

Revisiting the morphology and systematic placement of the enigmatic Cretaceous ommatid beetle *Bukhkalius lindae* (Coleoptera: Archostemata: Ommatidae)

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Abstract. The systematic position of *Bukhkalius lindae* (Jarzembowski *et al.* 2017) from mid-Cretaceous Burmese amber is revised based on a re-examination of the type specimen. Our observations confirm that *B. lindae* lacks unique apomorphies of *Tetraphalerus* Waterhouse, in which it was originally placed, including complete antennal grooves and mushroom-shaped micro-tubercles. It is well justified to place it into a separate genus, *i.e.*, *Bukhkalius* Kirejtshuk & Jarzembowski, 2020. The incomplete but distinct antennal grooves and the *Tetraphalerus*-like mouthparts of *B. lindae* suggest that it has a close affinity to *Tetraphalerus*. Therefore, *B. lindae* may represent a missing link bridging the morphological gap between extant ommatid subfamilies Tetraphalerinae and Ommatinae.

Keywords. Archostemata; Ommatidae; *Bukhkalius*; *Tetraphalerus*; Burmese amber.

INTRODUCTION

Extant Ommatidae is a small archostematan family, which can be divided into two subfamilies, Ommatinae *sensu stricto* and Tetraphalerinae (Bouchard *et al.*, 2011). Extant Tetraphalerinae comprises a single genus, *Tetraphalerus* Waterhouse, and two species, *T. bruchi* Heller and *T. wagneri* Waterhouse. Both occur in the southern half of South America (Hörschemeyer & Beutel, 2016). Seven apomorphies of *Tetraphalerus* have been identified by a morphology-based phylogenetic analysis, including head with antennal grooves below the eyes and mushroom-shaped micro-tubercles inserted with minute scales (Hörschemeyer, 2009).

Since Ponomarenko (1964), numerous Mesozoic compression-impression fossils have been placed in the extant genus *Tetraphalerus* by various authors (summarized in Kirejtshuk, 2020). However, the most characteristic feature of *Tetraphalerus*, ventrolateral antennal grooves, was not detectable in any of these compression-impression fossils. Recently, Jarzembowski *et al.* (2017) reported a new species, *T. lindae* Jarzembowski *et al.*, 2017, from

mid-Cretaceous Burmese amber, and assigned it to *Tetraphalerus*. The specimen, although nicely preserved, was poorly photographed and illustrated in Jarzembowski *et al.* (2017), which hindered an accurate evaluation of its systematic position within Ommatidae. Kirejtshuk & Jarzembowski (*in* Kirejtshuk, 2020) later recognized that *T. lindae* is probably not a member of the genus *Tetraphalerus*, and therefore erected a new genus *Bukhkalius* Kirejtshuk & Jarzembowski to accommodate *B. lindae* (Jarzembowski *et al.*, 2017). Unfortunately, the diagnosis of *Bukhkalius* was insufficiently proposed to justify such a taxonomic act. In this paper, we aim to clarify the external morphology of *B. lindae* based on new images under epifluorescence and confocal microscopy to evaluate its systematic position within the Ommatidae.

MATERIAL AND METHODS

The holotype of *Bukhkalius lindae* (Figs. 1-3), deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of

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Sciences, Nanjing, China, was re-examined. Additional *Omma* specimens in NIGP were also examined for comparison. The specimens were derived from amber mines near Noije Bum Village (26°20'N, 96°36'E), Hukawng Valley, Kachin State, northern Myanmar (Jarzembowski *et al.*, 2017). The amber piece containing *B. lindae* was further ground with emery papers of different grit sizes and polished with polishing powder to improve the visibility of the beetle's ventral side.

Photographs under incident light 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. Images under incident light and widefield fluorescence were stacked in *Helicon Focus 7.0.2* or *Zerene Stacker 1.04*. Confocal images were manually stacked in Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to enhance contrast.

RESULTS

Systematic Paleontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

Family Ommatidae Sharp & Muir, 1912

Subfamily Tetraphalerinae Crowson, 1962

Genus *Bukhkalius* Kirejtshuk & Jarzembowski, 2020

Type species: *Tetraphalerus lindae* Jarzembowski, Wang & Zheng, 2017.

