Short communication

New data on Ommatidae (Coleoptera) from mid-Cretaceous Burmese amber

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ABSTRACT

The relict family Ommatidae belongs, among other reticulated beetles (suborder Archostemata), to one of the most basal lineages of Coleoptera. Ommatids were much more diverse during the Jurassic and Cretaceous when the family attained a global distribution. Here we report two new species from mid-Cretaceous Burmese amber, *Stegocoleus arkonus* sp. nov. and *S. lawrencei* sp. nov. A key to the extinct beetle genus *Stegocoleus* is provided. The characteristically wide epipleural rims of *Stegocoleus* and the pronounced surface carinae probably served a protective function against potential predators.

1. Introduction

Beetles of the family Ommatidae Sharp & Muir, 1912 have been referred to as 'archaic beetles' by some authors in the past (Jarzembowski et al., 2018a, b), and rightfully so. Ommatidae represent one of the oldest and most basal beetle families, the earliest representatives being known from late Triassic (Crowson, 1962), although the origin of the family may be dated back to as early as the Permian (Tan et al., 2012). Only two relict ommatid genera with a highly disjunct distribution range survive to the present: *Omma* Newman, 1839 with four species occurring in Australia and *Tetraphalerus* Waterhouse, 1901 with two species in South America (Hörnschemeyer and Beutel, 2016). The family has been much more diverse in the Mesozoic era, only declining throughout the Cretaceous and Cenozoic (Ren and Tan, 2006). Some sixteen extinct genera are known mainly from the Jurassic and Cretaceous when the family had an apparently cosmopolitan distribution (Yamamoto, 2017; Jarzembowski et al., 2019).

The systematic position of the family Ommatidae has been debated in the past (Sharp and Muir, 1912; Atkins, 1963; Ponomarenko, 1969a; Lawrence, 1999), but it is currently placed in Archostemata, the smallest suborder containing the most ancient beetles with a suite of primitive features including reticulated elytra with rows of window punctures (Hörnschemeyer et al., 2016). Ancestral reticulated beetles probably fed on fungi-infested dead wood, as suggested by their strongly dorsoventrally compressed body and the life history of extant archostematans (Crowson, 1981). The extrinsic environmental factors that may have led to the decline of archostematan beetles remain largely a mystery, especially considering that their decline was not accompanied by any abrupt changes in the availability of the woody plants they inhabited (Ponomarenko, 2000; 2003), although Friedrich (2009) pointed out that their rather inefficient locomotory system and lack of cryptonephric Malpighian tubules that restrict them to permanently moist microhabitats may have played a role.

Although archaic beetles are rarely found in amber due to their large body size (Yamamoto, 2017), recent discoveries of new material from Burmese amber reveal a much higher diversity of ommatids during the mid-Cretaceous than today (Jarzembowski et al., 2018a; b, 2019). Here we describe two new species belonging to the enigmatic genus *Stegocoleus* Jarzembowski and

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Wang, 2016 known insofar only from Burmese amber (Jarzembowski and Wang, 2016). This genus is characterised by a very wide epipleural margin, which is otherwise found only in basal ommatids from the Jurassic and Cretaceous (Jarzembowski et al., 2013). We discuss the implications for the probable palae-oecology of these early archaic beetles.

2. Material and methods

The material described herein originates from an amber mine at the summit of the Noije Bum hill (26°20′ N, 96°36′ E) in the Hukawng Valley, Kachin State in northern Myanmar (Cruickshank and Ko, 2003: fig. 1). Amber from the mine was radiometrically dated at approximately 99 Ma, earliest Cenomanian (Shi et al., 2012), and likely originated from dawn redwood trees of the genus *Metasequoia* (Grimaldi & Ross, 2017). The samples were prepared using a handheld cutter and polished with different grades of sandpaper and rare earth powder. The specimens were studied under a Zeiss Discovery V20 stereo microscope fitted with an AxioCam MRc 5 camera and a Leica M165C stereomicroscope. The Zeiss Axio Imager 2 microscope was equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine. Photomi-crographs with a green background were taken under the eGFP mode, whereas ones with a red background were under the rhodamine mode. Body length is measured from the clypeus to the elytral apex and body width as the maximum width across the elytra. Measurements are taken as maximum distances across structures including any protruding plates, ridges, or spines. All studied material is deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The publication LSID is urn:lsid:zoobank.org:pub:FCF7F5B7-242B-4923-A5E7-7CD0D290F8F9.

3. Systematic palaeontology

Some previous authors have placed Ommatidae within the arch-ostematan family Cupedidae Laporte, 1836 *sensu lato* (e.g. Crowson, 1962; Jarzembowski et al., 2016; Kirejtshuk et al., 2016). Here, we treat Ommatidae as a family separate from Cupedidae based on the results of a recent molecular phylogenetic study (McKenna et al., 2015), in which there was strong support for Micromalthidae LeConte, 1878 as sister group of Ommatidae, placing it into a clade separate from Cupedidae. The morphological characters supporting the separate position of Ommatidae from Cupedidae have been discussed in detail by Lawrence (1999).

