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First boganiine beetle in mid-Cretaceous amber from northern Myanmar (Coleoptera: Boganiidae)

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ABSTRACT

Cretoboganium gei gen. et sp. nov., a new amber inclusion of the cucujoid family Boganiidae is described and figured based on a well-preserved adult from the mid-Cretaceous Burmese amber (Hukawng Valley, northern Myanmar), some 99 million years ago. Based on the presence of a pair of pronotal callosities, *Cretoboganium* can be firmly placed in the extant subfamily Boganiinae, a small group currently comprising two small austral genera. Our discovery represents the first fossil record for Boganiinae. It also demonstrates another example that an apparently austral group may have its sister group occurred in today's northern hemisphere. Together with the other fossil boganiid known from the Middle Jurassic of China, the finding suggests that Boganiidae is an ancient and relict group. Moreover, the present biogeographic distribution of Boganiinae is indicative of an earlier origin of this subfamily, which likely originated before the breakup of the Gondwanan supercontinent.

1. Introduction

With only 15 extant species placed in 6 extant genera, the cucujoid family Boganiidae is a small and distinctive beetle group, currently restricting to Australia, New Caledonia and southern Africa (Lawrence and Ślipiński, 2010; Escalona et al., 2015). All extant adults and larvae of Boganiidae seem to be pollenophagous. For example, *Boganium malleense* Escalona et al., belonging to the subfamily Boganiinae, occur in the flowers of *Eucalyptus gracilis* F. (Myrtaceae), and adults of *Athertonium* Crowson are collected in the blossoms of Myrtaceae, Elaeocarpaceae, Cunionaceae, Meliaceae and Lauraceae (Escalona et al., 2015). Although the phylogenetic relationships between Boganiidae and other cucujoid families remains unsettled, both morphological and molecular data indicate it as a member of the superfamily Cucujoidea (Lawrence et al., 2011; McKenna et al., 2015).

Fossil boganiids are very sparse. The firs described fossil species, *Palaeoboganium jurassicum* Liu et al., is from the Middle Jurassic Daohugou beds (Inner Mongolia, northeastern China), some 165 million years old (Liu et al., 2018). *Palaeoboganium jurassicum* was suggested as a potential pollinator of Jurassic cycads based on phylogenetic evidence (Liu et al., 2018). As such, our knowledge about the early evolutionary history and historical biogeography of this small peculiar family is lacking. Here we reported the first amber-entombed boganiid beetle with exquisite morphological details preserved in the Cretaceous amber from northern Myanmar.

2. Material and methods

The fossil species is described and figured based on a sole specimen preserved in Upper Cretaceous Burmese amber (Hukawng Valley, northern Myanmar; ca. 99 Ma). Observations and photographs were made using a Zeiss Discovery V20 stereo microscope and a Zeiss Axio Imager 2 light microscope with a digital camera attached respectively. The Zeiss Axio Imager 2 microscope was equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine. Photomicrographs with a green background were taken under the eGFP mode, and those with a red background were under the rhodamine mode. Extended depth of field images were digitally compiled using a Zerene Stacker v.1.0.4 software, and arranged in Adobe Photoshop CS5. The publication LSID is:urn:lsid:zoobank.org:pub:F9E63684-8BB6-40FE-AC61-D48C3FA3504F.

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3. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758
Family: Boganiidae Sen Gupta and Crowson, 1966
Subfamily: Boganiinae Sen Gupta and Crowson, 1966
Genus: *Cretoboganium* gen. nov.
ZooBank LSID: urn:lsid:zoobank.org:act:4A3787D5-34FF-48A3-8485-700A7117593D.

Type species. *Cretoboganium gei* sp. nov.

Diagnosis. *Cretoboganium* can be readily distinguished from all known extant and extinct genera of Boganiidae by the following combination of characters: frontoclypeal suture strongly curved (possible apomorphy); clypeal base not constricted; antennae short, with distinct 3-segmented antennal club; maxillary palp short; pronotum with a pair of large callosities; prosternal process distinctly dilated at apex; and elytra with regular puncture rows.

Etymology. Combination of the Latin word *creta*, meaning chalk, and the generic name *Boganium*; it is neuter in gender.

Description. Body (Fig. 1) comparatively large for Boganiidae (ca. 3 mm long), elongate, slightly flattened, subglabrous.

