

Proterosceliopsidae: A new family of Platygastroidea from Cretaceous amber

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Abstract

Proterosceliopsis was erected by Ortega-Blanco et al. (2014) in their treatment of scelionid genera in Cretaceous amber from Álava, Spain. The generic description appears to have been based on specimens in which only the dorsal aspects of the mesosoma and metasoma were visible, as characters of the mesopleuron, metapleuron, lateral pronotum, and ventral metasoma were not mentioned. We here provide a comprehensive description of the genus that includes characters from throughout the body and we reinterpret some of the characters presented by Ortega-Blanco et al. (2014). Our analysis of *Proterosceliopsis* in the context of extant and fossil platygastroids places this group as a lineage well outside of the current families. We here designate *Proterosceliopsis* as the type genus of a new family, Proterosceliopsidae Talamas, Johnson, Shih & Ren, **fam. nov.**, and describe five new species: *Proterosceliopsis ambulata* Talamas, Shih & Ren, **sp. nov.**, *P. nigon* Talamas, Shih & Ren, **sp. nov.**, *P. plurima* Talamas, Shih & Ren, **sp. nov.**, *P. torquata* Talamas, Shih & Ren, **sp. nov.**, and *P. wingerathi* Talamas, Shih & Ren, **sp. nov.** We provide a key to all presently known species in the genus. The oldest known specimen of Platygastriidae s.s., in Burmese amber, is presented and compared to Proterosceliopsidae **fam. nov.**

Keywords

fossil, morphology, Platygastriidae, Scelionidae

Introduction

Platygastroid wasps are numerous in Burmese amber, comprising 16% of Hymenoptera in a recent study by Zhang et al. (2018). Some Cretaceous taxa are recognizable among the extant fauna: Platygastridae, Sparasionini and *Archaeoteleia* Masner (Talamas et al. 2017a). Simultaneously, many cannot be confidently placed at the family level because of the morphological disparity of the Cretaceous fauna and because the classification of Platygastroidea is in a state of flux. Zhang et al. (2018) identified the Burmese amber specimens as Scelionidae, a family that has been used to accommodate taxa that are plesiomorphic, e.g. *Nixonia* Masner, *Archaeoteleia* Masner, *Sparasion* Latreille (Masner 1976), or feature characters that clearly exclude them from Platygastridae, e.g. *Janzenella* Masner & Johnson (Masner and Johnson 2007), *Plaumannion* Masner & Johnson (Masner et al. 2007), *Huddlestonium* Polaszek & Johnson (Masner et al. 2007) and *Neuroscelio* Dodd (Valerio et al. 2009).

The historical concept of Scelionidae was found to be polyphyletic in the molecular analysis of Murphy et al. (2007), which Sharkey (2007) used to treat Scelionidae as a junior synonym of Platygastridae. This resolved the issue of monophyly at the family level, but in doing so transferred the problem to the subfamilies, most of which are known to be polyphyletic. There is growing consensus among analyses that Platygastridae s.s. and the “main scelionid clade” of Murphy et al. (2007) are monophyletic lineages. The latter was retrieved in an analysis of the maxillo-labial complex by Popovici et al. (2017), and in unpublished molecular phylogenies of Platygastroidea that focus on relationships within Scelionidae (Chen et al.) and Platygastridae s.s. (Blaimer et al.). Both of these efforts include basal lineages and retrieve Platygastridae s.s. and the “main scelionid clade” as monophyletic taxa. A classification that employs the historical concept of Platygastridae and a modified concept of Scelionidae are thus well supported and provide cohesion with much of the taxonomic literature. Together, these taxa comprise the vast majority of platygastroid species, and a multi-family classification system provides better framework for higher taxonomy in the superfamily. We defer changes to family classification to the final results of the aforementioned analyses and note that while affinities are clearly present, we cannot place *Proterosceliopsis* in any of the existing or potential suprageneric taxa without drastically and unnecessarily altering their limits. Our analysis of *Proterosceliopsis* is made in the context of extant specimens from a broad geographic and taxonomic sampling, fossils from Lebanese, Burmese, Baltic, and Dominican amber, and with consideration of lineages for which additional families may be erected.

For the purposes of this paper, *Archaeoteleia*, *Neuroscelio*, *Huddlestonium* and *Plaumannion* are considered *incertae sedis* and are referenced by their generic names; Scelionidae refers to the “main scelionid clade” of Murphy et al. (2007); Platygastridae refers to the historical, pre-Sharkey (2007) concept of the family (=Platygastrinae + Sceliotrachelinae + *Orwellium* Johnson, Masner & Musetti); Nixonidae is treated as a monogeneric family (= *Nixonia*) sensu Mckellar and Engel (2012); and Sparasionini refers to the concept of Johnson et al. (2008a).

Criticism of previous taxonomy

Preservation artifacts complicate the taxonomic treatment of fossils. This problem is exacerbated when primary types do not display characters in sufficient detail to enable unambiguous determination at the species level. In the case of *Proterosceliopsis*, *P. masneri* Ortega-Blanco, McKellar & Engel can be reliably separated from the species here described from Burmese amber, but some of the most important generic characters are not visible in the specimens and are missing from the description presented by Ortega-Blanco et al. (2014). As a result, taxon-defining characters cannot presently be verified in the specimen that carries the name of a species, genus, and now, a family. We redefine *Proterosceliopsis* because we consider *P. masneri* and the specimens in Burmese amber to be congeneric based on the congruence of observable characters. In this case, attaching a concept to an existing name can be defended by the available data and reduces the number of superficially defined genera in Platygastroidea. We assert that dubiously delimited taxa can be avoided by a more rigorous approach to the treatment of fossils, one in which taxa are described only when based on well-preserved specimens and with the necessary background knowledge about the superfamily.

Material and methods

Informatics

The numbers prefixed with acronyms, e.g. “USNMENT” or “OSUC”, are unique identifiers for the individual specimens (note the blank space after some acronyms). Details on the data associated with these specimens may be accessed at the following link: purl.oclc.org/NET/hymenoptera/hol and entering the identifier in the form. Persistent URIs for each taxonomic concept were minted by xBio:D in accordance with best practices recommend by Hagedorn et al. (2013). Morphological terms were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010) using the text analyzer function. A table of morphological terms and URI links is provided in Appendix 1. Taxonomic synopses and matrix-based descriptions were generated from the Hymenoptera Online Database (hol.osu.edu) and the online program vSysLab (vsyslab.osu.edu) in the format of character: state. Characters that were not visible because of preservation or orientation of the insects are coded as “not visible”.

Imaging and microscopy

The amber pieces were cut and polished to optimize the viewing and photography of specimens for taxonomic study. Direct examination of the specimens was made with a Zeiss V8 stereomicroscope and an Olympus BX51 compound microscope.

Photographs were captured with multiple imaging systems: a Z16 Leica lens with a JVC KY-F75U digital camera using Cartograph and Automontage software; an Olympus BX51 compound microscope with a Canon EOS 70D digital SLR camera; and a Leica DM2500 compound microscope with a Leica DFC425 camera. Illumination was achieved with a lighting dome or with LED gooseneck lamps and mylar light dispersers. Images were rendered from z-stacks with Automontage, Helicon Focus or Zerene Stacker. In some cases, multiple montage images were stitched together in Photoshop to produce larger images at high resolution and magnification. Full resolution images are archived at the image database at The Ohio State University (specimage.osu.edu).

Dissections for scanning electron microscopy were performed with a minuten probe and forceps and body parts were mounted to a 12 mm slotted aluminum mounting stub (EMS Cat. #75220) using a carbon adhesive tab (EMS Cat. #77825-12) and sputter coated with approximately 70 nm of gold/palladium using a Cressington 108 auto sputtercoater. Micrographs were captured using a Hitachi TM3000 Tabletop Microscope at 15 keV.

Author contributions

EJT: photography, scanning electron microscopy, taxon concepts, manuscript preparation; NFJ: manuscript preparation; CKS: manuscript preparation, provision of Burmese amber; DR: manuscript preparation, provision of Burmese amber.

Collections

The amber specimens of *Proterosceliopsis* studied here were collected from Kachin (Hukawng Valley) of northern Myanmar, which was dated at 98.79+0.62 Ma (Cruikshank and Ko 2003, Shi et al. 2012), equivalent to the earliest Cenomanian and approximately 1 Myr within the boundary between the Early and Late Cretaceous (Walker et al. 2012). This deposit yielded many well-preserved insect fossils (Chen et al. 2018a–b, Li et al. 2018, Wang et al. 2016, Zhang et al. 2018).

Specimens on which this work is based are deposited in the following repositories with abbreviations used in the text:

- CCHH** Hoffeins Collection, Hamburg, Germany
- CNCI** Canadian National Collection of Insects, Ottawa, Canada
- CNU** Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China
- FSCA** Florida State Collection of Arthropods, Gainesville, FL, USA
- KUNH** Kansas University Natural History Museum, Lawrence, KS, USA
- OPPC** Ovidiu Popovici, personal collection, “A.I. Cuza” University, Faculty of Biology, Iasi, Romania

OSUC C.A. Triplehorn Insect Collection, The Ohio State University, Columbus, OH, USA

USNM National Museum of Natural History, Washington, DC, USA

Character annotations

1Rs (Fig. 15)	1 st radial sector vein
2Rs (Fig. 15)	2 nd radial sector vein
b (Fig. 15)	bullae
C, C+R (Fig. 15)	marginal vein
Cu (Fig. 15)	cubital vein
fas (Fig. 10)	facial striae
ff (Figs 43–44)	felt field
M (Fig. 15)	medial vein
mas (Fig. 10)	malar striae
mees (Figs 16, 20)	mesepimeral sulcus
ms (Figs 7–8, 10)	malar sulcus
net (Figs 16–17, 19)	netrion
p (Fig. 22)	cuticular pores
pp (Fig. 17)	mesopleural pit
prcs (Figs 16, 19, 21)	pronotal cervical sulcus
ps (Figs 1–6)	papillary (basiconic) sensilla
r (Fig. 15)	stigmatal vein
R1 (Fig. 15)	postmarginal vein
Rs+M (Fig. 15)	basal vein
sk (Figs 11–13)	skaphion
Sc+R (Fig. 15)	submarginal vein
S6 (Fig. 47)	metasomal sternites 6
T6–T8 (Figs 45–49, 55, 61)	metasomal tergites 6–8
tel (Figs 16, 19, 21)	transepisternal line

Results

Character discussion

Most of the diagnostic characters of *Proterosceliopsis* can be found in extant platygastroids but are present in a unique combination in this genus. Additionally, *Proterosceliopsis* exhibits significant differences from each of the taxa with which it shares characters. We present discussions of these characters and their distribution among platygastroid taxa as a prelude to the generic treatment.

Antenna

Bin (1981) defined the antennal clava in Telenominae (Scelionidae) based on the presence of papillary sensilla on the ventral side of the distal antennomeres (previously referred to as basiconic sensilla). The presence of these sensilla on female antennae is a synapomorphy for Platygastroidea (Austin et al. 2005), and Bin's definition of the clava has since been applied to all members of the superfamily. We continue to define the clava on the basis of papillary sensilla instead of relative antennomere size for multiple reasons: antennomeres can increase in size gradually (Figs 2–4); the size among antennomeres with papillary sensilla can be variable (Fig. 5); distinctly enlarged antennal segments may not have papillary sensilla, as in the clubbed antennae found in most males of *Helava* Masner & Huggert (Masner and Huggert 1989, Talamas and Masner 2016). The claval formula is often of taxonomic value, particularly at the species-level, and its use requires that specimens be preserved well enough to observe these structures. Small bubbles in the amber are sometimes visible at the tips of the sensilla (Fig. 6) and can be useful for identifying their presence.

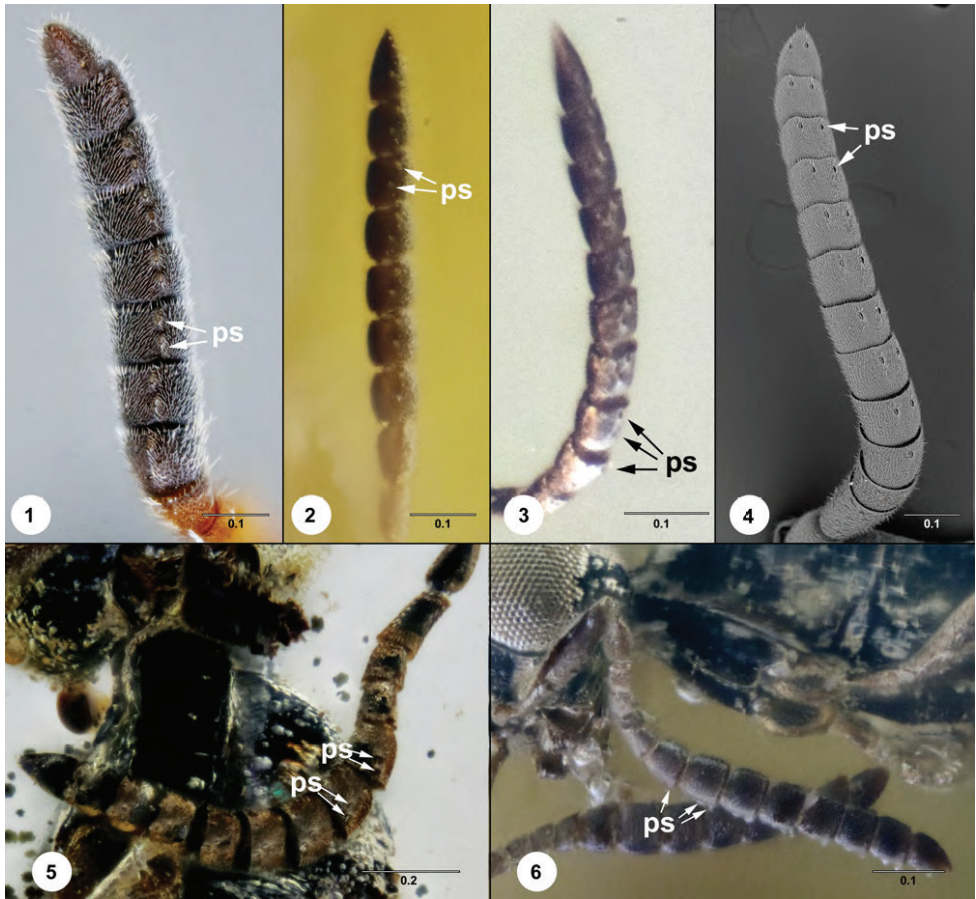
A transverse orientation of papillary sensilla is known only in *Nixonia* (Fig. 4) (Johnson and Masner 2006) whereas all other extant platygastroids have a longitudinal arrangement (Fig. 1). We found that in some species of *Proterosceliopsis* (Figs 3, 5) and Cretaceous *Electroteleia* Brues (Fig. 2) the sensilla are arranged at an oblique angle. This was found in multiple specimens in which the general shape of the antennomeres is intact, and thus we do not attribute this to taphonomic deformation. Instead, we consider that different arrangements of these sensilla were possible earlier in the history of Platygastroidea.

