

# On the origin of the desert locust *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae: Cyrtacanthacridinae)

## Hojun Song

Department of Entomology, The Ohio State University, 1315 Kinnear Road, Columbus, OH 43212, USA  
(song.131@osu.edu)

The locust genus *Schistocerca* (Stål) has a transatlantic disjunction, which has been controversial for more than a century. Among 50 species within the genus, only one species, the desert locust (*S. gregaria* Forskål), occurs in the Old World, and the rest occur in the New World. Earlier taxonomists suggested that the desert locust is a migrant from America, but this view was strongly challenged when a large swarm of the desert locust successfully crossed the Atlantic Ocean from West Africa to the West Indies in 1988. The currently accepted view, supported by this incident, is that the New World species are descendants of a *gregaria*-like ancestor, and the desert locust would be ancestral to the rest of the genus. However, there is surprisingly little evidence to support this view other than the 1988 swarm. I present the most comprehensive phylogenetic study that suggests that the desert locust originated from the New World, contrary to the accepted view. I also present a hypothesis about how the ancestral *Schistocerca* might have colonized the New World in the first place in light of phylogenetic relationships with other cyrtacanthacridine genera.

**Keywords:** *Schistocerca gregaria*; biogeography; locust swarm; phylogeny

## 1. INTRODUCTION

*Schistocerca* Stål is the largest and most diverse genus within the subfamily Cyrtacanthacridinae, containing ca. 50 species, widely distributed throughout the New World (Dirsh 1974). The desert locust, *Schistocerca gregaria* (Forskål), is the only Old World representative of the genus and it is one of the most notorious insects in the world. It is the biblical locust infamous for forming enormous swarms, and it annually causes severe agricultural and economic damage to African countries (Uvarov 1966, 1977; Showler 1995; Pener & Yerushalmi 1998). By contrast, the New World *Schistocerca* species have adapted to specific ecological niches, and most of them are sedentary.

The relationship between the desert locust and the New World species has been unclear, but based on the unbalanced number of species on each continent, the geographical distribution of *Schistocerca* is a clear case of transatlantic disjunction. How did such a disjunction arise? Because all the species occur in the New World except for the desert locust, earlier workers thought that the desert locust was a descendant of the American relatives. Two revisers of the genus, Scudder (1899) and Dirsh (1974), expressed a similar view that *Schistocerca* originated in America and from there populated the Old World after the genus diversified in the New World. In essence, their view requires a phylogeny that the desert locust is positioned within the New World clade (figure 1a). This scenario has been referred to as the New World Origin hypothesis of the desert locust.

In October 1988, there was a dramatic incident that radically changed this view. A large swarm of *S. gregaria* originating from West Africa successfully crossed the Atlantic Ocean to reach the West Indies (Kevan 1989; Ritchie & Pedgley 1989). This seemingly impossible flight

was later postulated to have lasted only a few days, considering the energy required to achieve the continuous flight of 5000 km (Kevan 1989). There had been records of locusts taken at sea (Howard 1917; Waloff 1946), but this was the first publicized incident of a successful flight. Because this effectively demonstrated that a locust swarm is capable of a transatlantic flight, orthopterists now had a reasonable explanation for the disjunction. Ritchie & Pedgley (1989) and Kevan (1989) proposed an alternative view that the New World species are descendants of a 'gregaria-like' ancestor from the Old World that crossed the Atlantic Ocean by flight. This view has been referred to as the Old World Origin hypothesis, and it is the currently accepted view on the diversification of *Schistocerca*. According to this view, the desert locust would be the remnant or descendant of the ancestor that gave rise to the New World *Schistocerca*, and it, in essence, requires a phylogeny that the desert locust is positioned basal to the rest of the New World species (figure 1b). Kevan (1989) also suggested a possibility that the New World *Schistocerca* could have been a result of multiple crossings by the ancestral *Schistocerca* from the Old World. This view was later expanded by Amedegnato (1993), but did not gain a wide acceptance. According to this Multiple Crossings hypothesis, the ancestral *Schistocerca* repeatedly crossed the Atlantic Ocean to give rise to several lineages in the New World. This hypothesis inherently assumes that the desert locust is the most recent ancestral stock that gave rise to the swarming species in the New World. If this is the correct view, it will require a phylogeny that has a large and diverse clade at the base, representing older lineages by the ancestral *Schistocerca* and another clade that has the desert locust at the base (figure 1c). This phylogeny superficially resembles that for the New World Origin hypothesis, but it differs in the position of

