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ARTICLE

Revisiting the morphology of the Cretaceous ommatid beetle *Clessidromma palmeri* (Coleoptera: Archostemata: Ommatidae)

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Abstract. The morphology of *Clessidromma palmeri* Jarzembowski *et al.* from mid-Cretaceous Burmese amber is revised based on a reexamination of the type specimen. Contrary to previous studies, our observation confirms that *Clessidromma* has open procoxal cavities. The characters such as platform on the ventral side of head, modified metacoxae, and ridges on head and pronotum are suggested to be diagnostic characters for *Clessidromma*. *Clessidromma zengi* Kirejtshuk from the same deposit is transferred into a new genus, as *Kirejtomma zengi* **comb. nov.**

Keywords. Archostemata; Ommatidae; *Clessidromma; Kirejtomma;* Burmese amber.

INTRODUCTION

Archostemata is a small suborder of Coleoptera, represented by only four extant families (excluding Jurodidae; Lawrence, 2016). Many Permian/Triassic coleopterans (*e.g.,* Permocupedidae, Tshekardocoleidae) were once placed in Archostemata due to their somewhat similar elytral structure (*e.g.,* Ponomarenko, 1969; Kirejtshuk *et al.,* 2014). A recent cladistic analysis, however, suggested that they are indeed stem-group beetles and should not be placed in Archostemata (Beutel *et al.,* 2008). Ommatidae is a small family of Archostemata (McKenna *et al.,* 2019), with three extant genera known to date (Hörnschemeyer & Beutel, 2016; Escalona *et al.,* 2020). Numerous Mesozoic ommatids have been found across Gondwana and Laurasia (*e.g.,* Ponomarenko, 1969; Tan & Ren, 2009; Ashman *et al.,* 2015). However, many characters in these compression-impression fossils are either not preserved or hard to interpret. Based on our preliminary examination, the morphological cladistic analysis of Ommatidae by Tan *et al.* (2012) seems to contain many coding errors, which was probably at least partly caused by the comparatively strong taphonomic artefacts in compression-impression fossils. The recent findings of relatively well-preserved ommatids in mid-Cretaceous Burmese amber have greatly increased our knowledge on the morphological disparity of this family (*e.g.,* Liu *et al.,* 2017; Jarzembowski *et al.,* 2019; Li *et al.,* 2020a, 2021a; Tihelka *et al.,* 2020). The morphological characters of the amber inclusions are less affected by taphonomic artefacts and could be crucial for further phylogenetic studies of Ommatidae.

Jarzembowski *et al.* (2018) reported a new ommatid species in a new genus, *Clessidromma palmeri* Jarzembowski *et al.,* from mid-Cretaceous Burmese amber. They mentioned that *C. palmeri* is unusual in Ommatidae in having tshekardocoleid-like fore legs. However, since the type specimen is strongly carbonized, it is extremely difficult to assess many of the characters of this species under incident light. After a detailed examination under fluorescence, it turns out that many structures were mistakenly illustrated in the original drawings, and some other important features were neglected in the original description by Jarzembowski *et al.* (2018). The clarified morphology of *C. palmeri* also permits a re-evaluation of the generic placement of an addition species previously assigned to *Clessidromma* (Kirejtshuk, 2020).

MATERIAL AND METHODS

The holotype of *Clessidromma palmeri* (Figs. 1-5), deposited in the Nanjing Institute of Geology and Paleontology (NIGP), Chinese

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Academy of Sciences, Nanjing, China, was re-examined. The specimen was derived from amber mines near Noije Bum Village (26°20′N, 96°36′E), Hukawng Valley, Kachin State, northern Myanmar (Jarzembowski *et al.,* 2018).

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 or a Zeiss Lumar V12 stereo microscope combined with a fluorescence imaging system. In some cases, the amber piece was immersed in mineral oil (CAS 8020-83-5) to reduce refraction (Fu *et al.,* 2021). Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using 488 nm Argon laser excitation line. Images under incident light and widefield fluorescence were stacked in Helicon Focus 7.0.2 or Zerene Stacker 1.04. Confocal images were stacked in Helicon Focus 7.0.2. 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
Genus *Clessidromma* Jarzembowski, Wang & Zheng, 2017

Type species: *Clessidromma palmeri* Jarzembowski *et al.,* 2017.

