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ARTICLE

New subfamily of ambrosia beetles (Coleoptera: Platypodidae) from mid-Cretaceous Burmese amber

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ABSTRACT
An ambrosia beetle described as *Palaeotylus femoralis* n. gen et sp. belonging to a new subfamily (Palaeotylinae n. subfam.: Coleoptera: Platypodidae) is described from Cretaceous Burmese amber. It differs from other subfamilies by the loose antennal club, 6-articled funicle, coarsely faceted eyes, tibiae with teeth at apex, bilobed meso- and meta-tarsomeres 2 and 3 and tarsomere 1 shorter than tarsomeres 2–4 combined. This is the first described Platypodidae from Burmese amber and the oldest documented ambrosia beetle that demonstrates glandular sac mycangia containing yeast-like propagules and hyphal fragments.

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Curculionoidea; Platypodidae; new taxa; Myanmar; Cretaceous

Introduction

Mesozoic Curculionoidea are well represented in Middle-Upper Jurassic impression fossils (Legalov 2010, 2011, 2012, 2013, 2015; Gratshev and Legalov 2011, 2014) as well as in Cretaceous amber from the Middle Neocomian–Lower Aptian (Kuschel and Poinar 1993; Kirejtshuk et al. 2009; Legalov 2012, 2015; Peris et al. 2014).

Cretaceous representatives of the Curculionoidea from amber include 20 described species in seven families (Kuschel and Poinar 1993; Gratshev and Zherikhin 2000; Poinar 2006, 2009; Cognato and Grimaldi 2009; Kirejtshuk et al. 2009; Poinar and Brown 2009; Soriano 2009; Davis and Engel 2014; Peris et al. 2014; Legalov and Poinar 2015; Poinar et al. 2016, 2017; Legalov et al. 2017; Legalov 2018a). However, representatives living inside trees such as the Platypodidae and Scolytidae comprise only 10% of the Cretaceous fauna. Members of the latter family have been described from Aptian Lebanese amber (Kirejtshuk et al. 2009) and Cenomanian Burmese amber (Cognato and Grimaldi 2009); however, no Platypodidae have been described from Cretaceous deposits.

Pinhole borers, the common name given to platypodids, are sometime placed in a subfamily, the Platypodinae, within the Curculionidae (Coleoptera: Curculionoidea) (Kuschel 1995; Kuschel et al. 2000; Marvaldi et al. 2002; Jordal 2014; etc.), a placement that has been 'contentious' (Peris et al. 2015) and 'is still debated' (Hulcr et al. 2015). In the present work, we follow those who consider the group as a separate family, the Platypodidae (Thompson 1992; Wood 1993; Morimoto and Kojima 2004; Bright 2014; Legalov 2015, 2018b).

Platypodids are common in wet tropical forests and are well known for their wood-boring activities and associations with symbiotic ambrosia fungi. The larvae of these ambrosia beetles develop on fungi growing in wood tunnels (Jordal 2015; Kirkendall et al. 2015). While members of the Platypodidae are considered to be the most ancient of fungus cultivating insects (Jordal 2015), no Cretaceous representatives have been described that show a close association with a symbiotic fungus. In the present study, we describe a new genus, species and subfamily of a pinhole borer in Burmese amber that possesses glandular sac mycangia containing yeast-like propagules and hyphal fragments.

Materials and methods

The amber specimen (Figure 1) originated from the Noije Bum 2001 Summit Site mine excavated in the Hukawng Valley in 2001 and located southwest of Maingkhwan in Kachin State (26°20′N, 96°36′E), Myanmar. Cruickshank and Ko (2003) have dated this site to the late Albian of the Early Cretaceous, placing the age at 97–110 million years ago (Ma). Shi et al. (2012) have determined the age for the site to be 98.8 ± 0.62 Ma or at the Albian/Cenomanian boundary. Araucarian trees have been determined as the source for the amber at the Noije Bum 2001 Summit Site based on nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers (Poinar et al. 2007).

The specimen was observed with a Nikon SMZ-10 R stereoscopic microscope (Nikon Instruments, Tokyo, Japan) and photographed with and Nikon Optiphot compound microscope (Nikon Instruments, Tokyo, Japan).

Results

It appears that a predator attacked the fossil beetle while it was inside its wood tunnel, resulting in a missing left middle

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Figure 1. Lateral view of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Arrow shows profemur. Scale bar = 0.6 mm.

