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Short communication

Zorotypus dilaticeps sp. nov., a remarkable zorapteran (Zoraptera) in mid-Cretaceous Burmese amber

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ABSTRACT

A seventh species of fossil zorapteran (Zoraptera) in mid-Cretaceous Burmese amber is described and figured from an apterous female (dealate). *Zorotypus* (*s. str.*) *dilaticeps* sp. nov. is exceptionally large in body size (ca. 3.9 mm), and can be readily distinguished from all other extinct and Recent members of the order by its distinctive head morphology and by unique spination of the metafemur and metatibia. Our new find sheds further light on the diversity and morphological disparity of fossil zorapteans during the Late Mesozoic.

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1. Introduction

The insect order Zoraptera is one of the smaller lineages of hexapods, comprising less than 50 species with a largely pantropical distribution (e.g., Engel, 2009, 2012, 2014; Yin et al., 2015; Yin and Li, 2017; Mashimo et al., 2018), although in North America and Asia there are species that extend beyond the otherwise tropical occurrence of most other species (e.g., Hinojosa-Díaz et al., 2006). Zorapterans are generally small insects, superficially resembling termites or barklice, and live gregariously. Most individuals within a species spend their lives living in subcortical habitats and are blind and wingless (dubbed, apterons). When resources become limited, their microhabitat degrades, or the population grows to a point of overcrowding, then a developmental shift is triggered such that newly laid eggs produce individuals with well-developed compound eyes and paddle-shaped, diaphanous wings. Such alates disperse to mate and form new colonies, at which point newly hatched individuals revert to the apteron morph. This mode of life is ancient among zorapterans as evidenced by apterons and alates in Cretaceous deposits (e.g., Engel and Grimaldi, 2002; Yin et al., 2018a).

Owing to their many peculiarities, consensus regarding a precise higher placement of Zoraptera among other polyneopteran lineages has yet to be achieved (summarized by Mashimo et al., 2014), with hypotheses supporting relationships as disparate as sister to Dictyoptera (e.g., Yoshizawa and Johnson, 2005; Wang et al., 2013), Embiodea (e.g., Engel and Grimaldi, 2000; Grimaldi and Engel, 2005; Yoshizawa, 2007, 2011), Dermaptera (Misof et al., 2014), or even outside of Polyneoptera and as sister to Paraneoptera (e.g., Hennig, 1969; Kristensen, 1981; Beutel and Weide, 2005). While studies based on Recent taxa alone have failed to resolve conclusively the phylogenetic affinities of this highly autapomorphic group, it may be hoped that the early fossil record of the order might shed some additional light on the matter (e.g., Engel and Grimaldi, 2002), particularly if stem-group zorapterans could be discovered in pre-Cretaceous deposits. Continuing efforts

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investigating the fossil history of Zoraptera during the last three decades have revealed four species in Miocene Dominican amber (ca. 25 Ma; Grimaldi, 1995) (Poinar, 1988; Engel and Grimaldi, 2000; Engel, 2008), six species in Upper Cretaceous Burmese amber (ca. 99 Ma; Shi et al., 2012) (Engel and Grimaldi, 2002; Yin et al., 2018a), and a single species in Lower Cretaceous Jordanian amber (ca. 113 Ma) (Kaddumi, 2005). Among these, one remarkable exemplar is *Xenozorotypus burmiticus* Engel & Grimaldi from Burmese amber. This species possesses plesiomorphically an additional vein (M3+4) in the hind wing, which is otherwise unknown in all other Zoraptera, living or extinct (Engel and Grimaldi, 2002). Another noticeable phenomenon drawn from these finds might be the unexpected high diversity of zorapterans in a single deposit (six species in amber from northern Myanmar), which is distinctly higher than that documented from any modern tropical forest (if not by the lack of proper sampling).

Here, we report the discovery of a distinctive new zorapteran, *Z. dilaticeps* sp. n., again from Burmese amber. Some diagnostic features of the new species were unique among the previous known species, thus improving our understanding of the morphological disparity of this group. Accordingly, the species number of Zoraptera in Myanmar amber raises to seven, and a total of eight are known during the Mesozoic, plus the Jordanian *Z. hudai* Kaddumi.