Order Coleoptera Linnaeus, 1758
Suborder Archostemata Kolbe, 1908
Family Ommatidae Sharp and Muir, 1912
Genus *Stegocoleus* Jarzembowski and Wang, 2016

Stegocoleus arkonus sp. nov.
(urn:lsid:zoobank.org:act:BEFA6EC0-F24D-4A82-9C65-E006CEA2542A)
(Figs. 1—4)

Diagnosis. The species can be distinguished from *Stegocoleus caii* by the epipleural rims up to two cells wide in the apical half (Fig. 1). It also lacks a well-defined neck region and possesses seven elytral
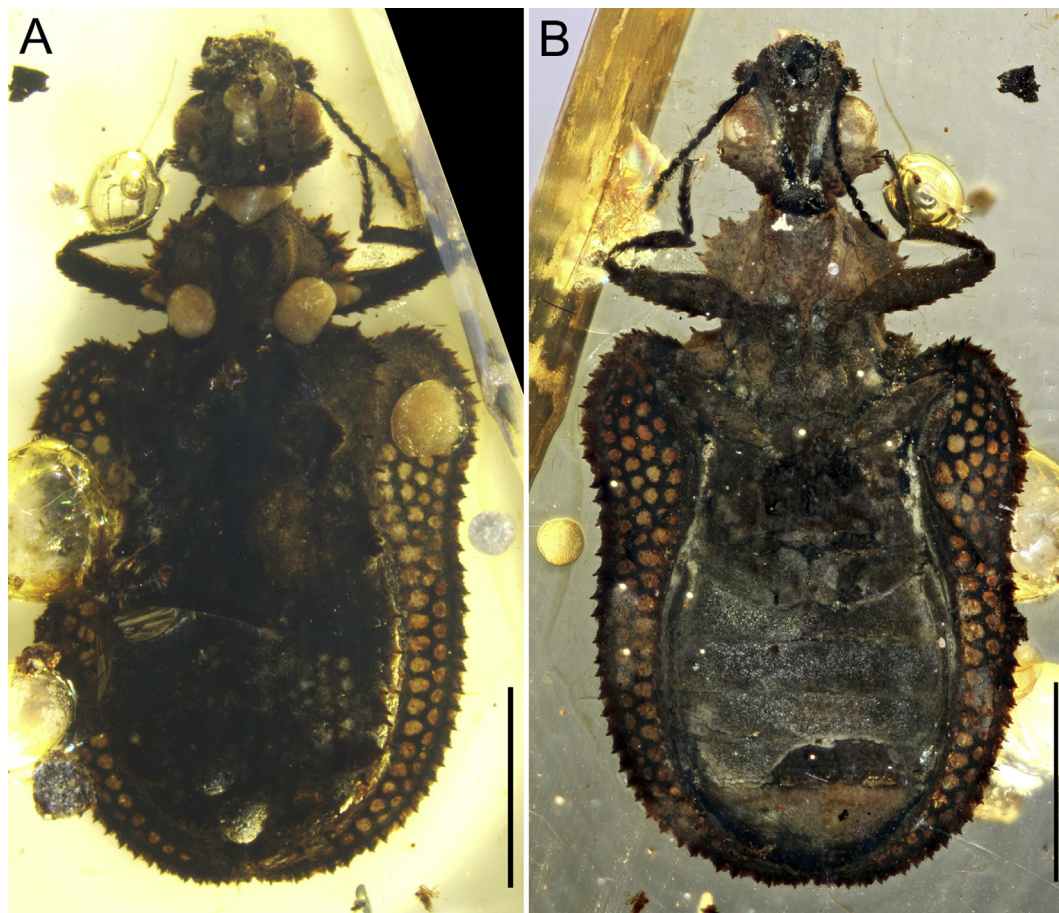

Fig. 1. Habitus photographs of *Stegocoleus arkonus* sp. nov. (holotype, NIGP170655) under normal reflected light; (A) dorsal and (B) ventral views. Scale bars = 2 mm.

carinae including a plate lining a part of the elytral base (Fig. 2, sc2). The abdomen is widest at the fifth ventrite. The species can be separated from *S. lawrencei* by a less ovate head, pronotal disc without spines, and epipleural rims only up to two cells wide in the apical half.

Description. Elongate, dorsoventrally flattened beetle with distinctly widened epipleural rims constituting up to 0.6 times of maximum abdomen width. Body length 8.34 mm, body width 4.41 mm. Body surface covered with scales, setae, elytra locally carinate. Colour uniformly dark brown to black.

Head prognathous, as long as wide, lacking spinal protuberances (Fig. 3A). Frons and vertex with four longitudinal rows of scales, with synocular scales distinctly larger than the medial two rows (Fig. 4A). Eyes protruding, glabrous, very finely faceted. Temples prominent, with scales, and appearing wider than eyes. Antennae 11-segmented, inserted laterally, sparsely pubescent, reaching slightly less than half of pronotum length (Fig. 4B). Antennomere 1 (scape) widened, with rows of scales, 2.5 times longer than the following segment; antennomere 2 (pedicel) ovate and widest medially; antennomere 3 elongate with setae located medially, 1.2 times longer than the following segment; antennomere 4 being 1.1 times longer than the following segment; antennomeres 6−10 subequal; antennomere 11 fusiform, 1.8 times longer than the preceding segment. Antennomeres pubescent, 5 basal segments more filiform. Antennal grooves prominent, widening towards the apex, and accommodating approximately half of the antenna length. Gula roughly triangular with a pointed apex (Fig. 4C). Head constricting gradually behind temples, with no pronounced neck region.

Prothorax 1.7 times wider than long, narrower than abdomen. Procoxae large, oval, separated by an elongated prosternal process (Fig. 4D). Protrochanter 2.5 times wider than mesotrochanter. Profemur widest medially, 1.5 times broader than mesofemur, longer than mesofemur and metafemur, at least half extending beyond the edge of the prothorax. Protibia slightly longer than mesotibia. Both profemur and protibia with scales, row of setae present. Protarsus 1.2 times longer than protibia, thinner, lacking scales but densely setate, protarsomere 5 approximately the same length as the two basal tarsomeres together. Claws lacking teeth, empodium not visible. Pronotal margin widened, with subequal spines, each bearing a single terminal scale. Pronotal disc elevated with two longitudinal rows of scales (Fig. 3C and 4F).

