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## *Pleuroceratos jiewenae* sp. nov.: A new Cretaceous phloeostichid beetle (Coleoptera: Cucujoidea: Phloeostichidae)

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### Abstract

Elucidating the phylogenetic affinities of enigmatic fossils is crucial for resolving the early diversification of the superfamily Cucujoidea, a diverse group of polyphagan beetles whose relationships remain contentious. The systematic position of the Cretaceous genus *Pleuroceratos* known from Burmese amber has been uncertain; the genus was previously placed into Silvanidae, Sphindidae, and Cucujoidea *incertae sedis*. Here we describe a new species, *Pleuroceratos jiewenae* sp. nov., from mid-Cretaceous Burmese amber and conduct a formal phylogenetic analysis to elucidate the position of the genus. We recover *Pleuroceratos* as nested within the family Phloeostichidae, represented in the modern fauna by four genera of fungivorous subcortical beetles with a highly disjunct distribution range. *Pleuroceratos* beetles are the sole fossil members of Phloeostichidae known to date and indicate that the family began to diversify by the mid-Cretaceous.

**Keywords:** Cucujoidea, Phloeostichidae, new species, fossil, Burmese amber, phylogeny

### Introduction

The superfamily Cucujoidea, consisting of over 10,000 described species in 26 families (Lord *et al.*, 2010; Leschen & Ślipiński, 2010; Ślipiński *et al.*, 2011; Robertson *et al.*, 2015; Alekseev, 2017), represents one of the taxonomically most challenging groups of beetles (Leschen *et al.*, 2005; Leschen & Ślipiński, 2010). The superfamily has historically acted as a taxon of convenience for small brown beetles with clubbed antennae that were difficult to place elsewhere. In particular, phylogenetic relationships within the early-diverging Cucujoidea ('lower Cucujoidea' or 'basal

Cucujoidea') have been difficult to resolve based on morphological (Leschen *et al.*, 2005) and molecular datasets (McElrath *et al.*, 2015; McKenna *et al.*, 2015, 2019; Zhang *et al.*, 2018), with analyses disagreeing about the monophyly and position of individual families. Fossils provide a crucial source of evidence for understanding the timing of the diversification of Cucujoidea and can inform our understanding of the group's phylogeny by revealing transitional states between modern families (Zhou *et al.*, 2018; Li *et al.*, 2019).

The unresolved phylogeny of Cucujoidea causes difficulties when trying to place Mesozoic fossil taxa. The enigmatic extinct genus *Pleuroceratos* Poinar & Kirejtshuk was described from mid-Cretaceous Burmese amber on the basis of a single specimen as the earliest representative of Silvanidae (silvanid flat bark beetles). However, the quality of preservation of the type specimen of *P. burmiticus* only permitted the dorsal side to be easily observed and the assignment was strongly informed by superficial similarities with the extant silvanid genus *Oryzaephilus* Ganglbauer (Poinar *et al.*, 2008). Recently, Liu *et al.* (2019) examined additional specimens and concluded that despite its silvanid appearance, *Pleuroceratos* does not belong to Silvanidae since it possesses some characters not found in any modern silvanid species, namely the transversely oval and externally open procoxae with partly exposed trochantins, and mesocoxal cavities closed or very narrowly open to the mesepimeron (Thomas & Leschen, 2010). The authors placed the genus as family *incertae sedis* within Cucujoidea.

Recently, further specimens of *P. burmiticus* were examined by Kirejtshuk *et al.* (2019) who transferred *Pleuroceratos* to Sphindidae (cryptic slime mold beetles). The authors justified this placement by the presence of separate transverse procoxae and further compared the

genus to the extant *Protosphindus* Sen Gupta & Crowson. However, the antennal club of *Pleuroceratos* is not compact or notably setose as is the case in all modern representatives of the family, the pronotal base is straight, and the presence of a dorsal mandibular mycangium could not be confirmed (Forrester & McHugh, 2010). Moreover, the separate transverse procoxae are not unique to Sphindidae and are found in a number of cucujoid families such as some Cryptophagidae, Cyclaxyridae, rhizophagine monotomids, some Passandridae, some Phalacridae, Propalticidae, and some members of Laemophloeidae.

Here we describe a second species of the genus, *P. jiewenae* **sp. nov.**, from Burmese amber and re-evaluate the systematic position of *Pleuroceratos* using a formal cladistic analysis.

## Materials and methods

### Preparation and photography

The studied specimen originated from an amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar. Amber from northern Myanmar is Albian to Cenomanian as indicated by zircon dating of the fossiliferous horizon and palaeontological evidence (Shi *et al.*, 2012; Mao *et al.*, 2018; Yu *et al.*, 2019). The fossilised resin was probably secreted by dawn redwood trees in a tropical rainforest palaeoenvironment in the vicinity of fresh or brackish water (Grimaldi & Ross, 2017; Smith & Ross, 2018; Li *et al.*, 2020). Burmese amber represents probably the largest Cretaceous insect Lagerstätte in terms of the number of described species (Cai *et al.*, 2019; Ross, 2019, 2020).

