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GEOGRAPHICAL VARIATION IN THE *NIGRICORNIS* GROUP OF OECANTHUS (ORTHOPTERA)

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THERE has been some disagreement among taxonomists working with the Orthoptera, as to whether the dark marked tree cricket described by F. Walker as *Oecanthus nigricornis* is really a distinct species from the pale one described later by Buetenmüller as *O. quadripunctatus*. The two insects are very similar morphologically, but differ in color characters and are usually separated by differences in the markings on the two proximal antennal segments. Caudell, Houghton (1909), E. M. Walker (1904) and Blatchley (1920) have mantained that they are only varieties, that numerous intergrades occur, and that it is impossible definitely to separate the two.

In working with these insects in New York state, P. J. Parrott (1914) and the writer became convinced that they were two distinct species. We found a difference in the choice of host plants for oviposition which was associated with the ecological distribution of the two species. *O. nigricornis* was found in berry plantings and on tall rank weeds or brushy growths of more woody plants such as willow, elder, sumac and grape. *O. quadripunctatus* was found only in old fields, especially where the wild carrot (*Daucus carota*) was abundant. This plant was preferred above all others for oviposition, but occasionally other pithy weeds one to two feet high were used, such as aster, small species of *Solidago*, and *Ambrosia artemisiifolia*.

These habit differences were associated with color characters, the most constant of which was the color of the abdominal sternites, which is difficult to determine in pinned specimens due to the shriveling and discoloration of the body on drying. We also found a constant difference in the morphology of the eggs of the two species.

Rehn & Hebard (1916), studying these insects in the southeastern states, believed that the two species were distinct. They state that in addition to coloration, *O. nigricornis* may be distinguished from the other by "the heavier pronotum, the greatest width of which more closely approximates the length of the same than in that species (*O. quadripunctatus*), while the head between the eyes is weakly but distinctly depressed, a condition not at all or rarely very weakly indicated in *quadripunctatus*." In the specimens examined by the writer, few of which were from the southeastern states, the depression between the eyes has not proven distinct or constant enough to be of any aid in separating the species. In specimens from Ohio and Iowa the pronotum of *nigricornis* averages slightly broader in proportion and also slightly larger in relation to the wings, but here again the difference is slight and the maximum for *quadripunctatus* overlaps the minimum for *nigricornis*.

When the writer moved to Oregon he found tree cricket eggs in berry canes deposited in a manner similar to *O. nigricornis* in the east. They proved to be the eggs of a physiological variety of the snowy tree cricket,

O. niveus, an account of which has been published (Fulton (1925)). The former species did not occur there, nor did *quadripunctatus,* but one very similar to both was found abundant in prairie regions where it was closely associated with a certain weed with sticky glandular hairs, called the gum plant (*Grindelia*). This insect had oviposition habits more like *O. quadripunctatus,* but the markings on the proximal antennal segments were very heavy and the ventral segments and sides of the abdomen were only slightly darkened, if at all. The species agreed with Saussure's description of *O. argentinus* and this identification was sustained by Caudell, who stated that he regarded it as merely a variety of *nigricornis.*

The problem of the relationship and distribution of the three species, or subspecies, at once suggested itself. From time to time the writer had opportunity to collect series in various parts of the country and to examine specimens loaned by other collectors.

The problem resolved itself into, first, an attempt to determine the western limits of *nigricornis* and *quadripunctatus* and the eastern limits of *argentinus,* and second, to find out if there is any blending between any or all of the species in question.

METHODS

In order to facilitate the tabulation of data, it was found advisable to originate a series of arbitrary classes based on the markings of the proximal antennal segments. At first, attempts were made to classify the material in a straight line series from light to dark markings, but it soon became evident that this would not work. It was found that dark body color is rather closely associated with certain types of antennal pattern, and that those with a heavy pattern diverge in two directions from a middle ground, one toward typical *nigricornis* with increasing body color and the other toward typical *argentinus,* without essential increase in body color.

After a number of changes 12 classes were decided on, which seemed to have approximately equal value and served well enough to show the differences in the tree cricket population of various regions with regard to this set of characters. Records were also kept on the degree and extent of dark body color, where this was possible. The frail integument of the abdomen makes records on coloration of that part untrustworthy except in fresh or liquid preserved material.

The 12 classes were based mainly on the markings of the first antennal segment. Numerous records showed that the degree of coloration of the second segment was closely correlated in the majority of specimens. The material was therefore classified on the basis of the pattern of the first segment alone except in doubtful cases. The 12 classes are illustrated in table II, and are described as follows:

1. With no markings.
2. With either the inner or outer elements of the pattern absent and the other reduced.
3. Space between the spot and line at least three times the average width of the line.
4. Space 2 times, but less than 3 times, the width of the line.
5. Space about the width of the line or a little over.
6. Space about one-half the width of the line or a little over. Space of fairly uniform breadth or the narrowest part proximad. Line quite heavy and of nearly uniform breadth.

7. Space distinctly less than one-half the width of the line, and narrowest proximad, or spot and line barely contiguous, leaving a notch distad. Line very heavy and of nearly uniform breadth or narrower distad. Little or no infuscation of the remainder of the segment.
8. Spot and line distinctly confluent; line very heavy. Little or no infuscation of the remainder of segment.

6′. Space about one-half the average width of the line or a little over, narrowest part distad. Line not unusually heavy and broadest distad. Segment often slightly shaded distad and proximad of the spot.
7′. Space distinctly less than one-half the width of the line, narrowest distad, or spot and line barely contiguous distad. Remainder of segment more or less shaded.
8′. Spot and line distinctly confluent, but usually leaving a notch of ground color proximad. Segment distinctly infuscated; palest areas bordering the line on both sides.
9′. Pattern decidedly obscured by a general dark infuscation of at least the distal two-thirds of the segment.

In scoring series of specimens on the above plan it is impossible to eliminate the personal element in the interpretation of doubtful specimens. It must be admitted that in series containing many atypical forms, no subsequent examinations would place all specimens in exactly the same classes again. The method serves to give a general idea of the complexion of a series, but conclusions must not be drawn too closely. This work was not intended as a study in evolution or heredity, but is merely an attempt to clear up a taxonomic problem. Better conclusions could be drawn from series which numbered in thousands, but the study has been limited to such collections as were available and to limited opportunity for travel. For several reasons these insects are not ideal material for a special study of variation.

The writer is fully aware that there is such a thing as "place variation," that a species varies somewhat in character from generation to generation or over longer periods of time. Only a few of these series were taken at the same place during different years. There the differences found are probably not greater than would be obtained by the law of chance if the second collection had been made the following day. Field observations on these insects covering seven years in New York and five years in Oregon have convinced the writer that they did not vary noticeably during that time in the characters used for separating the species.

RESULTS

The results of scoring all material examined are summarized in two tables. In table I are shown the actual numbers of individuals of each class; in table II the percent of each class is shown graphically only for the larger series. In many of these the number of individuals is much too small for drawing any quantitative conclusions. In several cases nothing is known about the ecological conditions where collections were made. In some series, especially those showing two distinct modes, the height of each mode depends entirely on the amount of collecting done in each of the two kinds of habitats, and not on the relative abundance of the two forms in that particular locality.

