

SHORT COMMUNICATION

## *Trihelota*, a new and unusual helotid beetle genus from mid-Cretaceous Burmese amber (Coleoptera: Helotidae)

Erik TIHELKA<sup>1)</sup>, Diying HUANG<sup>2)</sup> & Chenyang CAI<sup>1,2,\*</sup>

<sup>1)</sup>School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK

<sup>2)</sup>State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

\*) corresponding author, e-mail: cycai@nigpas.ac.cn

Accepted:  
16<sup>th</sup> September 2020

Published online:  
23<sup>rd</sup> September 2020

**Abstract.** A new genus belonging to the cucujoid family Helotidae, *Trihelota* gen. nov., is described from mid-Cretaceous (ca. 99 million years old) amber from Kachin State, northern Myanmar, containing a single species *T. fulvata* sp. nov. The minute fossil was documented using fluorescence microscopy and X-ray microtomography to reveal fine morphological details. *Trihelota* is characterised by its transverse head, antennal club about 1.5 times longer than wide, pronotum almost parallel-sided, and elytra not costate. Notably, each elytron possesses three coloured spots, a character unique within Helotidae. The new genus considerably expands the known morphological disparity of Cretaceous helotids. A key to extinct and extant genera of the family Helotidae is provided along with a checklist of fossil species.

**Key words.** Coleoptera, Cucujoidea, Helotidae, Cretaceous, Mesozoic, fossil, Burmese amber

**Zoobank:** <http://zoobank.org/urn:lsid:zoobank.org:pub:095E50C7-89F9-46E3-9EDB-14B9E0A30EC8>

© 2020 The Authors. This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Licence.

### Introduction

The family Helotidae is a small group of cucujoid beetles including approximately 100 extant species in five genera (WEGRZYNOWICZ 2000). The beetles are mainly distributed in warm regions of the Old World (LEE 2007, 2008, 2009a, b, 2010; LAWRENCE et al. 2010). The adults and larvae are attracted to fruits and tree sap, the larvae bore in wood to pupate (LEE et al. 2007). The family was regarded as one of the earliest diverging members of the traditionally understood superfamily Cucujoidea (CROWSON 1955, LAWRENCE & NEWTON 1995). LESCHEN et al. (2005) recovered the family as an early diverging member from their “basal Cucujoidea”. Recent molecular studies narrowed down the concept of Cucujoidea and transferred the families of the former cucujoid cerylonid lineage to the superfamily Coccinelloidea (ROBERTSON et al. 2015). Helotidae were confirmed as members of Cucujoidea *s. str.* and supported as a sister group to Erotylidae and Boganiidae or as sister to a clade including Protocucujidae and Sphindidae (BOCÁK et al. 2014; MCKENNA et al. 2015, 2019; ZHANG et al. 2018).

The fossil record of Helotidae is sparse (Tab. 1). The genus *Helota* MacLeay, 1825 is known from the Cenozoic

of China (LIN 1977, ZHANG 1989, ZHANG et al. 1994, WEGRZYNOWICZ 2007). The genus *Laodiscis* Lin, 1977 described from the Palaeocene of China was apparently placed into the family by accident and has been formally removed by LIU et al. (2019) and treated as family *incertae sedis*. The extant genus *Metahelotella* Kirejtshuk, 2000 is known from one species from Burmese (Kachin) amber mined in northern Myanmar, alongside the fossil genus *Burmahelota* Liu, Ślipiński, Ren & Pang, 2019 described from the same deposit. The oldest member of the family is the recently described *Palaeohelota parva* Liu, Ślipiński, Ren & Pang, 2019 from the Lower Cretaceous Yixian Formation of northeastern China (LIU et al. 2019). Here we describe a third helotid beetle from mid-Cretaceous Burmese amber, representing a new genus that documents the early diversity of the family in the Mesozoic.

### Materials and methods

The amber piece studied herein originates from mines near the summit of the Noije Bum hill (26°20'N 96°36'E) in the Hukawng Valley, Kachin State, northern Myanmar (CRUICKSHANK & KO 2003). In terms of the number of



Table 1. Overview of the fossil record of Helotidae. Minimum absolute ages in million years (Ma) are indicated in brackets.

Species	Deposit	Age
<b>Mesozoic: Cretaceous</b>		
<i>Palaeohelota parva</i> Liu, Ślipiński, Ren & Pang, 2019	Yixian Formation in Huangbanjigou, China	Barremian–Aptian (122.2 Ma)
<i>Burmahelota pengweii</i> Liu, Ślipiński, Ren & Pang, 2019	Burmese amber, Kachin State, Myanmar	Albian–Cenomanian (99 Ma)
<i>Metahelotella monochromata</i> Liu, Ślipiński, Ren & Pang, 2019	Burmese amber, Kachin State, Myanmar	Albian–Cenomanian (99 Ma)
<i>Trihelota fulvata</i> Tihelka, Huang & Cai <b>gen. &amp; sp. nov.</b>	Burmese amber, Kachin State, Myanmar	Albian–Cenomanian (99 Ma)
<b>Cenozoic: Miocene</b>		
<i>Helota senilis</i> Zhang, Sun & Zhang, 1994	Shanwang, Linqu County, China	Burdigalian (17.5 Ma)
<i>Helota palmus</i> Zhang, 1989	Shanwang, Linqu County, China	Burdigalian (17.5 Ma)
<i>Helota zhangii</i> Wegrzynowicz, 2007	Shanwang, Linqu County, China	Burdigalian (17.5 Ma)

