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Short communication

First definitive fossil agyrtodine beetles: An extant southern hemisphere group recorded from Upper Cretaceous Burmese amber (Coleoptera: Staphylinoidea: Leiodidae)

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ABSTRACT

Mesozoic leiodids are poorly known, and only one definitive leiodid is formally described from Burmese amber. Here we describe and illustrate the second definitive Mesozoic leiodid, *Cretagyrtodes glabratus* gen. et sp. nov., based on a single specimen from the Upper Cretaceous Burmese amber. The fossil is placed in Agyrtodini (subfamily Camiarinae) after maxillary palpomere 4 as wide as palpomere 3, and procoxal cavities closed behind. *Cretagyrtodes* is tentatively attributed to the extant "*Eupelates* group". The discovery of *Cretagyrtodes* in Burmese amber suggests that the south hemisphere endemic tribe Agyrtodini is probably an ancient group, which has showed its first appearance before the breakup of Pangaea.

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1. Introduction

The staphylinoid family Leiodidae (or round fungus beetles) is a worldwide, moderately large and diverse beetle group, comprising 4135 described species placed in 6 subfamilies (Newton, 2016). Among all extant subfamilies (Camiarinae, Catopocerinae, Cholevinae, Coloninae, Leiodinae and Platypsyllinae), Camiarinae contains the "leftover" leiodid lineages, which cannot be placed elsewhere in the family. A recent phylogenetic analysis of Camiarinae based on larval morphology indicated that Camiarinae and its tribes are paraphyletic, grouping possibly ancient and relict taxa (Kilian, 2012). All extant species of Camiarinae are restricted to the southern hemisphere, occurring in south-temperate forests and relatively high-altitude subtropical rainforests (Newton, 1985, 1998, 2016). Agyrtodini includes two distinctive generic groups, including a derived "*Agyrtodes* group" with specialized mouthparts and the "*Eupelates* group" with more generalized mouthparts (Newton, 1998). Camiarinae is divided into three paraphyletic tribes (Camiarini, Neopelatopini and Agyrtodini), but the "*Agyrtodes* group", including *Agyrtodes* Portevin, *Agyrtolasia* Szymczakowski, *Cholevomorpha* Blackburn, *Zeagyrtes* Broun, *Zearagytodes* Jeannel, and *Zeagyrtoma* Szymczakowski, represents a likely monophyletic group, as supported by both morphological (Newton, 1985, 1998) and molecular data (Seago, 2009). The "*Agyrtodes* group" have a large complex brush on the lacinia, a structure likely corresponding to feeding on fungi (Newton, 1998).

Fossil leiodids from the Mesozoic are sparse. Almost all definitive leiodid species reported from the Cenozoic (see summary in Cai and Huang, 2017). Recently, Cai and Huang (2017) reported a leiodid species belonging to the extant subfamily Coloninae, *Colonellus burmiticus* Cai and Huang, from the Upper Cretaceous Burmese amber, representing the oldest member of Leiodidae. Ponomarenko (1986) reported a fossil species placed in the formal genus "*Gurvanocoleus*", "*Gurvanocoleus*" *hirsutus* Ponomarenko, from the Lower Cretaceous of western Mongolia. Perkovsky (2002) regarded this species as a member of the extant tribe Agyrtodini. However, based on the poor preservation condition of the holotype of *G. hirsutus* (Ponomarenko, 1986; p. 102), we found no characters indicative of the placement in Agyrtodini, and even in the family

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Leiodidae. To date, no definitive fossils attributable to Agyrtodini are known. Here we report the first fossil of Agyrtodini and the second Mesozoic leiodid from the Upper Cretaceous Burmese amber.

2. Material and methods

The new species is described based on a sole adult preserved in a clear piece of Burmese amber (ca. 99 Ma). The amber specimen is derived from amber deposits in the Hukawng Valley of northern Myanmar. 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 red background were taken under the rhodamine mode. Photomicrographs with coloured background are taken using a confocal laser scanning microscopy (CLSM) Zeiss LSM 710 with ×10 objectives and using a laser at 488 nm. Extended depth of field images were then digitally compiled using Helicon Focus 3.10 software, and arranged in Adobe Photoshop CS5. The type specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The nomenclatural acts established herein are registered under ZooBank LSID urn:lsid:zoobank.org:pub:95889247-3336-43FA-8985-279E773070CF.

