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MESOCERATOCANTHUS FOSSILS FROM THE EARLY CRETACEOUS OF CHINA REINTERPRETED AS THE EARLIEST PASSALOIDS (COLEOPTERA: SCARABAEOIDEA)

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Abstract. The scarabaeoid beetle *Mesoceratocanthus* from the Early Cretaceous Yixian Formation was originally placed in the extant tribe Ivieolini (Hybosoridae). Our re-examination of the holotype and a new specimen demonstrates that *Mesoceratocanthus* does not possess the diagnostic characters of Ivieolini or Hybosoridae. Instead, it should be assigned to the passaloid lineage (Passalopalpidae + Passalidae) and appears closely related to the extinct family Passalopalpidae. The revised placement of *Mesoceratocanthus* further extends the earliest occurrence of the passaloid clade (~125 Ma, Barremian to early Aptian).

Key words. Scarabaeoidea. Hybosoridae. Passalopalpidae. Passalidae. China. Yixian Formation.

Resumen. El escarabajo scarabaeoideo *Mesoceratocanthus* de la Formación Yixian del Cretácico Inferior se asignó originalmente a la tribu existente Ivieolini (Hybosoridae). El nuevo examen del holotipo y de un nuevo espécimen demuestran que *Mesoceratocanthus* no posee los caracteres diagnósticos de Ivieolini o Hybosoridae. En cambio, debería asignarse al linaje passaloideo (Passalopalpidae + Passalidae) estando estrechamente relacionado con la familia extinta Passalopalpidae. La nueva asignación de *Mesoceratocanthus* cambia la primera aparición del clado passaloide (~ 125 Ma, del Barremiano al Aptiano temprano).

Palabras clave. Scarabaeoidea. Hybosoridae. Passalopalpidae. Passalidae. China. Formación Yixian.

SCARABAEOIDEA is one of the most speciose superfamilies in the beetle suborder Polyphaga, with about 2,500 genera and 35,000 described species (Scholtz & Grebennikov, 2016). Scarabaeoids are typically characterized by their lamellate antennal club, often highly modified prothorax for burrowing (with large coxae, usually with concealed trochantins and closed cavities), usually dentate protibia with a single terminal spur, and the absence of metacoxal plates (Browne & Scholtz, 1995). More than two hundred fossil scarabaeoid species have been described (reviewed by Krell, 2000, 2006, 2007), with the earliest undoubted taxa dating back to the Middle Jurassic (Bai *et al.*, 2012a). Molecular clock studies generally converged on a Jurassic origin of crown-group Scarabaeoidea (*e.g.*, Ahrens *et al.*, 2014), while earliest stem-scarabaeoids may have appeared during the Triassic (Zhang *et al.*, 2018; McKenna *et al.*, 2019).

Numerous fossil scarabaeoids have been discovered from the Lower Cretaceous Lagerstätte, Yixian Formation (~125 Ma) in northeastern China, including representatives of the extant Glaresidae (Bai *et al.*, 2010, 2014), Lucanidae (Bai *et al.*, 2012b), Glaphyridae (Nikolajev & Ren, 2011, 2013; Nikolajev *et al.*, 2011; Yan *et al.*, 2012a; Zhao *et al.*, 2016), Hybosoridae (Yan *et al.*, 2012b, 2013; Lu *et al.*, 2018), Pleocomidae (Nikolajev & Ren, 2012), and Scarabaeidae (Bai *et al.*, 2011), as well as the extinct Septiventeridae (Bai *et al.*, 2013). More recently, various well-preserved scarabaeoids have also been reported in the mid-Cretaceous Kachin amber, including representatives of the extant Glaresidae (Cai & Huang, 2018), Lucanidae (Cai *et al.*, 2017; Qiu *et al.*,

2017), Geotrupidae (Bai *et al.*, 2017), Passalidae (Boucher *et al.*, 2017) and Hybosoridae (Bai *et al.*, 2016), as well as the extinct Passalopalpidae (Boucher *et al.*, 2016). In the present study, we re-examine the *Mesoceratocanthus* fossils from the Yixian Formation, which were assigned to the family Hybosoridae by Nikolajev *et al.* (2010). Based on new compression fossils from the Yixian Formation, as well as new Kachin amber inclusions, our investigation instead suggests an affinity of *Mesoceratocanthus* with the extinct family Passalopalpidae from the mid-Cretaceous Kachin amber.