Malar sulcus

The malar sulcus found in *Proterosceliopsis* is unaccompanied by facial or malar striae (Fig. 7), a state which can be found in some Scelionidae (Fig. 8) and some Sparasionini (*Electroteleia*). In Platygastridae, the malar sulcus is present in only two genera: *Metacclisis* Förster and *Orseta* Masner & Huggert, each of which have both facial and malar striae (Fig. 10) (Masner and Huggert 1989), and *Orwellium*, which does not have facial or malar striae. The malar sulcus is entirely absent in *Nixonia* Masner (Fig. 9).

Palpal formula

Ortega-Blanco et al. (2014) recorded the palpal formula of *P. masner* to be 5:3. We observed 5-merous, cylindrical maxillary palps in *P. nigon*, *P. torquata*, and *P. wingerathi*; and at least 4 maxillary palpomeres in *P. plurima*. Two labial palpomeres are visible in *P. torquata*. Five-merous palpomeres were retrieved as the plesiomorphic condition for Platygastroidea in the phylogenetic analysis by Popovici et al. (2017) and are found in Sparasionini, *Nixonia*, and *Archaeoteleia*. This indicates that *Proterosceliopsis* is also

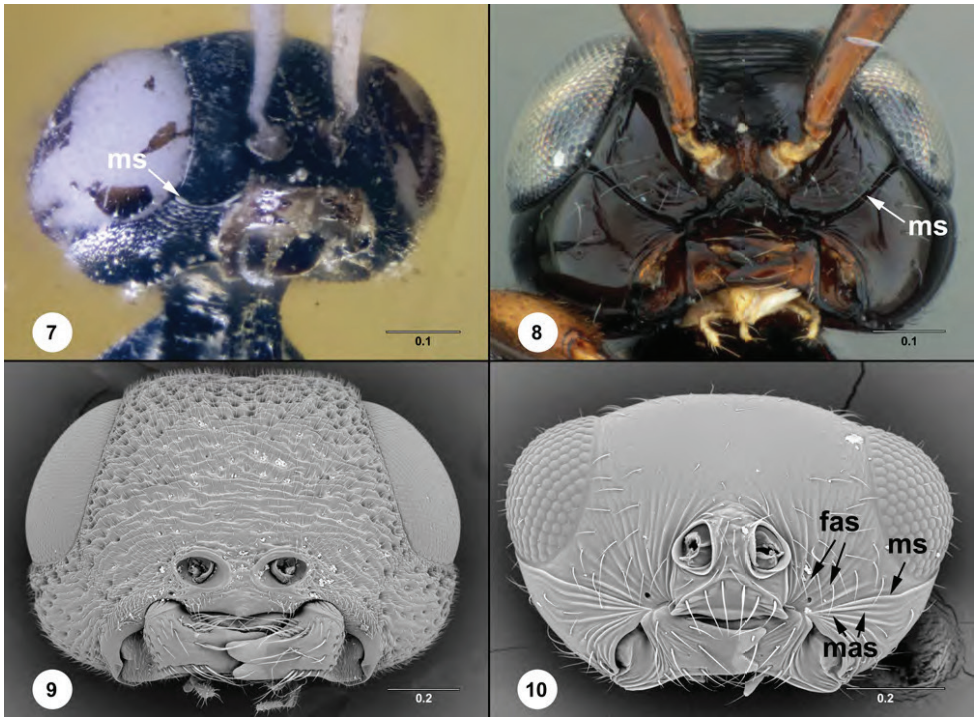


Figures 1–6. **1** *Sceliomorpha* Ashmead (DPI_FSCA 00008723), female antenna, ventral view **2** *Electroteleia* (DPI_FSCA 00010129), female antenna, ventral view **3** *Proterosceliopsis plurima* (CNU-HYM-MA-2016102), female antenna, ventral view **4** *Nixonia watshami* Johnson & Masner (OSUC 149432), female antenna, ventral view **5** *Proterosceliopsis nigon* (CNU-HYM-MA-2017566), female antenna, ventral view. **6** *Proterosceliopsis wingerathi* (CNU-HYM-MA-2016101), female antenna, lateral view. Scale bars in millimeters.

a basal lineage well outside of Scelionidae in which the palpal formula is 4:2 or less (Popovici et al. 2017), and Platygastridae in which the palpal formula is 2:1 or less (Popovici, personal communication).

Skaphion

The anterior mesoscutum in most species of *Proterosceliopsis* features a smooth, transverse structure to which we apply the term skaphion (Figs 11, 50, 58, 62). We do not assert that the skaphion of *Proterosceliopsis* is homologous with that found in scelionid genera (Figs 12–13) and note that it can be found in other Cretaceous taxa that do not belong to *Proterosceliopsis* or Scelionidae, e.g. *Electroteleia* (Fig. 14).



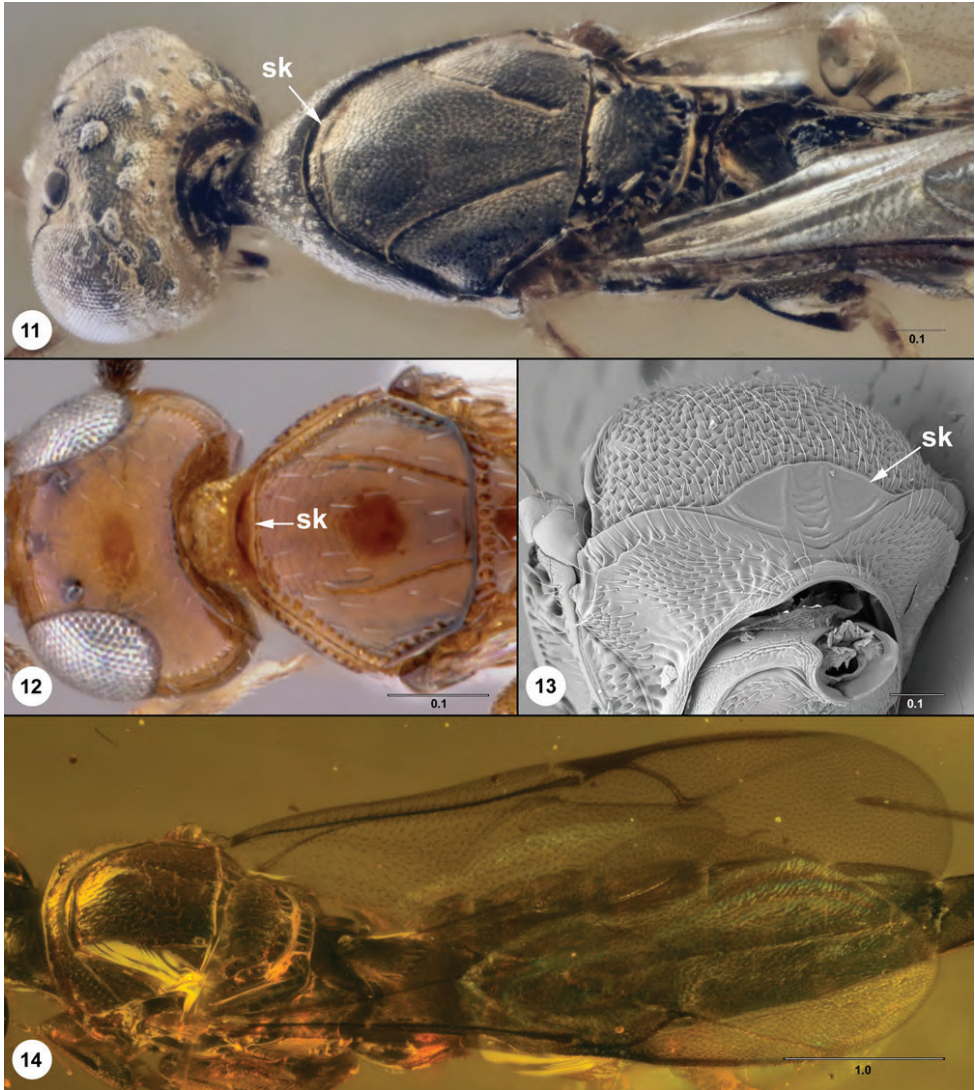
Figures 7–10. **7** *Proterosceliopsis plurima* (CNU-HYM-MA-2016102), head, anteroventral view **8** *Calliscelio* Ashmead (CNC494853), head, anteroventral view **9** *Nixonia watshami* (OSUC 149432), head, anteroventral view **10** *Metaclisis* (USNMENT01029162), head, anteroventral view. Scale bars in millimeters.

Costal vein

In *Proterosceliopsis*, the costal vein is present anterior to the fusion with R and extends proximally beyond the bulla (Fig. 15). This form is known from other Cretaceous platygastroids (Fig. 14), but not in extant taxa.

Setation of the pronotal cervical sulcus

The pronotal cervical sulcus can take many forms, including a distinct line of foveae (Fig. 18), a well-defined smooth groove (Fig. 19), or a weakly defined furrow along the lateral pronotal rim (Fig. 17). In *Nixonia*, Johnson and Masner (2006) reported an area of dense setation along the anterior margin of the lateral pronotum that is often associated with solidified exudate (Fig. 20). Setation along the pronotal cervical sulcus is found in *Proterosceliopsis* (Fig. 16, 52, 59) and many platygastroids (Figs 19, 26), and often contains what appears to be solidified exudate. The unpublished phylogenetic



Figures 11–14. **11** *Proterosceliopsis torquata* (CNU-HYM-MA-2016106), head and mesosoma, dorsal view **12** *Calotelea* Westwood (OSUC 56216), head and mesosoma, dorsal view **13** *Nyleta striaticeps* Dodd (OSUC 174452), mesosoma, anterior view **14** *Electroteleia* (CNU-HYM-MA-2016103), mesosoma and metasoma, dorsolateral view. Scale bars in millimeters.

analysis of Platygastriidae (Blaimer et al.) indicates that stem lineages of this family have a setose pronotal cervical sulcus. Figures 65–66 illustrate the oldest known platygastriid, in Burmese amber, that exhibits this character, consistent with our treatment of it as a plesiomorphy for Platygastriidae that varies significantly in some derived platygastriid lineages (Figs 21–26). Figures 21–22 illustrate the unusual form found in *Sacespalus*

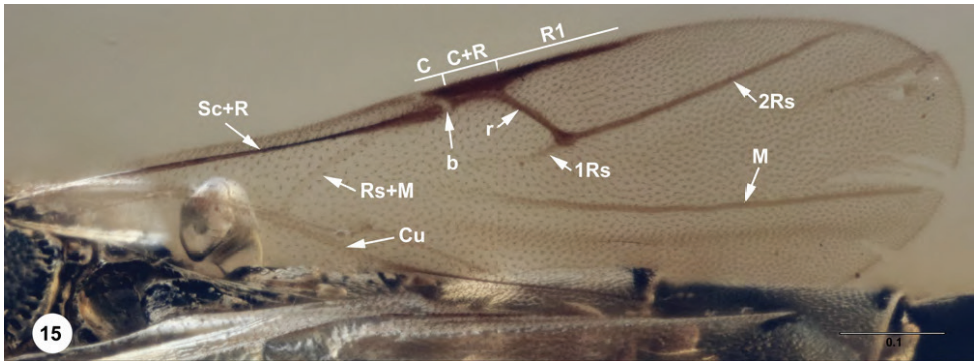


Figure 15. *Proterosceliopsis torquata* (CNU-HYM-MA-2016106), fore wing, dorsal view. Scale bar in millimeters.

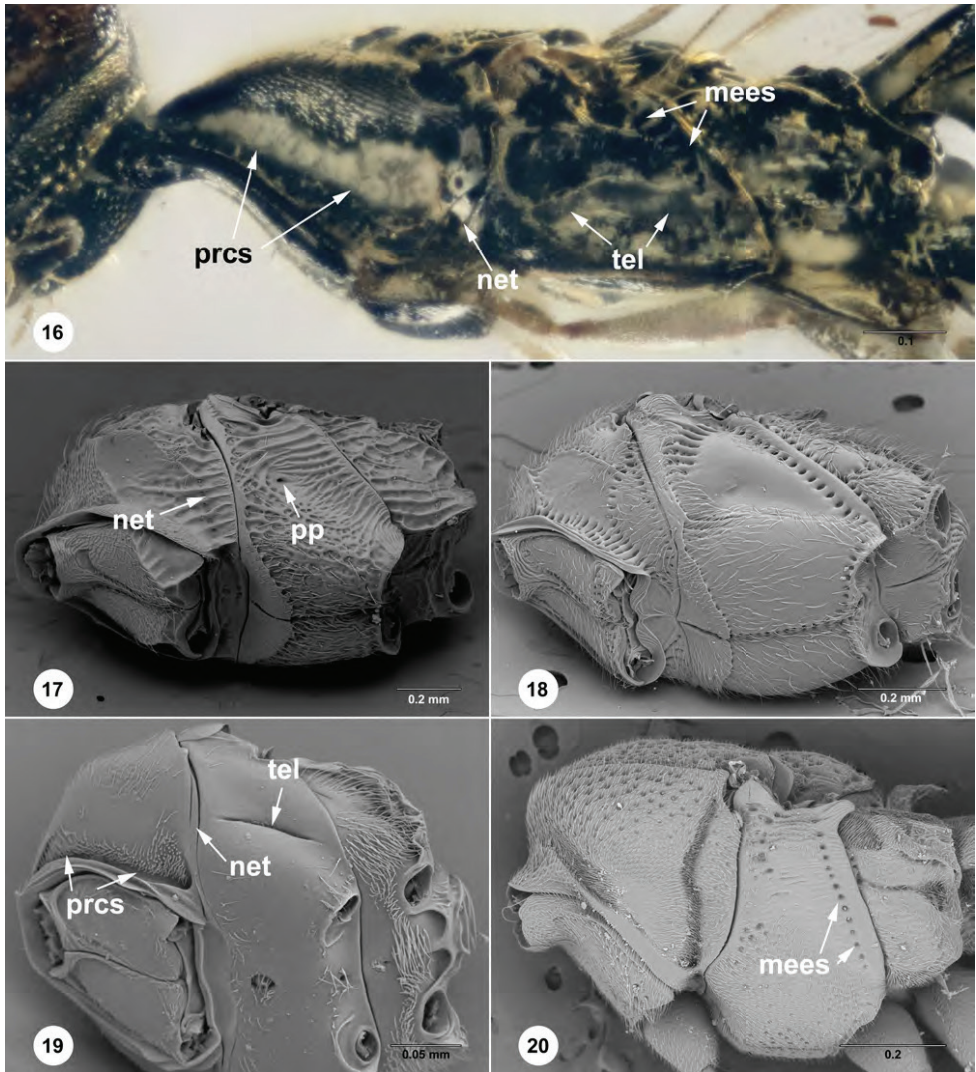
in which setation is absent and the pronotal cervical sulcus is broadly expanded. Pores can be seen in the ventral portion of the pronotal cervical sulcus of *Sacespalus* (Fig. 22), which is congruent with the hypothesis that this character is associated with glandular secretions. We do not know of any scelionids with a setal patch along the anterior portion of the lateral pronotum but note that the antespирacular setal patch (sensu Yoder et al. 2012) in Scelionidae is associated with cuticular pores (Fig. 28). Based on the pronotal position of these setal patches, we suspect that they have similar function.