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Family Leiodidae Fleming, 1821
Subfamily Camiarinae Jeannel, 1911
Tribe Agyrtodini Jeannel, 1936

Genus ***Cretagyrtodes*** gen. nov.
Type species: *Cretagyrtodes glabratus* gen. et sp. nov.

Etymology. The genus name is composed of the prefix *Creto-* derived from the Cretaceous and the extant genus *Agyrtodes*. The gender of the name is masculine. The genus is registered under LSID urn:lsid:zoobank.org:act:C700B63C-2987-40C5-AF34-75A0CA579311.
Diagnosis. *Cretagyrtodes* can be distinguished from other genera of Leiodidae based on the combination of features: body ovoid-shaped in dorsal view; antenna and leg short; antennae slightly clubbed, with distinctly reduced and subquadrate antennomere 8; head without occipital carina; apex of galea with dense long setae; dorsum glabrous, elytron transversely striolate; and mesoventrite strongly carinate. In addition, *Cretagyrtodes* differs from extant genera of the *Eupelates* group by its entirely glabrous body surface.
Description. Body small among Agyrtodini (1.56 mm long). Body shape ovoid, convex, dorsum without pubescence or punctures. Unicolour, elytra not patterned.

Head (Fig. 2A) without occipital carina. Frontoclypeal suture absent (Fig. 2A). Labrum (Fig. 2A) very short and transverse, slightly cleft apically. Antenna (Fig. 2A) with broad scape and pedicel, "stem" (antennomeres 3–6) elongate and slender, with loose 5-segmented antennal club. Club segments (Fig. 2B) slightly longer than wide, with antennomere 8 subquadrate, smaller than antennomeres 7 and 9. Antennal insertion (Fig. 2A) concealed. Eye (Fig. 2A) moderate, positioned posteriorly and protruding laterally, with coarse facets. Mandible stout, curving externally. Maxilla elongate; galea (Fig. 3) long and broad, with clump of dense setae at