Head (Fig. 2A) strongly transverse, not declined. Occipital region without transverse ridge. Frontal region without median endocarina. Eyes (Fig. 2B) large, entire, strongly laterally protuberant, coarsely facetted, without interfacetal hairs. Antennal insertions (Fig. 2B) slightly concealed from above. Frontoclypeal suture distinctly impressed, curved; base of clypeus not impressed laterally, its anterior edge rounded, without teeth. Labrum concealed beneath clypeus. Antennae (Fig. 2B) with eleven antennomeres, with distinct, 3-segmented club (Fig. 3D). Mandible small. Maxilla (Fig. 2C) with setose galea; maxillary palp short.

Pronotum (Fig. 2A) setose, strongly transverse, about 0.65 times as long as wide, widest slightly before middle; sides strongly curved, not explanate; lateral pronotal carinae complete, simple, visible for their entire lengths from above, with raised margin; anterior angles rounded, with prominent callosities containing gland openings (Fig. 2B); posterior angles sharp and distinct; posterior edge weakly bisinuate, well margined; pronotal disc without sublateral carinae. Prosternum (Fig. 2C) in front of coxae slightly longer than shortest diameter of procoxal cavity. Prosternal process (Fig. 2C) complete, distinctly expanded apically; apex nearly truncate. Protrochantins exposed. Procoxal cavities strongly transverse, narrowly separated, externally broadly open. Scutellar shield not abruptly elevated, anteriorly simple, laterally expanded and rounded, posteriorly broadly rounded.

Elytra (Fig. 2D) about 1.6 times as long as wide and 2.9 times as long as pronotum, finely setose, with several indistinct rows of small punctures. Elytral apices meeting at the suture. Mesocoxal cavities moderately separated, subcircular. Metacoxae narrowly separated, not extending laterally to meet elytra. Hind wing, if present, not visible. Trochanterofemoral joint strongly oblique; tibial apices gradually widened at apex; tarsal formula 5-5-5 (Fig. 3A–C); penultimate tarsomere distinctly reduced and one preceding tarsomere lobed beneath (Fig. 3A–C); pretarsal claws usually simple.

Abdomen with five free ventrites; intercoxal process acute.

Cretoboganium gei sp. nov. (Figs. 1–4)

ZooBank LSID: urn:lsid:zoobank.org:act:6C581C66-8FDD-49AC-8A1F-DD937B0EA407.

Etymology. In honor of Mr. Chang Ge for his effort in sharing knowledge of Burmese amber and donating the holotype for our study.

Material. Holotype, NIGP167701, sex undetermined; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Mid-Cretaceous amber

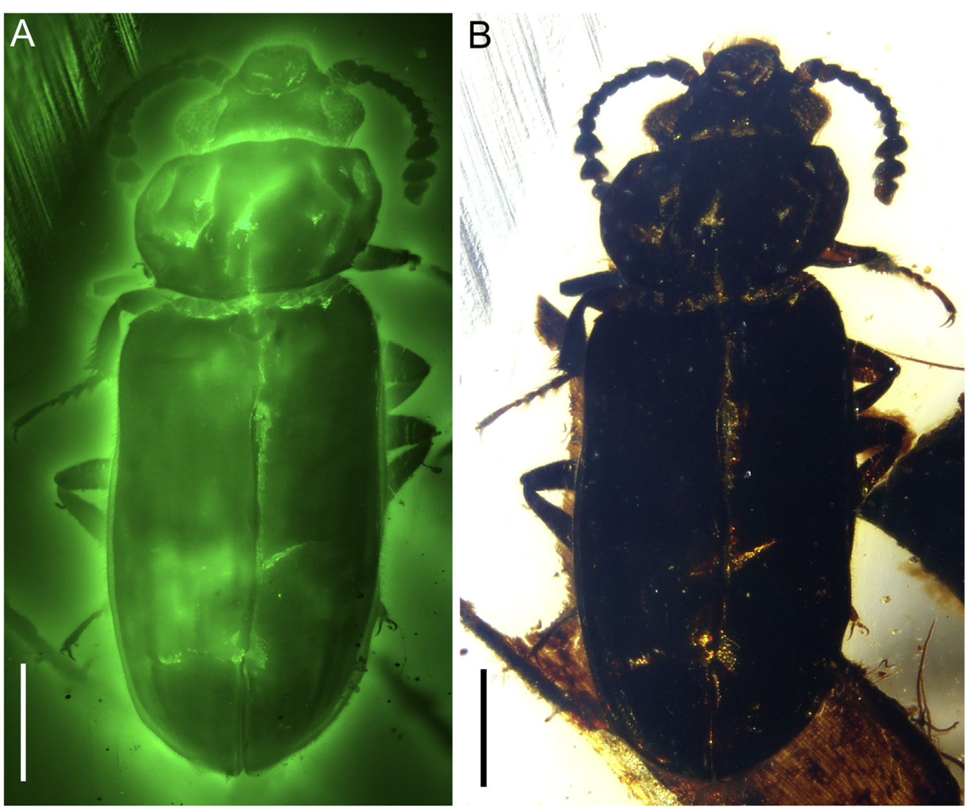

Fig. 1. Microphotographs of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov. from Upper Cretaceous Burmese amber. A. dorsal view, under green fluorescence; B. dorsal view, under normal reflected light. Scale bars: 500 μm (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