Mesoventrite subrectangular, divided by a posteromedial groove. Scutellum not visible. Mesocoxa rounded, wider than procoxa, adjacent, separated by only a small space and a short metaventrite process extending to their half. Mesotrochantins small. Metafemur extending beyond the abdominal margin but not beyond the epipleural rim. Mesotibia slender, 1.2 times longer than metatibia. Longest basal mesotarsomere as long as the following three segments and 1.3 times longer than the elongate apical tarsomere. Metafemur obclavate, just reaching to the abdominal
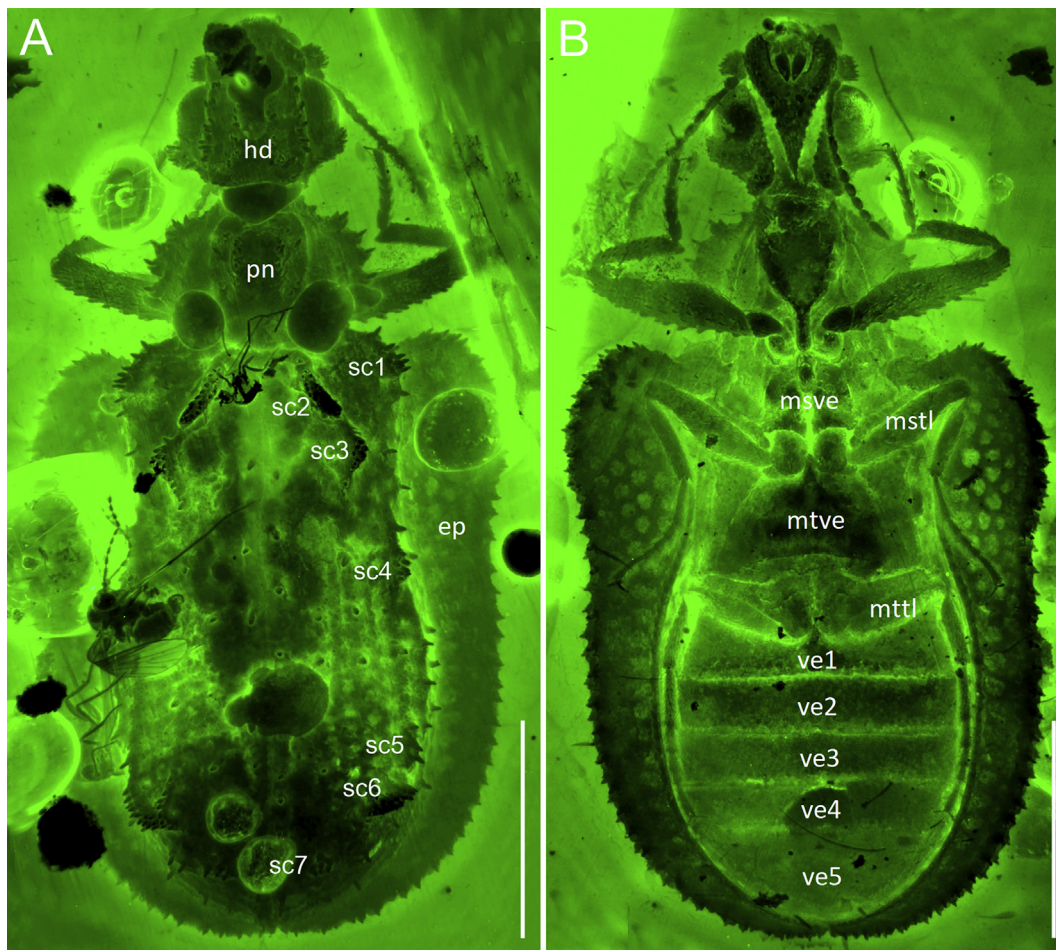

Fig. 2. Habitus photographs of *Stegocoleus arkonus* sp. nov. (holotype, NIGP170655) under green fluorescence; (A) dorsal and (B) ventral views. ep = epipleural rim, hd = head, mstl = mesothoracic leg, mttl = metathoracic leg, msve = mesoventrite, mtve = metaventrite, pn = pronotum, sc1−7 = surface carinae 1−7, ve1−5 = ventrites 1−5. Scale bars = 2 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

margin. Metatibia thinner than metafemur, 1.2 times longer than basal metatarsomere. Metatarsus only slightly narrower than metatibia, metatarsomere 1 markedly long, metatarsomeres 2−4 successively shorter, metatarsomere 5 as long as the two preceding segments together.

Elytra elongate, 2.1 times wider than pronotum, and with distinctly widened epipleural rims bearing up to four window punctures arranged into irregular rows. Elytra widest just after humeri, constricting towards the first third before gradually tapering apically so the epipleural rims are only one cell wide before the apex. Elytra with surface carinae bearing scales (Fig. 4G), with one at the margin of the elytral base (Fig. 2A: sc2), and the most prominent carinae located anteromedially (Fig. 2A: sc2, sc3). Abdomen rounded apically, widest at third ventrite and gradually narrowing posteriorly, with 5th ventrite longer than others. Glandular openings or pits not visible.

Holotype. NIGP170655, sex undetermined.

Type locality and horizon. Amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; Albian/Cenomanian boundary, mid-Cretaceous.

Etymology. The specific epithet is derived from Arkona, the last fortified stronghold of the Rani Slavs in the 12th century, after the characteristically expanded epipleural rims that presumably fulfilled a defensive function and after the impeding decline of the family throughout the Cretaceous.

Stegocoleus lawrencei sp. nov.

(urn:lsid:zoobank.org:act:57DFCDAC-8EEB-4238-9ED0-A9D92F95C7CD)

(Figs. 5−7)

Diagnosis. Species closely resembling *Stegocoleus caii* but can be easily differentiated by the shape of prontum with elevated pronotal disc bearing two protrusions (Fig. 5A, 6A) as opposed to two distinct spiny protrusions separated by a deep suture in *S. caii*. Gula subtriangular (Fig. 6B), in contrast to the holotype of *S. caii* illustrated by Jarzembowski and Wang (2016). Unlike in *S. caii*, the scutellum is subrhombical and widest medially (Fig. 7A). The species can be distinguished from *S. arkonus* by its ovate head with a distinctly constricted neck and epipleural rims with more than two cells in the apical half.

