geodiversitas

2023 • 45 • 24

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art. 45 (24) — Published on 14 December 2023
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Couverture / *Cover* :
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Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie***, ***Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Crayfishes from the Jehol biota

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Submitted on 16 May 2023 | accepted on 24 September 2023 | published on 14 December 2023

urn:lsid:zoobank.org:pub:73B795BD-23BA-44AA-98CA-0F62DAA3CAD7

Audo D., Kawai T., Letenneur C. & Huang D. 2023. — Crayfishes from the Jehol biota. *Geodiversitas* 45 (24): 689-719. https://doi.org/10.5252/geodiversitas2023v45a24. http://geodiversitas.com/45/24

ABSTRACT
Crayfishes are well-known freshwater invertebrates with important economic, ecological and cultural significance. In East Asia, crayfishes are represented by a single family, Cambaroididae Villalobos, 1955 with a single genus, *Cambaroides* Faxon, 1884 which phylogenetic relations to other northern hemisphere crayfishes has been debated. Here, we review crayfishes from the Early Cretaceous Jehol biota, China, where three species of crayfishes have been described from. We observed that specimens correspond either to exuviae or body fossils, the later sometimes including preserved gastroliths. Our investigation also shows it is not possible to find any distinction between the species, leading to only one species to be recognized in the Jehol biota. Furthermore, the extinct family Cricoidoscelosidae Taylor, Schram & Shen, 1999 and its unique genus *Cricoidoscelosus* Taylor, Schram & Shen, 1999 are based upon characters insufficient to warrant a separate family. Perhaps the most important of these, the annulated pleopods is a plesiomorphic character of Astacoidea, with annulations most likely more visible due to fossilization. In fact, based upon the shape of the male gonopods and epistome, the general habitus, the possible presence of an *annulus ventralis* in females and ischial hooks in males, crayfishes from the Jehol biota can be assigned to Cambaroididae, which are currently restricted to East Asia. This suggests that members of Cambaroididae have inhabited East Asia since at least the Early Cretaceous.

KEY WORDS
China,
Early Cretaceous,
Konservat-Lagerstätte,
Yixian Formation,
Decapoda,
Astacoidea,
Cambaroididae,
freshwater,
gastroliths,
exuvia,
new synonym,
neotypification.

RÉSUMÉ

Écrevisses du biote de Jehol.

Les écrevisses sont des invertébrés d'eau douce bien connus : elles sont importantes économiquement, du point de vue de l'écologie, et ont également un fort impact culturel. À l'est de l'Asie¸ les écrevisses sont représentées par une seule famille, les Cambaroididae Villalobos, 1955, comprenant un seul genre, *Cambaroides* Faxon, 1884, dont les relations phylogénétiques avec les autres écrevisses de l'hémisphère nord sont encore mal comprises. Nous révisons ici des écrevisses du biote de Jehol (Crétacé inférieur) parmi lesquelles trois espèces ont été décrites. Nous observons que les spécimens correspondent soit à des exuvies, soit à des corps, ces derniers incluant parfois des gastrolithes. Notre travail montre aussi qu'il n'est pas possible de différencier ces trois espèces, suggérant ainsi qu'une seule espèce est présente dans le biote de Jehol. De plus, la famille fossile de Cricoidoscelosidae Taylor, Schram & Shen, 1999, et son unique genre *Cricoidoscelosus* Taylor, Schram & Shen, 1999 s'appuient sur des critères insuffisants pour justifier son maintien. Le plus important de ces critères, les pléopodes annelés, est plésiomorphe pour les écrevisses ; par ailleurs, la fossilisation accentue la visibilité de ces annulations. En se basant sur la forme des gonopodes mâles, sur celle de l'épistome, sur l'aspect général, et sur la présence probable d'un *annulus ventralis* chez les femelles et de crochets ischiaux chez les mâles, les écrevisses du biote de Jehol peuvent être assignées à la famille des Cambaroididae, actuellement présente à l'est de l'Asie. Ceci suggère que des membres des Cambaroididae ont habité cette région depuis le Crétacé inférieur.

MOTS CLÉS
Chine,
Crétacé inférieur,
Konservat-Lagerstätte,
Formation Yixian,
Decapoda,
Astacoidea,
Cambaroididae,
eau douce,
gastrolithes,
exuvies,
synonyme nouveau,
néotypification.

INTRODUCTION

Crayfishes are among the largest freshwater invertebrates, as such, they have great environmental, cultural and economic significance (Swahn 2004; Souty-Grosset *et al.* 2006; Kozák 2015; Patoka *et al.* 2016; Kawai & Coughran 2021). Freshwater crayfishes are also the subject of extensive research and act as animal models, notably on vision studies, at least since the 19th century (Huxley 1880; Exner 1891; Vogt 1975; see also Crandall *et al.* 2000 and references therein). Some of the core questions in crayfish research concern their biogeographic distributions (Scholtz 1998; Ďuriš & Petrusek 2015; Pârvulescu *et al.* 2019). Among these is the biogeographic evolution of northern hemisphere crayfishes (Astacoidea Latreille, 1802) in which there are three lineages: 1, Astacidae Latreille, 1802, in west North America (*Pacifastacus* Bott, 1950) and from Europe to west Asia; 2, Cambaridae Hobbs, 1942, in east North America; and 3, Cambaroididae Villalobos, 1955 (*Cambaroides* Faxon, 1884), in East Asia (Scholtz 1998; Ďuriš & Petrusek 2015). This distribution is peculiar, as the repartition area of Astacidae is divided in two by the Atlantic and the repartition area of Cambaridae. Similarly, the biogeographic and evolutionary relationships of *Cambaroides* (East Asia) are still unclear. *Cambaroides* was initially believed to be part of Cambaridae (Hobbs 1988; Crandall & Buhay 2008), primarily based on the presence of ischial hooks and the shape of gonopodes in males (see Kawai *et al.* 2016 for illustrations), but is now considered as a distinct lineage of Astacoidea (in the family Cambaroididae), generally placed as a sister group to other northern hemisphere crayfishes (Braband *et al.* 2006; Breinholt *et al.* 2009, Crandall & De Grave 2017; Grandjean *et al.* 2017). For these reasons, studying fossil crayfishes in East Asia is important to know their significance in the diversification and evolution of crayfishes in the northern hemisphere. As an example, from Europe, the revision of *Emplastron edwardsii* (Van Straelen, 1928a) from the Thanetian (Palaeogene) of Sézanne (France) showed that it belongs to European Astacidae, not to Northern American groups, as the accompanying fauna suggested (O'Flynn *et al.* 2021, see also Van Straelen 1928a).

In the present publication, we review crayfishes from the Jehol biota, in the Yixian Formation Konservat-Lagerstätte. Three species have been described in this biota (*Astacus licenti* Van Straelen, 1928, *Astacus spinirostrius* Imaizumi, 1938 – currently placed in synonymy with the first – and *Cricoidoscelosus aethus* Taylor, Schram & Shen, 1999). These fossil crayfishes were considered as belonging to two families: Cambaridae and Cricoidoscelosidae Taylor, Schram & Shen, 1999 (Taylor *et al.* 1999; Shen *et al.* 2001). These publications being earlier than the new notions about *Cambaroides* relationships, and two families being purportedly present in north-eastern China warranted a review of the crayfishes of the Jehol biota.

MATERIAL AND METHODS

MATERIAL

The present study is based upon 109 fossil specimens (full list in "examined material") from north-eastern China, mainly Liaoning Province, some from Inner Mongolia, with one specimen coming from Hebei Province. All specimens, except three, are housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Science (Nanjing, China) and the three remaining specimens are from Tohoku University (Sendai, Japan). These specimens include one of the two syntypes of *Astacus spinirostrius* Imaizumi, 1938, the holotype of *Cricoidoscelosus aethus* Taylor, Schram & Shen, 1999, referred material published in Taylor *et al.* (1999), Shen *et al.* (2001) and new, unpublished material (see also Appendix 2).

Extant crayfishes from the zoological collections of Muséum national Histoire naturelle (Paris – MNHN-IU) were used for comparison and include an assortment of representatives of Astacidae, Cambaridae, Cambaroididae (*Cambaroides*) and Parastacidae Huxley, 1879. In total, 48 specimens including male and female of each taxa whenever possible were used, and including one female *Polycheles typhlops* Heller, 1862 for comparison (MNHN-IU-2022-4080).

Astacidae: *Astacus astacus* Linnaeus, 1758 (MNHN-IU-2022-4069, one female and one male); *Austropotamobius fulcisianus* (Ninni, 1886) (MNHN-IU-2021-6684, one male; MNHN-IU-2022-4070, two females); *Pontastacus leptodactylus* (Eschscholtz, 1823) (MNHN-IU-2022-4071, six males); *Pacifastacus leniusculus* (Dana, 1852) (MNHN-IU-2022-4072, one female; MNHN-IU-2022-4073, one male).

Cambaridae: *Cambarus bartonii* (Fabricius, 1798) (MNHN-IU-2022-4074, three males and three females); *Faxonius limosus* (Rafinesque, 1817) (MNHN-IU-2022-4075, one male).

Cambaroididae: *Cambaroides dauricus* (Pallas, 1772) (MNHN-IU-2022-4076, four females, five males; MNHN-IU-2022-4077, three females, six males; MNHN-IU-2022-4068, three males); *Cambaroides japonicus* (de Haan, 1841) (MNHN-IU-2022-4078, two females, one male).

Parastacidae: *Astacoides madagascariensis* (H. Milne Edwards & Audouin, 1839) (MNHN-IU-2022-4079, three males).

A few other specimens illustrated in Figures 1 and 2 were also used to compare the aspects of pleopods in *P. licenti* to that of other decapods.

Documentation of specimens in macrophotography

Specimens were documented both with the help of stereomicroscopes and cross-polarized-light macrophotography, the later to reduce specular reflexion which usually decrease contrasts (Bengtson 2000). Black-light autofluorescence (blue to UVA; Haug *et al.* 2009) was attempted, but the specimens do not present noticeable autofluorescence with our "black-light" setup (two Velleman® 15W, 850 lumens spiral lamps with an emission peak at 365 nm).

Measurements and statistics

Measurements were conducted on photographs with the free software ImageJ (Schneider *et al.* 2012) and statistical analyses made with Scipy 1.10.1 (https://scipy.org/) and Matplotlib 3.7.1 (https://matplotlib.org/) for Python 3.10.2 (https://www.python.org/). Measurements are summarized in Appendix 2. Measurements always correspond to the maximum length parallel or perpendicular to the anteroposterior axis for the cephalothorax, pleon and telson. Usually, CL is measured from the back of the ocular incision to the posterior part of cephalothorax. In our case, since the ocular incision was not always visible enough, we include the length of rostrum in this measurement. First pereiopod propodus length includes the whole propodus, from the tip of the fixed finger to the articulation between propodus and carpus. In the Appendix 2, measurements on an orange background are deemed less precise due to preservation.

Photogrammetry

Despite being extremely flattened, several fossils still retain some details in volumes, most notably imprints of the gastroliths, spines, and to a smaller extent, of the general morphology.

We made around 60 to 200 photographs for each specimen, in circular arcs, taking care to observe specimens from various angles. Photographs were made with an Olympus TG-5 camera, using the macrophotography autostacking feature, allowing a greater depth of field than usual photographs on handheld photographs. Photographs were then processed by the free open-source software Meshroom (Alicevision – version 2021.1.0) using default settings. This generated textured meshes which usually still incorporated unwanted background elements. These meshes were trimmed and optimized with the free open-source software Meshlab (version 2022.02, removal of non-manifold edges and vertices, fusion of duplicate vertices, removal of zero area faces). Finally, the resulting optimized meshes were reinjected in Meshroom for retexturing.

