Palaeoentomology 005 (3): 246–253
https://www.mapress.com/j/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.5.3.7
http://zoobank.org/urn:lsid:zoobank.org:pub:D284C0E1-09BB-4CFE-BDD5-FE73E34EDE4C

Homalenchodes, a new genus of Serropalpini from mid-Cretaceous amber of northern Myanmar (Coleoptera: Tenebrionoidea: Melandryidae)

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Abstract

A new fossil genus and species of the family Melandryidae, *Homalenchodes jarzembowskii* Li, Hsiao, Yoshitomi & Cai **gen. et sp. nov.**, is described and illustrated from the mid-Cretaceous Burmese amber. *Homalenchodes* is likely closely related to the serropalpin genus *Enchode*s LeConte, based on their simple maxillary palps, complete prosternal process, exposed protrochantins, ventrally lobed penultimate metatarsomeres, and absence of transverse rows of bristles or spines along the meso- and metatibiae.

Keywords: Melandryidae, *Enchode*s, fossil, Cretaceous, Burmese amber

Introduction

Melandryidae is a moderately diverse cosmopolitan family, with some 420 described extant species (Nikitsky & Pollock, 2010). Most melandryids inhabit dead wood and feed on wood-destroying fungi in the larval stage (Nikitsky & Pollock, 2010). The systematics of Melandryidae has been quite problematic. Even after the removal of various groups once included in the family (*e.g.*, members of Synchroidae, Pythidae, Stenotrachelidae and Tetratomidae; summarised by Nikitsky & Pollock, 2010), the currently defined Melandryidae is still likely to be non-monophyletic, as suggested by phylogenomic studies (McKenna *et al.*, 2019; Cai *et al.*, 2022). Analyses with denser taxon sampling revealed at least four independent melandryid lineages, represented by Osphyinae, Orchesiini, Serropalpini, and Dircaeini + Hypulini + Melandryini, respectively (Bocak *et al.*, 2014; Gunter *et al.*, 2014).

The majority of melandryid fossils were reported from amber deposits (as listed by Tihelka *et al.*, 2020). Among them, only four monotypic genera have been described from Mesozoic: *Archaeoxylita* Nikitsky from Upper Cretaceous Taimyr amber (Nikitsky, 1997), *Archaeserropalpus* Nikitsky and *Pseudocuphosis* Nikitsky from Upper Cretaceous New Jersey amber (Nikitsky, 2002), and *Longicrusa* Tihelka, Huang & Cai from mid-Cretaceous Burmese amber (Tihelka *et al.*, 2020). In the present study we describe a new melandryid genus from Burmese amber, which adds another piece to the earliest palaeodiversity of this family.

Material and methods

The Burmese amber specimen studied herein (Figs 1–3) originated from amber mines near Noije Bum (26°20′ N, 96°36′ E), Hukawng Valley, Kachin State, northern Myanmar. The type specimen is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery paper of different grit sizes, and finally polished with polishing powder.

Specimens of extant Melandryidae used for comparison are deposited in the Australian National

 Submitted: 14 Jun. 2022; accepted by D. Azar: 17 Jun. 2022; published: 27 Jun. 2022

Insect Collection (ANIC), Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra, Australia, and Ehime University, Matsuyama, Japan.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 561 nm (DPSS 561-10) laser excitation line (Fu *et al*., 2021). Images were stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC, and were further processed in Adobe Photoshop CC to adjust brightness and contrast.

The Melandryidae classification system follows Nikitsky & Pollock (2010), even though it is likely unnatural to some extent.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Superfamily Tenebrionoidea Latreille, 1802
Family Melandryidae Leach, 1815
Subfamily Melandryinae Leach, 1815
Tribe Serropalpini Latreille, 1829

Genus *Homalenchodes* Li, Hsiao, Yoshitomi & Cai gen. nov.

Type species. *Homalenchodes jarzembowskii* **sp. nov.**

Etymology. The generic name is a combination of the Greek "*homalós*", smooth, referring to the absence of longitudinal striae on its elytra, and "*Enchodes*", a presumably closely related genus. The name is feminine in gender.

