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# A close affinity of the enigmatic genus *Stegocoleus* with *Lepidomma* revealed by new fossil evidence (Coleoptera: Archostemata: Ommatidae)

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## Abstract

*Stegocoleus* Jarzembowski & Wang is an enigmatic genus in the family Ommatidae, known to date only from Burmese amber. This genus possesses a unique combination of characters, including antennal grooves on the ventral side of head, well-developed epipleural rims, and presence of separated procoxae, which makes its systematic position unclear. Here we report two new species of *Lepidomma* from mid-Cretaceous Burmese amber, *L. longisquama* **sp. nov.** and *L. jarzembowskii* **sp. nov.** Based on these well-preserved specimens and new morphological details revealed by widefield fluorescence and confocal microscopy, we discuss the morphological similarities between *Lepidomma* and the enigmatic *Stegocoleus*. We suggest that *Stegocoleus* is not a basal ommatid, but a highly derived form of ommatid beetles.

**Keywords:** Archostemata, Ommatidae, *Stegocoleus*, *Lepidomma*, Burmese amber

## Introduction

Ommatidae is a small family in the ancient beetle suborder Archostemata, with only three extant genera and seven extant species (Beutel *et al*., 2008; Escalona *et al*., 2020). The family was much more diverse in the Mesozoic, with more than 150 fossil species described to date (Kirejtshuk, 2020). Although some authors regard Ommatidae as a subfamily within Cupedidae *sensu lato* (*e.g*., Ponomarenko, 2000; Kirejtshuk, 2020), in this paper we treat Ommatidae and Cupedidae as separate families based on recent molecular phylogenetic studies (McKenna *et al*., 2015, 2019).

*Stegocoleus* Jarzembowski & Wang is an enigmatic ommatid genus with three described species known only from mid-Cretaceous Burmese amber (Jarzembowski & Wang, 2016; Tihelka *et al*., 2020). While some features such as short antennae, and simple tarsi are typical of ommatids, *Stegocoleus* also possesses several characters unusual for the family (Jarzembowski & Wang, 2016). Among Archostemata, antennal grooves located on the ventral (ventrolateral) side of head as in *Stegocoleus* are otherwise known only in the extant ommatid genus *Tetraphalerus* Waterhouse. The well-developed epipleural rims, that in *Stegocoleus* give the beetle's bodies a conspicuous and sometimes almost heart-shaped appearance, are characteristic of the ommatid tribe Brochocoleini. The presence of separated procoxae is unique within Ommatidae but is typical for Cupedidae. Based on this mixed set of characters, Jarzembowski & Wang (2016) suggested that *Stegocoleus* might represent a stem-group ommatid.

*Lepidomma* Jarzembowski, Wang & Zheng is a typical ommatid genus, with only one species previously reported from Burmese amber (Jarzembowski *et al*., 2019). Perhaps the most eye-catching feature of this genus is its outwardly directed scales borne on the epipleural rim. However, the detailed external morphology of *Lepidomma* is poorly known, since the reported specimens are strongly carbonised and appear to be almost completely black under incident light.

In this study, we examined several previously published and newly discovered specimens of *Lepidomma*.

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Based on these well-preserved specimens, we discuss the morphological similarities between *Lepidomma* and *Stegocoleus*, which sheds new light on the systematic position of the latter genus.

## Material and methods

The Burmese amber specimens studied herein originate from amber mines near Noije Bum Hill (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber pieces were trimmed with a small table saw, ground with emery papers of different grain sizes, and finally polished with polishing powder.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope or a Zeiss Lumar V12 stereo microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope. In the multicoloured images, colours were coded based on Z-depth. Images were stacked in Helicon Focus 7.0.2, Zerene Stacker 1.04, or ZEN 2.3 (Blue Edition) to increase the depth of field, and further processed in Adobe Photoshop CC to enhance contrast.

The following specimens were examined for this study:

*Lepidomma jarzembowskii* **sp. nov.**: NIGP173372 (holotype).

*Lepidomma longisquama* **sp. nov.**: NIGP173371 (holotype).

*Lepidomma tianae* Jarzembowski, Wang & Zheng: NIGP169479 (holotype).

*Lepidomma* sp.: NIGP169480 (originally identified as *Lepidomma* affl. *tianae* in Jarzembowski *et al*., 2019).

*Stegocoleus arkonus* Tihelka, Huang & Cai: NIGP170946 (holotype, incorrectly labeled as NIGP170655 in Tihelka *et al*., 2020), NIGP173373.

*Stegocoleus caii* Jarzembowski & Wang: NIGP157004 (holotype), NIGP173374 (paratype, originally labeled as a Xia collection specimen in Jarzembowski & Wang, 2016).

*Stegocoleus lawrencei* Tihelka, Huang & Cai: NIGP170947 (holotype, incorrectly labeled as NIGP170656 in Tihelka *et al*., 2020).

## Systematic palaeontology

### Order Coleoptera Linnaeus, 1758

### Suborder Archostemata Kolbe, 1908
### Family Ommatidae Sharp & Muir, 1912

### Genus *Lepidomma* Jarzembowski, Wang & Zheng, 2019 stat. resurr.

**Type species.** *Lepidomma tianae* Jarzembowski, Wang & Zheng, 2019, by original designation.

**Species included.** *Lepidomma tianae* **comb. rev.**, *Lepidomma longisquama* **sp. nov.**, *Lepidomma jarzembowskii* **sp. nov.**

**Remarks.** *Lepidomma* was synonymised with *Clessidromma* Jarzembowski, Wang & Zheng by Kirejtshuk (2020), based primarily on their superficially similar pronotal shape. However, the synonymisation was made without examining specimens of either genus (A.G. Kirejtshuk, pers. comm.). All three specimens of *Lepidomma* and *Clessidromma* described by Jarzembowski *et al*. (2018, 2019) are strongly carbonised and appear almost completely black in the original published photos, which makes a proper evaluation of their systematic position difficult.

