C. R. Palevol 16 (2017) 5–11

Contents lists available at ScienceDirect

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General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

An apterous scelionid wasp in mid-Cretaceous Burmese amber (Hymenoptera: Scelionidae)

Une guêpe scélionide sans aile dans l'ambre du Crétacé moyen birman (Hymenoptera : Scelionidae)

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ARTICLE INFO

Article history:
Received 30 October 2015
Accepted after revision 6 March 2016
Available online 13 May 2016

Handled by Annalisa Ferretti

Keywords:
Aptery
Cenomanian
Myanmar
Parasitoid
Platygastroidea
Taxonomy

ABSTRACT

A remarkably specialized parasitoid wasp of the family Scelionidae (Platygastroidea) is described and figured from mid-Cretaceous (Cenomanian) amber of the Hukawng Valley in northern Myanmar. *Geoscelio mckellari* Engel and Huang, gen. et sp. nov., is unique for its combination of a compact body, 12 antennal flagellomeres, a 1-2-2 tibial spur formula, a distinct malar sulcus, deeply impressed notauli, complete reduction of the wings, and basal crenulae on the metasomal terga and sterna, among many other features, and is placed within a separate tribe, Geoscelionini Engel and Huang, trib. nov. This is the first flightless species of Platygastroidea known from the Mesozoic, and its affinities with other Mesozoic and extant lineages are discussed.

Mots clés :
Absence d'ailes
Cénomanien
Myanmar
Parasitoïde
Platygastroidea
Taxonomie

RÉSUMÉ

Une guêpe parasitoïde remarquablemeent spécialisée de la famille des Scelionidae (Platygastroidea) est décrite et figurée de l'ambre du Crétacé moyen (Cénomanien) de la vallée de Hukawng dans le Nord du Myanmar. *Geoscelio mckellari* Engel et Huang, gen. et sp. nov., est unique par sa combinaison d'un corps compact, d'antennes à 12 flagellomères, d'une formule 1-2-2 d'éperons tibiaux, d'un sulcus malaire distinct, de notauli profondément impressionnés, d'une réduction complète des ailes, de crénulae basales sur les terga et

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http://dx.doi.org/10.1016/j.crpv.2016.03.005
1631-0683/

sterna métasomaux, parmi plusieurs autres caractères, et est placée dans une tribu séparée, Geoscelionini Engel et Huang, trib.nov. C'est la première espèce non volante de Platygastroidea connue du Mésozoïque, et ses affinités avec d'autres lignées mésozoïques et actuelles sont discutées.

1. Introduction

It is a well-known fact that the parasitoid wasp family Scelionidae is remarkably diverse in Cretaceous ambers (Engel, unpubl. data; Grimaldi and Engel, 2005; Grimaldi et al., 2002; Ortega-Blanco et al., 2014). Indeed, individuals of scelionids are also among the most abundant of hymenopteran fossils in most fossiliferous resins from the Mesozoic, and one might regard the Cretaceous as the 'Age of Platygastroids'. Yet, despite this staggering breadth in numbers, the diversity is often tightly confined to those more early-diverging groups among the Scelionidae, with many resembling the putatively basal Nixoniini, Sparasionini, and 'lower' Scelioninae (Johnson et al., 2008a; Ortega-Blanco et al., 2014). More specialized scelionids and certainly platygastrids have been hitherto absent, although such forms are well documented among the Cenozoic, particularly the Eocene fauna of Europe (e.g., Brues, 1940; Kononova and Simutnik, 2010, 2013; Masner et al., 2007a; Szabó and Oehlke, 1986). Today the superfamily comprises approximately 5400 species (Aguiar et al., 2013), and encompasses a diversity of parasitoids of insects and spiders, including idiobiont egg parasites as well as koinobionts of various immature insects, although the available biological data is rather taxonomically restricted (Austin et al., 2005). The paleobiology of the numerous fossil species is unknown, but might encompass the putatively groundplan condition of egg endoparasitoidism (Austin et al., 2005).

Here, we report the first rather specialized scelionid wasp from the Mesozoic. The new genus and species is the first truly wingless scelionid found from the Cretaceous. While it is still representative of the lower 'Scelionidae' owing to its primitive retention of traits, such as 12 flagellomeres in the antenna and a 1-2-2 tibial spur formula (Masner, 1976, 1980), the loss of wings and reduction of the basal pteralia is quite specialized, analogous to conditions seen among some modern scelionids in the subfamily Teleasinae or even scattered genera from elsewhere across the family (Austin et al., 2005). The present contribution is meant to document this unique form, and highlight the morphological diversity and disparity present among these otherwise lower members of the superfamily.

