

Mid-Cretaceous coastal amber forest palaeoenvironment revealed by exceptionally preserved ostracods from an extant lineage

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Abstract

As a famous fossil Lagerstätte, the mid-Cretaceous (ca. 100 Ma) amber from Kachin, northern Myanmar, harbors one of the most diverse Mesozoic palaeobiotas yet discovered. Over the past few years, reports of organisms trapped in Kachin amber have increased exponentially. Ostracods, as fully aquatic animals, are so far represented in Kachin amber by two records of specimens without soft parts (1 valve and two carapaces) as well as an exceptional assemblage with well-preserved soft parts comprising 39 specimens of three species assigned to the families Candonidae and Loxoconchidae. Since the last-mentioned focused on the exceptional preservation of giant sperm and reproductive organs in only one species, we here present in-depth morphological descriptions of all three species including a new genus: *Myanmarcypris hui* Wang et al., 2020, *Electrocypris burmitei* gen. et sp. nov., and *Sanyuania* sp. We further describe taphonomic traits indicating that the studied ostracods were quickly surrounded by resin and instantly immobilized. The palaeoenvironment is considered to be a vegetated brackish (mesohaline-oligohaline) lagoon.

Key Words

Candonidae, Kachin amber, Loxoconchidae, ostracods, palaeoenvironment, taphonomy

1. Introduction

Calcified bivalved carapaces of ostracods (Crustacea) have a high potential to be preserved as microfossils, and consequently ostracods have been the most common fossil arthropods since the Ordovician (Rodríguez-Lazaro and Ruiz-Muñoz 2012). However, ostracod soft parts (body and appendages) are rarely fossilized (Matzke-Karasz and Smith 2020). Furthermore, as fully aquatic animals, ostracods are scarcely trapped in amber in contrast to water-bound insect larvae. The few cases known include those from Cenozoic ambers from early Miocene in Mexico and the Eocene of the Baltic region (e.g. Keyser and Friedrich 2017; Matzke-Karasz et al. 2019). Kachin amber containing the most diverse biota of all known Cretaceous ambers provides a unique window

into mid-Cretaceous ecosystem (Yu et al. 2019). Over the past two decades, more than 500 families of invertebrates, vertebrates, protists, plants, and fungi have been reported, including scorpions, spiders, insects, frogs, a feather and a lizard (Ross 2019; Ross 2020). However, for Kachin amber, only three ostracod specimens were found, without soft parts, prior to the discovery of the material on which the current study is focused (Xing et al. 2018; Wang et al. 2020a). Wang et al. (2020b) first reported ostracods with soft parts (appendages and reproductive organs) in a single piece of mid-Cretaceous Kachin amber (approximately 100 million years old) and erected a new species and genus, *Myanmarcypris hui* Wang et al., 2020 and gave only brief consideration to two additional species in the same assemblage. In the present study we provide a full taxonomic, taphonomic

and palaeoenvironmental appraisal of the exceptionally preserved ostracods in this amber piece, adopting a palaeobiological approach to compare them with living relatives from the same Paracypridinae lineage, and the Loxoconchidae, respectively.

2. Materials and methods

The amber piece used for this study is from an amber mine near Noije Bum Village, Tanai Town, Hukawng Valley in Kachin Province, northern Myanmar (approx. latitude 26°13'47"N, 96°36'15"E). Grimaldi et al. (2002) and Ross et al. (2010) provided a general introduction to the amber deposit and its geological settings. The age of the studied amber was considered to be late Albian–early Cenomanian according to an ammonite trapped in the amber (Yu et al. 2019), which is also supported by U-Pb zircon dating of the volcanoclastic matrix with a maximum age of 98.79 ± 0.62 Ma (earliest Cenomanian) (Shi et al. 2012).

The elliptical amber piece (Suppl. material 1: Fig. S1; length 18 mm, width 14 mm, height 4 mm; volume approx. 0.78 cm^3) is permanently curated in the Lingpoge Amber Museum (Building No. 59, No. 2338 Duhui Road, Minhang District, Shanghai 201108, China) in compliance with the International Code of Zoological Nomenclature (Ride et al. 1999) and the instruction of International Palaeontological Society (Szwedo et al. 2020). This amber piece was acquired in 2016 and has been deposited in the Lingpoge Amber Museum (Shanghai) since January 2017, before the Myanmar military closed the Kachin amber mining in November 2017. The specimen is permanently housed in the Lingpoge Amber Museum in Shanghai (Building No. 59, No. 2338 Duhui Road, Minhang District, Shanghai 201108, China) which is a private museum (Director: Fangyuan Xia; Email: 138120076@qq.com). The fossils in the Lingpoge Amber Museum are held safely in trust for the benefit of researchers and educators throughout the world; the specimens reported in this study may be accessed by contacting, in the first instance, the corresponding author.

To further support unlimited access to the primary types of *Electrocypria burmiti* gen. et spec. nov. described in the present work, our tomographic data (virtual types) have been incorporated into the collection of the Chinese Academy of Sciences (NIGP175852) and cross referenced between the NIGP and the Lingpoge Amber Museum. Additionally, the data will be deposited in the Geobiodiversity Database (GBDB, <http://www.geobiodiversity.com>).

The studied ostracods were scanned at the micro-CT laboratory of Nanjing Institute of Geology and Palaeontology (NIGPAS), using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa, to three-dimensionally reconstruct the ostracods. Wang et al. (2020b) provide more detailed information on tomographic methods.

Volume data processing was performed using software VGStudio Max (version 3.0; Volume Graphics) and the open source volume exploration tool Drishti v2.6 (Limaye 2012).

For the analysis of morphological details, volume renderings from Drishti were used and the chaetotaxy was identified at the model itself by using a red-cyan 3D mode, so that the position of every detail could be identified in three dimensions (e.g., Suppl. material 2: Fig. S2). By using manipulation tools (rotate, zoom, clip, carve, etc) every desired view could be adjusted. Drawings were made by choosing an optimal view of each appendage, and using a screen shot as a basis for the drawing to then add all morphological details. This process is very similar to the drawing process from a light microscope with a camera lucida, where several focus levels are integrated in a final drawing.

3. Systematic palaeontology

Terminology for the appendages, segment numbering, and their chaetotaxy was adopted from Meisch (2000) and Maddocks (1992). Hierarchical taxonomic positions of non-marine taxa are based on the checklist by Meisch et al. (2019). The higher classification follows Smith et al. (2015).

The line drawings of appendages in this study can only reflect those anatomical details which are clearly observable in the available tomographies. A seta missing in a certain place where it would be expected in related modern species does not mean that it was not present in the amber-entrapped animal when it was still alive. Consequently, missing features such as setae cannot be used as a taxonomic feature in the following species descriptions – only the presence of a seta can. This shortcoming limits the possibilities of comparing the Myanmar amber ostracods to known species in related modern taxa. Drawings of the appendages may appear coarse and sometimes schematic compared to those of living ostracods, but since they are based on tomographic data of what is left of the appendages, this deficiency is inevitable.

Abbreviations

A1	first antenna (antennula);
A2	second antenna (antenna);
H	height;
HP	hemipenis;
L	length;
L5–L7	fifth to seventh limbs;
LV	left valve;
Md	mandibula;
Mxl	maxillula;
RV	right valve;
UR	uropodal ramus;
W	width.

Class Ostracoda Latreille, 1802
Order Podocopida Sars, 1866
Suborder Cypridocopina Jones, 1901
Superfamily Cypridoidea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Paracypridinae Sars, 1923
Tribe Renaudocypridini, McKenzie, 1980
Genus *Myanmarcypris* Wang et al., 2020

***Myanmarcypris hui* Wang et al., 2020**

Figs 1–7; Suppl. material 3: Movie S1, Suppl. material 4: Movie S2,
 Suppl. material 5: Movie S3

Material. 31 specimens, 5 of which were analyzed using
 3D X-ray microscopy: adult male, holotype (BA19005-1)

– L = 600 μ m, H = 356 μ m, W \approx 290 μ m; paratypes: adult female, (BA19005-2) – L = 609 μ m, H = 382 μ m, W \approx 300 μ m; A-2 juvenile (BA19005-3) – L = 400 μ m, H = 261 μ m, W \approx 175 μ m; A-3 juvenile (BA19005-4) – L = 313 μ m, H = 204 μ m, W \approx 161 μ m; A-4 juvenile (BA19005-5) – L = 226 μ m, H = 156 μ m, W \approx 120 μ m; material not tomographed: BA19005-11–36 (Suppl. material 1: Fig. S1).

Emended description. Carapace (Figs 1, 2): Adults small, in lateral view subtriangular. Female with higher and more pointed dorsal peak than male. In dorsal view, anterior and posterior ends blunt, not pointed. Valves thick and strongly reticulate, with prominent transverse muri, except for the dorsal region, which is smooth. In adults, a conspicuous antero-ventral lateral node present on each of the valves (Figs 1E, J, 2A). Antero-dorsally with smooth

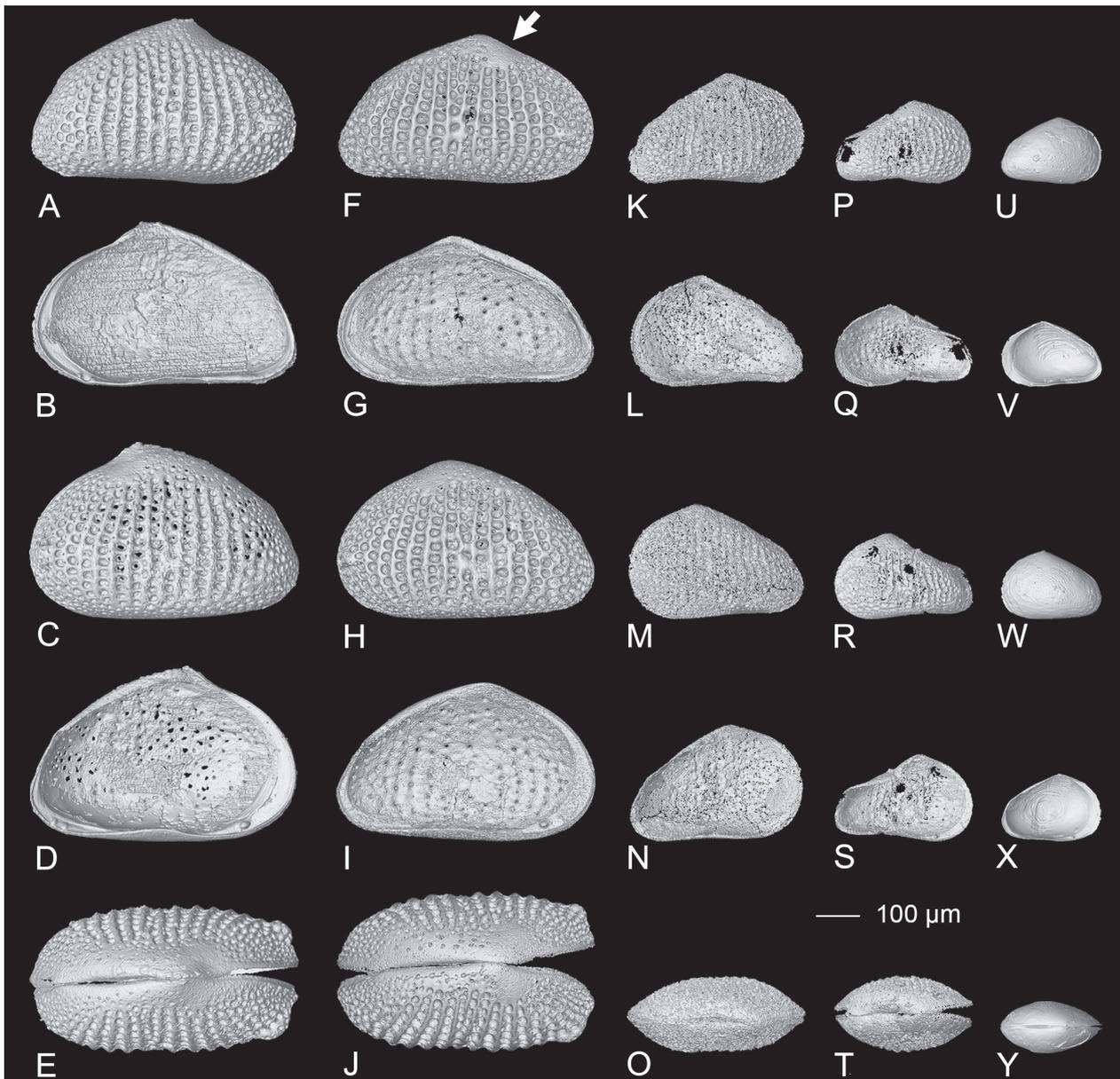


Figure 1. Microtomographic reconstruction of *Myanmarcypris hui*, surface rendering. A–E. Female, BA19005-2; F–J. Male, BA19005-1; K–O. Juvenile (A-2) BA19005-3; P–T. Juvenile (A-3), BA19005-4; U–Y. Juvenile (A-4), BA19005-5. First (uppermost) row: RV externally; second row: RV internally; third row: LV externally; fourth row: LV internally; fifth row: dorsal view of carapace, anterior to right. Arrow: smooth eye spot. Note: **D** and **E** are from Wang et al. (2020b).

