

Revision of the Alutacea Group of Genus *Schistocerca* (Orthoptera: Acrididae: Cyrtacanthacridinae)

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ABSTRACT The North American Alutacea Group of the genus *Schistocerca* is revised based on phylogenetic analysis and morphological comparison. Phylogenetic analysis suggests that *Schistocerca alutacea sensu* Dirsh is paraphyletic because *S. alutacea albolineata sensu* Dirsh is sister to *S. obscura*. Here, I recognize the monophyletic Alutacea Group consisting of six species: *S. alutacea*, *S. rubiginosa*, *S. lineata*, *S. shoshone*, *S. albolineata*, and *S. obscura*. Previous taxonomic confusion on these species is discussed, and their taxonomic ranks are accordingly raised from subspecies to species level. Neotypes of *S. alutacea* and *S. rubiginosa* are designated, and *S. insignis* is synonymized under *S. albolineata* syn. nov. Also, I argue for the validity of the name *S. lineata* and discuss the previous misapplication of nomenclature. Discussion of color variation and an identification key for all North American *Schistocerca* species are presented.

KEY WORDS North American *Schistocerca*, Alutacea Group, systematics, phylogeny, genitalia

THE LOCUST GENUS *Schistocerca* Stål is a biologically fascinating group. The genus is famous for its African species, *S. gregaria* (Forskål), perhaps one of the most notorious insects in the world. *Schistocerca gregaria*, the desert locust, is capable of forming an enormous swarm consisting of billions of individuals through density-dependent phase changes (Uvarov 1977, Pener and Yerushalmi 1998). Although the well-known desert locust is important and interesting in many aspects, *Schistocerca* is in fact a New World genus, containing about 50 species (Dirsh 1974). Indeed, the desert locust is the only Old World representative of the genus, and this transatlantic disjunction sparked heated debates concerning its origin among entomologists (Kevan 1989, Ritchie and Pedgley 1989). New World *Schistocerca* species are highly diverse and have adapted to different environments. For example, some species form a large swarm comparable with that of the desert locust (Harvey 1981). Most *Schistocerca* species are, however, sedentary, meaning that they do not form a swarm. They nevertheless have an extremely strong flight capacity. Certain species show density-dependent aposematism, which became a prime example of novel insight into the evolution of warning coloration (Sword 1999). These sedentary species also have high host preference within nymphal stage, which is very curious given that most grasshopper species are generalists. *Schistocerca ceratiola* Hubbell and Walker, endemic to central Florida, is one of few monophagous and noc-

turnal species of grasshoppers (Hubbell and Walker 1928).

Despite these attractive aspects of the genus, taxonomy of *Schistocerca* is surprisingly poorly understood. This dichotomy can certainly be attributed to the variability within a species and the similarity across the species. Some widespread species, such as *S. lineata* Scudder and *S. nitens* (Thunberg), have many local populations adapted to specific habitats, which introduces difficulty in taxonomic studies. Other species, such as species within the Americana and Alutacea Groups, are so similar externally that a careless synonymy is quite possible. These factors coupled with an inadequate taxonomic method are the exact reasons why the most recent revision of the genus (Dirsh 1974) is considered to be problematic.

In his revision, Dirsh (1974) used morphometric characters exclusively to define species, resulting in numerous synonyms. He modified the morphometric technique, initially used to differentiate the phase of a locust species (Uvarov 1966), to characterize each species using the proportional value of several measurements of characters including length of body, length of pronotum, length of tegmina (forewing), length and width of hind femur, and width of head. He created a pentagram using the proportional values and visually compared the shape for each species. Although these characters themselves are useful in differentiating species in some cases, the method failed to differentiate closely related species that are only distinguishable by internal male genitalia. As a result, Dirsh (1974) recognized 22 species and 21 subspecies. The most problematic species is *Schistocerca nitens*,

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under which Dirsh synonymized 16 names. No one has yet re-evaluated his treatment. Other taxonomically problematic species are *S. americana* (Drury) and *S. alutacea* (Harris). Dirsh (1974) changed the rank of any species that shared a similar pentagram, creating 11 subspecies under *S. americana* and 7 under *S. alutacea*. Several workers doubted his taxonomic concept and initiated a series of hybridization experiments to test the biological meaningfulness of the revision (Harvey 1979, 1981, 1982, Jago et al. 1979, 1982). These works focused on the subspecies of *S. americana*, including some of the most destructive locust species in the world, and resulted in a reclassification that yielded five species and four subspecies (Harvey 1981). However, no similar attempt has been made for the sedentary species in North America, *S. alutacea*.

In this study, I re-evaluate Dirsh's synonymy based on the morphological characters and known ecology. Several ecological studies on North American *Schistocerca* have been published since Dirsh's revision (Sword and Chapman 1994, Chapman et al. 1995, Howard 1995, Sword and Dopman 1999, Capinera et al. 2001), and most of them use the names before the synonymy. Here, I attempt to resolve long-standing taxonomic confusions marred by disagreements among orthopterists. I also test previous phylogenetic relationships among the North American *Schistocerca* species suggested by Hubbell (1960) and Dirsh (1974) in light of the morphological phylogeny.

Color Variation in *Schistocerca*

Schistocerca is known as a taxonomically difficult group mainly because of its color variation (Hebard 1923, Hubbell 1960). Dirsh's (1974) revision is a good example of how color variation can affect the taxonomic concept. His justification for synonymy, in addition to the morphometric technique, stemmed from his erroneous claims to have found the intermediate forms of all possible combinations with overlapping geographic distributions (Dirsh 1974). Variability of color in grasshoppers is well known and sometimes ineffective in differentiating species (Hubbell 1960). This is especially true for the North American *Schistocerca* species. Hubbell (1960) analyzed the variability of color patterns in *S. lineata*, *S. alutacea*, and *S. rubiginosa* (Harris), and here I briefly review his work and other studies (King and Slifer 1955, Chapman et al. 1995, Sword and Dopman 1999).

The dorsal stripe, which extends from the vertex to the anterior tip of pronotum, is one of several variable color patterns in *Schistocerca* (Rehn 1901, 1902). In early 1900, *S. alutacea* was known to be always striped, whereas *S. rubiginosa* was thought to be unstriped. Rehn (1901, 1902) observed a striped form and an unstriped form in copula and suspected that *S. rubiginosa* was just an unstriped form of *S. alutacea*. After examining a large number of specimens of both species identified by unique phallic morphologies, Hubbell (1960) concluded that *S. alutacea* is always striped, and *S. rubiginosa* can be either striped or unstriped. He then plotted the occurrence of a dorsal

stripe in *S. rubiginosa* against the collecting localities of the specimens and found that the southern populations gradually lose the dorsal stripe. Similar phenomenon is found in *S. shoshone* (Thomas). Originally, the species was described based on the striped form, and Scudder (1899) described two additional species based the absence of the dorsal stripe. Hebard (1935), when synonymizing unstriped *S. venusta* Scudder under striped *S. shoshone*, hypothesized that *S. venusta* was nothing more than an unstriped form of *S. shoshone*. Chapman et al. (1995) suggested that these two forms are associated with different host plants. Individuals that feed on jojoba, *Simmondsia chinensis* (Link) C. Schneid (Buxaceae), were always striped, and individuals that feed on mesquite, *Prosopis velutina* Wootton (Caesalpiniaceae), were always unstriped. Chapman and Sword (unpublished data) performed several crossing experiments between striped and unstriped forms and found that offspring were always striped regardless of the sex of the parents, confirming Hebard's (1935) hypothesis on the variability of the stripe.

Hubbell (1960) also studied regional variations in body color, markings of head and thorax, mesepimeral stripe, tegminal maculation, and hind tibiae. He demonstrated that different populations of a single species could vary considerably in color patterns and that color alone could not be used as a definite diagnostic character. For example, he showed that color of the hind tibiae varied according to the populations, especially in *S. lineata*. The hind tibiae were yellowish or brownish in the eastern populations, coral pink or red in the midwestern populations, and black in the southwestern populations. A similar phenomenon can be observed in *S. albolineata* (Thomas), whose Arizona populations have red hind tibiae, whereas Texas and Mexican populations have black hind tibiae (unpublished data). King and Slifer (1955) found that in *Melanoplus mexicanus mexicanus* (Saussure), color of the hind tibiae was determined by the Mendelian genetics of an autosomal gene, which could explain the color variation of hind tibiae in *Schistocerca*.

Schistocerca lineata is one of the most polymorphic species in the genus, and Hubbell (1960) showed that coloration intensifies toward southwestern regions. Populations in Illinois, Indiana, Michigan, and Ohio were lightly colored, whereas those in Oklahoma and Texas were conspicuously colored. He hypothesized that the variation could be associated with food preference of a local population and was not necessarily related to the habitat. Dirsh (1974) proposed that the conspicuously colored form was a hybrid between *S. albolineata* and *S. lineata*, which he used as a reason for his synonymy. However, this Texas population is not a hybrid, but an aposematic population of *S. lineata* that probably feeds on toxic *Ptelea trifoliata* L. (Rutaceae) (Sword and Dopman 1999). Sword and Dopman (1999) studied several populations of *S. lineata* in Texas that used different host plants as a nymphal instar. They showed that the intensity of density-dependent aposematism was different in populations associated with toxic *P. trifoliata* and populations as-