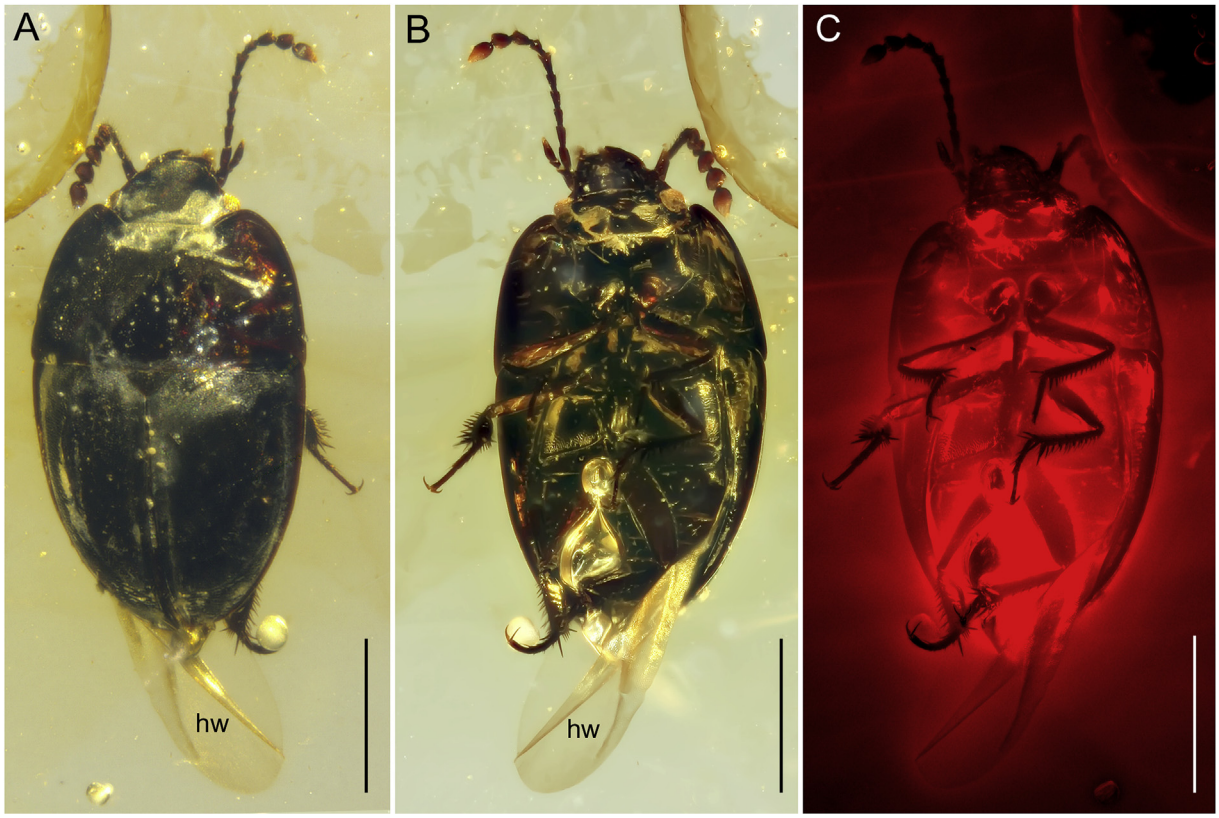


Fig. 1. Microphotographs of holotype (NIGP166150) of *Cretagyrtodes glabratus* gen. et sp. nov. from Upper Cretaceous Burmese amber. A. Dorsal view, under normal reflected light; B. Ventral view, under normal reflected light; C. Ventral view, under red fluorescence. hw, hind wing. Scale bars: 500 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

apex; lacinia short, with dense setae at apex. Maxillary palpus (Fig. 3) elongate, 4-segmented, palpomere 4 slender, tapering, distinctly longer than palpomere 3; apex of palpomere 4 with minute sensillae (Fig. 3A). Labial palpus short. Mentum (Fig. 3B) trapezoidal, narrowed distally.

Pronotum (Fig. 1A) transverse, widest toward posterior margin. Anterior pronotal margin of concave; posterior pronotal margin straight; side slightly curved. Prosternum (Fig. 2D) short and transverse. Hypomeron (Fig. 2D) broad, smooth, without visible glandular openings. Procoxal cavities (Fig. 2D) narrowly separated by prosternal process and closed by blunt postcoxal process.

Elytron with fine transverse striolae (Fig. 2F). Sutural stria present; longitudinal striae absent from disc. Elytral apex bluntly pointed. Epipleuron concave, laterally delimited by pronounced longitudinal bead. Hind wing (Fig. 1A, B) present, not reduced. Mesoventrite (Fig. 2D) with strongly raised median carina, appearing as triangular plate vertical to mesoventrite. Mesocoxal separation formed anteriorly by mesoventral process and posteriorly by non-carinate median metaventral projection. Mesosternal microsculpture (Fig. 2D) of shallow, irregular striolae, most pronounced laterally and posteriorly. Metaventrite (Fig. 2D) broad, not carinate.

Legs short. Protrochantin exposed (Fig. 2D); procoxa conical in shape (Fig. 2A), strongly projecting ventrally; Mesocoxa ovate, rounded. Metacoxa flattened, triangular, tapering laterally. All femora short, flattened, with paired apical flanges and posterioventral grooves for reception of tibiae. External margin of tibiae with dense strong spines. Protibia shorter than other tibiae, expanded apically; meso- and metatibia straight. All tarsi 5-segmented. Protarsus short, basal four tarsomeres very short, narrow, tarsomere 5 long; meso- and metatarsi with tarsomere 5 longest. Pretarsal claw simple (Fig. 2C). Empodial setae present (Fig. 2C).