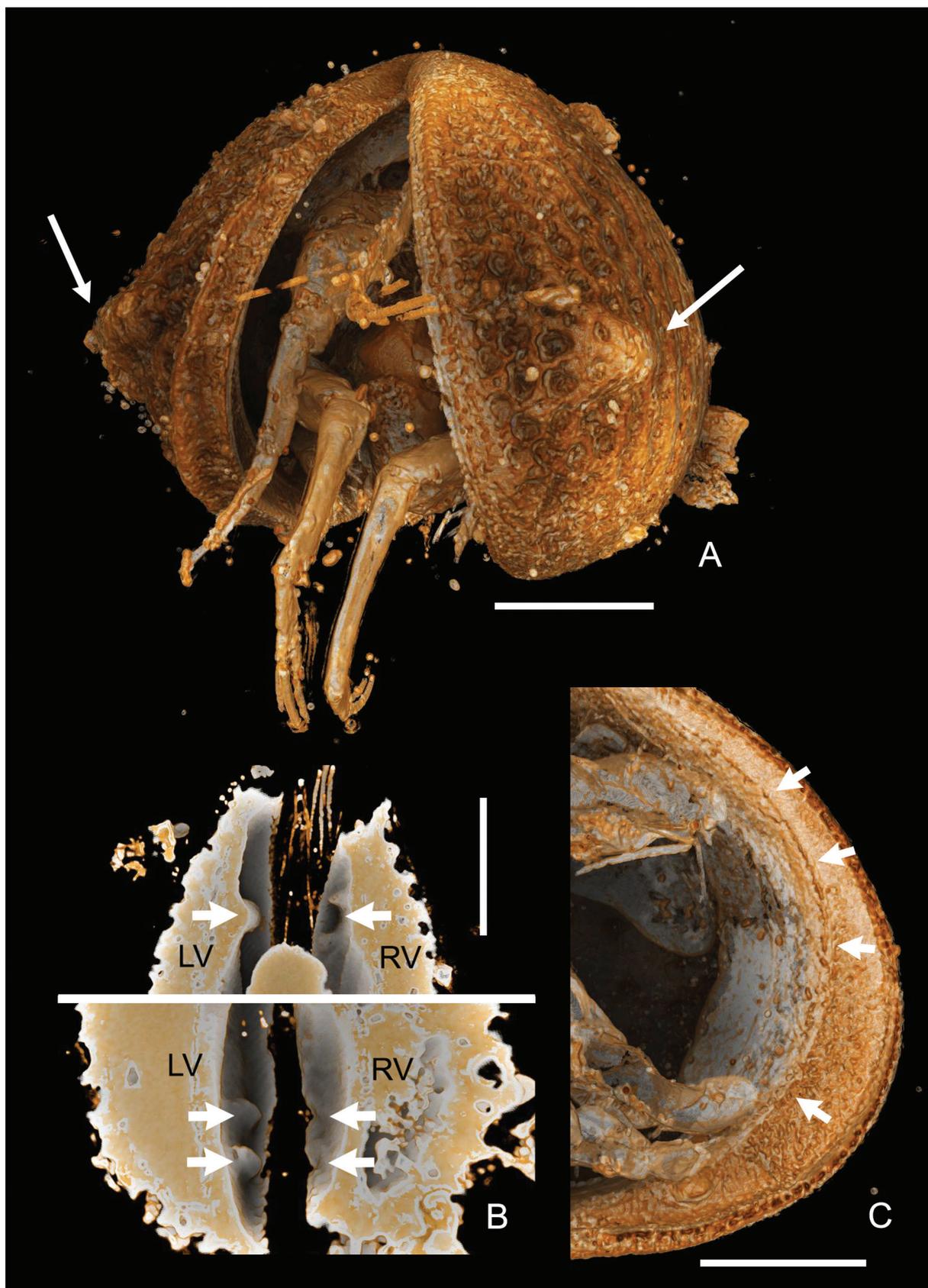


Figure 2. Microtomographic reconstruction of *Myanmarcypris hui* (volume rendering). **A.** Holotype, male, oblique anterior view with pairs of A1 and A2 reaching through gaping carapace. Arrows indicate pair of antero-lateral nodes on the ornamented carapace surface; **B.** Section of carapace of adult female paratype, dorsal view through ventral carapace gap. Upper part arrows showing single tooth in anterior LV and corresponding socket in RV. Lower part arrows showing pair of teeth and sockets in the posterior part of the valves. **C.** male holotype, anterior part of internal view with arrows pointing to inner list. Scale bars: 100 μm .



Figure 3. Microtomographic reconstruction of soft parts of male holotype of *Myanmarocypris hui* (BA19005-1), and female soft parts of *Myanmarocypris hui* (BA19005-2), surface renderings. A–N. With same scale, BA19005-1; O–AC. With same scale, BA19005-2; A. A1, right; B. A1, left; C. A2, right; D. A2, left; E. Md, right; F. Md, left; G. Mxl, right; H. L5, right; I. L5, left; J. L6, right; K. UR; L. Zenker organ, right; M. Zenker organ, left; N. Sperm duct; O. A1, right; P. A1, left; Q. A2, right; R. A2, left; S. Md, right; T. Md, left; U. Mxl, right; V. Mxl, left; W. L5, right; X. L5, left; Y. L6, right; Z. L6, left; AA. L7, right; AB. L7, left; AC. UR.

eye-spot (Fig. 1F). Normal pores distributed all over the valves except dorsal area. LV overlaps RV along dorsal and ventral margins. Hinge adont. Well-developed calcified inner lamella in adult carapaces, broader anteriorly than posteriorly, and anteriorly with inner list (Fig. 2C). Ventral margin of calcified inner lamella with conspicu-

ous anterior tooth in LV and corresponding socket in RV, and two smaller posterior teeth in LV with corresponding sockets in RV, the latter much less developed than anterior socket (Fig. 2B). No central muscle scars preserved. Preserved juveniles show similar carapace ornamentation as adults except for A-4 stage, which is smooth (Fig. 1).

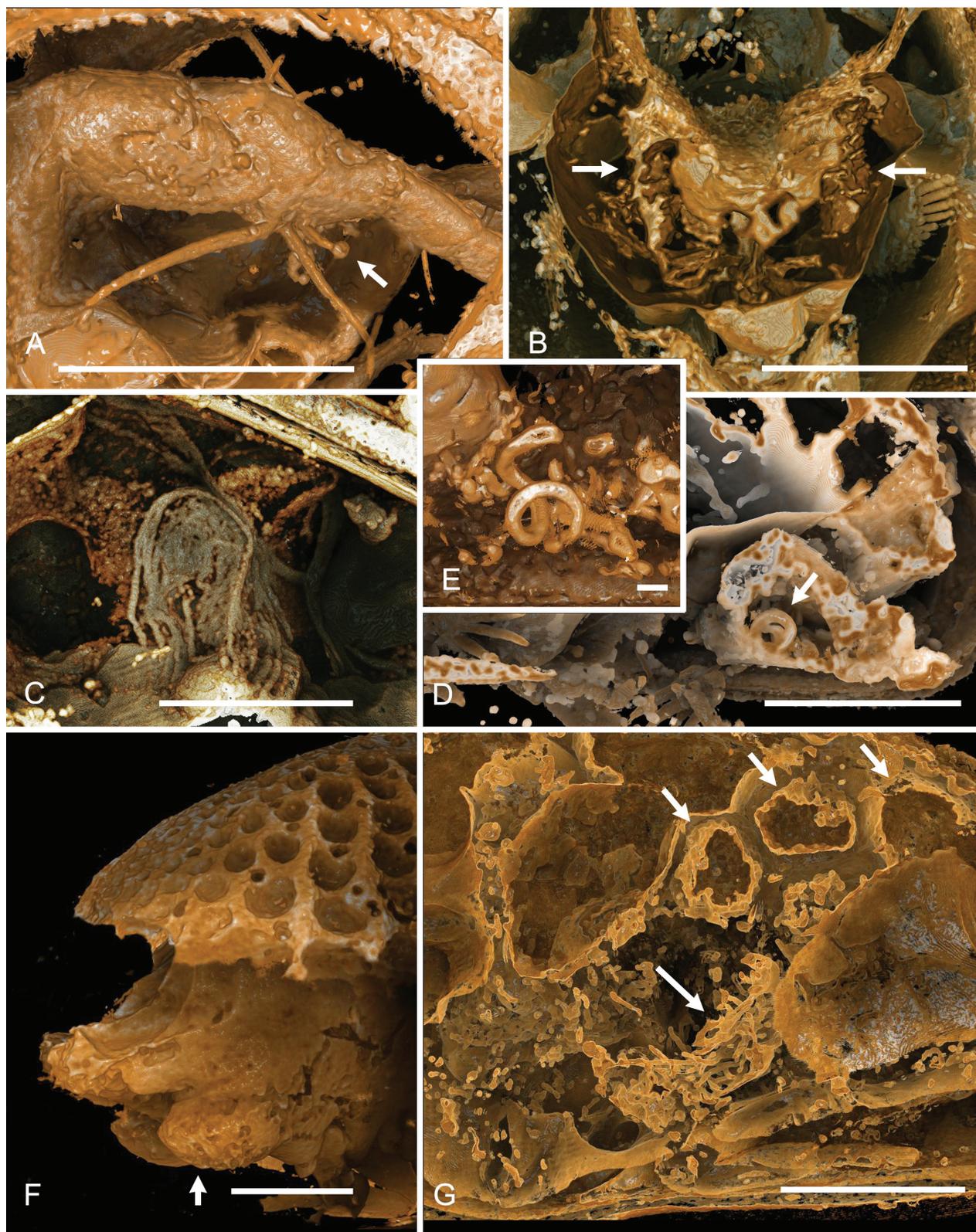


Figure 4. Microtomographic reconstruction of adult male (BA19005-1) and adult female (BA19005-2) *Myanmarcypris hui* (volume rendering). **A.** Male A1 with prominent Rome Organ (arrow); **B.** Male with pair of Zenker Organs in their body cavity (arrows); **C.** Loop of long sperm duct (vasa deferentia) in body cavity of male; **D.** Posterior body of male with hemipenis, which partly exposes coiled internal sperm duct (arrow); **E.** Detail of preserved sperm duct in hemipenis; **F.** Posterior body of female, with female genital lobes exposed (arrow); **G.** Section of female posterior body with eggs (short arrows) and stored spermatozoa (long arrow). Scale bars: 100 µm (A–D, F–G); 10 µm (E).

