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The Sibling Species of the Alutacea Group of the Bird-Locust Genus *Schistocerca*

(Orthoptera, Acrididae, Cyrtacanthacridinae)

BY
THEODORE H. HUBBELL

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
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(Continued on back cover)

HUBBELL - SCHISTOCERCA Errata

p. 5, line 4 - "Schistocera" should be "Schistocerca".
p. 23, line 6 - "This" should be "The";
line 23 - "disal" should be "distal".
p. 28, line 3 - "(VI, c, d)" should be "(XI, a-e)",
line 4 - "narrower" should be "longer".
p. 70, line 6 from bottom - "T. B. Smith" should be "J. B. Smith".
p. 77, line 25 - "Cimmaron" should be "Cimarron".
Plate X. Figures "b" and "c" apply to the entire range of the three species, but figure "a" only to New England-New Jersey; the means in the columns for length of hind femur and for breadth of head, therefore, should be, respectively, for alutacea, 17.82, 4.51; for lineata, 17.54, 4.83; for rubiginosa, 15.60, 4.56.
Plate XVI, explanation of plate, lines 2 and 4, delete "left".

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THE SIBLING SPECIES OF THE ALUTACEA GROUP OF THE BIRD-LOCUST GENUS *SCHISTOCERCA* (ORTHOPTERA, ACRIDIDAE, CYRTACANTHACRIDINAE)

THE numerous species of the genus *Schistocera* Stål, a member of the Group Cyrtacanthacres, constitute a characteristic and conspicuous element in the New World acridid fauna. Only the generotype, *Schistocerca gregaria* Forskål, occurs in the Old World; it is the desert locust or biblical locust of North Africa and the Near East. Excluding that species, the range of the genus extends from southern Canada to Chile and Argentina, with the largest number of species occurring in the tropics. From México southward the most important plague locusts are members of this genus. They undergo cycles of population increase, at the peaks of which their swarms may devastate crops and other vegetation over large areas. Much attention has been devoted to the life history, ecology, and behavior of the relatively few plague species, but the biology of most of the others is little known.

Being for the most part large and conspicuous insects, these locusts have long attracted the attention of collectors and of entomologists, with the result that more than 120 species and subspecies have been named, many of them based on single specimens or small series. Most of these names are currently in synonymy, but the exact status of many of them is uncertain, and the present assignments of some are certainly erroneous. A revision based on the study of large series from many localities would do much to clarify the systematics of the genus and resolve many of the nomenclatural problems. More than this will be needed, however, for the true relationships of many of the forms can be worked out only through planned field observation and experiment. Some of the species are known to be strongly polymorphic, and others may prove to be so. Within what appear to be single species, differentiated local populations exist, sometimes in close proximity but in different environments. What have been taken to be highly variable species may in reality be complexes of morphologically similar but distinct species, as is here demonstrated in the Alutacea Group. Many of the problems of specific identity and intraspecific variation in this difficult genus will require for their solution studies of ecology, life history, physiologic response to environmental factors, behavior, or cytogenetics, to mention only some of the possible lines of attack. Examples of such unsolved problems in the Alutacea Group will be pointed out. Furthermore, in answering some of the questions posed by morphotaxonomy, field observation and laboratory experiment are certain to reveal previously unsuspected com-

plexities that call for further analysis, and thus lead step by step into fundamental considerations of population dynamics and evolutionary mechanisms. Fortunately, much that has been learned about the few species of great economic importance can be used in interpreting situations encountered in the others.

SPECIES GROUPS OCCURRING NORTH OF MÉXICO

Ten species of *Schistocerca* are currently recognized in North America north of México. They appear to fall naturally into seven groups, of which only three have more than a single species in the area specified. This paper deals critically with the members of one of these, the Alutacea Group, but to place this group in proper setting the other groups are here briefly reviewed. The first stands well apart from the others, and perhaps ought to be given at least subgeneric status, but this would not be justified except after revision of the entire assemblage. It includes the small, slender, big-eyed *Schistocerca ceratiola* Hub. and Walk., distinctive in many morphological features, endemic to north-central Florida, and so far as known unique in its nocturnal habits and restriction to a single food-plant. If it has any close allies they are probably to be sought among the West Indian species. Also standing apart, but somewhat less deviant, is *Schistocerca damnifica* (Sauss.), a compact species with strongly tectate pronotum that ranges from southeastern Iowa and eastern Texas to New Jersey and Florida, its southeastern Coastal Plain populations being distinguished as the subspecies *damnifica calidior* R. and H.

The other North American species are all more similar to the generotype than those just mentioned. Two of them, *Schistocerca americana* (Drury) and *S. vaga* (Sc.), are long-winged, strong-flying insects only distantly allied to the species with which we are concerned. Although each is the only representative of its group in our territory, they show certain resemblances. Both are brownish in general coloration, with maculate tegmina, a light middorsal stripe on head and pronotum that continues more or less distinctly on the upper margins of the closed tegmina, and a dark blotch bordered above and below by lighter bands on the prozonal section of the pronotal lobes. They also agree in having short antennae, a supra-anal plate (tergiproct) with median sulcus not abruptly terminated by a transverse carina and without distinct admesal prominences, and a V-notched male subgenital plate; they differ in form of pronotum, male subgenital plate, coloration, and other features. *Schistocerca americana,* the well-known American locust, is reddish or yellowish brown with large, conspicuous dark blotches and a pale precostal basal streak on the tegmina; the dark

marking on the lateral pronotal lobes is divided by a pale horizontal line to give three light bands. This species is common in the southern half of the United States and extends at least to southern México; in the West Indies it appears to have developed insular subspecies. *Schistocerca vaga* (Sc.) of the southwest is darker and usually grayer in coloration, the dark tegminal markings being much smaller, more numerous, less regular, and less contrasted, and a precostal light line being absent; the dark blotch on the pronotal lobes is undivided, and the light bar along the lower margin is broader. This species occurs from Texas and California south to Nicaragua, and Rehn has described a short-winged subspecies, *vaga brevis*, from Clarion Island, México.

The members of the Alutacea, Shoshone, and Obscura groups share certain characteristics which distinguish them from other groups and indicate their common ancestry. In comparison with *americana* and *vaga* the form of the body averages more robust and the size of the tegmina and wings smaller for a given body size, especially in the female. The antennae tend to be unusually long for the genus, especially in the male. The most evident resemblances are those of coloration; in spite of a great amount of inter- and intraspecific variation, the general pattern, including the nature of the polymorphism itself, is common to all three groups. In all but one of the species at least some individuals are greenish or show a green tinge in the yellowish parts of the pattern, something that is never seen in *americana* or *vaga*. In all species some or all of the individuals have a yellow middorsal stripe extending from the vertex to the tip of the closed tegmina, or at least to the end of the pronotum. Except for this stripe (when present), and the proximal infuscations which often border it, the tegmina are either unicolorous (in various shades from dark brown to light green) or, if maculate, are neither contrastingly so nor furnished with whitish streaks in the precostal or radial areas.

The Obscura Group includes three nominal species occurring in the United States—*Schistocerca obscura* (Fabr.), *S. albolineata* (Thos.), and *S. chinatiensis* Tinkham—and a fourth, *S. insignis* Hebard, described from México. The group may be characterized as follows: male subgenital plate deeply fissate (depth of cleft 0.31–0.44 times length of dorsal margin), the apical lobes large, thin, in normal position outwardly flared, strongly convex on outer margins with narrowly rounded apices adjacent to straight inner margins; supra-anal plate (tergiproct, Pl. V, c) with medio-proximal sulcus narrowing to point of closure (by contact of bordering ridges or very short apical connecting ridge), without or with mere traces of admesal elevated points on surface on either side of point of closure; prosternal spine relatively short, slender, straight, tapering to a point; median carina of prono-

tum low but distinct and percurrent except where cut by sulci; antennae very long, especially those of male; thoracic surface more hirsute than in related groups. The basic coloration is the same in all the species, though strikingly modified in some: head and pronotum dark reddish or purplish brown varying (in *insignis*) to olivaceous, facial region concolorous and generally darker than in members of Alutacea and Shoshone groups; tegmina immaculate, dark reddish or blackish brown ("liver-colored"); at least the following strikingly contrasted yellow or greenish yellow markings present; a middorsal stripe from vertex to tip of closed tegmina (rarely faint or absent), a vertical line below front part of eye, a spot on caudal genicular lobe of hind femur or entire lobe, and (nearly always) a mesepimeral blotch or bar; caudal femur with external pagina yellowish, whitish, or greenish, with or without dark markings, dorsal surface with two preapical dark cross-bars, usually distinct but sometimes faint. In addition to the above, *S. albolineata* and *S. chinatiensis* have the following yellow markings: a vertical line behind and below the eye, a conspicuous horizontal band on the lateral lobe of the pronotum between the first and the principal sulcus, and a metepimeral blotch smaller than that on the mesepimeron; the dorsal bars and also the genicular region of the caudal femur are very dark or black, and the bars are confluent with a longitudinal dark streak on the upper part of the external pagina. In *obscura* and *chinatiensis* the caudal tibiae are dark brown to purplish black, or black on the extensor and partly or entirely greenish, yellowish, or brown on the flexor surface; in *albolineata* they are red.

Schistocerca obscura occupies the southeastern United States and extends west to the edge of the Great Plains in Kansas and to the Edwards Plateau in Texas; southward it follows the coastal plain as far as Veracruz in México. *S. albolineata* occurs from the Big Bend region of Texas and southern Arizona to Sonora and Sinaloa in México, the latter being the type locality of *S. mexicana* Sc., synonymized by Hebard (1932:281). *Schistocerca chinatiensis* was described from the Chinati Mountains in trans-Pecos Texas, and specimens are in the UMMZ collection from Carlsbad, New Mexico, and Sierra de Mapimi in Durango, México. *Schistocerca insignis*, recorded only from Guadalajara in Jalisco, México, is very similar to *chinatiensis* except for its larger size, olivaceous black dorsum of head and pronotum, and weaker dark markings on the caudal femur, which is greenish above and yellowish on the outer face. The relationships of the species of this group are evidently very close; it seems probable that *chinatiensis* is at most a subspecies of *insignis*, and not impossible that *albolineata* is also a part of the same polytypic species.

The Shoshone Group includes *Schistocerca shoshone* (Thos.) (= *obli-*

guata Sc.) of the western and southwestern states and northwestern México, and a still undeciphered and nameless complex of related populations inhabiting the forested mountain slopes in western Colorado, Utah, Nevada, and Arizona. Hebard (1929:369; 1935:299) has briefly discussed the mountain populations and pointed out that they have been incorrectly referred by various authors to *venusta* Sc. and *lineata* Sc.; *venusta* he has placed (1935:299) as a synonym of *shoshone* based on the striped color phase, and *lineata* is a member of the related Alutacea Group. Among the distinguishing features of the Shoshone Group are the following: general coloration yellowish or olive green, with or without a paler mediodorsal stripe; all dark markings except genicular arcs of caudal femora greatly reduced or absent, including the dots on sides of abdominal tergites normally present in members of this genus; tegmina unmarked except for a faint to distinct pale humeral dot and the dorsal pale stripe when the latter is present; caudal tibiae pinkish or red; pronotal carina percurrent except for interruptions by sulci, distinct or faintly cristate; thoracic surface less hirsute than in Alutacea Group and distinctly less than in Obscura Group; prosternal spine much as in Alutacea Group, thicker and apically blunter than in Obscura Group; male subgenital plate less deep at base than in Alutacea Group, its apex somewhat more deeply notched (depth of notch 0.26–0.33 of length of dorsal margin), apical lobes in most populations like those in Alutacea Group, in some approaching the condition characteristic of the Obscura Group.

The relationships of the Shoshone and Alutacea groups are evidently very close. In both the median sulcus of the supra-anal plate (tergiproct) is relatively short and wide, with sides subparallel or little convergent distad, and is partly or completely interrupted at the level of the proximal ends of the distomarginal carinae by a divided or complete transverse carina of which the ends form nodular prominences. In both groups the fore and often the middle femora of males tend to be more or less swollen, which is not true in the Obscura Group. Furthermore, in the western populations of *S. lineata* (a member of the Alutacea Group), one of the less common color phases is immaculate and yellowish green, with red caudal tibiae, individuals of this coloration being almost indistinguishable in appearance from *shoshone*, from which, however, they are separable by the black dots on the abdominal tergites and differences in the concealed male genitalia. Although characteristic distinctions between the two groups as such have not been found in the genital structures, the species all show phallic differences, and these are maximal between members of the Shoshone Group and of the western populations of *lineata* (Alutacea Group), the only ones with adjoining distributions.

The Alutacea Group

Although the systematics of the Alutacea Group are the subject of this paper, a satisfactory definition of the assemblage is hard to make because of the great individual and regional variation that exists in one of its species. The unity of the group is evidenced as much by the continuity of variation, parallel polymorphism, and geographic distribution of its members as by a distinctive combination of morphological characteristics. This becomes evident when we try to list those features which are not shared with the Obscura and Shoshone groups or with the latter alone, as discussed above. Excluding those, the Alutacea Group may be characterized as follows: dorsum of pronotum weakly tectate to transversely convex on prozona, usually a little tumid on anterior part of metazona and subplanate toward caudal margin; median pronotal carina either weak but percurrent (except where cut by sulci), or (in many of the individuals with mediodorsal stripe) subobsolete, the entire breadth of stripe in such individuals often slightly tumid and elevated ("callose"); tergiproct as described for Shoshone Group, but transverse carina more often complete than interrupted mesad; male subgenital plate in side view deeper at base and appearing less elongate than in the other groups, its apex with an open U- or V-shaped notch smaller than in other groups (depth 0.18–0.27 times length of dorsal margin), apical lobes relatively small, sub-triangular, or convex on outer margins, usually about as heavily sclerotized as remainder of plate, rarely (in large Texas *lineata*) showing slight approach to Obscura type; prosternal spine straight or slightly retrorse distad, subcylindrical to weakly conical, moderately slender to stout, sometimes slightly bulbous toward tip, apex rounded or bluntly pointed; thoracic surface less pilose than in Obscura Group, more so than in Shoshone Group. Coloration moderately to extremely variable, as later described, differing from that of other groups as follows: (contrasted with Obscura Group)—dark individuals with facial region usually paler than dorsal parts of head and pronotum (except in *alutacea*); lateral lobes of pronotum either concolorous with dorsum, or, when pale, uniformly so below shoulders or with broken dark areas and spots more or less concentrated along sulci, lacking a contrasted yellow bar between first and principal sulci; mesepimeron without a yellow blotch or bar except in some individuals of *lineata*, the proportion of individuals with such a marking increasing toward the western and southern edges of the range of that species; metepimeral yellow markings almost never indicated; (contrasted with Shoshone Group)—coloration not uniform yellowish green or olivaceous green except in rare western individuals of *lineata*; sides of abdominal tergites almost always marked with black dots which are usually distinct and in material of

lineata from central and coastal Texas are often amplified into slanting linear markings; caudal tibiae normally yellowish, brownish, or blackish, only in certain western populations of *lineata* red in a small or large percentage of individuals.

For many years the Alutacea Group has been considered to comprise two entities: *Schistocerca alutacea* (Harris), thought to be a highly plastic and variable species occupying much of the eastern United States east of the Prairie Region, and the even more variable *S. lineata* Scudder, with a range bordering that of *alutacea* in the Prairie Region and occupying the whole breadth of the Great Plains from southern Alberta to Texas. In recent literature the question as to whether they may be intergrading subspecies of a single species has been discussed.

The situation revealed by the present study is quite different, and will be briefly summarized here to facilitate presentation of the material which follows. Three very similar (sibling) species are involved instead of two: *S. alutacea* (Harris), *S. rubiginosa* (Harris), and *S. lineata* Scudder. They are distinguishable by genitalic characters of the male and by associated features; two of them are polymorphic and show parallel variations in coloration and structure; and none of the three is distributed as either of the currently recognized species was supposed to be.

Schistocerca alutacea inhabits the Atlantic and Gulf Coastal Plains, from Massachusetts to eastern Texas, and the southern Great Lakes Region, and has outlying colonies in Tennessee, northern Alabama, and Arkansas. It is a characteristic inhabitant of relatively moist situations such as marshes, open brushy swamps, and weed and shrub thickets on seepage slopes and damp ground. *Schistocerca rubiginosa* occupies the Atlantic and Gulf Costal Plains from New Jersey to eastern Texas, and is characteristic of drier habitats, including open grassy pine and oak forests and xeric ruderal situations. *Schistocerca lineata* has by far the most extensive range; it occurs in the Great Plains and Prairie Region from southern Alberta and Manitoba to eastern New Mexico and southern Texas, and extends eastward to the Atlantic Coast in a broad belt that includes southern Michigan and northern Kentucky. Along the east coast it occurs in the Coastal Plain and margins of the Piedmont from southern New Hampshire and Massachusetts to Virginia and northernmost North Carolina. In the prairie and plains regions it is present on various types of soils and in situations ranging from dry grassland and open xeric forest to weed thickets and tall grass prairie; eastward it seems to be increasingly restricted to xeric environments on sandy soils, such as grassy oak dune forests and beaches, open pine barrens, and such xeric ruderal situations as brushy pastures and old fields.

Since most of the taxonomic confusion in this group has resulted from

misinterpretation of differences in coloration, a brief discussion of the most striking of these differences, the presence or absence of a middorsal yellow stripe, is needed at this point. In the Alutacea Group (as in several others) "striped" and "unstriped" individuals may occur in the same species. The extreme of the striped color phase has a contrastingly pale yellowish stripe extending from the vertex of the head to the tips of the closed tegmina; the unstriped phase has no trace of such a marking.

All individuals of *alutacea* are striped. In the other two species both striped and unstriped phases occur, as well as intermediate conditions, although most individuals can be classed as striped or unstriped. In *rubiginosa* the great majority are unstriped, but narrowly striped individuals are numerous in some populations, especially northward. Nearly all western specimens of *lineata* have a much broader and more conspicuous stripe than is ever seen in the other two species, although some unstriped ones occur; eastward, however, the proportion of weakly striped or unstriped individuals increases, until in the populations along the Atlantic Coast the unstriped phase strongly predominates. Presence or absence of the stripe is by no means the only variation in coloration, which is moderate in *alutacea,* considerable in *rubiginosa,* and very great in *lineata,* but it is the only aspect of such variation which needs mention at this point. Its significance in relation to the historic development of species concepts in this group will become evident in the following survey.

In summary, we here recognize three species in the Alutacea Group. All three are present in the Atlantic Coastal Plain from New Jersey to northernmost North Carolina; in New England and the southern Great Lakes Region two occur, *alutacea* and *lineata;* two also occur in the Atlantic and Gulf Coastal Plain from North Carolina to Texas, *alutacea* and *rubiginosa;* and only one, *lineata,* is present in the Prairie Region and Great Plains.

HISTORICAL REVIEW

Although the first species of the Alutacea Group was described more than a century ago, and the literature dealing with its members now comprises more than two hundred titles, it is only now that the systematics of the group are becoming understood. The reasons for this slow progress are to be found partly in the actual situation and partly in the method of approach. A review of the more important contributions to the subject will not only illustrate the transition from the typological to the biological species concept, but also that part which accident and authoritative opinion may have in the formulation and maintenance of an erroneous hypothesis.

In 1841 Harris described *Acrydium alutaceum,* based on a striped female

specimen from Martha's Vineyard, off the coast of Massachusetts. Although the type has been destroyed, the application of this name is not in doubt for reasons given elsewhere. Harris also possessed an unstriped female specimen from South Carolina which he named and described in manuscript; in 1862, Scudder, quoting verbatim from that manuscript, published Harris' second species as *Acridium rubiginosum*, and associated with Harris' type other specimens from Massachusetts, Connecticut, Alabama, and "Southern States." In this instance, also, the identity of the species is not in question even though the type has not been found, for among the species which might fit the description only *rubiginosa* and *alutacea* occur in South Carolina, and the latter is always striped.

The genus *Schistocerca* was distinguished (as a subgenus of *Acridium*) by Stål in 1873, and to it both of Harris' species were assigned by later American authors. In 1899 Scudder published a comprehensive revision, "The Orthopteran genus *Schistocerca*," in which he recognized 42 species, of which 23 were described as new. Among these was the third species of the Alutacea Group, *S. lineata* Scudder, described from Kansas, Texas, and Coahuila, México. Although this study suffers from the same defects as his earlier work on the North American Ceuthophili, and has caused much subsequent confusion, we need consider here only his treatment of the species with which we are concerned. He placed all the species now assigned to the Obscura, Shoshone, and Alutacea groups in the first section of his key, distinguished by long antennae; they also all fall in the subsection characterized by having the pronotum rounded obtuseangulate behind. Aside from this they are grouped or separated in a manner unrelated to their affinities as now understood; *alutacea* stands next to *obscura* in a section of the key other than that containing *rubiginosa*; *lineata* and *albolineata* are associated, and *shoshone* and its synonym *venusta* are respectively Nos. 34 and 31 in his sequence. Because some of the characters he used are of real significance Scudder's classification is not wholly arbitrary; its artificiality is the result of his dependence on a few "key characters" and the fact that some of them, in particular the presence or absence of a middorsal light stripe, are subject to variation within species. For the same reason some of his "species" were actually composites. As his records and collection show, he included under *rubiginosa* unstriped material of *lineata*, under *alutacea* striped material of *lineata* and of members of the Shoshone Group, and under *albolineata* material of *lineata*. Like that of other workers of his time, his species concept was typological, and most other students, before and after the appearance of this revision, made similar mistakes in identification.

Morse (1898) distinguished two species in New England on the basis

of differences in morphology, coloration, and habitat. One, which he correctly identified as *alutacea,* was said to have the head and pronotum narrower, the vertex and facial costa narrower and more prominent, both fore and hind femora more slender, and the general coloration varying from olive green through yellowish to deep reddish brown in life, with a bright yellow middorsal stripe. This species he found most at home in the long sedge and coarse weeds of moist meadows and bushy swamps, but flying freely and often alighting on bushes and trees. The other, which Morse, following Scudder, identified as *rubiginosa* (actually *lineata*) was said to differ in form from *alutacea* as indicated above, and to be much more uniform in coloration, never showing any olivaceous tinge, though males taken late in the season have much of the rusty color replaced by gray; the tegmina are often almost immaculate, and the dorsal stripe, when rarely present, is not of the bright yellow characteristic of *alutacea.* This species he found to be more widely distributed, in New England, than *alutacea,* and to prefer drier situations, occurring most frequently in bushy pastures and wild land on sandy soil and along railroad embankments. Morse was an acute observer, and examination of his collections shows that he had correctly identified all but a very few of his New England specimens, aside from the misapplication of the name *rubiginosa.*

In 1901 Rehn announced that he had taken *rubiginosa* and *alutacea* in coitus, and the following year he published two short notes which are here quoted because of the enduring influence they have exerted on subsequent taxonomic thinking about the species of the Alutacea Group. The first (1902) is as follows: "On September 2, 1901, while collecting between Atsion and Quaker Bridge, Burlington County, New Jersey, the writer secured specimens of *Schistocerca alutacea* and *rubiginosa.* The most interesting thing in connection with the captures was the finding of one sex of one form paired with the opposite sex of the other form. This evidence, together with the close relationship of the forms, leads one to question the absolute distinctness of the two. Specimens in the collection of the Academy of Natural Sciences of Philadelphia, taken on the above-mentioned date, are perfectly typical of the two forms, and the two would be flushed from the same bush, but others are an apparently intermediate phase, in which the dorsal stripe does not extend beyond the tip of the pronotum to any marked degree. The last-mentioned specimens would possibly be considered representative of the brown phase of *S. alutacea,* but the whole matter seems deserving of more attention, as apparently too much stress has been laid on variable or uncertain color characters." In the second note (1902*a*) Rehn synonymized *rubiginosa* under *alutacea,* with the following comments: "The above synonymy is established after an examination of the sixty-seven

available local specimens. The striped phase (*alutacea* s. st.) and the reddish form with the mottled tegmina (*rubiginosum* Scudder [sic!]) are connected by a series of seventeen specimens, which show indisputable evidence of intergradation. In many reddish specimens the dorsal line is well marked, on others present on the pronotum alone, and in some green specimens the tegmina are distinctly mottled. The structural differences ascribed to the two forms are not of any value, specimens typical of either one of the forms, according to these slight structural discrepancies, being the reverse when coloration is considered."

Both Morse and Rehn were beginning to apply observations on behavior and ecology to the interpretation of a systematic problem, and were taking variation into account—in other words, were thinking of species as populations, not as specimens. The differences in their conclusions were determined in part by circumstance. In New England Morse was dealing with only two species; in New Jersey three are now known to occur, and their habitats are often in close proximity. All of them fly freely when disturbed, so that it would not be remarkable if two species were taken together in a limited area. Furthermore, and perhaps coincidentally, about one half of the individuals of *rubiginosa* in New Jersey have a more or less conspicuous middorsal light stripe, which may extend from the head only to the rear edge of the pronotum or to the tip of the closed tegmina. Examination of part of Rehn's material explains his observations; at Atsion-Quaker Bridge he was dealing in part with striped *alutacea* and in part with striped, half-striped, and unstriped *rubiginosa,* and the intermediates he lists in his second note are in part referable to *rubiginosa,* in part to *lineata.* Collections that I have examined from a number of localities in New Jersey show a mixture of species: *alutacea* and *rubiginosa,* often taken on the same day by the same collector, from Atsion, Whitings, Stafford's Forge, Lakehurst, and Manahawkin; *alutacea* and *lineata* from Cape May, Sea Island Junction, and East Plains. Individuals with tegmina immaculate or maculate to varying degrees are to be found in all three species, and this character varies semi-independently of the presence or absence of a stripe. It is no wonder that Rehn, unaware of the diagnostic phallic characters, concluded that he was dealing with a single highly variable species.

In his "Researches" (1904) and "Further Researches" (1907) Morse recorded his observations on *alutacea* and *"rubiginosa"* in the southeastern Coastal Plain. In the first paper he wrote that "typically these two species differ in color, structure, and haunts," but with greater field experience and more material he found the same difficulty in separating them as had Rehn. In his 1907 paper he qualified his original opinion as follows: "It is very probable that some so-called species are but forms of one which

varies greatly in color and structure. In New England the two forms known as *alutacea* and *rubiginosa* seem to be constantly different structurally, though *rubiginosa* has a color variety resembling *alutacea*. Southward and westward the structural gap between the two seems to be bridged, and both vary much in size, color, form, and proportions of parts."

Henry Fox, an observant field naturalist, came slightly closer to solving the riddle. In his valuable papers on the Orthoptera of eastern Pennsylvania and New Jersey (1914) and of Virginia (1917), he distinguished, besides *alutacea* and *"rubiginosa,"* a third unnamed form which he found on the beaches and dunes in both states and described as being larger and more uniformly colored than the others. This form, which he recorded from New Jersey as "species cf. *obscura*" and from Virginia as *"alutacea* maritime race (*rubiginosa*?)," actually represents *lineata* in an optimum condition. Fox was, however, as confused as others by the striped and unstriped, maculate and immaculate color phases, and commented that "intermediates between *alutacea* and *rubiginosa* are common and hard to ascribe to either race." Inspection of his New Jersey series of *alutacea* shows that they include striped specimens of *rubiginosa* and at least one specimen of *lineata*; his New Jersey *"rubiginosa"* include a few unicolorous specimens of *lineata*; and at least two (Tappahanock and Charlottesville) and perhaps all of his Virginia records of *"alutacea* phase *rubiginosa"* were based on specimens of *lineata*.

In their comprehensive, detailed, and generally excellent report on the Orthoptera of the Coastal Plain and Piedmont regions of the southeastern United States, Rehn and Hebard (1916:196–201) published a seemingly conclusive analysis of the *alutacea-rubiginosa* problem, and summarized their findings in a section entitled "Individual variability and dimorphism in *Schistocerca alutacea* and *obscura*." They based their study on 261 specimens from twenty-four localities in North and South Carolina, Georgia, and Florida, mostly collected by themselves and accompanied by habitat notes, and also referred to the evidence also furnished by some 180 specimens from New Jersey, collected by Rehn, Fox, and others, on many of which field data were also available. In addition to the degree of development of the middorsal pale stripe, they considered variation in width of fastigium and frontal costa, breadth of head and pronotum, depth in relation to length of caudal femur, length and maculation of tegmina, and body size. For each of the localities in the southeastern Coastal Plain they gave the number of specimens classed as *alutacea* (total 83), as intermediate (total 12), and as *rubiginosa* (total 166), with added notes on the variation observed in the eleven larger series. No comparable breakdown was given of the New Jersey material, but a series of twelve specimens from Taunton

was said to furnish a particularly interesting illustration of intergradation. The habitat from which some of the collections were made was also concisely indicated, as "pine woods," "high bushes and 'bracken' along edge of swamp," etc.

The results of this study confirmed the previously expressed opinions of the authors that *alutacea* and *rubiginosa* clearly represent two color phases of a single species, striped and unstriped, with which conditions certain structural differences are usually but not invariably correlated. "If we were called upon to deal only with typical material, it would be an extremely simple matter to consider the two phases as species, but unfortunately a very considerable portion [4.6% of the 261 southeastern Coastal Plain specimens] of our series is not typical, but apparently, and when carefully studied actually, intermediate not only in color but so, more rarely, however, in structure and proportions. The yellow line narrows and finally dies out, the fastigium broadens out and the pronotum and head become more robust toward the '*rubiginosa*' type in the intermediates in certain extensive series [from New Jersey, South Carolina and Georgia]. The proportionate depth of the caudal femora in general is greater in the *rubiginosa* type, but this is by no means an absolute rule, as some series of that phase show all sorts of variation in this respect. The '*alutacea*' phase, however, is more uniform in having the femora more slender. The number of scutes in the paginal pattern on the caudal femora also varies greatly and without phase correlation. . . . It is true that the striped types prefer moist areas with bracken, etc., while the brown forms are more at home in dry woods and brush, old fields and among dune thickets, although numerous specimens of each phase have been taken in the habitat preferred by the other. . . . The principle of dimorphism, which plays such an important role in the Orthoptera, satisfactorily explains to us the problem here considered. In the present case the color differences are quite decided, with a fair number of non-typical specimens nearer one type than the other and a relatively smaller number really intermediate. The structural differences generally correlated with the color differences, are typically quite appreciable, but their constancy fluctuates in different localities. . . . The final word on this very perplexing question can be said only after careful breeding experiments have been made. As far as the examination of dry material and field observations are concerned, we feel that little additional information, except purely statistical data, can be secured. We have had this problem in mind for over ten years, and have utilized every opportunity to secure data bearing upon it, with the results here summarized."

Nothing in this far from rigorous analysis precludes the possibility that the samples studied were mixtures of two or more species with overlapping

variation in coloration and structure. That this was in fact the case is shown by examination of some or all the specimens from sixteen of Rehn and Hebard's twenty-four southeastern Coastal Plain localities. Eight of these series proved to contain both *alutacea* and *rubiginosa* as determined by the phallic and other criteria used in the present study; the others consisted entirely of one or the other species. No evidence of intergradation was found; all the specimens cited as intergrades by Rehn and Hebard, though not identified as such in the collections, were evidently either individuals of *rubiginosa* with more or less well-developed dorsal stripe, or of *alutacea* with more or less distinctly maculate tegmina. The single specimen from Weldon, N. C., which I have not seen, may represent either *lineata* or *rubiginosa,* since both species are known from adjoining counties.

The weight of this authoritative pronouncement by the two leading students of North America Orthoptera was such that few doubts of its correctness have been expressed in the succeeding forty-four years. In his classic "Orthoptera of New England" Morse (1920:429) treated "typical" *alutacea* and *"rubiginosa"* [*lineata*] as color phases of a single species, but evidently with lingering reservations, for he wrote: "The two forms—which may be distinguished as the striped and the unstriped—of this species as found in New England, usually present certain differences in structure, color, and habitat that lead some entomologists to regard them as specifically distinct, but the consensus of opinion at the present time is that they should not be so regarded. . . . What the relation is between the two forms and their different environments has yet to be determined." Another who was not wholly convinced that *alutacea* and *rubiginosa* were "mere" color phases was Blatchley. In his widely used manual on the "Orthoptera of Northeastern America" (1920:314–17) he used for the latter the trinomial *S. alutacea rubiginosa,* although not in the accepted sense of a subspecies; he said of it: "I prefer to retain *rubiginosa* as a variety, since it can be readily separated by the characters given in the key and habitually occurs in drier situations than does typical *alutacea.*" Nevertheless he was no more successful than others in distinguishing the two; his *"alutacea"* included striped Indiana specimens of *lineata,* and his *"alutacea rubiginosa"* was a composite of unstriped *lineata* and true *rubiginosa.*

Acceptance of the hypothesis that *alutacea* and *rubiginosa* are color forms of a single species was made easier by the demonstration of the existence of "phase transformation" in various species of plague locusts. Uvarov propounded the phase theory in 1921, and experimental evidence soon verified the fact that marked changes in structure, coloration, and behavior occur in the progeny of normal "solitary" locusts reared under crowded conditions. Although this did not really bear on the *alutacea-rubiginosa*

problem, it lent support to the idea that the supposed "phases" of "*alutacea*" were somehow causally related to their occurrence in wetter or drier habitats, by showing that individual development may be strongly affected by differences in environmental factors.

Thus, it came about that for more than half a century following Rehn's placement of *rubiginosa* as a synonym of *alutacea* in 1902, an erroneous hypothesis concerning their relationship was accepted as demonstrated fact. In more recent years attention has been devoted principally to trying to discover the relation between *lineata* and the supposedly highly variable eastern *alutacea*. Between 1925 and 1938, Hebard published a series of valuable papers treating the Orthoptera of various mid-western and western states, in which he recorded data on the distribution and variation of *lineata*, distinguished it from *albolineata* and the red-legged montane populations of the Shoshone Group, corrected earlier misidentifications, and discussed its relationship to *alutacea*. In his Montana paper (1928) he suggested that the eastern limits of *lineata* might run through Minnesota, Iowa, Missouri, Arkansas, and eastern Texas; in his first Kansas paper (1931*a*) he referred all materials from that state to *lineata*, which he considered allied to but probably distinct from *alutacea*; in his Minnesota paper (1932*b*) *alutacea* was said to be confined in that state to the southeastern corner; and in his last paper of the state series, on Oklahoma (1938), he assigned all material from that state to *lineata*, the proper status of which, he wrote, was still undecided.

Froeschner is the latest author to discuss the *lineata-alutacea* problem. In his "Orthoptera of Iowa" (1954) he treated "*alutacea*" and *lineata* as distinct, but noted that Hebard had identified Iowa specimens in the Iowa State College collection as "*alutacea lineata*" and "*alutacea* × *lineata*," and remarked: "After puzzling over the local series of these two species one wonders if his [Hebard's] 1937 labelling was not correct after all." Froeschner was able to separate "*alutacea*" and *lineata* only by preponderance of several characters, those which he thought most reliable for recognition of *lineata* being as follows: (1) light brown ground color, usually deepened along either side of a prominent, pale middorsal stripe; (2) banded hind femora in specimens lacking the middorsal line; (3) numerous calloused yellow spots on dorsum and sides of thorax; and (4) flatter prozona, with lower median carina. Separating his series on these criteria, he stated that in Iowa *lineata* occurs west of a line from the middle of the northern border to the southeastern corner, "*alutacea*" east of a line from the middle of the northern border to the southwestern corner, so that the ranges of the two overlap widely, in a triangular area with apex at the middle of the northern border and base the whole southern border of the state.

In the present investigation large series have been examined from the regions covered by the publications cited immediately above, including all the specimens studied by Froeschner and a part of the material recorded by Hebard. As will be shown below, both of those authors, in the papers mentioned, were dealing with *lineata* only, and were trying to discriminate among the complex and confusing variations exhibited by its populations.

The comedy of errors would be incomplete without its final chapter, the history of the present investigation. Between the years 1923 and 1935, in the course of extensive field work in Florida and other parts of the Coastal Plain, I observed the same habitat preferences of striped and unstriped "*alutacea*" as had been so often reported, and the same intermingling of the two in certain situations. As I came to know the insects better I became aware of slight habitus differences that did not wholly correspond to those in coloration, and began a search for previously unused structural characters that might separate the "phases." Distinctive phallic characters were eventually discovered that not only permitted unerring differentiation of two kinds of males, but also made it certain that they represented two distinct species. By the study of mating pairs and of females found in association with only one kind of males, characteristics were also found by which females could be identified almost as surely as males. One of the species, *alutacea*, was found always to have a dorsal stripe, but either maculate or immaculate tegmina; the other, *rubiginosa*, also had either maculate or immaculate tegmina, but varied from (usually) unstriped to striped through intermediate conditions.

Additional observations, together with analysis of earlier collections and notes, showed that although the two species sometimes occurred together, this was almost always in ecotones, which in the Coastal Plain are numerous and often extensive. Certain types of pine flatwoods, for example, are a patchwork of slightly elevated drier areas and moist depressions; and high pine woods, turkey oak sand hill forest, and sand scrub may grade either abruptly or very gradually into swamp margin thickets, herb and shrub thickets on seepage slopes, or wet black pine shrubby flatwoods, to list only some of the more common transitions. In such ecotones the two species may mingle naturally, and only slight disturbance by the collector is enough to mix them more completely. In general, however, the difference in habitat preference between the two species proved to be much more clear-cut than previous investigators, confused by the variable striping of *rubiginosa*, had been led to believe. This observation has recently been confirmed by Friauf's detailed ecological study of the Orthoptera of an area on the St. John's River in northern Florida (1953).

At the stage in the investigation which I had then reached (1935) I

was as convinced that the *alutacea-rubiginosa* puzzle was solved as Rehn and Hebard had been, but it was fortunate that I did not publish my conclusions at that time. I then believed that only two species were involved: *alutacea* on the Coastal Plain and in the Great Lakes region, and *rubiginosa,* sympatric with *alutacea* over the whole range of the latter, and intergrading westward with its subspecies *lineata.* So plausible a case could have been made for this interpretation that no one might have questioned it for a long time. It was only when I resumed work on the problem after a rather long interval that I discovered the less obvious phallic characters that distinguish *lineata* and *rubiginosa,* and thus learned how much more complex the situation is than I had supposed. Subsequent study of large series from all parts of the range of the Alutacea Group has resulted in the interpretation here given. After the preceding survey it is perhaps needless to emphasize that no matter how well documented these conclusions appear, new evidence may at any time require their reexamination and perhaps their modification.

SOURCES AND AMOUNT OF MATERIAL STUDIED

Of the 2,921 specimens of the Alutacea Group dealt with in this paper, about one half are in the collection of the University of Michigan Museum of Zoology (UMMZ). Although this museum contains some of the material of earlier students of Orthoptera, including some 5000 specimens from the Morse and Scudder collections presented to it in 1929 by the Museum of Comparative Zoology, all but a small part of its large collections in this group have been assembled by the field work of staff members, students, and collaborators. Among those who have made the larger contributions are I. J. Cantrall, T. J. Cohn, J. J. Friauf, F. W. Walker, H. S. Wallace, and myself. Nearly all the specimens thus obtained are accompanied by detailed field notes, of which my own, for example, include 103 field observations on *alutacea,* 182 on *rubiginosa,* and 36 on *lineata.*

For the loan of the remaining material I am indebted to a number of institutions and individuals, listed below with the number of specimens furnished by each. The location of some of the more important series reported on by previous workers is also indicated by the names of those workers in parentheses.

