

Short communication

The first true Mordellidae (Coleoptera: Tenebrionoidea) from lower Cenomanian amber of Myanmar

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ABSTRACT

Primaevomordellida burmitina gen. et sp. nov. (Coleoptera: Mordellidae) is described on the base of two well-preserved specimens from Cenomanian Burmese amber. Due to the general body plan and the preservation of elongated pygidium, it is apparently the first true pintail beetle (subfamily Mordellinae). The simple hind leg structures placed the new species into the basal tribe Raynoldsiellini; however, the comparative morphology of the new species shows advanced characters similar to tribes Mordellini and Mordellistenini. The angiosperm plant records in Burmese amber forests were reviewed and the mordellids-angiosperm interactions are discussed.

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1. Introduction

The family Mordellidae, is thought to be among the most basal group of Tenebrionoidea based on molecular data (Hunt et al., 2007; McKenna and Farrell, 2009). All fossils attributable to Mordellidae refer only to Mordellinae, and Praemordellinae subfamilies, while so far there is no trace of Ctenidiinae.

The Cenozoic Mordellidae discovered in Fushun amber of the Eocene of China (Zhang and Hong, 1999), Kishenehn Fm., Eocene of Montana, USA (Huber and Greenwalt, 2011), Green River Fm., Eocene of Colorado, USA (Cockerell, 1925), Baltic amber of the Eocene Baltic gulf (Kubisz, 2003; Odnosum and Perkovsky, 2010; Perkovsky and Odnosum, 2013), Florissant Fm., Oligocene of Colorado, USA (Scudder, 1890; Cockerell, 1907), Rott Fm., Oligocene, Germany (Statz, 1952), Carbonate Fm., Oligocene, France (Nel, 1985), Mexican amber, Miocene, Mexico (Poinar, 1993),

Olympia beds Fm., Pleistocene, Washington, USA (Ashworth and Nelson, 2014) display close similarity to the extant species and they have been traditionally assigned in the major part of the cases to *Mordella* and *Mordellistena*. In comparison, the fossil records of Mesozoic mordellids are generally scarce, mainly found in the Late Jurassic Karabastau Fm., Russia (Scegoleva-Barovskaja, 1929) and the Early Cretaceous Yixian Formation of China (Liu et al., 2007, 2008). These Mesozoic mordellids have been placed into the subfamily Praemordellinae, because of the significant absence of pygidium and not-mordelloid hind legs. Mordellidae also recorded from Early Cretaceous Lebanese amber (Kirejtshuk and Azar, 2013). However, the specimen "RIH-5" is partly destroyed that made further research almost impossible.

Up to know if we exclude the suspected Mordellidae cited by Grimaldi et al. (2002), no published record and described taxa exist about Mordellidae in Burmese amber deposits. In the present paper we present and describe the first true Mordellidae; discuss comparative morphology of the new genus, additionally we reveal new knowledge concerning plant-insect interactions of the examined taxon.

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2. Materials and methods

Two specimens of Burmese amber from Hukawng Valley, Kachin Province (northern Myanmar) are stored in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing. The deposit in village Noije Bum was re-exploited in 1990s and since 2001 it has become the main source for excavation (Bao et al., 2018) (Fig. 1). The Burmese amber Lagerstätte has been dated as earliest Cenomanian, Cretaceous, ca. 99 Ma based on isotope analysis to the ash layers (Shi et al., 2012). Photomicrographs were taken using a Leica M205 A microscope system and Leica Application Suite (LAS Version 4.7) software; colour filters and agave syrup were applied to enhance the image quality. Hand drawings were created based on high-resolution images and illustrations from literature. CorelDRAW X7 (64-Bit) and Adobe Photoshop CS4 were applied for late image editing and text editing.

The familial/subfamilial classification in this paper follows that of Bouchard et al. (2005, 2011). The terminology and nomenclature follow "Handbook of Zoology" (Beutel and Leschen, 2016) and the recent research of current biology of Mordellidae (Ruzzier and Kovalev, 2016; Hsiao et al., 2018; Ruzzier, 2018). All measurements in the description are given in millimetres. This paper has been registered in ZooBank, the ICBN Official register of Zoological Nomenclature, with the unique digital ZooBank registration identifier (LSID urn: lsid: zoobank.org:pub:35AEC882-6ADC-4FBD-8A15-F83691E46379). The LSID number for the new taxa is given in the systematic paleontology section below.