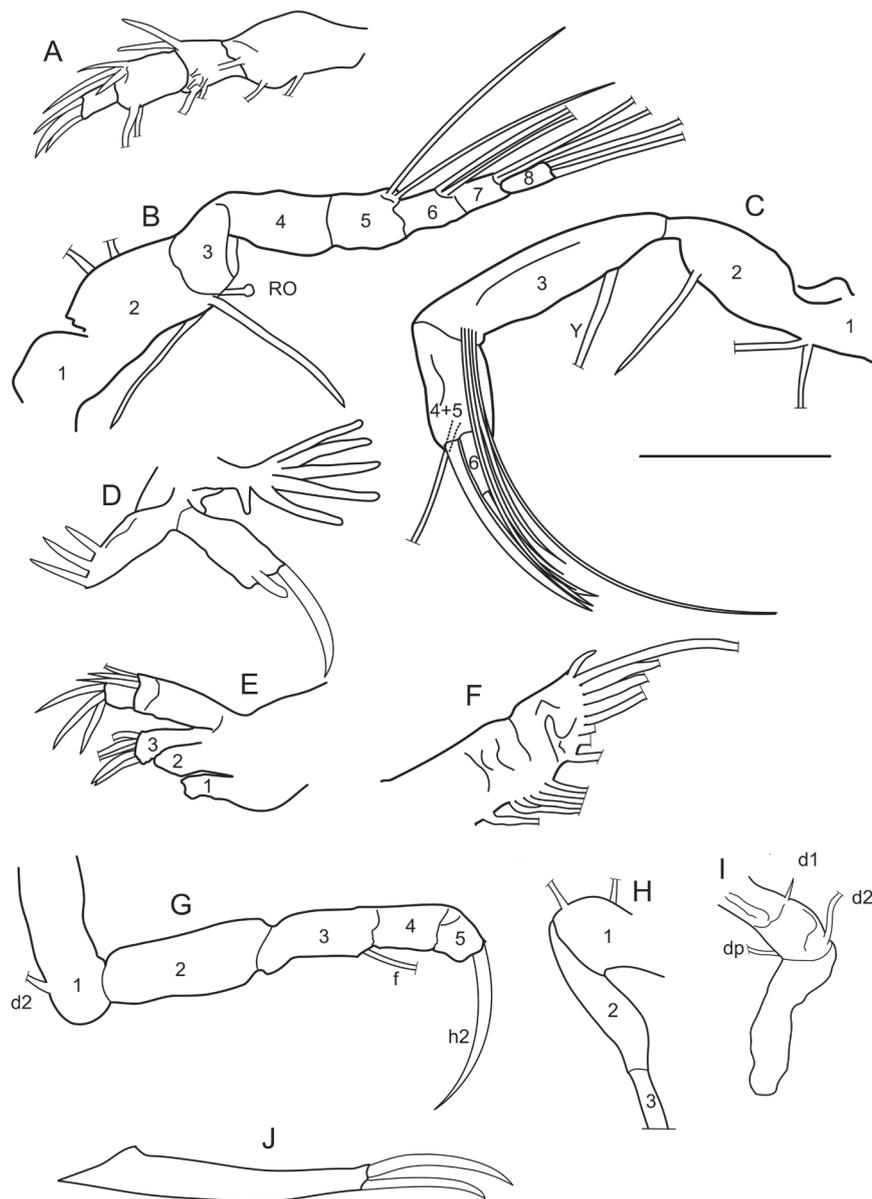


Figure 5. Drawings of appendages of *Myanmarocypris hui*, based on microtomography of adult male (BA19005-1) and adult female (BA19005-2). **A.** Right Md endopod (interior view); **B.** A1; **C.** A2; **D.** Male L5; **E.** Mxl palp and endites; **F.** Mxl branchial plate; **G.** L6; **H.** Female L7; **I.** Male L7; **J.** UR. Scale bar: 100 μ m. RO = Rome Organ; Y = Aesthetasc Y.

Soft Body (Figs 3–6): A1 (Figs 3A, B, O, P, 4A, 5B) with eight segments. Segments 1 and 2 fused forming large base, with two setae of unknown length originating dorso-median and long setae situated ventro-distally on segment 2. Only a little more distal, ventro-basally on segment 3, prominent Rome Organ with inflated tip (Figs 4A, 5B). Segment 3 short and sub-triangular. Segment 4 longer than twice its width. Segments 5 to 8 not fused and rectangular, with decreasing widths. Presence of setae confirmed for segments as figured. Setae at least as long as figured, possibly longer.

A2 (Male) (Figs 3C, D, 5C) Segment 1 (coxa) small, with 2 setae ventrally. Segment 2 (basis) elongate and carrying long ventro-apical seta. Segment 3 (first endopodal segment) elongate, with aesthetasc Y (ventro-median

and four natatory setae ventro-apically on the interior side of the appendage. Natatory setae possibly not complete and maximum length not known. Segments 4 and 5 possibly fused, together around half the length of segment 3. Apically with at least one seta subapical-exteriorly and three claws. Segment 6 small with at least one claw apically. Preservation of female A2 not sufficient for detailed chaetotaxy (Fig. 3Q, R).

Md (Figs 3E, F, S, T, 5A) Masticatory process of coxa too poorly preserved to describe morphology. Palp consisting of 4 separate segments and straight (i.e., not bent ventrally). Branchial plate not observed. Segment 1 (basis) with two setae ventrally, one at medium-length of the segment, the other more distally. Third seta originating on interio-apical margin. Shape of this segment subrectangular with

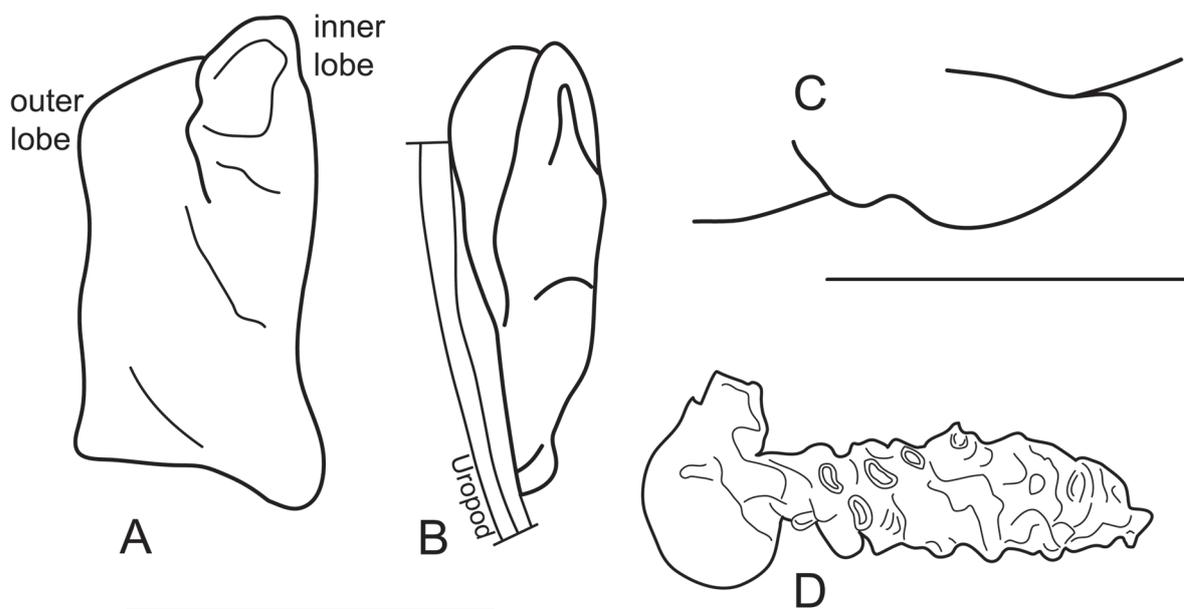


Figure 6. Drawings of appendages of *Myanmarocypris hui*, based on microtomography of adult male (BA19005-1) and adult female (BA19005-2). **A.** Hemipenis ventral view; **B.** Hemipenis, lateral view; **C.** Female genital lobe; **D.** Zenker Organ. Scale bars: 100 μm (**A–C**); 10 μm (**D**).

angulation on dorsal margin. Segment 2 square-shaped, with at least five setae apically (2 dorsally, 3 ventrally). Segment 3 rectangular with at least 5 setae confirmed 3 dorsally, 2 ventrally). Segment 4 much thinner than proximal segments, rectangular, distally with at least 1 claw and 2 setae.

Mx1 (Figs 3G, U, V, 5E, F) Protopod with branchial plate with at least 15 marginal setae. Three masticatory lobes (endites 1–3) with distal claws/setae. Palp with two segments, both with at least 3 setae on their apical margins.

L5 Male (Figs 3H, I, 5D) no setae on protopod confirmed. Branchial plate with six marginal setae. Palp (endopod) a jointed clasping organ, carrying a long claw/finger-like process distally, and a shorter (sensory?) process more ventrally. Masticatory process with three or more setae. Female L5 badly preserved (Fig. 3W, X).

L6 (Figs 3J, Y, Z, 5G) Walking leg with 5 segments. Segment 1 with setae d1 and d2. Segment 2 elongate with no seta preserved. Segments 3 and 4 separate, not fused. Segment 3 with seta f distally, segment 4 with no seta g observed. Segment 5 with long claw h2.

L7 (Figs 3AA, AB, 5H, I) Distal parts of this appendage not preserved. Bending of this appendage dorsally suggests it being used as a typical cleaning leg. Segment 1 (basis) with setae d1, d2 and dp present. Segment 2 (first endopodal segment) long, with no seta preserved. Segment 3 preserved in one of the male's L7, however, only partially.

Ur ramus (Figs 3K, AC, 5J) Elongate, only slightly bent, with two relatively long terminal claws of similar length preserved (approx. half the length of the posterior edge of the ramus). Posterior and anterior setae not observed.

HP (Figs 4D, E, 6A, B) nearly rectangular in lateral view, with outer distal lobe wider and shorter than inner lobe. Several loops of sperm duct preserved in HP (Fig. 4E).

Female genital lobes (Fig. 4F) formed as spindle-shaped projections towards posterior and extending

nearly to the posterior-most end of the soft body (i.e. basis of the UR). Inside the female BA19005-2, several eggs and stored spermatozoa are preserved (Fig. 4G).

Zenker Organs (Figs 3L, M, 4B, 6D) preserved in male BA19005-1 with five whorls of spines, one with the efferent part of the vas deferens attached. Vasa deferentia forming narrow U-shaped loops mid-laterally (Figs 3N, 4C).

Remarks. In the original description, it was stated that this species (and genus) belongs to the Candonidae because of the morphology of the Zenker Organ. Further, it was assigned to the Paracypridinae and tentatively to the tribe Renaudcypridini (Wang et al. 2020b) based on the presence of an internal antero-ventral tooth in LV and a corresponding socket in RV. This character has been defined as tribe-specific by Wouters (2001), while in the other tribes of the Paracypridinae the sockets are missing. As specified in the present analysis, the two postero-ventral teeth in LV of *M. hui* also possess corresponding sockets, albeit less pronounced than the anterior one. The other diagnostic features of the Renaudcypridini on L7 cannot be verified with the investigated specimens, namely the strong, spiny processes situated dorso-distally on each of the segments 3 and 4 and the arrow-shaped setules on the d2 seta. Nevertheless, we here assign this genus to the Renaudcypridini on the basis of the teeth/socket-characters of the valves, hoping that future findings of this species will offer more morphological characters to eventually verify, or falsify, this decision.

Although there is clearly some affinity with the genus *Renaudcypris* McKenzie, 1980, *Myanmarocypris* is easily distinguished by its dorsal hump, its strong and exceptional surface ornamentation and the striking antero-lateral nodes of the valves. Some living species of the cypridid subfamily Cypricerinae share carapace morphological characteristics with *M. hui*, notably the dorsal hump and the anterior tubercles. For example, *Strandesia martensi*



Figure 7. Microtomographic reconstruction of juvenile (A-2, A-3, A-4) soft parts of *Myanmarocypris hui* (BA19005-3, BA19005-4, BA19005-5), surface renderings. **A–U.** With same scale; **A–K.** Juvenile (A-2), BA19005-3; **L–U.** juvenile (A-3), BA19005-4; **V–AE** with same scale, juvenile (A-4), BA19005-5. **A.** A1, right; **B.** A1, left; **C.** A2, right; **D.** A2, left; **E.** Md, right; **F.** Mxl, left; **G.** L5, right; **H.** L5, left; **I.** L6, right; **J.** L7, right; **K.** UR; **L.** A1, right; **M.** A1, left; **N.** A2, right; **O.** A2, left; **P.** Md, right; **Q.** Md, left; **R.** Mxl, right; **S.** Mxl, left; **T.** L6; **U.** UR; **V.** A1, right; **W.** A1, left; **X.** A2, right; **Y.** A2, left; **Z.** Md, right; **AA.** Md, left; **AB.** L5, right; **AC.** L6, left; **AD.** L7, right; **AE.** L7, left.

Savatenalinton, 2015 from Thailand has a dorsal hump situated in front of mid-length, but in contrast to *M. hui* its RV overlaps the LV dorsally and it lacks internal ventral marginal teeth and sockets (Savatenalinton 2015). The genus *Sataracypris* Deb, 1983 from India also has a similar dorsal hump and has been tentatively assigned to the Cypricercinae pending redescription (Savatenalinton

2015). *Bradleytriebella tuberculata* (Hartmann, 1964) from Thailand has a prominent external tubercle close to the anterior margin of each valve, in a similar position to the node on each valve of *M. hui*, but it has no dorsal hump or internal ventral marginal teeth and sockets (Savatenalinton and Martens 2009a). Soft parts of *M. hui* are broadly similar to those of Cypricercinae, but

the morphology of the caudal ramus attachment, which in Cypricerinae features a diagnostic Triebel's loop, remains unknown for *Myanmarcypris* and *Sataracypris*. For now, therefore, we consider the carapace similarities of *M. hui* with cypricerine species to be examples of homeomorphy rather than close phylogenetic affinity.

