonal isolation (Alexander 1968). The geographical distribution of *ovisopis* is completely within that of *fultoni* and offers no support for geographical speciation. The seasonal life cycles, however, suggest that seasonal isolation was an essential part of the speciation process. The life cycle of *fultoni* at Gainesville has the very features that a common ancestor of *fultoni* and *ovisopis* should have: The partial late summer generation produces eggs that hatch into juveniles that either perish or contribute to the adult generation of the following spring. Evidence given above suggests that eggs laid later than September contribute little or nothing, because the juveniles that hatch in late fall die before reaching a winter-hardy stage. The evidence given above also suggests (and genetic theory supports) that occasional fall eggs (especially late ones?) hatch the following spring. These hatchlings would most likely become adults in the fall, at which time the laying of slow-to-hatch eggs would be adaptive. Fall adults that came from overwintering eggs would have a greater likelihood of producing reproductively successful progeny if they mated with like adults—rather than with adults of juvenile-overwintering parentage. As a consequence the reproductive behavior of the egg-overwintering fall adults and that of the other fall adults would be expected to diverge. The most obvious feature subject to selection would be mating season. Those egg-overwinterers that delayed mating until October and November would not only reduce the chances of an ill-adaptive mating with a juvenile-overwinterer but also increase the likelihood that the eggs they laid would not hatch until the following spring. Differences in pair-forming techniques would also be enhanced by selection, but loss of calling song by the phyletic line leading to *ovisopis* would be more likely after a stable, synchronized population of egg-overwinterers had developed.

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