Revised diagnosis: Body elongate. Head moderately elongate; temples short; antennal grooves short, only reaching anterior margin of eyes; antennae short, sub-filiform; separate mentum present. Pronotal disc without protuberances or ridges; propleura not reaching anterior prothoracic margin; procoxae contiguous. Elytra with indistinct longitudinal ridges (primary veins); lateral edge of elytra with double rows of teeth. Abdominal ventrites abutting.

Bukhkalius differs from *Tetraphalerus* in head only moderately elongate, antennal grooves incomplete, and mushroom-shaped micro-tubercles absent. *Bukhkalius* differs from the remaining genera in Ommatidae in the combination of antennal grooves present (though incomplete), separate mentum present, and propleura not reaching anterior prothoracic margin.

Remarks: The diagnosis provided in Kirejtshuk (2020) was insufficient, which cannot really differentiate *Bukhkalius* from *Omma* and *Omma*-like genera. For example, he claimed that "this new genus [*Bukhkalius*] differs from the genera with subglobose prothorax (*Cionocoleus*, *Cionocups*, *Omma*, *Polyakius* and *Rhopalomma*) in the clear 'neck' of the head". However, neck is clearly present

in both extant (Escalona *et al.*, 2020) and fossil ommatines. The neck in some fossil *Omma* (Figs. 4B, C) could be even narrower than that of *Bukhkalius*.

Bukhkalius lindae (Jarzembowski, Wang & Zheng, 2017) (Figs. 1-3)

Material examined: Holotype, NIGP166152.

Redescription: Body 4.1 mm long (from anterior end of mandibles to posterior end of folded elytra), 1.4 mm wide, with moderately short setae.

Head (Fig. 3A) prognathous, moderately elongate, distinctly flattened, constricted posteriorly to form a neck. Temples short. Posterior protuberances wide and indistinct. Compound eyes entire and finely faceted, without interfacetal setae. Antennal insertions lateral. Antennal grooves incomplete but distinct, only reaching anterior margin of eyes. Antenna short, extending beyond anterior prothoracic margin, but not reaching posterior prothoracic margin, 11-segmented and subfiliform, with thin setae; antennomere 3 slightly longer than 4. Labrum transverse. Mandible tridentate with vertically aligned teeth. Maxillary palps four-segmented, moderately long, extending well beyond apex of mandible when anteriorly directed; apical palpomere slender, not expanded, with small cavity near apex. Prementum with deep posteromedian pit. Separate mentum present, transverse. Labial palps three-segmented; apical palpomere slightly expanded, securiform. Gular sutures indistinct.

Pronotal disc longer than wide, without protuberances or ridges. Propleura probably not reaching anterior prothoracic margin, *i.e.*, notopleural suture joined by pleurosternal suture anteriorly (Fig. 3B). Prosternum in front of coxae moderately long. Procoxal cavities contiguous, broadly open externally. Mesoventrite at middle with acute anterior projection separating paired procoxal rests. Mesocoxal cavities contiguous. Metacoxae strongly transverse, contiguous, extending laterally to meet elytra. Elytra 1.7 times as long as wide combined, each with ten rows of maculated window punctures; longitudinal ridges (primary veins) indistinct; lateral edge of elytra with double rows of teeth. Femora stout. Tibiae thinner; tibial spurs well-developed. Tarsi five-segmented; tarsomeres simple, not bilobed; pretarsal claws simple.

Abdomen with five coplanar ventrites, separated by wide grooves; first and fifth ventrites longer than others.