2. Material and methods

The specimen discussed in the present work was obtained from the Hukawng Valley in northern Myanmar (26°21′33.41″N, 96°43′11.88″E; Cruickshank and Ko, 2003; Grimaldi and Ross, 2017). Maps showing the amber-yielding locality can be found in Kania et al (2015: fig. 1A–D), and Yin et al (2018b: fig. 1A–B). The age of Burmese amber has been established as earliest Cenomanian (98.79 ± 0.62 Ma) based on recent U–Pb dating of zircons (Shi et al., 2012), which corresponds with a general age predicted by Grimaldi et al. (2002) based on key inclusions. However, other workers have argued for slightly older ages, albeit at times on less than solid reasoning, either within the late Albian (Cruickshank and Ko, 2003; Ross et al., 2010), or right at the Albian-Cenomanian boundary (Rasnitsyn et al., 2016). The holotype (SNUC-Paleo-0033) is deposited in the Insect Collection of the Shanghai Normal University, Shanghai, China (SNUC). The amber piece was cut using a handheld engraving tool with a diamond blade, and polished using sandpapers of different grits and rare earth polishing powder. Photographs were made using a Canon 5D Mark III camera with a Canon MP-E 65 mm macro lens (Fig. 1A), or using a Canon G9 camera mounted on an Olympus CX31 microscope (Fig. 1B–G). Zerene Stacker Version 1.04 was used for image stacking. All images were arranged in Adobe Photoshop CS5 Extended. Morphological terminology follows Engel and Grimaldi (2002). This publication has been registered in ZooBank under LSID urn:lsid:zoobank.org:pub:92EF9CAC-E1EB-4F92-B2E0-04CD923E0CEC for nomenclatural purposes.

3. Systematic paleontology

Order Zoraptera Silvestri, 1913
Family Zorotypidae Silvestri, 1913

Genus *Zorotypus* Silvestri, 1913

Zorotypus (Zorotypus) dilaticeps sp. nov.
LSID urn:lsid:zoobank.org:act:ACB93517-812F-4A50-A105-18946E779FEC
(Fig. 1)

Etymology. The specific epithet is formed from the Latin *dilatus* (dilated, spread), and the suffix form of *caput* (head), referring to the strongly extended postocular regions of the head.
Type material. Holotype, SNUC-Paleo-0033, a complete but slightly distorted dealate female; lowermost Cenomanian, Hukawng Valley, northern Myanmar (SNUC).
Diagnosis. Body length nearly 3.9 mm. Head with postocular regions strongly dilated posterolaterally; antennae with nine antennomeres, scape three times as long as pedicel, all antennomeres distinctly elongate. Pronotum about as long as wide, meso- and metanotum transverse, with acute posterolateral corners. Metafemur with six major and twelve minor spines along ventral margin; metatibia with six acute spines and seven spine-like setae along inner margin.
Description. Dealate female. Measurements: body length 3.89 mm; antennal length 1.7 mm, length of antennomeres 1–9 (mm): 0.44(1), 0.15(2), 0.14(3), 0.15(4), 0.20(5), 0.23(6), 0.32(7), 0.22(8), 0.18(9); head length 0.85 mm, pronotal length 0.66 mm; mesonotal length approximately 0.40 mm; metanotal length approximately 0.31 mm; length of metafemur 1.0 mm, greatest width 0.38 mm; length of metatibia 1.29 mm; abdominal length 1.67 mm; cercus length 0.19 mm.