American Museum of Natural History, New York (125) (Beutenmüller, Morse, Fox); Academy of Natural Sciences of Philadelphia (114) (Rehn, Hebard, Bruner, Hancock, Fox); B. B. Fulton, North Carolina State College, Raleigh (28); Canadian National Collection, Ottawa (2); Chicago Natural History Museum (8); University of Colorado, Boulder (14); Uni-

versity of Connecticut, Storrs (25); University of Florida, Gainsville (42); H. F. Strohecker, University of Miami, Florida (23); Iowa State University, Ames (347) (Hebard, Froeschner); Illinois State Natural History Survey, Urbana (95) (McNeill, Hancock, Hart, Hebard); University of Kansas, Lawrence (22) (Hebard); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (90) (Scudder, Morse); University of Missouri, Columbia (14); Michigan State University, East Lansing (86); Oklahoma State University, Stillwater (17); Royal Ontario Museum, Toronto (3); Ohio State Museum, Columbus (110); Purdue University, Lafayette, Indiana (21) (Blatchley); Canada Department of Agriculture Research Laboratory, Saskatoon, Saskatchewan (5); U. S. National Museum, Washington, D. C. (25) (Caudell, Allard); University of Wisconsin Agricultural Experiment Station, Madison (16).

At various times I have also been able to examine additional material of the Alutacea Group in the collections of the Museum of Comparative Zoology, the Academy of Natural Sciences of Philadelphia, the U. S. National Museum, and the University of Kansas.

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The drawings on Plate XVI and the photographs on Plates XVII–XXIII are the work of the Museum of Zoology artist, William L. Brudon, to whom I am also indebted for suggestions and help in the presentation of the other graphic material.

METHODS OF STUDY

In order to use the male genitalic characters and to study their variation, it is necessary to expose or remove the phallus. Some or all of the males of each series were relaxed, and the epiphallus and phallus were extruded by first pulling the margin of the pallium back and then inserting

a small probe or the tips of a fine-pointed pair of forceps under the ventral lobe and lifting and pulling the phallic mass up and back. In properly relaxed specimens no more than this is necessary, but occasionally some membranes and muscles must be cut, or the membranous folds pushed aside from the sharp-pointed tips of the ancorae of the epiphallus to prevent its bridge from breaking. This basal or dorsal fold covering the cingulum and upper margins of the rami must be retracted or pushed forward to expose these structures and the phallotreme, which show the principal taxonomically important specific differences.

In addition to such treatment of most male specimens, the phallic mass was dissected out of several hundred individuals, cleaned of tissue by treatment with a solution of postassium hydroxide or with chloral hydrate-glacial acetic acid corrosive, and preserved in glycerine, either unstained or after staining with acid fuchsin.

All features of structure or coloration used by previous workers were studied, and a search was made for others that might prove of value. In order to analyze the nature and significance of variation in them, and to determine the degree to which such variation was correlated with ecological and geographic factors, objective measurements and estimates based on adequate samples were obviously needed. The following features were selected for measurement: length of body, pronotum, head, antenna, and caudal femur; breadth of head, interocular space, cephalic femur, and caudal femur; for the male cercus, proximal and disal breadth, dorsal and ventral length, and depth of distal emargination. With respect to coloration, the following measurements and estimates were recorded: pronotal stripe absent, indicated by mesal spot, or present, if present, breadth at principal sulcus; coloration of caudal tibiae; (on an arbitrary scale of 1 to 4, matched against standard examples of each step on scale) degree of completeness of dorsal tegminal stripe, intensity of humeral admesal infuscation of tegmina, dark punctation or maculation of head and pronotum, intensity of mottling of tegmina, size and conspicuousness of calloused yellow dots on thorax, size and intensity of black dots on sides of abdominal tergites, intensity of dorsal banding of caudal femur; other noteworthy features. Between eleven and twelve thousand such measurements and estimates were recorded, based on a total sample of 823 specimens from all part of the range of the three species—166 males and 63 females of *alutacea*, 108 males and 46 females of *rubiginosa*, and 291 males and 159 females of *lineata*. Included in these samples were series of up to 25 specimens taken in the same place at the same time, and other specimens selected to include the maximum structural and colorational variation found in various parts of the range of each species. The data thus obtained are summarized in the graphs and tables presented herein.

The data contained in the field notes concerning habitat and occurrence were also tabulated and analyzed in the attempt to discover correlations between environmental conditions and the structural and colorational characteristics of local populations; such conclusions as they suggest are discussed in a subsequent section.

DISCUSSION OF CHARACTERS

The primary morphological basis for separation of *alutacea, lineata,* and *rubiginosa* is found in the concealed male genitalia, discussed below. Once the males have been segregated on this basis, many other points of difference between the species can be demonstrated, which were previously unnoticed or, because of overlapping variation, considered to be weakly defined trends or "phase" differences. With the geographic distribution of the species worked out by means of the males, nearly all females can be identified with considerable certainty by locality, association with males, and the species characteristics common to both sexes.

The detailed analysis here presented was not primarily undertaken as an aid to identification of specimens, but to demonstrate the morphological distinctness of the three species in many characteristics, to determine the nature and amount of the geographic variation that occurs in them, and to permit assessment of the degrees of relationship existing between them.

The morphological comparisons between the three species are contained in this section, and are not repeated in the specific treatments. The data on which they are based are mostly given in the graphs and associated tabulations, reference to which is made by parenthesized plate-figure designations, thus (II, a).

Body Form and Size.—The body is very similar in general form in all three species, although males of *alutacea* average a little more slender and compressed than those of the other two. The females of all the species are much larger and proportionately more robust than the males (V–VIII; XIV, a–p; XVIII–XXIII). Since the extensibility of the abdomen prevents accurate measurement of body length, size is best expressed by the dimensions of selected body parts, of which length and breadth of pronotum are probably the most reliable, although length of hind femur and tegmen and breadth of hind femur and head show much the same trends; all of these measurements show a rather high degree of correlation. As shown in several of the graphs (I–V, XI), *lineata* averages larger than the other two species in all parts of its range, even in the east, where it is smallest and occurs sympatrically with *alutacea* and *rubiginosa*; it attains maximum size and robustness in the southern plains and coastal prairies from Kansas to south-

ern Texas. *Rubiginosa* shows a rapid and rather regular clinal increase in size from New Jersey southward, the largest individuals occurring in peninsular Florida; *alutacea*, in contrast, shows no striking trends in size, and is more constant in most characteristics throughout its range than either of the other two species.

HEAD.—Measured across the eyes, the head averages narrowest in *alutacea*, both in absolute dimensions (♂ I, b) and relative to other parts of the body (♂ ♀ VI, a–d). In this species, the frontal costa in both sexes averages a little narrower than in the others, and as seen from above is slightly but appreciably more protuberant in front of the eyes (XIV, a–o). In both sexes the interocular space is narrowest in *alutacea*, broader in *rubiginosa*, and widest in *lineata* (♂ III, b; ♂ ♀ VIII, a–d). As is usual, the eyes of the males of all three species are proportionately larger and more protuberant than those of the females; in *rubiginosa* the eyes are on the average larger and in dorsal view more strongly convex and protuberant than in the others (XIV, a–o). Antennal length is quite variable in the male, but in this sex averages slightly greater in *alutacea* than in the others, both in absolute dimensions (III, a) and relative to pronotal length (X, c); no significant differences were noted among the females, in which the antennae are much shorter than in the males. The breadth of the first segment is similar in all three species (♂ IV, b) and quite constant in relation to general body size; it is useful as a standard of comparison for other more variable structures of small size, such as the cerci.

PRONOTUM.—As noted above, pronotal length, measured along the middorsal line, is closely correlated with general body size and is perhaps its best single measure. The caudal breadth of the pronotum (measured across the disk of the metazona to the middle of the abrupt curvature that defines the humeral angle) is a function both of general size and of robustness (Tables 1 and 2, not graphed). Pronotal length and breadth are nearly the same in all regions in *alutacea*, whereas in *rubiginosa* and *lineata* they show a clinal increase from north to south, as noted above (♂ I, a). In all three species the prozona in some individuals is moderately tectate, in others almost evenly rounded and sometimes slightly tumid; tectation is somewhat more common and more pronounced in northern than in southern populations. The median carina varies in all three species from low but distinct and percurrent to a condition in which it is indistinguishably merged along most of its length in a medio-longitudinal callous area associated with the presence of a middorsal pale stripe; even then, however, it is almost always visible as a scarcely raised line on the metazona, and may be indicated on one or more of the prozonal lobes. In all three species the disk of the metazona is coarsely punctate. The prozonal dorsum on either

TABLE 1
CAUDAL BREADTH OF PRONOTUM, MALE

Species	No. Spec.	Max.	Min.	St. Dev.	Mean	St. Error Mean
alutacea						
New England	23	4.5	3.6	0.23	4.16	0.047
N. Y., N. J., Del.	20	4.5	3.7	0.22	4.07	0.050
Gr. Lakes reg.	30	4.4	3.5	0.25	4.03	0.045
Md.–S. Car.	30	5.1	3.5	0.49	4.30	0.089
Ga., Fla.–Tex.	55	4.6	3.3	0.26	4.06	0.036
rubiginosa						
New Jersey	31	4.4	3.4	0.28	3.76	0.050
Md.–S. Car.	26	4.7	3.2	0.33	3.98	0.064
Ga. Fla. Ala.	50	5.4	3.6	0.50	4.30	0.071
lineata						
New England	24	4.7	3.9	0.22	4.41	0.045
N. Y., N. J., Del.	23	5.0	3.9	0.31	4.42	0.064
Md.–N. Car.	19	5.0	4.1	0.31	4.55	0.071
Gr. Lakes reg.	58	4.8	3.6	0.26	4.17	0.034
S. Ind., S. Ohio	20	5.0	4.0	0.24	4.45	0.054
Iowa	15	5.2	4.4	0.25	4.80	0.065
Sask.–Neb. Colo.	22	5.4	4.3	0.36	4.71	0.077
Ks. Mo.–c. Tex.	51	5.9	4.4	0.45	5.09	0.062
So. Texas	16	6.6	4.9	0.44	5.70	0.111
N. M., W. Texas	7	5.7	4.5	0.37	5.05	0.195

side of the carina or median calloused area is covered with shallow impressions, large and small, irregular in outline, and separated by low, narrow smooth ridges; these impressions extend to the margins of the median carina in unstriped individuals and in some striped ones, but in other striped individuals are faint or obliterated in the median callous area. No consistent difference between the species has been observed in these features, but in western populations of *lineata* a high proportion of individuals have a broad median callous area on the prozona, correlated with the prevalence of a broad mediodorsal pale stripe. In *rubiginosa* the pronotum, especially in males, often flares a little cephalad to receive the broad head, a condition seldom noticeable in the others.

PROSTERNAL SPINE.—In all three species this varies from narrowly conical or subcylindrical with narrowly rounded tip to a much heavier condition with broadly rounded or even slightly bulbous tip; the shaft may be straight or its distal part bent slightly caudad so that the anterior face of the subconical tip appears obliquely truncate in side view. All these variations are represented in most large series from single localities, regard-

TABLE 2
CAUDAL BREADTH OF PRONOTUM, FEMALE

Species	No. Spec.	Max.	Min.	St. Dev.	Mean	St. Error Mean
alutacea						
New England	29	7.1	5.8	0.28	6.37	0.051
N. Y., N. J., Del.	20	7.0	5.4	0.45	6.17	0.102
Gr. Lakes reg.	19	6.6	5.4	0.33	6.15	0.075
Md.–S. Car.	8	6.9	5.8	0.38	6.26	0.135
Ga., Fla.–Tex.	16	7.6	6.0	0.59	6.37	0.148
rubiginosa						
New Jersey	5	6.1	5.2	0.31	5.60	0.139
Md.–S. Car.	13	6.6	5.2	0.43	5.90	0.117
Ga. Fla. Ala.	24	7.3	5.3	0.55	6.30	0.112
lineata						
New England	9	6.8	5.8	0.32	6.18	0.106
N. Y., N. J., Del.	7	6.7	5.8	0.41	6.30	0.153
Md.–N. Car.	3	6.7	5.9	0.68	6.45	0.390
Gr. Lakes reg.	18	6.8	4.8	0.51	5.70	0.119
S. Ind., S. Ohio	5	7.2	6.3	0.35	6.68	0.154
Iowa	20	7.1	4.7	0.76	6.24	0.170
Sask.–Neb. Colo.	10	7.0	4.3	0.81	5.84	0.256
Ks. Mo.–c. Tex.	69	8.1	5.8	0.56	6.76	0.067
So. Texas	10	8.8	7.3	0.47	8.18	0.148
N. M., W. Texas	6	6.7	5.8	0.46	6.22	0.189

less of species; in such series, however, there is often a preponderance of one or another form which may not be the same in two localities not distant from one another. No regional trends in form of the prosternal spine were observed.

TEGMINA AND WINGS.—The alar organs are very similar in size and form and vary to about the same extent in all three species (♂ II, b). A single female from Del Rio, Texas, is brachypterous (XXIII, a); other specimens taken with it have the tegmina and wings normally developed.

FORE AND MIDDLE LEGS.—The fore and middle femora of the male (IV, a) are proportionately thicker than those of the female; in *lineata*, as contrasted to the other two species, these femora are moderately to very strikingly swollen, the enlargement being less in *alutacea* and least in *rubiginosa* (VIII, a). The femora of the female are not enlarged, and the specific differences in the thickness of the fore femur are much less pronounced in this sex (VIII, b).

HIND LEGS.—Regional differences in the length and breadth of the hind

femora (II, a; V, a) are consistent with the variation in other measurements. In both sexes the hind femur of *alutacea* is considerably more slender (VII, c, d), distinctly narrower relative to breadth of head (VI, c, d), and slightly narrower relative to length of pronotum (VII, a, b) than in the other two species; this characteristic is helpful in identifying females of *alutacea*. In most of the areas where two or all three of the species occur sympatrically, the ratios of breadth head/breadth hind femur and breadth head/length hind femur, combined with average size differences (XI, a–g), will separate a majority of specimens.

Terminal Abdominal Structures of the Male.—The tergiproct or supraanal plate and the subgenital plate have not been found to differ significantly in the three species. The tergiproct (XVI, a, b) exhibits the group characteristics pointed out above in the discussion of the Shoshone and Alutacea groups. In all three species it varies considerably in basal breadth, degree of sinuosity of the margins, and extent of closure of the median sulcus by the transverse carina that marks the line of fusion between epiproct and basal region. The size, form, and degree of prominence of the raised points or ridges that terminate the carina are especially variable, but the points are apparently almost never entirely lacking. The subgenital plate (XIV, q–t) varies within the species in proximal breadth and in the exact shape of the distal lobes and the intervening U-shaped or rounded V-shaped notch; the lobes themselves are short and well sclerotized, and unlike the large, thin lobes of members of the Obscura Group they retain their shape in dried material, so that the notch remains open.

Cerci.—Unlike the structures just discussed, the cerci of *alutacea, lineata,* and *rubiginosa,* in spite of great variation, show average differences in size and facies (XV, XVI), which are clearly apparent when their measurements are graphed (IX, a–d; X, b). Those of *rubiginosa* are relatively small, generally taper more strongly toward a narrower apex, and are very shallowly notched at the tip. The cerci of *alutacea* and *lineata* are much alike in appearance, but differ slightly in proportions and more strongly in relation to certain other body measurements; compared with those of *rubiginosa,* they are larger, with more nearly parallel dorsal and ventral margins and moderately to deeply emarginate tip, the distoventral angle of which is usually more prominent than the distodorsal. From New England to the Carolinas *rubiginosa* is well separated from *lineata* and *alutacea* by cercal form and size alone, and in this region the two latter species are partially differentiated by the proximal cercal breadth/interocular distance ratio (XI, h–k, n). Along the Gulf Coast the overlap in cercal size between *alutacea* and *rubiginosa* is almost complete (XI, l), but the differences in

form and in the proximal cercal breadth/interocular distance ratio permit correct assignment of almost every specimen.

PHALLUS.—The primary diagnostic characters of the species reside in the distal parts of this complex organ. Though they are inconspicuous, once they have been seen and understood they can be used for identification without dissection; it is enough to simply retract the pallium and dorsal fold and pull down the ventral lobes, exposing the "basal eminence," rami of the cingulum, and phallotreme orifice. For critical study, however, it is necessary to remove the phallic mass and clear it of tissue, as already described. Semi-diagrammatic views of the diagnostic parts of the phallic complex are shown in Figure 1, and in Plate XVII these parts are shown as they appear in carefully made dry preparations.

The general structure of the phallus is extremely uniform throughout the genus *Schistocerca*. There is little or no difference between *alutacea*, *lineata*, and *rubiginosa* in the form of the epiphallus, basal valves of the endophallus, and ventral lobes. The parts found useful in the present study are here briefly described, the terminology being essentially that of Dirsh (1956). In resting position the base of the distal part of the phallus is covered dorsally by a fold of the ectophallic membrane; when this is retracted or folded back it exposes a median "basal eminence" above the zygoma, the sides of which are formed by the upper margins of two laterally concave plates, the rami of the cingulum, that extend ventrad on either side of the penial lobes and associated tissues. In dorsal aspect (Fig. 1, c–e) the upper margins of these lobes form a characteristic "figure," which includes the "basal eminence" with its membranous, gently convex dorsal surface, a constricted "waist," and a pair of divaricate, down-curving arms. The shape of this "figure" is highly diagnostic of the three species; some variation exists, but only in rare instances might *lineata* and *rubiginosa* be mistaken for one another on the basis of this character, and for *alutacea* it is completely distinctive. Between the divaricate arms formed by the margins of the rami appears the distal orifice of the phallotreme, a more or less transverse opening formed by the apices of the penial lobes, and continuous caudoventrad with the median cleft of the phallotreme. The form of the phallotreme orifice is as diagnostic as the ramal "figure" and even more reliable, but, on account of its small size, higher magnification and cleared preparations are required for its study. The phallotreme orifice of *alutacea*, however, is so much larger, broader, and more heavily sclerotized and deeply pigmented that it can be distinguished from those of the other two species even under low magnifications.

In *alutacea* (Fig. 1, a, c; XVII, e, f) the surfaces of the rami are deeply infolded so that in dorsal aspect the "basal eminence" appears transverse

and bilobate, the "waist" very much constricted, and the ramal margins strongly divaricate to accomodate the broad phallotreme orifice. In order to see the depth of the infolding of the ramal surfaces it is often necessary to push back a delicate fold of membrane attached to the surface of the

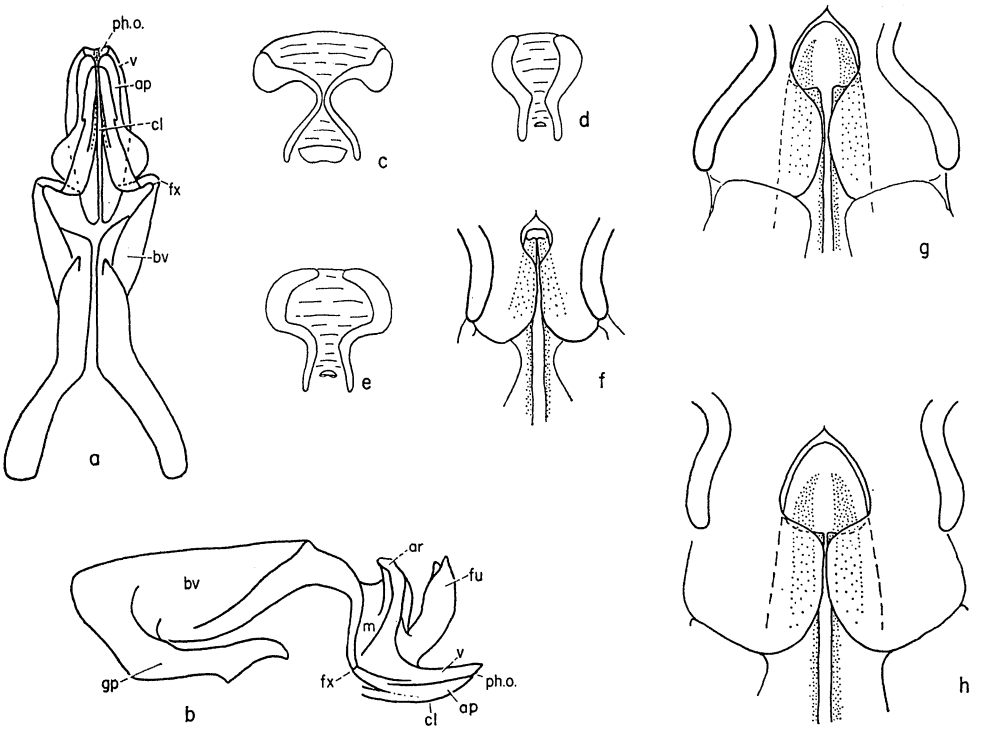

FIG. 1. Details of the concealed male genitalia.

a, b. *Schistocerca alutacea*, Stamford, Fairfield Co., Connecticut; endophallus, ventral and lateral views: ap, apical penial valves; ar, arch of the cingulum; bv, basal penial valves; cl, cleft of the phallotreme; fu, attachment to zygapophysis, severed in dissection; fx, flexible bend between apical and basal penial valves; gp, gonopore processes; m, membranous area; ph.o, distal orifice of phallotreme; v. dorsal penial valves (valves of cingulum). Terminology essentially that of Dirsh (1956).

c–e. Dorsal margins of rami of cingulum, enclosing "basal eminence" (attachment to zygoma), and cephalic face of tip of dorsal penial lobes at phallotreme orifice, sketched in dorsal view with camera lucida: c, *alutacea*, Sandfly, Chatham Co., Georgia; d, *lineata*, E. S. George Reserve, Livingston Co., Michigan; e, *rubiginosa*, Milton, Santa Rosa Co., Florida.

f–h. Details of the phallotreme orifice, caudal view, drawn from cleared preparations: f, *rubiginosa*, "Camp Torreya," Liberty Co., Florida; g, *lineata*, E. S. George Reserve, Livingston Co., Michigan; h, *lineata*, Denver, Denver Co., Colorado. All greatly enlarged.

"basal eminence" that may cover the upper end of the groove. As noted above, the phallotreme orifice is strikingly different in size, form, and coloration from those of *lineata* and *rubiginosa*; its opening is strongly transverse.

In *rubiginosa* (Fig. 1, e, f; XVII, c, d) the surfaces of the rami are much less deeply infolded and the general outline of the "basal eminence" is rounded subquadrate, a little wider than or about as wide as long, the caudal face in dorsal view appearing rather "square-cut." The phallotreme orifice is narrow and its cephalic margin does not project so far beyond the caudal marginal "shoulders" as in *lineata*; in dried preparations the cephalic margin often appears minutely biapiculate.

In *lineata* (Fig. 1, d, g, h; XVII, a, b) the "figure" formed by rami is always more or less hour-glass shaped, the "basal eminence" being more or less pyriform in outline, the "waist" little constricted and often very broad, especially in western and southwestern specimens. The phallotreme orifice is much narrower than that of *alutacea*, but somewhat broader than that of *rubiginosa*, and has its cephalic face prolonged as a submembraneous tip with parabolic outline, the two weak sclerotizations in the anterior wall not extending as far as the margin.

TERMINAL ABDOMINAL STRUCTURES OF THE FEMALE.—The form of the tergiproct, paraprocts, and last sternite does not differ significantly among the three species. The cerci of *rubiginosa* average a little smaller relative to other measurements than in the others, and are a little more pointed, but both tendencies are so slight and the variation so great that this difference is not useful in identification. The ovipositor (XIV, u–w) averages distinctly more elongate and slender in *alutacea* than in *lineata*, while that of *rubiginosa* is intermediate in form but closer to that of *alutacea*, as shown by the following ratios based on scattered sampling of the three species. Ventral valves (breadth of a single ventral valve at end of ventral basivalvula/length of apical part distad of this point): *alutacea*, 0.42–0.62, mean 0.52; *lineata*, 0.54–0.70, mean 0.63; *rubiginosa*, 0.48–0.67, mean 0.54. Breadth (as above)/length of "scoop" from ventro-lateral angle to tip: *alutacea*, 0.62–0.83, mean 0.70; *lineata*, 0.76–1.04, mean 0.94; *rubiginosa*, 0.58–0.93, mean 0.74. Dorsal valves (depth of valve at base of "scoop"/length of "scoop" from dorso-lateral angle to tip): *alutacea*, 0.54–0.73, mean 0.64; *lineata*, 0.70–0.93, mean 0.78; *rubiginosa*, 0.60–0.76, mean 0.67. Comparison of other ovipositor measurements gives comparable results.

COLOR AND COLOR PATTERN

Of the three species with which we are concerned, *alutacea* is by far the most uniform in color and pattern; *rubiginosa* is considerably more

variable, and *lineata* exhibits a very wide range of individual, local, and regional differences. Most of the basic elements of the color pattern are shared by all three species and many of the variations are probably allelomorphs of genes present in all. Other variations occur in only one of the species (most often *lineata*), and not infrequently in only a part of its range. Some of the elements vary independently of others, but many are more or less closely associated and probably genetically linked.

STRIPED AND UNSTRIPED PHASES.—The most striking difference in coloration (and the one which has caused the greatest taxonomic confusion) is that between individuals with a contrastingly pale middorsal stripe (XVIII, b; XIX; XXII, b) and others without trace of such a stripe (XVIII, a, c; XXII, f). In *alutacea* a complete dorsal stripe always extends from the vertex to the tips of the closed tegmina; in the other two species (XVIII; XX–XXII) both striped and unstriped individuals occur, though with varying incidence in different regions (XII; XIII). In these species, moreover, the full-length stripe is not a unitary characteristic. Although usually complete when present, it may sometimes be limited to the pronotum or to the head and pronotum; such a partial stripe is not uncommon in northern populations of *rubiginosa*.

The width of the stripe is quite constant in *alutacea* and *rubiginosa*, being moderate in the first and narrow in the second (XIII); in *lineata* it varies from a narrow line scarcely broader than the median carina of the pronotum (XX, e) to a broad band occupying as much as one third the breadth of the pronotum (XXII, b). When the stripe is broad on the pronotum it is also usually so on the anal margins of the tegmina (XXII, b, d), and vice versa (XXII, a), but this is not invariably the case (XX, e). In *lineata*, also, occasional individuals without a pronotal stripe have a moderately distinct stripe on the anal tegminal margins (XX, d). Although the stripe is usually of quite uniform width on the pronotum, in *lineata* it not infrequently broadens near the principal sulcus or on the metazona or both (XXI, c; XX, d); occasionally it may be fairly broad on the prozona and on the metazona taper to a narrow line or even disappear before reaching the caudal margin.

In color, the stripe also varies considerably. In *alutacea* it is normally bright yellow, often with a greenish and sometimes with an orange cast; in *rubiginosa* it is usually reddish yellow or light tan, sometimes pale yellow; in *lineata* it is commonly dull yellowish or pale tan in the east and in the more arid parts of its western range, but in the Prairie Plains from Iowa and eastern Kansas southward to southern Texas it is usually brighter and varies from a deep creamy yellow through greenish yellow, faintly orange

yellow, and light tan to a reddish brown contrasting little with the ground color.

In unstriped individuals of *rubiginosa* and *lineata* a considerable proportion (in some regions a majority) of specimens have a small pale dot or spot at the junction of the median carina with the principal sulcus (XII; XIII). In *lineata* the proportion so marked varies inversely with the prevalence of striping, increasing markedly from the border of the plains eastward. In a very small number of individuals the spot is attenuately prolonged forward and may be preceded by a few light dots in the midline, giving the appearance of a very thin broken median stripe, and suggesting that both the stripe and the dot may be the product of the same genes with appropriate modifiers.

GROUND COLOR.—The abdomen in all three species is yellowish, varying in tone from a clear bright yellow to faintly orange, buffy, greenish, grayish, or sometimes quite dark brown. Most males of *alutacea,* in life, have the face, sides of the thorax, and outer surfaces of the hind femora deep olivaceous or brownish green, the tegmina dark mahogany brown or even dark brown with a purplish tinge. These colors usually fade to reddish brown in dried material. Females of *alutacea* are less deeply colored, with the face and sides of the pronotum often paler than in the male and the upper parts of the lateral pronotal lobes often marked with two or three light blotches. *Lineata,* in the eastern part of its range, is generally rather dull or dilute reddish or yellowish brown or tan, sometimes with an olivaceous tinge on the sides of the body. Its face, unlike that of *alutacea,* is generally paler than the sides of the dorsum, the pale blotches on the upper pronotal lateral lobes are more often present, and general coloration in life is very rarely as intensive as is normal in that species. *Rubiginosa* is prevailingly reddish or yellowish brown in both sexes, with an increasing proportion of gray-brown individuals to the south.

Westward the variety of ground color in *lineata* increases. As Hebard (1931*a*) pointed out in his discussion of Kansas material, most specimens from the central Prairie–Plains area are some shade of brown, generally rather light, but even in dried material a considerable number have a faintly greenish tinge, and such specimens are much more noticeably green in life. In the large collection at hand from Iowa (reported on by Froeschner, 1954) most specimens are brownish, the tone ranging from light yellowish brown to deep reddish brown and in a few to mahogany brown almost as deep as the color of eastern male *alutacea.* A smaller number of individuals from scattered localities show a greenish cast, and one large series taken at Ames, Story County, is wholly of this color type. All the specimens in this

series (67 ♂, 45 ♀) are of dilute, brownish olive color, with the dorsal stripe narrow to broad, the tegmina immaculate, the hind femora without or with faint dorsal bars, and caudal tibiae varying from yellowish brown to blackish and to coral pink, the latter coloration prevailing. All these specimens are labelled in the same hand "Sept., 1932," and the series is doubtless a sample taken from a single genetically homogeneous population occupying a uniform environment. Specimens showing a more or less pronounced greenish cast have been seen from the following additional localities: Monona, Shenandoah, and Warren counties, Iowa; Boone County, Missouri; Barber, Grant, and Sedgwick counties, Kansas; Prowers and Pueblo counties, Colorado; Cleveland, Comanche, Garvis, Logan, Murray, and Payne counties, Oklahoma; Logan County, Arkansas; and Brazos, Carson, Collingsworth, and Sherman counties, Texas. One female from Grant County, Kansas, is almost uniformly pale yellowish green with a faintly indicated paler green stripe on the tegminal margins and no dark markings except scattered punctae along the carinae of the hind femur; in appearance it is very close to typical material of *shoshone*. Most specimens from southern Texas, possessing the striking coloration characteristic of that region, show a faint greenish tinge in the bright yellow parts of the pattern.

In most eastern specimens of *lineata* and in many western ones the dorsum and lateral lobes of the pronotum are concolorous, but in the central and southern Prairie-Plains a considerable proportion of striped individuals have the dorsum more or less darkened, increasing the conspicuousness of the mediodorsal stripe. This tendency reaches maximum expression in two regions—the northwestern part of the range (from Nebraska and northern Colorado to Canada) and southern Texas. In the northwestern populations (XX, a) the darkening often extends to the sides of the pronotum and the face. In the south Texas populations (XX, b, f; XXIII, b), on the contrary, these regions are lighter in color than usual so that the dorsal suffusion appears as two broad, strikingly contrasted dark bands bordering the mediodorsal stripe. Individuals with the admesal pronotal areas thus darkened almost invariably show a preanal infuscation of the tegmina, intensifying the contrast with the pale stripe along the anal margin, but the reverse is not always true.

Dark Markings of Head and Thorax (Fig. 2).—In northern populations of *alutacea* the facial region and sides of the thorax are generally dark in males and consequently show no evident maculation. The same is true to a less degree in females, but many of these are of somewhat lighter general tone and in about one fourth to one third the facial region is faintly to distinctly dark punctate. Southward the proportion of both sexes showing such markings increases, and the lateral lobes of the pronotum,

especially in the female, may be pale with a central dark macula or maculae and numerous small black dots; these markings may occasionally extend to the dorsum of the metazona. In *rubiginosa* the facial region and lateral lobes are sometimes quite dark, especially in northern populations, but seldom dark enough to obscure the presence of maculation. A much larger proportion of both males and females shows dark punctae on the face or on the face and pronotum than in *alutacea,* and in many southern females the entire dorsum and lateral lobes of the pronotum and much of the surface of the head are thickly dotted with small black spots

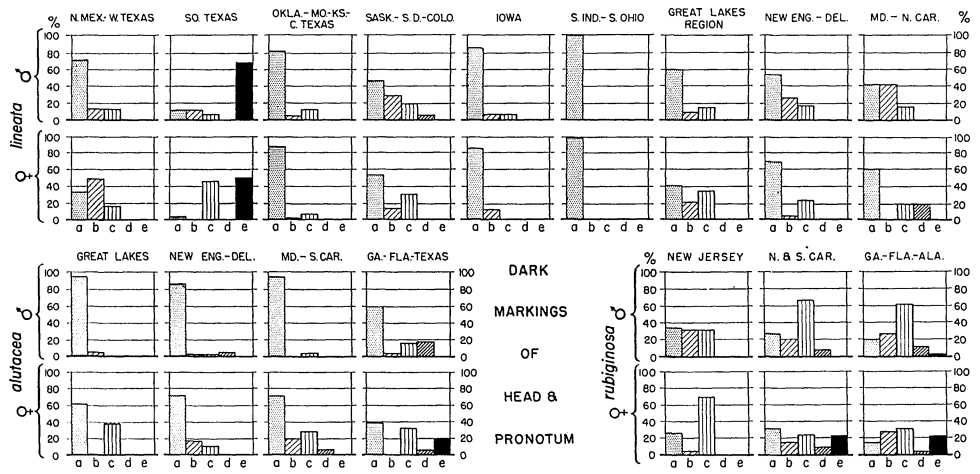

FIG. 2. Regional variation in dark markings of head and pronotum, *Schistocerca lineata, S. alutacea,* and *S. rubiginosa.*

a. Facial region of head and lateral lobes of pronotum without dark punctae or maculae, lateral lobes of pronotum usually concolorous with or only slightly lighter than dorsum, infra-ocular stripe of head usually faint or absent, occasionally distinct.

b. Facial region with faint dark punctae or maculae, infra-ocular stripe faint to distinct; lateral pronotal lobes without distinct markings.

c. Facial region with distinct dark punctae or maculae, infra-ocular stripe usually distinct, pronotal lateral lobes without dark markings.

d. Facial region strikingly dark-punctate, maculate, or mottled, infraocular stripe usually intense, rarely faint. Pronotal lateral lobes (and sometimes dorsum) with distinct dark maculae on a lighter ground color.

e. Facial region as last (in *lineata* generally yellowish or greenish) with contrasted markings, infra-ocular stripe usually intense, rarely faint. Pronotal lateral lobes strikingly maculate; in *rubiginosa* lateral lobes concolorous with dorsum, with or without a few pale markings in middle, and (usually together with dorsum) dotted with many small or medium sized dark spots; in *lineata* pronotal lateral lobes yellowish, distinctly paler than admesal areas of dorsum, usually with distinct blackish markings along sulci or spreading into an irregular central blotch of variable form and size.

(XVIII, g). In most populations of *lineata* the facial region is not or only faintly dark-punctate in both sexes, and the lateral lobes of the pronotum are without dark maculae. In the south Texas populations, however, most individuals have a medial spot on the clypeus and the areas between the facial carinae more or less maculate or suffused with black, the black infraocular stripe intense, and the dorsum on either side of the median stripe and the postocular regions deep black, so that the yellow parts of the head (facial carinae, labrum, etc.) stand out in sharp contrast. In these populations, also, the lateral lobes of the pronotum are prevailingly bright yellow, with the sulci and a more or less irregular and broken central blotch contrastingly blackened.

YELLOW THORACIC SPOTS.—Many of the species of the genus *Schistocerca* exhibit small yellow dots or spots on the pronotum and meso- and metapleura, and such spots are more or less evident in all three of the species here treated. In northern populations of *alutacea* they are lacking in about half the males and a smaller proportion of females, and in the rest are faint to distinct, but nearly always small; in southern populations they are present in a greater proportion of individuals, and are sometimes moderately conspicuous in females. The same is true of *rubiginosa*, except that in the north only a minority of both sexes has them; in the south they are present in about half the specimens examined, and while usually small and inconspicuous, are sometimes fairly large in females. In one South Carolina and two south Florida females those on the sides and dorsum of the metazona are conspicuously ringed with black.

One of the characteristics cited as a distinction between the western *lineata* and the eastern *"alutacea"* is the greater size and conspicuousness of the yellow spots in the former. Reference to Figure 4, B will show that while there is an average eastward decline in degree of development of these spots, in western populations they are absent or small in from one third to three fourths of the specimens examined, unusually large and conspicuous in only half or a smaller proportion of them. In south Texas populations they are generally conspicuous in the dark bands on the pronotal dorsum, but are lost in the yellow suffusion of the lateral lobes. When well developed the spots generally occupy small, slightly elevated callous areas.

YELLOW MESEPIMERAL STRIPE.—The presence of a yellow stripe covering a part or the full breadth of the mesepimeron has often been used in the past as a character to distinguish *obscura* (in which it is almost always present) from *"alutacea"* (in which it was supposed not to occur). Such a stripe is, in fact, never present in *rubiginosa*, and almost never in *alutacea*. The only exceptions to the latter statement that I have encountered are three Florida females, one from Liberty County and two from Putnam

County, in which a partial stripe is weakly indicated. In *lineata*, on the contrary, some individuals in all regions show traces of a yellow mesepimeral stripe, and in the western parts of the range a certain number have as conspicuous a stripe as that normally present in *obscura* (XXIII, b, e), the proportion of such individuals rising to 81 per cent in the south Texas populations (Fig. 4 D).

TEGMINAL MACULATION.—Individuals with unspotted and with spotted tegmina occur in all three species, spotted tegmina being in all instances commoner in the female than in the male (Fig. 3). In *alutacea* and in *rubiginosa* the proportion with the spotted tegmina increases southward, but such a trend is not clearly indicated in *lineata*. In the regions of sympatry the proportion of individuals of *alutacea* with unspotted tegmina is far higher in both sexes than in either of the other species. Southern females of *rubiginosa* are unusually variable in respect to this character; in some (XVIII, g) there are numerous rather small maculations, while in others (including specimens from South Carolina, Georgia, and Florida) the maculae are in part fused into solid dark blotches of small and large size.