Several juvenile specimens were embedded in the same amber piece (Wang et al. 2020b), allowing for the presentation of an ontogenetic series from A-4 to A-2 (Fig. 1K–Y), including soft parts (Fig. 7, Suppl. material 3: Movie S1, Suppl. material 4: Movie S2, Suppl. material 5: Movie S3) (no A-1 specimen found). These juveniles lack the pair of antero-lateral nodes present in the adults' valves. The A-4 specimen even lacks the pronounced surface ornamentations of older stages (Fig. 1U).

Family Candonidae Kaufmann, 1900

Subfamily Paracypridinae Sars, 1923

Electrocypria gen. nov.

<http://zoobank.org/9AC4D9B2-3D6C-422A-9319-EBA9E4430951>

Type species. *Electrocypria burmitei* sp. nov.

Etymology. Name referring to 'electrum', the Latin term for amber + cypria, a common epithet in candonid ostracods.

Diagnosis. Small ostracods of the family Candonidae, with subrectangular (male) to trapezoidal (female) lateral carapace shape. Dorsal margin with greatest height at about 1/3rd of length, tapering down in straight line from there towards anterior and posterior ends. Anterior end curved broadly, posterior end with narrow curve, but not pointed. Calcified inner lamella not broad. Female higher than male. Fusiform in dorsal view with greatest width at mid-length. A1 with segments 3 to 8 separate (not fused). Natatory setae present on A2. L7 with segments 3 and 4 clearly separate, each without dorso-apical, marginal spiny processes (hooks). Terminal segment short (not longer than wide), carrying a robust and long claw h2 and a long reflexed seta h3. UR with anterior and posterior claws of the same length.

Remarks. The new genus is excluded from the Ilyocyprididae and Notodromadidae by its carapace morphology, and from the most Cyprididae subfamilies by its lack of a terminal pincer on the L7 (see, e.g., Horne et al. 2019). We are aware of some extant cypridid genera of the subfamily Cypridopsinae with non-pincer L7 (e.g., *Neocypridopsis* Klie, 1940; *Paranadopsis* Almeida et al., 2021; *Cypridopsis* Savatentalinton, 2020) or incomplete pincer structure (e.g., *Brasilodopsis* Almeida et al., 2021) but all of these share the cypridopsine character of a reduced UR, unlike *Electrocypria* which has a fully developed UR. There is also the genus *Batucyprretta* (subfamily Batucyprrettinae) with a much reduced UR and lacking the L7 pincer, considered by its describing authors (Victor and Fernando 1981) to be transitional to the Cypridopsinae. The cyprid genus *Zonocyprretta* De Deckker, 1981 (subfamily Bradycypridinae) lacks the L7 pincer and has a

fully-developed UR, but differs from *Electrocypria* by virtue of other features including marginal septa in the valves.

Within the three subfamilies of the Candonidae, *Electrocypria* is best allocated to the Paracypridinae, foremost because of the natatory setae observed in the female specimen. Such natatory setae are not present in the Candoninae. The third subfamily, Cyclocypridinae, can be excluded by the valve morphology and shape, as well as by the cyclocypridine L7 morphology with segments 3 and 4 being fused, and the terminal segment carrying a long reflexed seta h3 and two short h1 and h2 setae distally. The genus *Electrocypria* therefore belongs to the subfamily Paracypridinae, which is currently subdivided into three tribes, these being the marine Paracypridini and the marine to brackish Thalassocypridini and Renaudocypridini. Although the carapace morphology may point to the Thalassocypridini, *Electrocypria* cannot be allocated to this tribe because of its L7 morphology, with segments 3 and 4 not being fused, a short terminal segment and its two long h setae distally. In the Thalassocypridini, segments 3 and 4 of L7 are fused, the terminal segment is long and bears only a long reflexed seta, while the other two h setae are short. *Electrocypria* does not qualify as a Renaudocypridini because of the lack of a unique feature of this tribe: the strong, spiny processes situated dorso-distally on both segments 3 and 4 of L7. In *Electrocypria* the dorsal edges of these segments are clearly smooth. Also, Renaudocypridini possess a well-developed tooth in the antero-ventral area of the inner lamella in the LV, complemented by a defined socket on the inner lamella of the RV (Wouters 2001) – characters that could not be observed in *Electrocypria*. Species of the third tribe, Paracypridini, typically show wide calcified inner lamellae with narrow vestibula and broad fused zones with radial pore canals in their well-calcified carapaces. These characters are not present in *Electrocypria*. The genera of the Paracypridini are more diverse in their soft body features than those of the Thalassocypridini and Renaudocypridini, as shown in the detailed review of anatomical features in the Paracypridinae by Maddocks (1992). The anatomy of A1 with its varying degrees of segment fusion and the variable combination of L7 features in the different genera may serve as examples. However, none of these mosaic patterns of characteristics fits to those observed in the type species of *Electrocypria*. Due to the valve morphology, combined with the lack of congruence in important soft body features with any genus of the Paracypridini, we refrain from attributing *Electrocypria* to this tribe. Consequently, we cannot allocate the genus *Electrocypria* to any of the currently accepted three tribes of the Paracypridinae.

Electrocypria burmitei sp. nov.

<http://zoobank.org/5BE413FE-3EC1-48ED-9C82-EF25C4776D2F>

Figs 8–13; Suppl. material 6: Movie S4, Suppl. material 7: Movie S5

Etymology. Referring to 'burmite', which is one of the names of amber from Myanmar.



Figure 8. Microtomographic reconstruction of *Electrocypria burmitei* gen. et sp. nov., surface rendering. A–E. Male, BA19005-6; F–J. Female, BA19005-7. First (uppermost) row: RV externally; second row: RV internally; third row: LV externally; fourth row: LV internally; fifth row: dorsal view of carapace, anterior to right.

Material. Seven specimens enclosed in one amber piece (BA19005-6, 7, 37–41) (Fig. S1), two of which (male holo- and female paratype) were analyzed using 3D X-ray microscopy. The species description is based on the tomographic data.

Type locality and stratigraphy. Hukawng Valley, Kachin Province, northern Myanmar; upper Albian–lower Cenomanian.

Types. Holotype: BA19005-6 (male); Paratype: BA19005-7 (female).

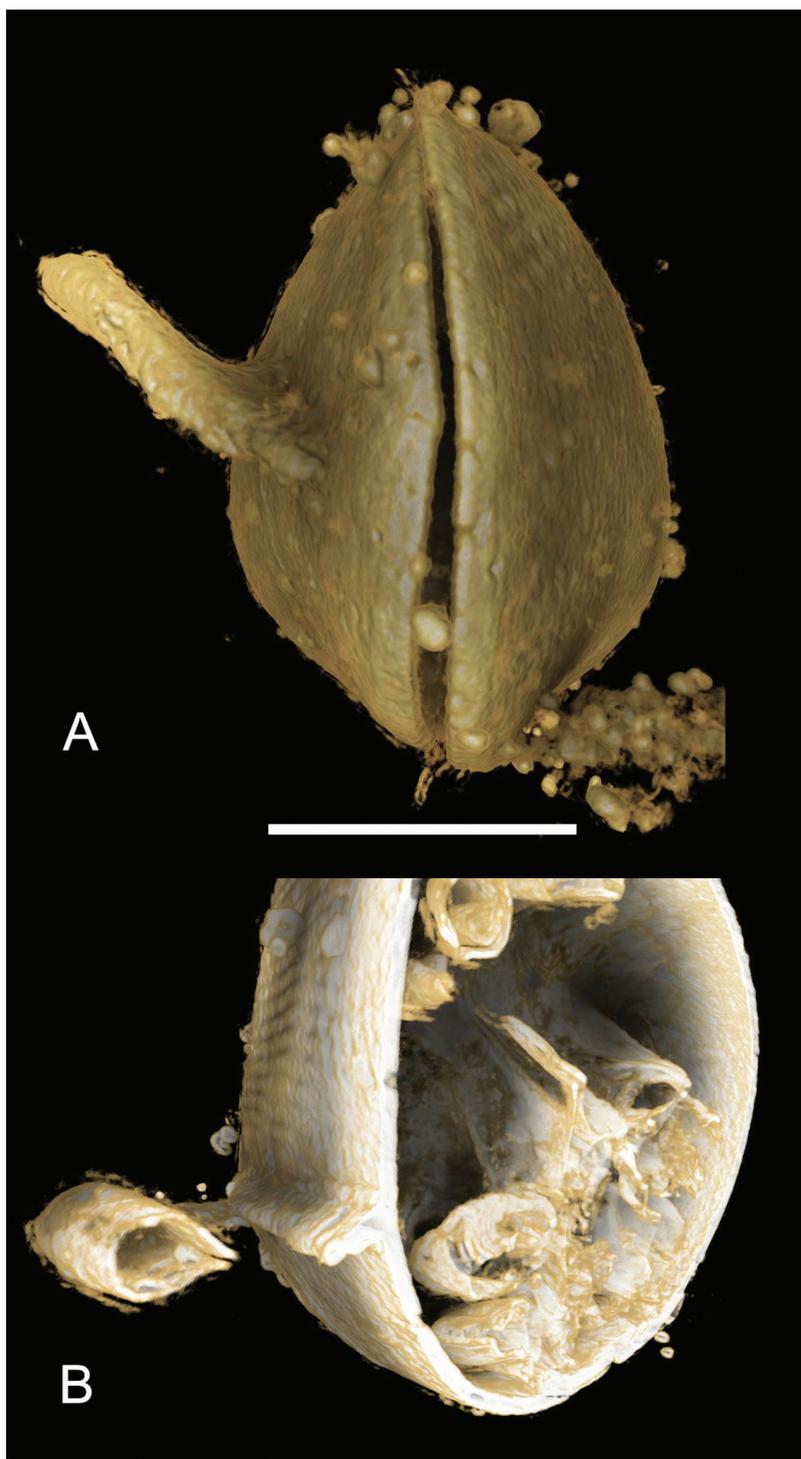


Figure 9. Microtomographic reconstruction of *Electrocypria burmitei* gen. et sp. nov., volume rendering. **A.** Male, BA19005-6, anterior view, with solidified body liquid extruding from breakage of RV; **B.** Cross section of same specimen, showing extrusion along the breakage in detail. Scale bar: 100 μm .

Repository. Lingpoge Amber Museum (Shanghai).

Dimensions. L = 470 μm , H = 200 μm , W \approx 160 μm (male, holotype); L = 470 μm , H = 217 μm , W \approx 145 μm (female, paratype).

Diagnosis. see diagnosis of the currently monospecific genus.

Description (The species description is based on the tomographic data, NIGP175852). Carapace (Figs 8, 9): LV overlaps RV along the dorsal and ventral margins.