Figure 2. Lateral view of head of *Palaeotylus femoralis* n. gen et sp. in Burmese amber showing portions of antenna and mouthparts. Arrow shows profemur. Scale bar = 136 µm.

leg and missing portions of the right foreleg and right middle leg. The attack caused the beetle to fall into some resin, along with fungal sporodochia and fibers of the host wood. The presence of femoral mycangia shows that the fossil platypodid was a true ambrosia beetle. The associated fungus has been described by Poinar and Vega (in press).

Description

Superfamily: Curculionoidea Latreille, 1802
Family: Platypodidae Shuckard, 1840
Subfamily: **Palaeotylinae** Poinar, Vega et Legalov, n. subfam.

LSID: urn:lsid:zoobank.org:act:67FDBAD5-2A5E-4D0E-824C-EA7C890D705C
Type genus *Palaeotylus* Poinar, Vega et Legalov, n. gen.

Diagnosis

Head as wide as pronotum. Eyes transversally-oval, coarsely faceted. Antennal scape short, no longer than most funicular segments. Flagellum 9-articled, with 6-segmented funicle and three segmented club. Posterior margin of pronotum laterally straight in pleural area. Disk without mycetangia pores. Elytra elongate, almost cylindrical. Surface of elytral apex rugose with connected ridges surrounding small depressions. Precoxal portion of prosternum elongated. Ventrites 1 and 2 equal in length. Ventrite 3 shorter than ventrite 2. Ventrite 5 elongate. Femora moderately narrow. Tibiae of mid and hind legs weakly flattened and curved, subequal in length to femora, with short apical tubercles. Tibia of fore leg narrow and greatly elongated, partly deformed. Apex of protibia with 4 teeth. Mesotarsus and metatarsus with 5 tarsomeres (tarsomeres 2 and 3 bilobed) terminated with free, paired claws. Femora of fore- and mid-legs with glandular sac mycangia containing yeast-like propagules and hyphal fragments.

Included genera: Type genus only.

Comparison

The new subfamily differs from other subfamilies in the Platypodidae in the loose antennal club, 6-articled funicle, coarsely faceted eyes, tibiae with teeth at apex, bilobed meso- and meta-tarsomeres 2 and 3, tarsomere 1 shorter than tarsomeres 2–4 combined.

Comments

The new subfamily can be placed in the family Platypodidae based on the presence of mycangia, elongated tarsi, head as wide as pronotum and tibiae without denticles on the outer margin or apical spurs.

Palaeotylus Poinar, Vega et Legalov, n. gen.
LSID: urn:lsid:zoobank.org:act:D6550C86-C9AF-46A4-940D-8DCB501852F9
Type species: *Palaeotylus femoralis* Poinar, Vega et Legalov, n. sp.

Diagnosis

As for subfamily.

Included species: Type species only.

Etymology

The generic name is formed from the Greek 'paleo' = old, ancient and the Greek 'thylasos' = sac, pouch in reference to the mycangia in the femora of the beetle.

Palaeotylus femoralis Poinar, Vega et Legalov, n. sp.
(Figure 1–11)
LSID: urn:lsid:zoobank.org:act:A5CC9353-14BC-4827-A3A6-6A51A8CA90A8

Etymology

The specific epithet is from the Latin 'femur' = femur and the Latin suffix 'alis' = pertaining to, in reference to mycangia located in the pro- and meso-femora of the fossil.

Type material

Holotype female # B-F-7 deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, OR, 97331.

Locality and strata

Hukawng Valley southwest of Maingkhwan in Kachin State (26°20′N, 96°36′E), Myanmar, early Cenomanian (mid-Cretaceous).

Description

Body dark brown, length 3.3 mm. Legs and antennae yellow-brown. Body distinctly sclerotized, convex dorsally. Rostrum reduced. Eyes slightly convex, transversally-oval, coarsely faceted, with about 10 rows of facets perpendicular to maximum length. Mandibles large, labial palpi 3-segmented; antennae inserted under eyes. Antennomeres 1–7 conical. Flagellum 9-segmented. Size and shape of antennomeres as depicted in Figures 3–4. There are 6 antennomeres in the funicle, with the 6th structurally different from the remainder. This antennomere appears to be disfigured and has a portion of the segment protruding outward. This condition occurs on the 6th antennomere on the opposite side as well. The three club segments are quite large and are attached to each other with short connectors, that vary slightly in length.