In the type species of *Clessidromma*, *C. palmeri* Jarzembowski, Wang & Zheng, the medial portion of the ventral surface of the head forms a distinctly elevated platform, extending to the posterior end of the neck, whereas such a structure is absent in *Lepidomma*. More importantly, *Clessidromma* lacks the elytral carinae and ridged scales that are present in *Lepidomma* and *Stegocoleus*. We therefore consider *Lepidomma* as a separate genus from *Clessidromma*, and formally resurrect the genus *Lepidomma*.

***Lepidomma longisquama*** Li & Cai, **sp. nov.** (Figs 1–2)

**Material.** Holotype, NIGP173371, sex unknown.

**Etymology.** The specific name is derived from the Latin "longus", long, and "squama", scale, referring to its comparatively elongate scales on the lateral elytral margins.

**Diagnosis.** *Lepidomma longisquama* **sp. nov.** is similar to the other two *Lepidomma* species. However, compared to them, the scales on the lateral edges of the elytra are much more elongate in *L. longisquama* (Fig. 1). Besides, in *L. jarzembowskii* **sp. nov.** and *L. tianae* the scales on the lateral sides of the elytral disc form small patches (Figs 3B, 5C), while in *L. longisquama* the scales on the lateral sides of elytral disc are more or less continuous (Figs 1C, 2E). In *L. tianae* there is a pair of carinae or protuberances located at exactly the apex of the elytra, and the carinae are almost contiguous with the elytra closed (Fig. 5E), while in *L. longisquama* the carinae at this position are either absent or much weaker.

**Locality and horizon.** Amber mine located near

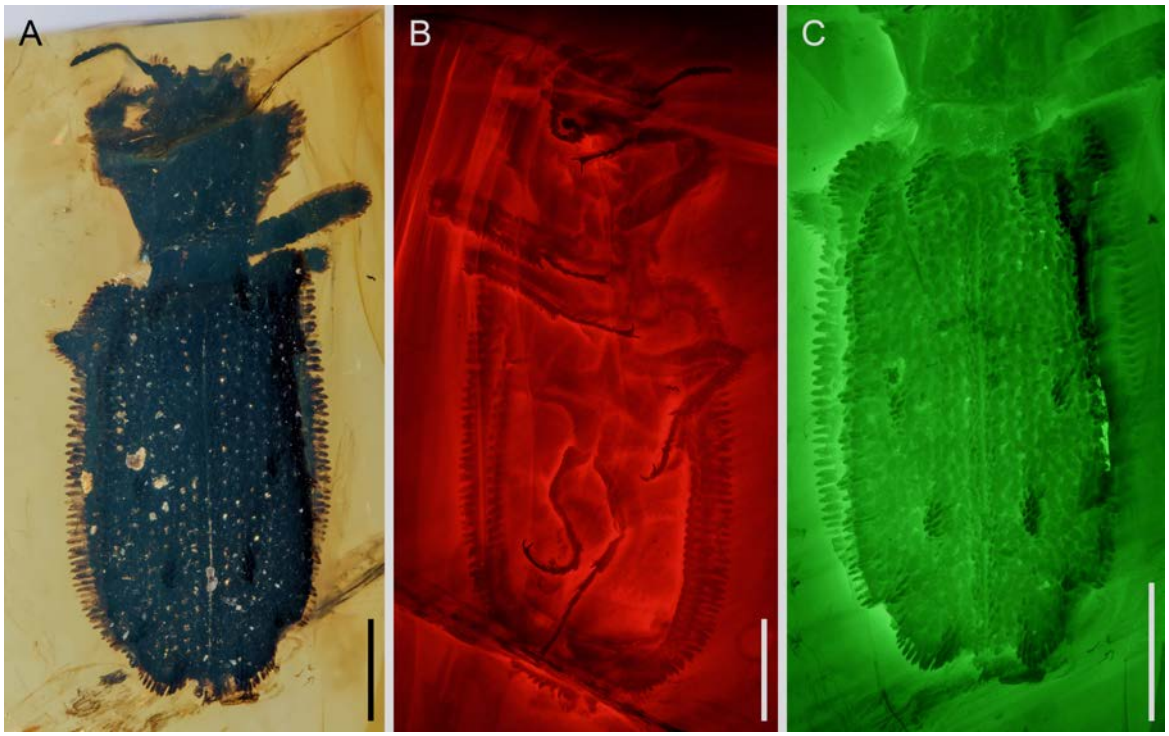


**FIGURE 1.** General habitus of *Lepidomma longisquama* **sp. nov.**, holotype, NIGP173371. **A**, Dorsal view, under incident light. **B**, Ventral view, under widefield fluorescence. **C**, Elytra, under widefield fluorescence. Scale bars: 1 mm.

