Dictyorachys gen. nov., an enigmatic genus of jewel beetles from mid-Cretaceous amber of northern Myanmar (Coleoptera: Buprestidae)

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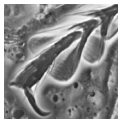

The mid-Cretaceous Burmese amber has yielded a wide diversity of polyphagan beetles, but the fossil record of Buprestidae is comparatively sparse. Cretaceous buprestids in amber with exquisite morphological details are invaluable for understanding character evolution and the origin and diversification of extant subfamilies. Here we report an enigmatic jewel beetle, *Dictyorachys callidictyus* Li, Volkovitsh & Cai gen. et sp. nov., based on a well-preserved specimen entombed in mid-Cretaceous amber from northern Myanmar. The unusual character combination of *Dictyorachys* is not consistent with any of the known buprestid subfamilies, which is therefore tentatively classified as Buprestidae *incertae sedis*. • Key words: Buprestoidea, fossil, Cretaceous, Burmese amber.

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Buprestidae is one of the hyperdiverse polyphagan beetle families, with about 520 genera and 15,000 species distributed worldwide (Bellamy & Volkovitsh 2016). Schizopodidae, the sister group of Buprestidae, had also been considered as a subfamily in Buprestidae by some researchers (*e.g.*, Hołyński 1993, Volkovitsh 2001).

The internal classification of Buprestidae has been quite contentious, as different authors proposed different classification systems based on their understanding of the morphological characters (*e.g.*, Nelson 1981, Hołyński 1993, Kolibáč 2000, Bellamy 2003). The current classification compiled by Bellamy (2008a–d, 2009) recognized 49 tribes in six subfamilies. Evans *et al*. (2015) conducted the only densely sampled molecular phylogenetic study on Buprestidae. In their results, Julodinae was grouped together with Haplostethini, a tribe of Polycestinae. The remaining Polycestinae was monophyletic, and sister to Julodinae + Haplostethini. Buprestinae and Chrysochroinae were polyphyletic and mixed together, with the monogeneric Galbellinae also nested in this group. Agrilinae as a whole was recovered as monophyletic, but none of the four agriline tribes was sufficiently supported. The analysis on the whole Elateriformia by Kundrata *et al.* (2017), though with less dense taxon sampling, yielded similar results regarding the relationships within Buprestidae.

The fossil record of Buprestidae is not rare (as listed in Bellamy 2008a–d). However, many of the fossils reported in the old literature, including isolated elytra from the Triassic of Australia (Etheridge & Olliff 1890, Dunstan 1923), were poorly preserved and (or) insufficient described and figured, making it impossible to justify the familial placement (Alexeev 1999). Additionally, due to the somewhat similar body shape, it would be sometimes difficult to differentiate Buprestidae and, for example, Elateridae in the fossil record (Bellamy 1995, Alexeev 2008, Dong & Huang 2011, Kundrata *et al*. 2020). Jurassic and Cretaceous buprestids have been known from Germany, Spain, Mongolia, Kazakhstan, Russia and China (*e.g.*, Alexeev 1993, 2000, 2009; Yu *et al*. 2013, 2015). Recently Jiang *et al*. (2021) described a buprestid adult from mid-Cretaceous Burmese amber, which was placed in Agrilinae and possibly closely related to extant *Agrilus* Curtis, 1825. Larvae of Bupre-