Netrion

A netrion is clearly present in 3 of the 5 species that we here describe. Mikó et al. (2007) reported that in *Nixonia* the trachea associated with the anterior thoracic spiracle extends ventrally between the netrion sulcus and the posterior pronotal inflection. Externally this results in the netrion sulcus dorsally terminating anterior to the anterior thoracic spiracle (Fig. 20). This character can be used to separate *Nixonia* from nearly all other platygastroids, in which the netrion sulcus, when present, terminates posterior or ventral to the anterior thoracic spiracle (Figs 16–18, 20).

Transepisternal line

Among extant platygastroids, the transepisternal line is found exclusively in Platygastriidae (Fig. 19). We treat it as a plesiomorphy for Platygastriidae based on its presence in the Cretaceous specimen illustrated in Figs 65–66, and because it is found in stem lineages of the family based on a preliminary analysis of molecular data (Blaimer et al.). The internal anatomy associated with this structure has yet to be examined in detail and will likely shed light on its function and evolution within Platygastriidae. The transepisternal line in *Proterosceliopsis* is clearly present in all specimens from Burmese amber (Figs 16, 53) suggesting a close relationship between Proterosceliopsidae and Platygastriidae.

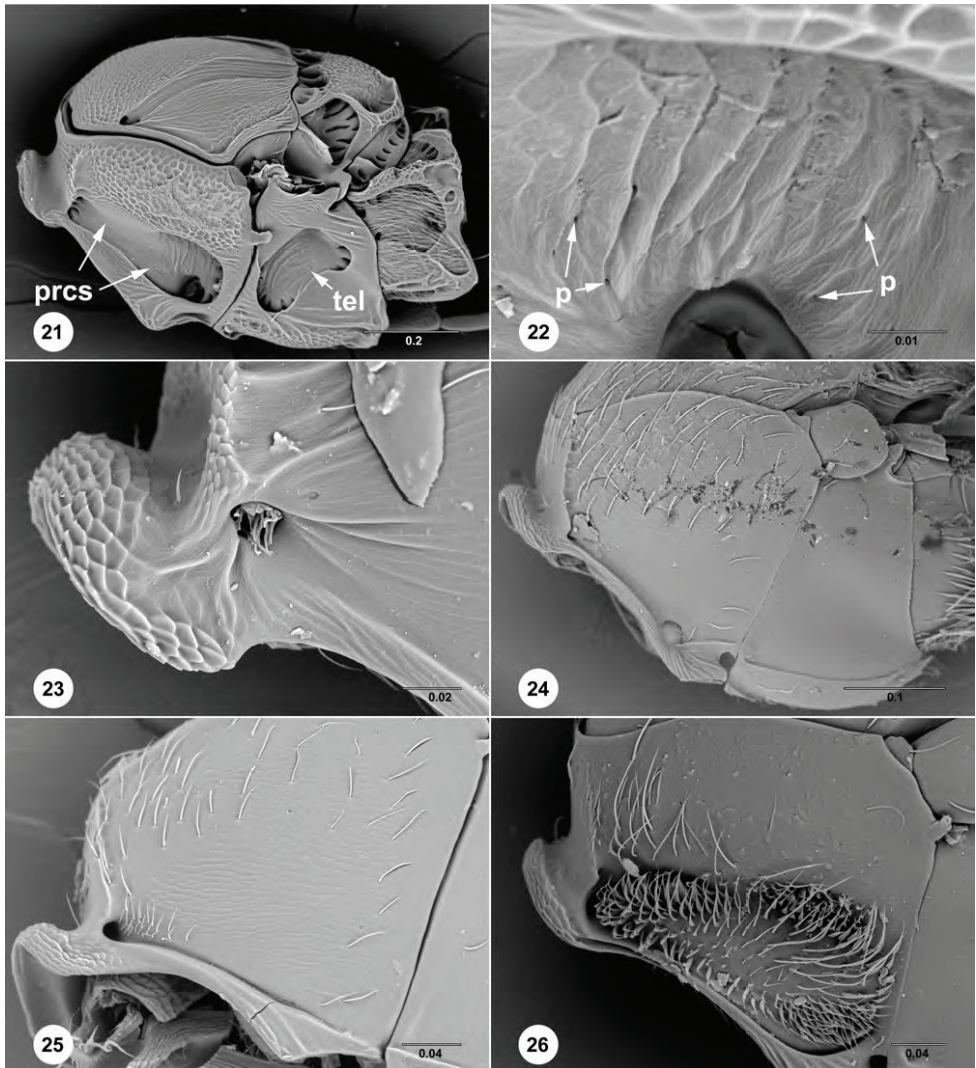


Figures 16–20. **16** *Proterosceliopsis plurima* (CNU-HYM-MA-2016102), mesosoma, lateral view **17** *Scelio* Latreille (USNMENT00989612_3), mesosoma, ventrolateral view **18** *Archaeoteleia gracilis* Masner (OSUC 163002), mesosoma, ventrolateral view **19** *Fidiobia* (USNMENT01197212_2), mesosoma, ventrolateral view **20** *Nixonia watshami* (OSUC 149432), head, lateral view. Scale bars in millimeters.

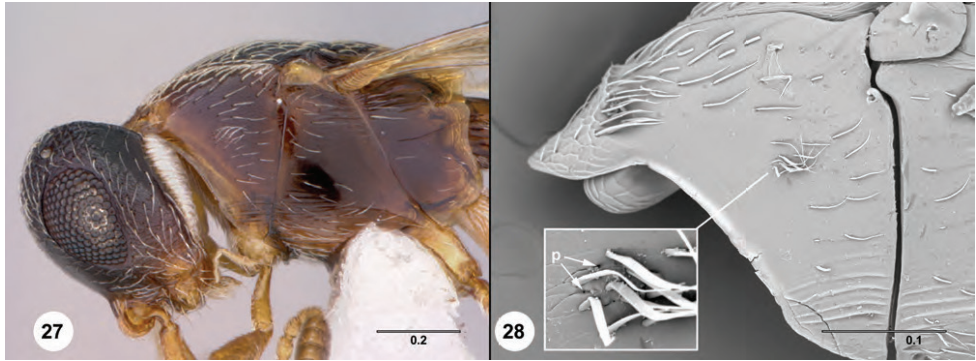
Mesepimeral sulcus

The presence of a fully developed mesepimeral ridge was retrieved by Vilhelmsen et al. (2010) as a potential autapomorphy for Proctotrupoidea s.s. This ridge corresponds externally to the mesepimeral sulcus, which is found in all platygastroid families except Platygastriidae (Figs 16–20). We consider the loss of the mesepimeral sulcus to be an apomorphy for Platygastriidae, but whether this internally corresponds to loss of the mesepimeral ridge has yet to be investigated. Some examples of an absent or weakly

indicated mesepimeral sulcus can be found in Scelionidae. In some cases, these are clearly secondary derivations that occurred at the species level (Fig. 17). In the unusual *Doddiella* Kieffer (Scelionidae) the mesepimeral sulcus is not indicated externally but the mesepimeral ridge can be seen through the semitransparent exoskeleton (Fig. 27). The presence of the mesepimeral sulcus in Proterosceliopsidae provides a reliable mesosomal character to separate it from Platygasteridae.



Figures 21–26. **21** *Sacspalus* Kieffer (USNMENT01197981_1), mesosoma, lateral view **22** *Sacspalus* (USNMENT01197981_1), ventral portion of pronotal cervical sulcus, lateral view **23** *Leptacis* Förster (USNMENT00872705), anterior portion of pronotal cervical sulcus, lateral view **24** *Synopeas* Förster (USNMENT00989616_3), mesosoma, lateral view **25** *Platygaster* Latreille (USNMENT01197214_1), pronotum, lateral view **26** *Trichacis* Förster (USNMENT00989620), pronotum, lateral view. Scale bars in millimeters.



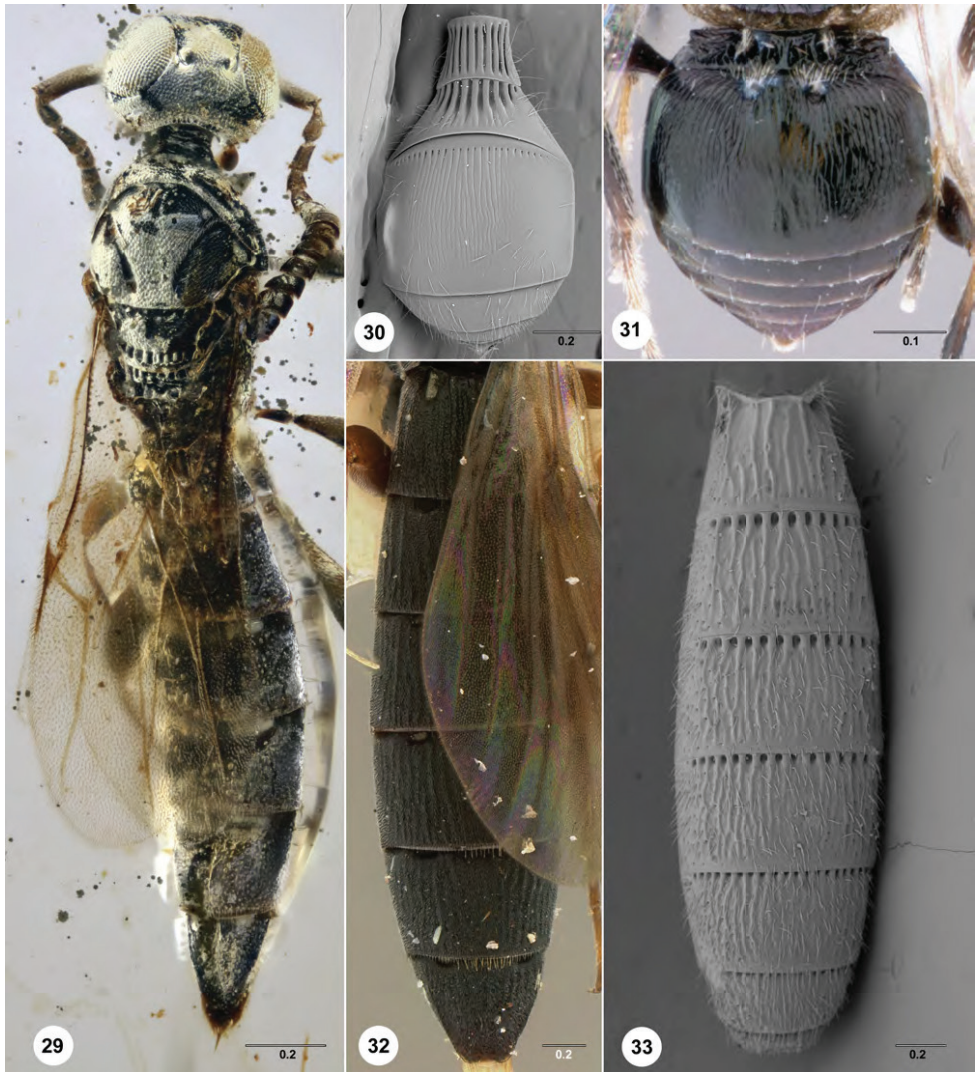
Figures 27, 28. **27** *Doddiella* (OSUC 56323), head and mesosoma, lateral view **28** *Doddiella* (USNM-ENT00872797), pronotum and mesopleuron, lateral view. Scale bars in millimeters.

Setation and sulci of the metasoma

Proterosceliopsis from Burmese amber and *Nixonia* share the presence of transverse, depressions along the anterior margins of T1–T5 (Figs 29, 32) and S1–S5 (Figs 34, 37). In *Nixonia*, these depressions have visible setation. In *Proterosceliopsis* they appear to have very fine setation, but the cloudy exudate prevents an unobscured view. In *P. torquata* these depressions are not clearly visible on T6, and in *P. plurima* they are not clearly present on S6. In the other Burmese species of *Proterosceliopsis*, and in all species of *Nixonia*, these depressions are present on T6 and S6. We suspect that they are present on T6 and S6 in all species of *Proterosceliopsis*, but the preservation of these specimens prevents us from reaching a confident conclusion.