Figure 1. General habitus of *Clessidromma palmeri,* holotype, NIGP166270, under incident light. (A) Dorsal view. (B) Ventral view. Scale bars: 2 mm.

Composition: Only *Clessidromma palmeri*.

Revised diagnosis: Head roughly hexagonal; dorsal surface with a transverse carina separating vertex and frons; medial portion of ventral surface forming a distinctly elevated platform. Pronotal disc with three longitudinal ridges; lateral edges dentate. Pro- and mesocoxae oblong. Metacoxae with a longitudinal carina medially.

Remarks: Kirejtshuk (2020) merged the genus *Lepidomma* into *Clessidromma*. However, *Lepidomma* actually differs distinctly from *Clessidromma* (Li *et al.*, 2020b). In *C. palmeri,* the medial portion of the ventral surface of the head forms a distinctly elevated platform, extending to the posterior end of the neck (Fig. 4A). This elevated platform is unknown in any other ommatids, and could be regarded as a diagnostic character of the genus. Such a structure is obviously absent in *Lepidomma* (fig. 6A in Li *et al.,* 2020b). The metacoxa of *C. palmeri* is somewhat aberrant (Figs. 4D, 5F). Though the exact structure of the metacoxa is hard to determine due to the poor preservation of the specimen, it surely lacks the posterior excavation for reception of metafemur, and therefore differs from most other ommatids and cupedids, including *Lepidomma*. *Lepidomma* is characterized by a special type of scales with distinctive ridges running down the sides (fig. 4D in Li *et al.,* 2020b), which is absent in *C. palmeri*. Besides, there are three longitudinal ridges on the pronotal disc of *C. palmeri* (Fig. 3B), while no such ridges are present in *Lepidomma* (fig. 4C in Li *et al.,* 2020b).

Clessidromma palmeri Jarzembowski, Wang & Zheng, 2017
(Figs. 1-5)

Material examined: Holotype, NIGP166270, strongly carbonized and crazed, with right portion of prothorax partly polished away. The network of cracks makes it sometimes difficult to determine the real boundaries of sclerites.

Redescription: Body slender and elongate, about 8.6 mm long and 2.2 mm wide, tuberculate, with thin setae and scales.