Dorsal margin with greatest height at about 1/3rd of length, tapering down in straight line and same angle to anterior and posterior ends. Hinge well-developed, straight, between highest point and posterior end. Both anterior and posterior margins nearly equicurvate, with the latter curved much narrower than the former, but lacking an acute angle or pointed tip. Fusiform in dorsal view with greatest width at mid-length. Ventral margin slightly concave at mid-length. Calcified inner lamella relatively

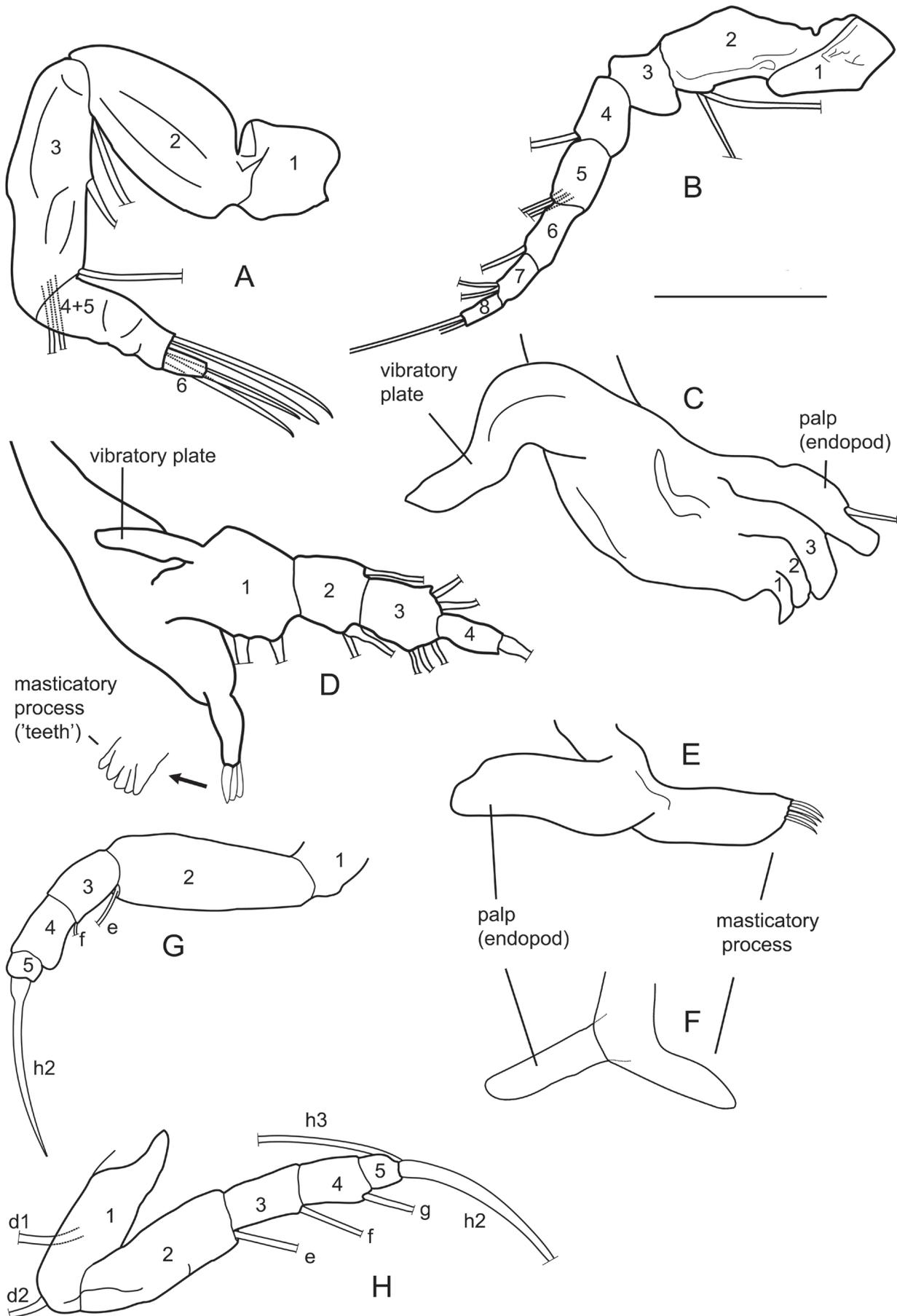


Figure 10. Drawings of appendages of *Electrocypria burmitei* gen. et sp. nov., based on data of adult male (BA19005-6) and adult female (BA19005-7). **A.** A2; **B.** A1; **C.** Mx1; **D.** Md; **E.** male L5; **F.** female L5; **G.** L6; **H.** L7. Scale bar: 50 µm.

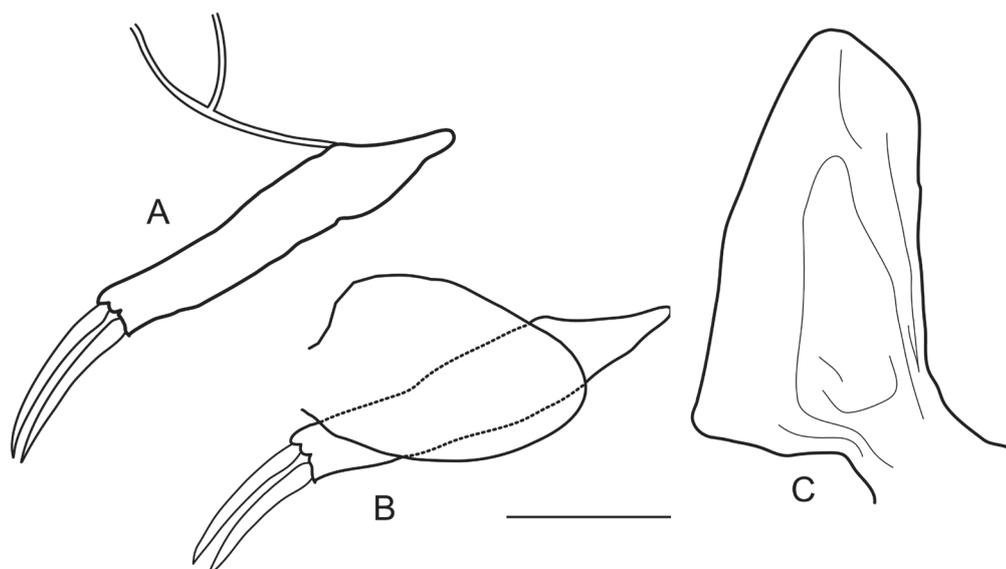


Figure 11. Drawings of appendages of *Electrocypria burmitei* gen. et sp. nov., based on microtomography of adult male (BA19005-6) and adult female (BA19005-7). **A.** UR with proximal attachment; **B.** UR with female genital lobe; **C.** Hemipenis, ventral view. Scale bar: 50 μ m.

narrow at free margin, slightly broader at posterior end, and broadest at anterior end. Central muscular scars not visible. Normal pores scattered over smooth surface.

Soft Body (Figs 10–13): A1 (Figs 10B, 12A, B, N, O, 13A) with eight segments. Segments 1 and 2 fused forming large base, with two long setae originating ventro-distally on segment 2. Segment 3 short and asymmetric, sub-triangular, with ventral extension. Segment 4 connected to segment 3 with ventral inclination. Segments 4 to 8 all separate (not fused) and rectangular, with decreasing widths. Presence of setae confirmed for segments as figured. Setae on segment 8 at least as long as figured, possibly longer.

A2 (Figs 10A, 12 C, D, P, 13A) Segment 1 (coxa) sub-rectangular, segment 2 (basis) elongate and carrying long ventro-apical seta. Knee between segment 2 and 3. Segment 3 (first endopodal segment) very similar to segment 2 in shape and length, also carrying ventro-apical seta. Exopod not confirmed, but aesthetasc Y present. Natatory setae not observed in male, but at least 2 natatory setae present in one of the female's A2 (Fig. 12P); their exact point of origin at segment 3 is unclear. Segments 4 and 5 possibly fused, since clear segmental boundary could not be confirmed. Their length approximately half the length of segment 3. Apically with at least three claws (G1, G2, G3). Segment 6 small with at least one claw apically (GM or Gm).

Md (Figs 10D, 12E, F, Q, 13B) Masticatory process of coxa with teeth (total number uncertain). Palp consisting of 4 separate segments and remarkably straight (i.e., not bent ventrally towards mouth). Segment 1 (basis) with vibratory (branchial) plate on dorsal edge (no setae observed), and two thick setae ventrally, one at medium-length of the segment, the other more distally, but still at a considerable distance to segment 2. Shape of this segment obliquely trapezoidal due to angulation on dorsal margin. Segment 2 nearly square-shaped, with at least three setae apically (one dorsally, two ventrally). Segment

3 more elongate, with shoulders distally towards segment 4. On these shoulders, at least 5 setae confirmed (2 dorsally, 3 ventrally). Segment 4 much thinner than proximal segments, distally at least one thick seta or claw present.

Mx1 (Fig. 10C) Protopod with branchial plate (no setae confirmed), three masticatory lobes (endites 1–3) and palp. Palp possibly two-segmented, as dorsal seta might indicate. Distal claws and/or setae not confirmed.

L5 Male (Figs 10E, 12G, H, 13C): no setae on protopod confirmed. Palp (endopod) truncated, possible finger-like process of this clasping organ not observed. Masticatory process with several distal setae. Female (Figs 10F, 12R): masticatory process and palp preserved with no detail.

L6 (Figs 10G, 12I, J, S) Walking leg. Segment 1 small, segment 2 elongate with seta e distally. Segments 3 and 4 separate, not fused. Segment 3 with seta f distally, segment 4 with no seta g observed. Segment 5 with long claw h2.

L7 (Figs 10H, 12K, L, T, U, 13D) Cleaning leg, directed dorsally. Segment 1 (basis) with setae d1 and d2 present. Segment 2 (first endopodal segment) long, with distal seta e. Segments 3 and 4 separate, not fused. Segment 3 with seta f, segment 4 with seta g distally. Segment 5 short, nearly quadrate; distally long claw h2 and long reversed seta h3 present.

Ur ramus (Figs 11A, B, 12M, V, 13E) Relatively stout and straight, with two relatively long terminal claws of similar length preserved (approx. half the length of the posterior edge of the ramus). Posterior and anterior setae not observed. UR attachment simply branched.

HP (Figs 11C, 13F) roughly triangular in lateral view, with no differentiation of lobes observed. Greatest length of HP nearly a quarter of carapace length.

Female genital lobes (Figs 11B, 13G) formed as spindle-shaped projections towards posterior and extending nearly to the posterior-most end of the soft body (i.e. basis of the UR).

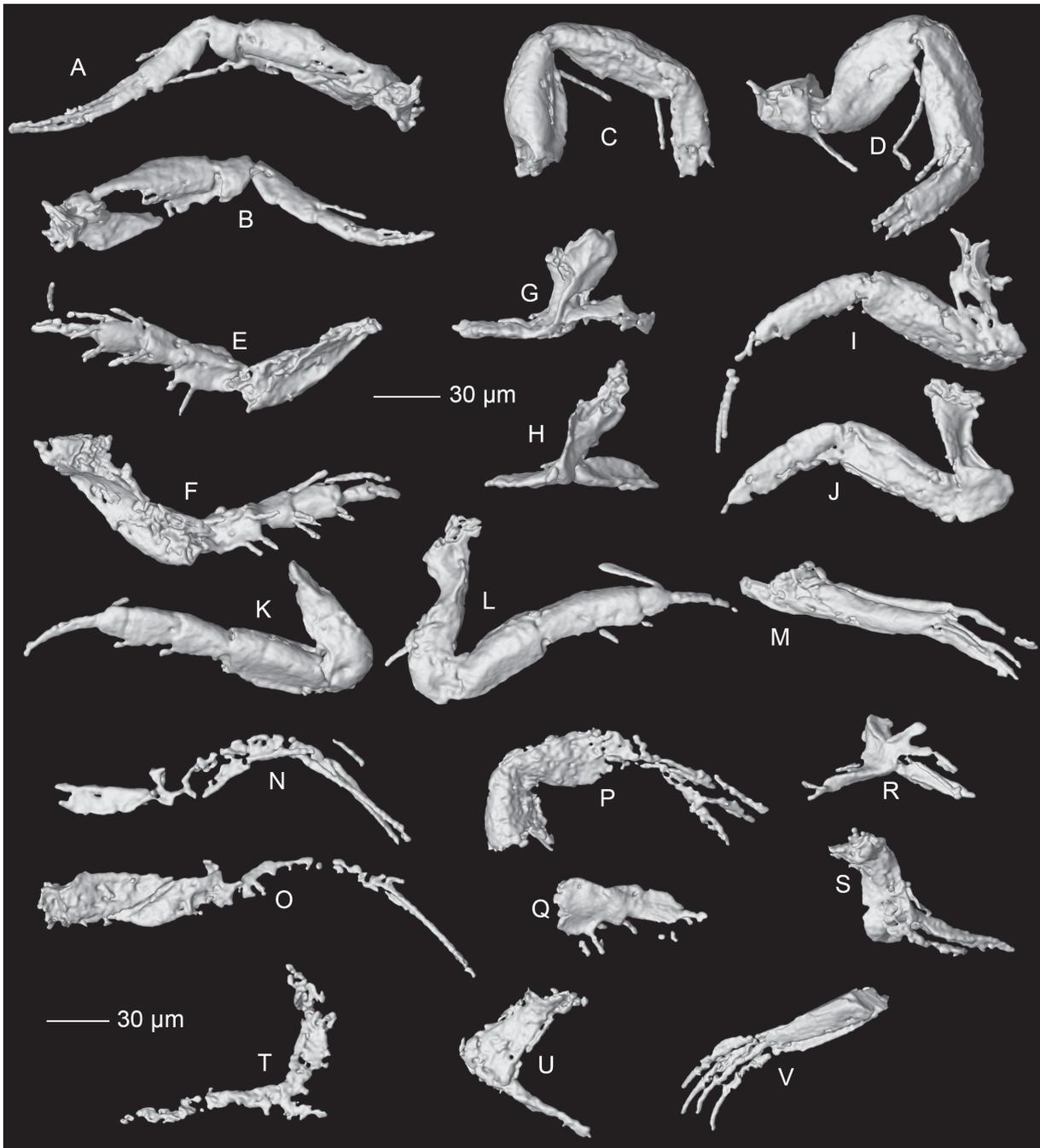


Figure 12. Microtomographic reconstruction of soft parts of male (BA19005-6) and female (BA19005-7) *Electrocypria burmitei* gen. et sp. nov., surface renderings. A–M. With same scale, male (BA19005-6); N–V. With same scale, female (BA19005-7). A. A1, right; B. A1, left; C. A2, right; D. A2, left; E. Md, right; F. Md, left; G. L5, left; H. L5, right; I. L6, right; J. L6, left; K. L7, right; L. L7, left; M. UR; N. A1, right; O. A1, left; P. A2, right; Q. Md, right; R. L5, left; S. L6, left; T. L7, right; U. L7, left; V. UR.