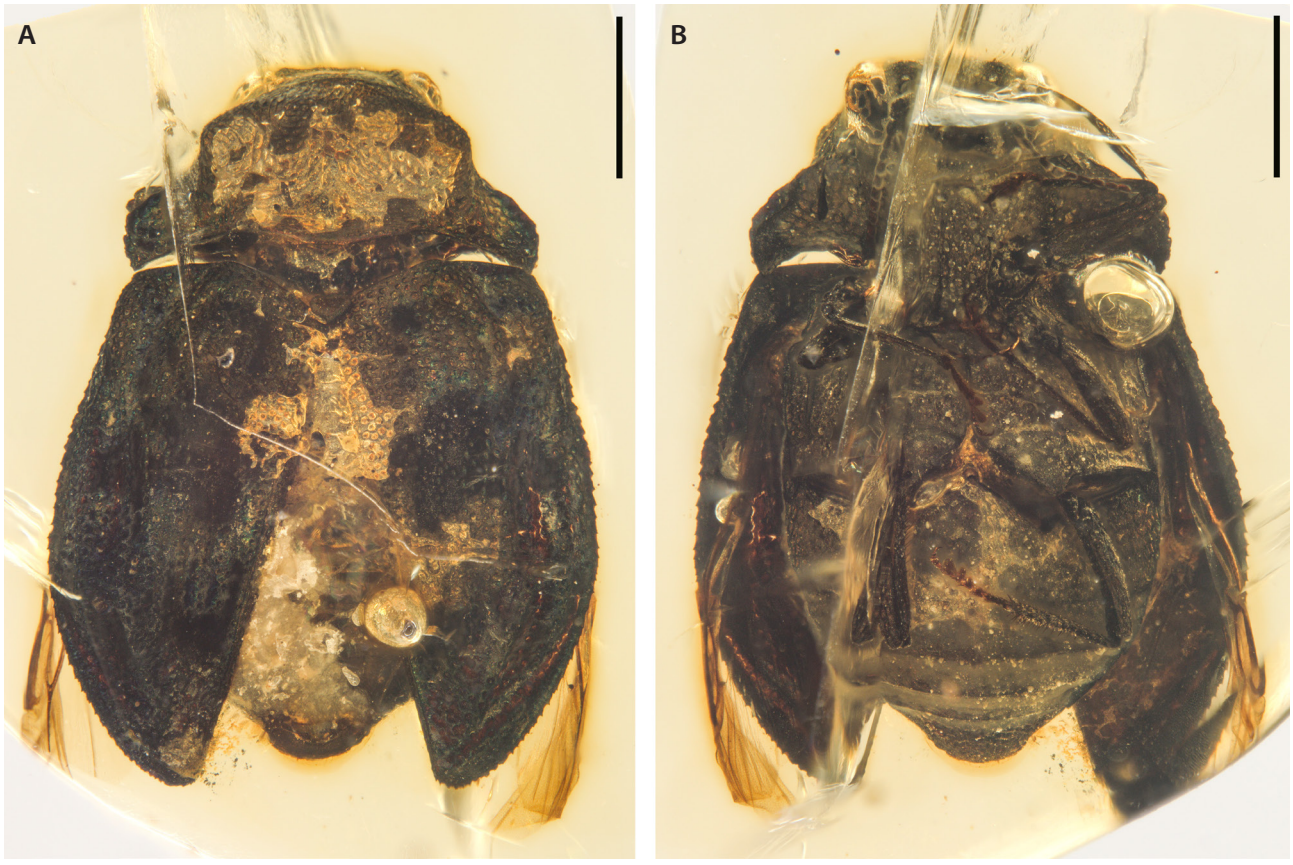

Figure 1. General habitus of *Dictyorachys callidictyus* Li, Volkovitsh & Cai gen. et sp. nov., holotype, NIGP201153, under incident light. A – dorsal view. B – ventral view. Scale bars: 1 mm.

stidae are also known from Burmese amber (Haug *et al.* 2021).

In this study, we report the second adult of Buprestidae from Burmese amber, which has an unusual morphology and cannot be assigned to any existing subfamily or tribe.

Materials and methods

The Burmese amber specimen studied herein originated from amber mines near Noije Bum (26° 20′ N, 96° 36′ E), Hukawng Valley, Kachin State, northern Myanmar. The 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 papers of different grit sizes, and finally polished with polishing powder.

Brightfield images were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. 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, Li *et al.* 2023). Brightfield and widefield fluorescence images were stacked with Helicon Focus 7.0.2 or Zerene Stacker 1.04. Confocal images were stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

The general morphological terminology follows Lawrence & Ślipiński (2013). The terminology for antennal structures follows Volkovitsh (2001).

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Superfamily Buprestoidea Leach, 1815
Family Buprestidae Leach, 1815
Subfamily *Incertae sedis*

Genus *Dictyorachys* Li, Volkovitsh & Cai gen. nov.

Type species. – *Dictyorachys callidictyus* Li, Volkovitsh & Cai sp. nov.

