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Phylogenetic perspectives on the evolution of locust phase polyphenism

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Abstract

Locust phase polyphenism is a spectacular example of density-dependent phenotypic plasticity. It is generally interpreted as an adaptation to heterogeneous environmental conditions brought on by high population density. However, several nonlocust species are known to express phase-like traits, which is difficult to explain from an adaptive perspective alone. Here I attempt to explain this phenomenon by 1) taking a reaction norm perspective in understanding the mechanisms underlying locust phase and 2) taking a phylogenetic perspective to study how individual reaction norms of locust phase might have evolved. I argue that locust phase polyphenism is a complex syndrome resulting from interactions among different density-dependent plastic reaction norms, each of which can follow a separate evolutionary trajectory, which in turn can be reflected in a phylogeny. Using a phylogeny of Cyrtacanthacridinae (Orthoptera: Acrididae), I explore the evolution of plasticity in density-dependent color change. I demonstrate that locusts and closely related nonlocusts, express similar phenotypic plasticity due to phylogenetic conservatism. Finally, I argue that it is crucial to study the evolution of locust phase polyphenism from both adaptive and phylogenetic perspectives.

Key words

locust phase polyphenism, reaction norm, phenotypic plasticity, phylogeny, phylogenetic conservatism, Cyrtacanthacridinae

Introduction

Locusts are a group of grasshoppers that can form dense migrating swarms through extreme density-dependent phenotypic plasticity, in which cryptic, solitary individuals transform into conspicuous, gregarious individuals, in response to change in population density (Pener 1983, Uvarov 1966). In addition to color and behavior, biochemistry, reproductive physiology, and morphology also change, and this suite of complex phenomena is often referred to as locust phase polyphenism (Uvarov 1966, Pener 1991, Pener & Yerushalmi 1998, Simpson *et al.* 1999).

Density-dependent phase polyphenism has been documented in many insects in addition to locusts (Applebaum & Heifetz 1999, Harvell 1994), and it is usually interpreted as an adaptation to unpredictable and heterogeneous environmental conditions brought on by high population density (DeWitt *et al.* 1998). Scientists have argued that the evolution of phenotypic plasticity, such as locust phase polyphenism, can be best understood from a reaction norm perspective (Schlichting & Pigliucci 1998, Sword 2002). A reaction norm is the set of phenotypes that can be produced by an individual genotype exposed to different environmental conditions (Schlichting & Pigliucci 1998), which can evolve by selection (Bradshaw 1965,

Schlichting 1986) or by genetic drift (Sword 2002). For example, cryptic and conspicuous coloration produced by locust nymphs in response to low and high population density can be viewed as a kind of plastic reaction norm. Therefore, locust phase can be understood as a collective expression of different reaction norms for color, behavior, physiology, and morphology.

Since Sir Boris Uvarov (1921) established the phase theory based on observations of *Locusta migratoria*, more than 15 species of acridids have been identified as expressing locust phase polyphenism (COPR 1982, Jago 1985). Taxonomically, these locust species belong to at least 6 different subfamilies within Acrididae (Table 1). Occurrence of locust species in phylogenetically distant groups led scientists to assume that locust phase is an evolutionary labile trait, a product of numerous convergent evolution events (Jago 1985, Pener 1991). However, this assumption is problematic in two aspects. First, locust phase is not a simple binary character that can be gained or lost. Rather, it is a composite character consisting of numerous density-dependent reaction norms. There are many grasshopper species that express phase-like characters, but do not form swarms (Applebaum & Heifetz 1999, Jago 1985, Pener 1991). This may indicate that different reaction norms of locust phase do not necessarily evolve together. Second, the distribution of locust species within each subfamily of Acrididae does not seem to be random. For instance, there are 4 locust species in *Schistocerca* and 3 in a likely monophyletic group of *Nomadacris-Patanga-Austracris* (Jago 1981, Key & Rentz 1994) (Table 1). This pattern suggests that closely related species might express phase traits because the evolution of the traits happened in their common ancestor.

The role of phylogeny in evolution of locust phase polyphenism has not been explicitly studied, although there have been some speculations (Song 2004a, Sword 2002, Sword 2003). This may be because phylogenetic analyses of phenotypic plasticity are rare in general, due to the difficulty in quantifying expression of plasticity to get the necessary data (Pigliucci 2001). Nevertheless, observations based on a locust genus *Schistocerca* are revealing and might provide an insight into the evolution of locust phase polyphenism from a historical perspective.

The genus consists of about 50 species, 3 of which exhibit distinct locust phase polyphenism (*S. gregaria*, *S. cancellata*, and *S. piceifrons*) (Harvey 1981). Presently, not much is known about the supposedly 4th locust species, *S. interrita* (SENASA 2005). The rest of the genus is nonswarming and sedentary, although some species occasionally cause agricultural damage (Dirsh 1974). *Schistocerca* has a unique biogeographic distribution where all members of the

Table 1. A list of known locust species. Locusts belong to at least 6 different subfamilies of Acrididae, indicating that locust phase polyphenism has evolved multiple times. Information taken from the International Society of Pest Information website (<http://www.pestinfo.org/Literature/locspec.htm>).

Common name	Species name	Subfamily
Desert locust	<i>Schistocerca gregaria</i>	Cyrtacanthacridinae
Central American locust	<i>Schistocerca piceifrons</i>	Cyrtacanthacridinae
South American locust	<i>Schistocerca cancellata</i>	Cyrtacanthacridinae
Peru locust	<i>Schistocerca interrita</i>	Cyrtacanthacridinae
Red locust	<i>Nomadacris septemfasciata</i>	Cyrtacanthacridinae
Bombay locust	<i>Patanga succincta</i>	Cyrtacanthacridinae
Spur-throated locust	<i>Austracris guttulosa</i>	Cyrtacanthacridinae
Sahelian tree locust	<i>Anacridium melanorhodon</i>	Cyrtacanthacridinae
Migratory locust	<i>Locusta migratoria</i>	Oedipodinae
Brown locust	<i>Locustana pardalina</i>	Oedipodinae
Australian plague locust	<i>Chortoicetes terminifera</i>	Oedipodinae
Sudan plague locust	<i>Aiolopus simulatrix</i>	Oedipodinae
Italian locust	<i>Calliptamus italicus</i>	Calliptaminae
Moroccan locust	<i>Dociostaurus marrocanus</i>	Gomphocerinae
Siberian locust	<i>Gomphocerus sibiricus</i>	Gomphocerinae
Yellow-spined bamboo locust	<i>Ceracris kiangsu</i>	Acridinae
Rocky Mountain locust (extinct)	<i>Melanoplus spretus</i>	Melanopliinae

genus occur in the New World except for a single species, the desert locust *S. gregaria* (Dirsh 1974). The subfamily Cyrtacanthacridinae, to which *Schistocerca* belongs, however, mostly occurs in the Old World (Uvarov 1923).