Pronotum elongate, flattened dorsally. Posterior margin of pronotum laterally straight in pleural area. Sides of pronotum non-carinate; scutellum triangular. Elytra almost cylindrical, about 2.5 times as long as pronotum. Humeri weakly rounded, with flattened intervals. Surface of elytral apex rugose with connected ridges surrounding small depressions. Precoxal portion of prosternum elongated. Postcoxal portion very short; procoxal cavities contiguous. Metaventrite and metanepisternum near metaccoxa not impressed. Metaventrite elongated and flattened, punctate, 3.8 times as long as metacoxal cavity length.

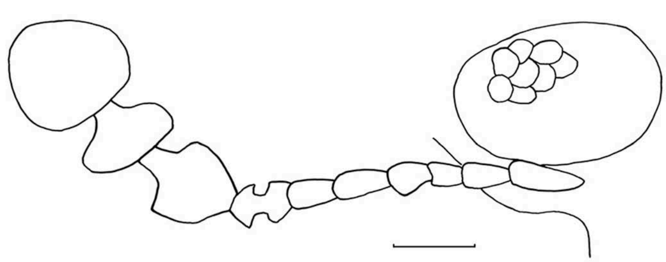

Figure 3. Drawing of antenna and eye of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Scale bar = 0.1 mm.

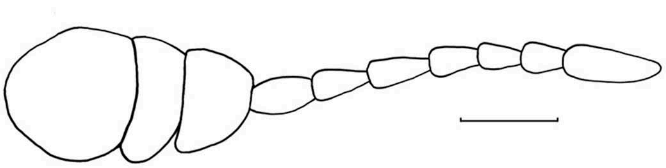

Figure 4. Reconstruction of antenna of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Scale bar = 0.1 mm.

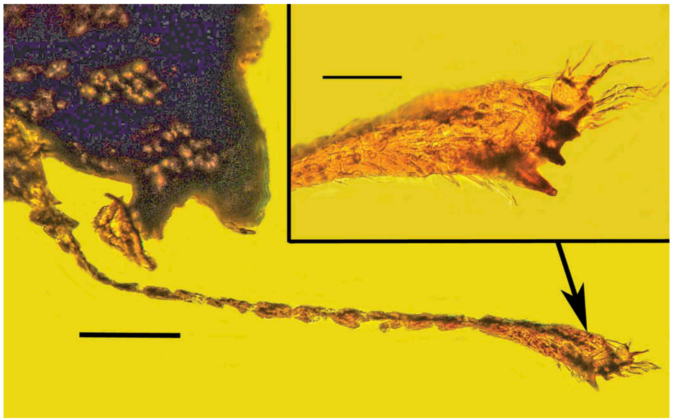

Figure 5. Modified, partly deformed protibia of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Arrow shows apex of protibia bearing 4 teeth. Scale bar = 220 µm. Insert shows detail of protibial apex attached to tarsomere 1 bearing filaments. Scale bar = 58 µm.

Figure 6. Midleg showing curved tibia and tarsus of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Scale bar = 93 µm.

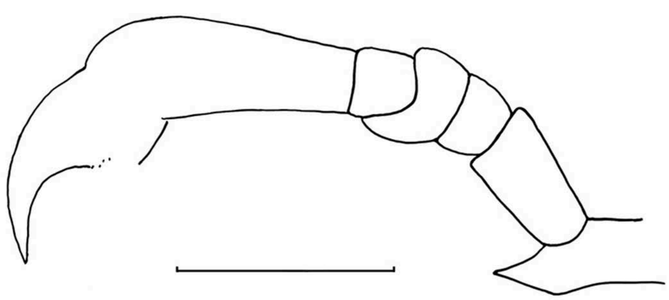

Figure 7. Drawing of midleg tarsus of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Scale bar = 93 µm.

Abdomen convex. Ventrites free with ventrites 1 and 2 equal in length. Ventrite 1 without tooth. Ventrite 3 0.8 times as long as ventrite 2. Ventrite 4 1.2 times as long as ventrite 3. Ventrite 5 elongate, 1.4 times as long as ventrite 3. Procoxae elongated. Mesocoxae round. Metacoxae transverse oval. Legs long. Femora moderately narrow, without teeth. Tibiae weakly flattened and curved, subequal in length to femora, without apical spurs. Protibiae apically with two terminal teeth and one subterminal tooth on inner side, lacking transverse rugae. Metatibia with 3 small protuberances apically.

Figure 8. Hind leg tarsus of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Scale bar = 82 µm.

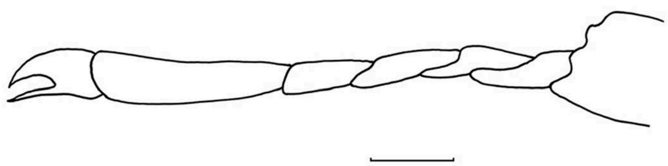

Figure 9. Drawing of hind leg tarsus of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Scale bar = 82 µm.

