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A new genus and species of soldier beetle from Upper Cretaceous Burmese amber (Coleoptera, Cantharidae, Malthininae)

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Abstract

A new Upper Cretaceous genus and species of soldier beetles, *Archaeomalthodes rosetta* gen. et sp. nov., is described and illustrated from an individual preserved in Upper Cretaceous (Cenomanian, ca. 99 Ma) amber from northern Myanmar. It is undoubtedly placed in extant subfamily Malthininae based on its small-sized body, somewhat abbreviated elytra and fusiform terminal maxillary palpomere, representing the oldest documented occurrence of Malthininae. It suggests that this

subfamily is an ancient group, which originated at least in the earliest Late Cretaceous. Our discovery sheds light on the palaeodiversity of Cantharidae in the Late Mesozoic. Together with other previously reported fossil cantharids, it is likely that Malthininae has been fairly speciose during the early evolution of Cantharidae. On the other hand, a morphological similarity between *Archaeomalthodes* and Recent malthinines and the occurrence of flowering plants in the Burmese amber implies a potential flower-visiting behaviour of this fossil species.

Keywords:

Cantharidae

Malthininae

Upper Cretaceous

Burmese amber

1. Introduction

The family Cantharidae is a moderately large group of soft-bodied, often brightly colored terrestrial beetles, also known as soldier beetles. The family consists of five subfamilies, over 130 genera and 5000 species, occurring on all the world's habitable continents. (Delkeskamp, 1977, 1978; Ramsdale, 2010). Cantharids are usually found in forested habitats and are often observed visiting flowers. The adults are opportunistic predators of foliage-frequenting invertebrates and also feed on nectar or pollen (Ramsdale, 2010). The larvae are geophillic and live in micro-habitats with high relative humidity. They are liquid-feeding predators and feed on various soft-bodied invertebrates as earth worms (Lumbricidae), slugs (Gastropoda), and larvae and eggs of various insects (Balduf, 1935; Janssen, 1963; Langenstück et al., 1998; Ramsdale, 2010). The monophyly of Cantharidae is well supported by the following synapomorphic characters: 1) larval velvety appearance caused by dense and minute cuticular process; 2) presence of paired lateral glandular pores on abdominal tergites 1–8

of adults, and thoracic and abdominal tergites 1–8 or 1–9 of larvae (Šulc, 1949; Fitton, 1975; Ramsdale, 2010). Branham and Wenzel (2000) performed cladistics analysis of Lampyridae and related Cantharoid families using adult characters and recovered non monophyletic Cantharidae embedded in a clade consisting of Omethidae, Phengodidae and Telegeusidae. However, all recent molecular phylogenetic studies support the monophyly of Cantharidae (Bocakova et al., 2007; Kundrata and Bocak, 2010; Kundrata et al., 2014; McKenna et al., 2015), but the results are not conclusive because of insufficient number of Cantharidae were included in studies focused on other elateroid groups. The phylogenetic position of Cantharidae is far from stable. It was formerly placed in the superfamily Cantharoidea (Crowson, 1972), which was subsequently transferred to expanded Elateroidea (Lawrence, 1988). Crowson (1972) linked Cantharidae to Omethidae. Bocakova et al. (2007) proposed the Lampyridae as the sister group of Cantharidae and such relationship was also agreed by Kundrata et al. (2014), while Kundrata and Bocak (2010) supported the relationship Cantharidae + (Lampyridae + Lycidae). McKenna et al. (2015) recovered Cantharidae as the sister group to the clade including Omalisidae, Drilidae, Elateridae, Rhagopthaimidae, Phendodidae and Lampyridae.

Brancucci (1980) published the only comprehensive phylogeny of Cantharidae based on morphological characters of adults and divided it into five subfamilies: Cantharinae, Silinae, Dysmorphocerinae, Chauliognathinae and Malthininae. This classification has been in use by subsequent taxonomists. The subfamily Malthininae is a speciose group of Cantharidae with four tribes (three extant and one extinct) and fourteen genera (one extinct) (Brancucci, 1980; Kazantsev and Brancucci, 2007; Kazantsev, 2013). It is characterized by small-sized body (1.2–5 mm); radially symmetrical terminal maxillary palpomere, with pointed apex; somewhat abbreviated elytra, with mostly exposed metathoracic wings; basal piece of aedeagus (=phallobase) enlarged, strongly sclerotized, and expanded ventrally. Malthinines are distributed worldwide, appearing mainly in spring and visiting flowers diurnally, with phototaxis at night as other cantharids. Malthininae