3. Systematic paleontology

Order: Coleoptera Linnaeus, 1758

Suborder: Polyphaga Emery, 1886

Superfamily: Tenebrionoidea Latreille et al., 1802

Family: Mordellidae Latreille et al., 1802

Subfamily: Mordellinae Latreille et al., 1802

Tribe: Raynoldsiellini Franciscolo, 1957

Diagnosis. Tribe Raynoldsiellini Franciscolo, 1957 represented by only one extant monotypic genus, *Reynoldsiella parallela* Ray, 1930, recorded hitherto only from Venezuela. The most important differential character for Raynoldsiellini Franciscolo, 1957 is metatibiae without any kind of ridges, including the subapical one (Franciscolo, 1957; Peris and Ruzzier, 2013).

Primaevomordellida gen. nov.

LSID urn: lsid: zoobank.org: act:5CC9AB4D-97B1-4F73-8412-9C0F68453EF7

Type species: *Primaevomordellida burmitina* gen. et sp. nov.

Diagnosis. *Primaevomordellida* gen. nov. differs from *Reynoldsiella* mainly based on the following characters: (1) eyes small, glabrous; (2) metafemora not greatly enlarged; (3) subapical spurs on metatibiae long, about half length of metatibiae; (4) pygidium sharply elongated, length ratio between pygidium and hypopygium 4:1; (5) branches of right genital parameron with equal length.