DISCUSSION

Bukhkalius lindae was originally placed in the extant genus *Tetraphalerus* by Jarzembowski *et al.* (2017). In fact, it has many characters different from extant *Tetraphalerus* based on our examination. The most important feature defining the extant *Tetraphalerus* is the presence of distinct antennal grooves on the ventrolateral side of the head, which extend up to the posterior margin (Beutel *et al.*, 2008). Although Jarzembowski *et al.*

(2017) mentioned that the lateral notch between protuberance P1 and P2 may indicate a presence of antennal grooves for *B. lindae*, our observation clearly shows that it lacks complete antennal grooves (Fig. 3A). Extant species of *Tetraphalerus* have mushroom-shaped micro-tubercles, each inserted with a short and stout seta (Hörnschemeyer, 2009). It is clear that *B. lindae* does not possess this special form of micro-tubercles. Indeed, to our knowledge, such a peculiar structure is not known in any other extant or fossil archostematan beetles. Extant species of *Tetraphalerus* have a strongly elongated head, *i.e.*, more than 1.3× longer than wide (Hörnschemeyer, 2009), whereas the head of *B. lindae* (excluding neck) is approximately as long as wide (Fig. 3A). Besides, we were unable to detect the well-developed protuberance above eye (P2) in *B. lindae* as illustrated in fig. 2 in

Jarzembowski *et al.* (2017). Based on these morphological differences, we suggest that it is plausible to place *B. lindae* into a separate genus.

Interestingly, *B. lindae* displays some similarities with the extant *Tetraphalerus*. In extant Ommatinae (*Omma* Newman and *Beutelius* Escalona *et al.*, 2020), if the propleuron is not fused with the prosternum, the notopleural suture is complete and never joined by the pleurosternal suture, *i.e.*, propleuron reaches anterior prothoracic margin (Escalona *et al.*, 2020; incorrectly coded in Lawrence *et al.*, 2011). In contrast, the propleuron of the extant *Tetraphalerus* does not reach the anterior prothoracic margin, even though it is very close (Friedrich *et al.*, 2009; R.G. Beutel, *pers. comm.*; incorrectly coded in Beutel *et al.*, 2008). Similarly, the propleuron of *B. lindae* also seems not to reach the anterior prothoracic margin (Fig. 3B). The