The specimen was polished with different grades of sandpaper of gradually finer grits and polishing powder. Photographs were taken using a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and with an attached Canon MT-24EX twin flash. For fluorescence microscopy, a Zeiss Axio Imager 2 microscope equipped with a mercury lamp and set to the eGFP mode was used. The type specimen is deposited in the amber collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences in Nanjing, China.

### Phylogenetic analysis

A phylogenetic analysis was conducted to elucidate the systematic position of *Pleuroceratos* within ‘basal Cucujoidea’. The genus was scored for morphological characters using the matrix (ninety-nine characters)

compiled by Leschen *et al.* (2005) for representatives of ‘basal cucujoid’ genera. We were able to score 33 characters out of the total 66 available characters for adults. The 33 larval characters could not be scored. The resultant character matrix is made available in the Appendix. Two members of the family Trogossitidae (*Eronyxa* Reitter, and *Thymalus* Latreille) and a single member of Derodontidae (*Derodontus* LeConte) were used as outgroups. Representatives of the following 23 ingroup families were sampled: Biphyllidae, Boganiidae, Byturidae, Cavognathidae, Cryptophagidae, Cucujidae, Cyclaxyridae, Erotylidae, Helotidae, Hobartiidae, Kateretidae, Laemophloeidae, Lamingtoniidae, Monotomidae, Nitidulidae, Passandridae, Phalacridae, Phloeostichidae, Propalticidae, Protocucujidae, Silvanidae, Smicripidae, and Sphindidae. Maximum parsimony analyses were conducted in TNT v. 1.5 (Goloboff & Catalano, 2016) using implied weighting. The recommended concavity value (K) of 12 was used (Goloboff *et al.*, 2018). Collapsing rules were set to ‘none’ and the analysis was run using default settings in ‘New Technology Search’. A majority-rule consensus tree was computed. To assess tree support, nonparametric bootstrap analysis was run with 1,000 replicates. GC, or ‘group present/contradicted’, values were calculated with 1,000 replicates (Goloboff *et al.*, 2003). Character states were mapped using ASADO v. 1.61 (Nixon, 2004).

## Systematic palaeontology

### Order Coleoptera Linnaeus, 1758

### Suborder Polyphaga Emery, 1886

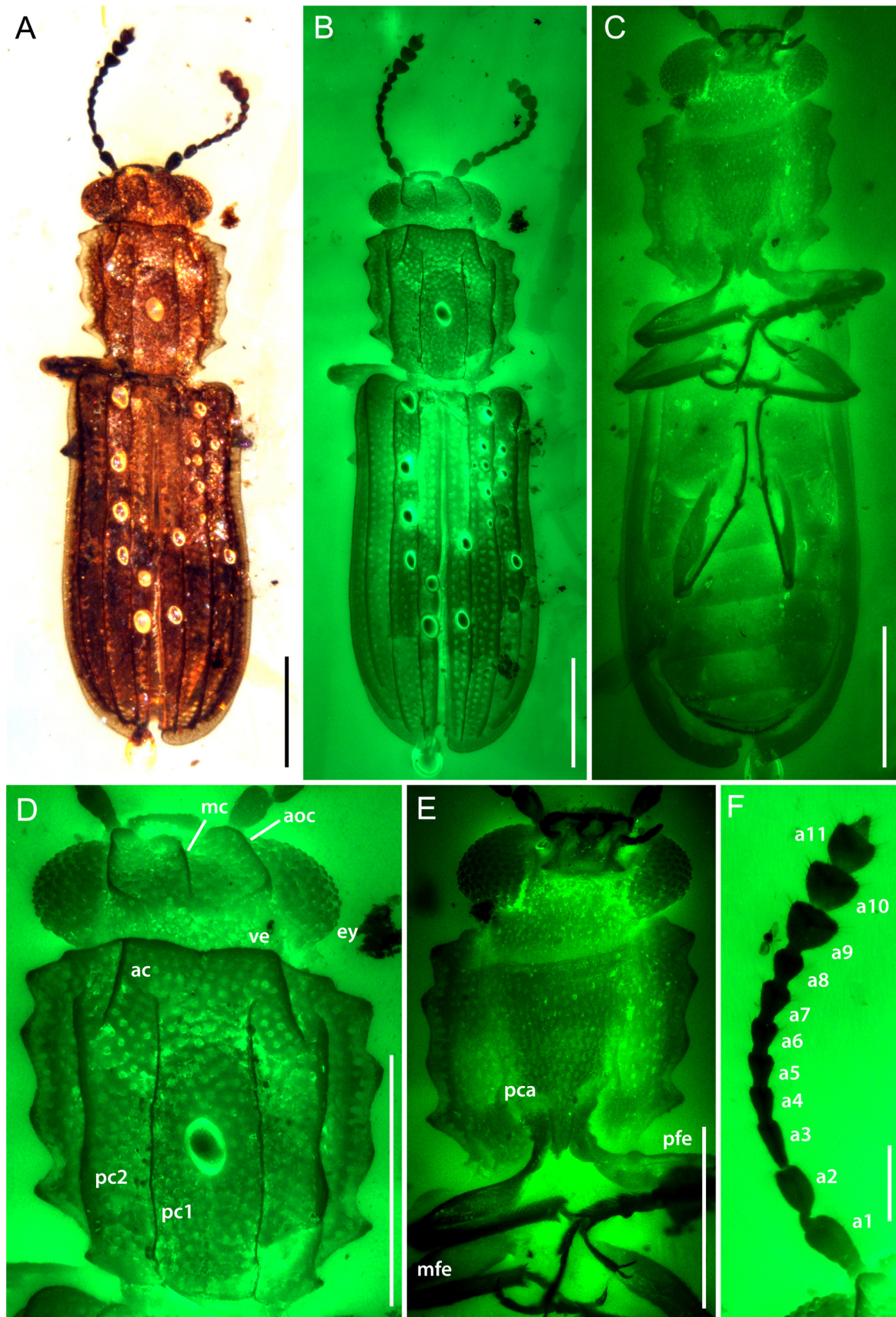
### Superfamily Cucujoidea Latreille, 1802