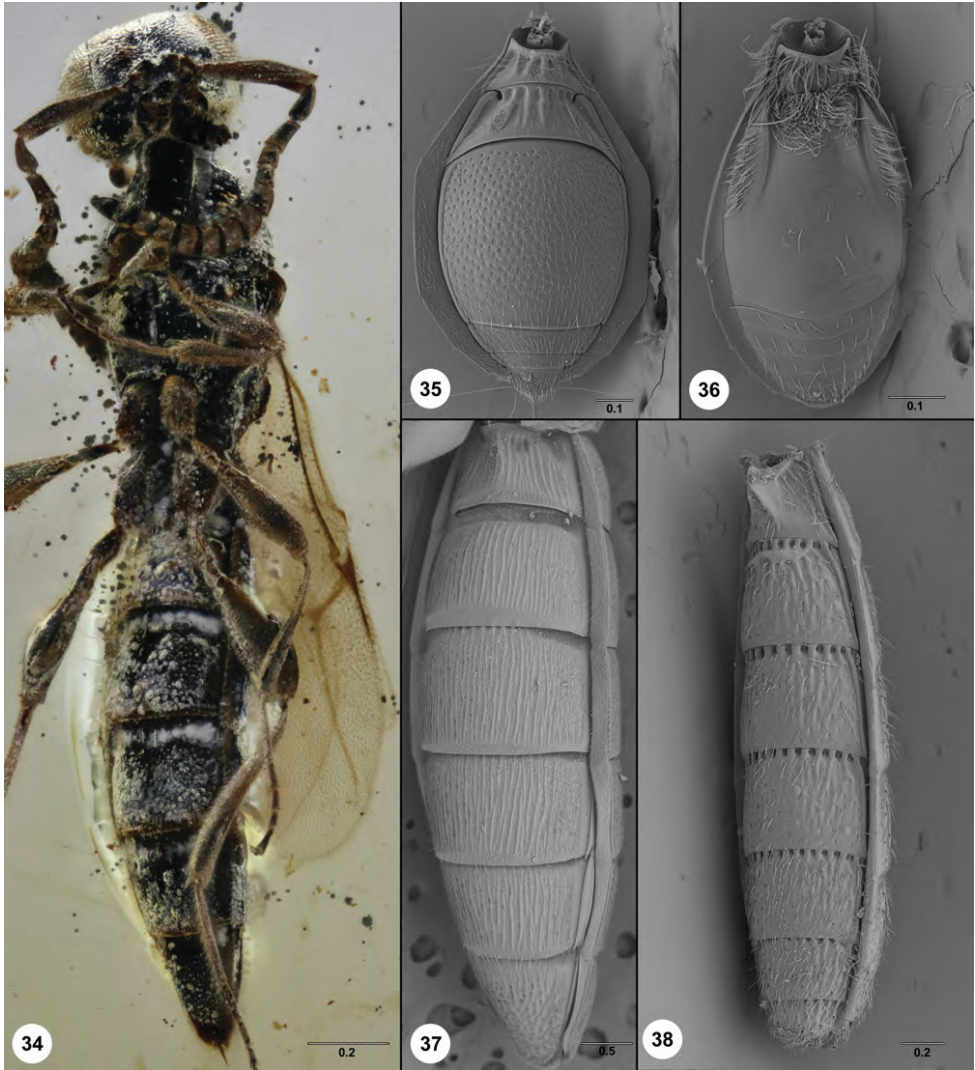
The two components of this character, setation/glandular secretion and sulci along the anterior tergites and sternites, vary independently among platygastroid families. Sparasionini and *Archaeoteleia* feature transverse sulci across the anterior margins of the external tergites and sternites (Figs 33, 38, 44), which may sometimes be reduced on T6 and S6 in females of *Electroteleia* (Sparasionini) and in *Archaeoteleia*. These sulci are found in all specimens that we examined in Lebanese amber, which constitute the oldest platygastroid fossils, and we consider it likely that this is the plesiomorphic condition for Platygastroidea. The metasoma in Sparasionini and *Archaeoteleia* lacks setation on the anterior tergites and sternites beyond T1 and S1, but there may be numerous felt fields (Fig. 44).

In Platygastriidae and Scelionidae, the anterior portions of T1–T2 and S1–S2 typically feature a transverse line of foveae or pits, which may or may not be clearly defined (Figs 30–31, 35–36). The transverse sulci in scelionids are not associated with setation, and patches of dense setae tend to be located on the lateral portion of the tergite, sometimes in well-defined pits (Figs 39–40). Some teleasines (Scelionidae) exhibit a transverse sulcus along anterior T3 and S3 (Fig. 30, 35) and setal patches with pores on T4–T5 (Fig. 42). Platygastriidae exhibits the greatest variation in the size, location, and shape of setal pits on metasomal segments 1 and



Figures 29–33. **29** *Proterosceliopsis nigon* (CNU-HYM-MA-2017566), head, mesosoma, metasoma, dorsal view **30** *Trimorus* Förster (USNMENT01197861), metasoma, dorsal view **31** *Amitus* Haldeman (OSUC 404941), metasoma, dorsal view **32** *Nixonia krombeini* Johnson & Masner (OSUC 146429), metasoma, dorsal view **33** *Sparasion philippinensis* Kieffer (USNMENT00872835), metasoma, dorsal view. Scale bars in millimeters.

2. They may be present laterally or medially, as a broad transverse patch that spans the width of the tergite or sternite (Fig. 43), in well-defined pits (Fig. 31), or they may be absent entirely (e.g. *Orwellium* Johnson, Masner & Musetti). Felt fields, which are absent in *Nixonia* and *Proterosceliopsis*, are found only on S2 in Platygastriidae and Scelionidae, with a few exceptions (e.g. *Heptascelio* Kieffer (Johnson

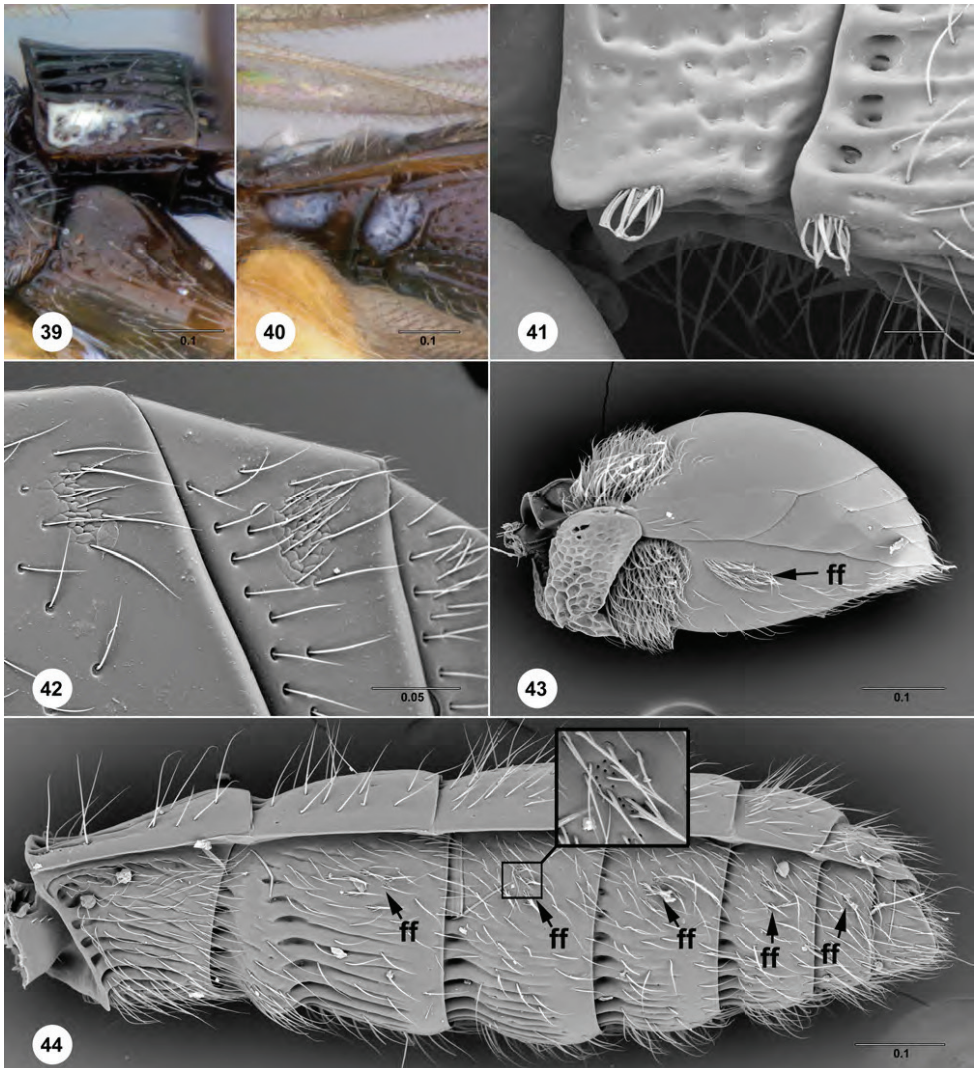


Figures 34–38. **34** *Proterosceliopsis nigon* (CNU-HYM-MA-2017566), head, mesosoma, metasoma, ventral view **35** *Dvivarnus mikuki* Talamas & Mikó (USNMENT01059135), metasoma, ventral view **36** *Trichacis* (USNMENT01059347), metasoma, ventral view **37** *Nixonia watshami* (OSUC 149432), metasoma, ventral view **38** *Sparasion philippinensis* (USNMENT00872835), metasoma, ventral view. Scale bars in millimeters.

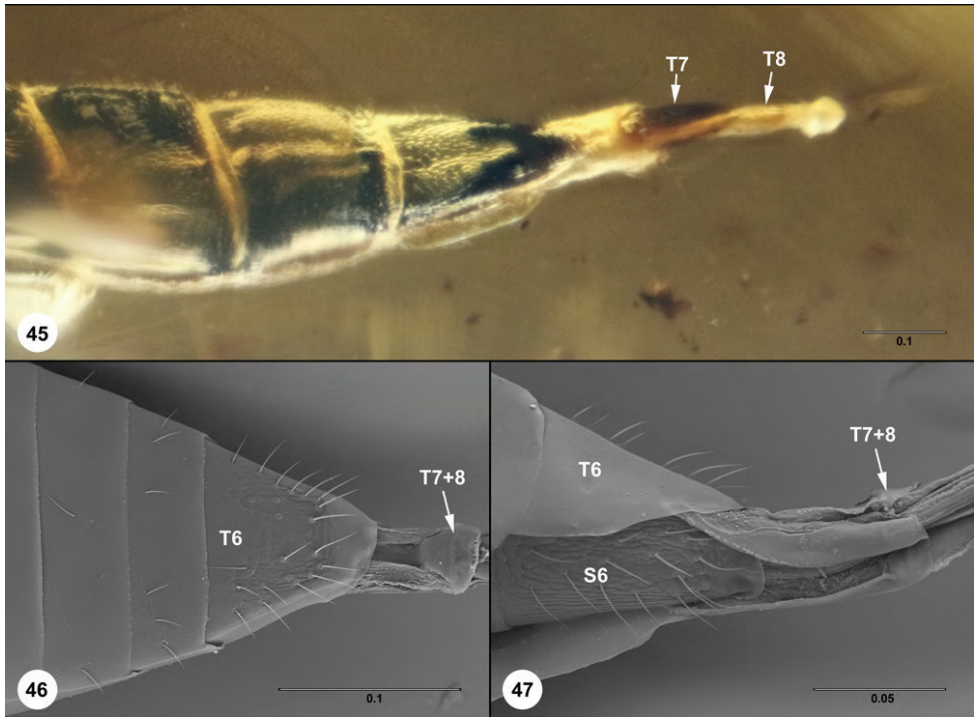
et al. 2008b)). *Neuroscelio doddi* Galloway, Austin & Masner exhibits an unusual and noteworthy form of sternal setation in which dense tufts are located medially on S1–S2 (Fig. 41).

Setal patches on the metasoma and pronotum, which are often associated with pores in the integument, clearly warrant further examination. A survey of platygas-

triod morphology with a scanning electron microscope has revealed an array of additional pore locations and forms on the head and mesosoma. Our present analysis of these characters, which provides only a broad overview as it relates to family level classification of *Proterosceliopsis*, will be developed further in future projects. The presence of cuticular pores and solidified exudate in the same locations point to the activity of internal glands.



Figures 39–44. **39** *Trichoteleia bidentata* Talamas (CASENT 2132802), T1, lateral view **40** Scelioninae (OSUC 254572), S1-S2, ventrolateral view **41** *Neuroscelio doddi* (OSUC 147252), S1-S2, ventrolateral view **42** *Dviivarnus mikuki* (USNMMENT01059135), T3-T5, dorsal view **43** *Helava alticola* Masner & Huggert (USNMMENT00989211), metasoma, lateral view **44** *Archaeoteleia gracilis* (OSUC 163002), metasoma, lateral view. Scale bars in millimeters.



Figures 45–47. **45** *Proterosceliopsis ambulata* (CNU-HYM-MA-2016105), distal metasoma, dorsal view **46** *Fidiobia* (USNMENT01197212_2), distal metasoma, dorsal view **47** *Fidiobia* (USNMENT01197212_2), distal metasoma, ventrolateral view.

Ovipositor system

Ortega-Blanco et al. (2014) interpreted T7+8 to be the ovipositor, which they described as short and broad. We here clarify that these sclerites are not the ovipositor, but they could be considered part of the *ovipositor system* sensu Austin and Field (1997). The known diversity of ovipositor systems in Platygastroidea has expanded in recent years, with at least two derivations of a telescoping ovipositor system found in Platygastriidae (Talamas et al. 2017b). Extension of the ovipositor system in *Proterosceliopsis* appears to operate via telescoping membrane between T6 and T7, with T7 and T8 clearly present as separate sclerites in some specimens (Fig. 45). The unpublished phylogenetic analyses suggest that conjunctival expansion between T6 and T7 occurred independently in Scelionidae and *Archaeoteleia*. The placement of *Proterosceliopsis* well outside of these families indicates that expansion of conjunctiva between T6 and T7 into a telescoping ovipositor system has occurred at least three times: in *Proterosceliopsis*, *Archaeoteleia*, and Scelionidae. We also have found evidence of conjunctival expansion between T6 and T7 in the platygastriid genus *Fidiobia* Ashmead. It does not appear to be telescoping but provides clear evidence of yet another independently derived elongation of conjunctiva between T6 and T7 (Figs 46–47), lending evidence to the plasticity of this morphological system.

Taxonomy

Proterosceliopsidae Talamas, Johnson, Shih & Ren, fam. nov.