One example is provided in Appendix 3.

Radiographic imagery of extant specimens

Extant specimens were first radiographed using a Faxitron X-ray cabinet X-ray system (power between 60 to 70 kVp) to search for gastroliths. Resulting raw files were processed with ImageJ and GIMP (version 2.10.30, open source software). Only one male *Austropotamobius fulcisianus* (MNHN-IU-2021-6684 – ex AS32, Fig. 14) has gastroliths clearly visible in radiographic images. Additionally, the radiographic images can help interpret more easily fossils: as with fossils, structures appear superimposed.

The problem of "cosmetic enhancements"

Most specimens were acquired from local fossil collectors and dealers who regularly paint over parts of fossils to give them a more complete or visually pleasing aspect. This practice can lead to "faked fossils" – intentionally or not – see Selden *et al.* (2019) for the case of *Mongolarachne chaoyangensis* Cheng, Liu, Huang, Liu, Li & Li, 2019: a poorly preserved fossil crayfish painted to resemble a large fossil spider, which was published as a spider and subsequently exposed as a fake just a few months after. We found that our UV fluorescence macrophotography setting was not sufficient to distinguish clearly areas that were painted over, due to the little to no autofluorescence of the fossils themselves. Therefore, we relied on close inspection of the fossil under stereomicroscope to distinguish areas that are simply painted from genuine fossils. It is to be noted that paint regularly hindered the observation of the finer structures of the fossils and as a result decrease the scientific value of some specimens.

Palaeoart

The preservation of fossil crayfishes from Jehol allows the observation of the outline of crayfishes quite easily, but this outline is not enough to really compare it to other crayfishes: for instance, elements with diagnostic characters such as the rostrum, carinae, grooves and even the shape of tailfan are often difficult to observe. Previous reconstructions by Taylor *et al.* (1999) proposed a sketch reconstruction of the dorsal view for *P. licenti*, and of the lateral view for *C. aethus*. This change in orientation complicates comparisons between the two species. Thus, we herein provide both a dorsal view and lateral view reconstructions summarising our observations and providing a visual of what Jehol crayfishes may have looked like in life. We also share the conclusion of Davis *et al.* (2022) concerning the importance of palaeoart and documenting its creation.

Obviously, fossils, especially flattened ones, have lost many details of the original animal. Thus, we based our reconstruction on the modern-day East Asian crayfish genus *Cambaroides*, using images and actual specimens of *C. japonicus* De Haan, 1841 and *C. dauricus* Pallas, 1772 to adjust the position and fill-in parts too poorly preserved on fossils. This choice follows our conclusions that Jehol crayfishes are fossil relatives to extant *Cambaroides*. Our process was iterative, drafting reconstruction from the best overall preserved specimens (detailed below) and extant relatives and confronting these reconstructions to fossil specimens to check proportions and the aspect of structures. Major fossil specimens used: the overall proportion of the cephalothorax is based mostly upon specimens NIGP-Shen-71, 126347, sp21, and Shen-68; the shape and ornamentation of the claw is closely based upon specimen NIGP-175159 for ornamentations, with contribution from specimens NIGP-DYH-6, Shen-32, Shen-35; grooves and carinae are mostly based upon specimens NIGP-Shen-1, Shen-62, and Shen-GM1; rostrum is based upon specimen NIGP-Shen-39, NIGP-Shen-42, Shen-62, 126337-126338, 126342, 126347; ornamentation of the cephalothorax, pleon and tailfan are based mostly on specimens NIGP-Shen-GM1, Shen-32, Shen-71, Shen-3, 126354.

Colour

Considering the diversity of colour in extant crayfishes (usually from greenish, brown, red, more rarely blue and shades in-between), including intraspecific variations, we chose not to represent the colour of the crayfish and use a tan colour reminiscent of some old scientific drawing of both extant of fossil specimens.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder ASTACIDA Scholtz & Richter, 1995
Superfamily ASTACOIDEA Latreille, 1802
Family CAMBAROIDIDAE Villalobos, 1955

Genus *Palaeocambarus* Taylor, Schram & Shen, 1999

Palaeocambarus Taylor, Schram & Shen, 1999: 122-130, figs 2, 4-6. — Type species: *Astacus licenti* Van Straelen, 1928b, by monotypy.

Cricoidoscelosus Taylor, Schram & Shen, 1999: 130-135, figs 3, 7, 8, **n. syn.** — Type species: *Cricoidoscelosus aethus* Taylor, Schram & Shen, 1999.

ORIGINAL DIAGNOSIS (Taylor *et al.* 1999). — “Entire dorsal surface of cuticle covered with fine granulations. Rostrum with basal lateral spines. Elongate, bladelike scaphocerite. Chela of first pereiopod long and narrow with extensive pitting and spination. No hooks visible on ischia. Pleura large and rounded on abdominal segments 2-5, 2nd pleuron being largest. Pleopods elongate and blade like, with no specialization on first. Telson subrectangular with pair of large lateral spines and rounded distal margin.” (Taylor *et al.* 1999).

EMENDED DIAGNOSIS (present work). — Pyriform cephalothoracic shield, longer than wide; rostrum in two parts, proximal part wide, less than half total rostrum length, tapering distally, flanked by a pair of lateral spine at the tip of supra-orbital carina, acumen (distal part) blade-like; deep-curved cervical groove, crossing median-line; subdorsal carina extending into the rostrum and on the cephalic region; postorbital carina double: dorsal part near subdorsal carina, formed of two spines aligned horizontally, each extending posteriorly in a short carina; ventral part formed of at least four spines posterior to the ocular incision; postrostral carina on median dorsal line, formed of at least four spines on the anterior half of the cephalic region, posterior to the rostrum; epistome with a wide cephalic lobe forming three spines anteriorly, no spine on the rest of epistome; telson with diaeresis and rigid distal portion; pleopods 1-2 forming copulatory gonopods in males; uropodal exopodite with a diaeresis and rigid distal portion.

COMMENTS

Taylor *et al.* (1999) described a new species, genus and family of crayfish from the Jehol biota. Following their revision, the two species they considered valid in Jehol biota therefore belonged to two distinct genera (*Palaeocambarus* and *Cricoidoscelosus* Taylor *et al.* 1999) and two distinct families (Cambaridae and Cricoidoscelosidae respectively). Concerning Cricoidoscelosidae, we herein consider that diagnostic characters used in the erection of this family are not sufficient to distinguish a new family: some of them are common to all crayfishes, such as the bladelike scaphocerite, well-developed first chelae and large rostrum with large lateral spines (observed in several species of Cambaridae, Astacidae, *Cambaroides* and Parastacidae) or the gonopores on the coxa (not sternite) of females (plesiomorphic condition, occurring in most decapods). The first pleopod being styliform in males (first gonopod) is an important diagnostic character, but only excludes Parastacidae from consideration. Rounded pleurae, as observed in Shen *et al.* (2001), were not observed in all specimens: our observations led us to believe this is only a preservation artefact, due to flattening of the specimens. More importantly perhaps, the namesake character for Cricoidoscelosidae, the pleopods formed of numerous rings (multiarticulated – Fig. 1A, B) is also visible in other crayfishes such as *Cambaroides* (Fig. 1C) and even fossil *Austropotamobius* Skorikov, 1907 (Fig. 1D). In fact, the presence of multiarticulated pleopods in other decapods, such as dendrobranchiate shrimps (Fig. 1E) and in polychelidans (Fig. 1F) suggests that multiarticulated pleopods are in fact a plesiomorphic character state for decapod crustaceans. It is worth mentioning that fossilization appears to make pleopod annulations more visible (Fig. 1A, B, D, E) than in specimens preserved in alcohol (Fig. 1C, F). We were not able to observe the variations noted by Taylor *et al.* (1999) or Shen *et al.* (2001): our observations suggest that the variations may be due to variation in preservation, or angle at which these structures are flattened.

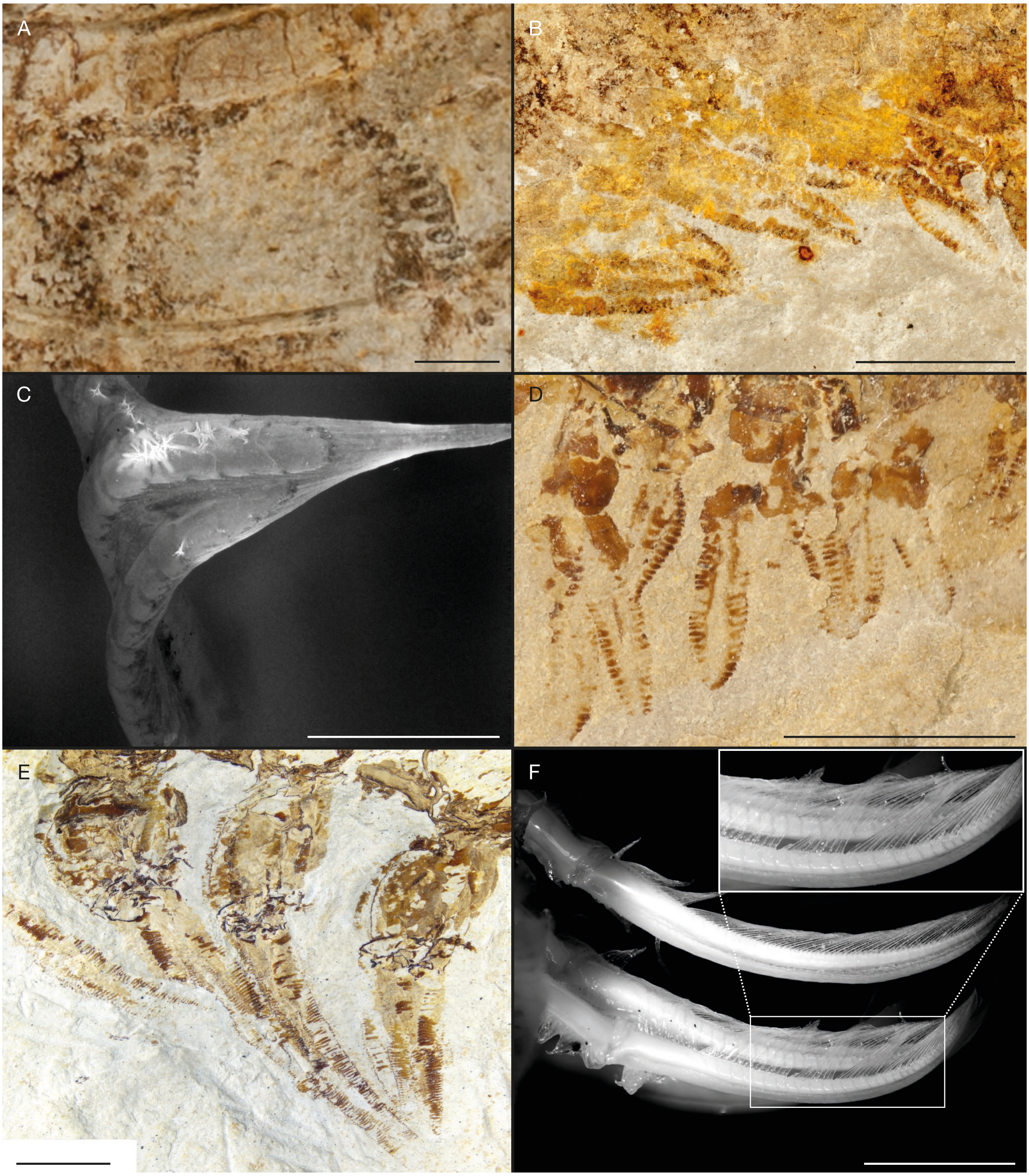

FIG. 1. — Pleopods of different decapod crustaceans, fossil and extant: **A**, **B**, *Palaeocambarus licenti* (Van Straelen, 1928b) seen in ventral view (**A**, holotype of *Cricoidoscelosus aethus* Taylor, 1999, NIGP-126337) and lateral view (**B**, specimen NIGP-Shen-2), both from the Early Cretaceous of China; **C**, pleopod 4 of a female *Cambaroides dauricus* (MNHN-IU-2022-4077, extant, Mandchuria); **D**, *Austropotamobius llopisi* (Vía, 1971) (female ? – specimen MUPA-LH-14011), from the Early Cretaceous of Spain; **E**, *Palaeobenthesicymus libanensis* (Brocchi, 1875) (specimen MNHN.F.A30607) from the Santonian of Lebanon; **F**, female *Polycheles typhlops* Heller, 1862 (MNHN-IU-2022-4080, extant, New Caledonia). Photographs: D. Audo. Scale bars: A, C, 1 mm; B, D, E, F, 5 mm.

