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A new scaly archaic beetle (Coleoptera: Archostemata) from mid-Cretaceous Burmese amber



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Edmund A. Jarzembowski ^{a, b, *}, Bo Wang ^{a, c}, Daran Zheng ^{a, d}

^a State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and

Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

^b Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK

^c Shandong Provincial Key Laboratory of Depositional Mineralization & Sedimentary Minerals, Shandong University of Science and Technology, Qingdao,

Shandong 266590, China

^d Department of Earth Sciences, University of Hong Kong, Hong Kong Special Administrative Region, China

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1. Introduction

About two hundred species of fossil Cupedina (Archostemata + Myxophaga) have been described from the Permian onwards, and archostematans are notable constituents of Mesozoic insect faunas, even occurring in regions from where they have now vanished (Kirejtshuk & Ponomarenko, 2015). Previously known from adpressions in Cretaceous non-marine sediments, some exceptionally well preserved as in northeastern China (Zhang et al., 2015), these archaic beetles have been discovered recently as amber inclusions in northern Myanmar (Xia et al., 2015). Archostematans are, nevertheless, scarce in Burmese amber, which is surprising considering the modern association of these beetles with wood, and they are usually represented by smaller forms as might be expected. Here we describe a new archaic beetle from this fossil resin belonging to the ommatines, a group of 'living fossils' peculiar to the modern fauna of Australia and South America.

* Corresponding author. State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China.

E-mail address: jarzembowski2@live.co.uk (E.A. Jarzembowski).

ABSTRACT

A rare ommatine beetle, *Lepidomma tianae* gen. et sp. nov. (Insecta: Coleoptera: Archostemata), is described in burmite from northern Myanmar (Kachin). It has unusual scale-lined elytra and belongs to the equally unusual clessidrommatin stem group apparently endemic to the West Burma Block. These beetles were possibly adapted for life on trees and shrubs.

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Almost a centimetre long, it belongs to a rare species, only one or two specimens being known from over 100,000 inclusions. The beetle is attributed to a recently erected fossil tribe, Clessidrommatini Jarzembowski, Wang & Zheng, 2018, originally based on a single amber find, which is of interest because it appears to be characteristic of Burmese amber (see below). Opinion is still divided as to whether ommatines are a subfamily of reticulated beetles/cupedids *sensu lato* (Kirejtshuk et al., 2016), or a separate family (Lawrence and Ślipiński, 2013). For consistency with other burgeoning studies of amber-hosted archostematans, we consider cupedids and ommatines in the broad sense (the latter including fossil notocupedins and brochocoleins and living and fossil tetraphalerins and ommatins).

2. Geological setting

Burmese amber (burmite) from northern Myanmar contains the most diverse biota in amber known from the Cretaceous: all the major divisions of extant insects (orders) are represented, beetles (Order Coleoptera Linnaeus, 1758) being one of the most diverse, but many species are still undescribed. Previously considered as reworked from the late Albian, the amber is now considered to be early Cenomanian (Smith and Ross, 2018) with U-Pb dating of zircons from the tuffaceous matrix giving an age of ca. 98.8 ± 0.6 Ma (Shi et al., 2012).

Amber has been found in several localities in Myanmar, but the principal supply is from Myitkyina District, Kachin State, in the Hukawng Valley; a major mining area is located near Noije Bum Village in Tanaing or Tanai (Danai) Township (Kania et al., 2015: fig. 1, location map); Jarzembowski et al., 2017a: Fig. S1 (view)). The Kachin amber is prepared for the international jewellery trade and exported particularly to neighbouring China. In addition to overpreparation for display purposes, there is a degree of natural deformation and obscuration of the otherwise excellent amber inclusions, the latter affecting the material described below.