assume end-to-end position during copulation (Fig. 1), as opposed to the male-above female position in the remaining subfamilies. The placement of Malthininae within Cantharidae varies between morphological and molecular phylogenetic studies. According to the morphological phylogeny of Brancucci (1980), Malthininae was regarded as a derived group and sister taxon to Dysmorphocerinae. However, the molecular phylogenies revealed its basal position of this family (Bocakova et al., 2007; Kundrata and Bocak, 2010; Kundrata et al., 2014).

Up to date, twenty-five fossil species in sixteen genera of Cantharidae have been described, classified in all extant subfamilies except Chauliognathinae. The oldest, unnamed, fossil classified in Cantharidae was reported by Jell (2004) from the Late Cretaceous Koonwarra fossil bed in Victoria, Australia (116 Ma) but most of fossil cantharids mostly originated from Baltic amber with few taxa described from Tertiary outcrop of Brunstatt (France), Chiapas, Dominican, Rovno and Burmese amber (Förster, 1891; Schaufuss, 1892; Yablokov-Khnozoryan, 1960; Wittmer, 1963; Kuśka, 1992, 1996; Kuśka and Kupryjanowicz, 2005; Kuśka and Kania, 2010; Kazantsev, 2010, 2013; Kazantsev and Perkovsky, 2014; Alekseev and Kazantsev, 2014; Poinar and Fanti, 2016).

Burmese amber is the important fossiliferous resin from the Upper Cretaceous and is renowned for yielding rich and exquisitely preserved insects (Cai et al., 2016; Engel and Grimaldi, 2008, 2014; Engel et al., 2007; Grimaldi et al., 2002; Ross et al., 2010). In the present paper, we describe a new genus and species of Cantharidae based on an individual preserved in the Late Cretaceous Burmese amber. The new genus belongs to the extant tribe Malthodini (subfamily Malthininae), representing the oldest fossil record for this subfamily.

2. Material and methods

The single specimen is derived from amber deposits in Kachin (Hukawng Valley) of Northern Myanmar, approximately 100 km southwest of the Village of Tanai. The age of the amber deposits generally considered to be the earliest Cenomanian (Grimaldi et al., 2002) or possibly latest Albian

(Ross et al., 2010). The recent U-Pb zircon dating constrained the Burmese amber to a maximum age of 98.79 ± 0.62 Ma, which is equivalent to the Late Cretaceous (earliest Cenomanian; Shi et al., 2012).

The fossil-containing amber was prepared using a mini table-saw, polished with emery papers with different grain sizes, and finally lustrated with polishing powder. The type specimen is housed in the Key Laboratory of Insect Evolution & Environmental Changes, Capital Normal University in Beijing, China. The specimen was examined using a Leica M205 C stereomicroscope and the photographs were taken using a Leica DFC490 digital camera or Nikon COOLPIX P310 digital camera. Images were post-processed using the software Helicon Focus 6.3.5 (Helicon Soft Ltd.). The morphological terminology follows Ramsdale (2010), and the classification of subfamilies and tribes of Cantharidae follows Brancucci (1980) and Kazantsev (2013).

3. Systematic paleontology

Order: Coleoptera Linnaeus, 1758

Superfamily: Elateroidea Leach, 1815

Family: Cantharidae Imhoff, 1856

Subfamily: Malthininae Kiesenwetter, 1852

Tribe: Malthodini Böving and Craighead, 1930

Genus: *Archaeomalthodes* Hsiao, Ślipiński and Pang, gen. nov.

Type species. *Archaeomalthodes rosetta* gen. et sp. nov., here designated.

Etymology. The genus name is composed of the prefix *Archaeo-* meaning “ancient” and the root genus *-malthodes* derived from the type genus of the tribe Malthodini. It is masculine in gender.