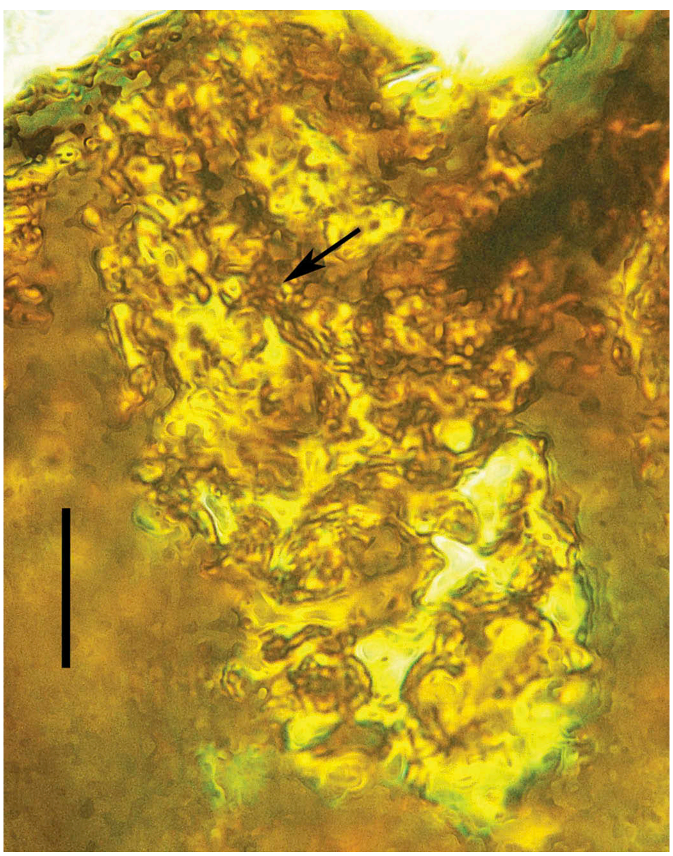

Figure 10. Portion of the profemur mycangium of *Palaeotylus femoralis* n. gen et sp. in Burmese amber showing hyphal fragments and yeast-like propagules (arrow). Scale bar = 18 µm.

Tarsi long and narrow. Tarsomeres 1–3 (on middle and hind legs) narrowly bilobed; Tarsomere 4 conical. Tarsomere 5 long-conical. Claws free, widely separated, without teeth but expanded at base. Protarsi: Tarsomere 1 quite modified and expanded, bearing filaments, tarsomeres 2–5 damaged and broken during fossilization. Mesotarsi: tarsomere 1 subequal to tarsomere 2; tarsomere 3 globose, shorter than tarsomere 2 and tarsomere 4; tarsomere 4 globose, larger than tarsomere 3; tarsomere 5 longer than tarsomeres 1, 2, and 3 combined. Metatarsi: tarsomere 2 longer than tarsomere 1; tarsomere 3 longer than tarsomere 2; tarsomere 4 slightly shorter than tarsomere 3; tarsomere 5 longer than tarsomeres 3 and 4 combined.

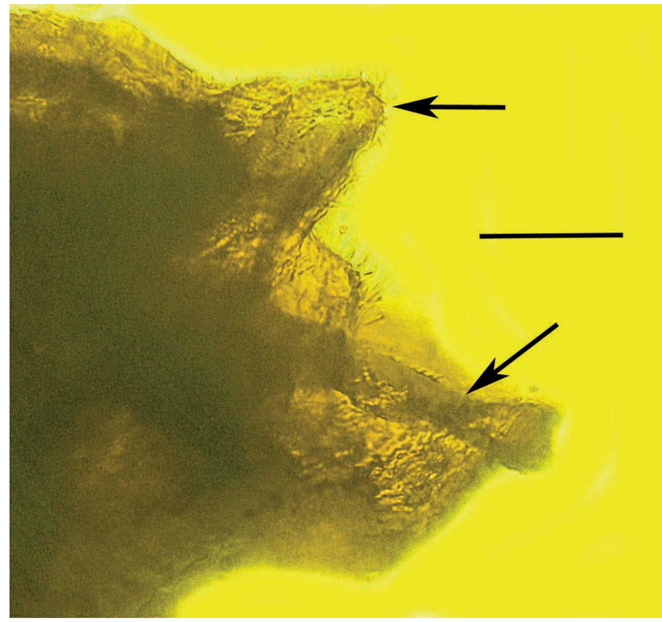

Figure 11. Terminus of *Palaeotylus femoralis* n. gen et sp. in Burmese amber. Top arrow shows cercus. Bottom arrow shows apex of ovipositor (spiculum ventrale). Scale bar = 70 µm.