described taxa, their diversity, and quality of preservation, Burmese (Kachin) amber represents one of the most important Cretaceous fossil insect assemblages (GRIMALDI et al. 2002; ROSS 2019, 2020; CAI et al. 2020; YIN 2020). The deposit has been conservatively dated using zircons to  $98.8 \pm 0.6$  Ma (SHI et al. 2012, MAO et al. 2018). A late Albian to early Cenomanian age of Burmese amber is moreover congruent with palaeontological findings (ZHERIKHIN & ROSS 2000, GRIMALDI et al. 2002, YU et al. 2019). The fossil resin most likely originated from dawn redwood (*Metasequoia*) trees; the palaeoenvironment has been reconstructed as a near-seashore tropical rainforest (GRIMALDI & ROSS 2017). The amber from Hukawng Valley is distinct from ambers collected in other parts of Myanmar, such as the Late Cretaceous deposit near Tilin (ZHENG et al. 2018).

Photographs under normal reflected light were taken with a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5 $\times$ ), and with an attached Canon MT-24EX twin flash. Epifluorescence photomicrographs were taken using a Zeiss Axio Imager 2 microscope, which is equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine. Photomicrographs with a green background were taken under the eGFP mode (Zeiss Filter Set 10; excitation/emission: 450–490/515–565 nm). Extended depth of field images were then digitally compiled using Zerene Stacker 1.04 software.

Due to the small size and peculiar nature of preservation of the fossil that renders its ventral side difficult to observe, high-resolution X-ray microtomography (micro-CT) was used to observe important morphological characters. The specimen was scanned using Zeiss Xradia 520 versa at the micro-CT laboratory of the Nanjing Institute of Geology and Palaeontology, CAS in Nanjing, China. A CCD-based 4 $\times$  objective was used, providing isotropic voxel sizes of 3.74  $\mu$ m with the help of geometric magnification. Throughout the course of the scanning, the acceleration voltage for the X-ray source was 40 kV. To improve the signal-to-noise ratio, 2,601 projections over 360 $^\circ$  were collected, the exposure time for each projection was 4 s. The tomographic data were analysed using Avizo software (version 2019.1).

The type specimen is deposited in the amber collection of the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

## Systematic Entomology

Order Coleoptera Linnaeus, 1758  
 Superfamily Cucujoidea Latreille, 1802  
 Family Helotidae Chapuis, 1876

### *Trihelota* gen. nov.

(Figs 1–4)

**Type species.** *Trihelota fulvata* sp. nov., here designated.

**Diagnosis.** Head transverse. Antennal club approximately 1.5 times longer than wide. Pronotum almost parallel-sided, broadest medially, not distinctly narrowing anteriorly, 1.1 times longer than wide, basal pronotal margin distinctly bisinuate. Pronotal disc with a smooth surface, with irregularly scattered punctation surrounding the centre of the disc. Elytra smooth, lacking elevated costae, elytral striae not punctate, incomplete, and faintly impressed. Each elytron with three coloured spots.

**Etymology.** The generic epithet is a combination of the Latin prefix *tri-*, referring to the three characteristic elytral spots, and *Helota*, the type genus of the family. Gender feminine.

### *Trihelota fulvata* sp. nov.

**Type material.** HOLOTYPE (NIGP173378): a well-preserved specimen of indeterminate sex; late Albian to early Cenomanian Burmese (Kachin) amber, Hukawng Valley, northern Myanmar.

**Diagnosis.** As for the genus, with additional characters: body length 3.07 mm, antennomeres 9–11 of subequal length, lateral margin of each elytron apically with 7 stout setae and 5 weak incisions.

**Description.** Body distinctly elongate, 3.5 times longer than wide, approximately parallel-sided, with dispersed deep punctures dorsally, subglabrous. Body length 3.07 mm from clypeus to elytral apex, 0.87 wide across the broadest point of the elytra. Body uniformly dark brown to black, appendages brown, elytra with a metallic violet hue (Figs 1, 2).

Head transverse, 0.5 mm long, 1.4 times wider than long, broadest across the eyes. Frontoclypeal suture absent. Clypeus broadly rounded apically. Mandibles broad, strongly curved. Terminal maxillary palpomere fusiform and elongate, broadest medially (Fig. 3A). Antennal insertions dorsally concealed, located anteriorly of eyes. Antenna 11-segmented with distinct and compact 3-segmented club approximately 1.5 times longer than