2. Material and methods

A unique individual was discovered in a large piece of mid-Cretaceous amber from the Hukawng Valley (Kachin State) in northern Myanmar. Through trimming of the piece, the wasp was isolated into a largely clear, light yellow block of amber, square in shape and with dimensions of approximately 8 mm long, 8 mm wide, and 1.5 mm deep. The piece includes a few isolated plant trichomes and other minor organic debris, but none of these are in a position to obscure the wasp, and there are minimal internal distortions from flow lines within the resin, fractures, or bubbles. There is a sizeable bubble beneath the apex of the metasoma that extends along the left side and expands along the posterior of the mesosoma and around the mesosomal-metasomal articulation (Fig. 1), but really only poses a challenge for views of the apicalmost sterna. Fine internal fractures filled with air also extend around the margins of the metasoma, most prominently along the right side, but these are short and slightly reflective; they do not impose restrictions on structural views of the inclusion. The antennae are extended to the left of the inclusion, and the legs are positioned beneath (but not fully tucked under) and outward from the body. The head is somewhat dipped downward and with the mouthparts positioned toward the propleura, and therefore everything other than the mandibles are rendered impossible to observe.

We have provided the description here with the goal of furthering paleontological work on Hymenoptera, and expanding our knowledge of character diversity among lower Platygastroidea, so that this might inform future phylogenetic inquiry and the discovery of explanatory patterns (sensu Grimaldi and Engel, 2007). Morphological terminology used in the description generally follows that of Masner (1976) and Mikó et al. (2007), while the higher classification adopted is modified from that of Masner (1976), Johnson and Masner (2006), Johnson et al. (2008b), and Masner et al. (2007a). We follow the position of Engel and Krombein (2012) and McKellar and Engel (2012) in the retention of multiple families within Platygastroidea, and advocate for the elevation of at least Nixoniini and Sparasionini, if not other clades, to familial rank alongside Platygastridae s.str. and a more narrowly circumscribed Scelionidae. Measurements were taken with ocular micrometers attached to an Olympus SZX12 stereomicroscope and an Olympus BX41 compound microscope. Microphotographs were prepared with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens.

The amber-bearing deposits of the Hukawng Valley have been studied geologically and mapped by Cruickshank and Ko (2003), while the age has been most extensively covered by Shi et al. (2012). Grimaldi et al. (2002) and Ross et al. (2010) provide further information on the locality, as well as a preliminary overview of the biotic diversity and abundance of various lineages. The taxonomic actions established herein are registered under ZooBank LSID urn:lsid:zoobank.org:pub:2AC79FD9-48AF-41D5-A6C8-FB04960CE84A.

Fig. 1. Holotype female (NIGP 163293) of *Geoscelio mckellari* Engel and Huang, gen. et sp. nov. in mid-Cretaceous amber from Myanmar (both images to the same scale; scale bar = 0.5 mm). **A**. Dorsal view. **B**. Ventral view.
Fig. 1. Holotype femelle (NIGP 163293) de *Geoscelio mckellari* Engel et Huang, gen. et sp. nov. dans l'ambre du Crétacé moyen du Myanmar (les deux images sont à la même échelle ; barre d'échelle = 0,5 mm). **A**. Vue dorsale. **B**. Vue ventrale.

Fig. 2. Ventral-oblique facial view of holotype female (NIGP 163293) of *Geoscelio mckellari* Engel and Huang, gen. et sp. nov. in mid-Cretaceous Burmese amber (scale bar = 0.25 mm).
Fig. 2. Vue faciale oblique-ventrale de l'holotype femelle (NIGP 163293) de *Geoscelio mckellari* Engel et Huang, gen. et sp. nov. dans l'ambre du Crétacé moyen du Myanmar (barre d'échelle = 0, 25 mm).