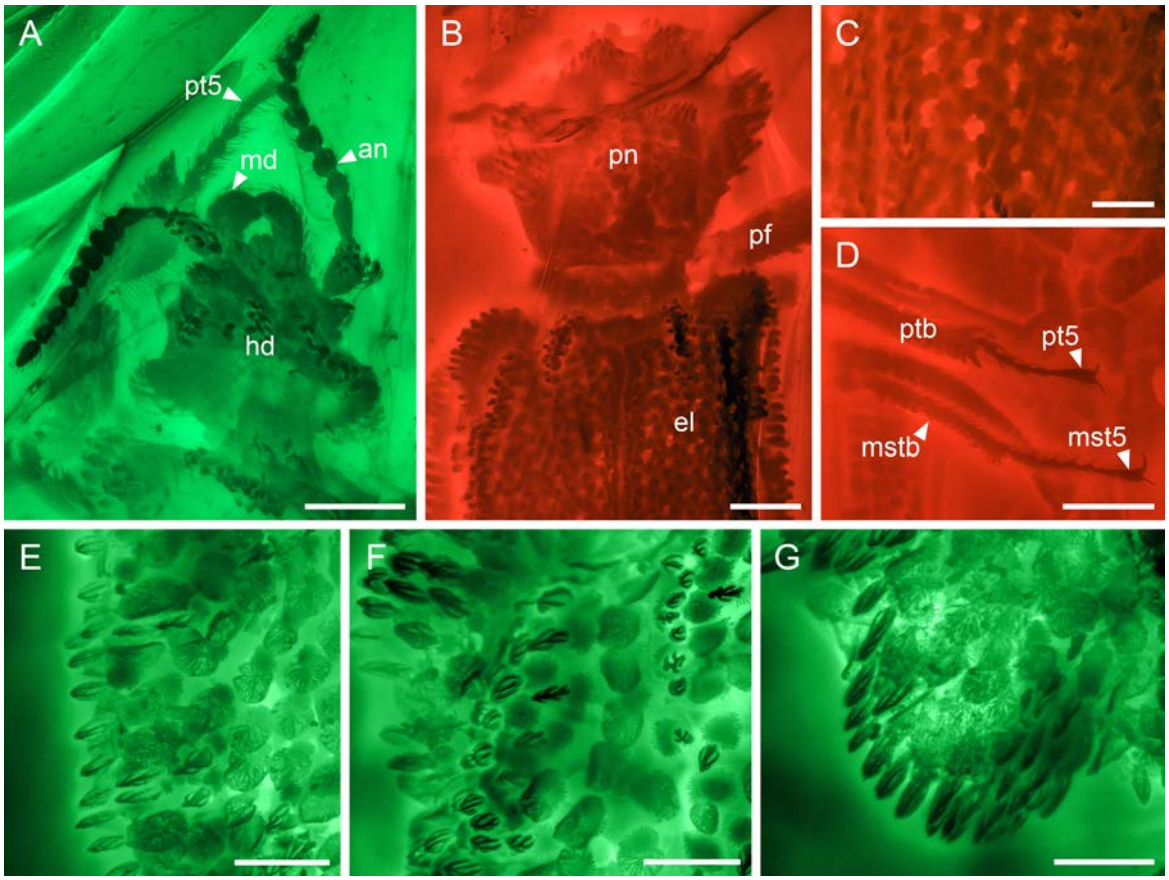


**FIGURE 2.** Details of *Lepidomma longisquama* **sp. nov.**, holotype, NIGP173371, under widefield fluorescence (**A**–**D**) or confocal microscopy (**E**–**G**). **A**, Head, dorsal view. **B**, Prothorax and anterior portion of elytra, dorsal view. **C**, Window punctures on elytra, dorsal view. **D**, Pro- and mesothoracic legs. **E**, Scales on lateral margin of elytral disc, dorsal view. **F**, Anterior elytral carina, dorsal view. **G**, Posterior elytral carina, dorsal view. Abbreviations: an, antenna; el, elytron; hd, head; md, mandible; mst5, mesotarsomere 5; mstb, mesotibia; pf, profemur; pn, pronotum; pt5, protarsomere 5; ptb, protibia. Scale bars: 500 μm in **A**–**B**, **D**, 200 μm in **C**, **E**–**G**.

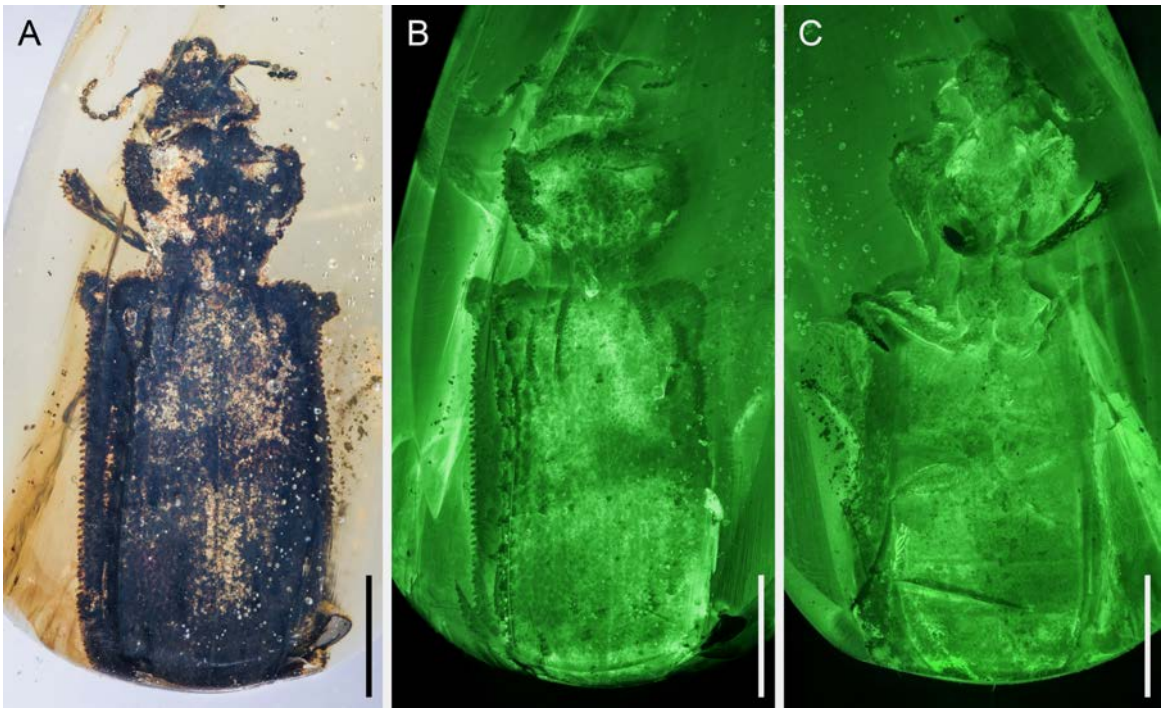


**FIGURE 3.** General habitus of *Lepidomma jarzembowskii* **sp. nov.**, holotype, NIGP173372. **A**, Dorsal view, under incident light. **B**, Dorsal view, under widefield fluorescence. **C**, Ventral view, under widefield fluorescence. Scale bars: 2 mm.