MATERIALS AND METHODS

The holotype of *Mesoceratocanthus tuberculifrons* Nikolajev, Wang, Liu & Zhang, 2010 (NIGP151840, Fig. 1.1–1.4) was collected from the Yixian Formation at Yangshuwanzi, Bisiyingzi Town, Ningcheng County, Chifeng City, Inner Mongolia, China. The specimen NIGP177046 (*Mesoceratocanthus* cf. *tuberculifrons*, Fig. 1.5–1.6) was collected from the Yixian Formation at Huangbanjigou, Shangyuan Town, Beipiao City, Liaoning Province, China. Additional fossils of *Passalopalpus cheni* Boucher, Bai, Wang, Zhang & Yang, 2016 (NIGP177332–177335) from Kachin amber (Noije Bum, Hukawng Valley, Kachin State, northern Myanmar; ~99 Ma) were also examined for comparison. The specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Where necessary, compression fossils were moistened with 70% ethanol to improve the contrast of morphological characters. Scanning electron microscope (**SEM**) images were obtained with a Hitachi SU 3500 scanning electron microscope, operating with an accelerating voltage of 20 kV and a pressure of 60 or 80 Pa. Energy dispersive X-ray spectroscopy (**EDS**) analyses were conducted with a TESCAN MAIA3 field emission scanning electron microscope. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm Argon laser excitation line. Images under incident light were stacked in Helicon Focus 7.0.2. Confocal images were semi-manually stacked in Helicon Focus 7.0.2 and Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

RESULTS AND DISCUSSION

Nikolajev *et al.* (2010: 444) placed *Mesoceratocanthus tuberculifrons* in the family Hybosoridae, based on "mandibles and labrum prominent, antennal club three-segmented, and pro- and mesocoxae contiguous". However, a three-segmented antennal club and well-developed mandibles and labrum are common and widely distributed characters within Scarabaeoidea. Further, the specific form of the mandibular dentition (Fig. 2.1) and antennal club lamellae (Figs. 2.2, 3.5, S1.2) are uncharacteristic of the Hybosoridae, which are characterized by far more compact, appressable antennal club segments and lack of stout subapical mandibular teeth. Additionally, our observations of the holotype and the new material indicate that the pro- and mesocoxae are clearly separated in *Mesoceratocanthus* (Figs. 2.4–2.5, 3.2, 3.4). Nikolajev *et al.* (2010) further assigned *Mesoceratocanthus* to Ivieolini, a morphologically divergent tribe in subfamily Ceratocanthinae. Most members in Ceratocanthinae are capable of rolling themselves into a nearly-perfect ball (*e.g.*, Ballerio *et al.*, 2011), while *Ivieolus* Howden & Gill, 2000, the only extant genus in Ivieolini, has an elongate body and is incapable of deflexing itself (Ballerio & Grebennikov, 2016). The key character presented by Nikolajev *et al.* (2010) as evidence of a relationship between *Mesoceratocanthus* and Ivieolini is the presence of a so-called "deep V-shaped groove" on the pronotum. However, it is unclear if this V-shaped structure is present on the beetle's dorsal surface at all. Based on our observation, the "V-shaped groove" (Figs 2.3, 3.3) actually represents the sutures between the mesoventrite and mesanepisterna (*e.g.*, Reyes-Castillo, 1970; Boucher, 2006; see also fig. 2D in Bevilaqua & Fonseca, 2020).