Other specimens examined fell in the above classes as follows: Mineral Springs, Ind., 3 in class 4; Montreat, N. C., 1 in class 9; Pascagoula, Miss., 2 in class 4; Grant Co., Okla., 1 in class 7; Bozeman, Mont., 2 in class 5;

TABLE I.

Series	Locality	No. of specimens of each class. Upper rows refer to upper series 6′ to 9′.									6-6′ intermediate	Total
							6′	7′	8′	9′		
		1	2	3	4	5	6	7	8			
1	Geneva, N. Y. various dates				2	5		7	1			15
2	Newark, Ohio Aug. 25, Sept. 5, 1921			2	11	5		3	23	10		54
3	Gainesville and Newberry, Fla., July-Nov.			5	10	2			.			17
4	Oskaloosa, Iowa, Sept. 4, 1924				11	23		2		1		37
5	ditto				18	33	1	7				59
6	ditto				6	10	1	2	3	1		23
7	ditto					1	1	10	15	6		33
8	ditto total of 4, 5, 6 and 7				35	67	2	21	18	7	1	152
9	Ames, Iowa Aug. 13, '23			1	20	33						54
10	Ames, Iowa, Aug. 27, '24			2	21	49	1	1				74
11	Ames, Iowa, Aug. 28, '24			1	4	17						22
12	Ames, Iowa Aug. 13, '24					14	14 6	6	1		2	43
13	Ames, Iowa Aug. 27, '24					1	14	8	2	1	3	29
14	Ames, Iowa Aug. 26, '24				1	9	6 1	4	1		1	23
15	Ames, Iowa Aug. 28, '24				1	1	5	17	8	1		33
16	Ames, Iowa Aug. 24, '24				19	26	3	4	1			53
17	Ames, Iowa Aug. 13, '24				1	8	7 2	1				19
18	Ames, Iowa Aug. 26, '24					8	4	3				15
19	Ames, Iowa Oct. 10, '24				1	11	4	3			6	25
20	Ames, Iowa, total of 9 to 18			4	68	177	58 9	47	13	2	12	390
21	Sioux City, Iowa Aug. 16, '25				13	30	4 1	15 7	1 10		2	83
22	Lake Okoboji, Iowa Aug. 18, '25			1		2	3 1	5 1	2			15
23	Brookings, S. D. Sept. 18, '23			1	2	6	4 1	10	4		1	29
24	Brookings, S. D. various dates			1	1	2	8 1	12	1			26
25	Lake Hendricks, S. D., Aug. 17, '23				1	1		6 3	3			14

TABLE I—Continued.

Series	Locality	No. of specimens of each class. Upper rows refer to upper series 6′ ot 9′.									6-6′ intermediate	Total
							6′	7′	8′	9′		
		1	2	3	4	5	6	7	8			
26	Arco, Minn., 1911							5				5
27	Canton, S. D. Aug. 26-28, '23		1	3	3	6	3 1	5 4				26
28	Yankton, S. D. Sept. 27, '23				7	8	2	1				18
29	Volin, S. D. Aug. 29, '23				2	3	1					6
30	Eastern, S. D., total of 23 to 29		1	5	16	26	15 6	39 7	8		1	124
31	Capa, S. D. various dates			3	1	2	2 2	3	1			14
32	Pierre, S. D. Sept. 10, '21			1	1	1						3
33	Martin, S. D. Sept. 3, '23	9	30	1				6	9			55
34	Aweme, Manitoba			3	2	9	8	8	2		3	35
35	Bismarck, N. D. Sept. 13, '21			5	5	7	4 6	7	5		2	41
36	Whitewood, S. D. Sept. 9, '23					4	1 2	6	2			15
37	Kansas 36 localities		1		3	2	5	2 44	31			88
38	Galveston, Texas May			1		3						4
39	Brownsville, Texas June					6	10	1				17
40	Fort Collins, Colo. Aug. 16, '23				4	15	1	32	25			77
41	Mesa Verde, Colo. Aug. 14, '24				1	8	2					11
42	Montezuma Co., Colo.				2	10	5					17
43	Wray, Colo.						1	2	2			5
44	Williams, Ariz. Aug. 14, '21					3	5					8
45	Arizona, other localities				2			5	1			8
46	Big Timber, Mont. Aug. 12, '25		1	2	31	46	2					82
47	Boise, Idaho		1	7	12	6	1					27
48	La Grande, Ore. Aug. 16, '19					1	4	9	2			16
49	Corvallis, Ore. Aug. 24, 28, '19						1	21	9			31
50	Corvallis, Ore. Sept. 6, '23						2	26	3			31

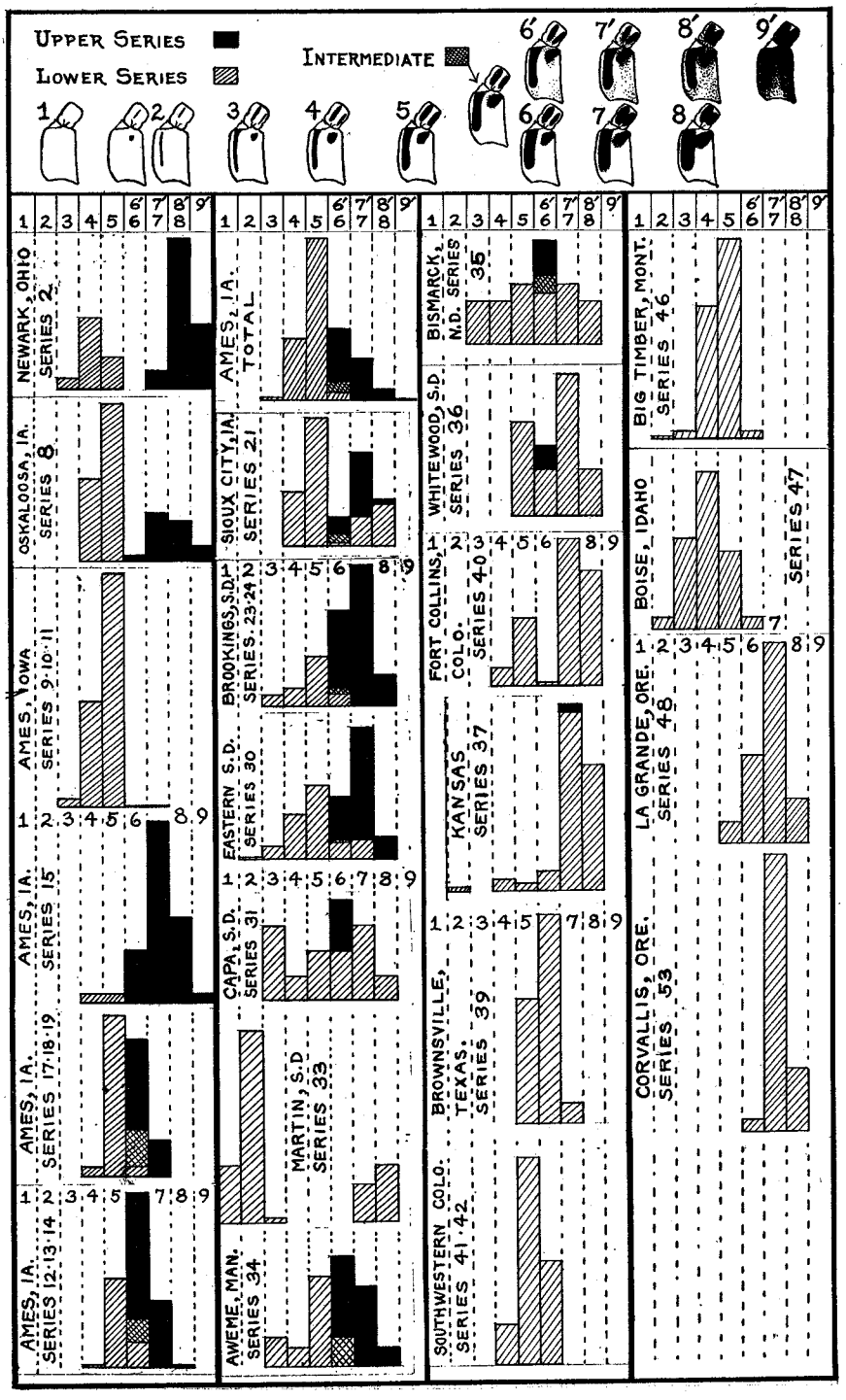
TABLE I—Continued.