3. Systematic palaeontology

Geoscelionini Engel and Huang, trib. nov.
Type genus: *Geoscelio* Engel and Huang, gen. nov.
Diagnosis: ♀: Small wasps, less than 2 mm in length, body compact, with ovoid metasoma (Fig. 1); head broad, transverse in dorsal view, without transverse ledge; frons without distinct scrobe or facial depression (Fig. 2), broadly convex, submedian carina present (Fig. 2); lower frons without fanlike facial striae (Fig. 2), upper frons with longitudinal striae extending to occipital carina; striae absent between submedian carina and malar sulcus, and on gena; internatennal process weakly produced, torulus opening slightly laterally; antenna with elongate scape (Figs. 1 and 2), scape length great than height of compound eye; first flagellomere distinctly longer than pedicel; flagellum not strongly clavate, basal flagellomeres distinctly longer than wide, gradually reducing in length to become about as long as wide, forming a weak clava apically (flagellomeres V–XII); orbital carina present; compound eye glabrous, with inner orbits approximately parallel, interocular width slight greater than compound eye length; lateral ocelli much closer to inner orbit of compound eyes than to median ocellus, yet distinctly separated from inner orbit by about one-half of ocellar diameter; malar sulcus present, extending to lower posterior angle of compound eye (Fig. 2); clypeus appears strongly transverse with minute medioapical emargination; mandible short, stout, broad apically, with three strong apical teeth (Fig. 2); occipital carina present, complete, with anterior crenulae (Fig. 3A), with occiput depressed relative to carina.

Mesosoma compact, robust (Fig. 1); pronotum short, transverse, with distinct transverse pronotal carina; pronotal carina interrupted medially (Fig. 3A), posteriorly bordered by single row of areolae except medially, anterolateral corners acute, slightly projecting; vertical epomial carina present; humeral carina present; lateral surface

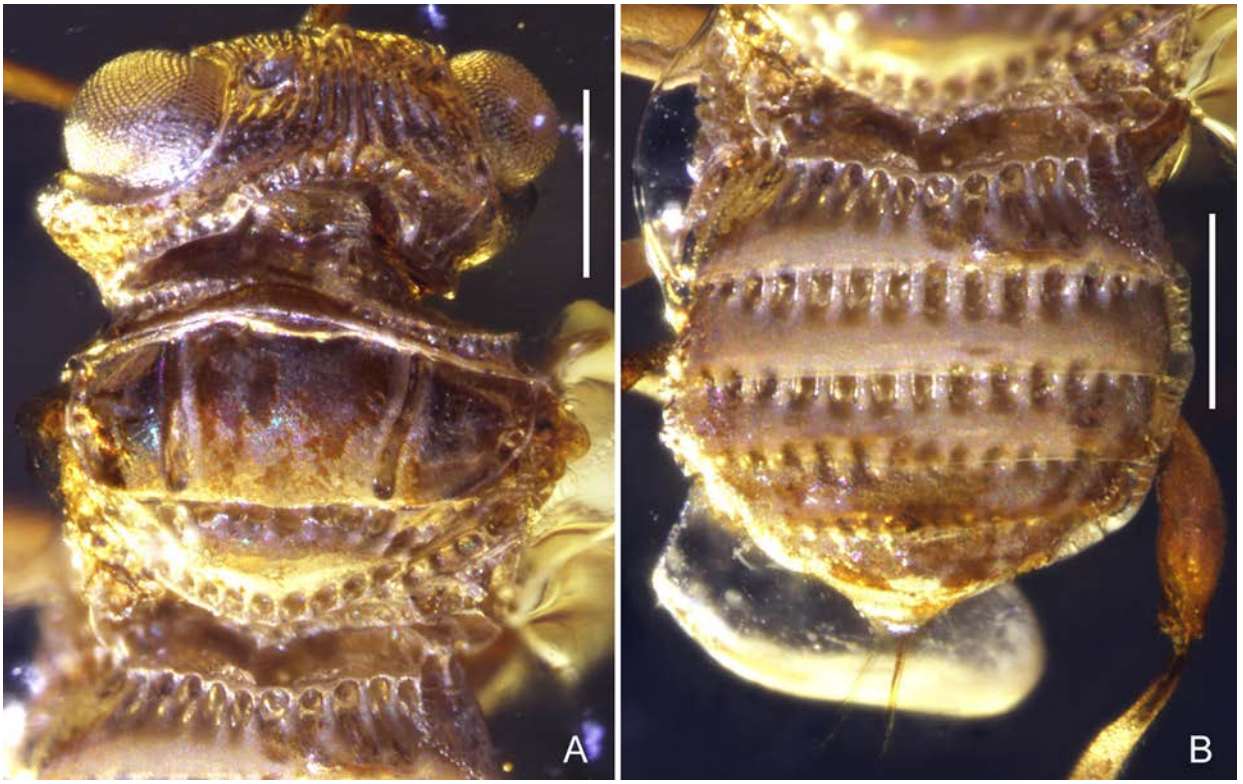

Fig. 3. Dorsal details of holotype female (NIGP 163293) of *Geoscelio mckellari* Engel and Huang, gen. et sp. nov. **A**. Detail of posterior of head and mesosoma (scale bar = 0.25 mm). **B**. Detail of metasomal terga; note that margins of metasoma have thin fractures filled with air extending from them (scale bar = 0.25 mm).