<http://zoobank.org/A482A28F-562C-4318-A681-47F326D152E3>

Diagnosis. Antenna with 14 or 15 antennomeres; malar sulcus present (Fig. 7); facial striae absent (Fig. 7); malar striae absent (Fig. 7); pronotal cervical sulcus present as a furrow of fine setation associated with glandular excretion (Figs 16, 48–49, 51–53, 59); mesopleuron with transepisternal line and mesepimeral sulcus (Figs 16, 51–53, 59, 63); T3–T5 and S3–S5 anteriorly with depressions associated with glandular excretion (Figs 29, 34, 56, 58, 62).

***Proterosceliopsis* Ortega-Blanco, McKellar & Engel**

http://bioguid.osu.edu/xbiod_concepts/352921

Proterosceliopsis Ortega-Blanco, McKellar & Engel, 2014: 554 (original description.

Type: *Proterosceliopsis masneri* Ortega-Blanco, McKellar & Engel, by monotypy and original designation. Diagnosis); Talamas, Johnson, Buffington and Ren 2017: 251, 253 (description, keyed).

Diagnosis. See family diagnosis.

Description. Head: Facial striae: absent. Malar sulcus: present. Malar striae: absent. Orbital carina: absent. Setation of compound eye: absent. Torulus: opening anteriorly. Frontal ledge: absent. OOL: lateral ocellus separated from compound eye by less than one ocellar diameter. Macrosculpture of head: absent. Hyperoccipital carina: absent. Occipital carina: present, continuous dorsally and ventrally extending to posterior articulation of the mandible.

Mesosoma: Propleural epicoxal sulcus: absent. Posterolateral corner of propleuron: strongly pointed. Pronotal cervical sulcus: furrow of dense fine setae. Epomial carina: absent. Transverse pronotal carina: absent. Antero-admedian lines: absent. Macrosculpture of mesosoma: absent. Orientation of notauli: converging posteriorly. Mesoscutal humeral sulcus: indicated by smooth furrow. Posterior mesoscutellar sulcus: foveate. Sculpture of metanotal trough: foveate. Metascutellum: undifferentiated from metanotal trough. Ventral mesopleural furrow: present. Ventral mesopleural carina: present. Mesopleural carina: absent. Anterior mesepisternal area: absent. Episternal foveae: absent. Transepisternal line: present. Mesopleural pit: absent. Prespecular sulcus: absent. Mesepimeral sulcus: present. Metapleural carina: present. Ventral metapleural area: convex and without macrosculpture. Dorsal metapleural area: convex and without macrosculpture. Ventral surface of metapleuron: setose. Sculpture of dorsal propodeum: coarsely rugose. Setal patch on anterodorsal surface of hind coxa: present.

Fore Wing: submarginal (Sc+R), marginal (C+R), postmarginal (R1) and stigmal vein (r) present; C extending proximally past bulla; 1Rs short and nebulous; 2Rs sclerotized and extending to wing margin. Basal vein (Rs+M) and M+Cu nebulous to weakly sclerotized. Median vein (M) present as a nebulous line in distal portion of the wing; tibial spur formula: 1-2-2.

Metasoma: T1–T5 with depressions anteriorly (unclear in *P. masneri*); S1–S5 with depressions anteriorly; 6–7 visible tergites when ovipositor not extruded. T7+T8 extruded with ovipositor system (based on *P. ambulata*).

Distribution. The presence of *Proterosceliopsis* in Burmese and Álava (Spain) amber indicates that this was a widespread genus.

Comments. Our generic description of *Proterosceliopsis* is based largely on specimens from Burmese amber, which provide far greater detail than the original description, and the two descriptions are congruent as far as can be observed. However, it should be noted that depressions along the anterior margin of the metasomal tergites in *Proterosceliopsis masneri* are not mentioned or illustrated in Ortega-Blanco et al. (2014). In their photographs of the dorsal habitus (Fig. 6A–B) it is unclear if these depressions are present. In cases where exudate is absent, photography of these depressions can be difficult, particularly in darkly colored specimens and when the amber is turbid.

Key to species of *Proterosceliopsis* (females)

- 1 Antenna with 15 antennomeres.....*P. plurima* Talamas, Shih & Ren, sp. nov.
- Antenna with 14 antennomeres 2
- 2 T1 with horn (Fig. 58)..... 3
- T1 without horn (Figs 29, 48, 62) 4
- 3 T6 distinctly the longest tergite (Fig. 58)
..... *P. torquata* Talamas, Shih & Ren, sp. nov.
- T1–T6 approximately equal in length.....
..... *P. masneri* Ortega-Blanco, McKellar & Engel
- 4 T1 evenly convex and without macrosculpture or raised area (Figs 48, 50); antenna with 7 clavomeres; A7 distinctly transverse (Fig. 49).....
..... *P. ambulata* Talamas, Shih & Ren, sp. nov.
- T1 medially with raised area of longitudinal striation (Fig. 29); antenna with more than 7 clavomeres; A7 about as long as wide (Figs 5–6) 5
- 5 Antennae with 9 clavomeres (Fig. 5); T2 without striae posterior to transverse sulcus (Fig. 29) *P. nigon* Talamas, Shih & Ren, sp. nov.
- Antennae with 8 clavomeres (Fig. 6); anteromedial T2 with longitudinal striae posterior to transverse sulcus (Fig. 62)
..... *P. wingerathi* Talamas, Shih & Ren, sp. nov.

***Proterosceliopsis ambulata* Talamas, Shih & Ren, sp. nov.**<http://zoobank.org/96EBF28B-6654-48F5-8FD0-AE1B106985F3>http://bioguid.osu.edu/xbiod_concepts/451148

Figures 45, 48–50

Diagnosis. *Proteroscelio ambulata* shares with *P. wingerathi*, *P. nigon* and *P. masneri* the roughly equal lengths of metasomal segments 1–6. It can be separated from all of these by the evenly convex form of T1, which has a horn in *P. masneri* and an anteromedian area of prominent striae in *P. nigon* and *P. wingerathi*.

Description. Head: Number of antennomeres in female: 14. Number of clavomeres in female: 7. Claval formula in female: 1-2-2-2-2-2. Number of mandibular teeth: 3. Number of labial palpomeres: not visible. Number of maxillary palpomeres: not visible. Shape of clypeus: narrow, transverse. Central keel: absent. Antennal scrobe: undifferentiated sculpturally from remainder of frons. Anterior margin of occipital carina: simple.

Mesosoma: Pronotal prespiracular depression: present, without striation. Netrion: absent. Skaphion: present. Posterior notaulus: reaching posterior margin of mesoscutum. Width of notaulus: expanding posteriorly. Parapsidal lines: absent. Mesoscutal suprahumeral sulcus: indicated by smooth furrow. Scutoscutellar sulcus: simple. Postacetabular carina: absent. Postacetabular sulcus: absent. Mesopleural epicoxal sulcus: present. Episternal foveae: absent. Metapleural sulcus: present as a transverse furrow. Lateral propodeal carina: present laterally as two small posteriorly-pointing projections.

Metasoma: Horn on T1 in female: absent. Sculpture of T1: weakly longitudinally striate throughout. Macrosculpture of T2–T5: absent. Anterior tergal depressions: visible on T1–T6. Median keel on S2: absent. Macrosculpture of S3–S6: absent. Anterior sternal depressions: visible on S1–S6.

Etymology. This species is given the name “ambulata” because the holotype specimen appears to be walking.

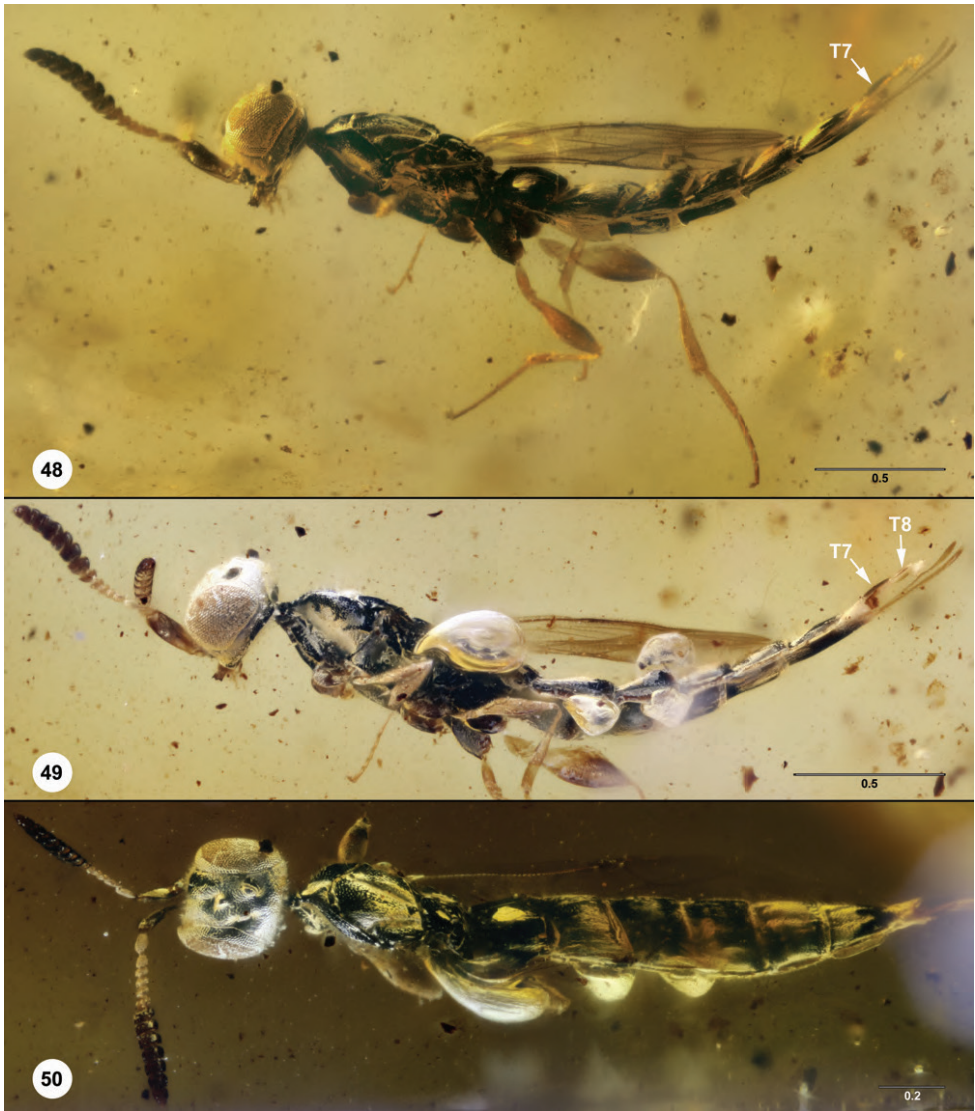
Link to distribution map. [<http://hol.osu.edu/map-large.html?id=451148>]

Material examined. Holotype female: **MYANMAR:** CNU-HYM-MA-2016105 (deposited in CNU).

***Proterosceliopsis masneri* Ortega-Blanco, McKellar & Engel**http://bioguid.osu.edu/xbiod_concepts/352922

Proterosceliopsis masneri Ortega-Blanco, McKellar & Engel, 2014: 555, 568 (original description, diagnosis, keyed).

Comments. *Proterosceliopsis masneri* may eventually be considered a *nomen dubium* as a species due to the paucity of detailed information on its morphology. The study of additional material from Álava amber is needed to clarify characters on this species, particularly the lateral mesosoma and structures on the anterior portions of the metasomal segments.



Figures 48–50. *Proterosceliopsis ambulata* (CNU-HYM-MA-2016105) **48** habitus, lateral view (left side) **49** habitus, lateral view (right side) **50** head, mesosoma, metasoma, dorsal view. Scale bars in millimeters.

***Proterosceliopsis nigon* Talamas, Shih & Ren, sp. nov.**

<http://zoobank.org/79232690-93E4-4F06-8157-76573017F84A>

http://bioguid.osu.edu/xbiod_concepts/463679

Figures 5, 29, 34

Diagnosis. *Proterosceliopsis nigon* is most similar to *P. wingerathi*, from which it can be separated by having 9 clavomeres and T2 without striation posterior to the transverse anterior depressions.

Description. Head: Number of antennomeres in female: 14. Number of clavomeres in female: 9. Claval formula in female: 1-2-2-2-2-2-2-2. Number of mandibular teeth: not visible. Number of labial palpomeres: not visible. Number of maxillary palpomeres: at least 5. Shape of clypeus: narrow, transverse. Central keel: absent. Antennal scrobe: indicated by faint transverse rugae. Anterior margin of occipital carina: crenulate.

Mesosoma: Pronotal prespiracular depression: present, without striation. Netrion: absent. Skaphion: present. Posterior notaulus: not reaching posterior margin of mesoscutum. Width of notaulus: expanding posteriorly. Parapsidal lines: present. Mesoscutal suprahumeral sulcus: simple, without furrow or cells. Scutoscutellar sulcus: crenulate. Postacetabular carina: present directly posterior to acetabulum. Postacetabular sulcus: present as simple furrow. Mesopleural epicoxal sulcus: present. Metapleural sulcus: present as a transverse furrow. Lateral propodeal carina: present and continuous dorsally, forming lamella surrounding metasomal depression, medial portion raised and projecting dorsally. Metasomal depression: excavate, interior surface with striae dorsomedially.

Metasoma: Horn on T1 in female: absent. Sculpture of T1: longitudinally striate medially. Macrosculpture of T2–T5: absent. Anterior tergal depressions: visible on T1–T6. Median keel on S2: absent. Macrosculpture of S3–S6: longitudinal median carina on S3–S4, otherwise absent. Anterior sternal depressions: visible on S1–S6.

Etymology. This word “nigon” is Anglo-Saxon for “nine”, referring to the number of clavomeres in this species, and is treated as a noun in apposition.

Link to distribution map. [<http://hol.osu.edu/map-large.html?id=463679>]

Material examined. Holotype female: **MYANMAR:** CNU-HYM-MA-2017566 (deposited in CNU). *Other material:* (1 female) **MYANMAR:** OPPC1718 (deposited in OPPC).

