

# Phylogeny of the grasshopper family Pyrgomorphidae (Caelifera, Orthoptera) based on morphology

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**Abstract.** The family Pyrgomorphidae (Orthoptera: Caelifera) is considered one of the most colourful grasshopper families, which contains about 500 species distributed worldwide. Commonly referred to as gaudy or bush grasshoppers, many pyrgomorphs are known to be aposematic and capable of sequestering plant secondary compounds. Several species are considered important agricultural pests, while some species are culturally important. Nevertheless, the phylogeny of this family has never been proposed using modern cladistic methods. In this study, we present a phylogenetic analysis of Pyrgomorphidae, based on 119 morphological characters with 269 character states, covering 28 out of 31 current recognized tribes. We recovered the monophyly of the family and one of the two currently recognized subfamilies, Orthacridinae. Pyrgomorphae was recovered as paraphyletic. Based on the most parsimonious tree, we propose four main clades and discuss the biology and biogeography of members of these clades. This is the first step towards building a natural classification for Pyrgomorphidae, which is an excellent model system for studying the evolution of interesting traits such as wing development, warning coloration and chemical defence.

## Introduction

The family Pyrgomorphidae (Orthoptera: Caelifera: Pyrgomorphae) contains some of the most colourful grasshoppers in the world. Often featured in display collections of large and showy insects, pyrgomorphs can be easily recognized by their vibrant and contrasting body colours, often brightly coloured hindwings, and conspicuous spikes and tubercles on pronotum (Fig. 1). Commonly referred to as gaudy or bush grasshoppers, many of these brightly coloured pyrgomorphs are known to be aposematic and capable of sequestering plant secondary compounds, such as cardiac glycoside from the toxic plants they are associated with (Rowell, 1967; Whitman, 1990; Chapman *et al.*, 1986; Rentz *et al.*, 2003). Some of these aposematic species are known to possess a specialized mid-dorsal abdominal gland, which is apparently used for releasing toxic chemicals through dorsal openings in the abdomen when disturbed (Whitman, 1990). While the family is most well known for its colourful members, only about 10% of the 482 known species are brightly coloured and aposematic; the majority of pyrgomorphs are in

fact cryptically coloured and probably not aposematic, and less familiar to the general public (Fig. 1D, F, H).

Some pyrgomorphs are economically important pests, attacking many types of crops and ornamental plants. There are at least 20 genera recognized as moderate to serious pests (COPR, 1982). For example, *Zonocerus elegans* (Thunberg) and *Z. variegatus* (Linnaeus) are major pests in sub-Saharan Africa that attack a wide range of broad-leaved plants, including many crops. They tend to form large aggregations as young instars, which can lead to localized outbreaks (COPR, 1982). The species in the African genus *Phymateus* Thunberg (Fig. 1B) are also pests of many crops, including, coffee, vine, fig, citrus, as well as various fruit trees and grains. Like *Zonocerus* Stål, the young instars of *Phymateus* show gregarious behaviours and are also capable of sequestering toxic chemicals, which deter or even kill vertebrate predators (COPR, 1982). In Mexico, *Sphenarium purpurascens* Charpentier is an important pest of crop plants, including corn, bean, alfalfa and sorghum, and it often reaches high density. Interestingly, this species does not produce toxic chemicals although the individuals are often brightly coloured. In fact, this species is harvested and used as human food, locally known as ‘chapulines’ (Ramos-Elorduy *et al.*, 1997) in parts of Mexico. Other genera that include pest species are *Orthacris*

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**Fig. 1.** Habitus images of some live pyrgomorphids. (A) *Petasida ephippigera* (Australia); (B) *Phymateus morbillosus* (South Africa); (C) *Sphenarium histrio* (Mexico); (D) *Chrotogonus hemipterus* (Mozambique); (E) *Monistria* sp. (Australia); (F) *Pyrgomorpha conica* (Greece); (G) *Dictyophorus* sp. (South Africa); (H) *Atractomorpha acutipennis acutipennis* (Mozambique) and (I) *Taphronota ferruginea* (Guinea). Photo credits: (A) Nathan Litjens; (B, G, I) Piotr Naskrecki; (C, D) Ricardo Mariño-Pérez; (E) Hojun Song; (F) Roy Kleukers; (H) Bert Foquet. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

Bolívar, *Neorthacris* Kevan & Singh, *Colemania* Bolívar, *Chlorizeina* Brunner von Wattenwyl, *Aularches* Stål and *Tagasta* Bolívar in Asia; *Desmopterella* Ramme in Papua New Guinea and adjacent areas; *Poekilocerus* Serville, *Chrotogonus* Serville, *Atractomorpha* Saussure and *Pyrgomorpha* Serville in both Africa and Asia; and *Rutidoderes* Westwood, *Phyteumas* Bolívar, *Taphronota* Stål, *Maura* Stål, *Dictyophorus* Thunberg, *Pyrgomorphella* Bolívar and *Rubellia* Stål in Africa only (COPR, 1982).

Pyrgomorphidae is easily diagnosable from other grasshopper families by the presence of a groove in the fastigium (Kevan & Akbar, 1964) and distinctive phallic characteristics such as the cingulum extending around to the ventral side, the medially directed endophallic apodemes, and the ejaculatory sac open to the genital chamber (Kevan & Akbar, 1964; Eades, 2000). The family is the sole member of the superfamily Pyrgomorphoidea, which is sister to the superfamily Acridoidea, which includes familiar families such as Acrididae and

Romaleidae (Flook *et al.*, 1999; Song *et al.*, 2015). Pyrgomorphidae currently includes 482 valid species belonging to 150 genera, mostly distributed in the Old World (Africa, Asia and Australia). In the New World, there are only 30 species in 13 genera known from Central and South America. Bolívar (1882–1917) and Kevan (1948–1990) were the most prolific taxonomists who worked on this group, each describing 85 and 79 species, respectively. Kevan was an important figure in pyrgomorph taxonomy as he established a provisional classification scheme by recognizing several tribes and series (Kevan, 1976; Kevan *et al.*, 1969, 1970, 1971, 1972, 1974, 1975). By the 1960s, over 90% of the known species had been described. However, this is not to say that the discovery of pyrgomorph diversity is complete; rather, it is a testament to the lack of taxonomic expertise in this group over many decades.

There has never been a modern cladistic analysis of the family based on comprehensive taxon sampling, and the phylogenetic relationships among the genera and tribes within Pyrgomorphidae remain unresolved. The only available hypothesis of the evolutionary relationships among different lineages within the family is the one proposed by Kevan & Akbar (1964) based on their interpretation of the morphology and biogeography. In their work, they provided a provisional arrangement of tribes, subtribes and genera in five series, and the work became the basis for their subsequent studies of male genitalia diversity, which resulted in recognizing two informal groups, ‘A’ and ‘B’ (Kevan, 1976; Kevan *et al.*, 1969, 1970, 1971, 1972, 1974, 1975) (Table 1). Subsequently, Eades & Kevan (1974) erected the subfamily Pyrgacrinae for a newly described genus *Pyrgacris* Descamps, which is endemic to the remote island of Réunion (Descamps, 1968). They assigned this subfamily to Pyrgomorphidae, but discussed its similarities with Acrididae. Later, Pyrgacridinae was included as a subfamily of Pyrgomorphidae in the works of Dirsh (1975), Kevan (1982), Otte (1994) and Vickery (1997). However, Eades (2000) argued that there was enough evidence to elevate the subfamily Pyrgacrinae to its own family and placed it in the superfamily Acridoidea based on the morphology of internal genitalia, which resemble Acridoidea more than Pyrgomorphoidea. Recent molecular work by Leavitt *et al.* (2013) and Song *et al.* (2015) found Pyrgacrididae to belong to Acridoidea, rather than Pyrgomorphoidea, corroborating the hypothesis of Eades (2000). Based on these studies, Pyrgomorphidae is currently divided into two subfamilies, Orthacridinae and Pyrgomorphinae (Table 1), which correspond to the groups ‘A’ and ‘B’ of Kevan *et al.* (1969, 1970, 1971, 1972, 1974), respectively. The defining characteristics of each group are summarized in Table 2.

Given the conspicuousness of many pyrgomorph species, their interesting biology and cultural and economic importance, it is surprising that the taxonomy of the family has not been revised in the past 50 years and that there is no phylogenetic hypothesis based on a modern cladistic analysis available. In this study, we present the first phylogenetic hypothesis of Pyrgomorphidae based on 28 out of the 31 currently known tribes and many external and internal morphological characters. Specifically, we aim to test the monophyly of the family and subfamilies and to describe phylogenetic relationships among major clades within

the family. We also provide a discussion about the evolution of important morphological characters; this study is intended to establish a basis for future studies on the evolution of this family of grasshoppers.