Fig. 3. Détails dorsaux de l'holotype femelle (NIGP 163293) de *Geoscelio mckellari* Engel and Huang, gen. et sp. nov. **A**. Détail de la partie postérieure de la tête et du mésosoma (barre d'échelle = 0, 25 mm). **B**. Détail de terga métasomal. À noter que les marges du métasoma ont de fines fractures remplies d'air les prolongeant (barre d'échelle = 0,25 mm).

of pronotum slightly depressed; mesoscutum wider than long, almost rectangular, with faint parapsidal lines present; skaphion present, narrow (Fig. 3A), with faint indication of antero-admedian lines; notauli broad and deeply impressed, percurrent (Figs. 1A, 3A); transscutal sulcus prominent, with faint posterior crenulae; mesoscutellum wider than long, unarmed (Fig. 3A), with narrow axilla; metanotum short, largely obscured by posterior border of mesoscutellum, unarmed; legs long, slender, femora slightly crassate (Fig. 1B), tibial spur formula 1-2-2; tarsi pentamerous; pretarsal claws simple, with small arolium; wings lacking (at most represented by tiny, hooked sclerite scarcely exceeding tegular posterior border), with small tegula retained (Figs. 1, 3A).

Metasoma compact, ovoid (Figs. 1, 3B); six terga and sterna visible externally, spiracles obscured; terga slightly convex, sterna slightly convex; laterotergites not developed (similar in this regard to *Archaeoscelio* Brues); terga I–III subequal in length, none greatly enlarged relative to other terga (Fig. 3B); base of terga and sterna I–V crenulate (Fig. 3A), weakly so on segment V.

Remarks: In a multi-familial system of Platygastroidea in which Nixoniidae is considered distinct, the present group apparently would form a tribe or subfamily in that 'family' but for now is placed in 'Scelionidae s.l.' and pending clarification of basal divergences and clades in among platygastroids. The genus *Archaeoscelio* Brues might be best incorporated into Geoscelionini owing to its lack of laterotergites and lower facial striae, its broad tridentate mandible, and its primitive antennal form (Brues, 1940; Masner et al., 2007a). If this is the case, then the circumscription of the tribe should be somewhat emended, as *A. rugosus* Brues and *A. filicornis* Brues have a more derived, 1-1-1 tibial spur formula, and lack a skaphion and notauli, among other differences (Brues, 1940; Masner et al., 2007a). Alternatively, the lack of laterotergites could indicate a position for both of these extinct genera outside and more basal to Nixoniidae, or could be secondarily lost in *Archaeoscelio* (as is the case with genera such as the mid-Eocene *Cobaloscelio* and the extant *Plaumannion*, *Huddlestonium*, and *Tyrannoscelio*, all of which are apparently along the stem to Platygastridae s.str.: Masner et al., 2007a, 2007b), and with the 1-1-1 tibial spur formula betraying its more derived placement. Such clarification awaits future paleontological study of Cretaceous Platygastroidea as these taxa should have considerable importance for resolving divergences among the varied groups. The tribal name is registered under ZooBank LSID urn:lsid:zoobank.org:act:A2AFA77F-F18D-48FF-BCB0-3BDDAD55AB20.

Geoscelio Engel and Huang, gen. nov.

Type species: *Geoscelio mckellari* Engel and Huang, sp. nov.

Diagnosis: As for the tribe (*vide supra*).

Etymology: The new genus-group name is composed of the Greek prefix *geo*–, referring to *gaia* and meaning, "earth", and *Scelio*, type genus of the family, and as a reference to the 'grounded' aspect of the wasp's putative life history, the result of its complete aptery. The name's gender is masculine. The generic name is registered under ZooBank LSID urn:lsid:zoobank.org:act:3ABF29D3-07C7-492B-BA1F-D47149F5DC3B.

Geoscelio mckellari Engel and Huang, sp. nov.

Figs. 1–3

Diagnosis: As for the genus (*vide supra*).