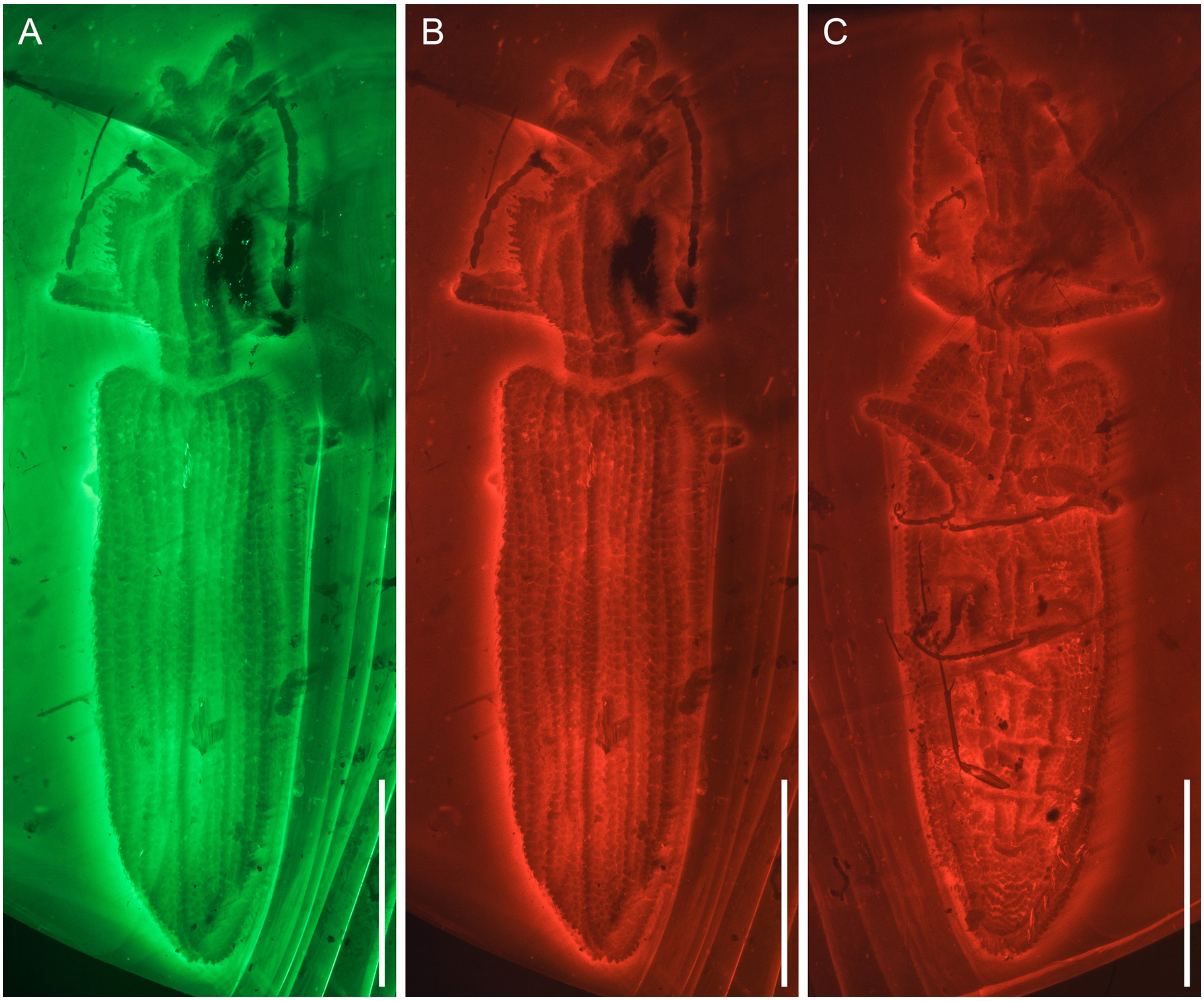

Figure 2. General habitus of *Clessidromma palmeri,* holotype, NIGP166270, under widefield fluorescence. (A, B) Dorsal view. (C) Ventral view. Scale bars: 2 mm.

Head (Figs. 3A, 4A) prognathous, roughly hexagonal, constricted posteriorly to form a neck. Vertex and frons separated by a somewhat v-shaped transverse carina. Ventral surface of head forming a distinctly elevated platform medially, extending to posterior end of neck (Figs. 4A, 5A). Compound eyes entire and finely facetted, without interfacetal setae. Antennal insertion area located anteriorly, anteromesad anterior margin of compound eyes, separated by more than two but less than three diameters of antennomere 1. Antennae (Figs. 3A, B, 4A) 11-segmented, fili-moniliform, with thin setae on all segments, extending beyond anterior prothoracic margin, but not reaching posterior prothoracic margin; antennomere 3 about twice as long as 4. Mandibles (Fig. 5A) long, with three vertically aligned teeth. Maxillary and labial palps seemingly short (Fig. 5A). Posteromedian pit on prementum not observed. Separate mentum probably absent.

Pronotal disc (Fig. 3B) gradually narrowed posteriorly, abruptly constricted behind procoxae; anterior extension forming a collar-like, centrally notched neck shield; lateral edges serrate. Notopleural sutures not observed (Fig. 5B). Prosternum (Fig. 4B) comparatively small; lateral edges slightly arcuate; prosternal process short and narrow, not reaching middle region of procoxae. Procoxal cavities contiguous, posteriorly open (Figs. 4B, 5B). Procoxae oblong (Fig. 5B).