Diagnosis. Body small-sized, about 2.5 mm long; eyes large, globular and prominent; frons somewhat concave; terminal maxillary palpomere fusiform, radially symmetrical with pointed apex; inflexed outer margin of mandible with a tooth; antennae filiform, extending to apical third of elytra. Pronotum trapezoidal, transverse with lateral margins straight; disc somewhat convex centrally. Elytra somewhat abbreviated, exposing caudal abdominal segments; densely and coarsely punctate; metathoracic wings completely covered by elytra. Abdomen with eight ventrites with ventrite 8 broadly ensiform.

Archaeomalthodes can be separated from *Prosthaptus* Gorham by having inflexed outer margin of mandible with a tooth. It can easily be distinguished from *Malthodes* (*Malthodes*) Kiesenwetter, *Malthodes* (*Podistrina*) Fairmaire, *Maltypus* Motschulsky, *Frostia* Fender and *Protomaltypus* Wittmer by its wings completely covered by elytra. It resembles *Inmalthodes* Pic by having the wings covered by elytra, but it can be distinguished from *Inmalthodes* by the lateral margins of pronotum straight, and elytra not covering caudal abdominal segments.

Archaeomalthodes rosetta Hsiao, Ślipiński and Pang, sp. nov.

(Figs. 2–4)

Etymology. The specific epithet is derived from the Rosetta Stone, referring to the fact that its discovery is the key in the process of studying on the paleobiology of Cantharidae. Rosetta Stone is the rock stele inscribed with a decree on behalf of Ancient Egyptian King and provided the key factor to research on Ancient Egyptian history and hieroglyphs. This term is also used idiomatically to refer to the small but representative key in the process of solving mysteries.

Holotype. Male; No. CNU-COL-MA20160200; earliest Cenomanian, Hukawng Valley, northern

Myanmar; deposited in in the Key Laboratory of Insect Evolution & Environmental Changes, Capital Normal University in Beijing, China.

Diagnosis. As for the genus (*vide supra*).

Description. Male. Total length 2.50 mm (from the anterior margin of the clypeus to the apices of elytra); width 0.70 mm (widest part of both elytra). Body ca. 3.60 times as long as wide. Eyes black, body and legs completely brown; body closely covered with fine yellowish pubescence.

Head (Fig. 3A) 0.40 mm long and 0.60 mm wide, ca. 0.65 times as long as wide; frons somewhat concave; anterior margin of clypeus arcuate; disc densely and coarsely punctate. Eyes large, globular and prominent, laterally protruding, ratio of eye diameter to interocular space 1.00 : 1.50. Terminal labial palpomere rounded ax-shaped. Terminal maxillary palpomere (Fig. 3B) fusiform, radially symmetrical, with pointed apex. Antennae (Fig. 3C) filiform, extending to apical third of elytra, 2.10 mm long; scape clavate, pedicel short and expanding apically, antennomeres 3–11 subcylindrical; relative lengths of antennomeres 1–11 as 19 : 10 : 17.5 : 17.5 : 17.5 : 17.5 : 16.5 : 17 : 16 : 16.5 : 20. Mandible (Fig. 3B) with single tooth on inflexed outer margin.

Pronotum (Fig. 3F) trapezoidal, 0.40 mm long and 0.60 mm wide, nearly as wide as head, ca. 0.65 times as long as wide; anterior and posterior margins moderately arcuate; lateral margins straight; anterior angles rounded; posterior angles obtuse; disc longitudinally convex at median portion, densely and coarsely punctate. Prosternum short. Mesoventrite short. Metaventrite transverse. Scutellum triangular, with rounded apex.

Elytra (Figs. 3D–E) somewhat abbreviated, exposing caudal abdominal segments; 1.70 mm long and 0.70 mm wide, ca. 2.40 times as long as wide and 1.15 times as wide as pronotum; lateral sides somewhat constricted in basal one-fourth, widening from this point to middle, roundly narrowing posteriorly in apical half; disc densely and coarsely punctate, punctures arranged in

longitudinal rows. Wings completely concealed beneath elytra.

Abdomen (Figs. 4) 1.60 mm long and 0.70 mm wide, with eight ventrites; first five abdominal segments broad, as wide as elytra; last three abdominal segments narrow, exposed; ventrite 8 broadly ensiform.