The generic name *Enchodes* LeConte has been sometimes mistakenly treated as masculine (*e.g*., Jung, 2019). According to Article 30.1.4.4 of ICZN (1999), "a compound genus-group name ending in the suffix -*ites*, -*oides*, -*ides*, -*odes*, or -*istes* is to be treated as masculine unless its author, when establishing the name, … treated it as such by combining it with an adjectival species-group name in another gender form". When establishing genus *Enchodes*, LeConte (1866) added a single previously described species, *Dircaea sericea* Haldeman, citing it as *Enchodes sericea* (Haldeman). Thus, the name should be feminine in gender.

Diagnosis. Body relatively small, strongly elongate. Compound eyes coarsely facetted (Fig. 2A, B). Antennae long, filiform. Maxillary palps simple (Fig. 2A). Pronotum widest posteriorly, with somewhat produced posterior pronotal angles (Fig. 2B). Prosternal process complete, gradually narrowed posteriorly, slightly extending beyond posterior procoxal margin (Fig. 2A). Procoxae narrowly separated (Fig. 2A). Protrochantins well exposed (Fig. 2A). Elytra without longitudinal striae (Fig. 2E). Meso- and metatibiae without transverse rows of bristles or spines (Fig. 2D). Metatibial spurs normal-sized (distinctly shorter than half length of metatarsomere 1) (Fig. 2D). Penultimate tarsomeres ventrally lobed in all three pairs of legs (Figs 2C, 3).

Remarks. *Homalenchodes* shares with Synchroidae a similar elongate habitus, lateral and oval eyes, and transverse head and pronotum. In fact, the adults of Synchroidae have an appearance similar to Melandryidae, but these two families are otherwise readily separable based on larval characters (Crowson, 1966). Nevertheless, synchroids are generally characterised by the long interfacetal setae (absent in *Mallodrya* Horn, although this genus might have been inappropriately placed in Synchroidae and needs to be further evaluated; Hsiao *et al*., 2018), unmargined posterior edge of pronotum (distinctly margined in *Mallodrya*), prosternal process markedly extending beyond procoxae with long oval apex (prosternal process laminate, ending just before the posterior edges of procoxae in *Mallodrya*), and unlobed penultimate tarsomeres (Ślipiński & Lawrence, 2010; Hsiao *et al*., 2018), while *Homalenchodes* has no interfacetal setae, a margined posterior edge of pronotum, a posteriorly gradually narrowed prosternal process with acute apex, slightly extending beyond posterior edges of procoxae, and lobed penultimate tarsomeres. Therefore, here we believe that it is appropriate to place *Homalenchodes* in the (currently non-monophyletic) family Melandryidae.

Homalenchodes jarzembowskii Li, Hsiao, Yoshitomi & Cai sp. nov.

(Figs 1–3)

Material. Holotype, NIGP180475.

Etymology. The species is named in honor of the palaeoentomologist Dr Edmund A. Jarzembowski.

Diagnosis. As for the genus.

Locality and horizon. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Description. Body strongly elongate, about 2.7 mm long, 0.6 mm wide. Surface finely punctate and with fine hairs.

Head well exposed from above. Compound eyes lateral, large, emarginate in front of antennal insertions, coarsely facetted on the surface, without interfacetal setae. Antennal insertions fully concealed from above, widely separated. Subantennal grooves absent. Antennae 11-segmented, long, filiform; antennomere 1 elongate, almost parallel-sided; antennomere 2 short, subquadrate; antennomeres 3–11 elongate, subequal. Clypeus with

FIGURE 1. General habitus of *Homalenchodes jarzembowskii* Li, Hsiao, Yoshitomi & Cai **gen. et sp. nov.**, holotype, NIGP180475, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars = 1 mm.

anterior margin convex. Mandibles bilobed apically. Maxillary palps 4-segmented, simple, not clearly serrate; palpomere 1 small; palpomere 4 possibly securiform. Mentum subtrapezoidal. Submentum relatively smooth, with hairs somewhat denser than other regions.