Etymology. – The generic name is formed based on the Greek "*diktyo*", referring to the reticulate sculpture on

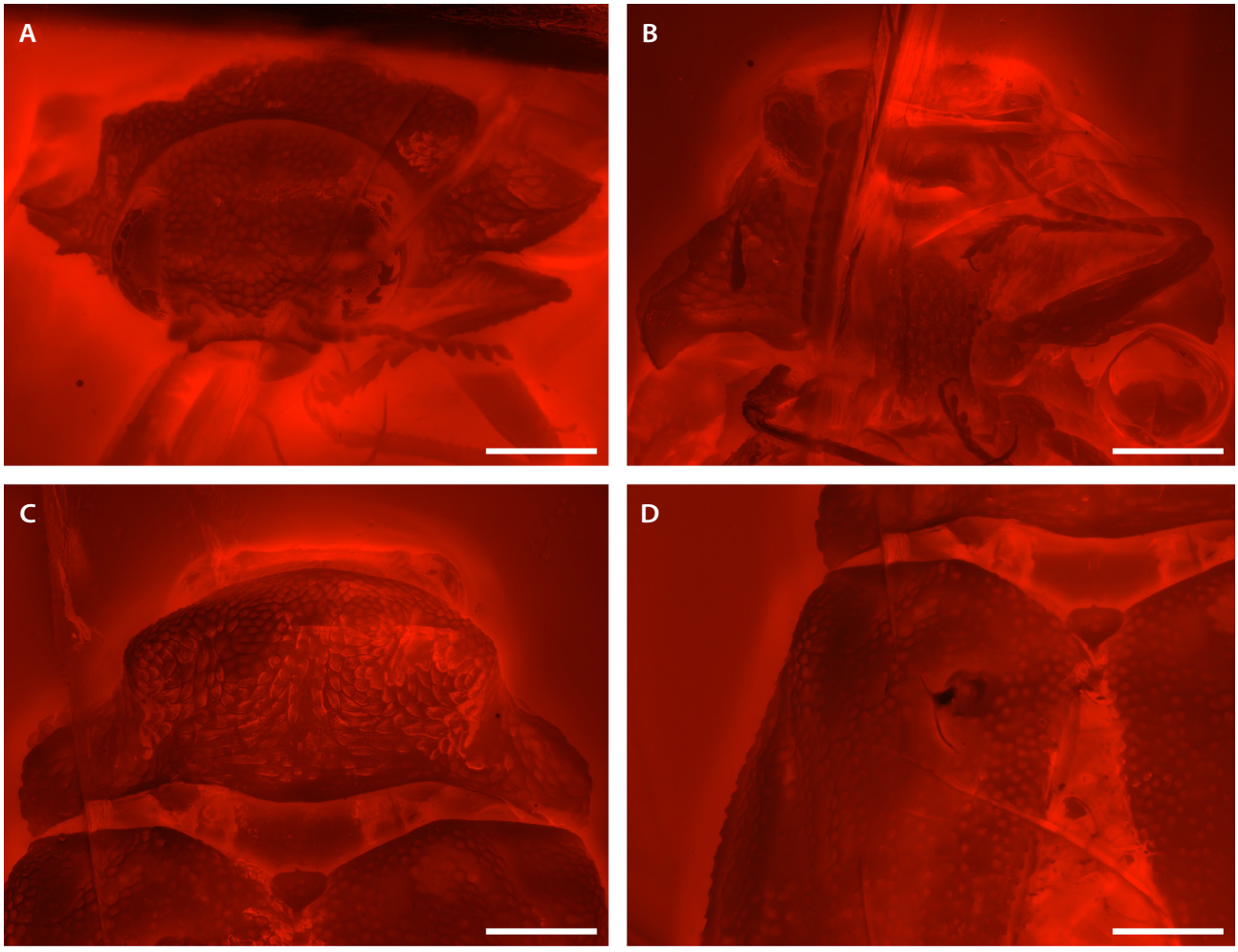

Figure 2. *Dictyorachys callidictyus* Li, Volkovitsh & Cai gen. et sp. nov., holotype, NIGP201153, under widefield fluorescence. A – head and prothorax, anterior view. B – head and prothorax, ventral view. C – prothorax, dorsal view. D – elytral base, dorsal view. Scale bars: 500 μm.

its head and pronotum, and the generic name *Trachys* Fabricius, 1801, referring to its broad body shape similar to some Tracheini. The name is masculine in gender (ICZN 2009).