From our assessment, the epistome of *Palaeastacus* (Fig. 2A-C) is similar to that of *Cambaroides* (Fig. 2D, see also Kawai *et al.* (2003) for illustrations of epistomes in several *Cambaroides*): there is no spine on the epistome except for that of the cephalic lobe (Fig. 2A, C; contrary to Astacidae, which have spines; see Fig. 2E), a wide cephalic lobe (about 30% of the total width, contrary to North American Cambaridae (Fig. 2F) and *Pacifastacus*, in which the cephalic lobe is narrower than 30% of total width; see NIGP-Shen-12, NIGP-Shen26, NIGP-Shen-38), and there is a cephalic median central projection on the cephalic lobe (Fig. 2C, as in *Cambaroides* Fig. 2D). Beside the rostrum, the presence of a telson diaeresis (articulation), two pairs of gonopods, the probable presence of ischial hooks (on the holotype of *C. aethus*, NIGP-126337, Figs 3A-3D, possibly on specimen NIGP-Shen-22, Fig. 3E-F, although our evidence is ambiguous due to preservation, ischial hooks may be present on specimens and NIGPAS-Shen-3, 5, 14, 32), all are similar to *Cambaroides*. We note that it is not unexpected that Taylor *et al.* (1999) and Shen *et al.* (2001) could miss this structure: it is only present in males of *Cambaroides* and Cambaridae, is rather small and placed on the inner margin of the ischium of periopods 2-4 (often only on two pairs: Fig. 4A, compare with Fig. 4B), so is rarely noticeable in fossils, and is even difficult to see on radiographic images of extant specimens. Examination of the neotype NIGP-126342 shows that the sternite between pereiopods 4-5 (Fig. 4C, D) does not form an annulus ventralis with a hemicircular fold like that of *Cambarus*. It resembles, however, the smaller annulus ventralis found in *Cambaroides*. For these reasons, we propose an assignment to Cambaroididae Villalobos, 1955. This placement is in line with the geographic origin of *Palaeocambarus*, indeed, Cambaroididae are only known to occur in East Asia (eastern China and Russia, North and South Korea, Japan, Mongolia: Kawai *et al.* 2003, 2016). Ďuriš & Petrusek (2015) and Schram & Koenemann (2022) also suggested a possibly close relationship between *Palaeocambarus* and modern East-Asian crayfishes.

For all these reasons, we consider *Palaeocambarus* Taylor, Schram & Shen, 1999 and *Cricoidoscelosus* Taylor, Schram & Shen, 1999 to be synonyms. Since these two genera were simultaneously published, we consider *Palaeocambarus* as the senior name, under the first reviser principle (ICZN 1999: art. 24.2): we believe this choice is more appropriate as the name *Cricoidoscelosus* refers to the annular pleopods, a character we do not consider as diagnostic, and also, *Palaeocambarus* appears before *Cricoidoscelosus* in the text, in Taylor *et al.* (1999).

Although Taylor *et al.* (1999) assigned *Palaeocambarus* to Cambaridae, and we assign it to Cambaroididae, these assignments are not so different, indeed, Taylor *et al.* (1999) considered *Cambaroides* as a Cambaridae. So, in this regard, we agree with Taylor *et al.* (1999) that *Palaeocambarus* belongs to the same family as modern-days East Asian crayfishes.

Another consequence of this synonymy and new familial assignment is the synonymy of Cricoidoscelosidae Taylor, Schram & Shen, 1999 to Cambaroididae Villalobos, 1955. Schram & Koenemann (2022) suggested that Cricoidoscelosidae may have precedence over Cambaroididae. We consider that Cambaroididae have precedence over Cricoidoscelosidae as this family was published as a subfamily earlier than Cricoidoscelosidae. Also, the name Cricoidoscelosidae refers to a character of taphonomic significance, which has little to contribute to the classification of crayfishes.

Palaeocambarus licenti (Van Straelen, 1928)

(Figs 1A; 2B, C; 3; 4C, D; 5-8; 10-13)

Astacus licenti Van Straelen, 1928b: 133-138, pl. 1, figs 1-2. — Imaizumi 1938: 173-176, pl. 23, figs 1, 2, 4-6, 11.

Astacus spinirostrius Imaizumi, 1938: 176-178, pls 12, 23, figs 9, 10, 12, 13.

Cricoidoscelosus aethus Taylor, Schram & Shen, 1999: 130-135, figs 3, 7, 8. — Schram & Shen 2000: 416-418, pl. 1. — Shen *et al.* 2001: figs 1c, 2a, 3a, 3b. — Shen 2008: figs 62-65. — Schweitzer *et al.* 2010: 32. — Crandall & De Grave 2017: 616, 636. — Bell *et al.* 2020: 1023-1030, **n. syn.**

Palaeocambarus licenti – Taylor *et al.* 1999: 122-130, figs 2, 4-6. — Shen *et al.* 2001: figs 1a, 1b, 2b, 2c, 3c. — Shen 2008: figs 66-67. — Schweitzer *et al.* 2010: 32. — Bracken-Grissom *et al.* 2014: 465. — Crandall & De Grave 2017: 616, 631. — Bell *et al.* 2020: 1026. — Xing *et al.* 2020: fig. 4.

Type locality and horizon. — Barremian (*c.* 125 Ma; Lower Cretaceous) of Yixian Formation, Lingyuan, Liaoning province, China (Swisher *et al.* 1999).

Type material. — Holotype of *Astacus licenti* by original designation (Van Straelen, 1928) not found, probably lost.

Neotype. — NIGP-126342, herein designated (Fig. 5).

Description. — See Appendix 1.

Examined material. — 106 specimens from NIGPAS collections and three from Tohoku University collections: NIGP-DYH-3-6, NIGP-Shen-1 (Figs 6A-C), Shen-2-3 (Fig. 1B), Shen-4-6, Shen-11-20, Shen-22-23 (Fig. 3E, F), Shen-26 (Fig. 2A, B), Shen-29, Shen-32-36, Shen-38-39; Shen-40 (Fig. 2C), Shen-42, Shen-47, Shen-50-56, Shen-58, Shen-62, Shen-64, Shen-66-68, Shen-71, Shen-a-b-c, Shen-f-g-h, Shen-GM1 (Fig. 6D, see also Appendix 3), Shen-RT132 (Fig. 13C), Shen-RT141, Shen-145, one specimen from Shen where the number “53” is crossed, NIGP-126337 (holotype of *C. aethus*, Figs 1A; 3A-D), 126338-126347, 126353 (Fig. 12B, C), 126354 (Figs 13A, B), 126366, new unpublished specimens in NIGP collections: NIGP-175159 (Fig. 7), 175159 (Fig. 7), and research specimens without collection number herein numbered sp1-31 (sp11: Fig. 12A), Tohoku-U-57254, U-57267 and U-57272 (Fig. 8; see also Appendix 6).

REMARK ON THE TYPE

The original type material of *Palaeocambarus licenti* consists of three specimens, one holotype (“type”, Van Straelen 1928b: Fig. 1), and two paratypes (only one originally illustrated). This material was supposedly initially housed in the Huangho Paiho Museum (Tianjin, China). Enquiries were made to try to locate this material again, but were unsuccessful as the specimens do not appear to be in Tianjin Natural History Museum (successor to the Huangho Paiho Museum listed by Van Straelen 1928b) nor in the Royal Belgian Institute of Natural Sciences (where Van Straelen used to work). For this reason, and in order to preserve nomenclatural stability, we herein designate the specimen NIGP-126342 as the neotype of *P. licenti*. This specimen preserves well the rostrum, first pereiopod, epistome, parts of the tailfan and even what is possibly the annulus ventralis, all of which are important for taxonomy. Besides, Van Straelen (1928b) indicates that the now lost holotype and paratypes come from the south-west of Moukden (present day Shenyang). No outcrops of the Yixian