Pronotum widest posteriorly, with slightly produced posterior pronotal angles; disc without depression medially; posterior edge margined. Notosternal sutures distinct. Prosternum about as long as longitudinal procoxal diameter; prosternal process complete, gradually narrowed posteriorly, slightly extending beyond posterior procoxal margin, apically acute. Procoxal cavities narrowly separated, externally broadly open. Protrochantins well exposed.

Scutellar shield transverse, subtrapezoidal, widest posteriorly; posterior edge slightly rounded, without notch. Elytra long, about 3.1 times as long as width combined, at base almost as wide as pronotum, apically separately rounded; surface without longitudinal striae. Mesocoxal cavities narrowly separated. Metacoxae almost contiguous; coxal plates absent.

Legs slender. Protrochanter small, obliquely attached to profemur, with profemur abutting procoxa. All tibiae with 2 spurs, without transverse rows of bristles or spines. Metatibial spurs normal-sized. Tarsi 5-5-4; penultimate tarsomeres ventrally lobed in all three pairs of legs; metatarsomere 1 long, distinctly longer than metatarsomeres 2–4 combined. Pretarsal claws simple.

Abdomen with five ventrites. Ratio of ventrite lengths along middle: 3.2:2.4:2.1:1.7:2.4. Ventrite 5 apically rounded, without emargination.

FIGURE 2. Details of *Homalenchodes jarzembowskii* Li, Hsiao, Yoshitomi & Cai **gen. et sp. nov.**, holotype, NIGP180475, under confocal microscopy. **A**, Head and prothorax, ventral view. **B**, Head and prothorax, dorsal view. **C**, Abdominal base and fore leg. **D**, Abdominal apex and metatibia, ventral view. **E**, Elytral apex, dorsal view. Abbreviations: an1–9, antennomeres 1–9; el, elytron; ey, compound eye; lbp, labial palp; md, mandible; mstb, mesotibia; msts, mesotarsus; mtc, metacoxa; mttb, metatibia; mtv, metaventrite; mxp, maxillary palp; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; ptcn, protrochantin; pts, protarsus; v1–5, ventrites 1–5. Scale bars: 200 µm.

Discussion

In the *Handbook of Zoology* (Nikitsky & Pollock, 2010), Melandryinae was suggested to be divided into eight tribes. As the detailed diagnoses for tribes have not been published yet, the tribal assignment for *Homalenchodes*

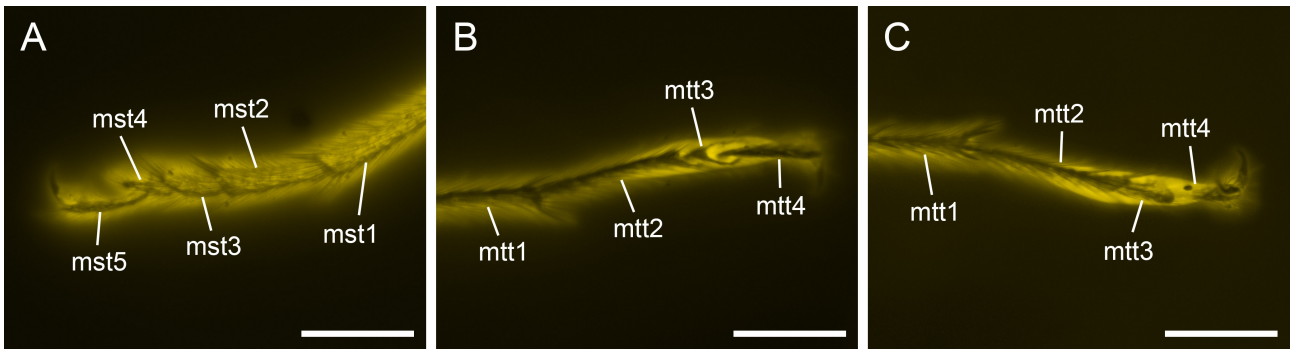

FIGURE 3. Details of *Homalenchodes jarzembowskii* Li, Hsiao, Yoshitomi & Cai **gen. et sp. nov.**, holotype, NIGP180475, under confocal microscopy. **A**, Mesotarsus, lateral view. **B**, Metatarsus, dorsal view. **C**, Metatarsus, ventral view. Abbreviations: mst1–5, mesotarsomeres 1–5; mtt1–4, metatarsomeres 1–4. Scale bars = 100 μm.