Series	Locality	No. of specimens of each class. Upper rows refer to upper series 6′ to 9′.									6-6′ intermediate	Total
							6′	7′	8′	9′		
		1	2	3	4	5	6	7	8			
51	Corvallis, Ore. Sept. 2, '23						1	15	3			19
52	Corvallis, Ore. Other specimens							25	5			30
53	Corvallis, Ore. Total of 49 to 52						4	87	20			111
54	Medford, Ore. Aug. 3, '21							4	2			6
55	Forest Grove, Ore. Oct., 1906							2	1			3

Billings, Mont., 3 in class 4; Tempe, Ariz., a bottle of specimens collected by R. M. Wilson from alfalfa were examined several years ago and notes taken at the time show that they all had the heavy antennal markings and would fall in class 7 or 8.

Further data on the series of specimens from which data was taken: (2) Newark, Ohio, from *Ambrosia trifida,* river bottom land, and *Daucus carota,* upland fields. (3) Gainesville and Newberry, Fla., collected by Fred Walker, the Newberry specimens from dog fennel. (4) Oskaloosa, Iowa, from *Ambrosia artemisiifolia* on side and top of hill pasture, growing in clumps. (5) from *Solidago* clumps in the same pasture. (6) from *Polygonum* and *Bidens* in a wet gully, same field as last. (7) from tall *Solidago* and *Ambrosia trifida* along fence surrounding above field. (9) Ames, Iowa, from *Ambrosia artemisiifolia* and other small weeds, river terrace pasture. (10) same place, following year. (11) from *A. artemisiifolia,* another river terrace pasture 5 miles from (9). (12) from *Cannabis sativa* and *Vernonia,* creek bottom land, one-quarter mile from (9). (13) same place following year. (14) from same plants two miles down stream from (12). (15) from *Ambrosia trifida* and *Helianthus* along fence half mile from (11). (16) from various kinds of weeds on terrace above creek. (17), (18), (19) three collections from same raspberry planting. (21) Sioux City, Iowa, mainly from *Erigeron canadensis* and *Helianthus tuberosus,* all from same field. (22) Lake Okoboji, Iowa, from various weeds in low meadows adjacent to lake. (23) to (33) and (36) loaned by H. C. Severin. (23), (24), (25), Brookings and Lake Hendricks, S. D., low prairie. (27), (28) Canton and Yankton, S. D., valley land with natural tree growth. (29) Volin, prairie. (31) (32), Capa and Pierre, S. D., central part, latter in Missouri Valley, former in a branch valley 35 miles southwest. (33) Martin, S. D., sand hill area with sparse vegetation. (34) Aweme, Manitoba, loaned by E. R. Buckell, collected by N. Criddle. (35) Bismarck, N. D., mainly from *Grindelia,* Missouri river bottom land. (36) Whitewood, S. D., in Black Hills altitude 3,700; pine, spruce and oak forest region. (37) Kansas, from University of Kansas collection, a few specimens each from many localities scattered over entire state. (38), (39) collected by Snow, University of Kansas collection. (40) Fort Collins, Colo., mostly from tall weeds in low ground, those in classes (4) and (5) from sage brush. (41), (42), (43), collected by C. J. Drake and H. H. Knight. (44) Williams,

TABLE II.


UPPER SERIES
LOWER SERIES
INTERMEDIATE
1
2
3
4
5
6
6'
7
7'
8
8'
9
9'
AMES, IA.
SERIES 12·13·14
AMES, IA.
SERIES 17·18·19
AMES, IA.
SERIES 15
AMES, IOWA
SERIES 9·10·11
NEWARK, OHIO
SERIES 2
OSKALOOSA, IA.
SERIES 8
AMES, IA.
TOTAL
SIOUX CITY, IA.
SERIES 21
BISMARCK, N.D.
SERIES 35
WHITEWOOD, S.D.
SERIES 36
BIG TIMBER, MONT.
SERIES 46
AWEME, MAN.
SERIES 34
MARTIN, S.D.
SERIES 33
CAPA, S.D.
SERIES 31
EASTERN S.D.
SERIES 30
BROOKINGS, S.D.
SERIES 23·24
FORT COLLINS, COLO.
SERIES 40
KANSAS
SERIES 37
BOISE, IDAHO
SERIES 47
SOUTHWESTERN COLO.
SERIES 41·42
BROWNSVILLE, TEXAS.
SERIES 39
CORVALLIS, ORE.
SERIES 53
LA GRANDE, ORE.
SERIES 48

Ariz., from *Chrysothamnus*. (45) Arizona, several isolated records, mostly from University of Kansas collection. Localities given: S. Ariz. (2 in class 4), Bill Wm's. Fork (1 in class 8), Cochise Co., San Rita Mtns., Douglas, Tucson, Phoenix. (46) Big Timber, Mont., from *Grindelia* and *Helianthus*, collected by J. R. Parker. (47) Boise, Ida., loaned by Claude Wakeland. (48) La Grande, from weeds in mountain side gully and field in valley several miles north. (49)-(53) Corvallis, Ore., mainly from *Grindelia*. (49) prairie near creek. (50) dry fields at foot of hill. (51) hillside prairie, mostly on *Hypericum*. (52) miscellaneous specimens, all from prairie. (54) Medford, Ore., from *Grindelia* along railroad.