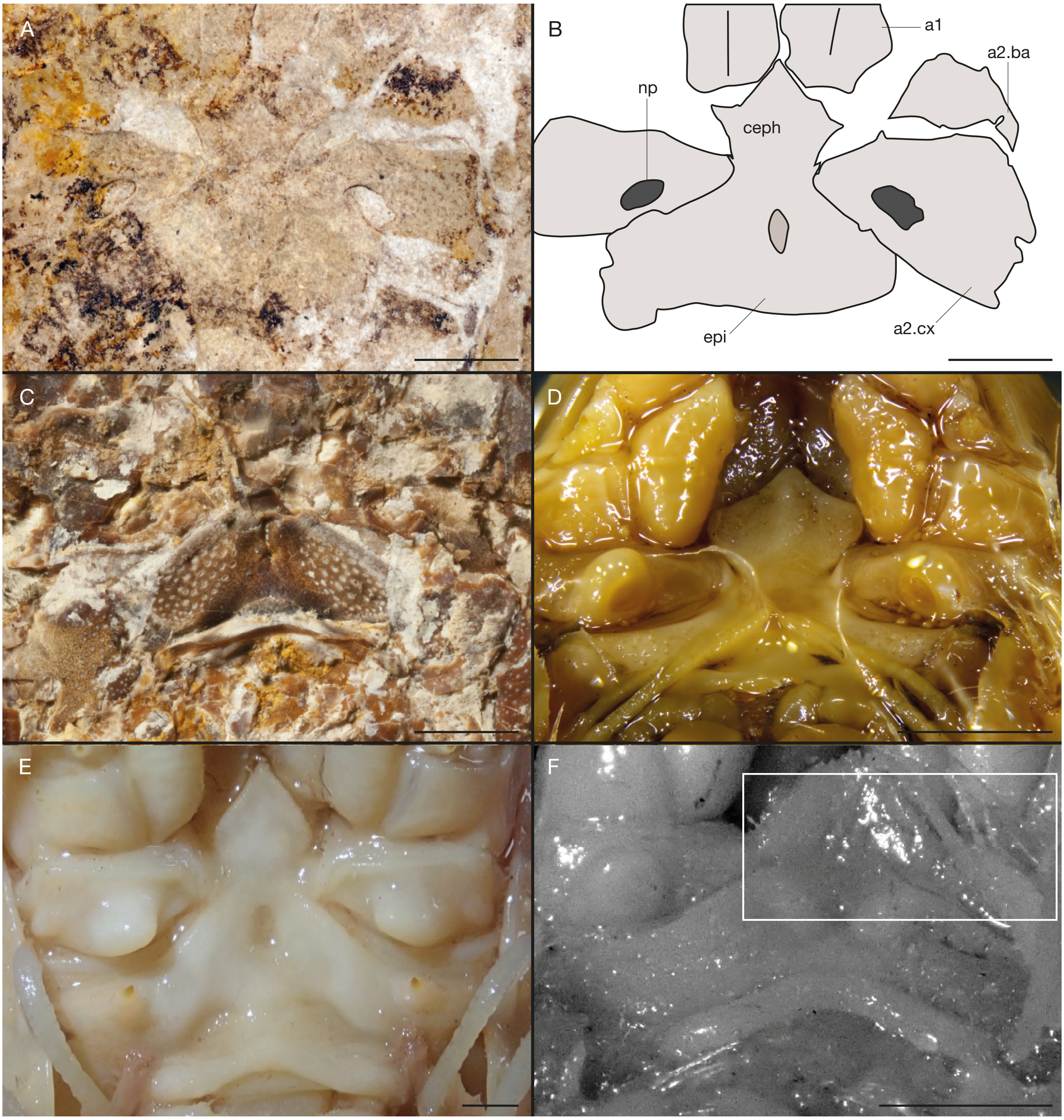

Fig. 2. — Comparison of epistomes in fossil and extant crayfishes: **A**, **B**, epistome of *P. licenti* (NIGP-Shen-26), photo (**A**) and interpretative line-drawing (**B**); **C**, epistome of *P. licenti* (NIGP-Shen-40); **D**, epistome of a female *Cambaroides dauricus* (Pallas, 1972) (MNHN-IU-2022-4077, extant, Mandchuria); **E**, *Cambarus bartonii* (Fabricius, 1798) (MNHN-IU-2022-4074, extant, Philadelphia, United States); **F**, *Astacus astacus* (Linnaeus, 1758) (MNHN-IU-2022-4069, extant, Nissi, Greece). Photos of fossil specimens in cross-polarized light. Abbreviations: **a1**, antennula; **a2.ba**, antennal basipodite; **a2.cx**, antennal coxa; **epi**, epistome; **uo**, urinary orifice (nephropore). Photographs: D. Audo. Scale bars: 2 mm.

Formation are known in the immediate vicinity of Shenyang, suggesting that the type material came from further southeast of the city. Although the exact origin of the type material cannot be determined precisely, it may correspond to Chaoyang. From this point of view, the neotype NIGP-126342 from Lingyuan most likely comes from a relatively similar outcrop.

Comments

Number of species in Jehol biota

To date, three separate species of crayfishes from the Jehol biota have been described. To justify the second species, *A. spinirostrius*, Imaizumi (1938) argued that it differed from *A. licenti* by the presence of dorsal spines

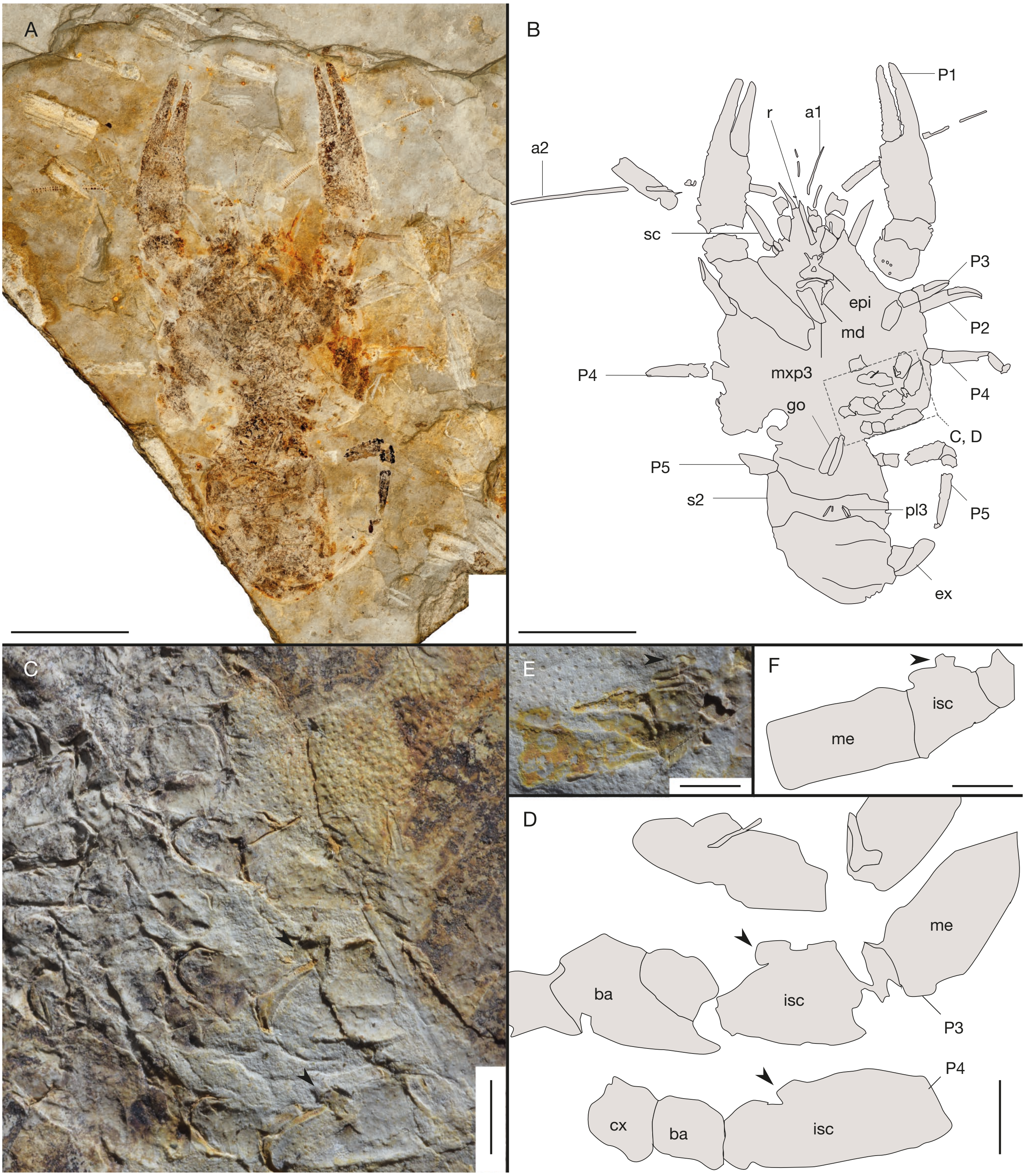

Fig. 3. — Ischial hooks in *P. licenti*: **A**-**D**, on specimen NIGP-126337 (holotype of *Cricoidoscelosus aethus*), ventral view in cross-polarized light (**A**) and interpretative line-drawing (**B**); **C**, **D**, detailed view of the base of P2-P4 (th5-th7) (**C**), and interpretative line drawing (**D**) – note that **C** and **D** are aligned horizontally for convenience; **E**, **F**, on specimen NIGP-Shen-22, detail of the ischium of P4 (th7). Abbreviations: **a1**, antennula; **a2**, antenna; **ba**, basipod; **cx**, coxa; **epi**, epistome; **ex**, uropodal exopod; **go**, male gonopod; **isc**, ischium; **md**, mandible; **me**, merus; **mxp3**, maxilliped 3 (thoracopod 3); **P1**-**P5**, pereiopods 1-5 (thoracopod 4-8); **pl3**, pleopod 3; **r**, rostrum; **s2**, pleonite 2; **sc**, scaphocerite. Photographs: A, D. Audo; C, E, D.-Y. Huang. Scale bars: A, B, 20 mm; C-F, 2 mm.

on the rostrum (lacking in *A. licenti*), possibly the shape of cervical groove, the absence of spine on gastric region (present in *A. licenti*), trigonal s2 tergopleuron (?) (more rounded in *A. licenti*) and uropodal exopodite shorter than endopodite (inverse in *A. licenti*). These characters were rejected by Taylor *et al.* (1999) who suggested they

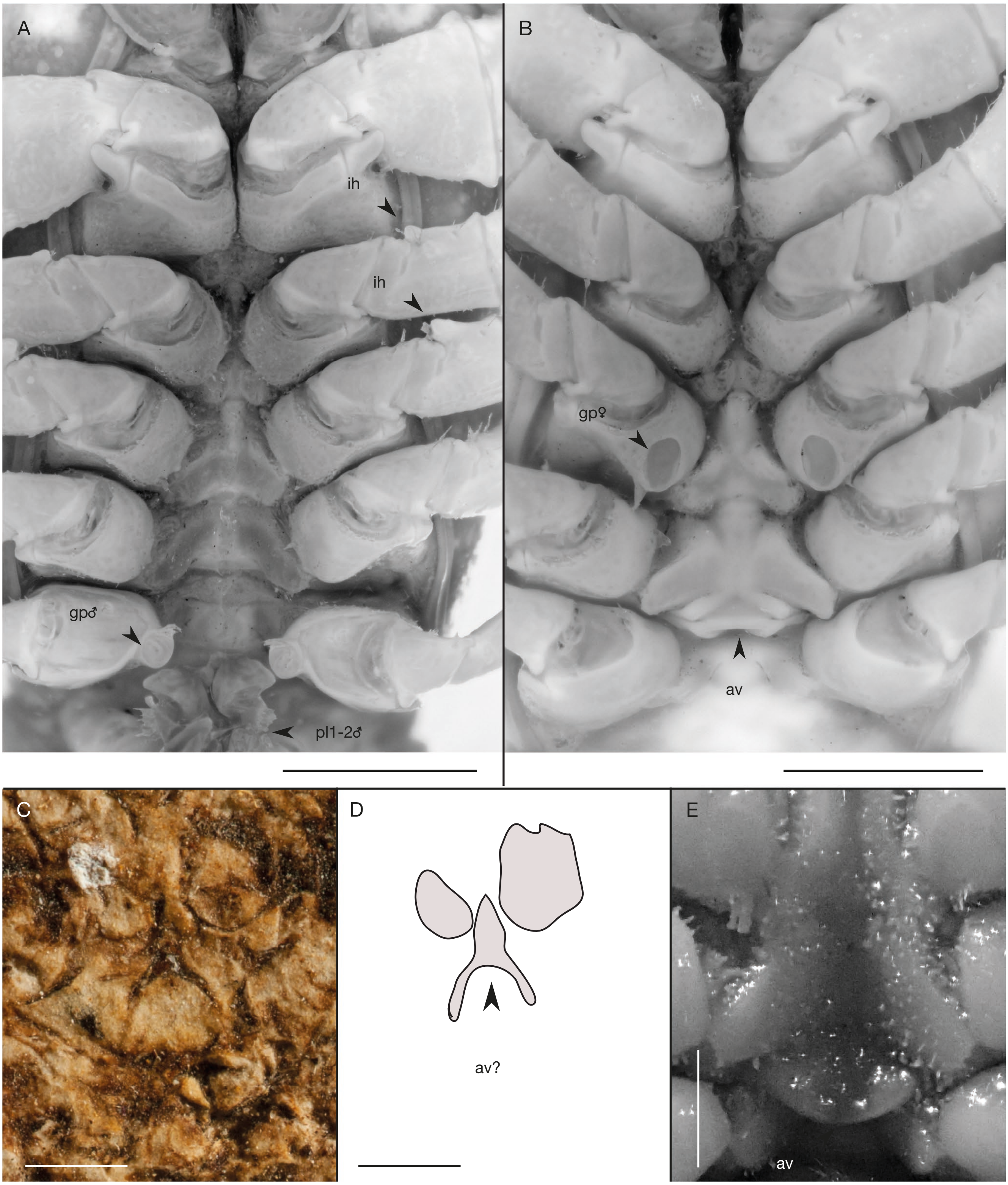

Fig. 4. — Sexual dimorphism: **A**, **B**, *Cambaroides dauricus* (AS11, extant, Mandchuria) male (**A**) and female (**B**); **C**, **D**, possible annulus ventralis in *Palaeocambarus licenti* (Van Straelen, 1928) specimen NIGP-126342 from the Early Cretaceous of China, photograph (**C**) and interpretative line-drawing (**D**); **E**, annulus ventralis in *Cambarus bartonii* (Fabricius, 1798) (AS90, extant, Philadelphia, United States); Abbreviations: **av**, annulus ventralis; **av?**, potential annulus ventralis; **gp♀**, female gonopore; **gp♂**, male gonopore; **pl1-2♂**, pleopods 1-2 (male gonopods). Photographs: D. Audo. Scale bars: A, B, E, 5 mm; C, D, 2 mm.