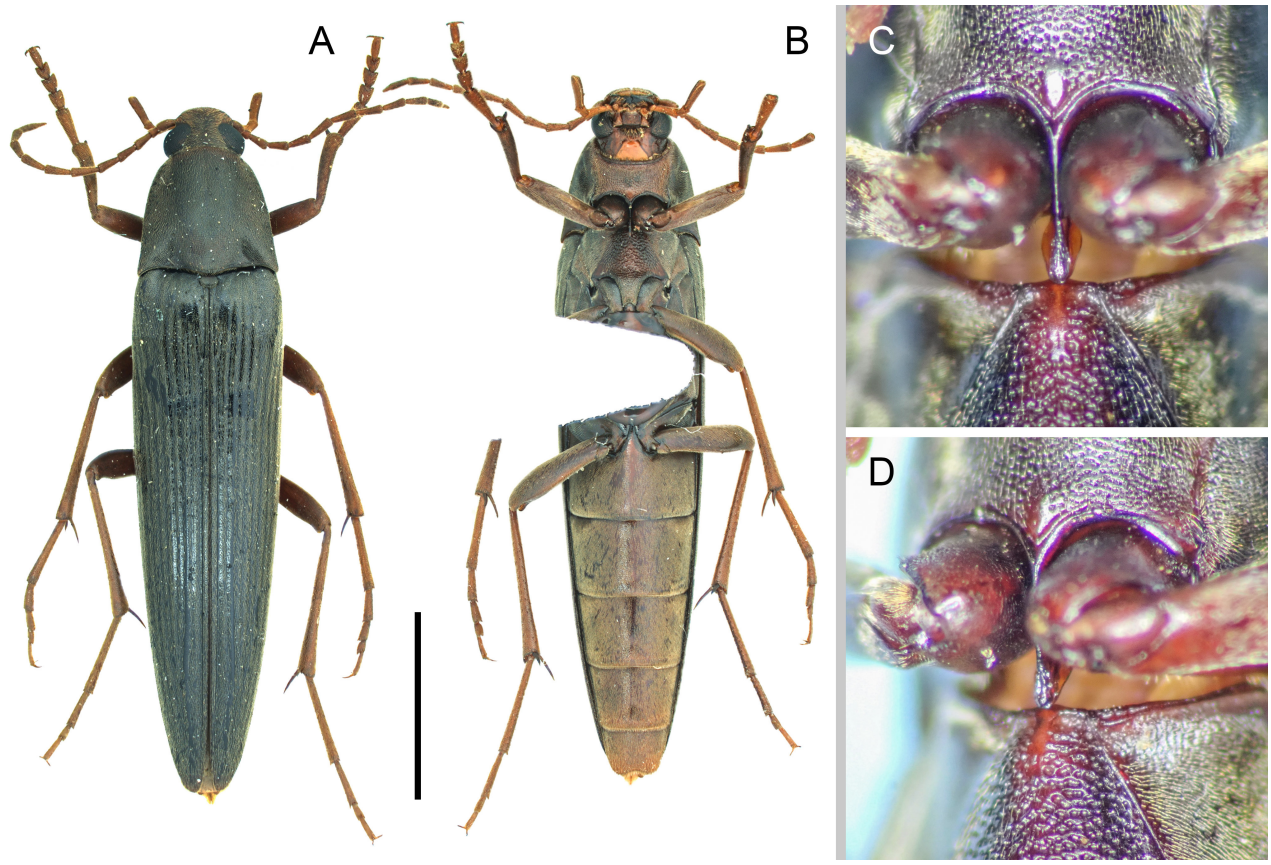

FIGURE 4. Extant *Enchodes crepuscula* (Lewis), deposited in Ehime University. **A**, Habitus, dorsal view. **B**, Habitus, ventral view. **C**–**D**, Prosternal process, ventral view. Scale bar = 4 mm in **A**, **B**.