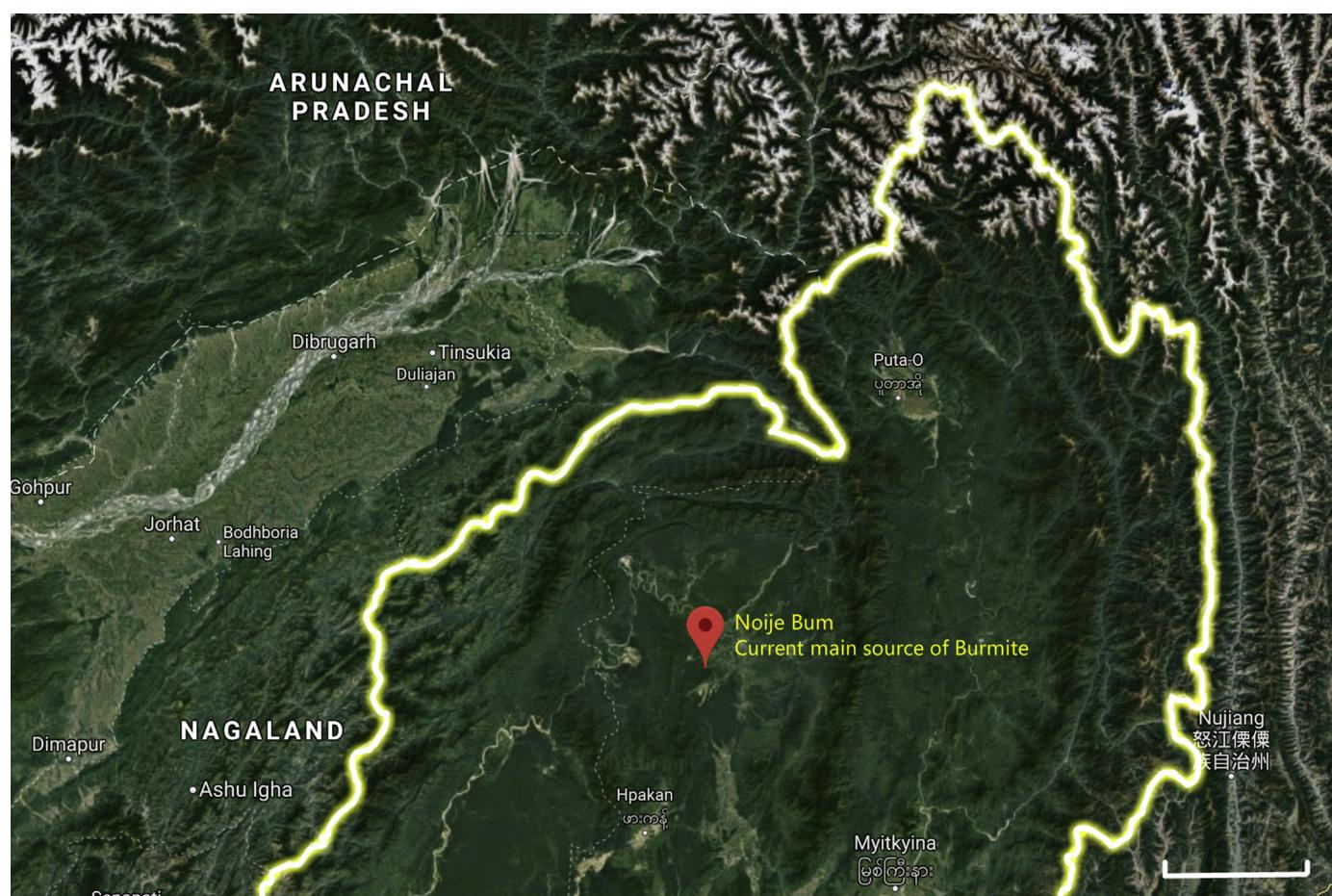


Fig. 1. Location of recent amber mining area in the Hukawng Valley, Myitkina Province, Myanmar. The border line of Republic of the Union of Myanmar is marked by yellow line. The current main source of Burmite is marked by red icon. Satellite map source from Google, scale bar 50 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Etymology. Primaev (Latin) – primaevus, means original; primaevomordellida refers to the first true pintail beetle.

Primaevomordellida burmitina sp. nov.

(Figs. 2 and 3)

LSID urn: lsid: zoobank.org: act:5BBB6443-3582-4E0B-94F8-7066CF4AC45A

Diagnosis. As for the genus.

Type material. Holotype NIGP168789 (Male) and paratype NIGP168790 (sex undetermined) (reference numbers for collection of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing).

Etymology. Burmitina (Latin), related to mineralogical name burmite.

Description. Dimensions: holotype NIGP168789 is 3.0 mm in length, of the paratype NIGP168790 is 2.9 mm (pygidium excluded); body profile typically mordelloid, slightly arched in lateral view. General colour of the body integuments black, except for the orange anterior legs.

Head: head large, almost as the prothoracic width, strongly declined; eyes lateral, moderately small, finely faceted and glabrous, not reaching occiput. Occipital region wide and flat, matching perfectly with the anterior edge of pronotum. Antennae comparatively short, filiform and feebly serrate; antennomeres covered of setae. Apical palpomere securiform.

Prothorax: pronotum trapezoid in dorsal view, slightly narrowed in front and as wide as elytra at base; disc of the pronotum smooth and covered of short and dense recumbent hairs. Anterior legs simple; tibiae slender and linear, tarsus with all the five segments feebly dilated; tarsomere one to four bearing short spines at the detail margin; apical spurs on pro tibia present.

Meso and metathorax: scutellum triangular. Elytra, in dorsal view, subparallel at the humeri, gradually curving up to apex proximity; integuments covered with by fine setae. Metaepistena typically mordelloid, of the *Mordellistena*-type.

Coxal plate expanded, widely rounded at the posterior margin, typically mordelloid; trochanter reduced.

Metafemora laterally compressed and feebly expanded. Metatibiae elongated, subconical, with obliquely truncated apexes; metatibiae missing of any kind of ridge including the sub apical one; apical margin of hind tibiae bearing comb-like setae; ventral side of metatibiae and metatarsomeres presenting fine spine-like setae; Apical spurs on posterior tibiae present, equal in size and

approximately half of length of metatibiae. Tarsal formula 5-5-4; Pro- and mesotarsomeres cylindrical, slightly torso-ventrally compresses, onlychium instead apically on the fourth tarsomere; metatarsi laterally compressed, slender, presenting comb-like setae at the apical margin; length ratio of the four hind tarsomeres 3:2:1:1. Claws small and bi-cleft.

Abdomen: visible abdominal sternites with length ratio 3:3:3:4:8. Pygidium subconical, elongated and pointed at apex; pygidium length about four times the hypopygium. Genital organs of holotype partially exposed. Apical part of penis visible, pointed.