Remarks. *Electrocypria burmitei* gen. et sp. nov. possesses relatively long setae on A1, as well as at least 2 natatory setae on A2, however, the latter are only preserved partly, and possibly not at their full lengths. It is therefore impossible to evaluate the swimming capability of this species.

The straight appearance of the Md palp results from segment 2 being nearly square-shaped and not as wedge-shaped as is often the case in other Cypridoidea. None of the L5s is completely preserved in either specimen and

it remains unclear how the male claspers look in *E. burmitei* gen. et sp. nov. While L6 is formed as a walking leg with a long distal claw and segments 3 and 4 not fused, L7 is formed as a 5-segmented cleaning leg with setae e, f and g present, as well as long terminal h2 and h3 setae/claws. The holotype shows a linear breakage in its LV, in parallel to the dorsal margin, as well as minor breaking marks in its RV. The external pressure of the resin seems to have squeezed body liquid out of the animal on the LV into the surrounding resin (Figs 8A, B, 9A, B).

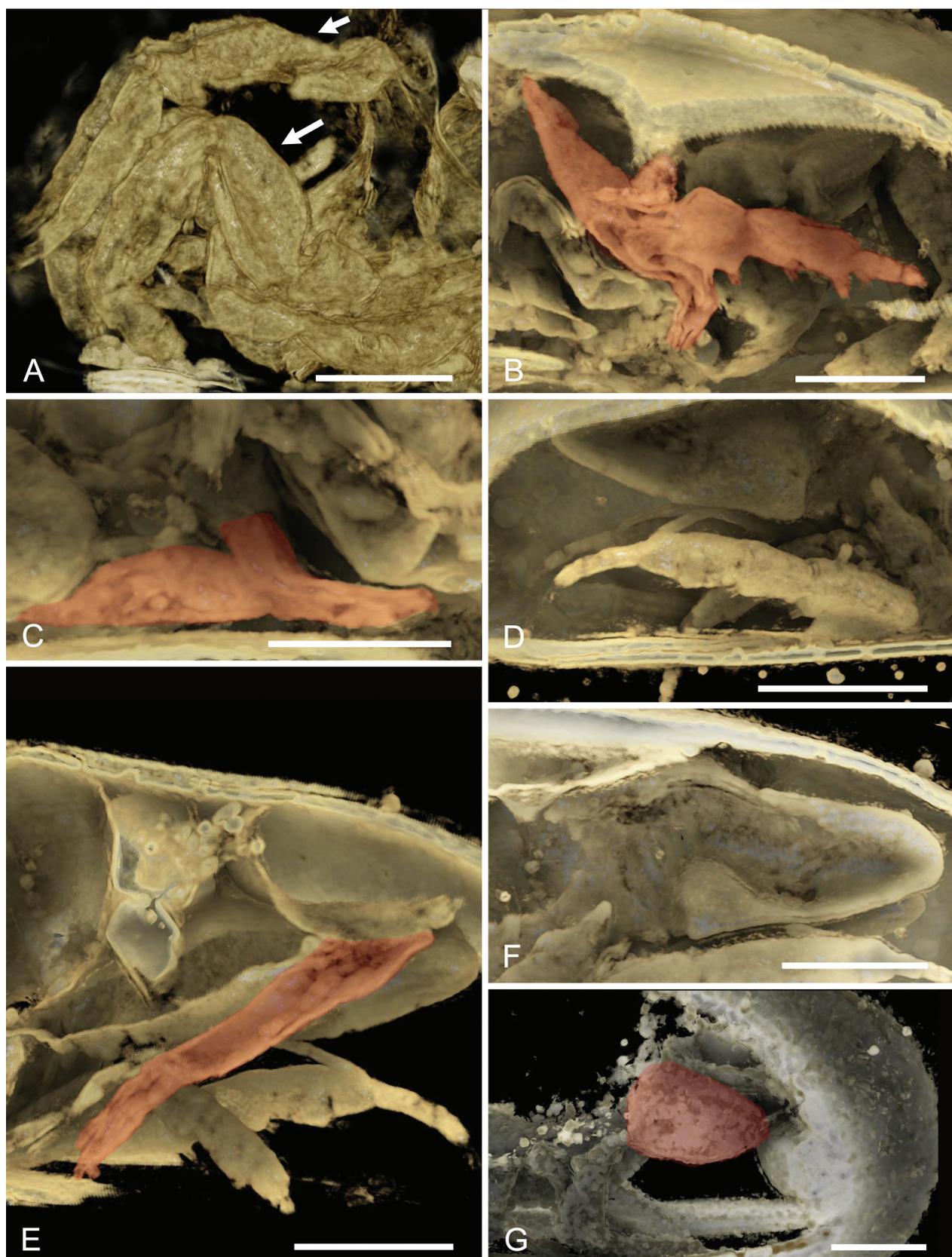


Figure 13. Microtomographic reconstruction of *Electrocypria burmitei* gen. et sp. nov., based on data of adult male (BA19005-6) and adult female (BA19005-7), volume rendering. **A.** A1 (short arrow) and A2 (long arrow); **B.** Right Md (highlighted); **C.** Male L5 (highlighted); **D.** Left L7; **E.** UR (highlighted); **F.** Right HP, interior view; **G.** Female genital lobe (highlighted). Scale bars: 50 μm .

Suborder Cytherocopina Baird, 1850
Superfamily Cytheroidea Baird, 1850
Family Loxoconchidae Sars, 1925

Genus *Sanyuania* Zhao & Han, 1980

Type species. *Sanyuania psaronius* Zhao & Han, 1980.

***Sanyuania* sp.**

Figs 14–16; Suppl. material 8: Movie S6

Material. Single male specimen; BA19005-8.

Dimensions. L = 245 µm, H = 116 µm, W ≈ 120 µm.

Description. Carapace (Figs 14A–E, 16A, C) small subtriangular shape in lateral view. Greatest height at ¼ of length. Anterior margin broadly rounded. Posterior margin narrowly rounded. Dorsal margin straight, moderately sloping down from the greatest height to the posterior margin. Ventral margin straight in middle part in both valves, with slightly concave regions in the very middle, forming distinct flaps as an area of valve overlap (LV>RV) (Fig. 16A). From posterior third, ventral margin ascending towards posterior end. Carapace in dorsal view elliptical, with posterior and anterior part compressed and central region strongly protruding. The valve's lateral surface punctate in the flat anterior and posterior marginal regions, while pitted (i.e., covered with wider and deeper depressions) in the central region and dorsally. Valves thick in cross section (Fig. 16C). Inflated central region with distinct sulcus mid-dorsally. Inner calcified lamella wide. Central muscular scar pattern, pore morphology and detailed hinge elements not preserved.

Soft parts almost all preserved, but with a low degree of detail.

A1 (Figs 14F, G, 15A, 16D) rod-shaped. Segmentation and setation not preserved.

A2 (Figs 14H, I, 15B, 16D) more robust than A1, number of segments unknown. With prominent knee between protopodite and endopodite, close to which the spinneret seta (exopodite) originates, the only preserved setation of both A2 in this specimen.

Between the right A2 and the internal side of RV, a roundish, disk-shaped body is preserved, which we tentatively interpret as the sac of the spinneret gland containing the secretion (Fig. 16D).

Md (Figs 14J, K, 15E, 16B, E) Masticatory process of coxa preserved, reaching into the oral opening, but teeth only weakly preserved. The palp's segmentation and setation not preserved. Vibratory plate not preserved.

Mxl (Figs 14L, M, 15C, 16B) Protopod with three masticatory lobes (endites 1–3) and two-segmented palp, without any claws/setae preserved; branchial plate preserved.

L5 (Figs 14N, O, 15F, 16F) Walking leg, elongate, with long endopodite consisting of indeterminate number of segments.

L6 (Figs 14P, Q, 15G, 16F) Presumed walking leg, protopodite elongate, endopod not well preserved.

L7 (Figs 14R, 15H) Walking leg, elongate protopodite and long endopodite, the latter with at least three segments.

HP (Figs 15D, 16F, G) almost triangular in shape, apically forming distinct tip, shaped like an arrowhead.

Remarks. We assign the studied specimen to the genus *Sanyuania* within the Loxoconchidae, mainly based on shape, ornamentation and morphology of its carapace. Preserved soft parts, although with little detail, and without genus-specific features being observable, at least do not oppose this assignment. The morphology of the preserved hemipenes is clearly in line with Hartmann's (1966: 758) description of hemipenes typical of Loxoconchinae as consisting of a voluminous capsule and a triangular, distally rounded top piece. A direct comparison of our specimens' hemipenis with that of *Sanyuania segersi* Savatnalinton & Martens, 2009a shows a high degree of similarity (Savatnalinton and Martens 2009a: fig. 5A) with its triangular (arrow-head-like) distal tip on a broad, rounded main body. Regarding the shape of the carapace, as well as the flattened anterior and posterior margins, our specimen is most similar to *S. cuneata* Zhao & Whatley, 1992. However, the surface ornamentation of the valves with broader pits centrally and smaller ones marginally, comes closer to that of *S. wangi* Zhao & Whatley, 1992. None of the known *Sanyuania* species, however, possess the mid-dorsal sulcus featured in our specimen. Clearly our data on this single specimen are too limited for more certainty; more specimens are needed for a full taxonomic assessment. We therefore present this specimen in open nomenclature here.

4. Discussion

4.1. Taphonomy

The potential for aquatic organisms to be trapped in amber is well-established from studies of modern tree resin in a swamp forest and supported by quite numerous fossil examples (Schmidt and Dilcher 2007). Previously reported invertebrates trapped in amber have included ostracods (e.g., Keyser and Weitschat 2005), although it should be noted that the example illustrated by Schmidt and Dilcher (2007: fig. 2J) is not an ostracod but perhaps a cladoceran branchiopod. In total, 39 ostracod specimens have been found in a single piece of amber of less than 1 cm³ volume. All of our preserved ostracods have articulated valves, most of them preserved with soft parts, and they include juveniles as well as adults, all of which suggests optimal environmental conditions immediately prior to the ostracods becoming trapped in the tree resin. We interpret this to indicate in-situ preservation of the ostracod specimens after a rapid burial in the plant sap; such an assessment of the coenosis according to criteria used for ostracods preserved in sediments is legitimate and represents as close an approximation to a biocoenosis as is possible in