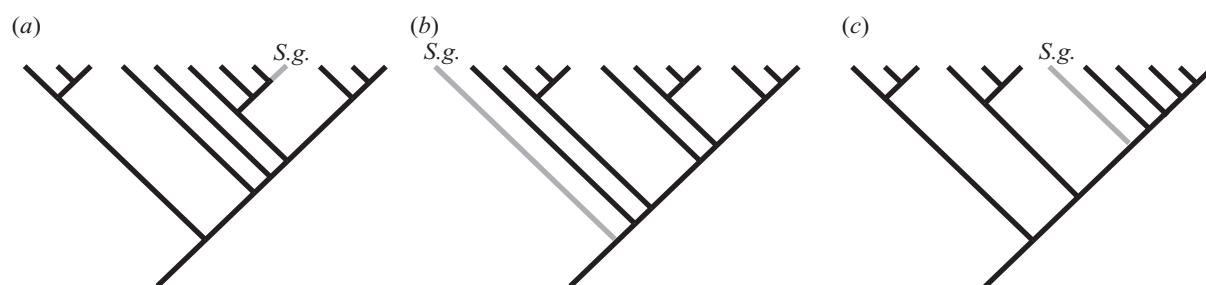


Figure 1. Three contrasting hypotheses on the origin of the desert locust. Each cladogram represents a simplified version of *Schistocerca* phylogeny. *S.g.* is an abbreviation of *Schistocerca gregaria*. (a) Presumed phylogeny of the New World Origin hypothesis. If the desert locust colonized the Old World after *Schistocerca* diversified in the New World, *S. gregaria* would be positioned deep among the New World clades. (b) Presumed phylogeny of the Old World Origin hypothesis. If the New World species were descendants of a 'gregaria-like' ancestor, *S. gregaria* would be basal to the rest of the genus, reflecting its ancestry. (c) Presumed phylogeny of the Multiple Crossings hypothesis. If the ancestral *Schistocerca* colonized the New World multiple times, there would be several lineages at the base and another clade with the basal *S. gregaria*, reflecting its ancestry.

*S. gregaria*. The Multiple Crossings hypothesis should be considered as a variety of the Old World Origin hypothesis because it assumes that the Old World is the originating point for the ancestral *Schistocerca*.

Although the Old World Origin hypothesis seems to be the simplest explanation for the biogeography of *Schistocerca*, there is, however, surprisingly little evidence for it other than the 1988 swarm. If the ancestral desert locust gave rise to numerous New World species, why has there been no diversification in the Old World? *Schistocerca gregaria* is morphologically similar enough to once be included as a subspecies of New World *S. americana* (Drury) (Dirsh 1974), and several hybridization studies suggested a close relationship between the desert locust and the New World swarming species (Harvey 1979; Jago *et al.* 1979). However, the Old World Origin hypothesis assumes that the desert locust has not evolved much while the rest of the genus greatly diversified, which is a very curious assumption. Furthermore, Cyrtacanthacridinae has only two New World representatives, *Schistocerca* and the Galapagos endemic *Halmenus* Scudder, which have been suggested to be closely related (Dirsh 1969, 1974). The Old World Origin hypothesis does not account for *Halmenus* (Chapman *et al.* 2000).

I conducted a cladistic analysis to test the hypotheses of origin. Specifically, I attempt to address three questions. (i) What is the position of *S. gregaria* within the *Schistocerca* clade? (ii) What is the relationship between *Schistocerca* and *Halmenus*? (iii) What is the relationship between *Schistocerca* and the Old World cyrtacanthacridine genera? Based on the present findings, I propose a novel view on the origin of the desert locust and the biogeography of *Schistocerca*. Also, I discuss the potential taxonomic implications resulting from the current phylogeny.

## 2. MATERIAL AND METHODS

The parsimony analysis was performed using 33 *Schistocerca* species and 15 cyrtacanthacridine outgroup species (see electronic Appendix A). *Schistocerca* is a taxonomically problematic group, and it is currently being revised (H. Song, unpublished data). Because *S. nitens nitens* (Thunberg) may consist of multiple species, I designated an alphabetical letter to each morphologically distinct geographical form.