Description. Body elongate, dorsoventrally flattened. Distinctly widened elytral epipleura constituting up to 1.2 times of maximum abdomen width. Body length 8.48 mm, body width 4.79 mm. Pronotal and elytral surface with seven local carinae, integument with scales and setae.

Head elongate, 1.3 times longer than wide, with dorsal longitudinal protuberances (Fig. 6A). Eyes ovate, rounded laterally. Temples prominent, wider than eyes. Fili-moniliform antennae 11-segmented, sparsely pubescent, barely reaching to the first quarter of pronotum length. Antennomere 1 (scape) inserted under a scaly tuft, dilated, 1.3 times longer than the following segment; antennomere 2 (pedicel) square-like; antennomere 3 being 1.4 times longer than preceding segment; antennomere 4 being 1.3 times longer than preceding segment, antennomeres 5−8 filiform, apparently similar in size; antennomeres 9−11 wider than preceding segments, lengthening apically; antennomere 11 fusiform, 1.3 times longer than preceding segment. Antennal grooves pronounced, widest basally, and accommodating eight antennomeres. Gula somewhat triangular with a pointed apex (Fig. 6B). Head constricting behind temples, forming a short and narrowed neck.
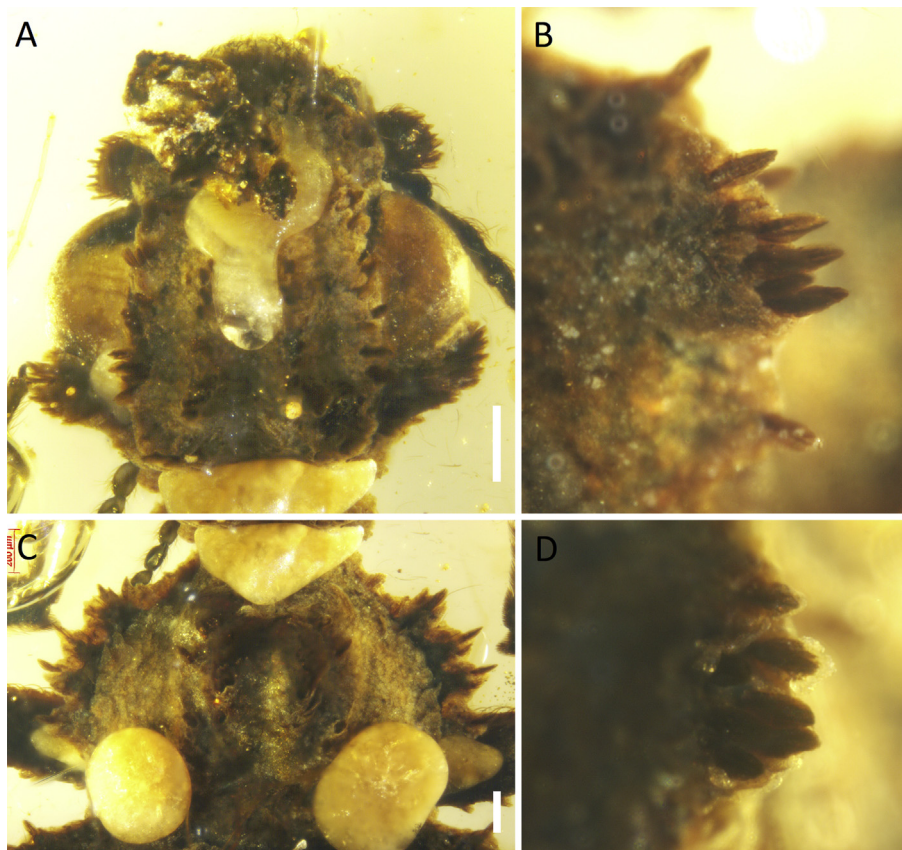