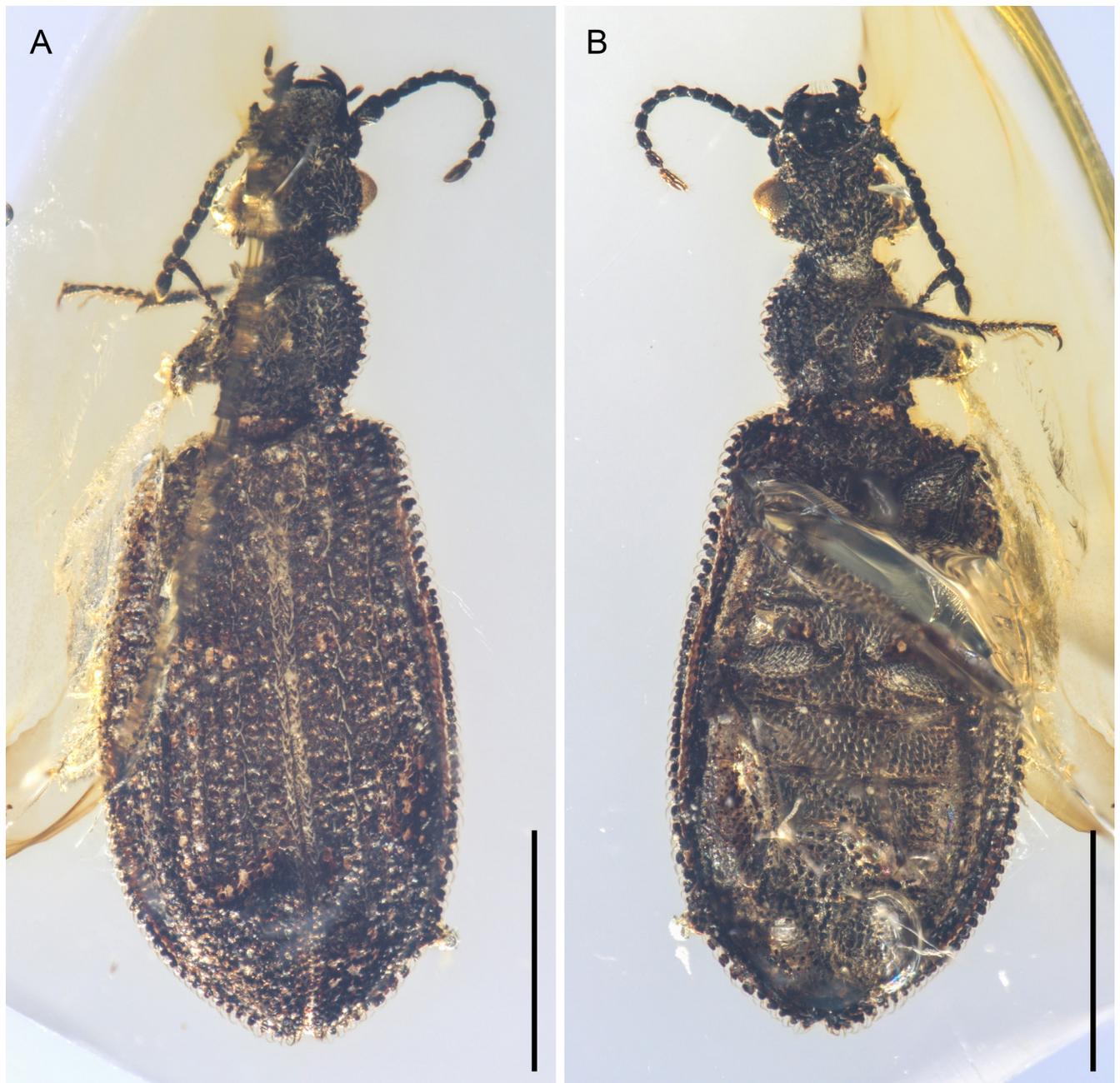


Figure 1. General habitus of *Bukhkalius lindae*, holotype, NIGP166152, under incident light. (A) Dorsal view. (B) Ventral view. Scale bars: 1 mm.

mouthparts of *B. lindae* and extant *Tetraphalerus* (fig. 3C in Beutel *et al.*, 2008) are very alike, though the maxillary palps of *B. lindae* is longer. In extant Ommatidae there is a sensorial cavity on the apical maxillary palpomere. The apical maxillary palpomere is expanded in *Omma* and *Beutellius*, so the cavity tends to be relatively small compared to the palpomere (figs. 4-7 in Lawrence, 1999). In contrast, the apical maxillary palpomere is slender in *Tetraphalerus*, so the cavity is relatively large (fig. 3D in Beutel *et al.*, 2008). The shape and relative size of the cavity on the apical maxillary palpomere of *B. lindae* match well with that of *Tetraphalerus* (Fig. 3A). In most archostematanans a separate mentum is absent (although Escalona *et al.*, 2020 described a mentum in *Omma* and *Beutellius*, the mentum actually corresponds to the prementum as defined by Beutel *et al.*, 2008 and Hörnschemeyer, 2009), whereas the mentum of *Tetraphalerus* is recog-

nizable as a transverse sclerite between submentum and prementum (Beutel *et al.*, 2008; incorrectly coded in Hörnschemeyer, 2009). A distinct transverse mentum is also present in *B. lindae* (Fig. 3A). Besides, in *B. lindae* there is a pair of possibly short antennal grooves, extending merely to the anterior edge of the compound eyes (Fig. 3A). Here we tentatively suggest that this structure may represent an early evolutionary stage of the well-developed antennal grooves in extant *Tetraphalerus*. Given the above discussions, we suggest that the enigmatic *Bukhkalius* is probably an early lineage closely related to the South America endemic *Tetraphalerus* and should be included in Tetraphalerinae.

Numerous Mesozoic "*Tetraphalerus*" species have been reported from Russia (*e.g.*, Ponomarenko, 1966), Mongolia (*e.g.*, Ponomarenko, 1997), Kazakhstan (*e.g.*, Ponomarenko, 1964), Kyrgyzstan (Ponomarenko, 1969),