In 1988, a swarm of the desert locust originating from West Africa, successfully crossed the Atlantic Ocean and reached the West Indies (Kevan 1989, Ritchie & Pedgley 1989). Based on this event, scientists hypothesized that the New World *Schistocerca* descended from a *gregaria*-like ancestor that colonized the New World via westward transatlantic flight (Kevan 1989, Ritchie & Pedgley 1989). Many extant *Schistocerca* species express density-dependent color change similar to that of *S. gregaria* (Duck 1944; Kevan 1943; Rowell & Cannis 1970; Sword 1999, 2003). Sword (2002) suggested that this may be because variation for the expression of density-dependent color polyphenism is an ancestral state for the lineage supposedly present in the *gregaria*-like ancestor.

I presented the first phylogenetic analysis of *Schistocerca* based on morphological data and suggested a different biogeographic scenario (Song 2004a). The phylogeny placed *S. gregaria* in the middle of the New World species, suggesting that the genus could not have descended from the *gregaria*-like ancestor. Rather, I proposed that the desert locust originated from the New World and colonized the Old World via eastward transatlantic flight after the genus had already diversified in the New World. The desert locust was positioned in a clade that roughly corresponded to the Americana Complex *sensu* Harvey (1981). The clade contained both locust and sedentary species, but 3 locust species, *S. gregaria*, *S. piceifrons*, and *S. cancellata*, did not form a monophyletic group. Some of the sedentary species in this clade, such as *S. americana*, are known to express density-dependent color change that closely resembles that of locusts (Harvey 1981, Sword 2003). This suggests that the

ultimate expression of locust phase polyphenism may be plastic even among closely related species, but individual reaction norms, such as density-dependent color change, may be phylogenetically conserved.

The aim of this study is to examine how general this trend is in other locust species. If locust species and closely related sedentary species share certain phase-like traits, then the presence of such traits can be reliably attributed to common ancestry (Brooks & McLennan 1991). These traits can be further shaped by adaptation or drift (Sword 2002). Here I present a preliminary phylogeny of Cyrtacanthacridinae which contains several locust species. I perform a character mapping analysis based on literature data and demonstrate the generality of this phenomenon. I argue that the evolution of locust phase polyphenism should be understood from both process and pattern perspectives.

Materials and methods

Cladistic analysis.—I performed a cladistic analysis using 65 cyrtacanthacridine species comprising 26 genera. Eight outgroup taxa belonging to 4 subfamilies of Acrididae were used. I chose the characters through a comprehensive study of both external and internal morphology. Internal structures were dissected and prepared using a procedure described in Song (2004b). In most cases, I examined multiple specimens and only used invariable characters. Particular attention was paid to known swarming species and only the characters that do not appear to be affected by phase transition were used. A data matrix consisting of 71 morphological characters with 190 character states was compiled in WinClada (Nixon 2002) where nonapplicable data were scored as a '-' and missing data were scored as a '?' (Appendix A & B). All characters were coded

non-additively, except for one: the shape of male subgenital plate. For male cerci, male subgenital plate, and phallic complex, the additive multistate character coding scheme was used. The Parsimony Ratchet (Nixon 1999) as implemented in NONA (Goloboff 1995) was used for initial tree searches. Five repeated runs of 100 iterations were performed (10 to 18% of characters sampled with one tree held each time). Trees from the ratchet were more thoroughly searched in NONA (Goloboff 1995) "mult* 100," "max*," and "best" commands. Bremer support values (Bremer 1994) were calculated up to 5, using the commands "amb," "sub 5," "find*," and "bs" in NONA (Goloboff 1995). WinClada (Nixon 2002) was used to view the trees.

Character mapping.—A character mapping analysis is a powerful tool for studying the evolution of a particular trait from a phylogenetic perspective (Brooks & McLennan 1991). When closely related species share a certain character, we can infer that it is due to common ancestry, which is the most parsimonious explanation (Miller & Wenzel 1995). When applied to the study of phenotypic plasticity evolution however, several difficulties become apparent. Controlled experiments are required to confirm whether a species expresses phenotypic plasticity or not. Ideally, all ingroup species must be studied in the same experimental settings, but this is practically impossible. In the absence of such data, one must rely on literature data, but with caution.

In the case of Cyrtacanthacridinae, there are only a few studies that empirically tested the presence of phenotypic plasticity in a given species: Kevan (1943) on *Schistocerca flavofasciata*, Duck (1944) on *S. obscura*, Rowell & Cannis (1970) on *S. nitens*, Antoniou & Robinson (1974) on *S. pallens*, Antoniou (1970) on *Patanga succincta*, Antoniou (1973) on *Ornithacris turbida*, Sword 1999 on *S. lineata*. Information on most species in the subfamily was purely observational, reported from various agricultural, taxonomic, and ecological reports. Lack of report on phenotypic plasticity in a certain species does not necessarily mean that the species lack genetic variation for plasticity.

The purpose of this study was to show that many species retain genetic variation for the expression of density-dependent phase polyphenism due to common ancestry. It was not my intention to propose a certain evolutionary pathway for a particular reaction norm. In this study, I mainly focused on density-dependent color change. In order to cope with incomplete literature data, I explicitly made the following assumptions. When a study specifically reported and described density-dependent color change in a species (regardless of the nature of the study), it was treated as the presence of plasticity in color. When a study specifically reported a lack of density-dependent color change, it was treated as the absence of plasticity in color. When there was no mention whatsoever, it was treated as unknown. These assumptions were made in order to study the pattern, and whether the species indeed possesses phenotypic plasticity for a certain trait will have to be verified experimentally.

In most cases, density-dependent color change was expressed as a combination of 2 independent traits. First was the development of black pigmentation in response to crowding. Nymphs in isolated conditions had naturally little or no black marking on their pronotum and hind femur, although some individuals exhibited more black pigmentation than others. In some species, crowded nymphs would exhibit a marked increase in black pigmentation. Second was background coloration. Isolated nymphs were usually green, with variable hues. When crowded, some species developed red, yellow, orange, or brown coloration. In many cases, the back-

ground coloration seemed to be species-specific, although variation in expression was also reported. The presence and absence of the plasticity for black pigmentation and background coloration were mapped on the preliminary phylogeny, to study how these characters were distributed within the subfamily. In addition, I noted whether a species in question was known to be sedentary, occasionally aggregating, or swarming. A caution must be made when studying density-dependent behavioral plasticity because many animals are known to form a dense group without plasticity (Sword 2005). All swarming species in Cyrtacanthacridinae were, however, clearly reported to possess density-dependent behavioral plasticity.