## Materials and methods

### Taxon sampling

Our study included 44 terminals (three outgroups and 41 ingroup taxa). The ingroup taxa comprised 41 species from different genera representing 28 out of the 31 currently known tribes (90%) of Pyrgomorphidae (Figs 2–8). The remaining three tribes, Bruniellini (Philippines), Fijipyrgini (Fiji) and Malagasphenini (Madagascar), were not included because specimens from these tribes were not available at the time of the study. For outgroup taxa, we included three species representing three families (Pamphagidae, Lentulidae, and Acrididae) of the superfamily Acridoidea. The specimens used in this study were borrowed from the following institutions: Academy of Natural Sciences of Drexel University, Philadelphia, PA, U.S.A. (ANSP); the Natural History Museum, London, U.K. (BMNH); and the Muséum National d’Histoire Naturelle, Paris, France (MNHN). Although the specimens were already identified in several cases by well-known orthopterologists, such as Descamps, Kevan, Hebard and Key, among others (see Table S1), the works of Dirsh (1963, 1965), Kevan (1976), Kevan *et al.* (1969, 1970, 1971, 1972, 1974, 1975) and Rentz *et al.* (2003) were used to confirm the identifications. The classification used in this work followed the current systematic arrangement adopted by the Orthoptera Species File (Cigliano *et al.*, 2017). Primarily this classification follows the groups ‘A’ and ‘B’ and the tribes recognized by Kevan (1976) and Kevan *et al.* (1969, 1970, 1971, 1972, 1974, 1975).

### Character sampling

We consulted Dirsh (1963, 1965), Kevan *et al.* (1969, 1970, 1971, 1972, 1974) and Rentz *et al.* (2003) to obtain characters that had been traditionally used in the pyrgomorph taxonomy. Additionally, we conducted a comprehensive study of both external and internal morphology in search of additional characters. We followed Dirsh (1965) and Rentz *et al.* (2003) for external morphology terminology and Kevan (1976), Kevan *et al.* (1969, 1970, 1971, 1972, 1974, 1975) and Eades (2000) for genitalia (epiphallus, ectophallus and endophallus) terminology. The complete list and description of the 119 morphological characters are presented in File S1. The character matrix is presented in Table S2.

The dissection procedure was based on Hubbell (1960). Dried museum specimens were relaxed by soaking their posterior portion of abdomen under boiling water for a few minutes until they were soft enough to extract internal genitalia. This was done by inserting a tip of forceps under the phallic structure and by gently pulling it. Dissected phallic structures were placed in 10% KOH solution for 30–120 min to dissolve muscle tissues. Dissolved muscles were removed

**Table 1.** Tribes for each subfamily of Pyrgomorphidae (taken from Orthoptera Species File) with their corresponding Group and Series (Kevan, 1976; Kevan *et al.*, 1969, 1970, 1971, 1972, 1974, 1975).

Subfamily Orthacridinae	Kevan Group and Series	Subfamily Pyrgomorphinae <sup>a</sup>	Kevan Group and Series
Fijipyrgini Kevan, 1966	A/I	Desmopterini Bolívar, 1905	B/V
Verduliini Kevan & Akbar, 1964	A/I	Monistrini Kevan & Akbar, 1964	B/V
Brunniellini Kevan, 1963	A/I	Petasidini Key, 1985	B/V <sup>b</sup>
Psednurini Burr, 1904	A/I	Chlorizeinini Kevan & Akbar, 1964	B/VI
Mitriccephalini Kevan & Akbar, 1964	A/I	Poekilocerini Burmeister, 1840	B/VI
Geloiini Bolívar, 1905	A/II	Phymateini Bolívar, 1884	B/VI
Sagittacridini Descamps & Wintrebert, 1966	A/II	Schultheysiini Kevan & Akbar, 1964	B/VII
Gymnohippini Kevan & Akbar, 1964	A/II	Taphronotini Bolívar, 1904 <sup>a</sup>	B/VII
Malagasphenini Kevan & Akbar, 1964	A/II	Dictyophorini Kirby, 1902	B/VII
Chapmanacridini Kevan & Akbar, 1964	A/III	Tagastini Bolívar, 1905	B/VIII
Ichthiacridini Kevan, Singh & Akbar, 1964	A/III	Pseudomorphacridini Kevan & Akbar, 1964	B/VIII
Ichthyotettigini Kevan, Singh & Akbar, 1964	A/III	Atractomorphini Bolívar, 1905	B/VIII
Orthacridini Bolívar, 1905 <sup>a</sup>	A/III	Sphenariini Bolívar, 1884	B/IX
Popoviini Kevan & Akbar, 1964	A/III	Omurini Kevan 1961	B/IX
Nereniini Kevan 1964	A/IV	Pyrgomorphini Brunner von Wattenwyl, 1882 <sup>a</sup>	B/X
		Chrotogonini Bolívar, 1904	B/X

<sup>a</sup>Groups not supported in this study.

<sup>b</sup>Petasidini was included by Kevan *et al.* (1974) in Monistrini, Key (1985) elevated to tribe level and Otte (1994) assigned to subfamily Pyrgomorphinae.

**Table 2.** General characteristics of groups A and B of Kevan *et al.* (1969a,b,c,d; 1972).

Group A	Group B
Metasternal pits usually large, connected by one suture Body form generally cylindrical or elongated	Metasternal pits usually small, joined by two sutures Body form usually but not always distinctly fusiform, or heavy or robust, or both
Hind femora often having both basal lobes subequally produced or the dorsal more prominent	Hind femora always with ventral basal lobe more prominent
Fastigium of vertex often (but by no means usually) short and blunt	Pronotum sometimes with large tubercles
Predominantly 'Gondwanian'; absent from Palaearctic and South American regions but occurring in Mexico; poorly represented in Africa (except Madagascar)	Predominantly circumtropical and subtropical (poorly represented in the Americas), some extending to Palaearctic region; very strongly represented on Africa but few species in Madagascar; Australian Pyrgomorphidae belong mostly to this group

in 70% ethanol and the entire structure was rinsed thoroughly. The epiphallus was separated from the ecto-endophallus complex. Both pieces were placed in genital vials with glycerine.