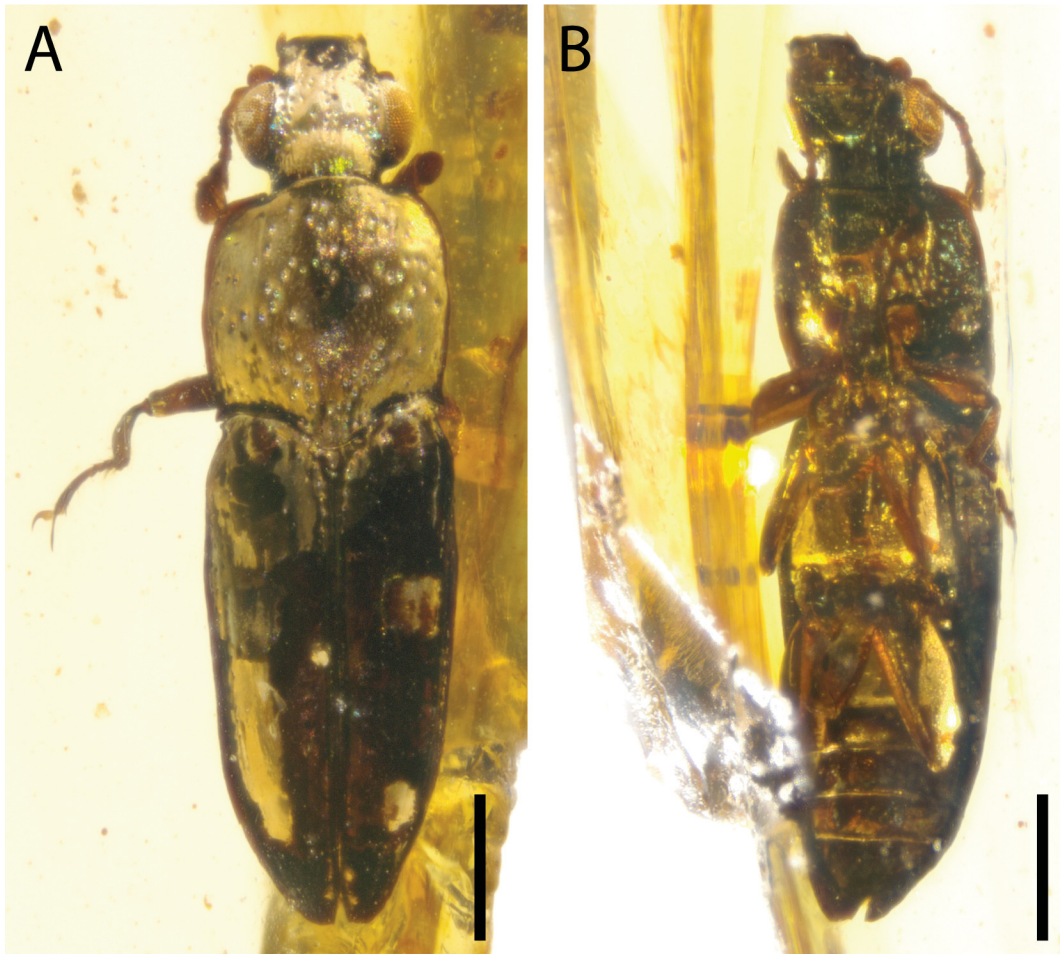


Fig. 1. Habitus of *Trihelota fulvata* gen. & sp. nov. (NIGP173378) under normal reflected light. A – dorsal view; B – ventral view. Scale bars: 500 µm.

wide, reaching to the anterior quarter of the pronotum, sparsely setose (Figs 3A, 4D). Antennomere 1 enlarged and globular, antennomere 2 1.2 times longer than the preceding segment and about as half as wide, antennomere 3 as wide as the preceding segment, 0.6 times as long; antennomere 4 0.8 times the length of the preceding segment; antennomeres 5–8 gradually lengthening apically, antennomeres 9–11 of subequal length, forming a compact club with dense short setae, broadest at antennomere 10, apex of antennomere 11 broadly rounded. Eyes large and hemispherical, distinctly protruding dorsally and laterally. Frons with prominent punctures, denser along the sides and the midline. Vertex with smaller but more densely packed punctures. Ventral side of head with short subantennal grooves not extending beyond the eyes.

Pronotum 0.94 mm long, 1.1 times longer than wide, longest medially, approximately parallel-sided, broader than the head. Anterior angles smoothly rounded. Lateral pronotal carina with distinct bead. Pronotal disc moderately convex and glabrous, with deep punctures separated by between one to seven times their width scattered around the medial area of the disc. Posterior margin deeply bisinuate, medial posterior projection of pronotum deeply rounded. Posterior angles strongly acute and projecting, pointing laterally at approximately 45° from the body axis (Fig. 3C: pa). Scutellum minute,

subtriangular, broadest in anterior quarter. Prosternum flat in lateral view, prosternal area in front of procoxae 2.9 times longer than maximum procoxal diameter. Procoxal cavities oval, separated by slightly more than their width. Prosternal process wide, apically truncate, reaching anterior mesoventral process. Anterior prosternal process broadly rounded. Mesocoxae longitudinally oval, separated by over three times their maximum width. Metaventricle medially depressed. Metacoxae horizontally oriented, not extending to meet elytra, longitudinally oval, widely separated.

Legs elongate and slender. Trochanterofemoral joint strongly oblique. Femora widened, ventrally grooved for the reception of tibiae. Tibiae slender, equally wide throughout, protibiae strongly bent in holotype, terminating with a pair of small spurs and a small brush of setae. Tarsal formula 5-5-5, not lobed, with elongate setae ventrally (Fig. 3B). Ultimate tarsomere longer than the preceding four segments. Claws simple, not toothed. Empodium well-developed, bisetose.