3. Material and methods

The holotype is in a cloudy, slightly oxidised amber cabochon, yellowish brown in colour, with a fine debris and bubble flow obscuring the ventral surface; the second specimen is in pale yellow amber but with the venter partly polished away. The specimens were examined under an Olympus SZX7 binocular microscope and Zeiss Stereo Discovery V16 microscope system with fibreoptics and top and bottom illumination. Photographs were taken with a Zeiss Axiocam 512 digital camera mounted on the microscope and operated with Zen 2.3 pro software. Only standard degreasing and local immersion in glycerol (under a cover slip) to minimize surface interference were undertaken during examination.

Drawings were prepared from both photographs and specimens by hand (EAJ). Drawing conventions are: solid line, distinct margin; dashed, indistinct or damaged; dotted, extrapolated; dashed and dotted, folded. For morphology, we follow terminology used by Jarzembowski et al. (2018); for additional terminology, see Figs. S3–6 herein. The abbreviations used are NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS).

All taxonomic acts established in the present work have been registered in ZooBank (see new taxonomic LSIDs below) together with the electronic publication LSID: urn:lsid:zoobank.org:pub: 14AAED42-87C4-40D3-978B-F5E9C010B3E7.

4. Systematic palaeontology

Class Insecta Linnaeus, 1758 Order Coleoptera Linnaeus, 1758 Suborder Archostemata Kolbe, 1908 Family Cupedidae Laporte, 1836 s.l.

Subfamily Ommatinae Sharp & Muir, 1912 Tribe Clessidrommatini Jarzembowski, Wang & Zheng, 2018

Comment. The circumscription is corrected to: procoxae (foreleg bases) located on or bottom of prothorax; expanded pronotum forming a distinct collar. It postdates the recent classification in Yamamoto (2017) therefore the key differences are as follows. The relatively weakly developed elytral venation/window cells and unraised abdominal ventrites readily distinguish this tribe from notocupedins; the narrow, unpunctured epipleural rim from brochocoleins; the expanded pronotum from ommatins; and simple head form from tetraphalerins. It shares, however, an elongated third antennomere with the latter three (short in notocupedins) and an unelongated head with ommatins.

Composition. Two genera, both from Burmese amber: *Clessidromma* Jarzembowski, Wang & Zheng, 2018 and *Lepidomma* gen. nov. (below).

Remarks. The above circumscription follows Jarzembowski et al. (2018) except that the expanded pronotum has been added and is

a potential autapomorphy (the pronotum is rounded in ommatins) as shared by *Clessidromma* and *Lepidomma*, covering the neck and back of the head respectively. The expanded pronotum in the latter resembles a wavy-edged Elizabethan collar, but its function was perhaps protective rather than decorative as another Burmese amber archostematan, *Mallecupes cleevelyi* Jarzembowski, Wang & Zheng, 2017b, has well-developed, outward pointing spines in the neck area. (The amber forest contained diverse invertebrate and vertebrate predators including entomophagous geckos: Arnold and Poinar, 2008).

Lepidomma appears to have more posteriorly located procoxae unlike *Clessidromma*, suggesting convergence in the latter with earlier (pre-Cretaceous) archostematans (Jarzembowski et al., 2018), although this feature has been phylogenetically scored as a simple extension of the prosternum (Beutel et al., 2008). More material is needed to analyse the situation in *Lepidomma*.

Genus Lepidomma gen. nov.

urn:lsid:zoobank.org:act:8EE5E37E-7799-4732-BF08-64095C06A306.

Type species: *Lepidomma tianae* sp. nov. by monotypy; mid-Cretaceous (lower Cenomanian), northern Myanmar.

Derivation of name. From the Greek for scale (lepidos) and the generic name *Omma*; gender neuter.

Diagnosis. Small ommatine with broad body and head (including mandibles), body about 2.4 times longer than broad; beady eyes, third antennomere as long as second and fourth together; pronotum broader than long, extending over posterior part of head, with slightly serrated anterior and lateral margins, wavy anterior margin and oblique posterior-lateral sides; short metaventrite; evidently short metafemur; scales and tuberculation well developed (latter passing into serration locally) but elytral striation less so, cells small (obscured).