Noije Bum, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

**Description.** Head (Fig. 2A) prognathous, subtriangular, 1.2 mm long (including mandibles, excluding neck) and 1.2 mm wide, distinctly narrowed behind temples, with patches of scales on dorsal protuberances. Temples prominent, with scales, semi-encircling eyes. Labrum with emarginate apex. Mandibles setose, with vertically arranged teeth. Antennae 11-segmented, inserted anterolaterally on head; antennomere 1 (scape) widened, covered with scales; antennomeres 2–11 covered with setae; antennomere 3 elongate; antennomeres 4–10 moniliform; antennomere 11 fusiform.

Pronotal disc (Fig. 2B) subtrapezoidal, 1.8 mm long and 1.9 mm wide, narrowed posteriorly; anterior edge with two scaly protuberances extending anteriorly, forming a collar-like structure; lateral edge raised, also with scales; anterior angles rounded, slightly produced. Prosternum transverse; anterior edge concave, fitting against the somewhat globular neck base; prosternal process incomplete and short, narrowed apically. Mesoventrite at middle with acute anterior projection separating paired procoxal rests.

Elytra 1.65 times as long as their combined width, subparallel, gradually tapering in the apical quarter, with rows of window punctures (Fig. 2C). Elytral disc with surface carinae bearing scales; three pairs of prominent carinae located near elytral base (Fig. 2B, F); one pair of prominent carinae located near elytral apex (Fig. 2G); sides of elytral disc with more or less continuous scales (Fig. 2E).

Legs (Fig. 2D) with scales and setae, but tarsus with setae only. Procoxae oval, contiguous. Femora stout. Tibiae thinner; tibial spurs well-developed. Tarsi slender, five-segmented; tarsomeres without ventral lobes; tarsomere 5 more than twice as long as the preceding segment; pretarsal claws simple.

Abdomen with five flattened ventrites, with edges abutting; ventrite 5 nearly twice as long as ventrite 4.

*Lepidomma jarzembowskii* Li & Cai, **sp. nov.** (Figs 3, 4)

**Material.** Holotype, NIGP173372, sex unknown.

**Etymology.** The species is named after the palaeoentomologist Dr Edmund A. Jarzembowski, in recognition of his contribution to the study of fossil archostematans.

**Diagnosis.** *Lepidomma jarzembowskii* **sp. nov.** is similar to the other two *Lepidomma* species. The differences between *L. jarzembowskii* and *L. longisquama* **sp. nov.** have been noted above. The posterior portion of the *L. jarzembowskii* holotype is polished away; therefore the shape and position of its posterior elytral carinae remain unknown. However, *L. jarzembowskii* appears to be slimmer than *L. tianae*. Moreover, the elytral margins of *L. tianae* are slightly curved, while the elytra margins of *L. jarzembowskii* are much straighter, at least in the anterior half.