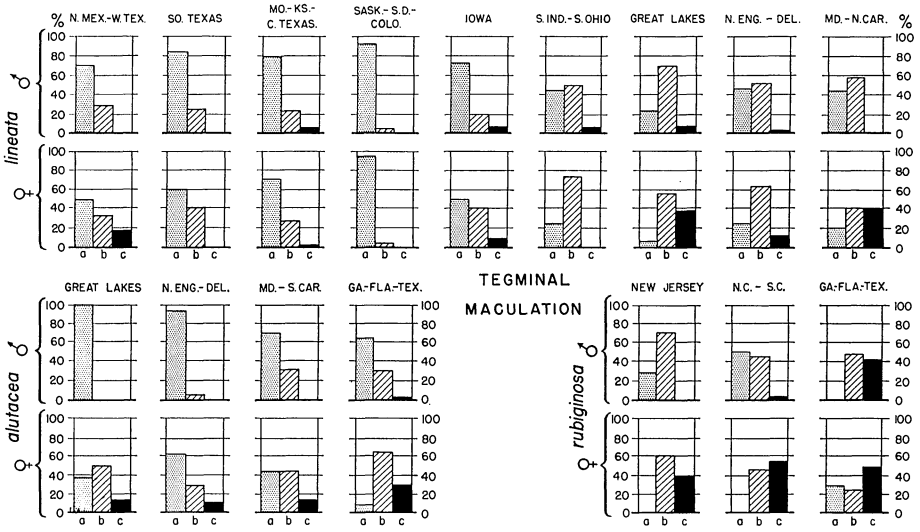

FIG. 3. Regional variation in maculation of tegmina, *Schistocerca lineata*, *S. alutacea*, and *S. rubiginosa*.

a. Tegmina unicolorous or (in *lineata*) with dark humeral stripe, immaculate.

b. Tegmina faintly maculate.

c. Tegmina distinctly to strongly maculate, or sometimes (in *rubiginosa*) with many small dots or with fusing dark blotches.

Black Abdominal Spots.—The presence of a row of black dots along the caudal margins of abdominal tergites 2–7 is an almost constant generic characteristic. Nevertheless the size, intensity, and form of these dots varies individually and regionally in the Alutacea Group, and the presence of large, conspicuous abdominal spots has been used as one of the diagnostic features distinguishing "*lineata*" from "*alutacea*." Actually the variation is nearly the same in all three species, from entirely absent to large and conspicuous. The proportion of individuals with large, conspicuous dots is, however, much smaller in *alutacea* and *rubiginosa* than in western populations of *lineata*, but not than in eastern populations of the latter. In *lineata*, furthermore, a small percentage of the westernmost populations has the dots enlarged until they are coalescent; and in a larger proportion of the south Texas populations the lower spots are obliquely elongated in a cephalo-dorsal direction, extending toward the cephalic margin of the tergite as lines or bars (Fig. 4, A).

Fore and Middle Legs.—Only in *lineata* does the coloration of these show noteworthy variations. Although in most regions they are of the general body color, in many of the specimens from south Texas and in a single female from Murray County, Oklahoma (which also possesses the coloration characteristic of south Texas material), there is a narrow black pregenicular ring on the dorsal and lateral faces of the fore and middle femora, sometimes extending onto the inner face. The genicula and apex of the tibia are also briefly blackened. In a few south Texas individuals the caudal faces of the fore and middle tibiae are also black. Three males from near Galeana, Nuevo León, México, have the femoral rings faintly indicated and the caudal surfaces of the tibiae blackened.

Hind Femur.—In all three species the dorsal surface of the hind femur may be without dark markings (except for the frequent presence of dark punctae along the carinae), or it may have a pair of faint or distinct dark crossbars, one near the proximal, the other near the distal third of the length. When these bars are faint only the subproximal or more rarely only the subdistal may be present. In northern populations of *alutacea* three fourths or more of the males and about half the females lack any trace of the bars, and when present they are usually faint. In the south most specimens of both sexes of this species have faint bars (XIX, e), and distinct bars are present in a few females from west Florida. In the New Jersey series of *rubiginosa* five out of every six males and nearly all the females have faint bars, but in the large series from the southeastern and southern Coastal Plain the proportion of unbarred to faintly barred is about 4:3 in the males and 1:2 in the females, distinct bars being present in a small percentage of both sexes. In *lineata* (Fig. 4, C) the populations east of Iowa

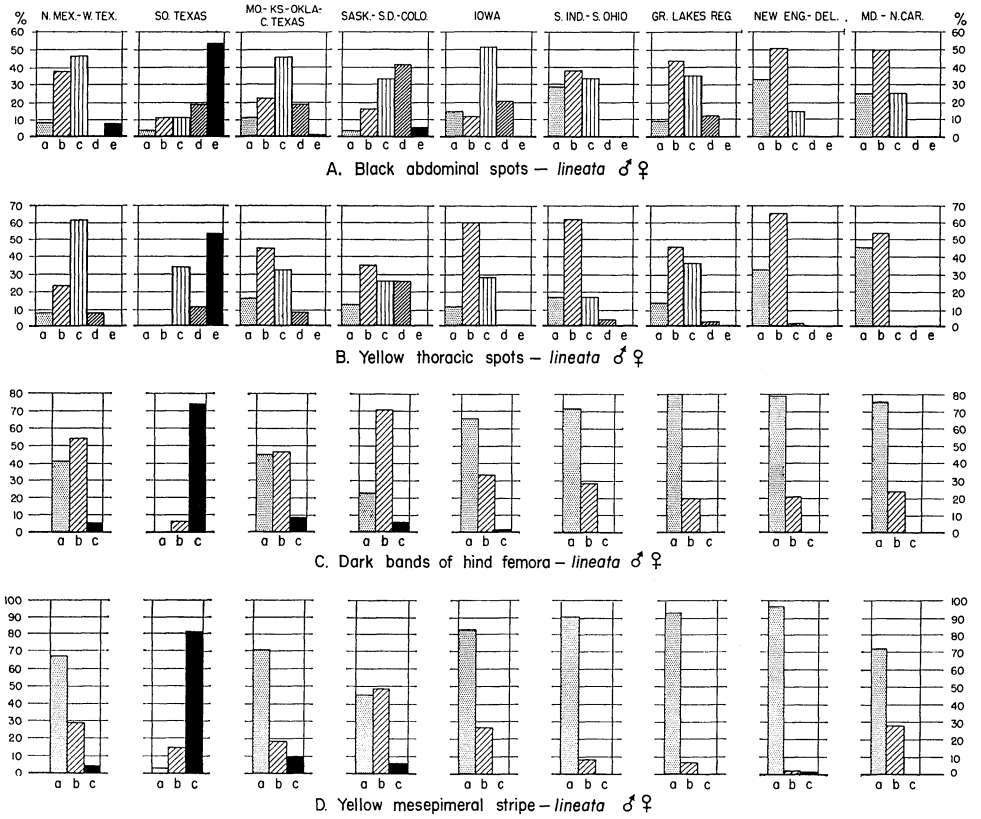

FIG. 4. Regional variation in elements of the color pattern, *Schistocerca lineata*; sexes combined.

A. Size, intensity and form of black dots on abdominal tergites 2–8: a, faint or absent on proximal tergites, absent distad; b, small or faint; c, of moderate size, distinct; d, very large and dark, but rounded; e, lower ones obliquely elongated in a cephalo-dorsal direction, or modified into oblique lines or bars, sometimes fusing into blotches.

B. Size and intensity of callose yellow spots on sides of thorax and dorsum of pronotum: a, absent; b, faint; c, distinct, of moderate size; d, large and conspicuous; e, fusing into or scarcely distinguishable from yellow areas on sides of pronotum, conspicuous on dorsum.

C. Presence and intensity of dark transverse dorsal bands of hind femora: a, absent; b, one or both bands weakly indicated; c, both bands distinct, moderately to very dark; in south Texas material, and occasional more northern specimens, genicular region of hind femora also often more or less darkened, and narrow pregenicular dark annuli often present on fore and middle femora.

D. Presence, size and intensity of yellow mesepimeral band: a, absent; b, faintly indicated or small; c, distinct, large, and often strikingly contrasted with darker surrounding areas.

run 65–80 per cent unbarred to 20–35 per cent faintly barred. From Iowa westward unbarred and faintly barred specimens each constitute 40–50 per cent of the population, 5–10 per cent being heavily banded, except in two areas—the northwest, where faint banding prevails, and south Texas (XX, b, f), where the proportion of heavy black femoral bars rises to 74 per cent. In this latter region, also, as well as to the south in Nuevo León, the genicular area of the femur is generally infuscated and a continuous dark bar often extends across the dorsum at the base of the genicular arcs, giving the femur a three-banded appearance not seen in other regions.

HIND TIBIAE.—In *alutacea* and *rubiginosa* and in the eastern populations of *lineata* (Fig. 8) the hind tibiae are invariably yellowish or brownish in color. Yellowish and brownish tibiae occur as occasional or prevalent variations throughout the areas inhabited by *lineata*, but from the Great Lakes region westward an increasing but locally variable proportion of individuals have the extensor surface of the tibia blackened part or all the way from the base to the tip, while the flexor surface remains pale or is darkened proximad or rarely almost to the distal end. Somewhat farther west, beginning in Iowa, Missouri, and Arkansas, individuals with clear coral pink or red tibiae begin to appear, and in the region bounded by central Iowa, South Dakota, eastern Colorado, northern Texas, and western Arkansas this type of tibial coloration is of sporadic occurrence and often dominant in localized populations. It is generally but not invariable associated with the greenish or yellowish green type of body coloration described above. In a few specimens from Kansas and Oklahoma and one from Gonzales County, Texas, the extensor face of the tibia is black, the flexor surface coral pink.

ECOLOGY

HABITAT.—In spite of the extensive literature on the members of the Alutacea Group we know relatively little about their ecological relations. This is particularly true in the east, where the three species have been confused, vitiating much of the published information concerning habitats. Some of it can be assorted to species, however, by re-examination of the specimens recorded as "*alutacea*" and "*rubiginosa*" by the various authors, and most of the data on occurrence in New England, the Atlantic Coastal Plain, and the Great Lakes region comes from such reinterpretation of observations by Blatchley, Fox, Hebard, Morse, Rehn, and others. This leaves much to be desired, however, and there is need for many more detailed ecological studies similar to those made by Cantrall (1943) on *lineata* in southern Michigan, by Criddle (1932) and Anderson and Wright

(1952) on *lineata* in Alberta and Montana, and by Friauf (1953) on *alutacea* and *rubiginosa* in northern Florida. Such studies would be of particular value in New Jersey, where all three species are sympatric, in order to determine the extent to which they are ecologically separated in that region.

The present summary is based in part on such published information as can be reliably assigned to species by re-examination of the specimens or on geographic grounds, in part on data from specimen labels, and in part on field notes sent me by other students. To a large extent, however, it rests upon my own extensive field observations on *alutacea* and *rubiginosa* in Florida and other parts of the southeastern Coastal Plain, and my less numerous ones on *alutacea* and *lineata* in Michigan, Ohio, Tennessee, Oklahoma and Texas.

By roughly classifying the types of environment in which species of this group have been found, listing them in order from wettest to driest, and tabulating under them the number and percentage of occurrences recorded in the sources listed above, the ecological preferences of the species can be seen to differ notably (Table 3). The table may be misleading in that it groups certain geographically separated habitats that may not in fact be similar in important respects, that presence or absence in certain habitats is a result not of ecological preference but of species range, and that the habitat categories themselves are not clearly defined and may not be mutually exclusive. Nevertheless certain generalizations are possible from inspection of the data thus arranged.

Schistocerca alutacea shows a strong preference for shrubby, fairly moist to wet situations, including open shrub-filled bogs and swamps, marshes, and thickets bordering mesic forests. In the southeastern Coastal Plain, as recorded by Friauf (1953) and confirmed by my own observations, it is a characteristic inhabitant of shrubby seepage slopes around bayheads and bordering swamps, and of thickets of gallberry, palmetto, and other shrubs in the lower parts of undulating wet flatwoods of slash and black pine. Although in the south it is not infrequently found in association with *rubiginosa*, such occurrence is almost always in marginal environments such as shrubby high pine forest and the shrubby ecotones between turkey oak or high pine and bayhead or swamp. Near the shores of Lake Erie and southern Lake Huron and Lake Michigan, in Ontario (Urquhart, 1942), Ohio, Michigan, Indiana, and Illinois, *alutacea* occurs in marshy situations, in tall herbaceous growths on moist soil, and in rank weed and shrub growths in cleared forest land. Nearly all records are from regions of sandy soil. The scattered occurrence of *alutacea* in relatively dry situations is generally attributable to proximity to more favored habitats and to disturbance. Being a fairly strong flier, like the other members of the group,

TABLE 3
OCCURRENCE IN VARIOUS HABITATS

Habitat	*alutacea*		*rubiginosa*		*lineata*	
	Number occur.	Per cent total	Number occur.	Per cent total	Number occur.	Per cent total
Hydric–Mesic						
Emergent vegetation and wet marshes	26	12.7	4	1.3	3	2.0
Moist meadows	18	8.9	..	..	4	2.7
Shrubby bogs, swamps, and swamp margins	50	24.8	12	4.0	2	1.3
Shrubby mesic forest margins and ecotones	40	19.8	41	12.8	..	..
Palmetto-gallberry thickets in low flatwoods	19	9.5	9	3.0	..	..
Weed thickets and tall prairie herbage	15	7.4	..	..	18	12.0
Xeromesic–Xeric						
High pine and dry shrubby flatwoods	19	9.5	72	23.1	1	0.7
Open upland shrubby hardwoods and dry hammock	5	2.4	17	5.5	3	2.0
Dry brushy old fields and fence rows	3	1.5	3	1.0	12	8.0
Scrubby open oak forest on dunes and sand hills	3	1.5	67	21.5	29	19.3
Coastal plain sand scrub	1	0.5	74	23.8	1	0.7
Ruderal dry grassland, sandy soil	3	1.5	12	4.0	48	32.0
Stream margins and gullies, Western Plains	..	..	..	..	..	N* (?)
Dry prairie short-grass plains	..	..	..	..	12	8.0
Beaches and grassy dunes	..	..	..	..	17	11.3
Total	202	100	311	100	150	100

* Numerous general references in literature to occurrence in such environments, sometimes in injurious numbers.

alutacea is quite subject to accidental local dispersal, and individuals found in xeric situations are to be classified, in Cantrall's terminology, as "erratics." Where, as in Florida, the edaphic pattern closely intermingles wet and dry situations and multiplies the extent of the ecotonal transitions

there must be fairly frequent contact between *alutacea* and *rubiginosa*, and similar conditions in New Jersey and the Great Lakes region must often bring *alutacea* and *lineata* together. Nevertheless no morphological evidence of hybridization has been observed between *alutacea* and either of the others.

With respect to *rubiginosa* we may suppose that in the Pine Barrens of New Jersey it occurs in open shrubby pine and oak forests and in grassy situations on sandy soil, as it does farther south, but unfortunately we do not have any clear idea of its ecological relations with *lineata*, which has somewhat similar habitat preferences. In the southeastern Coastal Plain, *rubiginosa* is a characteristic and often abundant species of the high pine and turkey oak forests of the sand hills, and is also of regular occurrence in the "sand scrub" of the coastal dunes and the deep sands in the interior of the Florida peninsula. At Welaka in northern Florida Friauf (1953) found it dominant in dry ruderal grassland and in xeric live oak hammock, in the herbaceous and scattered shrub strata; he also records it as occasional in sand scrub, dry grassy long-leaf pine flatwoods, and shrubby long-leaf pine flatwoods, and comments on its sharp ecological separation from *alutacea*. Farther inland, in Georgia and South Carolina, *rubiginosa* occurs also in open shrubby hardwood and pine forests on clay soils, though it is more characteristic of sandy situations.

Schistocerca lineata is more difficult to characterize ecologically, both because of its very extensive range and the varied habitats it is reported from, and because I have had less field experience with it. Most of the data on its habitat preferences in the east are taken from the literature, evaluated as described above, all records having appeared under the names "*alutacea*" and "*rubiginosa*." In New England, according to Morse (1920), *lineata* "inhabits dry areas on sandy and gravelly soils, railroad embankments, etc., clothed with bunch-grass, scrub-oak, sweet-fern, and pitch-pine thickets." On Long Island it occurs "in the driest situations" (Davis, 1913*a*). In New Jersey it occurs on the Piedmont and in the Pine Barrens "in dry open woods, especially oak scrub" (this probably including *rubiginosa*), and "on the barrier beaches in tracts characterized by an abundance of bayberry bushes (*Myrica*)" (Fox, 1928, and personal communication). In Virginia it occurs along the coast on the upper edges of the shingle and sandy beaches (Ferguson and Jones, 1949), on the dunes in wax-myrtle thickets (*Myrica*) and bunch-grass (Fox, 1917), and in open oak dune forests (R. D. Alexander, field notes). Inland in that state it is known from the Piedmont region and occurs on brushy slopes in the Massanutten and Bull Run Mountains (Allard, field notes). It has also been found on the slopes of the Appalachian Mountains at Hot Springs (Hebard, 1945), at

Covington (Fox, 1917), and at Pearisburg, Blacksburg, and Christiansburg by myself; at Covington it occurred in scrubby undergrowth of open oak-hickory-chestnut woods on steep mountainsides, and at the three localities where I found it, in weed patches and among shrubs and chestnut shoots in dry brushy pastures on shaly slopes.

In the Great Lakes region, also, *lineata* has most often been found in xeric or xeromesic environments on sandy soils. Urquhart (1942) recorded it as occurring at Grand Bend, Ontario, in an open, low scrubby growth of tree seedlings and sprouts—birch, ash, oak, and poplar—on sandy land about a mile from Lake Huron that had been burned over five years earlier. At the E. S. George Reserve in southeastern Michigan, Cantrall (1943) found *lineata* numerous in the mixed grass-herbage in dry sandy upland fields surrounded by xeromesic oak-hickory forest. From the sandy region around the south shore of Lake Michigan, in Michigan, Indiana, and Illinois, the species has been reported by Blatchley (1903, 1920), Hancock (1911), Hebard (1934), Hubbell (1922), Shelford (1913), and Strohecker (1937), in situations of which the following are representative: abandoned sandy fields overgrown with tall grass and tall weeds, *Rubus* (dewberry and blackberry), and various shrubs; dry upland pastures and open xeric woodland; open black oak dune forests and adjoining tracts covered with bunch grass and low shrubs. Hart (1906) and Hart and Gleason (1907) found it in the sandy "blowout" areas along the Illinois River in Mason and Morgan counties, Illinois, and on the Moline Sand Hill on the bank of the Rock River in Rock Island County, in the bunch-grass association and open black-jack forests. McNeill (1891) stated that at Moline it occurred sparingly along railroad embankments and on waste sandy land, but was abundant at Colona in Henry County in a patch of tall "Johnson grass" (*Andropogon* sp. according to McNeill). Young and Cantrall (1955) found *lineata* present over a period of three years in several relict prairie areas in the vicinity of Switz City, Greene County, southern Indiana, in which occur several distinct facies of "associations" dominated by *Andropogon furcatus,* the big bluestem. Here the species was co-dominant among the acridids with *Melanoplus differentialis* and *M. f-r. femur-rubrum.* The flora included, beside *Andropogon furcatus,* the grasses *Panicum virgatum* and *Sorghastrum nutans,* and the forbs *Helianthus grosseserratus, Aster* spp., and *Solidago* spp. In one or more of them also occurred species of *Baptisia, Cassia, Desmodium, Lespedeza,* and *Melilotus* (legumes); *Achillea, Ambrosia, Brauneria, Cirsium, Lactuca, Rudbeckia,* and *Vernonia* (composites); *Acalypha, Apocynum, Carex, Convolvulus, Daucus, Euphorbia, Fragaria, Hypericum, Oxalis, Potentilla,* and *Pycnanthemum* (forbs of various groups); and *Ceanothus, Cornus, Quercus, Rhus, Rubus,* and *Sassafras*

(shrubs and small trees in or near edges of stands). These edaphic prairie relicts are apparently very similar to the tall-grass prairie associations which formerly dominated the eastern margin of the Plains region, and it is of interest that the *lineata* collected in them are more similar in facies to series from Iowa than to those from the sand areas near the shores of the Great Lakes.

In the Prairie region *lineata* is a characteristic and abundant insect in the areas of tall-grass prairie still remaining, and in Iowa, according to Froeschner (1954), it is now most frequently encountered in moist open fields and meadows. In that state Ball (1897) found the brownish forms, which he called *emarginata*, along railroad embankments and in hazel brush thickets, while he took larger and more brightly colored specimens in a low marshy place overgrown with willows. Other Iowa records include those of Bessey (1877, in tall grass prairie on low lands), Drake and Richardson (1935, feeding in injurious numbers on cereal or clover plants in the counties bordering the Missouri River, and very abundant on willows along the sandy shores of the river and its tributaries), Hendrickson (1930, a characteristic species of the tall-grass prairie, *Andropogon scoparius–Bouteloua curtipendula* association, along the bluffs of the Missouri and Big Sioux rivers), Knutson (1940, in tall grass and open sandy woods), and Osborn and Gossard (1891, injurious to sugar beets at Ames).

In the Ozark region records of *lineata* are few. Morse (1907) collected it on Magazine Mountain, Arkansas, at the west end of the summit (elevation 2600 ft.) where the open xeric oak forest had been cleared and the sandy, rocky soil was densely covered with tall grass, goldenrod, blueberries, and a variety of other shrubs and tree seedlings. Although I was unable to find *lineata* at that place in 1954, I have encountered the species at lower elevations in the Ozark region, once at Booneville in Logan County, Arkansas, where it was present in tall grass and weeds bordering the forested edge of a dry pasture on sandy loam, and once at Cornell in Wagoner County, Oklahoma, on a xeric rocky hillside in open oak-hickory forest with undergrowth of oak shoots, poison oak, tall grass, and scattered weeds.

Much more information is available on the occurrence of *lineata* in Oklahoma and northern Texas, mostly derived from many field records by W. F. Blair, L. G. Duck, and myself, and from data published by Hebard (1938), Isely (1934, 1935, 1937), Morse (1907) and C. C. Smith (1940). In the prairie, savanna, and mixed-grass plains regions (Blair and Hubbell, 1938; Duck and Fletcher, 1943; N. D.; Tharpe, 1939, 1952) the species occurs in a rather wide variety of situations. On the sandstone ridges of the east central savannas and on the slopes of the Wichita Mountains in Oklahoma *lineata* occurs with high frequency and often in large numbers in

open post oak–blackjack forest with undergrowth of oak seedlings and other shrubbery and patches of tall grass and forbs, usually on sandy or rocky but occasionally on red clay soils. In northern Texas it has been taken in similar situations in the Eastern and Western Cross Timbers belts in Dallas, Ellis, Johnson, and Tarrant counties. In both states it is often abundant in the tall-grass prairie environment, along weedy roadsides, in sandy fields, and in pastures and rangeland, generally on sandy but sometimes on red clay soils. In such places the vegetation usually includes such grasses as sand dropseed, big and little bluestem, Johnson grass, and hairy and blue grama, and numerous forbs among which broomweed and sunflowers are conspicuous. Morse (1907) stated that in this region *lineata* "is usually found among the sunflowers and other coarse weeds along gullies, roadsides, and fences," and that "in the semi-arid prairies and plains it finds shelter in patches of weeds (*Ambrosia, Euphorbia, Grindelia,* etc.)."

Throughout the Prairie-Plains from South Dakota, Iowa and eastern Colorado to Texas the sandy river bottoms, with their patches of tall grass and weeds and fringes of willows or cotton woods, are a favored habitat for *lineata.* The species is also often abundant in the sand sage–grassland, and still more so in the denser vegetation of the stabilized dunes along the Cimarron, Canadian, and other streams in western Oklahoma and the Texas panhandle; in these environments the vegetation includes the tall grasses (bluestem, sand bluestem, little bluestem, and sand dropseed), the forbs (broomweed, western ragweed, and numerous weedy annuals), abundant sand-sage (*Artemisia filifolia*) on the flats, and on the dunes a scattered growth of shrubs and small trees, including hackberry, chittum, American elm, post oak, and blackjack. In the mixed-grass eroded plains of western Oklahoma and their southern extension as the mesquite plains of northern Texas, *lineata* often occurs in areas with rocky red clay soil, a short-grass cover in the more exposed areas, tall grass and weeds in the gulleys and on protected slopes, and scattered mesquite shrubs increasing in abundance southward. In Beckham County, western Oklahoma, Blair and I found *lineata* numerous on sand hills covered with low shinnery oak thickets (*Quercus* spp.) interspersed with tall grass, mostly *Andropogon scoparius.*

Along the western edge of its range, from Alberta to New Mexico, *lineata* is increasingly confined to gullies and stream margins in the arid high plains, and to open woodland or shrubby thickets on mesa and valley slopes and mountain hillsides. At Higdon Ranch in southeastern Alberta, Tinkham (1939) found it common in tall grass and shrubbery on steep south-facing slopes of the valley of the Milk River, and Brooks (1958) says that it occurs in rough, eroded valleys at Medicine Hat, Comrey, and Manyberries, Alberta, at Coronach, Saskatchewan, and near Lyleton, Manitoba.

Anderson and Wright (1952) report that near Decker in Bighorn County, Montana, *lineata* was observed infrequently along Hanging Woman Creek, where it was confined to moist shaded ravines and gullies in which shrubs were growing. Along the front of the Rockies in Colorado, H. S. Wallace found *lineata* at Denver only in the valley of Clear Creek and around the margins of a small swampy area; near Colorado Springs H. B. Baker collected specimens on the slopes of Austin Bluffs, in tall grass in open, park-like forest of scrub oak, and sometimes on the foliage of the oaks. At Black Mesa at the western end of the Oklahoma panhandle I found *lineata* below the rimrock in patches of tall grass and weeds among scattered piñons and junipers on the steep, boulder-strewn slopes. Most of the specimens seen from eastern New Mexico were collected in and near stream valleys, but E. R. Tinkham informs me that he found *lineata* abundant in the Mescalero Sands, 45 miles east of Roswell, on low, stabilized dunes covered with a moderately dense stand of shinnery oak (*Quercus harvardii*) about two feet high, interspersed with scattered clumps of tall grass and some forbs, conspicuous among which were *Verbena fragrans*, a tall *Asclepias*, *Comelina* sp., and a prickly *Solanum*. Here the insects were so numerous that they flew up in clouds when disturbed; many were seen eating the leaves of the oaks. In trans-Pecos Texas, Strohecker collected *lineata* under xeromesic conditions at the mouth of McKittrick's Canyon in the Guadalupe Mountains near Frijole, where it occurred on the canyon floor in the arborescent vegetation consisting of various shrubs and small trees with *Juglans* predominant. F. M. Gaige found *lineata* perched on manzanita shrubs on the upper slopes of Cherry Canyon in the Davis Mountains, and Tinkham (1948) recorded it from the oak zone (*Quercus virginiana*) at 5200 ft. on a north slope near the base of the Blue Mountains (Chinati Mountains).

The bright, contrastingly colored phase characteristic of south Texas has been taken outside that region only on the eastern edge of the Arbuckle Mountains in Murray County, Oklahoma. Here L. G. Duck (notes) found it in Turner Fall State Park, six miles southeast of Davis, in tall-grass prairie on gray-white limestone soil with many limestone outcrops. Most of the data on its occurrence in south Texas are derived from the field notes of T. J. Cohn; Strohecker furnished information on material he collected in Bexar County, and I encountered this form in Val Verde and Medina counties. Until Cohn's 1958–1959 field work showed otherwise, I had thought this phase of *lineata* restricted to the Black and Coastal Prairie regions, but he found it as frequent and numerous along the eastern rim and in the dissected margins of the Edwards Plateau as in the Prairies. On the plateau, at elevations of 1800–2300 ft. in Edwards and Real counties, *lineata* was taken in open, scrubby oak and oak-juniper forest, where the

scattered ground cover of low oak and other shrubs exposed much rocky soil, and patches of tall grass and weeds occurred in protected sites. In the dissected plateau margins, in Bandera, Bexar, Blanco, and Comal counties, the species was taken at elevations of 1000–1500 ft. in similar situations, usually with a good growth of tall grass and patches of tall weeds, and with more numerous trees and shrubs, the latter often including Mexican persimmon, catclaw, *Lizzia,* and an aromatic rosaceous bush. In the Black Prairie region in Bexar, Guadeloupe, and Travis counties, at elevations of 500–800 ft., *lineata* was taken by Cohn and Strohecker in the following situations, all with heavy clay-loam soil: in knee-high growth of grass (chiefly *Sorghastrum nutans*) and weeds in mesquite-dotted field; in heavily overgrazed pasture with many clumps of tall weeds, much *Gutierrezia,* and scattered mesquite and other thorny shrubs; and in open stand of *Quercus fusiformis, Diospyros texana, Juniperus virginiana,* and *Colubrina texensis*; most of the *lineata* taken on the latter though not seen feeding upon it.

On the top of Dunlay Hill in Medina County, south Texas, an extremely xeric, rocky situation, I found bright-colored *lineata* in an area of low thorny scrub resembling that which covers extensive areas in northern Tamaulipas; the most conspicuous plants were huajillo (*Pithecolobium brevifolium*), various cacti, and scattered clumps of tall grass. At Del Rio I also collected this form in grassy mesquite scrub and in clumps of willows on the floodplain of the Rio Grande. The southernmost record for which habitat data are available is seven miles southeast of Galeana in Nuevo León, México, where Cohn collected three males, rather small and dark, but otherwise like south Texas specimens, on the west side of one of the ridges of the Sierra Madre Oriental, in a region generally characterized by dissected, forested slopes; these specimens, however, were in a small area of arid, thorny bushland with scattered patches of heavy weed growth, much like the characteristic Tamaulipan scrub.

At first sight there appears to be little in common between the extremes of the environments occupied by *Schistocerca lineata.* The species is abundant in sandy areas, but also occurs in stony, loamy, and heavy clay soils. Although often found in very dry situations, and in the east rarely taken except in xeric or xeromesic habitats, in the Prairie-Plains region *lineata* is often abundant under mesic conditions, being often concentrated in irrigated crop land and along the margins of streams. Since it is apparently not limited by type of soil nor by atmospheric humidity, and yet is not ubiquitous within its range, other factors must restrict its occurrence; most important of these appears to be its food habits.

Feeding Habits and Food Preferences.—Our knowledge concerning these subjects comes from field observations of feeding, examination of crop

contents and fecal pellets, laboratory experiments on food preferences, and the evidence afforded by mandibular morphology.

Isely (1944) showed that the mandibles of Orthoptera are modified in accordance with feeding habits into a number of distinct but intergrading types, of which only three need here be mentioned. Most acridine and oedipod grasshoppers have *graminivorous* mandibles, adapted to eating the siliceous leaves of grasses, and characterized by a series of parallel ridges on the incisor and molar surfaces, the latter being flattened and adapted to grinding in a manner analogous to that seen in hypsodont grazing mammals. In most Cyrtacanthacridinae the mandibles are forbivorous, herbivorous, or of intermediate form. The *forbivorous* mandible, adapted for eating the leaves of broad-leaved herbs (forbs, in the terminology of the ecologist), has the incisor and molar surfaces armed with jagged cusps rather than ridges; the molar surface is deeply cupped proximad, and surrounded by a number of tall, sharp dentes that are not arranged in rows. The *herbivorous* mandible of mixed feeders is similar, but the incisor dentes approach a ridge-furrow pattern, and the dentes of the molar area are arranged in rows to form a series of ridges.

My examination of the mandibles of *Schistocerca alutacea, S. rubiginosa,* and *S. lineata* shows that they are all very similar and forbivorous, deviating slightly toward the herbivorous type. This finding agrees with Isely's (1944) and Gangwere's (1956 and in Press) observations on *lineata,* but not with the former's statement that *alutacea,* along with *obscura* and *vaga,* has herbivorous mandibles. His placement of "*alutacea*" was evidently based on examination of a few worn mandibles of *rubiginosa,* as shown by examination of one of the east Texas specimens he recorded as *alutacea.*

Field observations on the feeding habits of *alutacea* and *rubiginosa* are few, and no laboratory experiments have been done on these species. Franklin (1950) says that *alutacea* is destructive in cranberry bogs in New Jersey, the young nymphs feeding on cranberry foliage and gouging or nipping off the small berries.The sharpness of the mandibular teeth in a number of *alutacea* specimens examined, by contrast with the worn condition in most specimens of *rubiginosa,* suggests that the former may, in general, feed upon softer or more succulent plants than the latter, which would not be unlikely considering the difference in their habitats. It is my impression that I have seen *rubiginosa* feeding on the foliage of dwarf oaks in northern Florida, but I can find no record of this in my notes.

A great deal more is known of the food habits of *lineata* than of the other two species. Criddle (1932) found the species on the north shore of the Saskatchewan River near Medicine Hat, Alberta, and in the Marias Hills in northern Montana, in both instances in association with what he

observed to be its favorite foodplant, wild liquorice (*Glycyrrhiza lepidota*); this is one of the few plants which remains green throughout the season in the dry habitats of *lineata* in the Prairie Provinces of Canada. He found that adults would also eat vetch (*Astragalus*), wild pea (*Lathyrus*), and beans (*Vicia*), as well as sweet clover (*Melilotus*) and alfalfa (*Medicago sativa*), while nymphs were fond of dandelion (*Taraxacum*). Grasses were avoided. Anderson and Wright (1952), in their excellent field study of range grasshoppers in Montana, confirmed and extended Criddle's observations. In Bighorn County, Montana, they found *lineata* most frequently feeding and perching on wild rosebush (*Rosa* sp.) or eating wild liquorice. Adults were also observed feeding very sparingly on stiff goldenrod (*Solidago rigida*) and coralberry (*Symphoricarpos orbiculatus*). Neither adults nor nymphs were seen to feed on any of the grasses of the study area, nor on dry plant materials on the ground, as do many of the grass-eating species; both nymphs and adults generally remained high on the shrubs when at rest.

The most thorough and comprehensive studies of the food habits of American Orthoptera are those of Gangwere (1956 and in Press). His field observations of *Schistocerca lineata* were made on the E. S. George Reserve in Livingston County, Michigan, where the species occurs in dry fields with mixed grass-herbage and scattered shrubby vegetation that includes *Poa compressa, Aristida, Rumex acetosella, Rubus, Solidago, Monarda, Cirsium, Setaria, Asclepias,* and other plants; the fields are bordered by oak-hickory forest. He observed adult feeding on the basal leaves of *Rumex acetosella,* and nymphal feeding on *Lespedeza capitata.* Crops of adults contained mostly fragments of dicot leaves and a much smaller proportion of grass leaves, while in the fecal pellets the proportions of these were nearly equal, probably because grass is more resistant to the digestive process. Gangwere's extensive preferential feeding experiments give much more complete information. Twelve of the species of plants most numerous in the fields where he caught the insects to be tested were offered in pairs to caged individuals which were not starved or thirsty, and the amounts of each plant that were eaten were recorded. Summarizing the results of many such trials, bush-clover (*Lespedeza capitata*) was markedly preferred over all other plants tested, followed in order by orchard-grass (*Dactylis glomerata*), wheatgrass (*Agropyron*) and tick-trefoil (*Desmodium illinoiense*) (equal), and horsetail (*Equisetum arvense*). The remaining species had a very low preference value; they are, in approximate order of choice, toadflax (*Linaria*) and wiregrass (*Poa compressa*) (equal); evening-primrose (*Oenothera*), wild carrot (*Daucus carota*) and goldenrod (*Solidago nemoralis, S. juncea*) (all equal).

In Isely's (1944) Texas feeding experiments he found that leaves of shrubs and trees were high on the list of preferred foods of all four species of *Schistocerca* he tested (*damnifica*, "*alutacea*," *obscura*, and *americana*), and that "*alutacea*" [*lineata*?] showed a definite preference for the leaves of post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*). This accords with Tinkham's field observation of *lineata* feeding on the leaves of shinnery oak (*Quercus harvardii*) in eastern New Mexico.

Mandibular morphology, field observation, examination of food residues, and experimental evidence thus combine to show that the species of the Alutacea Group are primarily feeders upon broad-leaved plants—forbs, shrubs, and trees—and that grasses, particularly the tough range grasses, are seldom eaten. With this established, the field observations on local and regional occurrence begin to fall into an understandable pattern. Wherever *lineata* occurs it is in association with forbs, shrubs, or trees which are acceptable foods; these may grow in moist or very dry places, but where they are absent *lineata* is also absent. One must presume, therefore, that the scarcity of records of *lineata* in the broad interpluves of the Staked Plains in Texas (Fig. 9) and the High Plains further north is owing primarily to absence of suitable food plants. This may also account for the restriction of *lineata* to relatively xeric situations, generally with sandy soil, in the eastern part of its range, since in the Prairie-Plains it shows no such limitation.

Coloration in Relation to Environment.—It is an observed fact that in populations of *Schistocerca lineata* living in dry environments, especially those with sparse vegetation on sandy soil, the general tone of the body coloration is prevailingly light brown or buffy, while in populations that occur in moister situations, in dense herbage or shrub growth, a greenish or brownish green overall tone is usual. My own field observations, together with study of the series of *lineata* at hand, show that in a population occupying a limited area of uniform environment body tone is generally quite uniform, and that populations in different environments in close proximity often differ strikingly in average coloration. Whether this is the result of differences in genetic constitution or is an environmentally controlled, phenotypic phenomenon is a problem that has not been studied in the Alutacea Group, but which may be considered in the light of other evidence.

In his paper on the Orthoptera of Kansas, Hebard (1931*a*) suggested that the brownish and greenish phases of *lineata* are caused by differences in the environment, the buffy insects developing in areas of drier herbage than the greenish ones. Whiting (1920) found that in the oedipod grasshopper, *Chortophaga viridifasciata*, temperature during post-embryonic development is the most important agent in color determination. Adults and

nymphs of this species may be dark brown, prevailingly green, light buff, or occasionally reddish or purplish. Whiting found that the progeny of green-green, brown-brown, and green-brown matings all turned out brown when reared under hot, dry conditions, and that green nymphs collected in the field soon turned brown when caged under the same conditions. Green nymphs reared in cooler, moister places usually remained green, but brown ones so reared did not turn green; when kept at a constant temperature of 55°F., green nymphs produced green adults, dark brown nymphs brown adults. At a constant temperature of 100°F., regardless of whether the surrounding air was very dry or saturated with water vapor, or of differences in light intensity, both green and brown adults and nymphs soon changed to a light buff color. Some adults and nymphs turned buffy soon after being exposed to the high temperature, but other nymphs passed through one or two ecdyses before changing. Two nymphs retained their green color through the last two molts and emerged as green adults, which turned buffy several days later; purple nymphs became buffy after one or two molts. The change was irreversible.