Scutellum relatively narrow (Fig. 5I). Elytra elongate (Figs. 2A, B), about 2.5 times as long as wide combined, with distinct longitudinal ridges (primary veins) and rows of maculated window punctures (Fig. 5I); humeri prominent (Fig. 3C); lateral edges serrate; explanate epipleura absent. Mesoventrite (Fig. 5C) long and narrow, with median discrimen, anteriorly with deep procoxal rests. Mesocoxae oblong (Fig. 5C). Metaventrite trapezoidal (Fig. 4D), possibly with an inverted Y-shaped ridge extending from anterior metaventral process to posterior corners. Metacoxae (Figs. 4D, 5F) with a longitudinal carina medially (? or simply oblong with no lateral extension, *i.e.,* somewhat similar to *Miniomma* Li *et al.,* 2020a).

Legs slender. Femora stout. Tibiae thinner, with well-developed tibial spurs (Figs. 5B, D-F). Tarsi five-seg-

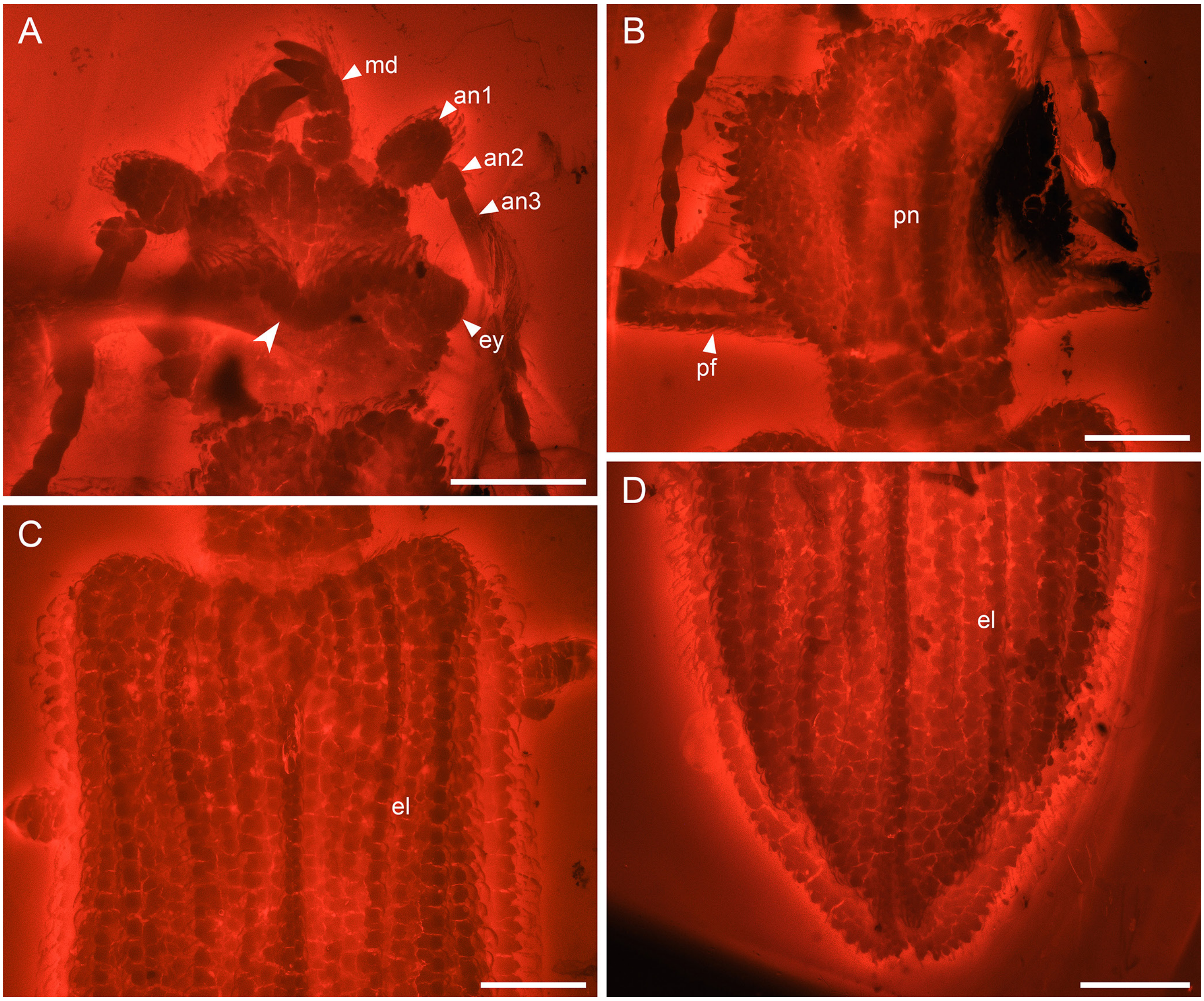

Figure 3. Details of *Clessidromma palmeri,* holotype, NIGP166270, under widefield fluorescence, dorsal view. (A) Head, showing the v-shaped transverse carina separating vertex and frons (arrowhead). (B) Prothorax. (C) Elytral base. (D) Elytral apex. Abbreviations: an1-3 = antennomeres 1-3; el = elytron; ey = compound eye; md = mandible; pf = profemur. Scale bars: 500 µm.

mented; tarsomeres simple, not bilobed. Pretarsal claws simple.

Abdomen (Figs. 4D, E) elongate, with five coplanar ventrites, separated by distinct grooves; ventrites 1-4 seemingly with a pair of longitudinal ridges (Fig. 5G; possibly being a taphonomic artefact); anterior margin of ventrite 5 seemingly emarginate (possibly being a taphonomic artefact).

Genus *Kirejtomma* Li & Cai gen. nov.

Type species: *Clessidromma zengi* Kirejtshuk, 2020.

Composition: Only *Kirejtomma zengi* **comb. nov.**

Diagnosis: Scales (scale-like setae) absent. Antennomere 3 distinctly longer than 4. Labrum with nearly straight