Legs moderately slender; femora mostly straight; profemur length 0.50 mm, mesofemur length 0.55 mm, and metafemur length 0.68 mm; tibiae mostly straight, with basal part feebly arcuate and paired tibial spurs, protibia length 0.48 mm, mesotibia length 0.55 mm, and metatibia length 0.70 mm; tarsal formula 5-5-5; tarsomere 4 expanded and ventrally bilobed, 0.30 mm long in protarsi, 0.35 mm in midtarsi, 0.35 mm in matatarsi; pretarsal claws simple.

Aedeagus (Figs. 4D–E) with pair of elongate, thin processes apically.

Remarks. The sexual dimorphism of morphology is common in extant cantharids. Males usually possess larger eyes, longer antennae, narrower body and modified last abdominal ventrite. Therefore, herein proposed diagnostic characters as considerably large eyes, antennae extending to apical third of elytra, and broadly ensiform abdominal ventrite 8 are probably limited to males only.

4. Discussion

Archaeomalthodes can be referred to the family Cantharidae based on the combination of following characters: head exposed, not concealed beneath pronotum; antennae 11-segmented; mesocoxae contiguous, tarsal formula 5-5-5, with tarsomere 4 expanded and ventrally bilobed and abdomen with eight ventrites. It can be placed in the subfamily Malthininae by its small body, fusiform terminal maxillary palpomere, filiform antennae and somewhat reduced elytra. It belongs to the tribe Malthodini evidenced by more or less concave frons and inflexed outer margin of mandible with a single tooth. The gular sutures which are the diagnosis for tribal classification cannot be observed from the position of this specimen. It cannot be attributed to any genus of Malthodini and thus it is considered as a new genus.

The oldest documented fossil cantharid was collected from the Koonwarra fossil bed in Victoria, Australia (Late Cretaceous, 116 Ma). The exposed head, nearly contiguous mesocoxae, and 5-segmented tarsi with tarsomere 4 expanded and ventrally bilobed suggests its possible placement in Cantharidae (Jell, 2004). However, with the missing antennal characters and pro- and hind legs its taxonomic placement remains unclear. Poinar and Fanti (2016) described a fossil cantharid from Burmese amber, *Ornatomalthinus elvirae*, which is the oldest and credible fossil record of the family. It was attributed to Cantharinae by its securiform terminal maxillary palpomere and pronotum without modified lateral margins. Our discovery of *Archaeomalthodes rosetta* is the oldest fossil record for Malthininae, dating the existence of this subfamily back to the Late Cretaceous. Together with both fossil taxa and other specimens without specific attribution from Burmese amber (Rasnitsyn and Ross, 2000; Poinar et al., 2007b), it highlights the palaeodiversity of Cantharidae in the Late Mesozoic. Furthermore, up to present, twenty-five fossil species of Cantharidae have been described and Malthininae is the major component, with ten species in three extant tribes and one extinct tribe. With the addition of our new discovery, it suggests that Malthininae possibly has been considerably speciose during the early evolution of solider beetles.

The extant malthinines are active during the daylight time and can be observed visiting flowers. Based on the overall morphological similarity between *Archaeomalthodes rosetta* and extant malthinines, and the occurrence of angiosperms in the Burmese amber (Santiago-Blay et al., 2006; Poinar and Chambers, 2005; Poinar et al., 2007a, 2008; Chambers et al., 2010; Ross et al., 2010), it is likely that *A. rosetta* had a similar diurnal flower-visiting behaviour. Additionally, it is possibly that this fossil species also mated with end-to-end position and can be attracted by light as its extant relatives. Eventually, with more well-preserved fossil records, we will be able to realize the palaeodiversity and paleobiology of early Cantharidae.

5. Concluding remarks

Our research describes a new fossil soldier beetle, *Archaeomalthodes rosetta* gen. et sp. nov. sharing many diagnostic characters with the extant cantharids to support its placement in the family Cantharidae, subfamily Malthininae, and tribe Malthodini. It represents the oldest occurrence of Malthininae and suggests that this subfamily is an ancient group, originated at least in the Late Cretaceous. Together with other documented fossil records, our discovery highlights the palaeodiversity of Cantharidae in the Late Mesozoic. The richness of malthinines fossil taxa implies that this subfamily possibly has been fairly speciose during the early evolution of cantharids. Based on the occurrence of flowering plants in the Burmese amber and overall morphological similarities between *Archaeomalthodes* and Recent malthinines, a potential flower-visiting habit is proposed for this species.