***Proterosceliopsis plurima* Talamas, Shih & Ren, sp. nov.**

<http://zoobank.org/8FBDF6FE-3BDC-499E-BDBF-BAF63B63943D>

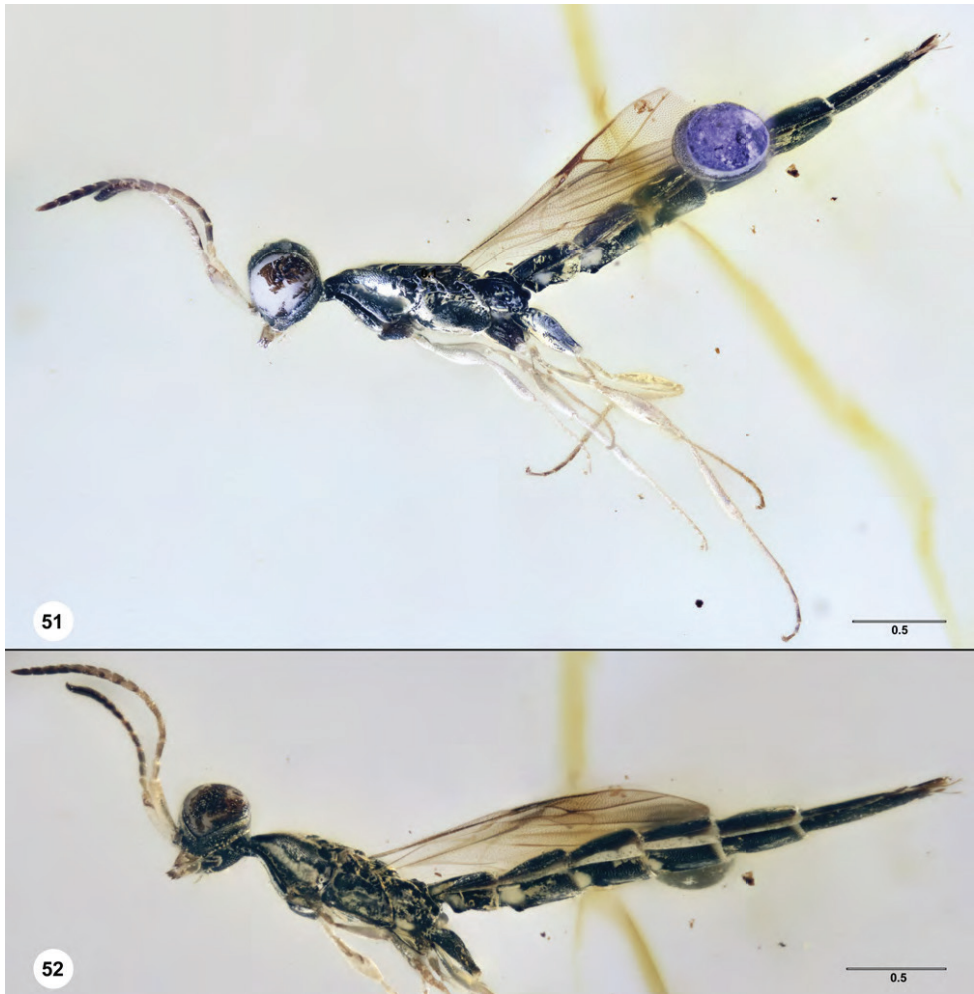
http://bioguid.osu.edu/xbiод_concepts/451147

Figures 3, 7, 16, 51–57

Diagnosis. The number of antennomeres in this species, 15, provides a simple means of separating it from other members of the genus. In *P. plurima* and *P. torquata* the 6th metasoma tergites and sternites are distinctly the longest. In the absence of antennal characters, these species can be separated on the form of the notaulus, which expands in width posteriorly in *P. plurima* and is of uniform width in *P. torquata*.

Description. Head: Number of antennomeres in female: 15. Number of clavomeres in female: 9. Claval formula in female: 1-2-2-2-2-2-2-1. Number of mandibular teeth: 3 on right mandible, 2 on left mandible. Number of labial palpomeres: not visible. Number of maxillary palpomeres: 4. Shape of clypeus: narrow, transverse. Central keel: present. Antennal scrobe: indicated by transverse rugae. Anterior margin of occipital carina: crenulate.

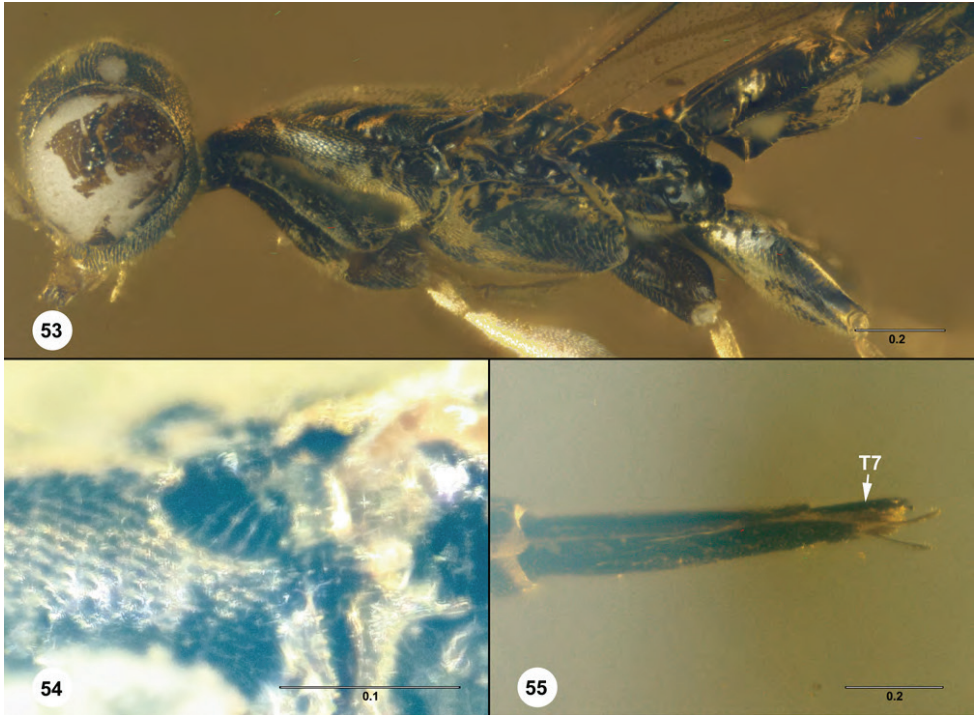
Mesosoma: Pronotal prespiracular depression: present, striate. Netrion: present. Skaphion: absent. Posterior notaulus: not reaching posterior margin of mesoscu-



Figures 51, 52. *Proterosceliopsis plurima* (CNU-HYM-MA-2016102) **51** habitus, lateral view (right side) **52** habitus, lateral view (left side). Scale bars in millimeters.

tum. Width of notaulus: expanding posteriorly. Parapsidal lines: absent. Mesoscutal suprahumeral sulcus: indicated by short line of cells. Scutoscutellar sulcus: simple. Postacetabular carina: present as short ridge laterally, carinae not meeting medially. Postacetabular sulcus: present as simple furrow. Mesopleural epicoxal sulcus: present. Episternal foveae: absent. Metapleural sulcus: present, anterodorsal portion comprised of cells. Lateral propodeal carina: present and continuous dorsally, forming lamella surrounding metasomal depression.

Metasoma: Horn on T1 in female: absent. Sculpture of T1: longitudinally striate medially. Macrosculpture of T2–T5: longitudinal median carina on T2 and T3, otherwise absent. Anterior tergal depressions: visible on T1–T6. Median keel on S2: present. Macrosculpture of S3–S6: longitudinal median carina on S3–S4, otherwise absent. Anterior sternal depressions: visible on S1–S5.



Figures 53–55. *Proterosceliopsis plurima* (CNU-HYM-MA-2016102) **53** head, mesosoma, anterior metasoma, lateral view (right side) **54** posterodorsal pronotum, lateral view **55** distal segments of metasoma, lateral view. Scale bars in millimeters.



Figures 56, 57. *Proterosceliopsis plurima* (CNU-HYM-MA-2016102) **56** habitus, dorsal view **57** head and mesosoma, ventral view. Scale bars in millimeters.

Etymology. The epithet “plurima”, meaning “abundant” or “numerous”, refers to the number of antennomeres in this species, which is the greatest known in Platygastroidea.

Link to distribution map. [<http://hol.osu.edu/map-large.html?id=451147>]

Material examined. Holotype female: **MYANMAR:** CNU-HYM-MA-2016102 (deposited in CNU).

Comments. The number of clavomeres is here coded as 9, a basiconic sensillum on A15 is visible, as are paired sensilla on A14–A8

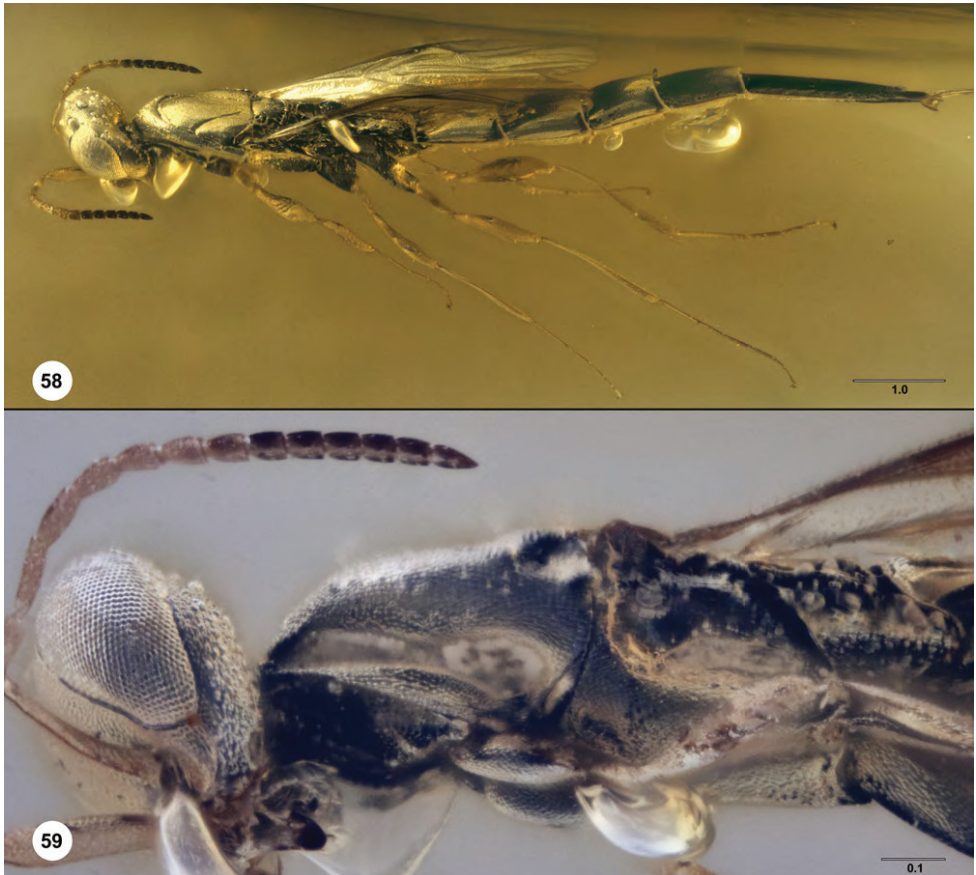
***Proterosceliopsis torquata* Talamas, Shih & Ren, sp. nov.**

<http://zoobank.org/E0A610BA-26A4-4BBA-96F2-3EA25A202E59>

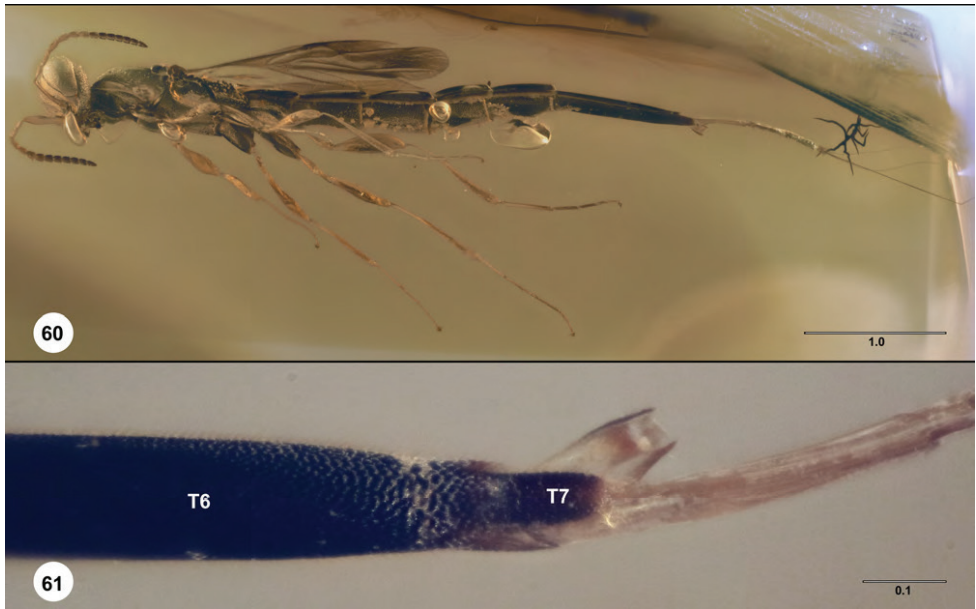
http://bioguid.osu.edu/xbiod_concepts/426419

Figures 11, 15, 58–61

Diagnosis. *Proterosceliopsis torquata* is most similar to *P. plurima*, with which it shares an elongate habitus, and having the 6th metasomal segment distinctly the longest. These



Figures 58, 59. *Proterosceliopsis torquata* (CNU-HYM-MA-2016106) **58** habitus, dorsolateral view **59** head and mesosoma, lateral view. Scale bars in millimeters.



Figures 60, 61. *Proterosceliopsis torquata* (CNU-HYM-MA-2016106) **60** habitus, ventrolateral view **61** distal segments of metasoma, dorsal view. Scale bars in millimeters.

can be separated by the presence of the horn on T1 in *P. torquata* (absent in *P. plurima*); the posteriorly expanded notauli in *P. plurima* (of uniform width in *P. torquata*), and by the number of antennomeres: 14 in *P. torquata* and 15 in *P. plurima*.