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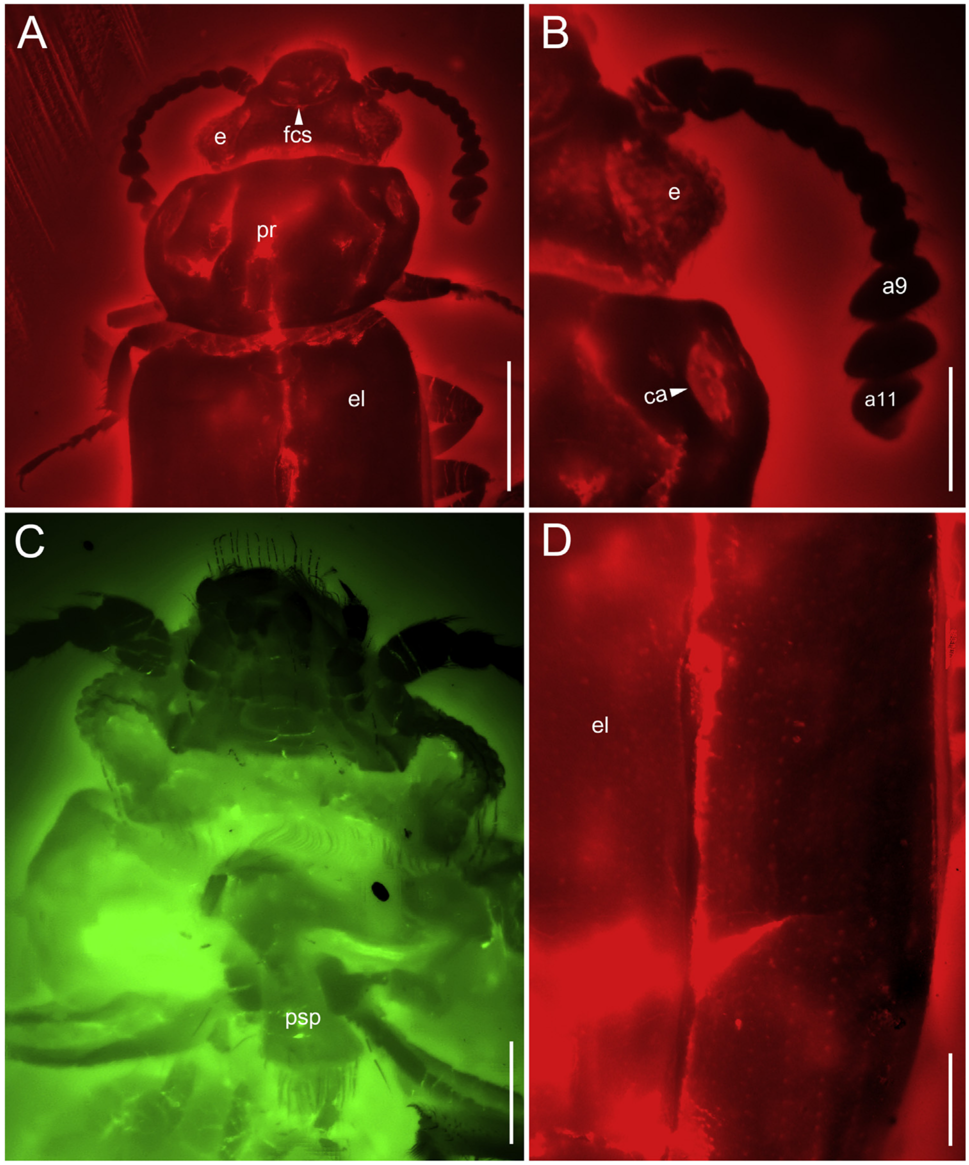

Fig. 2. Enlargements of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov., under fluorescence. A. dorsal view of head, pronotum and partial elytra; B. enlargement of A, showing details of eye, antenna and pronotal callosity; C. ventral view of head and prothorax; D. dorsal view of elytra, showing regular puncture rows. Abbreviations: a, antennomere; ca, callosity; e, eye; el, elytron; fcs, frontoclypeal suture; pr, pronotum; psp, prosternal process. Scale bars: 500 μm in A, 200 μm in others.