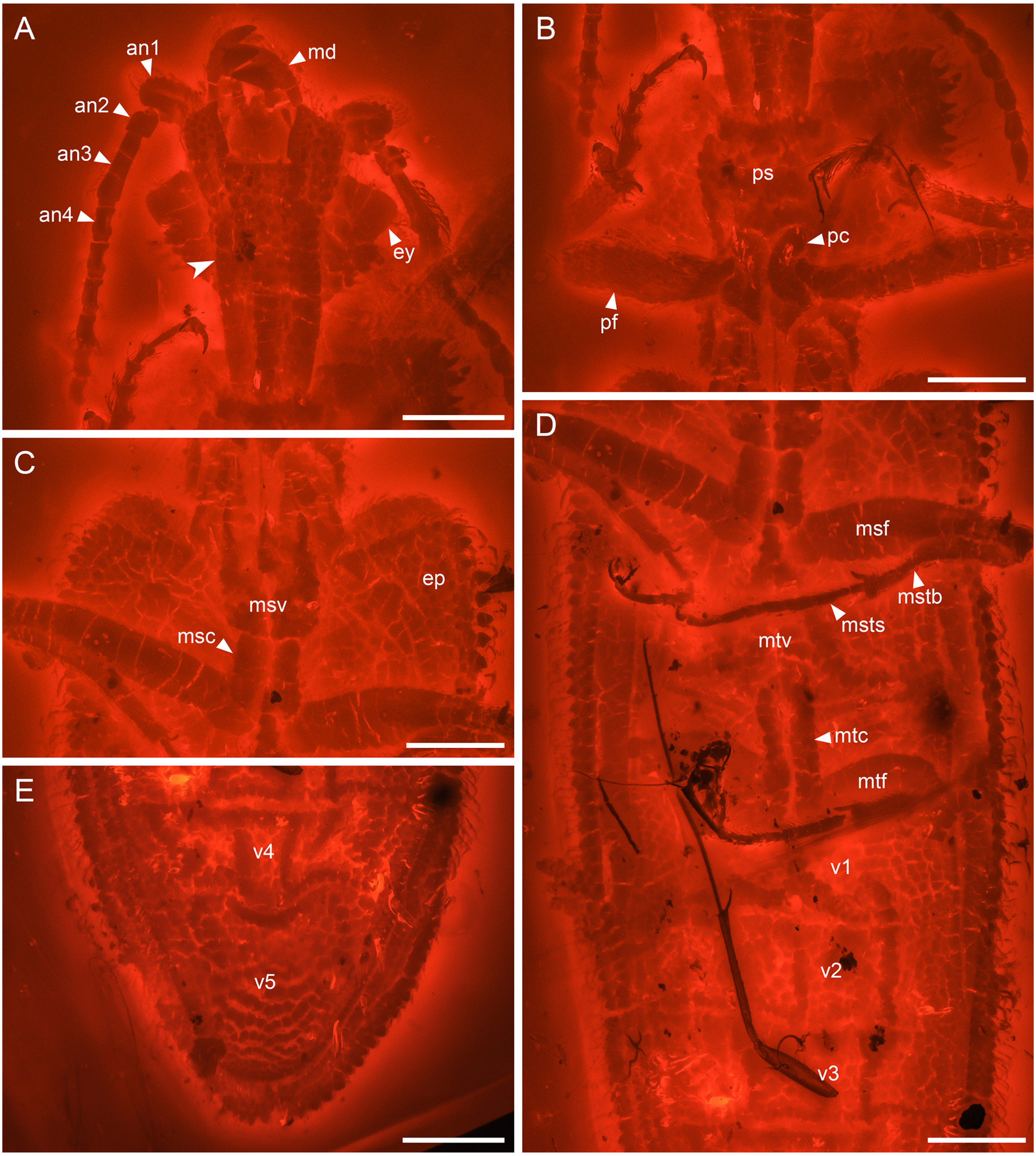

Figure 4. Details of *Clessidromma palmeri,* holotype, NIGP166270, under widefield fluorescence, ventral view. (A) Head, with arrowhead showing the elevated platform. (B) Prothorax. (C) Mesothorax. (D) Metathorax and abdominal base. (E) Abdominal apex. Abbreviations: an1-4 = antennomeres 1-4; ep = epipleuron; ey = compound eye; md = mandible; msc = mesocoxa; msf = mesofemur; mstb = mesotibia; msts = mesotarsus; msv = mesoventrite; mtc = metacoxa; mtf = metafemur; mtv = metaventrite; pc = procoxa; pf = profemur; ps = prosternum; v1-5 = ventrites 1-5. Scale bars: 500 μm.

anterior margin (not waveform). Pronotal disc expanding anteriorly; longitudinal ridges absent; lateral edges smooth. Pro- and mesocoxae subglobular. Metacoxae unmodified, with posterior excavations for reception of metafemora. Elytra without prominent longitudinal ridges (primary veins); explanate epipleura absent.

Remarks: Kirejtshuk (2020) reported a new species, *Clessidromma zengi* Kirejtshuk, from Burmese amber, and assigned it to genus *Clessidromma*. *Clessidromma zengi,* however, differs dramatically from *C. palmeri,* the type species of *Clessidromma,* and therefore is not a true member of *Clessidromma*. The head of *C. zengi* does not possess an elevated platform on the ventral side (fig. 9C in Kirejtshuk, 2020), and its pronotum and elytra lack any distinct longitudinal ridges (figs. 9D, 10A in Kirejtshuk, 2020). *Clessidromma zengi* has typical metacoxae for ommatid and cupedid archostematans (fig. 10D in Kirejtshuk, 2020). In addition, the lateral pronotal edges are dentate in *C. palmeri* (Fig. 3B), while they are relatively smooth in *C. zengi*. The pronotum of *C. zengi* is somewhat more similar to *Lepidomma*. However, it differs