A total of 57 characters with 148 character states were examined (see electronic Appendix B). Characters were chosen through a comprehensive study of both external and internal morphology. Except for the few cases where specimens were limited, multiple specimens from various localities were examined and compared for each species. Only invariable characters were used. Non-applicable characters were coded as '-'. All characters were run equally weighted with one character being additive and 56 non-additive (see electronic Appendix C). The additive character was the shape of the male cercus, and the hypothesis of the character transformation was made before the analysis. The Parsimony Ratchet implemented in NONA (Goloboff 1995), was run within WINCLADA (Nixon 2002). Five repeated runs of 100 iterations of the ratchet were performed with one tree 'hold' and 10–18% of characters sampled. The single resulting tree was saved and other most-parsimonious trees were searched using 'max\*' command in NONA. *Ornithacris turbida* (Walker) was used to root the tree.

## 3. RESULTS

The parsimony ratchet was used with various percentages of characters and consistently yielded a tree of 230 steps. The analysis resulted in 40 most-parsimonious trees (tree length of 230 steps, consistency index (CI) = 0.39, retention index (RI) = 0.77). A strict consensus of 40 most-parsimonious trees collapsed seven nodes mostly among the outgroups and produced a consensus tree of 245 steps (CI = 0.37, RI = 0.74; figure 2).

The monophyly of *Schistocerca* is supported by two synapomorphies: bilobate male subgenital plate and quadrate male cercus. The ingroup clade is highly resolved although there are some unresolved relationships among the outgroup taxa. The Bremer support value for the ingroup is low, as is typical in morphological analyses; however, the retention index is high, indicating that the homoplasious characters are useful in defining the ingroup. For example, the length of tegmina is a homoplasious character in terms of the entire phylogeny, but is a synapomorphy within *Schistocerca*.

### (a) Relationships within *Schistocerca*

*Schistocerca* is basally divided into two clades (figure 2). The smaller clade (figure 2a) included 11 species grouped by a slightly constricted pronotum. Of these, *S. gregaria*,