Description: ♀: Total length (as preserved, excluding antennae and ovipositor) 1.57 mm; integument generally brown to reddish brown throughout, generally impunctate and smooth except as noted, and without distinct setae over body. Head broad, width across compound eyes 0.64 mm, interocular distance 0.34 mm; integument of gena and between malar sulcus and submedian carina appearing weakly granulose. Antenna elongate, scape length 0.42 mm, slightly widening from base to apex; pedicel about twice as long as apical width, distinctly shorter than first flagellomere (Fig. 2); flagellomere I longest, about 4.5 times as long as apical width, flagellomeres II and III longer than wide, progressively shorter than flagellomere I; flagellomere IV slightly longer than apical width; flagellomeres V–XI forming weak clava, each about as long as apical width except flagellomere XII, which is slightly longer than wide and tapering to acute apex. Mandible stout, wider apically than at base, with three prominent, heavily sclerotized apical teeth visible on right mandible, teeth broadly separated by deep V-shaped incisions and arranged transversely along apical margin; anterior border with slight hump at base of first marginal tooth. Labrum not visible.

Pronotum strongly transverse, with exceptionally short posterior, elevated, dorsal-facing surface bordering mesoscutum, entirely consisting of single row of areolae interrupted medially against skaphion and anteriorly demarcated by transverse carina; otherwise pronotal surface sloping strongly to short medial collar between vertical epomial carinae; epomial carinae extending dorsally toward acutely pointed, dorsal anterolateral corners; lateral surface of pronotum slightly depressed and somewhat wrinkled, with large areolae ventrally along border with propleuron and mesepisternum (netrion lacking). Mesoscutum short, broad, medial width 0.63 mm, medial length 0.26 mm, surface weakly convex; narrow, short, skaphion present medially; notauli deeply and broadly impressed, not composed of areolae and not widening posteriorly, percurrent, separated by distance slightly more than their length, parapsidal line faintly indicated between notaulus and lateral border, mesoscutal lateral border with weak crenulae; transscutal sulcus deeply impressed, posteriorly with deep crenulae on mesoscutellum; mesoscutellum broader than long, medial length 0.19 mm, anterior width 0.35 mm, posterior border gently and broadly rounded, with overall hemispheric shape, and with posterior border composed of single row of deep areolae; tegula small, ovoid, with a small sclerotized hook slightly projecting beyond apical margin from beneath (highly reduced forewing?); mesepisternum weakly depressed, apparently smooth in area of depression but areolate anteriorly and posteriorly, apparently without sternaulus; metanotum short, surface composed of row of areolae and sloping, largely obscured by mesoscutellar posterior border in dorsal view; propodeum strongly declivitous, surface weakly areolate. Legs slender, with femora slightly crassate and longer than tibiae (less so for metafemur); inner surfaces of tibiae in apical halves and on tarsomeres with numerous, minute, fine setae; basitarsi longest tarsomeres, but shorter than combined lengths of remaining tarsomeres.

Metasoma compact, ovoid, medial length 0.66 mm, maximum width 0.64 mm (at apical margin of tergum II and base of tergum III); tergal posterior margins largely straight; sternal posterior margins somewhat concave; terga laterally slightly overlapping sterna; tergal bases with prominent, deeply impressed crenulae, weaker on tergum V and apparently lacking on tergum VI; tergum I with dorsal carina anterior to crenulae and defining sharp angle between tergal dorsal surface and precipitously declivitous anterior-facing surface bearing narrow articulation to propodeum; sterna with similar pattern of basal crenulae as on terga; apical segments not forming telescopic ovipositor tube; ovipositor exserted (as preserved), thin and about as long as medial length of terga II and III combined, without ovipositor tube, sheaths thin and about as long as ovipositor.

♂: Latet.

Holotype: ♀, NIGP 163293, Lowermost Cenomanian (near Albian boundary), Hukawng Valley, Kachin State, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Etymology: The specific epithet honors Dr. Ryan C. McKellar of the Royal Saskatchewan Museum, a prominent paleontologist who has contributed much to the study of amber as well as the Cretaceous record of Hymenoptera. The species name is registered under ZooBank LSID urn:lsid:zoobank.org:act:7A15E287-D0D2-4C63-BBA7-C7BAC9819E05.