Comparison. By contrast, *Clessidromma* is elongate, 4.1 times longer than broad; with a less broad head (including mandibles) and slightly filiform antennae; longer pronotum (a little longer than broad), but only covering the neck region and with curved posterior-lateral margins: it also lacks a well-developed scale cover and elytral tails, with a serrated elytral margin instead. *Clessi-dromma* shares, however, a similar size (length just under one centimetre), prominent eyes, a relatively long third antennomere, short antennae (only reaching middle of pronotum) and short metafemur (not reaching edge of hindbody) plus inconspicuous elytral venation.

Remarks. The ventral details are poorly discernible due to the black, opaque preservation of the specimens, coupled with much fine obscuring matter in the amber with the holotype; the jeweller's over preparation of the other material provides an internal view of the hindbody in the abdominal region.

Lepidomma tianae sp. nov.

urn:lsid:zoobank.org:act:5EE141E4-0D9B-40F6-A262-887FA87FA1FD. Figs 1-4, S1, S2.

Derivation of name. After Dr Tian Jiang (Beijing), palaeontologist. *Holotype*. Adult specimen, registration number NIGP 169479, deposited in Nanjing Institute of Geology and Palaeontology; sex unknown.

Other material. Lepidomma affl. *tianae*, adult specimen, registration number NIGP 169480, deposited in Nanjing Institute of Geology and Palaeontology; sex unknown.



Fig. 1. Lepidomma tianae gen. et sp. nov., holotype (NIGP 169479); probably Noije Bum, mid-Cretaceous. A, photograph of dorsal view; B, close-up of elytral (epipleural) rim showing lanceolate scales.

Locality and horizon. Probably mine near Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, northern Myanmar, 26° 15′ N., 96° 33′ E.; unnamed horizon, mid-Cretaceous, lower Cenomanian.

Diagnosis. As for genus.

Description. Body: black and flattened dorsoventrally, length (from anterior end of mandibles to posterior end of folded elytra), 8.9–9.4 mm, maximum width (across folded elytra), 3.4–4.2 mm. Cuticle coarsely tuberculate and often visibly serrated or scaly (see below).

Head: broad, slightly inclined, covered by pronotum up to eyes where edge covered by elongate scales (Fig. 3C, left); jaws setose apically; scaly basally, widely arched forward, dentition rotated vertically; labrum small and broad; last maxillary segment widened, but not extending much beyond labrum; antennae inserted anterolaterally on head and moniliform, not reaching posterior end of prothorax, and first antennomere (scape) covered in elongate scales (Fig. 3D); third antennomere tubular (slightly over two times as long as second and fourth segments).

Prothorax: shorter than broad and wider than head but narrower than hindbody (wings folded). Pronotum narrowed posteriorly to mesothorax, expanded anterolaterally and anteriorly towards head developing a serrated scaly edge (Fig. 3C right) and central transverse thickening; anterior extension forming a collar-like, slightly notched head shield; anterior angles rounded, curved outwards. Foreleg (proleg) apparently inserted posteromesally: profemur thick, extending beyond edge of prothorax, protibia thinner.

Hindbody: middle (meso-) leg: mesofemur thick, extending beyond edge of hindbody, mesotibia thinner, slightly shorter; mesotarsus shorter and thinner still, well clawed with five simple mesotarsomeres, first and last elongated, especially latter; scales and setae on leg segments but setae only on tarsus; metaventrite short and evidently broad, metacoxa large and transverse; elytra: moderately wide (nearly one and a half times as wide as prothorax) overlapping broad, flat abdomen and both rounded apically; elytra with pair of short, scaly tails; anterior (outer) margin of elytron curved, notably posteriorly, and distinctly scaly with large and small scales; humerus (shoulder) rounded; elytron convex in cross (transverse) section with discal fold set in from margin and with about twelve small scale tufts above; elytral disc comparatively flat with about seven longitudinal rows of weakly developed veins/ intercalaries and small cells (each with four or five maculae) obscured by scale cover (Fig. 3D); epipleural rim moderately wide, indistinct, but with numerous, outwardly directed large lanceolate (leaf-like) scales (Fig. 1B), pale brown in colour and some 0.25 mm long, with darkened, thickened mid rib and edging plus suggestion of ultrastructural parallel ribbing.