DISCUSSION OF RESULTS

An examination of the tables shows three general conditions in regard to the populations of these species, corresponding largely to three general regions, the eastern deciduous forest region, the great plains and the Rocky Mountain-Pacific Coast region.

In the eastern part of the country, extending a little west of the Mississippi, *nigricornis* and *quadripunctatus* seem to be fairly distinct, sufficiently so that one would be justified in calling them separate species. A few individuals may be found which would be difficult to place on the basis of antennal markings alone, but with fresh material or specimens in liquid, showing clearly the body color, especially the abdominal sternites (fig. I, A. B.), I believe practically all specimens could be properly identified. In this region the two crickets live in different environmental conditions.

By long experience in collecting these insects, the writer can tell at a glance which cricket would be found in any particular plant association in this region. *O. nigricornis* is found among the large, coarse, herbaceous plants with pithy stems or brushy growths of more woody plants or young trees of certain species. *Quadripunctatus* lives only among smaller species of pithy stemmed herbs. This well defined ecological distribution seems to be based on the oviposition habits which may be tested out in cages. If each species is given a choice of a number of different kinds of stems for oviposition, *nigricornis* will select large stems of about 6 to 10 mm. or even

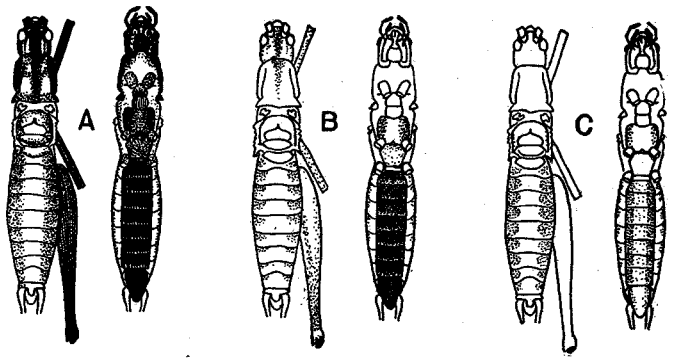


Fig. 1. Showing the extent of melanic color on the dorsal and ventral sides of the body with wings and legs removed except the right femora in the dorsal view. (A) Dark and (B) light colored specimens of O. nigricornis from eastern states. (C) Dark form of O. argentinus found in some western localities.

larger, while *quadripunctatus* will choose stems of 3 to 4 mm., or seldom as large as 5 mm. If given only one kind of plant, as raspberry for example, *nigricornis* will oviposit in the main part of the cane, while *quadripunctatus* will use the tips or leaf petioles, neither of which would be normal for the latter species.

At Oskaloosa, Iowa, where the two crickets are not as widely separated as they are further east, collections were made in an old pasture extending over a low hill. The fence along the bottom of the hill was surrounded by tall weeds, such as the giant ragweed (*Ambrosia trifida*) and a large species of golden-rod (*Solidago*). In the field, extending over the hill, there were many clumps of somewhat smaller golden-rod and the common ragweed (*Ambrosia artemisiifolia*). Series (4), collected only from the last named plant, contained only 3 specimens of *nigricornis* out of 37, and series (5), taken only from the clumps of golden-rod, contained 8 of the latter species out of 59. Some of these plants were of such size that the lower stems would come within the normal size range for oviposition by *nigricornis*. Series (6), collected from smartweed (*Polygonum*) and Spanish needle (*Bidens*), in a wet gully on the side of the hill, contained a considerable proportion of both forms, but none of doubtful taxonomic position. Series (7), taken from tall weeds along the lower fence, contained only one *quadripunctatus* out of 33. In all the specimens there was close correlation between the type of antennal markings and body color. All in classes (7′) and (8′) had black or very dark abdominal sternites and most of them were shaded on the sides of the abdomen, and had the typical dark areas on head and pronotum, as well as dark legs and antennae (Fig. I, A. B.). Two of the specimens in (6′) showed only faint color on the abdomen, the other was typically dark. These results show that at this locality, which is near the western limit of originally extensive deciduous forests, the two forms are fairly distinct both taxonomically and ecologically.

Series collected in the territory included in the great plains area are more difficult to interpret. This includes territory which is largely prairie, but which may have forest in the immediate vicinity of the larger streams. Here we find all three forms present, *nigricornis, quadripunctatus* and *argentinus,* and there are also more atypical specimens which are difficult to place. At Ames, Iowa, which is at about the eastern edge of this area, *argentinus* does not appear to be present, and the other two approach each other more closely and are more often associated than at Oskaloosa, 70 miles to the southeast. Series (11) shows a pure population of *quadripunctatus* taken on common ragweed (*Ambrosia artemisiifolia*) and vervain (*Verbena* sp.), all small plants, 1 to 2 feet high, growing at the top of a river terrace in an old pasture. Series (9) and (10) were taken on two successive years on the side and top of another terrace much closer to the stream, from the same plants as above with the addition of a small golden-rod. In series (10) only one typical specimen of *nigricornis* out of a total of 74 was found and that at the foot of the terrace. Compare these with series (15) taken from giant ragweed (*Ambrosia trifida*) and a *Helianthus* growing along a fence on level ground not over half a mile back from the terrace where series (11) was collected. Here we have only two specimens of *quadripunctatus* out of 33. No such pure populations are found in any of the other series taken around Ames, including those from creek bottom land collected largely from hemp (*Cannabis sativa*) and iron weed (*Vernonia*),

both large plants. The *nigricornis* present falls largely in the paler class (6′). There are many individuals which closely approach typical *argentinus* and fall in class (6) and many which seem to be intermediate in position between (6) and (6′).

All of the *quadripunctatus* in series (9), (10) and (11) have entirely pale bodies, while all of the *nigricornis* in series (15) have dark venters, but the typical dark areas of the head and pronotum are faint or narrow. In the other series there is a general correlation between antennal pattern and body coloration, but there are many exceptions. Many in the 6′ class show no dark color on the venter, some of the 7′ class are only faintly colored, while on the other hand many in class 5 and even a few in class 4 have a more or less dark colored venter. Specimens from the bottom land and berries are also larger on the average than the typical *quadripunctatus* from the river terraces.

At Sioux City, Iowa, which is at the western edge of the state and within the strictly prairie region, all three forms were found in the same field both on tall plants (*Helianthus*) and on small weeds (*Erigeron canadensis*). Series (21) was collected in a field on the side of a small valley which was fringed with trees, but not extensively wooded. There were some intermediate forms, but on the whole the three forms were more distinct than would be expected when finding them so closely associated. As can be noted in the percentage graph in table II, the modes come in classes 5, 7′ and 8. Class 6 was almost absent, while class 6′ and intermediate forms were few in number. There was close correlation between antennal pattern and body color. All in class 7′ had dark venters. One rather doubtfully assigned to 8′ had only a faintly colored venter. One in 6′ was entirely pale, while another was faintly shaded. One specimen in 4 had a faintly shaded venter.