**Locality and horizon.** Amber mine located near

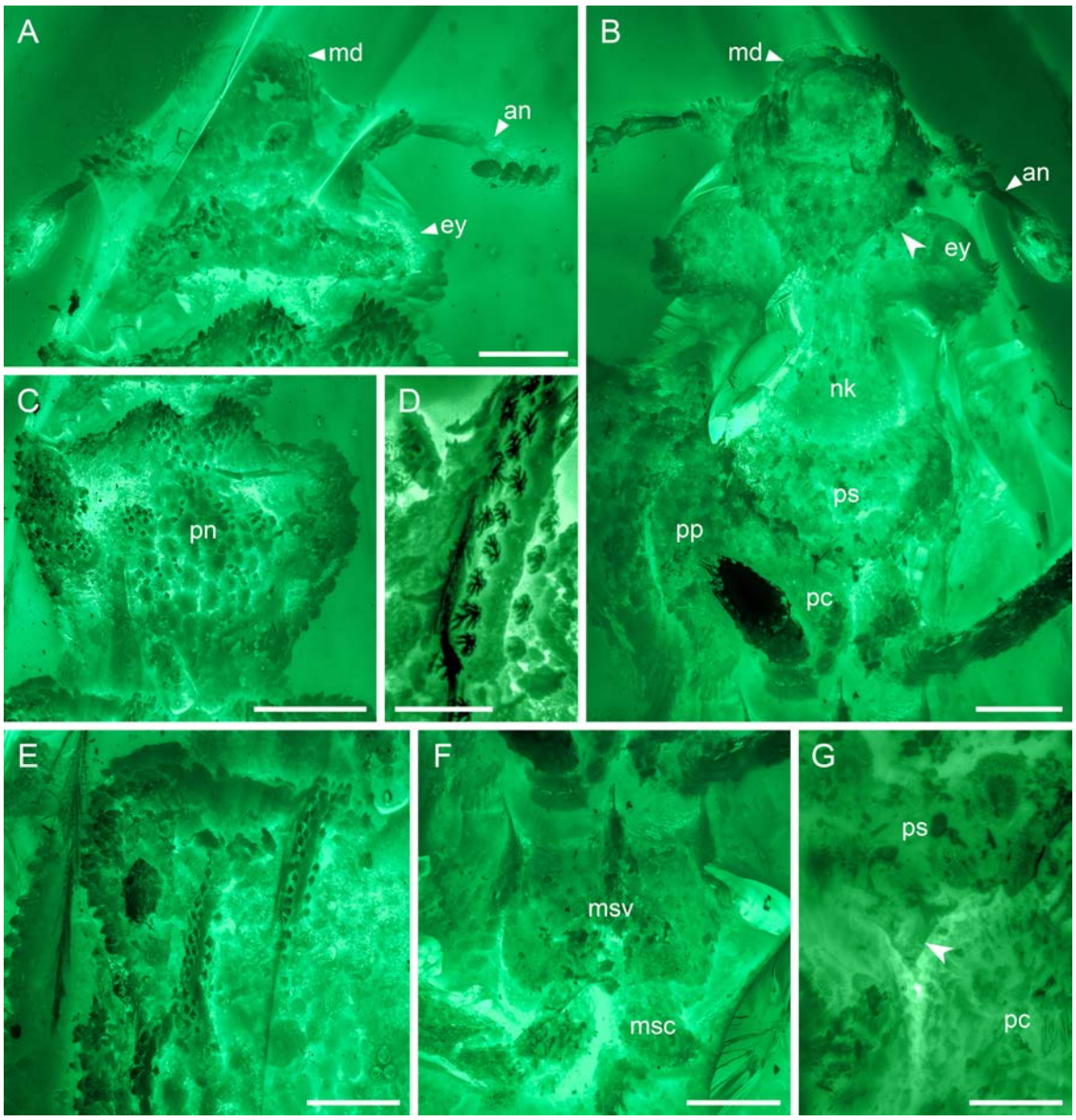


**FIGURE 4.** Details of *Lepidomma jarzembowskii* **sp. nov.**, holotype, NIGP173372, under widefield fluorescence (**A**–**C**, **E**, **F**) or confocal microscopy (**D**, **G**). **A**, Head, dorsal view. **B**, Head and prothorax, ventral view, showing the possible antennal groove (arrowhead). **C**, Prothorax, dorsal view. **D**, Anterior elytral carina, dorsal view. **E**, Anterior portion of left elytron, dorsal view. **F**, Mesothorax, ventral view. **G**, Prosternal process (arrowhead), ventral view. Abbreviations: an, antenna; ey, compound eye; md, mandible; msc, mesocoxa; msv, mesoventrite; nk, neck; pc, procoxa; pn, pronotum; pp, propleuron; ps, prosternum. Scale bars: 1 mm in **C**, 500 μm in **A**, **B**, **E**, **F**, 200 μm in **D**, **G**.

Noije Bum, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

**Description.** Head (Fig. 4A, B) prognathous, subtriangular, 1.5 mm long (including mandibles, excluding neck) and 1.8 mm wide, distinctly narrowed behind temples, with patches of scales on dorsal protuberances. Temples prominent, with scales, semi-encircling eyes. Mandibles setose apically; scaly basally, with vertically arranged teeth. Antennae 11-segmented, inserted anterolaterally on head; antennomere 1 (scape) widened, covered with scales; antennomeres 2–11 covered with setae; antennomere 3 elongate; antennomeres 4–10 moniliform; antennomere 11 fusiform. Inconspicuous grooves present on ventral surface between eyes and medial portion of head (Fig. 4B), possibly accommodating antennae.

Pronotal disc (Fig. 4C) subtrapezoidal, 2.7 mm long and 3.2 mm wide, narrowed posteriorly; anterior edge with two scaly protuberances extending anteriorly, forming a collar-like structure; lateral edge raised, also with scales; anterior angles rounded, slightly produced.

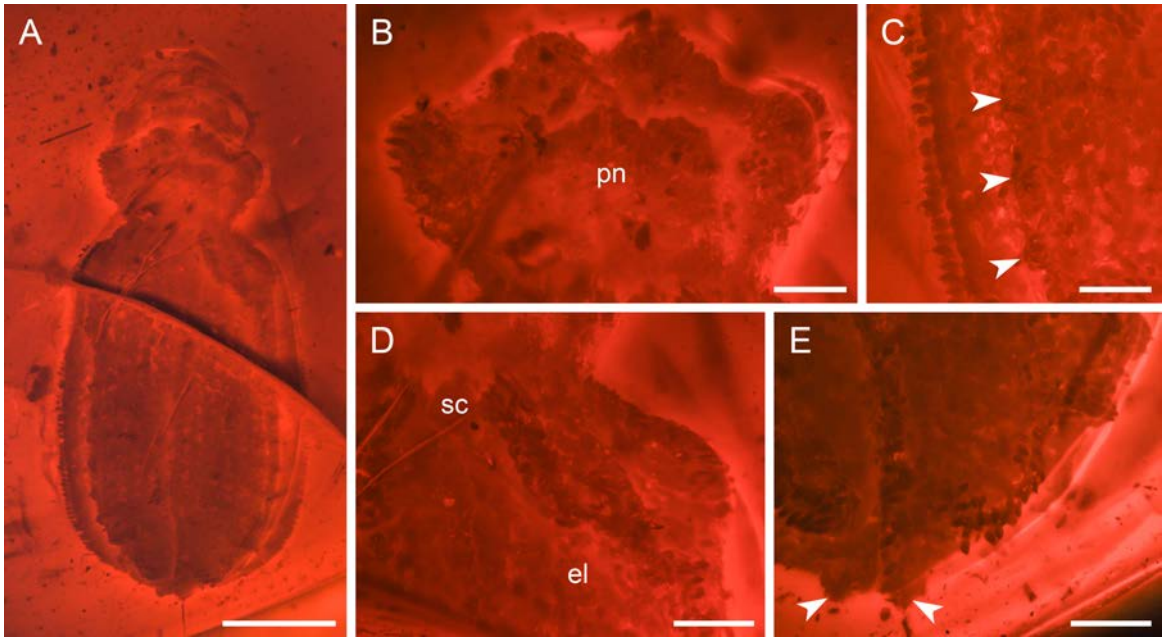


**FIGURE 5.** *Lepidomma tianae*, holotype, NIGP169479, dorsal view, under widefield fluorescence. **A**, General habitus. **B**, Prothorax. **C**, Patches of scales on lateral margin of elytral disc (arrowheads). **D**, Anterior portion of right elytron. **E**, Posterior portion of right elytron, showing the carinae at elytral apices (arrowheads). Abbreviations: el, elytron; pn, pronotum; sc, scutellum. Scale bars: 2 mm in **A**, 500 μm in **B**–**E**.