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[FIGURE CAPTIONS]

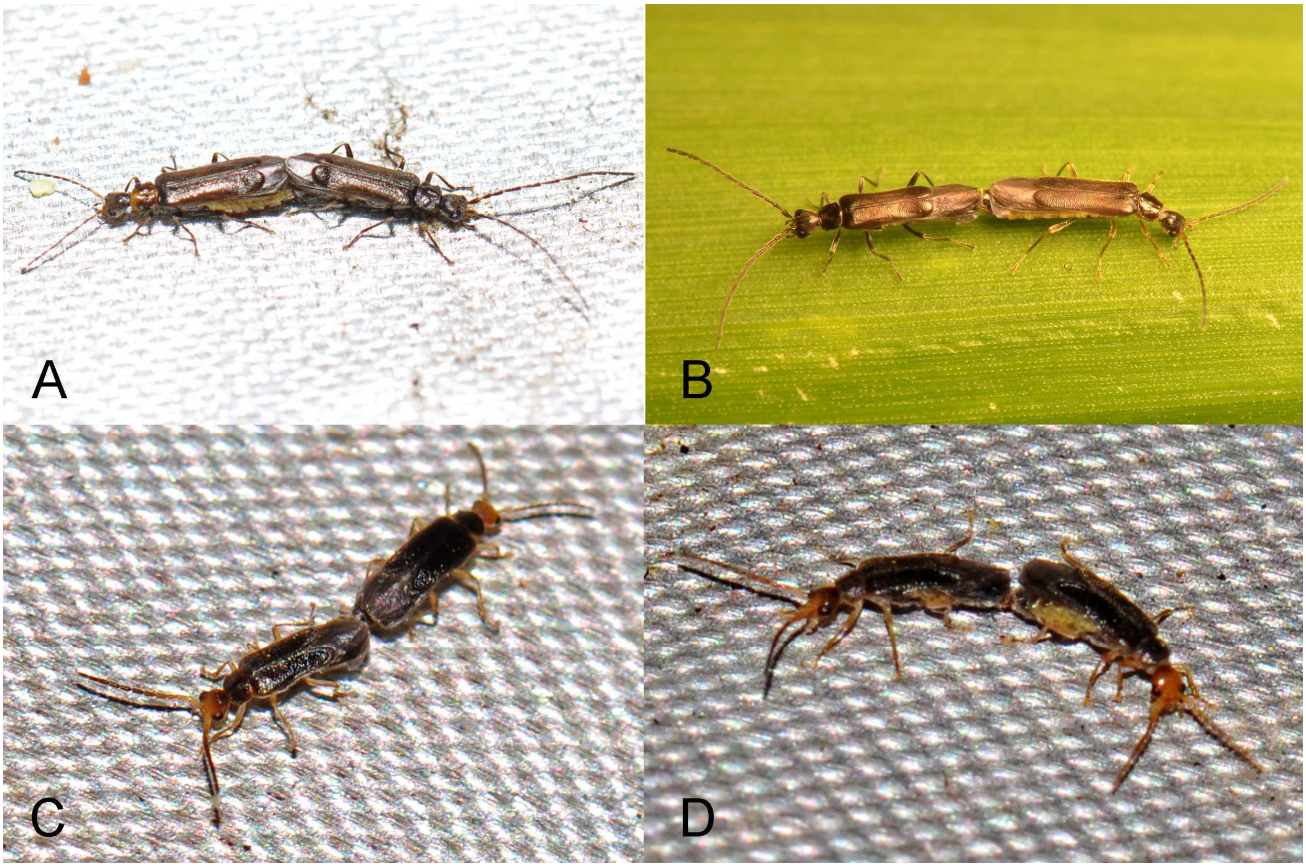

Fig. 1. The copulation of extant malthinine species, showing the end-to-end mating position. A–B. *Malthodes* spp.; C–D. *Maltypus* sp. A, C–D. Photographed by Wen-Chuan Liao; B. Photographed by Ren-Hou Liou.

Fig. 2. Lateral habitus of *Archaeomalthodes rosetta* Hsiao, Ślipiński and Pang, gen. et sp. nov., in Upper Cretaceous amber from Myanmar. Scale bar: 0.5 mm.