Many instances of color changes resulting in homochromy with the environment have been cited by Chopard (1938) and Ramme (1951, 1951*a*) in their reviews of the causes and significance of this phenomenon, upon which they are not agreed. Humidity has in some cases been assumed to be a determining factor for coloration. Thus, in the highly variable oedipod, *Locusta migratoria,* bright green nymphs develop only when fed with succulent moist food in a very humid atmosphere (Faure, 1932). A much more common and better substantiated control of coloration is the color of the background, affecting the prevailing wave length of light incident on the insect during certain critical stages in development. Ergene (1950), studying the slant-faced grasshopper *Acrida turrita,* found that in a given population the number of juvenile and adult individuals with "adaptive" coloration is greater than the number with "unadaptive," and that a large percentage of individuals removed into situations where they are not homochromous with the environment later seek out places where they are. He also found that the nymphs changed color only after a molt, but could change several times during the course of their development; if they remained as long as 14 days in a heterochromous background without molting and color change, their color remained fixed; yellow nymphs remained yellow in a yellowish environment, green nymphs remained green in a green one; adults placed in an environment with which their color did not harmonize were never observed to change; and blinded individuals did not undergo color change. In a later publication, however, Ergene (1954) states that green and yellow adults, blinded with opaque lacquer and

placed on a black background, became black, but if the tegmina were coated with opaque lacquer, excluding all light, they remained yellow or green under the lacquer. He concludes from this that the stimulus exerted by light of a given color acts directly on the hypodermis. Faure (1932) found that nymphs of the oedipod *Locusta migratoria* can adaptively change their colors through a range from dirty white to yellow, brown or black, depending on the quantities of orange-yellow and black pigments formed. In this species, according to Hertz and Imms (1937), the amount of black pigment seems to depend on differences in the intensity of the light incident from above and reflected from below, acting upon the eyes; the production of orange-yellow pigment is stimulated by yellow light (5500–6000Å), and inhibited by blue and violet light (5000–4500Å). Roonwal (1947) found the same type of response, with the same result of homochromy between insect and environment, in *Schistocerca gregaria*, a congener of the species here treated. Presumably all changes of this sort are mediated by hormones controlled by nerve centers in the head, and the latter in turn by stimuli received from the eyes. Being caused by alterations in the amounts of various pigments formed, they are not immediately reversible.

Other environmental factors that have been shown to affect the coloration of various acridids, including *Schistocerca gregaria*, and which are involved in the striking "phase changes" undergone by that and other species of plague locusts, include the effects of crowding and enforced activity of the nymphs, and of food (Faure, 1932; Stower, 1959). No indication of phase changes has been seen in the members of the Alutacea Group, but the possibility that some color differences in them may be caused by feeding on certain food plants cannot be ruled out. Color changes associated with ageing or with maturation of the gonads, such as have been observed in various African locusts and grasshoppers by Burtt and others, probably also occur in the Alutacea Group, but are apparently not considerable.

In the light of these findings, and in the absence of comparable studies on the species of the Alutacea Group, we may justifiably assume that the general tone of the body coloration is in one way or another determined by the local environment, just as Hebard postulated. One may then expect that successive generations in the same locale may differ in the proportion of buffy to greenish individuals according to the dryness or wetness, hotness or coolness of a given year, and also that the descendants of brownish individuals that migrate from a xeric hillside into an irrigated alfalfa field will be of the greenish phase. Observations and experiments to verify this hypothesis would be of interest.

The situation is different with respect to most of the other colorational

characters, which occur with varying incidence in different localities and broad regions (Figs. 8 and 9) and do not appear to be closely correlated with immediate environment. These include the presence or absence of the middorsal stripe and its breadth when present, the degree of development of dark femoral bands and yellow mesepimeral stripe, and variations in the dark markings of the head, pronotum, and tegmina, of the yellow thoracic dots, and of the size and shape of the black dots or blotches on the abdominal tergites. All these, as well as the differences in coloration of the hind tibiae, are probably controlled by allelic factors and modifying genes. King and Slifer (1955) have shown that in *Melanoplus bilituratus* (the lesser migratory grasshopper) red hind tibiae are caused by the presence of a dominant autosomal gene, individuals with blue hind tibiae being homozygous for the recessive allele; variations in the intensity of the red and blue are considered to be caused by modifying genes. Similar simple genetic mechanisms may account for the differences in tibial coloration in *Schistocerca lineata,* as well as for the variation in some of the other characters, and chromosomal linkage is probably responsible for much of the correlation observed.

Life History and Seasonal Distribution.—Criddle (1932) reared 31 males and 19 females of *lineata* to maturity at Aweme, Manitoba, from eggs laid by specimens collected at Medicine Hat, Alberta, and described and figured the eggs and nymphal stages. Tuck and Smith (1940) also described and figured the eggs of *lineata* in more detail, and pointed out characters that distinguish them from eggs of other midwestern grasshoppers, including *Schistocerca obscura.* Summarizing the data from these two sources, the life history of this species may be briefly described as follows.

The eggs are laid in the ground in the usual way, except that the female does not rake soil over the hole after withdrawing the abdomen. Each egg mass contains 35 to 64 eggs, and each female deposits at least 200 eggs. Criddle describes the egg as being Van Dyke brown, Tuck and Smith as being red in color, the latter authors using this as one of the characters to distinguish *lineata* eggs from the dark brown eggs of *S. obscura.* In *obscura* eggs, according to these authors, the boundaries of the cap cells are nearly or quite equally developed, and immediately before the micropyles are three rows of more heavily outlined, irregularly shaped, somewhat flattened cells which have no thickenings in the corners; in *lineata* the boundaries of the cap cells are not equally developed, the distal ones being more heavily outlined than the proximal, and the egg lacks the three differentiated antemicropylar rows of flattened cells. The duration of embryonic development is not stated by Criddle, but in his rearings the average time from hatching of the eggs to attainment of maturity was 39

days. First instar nymphs were pea-green, closely dotted with dull brown; second instars green, often suffused with brown on the abdomen; third, fourth and fifth instars either green or brownish cream color with many small round blackish spots and, in the two last instars, an increasing development of brown or black markings and suffusion on the dorsum and sides. All of the adults reared by Criddle were pale Van Dyke brown suffused with blacker shades on the head, pronotum, and tegmina, and with a wide median yellow stripe on the vertex and pronotum extending, in more creamy shades, along the anal margins of the tegmina.

No comparable studies have been made of *alutacea* or *rubiginosa*, or of *lineata* in the southern and eastern parts of its range. Tabulation of collection dates of adults of the three species, by region, by sex, by number of collections, and by number of specimens, shows that all three species have practically the same seasonal distribution. It is almost the same in both sexes, with only a slight tendency for earlier spring maturation and earlier fall disappearance of the males. Within each species the seasonal distribution is almost the same throughout all parts of the range except in the extreme south, where it is somewhat prolonged at both ends of the season. From Alberta to Massachusetts and south to Maryland and northern Texas *lineata* males and females begin to mature in middle or late June, increase to a peak of abundance in August, and then slowly decline, the latest records being in October in the northern states and in November in the latitude of Oklahoma and northern Texas. In south Texas the species is already abundant in mid-July, and presumably begins to mature somewhat earlier than farther north. The seasonal range of *alutacea* in the Great Lakes region and along the Atlantic Coast from New England to Delaware is from early July to late October, with peak abundance in August; in the southern Coastal Plain the same pattern exists, but adults appear in June and persist in small numbers into November. The seasonal distribution of *rubiginosa* is almost identical with that of *alutacea* in corresponding parts of their ranges, except that in Florida *rubiginosa* apparently survives longer in the fall, the latest records of both males and females being in early December.

RELATIONSHIPS AND EVOLUTIONARY HISTORY

Morphological evidence concerning the relationship to one another of *lineata, alutacea,* and *rubiginosa* is somewhat ambiguous, and needs to be considered along with ecological and geographic indications and collateral evidence of various kinds. *Schistocerca alutacea* appears clearly divergent from the other two species in the form of its concealed male genital struc-

tures, in its slightly more attenuate form with more slender and elongate hind legs and longer male antennae, and in being monomorphic with respect to the middorsal stripe and generally deeper and (in the male) more uniformly dark coloration. In the form of its cerci it closely resembles *lineata* and differs from *rubiginosa,* and, like *lineata,* conforms more nearly than *rubiginosa* to the prevailing conditions in the genus. Considering the pairs of measurements graphed on Plates VI–X, in body proportions *alutacea* is more widely separated by mean and/or trend than are *lineata* and *rubiginosa* in nine instances (VI, a–d; VII, a–d; IX, a), is closer to *lineata* than to *rubiginosa* in two (IX, b, d), and to *rubiginosa* than to *lineata* in one (X, c); in seven instances (VIII, a–d; IX, c; X, a, b) all three are about equally separated, though in two cases the means form the sequence *alutacea-rubiginosa-lineata* and in two others the sequence *rubiginosa-alutacea-lineata.*

Schistocerca lineata differs from both the others in the much more swollen fore and middle femora of the male, as well as in its much greater range of variability in form and coloration. In *Schistocerca rubiginosa,* besides the smaller and more tapering male cerci, the tendency toward broadening of the upper part of the head and increased prominence of the eyes constitutes a difference from the other species; the same tendency is seen in some individuals of *lineata,* but is the reverse of the trend seen in *alutacea.* The concealed male genitalia of *lineata* and *rubiginosa* are more similar to one another than are those of either species to the genitalia of *alutacea,* but on close examination they show many differences. The form of the "basal eminence" in *rubiginosa* is intermediate between those of *lineata* and *alutacea,* but closer to that of the former, while the form of the phallotreme orifice is distinctive in each species, that of *lineata* being, however, closer to the type prevailing in other species of the genus. Ecologically *lineata* shows a much wider range of adaptability than do the others, occupying both very dry and quite moist environments, while *rubiginosa* is more closely restricted to the former and *alutacea* to the latter.

Weighing the evidence summarized above, I draw from it the following conclusions. The Alutacea Group is monophyletic, containing the three closely related sibling species *lineata, alutacea,* and *rubiginosa,* superficially extremely similar, but showing many morphological differences when critically studied. *Alutacea* and *rubiginosa* both show more similarities to *lineata* than they do to one another, and the similarities between *rubiginosa* and *lineata* are considerably more numerous than those between *lineata* and *alutacea. Lineata* is not only the most widespread of the three, the most polymorphic and ecologically adaptable, but in several respects is closer to the morphological condition common to many species of the genus than

are *alutacea* and *rubiginosa*, as well as being situated closer to the main range of the genus. It appears highly probable, therefore, that both *alutacea* and *rubiginosa* have been independently derived from an ancestral *lineata* population, and that *alutacea*, being the most divergent both morphologically and ecologically, is the older of the two. Since all three are sympatric in parts of the Atlantic Coastal Plain, there can be no doubt that they are fully differentiated species.

The higher incidence of a middorsal stripe in the New Jersey populations of *rubiginosa* than in those farther south can conceivably be the result of introgression of *lineata* genes into the northern populations, but although not ruled out this is made less likely by the fact that where the two species are in contact the incidence of the stripe in *lineata* is very low. Between *alutacea* and *rubiginosa* no evidence of hybridization has been seen anywhere in the extensive area of sympatry, in spite of the frequent intermingling of individuals in ecotonal situations.

Evolutionary History.—Judging from the complete biological separation of the three species, the clear-cut and quite invariable morphological differences in the concealed male genitalia, the well-marked habitat shift that has occurred in *alutacea*, and the distributional evidence to be presented that all three were fully differentiated in early post-Wisconsin time, it appears reasonable to assume that the origin of *alutacea* and *rubiginosa* dates well back into the Pleistocene. It also seems reasonable to postulate that, in spite of Pleistocene expansions and contractions, the range of ancestral *lineata* had for its core the central and southern Prairie-Plains, where the modern form of the species finds its optimum environment and occurs in greatest numbers, most varied form, and with least restriction of habitat. Current uncertainties as to the distance to which the ice sheets exerted an influence on the climate, and debate concerning the amount of southward shift that took place in the biota during the glacial maxima (Deevey, 1949; Martin, 1958) scarcely affect this particular point, since the climatic changes recorded by the fossil vertebrate faunas in the late Pleistocene deposits of Meade County, Kansas (Hibbard and Taylor, 1960) do not seem to exceed the differences tolerated by *lineata* over the extent of its modern range. On the basis of the composition of the vertebrate faunas it is inferred that during the Yarmouth (pre-Illinoian) interglacial interval the climate of southern Kansas was warm-temperate, dry-subhumid, not greatly different from that of the present except that the winters may have been warmer during a part of the time. During the Illinoian glacial stage the climate was moister and the summers cooler, followed, in the Sangamon interglacial interval, by a return to conditions nearly like those of the present, though probably with somewhat cooler summers and much warmer winters.

Late in that interval, however, the climate again became more humid, with a rainfall of 40–50 inches and mild winters, while during at least a part of the Wisconsin glacial stage the climate was semiarid, with summers cooler and winters probably no warmer than those of today. The evidence concerning earlier glacial-interglacial climatic changes in this region is inconclusive, but suggests that they were similar to those of the late Pleistocene. The present climate of southern Kansas is more continental, with greater extremes of heat and cold, than any of those recorded in the late glacial sequence of deposits. Since *Schistocerca lineata* exists today both in southern Kansas and far to the north, as well as southward in much warmer regions under both arid and humid conditions, there seems no reason to suppose that it could not have inhabited the postulated area throughout the Pleistocene, perhaps with minor eastward or westward, northward or southward shifts in adjustment to changing moisture and temperature conditions.

The original homeland of *rubiginosa* was almost certainly the southeastern Coastal Plain, where it is today most abundant, largest, most varied, and least limited in habitat, and where the xeric and xeromesic environments in which it lives certainly existed throughout the Pleistocene, though doubtless fluctuating in extent. Northward, *rubiginosa* becomes less abundant and smaller, until in New Jersey it is not only depauperate but of restricted (though often locally abundant) occurrence.

The Coastal Plain is also just as clearly the region where *alutacea* originated, since the occurrence of that species elsewhere conforms to patterns that are common to many other species and attributable to postglacial movements. What part of the Coastal Plain may be considered its original territory is not, however, so evident. *Alutacea* is almost equally abundant in the southeast and, in suitable environments, as far north as Massachusetts; though somewhat more variable in the south, it is neither larger nor less restricted in habitat there than in other regions.

My interpretation of the evolutionary history of these three species, highly speculative for the earlier stages but much less so for the latest ones, is as follows. During one of the earlier interglacials ancestral *lineata* spread eastward to the Coastal Plain, either in the north, following the present pattern, or in the south. Since we do not know whether during the earlier interglacials there were climatic episodes similar to the post-Wisconsin Xerothermic Period, we cannot safely assume that there were times when a predecessor of the Prairie Peninsula permitted *lineata* to reach the coast in the north, but the possibility exists. If this indeed happened, the succeeding glacial episode would have isolated the eastern from the western population, leaving it to differentiate into *alutacea*. We know, from the

existence in the southeastern Coastal Plain and Piedmont of relict populations of such Prairie-Plains species as the grasshopper *Campylacantha olivacea*, that there have been times when elements of the plains fauna were able to spread into the southeast. Ancestral *lineata* apparently did so at least once (*rubiginosa*) and perhaps on two separate occasions. The circumstances under which this occurred, and the causes of the subsequent isolation of the southeastern population (s) are not known. In any event, in its earliest stages of differentiation the population which was to give rise to *alutacea* probably occupied both relatively moist and relatively dry situations, as *lineata* does today.

At some time, probably subsequent to the isolation of ancestral *alutacea*, but possibly at the same time if that event took place in the north, another *lineata* population spread into the southeastern Coastal Plain, there to evolve into *rubiginosa*. The pre-*alutacea* and pre-*rubiginosa* populations would have come into contact, either at once (if the former was already present in the southeast), or as the result of northward and southward spreading on the Coastal Plain if the two populations were northern and southern contemporaries. If, before this encounter, one or both of the populations had undergone genetic changes sufficient to cause partial reproductive isolation, then, according to current theory, selection might be expected to reinforce any incipient habitat differentiation and other barriers to mating. The end result would be the production of effective ecological and reproductive isolation of the two populations and their attainment of species status, one occupying dry and the other moist environments, as we see them existing sympatrically throughout the Coastal Plain today. The only essential difference between the hypothesis of an earlier northern or southern isolation of pre-*alutacea* and that of a simultaneous northern and southern isolation of the respective populations is that the first would permit more time for the *alutacea* stock to diverge, and for development of the required incipient reproductive isolation before it was put to the test.

In contrast to the foregoing, the post-glacial changes in the distribution of *lineata*, *alutacea*, and *rubiginosa* can be suggested with some confidence. They may be taken up in their probable sequence of occurrence, the two earlier episodes involving the spread of *alutacea* and *rubiginosa*, followed by retreat which left a prosperous colony of the former in the Great Lakes region and small relicts of both in other regions. The latest episode saw the eastward expansion of *lineata* to the Atlantic Coast, and the subsequent nearly complete isolation of its coastal from its interior populations.

Alutacea, along with other Atlantic Coastal Plain animals and plants, is believed to have entered the Great Lakes region via a narrow highway

which was later interrupted. During the recession of the Wisconsin ice sheet, at that stage when glacial Lake Lundy occupied the Erie and southern Huron basins, the ice front abutted on the highlands south of the Ontario basin and the Lundy drainage flowed to the Atlantic via the Mohawk and Hudson valleys. With further recession more northern outlets were uncovered, leaving the enlarged and now abandoned Mohawk-Hudson valley full of sand and gravel outwash and with marshes and swamps all along its course. As the climate warmed many of the Coastal Plain species of plants and animals, especially those of the sand beaches and coastal marshes, spread along this valley northward and westward until they reached the Great Lakes region. Peattie (1922) has discussed the plants which took part in this migration, and Thomas (1951) some of the animals. Among the latter, besides the marsh and bog inhabiting *Schistocerca alutacea,* were the arenophilous grasshoppers *Trimerotropis maritima* and *Psinidia fenestralis.* All of these found suitable environments along the sandy shores or on the outwash plains and sand- and gravel-filled valleys (such as that of the Grand River outlet across Michigan, clearly indicated on Figure 5 by the records of *alutacea*), and were able to persist in this region through the subsequent period of dessication that seems to have closed their route of entry. At present the *alutacea* populations of the Great Lakes region are separated from those of the east coast by a considerable gap in which the species is not known to occur.

The presence of isolated colonies of both *alutacea* and *rubiginosa* far north of their limits of continuous distribution along the Gulf Coast also requires consideration. Such colonies of *alutacea* have been found in the Ozark region (LeFlore County in extreme eastern Oklahoma and Rich Mountain in western Arkansas), in northeastern Alabama (Cheaha Mountain), and on the Cumberland Plateau in middle Tennessee, just south of the Kentucky border (Allardt, Fentress County). In all these places the species occurs in habitats that appear marginal for its requirements, and at Allardt the members of the colony are depauperate (Pls. I–V, Tennessee). Similar outlying colonies of *rubiginosa* are known from Choccolocco Mountain and Talladega County in northern Alabama. While these occurrences might be interpreted as the result of accidental dispersal, a much more probable explanation is that they are relicts of a once continuous distribution that included them. There is ample evidence that, with the warming trend of climate that followed the retreat of the Wisconsin ice and culminated in the period called the Climatic Optimum, elements of the southern fauna spread far north of their present limits (P. W. Smith, 1957). In many groups of animals and plants relicts dating from this expansion are numerous. On the summit of the Cumberland Plateau in northern Tennessee,

near Allardt, there exist sand areas suggestive of Georgia or Florida in their floral and faunal aspect. Their insect fauna includes, in addition to *Schistocerca alutacea,* such Coastal Plain and Piedmont Orthoptera as *Odontoxiphidium apterum, Conocephalus allardi, Pyrgocorypha uncinata, Neoconocephalus triops,* and *Tettigidea prorsa,* all more or less widely disjunct from their main areas of distribution to the south. The entire complex of southern species found here probably constitutes the residuum of a formerly larger assemblage of Coastal Plain immigrants.

Students of the Pleistocene are agreed that the Climatic Optimum was followed by a trend toward increasing aridity, culminating in the Xerothermic Period, during which a warm, dry climate prevailed over much of the northern part of the eastern United States. Recent radiocarbon dating (Zumberge and Potzger, 1955) puts the maximum of the Xerothermic Period shortly after 4000 years ago. As the aridity increased, the xeric oak-hickory forest, followed in turn by the grassland, spread eastward across the region between the Great Lakes and the Ohio River in a great tongue called the Prairie Peninsula (Transeau, 1935). Into this extension of the prairie environments moved many western species of animals, some of which eventually reached New England and the Atlantic Coastal Plain. Two Orthoptera which did so are the normally brachypterous *Phoetaliotes nebrascensis,* now restricted east of the Prairie Plains to colonies scattered from the southern Great Lakes region to Massachusetts (Morse, 1920), and *Schistocerca lineata,* which, once it had reached the sandy Coastal Plain, was able to maintain itself there and even spread southward along the coast to Virginia and North Carolina. Whether its scattered occurrence along the eastern edge of the Appalachians represents invasion from the seaboard, or spread through gaps in the mountains from the west, is uncertain. In the latter event, *lineata* was probably once widely distributed over Kentucky, West Virginia and Pennsylvania at the time of its maximum eastward expansion of range, but has now disappeared from most of that area. In Ohio it is restricted to the sandy regions bordering Lake Erie and the Maumee glacial outlet, and to relict prairie and ruderal prairie-like situations in the unglaciated sandy uplands in the southeastern part of the state. According to the hypothesis here stated, the meeting of *lineata* with its siblings on the Atlantic Coastal Plain is the most recent of the major events in the history of the Alutacea Group.

NOMENCLATURE, DIAGNOSES, RECORDS, AND REFERENCES

Although most specimens can be assigned to species with fair certainty on the basis of form, coloration, and measurements, critical identification

requires the examination of the concealed male genitalia. On account of the variability and overlap of most external characters construction of a simple key is not possible; in lieu of it a condensed diagnosis of the principal characteristics of each species is included in the following treatments.

Schistocerca alutacea (Harris)

(Plates XIV, i, j, o, p; XV, m–z; XVII, e, f; XIX)

1841. *Acrydium alutaceum* Harris, Rept. Ins. Inj. Veg., 139 [Martha's Vineyard, Massachusetts].

TYPE.—Destroyed. When examined in 1939 in the collection of the Boston Society of Natural History nothing remained of it but a fragment of intestine adhering to the pin. From the original measurements and descriptions it was evidently a female.

PLESIALLOTYPE.—Male, West Chop, Martha's Vineyard, Massachusetts, August, 1893 (A. P. Morse), here designated; in collection of Museum of Comparative Zoology.

At my request the late Dr. Frank Morton Jones made a thorough search on Martha's Vineyard for the species during several successive summers, without success. Fortunately, discovery of the topotypic male here designated plesiallotype (a specimen perfectly typical of the species treated in this paper as *alutacea*), taken in conjunction with the original description, permits assignment of Harris' name with certainty.

DIAGNOSIS.—General coloration of male very dark brown or olivaceous on head and thorax, tegmina dark brown, sometimes slightly purplish brown, usually unspotted, face usually dark; coloration of female often somewhat lighter, frequently reddish brown, tegmina plain or spotted; dorsum in both sexes with percurrent bright yellow stripe, often tinged with green and sometimes orange-yellow. Antennae of male relatively long (III, a; X, c); head relatively narrow and eyes little prominent (VI, c; X, a; XIV, i, o), the interocular space narrow (III, b; VIII, c, d) and the frontal costa narrow and in dorsal aspect projecting more strongly in front of eyes than in the other species (XIV, j, p); in dorsal view sides of prozonal part of pronotum subparallel, of metazona more abruptly flared caudad than in the other species, giving a more "shouldered" appearance (compare XIX, a, b, with XVIII and XX); hind femur relatively slender and elongate in both sexes (VI, c, d; VII); male cerci moderately large, subquadrate, distal margin more or less distinctly truncate-emarginate (XV, m–z), resembling those of *lineata* but larger, more deeply notched and more quadrate than those of *rubiginosa*; concealed male genitalia as shown in Figure 1, a, c, and Plate XVII, e, f; ovipositor more slender and elongate, with curvature

of scoop of dorsal valve less abrupt than in *lineata* and most *rubiginosa* (XIV, w).

NORMAL HABITAT.—Marshes, bogs, shrubby swamps, thickets of bushes and weeds in wet or moist environments, marginal thickets of mesic forest.

RANGE.—Sandy regions adjacent to the southern shores of Lakes Michigan, Huron, and Erie; southern New England and the Atlantic and Gulf Coastal Plains to eastern Texas and southern Florida; scattered records on the Piedmont and in northern Alabama, north-central Tennessee, and the Ouachita Mountains in Arkansas and easternmost Oklahoma (Fig. 5).

NOMENCLATURE.—The species has no synonyms. A great many of the

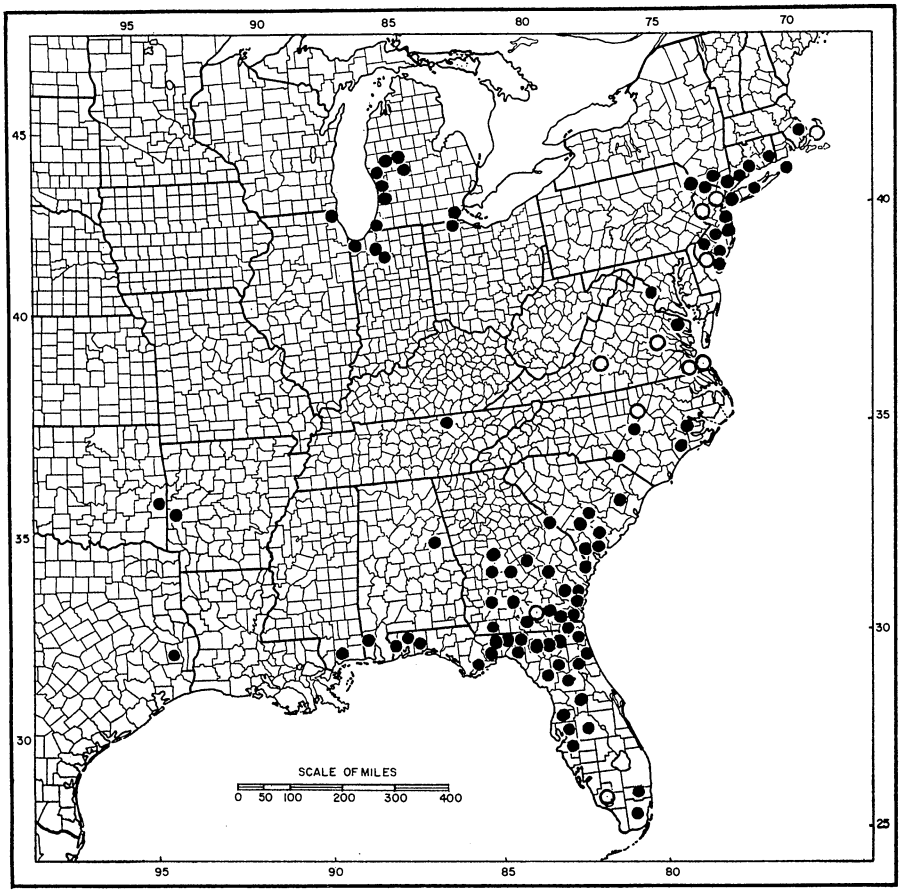

FIG. 5. Distribution of *Schistocerca alutacea* (Harris). Solid dots, specimens examined; open circles, reliable published records.

records that have been published under this name apply to *lineata* or *rubiginosa*.

RECORDS.—These include both the locality of specimens seen in the course of this study (769: 489 males, 280 females, *starred if previously recorded) and °published records that can be reliably assigned to this species, although the material on which they were based has not been seen.

ALABAMA: Clay-Cleburne Cos., *Chehawhaw [Cheaha] Mountain, 2000–2400 ft.; Houston Co., Cowarts; Lee Co., Chewacla State Park; Mobile Co., Mobile, 0.6 mi. E of Louisiana state line on US Hwy 90. ARKANSAS: Garland Co., Hot Springs; Polk Co., °Eagleton, 1500 ft., °Mena, 1150–1700 ft., *Rich Mountain Station, 1625 ft. CONNECTICUT: Fairfield Co., South Wilton, *Stamford; Middlesex Co., Haddam, *Deep River; New Haven Co., Cheshire, *New Haven, *North Haven. FLORIDA: Alachua Co., Cross Creek, Fairbanks, *Gainesville, Orange Heights, Waldo, Warburg Lake; Baker Co., Glen St. Mary; Broward Co., Ft. Lauderdale, 5.8 mi. N of Hammondville; Collier Co., °Chokoloskee; Columbia Co., Mt. Carrie; Dade Co., Paradise Key [Everglades Nat'l. Park]; Duval Co., *Atlantic Beach, Baldwin, *Jacksonville, 8.6 mi. N of Middleburg, °Pablo Beach [= Jacksonville Beach], °St Johns Bluff; Escambia Co., 2.6 mi. E of Alabama state line on US Hwy 90, *Ft. Barrancas; Franklin Co., *Carrabelle; Gilchrist Co., Trenton; Highlands Co.; Hillsborough Co., Little Manatee River at US Hwy 41; Indian River Co., Eau Gallie; Jefferson Co., Covington, 4.4 mi. NE of Fanlew, Lamont, Monticello, 3 and 7 mi. E of Thomas City, 0.7 mi. N jct. US Hwy 90 and Fla. Hwy 257; Lake Co., 3.3 mi. E of Altoona, Astor Park, Shore of Lake Harris, South shore of Lake Griffin, 2 mi. W of Tavares; Leon Co., 4 mi. SE of Woodville; Levy Co., Bronson, 3.8 mi. E of Otter Creek; Madison Co., Ashville, Logan Lake (6 mi. W of Greenville), Shady Creek; Manatee Co., Manatee; Marion Co., 4.3 mi. W of Dunnellon, Juniper Springs and other localities in Ocala Nat'l. Forest; Nassau Co., Fernandina Beach; Okaloosa Co., 4.8 mi. NW of Baker; Osceola Co.; Pasco Co., 2 mi. SE of Dade City; Pinellas Co., Tarpon Springs; Polk Co., 12 mi. N of Haines City, 3.7 mi. S of Lakeland; Putnam Co., Orange Mills, *Welaka; St. Johns Co., 2.1 mi. S of Durbin, Hastings; Santa Rosa Co., Milton; Suwanee Co., Houston, °Live Oak; Taylor Co., 4.5 mi. N of Boyd, 5.4 mi. E of Perry; Wakulla Co., Wakulla; Walton Co., °DeFuniak Springs. GEORGIA: Camden Co., 2.3 mi. N of Kingsland; Chatham Co., Hunter Field, Isle of Hope, *Sandfly, 9.4 mi. S of Savannah; Crawford Co., Gaillard; Decatur Co., *Between Climax and Bainbridge; Dougherty Co., *Albany; Glynn Co., 6.3 mi. S of Altamaha River on US Hwy 17, 1.2 mi. W of jct. Ga. Hwy 99 with US Hwy 17, *Brunswick, Fancy Bluff; Grady Co., Cairo; Laurens Co., Dublin, 8.6 mi. S of Garetta, 3.6 mi. W of Scott; Lowndes Co., Lake Park; Macon Co., Green's Mill; McIntosh Co., Darien; Pulaski Co., Hawkinsville; Richmond Co., 2.1 mi. SW of jct. Ga. Hwy 58 with US Hwy 1; Thomas Co., Thomasville; Tift Co., Tifton; Toombs Co., Vidalia; Ware Co., *Billy's Island, *Suwanee Creek (Lot 328, 12 Dist.), both in Okefinokee Swamp; Wayne Co., *Jesup. ILLINOIS: Lake Co., *Beach, *Waukegan. INDIANA: *Fulton Co.; *Lake Co., Millers, Mineral Springs [= Dune Acre]; Porter Co., Dune Park, Tremont Dunes; *Starke Co. °MARYLAND (Morse). MASSACHUSETTS: Barnstable Co., *Wellfleet (Cape Cod); Martha's Vineyard (type locality), *West Chop (plesiallotype); Norfolk Co., Needham; Plymouth Co., *Wareham. MICHIGAN: Allegan Co.; Berrien Co., *Warren Woods (E. K. Warren Preserve), *New Buffalo; Mecosta Co.; Monroe Co., 3 mi. W of Temperance; Montcalm Co.; Muskegon Co.; Newaygo Co.; Ottawa Co.; St. Joseph Co., Klinger Lake, near Sturgis. MISSISSIPPI:

Harrison Co., *Gulfport. NEW JERSEY: Atlantic Co., *Parkdale; Bergen Co., Tenafly; Burlington Co., *Atsion, New Lisbon, *Speedwell, Whitesbog; Camden Co., °Clementon; Cape May Co., Cold Spring, °Dennisville, Erma, *Sea Island Junction, °South Seaville, Swainton, Woodbine; Essex Co., °Caldwell, °Newark; Gloucester Co., °Glassboro, Wenonah; Middlesex Co., *Jamesburg, New Brunswick; Monmouth Co., Allaire, 2 mi. SE of Farmingdale; Ocean Co., Brookville, *Center of East Plains, *Lakehurst, Manahawkin, Palermo, *Stafford's Forge; Passaic Co., Ramsey; Sussex Co., Sussex. NEW YORK: *New York City, °Central Park; Orange Co., West Point, Pine Island; Rockland Co., *West Nyack; Westchester Co., Bronxville, Hartsdale, Katonah; Long Island, Flatbush, °Riverhead, *Wading River, Wood haven, °Wyandanch, °Yaphank; *Staten Island, °Arrochar, °Old Place, °Long Neck, °Richmond, °Richmond Valley, *Delaware. NORTH CAROLINA: Beaufort Co., "Dingo Bluff" [Pungo Bluff]; Craven Co., *New Berne; Harnett Co., Spout Springs; New Hanover Co., *Wilmington; Onslow Co., Camp Davis (Holly Ridge); Pender Co., Atkinson, Holly Shelter (12 mi. E of Burgaw); Scotland Co., *Gibson; Wake Co., °Raleigh. OKLAHOMA: LeFlore Co., 1 mi. NW of Page. PENNSYLVANIA: Delaware Co., *Tinicum [Tinicum Island is in New Jersey]; Pike Co., Milford. SOUTH CAROLINA. Bamberg Co., *Denmark; Beaufort Co., Hardeeville, Limehouse; Charleston Co., *Ashley Junction, Charleston, Seven Mile; Hampton Co., Gifford, *Yemassee; Jasper Co., 1.5 mi. S of Coosahatchee River on US Hwy 17, 5.6 mi. N of Ridgeland; Orangeburg Co., Four Hole Swamp; Williamsburg Co., Lane. TENNESSEE: Fentress Co., Allardt; Morgan Co., Clear Fork near Burrsville. TEXAS: Tyler Co., *Doucette. VIRGINIA: Allegheny Co., Covington (female, AMNH); Arlington Co., Summit; Buckingham Co., °Wingina; Nansemond Co., °Deanes; Norfolk Co., °Portsmouth; Richmond Co., *Naylor's.

REFERENCES IN LITERATURE.—The species has seldom been recorded under any other than its proper name, and the following references to *alutacea* apply to it wholly or in part.

Beutenmüller, 1894: 304, Pl. 9, fig. 2 (N.Y.); Blatchley, 1903: 294, fig. 63 (Ind.); *Idem*, 1920: 314, fig. 114 (Ind.; New England [not] to California and Mexico); Brimley, 1908: 18 (N.C.); *Idem*, 1938: 25 (N.C.); Davis, 1899; 80 (N.J.); *Idem*, 1913: 79 (N.J.); *Idem*, 1915: 95 (Fla.); *Idem*, 1923: 69 (N.Y.); *Idem*, 1926: 34 (Va.); *Idem*, 1928: 34 (N.Y.); Dozier, 1920: 355 (Fla.); Fernald, 1888: 114 (N.Eng.); Fox, 1914: 507 (N.J.); *Idem*, 1917: 219 (Va.); *Idem*, 1928: 50 (N.J.); Franklin, 1950: 17 (N.J.); Friauf, 1953: 108, 109, 115, 116, 117 (Fla.); Hancock, 1911: 330, 366, fig., p. 369 (Mich., part); Harris, 1841: 139 (original descr., Martha's Vineyard, Mass.); *Idem*, 1850: 150; 1852: 150; 1862: 173 (later editions); Headlee, 1922: 463 (N.J.); Hebard, 1934: 189 (Ill.); *Idem*, 1937–38: 277 (Pa.); Hubbell, 1922: 46 (Mich.); Kirby, 1910: 457 (Walker's *Cyrtacanthacris concolor, Acridium proprium, A. scutellare,* and *A. strenuum,* all Mexican; *Acrydium rubiginosum* Harris and *Acridium emarginatum* Dodge erroneously listed as synonyms); Knutson, 1940: 51 (E. Texas); Laird, 1943: 483 (male gonads of intermediate type, between fountain and radiating types, as in most Cyrtacanthacridinae); Morse, 1894: 105 (N.Eng.); *Idem*, 1898: 271, Pl. 7, fig. 32 (Mass., Conn., distinctions from *rubiginosa* [*lineata*] pointed out); *Idem*, 1899: 318 (N.Eng.); *Idem*, 1904: 39 (S. Car., Fla.); *Idem*, 1907: 13, 14, 15, 19, 42, 43 (Ala., Miss., Ark.); *Idem*, 1919: 35 (N. Eng.); *Idem*, 1920: 490, fig. 86, Pl. 22, fig. 2 (N.Eng., dorsum of head and pronotum figured in comparison with that of *rubiginosa* [*lineata*]); Newton and Gurney, 1956–57, Map 108, p. 226 (range, confused with those of *lineata* and *rubiginosa*); Nininger, 1915: Pl. 1, fig. 3b (mandi-

bular morph.); Rehn, 1901: 12; 1902: 89 (N. J., in copula with *"rubiginosa"*); *Idem,* 1902*a*: 312 (N.J., *rubiginosa* erroneously synonymized); *Idem,* 1904: 328 (N.J.); Rehn and Hebard, 1905: 40; 1907: 292 (Fla.); *Idem,* 1910: 632 (N.C.); *Idem,* 1916: 200–04 (N.J., N.C., S.C., Ga., Fla.; analysis of variation); Riley, 1884: 194 (E. U.S.); Scudder, 1862: 466 (Mass., Conn.); *Idem,* 1868: 4 (bibl.); *Idem,* 1899: 445, 464 (N. Eng., N. Y., Md., N. C., Ga., Fla., Ind., Ill., remaining records erroneous); *Idem,* 1900: 102 (N. Eng.); *Idem,* 1900*a*: 47 ("U. S. east of Sierra Nevadas, southern California"; *emarginata* Dodge erroneously synonymized); *Idem,* 1901: 5, 286 (bibl.); Sherman and Brimley, 1911: 389 (N. C.); Slifer, 1940: 207, Pl. 8, fig. 106 (spermatheca and associated glandular pouches, similar throughout genus); J. B. Smith, 1892: 34 (N. J., Mass.); *Idem,* 1900: 157; 1910: 183 (N. Y., N. J.); S. I. Smith, 1873: 370, 381 (Conn.); C. Thomas, 1873: 171 (N. Eng. to Fla.); Walden, 1911: 108, Pl. 9, fig. 5 (Conn.); Walker, 1870: 577 (U. S.; citations); *Idem,* 1871: 609 (Fla.). J. B. Smith (1900: 157) recorded *alutacea* under the name *obscura* from Newark, Caldwell, and Jamesburg to Cape May, N. J.

References to *alutacea* that are applicable wholly or in part to *rubiginosa* or to *lineata* are listed under those species. The following species have been incorrectly recorded as *alutacea*: *obscura* (Morse, 1904, Savanna and Tybee Island, Ga., Carrabelle, Fla. (part); Watson, 1918: 248, and 1926: 407, Fla.); *shoshone* or some member of its group (Anon., 1956: 747, near Hazen, Nev.; Caudell, 1903: 796, Grand Junction, Colo.; Rehn, 1901*a*: 334, Cuyamaca, Cal.; Woodworth, 1902: 18, Calif.). The Bahama Islands records of *alutacea* by Rehn (1906:115) and Bruner (1913: 495) are of doubtful validity.