Table 1. Taxonomic concept changes in North American *Schistocerca* species

Species Group	Currently recognized species	Original Description	Scudder (1899)	Hubbell (1960)	Dirsh (1974)	Harvey (1981)
Americana	<i>S. americana</i> (Drury, 1773)	<i>Gryllus americanus</i>	<i>S. americana</i>	<i>S. americana</i>	<i>S. americana americana</i>	<i>S. americana</i>
Nitens	<i>S. nitens</i> (Thunberg, 1815)	<i>Gryllus nitens</i>	<i>S. vaga</i>	<i>S. vaga</i>	<i>S. nitens nitens</i>	N/A
Ceratiola	<i>S. ceratiola</i> (Hubbell and Walker, 1928)	<i>Schistocerca ceratiola</i>	N/A	<i>S. ceratiola</i>	<i>S. ceratiola</i>	N/A
Damnifica	<i>S. damnifica</i> (Saussure, 1861)	<i>Acridium damnificum</i>	<i>S. damnifica</i>	<i>S. damnifica</i>	<i>S. damnifica</i>	N/A
Alutacea	<i>S. alutacea</i> (Harris, 1841)	<i>Acrydium alutaceum</i>	<i>S. alutacea</i>	<i>S. alutacea</i>	<i>S. alutacea alutacea</i>	N/A
	<i>S. rubiginosa</i> (Harris, 1862)	<i>Acridium rubiginosum</i>	<i>S. rubiginosa</i>	<i>S. rubiginosa</i>	<i>S. alutacea rubiginosa</i>	N/A
	<i>S. lineata</i> Scudder, 1899	<i>Schistocerca lineata</i>	<i>S. lineata</i>	<i>S. lineata</i>	<i>S. alutacea lineata</i>	N/A
	<i>S. shoshone</i> (Thomas, 1873)	<i>Acridium shoshone</i>	<i>S. shoshone</i>	<i>S. shoshone</i>	<i>S. alutacea shoshone</i>	N/A
	<i>S. albolineata</i> (Thomas, 1875)	<i>Acridium albolineata</i>	<i>S. albolineata</i>	<i>S. albolineata</i>	<i>S. alutacea albolineata</i>	N/A
	<i>S. obscura</i> (Fabricius, 1798)	<i>Gryllus obscurus</i>	<i>S. obscura</i>	<i>S. obscura</i>	<i>S. obscura</i>	N/A

sociated with palatable *Rubus trivialis* Michaux (Rosaceae). When crowded, nymphs from both populations produced an aposematic coloration, but *Ptelea*-associated nymphs were more intense in color. Sword (2002) suggested that the nymphal coloration associated with a host plant is genetic, not necessarily related to host plant, because he was able to rear different color phenotypes on the same standard diet (lettuce). The ontogenetic host specialization in relation to the aposematism is only known in Texas populations of *S. lineata*, and given the species' wide distribution, midwestern and eastern populations might have different ecologies (Sword and Dopman 1999).

North American *Schistocerca*

There are 10 *Schistocerca* species in North America north of Mexico (Table 1). Recently, Stidham and Stidham (2002) reported the occurrence of *S. camerata* Scudder in southern Texas, but because it is mainly distributed in Mexico, it is not treated in this revision. Hubbell (1960) recognized six species groups in North America: Americana, Nitens, Damnifica, Ceratiola, Obscura, Shoshone, and Alutacea Groups. However, this grouping is not based on a modern cladistic analysis, and each group might not represent a monophyletic clade. Here, I present a slight modification of Hubbell's grouping and tentatively recognize five species groups (Table 1).

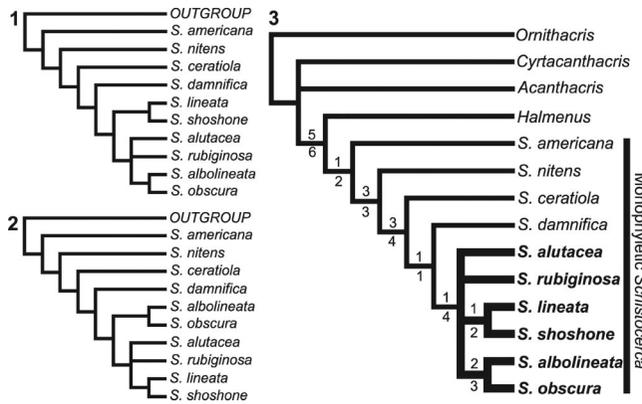
The Americana Group contains large grasshopper species including all three swarming species: the Central American locust *S. piceifrons* (Walker), the South American locust *S. cancellata* (Serville), and the desert locust *S. gregaria*. *S. americana* is the only North American representative, distributed from Florida to Texas. It occasionally forms minor swarms that cause damage in orange orchards in Florida (Harvey 1981, Capinera et al. 2001). The Nitens Group is a taxonomically problematic group, and perhaps contains more than 10 species. *S. nitens nitens sensu* Dirsh (1974) is extremely widespread and spans from the western United States to Brazil. I examined a large number of specimens bearing the identification label by Dirsh as *S. nitens nitens* and was able to distinguish several distinct forms based on color, male cerci, and male phallic complex.

It is not clear why he synonymized so many species under *S. nitens nitens*, most of which were soundly recognized by earlier taxonomists (Hebard 1923, 1924, 1932). North American *S. nitens* can be characterized by tectiform pronotum and mottled tegmina. It is sometimes called by its old name *S. vaga* (Scudder). Its distribution ranges from southern California to Mexico, with a population found in Hawaii (Bianchi and Kajiwara 1966, Sugerman 1966). The Ceratiola Group contains single species, *S. ceratiola*, which is endemic to Central Florida. It is unique in nocturnal habit as well as monophagy on Florida rosemary, *Ceratiola ericoides* Michaux (Hubbell and Walker 1928, Franz and Franz 1989). The Damnifica Group also contains one species, *S. damnifica* (Saussure), distributed in the eastern United States. This species is highly homogeneous in form and can be easily identified by having rusty brown color, highly tectiform pronotum, and slightly ensiform antennae. In the past, two subspecies of *S. damnifica* were described: the nominal subspecies and *S. damnifica calidor* (Rehn and Hebard). The only difference between the two is size, and here I follow Dirsh's (1965) synonymy in recognizing a single species with size variability. The remaining six species forming the Alutacea Group are subject of this study.

Materials and Methods

In this revision, I examined six species forming the Alutacea Group. These are *S. alutacea* (Harris), *S. rubiginosa* (Harris), *S. lineata* Scudder, *S. shoshone* (Thomas), *S. albolineata* (Thomas), and *S. obscura* (Fabricius). I directly compared all known type specimens with the original descriptions and Dirsh's revision.

This work was based on the study of specimens ($n = 7,882$) from the following institutions: Academy of Natural Sciences, Philadelphia, PA (ANSP); Brigham Young University, Arthropod Collection, Provo, UT (BYU); Reginald Chapman's personal collection (CHAP); Colorado State University Insect Collection, Fort Collins, CO (CSUC); Illinois Natural History Survey, Champaign, IL (INHS); University of Wisconsin Insect Research Collection, Madison, WI (IRCW); McGill University, Lyman Entomological



Figs. 1–3. Phylogeny of the North American *Schistocerca* species. (1 and 2) Two equally parsimonious cladograms produced from the analysis (L = 39; Ci = 82; Ri = 89). (3) Strict consensus cladogram (L = 40; Ci = 80; Ri = 87). Four cyrtacanthacridine outgroup taxa were collapsed as a single terminal in (1 and 2). Numbers above node are Bremer support values, and numbers below are the number of synapomorphies for that node.

Museum, Ste. Anne de Bellevue, QC, Canada (LEMQ); New Mexico State University Arthropod Museum, Las Cruces, NM (NMSU); Oklahoma State University, K.C. Emerson Museum, Stillwater, OK (OSEC); Ohio State University Insect Collection, Columbus, OH (OSUC); University of Kansas, Snow Entomology Collection, Lawrence, KS (SEMC); University of Arkansas Arthropod Museum, Fayetteville, AR (UARM); University of Michigan Museum of Zoology, Ann Arbor, MI (UMMZ); University of Minnesota Insect Collection, St. Paul, MN (UMSP); University of Nebraska State Museum, Lincoln, NE (UNSM); University of Idaho WFBarr Entomological Museum, Moscow, ID (WFRM). Hubbell’s genitalia collection from UMMZ was also studied. All existing type specimens were examined from the following institutions: Academy of Natural Sciences, Philadelphia, PA (ANSP); British Museum of Natural History, London, U.K. (BMNH); California Academy of Sciences, San Francisco, CA (CAS); Harvard University Museum of Comparative Zoology, Cambridge, MA (MCZ); University of Michigan Museum of Zoology, Ann Arbor, MI (UMMZ).

Male genitalia were extruded by inserting a probe under the epiproct using the technique described by Hubbell (1932). Ovipositors were dissected by making a slit at the distal part of abdomen (Cohn and Cantrall 1974). Genitalia were placed in 10% KOH solution for several hours to dissolve muscles. Cleared genitalia were placed in a vial filled with glycerin, and each genitalic specimen was given an identification number to associate with the pinned specimens. All illustrations were made using a drawing tube on a Wild dissecting microscope.

To test the previously suggested phylogenetic relationships, a cladistic analysis was performed using 10 North American *Schistocerca* species and 4 cyrtacanthacridine outgroup species. *Acanthacris*, *Cyrtacanthacris*, *Ornithacris*, and *Halmenus* (a genus endemic to the Galapagos) were used as outgroup taxa, and *Ornithacris* was used to root the tree. Twenty-two morphological characters with a total of 55 character

states were used in the cladistic analysis (Appendix A). Inapplicable characters were coded as “—.” All characters were equally weighted and treated as non-additive. Characters 0–1, 6–8, 9–10, 17–18, 19–20, and 21–22 were coded using a mixed-coding technique. The data matrix (Appendix B) was created in WinClada (Nixon 2002), and the cladistic analysis was carried out using NONA (Goloboff 1995). Search parameters include rs 0; hold 10,000; mult*100; and max*. From the obtained trees, any unsupported node was collapsed.

An electronic supplement of this study is now available (<http://www.schistocerca.org/alutacea.htm>). This website includes information on each species along with the images of all existing type specimens. It also contains an interactive identification key, a diagnosis, a distribution map, and a list of selected literature. PDF files of the original description are also linked to the website.

Results and Discussion

Phylogeny of North American *Schistocerca*

The cladistic analysis resulted in two most parsimonious trees of 39 steps (Figs. 1 and 2). The strict consensus of two most parsimonious trees collapsed one node and produced a consensus tree of 40 steps (consistency index [Ci] = 80; retention index [Ri] = 87; Fig. 3). Monophyly of the Alutacea Group was strongly supported in by four synapomorphies, although the relationship within the clade is largely unresolved. Among the most parsimonious trees, one topology (Fig. 1) suggests that *S. alutacea* and *S. rubiginosa* are sisters to *S. albolineata* + *S. obscura* clade by having constricted basal eminence of cingulum. The alternative topology (Fig. 2) suggests that they are sisters to *S. lineata* + *S. shoshone* clade supported by a pair of tubercles on male epiproct. Current data alone are insufficient in resolving this problem, but it is clear that the species in the Alutacea group are very closely related.