Diagnosis. – Body broad. Head hypognathous; frons wide, expanded toward vertex. Antennal insertions moderately separated (Fig. 4A). Antennae 11-segmented; antennomere 3 not longer than 2 (Fig. 4B). Head and pronotum with reticulate sculpture (Figs 4, 5A). Pronotal disc deeply depressed laterally (Fig. 2A, C). Lateral pronotal carinae anteriorly incomplete (Fig. 4B). Prosternal process apically very broadly rounded (Fig. 5E). Mesoventral cavities posteriorly largely bordered by metaventrite (Fig. 5E). Metakatepisternal suture indiscernible (Fig. 5F). Metacoxal plates not laterally dilated, with relatively straight anterior margin (Fig. 3A). Elytral striae poorly marked (Figs 3B, 5C). Hind wings likely with well-developed, elongate and distally closed radial cell (Figs 1A, 3A).

***Dictyorachys callidictyus* Li, Volkovitsh & Cai sp. nov.**
Figures 1–5

LSID. – urn:lsid:zoobank.org:act:1A9402B4-E25E-4384-BCBA-EE7276829844

Type. – Holotype, NIGP201153.

Type horizon and locality. – Unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar.

Material. – Type only.

Etymology. – The specific name is formed based on the Greek "*kalli*-", beautiful, and "*diktyo*", reticulum, referring to the beautifully distorted reticulate sculpture on its head and pronotal disc.