Schistocerca rubiginosa (Harris)

(Plates XIV, e–h, m, n, t, v; XV, a–l; XVII, c–d; XVIII)

1862. *Acridium rubiginosum* Harris, in Scudder, Boston Jour. Nat. Hist., 7: 467 [South Carolina (type); also listed by Scudder from Cape Cod, Mass., Conn., So. States, and Ala.].

TYPE.—Not found. It should have been in the Harris collection in the Boston Society of Natural History, or in the Scudder collection in the Museum of Comparative Zoology, but careful search in the former in 1939 and in the latter in subsequent years has been without result. Fortunately there can be no doubt concerning the identity of the species; only *alutacea* and *rubiginosa* occur in South Carolina, and *alutacea* always has a complete middorsal pale stripe, absence of which was the primary basis on which Harris described *Acridium rubiginosum*. A male with the following data, in the collection of the University of Michigan Museum of Zoology, is here designated plesiallotype: 1.1 mi. N of Limehouse on US Hwy 17, Beaufort Co., South Carolina, Aug. 20, 1947 (T. H. Hubbell; field cat. no. 2). The cerci of this specimen are almost exactly like XV, c, the concealed male genitalia like XVII, c, d, and its head and subgenital plate are shown in outline in XIV, g, h, t. Coloration of plesiallotype reddish brown, tegmina with numerous slightly darker brown small annular spots, pronotal lobes with paler blotches on upper half anterior to principal sulcus, pronotal dorsum unicolorous except for small pale spot at junction of low median carina with principal sulcus.

DIAGNOSIS.—General coloration in both sexes yellowish brown, reddish brown, or grayish brown, never with greenish tinge, face and sides of pronotum usually concolorous with or slightly paler than dorsum of head and pronotum, lateral lobes often with weakly indicated paler blotches or horizontal bars on upper half cephalad of principal sulcus; tegmina plain or spotted with darker brown, the spots varying from small and few or numerous to large and partly confluent, the latter condition commoner in the south and in the female than in the north and in the male; vertex, pronotum and anal margins of tegmina often unicolorous or the pronotum with dark spots, but anal tegminal margins frequently paler than remainder, and a mediodorsal yellowish or faintly orange stripe sometimes present on head, on pronotum, or on both, all these light markings varying independently to produce individuals with dorsal stripe on head only, on pronotum only, on head and pronotum, on tegmina only, or percurrent. Pronotal stripe, when present, usually narrow and never strikingly contrasted as in *alutacea*. Antennae of male relatively short (III, a; X, c); head relatively broad above and eyes more prominent than in *alutacea*, especially in male (VI, c; X, a; XIV, e–h, m, n), the interocular space relatively broad (III, b; VIII, c, d) and the frontal costa broader and projecting less strongly in front of eyes than in *alutacea* (XIV, e–h, m, n); sides of pronotum more nearly parallel than in *alutacea*, a little less expanded at shoulders (cf. XVIII, XIX); hind femur relatively stouter and shorter than in *alutacea* (VI, c, d; VII); male cerci distinctly smaller and more tapering than in *alutacea* and *lineata*, very shallowly notched at tip (XV, a–l); concealed male genitalia as shown in Figure l, e, f, and Plate XVII, c ,d; ovipositor generally shorter and stouter than that of *alutacea*, with scoop of dorsal valves shorter and deeper (XIV, v), but variable.

NORMAL HABITAT.—Xeric to xeromesic situations, especially on sandy soil, in open sunny forest, oak or pine but with broad-leafed tree seedlings or forbs in the undergrowth, and in sand scrub, dry flatwoods, and brushy or weedy fields and pastures; intermingling with *alutacea* in shrubby ecotones between dry and wet environments.

RANGE.—The Atlantic and Gulf Coastal Plains, from New Jersey to the Florida Keys and eastern Texas, with outlying colonies on the Piedmont of Virginia and the Carolinas, and in northeastern Alabama (slopes of Chocco-locco and Cheaha mountains) (Fig. 6.).

NOMENCLATURE.—*Rubiginosa* has no synonyms, and this name has itself stood in the synonymy of *alutacea* for nearly sixty years; most records, therefore, are under the latter name.

RECORDS.—Of this species, 901 specimens (557 males, 298 females, and

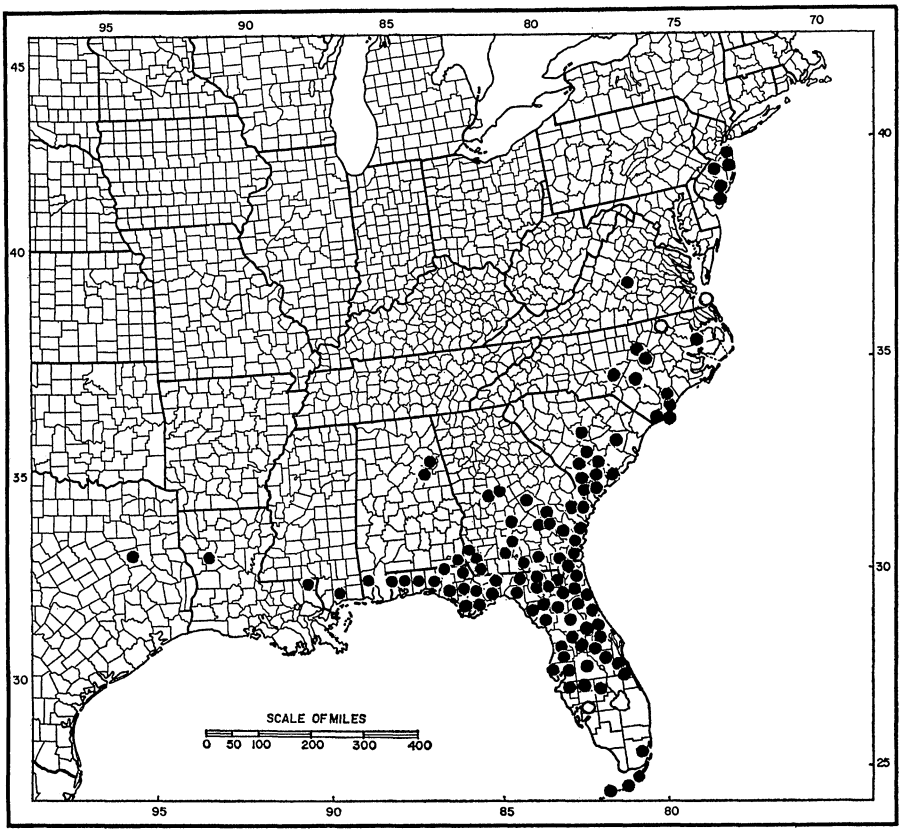

FIG. 6. Distribution of *Schistocerca rubiginosa* (Harris). Solid dots, specimens examined; open circles, reliable published records.

46 juveniles) have been studied. For the significance of the symbols in the following list of records, see *alutacea*.

ALABAMA: Calhoun Co., Choccolocco Mountain (Camp McClellan); Mobile Co., St. Elmo; Monroe Co., Little River State Forest; Talladega Co., E of Mumford on slopes of Cheaha Mountain. FLORIDA: Alachua Co., Alachua, Archer, Arredondo, 2 mi. N Cross Creek, Fairbanks, Gainesville and vicinity, Newberry (and 5 mi. N), Newnan's Lake, Paradise, 1 mi. S edge of Payne's Prairie on US Hwy 41; Bay Co, Auburn, Lynn Haven, Panama City (and 4 mi. N); Brevard Co., Eau Gallie, °LaGrange, Melbourne; Calhoun Co., Blountstown, Chipola River; Charlotte Co., *Punta Gorda; Clay Co., Gold Head Branch State Park, Highland; Collier Co.; Columbia Co., 3.5 mi. N Santa Fe River bridge on US Hwy 41; Dade Co., *Biscayne Bay, Bonefish Key, °Detroit [Homestead], °Miami, Paradise Key [Royal Palm State Park], Silver Palm; Dixie Co., Buies (near Steinhatchee River), near Hines (6 mi. S Steinhatchee River), Cross City (4 mi. N Shamrock); Duval Co., 2 mi. SE Arlington, *Atlantic Beach, *Jacksonville, *Pablo Beach [= Jacksonville Beach], San Pablo; Escambia Co., 2.6 mi. E of Alabama state line on US

Hwy 50; Flagler Co., 2 mi. W of Flagler Beach; Franklin Co., *Carrabelle (and 1 mi. inland), 7 mi. NE of Lanark; Glades Co., Palmdale; Gilchrist Co., 1.4 mi. W of Alachua Co. line on Fla. Hwy 26; Hamilton Co., 3 mi. S Jasper; Hardee Co., Wauchula; Hernando Co., Weekiwatchee Springs; Highlands Co., Hicoria, Tamiami Trail; Hillsborough Co., Dug Creek, Hillsborough River State Park, Little Manatee River at US Hwy 41, Plant City, Tampa; Holmes Co., Ponce de Leon; Indian River Co., 2.6 mi. S of Sebastian; Jackson Co., 3.9 mi. N of Alford, 3.7 mi. SE of Marianna; Jefferson Co., Covington, El Destino, Fanlew, Lamont (and 4.2 and 8 mi. south), Lake Miccosukee, Monticello, 0.7 mi. N of jct. Fla. Hwy 257 with US Hwy 90, Thomas City (and 3.2 and 6.8 mi. south); Lake Co., Alexander Spring Creek at Fla. Hwy 55 (and 1.4 mi. N), 3 mi. E of Altoona, Astor, 2.5 mi. W of Crow's Bluff, 4.5 mi. E of Eustis, 3.5 mi. NE of Fruitland Park, Leesburg and vicinity (and 6 mi. east), 2 mi. W of Tavares; Leon Co., 1.5 mi. W of Fanlew, Natural Bridge, °Tallahassee; Levy Co., 3.5 mi. W of Archer, Bronson (and 8.1 mi. W), Cedar Keys (and 4 mi. E on mainland), 3.6 mi. S of Otter Creek, Rosewood, Sumner, Wylly; Liberty Co., Alum Bluff, Bristol, Hosford, "Old Camp Torreya" (T. 2 N., R. 7 W); Madison Co., 3 mi. W of Ellaville; Manatee Co., Bradenton, Manatee; Marion Co., The Big Scrub (10 mi. SW of Ocala), 4 mi. W of Dunnellon, Eureka, Ocala Nat'l. Forest (numerous localities); Monroe Co., °Big Pine Key, °Long Key, *Key West; Nassau Co., Fernandina; Okaloosa Co., Delaco, Fort Walton; Orange Co., 2.3 mi. N of Ocoee, Orlando (and 2.5 mi. E, 5.5 mi. W, and 8.5 mi. NW), Tangerine; Osceola Co., 2.6 mi. E of St. Cloud; Pasco Co., 2 mi. SE of Dade City; Pinellas Co., 2.4 mi. E of Tarpon Springs; Polk Co., Bartow, Hesperides, Lake Streaty, 3 mi. E of Lakeland, 4.5 mi. E of Mulberry; Putnam Co., 2 mi. E of Melrose, Satsuma, *Welaka; Santa Rosa Co., 11.9 mi. NE of Milton; Seminole Co., Altamonte Springs; Sumter Co., 3.4 mi. N of Mable; Taylor Co., 2 mi. S of Athena, Boyd (and 4.5 mi. N), Hampton Springs, 4.6 mi. N of Salem; Volusia Co., Barberville (and 3.5 mi. NE), Benson Junction, 2.3 mi. W of Daytona Beach, Deland (and 2.5 mi. E), 4 mi. NE of DeLeon Springs, Glenwood, 5.4 mi. W of New Smyrna; Wakulla Co., St. Marks, 9.2 mi. N of Sopchoppy; Walton Co., De Funiak Springs, Mossy Head, Portland. GEORGIA: Appling Co., Baxley, north of Blarney; Bibb Co., Macon; Bryan Co., *Cannoche River near Groveland; Camden Co., 2.3 mi. N of Kingsland, 2.1 mi. E of Waverly; Charlton Co., Folkston, Okefinokee Swamp (*Billy's Island, *Suwanee Creek); Chatham Co., *Isle of Hope, *Sandfly, *Tybee [Island]; Clinch Co., *Homerville; Colquit Co., 3 mi. N of Norman Park; Crawford Co., Gaillard; Decatur Co., Bainbridge, *between Climax and Bainbridge, *Spring Creek; Dougherty Co., °Albany; Glynn Co., *Brunswick (and 10 mi. N), Fancy Bluff; Jackson Co., °Thompson's Mills; Jeff Davis Co., Hazelhurst; Laurence Co., 8.6 mi. S of Garetta; Liberty Co., Flemington; Lowndes Co., Lake Park, 6 mi. N of Valdosta; McIntosh Co., Darien, 7.5 mi. N of Eulonia; Richmond Co., °Augusta; Screven Co., 2.3 mi. N of jct. Ga. Hwy 24 and US Hwy 301; Tift Co., 5.4 mi. SW of Tifton; Toombs Co., 9.1 mi. S of Lyons, Vidalia; Wayne Co., *Jesup; Wilcox Co., near Bowen's Mill. LOUISIANA: Grant Par., °Lincecum [not Texas as cited by Scudder]; Natchitoches Par., Natchitoches; Washington Par., Bogolusa. MISSISSIPPI: Forrest Co., Hattiesburg; Harrison Co., *Nugent. NEW JERSEY: *Pine Barrens; Burlington Co., *Atsion, Medford, Pemberton, Rancocas, *Speedwell; Cape May Co., Erma, *Mt. Pleasant; Monmouth Co., Allaire, 2 mi. E of Farmingdale; Ocean Co., Brookville, *Lakehurst, Manahawken, *Stafford's Forge. [Many of the records of *alutacea* and *rubiginosa* from other New Jersey localities given by Rehn (1902, 1904), Fox (1914, 1928), and J. B. Smith (1892, 1900, 1910) are certainly applicable to *rubiginosa*, but cannot be assigned without examination of the specimens.] NORTH CAROLINA: Allegheny Co., Little River near Eunice; Beaufort Co., *"Dingo Bluff" [= Pungo Bluff]; Brunswick Co., Cape

Fear Peninsula (Ft. Smith), Cape Fear (Smith's Island), *Smithville [= Southport]; Craven Co., °New Berne; Cumberland Co., 3 mi. S of Fayetteville; Halifax Co., °Homestead, °Weldon; Harnett Co., Spout Springs (in sand hills SW of Lillington); Moore Co., *Southern Pines; New Hanover Co., Carolina Beach, *Wilmington, *Winter Park; Pender Co., Atkinson, Holly Shelter Refuge (13 mi. E of Burgaw); Wake Co., NW of Raleigh. SOUTH CAROLINA: Bamberg Co., *Denmark; Beaufort Co., Limehouse (plesiallotype); Charleston Co., *Ashley Junction, °Isle of Palms, Seven Mile; Colleton Co., 5 mi. SE of Islandton, 2 mi. N of Salkehatchie River on US Hwy 21, 3.7 mi. W of Walterboro; Dorchester Co., 2.2 mi. N of Grover; Hampton Co., *Yemassee; Jasper Co., 1.5 mi. S of Coosawhatchie River on US Hwy 17, 5.6 mi. N of Ridgeland; Orangeburg Co., Four Hole Swamp; Richland Co., *Columbia; Williamsburg Co., Salter's Depot. TEXAS: Anderson Co., *Elkhart; Smith Co., °Tyler.

REFERENCES IN LITERATURE.—Since 1904, *Schistocerca rubiginosa* has seldom been recorded under any other names than *alutacea* and *alutacea rubiginosa*, and without examination of the material on which they were based it is frequently impossible to assign records properly. From South Carolina southward, however, it is safe to assume that specimens said to be unstriped are *rubiginosa*, though the converse is not true. The following are believed to apply wholly or in part to this species.

As *rubiginosa* or *alutacea rubiginosa*: Blatchley, 1920: 316 (N. J. to Fla.; other records apply to *lineata*); Brimley, 1938: 25 (N. C.); Davis, 1913: 79; 1913*a*: 86 (N. J.); *Idem*, 1914: 196 (Fla.); Fox, 1914: 508 (N.J.); Friauf, 1953: 98, 99, 101, 103, 111, 112, 113 (Fla.); Harris, in Scudder, 1862: 467 (S. C., original descr.); Morse, 1904: 39 (S. C., Ga., Fla.); *Idem*, 1907: 18, 19, 42 (Miss.); Riley, 1884: 194 (E. U. S.); Scudder, 1868: 7 (bibl.); *Idem*, 1899: 455, 462 (N.C., Va., D.C., Ga., Fla., "Tex." [La.]; [probably not] Bahama Is.; the other U.S. records apply to *lineata*, those from México and Guatemala to other spp.); *Idem*, 1900*a*: 48 ("U.S. east of Rockies"); *Idem*, 1901: 10, 288 (bibl.); Seiss, 1901: 294 (N. J.); Sherman and Brimley, 1911: 389 (N. C.); C. Thomas, 1873: 170 (S. C. only; remainder apply to *lineata*); Walker, 1870: 578 (U.S.).

As *alutacea*: Allard, 1916: 277 (Ga.); Dozier, 1920: 355 (Fla.); Isely, 1937 (East Texas Timbers belt; Elkhart, Tyler); Isely, 1944: 56 (herbivorous type mandibles; oak leaves chosen); Knutson, 1940: 51, 52 (E Texas); Rehn, 1902: 89; 1902*a*: 312; 1904: 328 (N. J.); Rehn and Hebard, 1905: 40 (Fla.); *Idem*, 1907: 292 (Fla.); *Idem*, 1910: 632 (N. C.); *Idem*, 1914: 107; 1914*a*: 395 (Fla.); *Idem*, 1916: 200–04 (*alutacea* and *rubiginosa* treated as single variable species; N. J., N. C., S. C., Ga., Fla.); T. B. Smith, 1910: 183 (N. J., N. Y.).

Some of the records of *rubiginosa* and *alutacea rubiginosa* from the Atlantic seaboard and all those from west of the Appalachians apply to *lineata*, except those given by Scudder (1899: 463) from México, Yucatán, and Guatemala, unassignable, but almost certainly based on extra-limital species, and that from Inagua in the Bahamas, which might conceivably be *rubiginosa*, but probably is not.

Schistocerca lineata Scudder

1872. *Acridium emarginatum* Scudder, Final Rept. U. S. Geol. Surv. Nebr. and Adj. Terr. (Hayden), p. 250 (♂, ♀; Banks of the Platte River, [Nebr.]).

1899. *Schistocerca lineata* Scudder, Proc. Amer. Acad. Arts and Sci., 34: 455, 462 (♂, ♀; Barber Co., Kans.; Texas [Louisiana], Lincecum; San Antonio, Tex., Gulf coast of Texas; Montelovez [Monclova], Coahuila, Mex.).

1906. *Schistocera scudderi* Bruner, Proc. U. S. Natl. Mus., 30: 676 (new name for *lineata* Scudder, [not] preoccupied in *Schistocerca* by *Gryllus* (*Locusta*) *lineatus* Stoll [which is an *Acanthacris*].

TYPES.—I was unable to find the type material of Scudder's *emarginatum* in the collection of the Museum of Comparative Zoology or in the U. S. National Museum, nor is it mentioned in Gurney's 1950 manuscript list of the types of Orthoptera contained in the latter institution. It may have been overlooked, because the name has been attributed to Uhler and dismissed as a *nomen nudum*. Rehn and Hebard (1912: 95) designated as single type of *lineata* a male from Barber County, Kansas (Cragin, collector), in the Hebard Collection, ex Bruner (now a part of the collection of the Academy of Natural Sciences of Philadelphia). This specimen has been examined; it is referable to the species for which the name *lineata* has been used throughout this paper, and has a broad, percurrent, middorsal stripe.

DIAGNOSIS.—Coloration extremely variable, as discussed above; ground color yellowish brown, reddish brown, dark brown, olivaceous brown, olive green, or occasionally rather yellowish green; face usually paler than dorsum when the latter is dark; middorsal stripe present or absent, varying much in breadth and intensity of coloration when present, but much more frequently present and usually broader in western than in eastern populations; when absent, pronotum often with a small yellowish fleck at junction of median carina and principal sulcus, and anal margins of the tegmina sometimes slightly paler than remainder of the surface or more often concolorous; tegmina immaculate to distinctly maculate; median stripe often bordered by blackish on pronotum and tegmina, especially in western populations; caudal femora unmarked above, or carinae black-punctate, or faintly or strongly contrasted crossbars present at proximal and distal thirds and sometimes at genicula; mesepimeron with or without a yellow bar, this being more often present in western than in eastern populations; yellow dots of thorax and black dots of abdominal tergites inconspicuous to conspicuous, the latter conditions more frequent in western populations; coloration generally duller in eastern populations, averaging brighter and more variable in western ones, material from south Texas and México showing maximum intensity of coloration and contrast; hind tibiae yellowish, brownish, black on extensor surface, or coral red. Proportions of body

closer to those of *rubiginosa* than of *alutacea*; male antennae relatively short (III, a, c; X, c); head broader and eyes more prominent than in *alutacea*, but usually somewhat less so than in *rubiginosa* (VI, c; X, a; XIV, a–d, k, l), the interocular space broader, frontal costa less prominent, and eyes slightly more protuberant than in *alutacea*, not strongly different from condition in *rubiginosa* (III, b; VIII, c, d; XIV, a–d, k, l); sides of pronotum somewhat less abruptly expanded at shoulders than in *alutacea* (cf. XIX, XX, XXI); hind femur relatively stout compared with that of *alutacea*, more like that of *rubiginosa* (VI, c, d; VII); male cerci rather large, variable in shape, but approaching subquadrate, usually with moderately to deeply emarginate distal margin (XVI); concealed male genitalia as shown in Figure 1, d, g, h, and Plate XVII, a, b; ovipositor shorter and scoop of upper valve more strongly excavate than in *alutacea* (XIV, u).

NORMAL HABITAT.—Very xeric to mesic situations, always with trees, shrubs, or forbs which constitute the normal food of the species, generally on sandy but sometimes on clay or rocky soils, in open woodland or in prairie and plains environments, in more arid western regions concentrated along stream valleys, in gulleys, and on wooded slopes; often injurious to forb crops.

RANGE AND RELATIONSHIP TO SOUTHWESTERN POPULATIONS.—The Atlantic Coastal Plain and adjacent uplands from southern New England to northern North Carolina, with a few scattered records near the eastern base of the Appalachians in the middle Atlantic states, and even fewer in Kentucky and Tennessee; the sandy regions in southeastern Ohio, around the southern Great Lakes, and along the glacial outlets in Indiana and Illinois; relict prairie areas in central and southern Indiana and Illinois; northern limits extending from southern New Hampshire and Ontario through central Wisconsin and southeastern Minnesota to southernmost Manitoba, Saskatchewan, and Alberta; southward, occupying the whole breadth of the Prairie and Plains, and scattered through the Ozarks, reaching the Gulf Coast in southern Texas and occurring south to Galeana in Nuevo León, México (Figs. 7, 8, 9).

The western limits are uncertain. Material concerning the identity of which there is no doubt is known from as far west as central Montana and Wyoming, along the east front of the Rockies in Colorado, the Rio Grande Valley in New Mexico, and trans-Pecos Texas. *Lineata* has also been reported from western New Mexico, the vicinity of the Grand Canyon in Arizona, and along the Mexican border in that state. I have seen specimens from northwestern New Mexico, from Holbrook and the San Carlos Indian Reservation in Arizona, and (one female) from Salt Lake City, Utah, that closely resemble *lineata* in appearance and may actually be referable to that

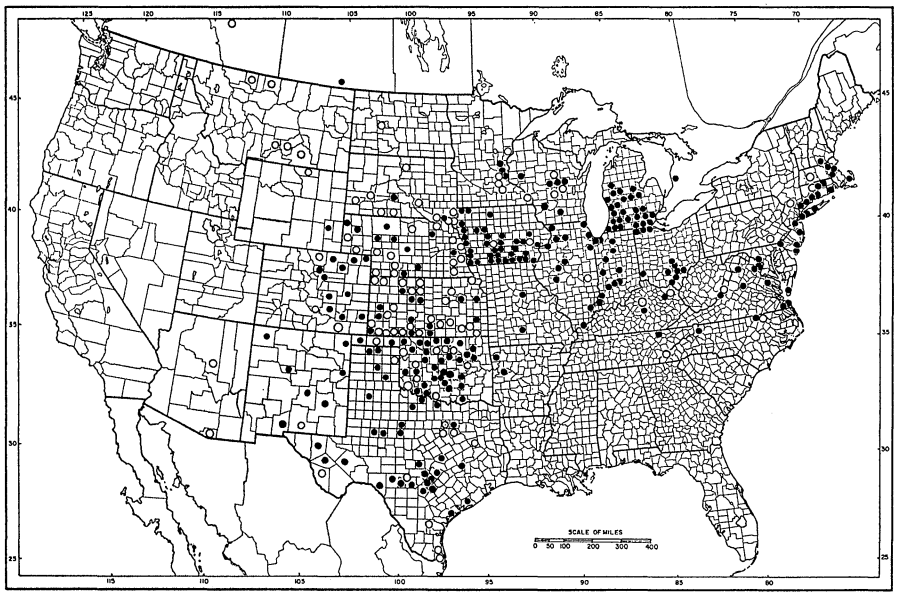

FIG. 7. Distribution of *Schistocerca lineata* Scudder. Solid dots, specimens examined; open circles, reliable published records.

species. A series from Craters of the Moon in Idaho looks like very intensively colored *lineata*, the dorsal stripe and mesepimeral band being bright greenish yellow, in strong contrast with the deep olivaceous brown ground color. In the males of all these western series, however, the "figure" formed by the dorsal margins of the rami of the cingulum is much constricted at the waist, in which respect they differ from typical *lineata* and agree with the group of western "red-legs" discussed in the introductory section. The relation of *lineata* to these populations, to the western "red-legs," and to the members of what I have here treated as the closely related Shoshone Group, is a difficult problem beyond the scope of this study. It is not impossible that all these will prove to be members of a single polytypic species complex.

NOMENCLATURE.—There can be no doubt that *lineata* is a strict synonym of *emarginata*, the latter having been adequately characterized by Scudder in the publication cited above. I have nevertheless kept to the former name throughout this paper since for the western populations it has been in continuous and unambiguous use for sixty years, during which time a considerable economic literature has grown up around it. The name *emarginatum* is generally attributed to Uhler or to Dodge, both of whom used it without characterization, and has been treated consistently as a *nomen*

nudum assigned [incorrectly] to the synonymy of *alutacea*. Since I myself have no strong feelings about strict priority in instances such as this, I shall leave it to those who do to argue the matter with their colleagues in the field of economic entomology.

RECORDS.—ALBERTA: °Manyberries; °Medicine Hat; °Comrey; °Higdon Ranch, valley of Milk River (all in southeastern corner). ARKANSAS: Logan Co., *Magazine Mountain (2600 ft.), Booneville; Washington Co., *Fayetteville. COLORADO: Boulder Co., Red Rocks, Chicken Ranch Gulch, 6700 ft. (both near Boulder); Denver Co., *Denver; El Paso Co., Colorado Springs and *Austin Bluffs nearby, °Manitou; Larimer Co., °Ft. Collins, °Timnath, °Windsor; Jefferson Co., Morrison (6–7000 ft.); Las Animas Co., °Garfield, °Trinidad; Lincoln Co., Smoky Hill to Denver; Logan Co., Crook, °Merino, °Sterling; Morgan Co., °Brush, °Orchard; Otero Co., La Junta, °Manton, °Nepesta, *Rocky Ford; Prowers Co., *Holly, *Lamar; Pueblo Co., *Pueblo (4700 ft.); Sedgwick

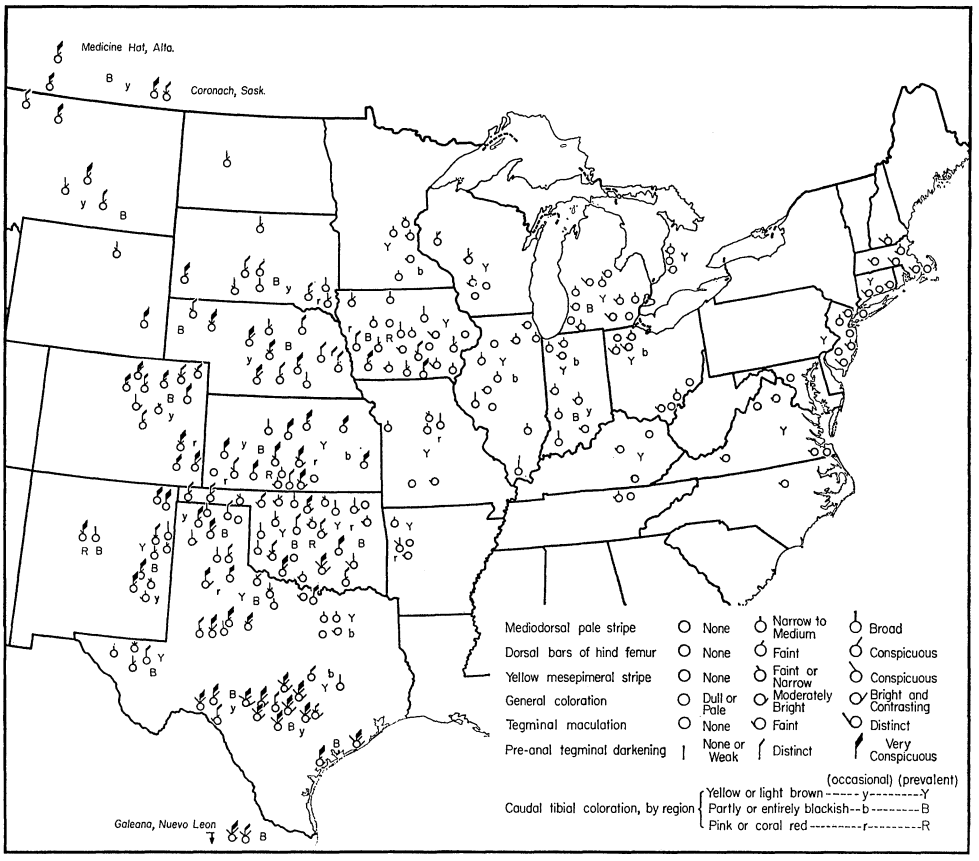

FIG. 8. Distribution of some of the principal color variants of *Schistocerca lineata* Scudder (generalized and semi-diagrammatic).

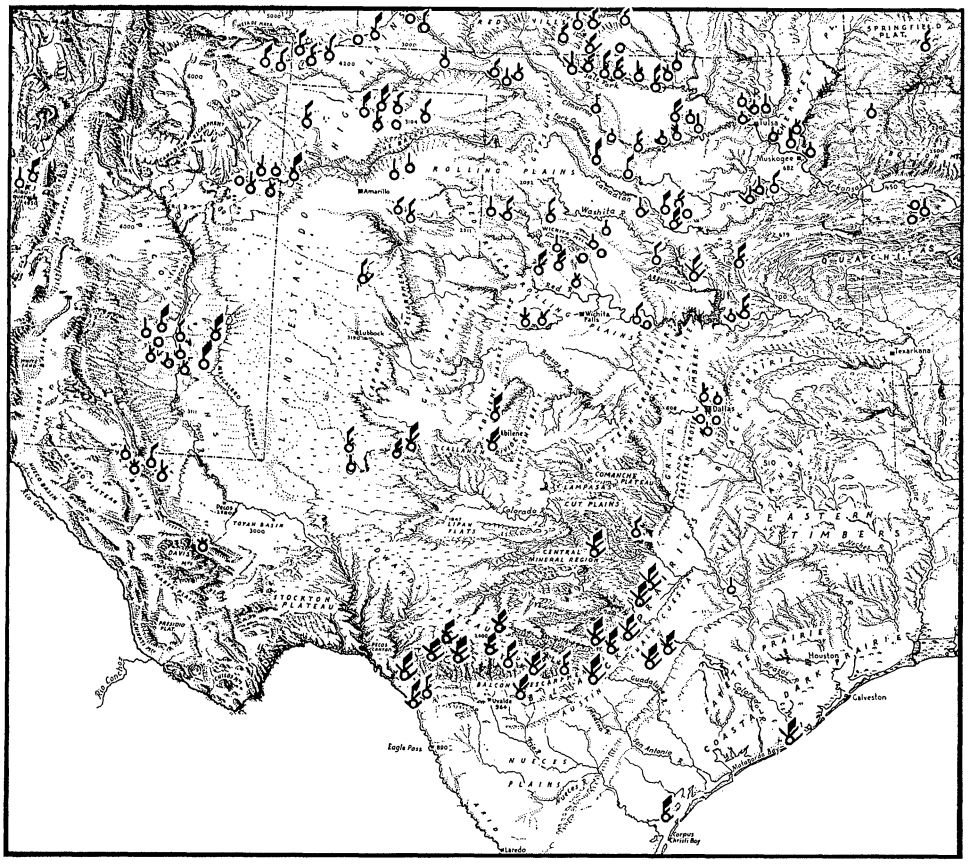

FIG. 9. Distribution of some of the principal color variants of *Schistocerca lineata* Scudder, in relation to physiographic and vegetational districts of Oklahoma, Texas, and adjoining regions. Symbols as in Fig. 8. Note association with stream valleys, and general absence from the High Plains and broad interfluves. Note also the concentration of the brilliantly colored south Texas type along the margins of the Edwards Plateau and in the Black and Coastal prairies, with a single occurrence east of the Arbuckle Mountains in Oklahoma, and the generally duller and less variegated coloration of the eastern (Missouri, Arkansas, eastern Oklahoma, and Dallas, Texas) and western (New Mexico and west Texas) populations as compared with those of the central Prairie-Plains region.