Results

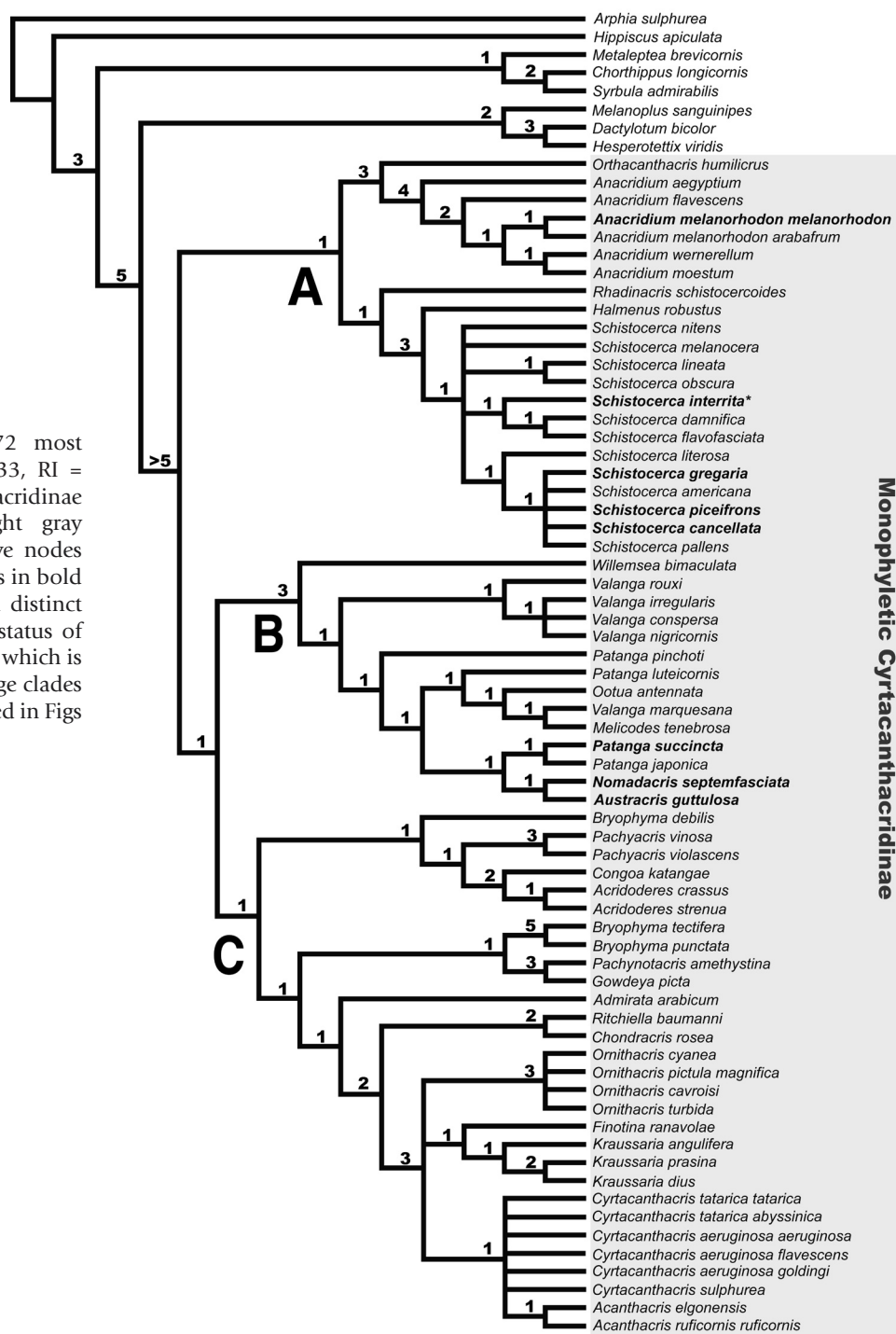
The cladistic analysis resulted in 72 most parsimonious trees (MPTs) (tree length of 345 steps, consistency index (CI) = 0.34, retention index (RI) = 0.77). A strict consensus tree of the 72 MPTs collapsed 8 nodes (Fig. 1, L = 357, CI = 0.33, RI = 0.76). The internal relationships were robust, but some apical relationships were not resolved. The monophyly of Cyrtacanthacridinae was strongly supported (Bremer support ≥ 5). The Bremer support values for the ingroup are low, which is typical in morphological analyses; however, the retention index is high, indicating that the homoplasious characters are useful in defining the ingroup relationships (Wenzel & Siddall 1999).

Distribution of locust species in relation to phylogeny.—Among 65 species in Cyrtacanthacridinae, 8 species are generally accepted as true locusts (Table 1). These locust species occurred in 3 distinct clades: 1 in *Anacridium*, 4 in *Schistocerca*, and 3 in *Nomadacris*-*Patanga*-*Austracris* (NPA) clade (Fig. 1). Within each clade, the locust species were closely related, although they did not form a monophyletic group (except *Anacridium* where there is only one locust species) (Figs 2,3). In all cases, nonlocust species that were most closely related to the locust species, were known to form occasional aggregations. The largest clade in the phylogeny contained no known locust species (Fig. 4), although *Kraussaria angulifera*, *Cyrtacanthacris tatarica*, and *Acanthacris ruficornis* were known to form occasional aggregations. These 3 genera were relatively closely related, and possibly monophyletic.

Distribution of density-dependent color change in relation to phylogeny.—The literature review resulted in partial or complete information on 35 ingroup species (53.8% of total ingroup species). Of these, the information on density-dependent color change was obtained for 28 ingroup species. In all cases, nymphs were reported to be green in their natural isolated settings. No homochromy was reported in Cyrtacanthacridinae (Rowell 1971). Plasticity for density-dependent color change was present in 24 species (85.7 % of the reported species) while it was absent in 4 species (14.3% of the reported species). This lack of plasticity was found in *Bryophyma debilis*, *Acridoderes strenua*, *Ornithacris cavroisi*, and *O. turbida*. They developed neither black pigmentation nor distinct background coloration when crowded (Fig. 4).

All species that were reported to have plasticity for color change exhibited the development of black pigmentation in response to change in density. The specific pattern of expression was also similar in that there was an increase in black pigmentation on the abdomen, pronotum, and wing pads. In general, closely related species exhibited a similar background coloration when crowded, although there were some exceptions.

Fig. 1. A strict consensus of the 72 most parsimonious trees ($L = 357$, $CI = 0.33$, $RI = 0.76$). The monophyly of Cyrtacanthacridinae is supported and shown by a light gray rectangular box. Numbers shown above nodes are the Bremer support values. Terminals in bold indicate the known locust species with distinct locust phase polyphenism. The locust status of *Schistocerca interrita* is not fully resolved, which is indicated by *. The cladogram has 3 large clades designated by A, B, C, which are presented in Figs 2-4 in detail.



Discussion

The phylogeny of Cyrtacanthacridinae shows a similar pattern to that observed in *Schistocerca* (Song 2004a). Locust species are often closely related, but not necessarily monophyletic, and other close relatives of the locusts express phase-like traits (Fig. 1). To understand this pattern, it is important to view locust phase polyphenism as a composite character, consisting of numerous density-dependent phenotypically plastic traits, which might follow different evolutionary trajectories. For example, the Bombay locust *Patanga succincta* is sister to a sedentary species *P. japonica*. The two species express similar density-dependent color change, but only *P.*

succincta is known to express density-dependent behavioral plasticity (Fig. 3). The Sahelian tree locust *Anacridium melanorhodon* and other sedentary *Anacridium* species, show a similar pattern (Fig. 2). This indicates that the traits we often associate with locust phase do not necessarily evolve together and their presence in sedentary species may be attributed to common ancestry.