Table 2. Diagnostic characters, distribution, phenology, preferred habitat, and known host plants for the species in the Alutacea Group

Species	Diagnostic characters	Distribution	Phenology	Preferred habitat	Known host plant
<i>S. alutacea</i>	Highly convex rami of cingulum; always with a yellow dorsal stripe	Eastern United States	May–Aug	Shrubby, moist to wet (Northeastern U.S.); dry, sand hill (Florida)	<i>Vaccinium macrocarpon</i>
<i>S. rubiginosa</i>	Slightly inflated head; cylindrical pronotum; small male cerci	Southeastern United States	May–Aug	Xeric, sandy soil	Unknown
<i>S. lineata</i>	Basal eminence broad in the middle; inflated male fore and middle femora	Entire North America	May–Oct	Variable	<i>Ptelea trifoliata</i> , <i>Rubus trivialis</i> , <i>Quercus</i> sp., <i>Glycyrrhiza lepidota</i> , <i>Taraxacum</i> sp.
<i>S. shoshone</i>	No marking on abdominal tergites	Western U.S.	June–Aug	Riparian, desert	<i>Simmondsia chinensis</i> , <i>Prosopis velutina</i>
<i>S. albolineata</i>	Male cerci with lower apical angle protruding more than upper	Southwestern United States and Mexico	Aug–Oct	Dry mountain	<i>Cercidium microphyllum</i> , <i>Cossypium hirsutum</i>
<i>S. obscura</i>	Male subgenital plate highly flared outward	Eastern United States	July–Sept	Open woodlands	<i>Celtis laevigata</i>

Present analysis (Fig. 3) contradicts the previously suggested phylogenies by Hubbell (1960) and Dirsh (1974). Hubbell (1960) suggested that *S. alutacea*, *S. rubiginosa*, and *S. lineata* are sibling species, distinguishable by only the subtle differences in genitalic morphologies. The current phylogeny suggests that *S. lineata* is in fact sister to *S. shoshone* and are united by inflated fore and middle femora. Dirsh (1974) did not synonymize *S. obscura* under *S. alutacea* because he considered the morphological differences to be sufficient enough. However, the present phylogeny suggests that *S. obscura* is sister to *S. albolineata*, which was considered as a subspecies of *S. alutacea* by Dirsh (1974). This result indicates that *S. alutacea sensu* Dirsh is paraphyletic, thus demonstrating the inadequateness of his synonymy.

North American *Schistocerca* species are ecologically sedentary, perhaps with an exception to *S. americana*. Although they possess a strong flight capacity, they mostly stay in the same habitat in their lifetime. Mass migration observed in other swarming species has never been reported in the species of the Alutacea Group. Occasionally, aggregation behavior has been observed in some species, causing minor damage to crops, but they do not have the characteristics of true swarming behavior such as cohesive flight or nymphal band movement (Chapman et al. 1995). Interestingly, however, the sedentary species of the Alutacea Group was recently found to possess a character, density-dependent polyphenism, known to be crucial in the swarming *Schistocerca* species (Sword 1999, 2002). The desert locust *S. gregaria* is usually solitary, but when population density increases, it behaves gregariously followed by changes in color patterns and shapes (Uvarov 1966). Although the sedentary species do not behave gregariously or change in morphology, they do change color in response to high density (Sword 1999). Sword (1999) discovered that the nymphs of *S. lineata* in Texas change color when reared in crowded condition. Nymphs associated with

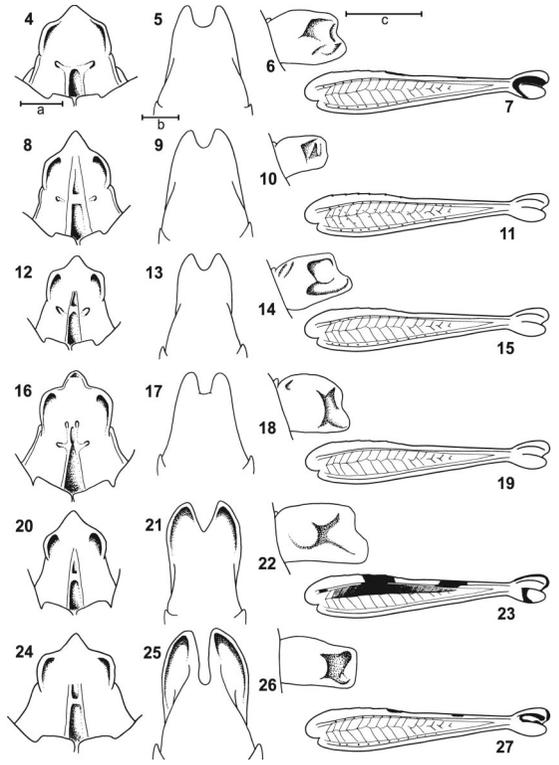
the toxic *Ptelea* were green when reared in isolation but turned bright yellow and black when reared in crowdedness. Sword (2002) later suggested that the density-dependent polyphenism in *S. lineata* is partially genetic, not necessarily related to the host plant the individuals feed on. Although not studied, it is possible that the closely related species in the Alutacea Group might have the similar polyphenism. This would indicate then that the density-dependent polyphenism is a phylogenetically informative character.

Another interesting point deduced from the phylogeny is the evolution of feeding habit. Most grasshopper species are polyphagous (Chapman 1990). Sword and Dopman (1999) discovered that the Texas populations of *S. lineata* were monophagous as nymphs but polyphagous as adults. The host association is also found in the Arizona populations of *S. shoshone* (Sword and Chapman 1994), and in the Texas populations of *S. obscura* (Chapman and Sword, unpublished data). The phylogeny suggests that *S. ceratiola* is basal to all the other sedentary North American species. *S. ceratiola* is one of few monophagous grasshopper species that specializes on *C. ericoides* (Hubbell and Walker 1928, Franz and Franz 1989). Therefore, it is possible that the common ancestor between *S. ceratiola* and other sedentary species evolved the intimate host–plant association. The extreme monophagy found in *S. ceratiola* is perhaps the result of the intensified dependency on the host plants. Because of this dependency, *S. ceratiola* might have developed the nocturnal habit to avoid predators. The ancestor of the Alutacea Group could have explored other niches but nevertheless retained the innate tendency to associate with the host plants in the local population. The fact that different local populations of *S. lineata* and *S. shoshone* have different host associations indicates that the nymphal monophagy is rather plastic in terms of choosing the host plants.

The Alutacea Group

The Alutacea Group consists of six closely related species: *S. alutacea* (Harris), *S. rubiginosa* (Harris), *S. lineata* Scudder, *S. shoshone* (Thomas), *S. albolineata* (Thomas), and *S. obscura* (Fabricius) (Table 2). It is characterized by four synapomorphies: round apex of male subgenital plate, rectangular male cerci, presence of small granules on pronotum and thorax, and constricted basal eminence of zygoma in male phallic complex. Useful plesiomorphic characters include unusually long antennae especially in males, robust body form, tegmina just slightly longer than the tip of abdomen, and tegmina colored in olive green or brown. The group is geographically confined in North America. Ecologically, the species in the group are arboreal and found in various woody habitats (Squitier and Capinera 2002a, Sword and Chapman 1994).

The Alutacea Group in the present sense is broader than in the sense of Hubbell (1960). He originally included three species, *S. alutacea*, *S. rubiginosa*, and *S. lineata*, within his Alutacea Group that were united by somewhat superficial characters. In this study, I have retained the species group name, but it now includes Hubbell's (1960) Alutacea, Obscura, and Shoshone Groups. Subspecies of *S. alutacea sensu* Dirsh (1974) are now considered valid species, with the exception of *S. insignis* Hebard, which is now a synonym of *S. albolineata*.

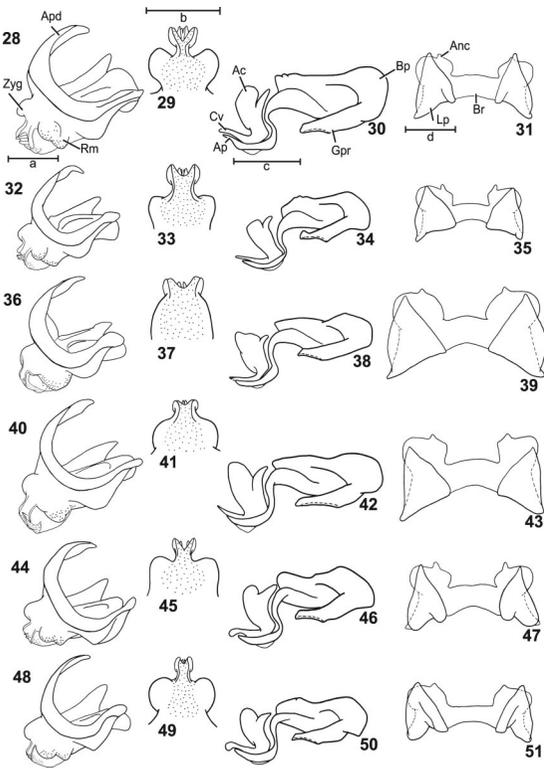


Figs. 4–27. External morphological characters of the species in the Alutacea Group. (4–7) *S. alutacea*; (8–11) *S. rubiginosa*; (12–15) *S. lineata*; (16–19) *S. shoshone*; (20–23) *S. albolineata*; (24–27) *S. obscura*; (4, 8, 12, 16, 20, and 24) male epiproct; (5, 9, 13, 17, 21, and 25) male subgenital plate; (6, 10, 14, 18, 22, and 26) male cercus; (7, 11, 15, 19, 23, and 27) hind femur pattern. Bar a = 1 mm for 4, 8, 12, 16, 20, and 24. Bar b = 1 mm for 5, 9, 13, 17, 21, and 25. Bar c = 1 mm for 7, 11, 15, 19, 23, and 27.