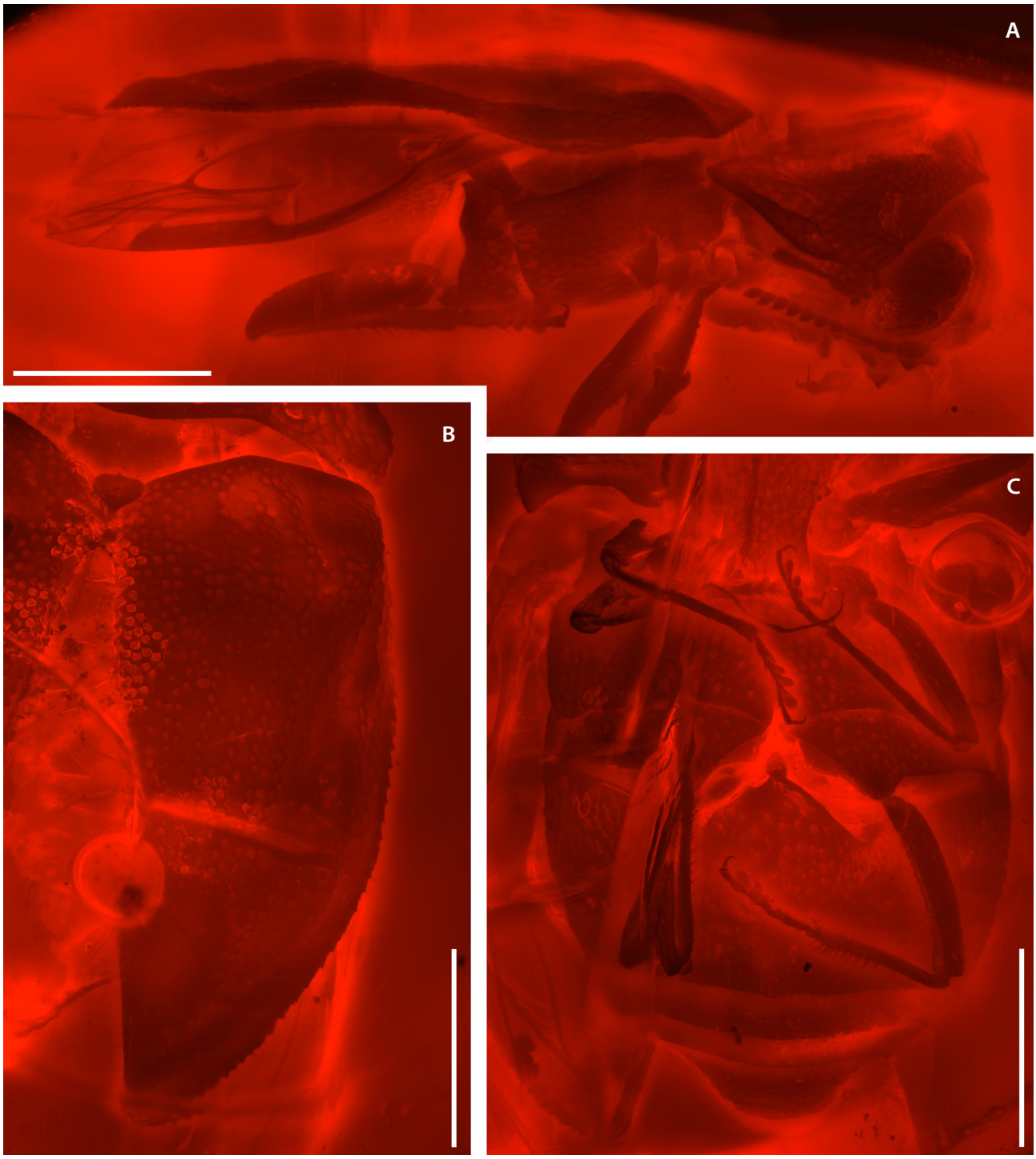

Figure 3. *Dictyorachys callidictyus* Li, Volkovitsh & Cai gen. et sp. nov., holotype, NIGP201153, under widefield fluorescence. A – lateral view. B – elytron, dorsal view. C – posterior body, ventral view. Scale bars: 1 mm.

Diagnosis. – As for the genus.

Description. – Body broad, about 4.3 mm long, 2.6 mm wide; dorsal surface almost asetose.

Head hypognathous due to inclined attachment of head base to prothorax; vertex wide, with median line reaching mid length of frons, flattened; frons without median depression, with a lateral area void of cells on each side (Fig. 4A); vertex and frons covered with reticulate sculpture of irregular cells. Eyes large, entire, vertically oval. Antennal insertions separated by about 0.4× distance between eyes. Antennae 11-segmented; antennomere 3