In this study, I chose to explore the evolution of density-dependent color change to demonstrate that individual reaction norms of locust phase polyphenism might be phylogenetically conserved. I subdivided it into 2 smaller components, black pigmentation and background coloration based on literature data.

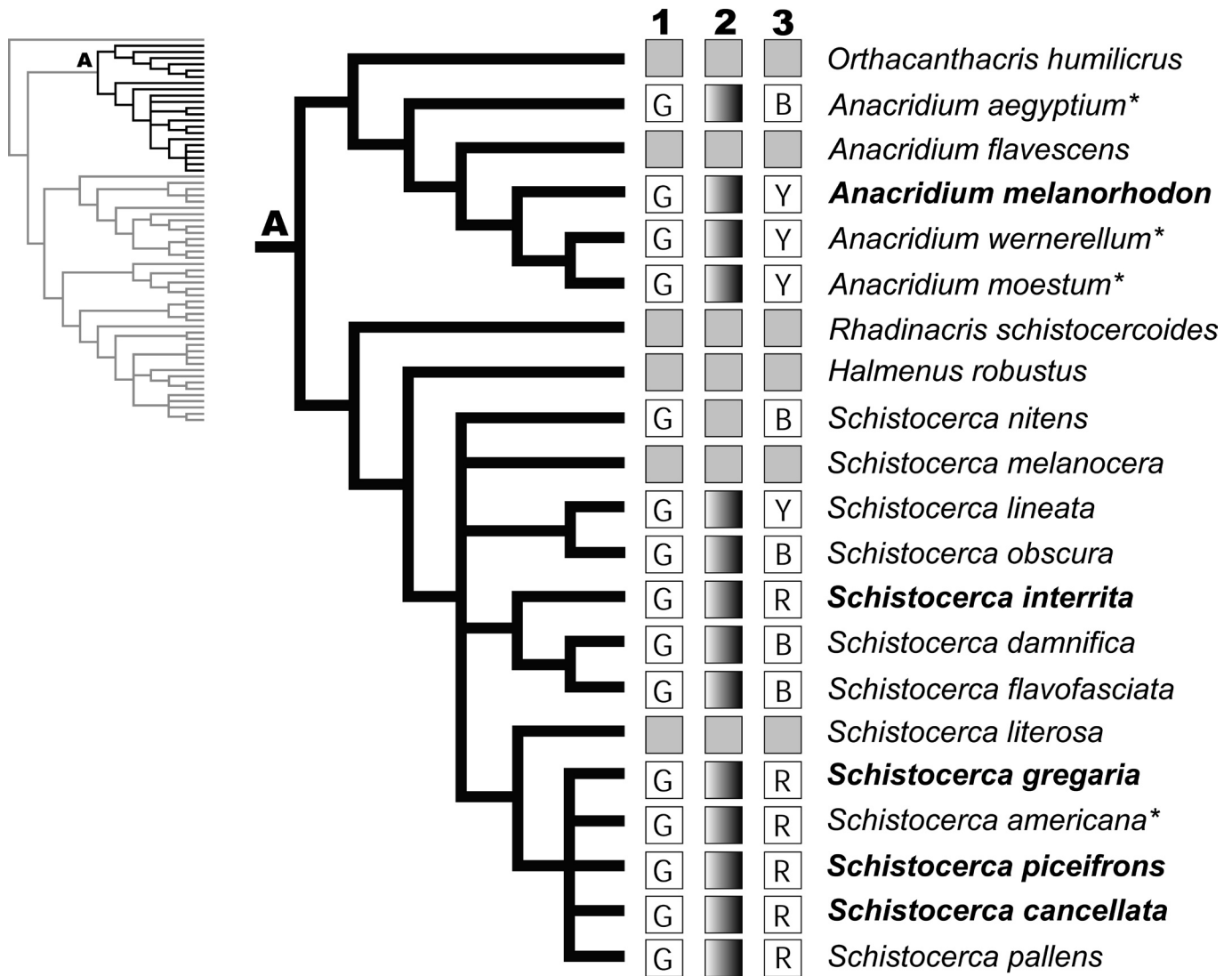


Fig. 2. Character mapping analysis of chromatic plasticity for clade A. Terminals in bold indicate the known locust species with distinct locust phase polyphenism. Terminals with * are the nonlocust species that occasionally aggregate. Column 1 is the nymphal color of the species in isolated condition (G for green, gray for unknown). Column 2 depicts whether or not the species develop black pigmentation when crowded (gradient for black pigmentation, white for no response, gray for unknown). Column 3 depicts background coloration of nymphs which develops when crowded (Y for yellow, B for brown, R for reddish-orange, G for green, gray for unknown). Subspecies of *Anacridium melanorhodon* were collapsed to one terminal.

Development of black pigmentation in response to change in density is widespread in grasshoppers (Applebaum & Heifetz 1999, Pener 1991, Rowell 1967, Rowell 1971). Wingpads, abdominal terga, and hind femora develop black pigmentation, and this pattern is similar across distantly related taxa within the subfamily. Tawfik *et al.* (1999) demonstrated that black pigmentation is induced by a neuropeptide, [His⁷]-corazonin. This neuropeptide and its function seem to be highly conserved across insects (Tanaka 2000). I found that numerous cyrtacanthacridine species express plasticity in development of black pigmentation, which may well be induced by [His⁷]-corazonin via the same underlying physiological mechanisms. If this is true, the presence of such plasticity in locust species can be attributed to a common ancestry. Four species in the largest clade (Fig. 4) however, do not express the plasticity for black pigmentation. This can be considered as at least 3 independent losses for the plasticity, which could have happened through selection or drift

(Sword 2002).