mostly represent variations in preservation. We agree with this view, as for instance, the spines dorsal to the rostrum are indeed actually part of the supraorbital carina, on the side of rostrum. Similarly, the relative sizes of the uropodal exopod and endopod appear different in different specimens due to incomplete preservation of the distal

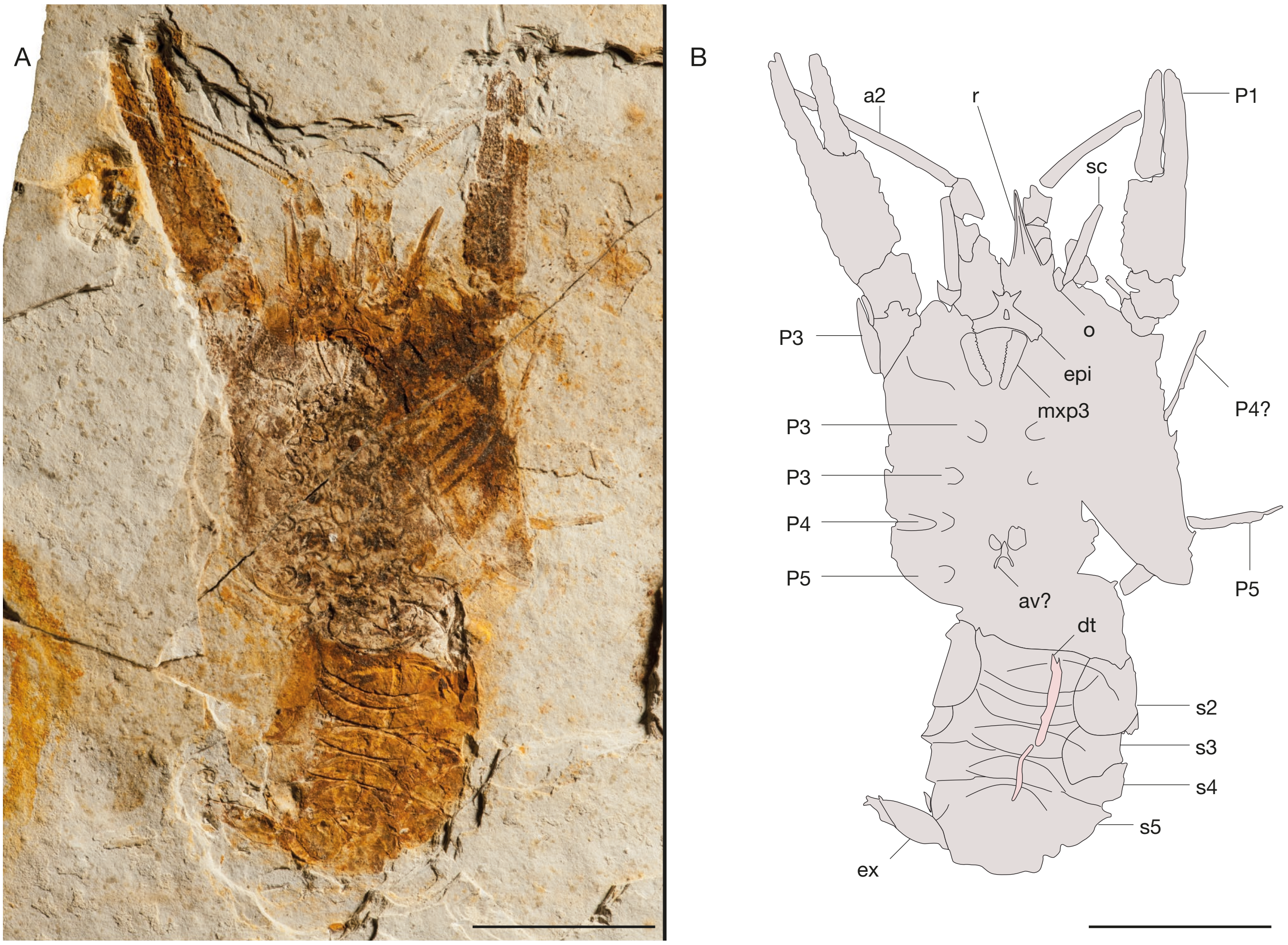

Fig. 5. — Neotype of *Palaeocambarus licenti* (Van Straelen, 1928), specimen NIGP-126342: ventral view in cross-polarized light (**A**) and interpretative line-drawing (**B**). Abbreviations: **a2**, antenna; **av?**, potential annulus ventralis; **dt**; digestive tract; **epi**, epistome; **ex**, uropodal exopod; **mxp3**, maxilliped 3 (thoracopod 3); **o**, eye; **P1**-**P5**, pereiopods 1-5 (th4-th8); **r**, rostrum; **s2**-**s5**, pleonites 2-5; **sc**, scaphocerite. Photograph: D. Audo. Scale bars: 20 mm.

part of these structures, or different orientations of the specimens in the sediment. However, we do not agree with Taylor *et al.* (1999), or Shen *et al.* (2001) that *C. aethus* can be distinguished from *P. licenti*. As explained above, the diagnostic characters of Cricoidoscelosidae, which are the same as those distinguishing *A. aethus* from *P. licenti* are, in our opinion extremely common within crayfishes or misinterpreted. For these reasons, we do not find any compelling characters allowing for the distinction of the three species described from the Jehol biota so far.

Nevertheless, due to the large number of available specimens, the relatively large distribution area where they are found, and the often highly endemic nature of many crayfish species (Crandall & Buhay 2008), it would not be impossible to have multiple species in the Jehol biota, especially as species may co-occur (Alda & Kawai 2022). We therefore performed a linear morphometric analysis based on measurements of as many specimens as possible, including type material of *Astacus spinirostrius* Imaizumi, 1938, and *Cricoidoscelosus aethus* Taylor, Schram & Shen, 1999 trying to find variations that could help characterize separate species. Results are given in table 2. As shown out of the eight elements studied, only the relative length of the pleon compared to that of uropodal exopod does not have a normal distribution: the distribution is asymmetrical but not bimodal (Fig. 9). A bimodal or multimodal distribution could have hinted at the presence of multiple species in our sample. While the present results cannot exclude the possibility of having multiple species, the parameter distribution is herein attributed to intraspecific variation and variations in preservation. As a result, we cannot at present consider there are more than one species of crayfish in Jehol biota. If more than one species is indeed present, the differences between species are likely mostly obfuscated by fossilisation. We thus herein consider *A. spinirostrius* Imaizumi, 1938 and *C. aethus* Taylor, Schram & Shen, 1999 to be more recent synonyms of *P. licenti* (Van Straelen, 1928).

Due to the aforementioned diagnostic characters, *Palaeocambarus* and *Cambaroides* are probably closely allied and forming a monophyletic group. A detailed comparison of *Palaeocambarus* to *Cambaroides* is complicated due to

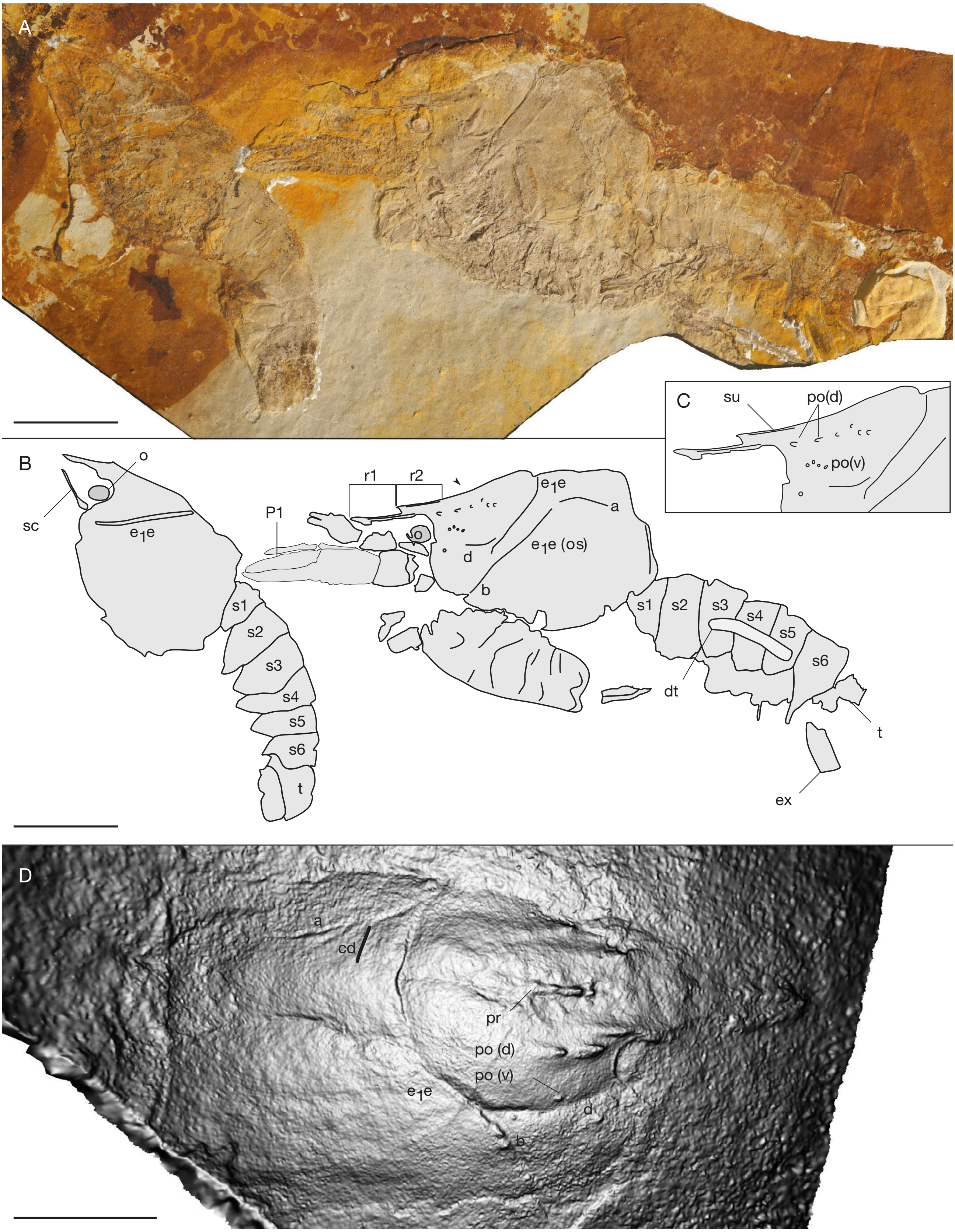

Fig. 6. — *Palaeocambarus licenti* (Van Straelen, 1928): three well preserved specimens NIGP-Shen-1, both in left-lateral view, in cross-polarized light (**A**), interpretative line drawing (**B**) and close-up of the cephalic area of one of the right crayfish in NIGP-Shen-1 (**C**), visualisation in Meshlab of the inverted surface volume of NIGP-Shen-GM1 from the photogrammetric model, with Minnaert shader (**D**). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **d**, gastro-orbital groove; **dt**, digestive tract; $\mathbf{e_1e}$, cervical groove; $\mathbf{e_1e}$ (**os**), cervical groove (opposite side); **ex**, uropodal exopod; **o**, eye; **P1**, pereiopod 1; **po** (**d**), postorbital carina (dorsal part); **po** (**v**), postorbital carina (ventral part); **pr**, postrostral carina; **r1**, acumen (distal part) of rostrum; **r2**, proximal part of rostrum; **s1**-**s6**, pleonites 1-6; **sc**, scaphocerite; **su**, subdorsal carina; **t**, telson. Photograph and photogrammetric model: D. Audo. Scale bars: A, B, 20 mm; D, 10 mm.