Key to North American *Schistocerca* Species

1. Mesosternum with lateral lobes longer than wide. Prosternal process always present. Male subgenital plate always bilobed. Usually moderate to large size 2, *Schistocerca* Stål
 Mesosternum with lateral lobes as wide as long or wider than long. Prosternal process present or absent. Male subgenital plate variable. Usually small to medium size. Other Acrididae
2. Small for the genus (♂ TL = 29–32 mm; ♀ TL = 39–41 mm), eyes highly prominent. Tegmina narrow, antennae much longer than the length of head and pronotum. Hind femur with two dark dorsal bands. Taken alive, color green. Museum specimens brown. Endemic in Central Florida, only found on Florida rosemary *Ceratiola ericoides*.
 *S. ceratiola* Hubbell and Walker
 body size moderate to large. Tegmina broad. 3
3. Tegmina much longer than the tip of abdomen, and posterior margin of tegmina colorless and transparent. Entire tegmina with distinct black patches or mottling 4
 Tegmina slightly longer than the tip of abdomen, and the entire tegmina brown, olive green, liver brown, or rusty brown, with or without slight mottling 5
4. Tegmina transparent with large distinct dark patches. Overall brown in color. Lateral lobe of pronotum with two dark markings. Median

- carina of pronotum low and prozona slightly constricted. Antennae as long as the length of head and pronotum. Hind femur without dorsal bands. Males slightly smaller than females. *S. americana* (Drury)
- Tegmina transparent with many irregular mottling. Overall gray in color. Lateral lobe of pronotum, with single dark marking and white marking at the base. Median carina of pronotum slightly tectiform, especially in females and prozona not constricted. Antennae slightly longer than the length of head and pronotum. Hind femur with two dorsal bands. Males much smaller than females.
 *S. nitens* (Thunberg)
5. Entire body rusty brown sometimes with slight mottling on tegmina. Median carina of pronotum distinctly elevated. Antennae shorter than the length of head and pronotum, and weakly ensiform *S. damnifica* (Saussure)
 Body color variable with tegmina uniformly brown or with slight mottling. Median carina



Figs. 28–51. Male genitalic structures of the species in the Alutacea Group. (28–31) *S. alutacea*; (32–35) *S. rubiginosa*; (36–39) *S. lineata*; (40–43) *S. shoshone*; (44–47) *S. albolineata*; (48–51) *S. obscura*; (28, 32, 36, 40, 44, and 48) cingulum; (29, 33, 37, 41, 45, and 49) “basal eminence” of zygoma; (30, 34, 38, 42, 46, and 50) endophallus; (31, 35, 39, 43, 47, and 51) epiphallus. Ac, arch of cingulum; Anc, ancora; Ap, apical valve of aedeagus; Apd, apodemes of cingulum; Bp, basal valve of aedeagus; Br, bridge of epiphallus; Cv, valve of cingulum; Gpr, gonopore process; Lp, lophus; Rm, rami of cingulum; Zyg, zygoma. Bar a = 1 mm for 28, 32, 36, 40, 44, and 48. Bar b = 1 mm for 29, 33, 37, 41, 45, and 49. Bar c = 1 mm for 30, 34, 38, 42, 46, and 50. Bar d = 1 mm for 31, 35, 39, 43, 47, and 51.

- of pronotum not elevated. Antennae, especially in males, much longer than the length of head and pronotum, and filliform 6, the Alutacea Group
- 6. Male epiproct without a pair of tubercles (Figs. 20 and 24). Apical lobes of male subgenital plate slightly or much flared outward (Figs. 21 and 25). Integument highly setose 7
- Male epiproct with a pair of tubercles (Figs. 4, 8, 12, and 16). Apical lobes of male subgenital plate not flared outward (Figs. 5, 9, 13, and 17). Integument moderately or sparsely setose 8
- 7. Male cerci highly bilobed, and lower apical angle protruding more than upper (Fig. 22). Apical lobes of male subgenital plate only slightly flared outward (Fig. 21). Upper carina and

- upper carinula of hind femora without a row of small dots. Two distinct dorsal bands on hind femora with upper half of medial area black (Fig. 23). Hind tibiae mostly red, sometime black or blue *S. albolineata* (Thomas)
- Male cerci not bilobed (Fig. 26). Apical lobes of male subgenital plate highly flared outward (Fig. 25). Upper carina and upper carinula of hind femora with a row of small dots (Fig. 27). Two dorsal bands on hind femur present or obliterated to no band. Hind tibiae purple, brown or black *S. obscura* (Fabricius)
- 8. Fore and middle femora of males distinctively inflated. “Basal eminence” of cingulum, hour-glass shaped, and very broad in the middle (Figs. 41 and 45) 9
- Fore and middle femora of males not inflated. “Basal eminence” of cingulum, slightly or highly constricted in the middle (Fig. 29 and 33) 10
- 9. Overall coloration olive green. Upper carina and upper carinula without a row of small dots (Fig. 19). Hind tibiae mostly red, pink, or orange. Posterior margin of abdominal tergites always without a row of black dots. Found in the southwestern United States (Arizona, California, Utah, Nevada, and Colorado) *S. shoshone* (Thomas)
- Coloration extremely variable (brown, olive green, or black and yellow). Upper carina and upper carinula with a row of small dots. Hind tibiae brown, red, or black. Posterior margin of abdominal tergites always with a row of black dots. Widespread in the United States *S. lineata* Scudder
- 10. Overall coloration rusty brown. Pronotum cylindrical, not narrowing toward head. Head slightly inflated. Dorsal longitudinal stripe usually absent, but can be present. Male cerci small, quadrate, length about the same as width, distal tip slightly bilobed (Fig. 10) *S. rubiginosa* (Harris)
- Overall coloration brownish to slightly olive green. Pronotum narrowing toward head. Head small and not inflated. Dorsal longitudinal stripe always present. Male cerci quadrate, length about the same as width, slightly inflated in the middle, distal tip bilobed (Fig. 6) *S. alutacea* (Harris)

Schistocerca alutacea Harris, 1841 stat. rev.
(Figs. 4–7 and 28–31)

Acrydium alutaceum Harris, 1841: 139
Schistocerca alutacea (Harris) (Bruner, 1893: 26)
Schistocerca alutacea (Harris) (Henderson, 1942: 101)
Schistocerca alutacea (Harris) (Hubbell, 1960: 62)
Schistocerca alutacea alutacea (Harris) (Dirsh, 1974: 194)

Male. Medium size (total length = 33–40 mm). Integument moderately setose. Median carina of pronotum distinct but not raised, with shallow sulci.

Hind angle of pronotum slightly angular. Lateral lobe of metazona with granules. Pronotum slightly narrowing toward head. Head small and not inflated. Fore and middle femur not inflated. Epiproct with a pair of tubercles (Fig. 4). Cerci quadrate, length about the same as width, slightly inflated in the middle, distal tip bilobed (Fig. 6). Apical lobes of subgenital plate not outwardly flared, notch U-shaped (Fig. 5). Phallus: Cingulum, surfaces of rami deeply infolded in the middle and highly convex, thus making "basal eminence" appear bilobate and highly constricted in the middle (Figs. 28 and 29). Endophallus, basal valves laterally semicircular, valves of cingulum straight, slightly protruding more than apical valves of aedeagus (Fig. 30). Epiphallus, distance between lophi as long as the length of base of a lophus (Fig. 31). Lophi inflated triangular. Color: Rusty brown to slightly olive green. Head yellow, rusty brown, olive green with faint to strongly dark subocular stripes. A pair of dark brown stripes between eyes from upper half of frontal ridge to occiput, often extending to pronotum. Head, pronotum, and tegmina with a yellow dorsal longitudinal stripe. Lateral lobe of pronotum without marking. Metazona sometimes with small granules. Epimeron without marking. Tegmina brown, sometimes with slightly mottling. Tegminal veins brown. Hind wing with slightly yellow tinge. Posterior margin of abdominal tergites with a row of black dots. Dorsal and ventral surface of hind femur light brown. Hind femur mostly without dorsal band, but sometimes with a trace. Medial area white, sometimes with irregular pattern of black dots. Carinula with a row of very small black dots (Fig. 7). Upper carina without dots. Hind tibia light brown, with tibial spines yellow with black tip.

Female. Much larger than ♂ (TL = 49–52 mm). Median carina of pronotum slightly more raised. Otherwise same as male. Ovipositor: Ventral valves long in profile. Base of dorsal valves distinctively angular. Egg guide slightly narrowing toward apex, slightly curved upward. Pigmentation covering Jannone's organ distinct, sclerotized linearly in the middle.

Diagnostic Characters. *Schistocerca alutacea* can be uniquely distinguished based on the highly convex rami of cingulum (Figs. 28 and 29). It always has a yellow dorsal longitudinal stripe. Front and middle femora of the males are never inflated.

Material Examined. 1,223 specimens (♂: 726, ♀: 497) from ANSP, CHAP, CSUC, INHS, IRCW, LEMQ, OSEC, OSUC, SEMC, UMMZ, and UMSP.

Type Material. NEOTYPE ♂ (MCZ, here designated) *S. alutacea* (Harris, 1841), with labels. "Mass. Martha's/Vineyard. West/Chop. Aug 1893," "West Chop, Mas./19 Aug 1893," "PROPERTY/M. C. Z./Harvard," "TOPOTYPE/*Schistocerca/alutacea* (Harris)," "PLESIALLOTYPE/*Schistocerca/alutacea* (Harris)," "PLESIALLOTYPE/See Hubbell/1960: 62," "NEOTYPE/*Schistocerca/alutacea* (Harris)/H. Song, 2003."

Distribution. Examined specimens were collected from Alabama, Arkansas, Connecticut, Florida, Georgia, Maryland, Michigan, Mississippi, New Jersey, New

York, North Carolina, Oklahoma, Pennsylvania, South Carolina, Tennessee, Virginia, and Wisconsin. This species is distributed mainly in the eastern United States.

Biology. *Schistocerca alutacea* prefers shrubby, moist to wet situations, including bogs, swamps, marshes, and thickets bordering mesic forests (Hubbell 1960). Besides wet habitats, Squitier and Capinera (2002a) found that the species also prefers dry sand hill. In Florida, nymphs occur starting in May, and adults can be frequently found in July and August (Squitier and Capinera 2002b).

Taxonomic Discussion. Although Hubbell (1960) considered the genitalic characters to be important for the Alutacea Group, Dirsh (1974) apparently overlooked these characters. His revision contained only two drawings of the cingulum of *S. alutacea alutacea*, and none for the other subspecies (Dirsh 1974). These drawings, however, failed to show the distinct "basal eminence" that Hubbell (1960) emphasized, making it difficult to validate Dirsh's taxonomic concept. I examined many phallic complexes of *S. alutacea* from various collecting localities, as well as the entire genitalia collection used by Hubbell, and I conclude that Hubbell's (1960) characterization was correct, thus reviving the taxonomic status to a valid species.

The type specimen in the collection of the Boston Society of Natural History was destroyed (Hubbell 1960). In the original description, Harris (1841) did not specify the sex of the type specimen, but the original measurement (length: 1.75 in; wingspan: 3 in) suggests that it was a female. Hubbell (1960) designated a plesiallotype, a male specimen topotypic of the type specimen, which, however, is not recognized by the International Code of Zoological Nomenclature (ICZN) (International Commission of Zoological Nomenclature 2000). Vickery and Kevan (1983) considered this plesiallotype as a neotype, but no formal action was taken. There is still some taxonomic confusion about the status of *S. alutacea* (Capinera et al. 2001), and I think it is necessary to designate a neotype. Therefore, I hereby designate Hubbell's (1960) plesiallotype as a neotype.