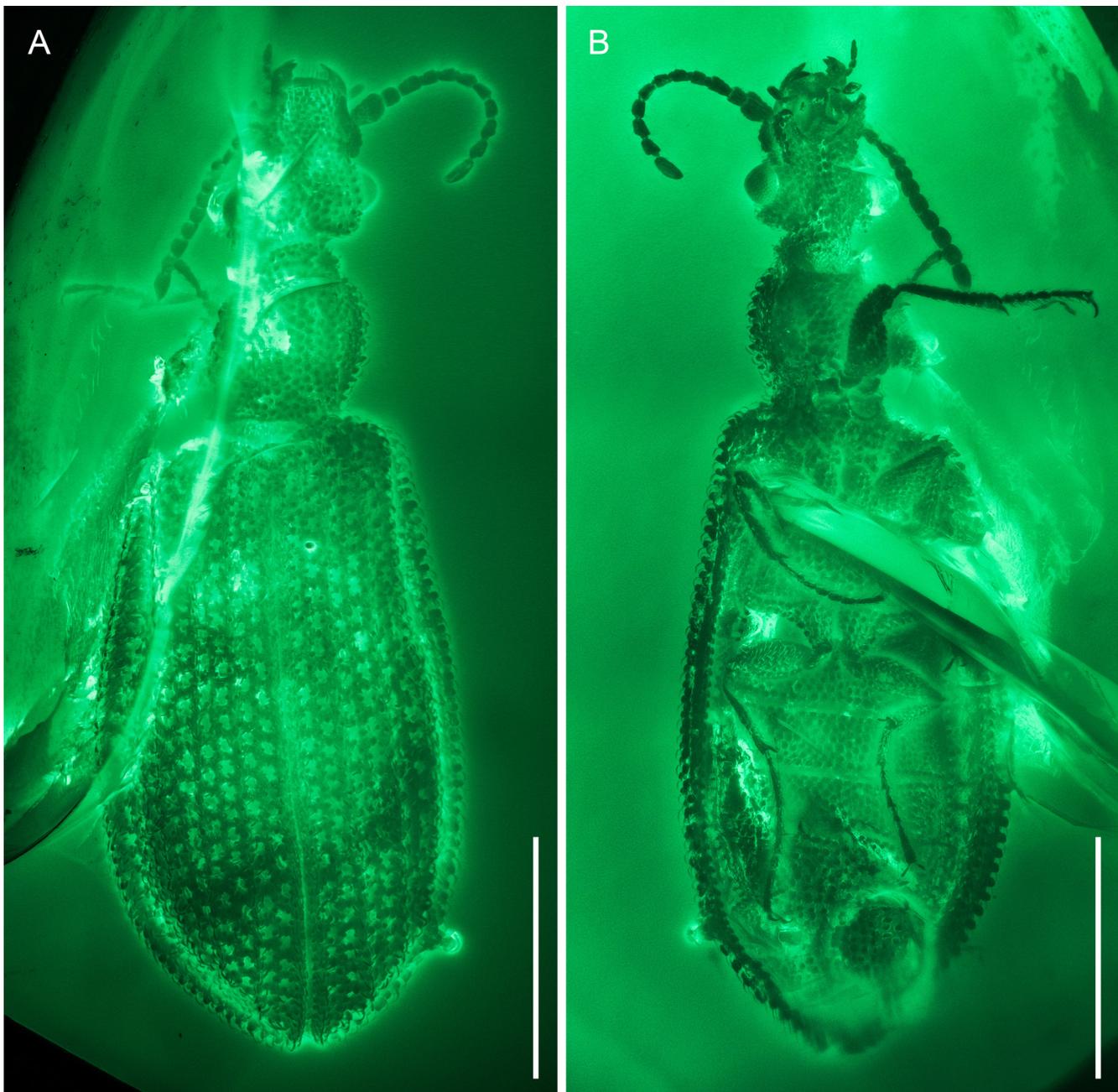


Figure 2. General habitus of *Bukhkalius lindae*, holotype, NIGP166152, under widefield fluorescence. (A) Dorsal view. (B) Ventral view. Scale bars: 1 mm.