has to rely partly on the overall habitus. *Homalenchodes* appears to fit best with Serropalpini, based on its strongly elongate body, posteriorly widest pronotum, somewhat produced posterior pronotal angles, strongly filiform antennae, and normal-sized metatibial spurs (Fig. 1).

Within Serropalpini, *Homalenchodes* is especially similar to *Enchodes* (Fig. 4). Both genera have simple maxillary palps (Fig. 2A), exposed protrochantins (Fig. 2A), and ventrally lobed penultimate metatarsomeres (at least in *E. orientalis* Nikitsky; Nikitsky, 1973). More importantly, they both have no transverse rows of bristles or spines along the meso- and metatibiae (Fig. 2D), while all other members of Serropalpini have such transverse bristle rows (Nikitsky & Pollock, 2010). The complete prosternal process and separated procoxae of *Homalenchodes* (Fig. 2A) are not typical for Serropalpini (or Melandryinae in general except for Orchesiini; Nikitsky, 1992; Eom & Park, 2001). Though Nikitsky & Pollock (2010) mentioned that the serropalpin genus *Ctenoplectron* Redtenbacher has complete prosternal process, our observation suggests that the prosternal process of *Ctenoplectron* does not reach the posterior procoxal edge (Fig. 5H). Interestingly, *Enchodes*