***Schistocerca rubiginosa* Harris, 1862 stat. rev.**
(Figs. 8–11 and 32–35)

Acridium rubiginosum Harris, in Scudder, 1862: 467
Schistocerca rubiginosa (Harris) (Hubbell, 1960: 66)
Schistocerca alutacea rubiginosa (Scudder) (Dirsh, 1974: 198)

Male. Medium size (TL = 34–39 mm). Integument without long setae. Median carina of pronotum distinct but not raised, with shallow sulci. Hind angle of pronotum slightly angular. Pronotum without pattern or granule. Anterior end of pronotum broad, and head slightly inflated. Overall pronotum cylindrical. Fore and middle femur not inflated. Epiproct with a pair of tubercles (Fig. 8). Cerci small, quadrate, length about the same as width, distal tip slightly bilobed (Fig. 10). Apical lobes of subgenital plate not outwardly flared, notch U-shaped (Fig. 9). Phallus: Cingulum, surfaces of rami infolded in the middle and moderately convex,

thus making "basal eminence" appear slightly bilobate and somewhat constricted in the middle (Figs. 32 and 33). Endophallus, basal valves laterally semicircular, valves of cingulum straight, slightly protruding more than apical valves of aedeagus (Fig. 34). Epiphallus, distance between lophi as long as the length of base of a lophus (Fig. 35). Lophi inflated triangular. Color: Rusty brown. Head rusty brown with numerous small black dots, with faintly brown subocular stripes. A pair of rows of black dots between eyes from fastigium to occiput. Dorsal longitudinal stripe rarely present. Epimeron without pattern. Antennae rusty brown. Tegmina rusty brown with slight mottling. Tegminal veins rusty brown. Hind wing with yellow tinge. Posterior margin of abdominal tergites with a row of black dots. Dorsal and ventral surface of hind femur rusty brown. No dorsal band on hind femur. Medial area white to light brown with irregular pattern of black dots (Fig. 11). Upper and lower carinula with a row of black dots. Upper carina with a row of dots. Hind tibia light to rusty brown, with tibial spines yellow with black tip.

Female. Much larger than ♂ (TL = 49–54 mm). Median carina of pronotum slightly more raised. Otherwise same as male. Ovipositor: Ventral valves long in profile. Base of dorsal valves distinctively angular. Egg guide slightly narrowing toward apex, slightly curved upward. Pigmentation covering Jannone's organ distinct, faintly sclerotized linearly in the middle.

Diagnostic Characters. *Schistocerca rubiginosa* can be distinguished by the slightly inflated head and the cylindrical pronotum. It also has the smallest male cerci (Fig. 10) compared with other species in the group. Overall coloration is almost always rusty brown, and most southern populations do not have a dorsal longitudinal stripe. This species is different from *S. alutacea* in the morphology of the rami of cingulum, which is only slightly convex (Figs. 32 and 33).

Material Examined. 1,292 specimens (♂: 795, ♀: 497) from ANSP, CSUC, IRCW, LEMQ, OSEC, SEMC, UMMZ, USNP, UNSM, and WFRM.

Type Material. NEOTYPE ♂ (UMMZ) *S. rubiginosa* (Harris, 1862), with labels. "BEAUFORT CO. S.C./1.1 mile N. Limehouse/(US17) 20 Aug, '47/2 T.H. Hubbell," "PLESIALLOTYPE/*Schistocerca/rubiginosa* (Harris)," "PLESIALLOTYPE/See Hubbell/1960:66," "Head and sub-/genital plate fig./Hubbell 1960: 14," "NEOTYPE/*Schistocerca/rubiginosa* (Harris)/H. Song, 2003."

Distribution. Examined specimens were collected mainly from the eastern United States including Connecticut, Florida, Georgia, Massachusetts, New Jersey, North Carolina, Tennessee, and South Carolina.

Biology. *Schistocerca rubiginosa* prefers xeric to xeromesic habitats, especially sandy soil (Hubbell 1960). In Florida, it is sympatric with *S. alutacea* and has a similar seasonal phenology (unpublished data).

Taxonomic Discussion. *Schistocerca rubiginosa* was considered a synonym of *S. alutacea* for almost 60 yr until Hubbell (1960) revised the group because of Rehn's (1901, 1902) erroneous observation. On the basis of morphological characters, I conclude that

Hubbell's (1960) characterization was correct, thus reviving the taxonomic status to a valid species.

As in *S. alutacea*, Hubbell (1960) designated a plesiallotype, which is not recognized by the Code (International Commission of Zoological Nomenclature 2000). Vickery and Kevan (1983) considered this as a neotype, but no formal action was taken. The rusty brown color of the species has sometimes caused misidentification, especially with female specimens, and even Dirsh erroneously identified it as either *S. damnifica* or *S. lineata* (unpublished data). Capinera et al. (2001) and Squitier and Capinera (2002a, b) did not recognize the species and considered it as a synonym of *S. alutacea*. To prevent further taxonomic confusion, I think it is necessary to designate a neotype. Thus, I hereby designate Hubbell's (1960) plesiallotype as a neotype.

Schistocerca lineata Scudder, 1899 stat. rev.

(Figs. 12–15, 36–39, and 28–31)

Acridium emarginatum Uhler, manuscript

Acridium emarginatum, nomen nudum Dodge, 1872: 15

Acridium emarginatum Scudder, 1872: 250

Schistocerca lineata Scudder, 1899: 465

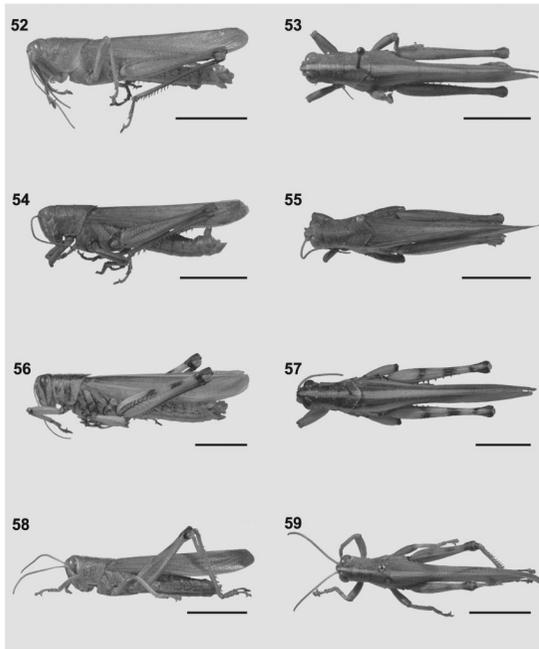
Schistocerca scudderi Bruner, 1906, unnecessary replacement name

Schistocerca lineata Scudder (Hubbell, 1960: 71)

Schistocerca emarginata (Scudder) (Vickery and Kevan, 1964: 1555; 1983: 725)

Schistocerca alutacea lineata (Scudder) (Dirsh, 1974: 204)

Male. Medium size (TL = 32–50 mm). Integument sparsely setose. Median carina of pronotum distinct and slightly raised, with distinct sulci. Hind angle of pronotum broadly angular. Lateral lobe of metazona mostly with granules. Pronotum slightly narrowing to head, and head medium size. Fore and middle femur highly inflated. Epiproct with a pair of tubercles (Fig. 12). Cerci quadrate, length about the same as width, slightly inflated in the middle, distal tip bilobed (Fig. 14). Lower apical angle of cerci protruding slightly more than upper. Apical lobes of subgenital plate not outwardly flared, notch U-shaped (Fig. 13). Phallus: Cingulum, surfaces or rami not infolded and sinuate, thus making "basal eminence" appear hourglass-shaped, and broad in the middle (Figs. 36 and 37). Endophallus, basal valves laterally semicircular, valves of cingulum straight, slightly protruding more than apical valves of aedeagus (Fig. 38). Epiphallus, distance between lophi as long as the length of base of a lophus (Fig. 39). Lophi inflated triangular. Color: Hubbell (1960) analyzed the color variation of the species, and here I categorize it into four distinguishable ecotypes: typical (Figs. 52 and 53), brown (Figs. 54 and 55), aposematic (Figs. 56 and 57), and olive green (Figs. 58 and 59). Here I characterize the typical form, and the differences among ecotypes are shown in Table 3. Head light to greenish brown with brown subocular stripes. A pair of light brown stripes between eyes from upper half of frontal ridge to occiput. Head, pronotum, and tegmina usually with a light



Figs. 52–59. Four ecotypes of *S. lineata*. (52–53) Typical form; (54–55) brown form; (56–57) aposematic form; (58–59) olive green form. Bar = 1 cm.

yellow dorsal longitudinal stripe. Lateral lobe of prozona without distinct marking. Metazona with small light yellow granules. Epimeron with small yellow granules. Tegmina light brown, with tegminal veins light brown. Hind wing with slightly yellow tinge. Posterior margin of abdominal tergites with a row of black dots. Dorsal and ventral surface of hind femur light brown. Hind femur without dorsal bands. Medial area light brown. Upper and lower carinula with a row of black dots (Fig. 15). Upper carina without dots. Hind tibia black especially on ventral side, with tibial spines yellow with black tip.

Female. Much larger than ♂ (TL = 45–69 mm). Median carina of pronotum slightly more raised. Fore and middle femur not inflated. Otherwise same as male. Ovipositor: Ventral valves long in profile. Base of dorsal valves distinctively angular. Egg guide highly narrowing toward apex, highly curved upward. Pigmentation covering Jannone’s organ distinct, sclerotized linearly in the middle.