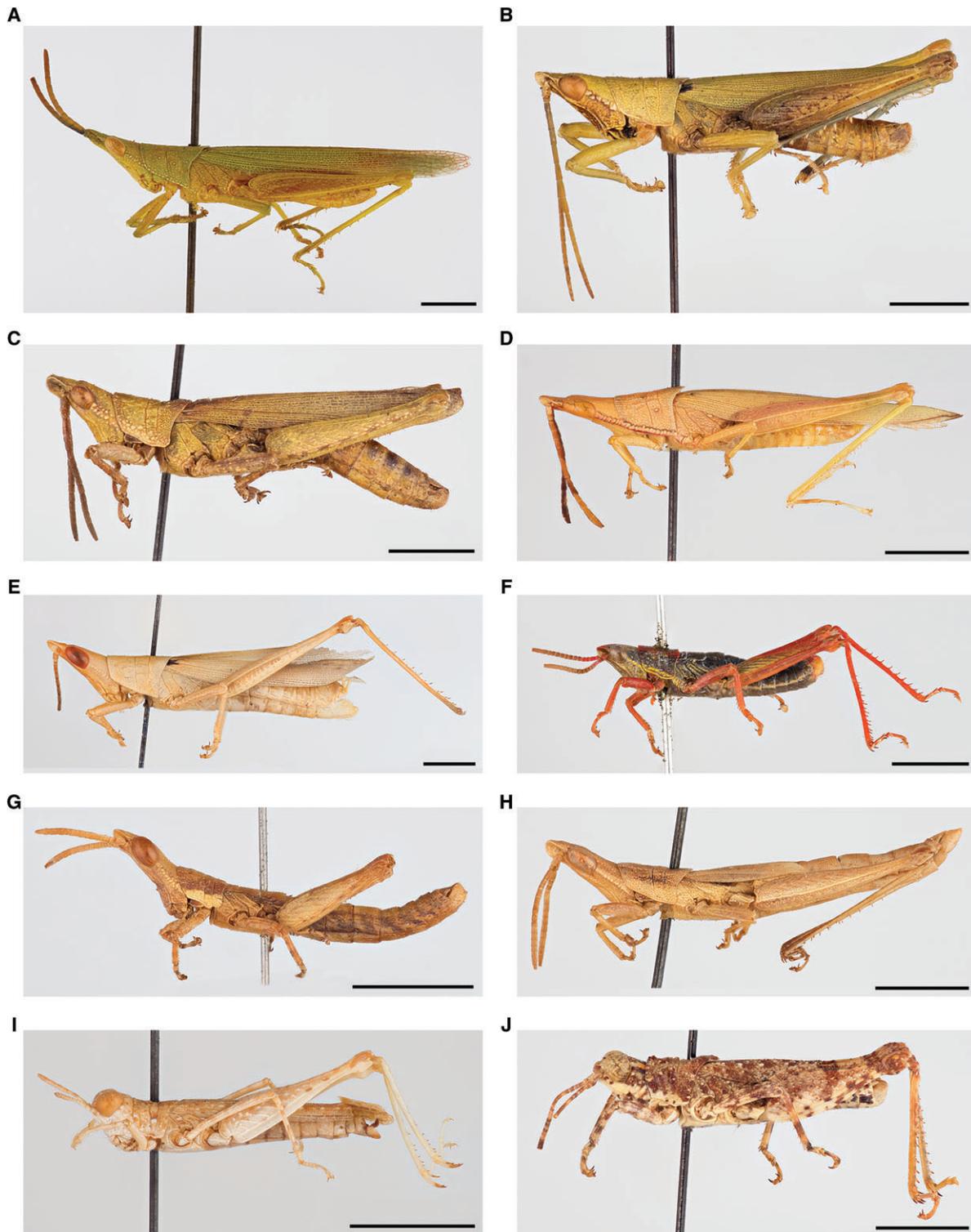
#### Digital imaging and illustration

All the specimens used in this study were photographed in lateral view (Figs 2–5). For the case of *Phymateus*, the ectophallus was photographed in posterior view and the internal genitalia (ecto/endophallus) was photographed in anterior, posterior, dorsal and ventral views (Fig. 6). Other specific close-up photographs were taken to illustrate certain characters and their states (Figures S1–S9). The images of all preserved specimens were taken using the Visionary Digital BK Plus Imaging System in combination with a Canon EOS 7D camera (Texas A&M, College Station, TX, U.S.A.) using 65 and 100 mm lenses to take multiple images at different depths of field. After this, Adobe LIGHTROOM 3 (v.3.2) was used to import the photos and

transform them from RAW files to TIFFs and then ZERENE STACKER (v.1.02) was employed to stack the image slices into a single focused image. Finally, Adobe PHOTOSHOP CS5 EXTENDED was utilized, when necessary, to adjust light levels, background colour and sharpness, and to add an accurate scale bar. Additionally, line drawings (Figs 7, 8) were made for important diagnostic characters using a camera lucida attached to a Leica M205C (Texas A&M). The illustrations were scanned and digitized using the Wacom Cintiq Tablet in Adobe PHOTOSHOP. Final composition of the plates was done in Adobe PHOTOSHOP.

#### Cladistic analysis

A data matrix (Table S2) consisting of 44 terminal taxa (41 ingroups and three outgroups) and 119 morphological characters with 269 character states was compiled in WINCLADA (Nixon, 2002). Nonapplicable data were recorded as '–' and missing data as '?'. Thirty characters were neomorphic and 89 were transformational (Serenó, 2007). For the uninformative states



**Fig. 2.** Lateral views: (A) *Atractomorpha aberrans* (Congo); (B) *Tagasta indica indica* (India); (C) *Pyrgomorpha vignaudi* (Central African Republic); (D) *Pseudomorpha notata* (Myanmar); (E) *Schulthessia biplagiata* (Madagascar); (F) *Parasphena imatogensis* (Sudan); (G) *Anarchita aptera* (India); (H) *Zarytes squalinus* (India); (I) *Tenuitarsus angustus* (Mauritania); (J) *Chrotogonus oxypterus* (India). Scale bar = 5 mm. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

we atomize the characters using contingent coding (Brazeau, 2011). All the characters were coded nonadditively and equally weighted. We searched for the most parsimonious trees in NONA (Goloboff, 1995) using the commands 'rs 0', 'hold 10000', 'mult\*1000', 'max\*' and 'best'. WINCLADA (Nixon, 2002) was used to view the trees and to calculate a strict consensus tree. The same data matrix was submitted to TNT (Goloboff *et al.*, 2003) for an independent analysis using a combination of sectorial search, drifting, tree fusing (Goloboff, 1999) and ratchet (Nixon, 1999). Bremer support values (Bremer, 1994) were calculated by holding suboptimal trees ten steps longer in TNT.

## Results and discussion

### Phylogenetic analysis

The analysis resulted in eight most parsimonious trees of 541 steps with a consistency index (CI) of 0.28 and retention index (RI) of 0.55 (File S2). One of the most parsimonious trees is shown as a preferred tree in Fig. 9. Understanding that any of the eight trees is equally parsimonious, we chose one that simplifies the analysis. As is evident in the consensus tree, the taxa with variable position in the phylogeny were in groups A (such as *Orthacris* and *Colemania*) and D (such as *Schulthessia* Bolívar), plus another three (*Humpatella* Karsch, *Chlorizeina* and *Desmopterella*) that we decided not to include in any of the four groups, and we provided a discussion based on morphology for these three genera of uncertain phylogenetic position. The objective of this paper was to provide a backbone for a natural classification based on morphology and the four groups that we proposed are recovered in the eight trees. The relationships of the taxa in groups B and C were recovered in all the eight trees. The strict consensus of these trees collapsed seven nodes ( $L = 560$ ,  $CI = 0.27$ ,  $RI = 0.52$ ). Bremer support values are shown in the consensus tree together with the number of synapomorphies per node (Fig. 10).

We recovered the family Pyrgomorphidae as a monophyletic group, which is supported by eight synapomorphies. Of these, one is the presence of a groove in the fastigium (Fig. 8A–H) and the others are the characters from the internal genitalia. Concerning the two subfamilies, Orthacridinae was recovered as monophyletic, while Pyrgomorphae was recovered as paraphyletic. Overall, our analysis found that Pyrgomorphidae consisted of four major clades, which we tentatively refer to as clades A, B, C and D. As most of the tribes included in this analysis were represented by only a single species, we were unable to test the monophyly of these tribes. However, we included multiple taxa for some of the tribes, for which we could test the tribe-level monophyly. We found Chrotogonini (two spp.), Sphenariini (four spp.), Phymateini (two spp.) and Psednurini (two spp.) to be monophyletic. Particularly, we found overwhelming support and numerous synapomorphies for Chrotogonini (16 spp.) and Psednurini (10 spp.). We recovered Pyrgomorphiini (four spp.), Orthacridini (three spp.), and Taphronotini (two spp.) as paraphyletic. Of these, all included members of Pyrgomorphiini (105 spp. in 29 genera), which is the most species-rich tribe within the family, were found in the clade D. Orthacridini (58 spp. in 11

genera) is the second most species-rich tribe and all its members were recovered as part of the clade A.

### Pyrgomorphidae is a monophyletic family

The present study represents the first modern cladistic analysis of the family Pyrgomorphidae, which we strongly recover as a monophyletic group based on the following seven characters: the groove in the fastigium, the reduction of posterior projections in the epiphallus, the reduction of ancorae in the epiphallus, club-shaped oval sclerites, cingulum extending and reaching the ventral side enveloping endophallus, the medially situated endophallic apodeme, and the unconstricted ejaculatory and sperm sacs. While we now recognize this family as a distinct member of the superfamily Pyrgomorpoidea (Cigliano *et al.*, 2017), there has been a tumultuous taxonomic history in determining its affinity within Caelifera.

Initially, Pyrgomorphidae was thought to be closely related to Pamphagidae because both families have the endophallic sclerites that are in ventral or medial position with respect to the spermatophore sac. Roberts (1941) described this arrangement as 'Chasmosacci' and both Dirsh (1956) and Amédég-nato (1976) suggested that the South African endemic family Lentulidae was also closely related to Pyrgomorphidae based on this genital arrangement. In his larger treatment of the classification of Acridomorpha, Dirsh (1975) elevated the 'Chasmosacci' to a superfamily status and erected Pamphagoidea, which Otte (1994) followed for establishing the higher-level classification of Orthoptera. However, the placement of Pyrgomorphidae within Pamphagoidea was challenged when Flook & Rowell (1997) used partial mitochondrial ribosomal RNA genes of 32 caeliferan taxa to resolve the phylogeny of Caelifera. Their study included three pyrgomorphs [*Prospheia scudderi* Bolívar, *Atractomorpha acutipennis* (Guérin-Méneville) and *Zonocerus elegans*], which did not recover a sister relationship between Pyrgomorphidae and Pamphagidae. Instead, Pyrgomorphidae was found to be an early-diverging lineage within Acridomorpha, a group of grasshopper-like families within Caelifera. This new phylogenetic position was strongly supported when Flook *et al.* (2000) used additional loci from three genes (12S, 16S and 18S) to test the relationships, which led to the erection of a new superfamily, Pyrgomorpoidea, which included only the Pyrgomorphidae. Flook *et al.* (2000) added Lentulidae to the analysis, which was found to be more closely related to Pamphagidae and quite divergent from Pyrgomorphidae. Eades (2000) used this finding and reinterpreted the homology of male phallic complex within Acridomorpha and hypothesized that Pyrgomorpoidea would be sister to Acridoidea (which includes both Pamphagidae and Lentulidae, as well as several other families). Indeed, the synapomorphies supporting Pyrgomorphidae are mostly male genitalia characters, which suggests that the previous hypothesis of 'Chasmosacci' was based on incorrect interpretation of genital homology.