Plasticity in background coloration seems more variable in expression than the expression of black pigmentation. When crowded, some species develop dull brown coloration (often known as green-brown polymorphism, Rowell 1971); some develop bright yellow coloration, and others develop a suite of different colors from yellow and orange to red. Different body parts may develop different coloration. It is difficult to say whether certain colors are homologous because the physiological mechanism for color expression is not fully understood. It is generally accepted that the expression of pigmentation is correlated with a simple redox shift at the cellular level (Lemberg & Legge 1949, Rowell 1971). For example, it could be possible that red is the result of a prolonged redox reaction, while yellow is the result of a short reaction. When mapped onto the phylogeny, closely related species generally have a similar expression. If the expression of background coloration is

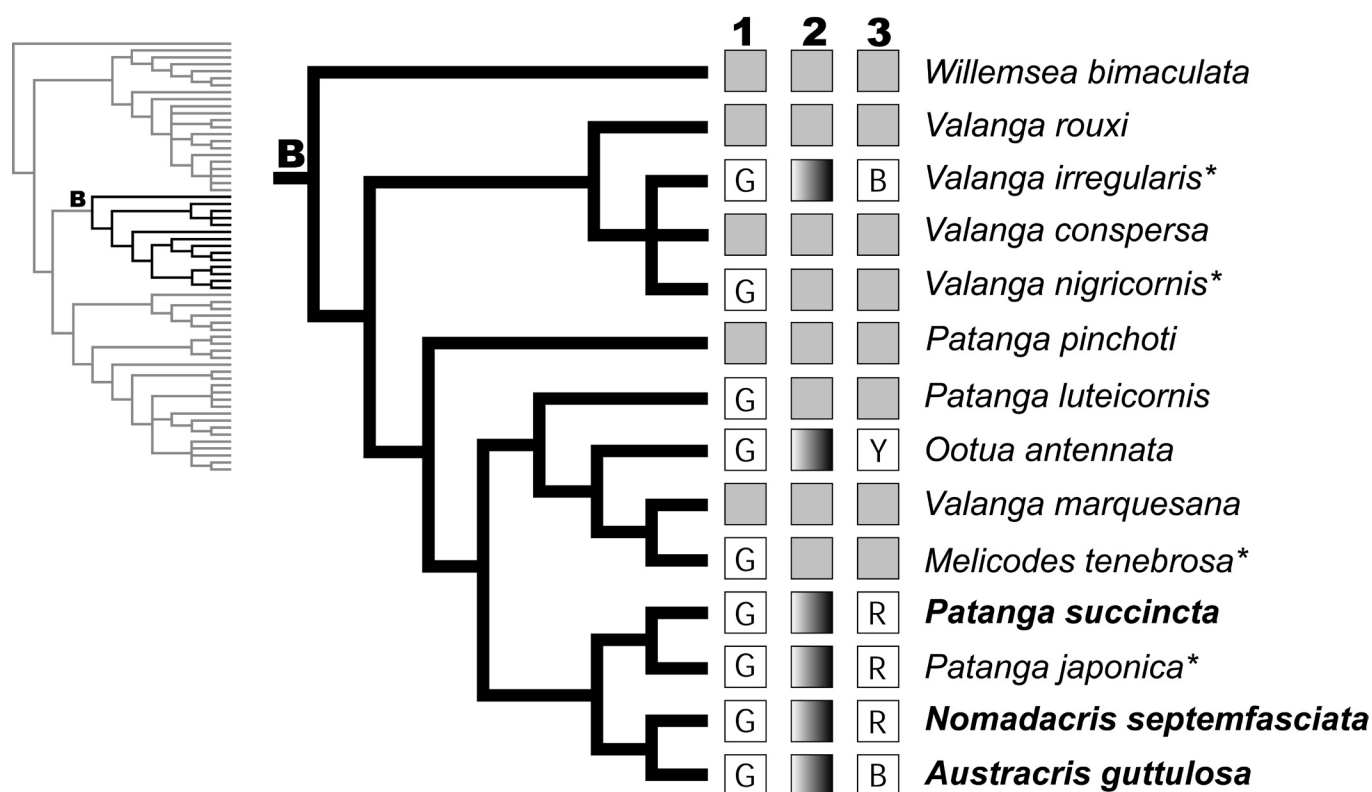


Fig. 3. Character mapping analysis of chromatic plasticity for clade B. See Fig. 2 legend for an explanation of the color coding. *Valanga* and *Patanga* are not monophyletic, reflecting unstable taxonomy.

intimately related to physiology, which is phylogenetically conserved, closely related species can exhibit this plasticity due to common ancestry.

The evolution of locust phase polyphenism is often viewed from an adaptive perspective. For example, density-dependent aposematism in the desert locust was shown to be adaptive (Sword *et al.* 2000). One can also easily imagine the adaptive significance of cohesive behavior, as in nymphal bands or adult swarms (Ellis & Pearce 1962, Romey 1997). And density-dependent pathogen resistance was found in the desert locust (Wilson *et al.* 2002). The present phylogeny, however, reveals that the physiological traits we commonly associate with locust phase are often present in sedentary species. It also suggests that the locust species are derived from the sedentary species, because in no case are the locust species basal to the sedentary ones. In other words, the phase-like traits might have originally evolved from totally different contexts.

This initial evolution of reaction norms could have happened in several ways, but might not have been directly related to swarming. I suspect that swarming behavior in locusts has evolved independently, because many animal species can form a dense migrating group (such as the swarms of honeybees, fish schools, and bird flocks) (Parrish & Hamner 1997).

Due to phylogenetic conservatism, locusts retain genetic variation for physiological mechanisms that underlie plastic reaction norms to evolve behavioral plasticity; they can utilize these to 'become a locust'. Because plastic reaction norms can be shaped by selection or drift (Sword 2002), they can also be lost by the same processes. A good example would be the southern subspecies of the desert locust, *S. gregaria flaviventris*, which expresses the plastic reaction norms in color, but has these much reduced in behavior from the

nominal subspecies (Harvey 1981, Waloff & Pedgley 1986). Weather conditions in southern Africa are not favorable for swarm breeding in *S. gregaria flaviventris* (Waloff & Pedgley 1986), and the reduced propensity to swarm may be an adaptive response to such environmental conditions.

Similarly, it would be possible for some nonlocusts, that already have all the physiological machinery due to common ancestry, to express hidden behavioral plasticity. For instance, *S. interrita* in Peru has long been known as a sedentary species (Blancas-Sanchez 1956); only recently has it been shown to express density-dependent changes in color and behavior (SENASA 2005). It is suggested this sudden explosion of locust phase in *S. interrita* is correlated to changes in climate due to El Niño (SENASA 2005). In other words, differential expression of locust phase polyphenism can occur through the local fine-tuning of the existing reaction norms (Sword 2002). Therefore, it is important to study the evolution of locust phase polyphenism from both adaptive and phylogenetic perspectives.