Remarks. The holotype and paratype shows natural black or deep brown colour on elytra. Fine setae are well developed on the beetle body (including legs, antennae), dorsally and ventrally, regularly in a posterior direction. The amber matrix is not clear, contains a large amount of organic impurities.

4. Discussion

4.1. Morphology

Six tribes, Raynoldsiellini, Conaliini, Mordellini, Mordellistenini, Mediumiugini and Stenaliini are included in subfamily Mordellinae, with a distinctive evolutionary trend of the hind leg structures (Jackman and Lu, 2002; Peris and Ruzzier, 2013).

The filiform antennae, the *Mordellistena*-type episterna and the elongated pygidium place *Primaevomordellida burmitina* gen. et sp. nov. into Mordellinae undoubtedly and the simple hind leg structure without appendix structures assignes it to the basal tribe Raynoldsiellini. Compared to *Reynoldsiella parallela*, *Primaevomordellida burmitina* gen. et sp. nov. shows similarities to species of tribe Mordellini and Mordellistenini. These similarities include the dilatation of antennae starts from the 5th antennomere, which occurs in almost all Mordellini species; the 4th segment of the maxillary palpus is expanded, securiform, which is typical in genus *Mordella*; the scutellum shape is triangular which is common for most of Mordellini and Mordellistenini species, while for *Reynoldsiella parallela* this is exactly semicircular; the pygidium is obviously elongated, narrow and sharp-pointed, similar with the genus *Mordellapygium* (Franciscolo, 1957; Jackman and Lu, 2002).

The anterior tibiae have a generally linear shape in the majority of Mordellidae. The most common shape of anterior tarsus is

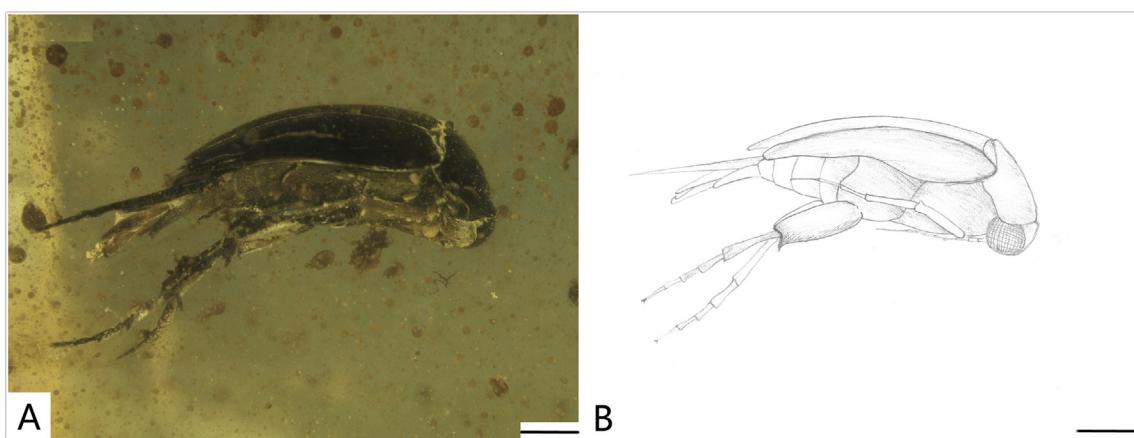


Fig. 2. *Primaevomordellida burmitina* gen. et sp. nov. general view, holotype NIGP168789. A. microscope photo, lateral view. B. Hand drawing. Scale bars 0.4 mm.