We instead suggest that *Mesoceratocanthus* is closely related to the passaloid lineage (Passalopalpidae + Passalidae) (*sensu* Boucher *et al.*, 2016) and most likely belongs to the Passalopalpidae. It is easy to separate *Mesoceratocanthus* from most other families in Scarabaeoidea based on some well-preserved characters. Trogidae and Glaresidae have contiguous mesocoxal cavities and five ventrites (mesocoxal cavities distinctly separated, six ventrites in *Mesoceratocanthus*). The poorly known Diphyllostomatidae also has virtually contiguous mesocoxae. Geotrupidae and Bolboceratidae have 11-segmented antennae and oval or round body shape (antennae likely 9-segmented, body elongated in

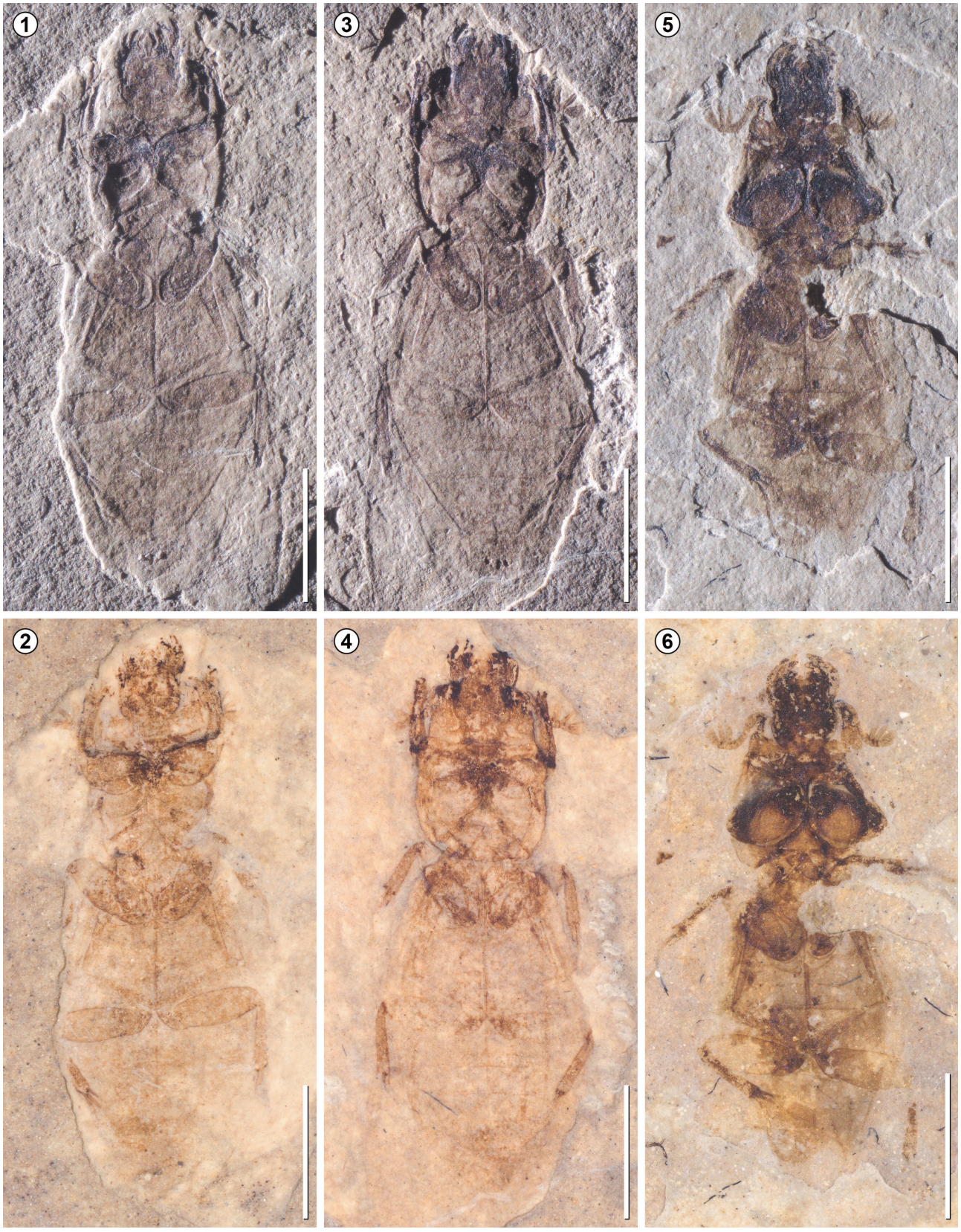

Figure 1. General habitus of ***Mesoceratocanthus***, under incident light, dry (**1, 3, 5**) and moistened with 70% ethanol (**2, 4, 6**). **1–2, *Mesoceratocanthus tuberculifrons***, holotype, **NIGP**151840a. **3–4, *Mesoceratocanthus tuberculifrons***, holotype, **NIGP**151840b. **5–6, *Mesoceratocanthus* cf. *tuberculifrons***, **NIGP**177046. Scale bars equal 3 mm.