### Family Phloeostichidae Reitter, 1911

### Genus *Pleuroceratos* Poinar & Kirejtshuk, 2008

**Included species.** *Pleuroceratos burmiticus* Poinar & Kirejtshuk, 2008 (type species), *P. jiewenae* **sp. nov.**

**Diagnosis.** Amended from Kirejtshuk *et al.* (2019). Body rather small (2.4–4.0 mm); elongate, slightly convex dorsoventrally. Dorsum mostly without visible hairs; anterior part of head, ventrum, antennae, and legs sparsely setose. Integument with coarse and dense punctation; head, pronotum, and elytra carinate. Head with one pair of adocular costae and one median costa, anterior part of frons slightly convex. Frontoclypeal suture present, gular sutures and antennal grooves absent. Mandibles tridentate apically. Antennal insertions barely concealed from above. Antennae 11-segmented, moderately long, not reaching to the elytral base, with three subapical antennomeres forming loose and sparsely



**FIGURE 1.** Habitus photographs and morphological details of *Pleuroceratos jiewenae* sp. nov. (holotype, NIGP173055). **A**, Dorsal view in reflected light. **B**, Dorsal view under green fluorescence. **C**, Ventral view under green fluorescence. **D**, Head and pronotum in dorsal view under green fluorescence. **E**, Head and pronotum in ventral view under green fluorescence. **F**, Antennae. Abbreviations: a1–11, antennomere 1–11; aoc, anterior pronotal costa; ac, adocular costa; pc1–2, posterior pronotal costa; ey, eye; mc, medial costa; mfe, mesofemur; pfe, profemur; pca, procoxa; ve, vertex. Scale bars (**A–E**) = 500  $\mu$ m, (**F**) = 100  $\mu$ m.

setose club. Pronotum transverse, slightly vaulted, its sides widely explanate and dentate laterally, disc with two to six longitudinal costae. Procoxae transversely oval; procoxal cavities externally open; protrochantins partly exposed. Elytra with rows of wide punctures between sharply elevated longitudinal costae, elytral sutural flange widened apically. Distance between oval mesocoxae smaller than between procoxae. Metaventrite slightly convex and with narrow median depression in distal half, without discrimen, its posterior edge deeply excised. Metepisterna rather narrow. Metacoxae narrowly separated. Trochanters elongate. Tibiae with rather thin, short spurs. Tarsi elongate, simple, lacking lobes.

***Pleuroceratos jiewenae* sp. nov.**

(Fig. 1)

**Holotype.** NIGP173055. Female, as indicated by the 5-5-5 tarsi.

**Etymology.** The new species is named after Ms Jiewen Zhao, the daughter of the donor of the amber piece, Ms Dan Zuo.

**Diagnosis.** The new species differs from *Pleuroceratos burmiticus* in the medial head costa reaching to the posterior third of the eyes and adocular costae approximately semi-rectangular, not triangular. Pronotal margin with five lateral carinae, with the posterior two approximately right-angled, spines acute and never bifid. Pronotal disc with two pairs of posterior longitudinal costae running from the pronotal base to the anterior fifth and a pair of anterior costae running from the anterior margin to the anterior quarter is located between the posterior costae. Each elytron with three longitudinal costae, the interval between the first and second longitudinal costae with three rows of punctures. Antennomeres 2 and 3 in the new species are subequal in length, while in *P. burmiticus*, antennomere 2 is slightly larger than antennomere 3.

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

**Description.** Body elongate, more or less parallel-sided, dorsoventrally compressed. Body length 2.47 mm from clypeus to abdominal apex, 0.78 mm wide across elytral base. Dorsum deeply punctate, glabrous. Body chestnut brown, appendages dark brown.