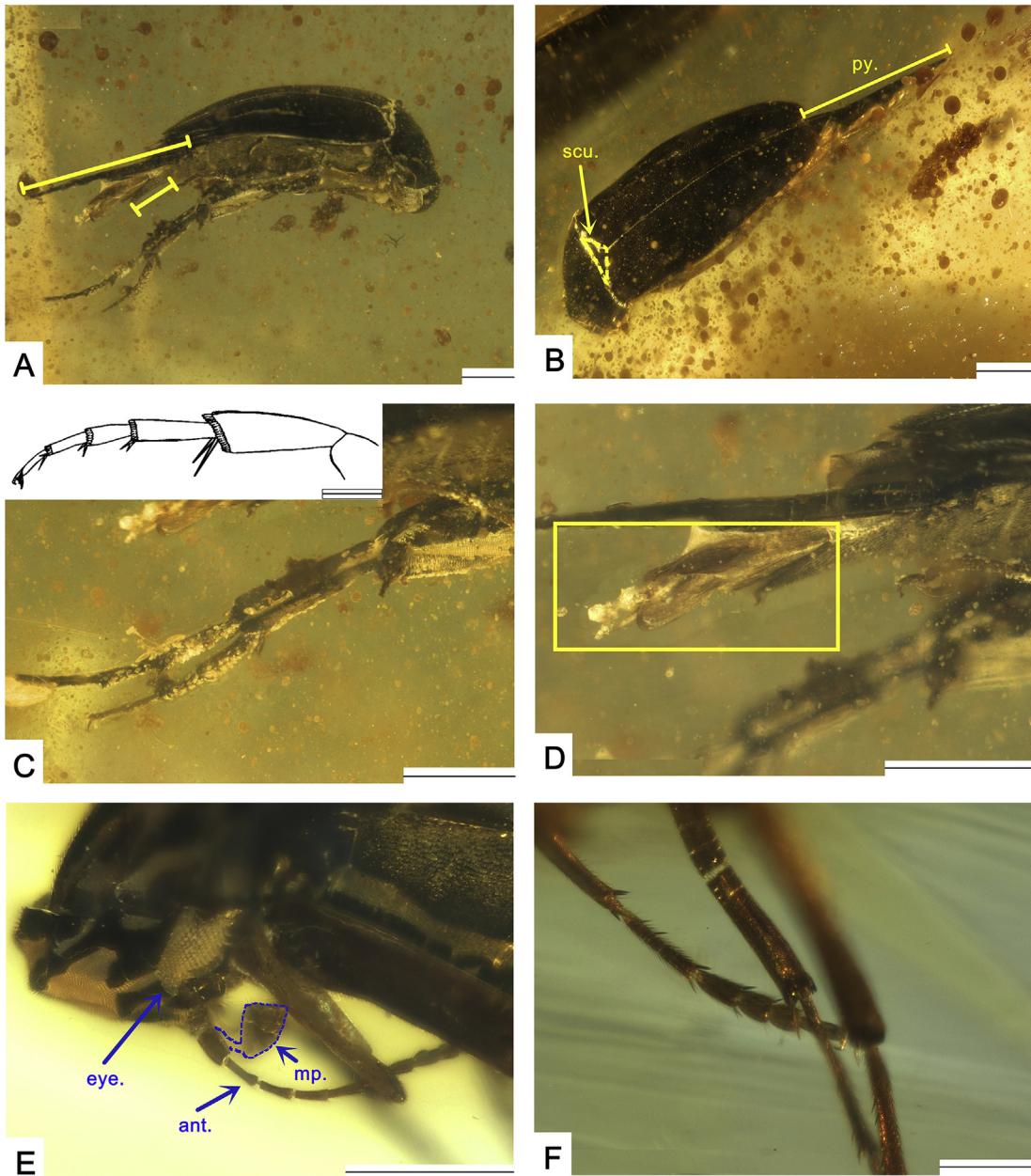


Fig. 3. Body structures of *Primaevomordellida burmitina* gen. et sp. nov. A. Lateral view, length of pygidium and last abdominal segment are indicated. B. Dorsal view, scu.- scutellum, py.- pygidium. C. hind leg structures, hand drawing is highlighted. D. Genital organ highlighted. E. Detail structures of head and mouthpart. eye.- eyes, ant.- antennae, mp.- maxillary palp. F. Fore legs structures. A–D from holotype NIGP168789, E–F from paratype NIGP168790. Scale bar A–E 0.4 mm, F. 0.2 mm.

simple and linear with all the five segments, featured in genera *Mordella* and *Mordellistena*. These characters also applied for *Primaevomordellida burmitina* gen. et sp. nov., which differs from the Mesozoic fossil Mordellidae species *Mediumiuga sinespinis* (Spain, Cretaceous) with appendix structures on mesotibiae and mesotarsi (Peris and Ruzzier, 2013). The metafemora and metacoxae are not well developed in *Primaevomordellida burmitina* gen. et sp. nov. This character together with the absence of pygidium are the common characters for other Mesozoic mordellid or mordellid-like fossils, e.g. *Praemordella* sp. from the Jurassic of Kazakhstan (Sciegoleva-Barovskaja, 1929), *Wuhua* sp. from the Jurassic of China (Wang and Zhang, 2011), as well as for *Mediumiuga sinespinis*, which made their taxonomic status doubtful.