Mesoceratocanthus). Pleocomidae have 11-segmented antennae, reduced mandibles, and open procoxal cavities (mandibles well-developed, procoxal cavities closed in *Mesoceratocanthus*). Belohinidae have short mandibles and a strongly convex body (mandibles long, body elongate in *Mesoceratocanthus*). It is more difficult to differentiate *Mesoceratocanthus* from the remaining families, including the most speciose and morphologically diverse Scarabaeidae. However, the prominent mandibles of *Mesoceratocanthus* that extend beyond the clypeus and labrum would be exceedingly unusual for Scarabaeidae. In addition, as stated above, the antennal lamellae of *Mesoceratocanthus* are digitiform and

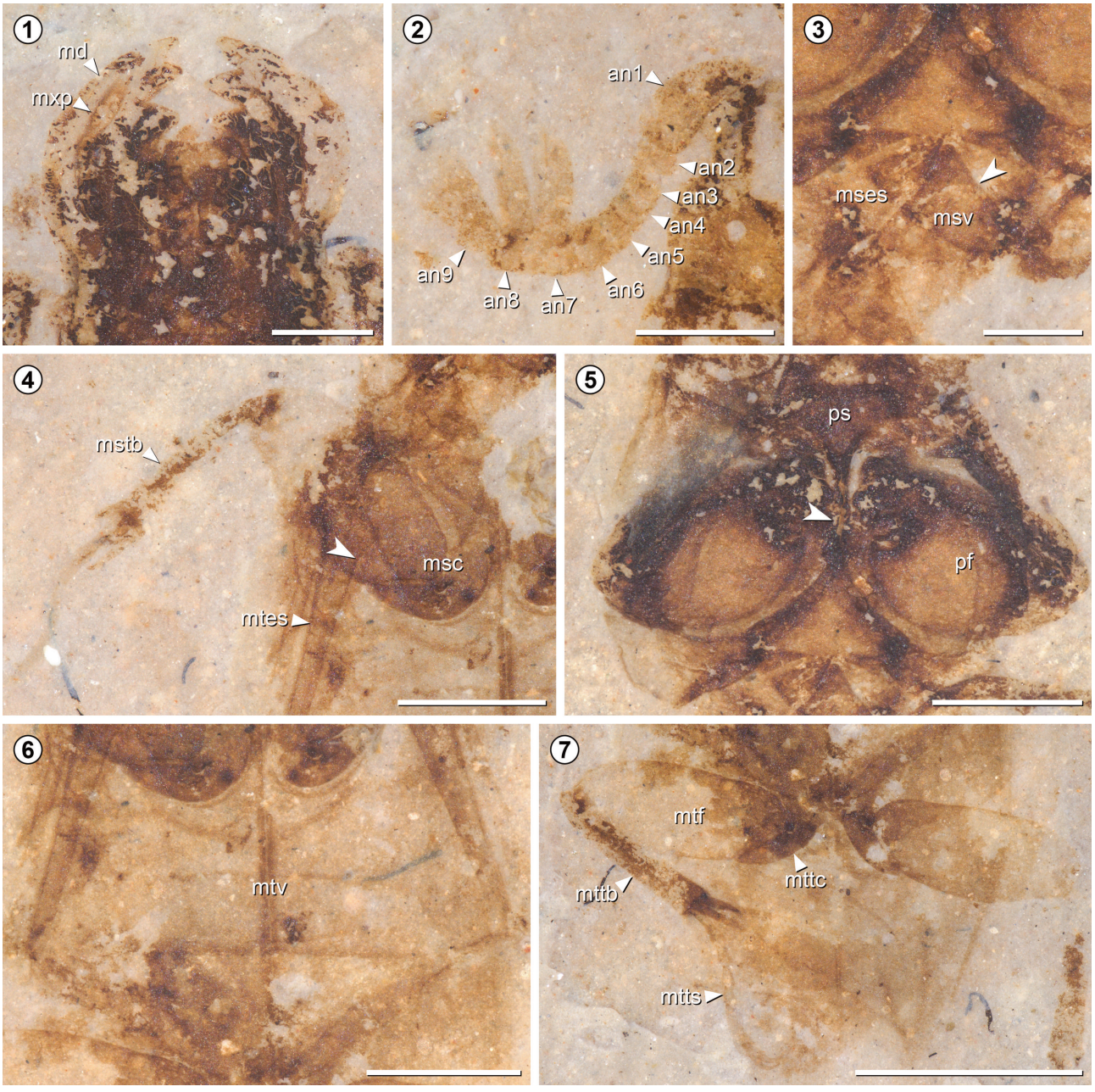

Figure 2. Details of ***Mesoceratocanthus*** cf. ***tuberculifrons***, **NIGP**177046, under incident light, moistened with 70% ethanol. **1,** Mouthparts; **2,** antenna; **3,** mesothorax; **4,** mid leg; **5,** prothorax; **6,** metathorax; **7,** hind legs and abdomen. Abbreviations: **an1–9**, antennomeres 1–9; **md,** mandible; **msc,** mesocoxa; **mses,** mesanepisternum; **mstb,** mesotibia; **msv,** mesoventrite; **mtes,** metanepisternum; **mtf,** metafemur; **mttb,** metatibia; **mttc,** metatrochanter; **mtts,** metatarsus; **mtv,** metaventrite; **mxp,** maxillary palp; **pf,** profemur; **ps,** prosternum. Scale bars equal 0.5 mm (**1–3**), and 1 mm (**4–7**).

non-appressable, in contrast to those of Scarabaeidae and Ochodaeidae which, are typically more compact or flattened and appressable. Lucanidae possess an antennal club similar to that of passaloids, but have a highly reduced labrum