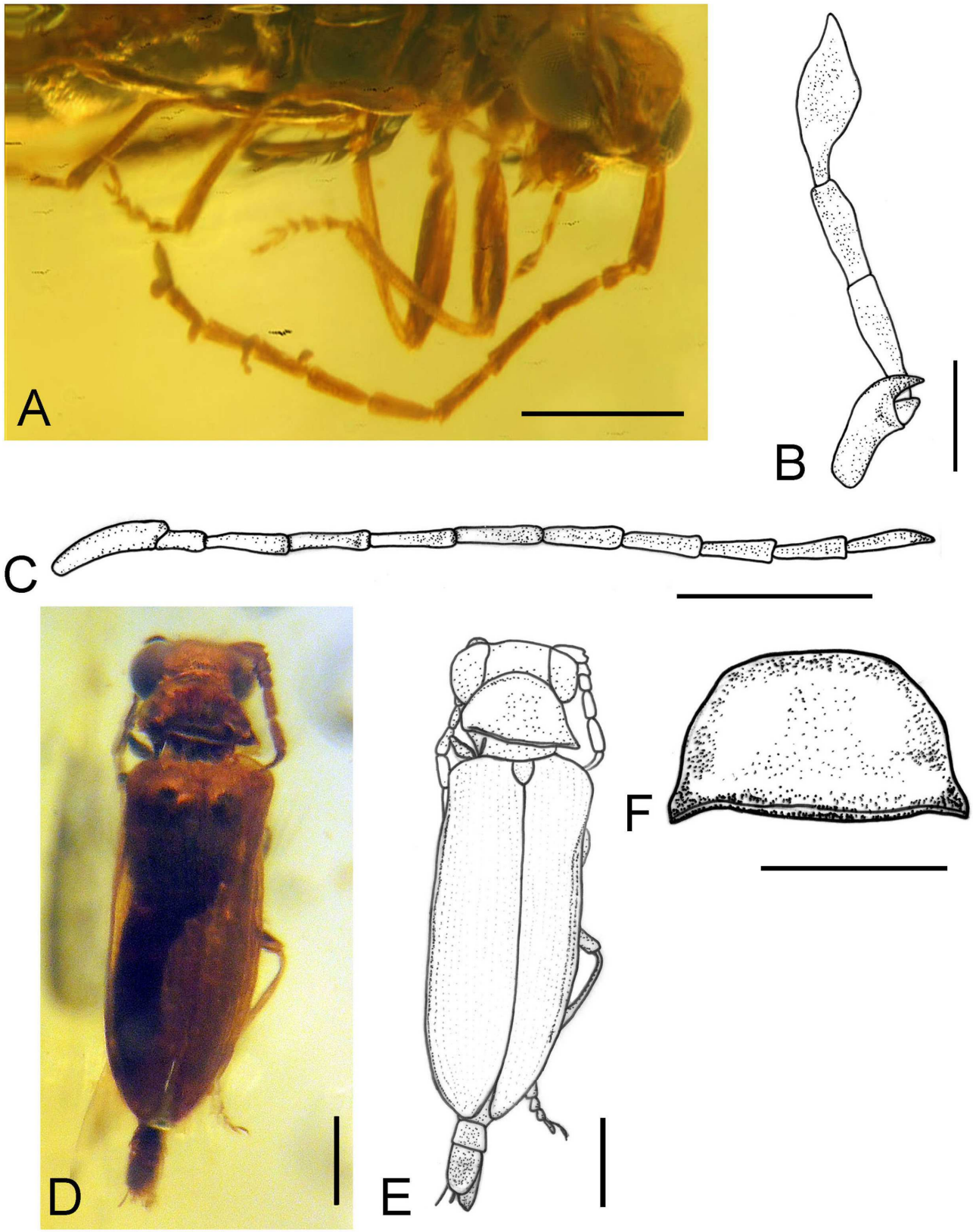

Fig. 3. *Archaeomalthodes rosetta* Hsiao, Ślipiński and Pang, gen. et sp. nov., A. head, antenna, pro- and mid legs; B. mandible and terminal maxillary palpomere; C. antenna; D–E. habitus, dorsal view: D. photograph; E. habitus drawing; F. pronotum. Scale bars: 0.5 mm in A, C–F; 0.1 mm in B.