4.2. Paleoecology

The feeding strategies of extant Mordellinae species are still under investigation. From the current knowledge, majority of Mordellinae members are featured by flower and pollen diet (Yang and Ren, 1999). They are widely distributed in all climate zones, and they have the highest species diversity in tropical regions. Larvae of mordellids usually develop in dead or decaying wood, except for few records of myrmecophilous species, life miners, stem forming species and frugivorous species; while adults are often found in warm forests or grasslands, preferring a diet of small flowers with umbel, corymb or head inflorescence (Borowiec and Kubisz, 1999). Even though the cooling trend of the last epoch of the Jurassic

continued into the first age of the Cretaceous, the average temperature increased again and constantly until the end of the Cretaceous (Barron and Washington, 1982; Huber et al., 2002), which stimulated the flourish of angiosperms (Scott et al., 1960; Krassilov, 1977). Chaboureau et al. (2014) used a fully coupled climate model driven by Mesozoic paleogeographic maps to explain that climate change from arid to temperate dominance may have set the stage for the ecological expansion of flowering plants. The Cenomanian Burmese amber forests were dominated by Araucariaceae trees (Poinar et al., 2007b). Several angiosperm species have been described from Burmese amber based on flowers, represented by (1) Lauraceae species, flowers small, radial symmetry, raceme or umbel inflorescence (Poinar, 2017); (2) Cunoniaceae species, flowers small with four or five sepals and petals (Poinar and Chambers, 2017); (3) Cornaceae species, flowers small, actinomorphic (Poinar et al., 2007a); (4) Monimiaceae species, flowers small, composed of a cup-shaped perianth of 8 fused tepals arranged in one series with 8 equal subsessile (Poinar and Chambers, 2005). The flower corollas are normally small and underdeveloped, indicating the primary stage of angiosperm plant evolution. However, some flowers (undescribed) and other insect group (e.g. Diptera, Blattodea, Permopsocida) already showed clear evidence of insect – plant interactions, although it is difficult to determine which insects were actual pollinators (Santiago-Blay, 2005; Huang et al., 2016; Vršanský and Wang, 2017). According to the flower shape and living environment, it is assumed that the potential flower plant nutrition available in Burmese amber forests for *Primaevomordellida burmitina* gen. et sp. nov. was considerable. The mouthpart structures, e.g. the expanded 4th maxillary palpus segment, might have been a benefit for pollen detecting and the elongated pygidium would assist the movement along stamen. However, the underdeveloped hind legs and coxal may have impeded their jumping and flying movement and may have related to their defensive strategy, which could be a trait to other Jurassic – Cretaceous Mordellidae or mordellid-like species. For future research, with potentially better-preserved specimens, the pollen or nectar collecting structure, e.g. manipes or lacinia, should be examined in detail. The potential pollen remains, preserved on beetle body surface or in amber matrix, will also provide good evidence for Cretaceous insect-plant interactions.

5. Conclusions

The first true pintail beetle *Primaevomordellida burmitina* gen. et sp. nov. (Coleoptera: Mordellidae: Mordellinae) is described based on two specimens from Burmese amber (lower Cenomanian, ca. 99 Ma). The morphological characters of the new species suggest their taxonomic assignment to the most basal tribe of Mordellinae: Raynoldsiellini, some detailed body structures also showed similarity with advanced Mordellinae taxa, e.g. genera *Mordella* and *Mordellistena*. The common Mordellidae featured by a typical flower and pollen diet; the angiosperm fossil records prove the potential nutrition for the new species in Burmese amber forests. However, since the angiosperm plants did not dominate the Burmese amber forests and the new species retains morphological traits of other Jurassic – Cretaceous Mordellidae or mordellid-like species, the insect-plant interactions were probably at a primary stage.

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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.2018.09.008>.