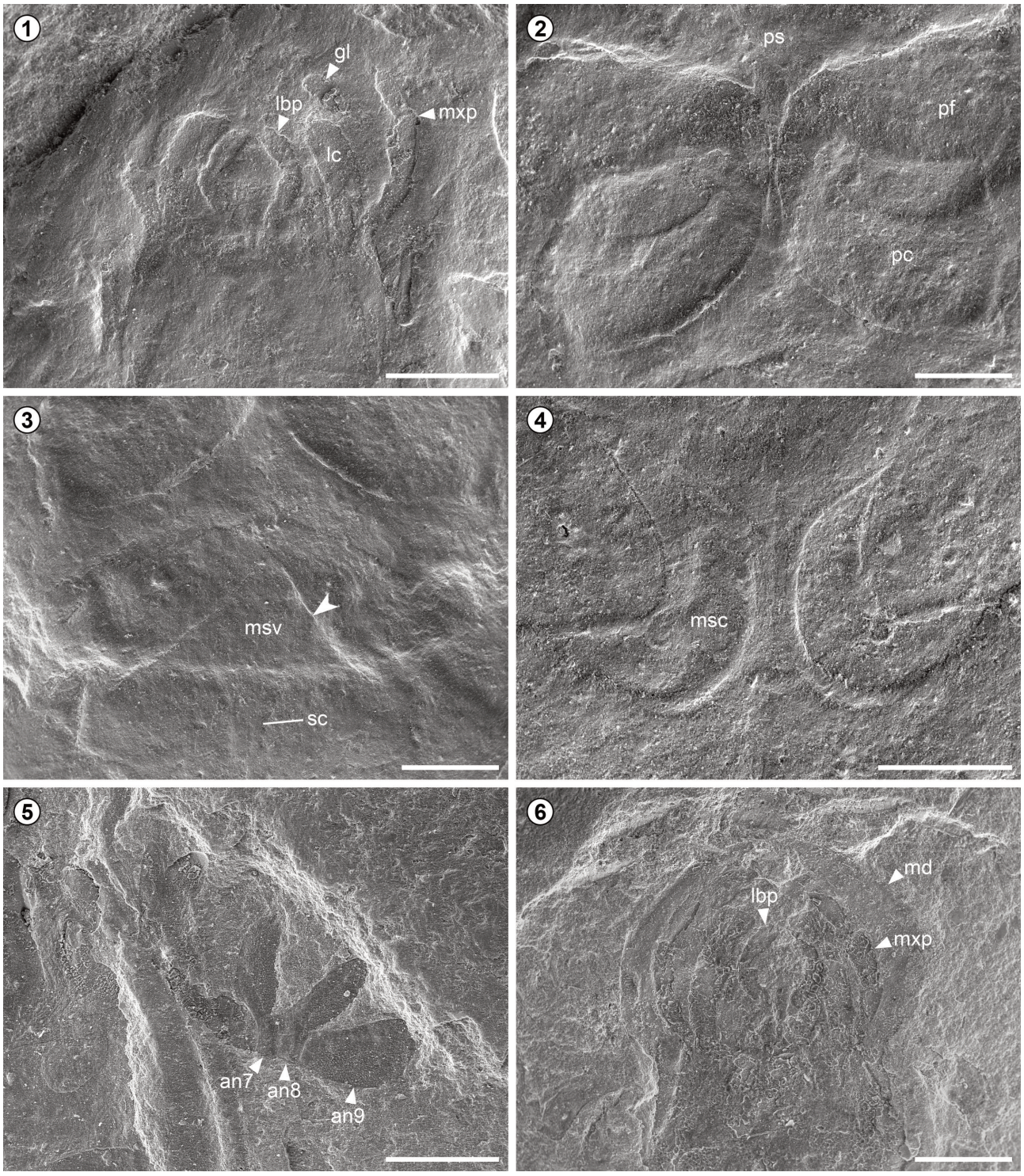

Figure 3. Details of ***Mesoceratocanthus***, under scanning electron microscopy. **1–4,** ***Mesoceratocanthus tuberculifrons***, holotype, **NIGP**151840a; **1,** mouthparts; **2,** procoxae; **3,** mesothorax, showing the sutures between mesoventrite and mesanepisterna (arrowhead); **4,** mesocoxae. **5,** ***Mesoceratocanthus tuberculifrons***, holotype, **NIGP**151840b, antennal club. **6,** ***Mesoceratocanthus*** cf. ***tuberculifrons***, **NIGP**177046, mouthparts. Abbreviations: **an7–9,** antennomeres 7–9; **gl,** galea; **lbp,** labial palp; **lc,** lacinia; **md,** mandible; **msc,** mesocoxa; **msv,** mesoventrite; **mxp,** maxillary palp; **pc,** procoxa; **pf,** profemur; **ps,** prosternum; **sc,** scutellum. Scale bars equal 0.5 mm.

and geniculate antennae (geniculate antennae absent in Sinodendrinae and some Aesalinae) (Scholtz & Grebennikov, 2016), neither of which is true of *Mesoceratocanthus*.

Moreover, the characteristics of *Mesoceratocanthus* match those of passalids and passalopalpids. The general body form and overall habitus of *Mesoceratocanthus* strongly resembles that of Passalidae and Passalopalpidae. In addition, the visible portions of the ventral cephalic anatomy (*i.e.*, the gula, gena, hypostoma, and mentum) are all consistent with passaloid anatomy, as are the visible portions of limbs