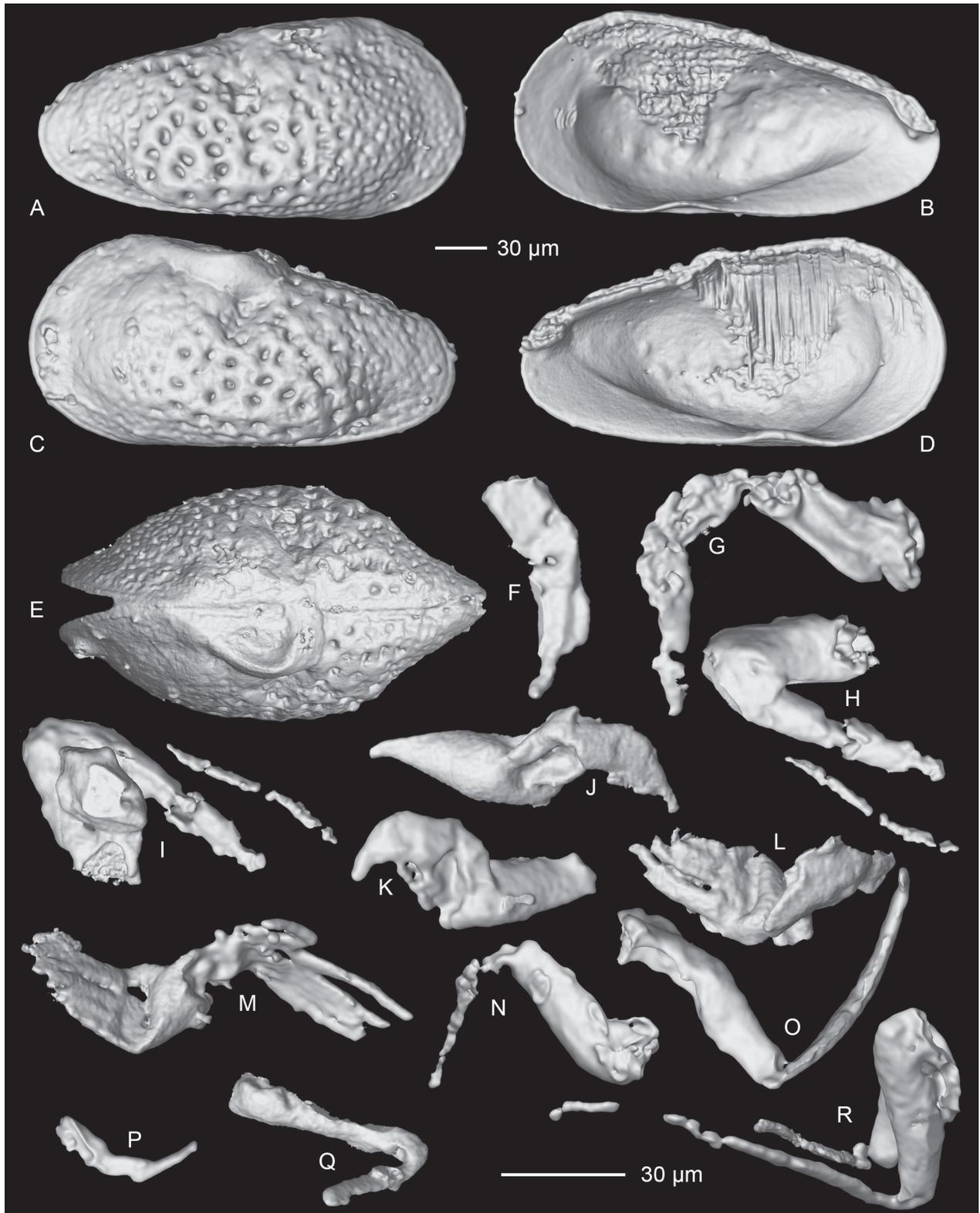


Figure 14. Microtomographic reconstruction of *Sanyuania* sp., based on microtomography of adult male (BA19005-8), surface rendering and soft parts of BA19005-8, surface renderings. **A–E.** With same scale, carapace; **F–R.** With same scale, soft parts. **A.** RV external; **B.** RV internal; **C.** LV external; **D.** LV internal; **E.** Dorsal view, anterior to left; **F.** A1, right; **G.** A1, left; **H.** A2, right; **I.** A2, left; **J.** Md, right; **K.** Md, left; **L.** Mxl, right; **M.** Mxl, left; **N.** L5, right; **O.** L5, left; **P.** L6, right; **Q.** L6, left; **R.** L7, right.

Cretaceous material. With three ostracod species, partly represented by specimens of different ontogenetic stages and sexes, the preserved death assemblage resembles a low energy thanatocoenosis with minimal post-mortem

disturbance (Boomer et al. 2003). Therefore the studied ostracod assemblage may be considered representative of the autochthonous ostracod population, allowing for an evaluation of the environmental conditions at the moment

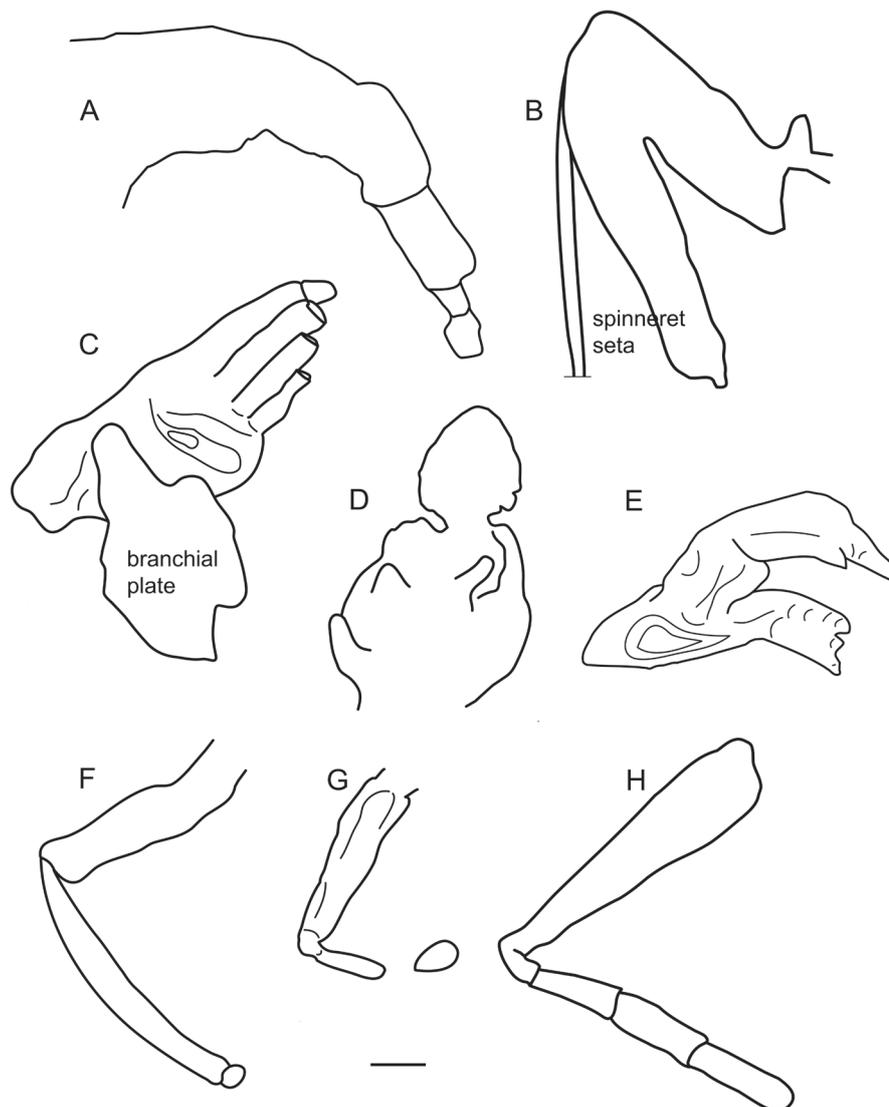


Figure 15. Drawings of appendages of *Sanyuania* sp., based on microtomography of adult male (BA19005-8). **A.** A1; **B.** A2; **C.** Mx1; **D.** HP; **E.** Md; **F.** L5; **G.** L6; **H.** L7. Scale bar: 10 μ m.

of embedding (Boomer et al. 2003; Matzke-Karasz et al. 2019). Moreover, reproductive organs of male and female *M. hui*, including giant sperms stored in a female's seminal receptacles (Wang et al. 2020b), indicate recent reproductive activity involving sexual intercourse and support the scenario of a thanatocoenosis.

Cypridoidean ostracods use their antennules and antennae, as well as their walking legs and uropodal rami for swimming and walking, respectively. During active movement, these appendages can be seen protruding from the carapaces (Schreiber 1922; Hunt et al. 2007). Such protruding appendages could also be observed in some of the trapped specimens, suggesting that they were trying to walk or swim in the resin before its viscosity impeded any further movement.

We conclude that the studied ostracods were quickly surrounded by resin fallen into the water or extruded from plant parts immersed in the water. The resin was not yet marginally hardened, and quite instantly immobilized the ostracods as they became embedded in this viscous matrix while swimming, climbing on vegetation, or walking

on the sediment surface. This conclusion is also consistent with one of the possibilities for embedding of aquatic organisms in resin: attaching to resin surface and struggling deeper (Schmidt and Dilcher 2007). The difference in pressure between the resin and internal body pressure becomes visible in the male *E. burmitei* gen. et sp. nov. (BA19005-6), where external pressure of the resin seems to have caused a linear breakage in the valve, through which body liquid was pressed out.

The above scenario resembles the taphonomic situation suggested for the ostracods from Mexican amber (Matzke-Karasz et al. 2019), while it differs from the entombment of the only three known ostracods preserved in Baltic amber, none of which seems to have been trapped in resin under water, but e.g. splashed (within a drop of water) or blown (dry) onto liquid tree resin (Keyser and Weitschat 2005; Keyser and Friedrich 2017).

Rare occurrences of marine organisms embedded in amber are usually interpreted as having formed in coastal forest settings by (e.g.) high tides, storm surges or wind and sea spray (Schmidt et al. 2018). In the case

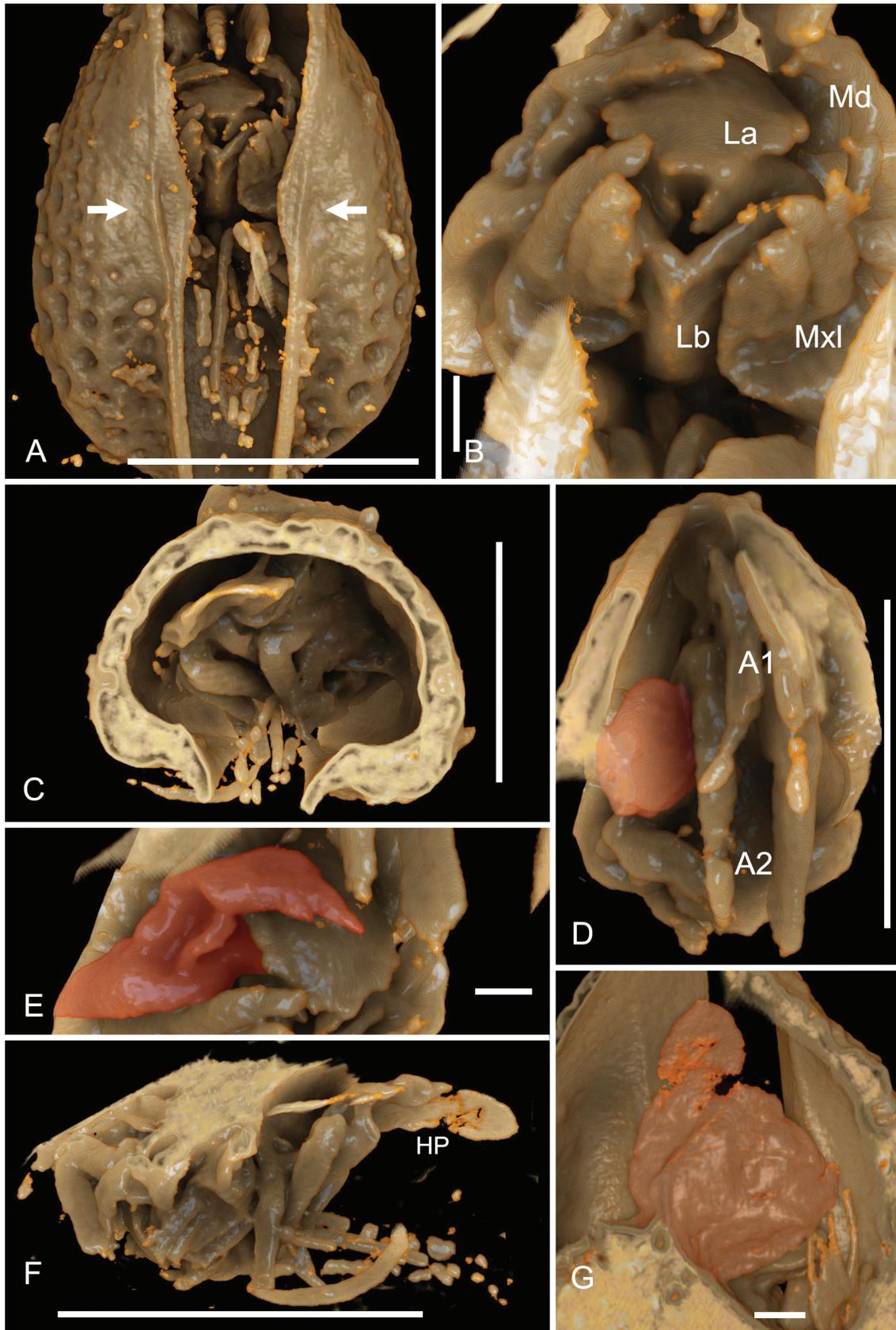


Figure 16. Microtomographic reconstruction of *Sanyuania* sp., based on data of adult male (BA19005-8), volume rendering. **A.** Oblique ventral view into gaping carapace with flaps for improved valve overlap (arrows); **B.** Mouth area from ventral, with labrum (la), labium (lb), mandible (Md) and maxillula (Mxl); **C.** Cross section in posterior region, with very thick and robust valves; **D.** Anterior body region with A1 and A2 and presumed sac of spinneret gland (highlighted); **E.** Mandible (highlighted); **F.** Soft body with L5, L6 and L7 and HP; **G.** HP in dorsal view (highlighted). Scale bars 100 µm (A, C, D, F); 10 µm (B, E, G).

of Burmese Cretaceous amber, in which freshwater organisms are common, marine fossils represented only by empty shells, such as an ammonite and gastropods (Yu et al. 2019) as well as a myodocopan ostracod (Xing et al. 2018), were probably subject to post-mortem transport before becoming embedded in resin. On the other hand, pholadid bivalves that apparently bored into the amber in which they were found are considered to be indicative of immediate proximity to fresh or estuarine waters (Smith and Ross 2017; Bolotov et al. 2021). The strong likelihood that our assemblage of 39 ostracods represents an in-situ thanatocoenosis is therefore of special importance for the palaeoenvironmental interpretation of Kachin amber (see next section).