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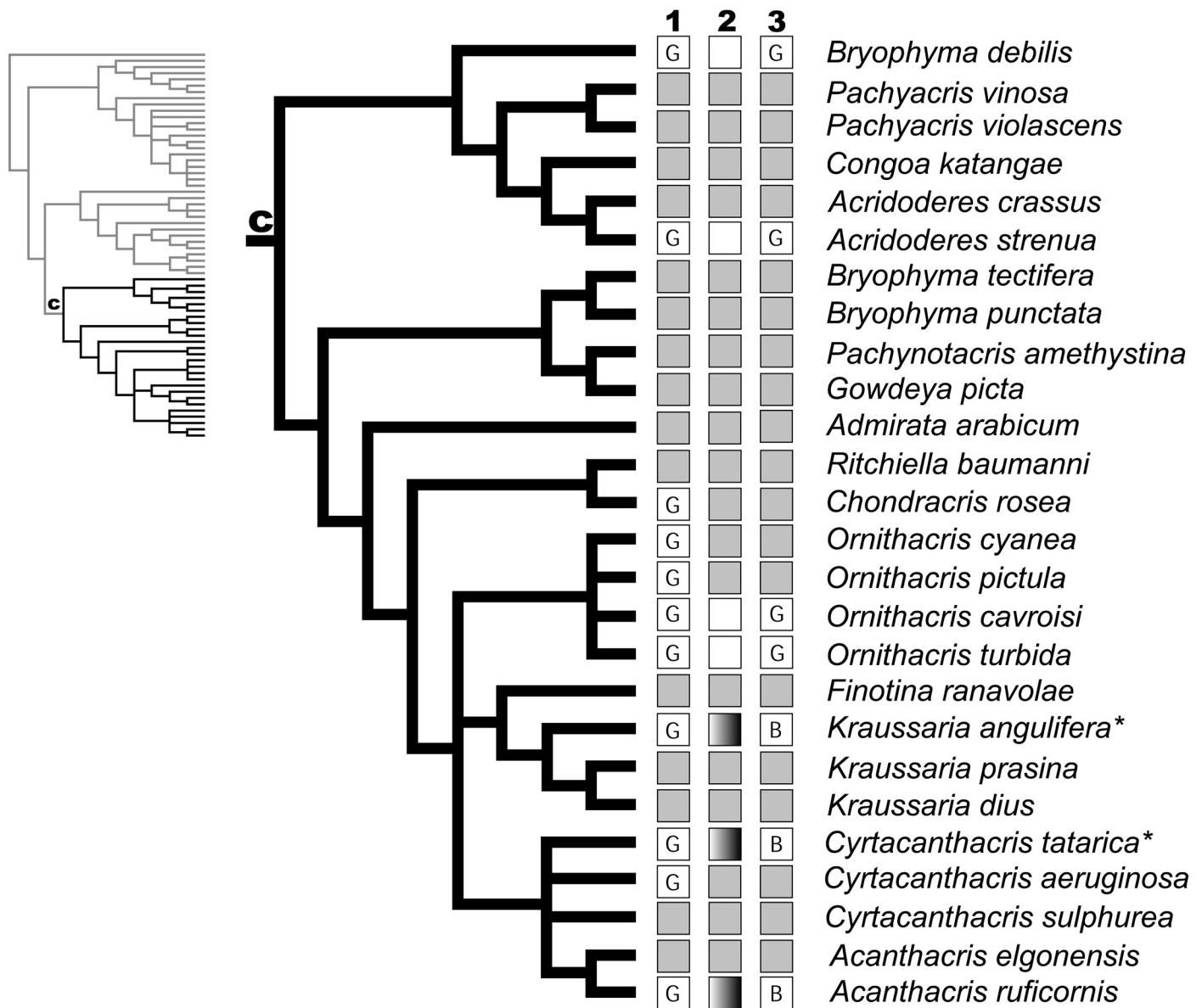


Fig. 4. Character mapping analysis of chromatic plasticity for clade C. See Fig. 2 legend for the explanation of the color coding. *Bryophyma* is not monophyletic. Four species shown here do not change color when crowded, which is unique for the subfamily. Subspecies of *Cyrtacanthacris tatarica* and *C. aeruginosa* were collapsed to single terminals.

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Appendix A. A list of characters and states used in the phylogenetic analysis that produced the trees in Figs 1-4.

0. Antennae length: as long as or slightly longer than head + pronotum = 0; much longer than head + pronotum = 1.
1. Head: overall shape: slanted = 0; straight = 1.
2. Head: frontal ridge: obliterated below ocellus = 0; ridge elongate below ocellus = 1.
3. Head: frontal ridge integument above ocellus: lightly punctured with a smooth background = 0; deeply punctured, like the surface of a golf ball = 1; rocky and rugose = 2.
4. Head: lateral foveolae: present adjacent to fastigium = 0; present laterally below fastigium = 1.
5. Head: fastigium shape (from 4:1): vertically elongated isosceles trapezoid = 0; horizontally elongated isosceles trapezoid = 1; lateral ridges round, forming water-drop shape = 2; broad and round, like half-ellipse = 3; indistinct = 4.
6. Head: lateral ocelli: distinct below fastigium = 0; projecting next to fastigium = 1.
7. Head: interocular distance: same as width of frontal ridge = 0; distinctly wider than width of frontal ridge = 1; narrower than width of frontal ridge = 2.
8. Thorax: sternum: mesosternal lobe: laterally wider than vertical length = 0; vertically longer than lateral width = 1.
9. Thorax: metathoracic episternum: median ridge absent = 0; median ridge present = 1.
10. Thorax: metapostnotum: slightly innervated to metathoracic epimeron = 0; strongly innervated to metathoracic epimeron = 1.
11. Pronotum: lateral carina: absent = 0; present = 1.
12. Pronotum: sulci: crossed by 1 sulcus = 0; crossed by 3 sulci = 1.
13. Pronotum: posterior margin of metazona: round = 0; obtusely angular = 1; acutely angular = 2.
14. Pronotum: profile of dorsal cross section: nearly flat or slightly convex = 0; roof-like and obtuse angular = 1; median carina raised as broad ridge = 2; median carina constricted and extremely raised = 3.
15. Pronotum: sculpting pattern of dorsum of prozona: no ridges = 0; reticulate, honeycomb-shaped ridges present = 1; thick irregular-shaped ridges present = 2.
16. Pronotum: background integument on dorsum of prozona: smooth = 0; minutely granulate = 1; velvety = 2.
17. Pronotum: sculpting pattern of lateral lobe of prozona: background integument shiny smooth = 0; background integument minutely granulose = 1.
18. Pronotum: sculpting pattern of lateral lobe of prozona: no pattern = 0; honeycombed ridges = 1; irregular ridges = 2; papillulate = 3.
19. Pronotum: sculpting pattern of lateral lobe of prozona: granules absent = 0; granules present = 1.
20. Pronotum: sculpture of dorsum of metazona: no pattern = 0; honeycomb shape = 1; irregular thick ridges = 2.
21. Tegmina: apex: round = 0; oblique = 1.
22. Tegmina: dark brown pattern: mottled = 0; medium sized pattern scattered = 1; forming distinct bands = 2; absent = 3.
23. Hind wing: color: transparent without any pattern = 0; colored hue at base = 1; dark brown band = 2; entire wing distinctly colored = 3.
24. Prosternal process: absent = 0; present = 1.
25. Prosternal process: overall shape (lateral view): cylindrical = 0; anterior portion strongly curved backward with an angle = 1.
26. Male hind femur: stridulatory pegs: absent = 0; present = 1.
27. Male hind femur: upper carina: smooth = 0; serrate = 1.
28. Male hind femur: lower carina: smooth = 0; serrate = 1.
29. Male hind femur: lower carinula: granules absent = 0; granules present = 1.
30. Male cerci: simple rod-like = 0; modified = 1.
31. Male cerci shape (from 30:1): simple triangular with pointed apex = 0; highly elongated, apex incurved = 1; elongated, narrowing toward apex and hooked downward = 2; simple lamelliform with tubercles on dorsal surface = 3; quadrate = 4.
32. Male cerci: simple triangular cerci: short and vertically wide at base = 0; long and vertically narrow at base = 1.
33. Male cerci: of quadrate type: apex nearly round = 0; apex clearly quadrate = 1.
34. Male subgenital plate: overall shape: apex divided into two lobes = 0; apex not divided = 1; apex divided into three narrow lobes = 2. [additive].
35. Male subgenital plate apex (of unilobed apex): overall simple conical structure = 0; lateral side expanded = 1.
36. Male subgenital plate shape: of conical type: entire structure tubular and phallus at the very base = 0; dorsal portion divided up to half way and phallus visible = 1; dorsal portion strongly divided and infolded in its entirety = 2.
37. Male subgenital plate: bilobed type: apex very small incision with small lobes = 0; apex deeply incised in the middle = 1.
38. Male furcula: absent = 0; present = 1.
39. Male furcula: small projection at base = 0; projecting angularly at base = 1; projecting perpendicularly at base = 2; distinctly elongate projection = 3.
40. Male epiproct: median projection: absent = 0; present, thus making the structure trilobate = 1.
41. Male epiproct: ridges forming lateral lobes: strongly converging in the middle of median lobes = 0; not reaching to middle = 1.
42. Male epiproct: median ridge on median lobe: absent = 0; present = 1.
43. Male epiproct: a pair of elongate ridges along basal-lateral sides: absent = 0; present = 1; robustly present and curved into the center = 2; as small tubercles = 3.
44. Female subgenital plate: lateral lobes: not projecting forward = 0; projecting forward as broad lobes = 1; sharply projecting forward as separate lobes = 2; lateral end projecting forward as small lobes = 3.