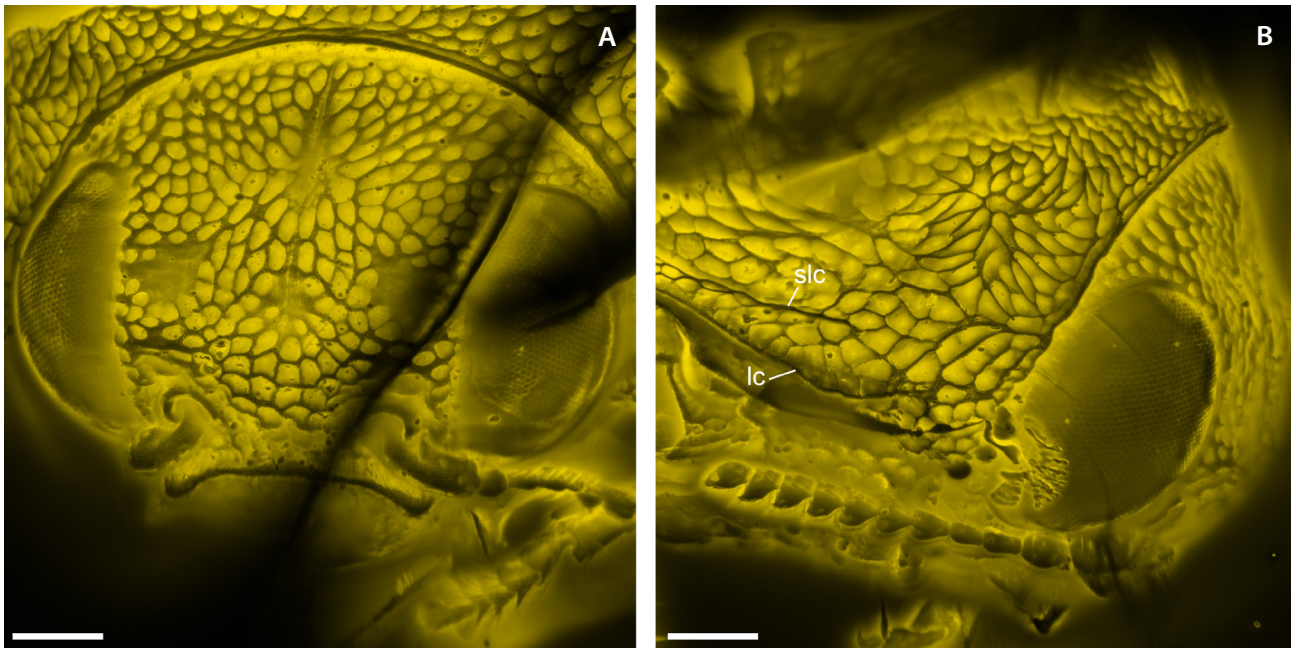

Figure 4. Details of *Dictyorachys callidictyus* Li, Volkovitsh & Cai gen. et sp. nov., holotype, NIGP201153, under confocal microscopy. A – head, anterodorsal view. B – head and prothorax, lateral view. Abbreviations: lc – lateral pronotal carina; slc – sublateral pronotal carina. Scale bars: 200 μm.

thinner and slighter shorter than 2; antennomere 4 slighter shorter than 3 and subequal to 3 in width; antennomeres 5–10 serrate, slightly trapezoid, each with a stout and long trichoid sensilla on external side (possibly of type U1 or A3, most clearly seen on antennomeres 7–10; Fig. 5I), with field of sensillae along inner margin (Fig. 5D); antennomere 11 obliquely fusiform, externally with a circular fossa (Fig. 5I). Clypeus anteriorly emarginate. Mandible short and broad.

Pronotum strongly transverse, widest basally, depressed laterally; anterior margin widely arcuate; posterior margin bisinuate; lateral carinae present in posterior $^{4}/_{5}$, incomplete anteriorly (Fig. 4B); sublateral carinae present in posterior $^{3}/_{5}$ (Fig. 4B); disc with distorted reticulate sculpture of irregular cells with central grains; hypomera without carina or groove, with similar reticulate sculpture as on pronotal disc. Prosternum moderately long; prosternal process subparallel-sided, weakly expanded near apex, apically very broadly rounded. Procoxal cavities moderately widely separated, externally open. Protrochantin exposed.

Scutellar shield transversely subtriangular; lateral angles broadly rounded (Fig. 5B). Elytra with sides subparallel anteriorly and arcuately converging posteriorly; apices conjointly rounded; lateral margins serrate along entire length; disc with more or less irregular punctation and with poorly marked striae. Mesoventrite short; mesoventral cavity large, laterally bordered by mesoventrite, posteriorly bordered by metaventrite. Mesocoxal cavities widely separated. Metaventrite broad; median discrimen present in anterior half; katepisternal suture indiscernible. Metacoxal plates not laterally dilated, with relatively straight anterior and sinuate posterior margins.

Hind wings likely with well-developed, elongate and distally closed radial cell.

Legs slender. Femora with groove on internal side (Fig. 3C). Tibiae slender; metatibia with setal comb along distal $^{2}/_{3}$ (Figs 3C, 5H). Tarsi 5-5-5; tibial spurs paired (as seen in fore and hind legs); tarsomeres 2–4 ventrally with membranous lobes; pro- and mesotarsomere 1 possibly also with weakly developed ventral lobe; metatarsomere 1 with dense stout setae. Pretarsal claws simple.

Abdomen with suture between abdominal ventrites 1 and 2 reduced; sternal groove likely absent.

Discussion

The combination of serrate antennae, widely separated mesocoxae, lobed tarsomeres 2–4, and obliterated suture between abdominal ventrites 1–2 could exclude *Dictyorachys* from other elateriform taxa except Buprestoidea. Schizopodidae can be easily ruled out as close relatives of *Dictyorachys* based on the very short prosternum and deeply bilobed tarsomere 4 (Nelson & Bellamy 1991, Hołyński 1993) (prosternum in front of coxae longer than procoxal cavities and tarsomere 4 not bilobed in *Dictyorachys*). Within Buprestidae,