Co., °Julesberg, Sedgwick; Weld Co., *Greeley, Roggen, °Windsor. CONNECTICUT: Fairfield Co., *Greenwich, *Noroton, *Stamford; Hartford Co., °Farmington, °Granby; Middlesex Co., *Deep River; New Haven Co., *New Haven, *North Haven, South Meriden, °West Rock, °Yalesville; Tolland Co., Mt. Hope; Windham Co., *Canterbury, *Plainfield, *Thompson. DELAWARE: Newcastle Co., Wilmington. ILLINOIS: Coles Co., °Charleston; Cook Co., *Cheltenham, *Chicago (and *Windsor and *Jackson Parks); Henry Co., *Colona; Jo Daviess Co., Galena; Kankakee Co., "Hopkins Park," *St. Anne;

Lake Co., *Beach, *Zion; Lee Co., *Amboy, Dixon; Massac Co., *Metropolis; McLean Co., °Normal; Mason Co., *Bath, *Bishop, *Devil's Hole, *Devil's Neck, *Forest City, *Havana, *Topeka; Morgan Co., *Meredosia; Rock Island Co., *Moline; Tazewell Co., Lake Delavan; Whiteside Co., Fulton (and 3 mi. south). INDIANA: Brown Co.; *Cass Co.; *Crawford Co.; Gibson Co.; Greene Co., *relict prairie areas in vicinity of Switz City, including *Lattas Creek Prairie; *Knox Co., 2 mi. S of Sandborn; *Lake Co., *Mineral Springs [= Dune Acres], *Miller; Marion Co.; *Marshall Co.; *Monroe Co.; *Porter Co., *Wicliffe [= Dune Acres]; *Vigo Co. IOWA: *Appanoose Co., Moulton; *Calhoun Co.; *Cass Co.; *Clarke Co.; *Davis Co.; *Decatur Co., Leon; *Fremont Co., near Hamburg State Park; *Greene Co., Jefferson; Guthrie Co., Panora; *Harrison Co., Mondamin; *Henry Co.; *Iowa Co.; Jefferson Co.; *Kossuth Co.; *Lee Co.; *Linn Co., Center Point; Lyon Co.; *Madison Co.; *Mahaska Co.; *Mills Co.; *Monona Co.; Monroe Co.; *Muscatine Co., Moscow; Osceola Co.; *Page Co., Shenandoah; *Plymouth Co.; *Polk Co.; *Pottawatomie Co.; *Poweshiek Co.; *Ringgold Co.; *Sac Co.; *Union Co.; *Van Buren Co.; *Warren Co., Indianola, Medora; Wayne Co.; Woodbury Co., Sioux City, Sergeant Bluff. KANSAS: *Allen Co.; *Barber Co., Aetna, 0.5 mi. S of Sun City, Medicine Lodge; °Butler Co.; °Cheyenne Co.; °Comanche Co.; °Dickinson Co.; *Douglas Co.; Edwards Co., 2 mi. E Kinsley; °Elk Co.; Ellis Co., Ellis; °Finney Co.; *Ford Co., Dodge City; *Graham Co.; *Grant Co., 10 mi. S Ulysses; *Harper Co.; Kearney Co., Lakin; *Kingman Co.; °Labette Co.; °Lane Co.; °Logan Co.; °Meade Co.; *Morton Co.; °Norton Co.; °Osborne Co.; °Rawlins Co.; °Reno Co.; °Riley Co.; °Rooks Co.; *Sedgwick Co.; °Seward Co.; °Smith Co.; °Stanton Co.; °Stevens Co.; *Wabaunsee Co.; *Wichita Co. KENTUCKY: Anderson Co., °Tyrone; Boyle Co., 5 mi. S of Danville; Carter Co., Aden Springs [=Aden = Saulsbury] 620 ft.; Rowan Co., 10 mi. SW of Morehead. MARYLAND: Montgomery Co., Chevy Chase Lake; St. Mary's Co., Piney Point. MASSACHUSETTS: Barnstable Co., *Cape Cod, °Hyannis, *Provincetown; Essex Co., °Andover, °Peabody; Hampshire Co., *Amherst; Middlesex Co., South Sudbury, Hopkinton; Norfolk Co., *Dedham; Suffolk Co., *Wellesley. MICHIGAN: Allegan Co., Allegan State Forest, T. 3N., R. 14W., Sec. 2; Barry Co., Gun Lake, Hastings (Yankee Springs); Berrien Co., *E. K. Warren Woods, *Sawyer Dunes, *New Buffalo, °Lakeside; Calhoun Co., Battle Creek.; Cass Co.; Gratiot Co.; Hillsdale Co., 5 mi. NE of Hillsdale; Ingham Co., East Lansing; Jackson Co., Big Portage Lake, Napoleon, Waterloo; Kalamazoo Co., Gull Lake Biol. Station; Kent Co., Grand Rapids, Wyoming Twp.; Lake Co., Baldwin; Lenawee Co., Camp Storer; Livingston Co., *E. S. George Reserve, Chilson, Strawberry Lake; Mecosta Co., Big Rapids; Midland Co.; Monroe Co., Temperance (1.8 and 3 mi. west); Montcalm Co., Stanton; Muskegon Co., Crystal Lake; Newaygo Co.; Ottawa Co., T. 7N., R. 13W., Sec. 22, T. 7N., R. 16W., Sec. 5, Holland; Saginaw Co.; St. Joseph Co., Klinger Lake, Three Rivers; Van Buren Co., Gobles, Lawton; Washtenaw Co., Portage Lake; Wayne Co., Inkster. MINNESOTA: Anoka Co., Andover, Fridley; Hennepin Co., °Ft. Snelling; Isanti Co., Brandford; Pine Co., °Friesland; *Ramsey Co., °Gray Cloud Island, °St. Anthony Park, °St. Paul; Rice Co., °Faribault, °Northfield; Scott Co., °Barden; Sherborne Co., Santiago; *Washington Co.; Winona Co., °Winona. MISSOURI: Boone Co., Columbia, Rocheport; Greene Co., Springfield; Jackson Co., Kansas City; Wright Co., Mountain Grove. MONTANA: Bighorn Co., °OW Ranch on Hanging Woman Creek (3800 ft.); °Hill Co.; Liberty Co., °Marias Hills; Stillwater Co., °Corinth, °Park City; Toole Co., °Sunshine Road Crossing of Marias River; Yellowstone Co., °Billings. NEBRASKA: °Southern Black Hills; °Valley of Platte River (type locality of *emarginata*); °Upper Missouri River; *Antelope Co., *Neligh; Boone Co., °Albion;; *Box Butte Co., Alliance; °Cass Co.; *Cherry Co., Valentine Wildlife Refuge; Cheyenne Co., °Sidney; °Cuming Co.; Custer Co., Anselmo; °Douglas Co., °Omaha; °Dundy Co., °Haigler; °Frontier Co.; Furnas Co., Cambridge; °Gage Co.;

Grant Co.; Kearney Co.; Keith Co., °Ogallala; °Knox Co.; °Lancaster Co.; Lincoln Co., °9 mi. W of Lincoln; °Red Willow Co.; °Rock Co.; Saunders Co., Cedar Bluffs; °Scotts Bluff Co.; Sioux Co., Bodarc; *Thomas Co., Halsey, Nebraska Nat'l. Forest, Thedford. NEW HAMPSHIRE: Hillsboro Co., *Manchester. NEW JERSEY: Atlantic Co., Ventnor, Reega; Burlington Co., °Beach Haven, °Spray Beach; Cape May Co., *Anglesea [= Five-Mile Beach], *Avalon, *Cape May, Palermo, *Piermont [=Avalon], *Sea Island Junction, °Townsend Inlet, Wildwood Junction; Middlesex Co., Jamesburg; Ocean Co., Cassville, Center of East Plains, °Seaside Park, Toms River. NEW MEXICO: Bernalillo Co., *Albuquerque; Chaves Co., 7 mi. S of Kenna, Mescalero Sands (45 miles E of Roswell), Ross; Doña Ana Co., °Las Cruces, °Mesilla; Lincoln Co.; Quay Co., Logan. NEW YORK: *New York City, and Van Cortlandt Park; Long Island, °Amagansett, °Aqueduct, *Calverton, *Central Park, °Cold Spring, Coney Island, °Coram, °Jamaica, °Montauk, °Riverhead, *Rockaway, Rockaway Beach, °Smithtown, °Wading River, °Wyandanch, *Yaphank; Staten Island, Concord Downs, °Kreischerville, °Long Neck, °Richmond Valley, *Watchogue; Rockland Co., °Sparkill; Westchester Co., Hartsdale, °White Plains. NORTH CAROLINA: Warren Co., Manson; Watauga Co., Blowing Rock. NORTH DAKOTA: Mercer Co., °Hazen. OHIO: Athens Co., °Athens, Buchtel; Butler Co., Reilly Twp.; Fairfield Co., Jacob's Ladder, Kettle Hills, Berne Twp., Madison Twp.; Fulton Co.; Gallia Co., Perry Twp.; Hocking Co., Good Hope Twp.; Jackson Co., Byer, Oak Hill, Washington Twp.; Lucas Co., Holland, 6 mi. W of Toledo, Swanton Twp.; Meigs Co., Salem Twp.; Monroe Co., Rinard's Mills; Noble Co., Sec. 19, Noble Twp.; Ross Co., Union Twp.; Scioto Co., Nile Twp.; Vinton Co., Harrison Twp.; Williams Co., Mud Lake, Sec. 13, Northwest Twp. OKLAHOMA: Alfalfa Co., Salt Fork of Arkansas River near Ingersoll (edge of Salt Plains); Beaver Co., Forgan; Beckham Co., 4.5 mi. NE of Erick, °Sayre; Blaine Co., °Watonga; Bryan Co., *Caddo; Canadian Co., El Reno; Cimmaron Co., Black Mesa (3 mi. N of Kenton); Cleveland Co., Norman; Comanche Co., *Cache, Fort Sill Military Res., *base and *summit of Mt. Sheridan; Cotton Co., east of Grandfield; °Ellis Co.; °Garfield Co.; Custer Co., °Butler, °Thomas; Garvin Co., *Pauls Valley; Grady Co.; *Grant Co.; *Harper Co., 4.5 mi. W of Laverne; Hughes Co., 2 mi. S of Calvin; Jackson Co., °Elmer; Jefferson Co., °Waurika; Kay Co., 9 mi. N of Tonkawa; Kingfisher Co.; Logan Co., Cimarron River banks near Guthrie, °Guthrie; Major Co.; °Noble Co.; Okmulgee Co., °Okmulgee; Osage Co., 4 and 14 mi. W of Turley; °Pawnee Co.; Payne Co., 6 mi. E of Cushing, *Perkins, *Stillwater; Pottawatomie Co., Shawnee; °Texas Co.; Tillman Co., °Grandfield; Tulsa Co., 4 mi. W of Sand Springs; Wagoner Co., Cornell; Washita Co.; Woods Co.; Woodward Co., Woodward. ONTARIO: Huron Co., *Grand Bend. RHODE ISLAND: Washington Co., *Kingston, *Wickford. SASKATCHEWAN: Coronach; Sec. 11, T. 2, R27W_2, on east fork of Poplar River. SOUTH DAKOTA: Bennet Co., °Martin; Bon Homme Co., °Springfield; Brule Co., °Chamberlain; Clay Co., °Vermilion; Custer Co., °Hermosa; Jones Co., *Capa; Lincoln Co., °Canton; Pennington Co., °Wasta; Todd Co., °Rosebud; Union Co., °Elk Point; Walworth Co., °Mobridge; Yankton Co., *Volin, *Yankton. TENNESSEE: Campbell Co., LaFollette (Cumberland Mountain); Obion Co., Samburg on Reelfoot Lake. TEXAS: *Gulf Coast; Anderson Co., *Elkhart; Aransas Co., 2 mi. N of Aransas Pass; Bandera Co., 7 mi. SW of Bandera (1500 ft.), 8 mi. NE of Tarpley (1500 ft.); Baylor Co., Seymour (Kemp Lake); Bell Co., 6 mi. SW of Kileen (900–1000 ft.); Bexar Co., 4 mi. NW of Helotes (1250 ft.), °San Antonio; Blanco Co., 8–10 mi. SE of Blanco (1200 ft.); Brazos Co., College Station; Cameron Co., °Brownsville; Carson Co., Skellytown; Collingworth Co.; Comal Co., 6 mi. NW of New Braunfels (1000 ft.); Culberson Co., Frijole, McKittrick's Canyon in Guadeloupe Mts. near Frijole; Dallam Co., Dalhart; Dallas Co., *Dallas; Donley Co., *Clarendon; Edwards Co., 23 mi. N of Bracketville (1800 ft.), 16 and 21 mi. SW of Rock Springs

(1900–2000 ft.); Ellis Co., °Waxahachie; Gonzales Co., Palmetto State Park (10 mi. SE of Luling, 300 ft.); Guadeloupe Co., 4 mi. S of Seguin (500 ft.); Hale Co., Plainview; Hansford Co., Spearman; Hays Co., 6 mi. W of San Marcos; Hemphill Co., °2 mi. N and °3 mi. S of Canadian River; Howard Co., 8.9 mi. E of Stanton; Jeff Davis Co., Davis Mts. (Cherry Canyon and °S base of Mt. Livermore); Jim Wells-Cameron Cos., °between Alice and Brownsville; °Johnson Co.; Jones Co., 3 mi. E of Hawley; Kerr Co., °Kerrville; Llano Co., 9 mi. E of Llano (900 ft.); Matagorda Co., 4 mi. SE of Sargent; Medina Co., Summit of Dunlay Hill; Mitchell Co., 1 mi. W of Colorado City (2100 ft.); Montague Co., *Bonita; Presidio Co., °Base of Blue Mts. (Chinati Mts., 5200 ft.); Real Co., 37 mi. N, 11 mi. NE of Leakey (2250–2300 ft.); Sherman Co.; °Tarrant Co.; Taylor Co., 11 mi. S of Abilene; Travis Co., Austin (Zilker Park, and 3.5 and 7.6 mi. E, 5 mi. NE, 500 ft.); Val Verde Co., Del Rio; Willacy Co., °Katherine; Wichita Co., °Wichita Falls. MEXICO: NUEVO LEON: 7 road mi. SE of Galeana, 5350 ft. ?COAHUILA: °"Montelovez" [Monclova].

REFERENCES IN LITERATURE.—The species has not been recorded under its nomenclatorially correct name *emarginata* since 1900, with one or two minor exceptions (in compiled works). The western populations have consistently been called *lineata* since the publication of Scudder's 1899 revision, except that red-legged specimens have often been misidentified as *albolineata*; in the east, however, *lineata* has been confused with *alutacea* and *rubiginosa*, striped specimens having been recorded as *alutacea*, unstriped ones as *rubiginosa* or *alutacea rubiginosa*. Without examination of the material it is often impossible accurately to assign such records, which may include two and sometimes all three of the species. Those here listed under the names used are believed to apply wholly or in part to *lineata*.

As *emarginata*: Ball, 1897: 240 (Iowa); Bessey, 1877: 210 (Iowa); Blatchley, 1891: 79 (Ind.); Bruner, 1877: 145, 1893: 26 (*amarginata*), 1895: Pl. 7, fig. 46 (*amarginata*); 1897: 134 (Nebr.); Dodge, 1872: 15 (Nebr.); Kellogg, 1905: 140, fig. 172; Lugger, 1898: 173, fig. (Minn.); McNeill, 1891: 73 (Ill.); Osborn, 1892: 117 (Iowa); *Idem*, 1939:80; Osborn and Gossard, 1891: 267 (Iowa); Scudder, 1872: 250 (Nebr., original description of *emarginata*); *Idem*, 1901: 7, 287, 348 (bibl.); C. Thomas, 1872*a*: 449 (Colo., Nebr.); *Idem*, 1873: 172 (Nebr.); *Idem*, 1876: 69 (Ill.); *Idem*, 1876*a*: 262 (Iowa, [not] Utah); *Idem*, 1878: 483 (Ill.); Townsend, 1893: 30 (N. Mex., ?Ariz.).

As *lineata*: Alexander, 1941:154 (Colo.); Anderson and Wright, 1952: 18, 37 (Mont.); Anonymous, 1953: 711 (Okla.); *Idem*, 1955: 761 (Ks.); ?Ball, 1936: 682 (Ariz.); ?Ball *et al.*, 1942: 325, 328 (Ariz.); Bragg, MS, 1936 (Okla.); Bruner, 1906: 676 (*lineata* unnecessarily renamed *scudderi*); *Idem*, 1908: 297 (cit.); Caudell, 1902: 86 (Okla.); Criddle, 1932: 98, figs. (Alta., Mont.); Froeschner, 1954: 247 (Ia.); Gillette, 1904: 38 (Colo.); Hauke, 1953: 51 (Nebr.); Hebard, 1925: 95 (S. D., Mont., Alta.); *Idem*, 1928: 265 (Mont.); *Idem*, 1929: 368 (Colo.); *Idem*, 1931*a*: 169 (Ks., Minn., Okla., Tex.); *Idem*, 1931: 392 (Alta.); *Idem*, 1932*a*: 254 (Mont.); *Idem*, 1932*b*: 254 (Minn., Tex.); *Idem*, 1936: 43 (N. Dak.); *Idem*, 1938: 19 (Okla.); Isely, 1934: 7; 1935: 72; 1937: 324, 339, 340; 1944: 56 (Tex.); Knowlton, 1952: 5 (Wyo.); Knutson, 1937: 45 (Iowa); *Idem*, 1940: 51 (Tex.); Knutson and Jaques, 1935: 182 (Iowa); Morse, 1907: 21, 43 (Okla., Tex.); Newton and Gurney, 1956–57: 247, map 110 (distr.); Rehn and Hebard, 1906: 399 (Colo.); *Idem*, 1912: 95 (lectotype in Hebard Coll.); Scudder, 1899: 445 (Ks., Tex., ?Mex.); *Idem*, 1900: 47 (checklist); *Idem*, 1901: 287 (bibl.); Slifer, 1943: 225, fig. (spermatheca, glandular pouches of female); C.

C. Smith, 1940: 69 (Okla.); R. C. Smith, 1954: fig. (Ks.); Smith *et al.*, 1943: 129, fig. (Ks.); Stroud, 1950: 663 (N. Mex.); Tinkham, 1939: 125 (Alta.); *Idem*, 1948: 607 (Tex., ?Ariz.); Tuck and Smith, 1940: 8, 33, fig. (egg); Whelan, 1938: 4 (Nebr.); Woodruff, 1937: 78 (Ks.)

As *alutacea*: Adams, 1915: 55, 167, Pl. 39, fig. 3 (Ill.); Anonymous, 1957: 701 (Wis.); Ball, 1897: 240 (Iowa); Blatchley, 1903: 294; 1908: 187 (Ind.); *Idem*, 1920: 314 (Knox Co., Vigo Co., Ind.); Bruner, 1885: 135; 1886: 199 (Ks.); *Idem*, 1983: 26; 1902: 48 (Nebr.); *Idem*, 1908: 296 (cit.); Cantrall, 1943: 108 (Mich.); Caudell, 1902: 86 (Okla.); *Idem*, 1904: 113 (Tex.); Cockerell, 1888: 301 (Colo.); Criddle *et al.*, 1924: 101 (Alta.); Ferguson and Jones, 1949: 443 (Va.); Forbes and Hart, 1900: 480, fig. 52 (Ill.); Fox, 1915: 311 (Ind.); *Idem*, 1917: 219, 220 (*alutacea*, maritime race, Va., N. J.); Froeschner, 1954: 247 (Iowa); Garman, 1894: 3, 8 (Ky.); Gurney, 1935: 188 (*alutacea*, unicolorous phase; Mass.); Hancock, 1911: 330, 366 (Mich., Ill., part); Hart, 1906: 79 (Ill.); Hart and Gleason, 1907: 233 (Ill.); Hebard, 1932*b*: 32 (Minn., Tex.); *Idem*, 1934: 189 (Ill.); *Idem*, 1945: 87 (Va.); Hendrickson, 1930: 60 (Iowa); Isely, 1905: 243 (Ks.); Knutson, 1937: 45 (Iowa); Knutson and Jaques, 1935: 182 (Iowa); Kostir, 1914: 374 (Ohio); Lugger, 1898: 172 (Minn.); McAtee and Caudell, 1918 (Md.); McNeill, 1891: 73 (Ill.); Mead, 1904: 111 (Ohio); Newton and Gurney, 1956–57: 226, Map 108 (in part); Osborn, 1892: 117 (Iowa); *Idem*, 1939: 80; Pettit and McDaniel, 1918: 21 (Mich.); Rathvon, 1863: 384 (Pa.); Rehn, 1901: 294; 1902: 89; 1902*a*: 312 (N. J., in part); *Idem*, 1907: 212 (Tex.); Rehn and Hebard, 1907: 292 (N.J.); *Idem*, 1909: 156 (N. Mex.); *Idem*, 1916: 204 (occurrence of *"alutacea"* in the western part of the Atlantic states attributed, probably correctly, to the species having "pushed in from the Mississippi valley drainage by way of the Tennessee valley."); Scudder, 1899: 445, 464 (in part; all records west of New England and east of Great Basin; that from "Montelovez" [Monclova], Coahuila, probably applies to *lineata*, and that from "Sierra Nola," México, cannot be assigned); *Idem*, 1900*a*: 47 (range, in part); *Idem*, 1901: 286 (bibl., in part); Scudder and Cockerell, 1902 (N. Mex.); Shelford, 1915: 55, 56, 167 (Ill.); S. I. Smith, 1873: 370, 381 (Conn.); Somes, 1914: 67 (Minn.); Strohecker, 1937: 233, 235 (Ill.); Tucker, 1907: 73 (Ks.); Urquhart, 1942: 98 (Ont.); Washburn, 1912: 117; 1912*a*: 13 (Minn.); Whelan, 1938: 4 (Nebr.); Young and Cantrall, 1955: 113 (Ind.).

As *rubiginosa, alutacea rubiginosa, alutacea* form, phase, or variety *rubiginosa*: Blatchley, 1903: 294 (Ind.); *Idem*, 1920: 316 (Ind.; other records include *rubiginosa*); Bruner, 1885: 135 (Ks.); *Idem*, 1893: 26 (Nebr.); *Idem*, 1908: 296 (citations); Davis, 1889: 80; 1913*a*: 85; 1923: 69 (N. Y., N. J.); *Idem*, in Leonard, 1928: 34 (N. Y.); Fernald, 1888: 114 (N. Eng.); Fox, 1914: 508 (N.J., part); *Idem*, 1917: 217 (Va.); Garman, 1894: 3, 8 (Ky.); Hancock, 1911: 330, 366 (Mich., Ill.); Hubbell, 1922: 46 (Mich.); Lugger, 1898: 174 (Minn.); McNeill, 1891: 73 (Ill.); Morse, 1894: 105; 1898: 27, Pl. 7, fig. 31; 1899: 318, 320; 1919: 35 (N. Eng.); *Idem*, 1904:39 (Va.); *Idem*, 1907: 18, 19, 42 (Ark., Okla., Tex.); *Idem*, 1920: 49, Pl. 22, fig. 1 (N. Eng.); Pettit and McDaniel, 1918: 21 (Mich.); Scudder, 1862: 467 (N. Eng. records appended to Harris' description); *Idem*, 1868: 7 (bibl.); *Idem*, 1899: 455, 462 (all except Yucatán and Guatemala records); *Idem*, 1900*a*: 102; 1901: 10, 288 (range, bibl.); Shelford, 1912: 70; 1913: 232, 259 (Mich., Ind.); S. I. Smith, 1873: 370, 381 (Conn.); Somes, 1914: 67 (Minn.); C. Thomas, 1873: 170 (all records except S. Car.); *Idem*, N. D. [1875?]: 3; 1876: 69 (Ill.); *Idem*, 1876*a*: 262 (Iowa; [not] Utah); Walden, 1911: 109, Pl. 9, fig. 6 (Conn.).

In addition *lineata* has been recorded under the following names: as *flavofasciatum* by Thomas, 1872: 265 (SE Colo.); as *albolineata* by Gillette, 1904: 38 (eastern Colorado material with red hind tibiae), and by Morse, 1907: 42 (Wichita Falls, Texas); as *shoshone* by Milliken, 1912: 232 (Dodge City, Kansas; description of ovipositing position); and as sp. cf. *obscura*, unicolorous phase by Fox, 1914: 508 (N. J., beaches).

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PLATE I

Geographic variation in length of pronotum and breadth of head of male

Measurements in millimeters: vertical line, range of variation; circle, mean; open bar, one standard deviation on each side of mean; solid bar, two standard errors on each side of mean; a, *Schistocerca alutacea*; l, *S. lineata*; r, *S. rubiginosa*.

(Geographic Regions and Size of Samples)

A. Northwestern Plains (Saskatchewan to South Dakota, Nebraska and Colorado); *lineata*, 24.

B. Southwestern Plains and Plateaus (southeastern New Mexico and southwestern Texas); *lineata*, 14.

C. Southern Texas (Coastal Plain Prairies and lower Rio Grande Valley); *lineata*, 29.

D. South-central Plains and Prairies (Kansas and Missouri to central Texas); *lineata*, 51.

E. North-central Prairie Region (Iowa); *lineata*, 25.

F. Eastern Prairie-Forest Transition (southern Indiana and Ohio); *lineata*, 20.

G. Northeastern Prairie-Forest Transition (southern Minnesota, Wisconsin); *lineata*, 10.

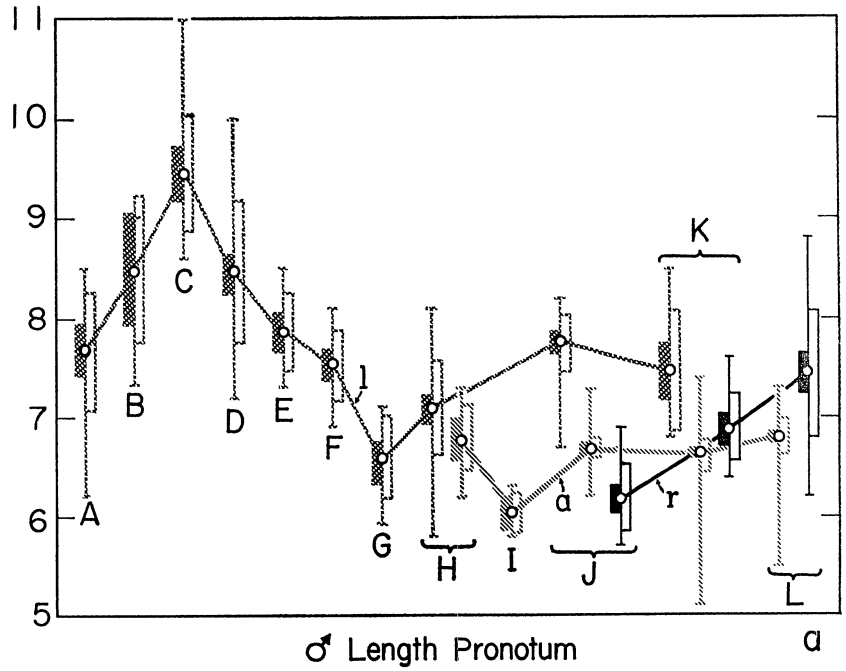
H. Southern Great Lakes Region (northern Illinois, Indiana and Ohio, and southern Michigan and Ontario); *lineata*, 48; *alutacea*, 15.

I. Interior Low Plateaus and Basins (Kentucky, Tennessee, northern Alabama); *alutacea*, 6.

J. Northeastern Atlantic Coastal Plain and adjacent Uplands (southern New England, Long Island, southeastern New York, New Jersey, Delaware); *lineata*, 47; *alutacea*, 63; *rubiginosa*, 31.

K. Middle Atlantic Coastal Plain and adjacent Piedmont (Maryland, Virginia, North and South Carolina); *lineata*, 19; *alutacea*, 25; *rubiginosa*, 26.

L. Southeastern and Gulf Coastal Plains (Georgia and Florida to southern Arkansas and eastern Texas); *alutacea*, 59; *rubiginosa*, 50.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♂ Length Pronotum
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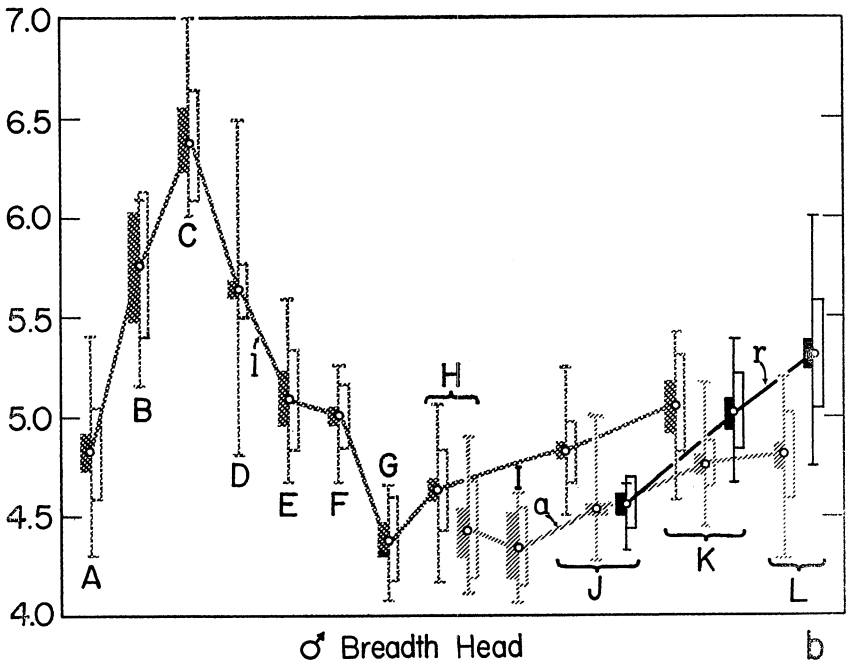
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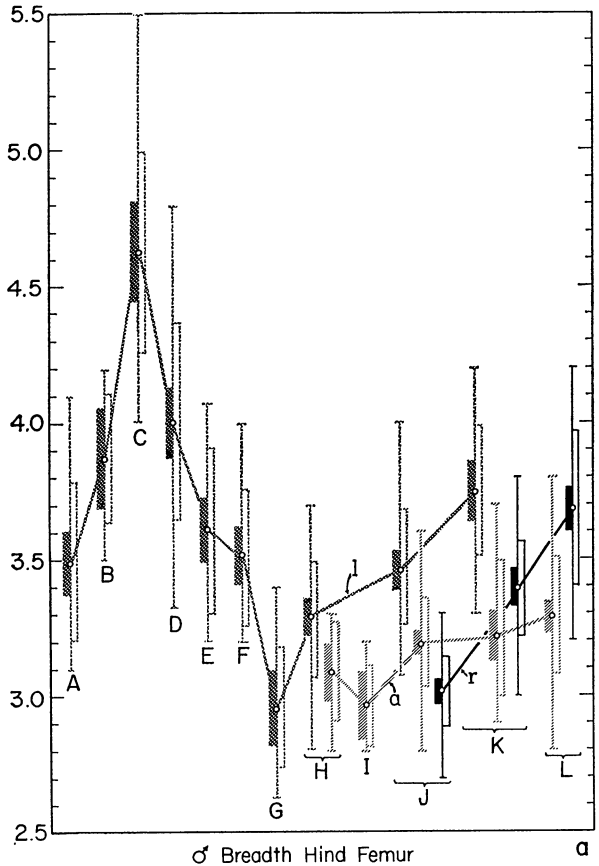
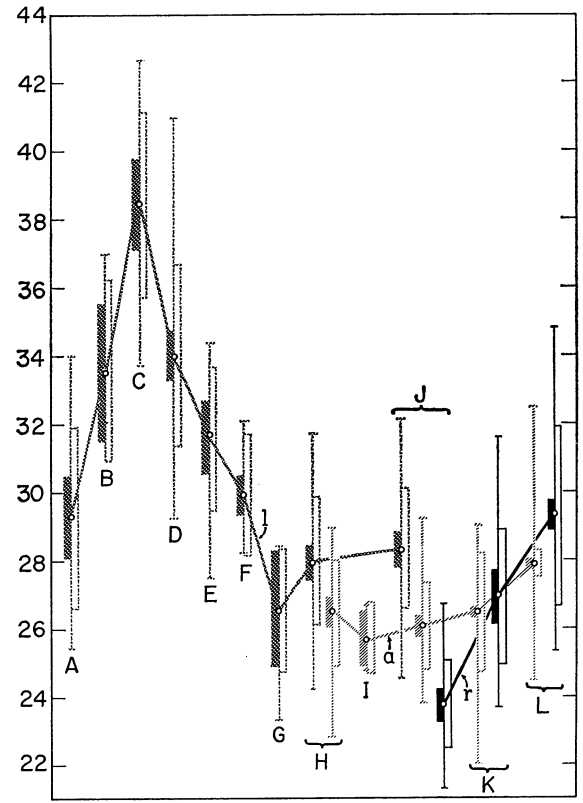
♂ Breadth Head
b

PLATE II

Geographic variation in breadth of hind femur and length of tegmen of male; measurements in millimeters. Explanation as for Plate I



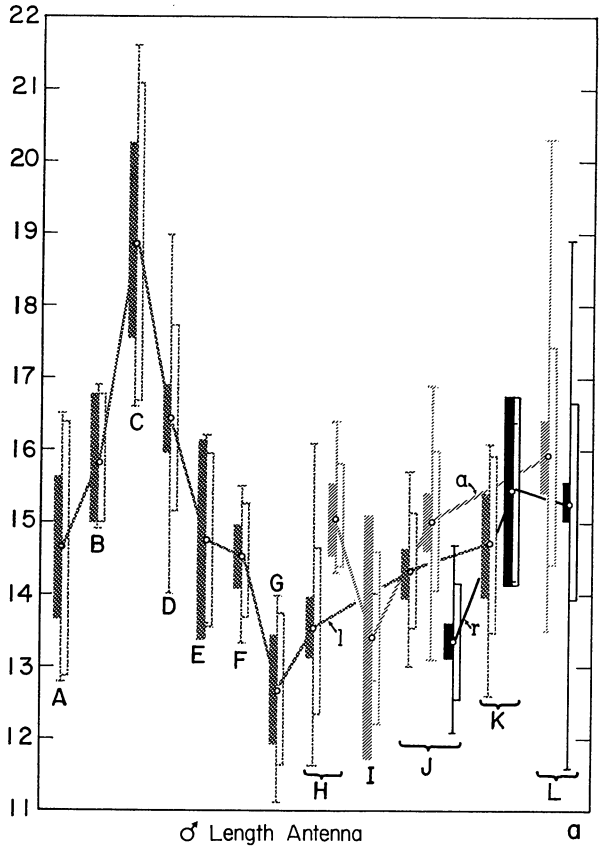
♂ Breadth Hind Femur a



♂ Length Tegmen b

PLATE III

Geographic variation in length of antenna and interocular distance of male; measurements in millimeters. Explanation as for Plate I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♂ Length Antenna
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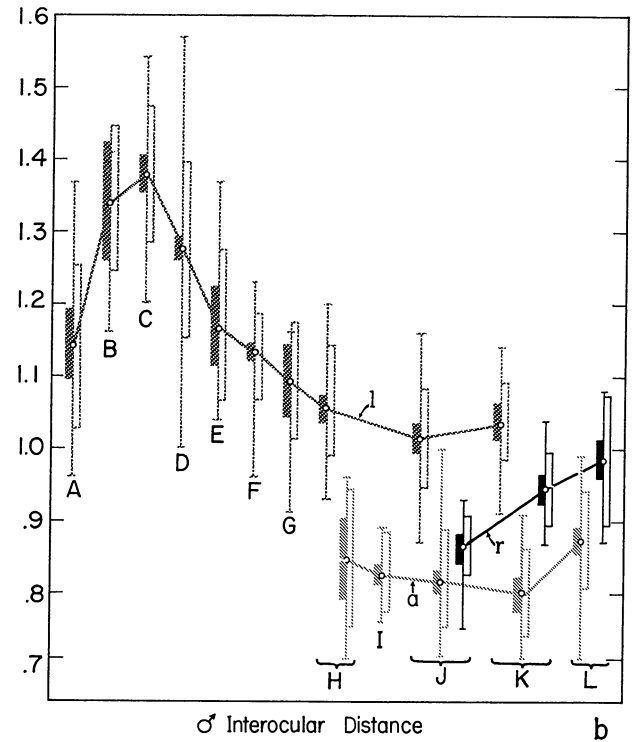
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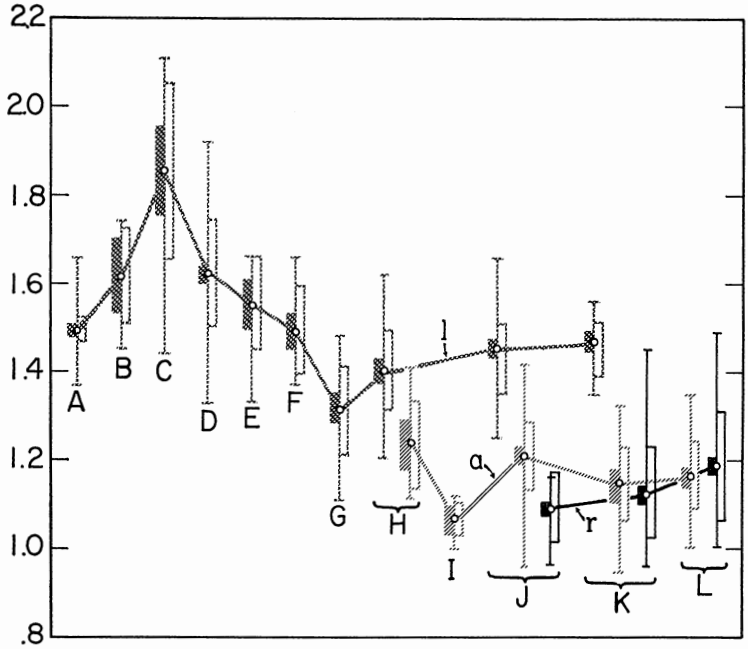
♂ Interocular Distance
b

PLATE IV

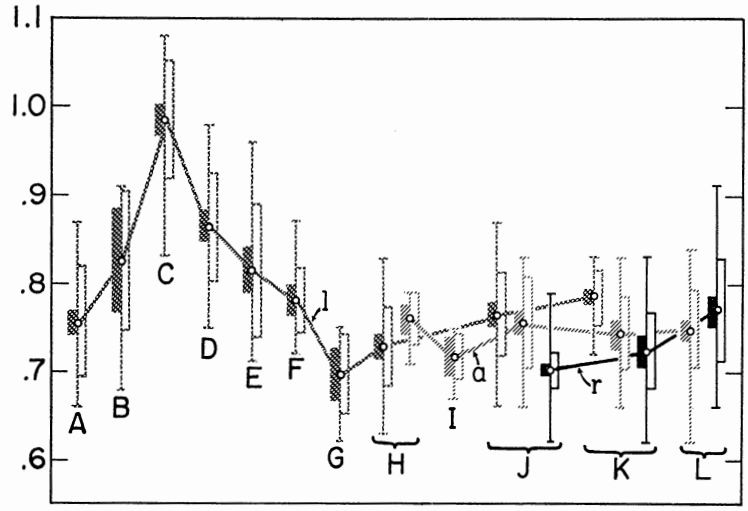
Geographic variation in breadth of fore femur and breadth of first antennal segment of male

Measurements in millimeters: a, *alutacea*; l, *lineata*; r, *rubiginosa*. For complete explanation see Plate I.

A, Northwestern Plains; B, Southwestern Plains and Plateaus; C, Southern Texas; D, South-central Plains and Prairies; E, North-central Prairie Region; F, Eastern Prairie-Forest Transition; G, Northeastern Prairie-Forest Transition; H, Southern Great Lakes Region; I, Interior Low Plateaus and Basins; J, Northeastern Atlantic Coastal Plain and adjacent Uplands; K, Middle Atlantic Coastal Plain and adjacent Piedmont; L, Southeastern and Gulf Coastal Plains.



♂ Breadth Fore Femur a



♂ Breadth First Antennal Segment b

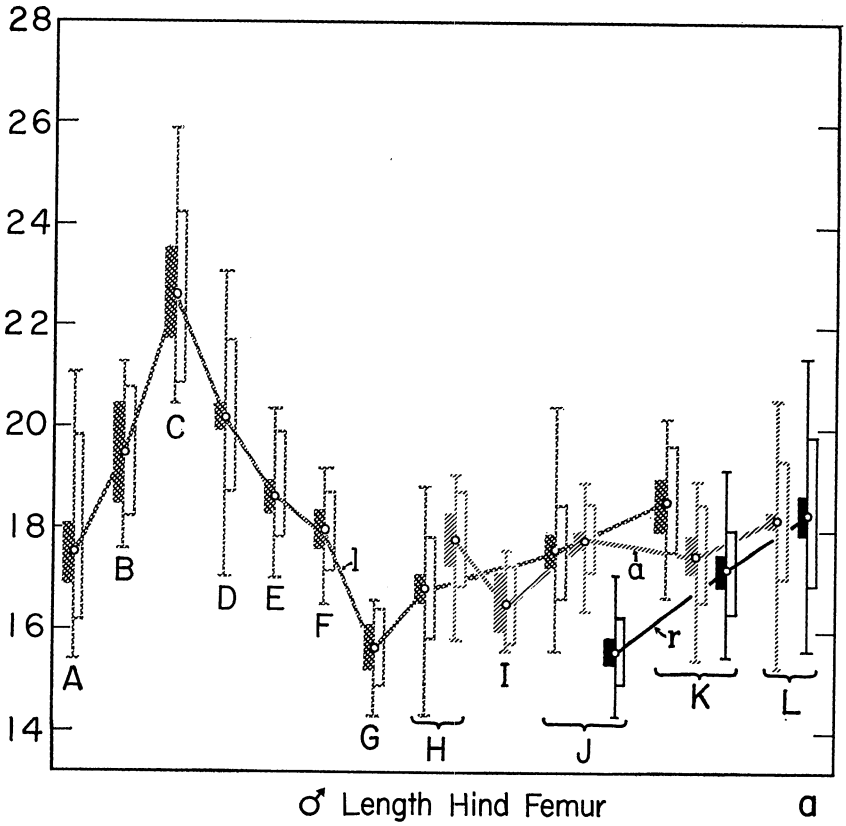
PLATE V

Geographic Variation in *alutacea* Group, and terminal abdominal structures of *Schistocerca obscura*

a. Geographic variation in length of hind femur of male, species of Alutacea Group; Measurements in millimeters. Explanation as for Plate I.

b. Left cercus, male, *Schistocerca obscura*, × 12, near Austin, Travis Co., Texas.

c. Epiproct and left cercus, male, same specimen as last, × 12.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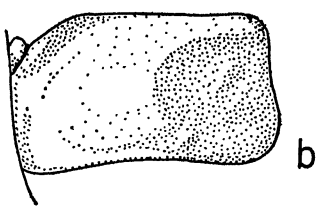
r
♂ Length Hind Femur
a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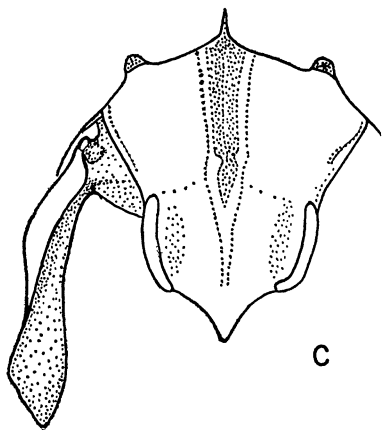
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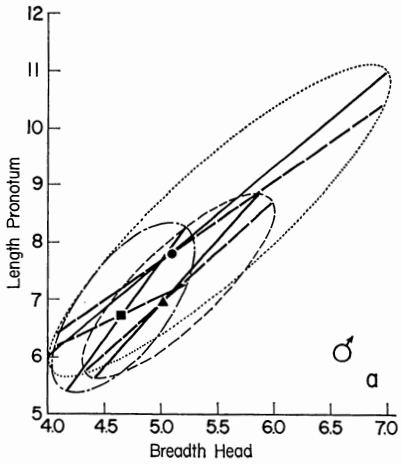
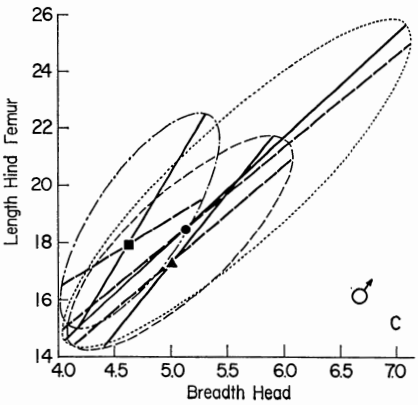
PLATE VI

Body proportions, *Schistocerca alutacea*, *S. lineata*, and *S. rubiginosa*

Measurements in millimeters. Ovals outline area occupied by dots of scatter diagrams. Samples represent entire geographic range of each species. Means: black square, *alutacea*; black circle, *lineata*; black triangle, *rubiginosa*. The regression lines are estimates based on summation of arrays; continuous line, Y on X; dashed line, X on Y.