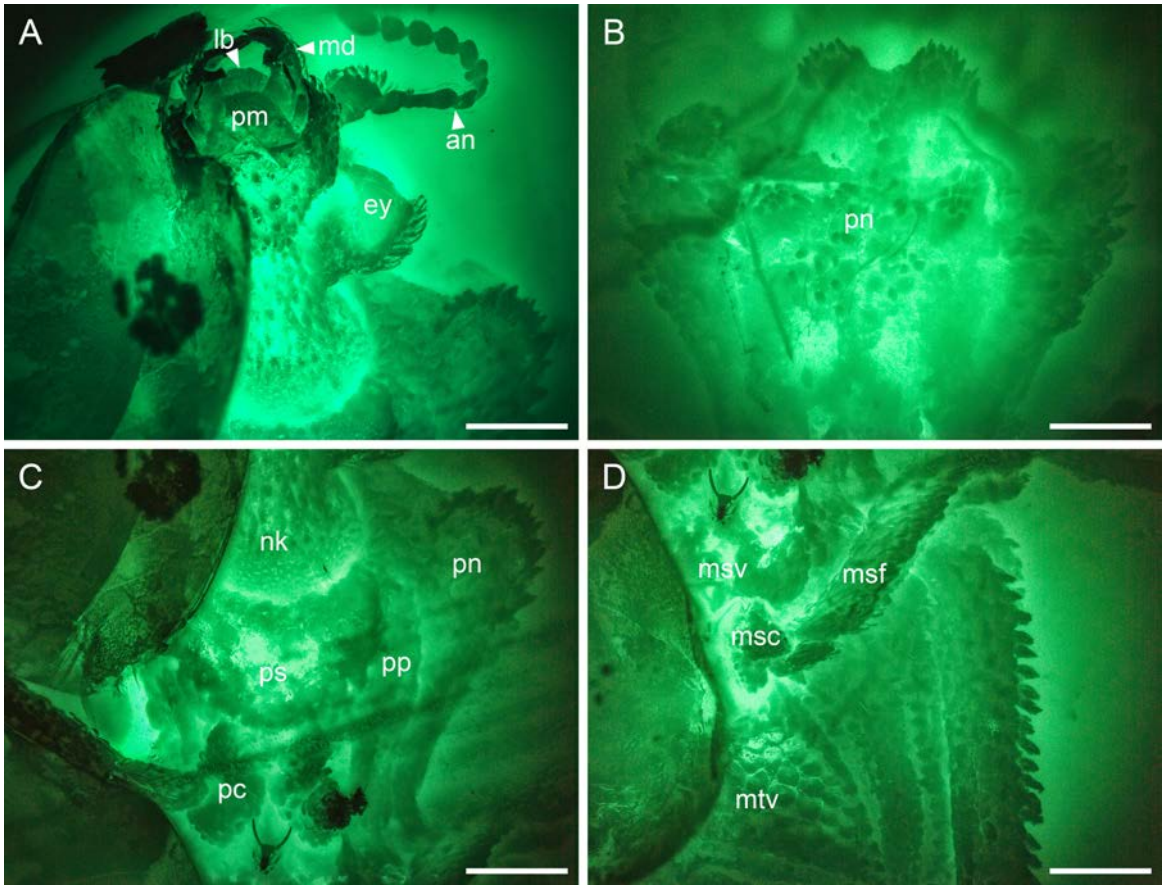


**FIGURE 6.** Details of *Lepidomma* sp., NIGP169480, under widefield fluorescence. **A**, Head, ventral view. **B**, Prothorax, dorsal view. **C**, Prothorax, ventral view. **D**, Meso- and metathorax, ventral view. Abbreviations: an, antenna; ey, compound eye; lb, labrum; md, mandible; msc, mesocoxa; msf, mesofemur; msv, mesoventrite; mtv, metaventrite; nk, neck; pc, procoxa; pm, prementum; pn, pronotum; pp, propleuron; ps, prosternum. Scale bars: 500 μm.