Fig. 7. — *Palaeocambarus licenti* (Van Straelen, 1928), specimen NIGP-175159 with well-preserved ornamentation of first pereiopod (thoracopod 4). Photograph: D.-Y. Huang. Scale bars: 20 mm.

the flattened preservation of fossil specimens. It however appears that specimens of *Palaeocambarus* differ from of all species of *Cambaroides* (based on data from Kawai *et al.* 2003, 2013, 2016; Kawai & Min 2005; Kawai & Barabanshchikov 2022; and observations of *C. dauricus* and *C. japonicus* from MNHN-IU collections) by a longer acumen of the rostrum, larger spines on postorbital carina and on median line in the cephalic area. For these reasons, and since no detailed phylogeny of the species of *Cambaroides* including *Palaeocambarus licenti* are available, we do not consider the two genera as synonym at present (Table 1).

DISCUSSION

Palaeobiogeography

The positive identification of close relatives to extant *Cambaroides* in the Early Cretaceous is important, as it ties in with the distribution of modern crayfishes, with *Cambaroides* known from continental East Asia, in the Japanese archipelago and Sakhalin islands (Kawai *et al.* 2003, 2013, 2016). This indeed shows that these crayfishes had enough time to both spread in East Asia, including the Japanese archipelago and Sakhalin islands before these were separated from continental Asia in Miocene (Fournier *et al.* 1994; Jolivet *et al.* 1994).

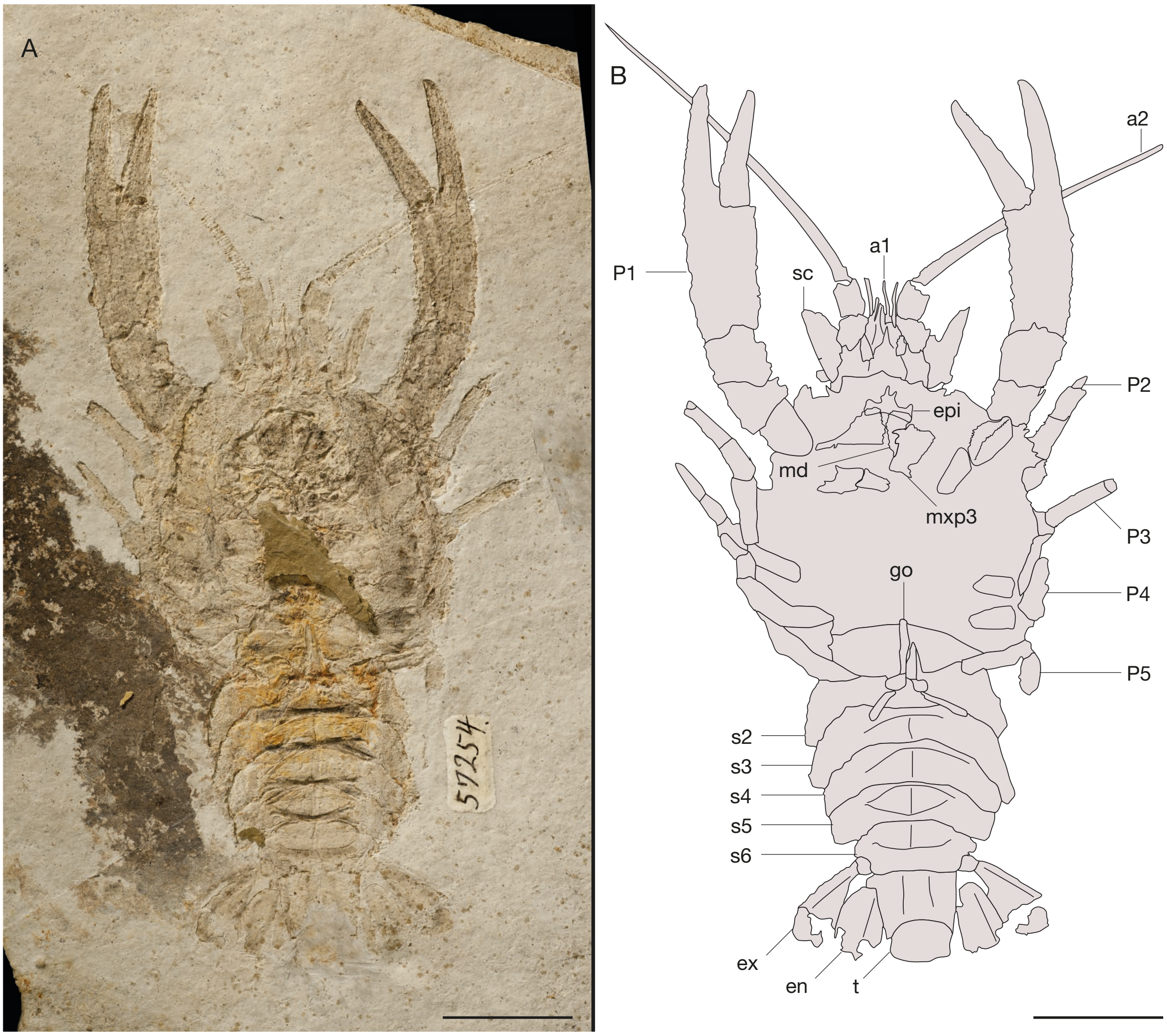

Fig. 8. — Syntype of *Astacus spinirostrius* (synonym of *P. licenti*), ventral view in cross-polarized light (**A**) and interpretative line-drawing (**B**), Abbreviations: **a1**, antennula: **a2**, antenna; **en**, uropodal endopod; **epi**, epistome; **ex**, uropodal exopod; **go**, male gonopod; **md**, mandible; **mxp3**, maxilliped 3 (th. 3); **P1**-**P5**, pereiopods 1-5 (th. 4-8); **s2**-**s6**, pleonites 2-6; **sc**, scaphocerite; **t**, telson. Photograph: D. Audo. Scale bars: 20 mm.

Preservation

Fossil ecdysozoans, notably arthropods, can either represent body fossils or exoskeletons discarded after ecdysis. During moulting (ecdysis), the old exoskeleton will be torn or disarticulate along a line of least resistance to allow the animal with its still soft, new exoskeleton to exit the old exoskeleton. In the case of decapod crustaceans, the break in the exoskeleton usually occurs at the articulation between the cephalothorax and pleon (disarticulation), and, in some groups, between the cephalothorax and pleon (disarticulation) and along the median line of cephalothorax (tearing). As a result, these empty exoskeletons can be identified by an at least partial disarticulation between the cephalothorax and pleon, a cut along the cephalothoracic shield median line or/and unusual position of some appendages (Schweigert 2007; Charbonnier *et al.* 2013; Audo 2016). Regularly however, the old exoskeleton will fold back due to its elasticity, giving

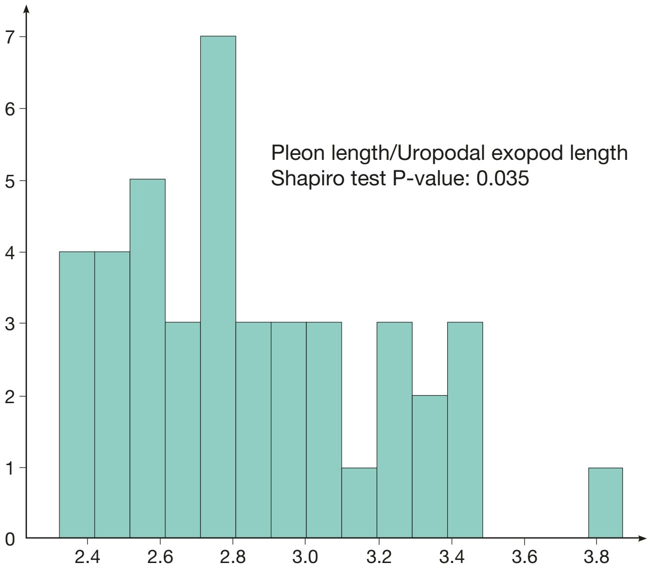

Fig. 9. — Distribution of pleon length to uropodal exopod length ratios.

Fig. 10. — Scientific reconstructions in dorsal view of *Palaeastacus licenti* (Van Straelen, 1928b). Drawing: C. Letenneur (UMR 7207 CR2P).

it an aspect very similar to that of the complete animal. Another clue allowing to distinguish body fossils from empty exoskeleton is the compaction: body fossils can also include soft-parts preservation (muscles notably). case of Solnhofen-type outcrops, most of the fossils actually correspond to empty exoskeleton, not body fossils (Audo *et al.* 2014; Schweigert 2007; see also Briggs *et al.* 2005 for a case in a xiphosuran).

The crayfishes from Jehol biota are preserved in connection, with fine anatomical details such as antennae and even traces of ommatidia preserved (Fig. 12A). We did not observe massive preservation of muscles or soft parts, and the fossils are usually as flat as most Solnhofen-type fossils or fossil from the Upper Cretaceous of Lebanon (when present, soft parts are flattened, see Briggs *et al.* 2005; Audo & Charbonnier 2013; Audo *et al.* 2014; Bicknell *et al.* 2019; Odin *et al.* 2019). Besides, some specimens only consist of an isolated cephalothorax, and others seems to have a partial disarticulation between the cephalothorax and pleon (posterior margin of cephalothorax raised

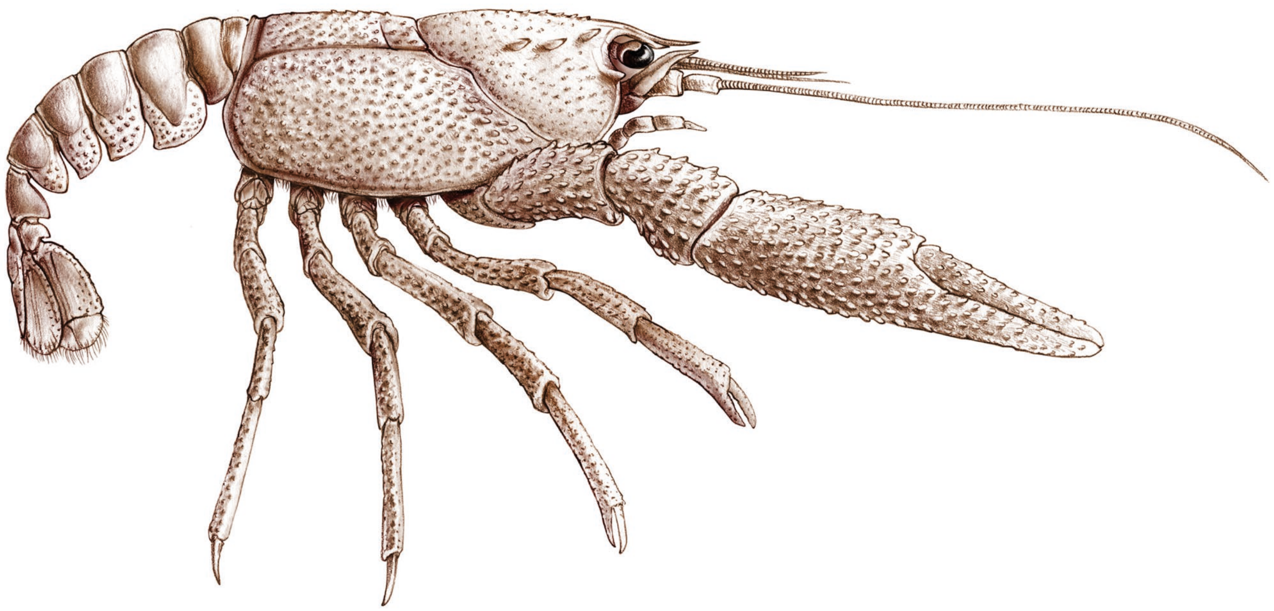

Fig. 11. — Scientific reconstructions in lateral view of *Palaeastacus licenti*. Drawing: C. Letenneur (UMR 7207 CR2P).