45. Female subgenital plate: egg guide (ventral view): projecting under sheath formed by lateral lobes = 0; lateral lobes fusing in the middle, projecting into the egg guide = 1.
46. Female subgenital plate: Egg guide: formed by wrapped sheath = 0; single rod-like structure = 1.
47. Phallic complex: overall size: small = 0; large = 1.
48. Epiphallus: independent, elongated horn-like ancora: absent = 0; present = 1.
49. Epiphallus: projection on lateral lobes (of 48:0): absent or only a trace of projection = 0; noticeably present as a knobby structure = 1.
50. Epiphallus: length of bridge between lophi: normal = 0; very wide = 1.
51. Epiphallus: length of bridge between lophi (from 50:0): narrower than width of single lophus = 0; as long as width of single lophus = 1; wider than width of single lophus = 2.
52. Epiphallus: lophi angle relative to bridge: projecting nearly perpendicular to bridge = 0; projecting nearly parallel to bridge = 1; twisted about 90 degrees and projecting = 2.
53. Epiphallus: projection of lophi (from 52:2): lophi projecting right below bridge = 0; lophi projecting much below bridge = 1.
54. Epiphallus: shape of lophi: apex divided into several small lobes = 0; a single lobe = 1.
55. Epiphallus: lophi shape (from 54:1): narrow triangular with pointed apex = 0; lamelliform with pointed apex = 1; broadly round with round apex = 2; laterally expanding with round apex = 3.
56. Ectophallic sclerite: absent = 0; two lobes connected by membrane = 1; single flimsy lobe = 2; single robust structure = 3.
57. Ectophallic sclerite: lateral overall profile (from 56:3): midprojection elongate and protruding broadly forward = 0; midprojection protruding below the lateral wings = 1; midprojection protruding as a small lobe = 2; midprojection not protruding = 3.
58. Ectophallic sclerite: midprojection shape (from 57:0): broad = 0; distinctly constricted in middle = 1; reduced = 2.
59. Cingulum: overall shape of lateral apodeme (dorsal view): U-shape = 0; relaxed bow-shape = 1; thickened arch = 2; inverted v-shape (center round rather than pointed) = 3.
60. Cingulum: overall shape: indistinct = 0; horn-like projection = 1; entirely covering apex of aedeagus = 2.
61. Cingulum: overall shape of zygoma and rami (from 60:2): simple and narrowing toward apex = 0; elongated, highly cuticular and fleshy = 1; rami distinct with membranous zygoma = 2; simply encapsulating apex of aedeagus = 3.
62. Cingulum: shape of rami and zygoma (from 61:2): short and apex highly membranous = 0; short and rami completely closed with less membrane at apex = 1; elongated like a snout with apex ring-like = 2.
63. Endophallus: valve of penis elongated, very narrow and thin in its entirety: absent = 0; present = 1.
64. Endophallus: apical valve: bilaterally symmetrical = 0; twisted = 1.
65. Endophallus: apical valve: apical valve of aedeagus and valve of cingulum fused = 0; two valves not fused = 1.
66. Endophallus: fused apical valves (from 65:0): apex flabby lobed = 0; apex branched = 1; apex like hollowed tube = 2; kidney-shaped solid lobe = 3.
67. Endophallus: apical valves (from 65:1): apex hollow tube = 0; apex modified as broad membranous lobes = 1; apex modified as thick fleshy lobes = 2; apex widely diverging sideways = 3.
68. Endophallus: vertical width of basal valves: narrow = 0; wide = 1.
69. Endophallus: gonopore process: weak and reaching only half way to flexure = 0; robust = 1.
70. Endophallus: "neck" between apex and flexure: disjunct = 0; weakly sinuate = 1; robustly sinuate = 2.

Appendix B. A data matrix used to produce the trees in Figs 1-4.