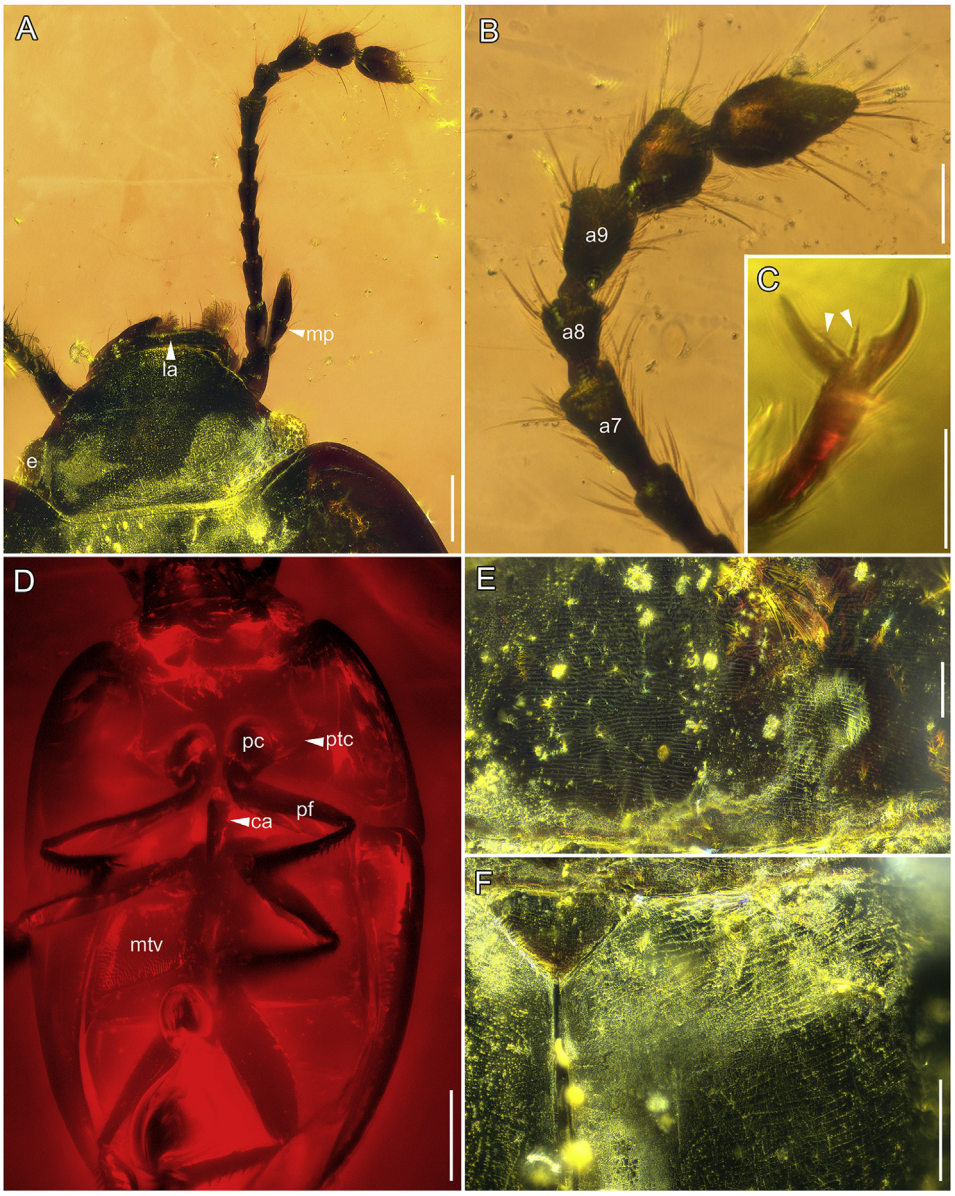


Fig. 2. Enlargements of holotype (NIGP166150) of *Cretagyrtodes glabratus* gen. et sp. nov., D under red fluorescence; others under reflected light. A. Dorsal view of head and right antenna; B. Apical antennomeres of right antenna, showing reduced antennomere 8; C. Pretarsal claw and empodial setae (indicated) of right proleg; D. Ventral view of thorax; E. Posterior part of pronotum, showing extremely fine transverse striolae; F. Anterior part of elytra, showing triangular scutellar shield and transverse striolae. a7–9, antennomeres 7–9; ca, carina; e, eye; la, labrum; mp, maxillary palpus; mt, metaventrite; pc, procoxa; pf, profemur; ptc, protrochantin. Scale bars: 100 μm in A and F; 200 μm in D; 50 μm in B, C and E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