Table 1. — Results of linear morphometric analyses on *P. licenti* (Van Straelen, 1928b).

Element	Requirements	Normal	Shapiro test P-value	Mean
Cephalothorax length / pleon length	None	Yes	0.384	1.277
Cephalothorax width / pleon width	Only dorsoventral	Yes	0.103	1.457
Rostrum length / width	Only dorsoventral	Yes	0.98	2.269
Propodus lenght / shield length	None	Yes	0.551	0.593
Propodus lenght / width	None	Yes	0.487	3.622
P1 Propodus / P1 dactylus	None	Yes	0.135	1.951
Pleon / Uropod length	None	No	0.035	2.85
Telson length / width	Only dorsoventral	Yes	0.574	1.056

a few millimetres above the pleon). These would suggest, at first glance, that several of these fossils corresponds to empty exoskeletons. Specimens with isolated cephalothorax (NIGP-126347, Shen-GM1 – see Fig. 6D and Appendix 3) or with strong disarticulation between the cephalothorax and pleon (NIGP-Shen-RT132, sp29, Fig. 13C) are most likely empty exoskeletons. As explained by Schram & Shen (2000), empty skeletons discarded after exuviations are interesting finds as crayfishes often eat this exoskeleton (Schram & Shen 2000), T. Kawai pers. obs.) 18 of these specimens preserve gastroliths remains, structures used to store calcium in the stomach during the intermoult period. The presence of a gastrolith is a clear indication of a body fossil, indeed, the gastroliths remains inside the stomach (Murakami & Kawai 2022; Fig. 14) where they are dissolved (Vogt 2002). Even more specimens show traces of the proctodeum (posterior alimentary tractus) infilled with sediment (Figs 5; 6A, B; 13A, B). It has been observed that some crayfishes can have sediment in the stomach and proctodeum, and empty exoskeletons do not (T. Kawai pers. obs.). This suggest again that specimens with sediment in the stomach/proctodeum are body fossils. We note that one specimen interpreted as an exuvia by Schram & Shen (2000) preserves parts of the proctodeum (Figs 13A, B), contrary to clear moulted exoskeleton (Fig. 13C) and is therefore probably a partially decayed body fossil. Also, several specimens preserve traces of mineralized muscles (Schram & Shen 2000), which contrary to what is known in Solnhofen are considerably flat. Considering specimens with gastroliths, soft parts and/or sediment in the proctodeum, more than half of the fossils are body fossils, not empty exoskeletons. It is notable however that all these fossils are highly compressed and some even shows a slight disarticulation between the cephalothorax and pleon. We suggest that while the taphonomy was conducive to the preservation of mineralized tissues, most of the soft parts were probably lost to decomposition. Another possible piece of evidence is the position of gastroliths in some specimens: in living animals, the pair of gastroliths are positioned dorsolaterally with both gastroliths almost touching dorsally; yet in some fossils (gastroliths not close one to the other: NIGP-Shen-12-13, Shen-52; gastroliths not in the same orientation: NIGP-126353; Fig. 12B, C), the position of the gastroliths seems to have settled on the bottom of a mostly empty exoskeleton after soft parts decomposed.

FIG. 12. — Eyes and gastroliths: detail of the eye of spec11 (**A**) and specimen with gastroliths NIGP-126353, whole specimen in dorsal view, in cross-polarized light (**B**) and close-up of the gastroliths imprint, in cross-polarized light (**C**). Photographs: D. Audo. Scale bars: A, 1 mm; B, 20 mm; C, 10 mm.

PALAEOECOLOGY

Taylor *et al.* (1999), suggested the first chelipeds (pereiopod 1/thoracopod 4 claws) are quite dissimilar to those of extant *Cambaroides*. Actually, species of *Cambaroides* have two main types of first chelipeds: the general type, for instance in *Cambaroides japonicus* (de Haan, 1841) (see Kawai & Labay 2011) and the narrow type, as in *Cambaroides schrenckii* (Kessler, 1874) (see Kawai *et al.* 2013). Among these two types, *Palaeocambarus licenti* has claws of the narrow type, similar to that of *C. schrenckii*. *Cambaroides shrenckii* lives in lentic waters (such as lakes, oxbow lakes) with a silty or sandy substrate with detritus and plant fragments, in meso- to oligotrophic conditions; in the case of juveniles, in less than 0.8 m deep waters, and deeper than 1 meter for adults (Kawai *et al.* 2013). *Palaeocambarus licenti* therefore probably inhabited a broadly similar habitat.

The Yixian Formation, and at large, the paleoenvironment where the Jehol Biota developed, were characterized by numerous lakes and forested area (Zhou 2006; Wang & Zhou 2008), in a relatively cold climate (mean annual temperature aroung 10°C: Amiot *et al.* 2015). Thus *P. licenti* probably had a very roughly similar environment to that of extant species of *Cambaroides*.

Within this environment and similarly to modern crayfishes (Arrignon 1981; Kozák *et al.* 2015; Thoma 2016), *P. licenti* probably fed on plant materials and small invertebrates such as insect larvae and small crustaceans (such as the abundant *Liaoningogriphus quadripartitus* Shen, Taylor & Schram, 1998 – Hemicaridea) that are all well-known is the Jehol biota (Chang *et al.* 2008). In turn, aquatic vertebrates such as *Monjurosuchus splendens* Endo, 1940 (Choristodera) and *Hyphalosaurus lingyuanensis* Gao, Tang & Wang, 1999 (Choristodera) may have predated

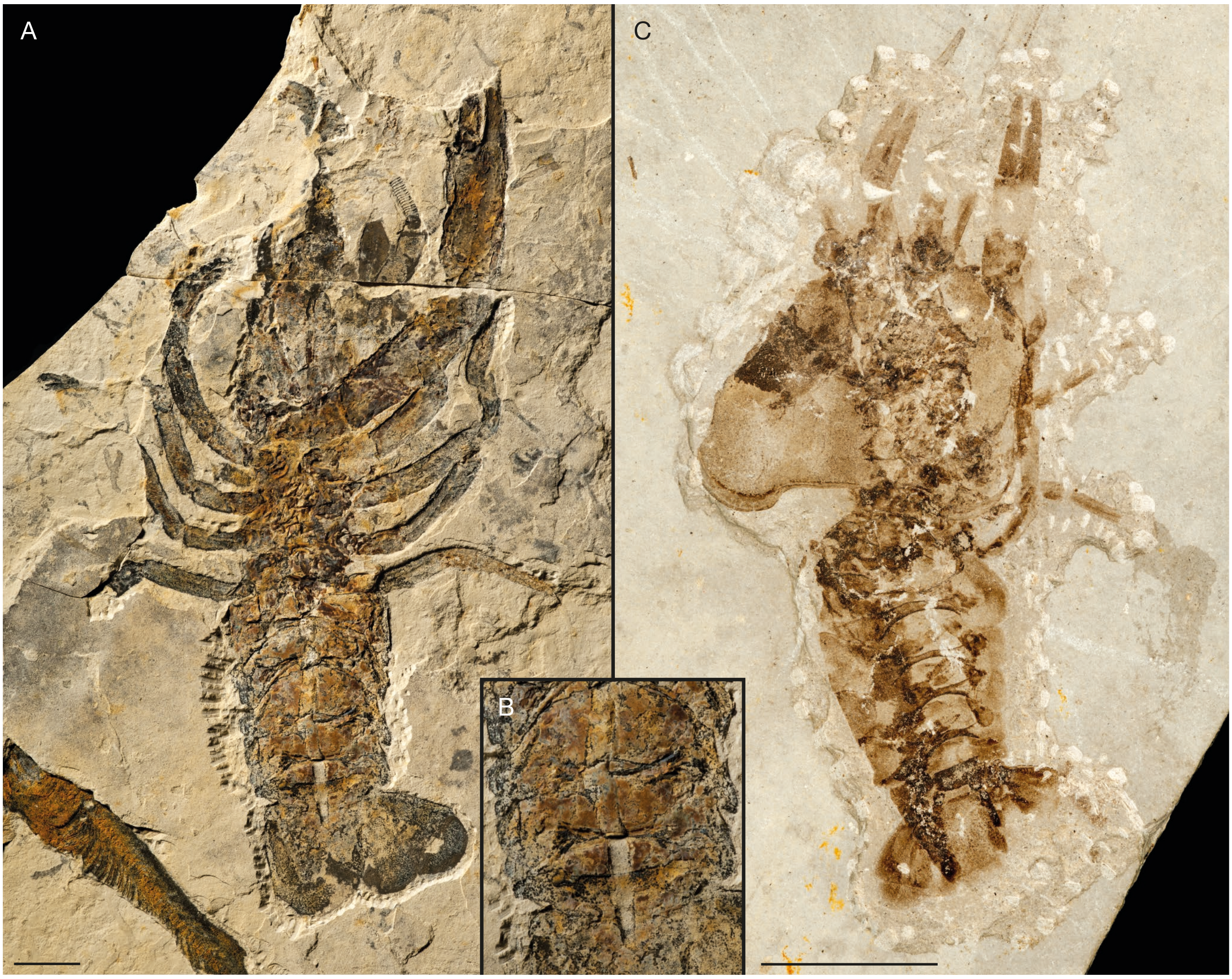

FIG. 13. — Two types of preservation: **A**, **B**, NIGP-126354, a possible fossil corpse (**A**) as shown by the presence of an infilled proctodeum (**B**); **C**, fossilized moult NIGP-Shen-RT132 (**C**) as shown by the disconnection of the cephalothorax shield, thinness of the exoskeleton and lack of fossilized soft-parts. Photographs: D. Audo. Scale bars: 10 mm.

on crayfishes although we are not aware of any crayfish in their gut content having been found. However, the lizard *Yabeinosaurus robustus* Dong, Wang & Even, 2017 at least occasionally ate crayfishes as proven by its gut-content (Xing *et al.* 2020).