(earliest Cenomanian or late Albian; Ross et al., 2010; Shi et al., 2012), Hukawng Valley in Tanai, Kachin State, northern Myanmar.

Diagnosis. Body relatively large (ca. 3 mm long), black; antenna short; and pronotal callosities very large.

Description. Body 3.09 mm long (measured from anterior margin of head to abdominal apex); black throughout the body.

Head strongly transverse; head surface glabrous. 0.44 mm long and 0.79 mm wide (across eyes). Eye large. Mandible small, not visible from above, apparently without teeth. Anterior margin of clypeus with dense anteriorly-directed setae. Antenna short, nearly asymmetric, with apical three antennomeres forming a distinct club; surface of antennomeres densely setose; antennomere 1 elongate and broad, antennomere 2 subquadrate, narrower than antennomere 1, antennomere 3 longer than wide, antennomeres 4–8 almost in the same length and width, antennomere 9 nearly twice as long as antennomere 8, antennomere 10 in the same width and shape as antennomere 9, antennomere 11 subconical, slightly narrower than antennomere 10. Maxillary palp short, palpomere 2 elongate, palpomere 3 very short, palpomere 4 fusiform, much longer than palpomere 3.

Pronotum strongly transverse, 0.68 mm long and 1.05 mm wide. Surface without punctures or setae. Pronotal callosities located near the anterior pronotal angles, prominent from above. Apex of prosternal process dilated apically, with dense posteriorly-directed setae. Elytra complete, 2.0 mm long and each 0.64 mm wide, with regularly arranged rows of small punctures. Humeral callus well developed. Legs moderately long; tibiae setose, expanded at apex, apical tibial edges fringed with spines; tarsomeres 1–3 successively shortened, tarsomere 4 much shorter and smaller than the rest, tarsomere 5 long, as long as tarsomeres 2–4 combined; ventral side of pro- and mesotarsomeres 1–3 covered with dense setae. Pretarsal claws long, curved. Genitalia not visible.

4. Discussion

The new genus *Cretoboganium* can be confidently attributed to the extant cucujoid family Boganiidae based on the following combination of morphological features: 1) head with distinct frontoclypeal suture; 2) protrochantins well developed; 3) all

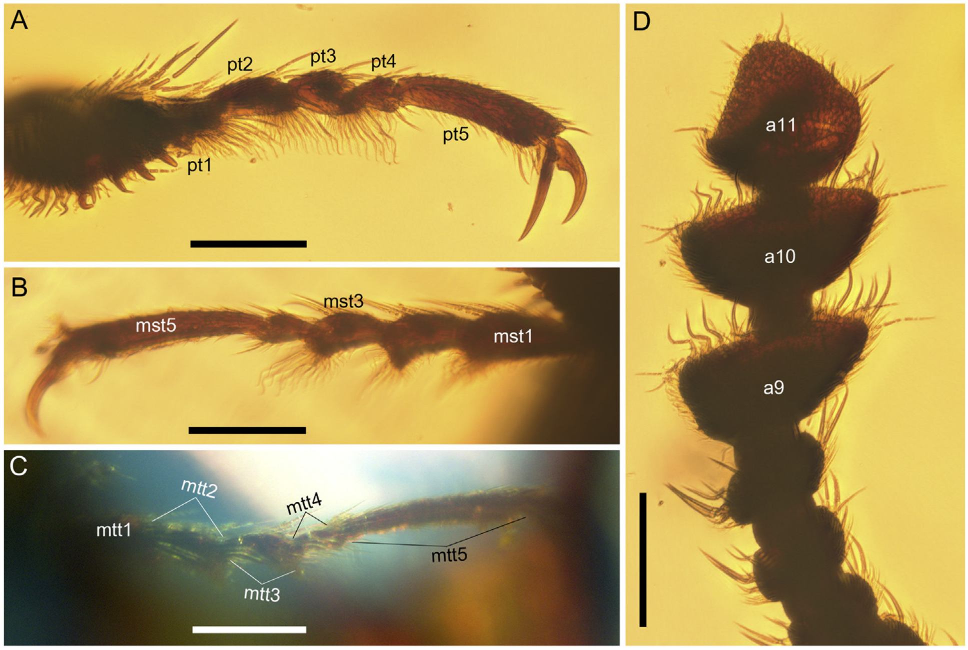

Fig. 3. Enlargements of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov., under transmitted light. A–C. pro-, meso- and metatarsus, showing reduced tarsomere 4; D. apical six antennomeres of right antenna, showing strongly clubbed antenna. Abbreviations: a, antennomere; mst, mesotarsomere; mtt, metatarsomere; pt, protarsomere. Scale bars: 100 μm.