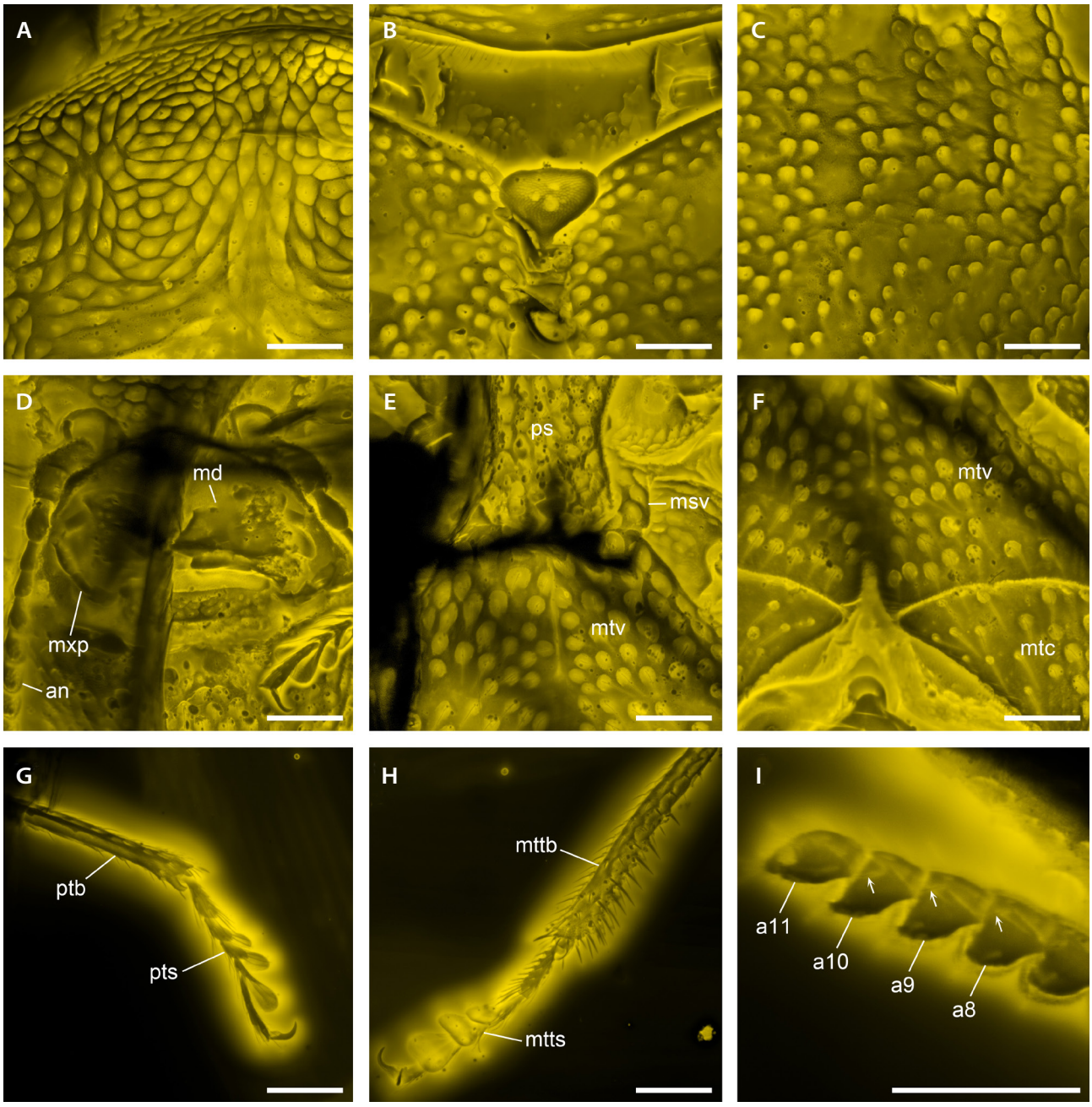

Figure 5. Details of *Dictyorachys callidictyus* Li, Volkovitsh & Cai gen. et sp. nov., holotype, NIGP201153, under confocal microscopy. A – pronotum, dorsal view. B – scutellum, dorsal view. C – anterior portion of elytron, dorsal view. D – mouthparts, anteroventral view. E – mesothorax, ventral view. F – metathorax, ventral view. G – fore leg. H – hind leg. I – antenna, external side. Abbreviations: a8–11 – antennomeres 8–11; an – antenna; md – mandible; msv – mesoventrite; mtc – metacoxa; mttb – metatibia; mtts – metatarsus; mtv – metaventrite; mxp – maxillary palp; ps – prosternum; ptb – protibia; pts – protarsus. Scale bars: 200 µm.