More recently, additional molecular studies consistently found a sister relationship between Pyrgomorpoidea and Acridoidea (Hong *et al.*, 2003; Lu & Huang, 2012; Leavitt

*et al.*, 2013; Zhang *et al.*, 2013; Song *et al.*, 2015). A recent divergence time estimate study of Orthoptera based on nine fossil calibration points proposed that the origin of Pyrgomorphidae could be dated to the Cretaceous period (Song *et al.*, 2015), suggesting that this family represents a much older lineage than other grasshopper families that it was originally associated with.

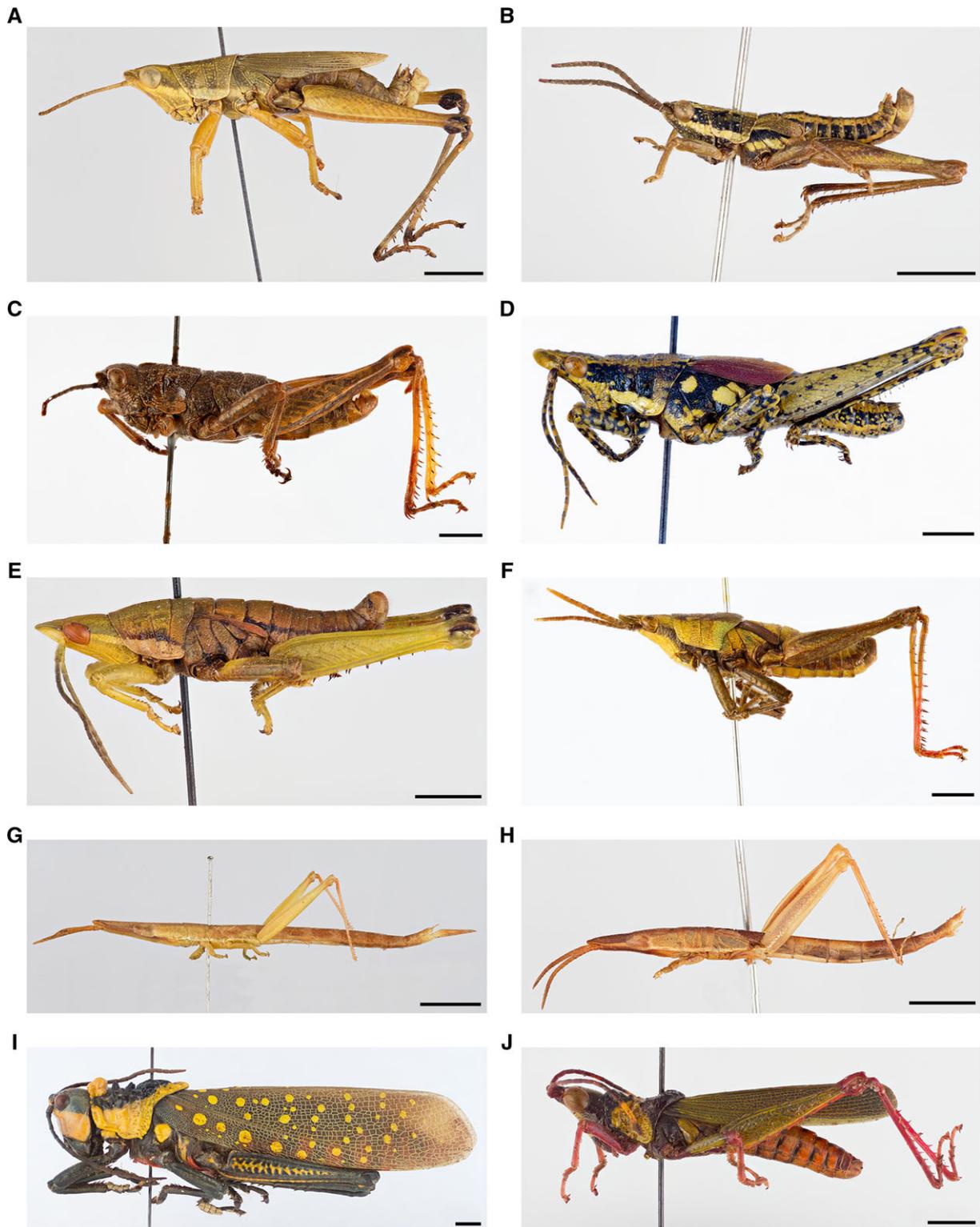
#### *Phylogenetic relationships within Pyrgomorphidae*

Our analysis found that the subfamily Pyrgomorphinae is paraphyletic, with the subfamily Orthacridinae monophyletic (Fig. 9). This is not surprising given that the classification scheme established by Kevan and his colleagues (Kevan & Akbar, 1964; Kevan, 1976; Kevan *et al.*, 1969, 1970, 1971, 1972, 1974, 1975) has not been stable. For example, Kevan (1976) concluded that there were not sufficiently distinctive features to divide the family into major subfamilies. Instead, they created two groups, 10 series and 30 tribes. Some tribes were quite large while others comprised a few genera, and six were monogeneric. These divisions were made based on internal genitalia and some external morphological characteristics (Table 1). On the other hand, Dirsh (1975) divided Pyrgomorphidae into 13 subfamilies, based mostly on external characteristics, which incompletely overlapped with Kevan's tribes. Dirsh (1975) argued that grouping based on internal genitalia was difficult because of the diversity in the secondary structures in almost every genus. However, Dirsh's classification was largely ignored by subsequent authors. Chinese authors have followed a different classification system, proposed by Yin (1982, 1984), who placed Pyrgomorphidae within Acridoidea and divided it into two families: Chrotogonidae, with four subfamilies (Taphronotinae, Chrotogoninae, Yunnanitinae and Mekongiellinae); and Pyrgomorphidae, with two subfamilies (Pyrgomorphinae and Atractomorphinae). Later, Xia *et al.* (1994) added two subfamilies (Aularchinae and Tagastinae) to Chrotogonidae, but this classification scheme had never gained wide acceptance. Xu *et al.* (2002) conducted a phylogenetic analysis based on 21 morphological characters and 10 representative pyrgomorph genera found in China, which did not find any support for the hypothesis of two families, but this finding did not lead to a revised classification.

Our result divides Pyrgomorphidae into four main clades (Fig. 10). The clade A (Figs 3G, H, 4G, H, 5) consists of the following tribes: Chapmanacridini (one sp.), Geloiiini (eight spp.), Gymnohippini (six spp.), Ichthiacridini (ten spp.), Ichthyotettigini (seven spp.), Mitricephalini (six spp.), Nereniini (26 spp.), Orthacridini (58 spp.), Popoviini (six spp.), Sagittacridini (three spp.), Psednurini (six spp.) and Verduliini (13 spp.). The members of this clade are typically small and have cylindrical body forms. In some cases, male cerci are enlarged and highly modified. In other cases, the posterior part of the abdomen is inflated. Wing reduction is widely present in this group. Based on our analysis, we identified five characters uniting this clade: (i) quadrate pronotum (except *Colemania* and *Caprorhinus* Saussure); (ii) posterior margin of pronotum in lateral view

extending to the first coxae (except *Mitricephaloides* Kevan); (iii) unconnected metasternal pits (except in *Meubelia* Willems and *Psednurini*); (iv) the absence of tegmina; and (v) the absence of hindwings, except in *Mitricephaloides*. Clade A is essentially equivalent to the subfamily Orthacridinae, i.e. group 'A' of Kevan *et al.* (1969, 1970, 1971, 1972, 1974). We predict that the three tribes not sampled in this study – Bruniellini (Philippines), Fijipyrgini (Fiji), and Malagasphenini (Madagascar) – are likely to be placed in this clade based on published descriptions of their morphology. The members of the clade A are distributed in both the New and Old World, but with a high level of endemism. There are two tribes endemic to Mexico (Ichthyotettigini and Ichthiacridini), three endemic to Madagascar (Geloiiini, Gymnohippini and Sagittacridini), and three endemic to Southeast Asia (Mitricephalini, Nereniini and Verduliini). The tribe Orthacridini is distributed in Africa and Asia and consists of 56 species in 11 genera. The tribe Psednurini is the most strongly supported group within the clade A (Bremer support of 9) and is represented by ten synapomorphies. This tribe (six spp. in three genera) is endemic to Australia and is associated with stiff grassy vegetation, the circular stems of which the grasshoppers grasp with their minute legs (Rentz *et al.*, 2003). The information on the biology and ecology of the tribes of clade A is very scarce. In studying Malagasy species, Braud *et al.* (2014) reported that *Gymnohippus marmoratus* Bruner lives in small salt-tolerant bushes in coastal dunes and that *Acanthopyrgus finoti* Bolívar inhabits medium-altitude forest in the highlands. Fontana *et al.* (2011) reported that the species of *Ichthyotettix* Rehn are found in partially stony to dry stony habitats with sparse bushes and very few herbs in Mexico. In general, Ichthyotettigini and Ichthiacridini are found in arid habitats in Mexico. Perhaps the best-studied species in this clade is *Colemania sphenarioides*, which is a major pest on sorghum and wheat on the Indian subcontinent. It appears in large numbers in cycles of ~10–15 years and has a mid-dorsal abdominal gland that secretes a pungent milky fluid that it can project up to 5 cm (COPR, 1982).