Fig. 3. Morphological details of *Stegocoleus arkonus* sp. nov. (holotype, NIGP170655) under normal reflected light; (A) head in dorsal view, (B) enlargement of elytral surface carinae 1 (sc1), (C) pronotum in dorsal view, (D) enlargement of elytral surface carinae 4 (sc4). Scale bars = 200 μm.
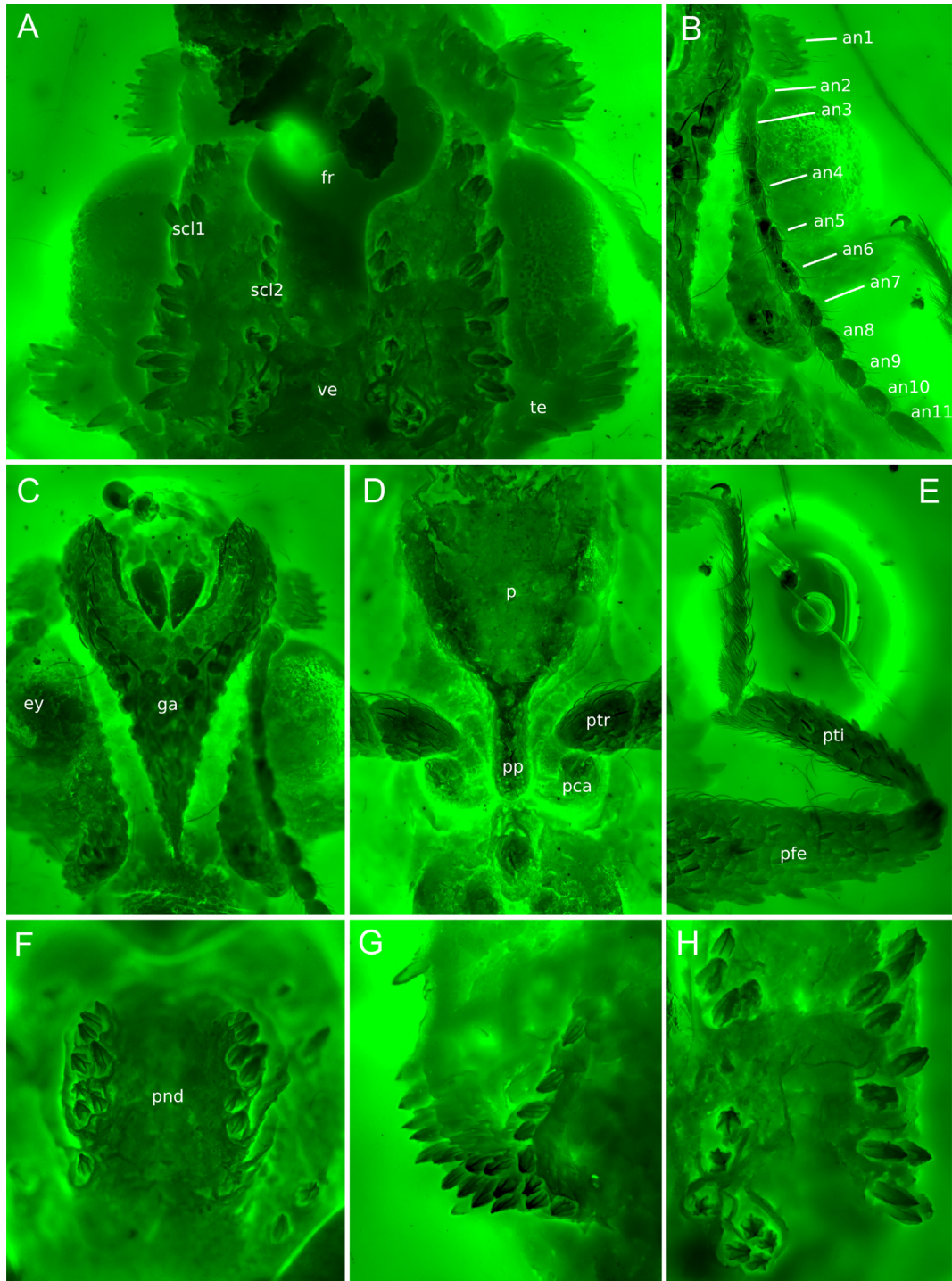
Fig. 4. Morphological details of *Stegocoleus arkonus* sp. nov. (holotype, NIGP170655) under green fluorescence; (A) head in dorsal view (B) antenna, (C) gula region and antennal grooves, (D) prothorax, (E) prothoracic leg, (F) pronotal disc, (G) elytral surface carinae 6, (H) surface carinae on head. Scale bars = 200 μm an1−11 = antennomeres 1−11, ang = antennal groove, ey = eye, fr = frons, ga = gula, p = prosternum, pca = procoxa, pfe = profemur, pnd = pronotal disc, pp = prosternal process, pti = protibia, ptr = protrochanter, scl1 = larger synocular head scales, scl2 = smaller medial head scales, te = temple, ve = vertex. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Prothorax 1.2 times wider than long, broader than head but narrower than abdomen. Procoxae large, oval, separated by an elongated prosternal process reaching to the posterior edge of procoxae. Protrochanter longer than mesotrochanter. Profemur clavate, 1.1 times broader than mesofemur, longer than mesofemur and metafemur, over half extending beyond the edge of the prothorax but not reaching further than the epipleural margin.

Protibia 0.4 times the length of the profemur, thinner, slightly longer than mesotibia. Both profemur and protibia with scales, setate. Protarsus longer than protibia, thinner, basal protarsomere 1.6 times longer than following segment, protarsomeres 2−3 subequal, protarsomere 5 as long as three preceding segments. Claws lacking teeth, empodium absent. Pronotal margin widest in the first third, with five lateral spines, with the
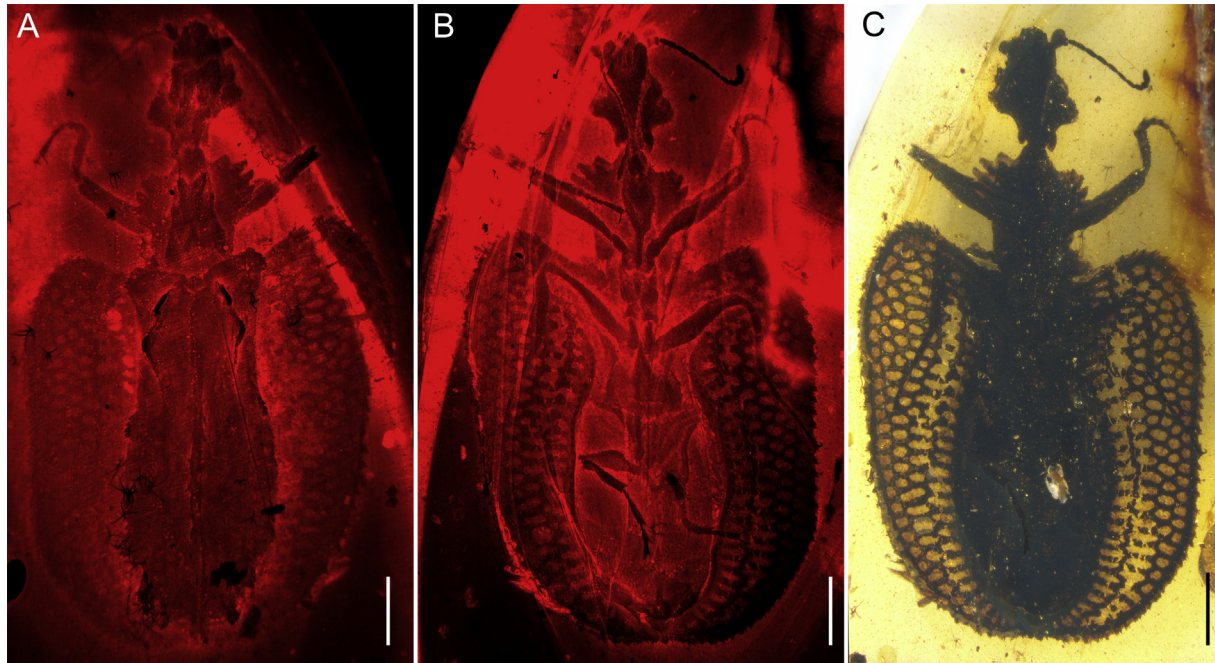
Fig. 5. Habitus photographs of *Stegocoleus lawrencei* sp. nov. (holotype, NIGP170656); (A) dorsal and (B) ventral views under green fluorescence, (C) dorsal view under normal reflected light. Scale bars = 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