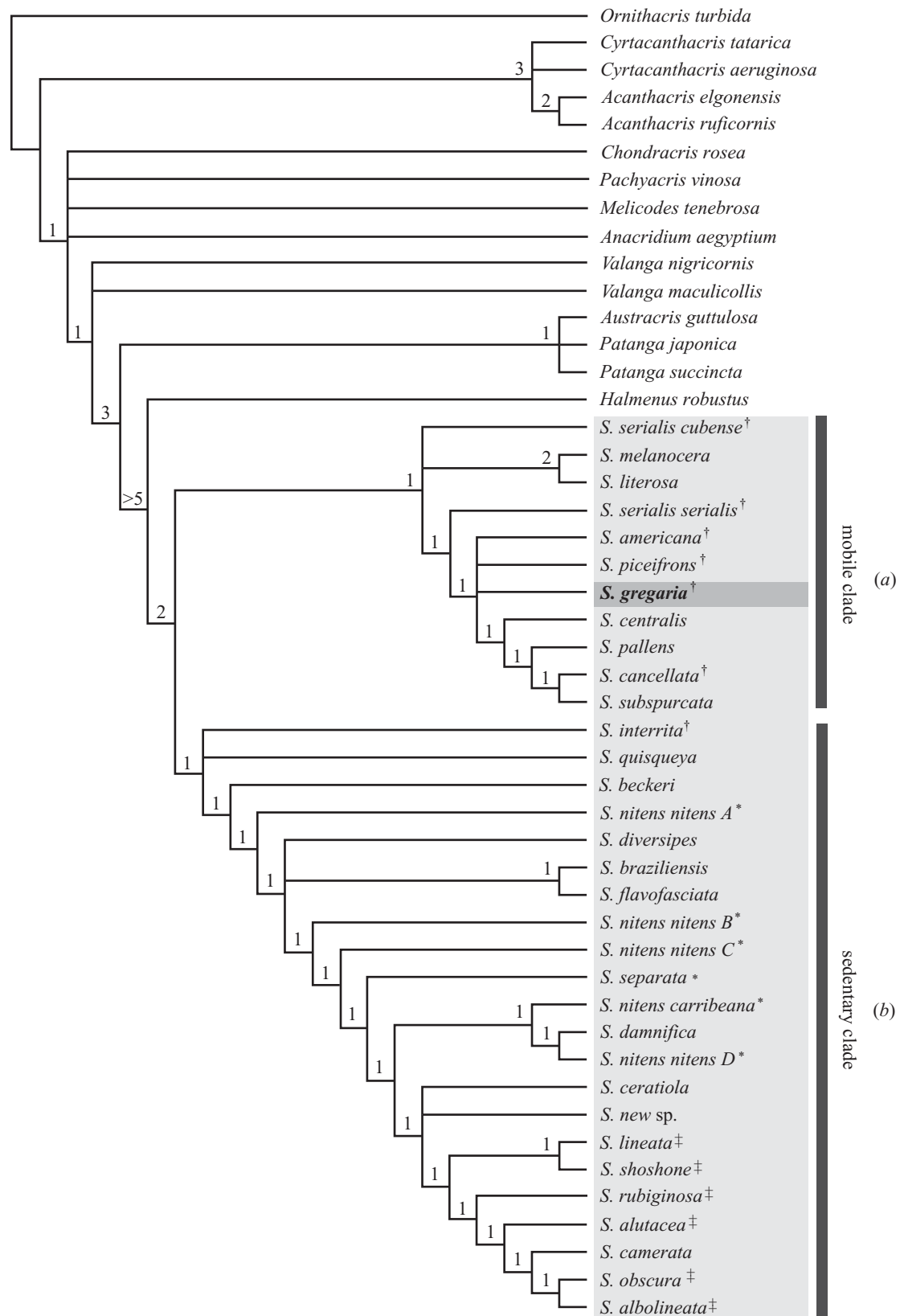


Figure 2. Strict consensus of 40 most-parsimonious trees (245 steps, CI = 0.37, RI = 0.74) with Bremer support values above the nodes. *Schistocerca* is a monophyletic group, shown by a light-grey rectangle. *Schistocerca gregaria* is positioned well within the ingroup, shown by a dark-grey rectangle. (a) Mobile clade that includes all swarming locust species and other species with long wings. (b) Sedentary clade that includes non-swarming species. Taxonomically problematic species in Dirsh's (1974) revision are indicated by a dagger for *S. americana sensu* Dirsh, an asterisk for *S. nitens sensu* Dirsh, and a double dagger for *S. alutacea sensu* Dirsh.

*S. piceifrons* (Walker) and *S. cancellata* (Serville) are known to swarm, but they do not form a monophyletic group. Two Galapagos endemic species, *S. melanocera* (Stål) and *S. literosa* (Walker), form a monophyletic clade by having male cerci that have the upper margin sharply protruding. Its position among other species is unresolved but generally basal in the clade. *Schistocerca serialis cubense* (Saussure) is not sister to the nominal subspecies *S. serialis serialis* (Thunberg). *Schistocerca gregaria* is positioned comfortably and unambiguously within the New World clade. The larger clade (figure 2b) is grouped by having a curved outer margin of tegmina and a moderately raised median carina of pronotum, and it includes the rest of the genus, all of which are sedentary. *Schistocerca nitens sensu* Dirsh is paraphyletic, indicating that his taxonomic concept is problematic (\* in figure 2). The same is true for *S. alutacea sensu* Dirsh (‡ in figure 2) and *S. americana sensu* Dirsh († in figure 2).

#### (b) *Relationships among cyrtacanthacridine genera*

*Schistocerca* is sister to the Galapagos endemic *Halmenus*, and this relationship is strongly supported by several synapomorphies, mostly of the male genitalia. *Halmenus* differs from *Schistocerca* by having highly reduced wings and a short conical male subgenital plate. The shape of the male subgenital plate in Cyrtacanthacridinae varies considerably, but most Old World genera have a pointed conical subgenital plate. *Schistocerca* and *Halmenus* are sister to the Australasian clade formed by *Austracris guttulosa* (Walker), *Patanga succincta* (Johannson) and *P. japonica* (Bolivar). Indo-Malaysian *Valanga* Uvarov is basal to the Australasian and New World taxa, but the monophyly of *Valanga* was not supported. The relationships among *Chondracris* Uvarov, *Pachyacris* Uvarov, *Melicodes* Uvarov, *Anacridium* Uvarov are largely unresolved. Basally, the African genera *Cyrtacanthacris* Walker and *Acanthacris* Uvarov form a monophyletic clade by having only six hind tibial spines and a twisted valve of cingulum, and are sister to the rest of the species.