At Lake Okoboji, in northwestern Iowa, the three forms were also found associated in low meadow land adjoining the lake. An examination of the several series from the eastern part of South Dakota shows that *nigricornis* and *quadripunctatus* predominate in that region as in Iowa, but that *argentinus* is present as a minor element of the population or at least certain individuals show definite *argentinus* tendencies. Much the same condition is found in the series from Aweme, Manitoba. The correlation of body color in the last locality was poor like that in the Ames series taken from berries.

In series (35), collected on the Missouri bottom lands at Bismarck, N. D., we find a fairly uniform distribution of specimens in all classes from 3 to 8, with a minor element in the population showing distinct *nigricornis* characters. None of those in 6′ have a very pronounced dark body color and could not be called typical *nigricornis*. A small series from Capa, S. D., (No. 31) shows the same condition, and series (36) from Whitewood, S. D., in the Black Hills, contains only one specimen similar to the above. The Kansas series contains only two specimens of typical *nigricornis*, from the northeastern part of the state near the Kansas river.

Typical *argentinus* forms the largest element in the Kansas series, taken from all parts of the state, a few specimens from each of 36 localities. It also predominates in the Whitewood, S. D., and Fort Collins, Colo., series, both from the western portion of the great plains region. At Fort Collins, the specimens in classes 4 and 5 were taken from semi-desert plants,

largely *Chrysothamnus*, while the typical *argentinus* came from a patch of marsh ground where the crickets were living on tall rank weeds.

Series (33), from the sand hills at Martin, S. D., contained 15 typical *argentinus* and 40 specimens of what I take to be an extreme form of *quadripunctatus*. These were different from any other series I have seen in having the antennal pattern extremely reduced. Some other series have a few individuals with one element of the pattern absent, but in the Martin series this was the mode and nine specimens had no trace of antennal pattern. It is not known whether the two groups were associated in nature or not.

Series (38) from Brownsville, Texas, contained many specimens in which the spot of the antennal pattern was reduced relatively more than the line. These fell in class 5, but many of them were not typical of *quadripunctatus*. There were relatively few typical *argentinus* and most of the specimens were somewhat intermediate between the two, with many irregularities in form of pattern.

In comparing the series from the great plains area we find extreme variation in the complexion of the tree cricket populations even in localities not far removed from each other. Most of them show that the three forms are quite close together and field notes show that in some cases they are associated in nature. While in most cases the typical forms outnumber the intermediate forms, there are enough of the latter to indicate hybridization or blending. *Nigricornis* becomes scarce toward the west and loses its typical coloration, *argentinus* extends eastward almost if not entirely to the limits of the true prairie region. *Quadripunctatus* ranges westward as an insect of the higher and dryer prairie and finally becomes an inhabitant

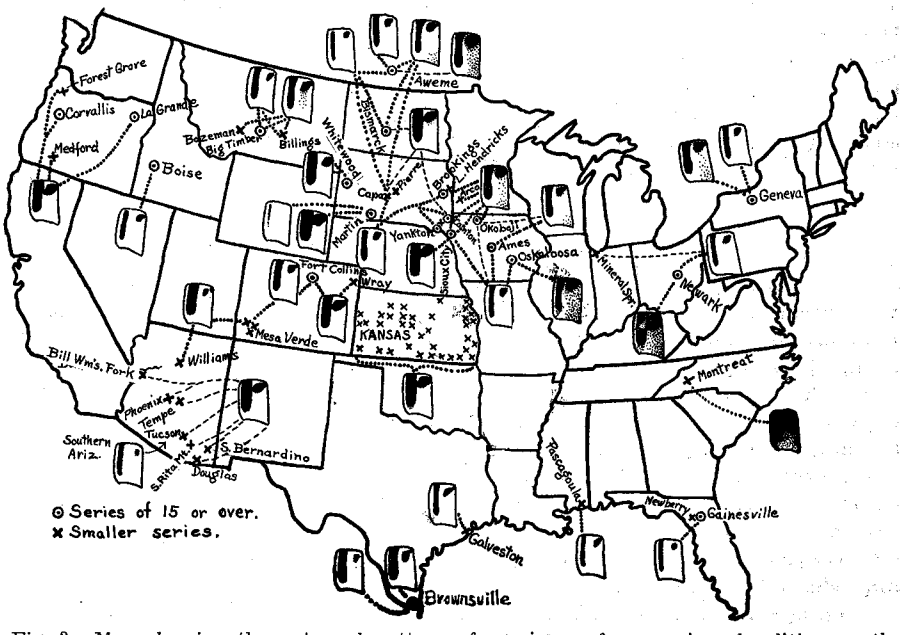


Fig. 2. Map showing the antennal pattern of specimens from various localities, or the commonest types of pattern found in series of specimens.

of the semi-desert. Whether these last are true *quadripunctatus* seems doubtful on the evidence of the egg characters as brought out later.

In the Rocky Mountain-Pacific region, the classes in the *nigricornis* group are entirely absent and classes with light antennal pattern extend only thru the Rocky Mountains, as indicated by available collections. No series of any size from this region shows a bimodal grouping of the population, but all fall into a fairly normal curve. In specimens from southwestern Colorado and Williams, Arizona, and two specimens in the Kansas University collection labelled S. Arizona, there is a peculiar reduction of the spot of the antennal pattern and frequently it is divided, leaving a small portion isolated on the extreme distal part of the first segment on the outer edge. In many of these specimens the line is as heavy as in typical *argentinus*. The few specimens examined from various other parts of Arizona (45) were mainly typical *argentinus*. I also have notes taken before the present study was started, on a series of specimens collected by R. M. Wilson on alfalfa at Tempe, Arizona. These were typical *argentinus* as shown by sketches made at the time. The abdomen was marked by lightly infuscated lines extending across all of the abdominal sternites on each side and by rows of lightly infuscated patches in a dorso-lateral position. These specimens must have been almost identical to average specimens from western Oregon, where the same body markings are present. (Fig. 1, C.)

Series (47) from Boise, Idaho, appears to be typical *quadripunctatus*. These were collected by Wakeland among weeds along irrigation ditches and the collector states that they sometimes oviposit in the twigs of prune trees, a habit which reminds us of *nigricornis* in the eastern states.

Series (46), Big Timber, Mont., collected from *Grindelia* and *Helianthus*, falls mainly in the *quadripunctatus* groups, but shows decided tendencies toward *argentinus*. Many specimens have the lightly infuscated stripes on the venter, and many have the reduced spot common in the southwestern states. The first named host plant is the favorite of typical *argentinus* in western Oregon. All series from western Oregon (49 to 55) show remarkable uniformity, with nearly all specimens falling in classes 7 and 8. Series (48) from La Grande, in eastern Oregon, has the same mode, but a larger proportion of specimens show a lighter antennal pattern.