Description. Head: Number of antennomeres in female: 14. Number of clavomeres in female: 8. Claval formula in female: 1-2-2-2-2-2-1. Number of mandibular teeth: not visible. Number of labial palpomeres: at least 2. Number of maxillary palpomeres: at least 5. Shape of clypeus: not visible. Central keel: present. Antennal scrobe: indicated by transverse rugae. Anterior margin of occipital carina: crenulate.

Mesosoma: Pronotal prespiracular depression: present, without striation. Netrion: present. Skaphion: present. Posterior notaulus: not reaching posterior margin of mesoscutum. Width of notaulus: uniform. Parapsidal lines: present. Mesoscutal supra-humeral sulcus: indicated by smooth furrow. Scutoscutellar sulcus: simple. Postacetabular carina: present as short ridge laterally, carinae not meeting medially. Postacetabular sulcus: present as simple furrow. Mesopleural epicoxal sulcus: present. Episternal foveae: absent. Metapleural sulcus: present as a transverse furrow. Lateral propodeal carina: present and continuous dorsally, forming lamella surrounding metasomal depression. Metasomal depression: deeply excavate, interior surface smooth.

Metasoma: Horn on T1 in female: present. Sculpture of T1: longitudinally striate medially. Macrosculpture of T2–T5: longitudinal median carina on anterior T2 and T3, otherwise absent. Anterior tergal depressions: visible on T1–T5. Median keel on S2: present. Macrosculpture of S3–S6: absent. Anterior sternal depressions: visible on S1–S6.

Etymology. The Latin adjectival epithet “torquata”, meaning “adorned with a necklace or collar”, is given to this species for the collar-like shape of the pronotum in dorsal view.

Link to distribution map. [<http://hol.osu.edu/map-large.html?id=426419>]

Material examined. Holotype female: **MYANMAR:** CNU-HYM-MA-2016106 (deposited in CNU). *Other material:* (1 female) **MYANMAR:** OPPC1801 (deposited in OPPC).

***Proterosceliopsis wingerathi* Talamas, Shih & Ren, sp. nov.**

<http://zoobank.org/B2655449-13F3-42BE-A67B-2562D53CB003>

http://bioguid.osu.edu/xbiod_concepts/451152

Figures 6, 62–64

Diagnosis. *Proterosceliopsis wingerathi* is most similar to *P. nigon*, from which it can be separated by having eight clavomeres and the presence of longitudinal striation in the anteromedial portion of T2.

Description. Head: Number of antennomeres in female: 14. Number of clavomeres in female: 8. Claval formula in female: 1-2-2-2-2-2-1. Number of mandibular teeth: 3 on right mandible. Number of labial palpomeres: not visible. Number of maxillary palpomeres: at least 5. Shape of clypeus: narrow, transverse, medially concave. Central keel: absent. Antennal scrobe: undifferentiated sculpturally from remainder of frons. Anterior margin of occipital carina: crenulate.

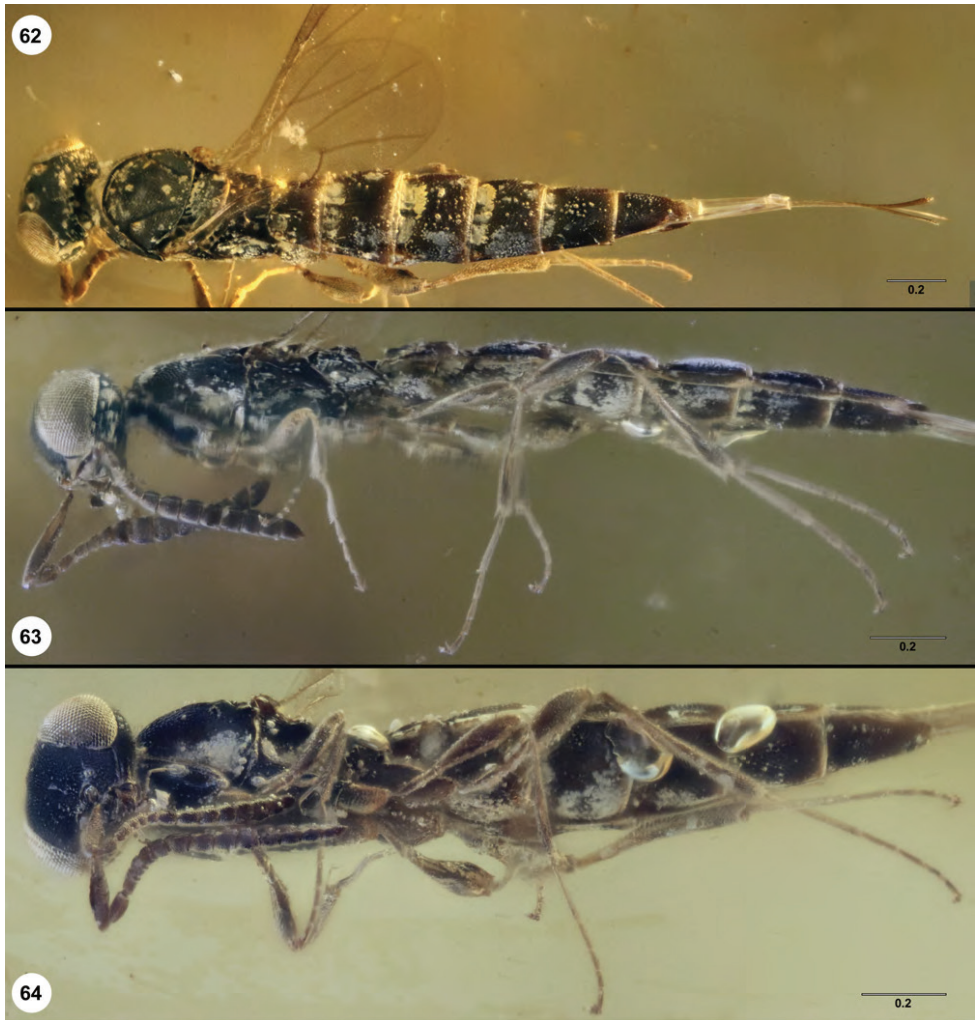
Mesosoma: Pronotal prespiracular depression: present, without striation. Netrion: present. Skaphion: present. Posterior notaulus: not reaching posterior margin of mesoscutum. Width of notaulus: uniform. Parapsidal lines: present. Mesoscutal suprahumeral sulcus: indicated by smooth furrow. Scutoscutellar sulcus: crenulate. Postacetabular carina: absent. Postacetabular sulcus: absent. Episternal foveae: absent. Metapleural sulcus: present as a transverse furrow. Lateral propodeal carina: present and continuous dorsally, forming lamella surrounding metasomal depression. Metasomal depression: excavate, interior surface with striae dorsomedially.

Metasoma: Horn on T1 in female: absent. Sculpture of T1: longitudinally striate medially. Macrosculpture of T2–T5: anteromedial T2 longitudinally striate, otherwise absent. Anterior tergal depressions: visible on T1–T6. Median keel on S2: absent. Macrosculpture of S3–S6: absent. Anterior sternal depressions: visible on S1–S6.

Etymology. This species is named for Jonathan Wingerath, Deputy Collections Manager for Paleobotany at the National Museum of Natural History, Washington, DC, to express our thanks for contributing his time and skills in preparing amber specimens for this and other projects.

Link to distribution map. [<http://hol.osu.edu/map-large.html?id=451152>]

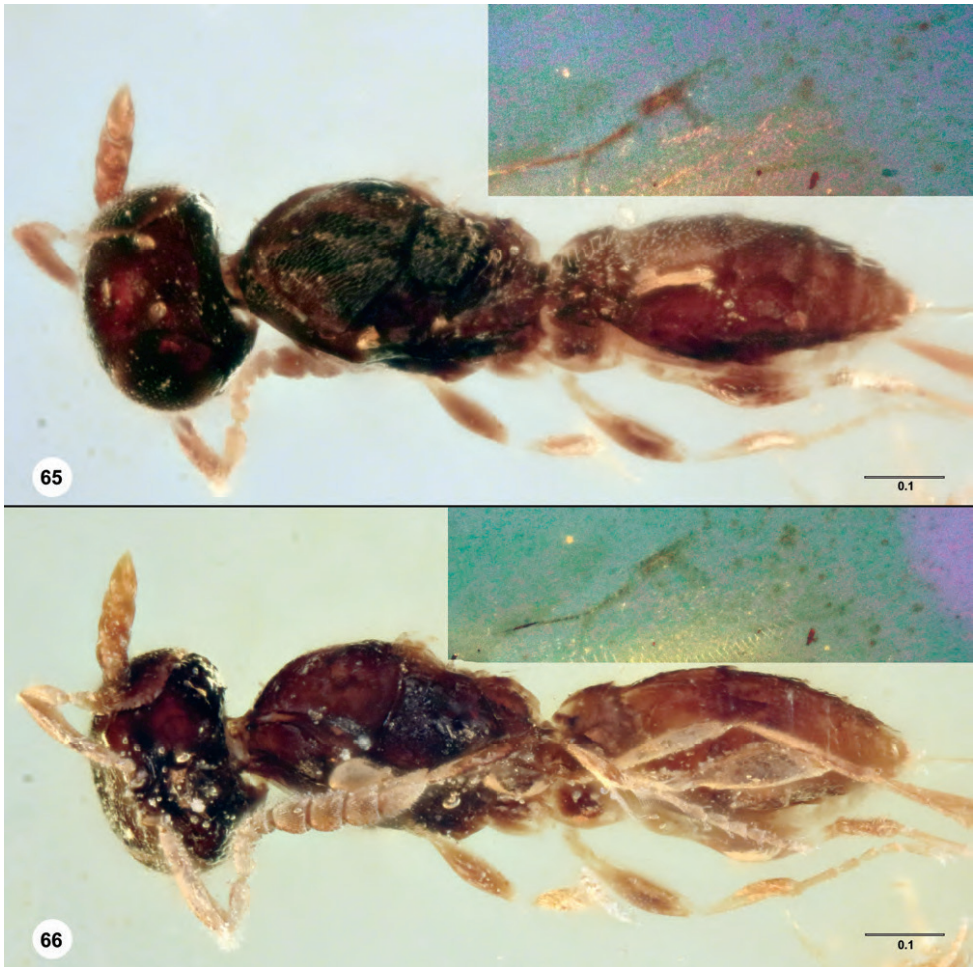
Material examined. Holotype female: **MYANMAR:** CNU-HYM-MA-2016101 (deposited in CNU).



Figures 62–64. *Proterosceliopsis wingerathi* (CNU-HYM-MA-2016101) **62** habitus, dorsal view **63** habitus, lateral view **64** habitus, ventrolateral view. Scale bars in millimeters.

Comments on Cretaceous Platygastriidae

The specimen illustrated in Figures 65–66 is the oldest representative of Platygastriidae known to us. It complies with the current and historical concepts of the family: 10-merous antennae; T2 as the largest tergite; malar sulcus absent; pronotal cervical sulcus is a furrow with what appears to be solidified exudate; transepisternal line present (not clear in photographs); S1 and anterior S2 with setal patches. Perhaps most interesting, this specimen has marginal, stigmal and (short) postmarginal veins, as in *Orwellium enigmaticum* Johnson, Masner & Musetti, which Johnson et al. (2009) considered to be the sister to the rest of Platygastriidae. This specimen is not sufficiently



Figures 65, 66. Platygastriidae, female (KU-NHM-ENT Bu-007) **65** head, mesosoma, metasoma, dorso-lateral view **66** head, mesosoma, metasoma, ventrolateral view. Insets are portions of image that have had the color altered to emphasize wing venation. Scale bars in millimeters.

well preserved to be described at the species level, but we consider it relevant to this paper because it supports our contention that the transepisternal line and glandular nature of the pronotal cervical sulcus are plesiomorphies for Platygastriidae.

Acknowledgements

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amber to EJT, including platygastriid specimen KU-NHM-ENT Bu-007, and facilitated examination of Lebanese amber. Former Smithsonian interns Dylan Johnston-Jordan, Melanie Anderson, Luke Kresslein, Anthony Cuminale, Colin Schwantes and Cate Paxton contributed many of the scanning electron micrographs. Ovidiu Popovici (“A.I. Cuza” University, Faculty of Biology, Iasi, Romania) provided images that enabled species determination of two female specimens in his collection. We thank the Florida Department of Agriculture and Consumer Services – Division of Plant Industry for their support on this contribution. This research was supported by the National Natural Science Foundation of China (No. 31730087 and 31672323), the Program for Changjiang Scholars and Innovative Research Team in University (grant number IRT-17R75), and Project of High-level Teachers in Beijing Municipal Universities (grant number IDHT20180518).