#### 4. DISCUSSION

The purpose of this study was to test the previous hypotheses about the transatlantic disjunction of *Schistocerca* (figure 1). The phylogeny places the desert locust within the New World clade (figure 2). Its position is unambiguous and robust because it would take at least three steps to pull *S. gregaria* out of the New World clade. In other words, the current phylogeny strongly favours the New World Origin hypothesis (figure 1a) rather than the accepted view of the Old World origin of the desert locust (figure 1b). It is also not consistent with the phylogeny proposed by the Multiple Crossings hypothesis (figure 1c). Instead of the desert locust being basal to the closely related species, *S. gregaria* is unambiguously placed within the smaller clade. This indicates that the ancestral desert locust did not give rise to the species in the smaller clade. *Schistocerca serialis* is morphologically very similar to the species in the Americana Group, but it is basal to the rest according to the current phylogeny. This would suggest that *S. serialis* went through an impressive morphological

convergence to resemble the rest of the clade, if the Multiple Crossings hypothesis is to be forced. This, of course, requires too many *ad hoc* explanations that are not testable. The most parsimonious explanation from the current phylogeny would be that the ancestral desert locust colonized the Old World from the New World. How could this colonization have happened?

Two possible colonization routes have been suggested. The first is by the Bering land bridge. Dirsh (1974) suggested that the ancestral desert locust might have migrated from America through Eurasia and Europe and finally reached Africa. However, this route is unlikely because there is no species closely related to the desert locust in northern North America or eastern Russia. If the colonization route was overland, it is reasonable to expect that there could be some relic populations. Of course, the absence of a population is insufficient evidence for rejecting a hypothesis, but there is an alternative route that is more parsimonious. This second route is a direct transatlantic flight from America to West Africa. The incident in 1988 demonstrates that a locust swarm is capable of a long-distance flight with favourable conditions (Kevan 1989). However, the prevailing wind direction between two continents does not favour the eastward flight route from America to Africa. The prevailing wind direction is westward from Africa to America owing to both Northern and Southern Trade Currents (Thurman 1975). The 1988 swarm took advantage of the Northern Trade Current. However, there is indeed an eastward wind current, the Equatorial Countercurrent, which blows eastwards along the equator. Therefore, it is possible that the ancestral desert locust might have taken advantage of this eastward current and colonized Africa. In other words, the New World Origin hypothesis has just as valid meteorological support as does the Old World Origin hypothesis. This indicates that the Old World Origin hypothesis cannot be preferred on the direction of the prevailing winds alone. It is impossible to directly demonstrate the eastward colonization, but the historical pattern deduced from the phylogeny clearly points to the New World Origin hypothesis.

Yet, a question remains. How did the ancestral *Schistocerca* reach the New World in the first place? This is an appropriate question because of the distribution of the subfamily Cyrtacanthacridinae. This subfamily contains approximately 35 genera, of which only two occur in the New World: *Schistocerca* and the Galapagos endemic *Halmenus*. The rest of the genera are distributed in the Old World, mainly in Africa (Uvarov 1923). Indeed, this is one of the reasons why the Old World Origin hypothesis was favoured initially. Earlier workers thought that the centre of origin for Cyrtacanthacridinae was Africa, and *Schistocerca* must have come from Africa (Vickery & Kevan 1983; Vickery 1989). Although the present study focused on the ingroup relationships, it included enough outgroup species to infer the biogeographic pattern of the subfamily.

The phylogeny (figure 3) suggests that the basal genera are from Africa, and there seems to be an eastward progression from Africa to Asia to the Indo-Pacific and Australia, and to the New World. *Schistocerca* and *Halmenus* form a strong monophyletic clade, indicating that the common ancestor of these two genera colonized the New World. This clade is, in turn, sister to the Australasian



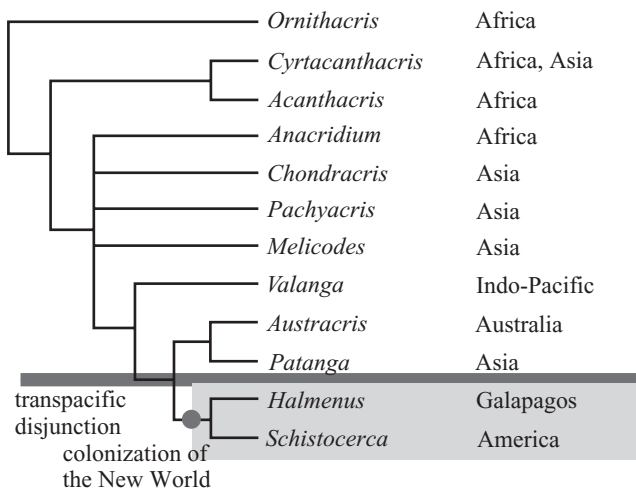


Figure 3. Simplified cladogram of the outgroup relationships. Normal geographical distribution is placed next to each terminal showing a biogeographic trend. Two New World genera, *Schistocerca* and *Halmenus*, form a monophyletic group, indicating that a common ancestor of both colonized the New World. This clade is, in turn, sister to the Australasian clade, suggesting a transpacific disjunction.