Spain (e.g., Soriano & Delclòs, 2006), and China (e.g., Tan et al., 2007, 2012). Ponomarenko (1969) even proposed two series, each including one of the only two extant *Tetraphalerus* species (*T. bruchi* and *T. wagneri*), to accommodate the Mesozoic "*Tetraphalerus*" species. His practice of placing Mesozoic "*Tetraphalerus*" into series was followed by other researchers (e.g., Soriano & Delclòs, 2006; Tan et al., 2007). In the cladistic analysis of Tan et al. (2012), the fossil "*Tetraphalerus*" species (including *Tetraphalerites* Crowson) form a monophyletic group together with extant species of *Tetraphalerus*. This Tetraphalerini clade was united by a single non-homoplasious change, i.e., the presence of ventrolateral antennal grooves on head. However, the character coding of their analysis was problematic. In Tan et al. (2012), all three Mesozoic "*Tetraphalerus*" fossils were coded as having antennal grooves. No antennal grooves, however,

were mentioned in the original descriptions of "*T.*" *brevicapits* Ponomarenko & Martínez-Delclòs or "*T.*" *glabratus* Ponomarenko (Ponomarenko, 1997; Ponomarenko & Martínez-Delclòs, 2000), and we failed to detect the antennal grooves in the original figures either. Contradictorily, Tan et al. (2012) even clearly stated that no antennal grooves were visible in "*T. decorosus*" (name actually unavailable due to failure to comply with the requirements of ICZN, see Dubois et al., 2013) in the description part of their own paper. To our knowledge, the most critical character of *Tetraphalerus*, ventrolateral antennal grooves, was not discernible in any Mesozoic specimens belonging to "*Tetraphalerus*". Although Tan & Ren (2009) claimed that the presence of antennal grooves is clearly evident in "*T. curtinervis* Tan et al., 2012, we cannot identify this structure based on the photos provided in the paper. Other vital diagnostic features, including the relatively