Elytra 2.06 mm long, 2.0 times longer than their combined width, broadest in the anterior third but approximately parallel-sided, gradually narrowing in the posterior quarter, with a violet metallic hue under some angles. Humeral projection short and pointed, directed laterally. Elytral surface glabrous, lacking costae, without punctate



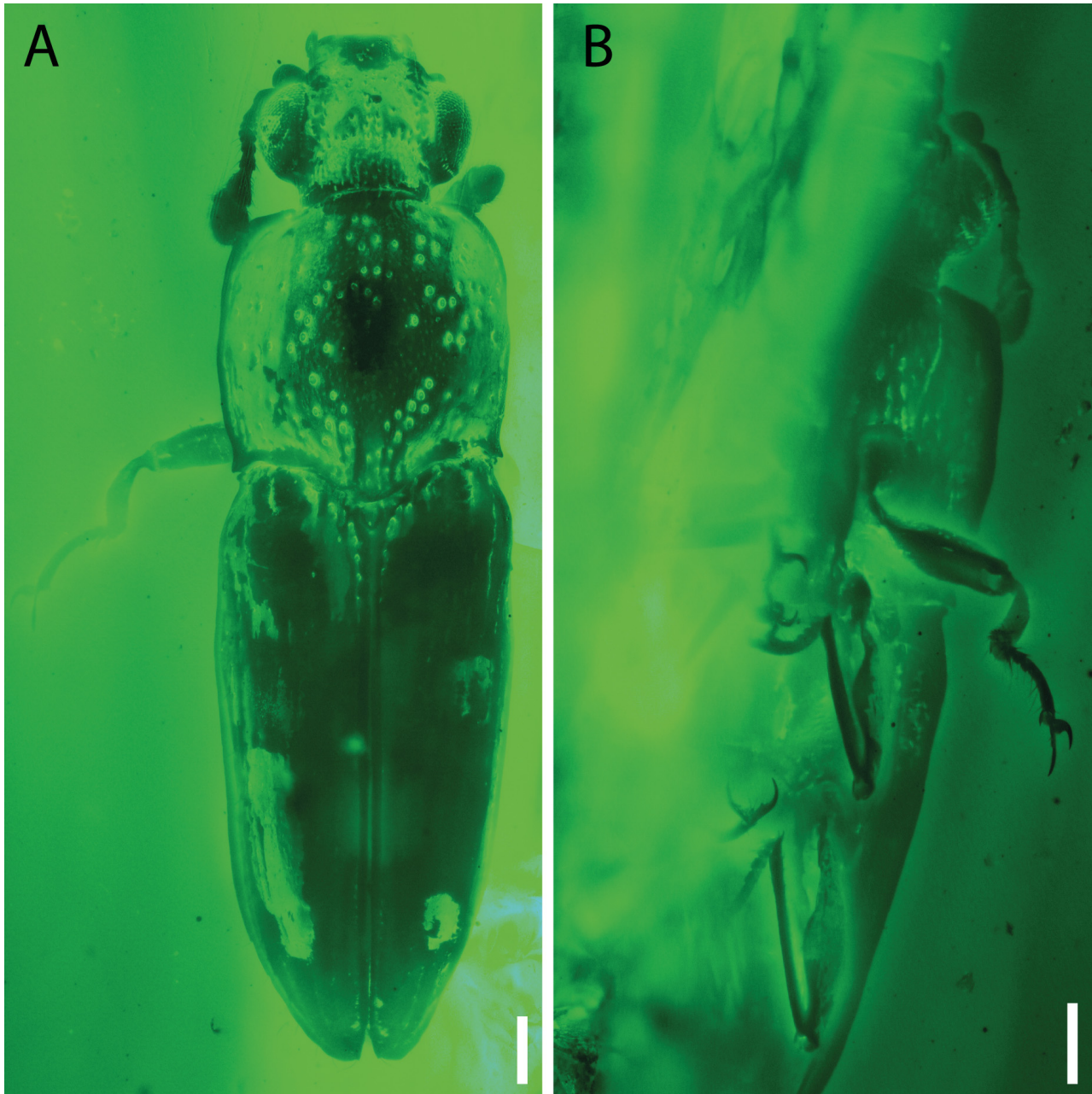


Fig. 2. Habitus of *Trihelota fulvata* gen. & sp. nov. (NIGP173378) under green epifluorescence. A – dorsal view; B – ventral view. Scale bars: 200  $\mu$ m.

striae. Elytral striae faintly impressed, incomplete. Each elytron with three oval, glabrous and apparently coloured spots, anteriormost spot smallest (Fig. 3C: es1–3). Apical third of lateral margin with 7 stout setae associated with five angular to minute indentations (Fig. 3D: ei1–5). Elytral apices with an apical indentation with a stout seta (Fig. 3D: ei5). Epipleura almost complete, widest basally (Fig. 4C).

Abdomen with five ventrites. Ventrites glabrous, with fine macrosculpture. Ratio of ventrite lengths (in mm): 0.20 : 0.09 : 0.10 : 0.10 : 0.42. Grooves for the reception of legs absent.

**Etymology.** Latin adjective *fulvus* meaning amber-coloured, in reference to the golden-yellow appearance of elytral spots in extant Helotidae and the colour of the amber piece in which the holotype is preserved.

### Key to the genera of Helotidae

This is a revised and expanded version of the key of KIREJTSHUK (2000), who conducted a generic revision of Helotidae. The key includes both extant and fossil genera, the latter of which are denoted with a dagger (†).