anteriormost shortest. Pronotal disc elevated and with two spiny protrusions (Fig. 6A).

Mesoventrite subrectangular, divided by a posteromedial groove. Scutellum subrhombical, widest in the middle of its length (Fig. 7A). Mesocoxa ovate, adjacent, with a short metaventrite process extending to their lower third. Mesotrochantins small. Metafemur extending beyond abdominal margin and reaching to about the second third of the epipleural rim. Mesotibia narrower than metafemur but wider than metatarsomeres. Metatarsomeres 1 and 5 subequal, metatarsomeres 2−4 gradually shortening apically. Metafemur broad, just reaching the abdominal margin. Metatibia thinner than metafemur, 1.2 times longer than basal metatarsomere. Basal metatarsomere 1.6 times longer than metatarsomere 5, metatarsomeres 2−4 successively shorter, apical metatarsomere 1.4 times longer than the preceding two segments together.

Elytra elongate, 2.8 times wider than pronotum, with well-developed irregular rows of window punctures, and distinctly widened epipleural rims with up to six window punctures. Elytral epipleura widest just after humeri, tapering apically, with up to three cells in the apical third. Elytra with surface carinae bearing scales, the most prominent carinae located anteromedially, but none lining the basal elytral margin (Fig. 7A; 7B). Sutural margin raised, with a jagged central ridge (Fig. 7B). Abdomen vase-shaped, widest at base and then widening between the first and third ventrite.

Holotype. NIGP170656, sex undetermined.

Type locality and horizon. Amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; Albian/Cenomanian boundary, mid-Cretaceous.

Etymology. The specific epithet is a patronym formed from the surname of Dr. John F. Lawrence, a world-leading coleopterist.

Key to Cretaceous beetles of genus **Stegocoleus**

1 (4) Elytral epipleural rims up to six cells wide. Head with a short and narrow neck. Elytral base not lined by a raised plate. . . . .
. . . . 2

2 (1) Gula subtriangular with a pointed apex. Pronotal disc with a single elevated region bearing two carinae. Scutellum subrhombical, widest medially . . . .
. . . . *Stegocoleus lawrencei* sp. nov.

3 (2) Gula not as above. Pronotal disc with two separate longitudinal spiny plates. Scutellum subtriangular, widest basally. . . . .
. . . .
. . . . *Stegocoleus caii* Jarzembowski and Wang (2016)

4 (1) Elytral epipleural rims up to four cells wide, up to two cells wide in the apical half. Head lacking an elongated neck region. Pronounced plate lining a section of the elytral base present. . . . .
. . . . *Stegocoleus arkonus* sp. nov.

4. Discussion

4.1. Systematic position

The placement of *Stegocoleus* into the family Ommatidae is well supported by the presence of short antennae, antennae not inserted dorsally, apical antennomere not parallel-sided, presence of antennal grooves, epipleura with cells, abdominal ventrites not overlapping, and simple tarsi (Lawrence, 1999; Tan et al., 2012). A distinctly expanded epipleura is furthermore considered an apomorphy of brochocoleine ommatids (Jarzembowski et al., 2013).

The two species described herein can be confidently placed into the genus *Stegocoleus* based on the combined presence of short antennal grooves accommodating over half the length of the antennae, procoxae not continuous and separated by a prosternal process, elytra with very wide epiplerual rims bearing more than three rows of irregular window punctures, and body surface with protruding processes. *Stegocoleus arkonus* and *S. lawrencei* show numerous typical archostematan characters, namely the presence of exposed metatrochantins and reticulate elytra.