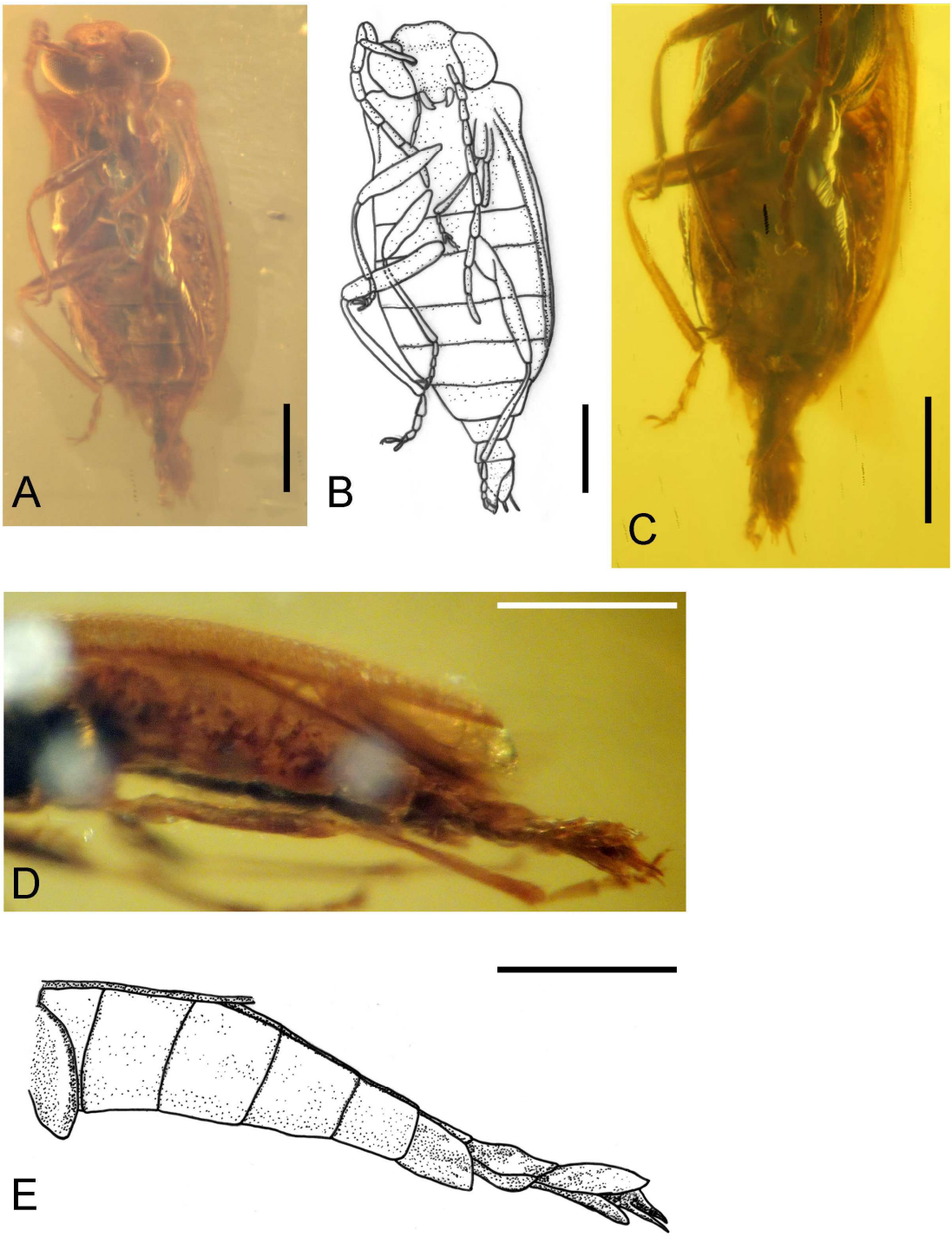

Fig. 4. *Archaeomalthodes rosetta* Hsiao, Ślipiński and Pang, gen. et sp. nov., A–B. habitus, ventral view: A. photograph; B. habitus drawing; C. abdomen, ventral view; D–E. abdomen, lateral view: D. photograph; E. habitus drawing. Scale bar: 0.5 mm.