- 1 Each elytron with two or three smooth oval spots with a distinctly reduced punctation that are of a different colour from the rest of the elytra. .... 2
  - Elytral surface without coloured smooth oval spots, at most with one isolated spot of the same colour as the rest of the elytra always located in the middle. ...
- ..... 5
- 2 Each elytron with two smooth oval spots. .... 3
  - Each elytron with three smooth oval spots. ....
- ..... † *Trihelota* Tihelka, Huang & Cai **gen. nov.**



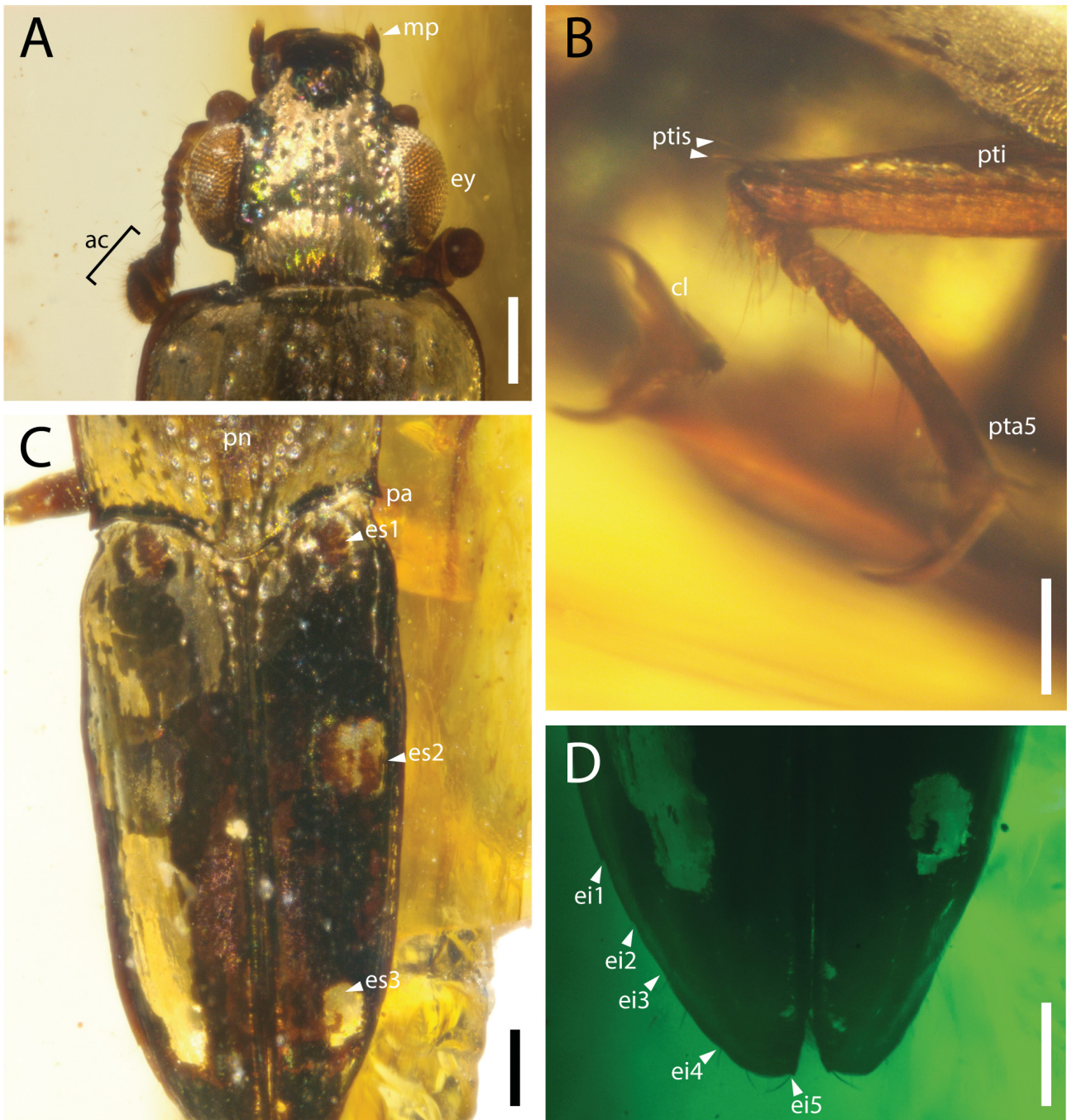


Fig. 3. Morphological details of *Trihelota fulvata* gen. & sp. nov. (NIGP173378) under normal reflected light and green epifluorescence. A – head in dorsal view under normal reflected light; B – prothoracic leg under normal reflected light; C – elytra under normal reflected light; D – elytral apex under green epifluorescence. Abbreviations: ac – antennal club; cl – claw; ei1–5 – elytral indentations 1–5; es1–3 – elytral spots 1–3; ey – eye; mp – apical maxillary palpomere; pa – posterior pronotal angle; pn – pronotum; pta5 – protarsomere 5; pti – protibia; ptis – protibial spurs. Scale bars: 100  $\mu$ m (B), 200  $\mu$ m (A, C, D).

3 Elytra with punctate striae. .... 4  
 – Elytral disc without punctate striae. ....  
 ..... †*Burmahelota* Liu, Ślipiński, Ren & Pang, 2019  
 4 Pronotum rugose, irregularly and coarsely punctate,  
 with raised patches. Elytra tuberculate or often sub-  
 costate. Head more elongate, convex anteriorly. An-  
 tennal club not more than 1.5 times as long as wide.  
 Males with slightly more curved protibiae than fem-  
 ales, or without sexually dimorphic protibiae, except for  
 frequently more raised brushes of long setae at tibial  
 apices. .... *Helota* MacLeay, 1825

– Pronotum more finely and evenly punctured, without  
 raised patches. Elytra never tuberculate or subcostate.  
 Head usually as long as wide, subtruncate anteriorly.  
 Antennal club usually about as wide as long. Males of  
 many species with rather curved protibiae. ....  
 .... *Neohelota* Ohta, 1929  
 5 Elytra costate or with elevated elytral intervals spaces. .. 6  
 – Elytra without costae. .... 7  
 6 Body size greater than 13 mm, elytra with distinct rows  
 of punctures between costae. ....  
 .... *Afrohelotina* Kirejtshuk, 2000