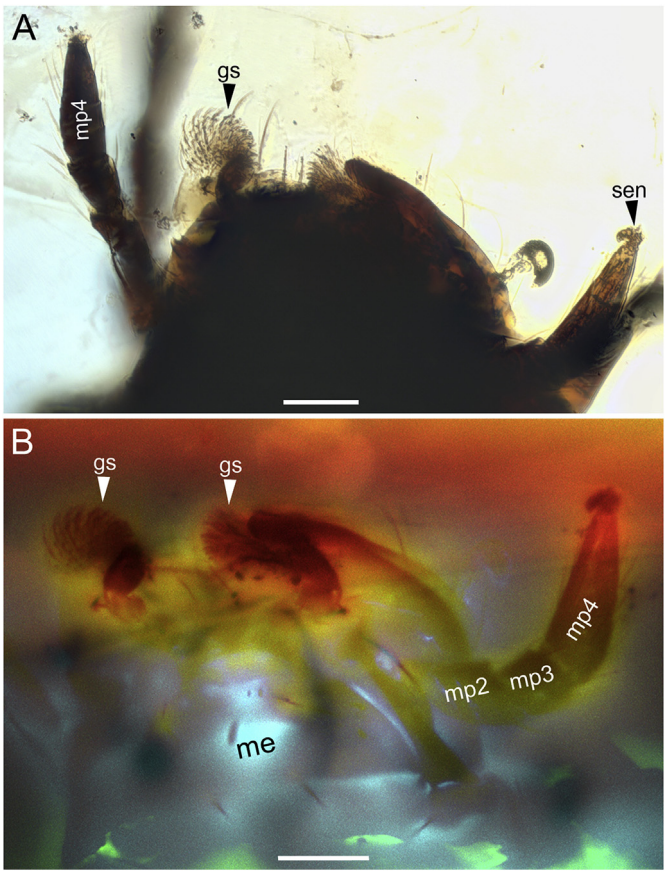


Fig. 3. Mouthparts of holotype (NIGP166150) of *Cretagyrtodes glabratus* gen. et sp. nov. A. Ventral view, under transmitted light; B. Ventral view, under confocal laser scanning microscopy. gs, galeal setae; me, mentum; mp2–4, maxillary palpomeres 2–4; sen, sensillae. Scale bars: 50 μm.

Abdomen rounded at apex. Abdominal sterna broad, strongly sclerotized.

Cretagyrtodes glabratus sp. nov.
Figs. 1–3

Etymology. The specific name refers to the glabrous body surface of the new species. The species is registered under LSID urn:lsid:zoobank.org:act:380B5A38-78F6-4E82-BDEC-B53FFCF6DBD6.
Holotype. NIGP166150, sex undetermined. Earliest Cenomanian, Hukawng Valley, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.
Diagnosis. As for the genus (*vide supra*).
Description. Total length 1.56 mm. Integument dark brown throughout. Head small, subtriangular, widest across eyes, 0.26 mm long and 0.45 mm wide. Eye laterally protruding, with a few dozens of ommatidia. Antenna (Fig. 2A) densely setose, antennomere 1 elongate, as long as antennomere 2; antennomere 2 slightly narrower than antennomere 1; antennomeres 3–6 almost slightly narrower than antennomere 2; antennomere 3 as long as antennomere 2; antennomeres 4–6 gradually shortened; antennomere 7 longer and wider than antennomere 6; antennomere 8 reduced (Fig. 2B); antennomere 9 much larger than antennomere 8; antennomeres 10 and 11 broader than antennomere 9; antennomere 11 narrowed toward apex. Pronotum transverse, glabrous, 0.49 mm long and 0.90 mm wide; surface with extremely fine transverse striolae (Fig. 2E), denser than those on elytra, without punctures. Scutellar shield large, triangular, wider than long. Elytron complete, 0.85 mm long and 0.52 mm wide; with very fine transverse and slightly oblique striolae. Legs short; protibia slightly broadened apically, with a row of about 15 spines along external margin, apex of protibia with two long spurs; protarsus with tarsomere 5 as long as tarsomeres 1–4 combined; tarsomeres 1–4 narrow, as broad as tarsomere 5. Mesotibia with at least two rows of spines and several spines along external margin, apex of mesotibia with two long spurs; mesotarsus with tarsomere 1 very short, tarsomeres 2–4 gradually shortened toward apex, tarsomere 5 as long as tarsomeres 2–4 combined. Metatibia with dense spines along external margin, apex of metatibia with two long spurs and several spines; metatarsus with tarsomere 1 very short, tarsomeres 2–4 longer than tarsomere 1, tarsomere 5 longest. Pretarsal claw long and slightly curved.