	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70
<i>Arphia sulphurea</i>	0112130101110230110000330-00000	---	10	--0	-110000001-010-0-1--01--001-0002										
<i>Hippiscus apiculata</i>	0112130101110222102020330-00000	---	10	--0	-110000011-010-0-1--01--001-0002										
<i>Chorthippus longicornis</i>	1010130101110020110000300-10000	---	10	--0	-110000101-000-0-2--00--001-0001										
<i>Syrbula admirabilis</i>	0010130101110020110000100-10000	---	10	--0	-110000101-000-0-2--00--001-0001										
<i>Metaleptea brevicornis</i>	0010130101110020110000300-00000	---	10	--0	-110001101-010-0-2--00--001-0001										
<i>Dactylotum bicolor</i>	010004100000100000001-3010000010--10--	100100011101010-0-0--023-001-0000													
<i>Hesperotettix viridis</i>	01100411000010000000103010000010--10--	100100311001010-0-0--023-001-0000													
<i>Melanoplus sanguinipes</i>	0110001100001020100000101000001--10--	130100111101000-120--023-001-0000													
<i>Cyrtacanthacris tatarica tatarica</i>	011000001000111021310010110110100-100-1110011111001-2010300020-1000-012														
<i>Cyrtacanthacris tatarica abyssinica</i>	011004001000112020310010110110100-100-1110010111001-2010300020-1100-012														
<i>Cyrtacanthacris aeruginosa aeruginosa</i>	111004011000112020310030110110100-100-1110011111001-2010300020-1000-012														
<i>Cyrtacanthacris aeruginosa flavescens</i>	011000001000112021310030110110100-100-1110011111001-2010300020-1000-012														
<i>Cyrtacanthacris aeruginosa goldingi</i>	011000001000112020310030110110100-100-1110011111001-2010300020-1000-012														
<i>Cyrtacanthacris sulphurea</i>	011000011000112020310010110110100-100-1110031111001-2010300020-1100-012														
<i>Acanthacris elgonensis</i>	011004101000112021310010110110100-11--1110011111001-2010300120-1102-012														
<i>Acanthacris ruficornis ruficornis</i>	011004001000112021310020110110100-11--111000111001-2010300120-1102-012														
<i>Ornithacris cyanea</i>	011000001000112110301021110100100-100-1211031111001-2110301020-1000-012														
<i>Ornithacris pictula magnifica</i>	011000011000113110301021110110100-100-1211001111001-2110301020-1000-012														
<i>Ornithacris cavroisi</i>	011000001000100110301021110100100-100-1211001111001-2110301020-1000-012														
<i>Ornithacris turbida</i>	011000001000100110301021110100100-100-1211011111001-2110301020-1000-012														
<i>Kraussaria angulifera</i>	011000001000112120311010110100100-11--1110001111001-2010300120-1002-012														
<i>Kraussaria prasina</i>	01100000100011111301030110100100-11--111011111001-2010300120-1001-012														
<i>Kraussaria dius</i>	0110000010001111130103011011100-11--111011111001-2010300120-1101-012														
<i>Finotina ranavolae</i>	011000001000112110301030110100100-100-1110011111001-2010300020-1101-012														
<i>Ritchiella baumannii</i>	011001111000111210202031110110100-100-111001111100010-11301020-0000-112														
<i>Chondracris rosea</i>	011001111000123210202031110111100-100-111001111100000-11302020-0000-012														
<i>Anacridium aegyptium</i>	01120210100010211121200210011011--2---	121011211100020-1131-221-0001-112													
<i>Anacridium melanorhodon melanorhodon</i>	11100212100010111130101210011011--2---	1210132111100010-1131-221-0001-112													
<i>Anacridium melanorhodon arabafum</i>	11100212100010111130101210011011--2---	121013211100010-1131-221-0001-112													
<i>Anacridium wernerellum</i>	01100212100010111130101210011011--2---	121013211100020-1131-221-0001-112													
<i>Anacridium moestum</i>	01100212100010111130101210011011--2---	121013211100020-1131-221-0001-112													
<i>Anacridium flavescens</i>	01100212100010111130101210011011--2---	1210102111100010-1131-221-0001-112													
<i>Orthacanthacris humilicrus</i>	01100210100010301100000210010011--11--	111100211100010-1133-32200003-112													
<i>Bryophyma debilis</i>	0111001010001111113010-0100110101-102-111103101101000-1233-0220001-0012														
<i>Bryophyma tectifera</i>	01120010100011211100002010011113--102-111100101101020-1331-020-0002-012														
<i>Bryophyma punctata</i>	01110010100011211130102010011113--102-111100101101020-1331-020-0002-012														
<i>Adramita arabicum</i>	011002101000112211211010100111101-102-111001111100010-1133-020-0001-012														
<i>Pachyacris vinosa</i>	01110010100011111101031100111101-100-111001011101000-11302020-001-3012														
<i>Pachyacris violascens</i>	01110410100011011110103010011101-100-111001001101000-11302020-001-3012														
<i>Acridoderes crassus</i>	010101101000121111011130100110101-102-101101101101020-1231-0220001-2112														
<i>Acridoderes strenua</i>	0101011110001111110112010011013--102-101101001101020-1132-0220001-0012														
<i>Congoa katangae</i>	01010100100011111101-30100110101-102-11110100110???-1???-2???-??-??12														
<i>Pachynotacris amethystina</i>	111004001000110110301033100111101-102-101100011101000-1233-32200000-012														
<i>Gowdeya picta</i>	011204101000101111202033100110101-102-101102011101020-1133-120-0002-012														
<i>Rhadinacris schistocercoides</i>	111000101000102111301030100100100-101-111100011000010-1132-0220001-0012														
<i>Willemsea bimaculata</i>	01110410100010011030103310010012--101-12110111110???-1???-2???-??-??12														
<i>Valanga irregularis</i>	01100000100010111030103010010012--101-121003111101010-1133-3222001-1012														
<i>Valanga rouxi</i>	01100000100010111030103010010012--101-121101111101010-1133-3222001-1012														
<i>Valanga marquesana</i>	11100000100011111020103010010012--101-121103011100020-1133-3222001-1012														
<i>Valanga conspersa</i>	01100400100010111030103010010012--101-121001111101010-1133-3222001-1012														
<i>Valanga nigricornis</i>	01100200100010111030101010010012--101-121001111101010-1133-3222001-1012														
<i>Melicodes tenebrosa</i>	01100000100011211030103010010012--101-121102011100020-1133-3222001-1012														
<i>Ootua antennata</i>	11100000100010011030203010010012--101-121102???1001-0-1133-3222001-1012														
<i>Patanga succincta</i>	01100000100010011030101010011012--101-1211013111100010-1133-0222001-1012														
<i>Patanga japonica</i>	01110000100010011030101010011012--101-121101111100020-1133-0222001-1012														
<i>Patanga luteicornis</i>	11100000100010011030103110010012--101-121101111100020-1133-3222001-1012														
<i>Patanga pinchoti</i>	01100102100010011030103010010012--101-121000111101020-1133-3222001-1012														
<i>Nomadacris septemfasciata</i>	01100200100010011030102111010012--101-1211013111100020-113003220001-1012														
<i>Austracris guttulosa</i>	01100000100010011030101011010012--101-121101311101010-1133-3222001-1012														
<i>Halmenus robustus</i>	010004121000100111301-3010000014-00--0121101011000011-1132-0221001-0012														
<i>Schistocerca gregaria</i>	01100000100010111030101010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca americana</i>	01100000100010111030101010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca piceifrons</i>	01100000100010111030101010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca cancellata</i>	01100000100010111030101010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca pallens</i>	01100000100010111030101010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca alutacea</i>	1110000010001111130103010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca obscura</i>	1110000010001111130103010010014-10--1121100011000021-1132-0221001-0012														
<i>Schistocerca damnifica</i>	01120000100012211120203010010014-10--1121100011000021-1132-0221001-0012														
<i>Schistocerca interrita</i>	01100000100011211120101010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca nitens</i>	01100000100011211030100010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca flavofasciata</i>	01100000100011211120103010010014-10--1121100011000021-1132-0221001-0012														
<i>Schistocerca melanocera</i>	01100000100010111130103010010014-10--1121100011000011-1132-0221001-0012														
<i>Schistocerca literosa</i>	01100000100010111130101010010014-10--1121100011000011-1132-0221001-0012														