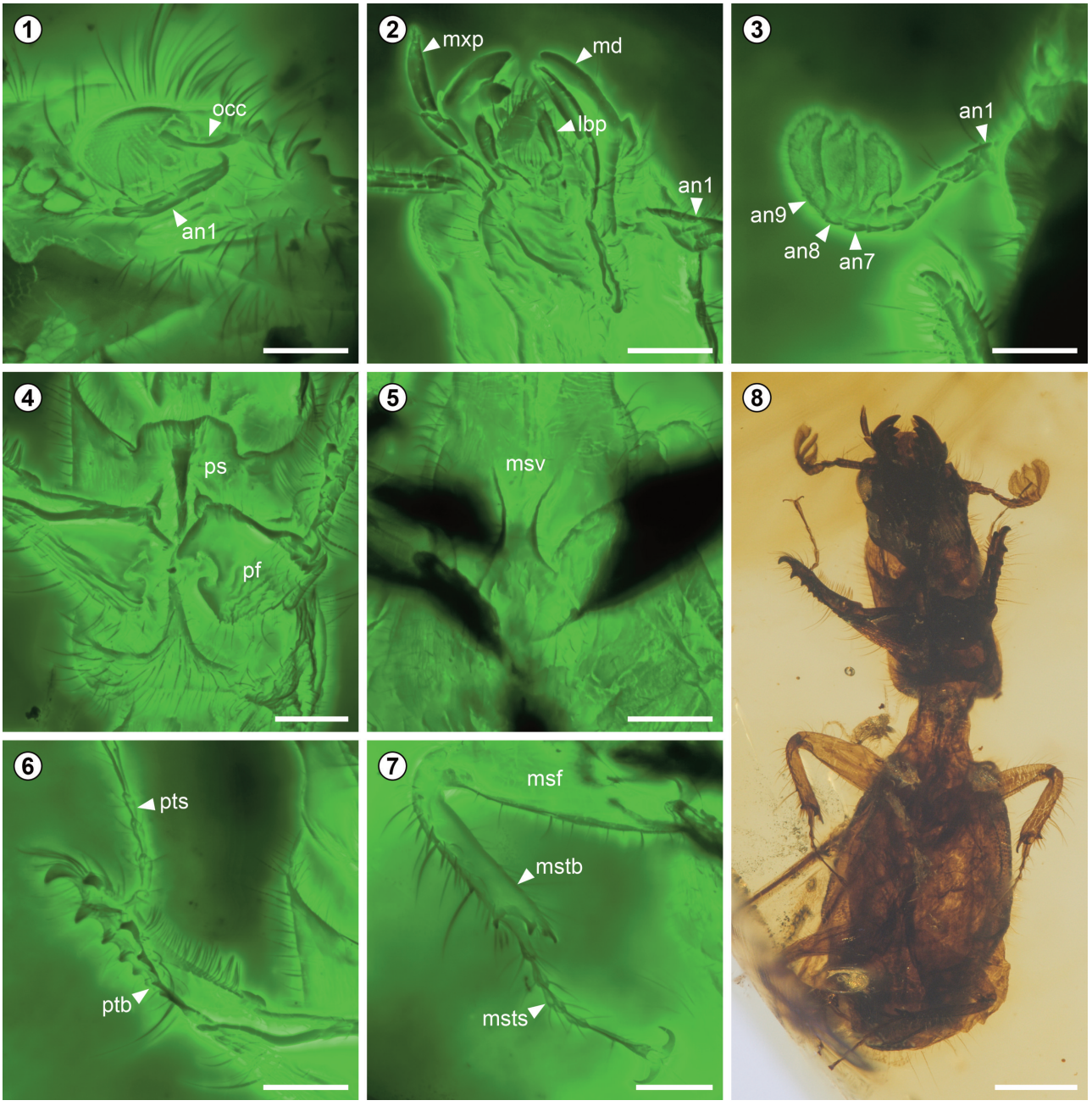

Figure 4. ***Passalopalpus cheni*** from Kachin amber, under confocal microscopy (**1–7**) or incident light (**8**). **1, NIGP**177332, head, lateral view. **2–8, NIGP**177333; **2,** mouthparts, ventral view; **3,** antenna, dorsal view; **4,** prothorax, ventral view; **5,** mesothorax, ventral view; **6,** fore leg; **7,** mid leg; **8,** general habitus. Abbreviations: **an1–9,** antennomeres 1–9; **lbp,** labial palp; **md,** mandible; **msf,** mesofemur; **mstb,** mesotibia; **msts,** mesotarsus; **msv,** mesoventrite; **mxp,** maxillary palp; **occ,** ocular canthus; **pf,** profemur; **ps,** prosternum; **ptb,** protibia; **pts,** protarsus. Scale bars equal 0.2 mm (**1–7**), and 0.5 mm (**8**).