EGG CHARACTERS

In studying the tree crickets in New York state it was found that the eggs of *quadripunctatus* could be distinguished from those of *nigricornis* by the structure of the cap at the cephalic end. The cap is a white covering delicately moulded into numerous minute ridges and projections which are arranged in spiral rows in two directions, similar to the scales of a pine cone. The projections gradually increase in length from the base of the cap, reaching a maximum near the apex and decrease again at the immediate apex. Subsequent descriptions of projections apply to those of maximum length unless otherwise stated. *O. nigricornis* egg caps were found to be broadly rounded and considerably broader than long, and the projections were short. In *quadripunctatus* eggs the cap tended toward a conical shape and averaged only a little broader than long, while the projections were finger-shaped and about twice as long as in the other species.

Comparing the eggs from a number of localities we find that they differ more or less in character in each place. (Fig. 3.) At Newark, Ohio,

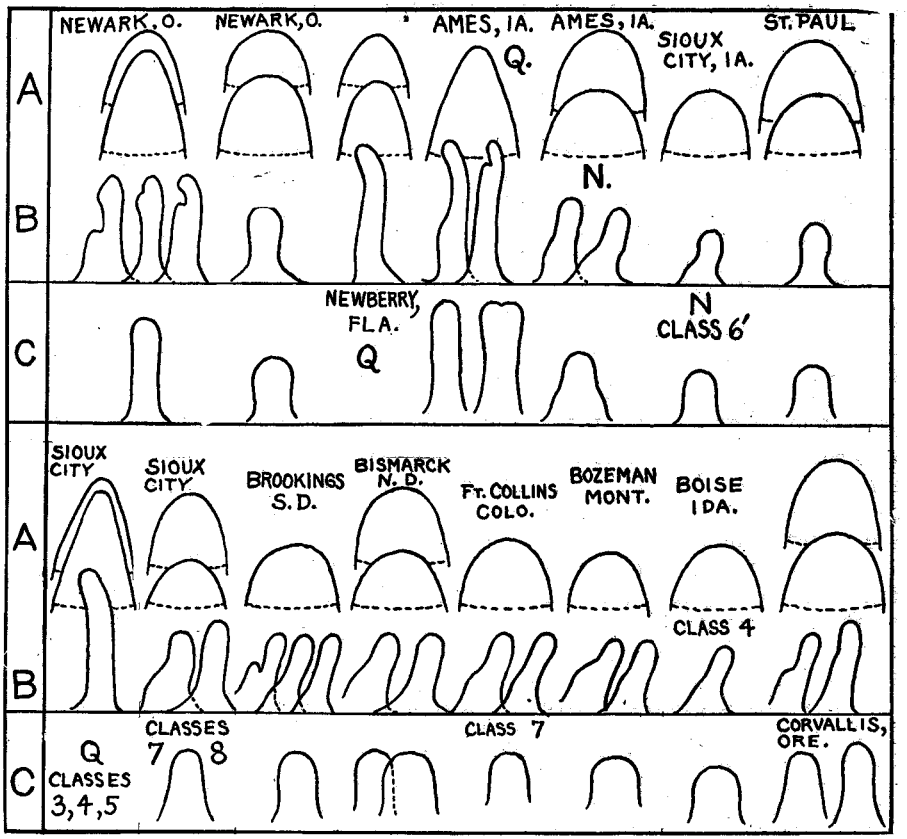


Fig. 3. Eggs of tree crickets. Vertical columns show details of eggs from one locality. (N) O. nigricornis. (Q) O. quadripunctatus. (Under Newark, O., left column is O. quadripunctatus; right, O. nigricornis.) When eggs were dissected from specimens the class of antennal pattern is given. In other cases, the eggs were taken from plants. Horiontal rows show: (A) Egg caps, with extremes figured in cases where considerable variation was found. (B) Types of longest projections found as seen at the edge of the cap. The right side is toward the apex of the cap in every case. (C) The same when viewed directly in the middle of the cap. Enlarged 25 diameters for caps, 400 diameters for projections.

the eggs of both species agree closely with the descriptions and drawings made of eggs of the same species at Geneva, N. Y., the only difference noted was that the eggs of *quadripunctatus* from Ohio showed a more pronounced conical shape of the cap and in the majority of them the length of the cap was greater than the diameter. Altho there is the same relative difference in length of cap projections in the two species, they are longer for both species in the Ohio eggs. This difference may possibly be accounted for by an improvement in the method of measuring them.

The projections of the Ohio *nigricornis* eggs are expanded a little near the tip, forming a rounded knob, and are slightly flattened so that the diameter measured on a transverse tangent with the egg surface is a little greater than the radial diameter. A few of the projections, especially toward the base of the cap, have a slight shoulder or buttress on the side toward the base, but this is not the rule. In the eggs of *quadripunctatus*

the projections are also knobbed and slightly flattened at the tip, and usually slightly curved near the tip. Many of them, possibly half, have a more or less abrupt shoulder of variable height. In some cases this forms a ridge or rib extending to the tip.

Eggs collected at Ames, Iowa, on the sites where series (11) and (15) were collected, show even greater differences between the two forms. The *nigricornis* eggs are very similar to those from Ohio, but the *quadripunctatus* eggs exhibit a longer and more conical shaped cap, while the projections are longer, more slender, less clubbed and most of them are provided with a shoulder or buttress.

Eggs collected in wild raspberry canes at St. Paul, Minn., and some from Brookings, S. D., in raspberry (8.5 mm. diameter), and a pithy weed stem (7 mm. diameter), are very similar to the *nigricornis* eggs found elsewhere.

Eggs found in *Grindelia* (5-8 mm. diameter) and wild rose (3 mm. diameter) at Bismarck, N. D., at the same time and place that series (35) was collected, are more like *nigricornis* eggs, altho the oviposition is more like that of *quadripunctatus*. The cap projections differ from *nigricornis* eggs in being broader and in the presence of a low shoulder or buttress on the majority of them.

Eggs collected at Bozeman, Mont., resembled those from Bismarck, but with a more pronounced and more constant development of the shoulder on the projections. At the time these eggs were collected, only two crickets could be found, both of which were placed in class 5, which is the commonest class in the Big Timber series (No. 46).

Eggs from Corvallis, Oregon, have a short rounded cap, but the projections are quite long and resemble those of *quadripunctatus*. Many of them have a shoulder, but probably most of the longer ones do not.

In order to obtain still more information on the egg characters, the dissected eggs from specimens in liquid and also some pinned ones were studied. In most of the series the females did not contain any well developed eggs if collected before September. Oskaloosa, Iowa, specimens showed the same type of eggs for *nigricornis* and *quadripunctatus* as found at Ames. Eggs were obtained from the following specimens of series (21), Sioux City: 1 from class 3, 4 from class 4, 5 from class 5, 2 from class 7, 4 from class 8, 1 from class 6′. Unfortunately, all female specimens in classes 7′ and 8′ were young and contained no eggs. All eggs from specimens in classes 3, 4 and 5 had the long conical cap with the long projections as at Ames. All other eggs had a short, rounded cap. The projections on eggs from classes 7 and 8 were slender, of medium length, many of them with a slight shoulder, and showed points of resemblance both to Corvallis, Oregon, eggs and to eggs from Bozeman, Mont., and Bismarck, N. D. Curiously enough, eggs from the one specimen of class 6′ had the short, stout projctions typical of *nigricornis* from Ohio.