The procoxae separated by a prosternal process is a problematic character of *Stegocoleus* that caused uncertainty about its systematic position in the past (Jarzembowski and Wang, 2016). As far as
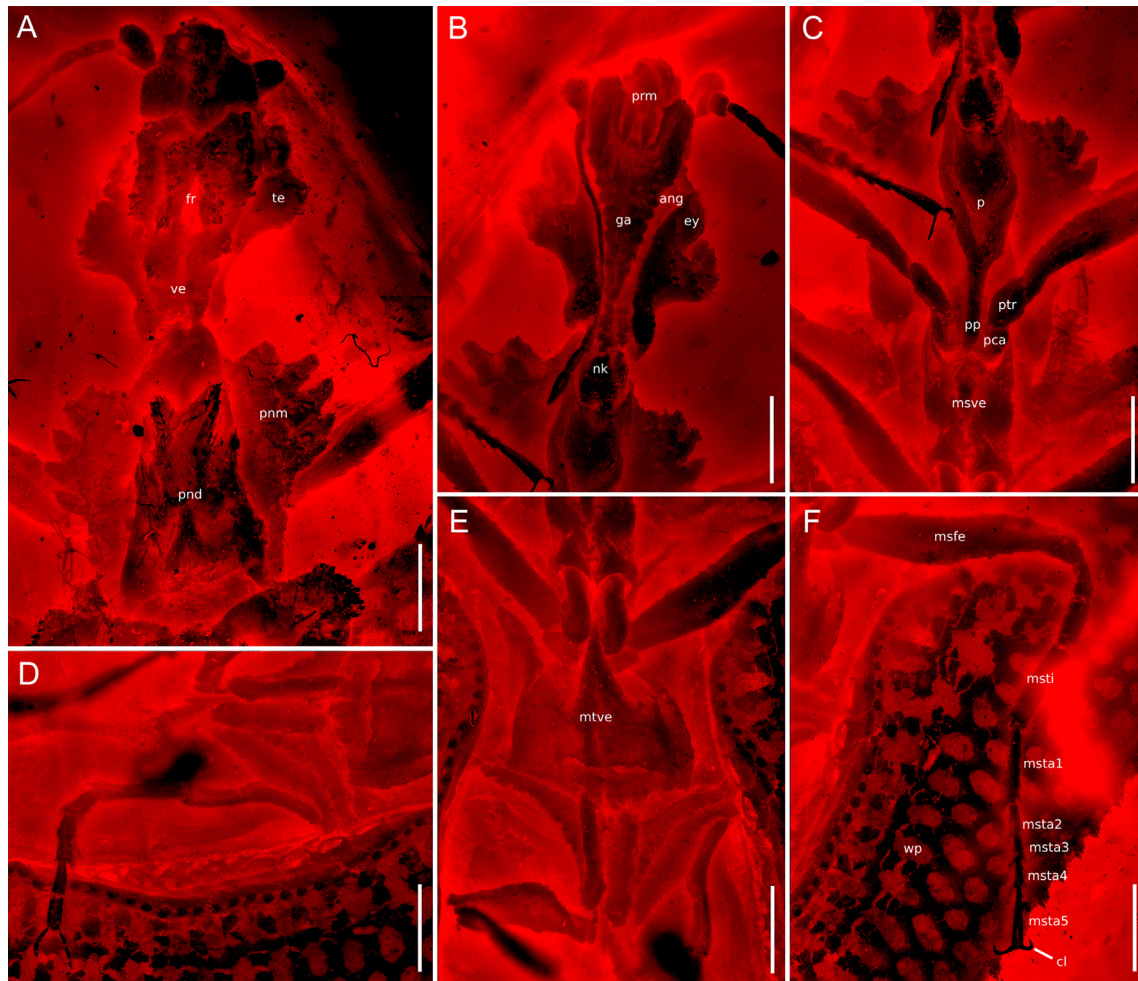
Fig. 6. Morphological details of *Stegocoleus lawrencei* sp. nov. (holotype, NIGP170656) under red fluorescence; (A) head and pronotum in dorsal view, (B) head in ventral view, (C) prothorax in ventral view, (D) metathoracic leg, (E) abdomen (F) mesothoracic leg. Scale bars = 500 μm ang = antennal groove, cl = claw ey = eye, fr = frons, ga = gula, msfe = mesofemur, msti = mesotibia, msta1−5 = mesotarsals 1−5, msve = mesoventrite, mtve = metaventrite, nk = neck, p = prosternum, pca = procoxa, pnd = pronotal disc, pnm = pronotal margin, pp = prosternal process, ptr = protrochanter, prm = prementum, te = temple, ve = vertex, wp = window puncture. Scale bars = 500 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

archostematans are concerned, Hörnschemeyer (2009) mentions the presence of separate procoxae only in Cupedidae. However, separate procoxae are probably not a cupedine autapomorphy, being apparently present in a basal micromalthid beetle from the Permian (Yan et al., 2019). Moreover, in *Stegocoleus* the prosternal process does not extend beyond the procoxae into a small meso-ventral cavity as is the case in Cupedidae (Lawrence, 1999).

4.2. Palaeoecology

Perhaps the most striking feature of *Stegocoleus* distinguishing it from all other Burmese amber taxa are the greatly expanded epipleural rims with more than three rows of irregular window punctures. Wide epipleural rims with several cells are present in Permian Tshekardocoleidae Rohdendorf, 1944 and early Creta-ceous Labradorocoleidae Ponomarenko (1969a),1969b (Ponomarenko, 1969a,b). Apart from these two families, a wide epipleuron bearing window punctures is known only from the ommatid tribe Brochocoleini (Tan et al., 2012). A similarly expanded epipleural rim, but without window punctures, developed independently in several other beetle groups including the Middle Jurassic trogossitid genus *Sinopeltis* Yu,

Leschen, Ren and Pang (2012) (Yu et al., 2012), the Cretaceous cupedid *Mallecupes qingqingae* Jarzembowski, Wang and Zheng (2017a), 2017b known from Burmese amber (Jarzembowski et al., 2017b), the extant subcortical calityin beetles (Kolibáč, 2013), and the extant *Mormolyce* Hagenbach, 1825 violin beetles (Lieftinck and Wiebes, 1968).