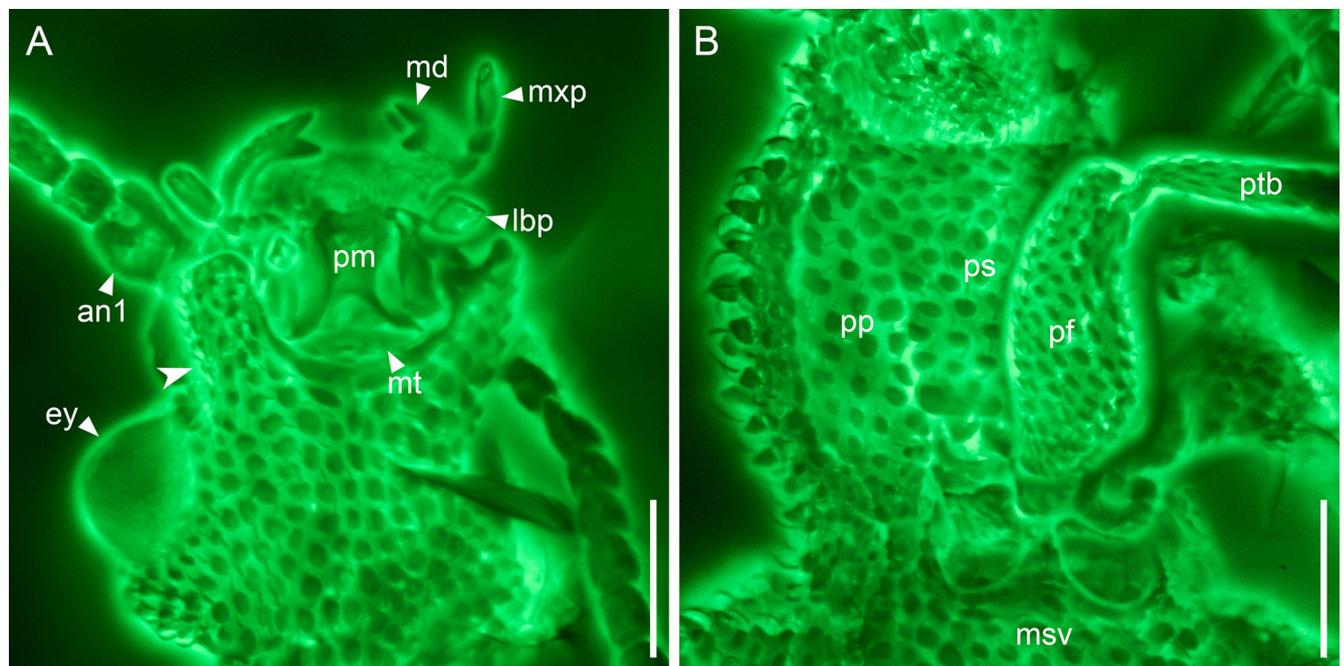


Figure 3. Details of *Bukhkalius lindae*, holotype, NIGP166152, ventral view, under confocal microscopy. (A) Head, showing the possibly incomplete antennal groove (arrowhead). (B) Prothorax. Abbreviations: an1 = antennomere 1; ey = compound eye; lbp = labial palp; md = mandible; msv = mesoventrite; mt = mentum; mxp = maxillary palp; pf = profemur; pm = prementum; pp = propleuron; ps = prosternum; ptb = protibia. Scale bars: 200 μ m.

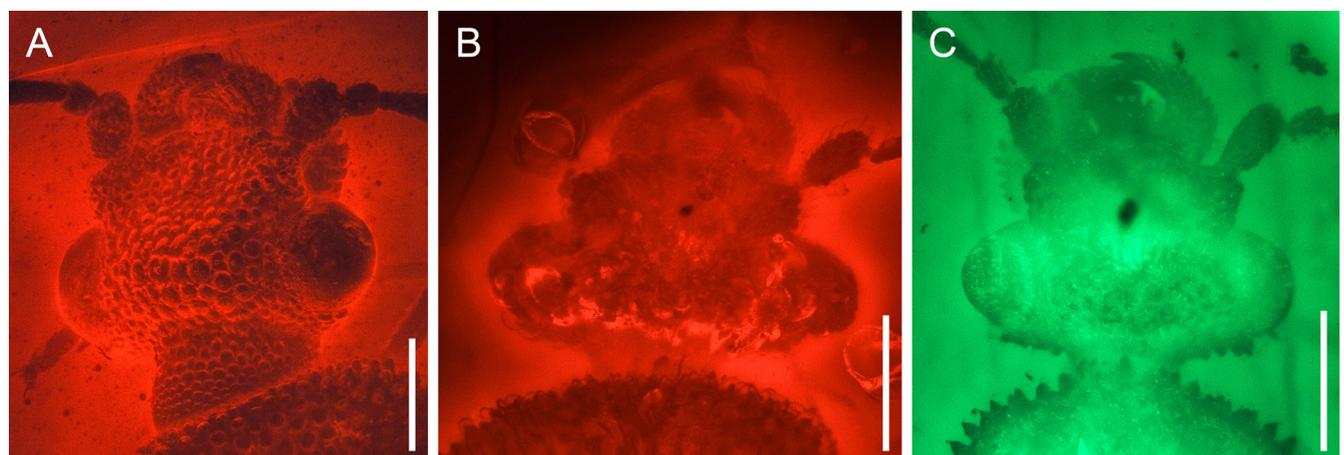


Figure 4. Head of fossil *Omma* species from Burmese amber, showing the well-defined neck region. (A) *Omma lii*, holotype, NIGP164898. (B) *Omma* sp. 1. (C) *Omma* sp. 2. Scale bars: 500 μ m.

large mushroom-shaped micro-tubercles and a separate mentum, were also not reported in these Mesozoic "*Tetraphalerus*". Therefore, we agree with Kirejtshuk (2020) that probably none of the Mesozoic species of "*Tetraphalerus*" should be placed in *Tetraphalerus*. The divergence between Ommatidae and Micromalthidae has been dated to Early Cretaceous, approximately 130 Ma (McKenna et al., 2019). It is reasonable to expect the divergence between two extant species of *Tetraphalerus* to happen much later than that. As such, it makes no sense to place the Early Cretaceous, or even Jurassic fossils into the *T. bruchi* and *T. wagneri* series.

DATA AVAILABILITY

The original series of confocal slices are available on Zenodo repository (<http://doi.org/10.5281/zenodo.4362699>).

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AUTHORS' CONTRIBUTIONS

Y.-D.L. and C.-Y.C. conceived the study. C.-Y.C. prepared the amber specimens. Y.-D.L. acquired and processed the photomicrographs. Y.-D.L. drafted the manuscript, to which C.-Y.C. contributed. All authors commented on the manuscript and gave final approval for publication.

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