(coxae, trochantero-femoral joints, femora, tibiae, and tarsomeres). Thus, although our interpretation relies on the overall habitus, it is important to note that, unlike other scarabaeoid families, there are no visible anatomical features inconsistent with a close affinity to the Passalidae and Passalopalpidae.

Passalidae is an extant, widespread, and mainly tropical family, with more than 700 described species and a high degree of morphological homogeneity (Boucher, 2006; Scholtz & Grebennikov, 2016). Boucher *et al.* (2016) reported a new family, Passalopalpidae (Fig. 4), from the mid-Cretaceous Kachin amber, and suggested it to represent the extinct sister group of Passalidae. *Mesoceratocanthus* shares several characters with Passalopalpidae. *Mesoceratocanthus* most likely had 9-segmented antennae (Figs. 2.2, S1.2); interpretation of the fossils is somewhat ambiguous, although the bulk of the evidence favors nine antennomeres. This is consistent with Passalopalpidae, in contrast to the 10-segmented antennae of Passalidae. In addition, the protibiae of *Mesoceratocanthus* are relatively narrow, only weakly expanded distally with tibial spines that are directed more ventrally, as in Passalopalpidae. The large and prominent procoxae also resemble those of Passalopalpidae. In *Mesoceratocanthus*, the mesocoxal cavities seem to be laterally bordered by the metanepisterna (Fig. 2.4), which is similar to the condition in Passalopalpidae (Boucher *et al.*, 2016, fig. 5). In Passalidae, the mesocoxal cavities are closed laterally by a broad meeting of the mesoventrite and metaventrite (Lawrence & Ślipiński, 2013; Bevilaqua & Fonseca, 2020, figs 2E, 3C,F). There are six almost completely visible sternites on the abdomen of Passalopalpidae (Boucher *et al.*, 2016). *Mesoceratocanthus* also have six well-developed abdominal ventrites, with the first one not separated by metacoxae (Nikolajev *et al.*, 2010, fig. 1C). Although some Passalidae (Passalinae) also have six abdominal ventrites, the first ventrite is only represented by two very small sclerites visible on the sides of the metacoxae (Matthews & Seeman, 2019). In addition, *Mesoceratocanthus* also shares a similar body shape with Passalopalpidae, with hind body widened postmedially. On the other hand, some other characters of *Mesoceratocanthus* are more similar to Passalidae. For example, the scutellum is well marked in *Mesoceratocanthus* (Fig. 3.3) and Passalidae, which, however, is not seen in Passalopalpidae (Boucher *et al.*, 2016, fig. 2). Besides, Passalopalpidae has very long maxillary palps, exceeding beyond the apex of mandibles (Boucher *et al.*, 2016), while in Passalidae and *Mesoceratocanthus* the maxillary palps are shorter, not reaching the mandibular apex.

Based on the above discussion, we suggest that *Mesoceratocanthus* represents an intermediate between the extinct Passalopalpidae and the extant Passalidae, and probably is more closely related to Passalopalpidae.

Mesoceratocanthus extends the known age of passaloids. Santos *et al.* (2021) report a putative passaloid fossil, *Protopassalus*, from a Brazilian fossil bed dated to the late Aptian (*ca.* 112–114 Ma). However, the placement of *Protopassalus* within the Passalidae is not accepted by a number of passalid researchers (Boucher, 2006; S. Boucher pers. comm.; Jimenez *et al.*, unpublished manuscript). Thus, the revised placement of *Mesoceratocanthus* establishes the earliest occurrence of the passaloid clade. This extended fossil record is accordant with the estimation based on paleobiogeography by Boucher (2006), who suggested the origin of primitive passalids (*i.e.*, passaloids) should be no later than Tithonian (*ca.* 145–150 Ma). The present study demonstrates that the combination of adpression and amber fossils can be used to more comprehensively reconstruct the complex evolutionary history of beetle clades.

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