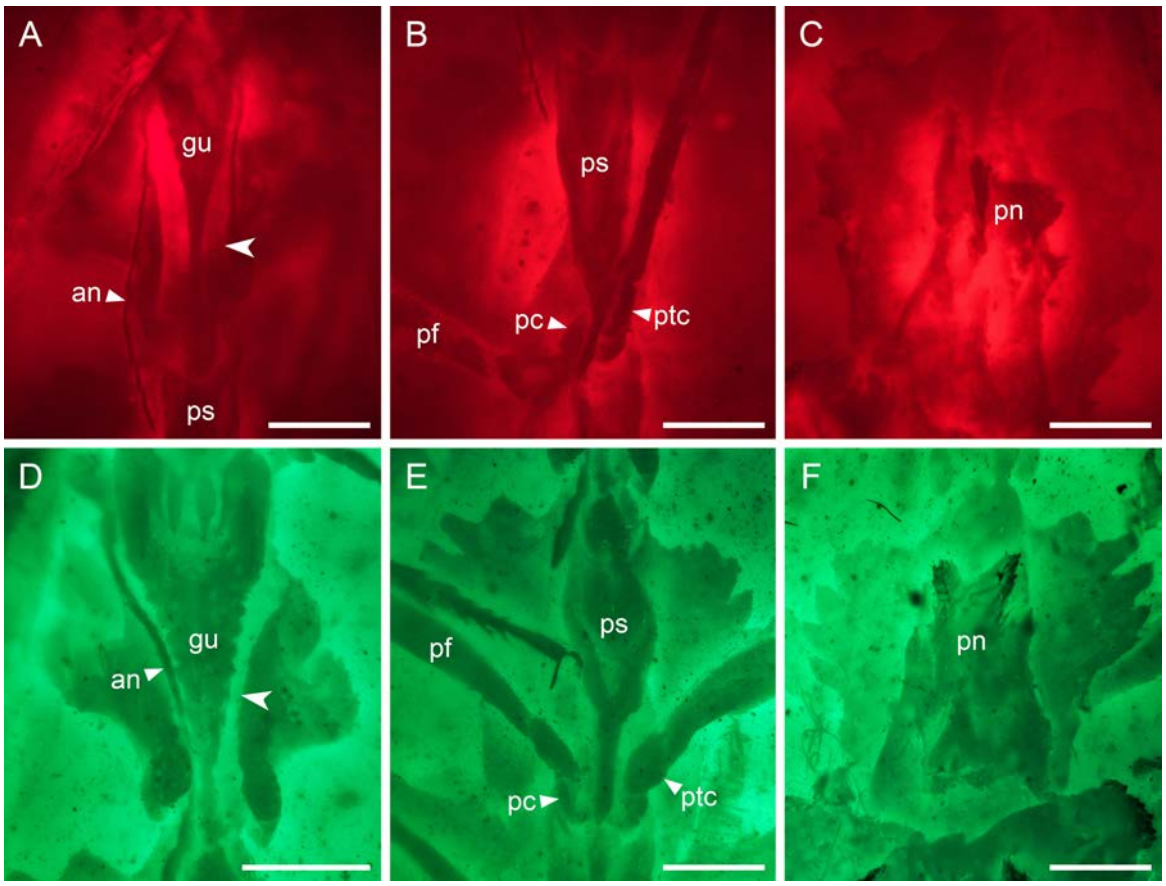


**FIGURE 7.** Comparison between *Stegocoleus caii*, NIGP157004 (**A**–**C**), and *S. lawrencei*, NIGP170947 (**D**–**F**) under widefield fluorescence. **A**, **D**, Head, ventral view, showing antennal grooves (arrowheads). **B**, **E**, Prothorax, ventral view. **C**, **F**, Prothorax, dorsal view. Abbreviations: an, antenna; gu, gula; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptc, protrochanter. Scale bars: 500 μm.

Prosternum (Fig. 4B) transverse; anterior edge concave, fitting against the somewhat globular neck base; prosternal process (Fig. 4G) incomplete and short, narrowed apically. Mesoventrite (Fig. 4F) at middle with acute anterior projection separating paired procoxal rests.

Elytra elongate, essentially parallel-sided in the anterior half. Elytral disc with surface carinae bearing scales; three pairs of prominent carinae located near elytra base (Fig. 4D, E); sides of elytral disc with small patches of scales.

Legs with scales and setae, but tarsus with setae only. Procoxae oval, contiguous. Femora stout. Tibiae thinner; tibial spurs well developed. Tarsi slender, five-segmented; tarsomeres without ventral lobes; tarsomere 5 more than twice as long as the preceding segment; pretarsal claws simple.

Abdomen with probably five flattened ventrites, with edges abutting.

## Discussion

Jarzembowski and Wang (2016) originally described *Stegocoleus* as a monotypic genus and designated five paratypes for *S. caii*. However, some of the paratypes obviously belong to different species. For example, the specimen illustrated in fig. 1A–E in Jarzembowski and Wang (2016) differs from the holotype of *S. caii* significantly and was later described as *S. arkonus* by Tihelka *et al*. (2020). Tihelka *et al*. (2020) furthermore recognised a third *Stegocoleus* species, *i.e*., *S. lawrencei*, which is morphologically similar to *S. caii*. Tihelka *et al*. (2020) noted three differences between *S. lawrencei* and *S. caii*: the shape of gula (since no gular sutures are visible here, the term "gula" here refers to the region between antennal grooves and does not necessarily correspond to the true gula), pronotum, and scutellum. However, the holotype of *S. caii* was poorly figured and illustrated in the original paper by Jarzembowski & Wang (2016). After a detailed examination under a fluorescence microscope, it turns out that the gula between antennal grooves was also subtriangular in the holotype of *S. caii* (Fig. 7A), and its two pronotal protrusions were similarly located on a laterally bordered elevated region (Fig. 7C). Besides, the holotype of *S. caii* was moderately distorted, which could probably account for its superficial difference in the shape