Integument generally light reddish-brown and smooth. Head (Fig. 1A; *h*) with postocular regions dilated posteriorly to form 'lobes' (Fig. 1A, upper box, indicated by arrows). Antenna long, with nine distinctly elongate antennomeres (Fig. 1B; *a1–9*); scape (a1) approximately 3 × as long as long as pedicel (a2), about as long as combined lengths of next three antennomeres (a2–4); pedicel not curved outward near base, subequal in length to antennomeres 3 and 4; antennomere 5 slightly longer than 4, antennomeres 6–9 distinctly larger than preceding antennomeres (Fig. 1B). Maxillary palpus (Fig. 1C; *mxp1–5*) with short palpomere 1, and elongate palpomeres 2, 3, and 5, palpomere 4 slightly longer than wide. Pronotum (Fig. 1A; *prn*) of medium size, about as long as wide; lacking crescentic ridges along anterior third; anterior margin straight; setae scattered, of approximately uniform length; mesonotum (Fig. 1A; *msn*) transverse, lacking thorn-like spines on anterolateral corners; metanotum (Fig. 1A; *mtn*) much broader than long, shorter than mesonotum; meso- and metanotum with distinct spinose posterolateral corners (Fig. 1A, lower box, indicated by arrows). Wings absent (shed). Metafemur (Fig. 1D) expanded, gently tapering toward apex; six large and strongly sclerotized spines (Fig. 1E; *1–4, 1′–2′*) and 12 shorter spines (Fig. 1E; *arrows*) present along posterior border of metafemoral ventral surface; spines slightly angled toward metafemoral apex; metatibia (Fig. 1F) longer than metafemur, slender, not dilated toward apex; with six short spines (Fig. 1F; *a–f*) in apical half of inner margin, and seven spine-like setae (Fig. 1F; *arrows*) in basal half; basal metatarsomere minute, distal metatarsomere elongate, about one-third length of metatibia; pretarsal claws simple. Abdominal terga with scattered, minute setae, lacking distinct, transverse rows of setae along posterior margins; terga lacking stiff, erect setae at posterolateral corners; sterna with sparse, minute setae. Cercus (Fig. 1G) elongate, narrowing toward apex; undivided; with scattered setae longer than cercus, lacking apical spine-like seta.

4. Discussion

Two new fossil species of *Zorotypus*, *Z. robustus* Liu, Zhang, Cai et al., and *Z. oligophleps* Liu, Zhang, Cai et al., were recently described from Burmese amber (Liu et al., 2018). *Zorotypus robustus* is morphologically extremely similar to the previously described *Z.* (*Octozoros*) *cenomanianus* Yin, Cai and Huang, sharing with it the