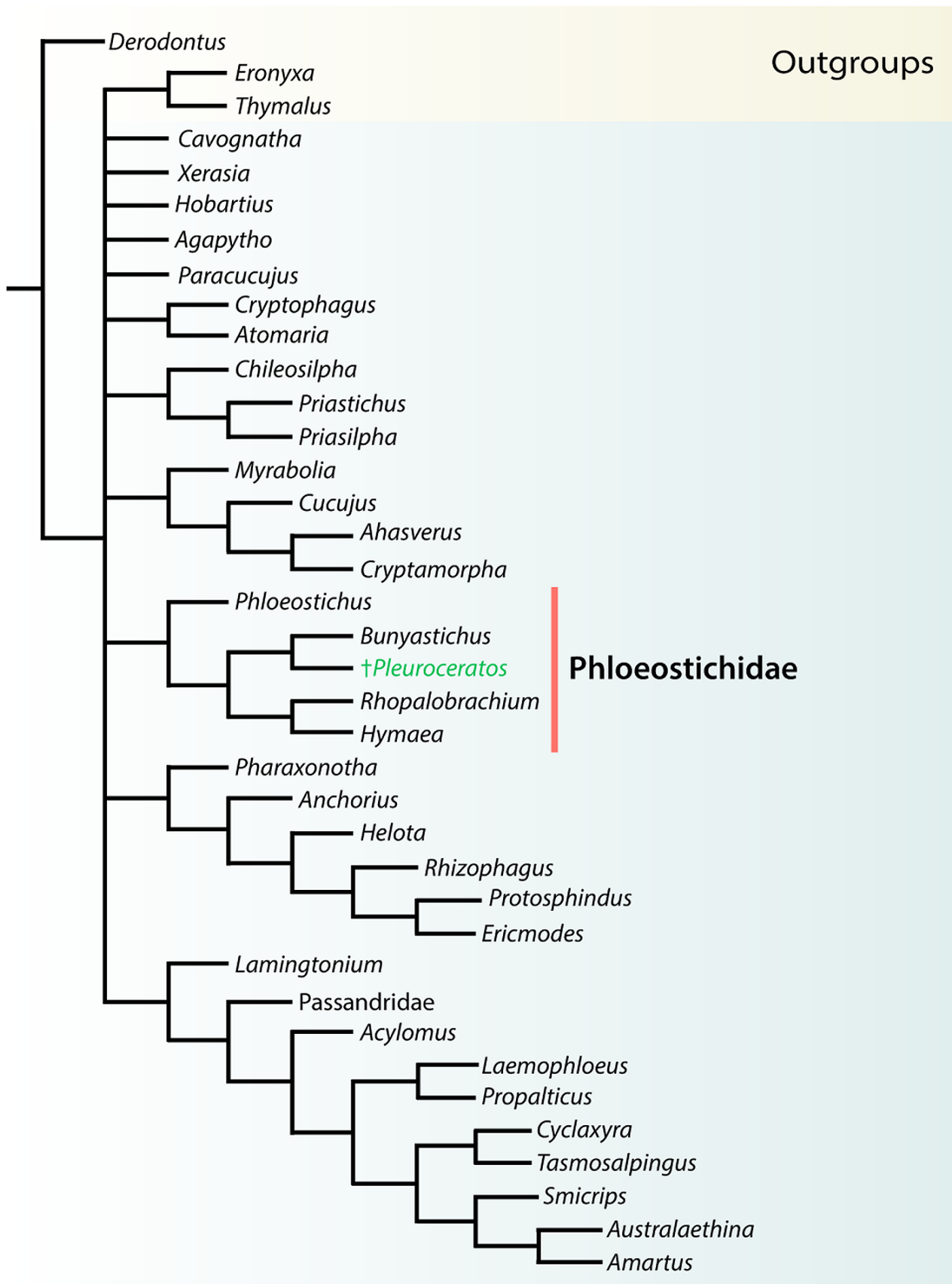
Head 0.4 mm long, approximately as long as wide, apparently slightly declined, with mouthparts oriented anteroventrally. Dorsum of head distinctly carinate (Fig. 1D). One pair of adocular costae reaching to the posterior third of the eyes and with apical portions bent medially at a right angle, each costa approximately the same height throughout, not forming a triangular spine (Fig. 1D: aoc).

A single costa is located medially, not exceeding the length of the adocular costae (Fig. 1D: mc). Frontoclypeal suture present. Gular sutures and antennal grooves absent. Mandibles elongate, lacking a mola, tridentate apically. Eyes ovoid, strongly protruding, without interfacetal setae. Antennal insertions barely concealed from above and located anterior to the eyes. Antennae 11-segmented, moderately long, reaching to the fourth lateral costa anteriorly, with a loose symmetrical three-segmented club (Fig. 1F). Antennomere 1 (scape) clavate, 1.25 times as long as the following segment; antennomere 2 (pedicel) clavate, as long as the following segment and wider; antennomeres 3–8 progressively shorter and broader apically; antennomeres 9–11 forming a loose club with the apical portion of the ultimate segment subtriangular. Antennomeres mostly glabrous, segments 4–11 with a group of elongate apical setae. Vertex of head without costae, densely punctate.