4. Discussion

The new genus *Cretagyrtodes* can be attributed to the staphylinoid family Leiodidae based on its clubbed antennae with distinctly reduced antennomere 8 and 5-segmented tarsi. The poorly defined subfamily Camiarinae includes many of the most plesiomorphic leiodids, morphologically more similar to the related family Agyrtidae than to more derived leiodids, such as Leiodinae, Catopocerinae (Newton, 1998; Seago, 2005). Although Camiarinae is not a monophyletic group and it is not supported by any discernable synapomorphies, *Cretagyrtodes* is tentatively placed in the subfamily based on its Agyrtidae-looking appearance, head without occipital carina, and antennomere 8 reduced. *Cretagyrtodes* is placed in Agyrtodini based on maxillary palpomere 4 as wide as palpomere 3, and procoxal cavities closed behind. Moreover, it can be placed in the "*Eupelates* group" of Agyrtodini (Newton, 1998), because it bears more generalized mouthparts, when compared to the "*Agyrtodes* group", extant taxa of which are characterized by the presence of highly specialized "spore brush" on the apex of lacinia (Newton, 1998; Seago, 2005).

The mouthparts of *Cretagyrtodes* are very distinctive among all known genera of Agyrtodini. The galea of *Cretagyrtodes* is broad and long, and its distal part is exposed from dorsal view, a character similar to that of some extant members of "*Eupelates* group", such as *Karinapelates* Salgado Costas and *Dontipelates* Salgado Costas (Salgado Costas, 2015). The biology of extant members of "*Eupelates* group" is poorly known, and the exact function of the specialized galea in several genera remains elusive. By contrast, many species of the "*Agyrtodes* group" characterized by "spore brush" on lacinia are known as feeders on tough, wood-associated "polypore" (Basidiomycota: Agaricomycetes: Polyporales, Hymenochaetales, etc.) fungi (Seago, 2009). Cai et al. (2016) reported a peculiar fossil proteinine rove beetle, *Vetuproteinus cretaceous* Cai et al., from the Upper Cretaceous Burmese amber. The mouthparts of *Vetuproteinus* possess a markedly enlarged protruding galea bearing a spore-brush-like structure, and it was inferred to be used to scrape fungal spores off surfaces and direct them into the mouth (Cai et al., 2016). In *Cretagyrtodes*, the apex of the galea is armed with dense long setae, rather than dense array of short, scale-like rasping teeth as in a so-called "spore brush". Thus, the exact function of the specialized gelea of *Cretagyrtodes* remains enigmatic.

Another interesting character of *Cretagyrtodes* is the presence of an acute mesoventral median carina. Within Agyrtodini, a mesoventral median carina is developed at least in *Agyrtodes*, *Agyrtolasia*, *Chelagyrtodes* Szymanowski, *Karinapelates* and *Dontipelates* (Seago, 2005; Salgado Costas, 2015). The mesoventral carina of *Cretagyrtodes* is acute and triangular in profile, very similar to that of *Agyrtolasia* (eastern Australia), *Dontipelates* (Chile), and some species of *Agyrtodes* (Seago, 2005, 2009; Salgado Costas, 2015).

Our discovery of an extinct taxon from Burmese amber belonging to an extant south hemisphere endemic group has important biogeographic implications. The distribution of the tribe Agyrtodini extended tremendously, from South America, New Zealand and Australia to Southeast Asia. *Cretagyrtodes* represents another example showing that some Recent austral-endemic taxa have their sister group apparently occurred in what is now the northern hemisphere (e.g., Grimaldi et al., 2002; Cai et al., 2012; Thayer et al., 2012; Jarzembowski et al., 2017).

5. Concluding remarks

Our discovery of *Cretagyrtodes glabratus* from the Upper Cretaceous Burmese amber represents the first fossil for the tribe Agyrtodini and for the subfamily Camiarinae. It suggests that the tribe is probably an ancient group, which originated before the breakup of Pangaea, and this tribe was widespread on Pangaea. It also represents the second definitive leiodid fossil from the Mesozoic.

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