clade of *Austracris* and *Patanga*. In other words, there is a transpacific disjunction within the subfamily. In explaining this kind of disjunction, it is tempting to invoke an ancient vicariance event such as the Gondwanaland distribution (Vickery 1989). However, there is an abundance of fossil evidence suggesting that the modern grasshoppers evolved during the Tertiary (Zeuner 1941, 1942*a,b,c*). Although the order Orthoptera is known from the Carboniferous, the family Acrididae evolved relatively recently, and all the known fossils are from the Oligocene and Miocene (Zeuner 1941; Lewis 1974, 1976). Cyrtacanthacridinae perhaps evolved even later. The exact time is unknown, but by this time, all the continents were already separated by the oceanic barriers, and nearing modern positions. Therefore, invoking the vicariant Gondwanaland distribution would be incongruent with the fossil evidence, and dispersal events need to be invoked. Although there is no reliable test to determine if the dispersal is responsible for the current biogeographic pattern, I argue that the dispersal could have been the sole mechanism for the subfamily. Species in Cyrtacanthacridinae are known for a strong flight capacity (Uvarov 1923; Dirsh & Uvarov 1953; Willemsse 1957; Mungai 1987*a,b*, 1992). They are usually large and possess long forewings. Many of them are capable of forming a large swarm that can migrate a long distance. Therefore, it is possible to propose that the genera in Asia, the Indo-Pacific and Australia are the result of a direct eastward colonization from Africa with a single transpacific migration from Australasian regions to America. This idea is consistent with the transpacific disjunction in many hemipterans and plants, and dispersal has been invoked as an explanation for them (Schuh & Stonedahl 1986).

Present analysis suggests a sister relationship between *Schistocerca* and *Halmenus*. Galapagos endemic *Halmenus* is a brachypterous genus containing only four species, and the loss of wings has been attributed to the rapid island brachypterism (Dirsh 1969; Amedegnato 1993). However,

the phallic structures of *Halmenus* are virtually identical to *Schistocerca*, suggesting that the divergence between two genera could have been very recent (Dirsh 1974). The ancestral *Halmenus* must have colonized the Galapagos Islands after the islands emerged, which would make *Halmenus* certainly less than 5 Myr old (Steadman & Ray 1982). According to the cladistic theory, sister taxa are of the same age by definition, and the current phylogeny would then suggest that *Schistocerca* is less than 5 Myr old. If this is true, the unbalanced dichotomy in the number of species between two genera can be attributed only to the extremely rapid diversification rate in *Schistocerca*. This would indicate a very high rate of speciation on the mainland and not on the islands, contrary to general proposals for the Galapagos Islands. However, if an extinct lineage that gave rise to *Halmenus* can be invoked, it becomes possible that the age of *Schistocerca* may be much older.

The phylogeny of *Schistocerca* reveals several interesting points about diversification of the genus. It suggests that the desert locust belongs to a smaller clade (figure 2*a*) that includes two Galapagos endemic species, all three swarming species together with six non-swarming species, which can be characterized by long transparent forewings and a slender body form. All 11 species within this clade are highly mobile and strong fliers, and thus the name 'mobile clade' seems to be suitable. Two Galapagos endemic species, *S. melanocera* and *S. literosa*, form a monophyletic group, which indicates that the common ancestor of these two colonized the island and diversified. Although the relationship is ambiguous, this Galapagos clade can certainly be basal to the rest of the mobile clade. This in turn suggests that the ancestor of the mobile clade must have possessed a strong flight capacity, which can explain why all the species within the mobile clade are strong fliers. Three swarming *Schistocerca* species are *S. piceifrons* (Central American locust), *S. cancellata* (South American locust) and *S. gregaria* (desert locust), which are all closely related within the mobile clade. The present phylogeny suggests that these three species do not form a monophyletic group, which indicates that the swarming behaviour has evolved multiple times even within *Schistocerca*. This result is congruent with experimental studies, which suggested that the swarming *S. cancellata* was closely related to non-swarming *S. pallens* (Harvey 1979; Jago *et al.* 1979). Swarming behaviour is, however, a complex composite character, and it might be inadequate to simply state that it evolved multiple times. To study the evolution of swarming behaviour, it is important to dissect and compare the behaviour into small components such as nymphal band formation, cohesive flight and response to density. It is also crucial to study the role of environment. Perhaps one reason for swarming could be that locusts happen to exist in environments that allow for a rapid population increase, such as deserts. However, different species seem to have different genetic variations for the swarming behaviour. For example, *S. piceifrons* and *S. pallens* are often sympatric in Mexico, but only *S. piceifrons* swarms despite the close phylogenetic relationship (Harvey 1983). However, the fact that all three swarming species belong to the same clade, although not monophyletic, suggests that the species within the mobile clade already possessed some propensity for