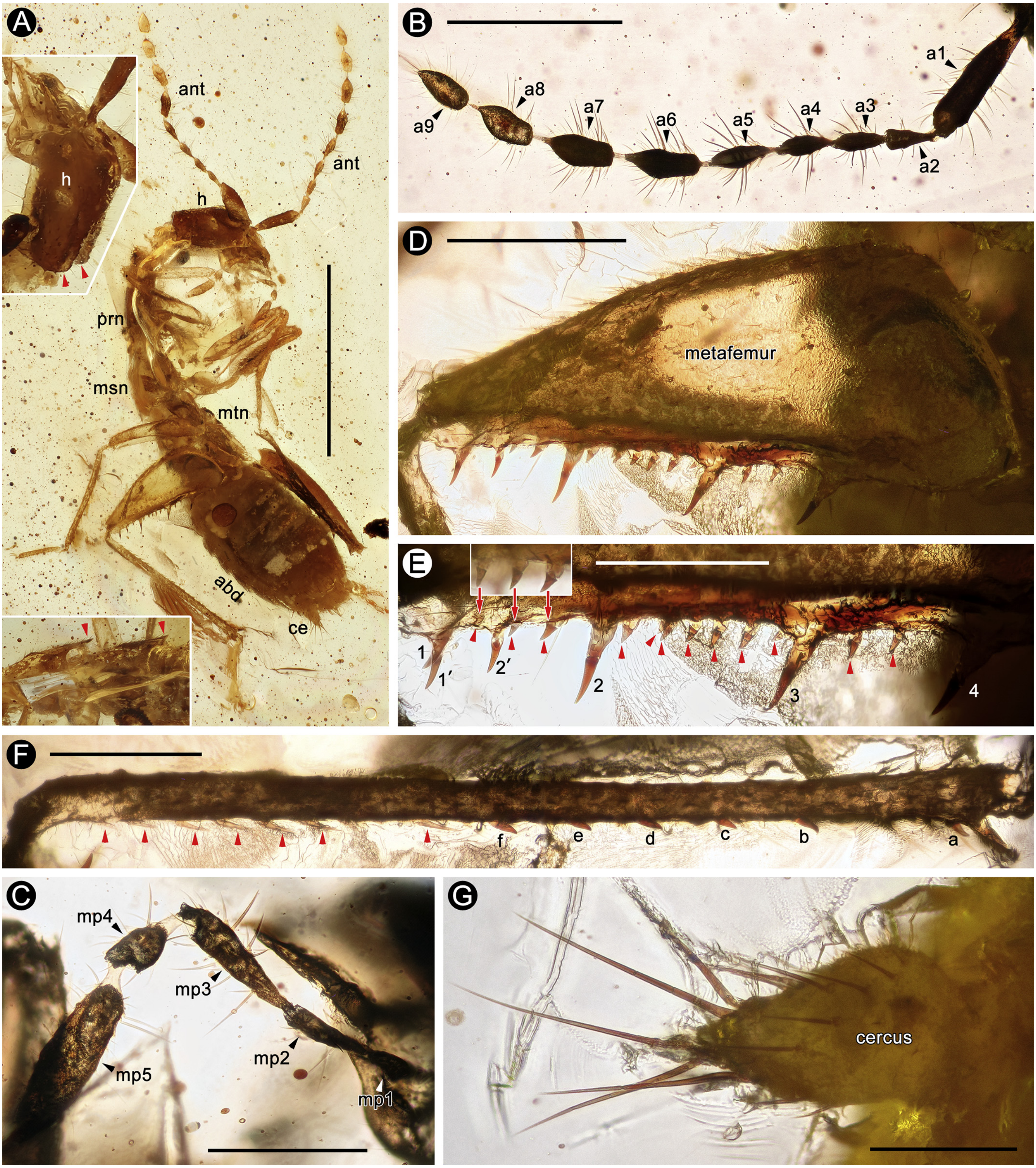

Fig. 1. *Zorotypus dilaticeps*, holotype (SNUC-Paleo-0033). A. Habitus (enlarged head in upper box, showing postocular extensions; lower box showing spinose posterolateral corners of meso- and metanotum). B. Antenna. C. Maxillary palpus. D. Metafemur. E. Spination of metafemur (numerals indicate major spines, arrows indicate minor spines). F. Metatibia (letters indicate spines, arrows indicate spine-like setae). G. Cercus. Abbreviations: 1–4, metafemoral spines 1–4; 1′ – 2′, metafemoral spines 1′ – 2′; a–f, metatibial spines a–f; a1–9, antennomeres 1–9; abd, abdomen; ant, antenna; ce, cercus; h, head; mp1–5, maxillary palpomeres 1–5; msn, mesonotum; mtn, metanotum; prn, pronotum. Scale bars: 2 mm in A; 0.5 mm in B; 0.3 mm in D, F; 0.2 mm in C, E; 0.1 mm in G.

identical shape and proportions of the antennomeres, presence of a large angulate projection on the anterolateral corner of the mesonotum, similar spination of the mesofemur, presence of a row of ctenidia along the posterior margin and a cluster of thickened setae at the middle of tergite X, a thin median projection of tergite XI, a row of erect spines on sternite X, and a pair of acute lateral projections of sternite XI. Most of these characters were listed in the ‘Diagnosis’ section for *Z. cenomanianus*, and combined as a reliable means for an unambiguous identification of this species (Yin et al., 2018a). *Zorotypus oligophleps*, described from an alate female with reduced wing venation (Liu et al., 2018), shares with *Z.* (*s.str.*) *denticulatus* Yin, Cai and Huang the similar form of the head that is distinctly border than the pronotum, and identical configuration and proportions of the antennomeres. The wings of *Z. denticulatus* are largely covered by transparent air bubbles, but it seems that wing venation in this species are also reduced, and similar to the condition in *Z. oligophleps* (Yin et al., 2018a). In fact, *Z. oligophleps* was separated from *Z. denticulatus* only based on the presence of an additional small spine on the apical portion of the metatibia in the latter species (Liu et al., 2018), which could fairly fall into the range of intraspecific or sexual variation in *Zorotypus*. With the lack of definitive characters for effective species discrimination, here we place *Z. robustus* as a junior synonym of *Z. cenomanianus*, and *Z. oligophleps* as a junior synonym of *Z. denticulatus*.