Pronotum transverse, 0.69 mm long, 1.1 times as long as wide, approximately parallel-sided with lateral projections, base distinctly narrower than elytral base. Pronotal surface densely punctate, irregularly arranged punctures deep and circular, separated by at most one time their diameter. Anterior pronotal angles not distinctly produced forward and approximately right-angled. Anterior and posterior margins of pronotum approximately straight. Lateral margins distinctly dentate with five subequally spaced projections. Anterior three lateral carinae oblique, remaining two more projecting and approximately right-angled. Pronotal disc with six longitudinal costae: two pairs of posterior longitudinal costae running from base to the anterior fifth (Fig. 1D: pc1–2), and a pair of shorter anterior longitudinal costae running between the two posterior pairs and reaching to the basal quarter (Fig. 1D: ac). Pronotal costae approximately equally high, posterior costae approximately straight, anterior costae slightly curving laterally distad.

Prosternum in front of coxae longer than the diameter of the procoxal cavities. Procoxal process complete, parallel-sided, gradually narrowing posteriorly, with lateral carinae. Procoxae moderately transverse and externally open, separated by slightly less than the procoxal diameter. Metepisterna narrow. Mesocoxal cavities rounded, separated. Metacoxae narrowly separated. Abdominal intercoxal process rather broadly rounded.

Legs rather long and slender. Trochantins partly exposed. Trochanters elongate. Femur widened medially. Tibiae with two thin spurs apically and a comb of spines or strong setae, reaching to approximately half of the basal tarsomere. Tarsi five-segmented, simple, lacking lobes. Basal four segments densely setose ventrally, apical tarsomere with rows of sparse setae. Claws simple, empodium not visible.



**FIGURE 2.** Strict consensus cladogram of two most parsimonious trees obtained in TNT v. 1.5 with ‘New Technology Search’ under implied weighting ( $K = 12$ ; tree length = 616 steps; consistency index = 0.203; retention index = 0.453), showing the systematic position of *Pleuroceratos* in relation to the former ‘lower Cucujoidea’.

Elytra 1.38 mm long, 2.1 times longer than their combined width. Elytral disc with ten rows of deep circular punctures. Three longitudinal costae present. Two rows of punctures located between the elytral suture and the first costa, three rows of punctures located between the first and second costae, three sutures located between the second and third costae, and two rows located between the third costa and the epipleural margin. Costae highest at elytral base. Medial elytral costa shortest, terminating in the apical quarter, remaining costae reaching to elytral margin. Epipleura narrow and almost complete, widest basally, reaching to the apex of the third ventrite. Elytral sutural flange widened apically. Elytral apices rounded. Abdomen with five ventrites, ventrites 1–4 subequal, ventrite 5 representing approximately half of the preceding segment.

## Discussion

### *Systematic position of Pleuroceratos*

The exquisite preservation of *Pleuroceratos jiewenae* **sp. nov.** provides access to morphological characters important for elucidating the systematic position of this enigmatic Cretaceous genus. Our parsimony analysis sampling a wide range of extant cucujiform families resulted into three most parsimonious trees. A strict consensus tree was calculated (tree length = 616 steps; consistency index = 0.203; retention index = 0.453) which recovered *Pleuroceratos* as a sister taxon to the genus *Bunyastichus* Leschen, Lawrence & Ślipiński within a monophyletic Phloeostichidae (Fig. 2).

The monophyly of the family Phloeostichidae was supported by the anterolateral genal projection (apomorphy), carinate sides of pronotum, well-developed metendosternal laminae, well-separated bases of frontal arms, and labrum partly or completely fused to head capsule. The genus *Pleuroceratos* indeed possesses all the diagnostic characters of Phloeostichidae (Leschen *et al.*, 2005; Lawrence & Ślipiński, 2010) including an elongate, parallel-sided, subglabrous and tuberculate body, 11-segmented antennae with a 3-segmented club, prothorax distinctly narrower than elytral bases, complete prosternal process, slightly transverse procoxae with exposed trochantins, mesocoxal cavities separated, abdomen with 5 ventrites, and enlarged femora. The genera *Bunyastichus* and *Pleuroceratos* share the presence of the frontoclypeal suture, antennal insertions somewhat concealed from above, and tridentate mandibles that distinguish both genera from other representatives of the family. However, *Pleuroceratos* differs from *Bunyastichus* in the presence of externally open procoxae and simple tarsi without

lobes. *Pleuroceratos* is furthermore distinguished from all members of the family by its carinate head and elytra, although lateral pronotal carinae are also found in the genera *Bunyastichus* and *Phloeostichus*.