Clade B (Figs 3I, J, 4A–F) consists of the following tribes: Dictyophorini (11 spp.), Monistrini (15 spp.), Petasidini (two spp.), Phymateini (22 spp.), Poekilocerini (four spp.), and Taphronotini (nine spp.). This clade is united by four synapomorphies: a convex shape of the upper and lower marginal areas of hind femur, thick carinae and carinulae in the hind femur (Fig. 7I), contrasting coloration in abdomen, and the presence of dorsal posterior processes of endophallic apodeme. The close relationships among some of the tribes included in the clade B have been proposed previously. For example, Kevan *et al.* (1972) placed the tribes Poekilocerini and Phymateini in the Series VI. Kevan *et al.* (1974) further divided Taphronotini into subtribes Aularchina and Taphronotina, and suggested a close relationship between Taphronotini and Dictyophorini. Key (1985) suggested a relationship between the tribes Monistrini, Petasidini and Poekilocerini. This group is mainly distributed in Africa, Madagascar, Asia and Australia, and includes some of the most familiar members of the family that are large and colourful. They commonly have a well developed and intricate pronotum with tubercles and spines (Fig. 8I, J). The tegmina are well



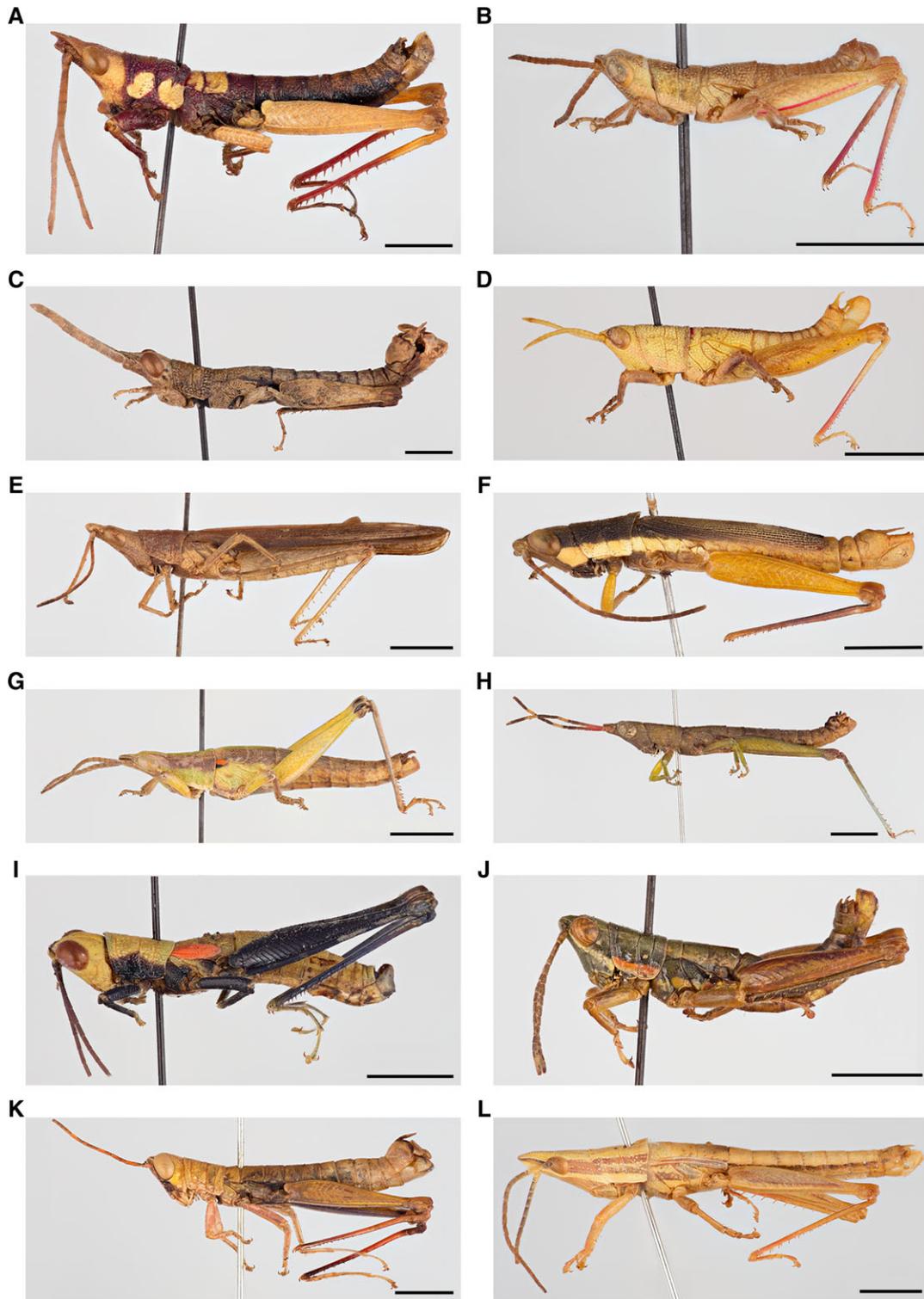
**Fig. 3.** Lateral views: (A) *Chlorizeina unicolor* (Thailand); (B) *Humpatella huambae* (Angola); (C) *Mekongiella kingdoni* (China); (D) *Rubellia nigrosignata* (Madagascar); (E) *Sphenarium histrio* (Mexico); (F) *Prospheia scudderi* (Guatemala); (G) *Psednura musgravei* (Australia); (H) *Psedna nana* (Australia); (I) *Aularches miliaris* (Thailand); (J) *Taphronota ferruginea* (Cameroon). Scale bar = 5 mm. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].



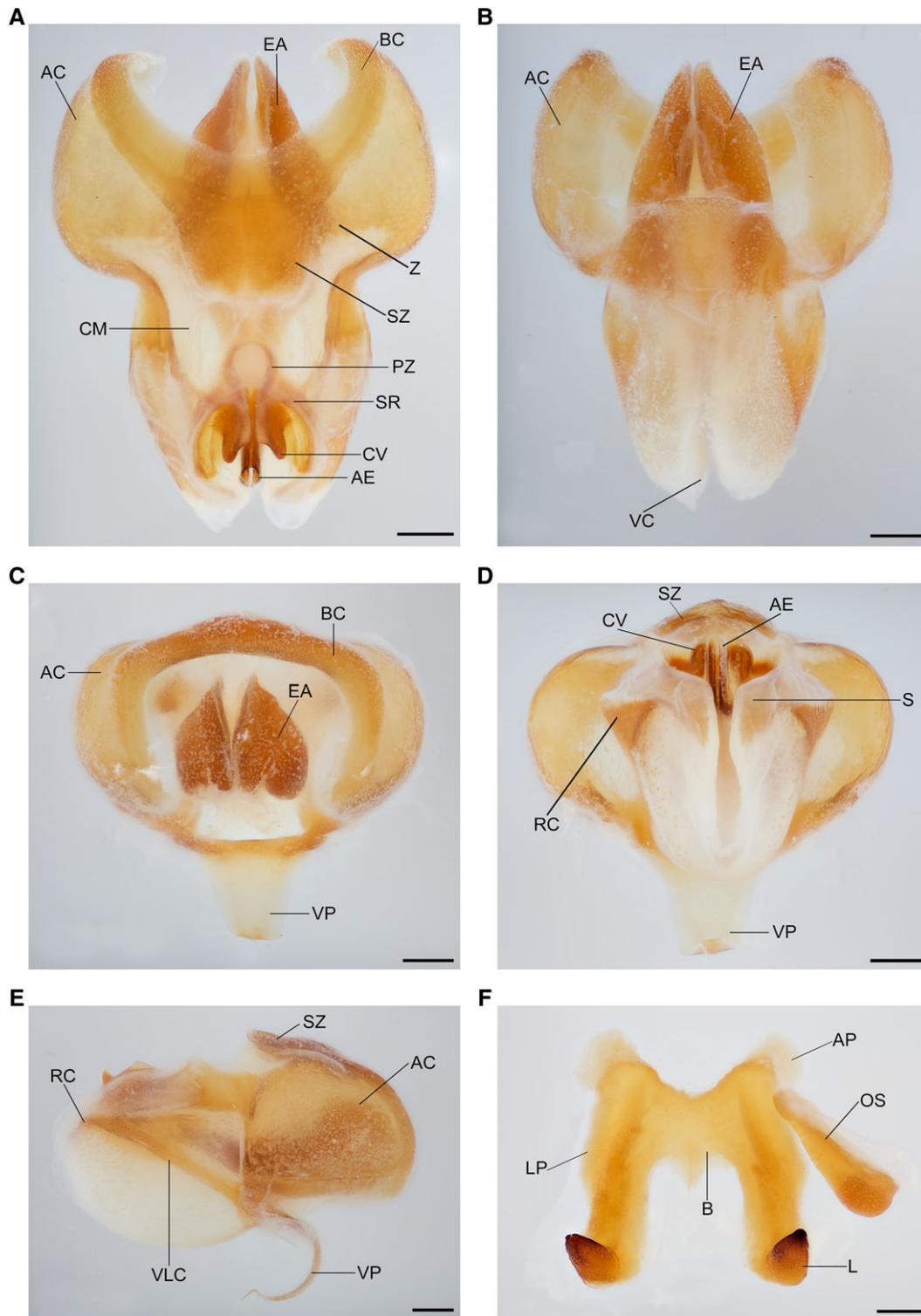
**Fig. 4.** Lateral views: (A) *Zonocerus variegatus* (Congo); (B) *Phymateus saxosus* (Madagascar); (C) *Petasida ephippigera* (Australia); (D) *Monistria concinna* (Australia); (E) *Poecilocerus pictus* (India); (F) *Dictyophorus spumans* (South Africa); (G) *Ichthyotettix mexicanus* (Mexico); (H) *Sphenacris crassicornis* (Mexico); (I) *Omura congrua* (Peru). Scale bar = 5 mm. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