New synonyms. It is somewhat unexpected to discover another new zorapteran from Burmese amber, especially one so soon after publication of an account describing two additional species from the same deposit (Yin et al., 2018a). *Zorotypus dilaticeps* is presently the eighth species of the order documented from the Mesozoic, and one of seven from the amber deposits of northern Myanmar. Both Engel and Grimaldi (2002) and Yin et al. (2018a) have drawn attention to the paleodiversity of zorapterans from Cretaceous tropical forests, and our discovery of yet another new species lends support to the hypothesis that the diversity of Burmese zorapterans may be somewhat greater than that observed within individual localities of modern tropical forests (Yin et al., 2018a).

The new species described here is so distinct that it is almost effortless to separate it from all other species at quick glance, although only a dealate female is available at this moment. *Zorotypus dilaticeps* is exceptionally large in size, with a body length effectively at 3.9 mm, while the total length of other Cretaceous species ranges from 1.15 mm (*Z. cretatus* Engel & Grimaldi) to 2.50 mm (*Z. hudai* (Kaddumi)) (Engel and Grimaldi, 2002; Kaddumi, 2005) (the length of *Z. denticulatus* Yin et al., is unknown as the holotype is lacking its abdomen, but the forebody length measures only 0.99 mm and it was likely under 2 mm in life: Yin et al., 2018a). The head of *Z. dilaticeps* is quite distinct, with a form not found in any other extinct or modern zorapterans, i.e., the postocular regions are strongly dilated posteriorly to form markedly lobes, with the connection of the pronotum deeply inserted between these posterolateral lobes (although the pronotum in the holotype is detached from position *in situ*). The elongate first antennomere (as long as antennomeres 2–4 combined), presence of six large and 12 minor spines arranged in a row on the ventral margin of the metafemur, and presence of six spines and seven spine-like setae along the inner margin of the metatibia also contribute to a unique combination of features for the new species. Interestingly, while spination of the legs serves as a frequently useful suite of characters to circumscribe species of zorotypids, it would be worthwhile to explore the potential variation in spination present in populations (or even among individuals within large colonies) of one or more of the more commonly encountered modern species. Such a population-level exploration would provide considerable insight into possible variations that may have existed in fossil species, thereby permitting greater clarity and confidence when establishing extinct taxa for this group.

The discovery of a male of *Z. dilaticeps*, preferably an alate individual, is desired to further decipher the exact affinities of the species in regard to its congeners, both living and fossil. Nevertheless, the diversity of Zoraptera from Burmese amber offers a tantalizing glimpse into the variety of zorapterans that were present in tropical wet forests of the Mesozoic.

5. Concluding remarks

With the discovery of *Zorotypus dilaticeps* sp. nov., diversity of Mesozoic Zoraptera has risen to eight species, seven of which are known from Burmese amber. Presently, only a single dealate female is available for the new species, but it will not be difficult to match it with its opposite sex should the male be discovered in the future. The larger body size and unique morphological features of the head and legs represent sufficiently distinctive traits to make a positive association with potential males, assuming there were not forms of distinct sexual dimorphism present in this taxon that are unknown among living species of the order. Our discovery sheds further light on the paleodiversity and morphological disparity of fossil zorapterans during the Late Mesozoic, and it is reasonable to expect that further zorapterans shall eventually be found in Mesozoic amber deposits in the future.

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