Jarzembowski et al. (2019) suggested that some Cretaceous ommatids may have lived on trees and shrubs. The strongly dorsoventrally compressed body of *Stegocoleus* and the presence of antennal grooves suggest they were associated with wood, just as modern ommatids. Lawrence (1999) considered the expanded epipleural rims to indicate a subcortical mode of life. Moreover, all the above-mentioned extant taxa with expanded epipleural rims are subcortical or associated with wood. The wide epipleura and surface carinae probably served a protective function against predators. When threatened, the beetles could have retracted their legs beneath the tough epipleural rims and their antennae into gular sutures. Like this, the beetle would be very difficult to hold on to or even turn around. The numerous surface carinae, ridges, and spines also probably fulfilled a protective role. Sharp spines in some insects can cause insectivores to regurgitate their prey and learn to avoid it afterwards (Ito et al., 2016).
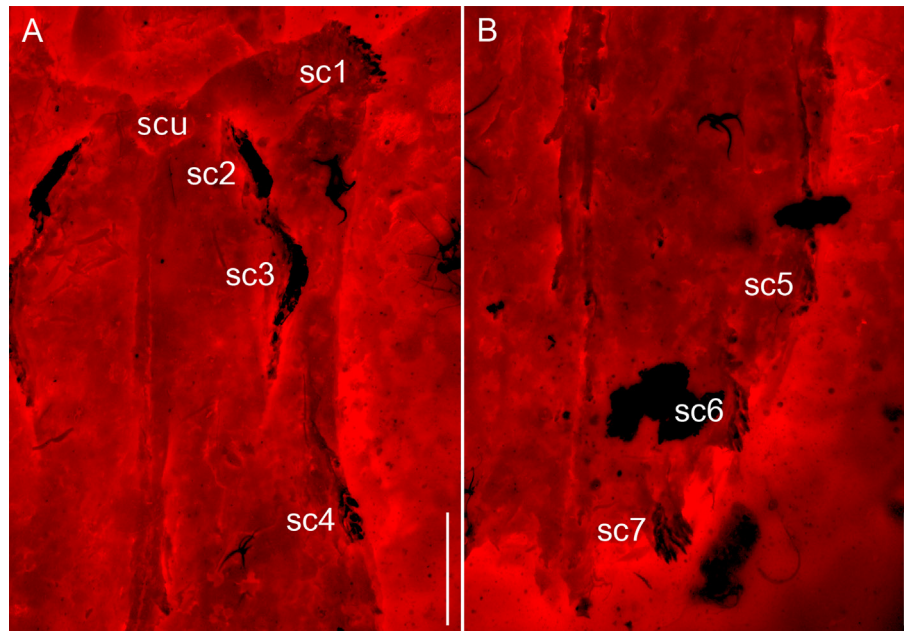
Fig. 7. Morphological details of *Stegocoleus lawrencei* sp. nov. (holotype, NIGP170656) under red fluorescence; (A) basal part of elytron (B) apical part of elytron. Scale bars = 500 μm sc1−7 = surface carinae 1−7, scu = scutellum. Scale bars = 500 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Ants today dominate many saproxylic microhabitats and are responsible for harvesting vast amounts of insect biomass annually (Del Toro et al., 2012). Molecular studies estimate that ants originated probably between the late Jurassic and the early Cretaceous, although the oldest fossils are from the Cretaceous (Brady et al., 2006, Moreau et al., 2006; Moreau and Bell, 2013; Peters et al., 2017), and could explain the appearance of these defensive adaptations in late Jurassic and early Cretaceous ommatids (Tan et al., 2012). Basal ants are known from Burmese amber (Zhang et al., 2018), including the now extinct trap-jaw unicorn ants that possessed massive mandibles that could presumably puncture and crush large insect prey (Perrichot et al., 2016). Jarzembowski et al. (2017a) discussed the evidence that saproxylic insects may have been subjected to predation pressure from these ants in the Burmese amber forest. It is not without interest that myrmecophilic sap beetles of the genus *Amphotis* Erichson, 1843 also possess widely expanded pronotal and epipleural rims that provide protection against ants (Olberg, 2015).

If the expanded epipleural and pronotal rims widespread in Cretaceous ommatids (Tan et al., 2012) indeed acted as a defence against ants, it is surprising why the only two surviving ommatid genera, *Omma* and *Tetraphalerus*, entirely lack these defences. The cyclical model of host-parasite coevolution (*sensu* Rothstein, 2001; Sasaki and Godfray, 1999) posits that as a predator shifts away from a well-defended prey species, the prey will gradually lose its costly defence mechanisms only to become exploited again once the predator shifts back to the now undefended species. This model could perhaps partly explain the lack of a wide epipleura in modern ommatids, but field studies in avians have not found unequivocal support for this hypothesis (Peer et al., 2007; Feeney et al., 2014). It seems more likely that these presumably costly defences simply allowed basal ommatids to coexist with early ants, while other archaic beetles had to rely on behavioural mechanisms to avoid ants (e.g. Reznikova and Dorosheva, 2004). Indeed, the decline of Archostemata coincided with the diversification of ants from the late Cretaceous to the early Eocene (Brady et al., 2006; Moreau

et al., 2006), suggesting that ant predation may have contributed to the downfall of these ancient beetles throughout the Cretaceous and the Cenozoic.

5. Concluding remarks

Beetles of the suborder Archostemata represent 'walking fossils' known since the Permian that have apparently undergone little morphological change since then (Ponomarenko, 1969a; Friedrich, 2009). While reticulated beetles are rarely found in fossilised resin (Yamamoto, 2017; Jarzembowski et al., 2018a), recent exploration of Burmese amber hints towards a much wider morphological disparity and ecological diversity in Cretaceous archostematans than today (Jarzembowski et al., 2018a; b, 2019). Here we describe two new species belonging to Ommatidae, *Stegocoleus arkonus* sp. nov. and *S. lawrencei* sp. nov., from mid-Cretaceous Burmese amber. Members of the genus *Stegocoleus* are unusual among archostematans, possessing widely expanded epipleural rims with up to six window punctures and elytral discs with numerous surface carinae. These morphological adaptations may have conferred protection against predators, namely early ants. Indeed, the rise of armoured ommatids in the Jurassic and Cretaceous (Tan et al., 2012) coincided with the origin of ants, while the decline of the Archostemata during the Late Cretaceous and Cenozoic (Ren and Tan, 2006) took place at a time of great ant diversification.

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