developed, although they are reduced in some cases. They exhibit aposematic coloration and feed on toxic plants, such as milkweeds (Whitman, 1990); the sequestration of secondary plant compounds as a chemical defence could be an important condition in this clade (Euw *et al.*, 1967; Modder, 1983; Chapman *et al.*, 1986; Agrawal *et al.*, 2012). There is also evidence of detoxifying and neutralizing cyanogenic glycosides in some of these grasshoppers (Idowu *et al.*, 2009; Bessie & Agboola,

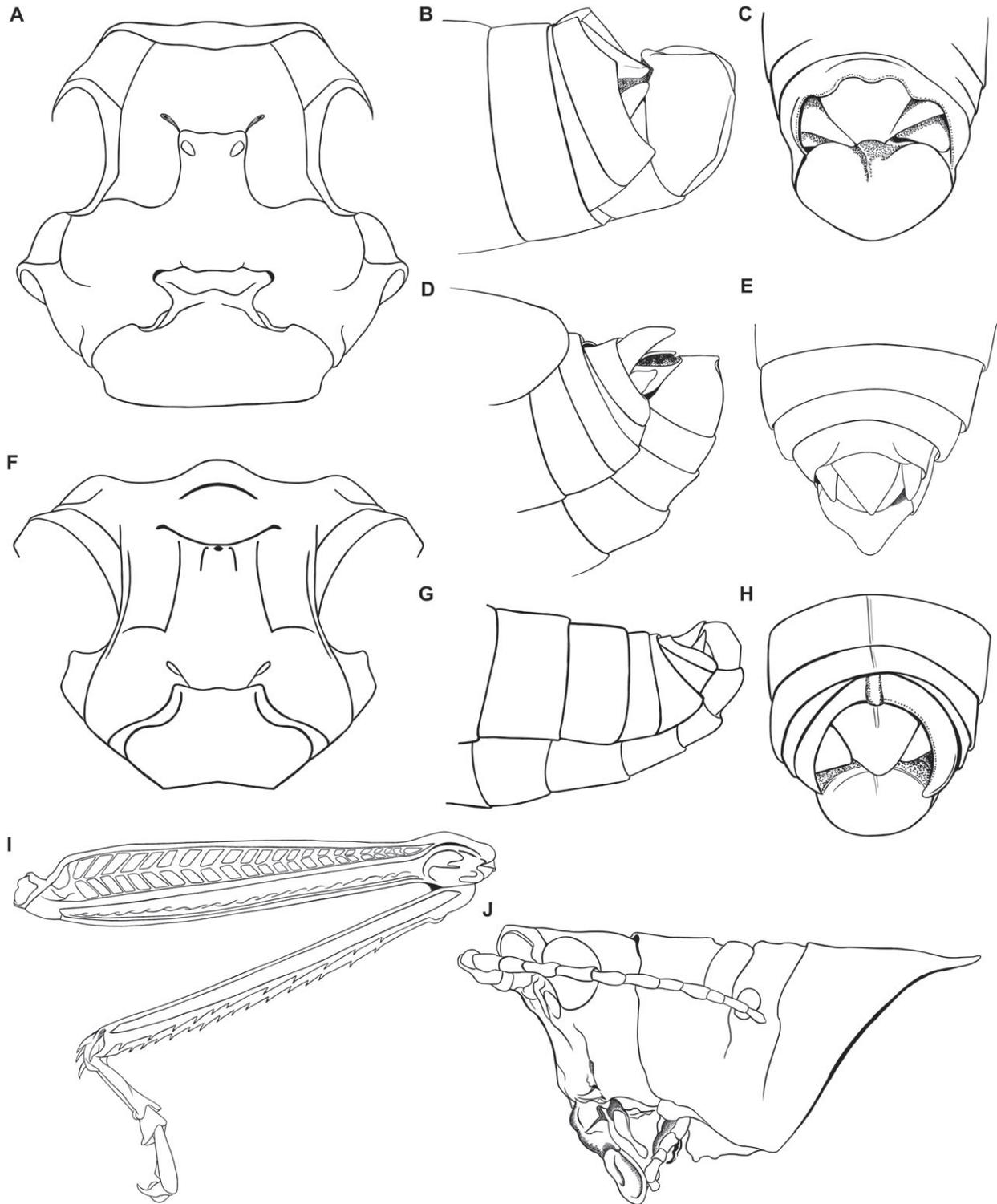
2013). Some species have a mid-dorsal abdominal gland that can produce chemical defence, such as *Zonocerus*, *Phymateus* and *Poecilocerus* (Whitman, 1990). There is only one other report of mid-dorsal abdominal gland outside this clade (i.e. *Colemania* in clade A). Others have different mechanisms of chemical defence, such as openings on the pronotum and abdomen (*Aularches* and *Taphronota*), for releasing toxic chemicals or production of toxic foams by combining haemolymph