Diagnostic Characters. *Schistocerca lineata* is the most polymorphic species in the Alutacea Group, and each local population is highly variable in coloration (Table 3) and perhaps host preference. Therefore, it is difficult to characterize this species except by the phallic morphology, where the “basal eminence” resembles an hour-glass and is broad in the middle (Figs. 36 and 37). This genitalic character was first introduced by Hubbell (1960). The species also possesses the inflated front and middle femora in males, which are also found in *S. shoshone*. However, *S. lineata* can

Table 3. Four ecotypes of *S. lineata* and their color variation

Ecotypes	Distribution	Head	Dorsal stripe	Epimeron	Tegmina	Hind femur	Hind tibia
Typical	Great Plains region	Light to greenish brown with brown subocular stripes	Light yellow	With small yellow granules	Light brown with light brown veins	Light brown without dorsal bands; carinula with a row of black dots; upper carina without dots	Black especially on ventral side, with tibial spines yellow with black tip
Brown	Great Lake regions	Brown with faint subocular stripes	Absent	Without pattern	Light brown with slight mottling, with brown veins	Brown without dorsal bands; carinula with a row of black dots; upper carina sometimes with a row of dots	Light brown, with tibial spines yellow with black tip
Aposematic	Southwestern U.S.	Yellow with black subocular stripes	Yellow	Entirely yellow without distinct marking, but sulci between episternum and epimeron black.	Yellowish brown, sometimes with slight mottling, with brown veins	Light brown to yellow with distinct black dorsal bands; carinula with/without a row of very small black dots; upper carina mostly without dots	Black especially on ventral side, with tibial spines yellow with black tip
Olive green	Western United States	Olive green with dark green subocular stripes	Bright yellow	With small yellow granules	Light brown to olive green, with lemon yellow veins	Olive green sometimes with two dorsal bands; carinula sometimes with a row of black dots, but usually absent; upper carina sometimes with dots, but usually absent.	Pinkish red, with tibial spines yellow with black tip

always be distinguished from *S. shoshone* by the presence of the black dots on the abdominal tergites.

Material Examined. 3,151 specimens (δ : 1656, ♀ : 1495) from ANSP, BYU, CSUC, INHS, IRCW, LEMQ, NMSU, OSEC, OSUC, SEMC, UARM, UMMZ, UMSP, UNSM, and WFRM.

Type Material. LECTOTYPE δ (ANSP) *S. lineata* Scudder, 1899, with labels. "Barbour Co./Kas. Cragin," "Schist./lineata/Scudder's/Type, 1899," "Ex Coll.L. Bruner/S. lineata Sc./Proc. Am. Ac. A.&S./Vol. XXXIV p. 466./Hebard Collection," "Schistocerca/lineata Sc./TYPE H86," "Sch. alutacea/lineata Sc./Lect./V.M.Dirsh det., 1972."

Distribution. This is the most widely distributed species of *Schistocerca* in North America. Examined specimens were collected from Arizona, Arkansas, Connecticut, Colorado, Delaware, Georgia, Indiana, Illinois, Idaho, Iowa, Kansas, Kentucky, Massachusetts, Maryland, Michigan, Minnesota, Mississippi, Nebraska, New Jersey, New Hampshire, New Mexico, New York, North Dakota, Ohio, Oklahoma, Rhode Island, South Dakota, Texas, Utah, Virginia, and Wisconsin. Its distribution extends north to Manitoba and Alberta, Canada.

Biology. *Schistocerca lineata* is abundant in sandy areas but is also frequently found in other habitats. Detailed account of its habitat association is found in Hubbell (1960). Criddle (1932) reported that the development takes 39 d from the time of hatching. He also noted that this species has five nymphal instars. Sword et al. have shown that the Texas population has a density-dependent polyphenism in nymphal instar, mediated by the host preference (Sword 1999, Sword and Dopman 1999, Dopman et al. 2002, Sword 2002).

Taxonomic Discussion. Here, I designate four ecotypes of *S. lineata*. Dopman et al. (2002) found that the populations associated with either *Ptelea* or *Rubus* form a monophyletic clade using 16S rRNA and 12S rRNA regions of the mitochondrial DNA. Although their study demonstrated the lack of gene flow between two host-associated populations, I am hesitant to create a new taxonomic concept at this moment, because not much is known about the populations in the midwestern and eastern United States. Highly conspicuous individuals from the southwestern states are more robust in form and slightly larger than nonconspicuous ones. In terms of coloration, specimens from Great Lake regions are brown and resemble *S. rubiginosa*. Aposematic specimens are never found in northern states, although the polymorphism of dorsal longitudinal stripe exists. In western states, specimens become almost indistinguishable from *S. shoshone* except on the basis of markings on abdominal tergites. These specimens have olive green hue, which is rarely observed in either southwestern or eastern populations. In all cases, however, crucial morphological characters, such as phallic complex and inflated male femur, are identical.

The main reason Dirsh (1974) changed the ranks of previously recognized species in the Alutacea Group was his claim to have found the hybrid between *S. lineata* and *S. albolineata*. I have examined several

specimens bearing labels by Dirsh (1974) stating, "Schistocerca alutacea lineata transient to albolineata." These specimens are, however, not hybrids, but aposematic individuals of *S. lineata* found in Texas. *S. lineata* is different from *S. albolineata* in terms of the phallic complex (Figs. 36–39) and the front and middle femora in males. Therefore, I argue that Dirsh's (1974) synonymy was based on the incorrect assumptions about the biology of the species, and here I revise the taxonomic status to a valid species.

There is also a long-standing confusion on the validity of the name *S. lineata*. Detailed account can be found in Appendix C, and here I argue that *S. lineata* is a valid name as *nomen protectum*.

Schistocerca shoshone Thomas, 1873 stat. rev.
(Figs. 16–19 and 40–43)

Acridium shoshone Thomas, 1873: 295

Schistocerca venusta Scudder, 1899: 467 (Hebard, 1935: 299)

Schistocerca obliquata Scudder, 1899: 470 (Hebard, 1932: 279)

Schistocerca shoshone (Thomas) (Henderson, 1942: 99)

Schistocerca alutacea shoshone (Thomas) (Dirsh, 1974: 200)

Male. Medium size (TL = 39–44 mm). Integument without long setae. Median carina of pronotum distinct and slightly raised, with distinct sulci. Metazona with numerous small granules. Hind angle of pronotum slightly angular. Fore and middle femur highly inflated. Epiproct with a pair of tubercles (Fig. 16). Cerci quadrate, length about the same as width, slightly inflated in the middle, distal tip bilobed (Fig. 18). Apical lobes of subgenital plate not outwardly flared, notch U-shaped (Fig. 17). *Phallus*: Cingulum, surfaces or rami not infolded and sinuate, thus making "basal eminence" appear hourglass-shaped and very broad in the middle (Figs. 40 and 41). Endophallus, basal valves laterally semicircular, valves of cingulum straight, slightly protruding more than apical valves of aedeagus (Fig. 42). Epiphallus, distance between lophi as long as the length of base of a lophus (Fig. 43). Lophi inflated triangular. Color: Mostly light olive green, occasionally lemon yellow or slight brown. Two forms can be distinguished based on the presence of dorsal stripe. *Unstriped form*: Head olive green to yellow with dark olive green to brown subocular stripe. No pair of stripes between eyes, and no dorsal longitudinal stripe on head and pronotum. Lateral lobe of pronotum without marking. Metazona sometimes with small granules. Antennae yellow. No pattern on epimeron. Tegmina light olive green to yellow without any pattern. Tegminal veins light lemon-yellow to brown. Hind wing with slightly yellow tinge. Posterior margin of abdominal tergites without a row of black dots. Dorsal and ventral hind femur yellow to olive green. Medial area white without any pattern. Hind femur without dorsal bands. Carinula without pattern (Fig. 54). Hind tibia pink, orange to red, with tibial spines yellow with black tip. *Striped form*: Head light

olive green to yellow with faint dark olive green to brown subocular stripes. A pair of olive green stripes between eyes from upper half of frontal ridge to occiput. Head, pronotum, and tegmina with a yellow dorsal longitudinal stripe. Lateral lobe of prozona with no apparent marking, and lower half of prozona and entire metazona with yellow granules. Second epimeron sometimes with yellow marking. Antennae, tegmina, hind wing, abdomen, and hind femur same as unstriped form.

Female. Much larger than ♂ (TL = 53–63 mm). Median carina of pronotum distinctly more raised. Fore and middle femur not inflated. Otherwise same as male. Ovipositor: Ventral valves short in profile. Base of dorsal valves distinctively angular. Egg guide highly narrowing toward apex, highly curved upward. Pigmentation covering Jannone's organ distinct, sclerotized linearly at the base.

Diagnostic Characters. *Schistocerca shoshone* can be easily distinguished by the absence of black markings on the abdominal tergites. These black markings appear to be the universal color pattern in *Schistocerca* species, but *S. shoshone* always lacks this pattern. This species is closely related to *S. lineata*, because both share the similar phallic morphology and inflated fore and middle femora in males.

Material Examined. 991 specimens (♂: 498, ♀: 493) from ANSP, BYU, CSUC, INHS, IRCW, LEMQ, OSEC, OSUC, NMSU, SEMC, UARM, UMMZ, UMSP, UNSM, and WFRM.

Type Material. 1. NEOTYPE ♂ lost. "Utah, Cache County, Logan" (Dirsh 1965) I was unable to find the neotype at ANSP. 2. LECTOTYPE ♂ (ANSP, dissected phallus stored in a vial) *S. venusta* Scudder, 1899, with labels. "Indio, Calif./9 July, 1897," "Schist./venusta/Scudder's/Type, 1899," "S.H.Scudder/Coll.," "Type/1829," "Lecto/type/R.&H. 1912," "venusta/Scudder." 3. LECTOTYPE ♂ (ANSP, dissected phallus stored in a vial) *S. obliquata* Scudder, 1899, with labels. "San Jose/del cabo/Mexico," "Schist./obliquata/Scudder's/Type, 1899," "Ex Coll.L.Bruner/S. obliquata Sc./Proc. Am. Ac. A.&S./Vol. XXXIV p. 471/Hebard Collection," "Schistocerca/obliquata Sc./TYPE H393," "Lectotype."

Distribution. *Schistocerca shoshone* occurs in the western United States including Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Texas, and Utah.

Biology. It is present in both riparian and desert habitats and prefers various woody plants (Sword and Chapman 1994). In Utah, it is frequently found in cornfields or other tall growing vegetation (Henderson 1942). This species is univoltine, and adults occur in June and July (Chapman et al. 1995).

Taxonomic Discussion. *Schistocerca shoshone* has both striped and unstriped forms that seem to be associated with certain host plants (Chapman et al. 1995). Because these two forms can apparently interbreed (Chapman and Sword, unpublished data), I hereby call these ecotypes of a single species.