### *The earliest fossil record of Phloeostichidae*

Phloeostichidae is a small family comprising only four extant genera with six species (Lawrence & Ślipiński, 2010). This rather obscure family has been recognised relatively recently, by Sen Gupta & Crowson (1969), as a heterogeneous group of enigmatic cucujoids. Subsequent revisions split Phloeostichidae *sensu* Sen Gupta & Crowson (1969) into five families (Crowson, 1973; Leschen *et al.*, 2005). Phloeostichidae in its present sense, containing the genera *Bunyastichus*, *Hymaea* Pascoe, *Phloeostichus* Redtenbacher, and *Rhopalobrachium* Boheman, appears monophyletic on morphological grounds (Leschen *et al.*, 2005). The phylogenetic position of Phloeostichidae has historically been uncertain (Leschen, 1996). McElrath *et al.* (2015) recovered Phloeostichidae as a sister group to a clade comprising Agapythidae and Priasilphidae based on an analysis of seven genes. McKenna *et al.* (2015) arrived at an identical topology when their six gene dataset was analysed with maximum likelihood, but recovered Phloeostichidae as a sister to Agapythidae, Cucujidae, and Priasilphidae when the genes were analysed using a Bayesian model. Analyses of larger datasets have arrived at substantially different results. Zhang *et al.* (2018) recovered Phloeostichidae as a sister group to a clade containing Laemophloeidae, Myraboliidae, Passandridae, Phalacridae, and Propalticidae based on an analysis of 95 protein-coding genes. An identical topology was arrived at by McKenna *et al.* (2019) based on an analysis of 89 genes.

Leschen *et al.* (2005) stressed the superficial similarity between *Bunyastichus* and some brontine Silvanidae. With its carinate head, pronotum, and elytra, *Pleuroceratos* also strongly resembles silvanids, explaining why it may have been misplaced earlier. It however differs from Silvanidae in having externally closed procoxal cavities with partly exposed trochantins, and apically widened elytral sutural flange. It is likely that the striking morphological similarities between *Pleuroceratos* and some extant members of Silvanidae and Sphindidae resulted from convergence due to a similar mode of life.

The biology of extant members of the family Phloeostichidae remains little known since the members of the family are small and infrequently collected. *Phloeostichus denticollis*, the only member of the family inhabiting the Northern Hemisphere has an Euro-Siberian distribution including Japan and occurs on maples,

beeches, firs, and larches in alpine and subalpine forests (Hirano & Kusano, 2014; Procházka & Schläghamerský, 2018). Most beetles are collected individually from under the bark of these trees, under moss covering bark, or are found in flight interception traps. The Australian *Hymaea* has been collected under tree bark of decaying logs and in ambrosia beetle galleries (Candy, 1990). Adults have mandibular cavities that have been interpreted as possible mycangia by Sen Gupta & Crowson (1966), although this hypothesis remains to be tested (Grebennikov & Leschen, 2010). *Rhopalobrachium* occurs throughout parts of Australia and South America. Representatives of the genus have been collected in beech forests (Cekalović, 1976) and gut dissections have revealed the presence of fungal hyphae, suggesting mycophagous habits (Lawrence & Ślipiński, 2010). The monotypic genus *Bunyastichus*, that has been recovered as sister to *Pleuroceratos* in our analyses, is endemic to northern Queensland, Australia. Little is known about its biology, aside from that the type series was collected from bunya pine trees (Leschen *et al.*, 2005). Considering these findings about the biology of extant phloeostichids, it is thus most likely that *Pleuroceratos* inhabited spaces under bark of the resin-producing trees in the Cretaceous Burmese rainforest and fed on fungi.

Up until now, the family Phloeostichidae was only known from the Recent fauna. The genus *Pleuroceratos*, reassigned to Phloeostichidae, thus represents the first fossil record of the family and provides evidence that phloeostichids began to diversify by the mid-Cretaceous. The disjunct distributional range of Phloeostichidae may suggest that the group had a wider distributional range in the past. Alternatively, the disjunct distribution may stem from our still incomplete understanding of this overlooked family as it is likely that many further species remain to be described. In either way, *Pleuroceratos* substantially expands the known morphological disparity of the family and represents an important calibration point for understanding the early diversification of Cucujoidea.

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## Appendix 1: Character state definitions (after Leschen et al., 2005)