coxae narrowly separated; 4) tarsi 5-segmented, with tarsomere 4 reduced; and 5) abdomen with five ventrites (Lawrence and Ślipiński, 2010; Escalona et al., 2015). Another important diagnostic character for modern Boganiidae, mandible with dorsal setose cavity, is unfortunately not visible from the holotype. Moreover, *Cretoboganium* can be referred to the extant subfamily Boganiinae as strongly evidenced by the presence of paired pronotal callosities and the comparatively short and somewhat fusiform apical maxillary palpomere (Escalona et al., 2015). The subfamily Boganiinae currently comprises only two extant genera: *Afroboganium* Endrödy-Younga & Crowson (South Africa and Namibia) and *Boganium* Sen Gupta & Crowson (South Australia, Victoria, Tasmania and southeastern Western Australia) (Escalona et al., 2015). *Cretoboganium* can be easily recognized from these extant genera by a strongly curved frontoclypeal suture, striate elytra, compact antennae with an abrupt antennal club, and very large pronotal callosities.

The most distinctive feature of *Cretoboganium* is the strongly curved frontoclypeal suture. The frontoclypeal suture of modern boganiid beetles are all straight or nearly so (Lawrence and Ślipiński, 2010; Escalona et al., 2015). To our knowledge, a strongly curved frontoclypeal suture in Boganiidae is confined to two extinct genera: *Cretoboganium* presented here and *Palaeoboganium* Liu et al. from the Middle Jurassic Daohugou beds (Liu et al., 2018). As in the Jurassic *Palaeoboganium*, the clypeal base of *Cretoboganium* is not constricted at base, a character also found in one of the two extant genera: *Afroboganium*. By contrast, the clypeal base of the Australian *Boganium* is more deeply constricted (Escalona et al., 2015). Although *Cretoboganium* shares with the older *Palaeoboganium* the curved frontoclypeal suture and unconstricted clypeal base, *Cretoboganium* differs significantly from the latter by having strongly clubbed antennae, well-developed pronotal callosities, and much smaller body size (11 mm long in *Palaeoboganium v.s.* 3 mm long in *Cretoboganium*).

Another interesting character of *Cretoboganium* is the striate and finely setose elytra. Among all extant Boganiidae, this character is absent in the subfamily Boganiinae, but it can be found in one of three genera of the other subfamily Paracucujinae, i.e., *Metacucujus* Endrödy-Younga and Crowson. The paracucujine genus *Paracucujus* Sen Gupta and Crowson also bears regularly striate elytra, but the elytra lack fine setae (Escalona et al., 2015). The Jurassic *Palaeoboganium*, as a sister group to *Paracucujus* + *Metacucujus*, appears to have glabrous and regularly striate elytra (Liu et al., 2018).

The discovery of *Cretoboganium* from the mid-Cretaceous Burmese amber (approximately 99 million years ago) stands for the first fossil member of the extant austral subfamily Boganiinae. Such an old and comparatively precise age of this clade is of great importance for further phylogenetic analysis and divergence time estimation in future. This discovery represents another example that current southern hemisphere endemic group may have its sister group apparently occurred in what is now the northern hemisphere (e.g., Thayer et al., 2012; Cai et al., 2012; Krishna et al., 2013; Cai and Huang, 2017a,b). There is high-resolution aeromagnetic data indicating that the eventual breakup (formation of first true ocean floor) between the Antarctic Peninsula and southernmost South America occurred at about 147 Ma (König and Jokat, 2006). This happened before the separations between Africa and South America, and between Antarctic and Australia (Jokat et al., 2003; König and Jokat, 2006). Therefore, it is very likely that Boganiinae first originated before the breakup of the Gondwanan supercontinent, at least about 147 million years ago. The previous find of a mid-Jurassic boganiid species from northeastern China (Liu et al., 2018) indicated Boganiidae as a very ancient group of Cucujoidea (Labandeira, 2000), and it was much more widespread in the Jurassic. Although there are no fossil boganiids documented from the Mesozoic of the southern hemisphere, we can expect such discoveries from the fossil deposits in the Gondwanan landmasses, such as the Late Jurassic of Australia (Talbragar fish beds; Cai et al., 2013; Ashman et al., 2015) and/or the Early Cretaceous of Brazil in the future.

Fig. 4. Dorsal reconstruction of *Cretoboganium gei* gen. et sp. nov. (with setae on dorsal surface omitted).

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