Dissected eggs from crickets collected on raspberry at Ames all had the short, rounded cap with short projections. A specimen of class 5 from the creek bottom land, series (12), also had eggs of this type. Most of the Ames specimens were collected before eggs were developed.

One specimen of *quadripunctatus* from Newberry, Fla., contained four well developed eggs. The cap was not excessively long and conical as in

Iowa, but resembled more the Geneva, N. Y., condition. The projections, however, were long and slender, as in Iowa specimens.

Eggs dissected from a dried specimen of class 4 from Boise, Idaho, had the short, rounded cap and short projections. The same was true of eggs from a Fort Collins, Colo., class 7 specimen, and also from a class 5 specimen, but in the latter case the projections were obscured.

The evidence from the egg characters indicates that the tree crickets found on raspberries and on tall bottom land weeds at Ames, Iowa, are *nigricornis* whether the antennal pattern is lighter than the typical condition or not. It indicates also that those with the light antennal pattern from Colorado and Idaho are not true *quadripunctatus*. The egg characters must be fairly constant for the latter species in the east, where the same general type is found in such widely separated localities as New York, Ohio, Iowa and Florida. At Sioux City, Iowa, the meager data seem to indicate that *quadripunctatus* is distinct there also, yet it seems improbable that it could exist without hybridizing when intimately associated with such closely related forms.

The egg characters point toward a close relationship between *nigricornis* and *argentinus*. *Nigricornis* eggs from Ames closely resemble those dissected from *argentinus* specimens from Sioux City, Iowa, and Fort Collins, Colorado.

CONCLUSIONS

The extent to which local environmental conditions may change the character of the tree crickets of the *nigricornis* group has not been determined. It seems hardly possible that all the results could be accounted for in this way. The environmental difference between a small ragweed growing in a pasture and a bramble or sunflower ten feet away, is hardly great enough to account for the differences in color, egg structure and habits, found between *nigricornis* and *quadripunctatus*. If environment were directly responsible for the differences, why should all three forms be found in the same field and on the same species of plants as at Sioux City, Iowa? Likewise in western Oregon, apparently similar differences in environment have little or no effect on the color characters, which hold remarkably constant.

On the other hand, we find in the far west little or no difference in the egg characters between series which fall largely in the pale classes of antennal pattern and those which are typical *argentinus*. Considering the extreme environmental differences that may be found in the western mountain regions, it seems entirely possible that color characters could be influenced to some extent at least by the physical environment.

On the whole, one is forced to the conclusion that in each locality the crickets have a certain genetic constitution differing more or less from those in other localities. In the eastern portion of the United States and Canada, *nigricornis* and *quadripunctatus* are fairly distinct, sufficiently so to be considered different species if they did not range beyond this region. Both forms are found in most of the eastern territory, but *nigricornis* ranges farther north and reaches the southern states only in the Appalachian Mountain regions. In the eastern portion of the great plains area, *nigricornis* becomes less distinct, by reduction of the average antennal pattern and body color, altho the eggs retain essentially the same character. In

this region it apparently blends or hybridizes with *argentinus,* which has eggs very similar to *nigricornis. Nigricornis* predominates in the eastern portion of the area and fades out to the west, while the reverse is true of *argentinus,* which also extends to the Pacific coast states.

The situation in regard to *quadripunctatus* is more uncertain. All known eggs of this form from the eastern states, so far examined, have shown distinct characters, even as far west as Sioux City, Iowa. No eggs were obtained of the extreme form found in the sand hills at Martin, S. D., but it seems plausible that this might represent the extreme western extension of true *quadripunctatus.* The few eggs obtained from apparently typical *quadripunctatus* from Colorado and Idaho were not like those found in the eastern states, but were more like the eggs of *argentinus.*

This evidence points to a closer relationship to *argentinus.* Either the two forms are less distinct in the far west or else true *quadripunctatus* extends only as far as the eastern portion of the great plains, and similar forms found in the far west are only variations of *argentinus,* possibly due to local environment. From a practical standpoint, the best we can do at present is to consider all series with the light antennal pattern and pale body color as *quadripunctatus.*

Until better characters for separating the tree crickets of this group have been discovered, it seems advisable to consider *nigricornis, quadripunctatus* and *argentinus* as subspecies. The greatest difficulty in identifying them will be found in the central portions of the country. There they exhibit little or no differences in the choice of environment. One would hardly expect such closely related races to be associated on the same plants without hybridizing to some extent. There is no experimental evidence to show whether this is the case or not, but many individuals are found which are intermediate in regard to the characters commonly used in separating them.

OTHER SPECIES

The only other known species of *Oecanthus* in the *nigricornis* group is *O. pini* Beutenmuller, which has characters distinct enough to justify its rank as a separate species. The antennal pattern is not very distinctive. It is usually like that of class 4 or 5, with the spot on the first segment small and round or with an outward extension along the distal border of the segment. The lines on the second segment are straight, parallel, of uniform width and usually well separated. In some specimens the outer elements of the pattern are faint or absent.

The most distinctive character about the species is the general ground color of the body. It could be confused only with specimens of related species discolored by too long confinement in the killing bottle. In dry specimens, it is a light yellowish or reddish brown, lighter on the lateral portions of the pronotal disk and ventral side of the thorax, and darkest on the median part of head and pronotum. The pale color is close to clay color, cinnamon, or cinnamon buff in Ridgway's "Color Standards and Nomenclature," while the darkest parts are near snuff brown, walnut brown, or burnt umber. The arrangement of the darker color is similar to typical *nigricornis,* but in the latter the dark color on the pronotum is fuscous or black on a pale buff or ivory yellow ground color. The venter of the abdomen is black in typical *nigricornis* as compared to dull brown in

pini. The first antennal segment is broader in *pini*, being nearly as wide as long; the ground color of the two basal segments is the same as the palest body color, while the remainder of the antenna assumes the darkest body color.

In life *pini* is easily recognized by the distinct green of the wing veins. The hind femora and dorsal part of the abdomen have enough green to give them an olive color. The head and thorax appear more reddish-brown in life and contrast sharply to the greenish color of the wings. Nymphs have greenish wing pads, a green abdomen with cream colored dorso-lateral stripes; the remainder of the body is light brown; the legs a light olive brown. The species has been found only on or near pines.

KEY TO NORTH AMERICAN OECANTHINAE*

On the basis of this and other recent work on the tree crickets, the following modified key is appended:

A. Front face of the proximal antennal segment with a small but prominent tubercle or knob on the distal border near the middle; no black markings. Hind tibiae armed with spurs only. Wings exceed the tegmina by at least half their length. Deciduous forest and thickets. Conn. to Ga., west to Iowa, Kansas, Texas. Recorded by Saussure from Mexico and Central America.

Neoxabea bipunctata (De Geer)

AA. Proximal antennal segment without a prominent tubercle on the distal border. Distal half of hind tibiae armed with several long spines and numerous small teeth.