### Adult characters

- (1) *Postocular constriction*: (1) absent; (2) present.  
(2) *Vertexal line*: (1) absent; (2) present.  
(3) *Median occipital stridulatory file*: (1) absent; (2) present.  
(4) *Paired occipital incisions*: (1) absent; (2) present.  
(5) *Frontoclypeal suture*: (1) present; (2) absent.  
(6) *Antennal insertions*: (1) exposed from above; (2) concealed by frontal ridge.  
(7) *Subantennal groove*: (1) absent; (2) not extending below or behind eye; (3) extending below or behind eye.  
(8) *Genal projection*: (1) absent; (2) anterior, truncate or rounded; (3) anterior, acute; (4) anterolateral.  
(9) *Anterior cervical sclerites*: (1) not contiguous with head capsule or placed in paired emarginations; (2) contiguous with head capsule and usually placed within paired emarginations on ventral edge of occipital foramen; (3) apparently absent.  
(10) *Apex of mandible*: (1) unidentate; (2) bidentate; (3) tridentate.  
(11) *Dorsal surface of mandible*: (1) without tubercle fitting into lateral clypeal emargination; (2) with tubercle fitting into lateral clypeal emargination.  
(12) *Dorsal surface of mandible*: (1) without cavity; (2) with glabrous cavity; (3) with setose cavity.  
(13) *Mandibular mola*: (1) present; (2) absent.  
(14) *Galea*: (1) at least 2.5X as wide as lacinia; (2) between 1X and 2.5X as wide as lacinia; (3) distinctly narrower than lacinia; (4) absent.  
(15) *Lacinal uncus*: (1) absent; (2) present.  
(16) *Lateral pronotal carinae*: (1) complete; (2) incomplete or absent.  
(17) *Sides of pronotum*: (1) without 4–6 sharp teeth; (2) with 4–6 sharp teeth.  
(18) *Anterior pronotal angles*: (1) absent or not produced forwards; (2) produced forwards.  
(19) *Anterior portion of prosternum at midline*: (1) longer than prosternal process; (2) as long as as prosternal process; (3) shorter than prosternal process.  
(20) *Anteromesal corner of hypomerone*: (1) without tooth; (2) with tooth.  
(21) *Apex of prosternal process*: (1) without lateral projections; (2) with lateral projections.  
(22) *Shortest distance between procoxal cavities*: (1) less than half as great as mid length of cavity; (2) more than half as great but less than mid length of cavity; (3) more than mid length of cavity.  
(23) *Notosternal suture*: (1) complete; (2) incomplete.  
(24) *Procoxa*: (1) without or with short, concealed lateral extension; (2) with long, concealed lateral extension.  
(25) *Protochantin*: (1) exposed; (2) concealed.  
(26) *Procoxal cavity*: (1) strongly transverse; (2) slightly transverse; (3) about as long as wide.  
(27) *Procoxal cavities externally*: (1) open; (2) closed.  
(28) *Procoxal cavity*: (1) without lateral notch, only slightly or gradually narrowed laterally; (2) with narrow lateral notch (less than 0.25X as wide as mid length of cavity).  
(29) *Procoxal cavity*: (1) internally open; (2) internally closed.  
(30) *Elytral punctation*: (1) not seriate or striate; (2) seriate or striate.  
(31) *Scutellary striole*: (1) absent; (2) present.  
(32) *Elytral sutural flange*: (1) not widened apically; (1) widened apically.  
(33) *Epipleuron*: (1) complete to apex; (2) incomplete or absent.  
(34) *Anteromesal corner of mesepisternum*: (1) without cuticular pocket; (2) with cuticular pocket.  
(35) *Shortest distance between mesocoxal cavities*: (1) less than half as great as shortest diameter of cavity; (2) more than half as great but less than shortest diameter of cavity; (3) more than shortest diameter of cavity.  
(36) *Meso-metaventral junction*: (1) dicondylic; (2) monocondylic; (3) simple.  
(37) *Mesocoxal cavities laterally*: (1) open (partly closed by mesepimeron); (2) closed (by meeting of mesoventrite and metaventrite).  
(38) *Metaventral discriemen*: (1) present; (2) absent.  
(39) *Metaventral transverse suture (katapisternal suture)*: (1) present; (2) absent.  
(40) *Metacoxae*: (1) contiguous or narrowly separated; (2) widely separated.  
(41) *Metacoxae*: (1) extending laterally to meet elytral epipleura, ventrite one not in contact with metepimeron; (2) not extending laterally to meet elytral epipleura, ventrite one in contact with metepimeron.  
(42) *Metacoxal carina*: (1) present; (2) absent.  
(43) *Metendosternal laminae*: (1) well developed; (2) reduced; (3) absent. Reduced laminae (2) tend to be slender and not broad and plate-like.  
(44) *Anterior tendons of metendosternite*: (1) narrowly separated; (2) widely separated.  
(45) *Radial cell of hind wing*: (1) complete; (2) incomplete (open basally) or absent.  
(46) *Free veins in medial field of hind wing*: (1) five; (2) four; (3) three or fewer.  
(47) *Tarsi in male*: (1) 5–5–5; (2) 5–5–4.  
(48) *Mesotarsomere four*: (1) not or slightly reduced and not enclosed within lobe on tarsomere three; (2) highly reduced and partly or entirely enclosed within ventral lobe on tarsomere three.  
(49) *Apex of terminal tarsomere*: (1) without fringe of short setae; (2) with fringe of short setae.  
(50) *Empodium*: (1) projecting between pretarsal claws; (2) absent or not visible between pretarsal claws.  
(51) *Number of basal ventrites connate*: (1) none; (2) two.  
(52) *Ventrite 1*: (1) not much longer than 2; (2) much longer than 2.  
(53) *Abdominal intercoxal process*: (1) acute or narrowly rounded; (2) broadly rounded; angulate or truncate.  
(54) *Abdominal tergite VII*: (1) concealed from above; (2) exposed from above.  
(55) *Functional spiracles on abdominal segment VII*: (1) present; (2) absent.  
(56) *Tergite VIII in male*: (1) completely dorsal; (2) with sides curved ventrally; (3) with sides and apex curved ventrally to form genital capsule.  
(57) *Anterior edge of sternite VIII in male*: (1) without median strut; (2) with median strut.  
(58) *Apex of sternite IX in male*: (1) with mesal lobe; (2) without mesal lobe.  
(59) *Anterior edge of sternite IX in male*: (1) without spiculum gastrale; (2) with spiculum gastrale.  
(60) *Base of tegmen*: (1) broadly rounded; (2) narrowly rounded to acute; (3) produced anteriorly forming strut.  
(61) *Parameres*: (1) free from one another; (2) fused into single piece.  
(62) *Parameres*: (1) articulated to phallobase; (2) fused to phallobase.