Dictyorachys obviously does not belong to Julodinae, as the latter has a very short prosternum, a concealed scutellum and antennomeres almost entirely covered with trichoid sensilla (Hołyński 1993, Volkovitsh 2001, Bellamy & Volkovitsh 2016) (scutellum exposed in *Dictyorachys*; antennomeres surface mainly glabrous with scattered trichosensilla externally). The mesoventral cavity of *Dictyorachys* is formed in part by the metaventrite. In most Polycestinae, the mesoventral cavity is formed by the mesoventrite only (Nelson 1981, Bellamy 1986). The few exceptions could be separated from *Dictyorachys* based on some other distinctive characters: Astraeusini has a concealed scutellum (Barker 1975), and Haplostethini has a complete carina on hypomeron (Willams & Weir 1987). Therefore, *Dictyorachys* likely does not belong to Polycestinae.

It would be much more difficult to determine whether *Dictyorachys* is more closely related to the Buprestinae + Chrysochroinae lineage or the Agrilinae lineage. It is also possible that *Dictyorachys* may belong to some previously unknown lineage. *Dictyorachys* has the antennal insertions separated by less than half the distance between eyes, mesoventral cavity posteriorly largely bordered by metaventrite, and antennomere 3 not longer than 2, which should generally favor an agrilinine placement (Holm & Bellamy 1985, Bellamy 1986, Hołyński 1993). However, Agrilinae is characterized by the presence of sternal groove on abdomen (although it may be somewhat reduced in some subtaxa) (Jendek 2001). No clear sternal groove could be confirmed in *Dictyorachys*. The lateral pronotal carina is incomplete anteriorly in *Dictyorachys*, while in Agrilinae the lateral pronotal carina is almost always complete (or rarely absent) (Lawrence *et al*. 2000–2018). Such an anteriorly incomplete lateral pronotal carina is commonly seen in Buprestinae or Chrysochroinae. Elytra of the most Agrilinae are covered by secondary tiled sculpture, without striae, while *Dictyorachys* has some poorly marked punctate striae on the elytra. The metacoxal plate of *Dictyorachys* is not laterally dilated, with anterior margin relatively straight, which also disfavors the agriline placement (Bellamy & Nelson 2002).

Dictyorachys is similar to Anthaxiini (Buprestinae) and many Acmaeoderini (Polycestinae) in head and pronotum with reticulate sculpture, and additionally to Neotropical members of Anthaxiini in pronotal disc with sublateral carina and body asetose (Bílý 2013). However, Anthaxiini has a more flattened pronotal disk with a straight base, and the radial cell on hind wings is small or reduced; Acmaeoderini has a peculiar type of dense and longitudinally parallel sculpture along the base of pronotum and a straight posterior pronotal margin (Volkovitsh 2008). The small size and broad body shape of *Dictyorachys* somewhat resemble Tracheini (Agrilinae). But Tracheini usually has a distally open radial cell (Good 1925, Kolibáč 2000) and no elytral striae, and none of Tracheini has such reticulate sculpture. The body and pronotal shape of *Dictyorachys* may also resemble some shortened members of Coraebini (Agrilinae), such as *Philocoroebus* Bellamy, 1991 and *Brachycoraebus* Kerremans, 1903. However, these coraebins generally have a shortened radial cell (Bellamy 1991, Kubáň *et al*. 2000) and lack elytral striae, and the sculpture is never completely reticulate. The metakatepisternal suture is indiscernible in *Dictyorachys*, which is unusual in Buprestidae, as extant Buprestidae usually has a distinctly curved metakatepisternal suture crossing midline, although in some small species the suture may also be indiscernible or poorly marked.

Most previously reported Mesozoic fossils were assigned to Parathyreinae (*e.g*., Alexeev 1993, 1999; Pan *et al.* 2011), although the validity of this extinct subfamily is dubious (Cai *et al*. 2015, Yu *et al*. 2015). These fossils always have the distinct (and straight) metakatepisternal suture, distinct elytral striae, and unreduced suture between abdominal ventrites 1 and 2, which clearly differ from *Dictyorachys*.

Given the discussion above, we prefer to place the newly discovered *Dictyorachys* in Buprestidae *incertae sedis*, without subfamilial or tribal attribution. The possibility also remains that *Dictyorachys* could represent an extinct family of the superfamily Buprestoidea. Further discoveries of related extinct or extant forms in the future may help us to better understand the systematic placement of this unusual taxon.

Data availability. The original confocal data are available in Zenodo repository (*https://doi.org/10.5281/zenodo.7909734*).

Acknowledgments

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