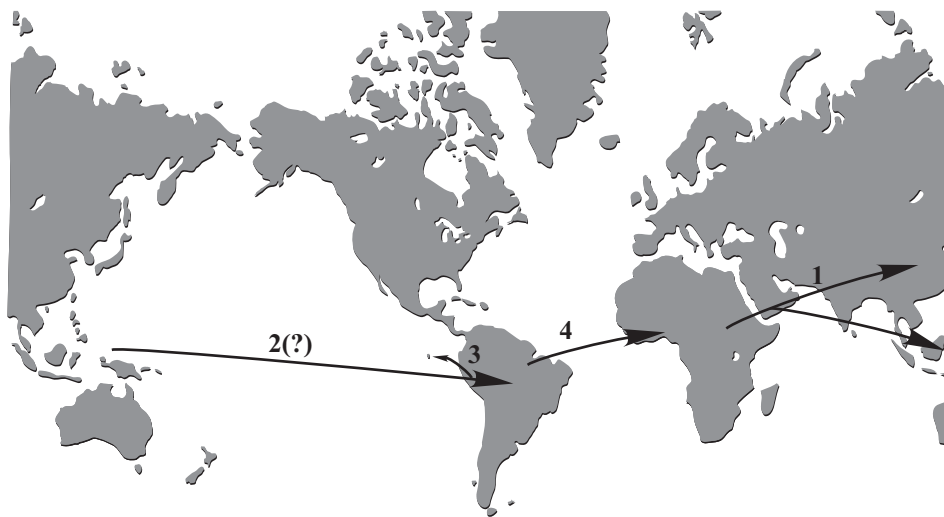


Figure 4. Novel hypothesis on the origin of the desert locust based on current phylogeny. (1) Ancestral cyrtacanthacridines colonized eastwards from Africa to India, Asia, the Indo-Pacific and Australia, giving rise to several genera. (2) Possible transpacific colonization of the New World by the common ancestor of *Schistocerca* and *Halmenus*. (3) Ancestral *Halmenus* colonized the Galapagos Islands after the islands emerged. The Galapagos Islands were later colonized once more by the common ancestor of *S. melanocera* and *S. literosa*. (4) Ancestral desert locust colonized Africa from South America possibly with a favourable wind condition along the Equatorial Countercurrent.

swarming. Perhaps the reason the desert locust is so problematic is because its ancestors already possessed this propensity.

The larger clade (figure 2*b*) contains mostly sedentary species. Sedentary *Schistocerca* species differ from the mobile species by having long antennae and shorter wings, and a robust body form (Hubbell 1960; Song 2004). Species in this 'sedentary clade' are ecologically arboreal and strong fliers, but they never form a swarm. Occasionally, aggregation behaviour has been observed in some species (Chapman *et al.* 1995), but they do not have the characteristic swarming behaviours such as cohesive flight or nymphal band formation. Interestingly, however, a species in the sedentary clade was recently found to possess a character, density-dependent polyphenism, important in the swarm formation of the desert locust (Sword 1999, 2002). Sword (1999) discovered that the nymphs of *S. lineata* in Texas change colour when reared in crowded conditions. The colour change was more intense in the population that primarily fed on toxic plants, suggesting that the aposematism can be mediated by the density and host preference. It is, however, not clear how widespread this phenomenon is within *Schistocerca*. Species in the Alutacea Group, to which *S. lineata* belongs, can certainly have this character because of a close relationship (Song 2004). By contrast, Rowell & Cannis (1971) found that *S. nitens* does not respond to the rearing density. Therefore, it is likely that the density-dependent polyphenism has evolved multiple times within *Schistocerca*.