- (63) *Penis*: (1) not divided into distinct basal and apical sections; (2) divided into distinct basal and apical sections.  
 (64) *Basal portion of penis*: (1) distinctly wider than apical portion; (2) as wide as or narrower than apical portion.  
 (65) *Base of penis*: (1) without median carina; (2) with median carina.  
 (66) *Anterior edge of penis*: (1) without struts; (2) with paired struts; (3) with single strut.

*Larval characters*

- (67) *Posterior edge of head capsule*: (1) not, or only slightly, emarginate; (2) distinctly emarginate.  
 (68) *Bases of frontal arms*: (1) contiguous; (2) well separated.  
 (69) *Median endocarina*: (1) absent; (2) present.  
 (70) *Paired endocarinae*: (1) absent; (2) present.  
 (71) *Stemmata*: (1) six; (2) five; (3) four or fewer.  
 (72) *Antennal length*: (1) less than 0.15X head width; (2) 0.15–0.5X head width; (3) more than 0.5X head width.  
 (73) *Sensorium*: (1) shorter than apical antennomere; (2) longer than apical antennomere.  
 (74) *Labrum*: (1) separated from head capsule by complete suture; (2) partly or completely fused to head capsule (suture incomplete or absent).  
 (75) *Apex of mandible*: (1) unidentate; (2) bidentate; (3) tridentate.  
 (76) *Accessory ventral process of mandible*: (1) absent; (2) present.  
 (77) *Mesal surface of mandibular base*: (1) with asperate or tuberculate mola; (2) with 1–3 hyaline processes; (3) simple.  
 (78) *Ventral mouthparts*: (1) strongly retracted; (2) protracted or slightly retracted.  
 (79) *Maxillary articulating area*: (1) well developed; (2) highly reduced or absent.

- (80) *Inner apical angle of mala or lacinia*: (1) rounded or truncate; (2) more or less acute (falciform).  
 (81) *Number of labial palpomeres*: (1) two; (2) one.  
 (82) *Labial palps*: (1) contiguous or separated by less than width of first palpomere; (2) separated by more than width of first palpomere.  
 (83) *Ligula*: (1) absent; (2) present.  
 (84) *Hypopharyngeal sclerome*: (1) absent; (2) present.  
 (85) *Hypostomal rods*: (1) subparallel; (2) diverging.  
 (86) *Ventral epicranial ridges*: (1) absent; (2) present.  
 (87) *Gula*: (1) wider than long; (2) longer than wide.  
 (88) *Thoracic and most abdominal terga*: (1) without long lateral processes; (2) with long lateral processes.  
 (89) *Mesocoxae separated by*: (1) less than two coxal diameters; (2) more than two coxal diameters.  
 (90) *Number of pretarsal setae*: (1) two; (2) one.  
 (91) *Abdominal tergites*: (1) without rows of asperities; (2) with curved rows of asperities.  
 (92) *Abdominal tergum IX*: (1) not forming articulated plate; (2) forming articulated plate.  
 (93) *Abdominal tergum IX*: (1) simple; (2) with paired urogomphi.  
 (94) *Urogomphi*: (1) straight; (2) curved upwards.  
 (95) *Urogomphi*: (1) subparallel; (2) strongly diverging.  
 (96) *Sternum IX*: (1) partly or entirely exposed; (2) completely concealed or apparently absent.  
 (97) *Segment X and anal opening*: (1) posterior or terminal; (2) posteroventral; (3) ventral.  
 (98) *Spiracles*: (1) annular; (2) annular—biforous.  
 (99) *Abdominal spiracles*: (1) not at ends of spiracular tubes; (2) at ends of short spiracular tubes on segments I–VIII; (3) at ends of long spiracular tubes on segments I–VIII; (4) at end of spiracular tubes on segment VIII only.