4. Discussion

Geoscelio mckellari is a fascinating discovery among Cretaceous platygastroid wasps, and reflects the considerable variety within this lineage that was already in place by the mid-Cretaceous. The retention of 12 flagellomeres not forming a pronounced apical clava (the clava is at best weakly indicated in *G. mckellari*), a 1-2-2 tibial spur formula, absence of a frontal depression on the head, and six largely equal metasomal terga are all putatively plesiomorphic characteristics, shared with only the genus *Nixonia* Masner among the modern fauna (Johnson and Masner, 2006; Masner, 1976; van Noort and Johnson, 2009). Indeed, these are likely groundplan features for the superfamily, with multiple independent reductions in the line leading

to the Platygastridae s.str. as well as the Scelionidae, a pattern that would accord with current phylogenetic evidence (e.g., Murphy et al., 2007).

While in the modern fauna it is only *Nixonia* that retains a full complement of 12 flagellomeres, there are various genera in the fossil record, particularly the Cretaceous, that have this same condition. Of special interest are the genera *Proteroscelio* Brues in Early Cretaceous Lebanese amber and Late Cretaceous Canadian amber (Brues, 1937; Johnson et al., 2008a), and *Proterosceliopsis* Ortega-Blanco et al. and *Bruescelio* Ortega-Blanco et al. in Early Cretaceous Spanish amber (Ortega-Blanco et al., 2014). All of these genera share the plesiomorphic retention of 12 flagellomeres, a 1-2-2 tibial spur formula, a convex frons (lacking a frontal depression), and, at least in the case of *Proteroscelio*, also retain a malar sulcus. Unlike *Geoscelio*, all are fully winged and have distinct laterotergites. *Proteroscelio* also lack an occipital carina, a submedian carina, a skaphion, and notauli, and have a more distinct clava, short basal flagellomeres, and a more elongate metasoma lacking basal crenulae on the terga and sterna (Johnson et al., 2008a). *Cretaxenomerus* Nel and Azar in Early Cretaceous Lebanese amber also have 12 flagellomeres and 1-2-2 tibial spurs, but this genus has the lateral ocelli positioned close to the median ocellus, lacks notauli and a skaphion, and has a rather elongate metasoma with a prominent ovipositor tube and tergum III enlarged relative to the other segments (Nel and Azar, 2005).

The compact form, 12 flagellomeres, and primitive absence of laterotergites are shared with *Archaeoscelio*, described from mid-Eocene Baltic amber (Brues, 1940; Masner et al., 2007a). Indeed, aside from the aforementioned features, there are many traits similar between these two genera, despite their separation by approximately 50–55 million years. Both have an overall compact habitus; have a broad, stout, tridentate mandible; have the apical seven flagellomeres forming a weakly delimited, non-abrupt clava; lack a facial depression; lack a sternaulus; and have basally crenulate terga and sterna. Nonetheless, there remain significant differences, such as the 1-1-1 tibial spur formula, lack of submedian and orbital carinae, lack of a malar sulcus, lack of a skaphion and notauli, and more convex mesosomal dorsum in *Archaeoscelio*, as well as the general integumental sculpturing of the body in both genera. In all of these respects, *G. mckellari* appears more plesiomorphic than *Archaeoscelio*, and the latter may be a stem-group to the platygastrid lineage.

For the time being, *G. mckellari* stands as an outlier among Cretaceous Platygastroidea. Nonetheless, it provides initial clues to specializations already in place by the mid-Cretaceous, likely associated with some aspect of parasitoidism on a particular host. Scelionids are endoparasitoids of spider and insect eggs, and some of the most noted genera with apterous females are those of the Baeini, compact spider parasitoids (Austin et al., 2005; Masner, 1976). Interestingly and not surprisingly, where wing reduction has taken place among modern platygastroids, it is almost universally associated with a shift to a soil or litter habitat (Austin et al., 2005), and this is likely the case for *Geoscelio* as well and suggests that their hosts were among the debris on the floor of the Burmese amber forest.

Acknowledgements

Support for this project was provided by the National Basic Research Program of China (2012CB821903) to H.D.-Y.; through collaborative project, “Biodiversity: Origin, Structure, Evolution and Geology” granted by the Lebanese University to D.A.; partially by U.S. National Science Foundation grant (DEB-1144162) to M.S.E.; and through a doctoral fellowship from the Fondo para la Innovación, Ciencia y Tecnología, Peru, to M.A. This work was also supported by the Visiting Professor Program at King Saud University, Deanship of Scientific Research. We are also grateful to two anonymous reviewers for their helpful comments on an earlier version of the manuscript.

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