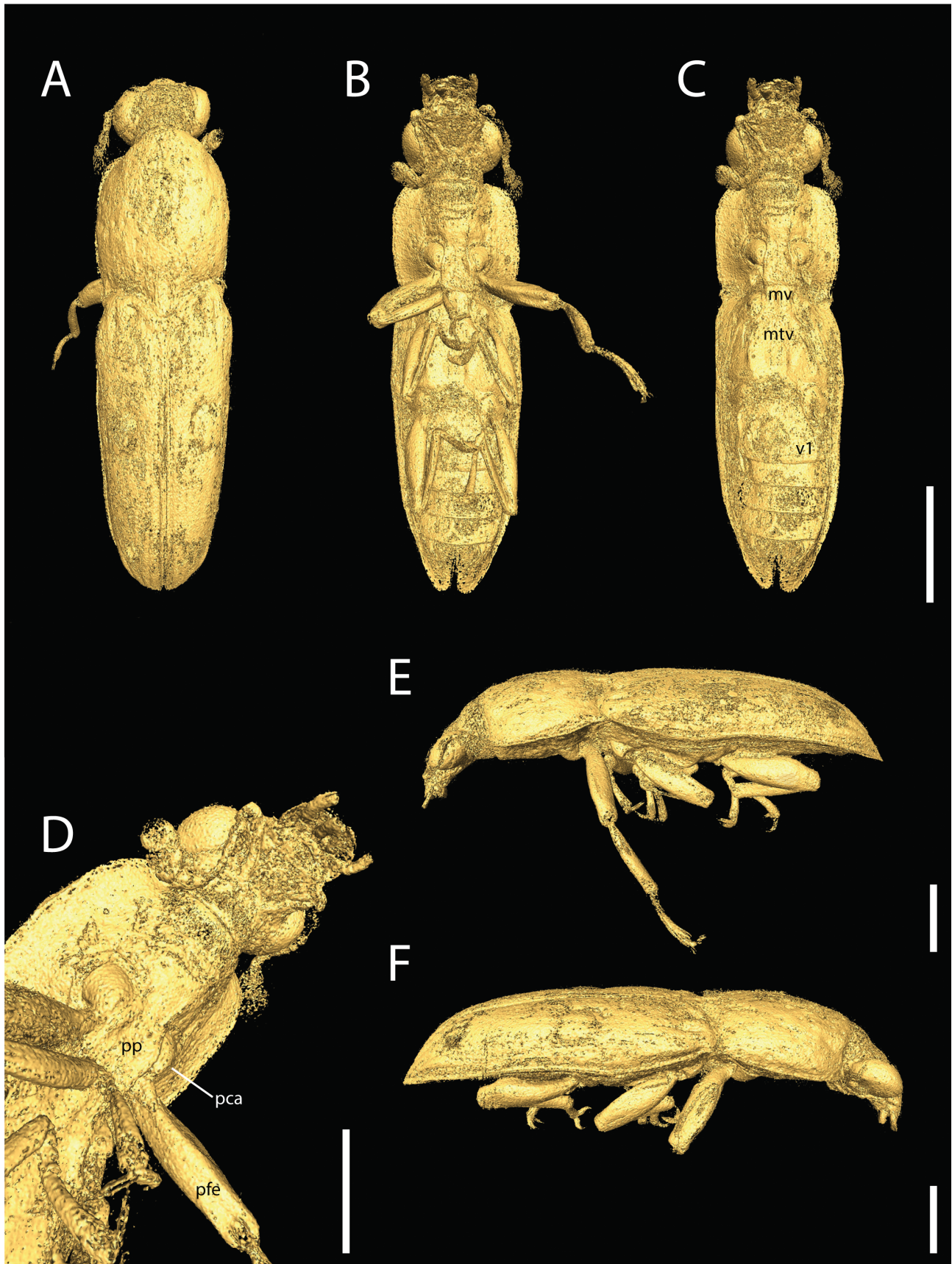


Fig. 4. Micro-CT reconstruction of *Trihelota fulvata* gen. & sp. nov. (NIGP173378). A – dorsal view; B – ventral view; C – ventral view with legs removed for clarity; D – head and thorax in ventral view; E–F – lateral view. Abbreviations: mvt – metaventrite; mv – mesoventrite; pca – procoxa; pfe – profemur; pp – prosternal process; v1 – ventrite 1. Scale bars: 500  $\mu$ m.



- Body size smaller than 5 mm, elytra without distinct rows of punctures between costae. ....  
..... †*Palaeohelota* Liu, Ślipiński, Ren & Pang, 2019
- 7 Head distinctly transverse. Pronotum with a deeply bisinuate base. Antennal club generally about twice as long as wide. Male protibiae usually more curved than in females. .... *Metahelotella* Kirejtshuk, 2000
- Head more elongate. Pronotum with a subtruncate base with four rather weak situations. Antennal club not more than 1.5 times as long as wide. Protibiae not sexually dimorphic. ... *Strophohelota* Kirejtshuk, 2000

### Discussion and conclusion

The new species can be unambiguously assigned to Helotidae on the basis of its elongate body, the large and distinctly protruding eyes, the subtrapezoid frontoclypeus, 11-segmented antennae with a distinct compact and 3-segmented antennal club, pronotum with a bisinuate posterior margin, and metacoxal cavities widely separated (KIREJTSHUK 2000, LAWRENCE et al. 2010, LIU et al. 2019). Besides these basic habitus characters, the fossil is also excluded from the remaining cucujoid families as well as from all families in Cleroidea and Coccinelloidea by the metacoxae not meeting the edges of elytral epipleura, metaventrite distinctly not as long as prothorax and mesoventrite, and metaventrite with a complete transverse suture (LESCHEN et al. 2005).