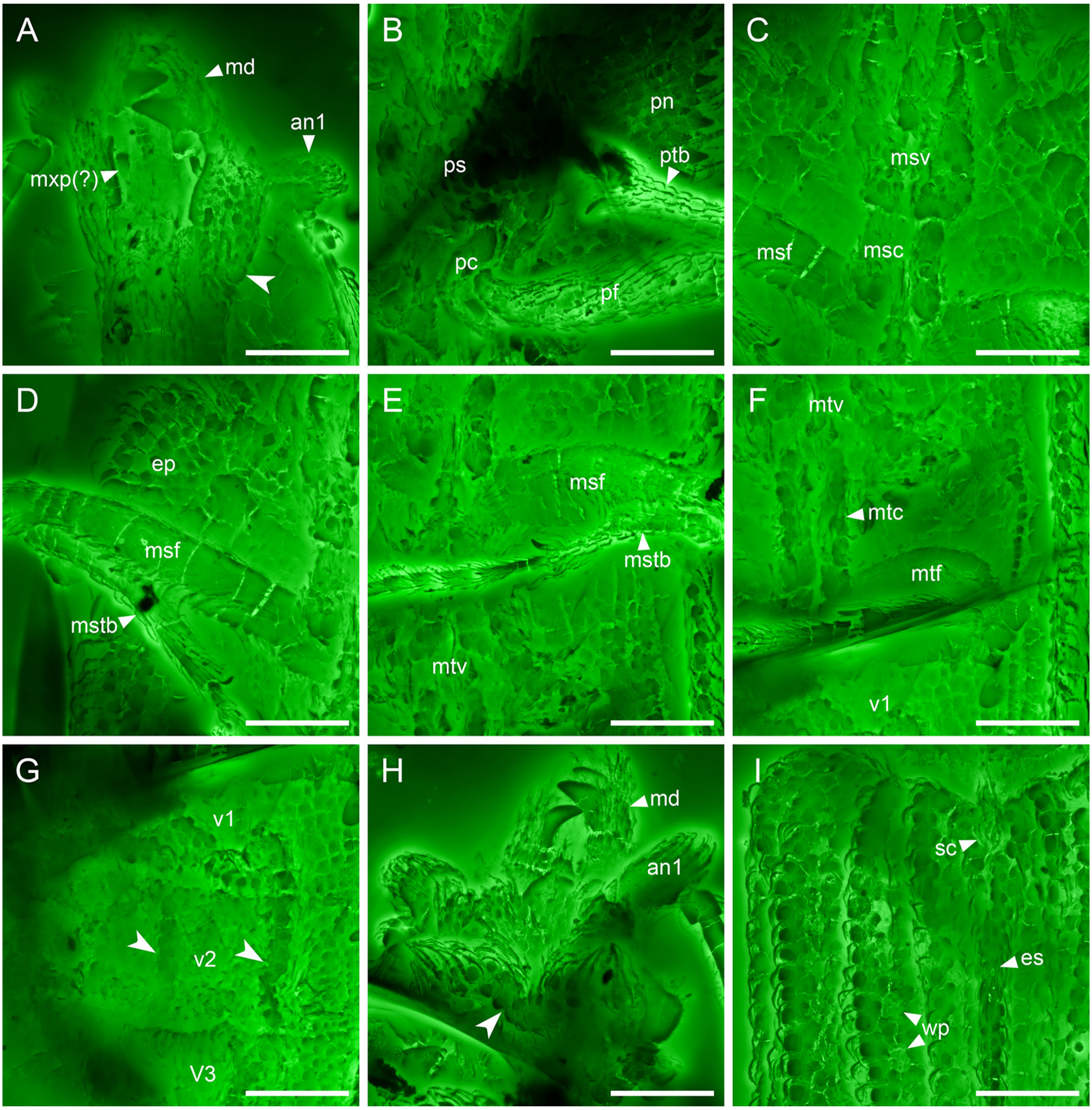

Figure 5. Details of *Clessidromma palmeri,* holotype, NIGP166270, under confocal microscopy. (A) Head, ventral view, with arrowhead showing the elevated platform. (B) Prothorax, ventral view. (C) Mesothorax, ventral view. (D) Mid leg and elytral epipleuron, ventral view. (E) Mid leg and metathorax, ventral view. (F) Hind leg, ventral view. (G) Abdomen, ventral view, with arrowheads showing the longitudinal ridges (? taphonomic artefact). (H) Head, dorsal view, showing the v-shaped transverse carina (arrowhead). (I) Elytral base, dorsal view. Abbreviations: an1 = antennomere 1; ep = epipleuron; es = elytral suture; md = mandible; msc = mesocoxa; mstb = mesotibia; msv = mesoventrite; mtc = metacoxa; mtf = metafemur; mtv = metaventrite; mxp = maxillary palp; pc = procoxa; pf = profemur; pn = pronotum; ps = prosternum; ptb = protibia; sc = scutellum; v1-3 = ventrite 1-3; wp = window punctures. Scale bars: 400 µm.

from *Lepidomma* in lacking the ridged scales and elytral carinae. The character combination of *C. zengi* does not fit into any other known ommatid genera as well. Thus we establish a new genus here to accommodate *C. zengi*. Thus *C. zengi* is here transferred into the new genus as *Kirejtomma zengi* **comb. nov.**

Etymology: The generic name is formed based on the generic name *"Omma"* and the surname of the Russian entomologist Alexander G. Kirejtshuk. The name is neuter in gender.

DISCUSSION

Jarzembowski *et al.* (2018) placed *Clessidromma* in a newly established tribe, Clessidrommatini, mainly based on its prothoracic structures. According to Jarzembowski *et al.* (2018), the foreleg insertion of *Clessidromma* is similar to tshekardocoleids, where the insertions are near the middle of the prothorax. Escalona *et al.