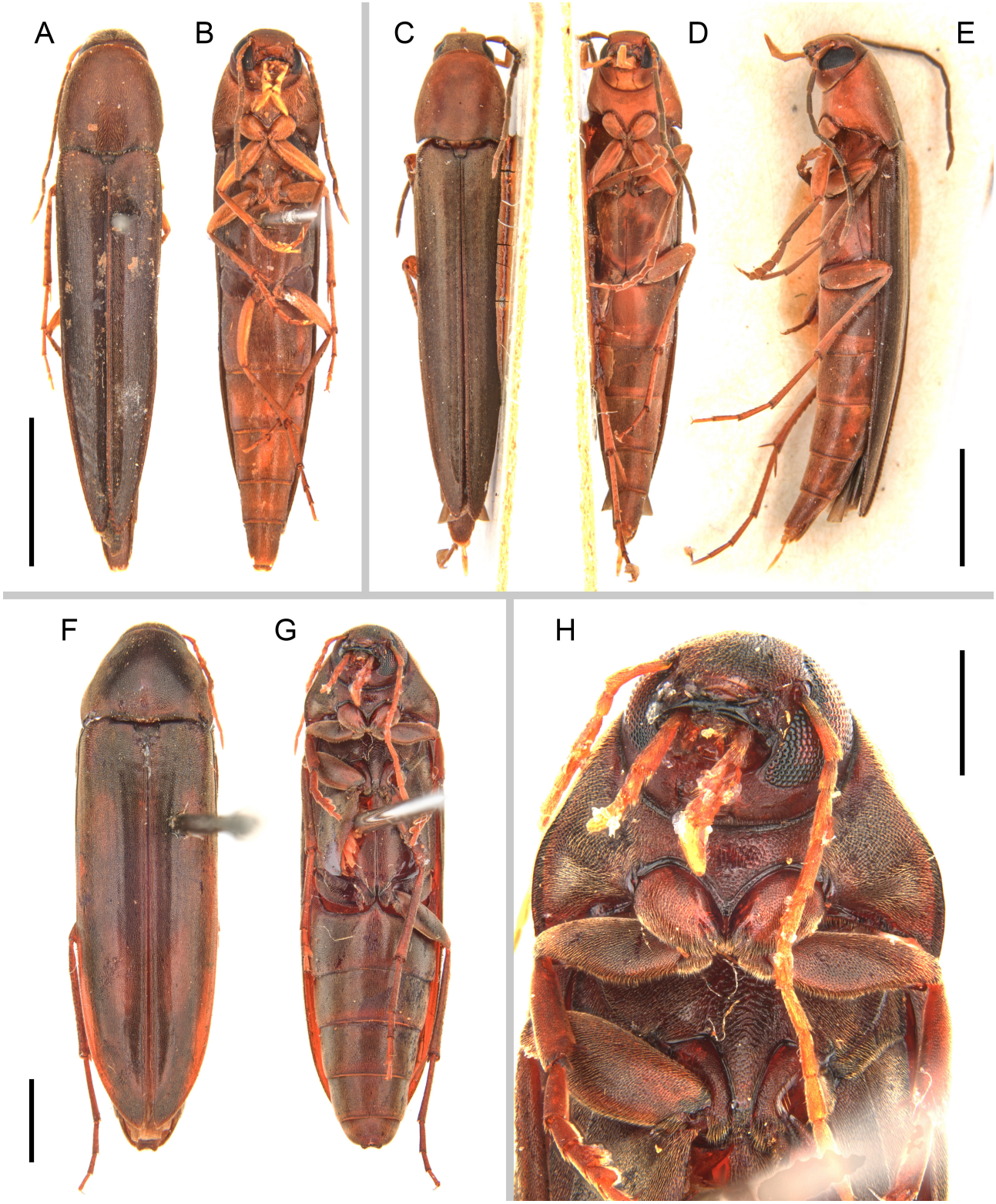

FIGURE 5. Extant *Ctenoplectron* spp., deposited in Australian National Insect Collection. **A**–**E**, *Ctenoplectron agile* Champion, dorsal (**A**, **C**), ventral (**B**, **D**), and lateral (**E**) views. **F**–**H**, *Ctenoplectron rufobrunneum* Lea, dorsal (**F**) and ventral (**G**, **H**) views. Scale bars = 2 mm in **A**–**G**, 1 mm in **H**.

shares with *Homalenchodes* the complete prosternal process surpassing posterior edge of procoxae. Although *Enchodes* was sometimes described as having contiguous procoxae, its procoxal cavities are actually separated by a very narrow prosternal process extending beyond the hind margin of coxae (Fig. 4C, D; Nomura, 1959; Nikitsky, 1973; Jung, 2019). Nevertheless, the prosternal process of *Homalenchodes* is gradually narrowed posteriorly, while in *Enchodes* it is narrowed abruptly before the midpoint of procoxae. *Homalenchodes* differs additionally from

Enchodes in the distinctly smaller size, more coarsely facetted compound eyes (Fig. 2A, B), and elytra without clear longitudinal striae (Fig. 2E).

It is noteworthy that based on his unpublished cladistic analyses, Nikitsky (*in* Nikitsky & Pollock, 2010) suggested that *Enchodes* has characters intermediate between Dircaeini and Serropalpini, and may deserve the state of an independent tribe. However, in the molecular analyses, *Enchodes* was grouped together with *Mikadonius* Lewis (another genus in Serropalpini), but not closely related to Dircaeini (Bocak *et al*., 2014; Gunter *et al*., 2014). Thus, in the present paper we believe that it is reasonable to placed *Homalenchodes* in Serropalpini, together with *Enchodes*.

Data availability

The original confocal data are available in Zenodo repository (https://doi.org/10.5281/zenodo.6657364).

Acknowledgements

We are grateful to Rong Huang for technical help with confocal imaging, and Alfred Newton for help with the zoological nomenclature. Liang Lü and Zi-Wei Yin provided helpful comments on the manuscript. Financial support was provided by the Second Tibetan Plateau Scientific Expedition and Research project (2019QZKK0706), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), and the National Natural Science Foundation of China (41688103).

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