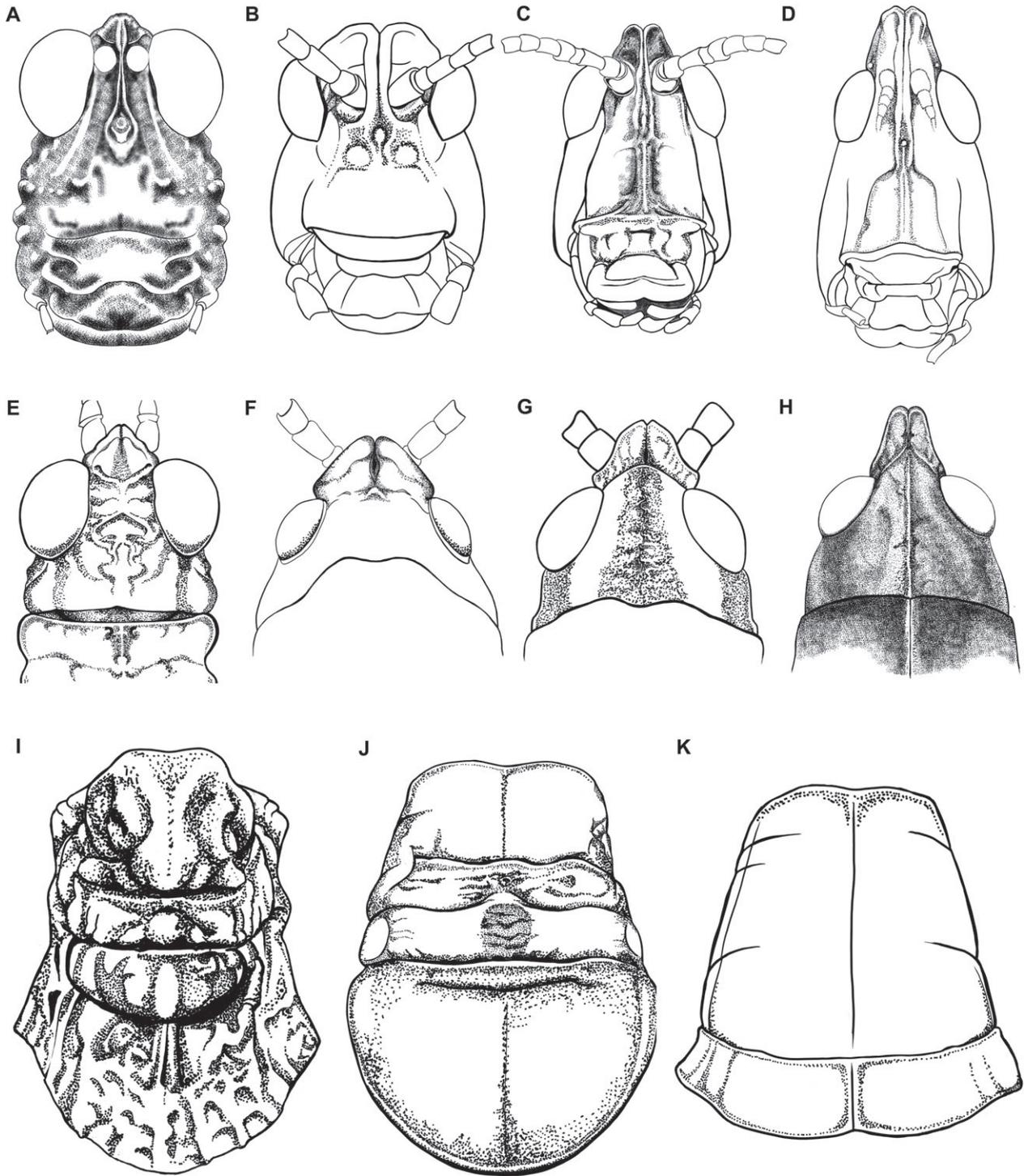
**Fig. 5.** Lateral views: (A) *Acanthopyrgus finoti* (Madagascar); (B) *Acropyrgus cadeti* (Madagascar); (C) *Pseudogeloius decorsei* (Madagascar); (D) *Gymnohippus marmoratus* (Madagascar); (E) *Desmopterella angustata* (Papua New Guinea); (F) *Mitricephaloides rhodopterus* (Malaysia); (G) *Caprorhinus kevani* (Madagascar); (H) *Chapmanacris sylvatica* (Ghana); (I) *Meubelia leytenis* (Philippines); (J) *Orthacris incongruens* (India); (K) *Modernacris controversa* (Solomon Islands); (L) *Colemania sphenarioides* (India). Scale bar = 5 mm. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].



**Fig. 6.** Ectophallus + endophallus of *Phymateus saxosus* (Madagascar): (A) dorsal view; (B) ventral view; (C) anterior view; (D) posterior view; (E) lateral view. (F) Ectophallus: dorsal view. AC, apodemal plate of cingulum; AE, aedeagus (aedeagal valves); AP, anterior projection of epiphallus; B, bridge of epiphallus; BC, basal thickening of cingulum; CM, central membrane of epiphallus; CV, valve of cingulum; EA, endophallic apodeme; L, lophus of epiphallus; LP, lateral plate of epiphallus; OS, oval sclerites; PZ, pseudoarch of epiphallus; RC, ramus of cingulum; S, sheath of ectophallus; SR, supramus of cingulum; SZ, suprazygomal plate of cingulum; VC, ventral cleft of cingulum; VLC, ventral longitudinal thickening of cingulum; VP, ventral process of cingulum; Z, zygoma of cingulum. Scale bar = 0.5 mm. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

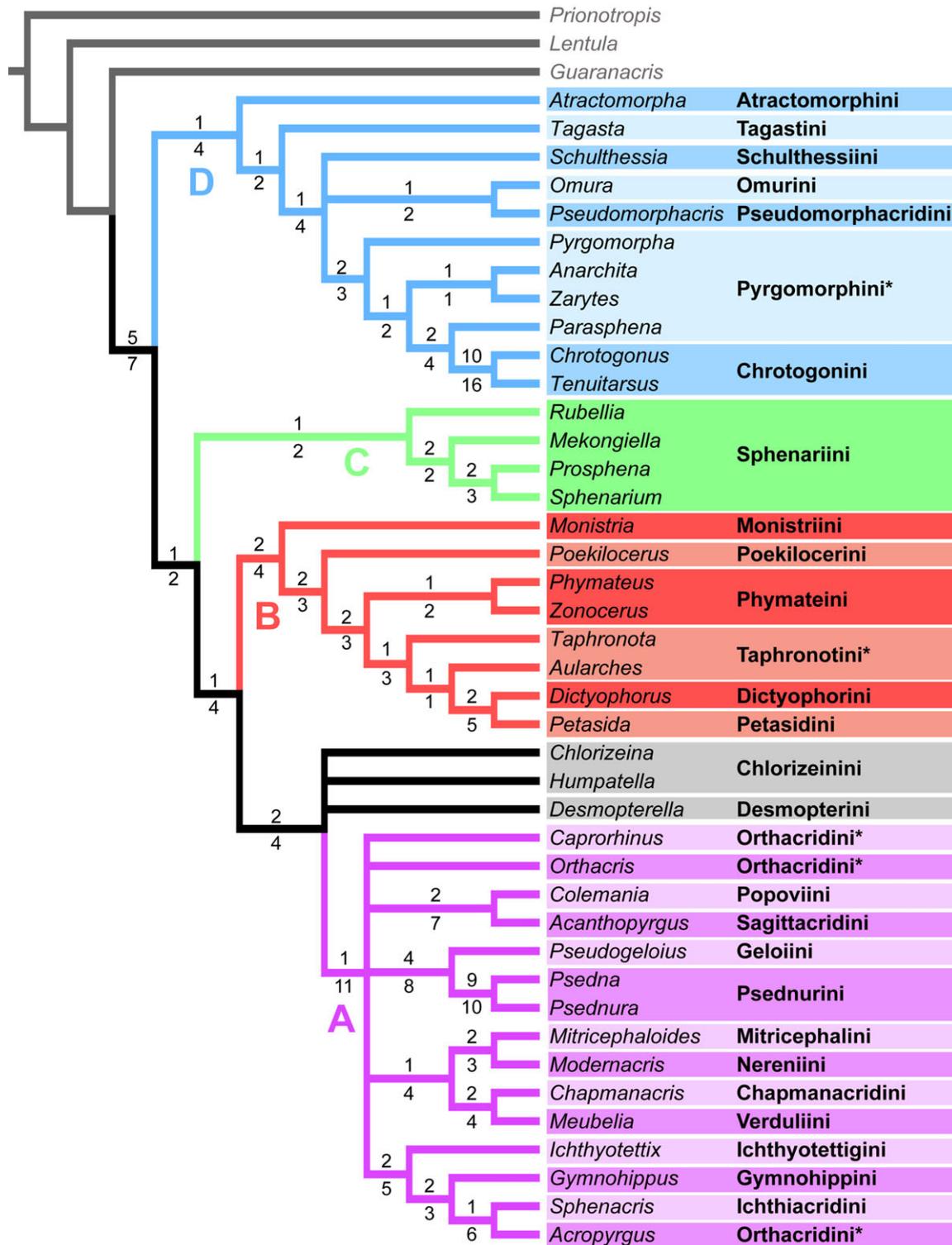


**Fig. 7.** (A) Meso- and metathorax of *Poeciloceris pictus* (India); (B, C) lateral and dorsal views of tip of abdomen of *Chrotogonus oxypterus* (India); (D, E) lateral and dorsal views of tip of abdomen of *Dictyophorus spumans* (South Africa); (F) meso- and metathorax of *Sphenarium histrio* (Mexico); (G, H) lateral and dorsal views of tip of abdomen of *Sphenarium histrio* (Mexico); (I) left hind leg in lateral view of *Dictyophorus spumans* (South Africa); (J) head and thorax in lateral view of *Poeciloceris pictus* (India).



**Fig. 8.** (A–D) Heads in frontal view: (A) *Chrotogonus oxypterus* (India); (B) *Dictyophorus spumans* (South Africa); (C) *Poecilocerus pictus* (India); and (D) *Sphenarium histrio* (Mexico). (E–H) Heads in dorsal view: (E) *Chrotogonus oxypterus* (India); (F) *Dictyophorus spumans* (South Africa); (G) *Poecilocerus pictus* (India); and (H) *Sphenarium histrio* (Mexico). (I–K) Pronotum in dorsal view: (I) *Dictyophorus spumans* (South Africa); (J) *Poecilocerus pictus* (India) and (K) *Sphenarium histrio* (Mexico).