The differences between the mobile and the sedentary clades can perhaps be explained in an evolutionary framework. When the ancestral *Schistocerca* colonized the New World, it gave rise to two lineages. The present study suggests that this ancestor must have possessed an enormous flight capacity for it to cross the Pacific. One lineage retained many ancestral characteristics and gave rise to the mobile clade. With the symplesiomorphic characters that were already adapted to long-distance migration, several

swarming species could have evolved. The other lineage quickly adapted to the different ecological niches and became sedentary. Although certain plesiomorphic characters such as the density-dependent polyphenism have been retained, the species in the sedentary clade have now completely lost the swarming capacity. *Schistocerca ceratiola* is a good example of the extreme adaptation to a specific environment. This nocturnal species is endemic to central Florida, and feeds exclusively on Florida rosemary, *Ceratiola ericoides* Michaux (Hubbell & Walker 1928). Its eyes have been enlarged to cope with the nocturnal habit, and the body has become very slender, perhaps to deal with life on rosemary. Other sedentary species have also adapted to various habitats and host plants, suggesting that the sedentary clade of *Schistocerca* in particular seems to have experienced some sort of adaptive radiation.

The phylogeny reveals several taxonomic problems in *Schistocerca*. The taxonomy of the genus is poorly understood, despite a revision by Dirsh (1974). His revision, which resulted in numerous synonymies, is problematic because Dirsh used an unjustified morphometric technique, a method originally devised to differentiate between phases of a swarming locust. In justifying the synonymy, Dirsh reasoned that any taxa that share similar morphometric ratios should be considered as one species. By doing so, he synonymized 11 names under *S. americana*, seven names under *S. alutacea* and 16 names under *S. nitens*. This scheme was severely criticized, and several hybridization studies were published to show the inadequacy of the revision (Harvey 1979, 1982; Jago *et al.* 1979, 1982). However, a comprehensive review of the genus is currently unavailable. Current phylogeny suggests that these three problematic species are all paraphyletic, again confirming the inadequacy of Dirsh's taxonomic concept. *Schistocerca americana sensu* Dirsh († in figure 2) has been reviewed by Harvey (1981) who raised sub-specific ranks of most taxa to the specific status. The Americana Complex *sensu* Harvey, however, did not include *S. centralis* or *S. subspurcata*, both of which are

undoubtedly related to *S. cancellata*. Harvey also did not include the rare *S. americana interrita*, but the current study suggests that this species does not even share any characters with the mobile clade, and thus a status change would be necessary. Two subspecies of *S. serialis* are not sisters in this study, and it is possible that two subspecies are actually valid species. *Schistocerca alutacea sensu* Dirsh (‡ in figure 2) has been recently reviewed by Song (2004) who raised the ranks based on morphological study of over 8000 specimens. The species of the Alutacea Group are morphologically distinct, especially in male genitalia, which Dirsh overlooked. Dirsh considered *S. obscura* distinct from *S. alutacea*, but the current topology suggests that it is sister to *S. alutacea albolineata sensu* Dirsh. Present analysis includes six taxa that were considered as *S. nitens*, but this species is largely paraphyletic (\* in figure 2). Moreover, specimens from different localities that were labelled as *S. nitens nitens* by Dirsh do not come out as a monophyletic group, which suggests that a taxonomic revision is much in need.

The biogeography of *Schistocerca* has attracted scientists for more than a century. The traditional view was simple and one-dimensional (Kevan 1989). It states that the ancestral *Schistocerca* colonized the New World from Africa by a transatlantic flight. However, this seemingly simple hypothesis is incapable of explaining the presence of *Halmenus* and other *Schistocerca* on the Galapagos Islands, the close biological relationships among swarming species, and the close relationship between *Schistocerca* and the Australasian genera. This study proposes an alternative view, that the ancestral cyrtacanthacridine colonized Asia, the Indo-Pacific and Australia, and somehow reached the New World, and there gave rise to *Schistocerca* and *Halmenus* (figure 4). After *Schistocerca* diversified in the New World, one lineage colonized the Old World by a transatlantic flight, which gave rise to the desert locust. This morphological phylogeny also provides a testable hypothesis for a molecular study, which is currently in progress.

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