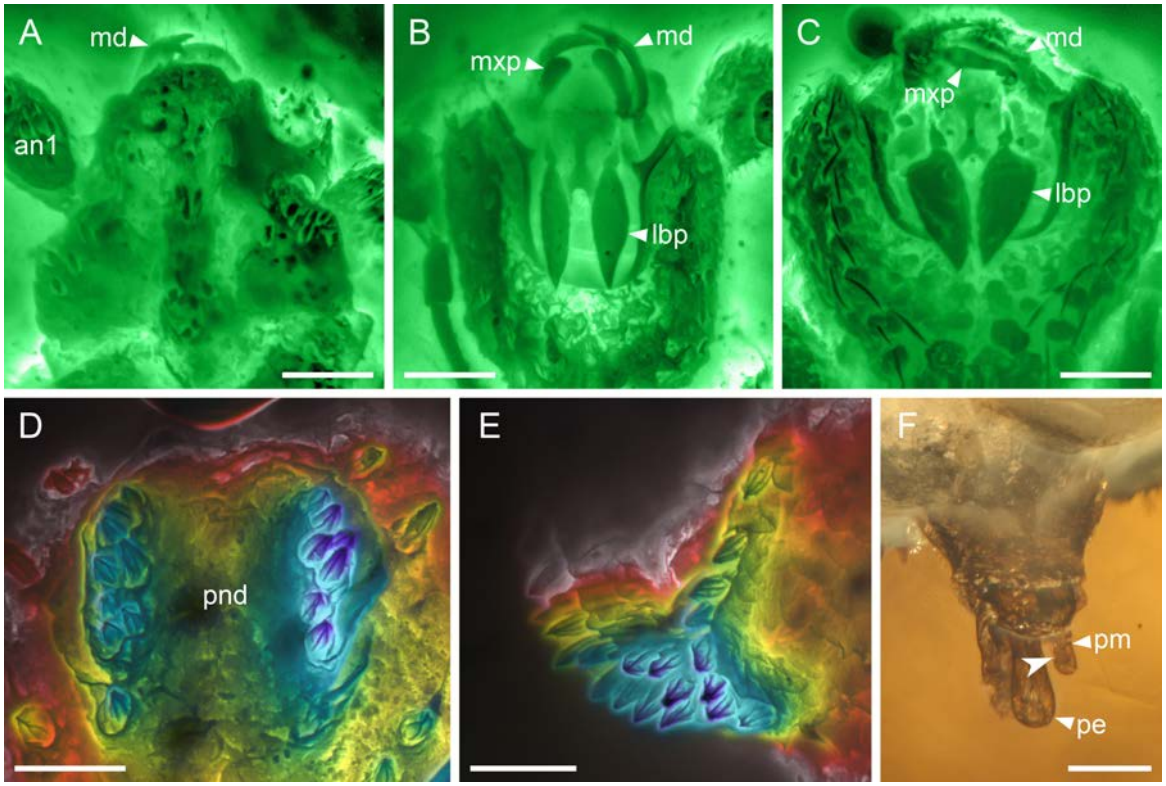


**FIGURE 8.** Details of *Stegocoleus*, under incident light (**F**) or confocal microscopy (**A**–**E**), with depth colour coding in (**D**–**E**). **A**, *S. lawrencei*, NIGP170947, anterior portion of head, dorsal view. **B**, *S. lawrencei*, NIGP170947, mouthparts, ventral view. **C**, *S. arkonus*, NIGP170946, mouthparts, ventral view. **D**, *S. arkonus*, NIGP170946, pronotal disc, dorsal view. **E**, *S. arkonus*, NIGP170946, posterior elytral carina, dorsal view. **F**, *S. arkonus*, NIGP173373, aedeagus, ventral view, showing the small mesal notch near apex of paramere (arrowhead). Abbreviations: an1, antennomere 1; lbp, labial palp; md, mandible; mxp, maxillary palp; pe, penis; pm, paramere; pnd, pronotal disc. Scale bars: 200 μm.

of scutellum. Even so, *S. lawrencei* may still be a valid species. In *S. lawrencei*, the prosternum broadens slightly in the anterior half, and then tapers posteriorly (Fig. 7E), while in the holotype of *S. caii*, the lateral prosternal margins are subparallel in the anterior half (Fig. 7B).

The male genital structures are preserved in one of our *S. arkonus* specimens. A small mesal notch can be seen near the apex of the paramere (Fig. 8F). A similar but larger notch is also found in some extant ommatid and micromalthid species, while cupedids do not possess such a structure on parameres (Hörnschemeyer, 2009). This confirms the placement of *Stegocoleus* in Ommatidae, rather than Cupedidae, and implies that the elongated prosternal process and separated procoxae evolved independently in Cupedidae and *Stegocoleus*. However, the penis of *S. arkonus* extends well beyond the apex of the paramere, which is different from most extant ommatids (figs 90–95 in Escalona *et al*., 2020).

Based on our observation, the enigmatic genus *Stegocoleus* shares many similarities with *Lepidomma*. *Lepidomma* have been noted to have a collar-like pronotal extension (Jarzembowski *et al*., 2019). A similar extension can also be found in some *Stegocoleus* species. Inconspicuous grooves are present in *Lepidomma* on the ventral head surface between the eyes and gula (Figs 4B, 6A), which may be homologous with the much more well-defined antennal grooves in *Stegocoleus*. *Lepidomma* and *Stegocoleus* share a special type of scales with distinctive ridges running down the sides (Figs 2F, 4D, 8D, E). Most importantly, *Lepidomma* and *Stegocoleus* both have scale-bearing carinae on the elytral surface, the shape and distribution of which, to our knowledge, have not been reported in any other archostematans. Tihelka *et al*. (2020) identified seven pairs of elytral carinae in *S. arkonus* and *S. lawrencei*. Well-corresponding counterparts of most of these carinae can be found in *Lepidomma*. The one located anteromarginally (surface carinae 1) is present in both *Lepidomma* and *Stegocoleus*. The two carinae in the anteromedial part of elytra and extending posterolaterally in *Lepidomma* probably correspond to the surface carinae 2 and 3 in *Stegocoleus*. The prominent posterior carina in *Lepidomma* corresponds probably to the surface carinae 7 in *Stegocoleus*.

Based on above similarities, we conclude that *Stegocoleus* is closely related to the typically-looking ommatid *Lepidomma*. Thus, *Stegocoleus* is not a stem

ommatids as suggested by Jarzembowski & Wang (2016), but a derived form of ommatids. Although Tan *et al*. (2012) placed all ommatids with wide epipleural rims into the extinct tribe Brochocoleini, this feature could have evolved convergently in brochocoleins and *Stegocoleus* as a response to similar ecological pressures, and thus may not be phylogenetically informative. The Brochocoleini united by wide epipleural rims in Tan *et al*. (2012) may be a problematic and heterogeneous assemblage and need to be reevaluated in further studies.


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