**Fig. 10.** Strict consensus tree. Seven nodes were collapsed from the most parsimonious trees (length = 560, consistency index = 0.27, retention index = 0.52). Bremer support values are shown in the upper part and the number of synapomorphies per node is shown in the lower part. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

with air through the spiracles (*Dictyophorus*) (Whitman, 1990). In Australia, *Petasida ephippigera* White (Fig. 1A) has a very strict diet of toxic shrubs and is not known to have any chemical release mechanism (Rentz *et al.*, 2003). These bright orange and blue grasshoppers are known as Leichhardt's Grasshopper in northern Australia and are culturally important, as they are known in Aboriginal dreaming stories as Alyurr, children of the lightning man (Lowe, 1995). Several members of clade B, including *Zonocerus*, *Phymateus*, *Taphronota* and *Poecilocerus*, are gregarious as nymphs in Africa and Asia (Whitman, 1990). The members of the Australian genus *Monistria* Stål are found in different habitats from coastal heaths to alpine woodlands; they are often abundant and can be destructive (Rentz *et al.*, 2003).

Clade C (Fig. 3C–F) consists of the genera *Rubellia*, *Mekongiella* Kevan, *Prospheia* and *Sphenarium*, and is united by two synapomorphies, triangular cerci and rectangular epiphallus. All genera included in this analysis are currently placed in the tribe Sphenariini (25 spp.). This tribe exhibits the most peculiar biogeographical patterns within the family. In our analysis, *Rubellia* is endemic to Madagascar, *Mekongiella* occurs in China, and *Prospheia* + *Sphenarium* occur in Central America. Kevan *et al.* (1972) further divided the tribe according to geographic distribution into subtribes: Rubellina (one sp.) (Madagascar), Sphenaxiina (two spp.) (East Africa and Socotra), Mekongianina (ten spp.) (China) and Sphenariina (12 spp.) (Central America). We find that the pyrgomorph species occurring in the New World do not form a monophyletic group, but belong to other clades (A and B), which suggests that the New World has been colonized by ancestral pyrgomorphs from the Old World multiple times. The genus *Sphenarium* is culturally important in Mexico because it used as human food in the southern parts, but is considered a major pest species in the central Mexico (reference). This genus consists of flightless, polyphagous and univoltine species (Sanabria-Urbán *et al.*, 2015). For the Malagasy endemic *Rubellia nigrosignata*, Braud *et al.* (2014) reported it as a moderately important pest which affects shrubs, fruit trees and occasionally rice.

Clade D (Figs 2 and 4I) consists of the following tribes: Atractomorphiini (29 spp.), Chrotogonini (17 spp.), Omurini (four spp.), Pseudomorphacridini (three spp.), Pyrgomorphini (105 spp.), Schultessiini (two spp.), and Tagastini (17 spp.). All these tribes are currently placed in the subfamily Pyrgomorphinae. This clade is characterized by the antennal base that is positioned in front of ocelli in lateral view, a row of tubercles between the eye and posterior border of head, a wider lower marginal area compared with upper marginal area, and the thick wing veins when functional tegmina are present. In general, the tribes belonging to the clade B have full tegmina and pale coloration, although in some taxa there are reductions in wing length. This clade is mostly distributed in the Old World with the exception of the representative of the tribe Omurini (*Omura* Walker), which is found exclusively in South America. The tribe Chrotogonini is the most strongly supported group within clade B, with 16 synapomorphies, the presence of the collar of prosternum being the most evident character. Kevan *et al.* (1975) discussed that typical Chrotogonini and Pyrgomorphini (Series X) have similar phallic structures and that the members of Chrotogonini

probably have a common origin with Pyrgomorphini. Interestingly, Kevan *et al.* (1975) placed the genera *Pyrgomorpha*, *Anarchita* Bolívar and *Zarytes* Bolívar in the same subtribe, Pyrgomorphina. It is important to point out that the tribe Pyrgomorphini comprises 105 species in 29 genera, which represents more than 20% of the species diversity in the family. Kevan *et al.* (1974) grouped the tribes Tagastini, Pseudomorphacridini and Atractomorphiini in the Series VIII. They suggested that the nearest relatives of Tagastini are Pseudomorphacridini, which are derived from Tagastini. They also suggested a probable affinity of these three tribes with Schultessiini. It is necessary to include more genera to resolve the phylogenetic relationships of this tribe. The genus *Atractomorpha* is the best studied and prefers riparian habitats; in Australia it can cause damage to some crops such as peanuts and tobacco and has the potential to attack cotton (Rentz *et al.*, 2003), while in India both nymphs and adults are important pests of tobacco and maize (COPR, 1982). The genus *Chrotogonus* can cause severe damage to cotton in Asia and cereals and coffee in Africa (COPR, 1982) and the genus *Pyrgomorpha* attacks useful plants such as castor, cotton, cucumber and wheat in Africa and Asia (COPR, 1982).

While most of the taxa included fall within the four clades discussed earlier, there are some groups whose phylogenetic positions our analysis is not able to clarify. We included two genera (*Chlorizeina* and *Humpatella*) representing the tribe Chorizeiniini (Fig. 3A, B), but this tribe is not recovered as a monophyletic group. Both *Humpatella* and *Chlorizeina* share a constricted bridge of epiphallus with *Tagasta* in clade D. The genus *Chlorizeina* has thick tegmina veins, which is only found in clade D. However, both genera have the upper basal lobe of hind femora as long as the lower basal lobe, pubescent hind tibiae, and a separation between the base of cerci and epiproct, which group them close to clade A. Nevertheless, the longitudinal length of fastigium of vertex is shorter than the dorsal length of eye, which is a state widely present in clades A, B and D. The lateral carina of pronotum is absent in *Humpatella* (as in the clades A and B) but present in *Chlorizeina* (as in the clade D). Finally, the posterior corners of last abdominal tergite are protruded as in the great majority of the clade A, but this state is also present in some members of clade D. The inclusion of additional genera will help to test the monophyly of the tribe and its position within Pyrgomorphidae. The tribe Desmopterini (Asia and Australia) includes nine other genera apart from *Desmopterella*. Although *Desmopterella* (Fig. 5E) is recovered as a sister group of the clade A because of the dorsoventral length of the medial area of hind femur, which is wider when compared with the upper and marginal areas, there are other characters, such as the oval eyes and foveolate texture of the lateral pronotum; both features are found in clades A and D. Interestingly, the veins on the tegmina are thin (contrary to that in the clade D). However, the radial sector is poorly developed, as is the case for the members of clade D, and the first part of the precostal area in tegmina is poorly developed, similar to several members of clades B and D. The general appearance of *Desmopterella* (form of pronotum, development of wings) as well as its distribution suggest that its current position in the phylogeny may not be

accurate. The inclusion of additional genera will help to define the placement of this group in the family.

#### Conclusion and future directions

Pyrgomorphidae is a charismatic family that is evolutionarily intriguing, but any attempt to study this family has been impeded by the lack of a robust phylogeny. Although our taxon sampling is limited and there are additional character systems such as female genitalia that have not yet been included, our study represents the first explicit phylogenetic hypothesis of the family, which encompasses the spectrum of diversity for the group. This work provides a phylogenetic basis for further testing the monophyly of tribes and subtribes, and represents the first step towards building a natural classification for the family.

We think that this family is an excellent model system for studying the evolution of warning coloration and chemical defence. The aposematic coloration is a difficult characteristic to define and usually involves brightly contrasting colours (Lev-Yadun, 2009), with the patterns being more important than the colours themselves (Dolenská *et al.*, 2009). If we use the abdominal coloration as a proxy for aposematic coloration, we can infer that a contrasting pattern has evolved at least twice, in clade B and in clade A. Furthermore, highly colourful members of *Parasphena* (clade D) and *Sphenarium* (clade C) (Fig. 1C) are not known to be chemically defended. Therefore, it is clear that the evolution of aposematism is more complex than was first thought and this requires more careful investigation. Moreover, some pyrgomorphs have a specialized gland for chemical defence which appears to be associated with aposematic coloration, but not always. However, the functional morphology and physiology of this gland are not well understood. The variation of body coloration and the modes of chemical defence within Pyrgomorphidae make the family a unique system for future studies of aposematism.

Based on the paraphyly and incongruence with previous data, our study clearly shows that much work is needed before proposing a new classification scheme. We consider that the addition of new evidence will allow us to refine diagnoses for groups at different levels and improve the taxonomy of Pyrgomorphidae.

#### Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12251

**File S1.** Description of characters and optimizations.

**Figures S1–S9.** Illustration of character states.

**Table S1.** Specimen information.

**Table S2.** Character matrix.

**File S2.** Eight most parsimonious trees.

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