In common with the genera *Helota*, *Neohelota* and the extinct *Burmahelota*, *Trihelota* gen. nov. possesses apparently coloured spots on the elytra (KIREJTSHUK 2000, LAWRENCE et al. 2010, LIU et al. 2019). However, unlike in the aforementioned genera, *Trihelota* gen. nov. has three spots on each elytron, a potential apomorphy of the genus. The pronotum slightly longer than wide and broadest medially is another unusual character within Helotidae and potentially apomorphic (LAWRENCE et al. 2010). The transverse head, shape of pronotum and lack of elytral costae strongly resemble the Oriental genus *Metahelotella*. The new genus is however differentiated by the distinctly shorter antennal club (twice long as wide in *Metahelotella*), and the absence of punctate elytral striae (LEE 2009b).

Assessing the precise systematic position of *Trihelota* gen. nov. will only become possible after a detailed phylogenetic study of extant Helotidae that will rigorously test the monophyly of the currently recognised genera. Nonetheless, the new fossil genus provides further evidence that the family Helotidae diversified before the mid-Cretaceous and gives valuable information about the early morphological diversity of the family. *Trihelota fulvata* gen. & sp. nov. confirms that both genera with and without coloured spots on the elytra were present during the Cretaceous (LIU et al. 2019) and will be useful for calibrating the evolutionary tree of Cucujoidea. The adaptive value of the distinctly spotted elytra of helotids remains poorly understood. They have been reported to fluoresce in live beetles (KIREJTSHUK 2000). Similar patterns are present in some other early diverging cucu-

joids such as Erotylidae which possess defensive glands (DRILLING et al. 2010), suggesting that the role of this colouration may be aposematic or mimetic. Regardless of its true function, the Burmese amber genera *Burmahelota* and *Trihelota* suggest that this potential adaptation and associated mode of life originated by the mid-Cretaceous.

### Acknowledgments

We are grateful to Dr. Yan Fang and Ms. Su-Ping Wu for technical help. We thank Richard Leschen, an anonymous reviewer and the manuscript editor Martin Fikáček for their valuable comments. This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences [XDB26000000 and XDB18000000]; the National Natural Science Foundation of China [41688103 and 41672011]; and the Second Tibetan Plateau Scientific Expedition and Research [2019QZKK0706].

### Digitally archived data

High resolution tomographic reconstructions and raw micro-CT data were uploaded to MendeleyData archive (data.mendeley.com) and are available from <http://dx.doi.org/10.17632/8532xrbkhhk.1>

### References

- BOCÁK L., BARTON C., CRAMPTON-PLATT A., CHESTERS D., AHRENS D. & VOGLER A. P. 2014: Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology* **39**: 97–110.
- CAI C., TIHELKA E., PAN Y., YIN Z., JIANG R., XIA F. & HUANG D. 2020. Structural colours in diverse Mesozoic insects. *Proceedings of the Royal Society B* **287**(1930) (20200301): 1–7.
- CROWSON R. A. 1955: *The Natural Classification of the Coleoptera*. N. Lloyd, London, 187 pp.
- CRUICKSHANK R. D. & KO K. 2003: Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* **21**: 441–455.
- DRILLING K., DETTNER K. & KLASS K. D. 2010: Morphology of the pronotal compound glands in *Tritoma bipustulata* (Coleoptera: Erotylidae). *Organisms Diversity and Evolution* **10**(3): 205–214.
- GRIMALDI D. A., ENGEL M. S. & NASCIMBENE P. C. 2002: Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* **3361**: 1–71.
- GRIMALDI D. & ROSS A. J. 2017: Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. Pp. 287–342. In: FRASER N. C. & SUES H.-D. (eds): *Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land*. Dunedin Academic Press, Edinburgh, 450 pp.
- KIREJTSHUK A. G. 2000: On origin and early evolution of the superfamily Cucujoidea (Coleoptera, Polyphaga). Comments on the family Helotidae. *Kharkov Entomological Society Gazette* **8**(1): 8–38.
- LAWRENCE J. F. & NEWTON A. F. 1995: Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779–1006. In: PAKALUK J. & ŚLIPIŃSKI A. (eds): *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy Crowson*. Museum i Instytut Zoologii, Warszawa, 1092 pp.
- LAWRENCE J. F., ŚLIPIŃSKIA. & LEE C. F. 2010: Helotidae Reitter, 1876/Chapuis, 1876. Pp. 292–295. In: LESCHEN R. A. B., BEUTEL R. G. & LAWRENCE J. F. (eds): *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. Walter de Gruyter, Berlin/New York, xiii + 786 pp.