Dirsh's (1974) redescription of *S. alutacea shoshone* is suspicious, because it states that the anterior femora

of males are slightly or not at all inflated. All type specimens as well as all the examined specimens possess this character, and usually the inflation is even more obvious than in *S. lineata*. Therefore, I argue that Dirsh's synonymy is erroneous, and I hereby revive the taxonomic status to a valid species.

***Schistocerca albolineata* Thomas, 1875 stat. rev., syn. nov.**

(Figs. 20–23 and 44–47)

Acridium albolineata Thomas, 1875: 897

Schistocerca mexicana Scudder, 1899: 468 (Hebard, 1932: 281)

Schistocerca insignis Hebard 1932: 279 (syn. nov.)

Schistocerca chinatiensis Tinkham 1948: 607 (Dirsh, 1974: 209)

Schistocerca alutacea insignis (Hebard) (Dirsh, 1974: 212)

Schistocerca alutacea albolineata (Thomas) (Dirsh, 1974: 209)

Male. Medium size (TL = 39–43 mm). Integument setose, with long setae on pronotum, thorax, cerci, and subgenital plate. Median carina slightly raised, with distinct sulci. Metazona with numerous small granules. Hind angle of pronotum slightly angular. Width of metazona slightly wider than width of prozona. Fore and middle femur not inflated. A pair of tubercles on epiproct absent (Fig. 20). Cerci quadrate, length 1.5 times longer than width, and bilobed (Fig. 22). Lower apical angle of cerci protruding more than upper. Apical lobes of subgenital plate slightly flared outward, notch round V-shaped (Fig. 21). Phallus: Cingulum, surfaces of rami deeply infolded in the middle and highly convex, thus making "basal eminence" appear slightly bilobate and somewhat constricted in the middle (Figs. 44 and 45). Endophallus, basal valves ventral angle protruding more than dorsal, valves of cingulum club-shaped and curved downward, protruding more than apical valves of aedeagus (Fig. 46). Epiphallus, distance between lophi longer than the length of base of a lophus (Fig. 47). Lophi lamelliform. Color: Olive brown. Head yellowish to olive brown with dark-brown to black subocular stripes. A pair of olive brown stripes between eyes from upper half of frontal ridge to occiput. Head and pronotum with a bright yellow dorsal longitudinal stripe, sometimes extending to tegmina. Epimeron often distinctly yellow. Antennae yellow. Lateral lobe of pronotum sometimes with a yellow rectangular spot. Tegmina uniformly olive brown, with veins light-brown to yellow. Hind wing with yellow tinge. Posterior margin of abdominal tergites with a row of black dots. Dorsal and ventral surface of hind femur yellow, with two distinct black dorsal bands. Posterior tip of hind femur black. Outer face of hind femur, upper half of medial area sometimes black and lower half white (Fig. 23). Carinula and carina without spots. Hind tibia mostly red or orange-red, but occasionally black or blue, with tibial spines yellow with black tip.

Female. Much larger than ♂ (TL = 49–61 mm). Median carina of pronotum more raised. Otherwise

same as male. Ovipositor: Ventral valves short in profile. Base of dorsal valves not angular. Egg guide not narrowing toward apex, slightly curved upward. Pigmentation covering Jannone's organ distinct, sclerotized circularly in the middle.

Diagnostic Characters. Males of *S. albolineata* possess elongated cerci with the lower apical angle protruding more than upper (Fig. 22), which is unique among the species in the Alutacea Group. The following characters can also be found in *S. obscura*, but the two species are never sympatric. They also have an elongated subgenital plate that is slightly flared outward (Fig. 21). The epiproct lacks a pair of tubercles (Fig. 20). The epiphallus is wide in the bridge between lophi (Fig. 47), and the apical valve of cingulum is clubbed (Fig. 46). Most known specimens have a bright yellow dorsal longitudinal stripe, two black dorsal bands on hind femur, and red hind tibia.

Material Examined. 240 specimens (δ : 140, ♀ : 100) from ANSP, BYU, NMSU, and UMMZ.

Type Material. 1. NEOTYPE δ (ANSP) *S. albolineata* Thomas, 1875, with labels. "Ajo, Pima Co. Ariz./ab.1800 feet (R&H)/IX, 18, 1922," "Schistocerca/alutacea albolineata Thom./V.M. Dirsh det. 1971," "NEO-TYPE." 2. HOLOTYPE δ (ANSP, dissected phallus stored in a vial) *S. mexicana* Scudder, 1899, with labels. "Sinaola, Mex./KOELS. J. BEHRENS," "Schist./mexicana/Scudder's/Type, 1899," "S.H.Scudder/Coll.," "Type 1830," "Holotype," "HOLOTYPE/Sch. mexicana/Scudder, 1899./V.M. Dirsh 1964." 3. HOLOTYPE δ (ANSP, dissected phallus stored in a vial) *S. insignis* Hebard, 1932, with labels. "Guadalajara Jalisco/9.19 1903. Mex./J.F. McClendon," "Schistocerca/insignis/Hebard,/TYPE 5509." 4. ALLOTYPE ♀ (ANSP) *S. insignis* Hebard, 1932, with labels. "Guadalajara Jalisco/9.18 1903. Mex./J.F. McClendon," "Schistocerca/insignis/Hebard,/Allotype ♀ ." 5. HOLOTYPE ♀ (CAS) *S. chinatiensis* Tinkham 1948, with labels. "Chinatis/3 miles W of/Schafter/19 Oct 46," "Type/Schistocerca/chinatiensis/msp. 1947 Tink.," "ERNEST ROBERT TINKHAM/COLLECTION—1988/DONATED TO THE CALIFORNIA/ACADEMY OF SCIENCES/by Marion Blair Tinkham," "California Academy/of Sciences/Type no. 16968."

Distribution. *Schistocerca albolineata* occurs in the southwestern United States including Arizona, New Mexico, and Texas. Its distribution extends south to Jalisco, Mexico.

Biology. *Schistocerca albolineata* prefers dry mountainous habitats. It usually feeds on various woody plants, and adults can be found in early September (unpublished data). On Tucson Mountain, AZ, I found a population of emerging adults feeding on foothill Palo Verde *Cercidium microphyllum* (Torrey) Rose and Johnston (Fabaceae). Howard (1995) found that the Arizona populations preferred cotton *Gossypium hirsutum* L. (Malvaceae).

Taxonomic Discussion. Although *S. albolineata* is the most homogeneous species in the Alutacea Group in terms of coloration, examination of a large number of specimens revealed that the color variation indeed

exists especially in hind tibia. Color variation in *Schistocerca* is well known (Hubbell 1960), and there seems to be the southward darkening progression in the species. *S. chinatiensis* Tinkham, described based on a local population from the Chinati Mountains, TX, has slightly darker coloration and black tibia. *S. insignis* Hebard, only known from eight specimens from Guadalajara, Mexico, is even darker in general coloration and has black tibia. Hubbell (1960) suggested that it is possible for *S. albolineata*, *S. chinatiensis*, and *S. insignis* to be of the same polytypic species, and I agree with his idea. All known specimens of the populations from Arizona, New Mexico, Texas, and Mexico possess the invariable diagnostic characters. Therefore, I accept Dirsh's (1974) synonymy of *S. chinatiensis*, and I hereby synonymize *S. insignis* under *S. albolineata* on the basis of morphological similarity. I also argue that Dirsh's synonymy overlooked the distinct morphological characters in *S. albolineata*, and I hereby revive the taxonomic status to a valid species.

Schistocerca obscura Fabricius, 1798

(Figs. 24–27 and 48–51)

Gryllus obscurus Fabricius, 1798: 194

Schistocerca obscura (Fabricius) (Scudder, 1899: 465)

Schistocerca obscura (Fabricius) (Dirsh, 1974: 181)

Male. Medium size (TL = 38–46 mm). Integument highly setose. Median carina of pronotum distinct and slightly raised, with distinct sulci. Hind angle of pronotum slightly angular. Width of metazona slightly wider than width of prozona. Fore and middle femur not inflated. A pair of tubercles on epiproct absent (Fig. 24). Cerci quadrate, length twice longer than width, not bilobed (Fig. 26). Apical lobes of subgenital plate strongly flared outward, notch deep (Fig. 25). Phallus: Cingulum, surfaces of rami deeply infolded in the middle and highly convex, thus making "basal eminence" appear bilobate and highly constricted in the middle (Figs. 48 and 49). Endophallus, basal valves ventral angle protruding more than dorsal, valves of cingulum club-shaped and curved downward, protruding more than apical valves of aedeagus (Fig. 50). Epiphallus, distance between lophi much longer than the length of base of a lophus (Fig. 51). Lophi lamelliform. Color: Olive green to liver color. Head yellowish to liver color with dark-brown to black subocular stripes. A pair of dark brown stripes between eyes from upper half of frontal ridge to occiput. Head and pronotum with a bright yellow dorsal longitudinal stripe, often extending to tegmina. Upper half of epimeron often distinctly yellow. Antennae yellow to orange. Lateral lobe of pronotum without pattern. Lower half of lateral prozona and entire metazona with yellow granules. Tegmina uniformly purplish liver color except for the extending dorsal longitudinal stripe. Tegminal veins same color as tegmina. Hind wing transparent with yellow tinge. Posterior margin of abdominal tergites with a row of black dots. Dorsal and ventral surface of hind femur yellowish olive to liver color, with two black dorsal bands which sometimes reduced to a trace. Medial area mostly white.

Upper and lower carinula on outer face with a row of small black dots (Fig. 27). Hind tibia brown to black with tibial spines yellow with black tip.

Female. Much larger than ♂ (TL = 52–70 mm). Median carina of pronotum more raised. Otherwise same as male. Ovipositor: Ventral valves long in profile. Base of dorsal valves distinctively angular. Egg guide slightly narrowing toward apex, ventral portion highly sinuate. Pigmentation covering Jannone's organ distinct, sclerotized circularly in the middle and patterns present on top.

Diagnostic Characters. *Schistocerca obscura* can be easily distinguished from other species in the Alutacea Group on the basis of the highly flared male subgenital plate (Fig. 25). Male cerci are elongated with length twice longer than width, and not bilobed (Fig. 26). It also has the epiproct lacking a pair of tubercles (Fig. 24), the wide epiphallus (Fig. 51), and the clubbed apical valve of cingulum (Fig. 50), which it shares with *S. albolineata*.

Material Examined. 985 specimens (♂: 495, ♀: 490) from ANSP, BYU, CHAP, CSUC, INHS, IRCW, LEMQ, NMSU, OSEC, OSUC, SEMC, UARM, UMMZ, UMSP, UNSM, and WFRM.