Fig. 2. Lepidomma tianae gen. et sp. nov., holotype (NIGP 169479); probably Noije Bum, mid-Cretaceous. Interpretive drawings A, dorsal view, representative striae/window cells shown in strip on right elytron; B, scale fringe on epipleural rim.

Remarks. The second specimen is smaller and slimmer than the holotype and might represent a second species of the new genus; Burmese amber inclusions, however, show both natural variation and deformation (including plastic), so we provisionally include this specimen above pending the discovery of more material.

5. Discussion

Perhaps not surprisingly in a basal group with comparatively few apomorphies, there is currently no consensus on the family group classification of cupedid beetles (Section 1). However, the presence of a discal fold in Lepidomma gen. nov. (as in all Burmese amber cupedids) is consistent with the presence of highly erect laterosternites found in this family (Kirejtshuk et al., 2016). The dense scale cover on the first antennomere (Fig. 3B) is a previously proposed ommatine autapomorphy (ommatid: Hörnschemeyer, 2009). Moreover, the well-separated, lateral antennal insertions and moniliform antennae shorter than the head and prothorax combined plus twisted mandibles of Lepidomma are considered typical ommatine crown features (ommatid: Lawrence and Ślipiński, 2013). The distinctive expanded pronota in clessidrommatins, developed into a wavyedged Elizabethan collar in *Lepidomma* are, however, unparalled in other archostematans and so far only reported from Burmese amber. A morphological precursor may be the transverse pronotum seen in Pareuryomma Tan, Wang, Ren & Yang, 2012 from the Lower Cretaceous (Yixian Formation) of northeastern China.



Fig. 3. *Lepidomma* affl. tianae gen. et sp. nov., other material (NIGP 169480); probably Noije Bum, mid-Cretaceous. A, photograph of ventral view; close-up of B, head showing mouthparts, left antennal base and scales; C, left eye (ridge) and pronotal edge showing large and small scales; D, window cells either side of elytral suture showing maculae (lateral tubercles) and covering scales.



Fig. 4. *Lepidomma* affl. tianae gen. et sp. nov., other material (NIGP 169480); probably Noije Bum, mid-Cretaceous. Interpretive drawing of ventral view, representative window cells shown in strip on right elytron.

The two Burmese genera are, moreover, rather different in body proportions. An arboreal lifestyle has already been suggested for *Clessidromma* with a body length 4.1 times greater than width (Jarzembowski et al., 2018). Lawrence (1999) associated the elongate body form (three or so times greater than width) of recent tetraphalerin ommatines and cupedines (cupedids sensu stricto) with surface living rather than subcortically in wood and playing dead or possum when threatened (thanatosis). These beetles like Lepidomma, however, lack the narrow waist of Clessidromma which is nevertheless seen in some adephagan beetles (sister suborder of the cupedinans pars: Ponomarenko, 2002). Thus in the latter, pedunculate scarite carabids (ground beetles) when threatened, e.g. by a rodent, not only pull in their appendages and stiffen up, but also arch their backs (Helzer, 2011). The ground beetles are otherwise broad bodied unlike Clessidromma, but extant Tetraphalerus Waterhouse, 1901 has a very similar inequality to this genus (4.2; Hünefeld et al., 2011, fig. 1) and this uncommon extant beetle is reported to live on shrubs in marginal situations rather than trees like Omma Newman, 1839 (Hörnschemeyer, 2005). The considerably lower inequality of Lepidomma (c. 2.4) is about midway between typical extant Omma (2.9 like the pedunculate scarite above; Lawrence and Ślipiński, 2013, fig. 54C) and the flat bug Dysodius Le Peletier & Serville, 1828 (1.7; Heyden and Díaz, 2016, fig 1), both associated with trees. The inequality probably reflects niche