Comments

Antennae, especially the last segment of the funicle and club segments deformed by stretching. Antennomere 7 (6th segment of funicle) is broken. A reconstruction of the antenna is presented in Figure 4.

Discussion

Only five Coleoptera families (Scolytidae, Platypodidae, Languriidae, Lymexylidae and Attelabidae) have mycangia (Sakurai 1985; Casari and Teixeira 2011; Toki et al. 2012; Hulcr and Stelinski 2017). The amber specimen has characters that are common in the Scolytidae, such as not having an elongated tarsomere 1 and loose club, but it differs by having a femoral mycangium, tibiae not having denticles on the outer margin (the tribe Scolytini does not have denticles but has a large mucro; our specimen does not have a mucro), head as wide as the pronotum and elongated tarsi. Also in the Scolytidae, the antennae are elbowed (geniculate), the club is normally compact and the funicle ranges from 1–7 segments (Chamberlin 1958).

The new subfamily lacks some characteristics of modern Platypodidae, such as the highly elongate tarsomere 1, mycangium on the pronotum or tibiae, and fused articles in the club. Nevertheless, the specimen is placed in the

Platypodidae; it has elongated tarsi, tibiae without denticles on the outer margin, and the head is as wide as the pronotum.

Some beetles of the Colydiinae live in habitats similar to Platypodidae. Our beetle is characterized by the 5-segmented tarsi, prosternum lacking lateral carina and contiguous procoxal cavities, but the Colydiinae always has 4-segmented tarsi, prosternum with lateral carina and separated procoxal cavities. The amber specimen is not an Attelabidae and it differs from Lymexylidae in the antennae with club, prosternum without lateral carina, and the bilobate tarsomere 2 and 3. It differs from Languriidae in the 3-segmented labial palpi, prosternum without developed lateral carina, contiguous procoxal cavities, and the long and narrow tarsi. In body shape, the amber specimen is similar to representatives of the family Bostrichidae, but it differs in the tibiae lacking apical spurs, slightly convex transverse eyes, and a large mycangium in the pro- and meso-femora.

It is not infrequent for a lineage from the mid-Cretaceous to possess characters that are found in several extant lineages. These Cretaceous lineages are known as intermediate or transitional fossils and contain both ancestral and derived features. An example is the Burmese amber bee, *Melittosphex burmensis* Poinar and Danforth, which has mainly bee characters, but also two ancestral wasp features (Danforth and Poinar 2011). While we acknowledge that *Palaeotylus femoralis* n. gen et sp. has some cucujiform and scolytid features, most of the characters are those of a pinhole borer.

Even though pinhole borers are quite common in the tropics, they are very rare as fossils (Legalov 2015). The earliest published fossil of this group was a member of the genus *Platypus* Herbst, 1793 in Eocene Baltic amber (Klebs 1910). Also recently described from Baltic amber was the genus *Eoplatypus* Cognato et Smith, 2017 of the tribe Tesserocerini (Peris et al. 2017). Platypodids were also discovered in Late Oligocene Sicilian Apenninian amber (Skalski and Veggiani 1990) and in mid-Tertiary Dominican and Mexican amber, including 14 species of two modern genera (Bright and Poinar 1994; Schedl 1962; Schawaller 1981; Davis and Engel 2007; Peris et al. 2015). The African *Periommatus severini* Strohmeyer, 1912 was apparently described in copal, however there is some question about the origin of the sample (Nunberg 1959).

Of special interest are the glandular sac mycangia containing yeast-like propagules and hyphal fragments in the pro- and meso-femora of the fossil, leaving no doubt about the ambrosia nature of the association. There are no records of such mycangia in the femora of extant ambrosia beetles.

This is the first described member of the Platypodidae in Burmese amber and represents the oldest known fossil ambrosia beetle that clearly shows an association with symbiotic fungi. The primitive features of the Palaeotylinae n. subfam., especially the structure of the antennae, shape of the legs, and femoral mycangia, allow it to be easily separated from previously known platypodid beetles. This discovery shows that ambrosia beetles were well established by the mid-Cretaceous and provides a minimum date that can be used in future studies establishing the evolutionary history of symbiotic associations between fungi and insects.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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