4.2. Palaeoenvironment and distribution

Previous work has established the palaeoenvironmental context of the Kachin amber as a coastal forest (Yu et al. 2019). This kind of coastal amber forest could have both terrestrial and marine organism preserved in resin (e.g., Girard et al. 2008; Girard et al. 2009; Masure et al. 2013; Saint Martin et al. 2015). The assemblage of 39 ostracods in a single piece of amber provides valuable new insight into the aquatic palaeoenvironment associated with the forest. *Myanmarcypris hui* belongs to the Paracypridinae, tribe Renaudcypridini. This is the only fossil record of the Renaudcypridini, so that palaeoenvironmental assessments must rely on what is known about extant representatives of this tribe. It contains only two genera, *Hansacypris* Wouters, 1984, known to occur in oligo- and mesohaline as well as in fully marine environments (Wouters 2001), and *Renaudcypris* McKenzie, 1980, which seems to have a preference for lower salinities than *Hansacypris*. Of the four known *Renaudcypris* species, only one (*R. gorongae* McKenzie, 1980) was described from a marine environment (a beach of Gorong Island); however, it was sampled in a section that was under strong freshwater influence from a rivulet causing salinity fluctuations. *Renaudcypris wolffi* (Harding, 1962) was reported from (e.g.) the oligohaline lake Te-Nggano (Rennel Island/Solomon Islands) with subterranean channels connecting it with the sea, and from brackish and freshwater sites in Papua New Guinea (Wouters 1984); *R. natans* Hartmann, 1984 (from a pond without connection to the sea on Rangiroa Atoll, French Polynesia) and *R. luzonensis* Wouters, 1986 (from Lake Taal, Philippines) clearly both thrive in full freshwater.

Living species of *R. gorongae* were recorded from a 1:1 mix of coralline sands and algae (McKenzie 1980); for *R. luzonensis*, Wouters (1986) reported them living on the lake bottom and on algae, while *R. natans* was found on a coralline rock with a layer of organic detritus. Given these ecological data of extant *Renaudcypris*, we here suggest that *M. hui*, being closely related to *Renaudcypris*, may indicate a palaeoenvironment of fluctuating salinity from fully freshwater to brackish waters,

accepting occasional marine influx. The presence of algae and organic detritus in the habitat is likely, as well as the possibility of occasional higher water energy (due to wave action, perhaps) and/or the presence of small predators, since the robust, ornamented shells of *M. hui* with their efficacious closure mechanism (3 teeth and corresponding sockets on the calcified inner lamellae) provide protection against both. Its longer natatory setae would allow this species to swim in the water column to cover short distances.

The autecology of *E. burmitei* gen. et sp. nov. cannot be inferred from its taxonomic relationships, because it is currently impossible to assign it to any of the existing three tribes within the Paracypridinae, and therefore an ecological approximation would remain doubtful. Unfortunately, the natatory setae of our two type specimens are only partly preserved, so that it is not even possible to evaluate the swimming ability of this species (although it was at least capable of swimming).

In contrast, Cytheroidea are always non-swimming, benthonic ostracods, crawling and burrowing on and in sediments or climbing on aquatic plants. A single specimen in our material could be ascribed to this superfamily, and here to the genus *Sanyuania*, of which six species have been described so far from China, Korea, Japan and Thailand. The geologically oldest of them, *S. psaronius* Zhao & Han, 1980 has a fossil record dating back to the Pliocene but has also living representatives, while the other species are all geologically younger, with *S. abei* (Choe, 1988) and *S. segersi* being known from living occurrences only. Our finding of a representative of a *Sanyuania* species pushes the roots of this genus c. 94 million years deeper in time. As to their habitat salinity preferences, the known species of this genus are very heterogeneous, inhabiting fully marine bottom mud (*S. abei*), ocean-connected and continental brackish water bodies (*S. psaronius*, *S. wangi*, *S. cuneata* and *S. sublaevis* Zhao & Whatley, 1992) as well as a fully freshwater river habitat (*S. segersi*) (Zhao and Han 1980; Choe 1988; Zhao and Whatley 1992; Tanaka 2006; Savatentalint and Martens 2009a). Consequently, the assignment of our Cretaceous specimen to the genus *Sanyuania* as such cannot help in narrowing down its salinity preference, but in concert with *M. hui*, for which we showed a close relationship with the predominantly brackish to freshwater genus *Renaudcypris*, the likelihood of a brackish environment in the oligohaline/mesohaline range increases.

4.3. Outlook

Through its taxonomy and morphology, the ostracod fauna that was found in a single amber piece sheds a light on the environmental settings and the process of entombment in the liquid plant resin. The presence of reproductive organs and sperms are the basis of substantiated conclusions on the cypridoidean reproductive strategies at the time. Unfortunately, the poor soft part preservation

in specimens of *E. burmitei* gen. et sp. nov. and *Sanyuania* sp. precluded some conclusions for the time being, but future amber-findings of these taxa will likely help in resolving (e.g.) the three following issues.

First, *E. burmitei* gen. et sp. nov. could not yet be assigned to one of the three existing tribes in Paracypridinae, but with only a few more taxonomically relevant characters at hand. In the future, it should be possible to either assign it to one of the existing tribes, or to expand the subfamily with the addition of a fourth tribe. Either case will help to consolidate an evolutionary tree of this rather enigmatic (due to rare findings of Renaudocypridini and Thalassocypridini) and ecologically diverse lineage.

Second, the genus *Sanyuania* could hold some key information on the family Loxoconchidae, but a few more specimens with good soft part preservation will be needed for unequivocal conclusions. *Sanyuania segersi*, a fully freshwater species from an inland river of Thailand, has been used by Savatnalinton and Martens (2009b) for a phylogenetic assessment of freshwater inhabiting lineages within the Loxoconchidae based on (soft part) morphological characters. This assessment could gain much more impact if soft parts of this ancient member of the genus could be analyzed in more detail in better-preserved specimens.

Third, Savatnalinton and Martens (2009b) found *S. segersi* to be morphologically close to *S. cuneata*, of which living representatives live under shallow-marine, mesohaline conditions (Tanaka 2006). Zhao and Whatley (1992) developed an evolutionary model of the genus suggesting a Holocene origin of *S. segersi*, branching off of Pleistocene representatives of *S. cuneata* or their ancestors, either inhabiting coastal or inland brackish water. New data on the soft parts of the *Sanyuania* species from Myanmar amber would considerably improve this tentative evolutionary model, shedding light on an Asian brackish-water ostracod genus of high interest with regard to regional Cenozoic faunal provinces (Tanaka 2006).

5. Conclusions

With rare exceptions, fossil ostracods are classified based on carapace alone – and must be, because normally it is only the calcified parts of the animal that are preserved. In very few cases ostracod soft parts were preserved and could provide unique taxonomic information through their morphological details (Matzke-Karasz and Smith 2020), which occasionally even call into question the taxonomy of extinct ostracods established on carapaces alone (Siveter et al. 2013). In our study, the preserved appendages and setae had a strong impact on the final taxonomic evaluation and we emphasize the value of fossil soft part preservation for key questions in ostracod evolution.

According to the taphonomy of the three studied ostracod species, we suggest that these ostracods were preserved in situ, having been quickly surrounded by resin and instantly immobilized when trapped in the amber.

After considering the present-day affinities of the embedded ostracods, the palaeoenvironment is suggested to have been a vegetated lagoonal setting with mesohaline to oligohaline water salinities being dominant. The resin producing trees and other coastal vegetation, in combination with surface barriers, created relatively still microhabitats along the Cretaceous coasts of Myanmar, where podocypid ostracods could thrive swimming and walking on submerged vegetation and in the organic detritus on the bottom.

Author statement

Tomographic data have been processed by He Wang and Renate Matzke-Karasz. Resulting models have been analyzed by all authors. The manuscript has been written by all authors and all agree with the presented ideas.

Ethical statement

We acknowledge the controversial nature of the study of fossils in amber from Myanmar and the need for vigilance regarding ethical and legal issues in palaeontology (e.g., Haug et al. 2020). Our research is limited to material acquired prior to the 2017 resumption of armed conflict in the region, and we hope that it will contribute to raising awareness of the current conflict in Myanmar and the hard work of Burmese miners, to the benefit of disadvantaged communities (Peretti 2021).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Supplementary material 1

Figure S1

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Figure (pdf file)

Explanation note: Light-microscopical images of the Kachin amber piece with 39 embedded ostracods mapped with their collection numbers. Revised from Wang et al. (2020b).

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Link: <https://doi.org/10.3897/fr.25.84604.suppl1>

Supplementary material 2

Figure S2

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Figure (pdf file)

Explanation note: View inside the anterior part of the carapace of the adult male *Myanmarcypris hui* specimen (BA19005-1). Data visualization by volume rendering in Drishti in red-cyan. In this mode the investigation of appendages and chaetotaxy were carried out by using tools such as rotate, zoom, clip, and

carve, and by modifying the two-dimensional transfer functions.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl2>

Supplementary material 3

Movie S1

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Movie (mp4. file)

Explanation note: Movie S1. Micro-tomographic reconstruction of *Myanmarcypris hui* juvenile (A-2), BA19005-3. Color code: A1: orange; A2: yellow; Md: light green; Mx1: light blue; L5: blue; L6: purple; L7: red; UR: olive.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl3>

Supplementary material 4

Movie S2

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Movie (mp4. file)

Explanation note: Movie S2. Micro-tomographic reconstruction of *Myanmarcypris hui* juvenile (A-3), BA19005-4. Color code: A1: orange; A2: yellow; Md: light green; Mx1: light blue; L6: purple; UR: olive.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl4>

Supplementary material 5

Movie S3

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Movie (mp4. file)

Explanation note: Movie S3. Micro-tomographic reconstruction of *Myanmarocypris hui* juvenile (A-4), BA19005-5. Color code: A1: orange; A2: yellow; Md: light green; L5: blue; L6: purple.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl5>

Supplementary material 6

Movie S4

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Movie (mp4. file)

Explanation note: Movie S4. Micro-tomographic reconstruction of *Electrocypria burmitei* gen. et sp. nov., BA19005-6, male. Color code: A1: orange; A2: yellow; Md: light green; L5: blue; L6: purple; L7: red; UR: olive.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl6>

Supplementary material 7

Movie S5

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Movie (mp4. file)

Explanation note: Movie S5. Micro-tomographic reconstruction of *Electrocypria burmitei* gen. et sp. nov., BA19005-7, female. Color code: A1: orange; A2: yellow; Md: light green; Mx1: light blue; L5: blue; L6: purple; L7: red; UR: olive; female genital lobe: blue-green.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl7>

Supplementary material 8

Movie S6

Authors: He Wang, Renate Matzke-Karasz, David J. Horne

Data type: Movie (mp4. file)

Explanation note: Movie S6. Micro-tomographic reconstruction of *Sanyuania* sp., BA19005-8. Color code: A1: orange; A2: yellow; Md: light green; Mx1: light blue; L5: blue; L6: purple; L7: red; HP: pink; presumed part of spinneret gland: pistachio; mouth: gray-green.

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Link: <https://doi.org/10.3897/fr.25.84604.suppl8>