partitioning in the woody biome (e.g. living on twigs versus trunks). Indeed, the hindbody of Lepidomma is rather similar to Omma in Burmese amber (Fig. S3) with the possible exception of having small elytral tails which are also present, although larger and cuticular, in extant Omma rutherfordi Lawrence, 1999. The latter also possesses scales and does not rely on thanatosis like some congeners. A distinctive feature of *Lepidomma* is the development of leaf-like scales, in addition to the more hair-like ones as on the antennal scape (first antennomere). The development of scales is usually associated with lepidopterans (moths and butterflies: Zhang et al., 2018) but is also a feature of some archaic beetles, and although not always readily visible in fossils, scales have been reported from younger adpressions (cupedine archostematans: Kirejtshuk et al., 2016). Unlike in lepidopterans, scales have not figured much in cupedid phylogenetic analyses (e.g. Tan et al., 2012), departing somewhat from the coarsely tuberculate, subcortical, lignicolous lifestyle typically associated with these beetles. In recent ommatines, scales are best developed in species of Omma and are white or yellow-brown, the latter the colour in Lepidomma, although this may be a taphonomic hue; the resulting colour pattern is thought to be protective, but mimetic rather than cryptic as in cupedines (Lawrence, 1999; Hörnschemeyer et al., 2002). Unfortunately, the scale patterning is currently unknown in Burmese inclusions. Lepidomma is, nevertheless, a specialised beetle with its distinctive pronotum and scaly elytra, suitable protection for an exposed lifestyle in the amber forest. Such specialisation is consistent with a high level of endemic taxa becoming apparent in the rapidly growing list for Burmese amber (e.g. in Hymenoptera and Odonata: Ross, 2018) and implies evolutionary time and separation. The amber locality lies in the West Burma terrane (Block, Plate or Platelette: Broly et al., 2015) of Gondwanan origin which separated and finally collided with the Eurasian marginal Sibumasu terrane in the Campanian (Heine and Müller, 2005; Seton et al., 2012). According to the generally accepted tectonic model, the West Burma terrane rifted from northwestern Australia, drifting in a northerly direction, during the Late Triassic to Late Jurassic (Metcalfe, 1998), although earlier (Devonian/ Triassic) rifting and collision has also been suggested (Metcalfe, 2013). The beetle evidence supports the older model because the order Coleoptera is unknown prior to the Late Palaeozoic and ommatine beetles diversified as late as the Middle Triassic (list in Kirejtshuk and Ponomarenko, 2015).

6. Conclusion

A rare, newly discovered archaic beetle, Lepidomma tianae gen. et sp. nov., adds to the diversity of stem cupedid (ommatine) beetles in Burmese amber with its well-developed scale cover and squat body form probably for a surficial, arborical existence in the coniferous amber forest. With an Elizabethan collar as a potential autapomorphy, it points to early ecological specialisation of the clessidrommatins by analogy with extant ommatins and carabids, prior to angiosperm dominance. The continuing flow of new forms from the Kachin amber at generic (and even higher) level contrasts with the now relict aspect of archaic beetles (e.g., only one new ommatine species has been described from the recent fauna in the past twenty years compared with eight from Burmese amber in the past two years). The insect disparity in Burmese amber may well be linked tectonically to West Burma's isolated trajectory across the neotethyan ocean in the late Mesozoic. More material is nevertheless needed to complete character analyses as discussed above and eliminate biases in rare beetle phylogeny: this should be achievable with the current interest in Burmese amber inclusions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10. 1016/j.cretres.2019.02.027