Species	Size of Sample		Means					
			L. pronotum		L. hind femur		Br. head	
	♂	♀	♂	♀	♂	♀	♂	♀
alutacea	168	63	6.72	9.94	17.86	24.56	4.65	5.72
lineata	255	158	7.78	10.52	18.41	24.08	5.10	6.29
rubiginosa	107	42	6.97	10.30	17.29	24.09	5.02	6.40


Length Pronotum
Breadth Head
♂
a


Length Hind Femur
Breadth Head
♂
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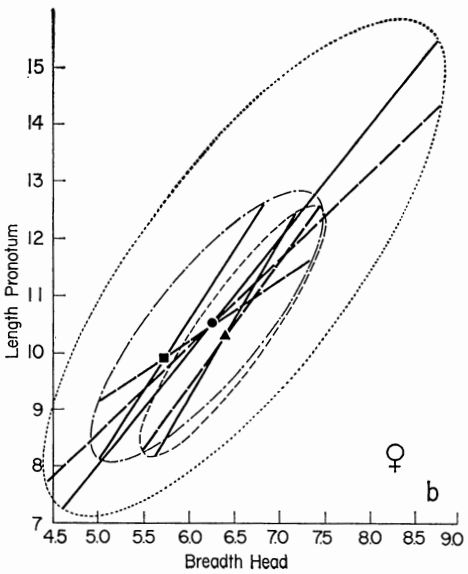

Length Pronotum
Breadth Head
♀
b

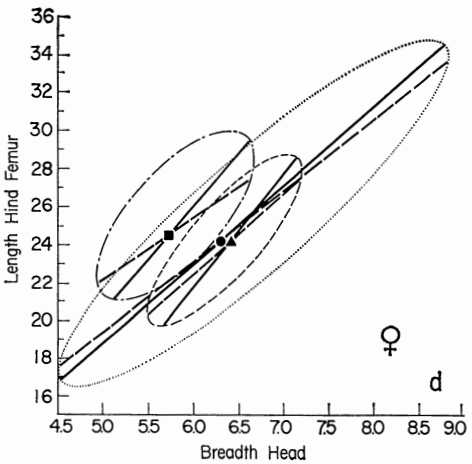

Length Hind Femur
Breadth Head
♀
d

PLATE VII

Body proportions, *Schistocerca alutacea, S. lineata, S. rubiginosa*; explanation of graphs as for Plate VI

Species	Size of Sample		Means					
			L. pronotum		L. hind femur		Br. hind femur	
	♂	♀	♂	♀	♂	♀	♂	♀
alutacea	168	63	6.72	9.94	17.86	24.56	3.24	4.37
lineata	255	158	7.78	10.52	18.41	24.08	3.64	4.68
rubiginosa	107	42	6.97	10.30	17.29	24.09	3.42	4.72

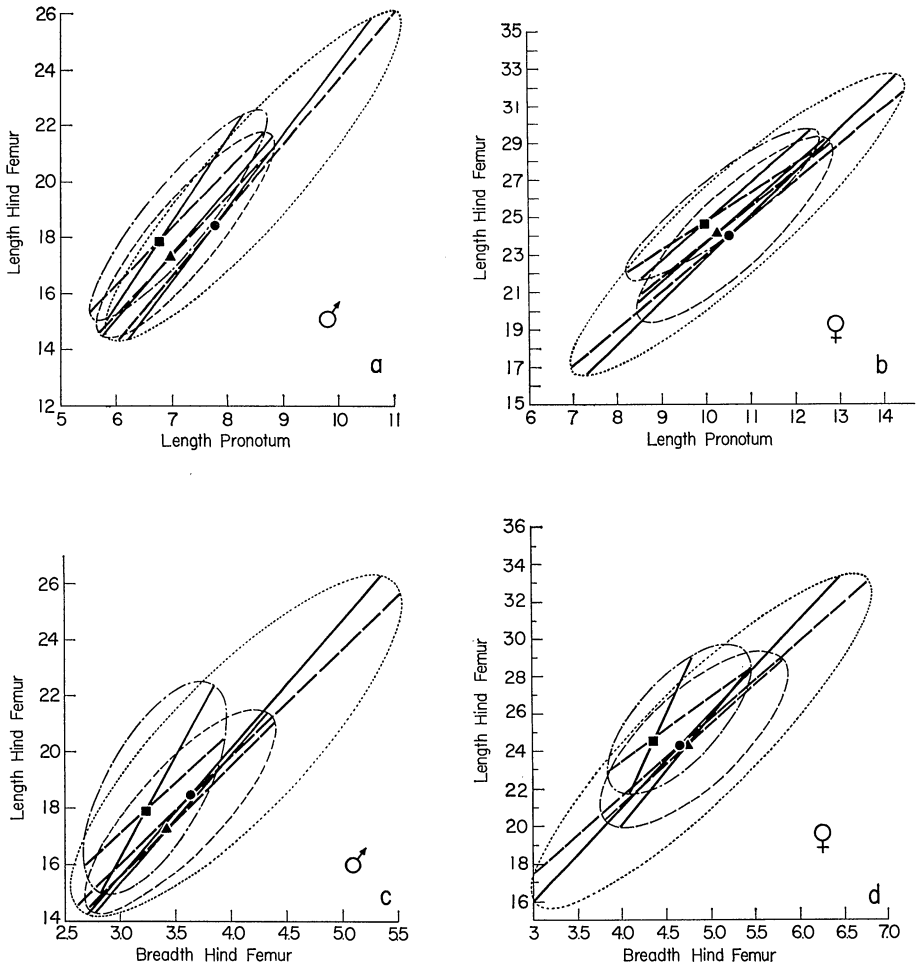
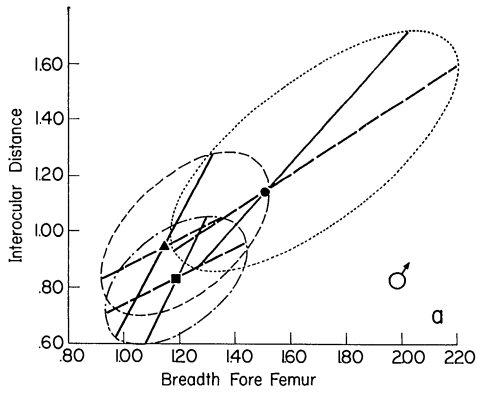

Length Hind Femur
Length Pronotum
♂
a
Length Hind Femur
Length Pronotum
♀
b
Length Hind Femur
Breadth Hind Femur
♂
c
Length Hind Femur
Breadth Hind Femur
♀
d

PLATE VIII

Body proportions, *Schistocerca alutacea, S. lineata, S. rubiginosa*; explanation of graphs as for Plate VI

Species	Size of Sample		Means					
			Interoc. dist.		Br. 1st ant. seg.		Br. fore femur	
	♂	♀	♂	♀	♂	♀	♂	♀
alutacea	168	63	0.83	1.35	0.75	0.89	1.18	1.25
lineata	255	158	1.14	1.66	0.80	0.86	1.51	1.36
rubiginosa	107	42	0.94	1.49	0.74	0.85	1.15	1.15


Interocular Distance
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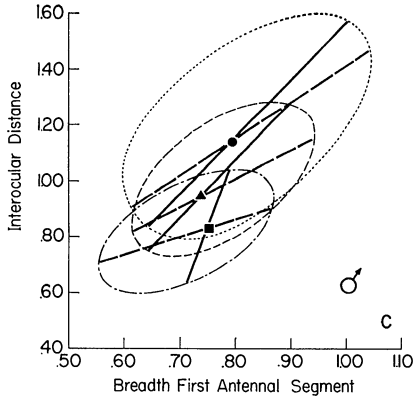
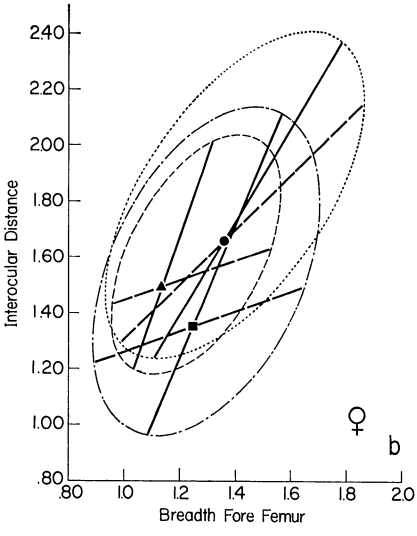
.80 1.00 1.20 1.40 1.60 1.80 2.00 2.20
Breadth Fore Femur
♂
a


Interocular Distance
1.60
1.40
1.20
1.00
.80
.60
.40
.50 .60 .70 .80 .90 1.00 1.10
Breadth First Antennal Segment
♂
c


Interocular Distance
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2.20
2.00
1.80
1.60
1.40
1.20
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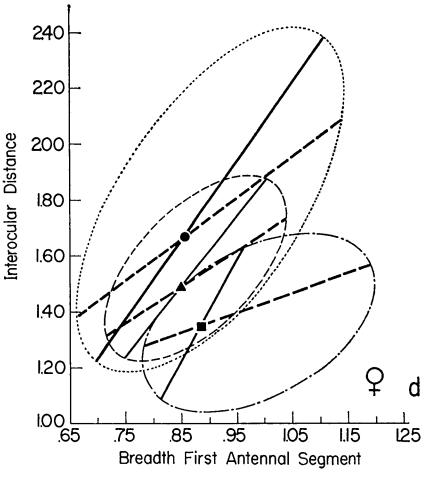
.80 1.0 1.2 1.4 1.6 1.8 2.0
Breadth Fore Femur
♀
b


Interocular Distance
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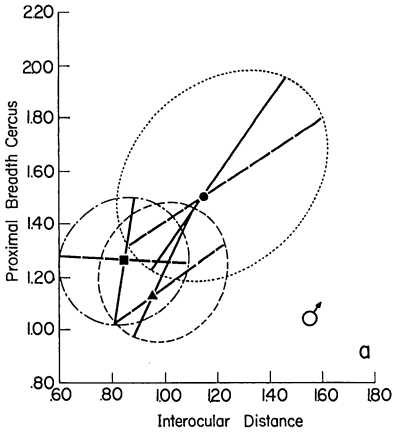
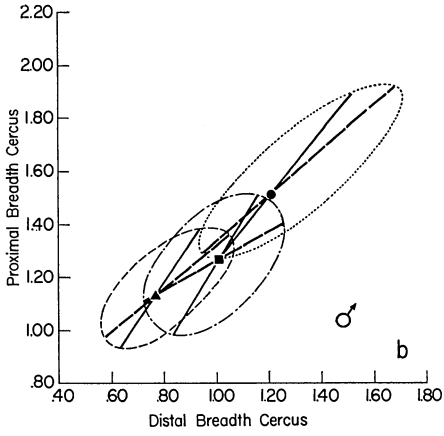
Breadth First Antennal Segment
♀
d

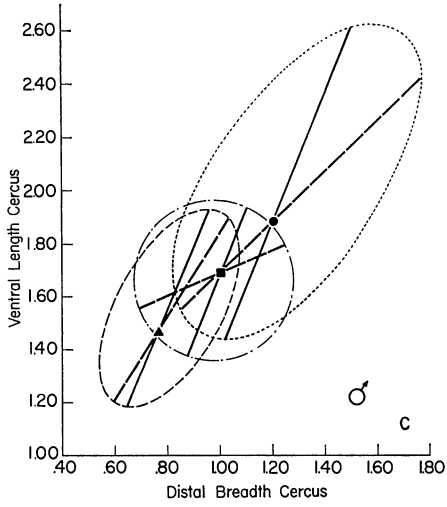
PLATE IX

Proportions of male cercus, *S. alutacea, S. lineata, S. rubiginosa*; explanation of graphs as for Plate VI

Species	Number of Specimens	Means				
		Interocular distance	Proximal breadth	Distal breadth	Ventral length	Depth/distal notch
alutacea	38	0.84	1.26	1.01	1.69	0.117
lineata	143	1.16	1.51	1.21	1.88	0.131
rubiginosa	31	0.95	1.13	0.77	1.45	0.045


Proximal Breadth Cercus
2.20
2.00
1.80
1.60
1.40
1.20
1.00
.80
.60
.80
1.00
1.20
1.40
1.60
1.80
Interocular Distance
♂
a


Proximal Breadth Cercus
2.20
2.00
1.80
1.60
1.40
1.20
1.00
.80
.40
.60
.80
1.00
1.20
1.40
1.60
1.80
Distal Breadth Cercus
♂
b


Ventral Length Cercus
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
.40
.60
.80
1.00
1.20
1.40
1.60
1.80
Distal Breadth Cercus
♂
c

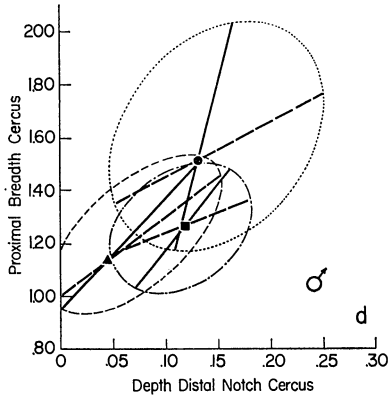
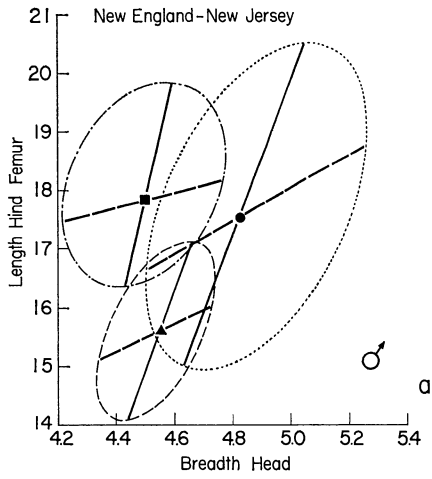
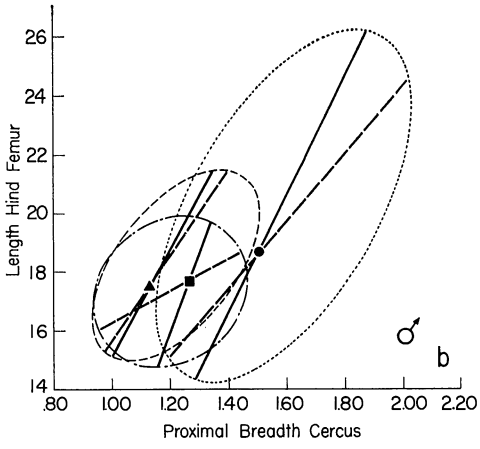

Proximal Breadth Cercus
2.00
1.80
1.60
1.40
1.20
1.00
.80
0
.05
.10
.15
.20
.25
.30
Depth Distal Notch Cercus
♂
d

PLATE X

Body proportions, male, *S. alutacea, S. lineata, S. rubiginosa*; explanation of graphs as for Plate VI

Species	Number of Specimens			Means				
	a	b	c	Length pro-notum	Length hind femur	Length antenna	Breadth head	Prox. br. cercus
alutacea	168	38	70	6.72	17.86	15.44	4.65	1.26
lineata	255	141	150	7.78	18.41	14.92	5.10	1.51
rubiginosa	107	30	44	6.97	17.29	14.86	5.02	1.13


New England-New Jersey
Length Hind Femur
21
20
19
18
17
16
15
14
4.2
4.4
4.6
4.8
5.0
5.2
5.4
Breadth Head
♂
a


Length Hind Femur
26
24
22
20
18
16
14
.80
1.00
1.20
1.40
1.60
1.80
2.00
2.20
Proximal Breadth Cercus
♂
b

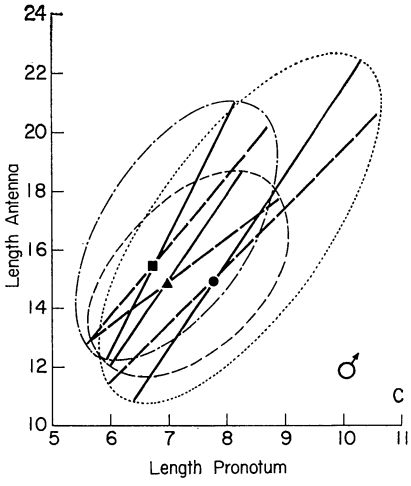

Length Antenna
24
22
20
18
16
14
12
10
5
6
7
8
9
10
11
Length Pronotum
♂
c

PLATE XI

Regional comparisons, body proportions of male, *Schistocerca alutacea*, *S. lineata*, *S. rubiginosa*

Measurements in millimeters. Area occupied by dots of scatter diagram ruled, mean shown by black symbol. *S. alutacea*, vertical ruling and square: sample size: a, 18; b, 36; c, 27; d, 25; e, 57; f, 35; g, 27; h–k and n, 17; l, o, 25; m, 88. *S. lineata*, oblique ruling and circle; sample size: a, 48; b, 24; c, 23; f, 24; g, 23; h–k and n, 29; m, 66. *S. rubiginosa*, horizontal ruling and triangle: sample size: c, 25; d, 26; e, 51; g, 25; h–k and n, 16; m, o, 21.

Means

Breadth of head/breadth of hind femur

S. alutacea: a, 4.42/3.09; b, 4.49/3.22; c, 4.58/3.17; d, 4.76/3.22; e, 4.81/3.29.
S. lineata: a, 4.63/3.28; b, 4.83/3.45; c, 4.83/3.50. *S. rubiginosa*: c, 4.56/3.02; d, 5.09/3.40; e, 5.31/3.68.

Breadth of head/length of hind femur

S. alutacea: f, 4.49/17.98; g, 4.58/17.60. *S. lineata*: f, 4.83/17.50; g, 4.83/17.57.
S. rubiginosa: g, 4.56/15.60.

Proximal breadth/distal breadth of cercus

S. alutacea: h, 1.33/1.07. *S. lineata*: h, 1.41/1.12. *S. rubiginosa*: h, 1.09/0.71.

Proximal breadth/depth of distal notch of cercus

S. alutacea: i, 1.33/0.135. *S. lineata*: i, 1.41/0.123. *S. rubiginosa*: i, 1.09/0.046.

Ventral length/distal breadth of cercus

S. alutacea: j, 1.73/1.07. *S. lineata*: j, 1.81/1.12. *S. rubiginosa*: j, 1.44/0.71.

Ventral length/proximal breadth of cercus

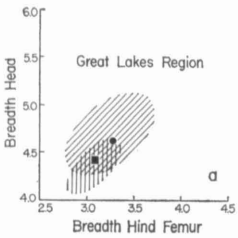
S. alutacea: k, 1.73/1.33; l, 1.65/1.21. *S. lineata*: k, 1.81/1.41. *S. rubiginosa*: k, 1.44/1.09; l, 1.46/1.14.

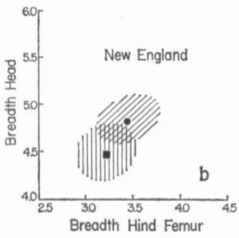
Interocular distance/breadth of fore femur

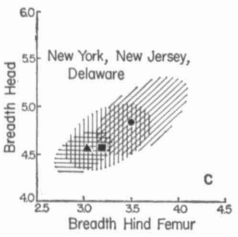
S. alutacea: m, 0.81/1.19. *S. lineata*: m, 1.02/1.45. *S. rubiginosa*: m, 0.90/1.13.

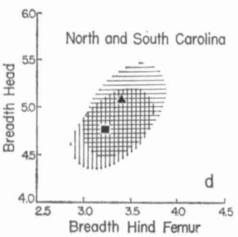
Proximal breadth of cercus/interocular distance

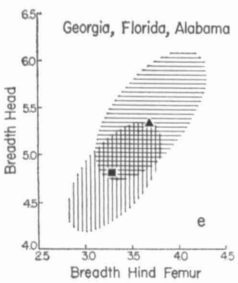
S. alutacea: n, 1.33/0.81; o, 1.21/0.86. *S. lineata*, n, 1.41/1.02. *S. rubiginosa*: n, 1.09/0.90; o, 1.14/0.94.

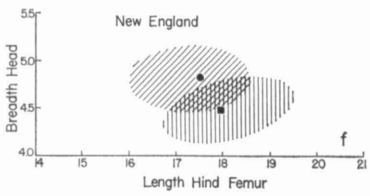

Great Lakes Region
Breadth Head
Breadth Hind Femur
a

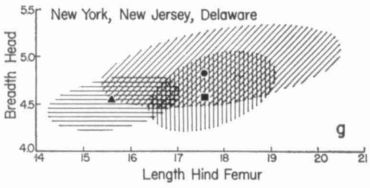

New England
Breadth Head
Breadth Hind Femur
b

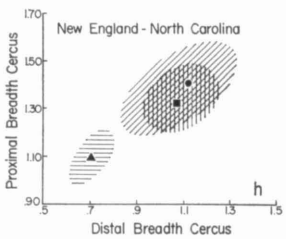

New York, New Jersey, Delaware
Breadth Head
Breadth Hind Femur
c

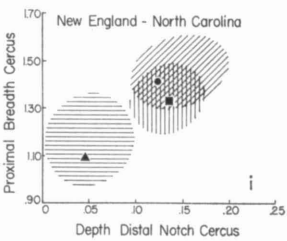

North and South Carolina
Breadth Head
Breadth Hind Femur
d

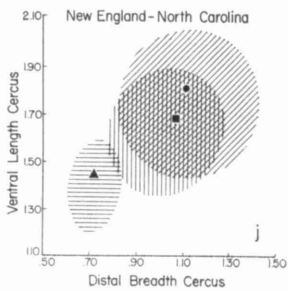

Georgia, Florida, Alabama
Breadth Head
Breadth Hind Femur
e

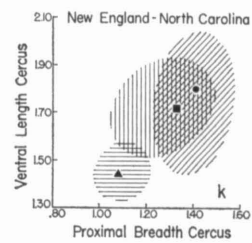

New England
Breadth Head
Length Hind Femur
f

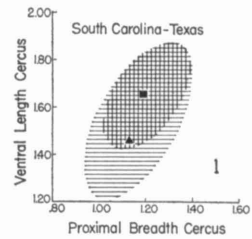

New York, New Jersey, Delaware
Breadth Head
Length Hind Femur
g

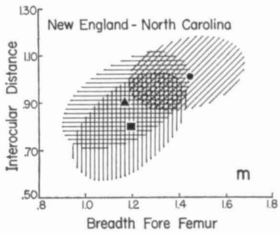

New England - North Carolina
Proximal Breadth Cercus
Distal Breadth Cercus
h

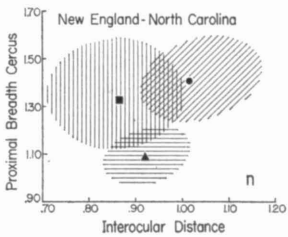

New England - North Carolina
Proximal Breadth Cercus
Depth Distal Notch Cercus
i


New England - North Carolina
Ventral Length Cercus
Distal Breadth Cercus
j


New England - North Carolina
Ventral Length Cercus
Proximal Breadth Cercus
k


South Carolina - Texas
Ventral Length Cercus
Proximal Breadth Cercus
l


New England - North Carolina
Interocular Distance
Breadth Fore Femur
m


New England - North Carolina
Proximal Breadth Cercus
Interocular Distance
n

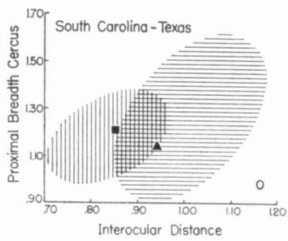

South Carolina - Texas
Proximal Breadth Cercus
Interocular Distance
o

PLATE XII

Geographic variation in pronotal coloration, *Schistocerca lineata*
Percentage scale at margin of graph. Sexes combined
Pronotum unstriped

A. Dorsum of pronotum unicolorous.
B. Dorsum of pronotum with small pale spot at intersection of median carina with principal sulcus.

Pronotum with medio-longitudinal dorsal pale stripe*

Stripe breadth class	Breadth in mm. measured just anterior to principal sulcus	
	♂	♀
1. Very narrow	0.04–0.39	0.40–0.79
2. Narrow	0.40–0.79	0.80–1.19
3. Average	0.80–1.19	1.20–1.59
4. Broad	1.20–1.59	1.60–1.99
5. Very broad	1.60 +	2.00 +

* SIZE OF SAMPLES.—Southern Texas, 20 ♂ + 18 ♀ = 38; South Dakota–New Mexico, 71 ♂ + 68 ♀ = 139; Kansas–central Texas, 107 ♂ + 147 ♀ = 254; Iowa, 168 ♂ + 145 ♀ = 313; Minn.–Wis.–Ill.–Ind., 92 ♂ + 78 ♀ = 170; Michigan–Ohio, 170 ♂ + 85 ♀ = 255; New England–Deleware, 142 ♂ + 49 ♀ = 191; Maryland–North Carolina, 21 ♂ + 3 ♀ = 24.

Region	Percentage distribution						
	A	B	1	2	3	4	5
Southern Texas	..	..	..	10.5	47.3	36.8	5.3
S. D.–Colo.–N. Mex.	1.4	0.7	7.9	41.0	43.0	5.9	..
Kansas–central Texas	4.1	7.4	4.5	32.8	45.1	5.3	0.8
Iowa	6.7	4.2	2.9	46.9	34.5	4.2	0.6
Minn.–Wis.–Ill.–Ind.	11.2	14.1	6.5	54.7	13.5	..	..
Michigan–Ohio	29.4	45.8	5.9	27.8	1.5	..	..
New England–Delaware	30.9	60.7	0.5	6.8	0.5	..	..
Maryland–North Carolina	37.5	58.2	..	4.2	..	..	..

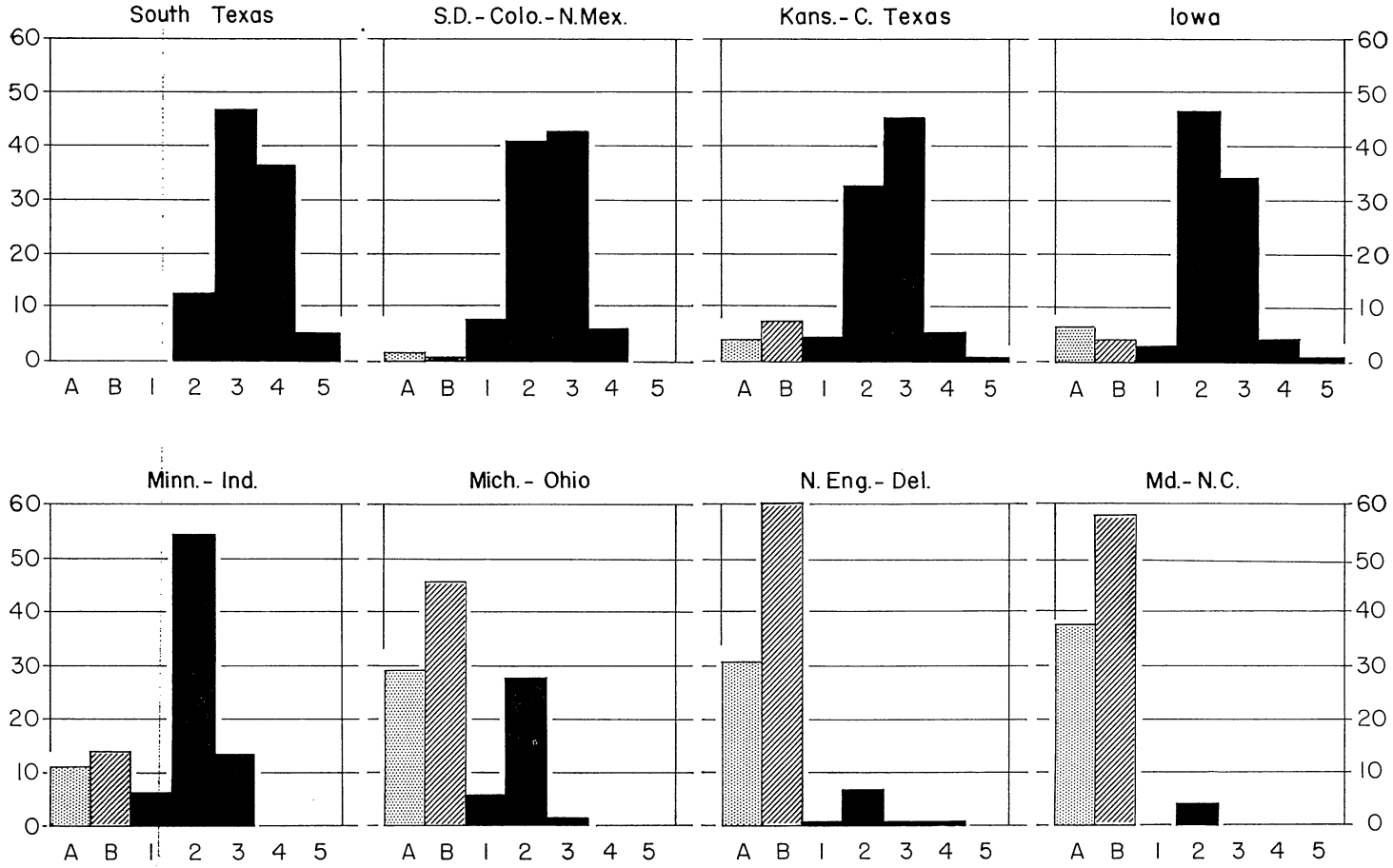

South Texas
S.D.-Colo.-N.Mex.
Kans.-C. Texas
Iowa
Minn.-Ind.
Mich.-Ohio
N. Eng.-Del.
Md.-N.C.
60
50
40
30
20
10
0
A B I 2 3 4 5

PLATE XIII

Geographic variation in pronotal coloration, *Schistocerca lineata*, *S. rubiginosa*, *S. alutacea*

Percentage scales at margins of graphs. Sexes combined. Only that part of the range of *S. lineata* is included in which the species is sympatric with one or both of the others. Symbols as in Plate XII.

SIZE OF SAMPLES.—*S. lineata*: Great Lakes region including Wisconsin and southeastern Minnesota, 236 ♂ + 146 ♀ = 382; New England, 103 ♂ + 36 ♀ = 139; New York–Delaware, 39 ♂ + 13 ♀ = 52; Maryland–Carolina, 21 ♂ + 3 ♀ = 24. *S. rubiginosa*: New Jersey–Delaware, 39 ♂ + 5 ♀ = 44; Maryland–South Carolina, 43 ♂ + 15 ♀ = 58; Georgia and west Florida to eastern Texas, 147 ♂ + 58 ♀ = 205; peninsular Florida, 321 ♂ + 197 ♀ = 518. *S. alutacea*: Great Lakes region, 46 ♂ + 22 ♀ = 68; New England, 73 ♂ + 58 ♀ = 131; New York–Delaware, 48 ♂ + 19 ♀ = 67; Maryland–South Carolina, 31 ♂ + 2 ♀ = 33; Georgia and west Florida to eastern Texas and Arkansas, 61 ♂ + 13 ♀ = 74; peninsular Florida, 178 ♂ + 127 ♀ = 305.

Region	Percentage distribution					
	A	B	1	2	3	4
Great Lakes–Minn.						
lineata	24.2	29.6	6.2	36.1	3.8	..
alutacea	..	..	1.4	72.1	26.5	..
New England						
lineata	30.9	61.2	..	6.6	0.7	0.7
alutacea	..	..	1.5	64.8	33.6	..
New York–Delaware						
lineata	30.7	59.6	1.9	7.7	..	..
rubiginosa	27.3	11.4	22.7	38.6	..	..
alutacea	..	..	3.0	89.5	7.5	..
Maryland–So. Car.						
lineata	37.5	58.2	..	4.2	..	..
rubiginosa	59.0	43.0	..	..	..	..
alutacea	..	..	6.0	94.0	..	..
Ga.–w. Fla.–Texas						
rubiginosa	53.1	42.0	0.5	4.4	..	..
alutacea		..	6.8	89.3	3.9	..
Peninsular Florida						
rubiginosa	53.2	49.7	0.4	1.2	0.6	..
alutacea	..	..	11.2	84.2	4.6	..

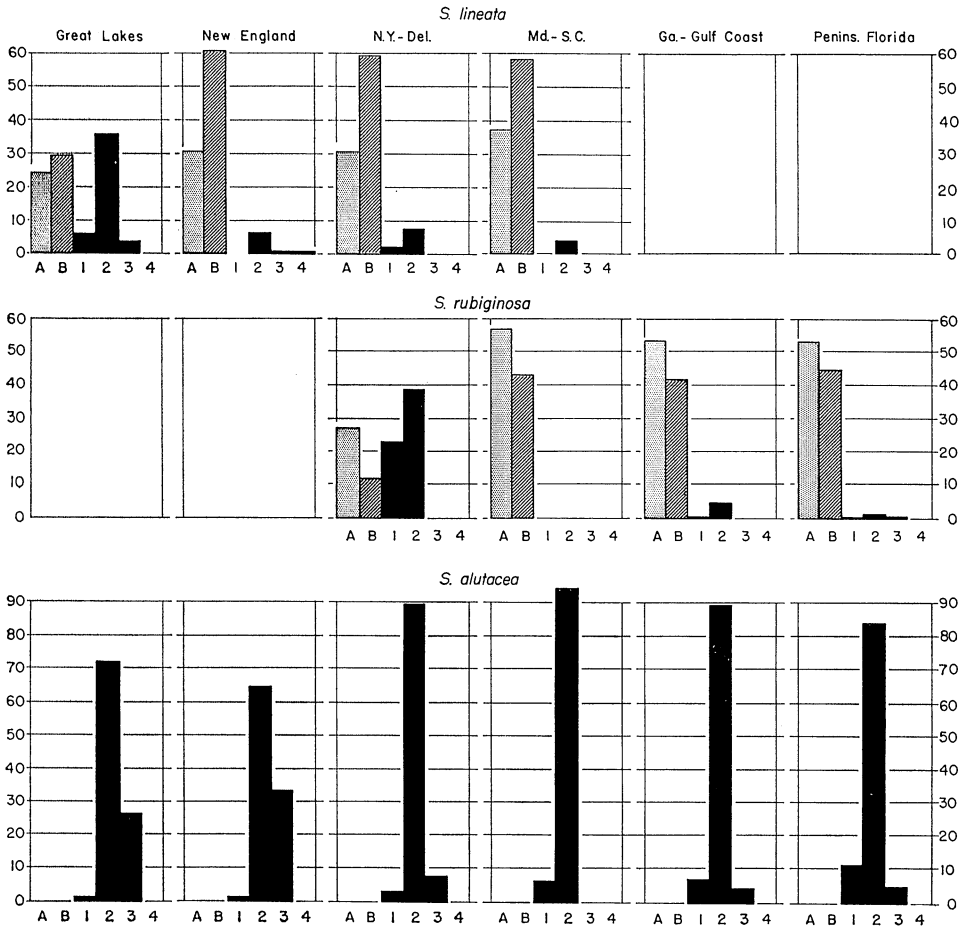

S. lineata
Great Lakes
New England
N.Y.- Del.
Md.- S.C.
Ga.- Gulf Coast
Penins. Florida
S. rubiginosa
S. alutacea
A B 1 2 3 4

PLATE XIV

Various structural details, *Schistocerca lineata, S. rubiginosa, S. alutacea*

Dorsal and cephalic outlines of head

a, b. *S. lineata,* ♂, Sun City, Barber Co., Kansas (topotypic).
c, d. *S. lineata,* ♂, Staten Island, New York, UMMZ.
e, f. *S. rubiginosa,* ♂, Spout Springs, Harnett Co., North Carolina.
g, h. *S. rubiginosa,* ♂, Limehouse, Beaufort Co., South Carolina.
i, j. *S. alutacea,* ♂, Stamford, Fairfield Co., Connecticut.
k, l. *S. lineata,* ♀, Concord Downs, Staten Is., New York.
m, n. *S. rubiginosa,* ♀, Dry margins of 4-Hole Swamp, Orangeburg Co., S. C.
o, p. *S. alutacea,* ♀, Stamford, Fairfield Co., Connecticut.

Outlines of male subgenital plate

q. *S. lineata,* Sun City, Barber Co., Kansas (topotypic).
r. *S. lineata,* Long Island, New York, AMNH.
s. *S. alutacea,* Stamford, Fairfield Co., Connecticut.
t. *S. rubiginosa,* Limehouse, Beaufort Co., South Carolina.

Outlines of ovipositor

u. *S. lineata,* Deep River, Middlesex Co., Connecticut.
v. *S. rubiginosa,* Ashley Junction, Charleston Co., South Carolina.
w. *S. alutacea,* Stamford, Fairfield Co., Connecticut.

Drawn with camera lucida. Figures a–p approximately × 4; figures q–x approximately × 10.