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Appendix I

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Term	Concept	URI	Preferred Term
T8	The tergum that is located on abdominal segment 8.	http://purl.obolibrary.org/obo/HAO_0000061	abdominal tergum 8
acetabulum	The scrobe that is located anteroventrally on the mesopsectus and accommodates the procoxa.	http://purl.obolibrary.org/obo/HAO_0000294	epinotemium
antenna	The appendage that is composed of ringlike sclerites and the anatomical structures encircled by these sclerites and that is articulated with the cranium.	http://purl.obolibrary.org/obo/HAO_0000101	antenna
antennal scrobe	The scrobe that is located dorsally of the antennal foramen and is for the reception of the antenna.	http://purl.obolibrary.org/obo/HAO_0001432	antennal scrobe
antennomere	The anatomical structure that is delimited by the proximal and distal margins of the antennal sclerite.	http://purl.obolibrary.org/obo/HAO_0000107	antennomere
anterior mesepisternal area	The area delimited anteriorly by the pronotal-mesoplectal suture, posterodorsally by the ventral limit of the subacopleural sulcus, and posteroventrally by the episternal foveal line.	http://purl.obolibrary.org/obo/HAO_0002459	anterior mesepisternal area
anterior thoracic spiracle	The spiracle that is located on the border of the pronotum and mesopleuron.	http://purl.obolibrary.org/obo/HAO_0000582	anterior thoracic spiracle
antepitracular setal patch	The setiferous patch that is located just anteriorly of the anterior thoracic spiracle.	http://purl.obolibrary.org/obo/HAO_0001985	antepitracular setal patch
basal vein	The wing vein that is basally located on the fore wing and connects or nearly connects the submarginal vein and the medial plus cubital veins.	http://purl.obolibrary.org/obo/HAO_0000170	basal vein
bulla	The anatomical region of the wing vein that is less melanized and more flexible than surrounding anatomical wing vein regions and corresponds to the intersection of the wing vein with a flexion line.	http://purl.obolibrary.org/obo/HAO_0000184	bulla
carina	The process that is elongate and external.	http://purl.obolibrary.org/obo/HAO_0000188	carina
central keel	The frontal line that is a carina.	http://purl.obolibrary.org/obo/HAO_0001929	central keel
clava	The anatomical cluster that is composed of apical flagellomeres bearing multiporous plates in female organism.	http://purl.obolibrary.org/obo/HAO_0000203	clava
clypeus	The area that corresponds to the site of origin of the clypeo-epipharyngeal muscle.	http://purl.obolibrary.org/obo/HAO_0000212	clypeus
conjunctiva	The area of the cuticle that is weakly sclerotized, with thin exocuticle.	http://purl.obolibrary.org/obo/HAO_0000221	conjunctiva
costa	The wing vein that is anterior to the subcosta and is connected to the humeral plate.	http://purl.obolibrary.org/obo/HAO_0000225	costa
coxa	The leg segment that is connected to the body and to the trochanter via conjunctivae and muscles.	http://purl.obolibrary.org/obo/HAO_0000228	coxa
cubital vein	The longitudinal vein that is posterior to the marginal vein.	http://purl.obolibrary.org/obo/HAO_0000237	cubital vein
dorsal metapleural area	The area that is delimited posterodorsally by the metapleural carina and anteroventrally by the metapleural sulcus.	http://purl.obolibrary.org/obo/HAO_0000261	dorsal metapleural area
egg	.	http://purl.obolibrary.org/obo/HAO_0000286	egg
episternal foveae	The row of impressions that is located on the anteroventral edge of the mesopleuron and is correspond to the site of origin of the mesopleuro-mesobasalar muscle.	http://purl.obolibrary.org/obo/HAO_0001509	episternal foveae
eye	The compound organ that is composed of ommatidia.	http://purl.obolibrary.org/obo/HAO_0000217	eye

Term	Concept	URI	Preferred Term
facial striae	The anatomical cluster anterior to the malar sulcus that is composed of carinae radiating from the pleurostomal condyle.	http://purl.obolibrary.org/obo/HAO_0002376	facial striae
felt field	The setiferous patch that is located sublaterally on an abdominal sternum.	http://purl.obolibrary.org/obo/HAO_0000322	felt field
fore wing	The wing that is located on the mesothorax.	http://purl.obolibrary.org/obo/HAO_0000351	fore wing
frons	The area that is located dorsally of the ventral margin of the antennal rim and ventrally of the anterior ocellus medial to the inner margins of the eye and malar line.	http://purl.obolibrary.org/obo/HAO_0001044	upper face
frontal ledge	The edge that traverses the upper face between the antennal foramen and the median ocellus separating a more horizontal dorsal and a more vertical ventral area.	http://purl.obolibrary.org/obo/HAO_0001886	frontal ledge
head	The tagma that is located anterior to the thorax.	http://purl.obolibrary.org/obo/HAO_0000397	head
hyperocipital carina	The carina that extends on the vertex between the outer orbits.	http://purl.obolibrary.org/obo/HAO_0000406	hyperocipital carina
integument	The anatomical system that forms the covering layer of the animal, ectodermal in origin and composed of epidermal cells producing the cuticle.	http://purl.obolibrary.org/obo/HAO_0000421	integument
lateral ocellus	The ocellus that is paired.	http://purl.obolibrary.org/obo/HAO_0000481	lateral ocellus
lateral propodeal carina	The carina that arises submedially from the anterior margin of the metapestral-propodeal complex, is longitudinal and extends towards the propodeal foramen.	http://purl.obolibrary.org/obo/HAO_0001919	lateral propodeal carina
malar striae	The anatomical cluster posterior to the malar sulcus that is composed of carinae radiating from the pleurostomal condyle.	http://purl.obolibrary.org/obo/HAO_0002373	malar striae
malar sulcus	The sulcus that extends between the ventral margin of the compound eye and the base of the mandible.	http://purl.obolibrary.org/obo/HAO_0000504	malar sulcus
mandible	The appendage that is encircled by one sclerite that is connected to the cranium proximolaterally and to the maxillo-labial complex proximomedially via conjunctivae and articulates with the cranium via the anterior and posterior cranio-mandibular articulations.	http://purl.obolibrary.org/obo/HAO_0000506	mandible
margin	The line that delimits the periphery of an area.	http://purl.obolibrary.org/obo/HAO_0000510	margin
mesepimeral ridge	The ridge that extends along the posterior margin of the mesoplectus.	http://purl.obolibrary.org/obo/HAO_0000537	mesepimeral ridge
mesepimeral sulcus	The sulcus that extends along the posterior margin of the mesoplectus, delimits the mesepimeral area and corresponds to the mesepimeral ridge.	http://purl.obolibrary.org/obo/HAO_0000538	mesepimeral sulcus
mesopleural carina	The carina that crosses the mesopleuron and limits ventrally the femoral depression.	http://purl.obolibrary.org/obo/HAO_0000559	mesopleural carina
mesopleural epicoxal sulcus	The epicoxal sulcus that is located on the mesopleuron.	http://purl.obolibrary.org/obo/HAO_0000560	mesopleural epicoxal sulcus
mesopleural pit	The pleural pit that is located on the mesopleuron.	http://purl.obolibrary.org/obo/HAO_0000561	mesopleural pit
mesopleuron	The pleuron that is located in the mesothorax.	http://purl.obolibrary.org/obo/HAO_0001354	mesopleuron
mesoscutal humeral sulcus	The sulcus that extends medially along the parasutural carina and corresponds to a shallow ridge.	http://purl.obolibrary.org/obo/HAO_0000569	mesoscutal humeral sulcus
mesoscutal supra-humeral sulcus	The sulcus that extends along the anterior margin of the mesoscutum between the anterior-most point of the preaxilla and the anteromedian line and corresponds to the vertical lobe of the mesoscutum.	http://purl.obolibrary.org/obo/HAO_0000570	mesoscutal supra-humeral sulcus
mesoscutum	The scutum that is located on the mesonotum.	http://purl.obolibrary.org/obo/HAO_0000575	mesoscutum

Term	Concept	URI	Preferred Term
mesosoma	The anatomical cluster that is composed of the prothorax, mesothorax and the metapetal-propodeal complex.	http://purl.obolibrary.org/obo/HAO_0000576	mesosoma
metanotal trough	The area that is concave, and is delimited medially by the mesoscutellum, laterally by the supraalar area and posteriorly by the mesoscutellar arm.	http://purl.obolibrary.org/obo/HAO_0000600	metanotal trough
metapleural carina	The carina that delimits the metapleuron dorsally from the propodeum, extends from just ventral of the metapleural arm to the metacoxal articulation and passes anteroventral to the propodeal spiracle.	http://purl.obolibrary.org/obo/HAO_0000609	metapleural carina
metapleural sulcus	The line that corresponds with the metapleural ridge.	http://purl.obolibrary.org/obo/HAO_0000614	metapleural sulcus
metapleuron	The area of the metapetal-propodeal complex that is located laterally of the metadiscrimen.	http://purl.obolibrary.org/obo/HAO_0000621	metapleuron
mesoscutellum	The area that is located posteromedially on the mesonotum, is delimited laterally by the metanotal trough and corresponds to the reservoir of the dorsal vessel.	http://purl.obolibrary.org/obo/HAO_0000625	mesoscutellum
metasoma	The tagna that is connected anteriorly to the metapetal-propodeal complex at the propodeal foramen and consists of abdominal segments.	http://purl.obolibrary.org/obo/HAO_0000626	metasoma
metasomal depression	The acetabulum that is concave, surrounds the nucha and accommodates the base of the metasoma.	http://purl.obolibrary.org/obo/HAO_0000627	metasomal depression
metasomal segment	The abdominal segment that is located in the metasoma.	http://purl.obolibrary.org/obo/HAO_0001969	metasomal segment
netrion	The area that is located posteroventrally on the pronotum and corresponds to the site of origin of first flexor of the fore wing muscle.	http://purl.obolibrary.org/obo/HAO_0000644	netrion
netrion sulcus	The sulcus that anteriorly delimits the netrion.	http://purl.obolibrary.org/obo/HAO_0000646	netrion sulcus
notaullus	The line that extends submedially along the mesoscutum and corresponds to the median border of the site of origin of the first mesopleuro-mesonotal muscle.	http://purl.obolibrary.org/obo/HAO_0000647	notaullus
occipital carina	The carina that surrounds dorsolaterally the occiput.	http://purl.obolibrary.org/obo/HAO_0000653	occipital carina
ocellar diameter	The diameter of the ocellus.	http://purl.obolibrary.org/obo/HAO_0002107	ocellar diameter
ocellus	The multi-tissue structure that is located on the top of the head, composed of the corneal lens, pigment cell, rhabdoms and synaptic plexus.	http://purl.obolibrary.org/obo/HAO_0000661	ocellus
orbital carina	The carina that is located on the face, parallels the inner orbit and is paired.	http://purl.obolibrary.org/obo/HAO_0000810	preorbital carina
ovipositor	The anatomical cluster that is composed of the first valvulae, second valvulae, third valvulae, first valvifers, second valvifers and female T9.	http://purl.obolibrary.org/obo/HAO_0000679	ovipositor
postacetabular sulcus	The sulcus that extends posteriorly along the epicnemial carina.	http://purl.obolibrary.org/obo/HAO_0000741	postacetabular sulcus
posterior mesoscutellar sulcus	The line that extends along the posterior margin of the mesoscutellum and corresponds to the posterior mesoscutellar ridge.	http://purl.obolibrary.org/obo/HAO_0000757	posterior mesoscutellar sulcus
posterior pronotal inflection	The inflection that extends along the posterior margin of the pronotum and articulates with the anterior mesopleural inflection.	http://purl.obolibrary.org/obo/HAO_0000761	posterior pronotal inflection
postmarginal vein	The abscissa that is marginal and located distal to the marginal vein.	http://purl.obolibrary.org/obo/HAO_0000783	postmarginal vein
prespecular sulcus	The sulcus that delimits anteriorly the speculum and corresponds to the anterior margin of the speculum.	http://purl.obolibrary.org/obo/HAO_0000816	prespecular sulcus
pronotal cervical sulcus	The sulcus that extends along the anterior margin of the pronotum and delimits the anterior rim of pronotum.	http://purl.obolibrary.org/obo/HAO_0000831	pronotal cervical sulcus

Term	Concept	URI	Preferred Term
pronotum	The notum that is located in the prothorax.	http://purl.obolibrary.org/obo/HAO_0000853	pronotum
propodeal epicoxal sulcus	The epicoxal sulcus that sets of the epicoxal lobe from the ventral part of the ventral propodeal area.	http://purl.obolibrary.org/obo/HAO_0000858	propodeal epicoxal sulcus
propopleuron	The pleuron that is articulated with the fore leg, connected dorsolaterally (anterolaterally) with the pronotum and ventrally (posteriorly) with the prosternum.	http://purl.obolibrary.org/obo/HAO_0000862	propopleuron
propodeal carina	The carina that is located on the propodeum.	http://purl.obolibrary.org/obo/HAO_0000864	propodeal carina
propodeum	The area of the metapleural-propodeal complex that is located posterior to the metapleural carina.	http://purl.obolibrary.org/obo/HAO_0001249	propodeum
sculpture	The area that is located on the sclerite and that is composed of repetitive anatomical structures.	http://purl.obolibrary.org/obo/HAO_0000913	sculpture
scutoseutellar sulcus	The sulcus that extends along the scutoseutellar suture.	http://purl.obolibrary.org/obo/HAO_0000919	scutoseutellar sulcus
segment	An anatomical structure that is metameric and is connected to other metameric subdivisions by muscles and is delimited by its sclerites.	http://purl.obolibrary.org/obo/HAO_0000929	segment
sensillum	A sense organ embedded in the integument and consisting of one or a cluster of sensory neurons and associated sensory structures, support cells and glial cells forming a single organized unit with a largely bonafide boundary.	http://purl.obolibrary.org/obo/HAO_0000933	sensillum
skaphion	The area that is anteriorly on the mesonotum and delimited posteriorly by the skaphion carina.	http://purl.obolibrary.org/obo/HAO_0000940	skaphion
spiracle	The anatomical cluster that is composed of the distal end of the trachea and the margin of the sclerite or conjunctiva surrounding the spiracular opening.	http://purl.obolibrary.org/obo/HAO_0000950	spiracle
sternite	The sclerite that is located on the sternum.	http://purl.obolibrary.org/obo/HAO_0000955	sternite
stigmatal vein	The vein that is adjacent proximally to the preostigma.	http://purl.obolibrary.org/obo/HAO_0002428	stigmatal vein
submarginal vein	Basal-most portion of the forewing vein complex that occurs behind the costal cell; measured from the constriction that delimits the humeral plate to the point at which the vein touches the leading edge of the wing apically.	http://purl.obolibrary.org/obo/HAO_0000972	submarginal vein
sulcus	The groove that corresponds to a ridge.	http://purl.obolibrary.org/obo/HAO_0000978	sulcus
tergite	The sclerite that is located on the tergum.	http://purl.obolibrary.org/obo/HAO_0001005	tergite
trachea	The cuticular invagination that is tubular, branched into tracheoles and bears the taenidia.	http://purl.obolibrary.org/obo/HAO_0002415	trachea
transpleuristernal line	The line that is longitudinal, extends ventrolaterally on the mesopleuron and corresponds with the site of origin of the second and third mesopleuro-third axillary sclerite of fore wing muscle and the second mesopleuro-mesonotal muscle.	http://purl.obolibrary.org/obo/HAO_0001205	transpleuristernal line
transverse pronotal carina	The carina that delimits posteriorly the pronotal neck.	http://purl.obolibrary.org/obo/HAO_0001031	transverse pronotal carina
venation	The anatomical cluster that is composed of abscissae.	http://purl.obolibrary.org/obo/HAO_0001096	venation
ventral metapleural area	The area that is located on the metapleuron anteroventrally of the metapleural sulcus.	http://purl.obolibrary.org/obo/HAO_0001062	ventral metapleural area
wing	The appendage that is between the notum and the pectus and is connected to the body by the axillary sclerite muscles.	http://purl.obolibrary.org/obo/HAO_0001089	wing