- LEE C. F. 2007: Revision of family Helotidae (Coleoptera: Cucujoidea): I. Gemmata group of genus *Helota*. *Annals of the Entomological Society of America* **100**(5): 623–639.
- LEE C. F. 2008: Revision of the family Helotidae (Coleoptera: Cucujoidea) II: the vigorsii group of the genus *Helota*. *Annals of the Entomological Society of America* **101**(4): 722–742.
- LEE C. F. 2009a: Revision of the family Helotidae (Coleoptera: Cucujoidea) III: The thibetana group and a checklist of *Helota* MacLeay species. *Annals of the Entomological Society of America* **102**(1): 48–59.
- LEE C. F. 2009b: Revision of the Family Helotidae (Coleoptera: Cucujoidea): IV. The Genus *Metahelotella*. *Annals of the Entomological Society of America* **102**(5): 785–796.
- LEE C. F. 2010: Revision of the family Helotidae (Coleoptera: Cucujoidea): V. species group classification of the genus *Neohelota* Ohta and revisions of *N. laevigata* and *N. helleri* species groups. *Annals of the Entomological Society of America* **103**(4): 500–510.
- LESCHEN R. A., LAWRENCE J. F. & ŚLIPINIŃSKI S. A. 2005: Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. *Invertebrate Systematics* **19**(1): 17–73.
- LIN Q. B. 1977: Fossil insects from Yunnan. Pp. 373–382. In: Nanjing Institute of Geology and Palaeontology (ed.): *Mesozoic Fossils from Yunnan, China (Fasc. II)*. Science Press, Beijing, 536 pp (in Chinese).
- LIU Z., ŚLIPINIŃSKI A., REN D. & PANG H. 2019: The first Mesozoic Helotidae (Coleoptera: Cucujoidea). *Cretaceous Research* **96**: 113–119.
- MAO Y. Y., LIANG K., SU Y., LI J. G., RAO X., ZHANG H., XIA F., FU Y., CAI C. & HUANG D. 2018: Various amber ground marine animals on Burmese amber with discussions on its age. *Palaeoentomology* **1**: 91–103.
- McKENNA D. D., WILD A. L., KANDA K., BELLAMY C. L., BEUTEL R. G., CATERINO M. S., FARNUM C. W., HAWKS D. C., IVIE M. A., JAMESON M. L., LESCHEN R. A. B., MARVALDI A. E., McHUGH J. V., NEWTON A. F., ROBERTSON J. A., THAYER M. K., WHITING M. F., LAWRENCE J. F., ŚLIPINIŃSKI A., MADDISON D. R. & FARRELL B. D. 2015: The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* **40**: 835–880.
- McKENNA D. D., SHIN S., AHRENS D., BALKE M., BEZA-BEZA C., CLARKE D. J., DONATHA., ESCALONA H. E., FRIEDRICH F., LETSCH H., LIU S., MADDISON D., MAYER C., MISOF B., MURIN P. J., NIEHUIS O., PETERS R. S., PODSIADŁOWSKI L., POHL H., SCULLY E. D., YAN E. V., ZHOU X., ŚLIPINIŃSKI A. & BEUTEL R. G. 2019: The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences* **116**: 24729–24737.
- ROBERTSON J. A., ŚLIPINIŃSKI A., MOULTON M., SHOCKLEY F. W., GIORGI A., LORD N. P., McKENNA D. D., TOMASZEWSKA W., FORRESTER J., MILLER K. B., WHITING M. F. & McHUGH J. V. 2015: Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology* **40**: 745–778.
- ROSS A. J. 2019: Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology* **2**: 22–84.
- ROSS A. J. 2020: Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019. *Palaeoentomology* **3**: 103–118.
- SHI G., GRIMALDI D. A., HARLOW G. E., WANG J., WANG J., WANG M., LEI W., LI Q. & LI X. 2012: Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* **37**: 155–163.
- WĘGRZYŃCZAK P. 2000: Catalogue of the Helotidae (Coleoptera: Cucujoidea). *Zoologische Mededelingen* **73**: 391–411.
- WĘGRZYŃCZAK P. 2007: Systematic position of the genus *Tarrodacne* Zhang, 1989 (Coleoptera: Helotidae non Erotylidae). *Annales Zoologici* **57**(4): 757–758.
- YIN Z. 2020: Discrimination of species of *Hapsomela* Poinar & Brown (Coleoptera: Staphylinidae: Scydmaeninae) in mid-Cretaceous Burmese amber. *Palaeoentomology* **3**(3): 309–316.
- YU T., KELLY R., MU L., ROSS A., KENNEDY J., BROLY P., XIA F., ZHANG H., WANG B. & DILCHER D. 2019: An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences* **116**: 11345–11350.
- ZHANG J. F. 1989: *Fossil Insects from Shanwang, Shandong, China*. Shandong Science and Technology Publishing House, Jinan, 551 pp (in Chinese).
- ZHANG J., SUN B. & ZHANG X. 1994: *Miocene Insects and Spiders from Shanwang, Shandong*. Science Press, Beijing, 298 pp (in Chinese).
- ZHANG S.-Q., CHE L.-H., LI Y., LIANG D., PANG H., ŚLIPINIŃSKI A. & ZHANG P. 2018: Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* **9** (205): 1–11.
- ZHENG D., CHANG S.-C., PERRICHOT V., DUTTA S., RUDRAA., MU L., KELLY R. S., LI S., ZHANG Q., ZHANG Q. Q., WONG J., WANG J., WANG H., FANG Y., ZHANG H. & WANG B. 2018: A Late Cretaceous amber biota from central Myanmar. *Nature Communications* **9** (3170): 1–6.
- ZHERIKHIN V. V. & ROSS A. J. 2000: A review of the history, geology and age of Burmese amber burmite. *Bulletin of the Natural History Museum Geology Series* **56**(1): 3–10.