* (2020) further explicitly stated that *Clessidromma* has externally closed procoxal cavities. However, a detailed examination reveals that the prothoracic structure of *Clessidromma* is actually similar to other ommatids, rather than tshekardocoleids. The procoxal cavities of tshekardocoleids are externally closed and indeed located well away from the posterior edge of prothorax (fig. 29 in Ponomarenko, 1969), whereas the mesoventrite of *Clessidromma* possesses well-developed procoxal rests (Fig. 4C), indicating that its procoxal cavities are in fact externally open. Besides, in Tshekardocoleidae, the procoxae are widely separated by the broad prosternal process, and the prosternal process extends far beyond the posterior end of procoxae. By contrast, *Clessidromma* has adjacent procoxae, and its prosternal process is reduced (Fig. 4B), which is typical in Ommatidae (Hörnschemeyer & Beutel, 2016).

Clessidromma superficially resembles *Tetraphalerus* Waterhouse in having a rather elongate body shape. The sharp edge of the ventral platform on head may possibly indicate the presence of a *Tetraphalerus*-like ventrolateral antennal groove. *Clessidromma* is additionally similar to *Tetraphalerus* in having longitudinal ridges on pronotum. However, *Tetraphalerus* is unique in Ommatidae (and differs from *Clessidromma*) in having antennomeres 5-11 without setae and mushroom-shaped tubercles (Beutel *et al.,* 2008). The separate mentum present in *Tetraphalerus* and related fossils (Li *et al.,* 2021b) is also not observed in *Clessidromma*. Considering the high morphological diversity found in fossil Ommatidae, the similarity between *Clessidromma* and *Tetraphalerus* might be merely homoplasious. The exact position of *Clessidromma* within Ommatidae requires further studies.

DATA AVAILABILITY

The original confocal data are available in Zenodo repository (http://doi.org/10.5281/zenodo.5214200).

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AUTHORS' CONTRIBUTIONS

Y.-D.L. and C.-Y.C. conceived the study. Y.-D.L. acquired and processed the photomicrographs. Y.-D.L. drafted the manuscript, to which C.-Y.C. contributed. Both authors gave final approval for publication.

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