Oecanthus

B. Front face of proximal antennal segment with a broad, white or ivory colored swelling at the inner edge, ornamented with black. Area between eyes usually tinged with yellow.

C. Swelling with a round or oval, black (or rarely brown) spot. Second segment wth a similar spot. Width of dorsal field of male tegmina nearly half of length. Deciduous trees and shrubs. Me., Ont., and B. C., to Ga., Cuba., Calf., Mexico and Central America.

O. niveus (De Geer)

CC. Swelling with a curved or "J-shaped" black mark; the proximal end curved toward the inner side. Second segment with elongated black mark. Width of dorsal field of male tegmina less than four-tenths of length; length 10 to 12 mm. Pronotum usually with a darker median streak. Deciduous trees and shrubs. Mass., Mich., Minn., S. D., to Fla., Kans., and Tex.

O. angustipennis Fitch

CCC. Swelling with a club-shaped black mark, broadest proximad. Second segment with elongated black mark. Width of dorsal field of male tegmina less than four-tenths of length; length 12.5 to 14 mm. On certain oaks, sometimes on hickory, beech and other deciduous trees. Conn., Long Island and N. C., to Ohio, Tenn., Mo., and Iowa.

O. exclamationis Davis

BB. Front face of proxmal antennal segment without a swelling on the inner edge; this edge nearly straight except at the base and nearly parallel with outer edge.

* Three other North Amercan species of *Oecanthus* have been described by C. F. Baker. The writer has not examined the types, but in the descriptions there is nothing to definitely separate *O. Rileyi* Baker from *niveus* or *O. rehnii* Baker from *argentinus*. *O. marcosensis* Baker is apparently only a dark form of the species commonly accepted as *californicus*.

C. Subgenital plate of female with a broad notch posteriorly, half as broad as widest part of the plate. Width of dorsal field of male tegmina about half the length (in one case as low as .44). Front side of proximal antennal segment never ornamented with more than a narrow dark line along the inner edge.

D. Typically pale straw color or ivory, with top of head and base of antennae purplish pink; proximal antennal segment without distinct markings. Large; male tegmina 13 mm. and over; female, 11 mm. and over; oviposter 6.5 mm. and over. Pronotum width at hind margin seldom greater than length in males, distinctly less in females; pronotum small in relation to tegmina so that width of hind border goes into length of tegmina 5 to 6 times. Hollow on side of terminal segment of maxillary palp rarely covers more than distal third of segment. In thickets of shrubs, vines and tall weeds. Long Island, southern Mich., and Minn., southeastern S. D. to Ga., Miss., and Kans., possibly to Tex.

O. latipennis Riley

DD. Brown to ivory with only a reddish tinge on top of head in pale forms; proximal antennal segment in many specimens with a dark line along the inner edge of front face. Smaller; male tegmina 10 to 13 mm.; female, 8 to 11.5 mm.; oviposter, 5 to 6 mm. Pronotum of male with width of hind border generally exceeding length by more than one-tenth; in females length seldom exceeds width by more than one-tenth. Pronotum larger in relation to tegmina, width of former included in length of latter 4 to 5 times. Hollow on side of terminal segment of maxillary palp covers distal 3-5 to 1-2 of segment. Thickets of shrubs and other low plants. Wash. (?), Ore., Ida., to Calif., Colo., Ariz., N. Mex., Tex., and Ark. (?).

O. californicus Saussure

CC. Subgenital plate of female with a narrow notch posteriorly, not more than one-fifth of widest part of plate. Male tegmina narrow; width of dorsal field rarely over four-tenths of length. Front side of proximal antennal segment, with few exceptions, ornamented with more than a narrow line along inner edge.

D. Head, pronotum, legs and antennae light to medium brown, sometimes reddish-brown; underside of abdomen dull brown. In life, wing veins green, dorsum of abdomen and hind femora olive green. In pines or near them. Mass., Conn., Long Island, N. J., Pa., N. C.

O. pini Beutenmuller

DD. Head and pronotum typically with a fuscous median stripe on pale yellowish ground color, (or these parts entirely pale or nearly entirely black). Sternites of abdomen typically entirely black; atypically lightly infuscated or pale. Proximal antennal segment ornamented as in classes 6′ to 9′, atypically as in 5 (table II). On tall weeds, shrubs, young trees or vines. Typical: Me., Ont., Minn., S. D., to eastern Kans., Mo., Ky., and Va.; in mountains to Tenn. and N. C. Atypical: Man., N. D. to Nebr., western Ia.

O. nigricornis nigricornis Walker

DDD. Body entirely pale or with abdomen lightly infuscated along each side of the sternites and dorso-laterally. Proximal antennal segments ornamented as in classes 6 to 8; atypically with line as in 6, but with spot reduced. Generally on weeds 1 to 3 feet high, or small shrubs. Great plains and west to Pacific.

O. nigricornis argentinus Saussure

DDDD. Body entirely pale. Abdominal venter lightly infuscated in some atypical specimens. Proximal antennal segments ornamented as in classes 1 to 5 (rarely as in 1 and 2). On small weeds 1 to 2 feet high. Typical: Me., southern Ont., Mich., Minn. to Fla., Miss. Atypical: B. C., Man., to Ariz., Tex.

O. nigricornis quadripunctatus Beutenmuller

SUMMARY

Three tree crickets of the genus *Oecanthus*, namely *nigricornis, quadripunctatus* and *argentinus*, differ from each other mainly in color characters and have been separated by the nature of the black markings on the two proximal antennal segments. There has been some dispute among taxonomists as to whether they represent distinct species.

In order to classify the material from various localities on the basis of the antennal pattern, twelve approximately equal, arbitrary classes were originated. The classes with light pattern (*quadripunctatus*) run in a straight line series up to a middle point and from there diverge in two directions, toward the extreme types of *nigricornis* and *argentinus*.

In the eastern portion of the U. S. corresponding roughly to the country originally largely covered with forest, *nigricornis* and *quadripunctatus* are present and distinct in color characters, ecological distribution and habits, as well as having distinct types of eggs. They could be considered separate species if they did not extend beyond this region.

In the great plains region, *nigricornis, quadripunctatus* and *argentinus* are found, with many intermediate forms. The three are often associated in the same field on the same kinds of plants. The characteristics which typify *nigricornis* gradually disappear from the population toward the west, while the reverse is true of *argentinus* characters, which come no farther east than the true prairie regions.

Only *argentinus* and *quadripunctatus* are found in the Rocky Mountain region and are not clearly separated. The former only has been found in the Pacific Coast region.

Quadripunctatus has the same distinct type of egg in N. Y., Ohio, Fla. and Iowa. In the western region the eggs of individuals falling in the *quadripunctatus* classes of antennal pattern are of a different type and resemble those of typical *argentinus*.

Until better characters are discovered for separating the three tree crickets of this group, it seems advisable to consider them as subspecies.

A revised key to the *Oecanthinae* of North America is appended, based on this and other recent work.

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