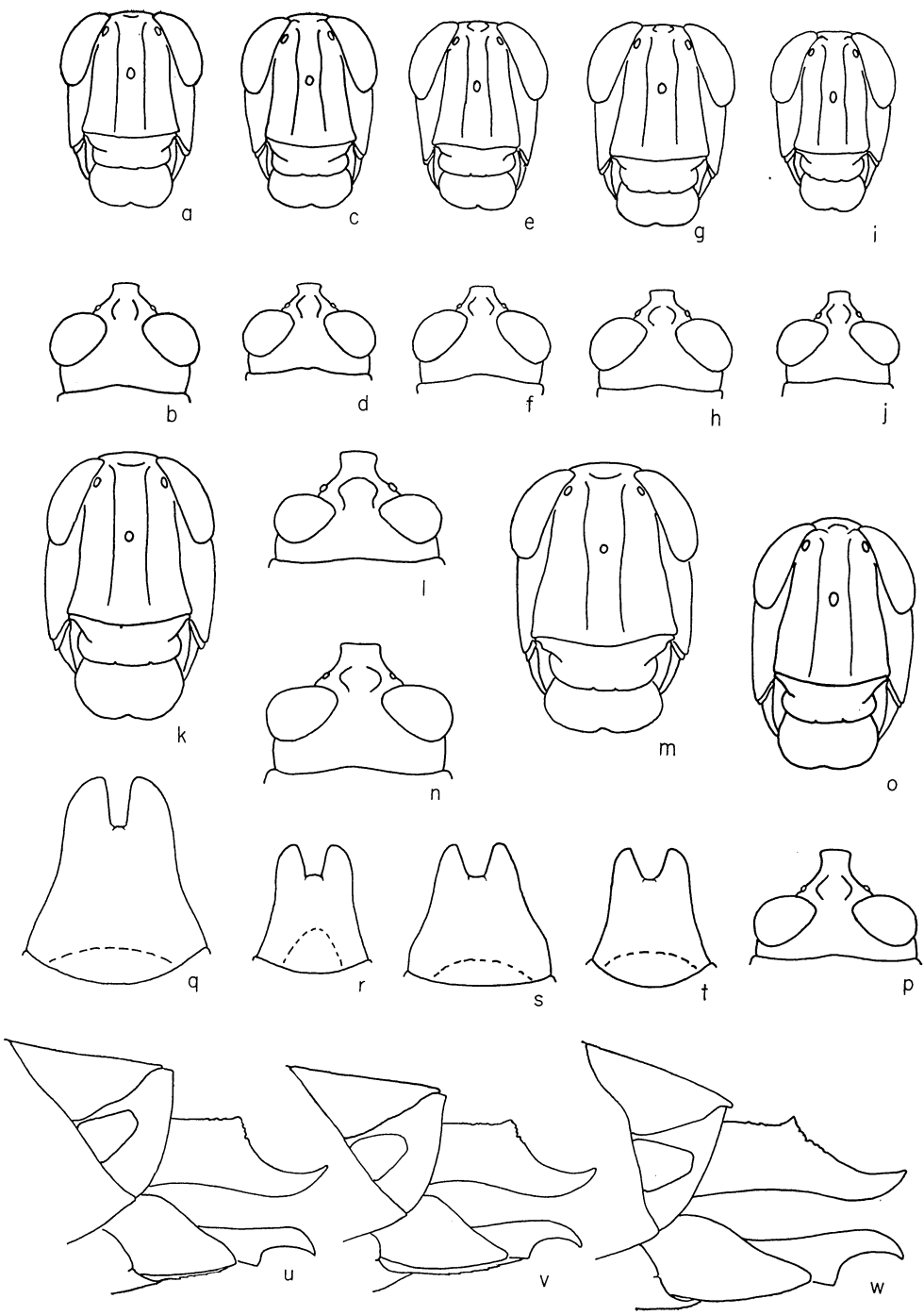

a
c
e
g
i
b
d
f
h
j
k
l
m
o
n
q
r
s
t
p
u
v
w

PLATE XV

Left cercus of male, *Schistocerca rubiginosa* and *S. alutacea*

Schistocerca rubiginosa (Harris)

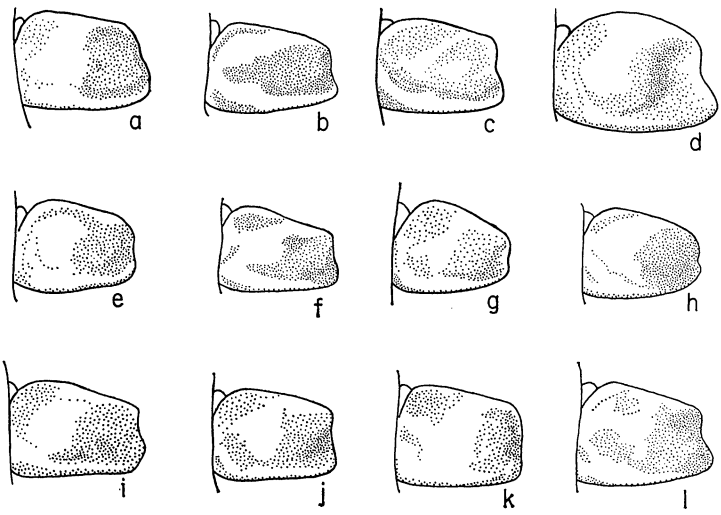
a–d. Lakehurst, Ocean Co., New Jersey (a, c, dorsum unstriped; b, d, head, pronotum and tegmina narrowly striped).
e–f. Folkston, Charlton Co., Georgia (e, dorsum unicolorous; f, head weakly striped, pronotum with central macula, tegmina unstriped).
g. Between Climax and Bainbridge, Decatur Co., Georgia (dorsum unicolorous).
h. Newberry, Alachua Co., Florida (dorsum unicolorous).
i–j. Gainesville, Alachua Co., Florida (i, dorsum unicolorous; j, dorsum unicolorous except pronotum with central macula).
k. Cross Creek, Alachua Co., Florida (dorsum unicolorous).
l. Elkhart, Anderson Co., Texas (head faintly striped, pronotum with central macula, tegmina unstriped.

Schistocerca alutacea (Harris)

m. Wareham, Plymouth Co., Massachusetts.
n. Sussex, Sussex Co., New Jersey.
o. Cold Spring, Cape May Co., New Jersey.
p. Manahawken, Ocean Co., New Jersey.
q–s. Waukegan, Lake Co., Illinois.
t. Beach, Lake Co., Illinois.
u–v. Hastings, St. Johns Co., Florida.
w. Lakeland, Polk Co., Florida.
x. Doucette, Tyler Co., Texas.
y–z. Mobile, Mobile Co., Alabama.

Drawn with camera lucida. All approximately × 12.

S. rubiginosa



S. alutacea

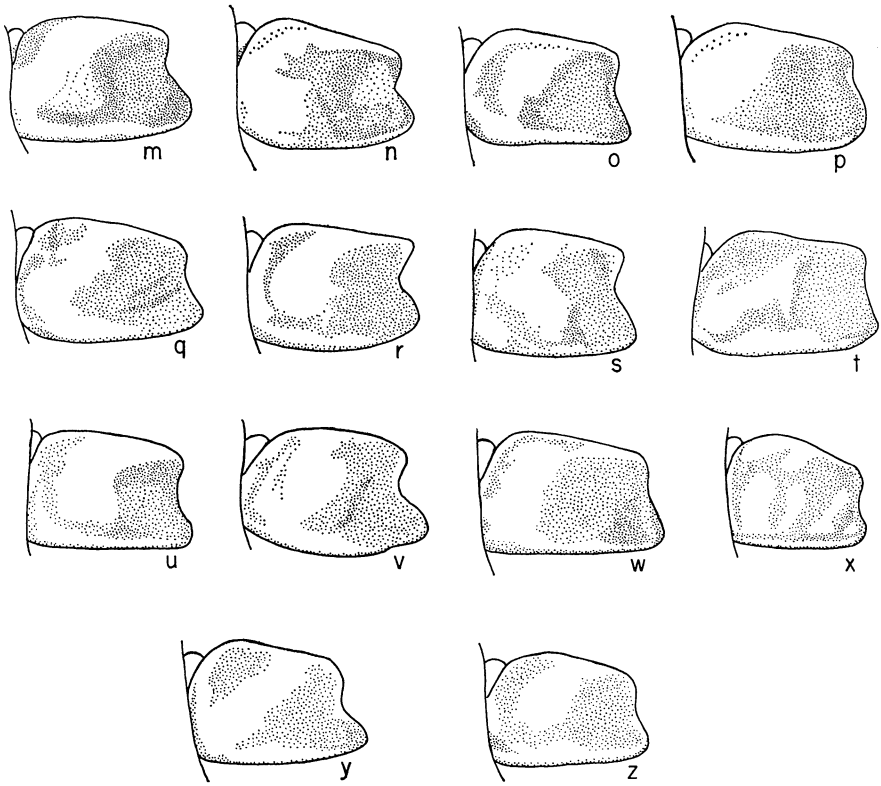


PLATE XVI

Epiproct and left cercus of male, *Schistocerca lineata*

a. Near Bandera, Bandera Co., Texas. Epiproct.
b. Austin, Travis Co., Texas. Epiproct and left cercus.

Left Cercus

c. Grand Bend, Huron Co., Ontario.
d. Ocean View, Norfolk Co., Virginia.
e–g. Provincetown [Cape Cod], Barnstable Co., Massachusetts.
h. Blowing Rock, Watauga Co., North Carolina.
i–l. Edwin S. George Reserve, Livingston Co., Michigan.
m. Lattas Creek Prairie, north of Switz City, Greene Co., Indiana.
n–p. Ames, Story Co., Iowa (all with red hind tibiae).
q. Andover, Anoka Co., Minnesota.
r. Cornell, Wagoner Co., Oklahoma.
s. Payne Co., Oklahoma (red hind tibiae).
t. Flushing, Payne Co., Oklahoma.
u. Colorado Springs, El Paso Co., Colorado.
v. Near Bandera, Bandera Co., Texas (same specimen as *a*).
w. Bexar Co., Texas.

Drawn with camera lucida. All approximately × 12.

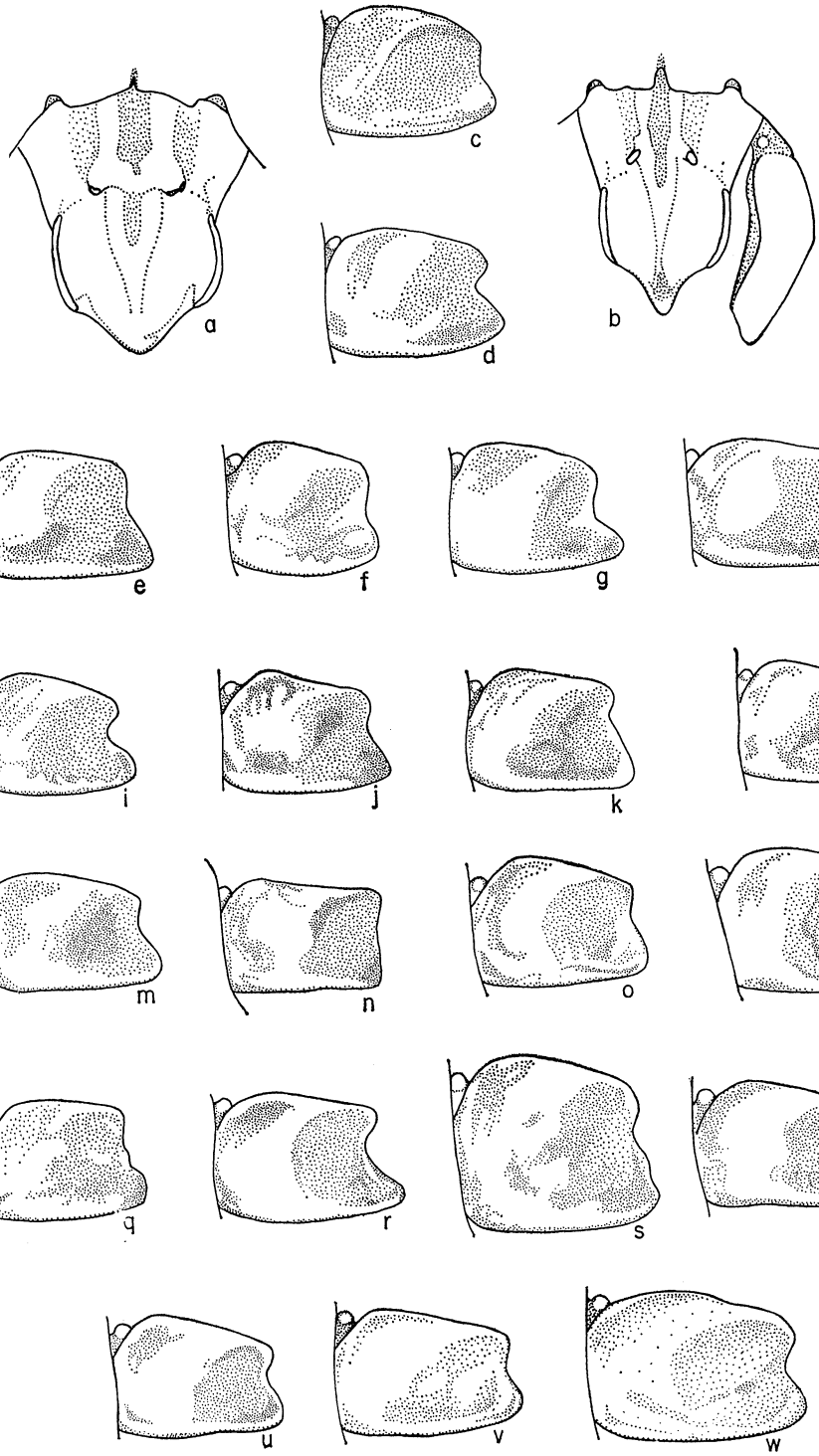

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PLATE XVII

Distal phallic structures, *Schistocerca lineata, S. rubiginosa, S. alutacea*

a, c, e. Oblique views of distal part of phallus, with dorsal fold of ectophallic membrane retracted and ventral lobes depressed to expose diagnostic structures. pht, distal orifice of phallotreme; vl, ventral lobe; z, summit of zygoma, between bases of rami of cingulum ("basal eminence").

b, d, f. Caudal views of distal part of phallus, ventral lobes omitted, showing distal orifice of phallotreme (pht), "basal eminence" (z), and rami of cingulum (rm).

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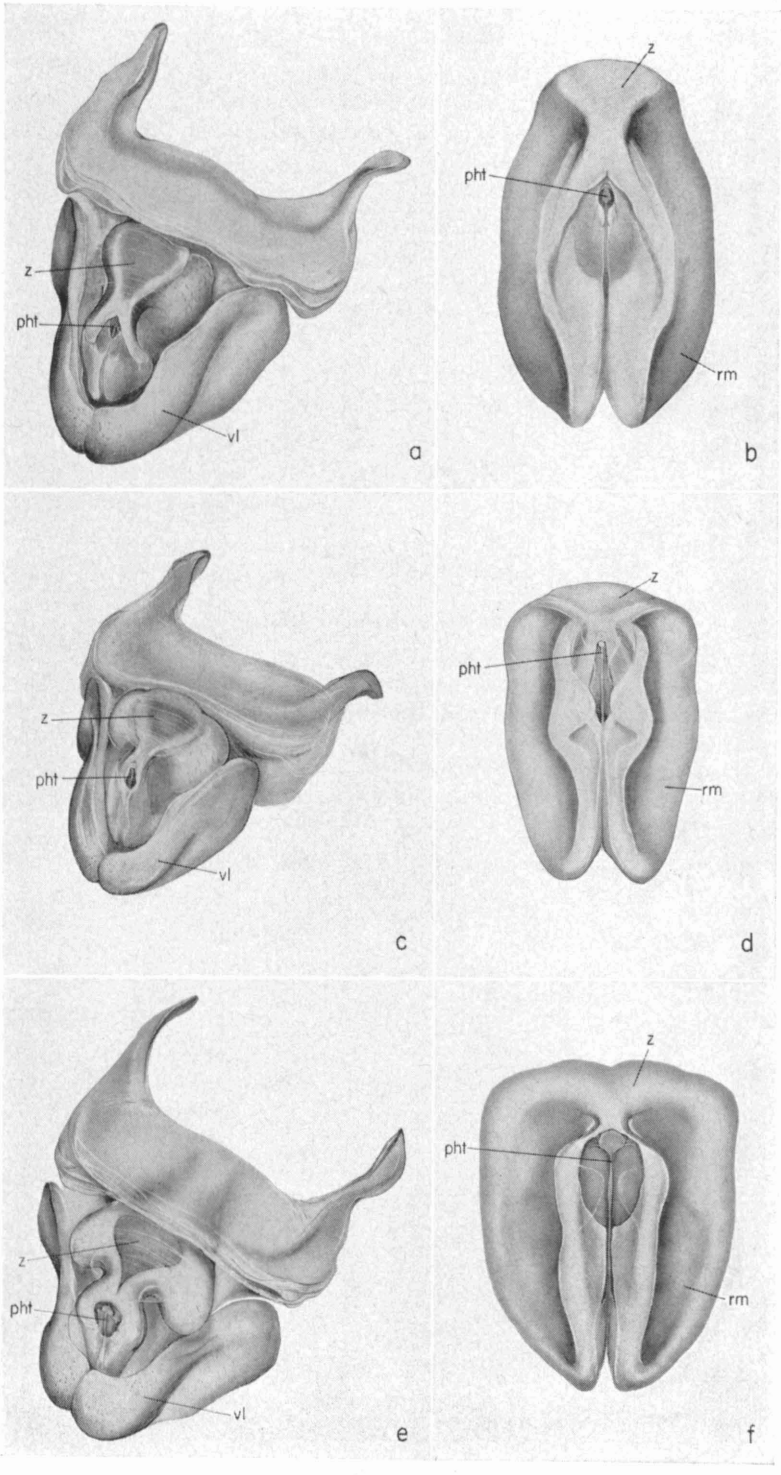
a, b. *Schistocerca lineata* Scudder. Erick, Beckham Co., Oklahoma.

c, d. *Schistocerca rubiginosa* (Harris). Near Islandton, Colleton Co., South Carolina.

e, f. *Schistocerca alutacea* (Harris). Jamesburg, Middlesex Co., New Jersey.

Figures a, c, e approximately × 18; figures b, d, f approximately × 27.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pht
vl
a
z
pht
rm
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z
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rm
f

PLATE XVIII

Schistocerca rubiginosa (Harris)

a. Male, Lakehurst, Ocean Co., New Jersey (31 mm.).
b. Male, Atsion, Burlington Co., New Jersey (31 mm.).
c. Male, Gainesville, Alachua Co., Florida (30 mm.).
d. Female, Fayetteville, Cumberland Co., North Carolina (53.5 mm.).
e. Female, Lakehurst, Ocean Co., New Jersey (44 mm.).
f. Female, Carabelle, Franklin Co., Florida (53 mm.).
g. Female, Tampa, Hillsborough Co., Florida (63.5 mm.).

Length as given above measured from tip of vertex to end of tegmen.

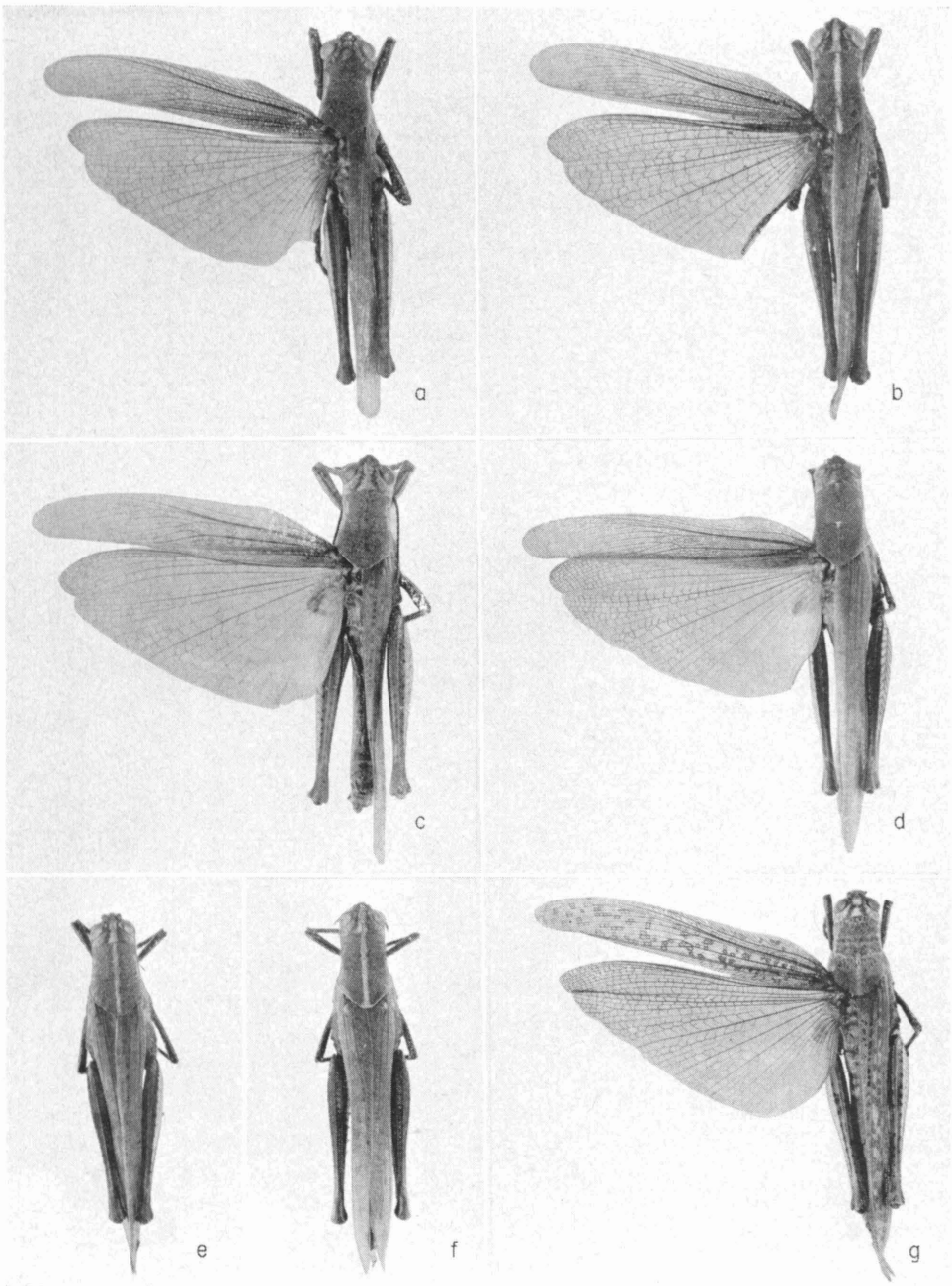
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PLATE XIX

Schistocerca alutacea (Harris)

a, b. Females, Wareham, Plymouth Co., Mass. (45 and 47 mm.).
c. Plesiallotypic male, West Chop, Martha's Vineyard, Mass., Aug., 1893 (35.5 mm.).
d. Female, near Toledo, Lucas Co., Ohio (51.5 mm.).
e. Male, near Lamont, Jefferson Co., Florida (37.5 mm.).
f. Female, near Aucilla, Jefferson Co., Florida (51.5 mm.).

Length as given above measured from tip of vertex to end of tegmen.

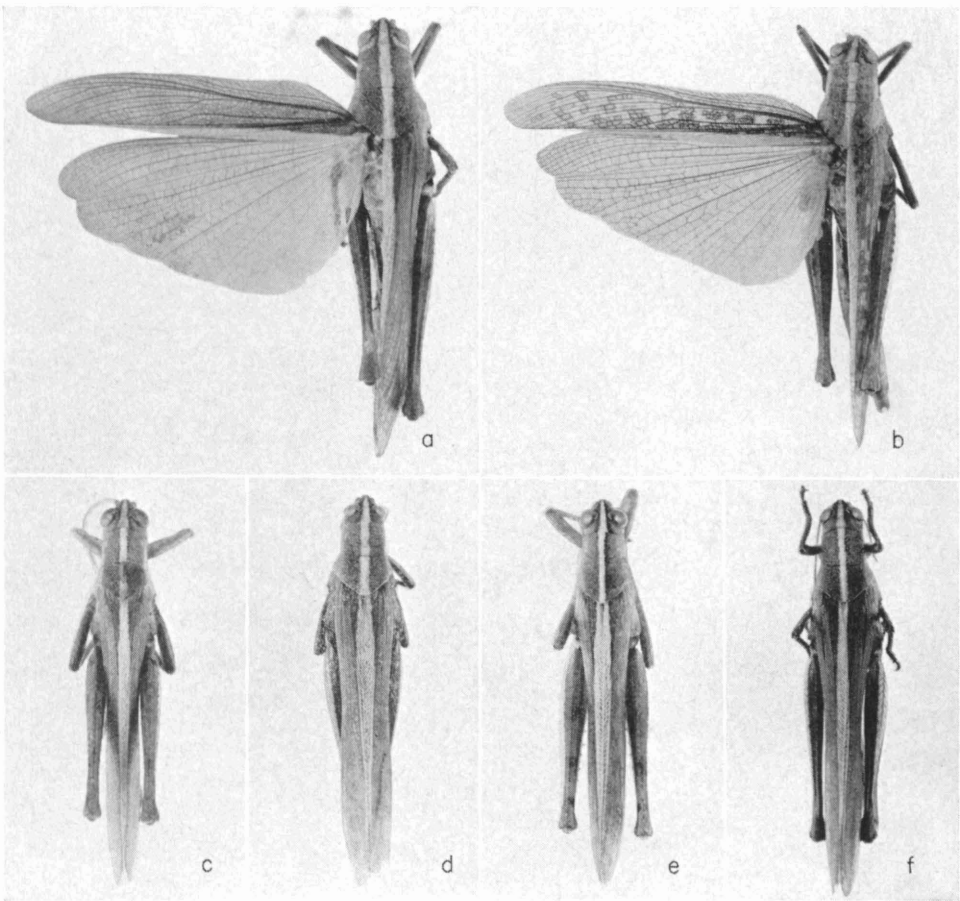
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PLATE XX

Schistocerca lineata Scudder, Western Plains and Southern Texas

a. Female, Coronach, southern Saskatchewan (44 mm.).
b. Female, Bexar Co., Texas (62 mm.).
c. Female, Boas, Chaves Co., New Mexico (57 mm.).
d. Female, near Kenna, Chaves Co., New Mexico (45 mm.).
e. Female, Del Rio, Val Verde Co., Texas (69 mm.).
f. Male, Austin, Travis Co., Texas (50 mm.).

Length as given above measured from tip of vertex to end of tegmen.

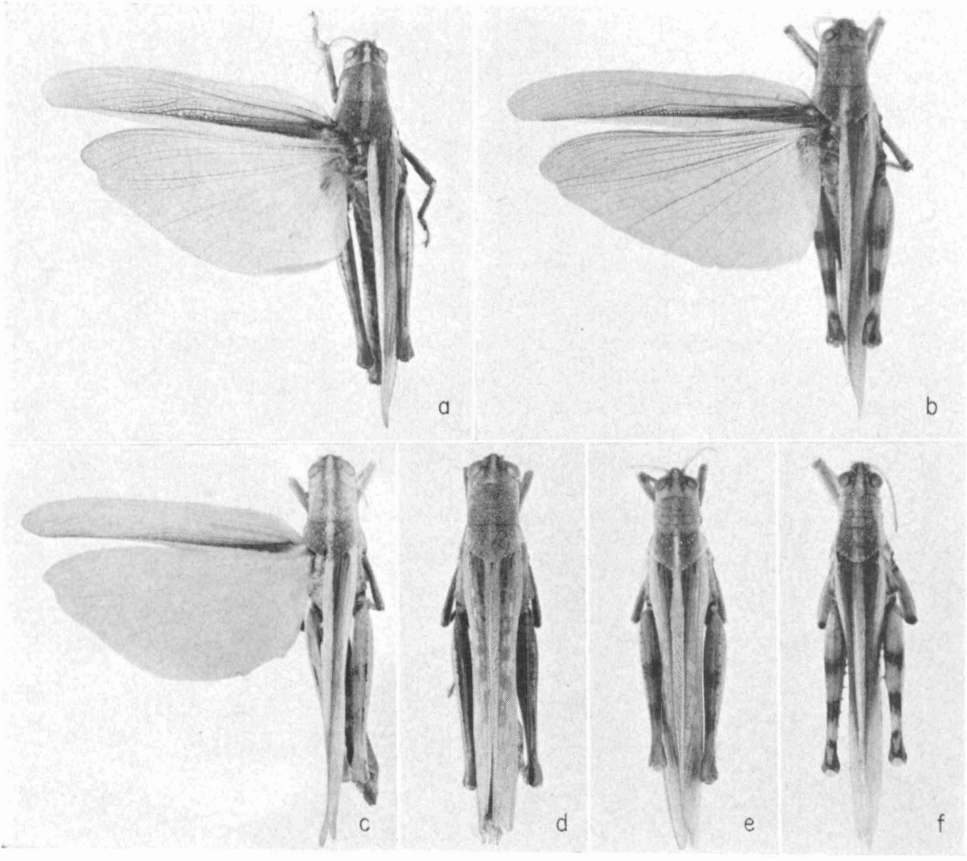
a
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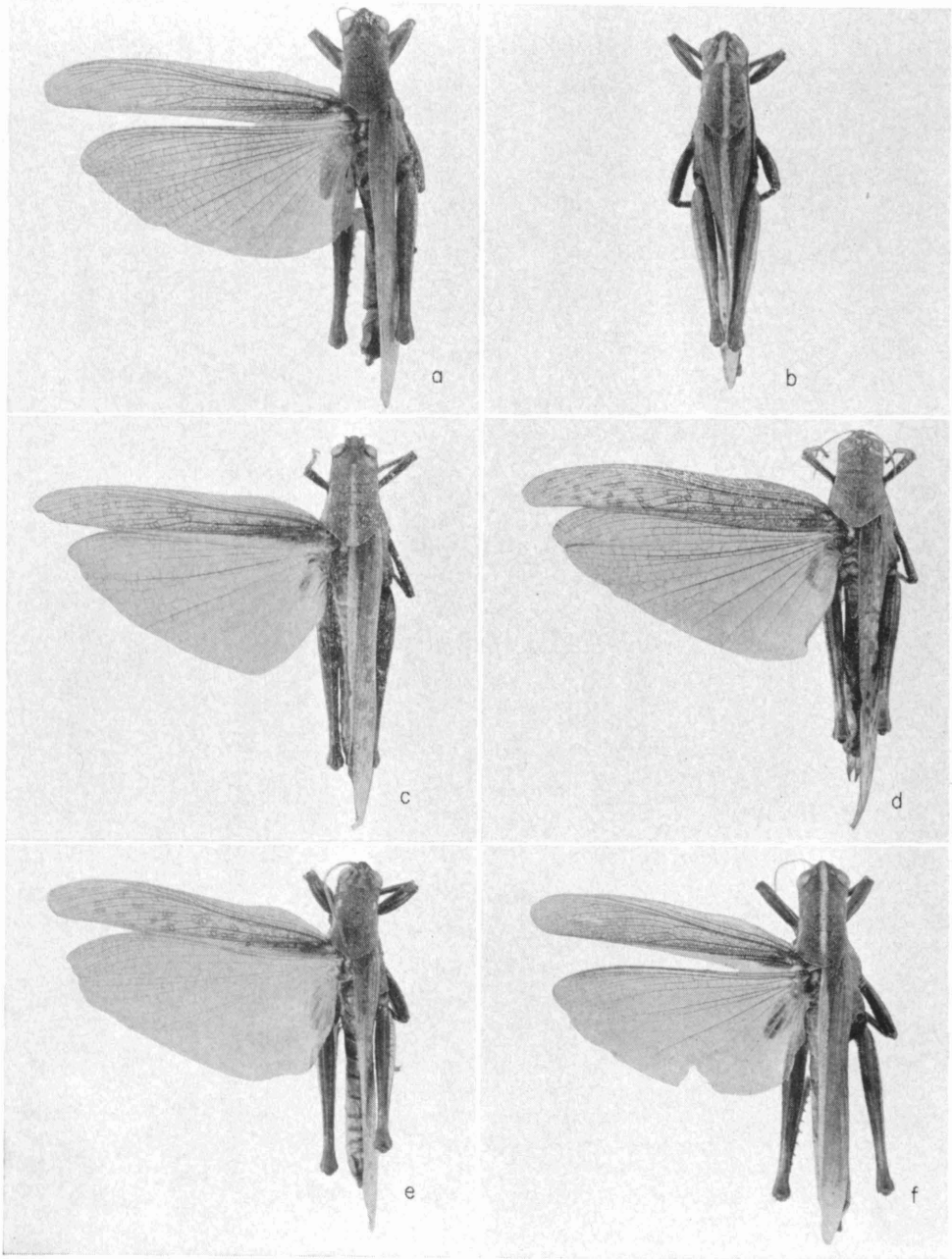
PLATE XXI

Schistocerca lineata Scudder, North Central and Northeastern Regions

a. Male, Manchester, Hillsboro Co., New Hampshire (37 mm.).
b. Male, Center of East Plains, Ocean Co., New Jersey (33 mm.).
c. Female, Grand Bend, Huron Co., Ontario (43.5 mm.).
d. Female, Big Portage Lake, Jackson Co., Michigan (48.5 mm.).
e. Male, Camp Stoner, Lenawee Co., Michigan (37.5 mm.).
f. Male, Jacob's Ladder, Fairfield Co., Ohio (34 mm.).

Length as given above measured from tip of vertex to end of tegmen.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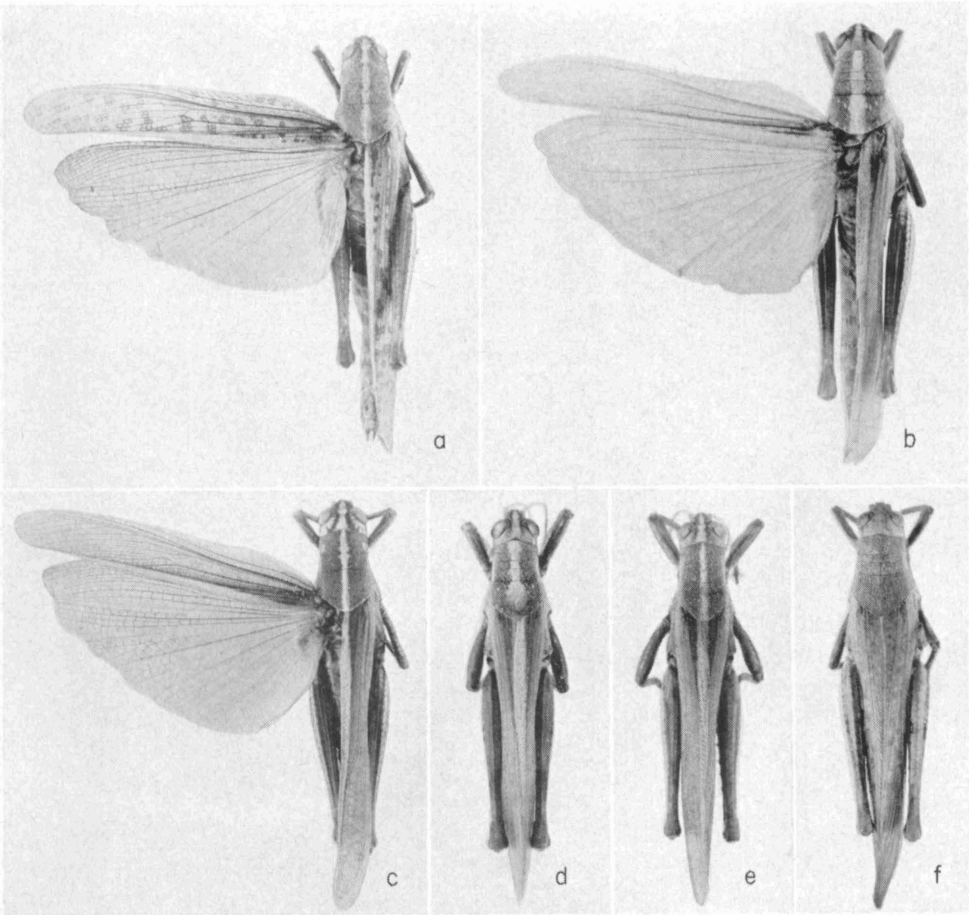

PLATE XXII

Schistocerca lineata Scudder, Central Plains and Prairies

a. Female, Moulton, Appanoose Co., Iowa (56 mm.).
b. Female, Sun City, Barber Co., Kansas (topotypic) (62 mm.).
c. Female, Norman, Cleveland Co., Oklahoma (54 mm.).
d. Male, Panora, Guthrie Co., Iowa (45 mm.).
e. Male, Iowa Co., Iowa (40 mm.).
f. Female, Lattas Creek Prairie, Greene Co., Indiana (52 mm).)

Length as given above measured from tip of vertex to end of tegmen.

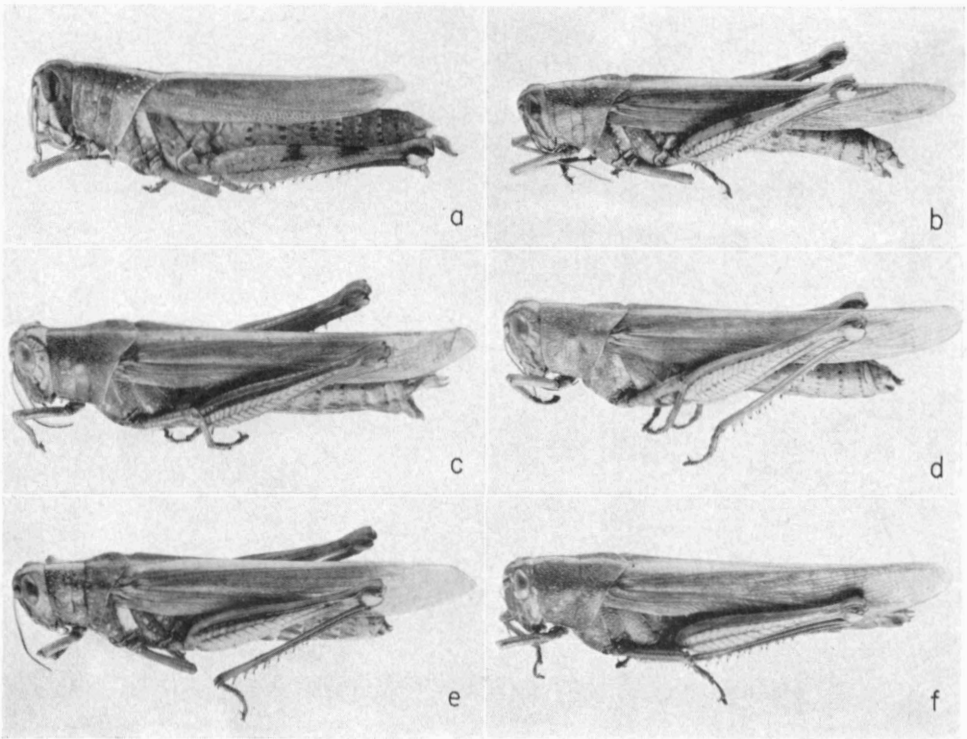

PLATE XXIII

Schistocerca lineata Scudder, Lateral Views of Female

a. Del Rio, Val Verde Co., Texas (59 mm. to tip of ovipositor).
b. Near Austin, Travis Co., Texas (67 mm.).
c. Dallas, Dallas Co., Texas (53 mm.).
d. Near Laverne, Harper Co., Oklahoma (57 mm.).
e. Cleveland Co., Oklahoma (60 mm.).
f. Temperance, Monroe Co., Michigan (51 mm.).

Length as given above measured from tip of vertex to end of tegmen, except as noted.

No. 88. An annotated list of the moths of Michigan exclusive of Tineoidea (Lepidoptera). By SHERMAN MOORE. (1955) 87 pp. $0.90

No. 90. The crane flies of Alaska and the Canadian northwest (Tipulidae, Diptera). The genus *Erioptera* Meigen. By C. P. ALEXANDER. (1955) 33 pp., 38 figs. $0.50

No. 98. A synopsis of the Tabanidae (Diptera) of Michigan. By KIRBY L. HAYS. (1956) 79 pp., 3 pls. $1.15

No. 104. Catalogue of the Odonata of Michigan. By EDWARD J. KORMONDY. (1958) 43 pp., 1 map $0.65

No. 107. The systematics of *Tetragoneuria,* based on ecological, life history, and morphological evidence (Odonata: Corduliidae). By EDWARD J. KORMONDY. (1959) 79 pp., 4 pls., 4 maps $1.20

No. 116. The sibling species of the Alutacea Group of the bird-locust genus *Schistocerca* (Orthoptera, Acrididae, Cyrtacanthacridinae). By THEODORE H. HUBBELL. (1960) 136 pp., 23 pls., 9 figs. $3.00