Type Material. 1. NEOTYPE ♂ (BMNH) *S. obscura* (Fabricius, 1798), with labels, "Allen Co Ks/Ele. 062,15/R.H. Beamer," "NEO-/TYPE," "Brit.Mus./1925–208," "Schistocerca/obscura/(Fabr)," "Schistocerca/obscura (Fabr, 1798)/V.M. Dirsh det., 1974."

Distribution. Examined specimens were collected from Alabama, Arkansas, Florida, Georgia, Kansas, Louisiana, Maryland, Mississippi, Missouri, Nebraska, New Mexico, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia. Its distribution extends south to Tamaulipas, Mexico.

Biology. Duck (1944) documented the bionomics of *S. obscura* after the grasshopper outbreak in Oklahoma. It prefers to feed on woody plants such as American elm and cotton. The species has five nymphal instars and emerges as an adult ≈50 d after hatching. Populations in central and south Texas are commonly associated with hackberry, *Celtis laevigata* Willd. (Ulmaceae) (Chapman and Sword, unpublished data). Its preferred habitat is fields and open woodlands (Capinera et al. 2001). Emerging adults were collected in August in Florida (unpublished data).

Taxonomic Discussion. Dirsh (1974) treated *S. obscura* as a species distinct from *S. alutacea* based on the shape of subgenital plate (Fig. 25). However, the present phylogeny suggests that *S. obscura* is sister to *S. albolineata* indicating the paraphyly of *S. alutacea sensu* Dirsh (1974). No taxonomic action is taken for *S. obscura* in this revision, but this species is now considered to be included in the Alutacea Group.

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Appendix A: Characters and Character States

0. Antennae length: as long as head + pronotum = 0; longer than head + pronotum = 1; shorter than head + pronotum = 2.
1. Antennae length (from 0:1): slightly longer than head + pronotum = 0; much longer than head + pronotum = 1.
2. Tegmina length: much longer than tip of abdomen = 0; slightly longer than tip of abdomen = 1; highly reduced = 2.
3. Distal end of tegmina color: partially transparent = 0; nontransparent = 1.
4. Tegmina pattern: no pattern or weak mottling = 0; distinct mottling = 1; numerous dark patches = 2; distinct bands = 3.
5. Outer margin of tegmina: straight = 0; curved = 1.
6. Male subgenital plate: subconical = 0; weakly trilobate = 1; bilobate = 2.
7. Shape of apical lobes of male subgenital plate (from 6:2): pointed = 0; round not flared outward = 1; round and flared outward = 2.
8. Width of apex of male subgenital plate (from 6:2): apex as long as base = 0; apex slightly narrower than base = 1; apex much narrower than base = 2.
9. Male cerci: conical = 0; quadrate = 1.
10. Quadrate male cerci (from 9:1): tapering toward apex = 0; not tapering toward apex = 1.
11. Male supra anal plate: a pair of tubercles absent = 0; a pair of tubercles present = 1.
12. Inflated male fore- and middle femur: absent = 0; present = 1.
13. Posterior margin of metazona: round = 0; semi-pointed = 1; highly pointed = 2.
14. Pronotum setae: sparse = 0; numerous = 1.
15. Pronotum with small granules: absent = 0; present = 1.
16. Prosternal process: curved backward and reaching sternum = 0; straight or only slightly curved = 1.
17. Apical valve of aedeagus: very long = 0; short = 1.
18. Endophallus (from 17:1): valve of cingulum pointed = 0; valve of cingulum clubbed = 1.
19. Epiphallus: bridge very long = 0; bridge short = 1.
20. Epiphallus (from 19:1): bridge shorter than the base of lophus = 0; bridge as long as the base of lophus = 1; bridge slightly longer than the base of lophus = 2.
21. Cingulum: elongated = 0; short = 1.
22. Basal eminence of cingulum (from 21:1): not constricted = 0; constricted = 1.

Appendix B: Character Matrix

	0	5	10	15	20
<i>Ornithacris</i>	0	00300	--0	00200000	0-0-0
<i>Cyrtacanthacris</i>	0	00200	--0	00200000	0-0-0
<i>Acanthacris</i>	0	11200	--0	00200000	0-0-0
<i>Halmenus</i>	0	2--01	--0	000001101110	
<i>S. americana</i>	0	00202011	100000001101010		
<i>S. nitens</i>	1000102021	10001001101110			
<i>S. damnifica</i>	2	11012021	10002101101210		
<i>S. ceratiola</i>	1110112011	1010110110110110			
<i>S. alutacea</i>	1110121111	11101111101111			
<i>S. rubiginosa</i>	1110121111	11011111101111			
<i>S. lineata</i>	1110121111	111111111101110			
<i>S. shoshone</i>	1110121111	111111111101110			
<i>S. albolineata</i>	1110122011	1001111111211			
<i>S. obscura</i>	1110122011	1001111111211			

Appendix C: Case for the Valid Taxonomic Usage of *S. lineata*

Schistocerca lineata has sometimes been called *S. emarginata* by a few authors (Vickery and Kevan 1964, 1967, 1983, Cantrall 1968, Sword and Dopman 1999, Sword 2001, Dopman et al. 2002, Sword 2002,) because of an invalid action by Vickery and Kevan (1964) to strictly adhere to the Principle of Priority. The taxonomic history of *S. lineata* is rather complex and is partially summarized in Hubbell (1960) and Vickery and Kevan (1964, 1983). Here, I explain how confusion arose and argue why *S. lineata* is the valid name.

Uhler characterized *Acridium emarginatum* only in a manuscript and never published it, and Dodge (1871) was the first one to use this name as *nomen nudum* when he listed several grasshopper species collected in Nebraska. Hayden (1872) characterized *A. emarginatum* and attributed this name to Uhler but noted that the name came only from the manuscript. Through this paper, Hayden (1872) inadvertently established himself as author of *A. emarginatum*. The type specimen of *A. emarginatum* was lost, and a neotype was never designated (Hubbell 1960). In 1899, Scudder (1899) incorrectly synonymized *A. emarginatum* with *S. alutacea* and described a new species, *S. lineata*. From 1899–1960, *S. lineata* was used continuously and unambiguously with two exceptions (Kellogg 1905, Osborn 1939). Kellogg (1905) used *S. emarginata* under a figure copied from Lugger (1898), and the figure alone is difficult to associate with the name because many *Schistocerca* species are externally similar. Osborn (1939) merely listed several names of injurious grasshoppers, and the name alone is difficult to associate with a taxonomic concept. In 1960, Hubbell (1960) published a thorough taxonomic revision on *S. lineata*, *S. alutacea* and *S. rubiginosa*. He acknowledged that *lineata* is a strict synonym of *emarginata* but nevertheless retained *S. lineata* because of the prevailing use. His revision effectively reversed the precedence under Articles 23.9 of the ICZN, and *S. lineata* became a valid name as *nomen protectum*. In 1964, Vickery and Kevan (1964) reinstated *S. emarginata* based on the Principle of Priority. Their justification

for this action came from the prevailing usage of the name between 1872 and 1898. However, *A. emarginatum* was the only available name during that period, and *S. lineata* was described in 1899. Because the name *emarginata* was already suppressed by Hubbell (1960) in accordance with the Code (International Commission of Zoological Nomenclature 2000), Vickery and Kevan (1964) could not have simply reinstated the name. To do so, they should have submitted a proposal to the Commission, which they never did. Between 1964 and 1974, *S. emarginata* was used once by Vickery and Kevan (1967). In the complete revision of the genus, Dirsh (1974) agreed with Hubbell's (1960) use of *lineata*, even though his discussion of synonymy indicated that *emarginata* has priority. Although he cited Vickery and Kevan (1964), Dirsh (1974) did not mention their action in the discussion perhaps because he rejected their proposal. Vickery and Kevan (1983), apparently troubled by Dirsh's revision, dismissed the revision in its entirety. Once again, they reinstated *S. emarginata*. Since then, *S. emarginata* (*lineata*) was used in a series of ecological studies by Sword and Dopman (1999), Sword (2001), Dopman et al. (2002), and Sword (2002).

It is true that the name *A. emarginatum* (or *S. emarginata*) is older, thus taking precedence to *S. lineata*. Hayden's (1872) description is sufficient to make him an author but insufficient to distinguish *A. emarginatum* from other *Schistocerca* species. With inadequate characterization and no type specimen available, the name itself has a dubious status. Hubbell (1960) discovered this older name but nevertheless used *S. lineata* in his revision because of the prevailing use of the latter name. Because the name *emarginatum* had not been used in the primary zoological literature for >50 yr, and because the later name *lineata* was being used prevalently, Hubbell (1960) did not consider it necessary to keep the antiquated name *emar-*

ginatum. To reverse the precedence based on the 50-yr rule, one needs to apply to the Commission only if it is proposed from 1961. Interestingly, Hubbell's paper was published on 29 December 1960. Therefore, one can assume that, under the rules in existence at that time, Hubbell (1960) did not need the action of the Commission to declare a name as *nomen oblitum*. Hubbell (1960) appreciated the objectives of the Code, which are to promote stability and not upset a long-accepted name in its accustomed meaning. Vickery and Kevan's (1964) subsequent actions were erroneous and irrelevant. Indeed, resurrecting an obscure name has a negative effect in maintaining stability of taxonomy. Cohn (1999) criticized the use of an obscure name that takes precedence to a widely used later name, using an example of *Romalea microptera* (Beauvois, 1817). Kevan (1980) discovered an older name of this common Eastern lubber grasshopper and argued for its name change to *Romalea guttata* (Stoll, 1813) on the basis of Principle of Priority. This name had not been used for >150 yr, and it should have been suppressed because introduction of this name would endanger the stability of already well-established use of *R. microptera*. As a result, both names were used to refer to one taxonomic concept since 1980, which is, of course, far from the stability that ICZN strives for. Similar confusion has already happened in *Schistocerca* where some researchers used *S. emarginata* (Sword and Dopman 1999, Sword 2001, Dopman et al. 2002, and Sword 2002) and others used *S. lineata* (Otte 1970, Helfer 1972, Capinera and Sechrist 1982, Richman et al. 1993, Hubbell 1960) to refer to the same taxonomic concept. To maintain the stability and universality of a taxonomic name, partially hindered by Vickery and Kevan's (1964) action, I argue that Hubbell's (1960) initial action was correct, effectively making *S. lineata* a valid name as *nomen protectum*.