CONCLUSION

Crayfishes have probably conquered freshwater in the Permian, with the earliest traces known so far found in North America (Hasiotis *et al.* 1993; Hasiotis 1999; Audo *et al.* in press). Due to the very limited fossil record of freshwater crayfishes, it is not possible to know if at the time crayfishes were already widespread all over Pangea or not. However, if they were not yet present in Northern China, crayfishes may have invaded this area from the rest of Pangea as early as Triassic as *Camborygma litonomos* Hasiotis & Mitchell, 1993, ichnofossils usually attributed to crayfishes, are known from Henan Province (Zheng *et al.* 2023), after the closure of the Ural seaway (Fokin *et al.* 2001). Astacoidea (northern hemisphere crayfishes) and Parastacoidea (southern hemisphere crayfishes) probably diverged around the Permian-Triassic (Bracken-Grissom *et al.* 2014) or the Middle Triassic (Wolfe *et al.* 2019), long before the breakup of Pangea, which is dated around the Callovian (Enay *et al.* 1993). Moreover, it is probable that *Cambaroides* diverged early from other northern hemisphere crayfishes (Astacoidea) as, based upon molecular studies the family has been interpreted as a sister group of other Astacoidea (Astacidae + Cambaridae: Breinholt *et al.* 2009; Grandjean *et al.* 2017; Wolfe *et al.* 2019), as a sister group of Astacidae (Bracken *et al.* 2009) or as a sister group of *Pacifastacus* (from North-Eastern America: Crandall *et al.* 2000) – see also Kawai *et al.* (2021). Therefore, finding Early Cretaceous relatives to *Cambaroides*,

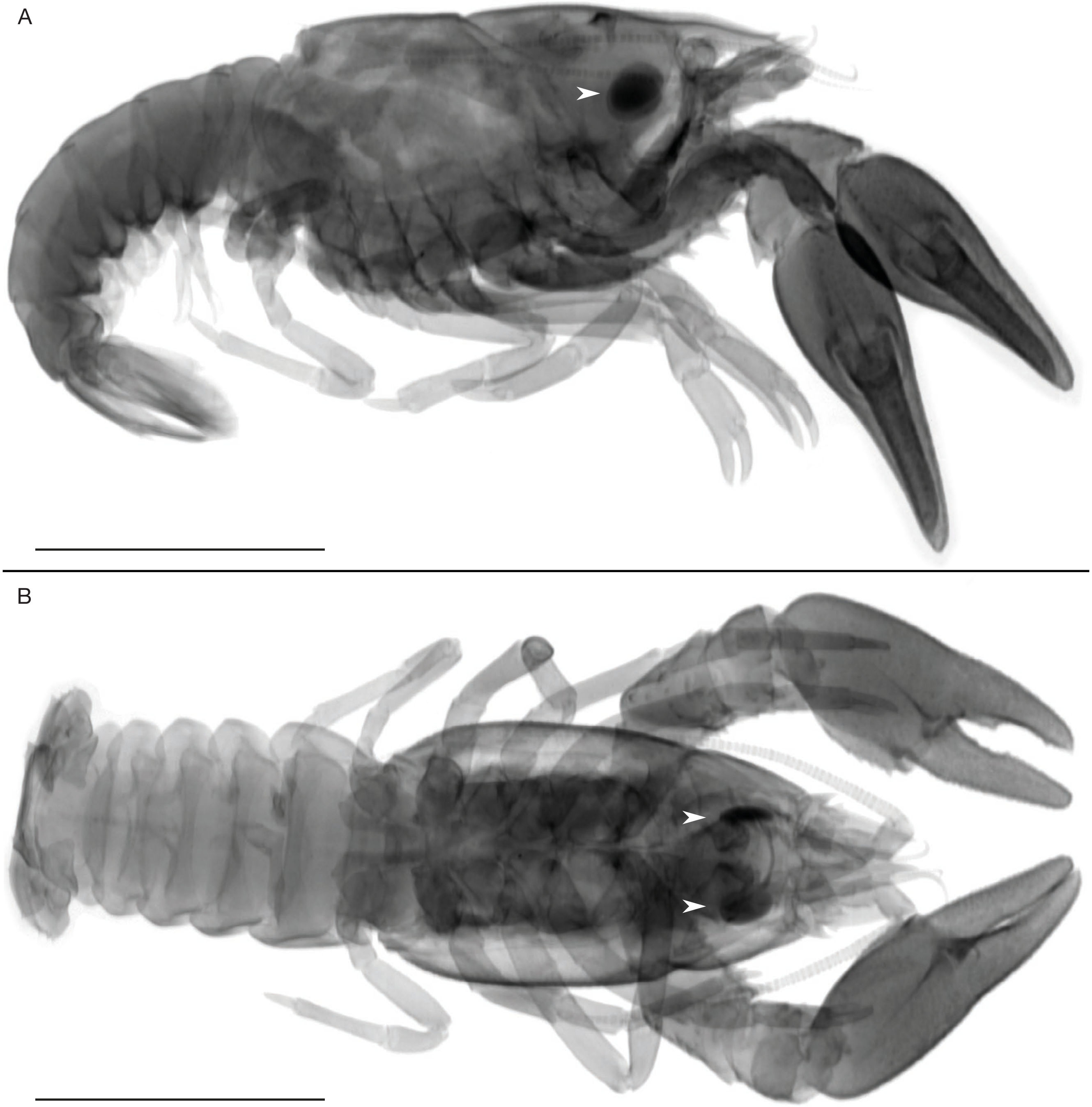

FIG. 14. — Radiographs of *Austropotamobius fulcisianus* MNHN-IU-2021-6684 (ex MNHN-IU-AS32, identification: T. Kawai) from Richelieu, Indre-et-Loire, France showing the position of gastroliths in an extant crayfish (arrows). Scale bars: 20 mm.

which are endemic to East Asia, is not surprising and shows that the lineage leading to *Cambaroides* was established in East Asia since at least Early Cretaceous.

Detailed comparisons with modern crayfishes are difficult, due to the preservation of fossil specimens. However, it is possible that the simple annulus ventralis typical of *Cambaroides* had appeared before that period, as it seems to also occur in *Palaeocambarus licenti*. Hopefully, other, perhaps older fossil crayfishes will one day be found in East Asia and help refine our understanding of East Asian crayfishes.

Acknowledgements

We thank the two reviewers, Sammy De Grave and Sylvain Charbonnier for helping improve this manuscript. We are indebted to Yanbin Shen (NIGPAS) for letting us access his material, giving multiple specimens, and constructive discussions. We are grateful to Daojun Yuan (NIGPAS) who helped access the specimens in the NIGPAS palaeontological collections, Laure Corbari and Paula Martin-Lefèvre (MNHN) for the access to comparison material. We also thank Zouhaira 'Zora' Harakati Gabsi (MNHN) for access to the X-ray facilities and explanation on how to operate it. This work was supported by the National Natural Science Foundation of China (41925008 and 42288201), and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000).

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Submitted on 16 May 2023;
accepted on 24 September 2023;
published on 14 December 2023.

Appendix 1. — Descriptive table of *P. licenti* (Van Straelen, 1928).

			Description	**Observed on specimens**
Cephalothoracic shield (Carapace)	Outline	Outline in dorsoventral view	pyriform, tapering anteriorly in the cephalic region, wider around the branchial region, with lateral sides slighty curved, longer than wide (up to 1.9 times longer than wide, depending on the preservation), with ocular incisions opening forward, posterior margin slightly concave, straight medially	NIGP-DYH-4, NIGP-DYH-6, NIGP-Shen-12, NIGP-Shen-16, NIGP-Shen-17, NIGP-Shen-18a, b, NIGP-Shen-19, NIGP-Shen-23, NIGP-Shen-35, NIGP-Shen-40, NIGP-Shen-42, NIGP-Shen-71, NIGP-Shen-F, NIGP-Shen-RT145, NIGP-126337, NIGP-126342, NIGP-126347, NIGP-126353, sp 1, sp2, sp4, sp5, sp7-10, sp11, sp16-17, sp20, sp23, sp24-25, sp26-27, sp29, sp31, Tohoku-U-57254
		Outline in lateral view	roughtly subrectangular, with straight dorsal margin, curved ventral margin, sinuous posterior margin and anterior margin cut by ocular and antennal incisions	NIGP-DYH-5, NIGP-Shen-1-3, NIGP-Shen-5-6, NIGP-Shen-11, NIGP-Shen-33-34, NIGP-Shen-50-51, NIGP-Shen-62, NIGP-Shen-68, NIGP-Shen-b-c, NIGP-Shen-GM1, NIGP-126340, NIGP-126366, sp22, Tohoku-U-57272
		Proportions height/width	probably slightly wider than high	All specimens except NIGP-Shen-20 and NIGP-Shen-56, based upon the slightly higher number of specimens in dorsoventral compression instead of lateral view
		Rostrum	comprising a proximal and distal part; proximal part wide, a little less than half the total length of the rostrum (from the tip to the ocular incision), tapering distally, flanked by a pair of lateral spines forming the tip of supra-orbital carina; distal part narrow, blade-like, fringed by a thin carina; axial area with a depression/wide groove	NIGP-Shen-1-2, NIGP-Shen-12, NIGP-Shen-32, NIGP-Shen-39, NIGP-Shen-42, NIGP-Shen-a, NIGP-Shen-GM1, NIGP-RT132, NIGP-RT143, NIGPAS-126338-126339, NIGP-126342-126343, NIGP-126346-126347, sp2, sp6, sp8, sp11, sp18, sp24-25
		Dorsal margin	straight, lined by a shallow groove	NIGP-DYH-5, NIGP-Shen-1-3, NIGP-Shen-5-6, NIGP-Shen-11, NIGP-Shen-19-20, NIGP-Shen-33-34, NIGP-Shen-50-51, NIGP-Shen-62, NIGP-Shen-68, NIGP-Shen-b-c, NIGP-Shen-GM1, NIGP-126340, NIGP-126366, sp22, Tohoku-U-57272
		Ocular incision	shallow	
		Antennal spine	short and blunt	
		Antennal incision	shorter and shallower than ocular incision	
		Pterygostomian spine	none, pterygostomian angle slightly rounded	
		Ventral margin	curved, lined by a groove, seemlessly connecting to the ventral/branchial part of posterior margin	
		Posterior margin, articular area	straight, lined by a shallow groove	
		Posterior margin, branchial area	curved, lined by a groove	

Appendix 1. — Continuation.

			Description	**Observed on specimens**
	Grooves	Branchiocardiac (a)	extending from the cervical groove, subparallel to median line	NIGP-DYH-5-6, NIGP-Shen-1, NIGP-Shen-3, NIGP-Shen-5-6, NIGP-Shen-11, NIGP-Shen-15, NIGP-Shen-17, NIGP-Shen-32-33, NIGP-Shen-39-40, NIGP-Shen-51, NIGP-Shen-53, NIGP-Shen-58, NIGP-Shen-62, NIGPAS-126338, NIGPAS-126344, NIGPAS-126347, NIGPAS-126353, NIGPAS-126366, NIGP-Shen-a, NIGP-Shen-b-c, NIGP-Shen-GM1, sp3, sp8, sp15-17, sp20, sp22, sp24, sp27, Tohoku-U-57254, Tohoku-U-57272
		Antennal (b)	oblique, forming an angle of around 40° compared to dorsal median line, joined posteriorly to the cervical groove	
		Hepatic (b1)	not visible / not present	
		Postcervical (c)	not visible / not present	
		Cardiac (ca)	extending from the branchiocardiac groove, parallel to the cervical groove, fading just before reaching median line	
		Gastro-orbital (d)	extending anteriorly from the mid-height of the cervical groove, covering halft the distance toward the anterior margin	
		Cervical (e1e)	deep, curved, crossing median line around the mid-lenght of shield in medium to large specimens, slightly behind the mid-length of the shield in small specimens (= cephalic region proportionally bigger in small specimens than in larger ones)	
	Spines and carinae	Subdorsal	parallel to median line, ending in the spine of the proximal part of rostrum, anteriorly, ending posteriorly a short distance posterior to the level of ocular incision	NIGP-Shen-1, NIGP-Shen-3, NIGPAS-126346, NIGPAS-126347, NIGP-Shen-GM1, Tohoku-U-57272
		Postorbital	paired, dorsal part very close to the subdorsal carina, formed of two spines each continued posteriorly by a short carina fading posteriorly; ventral part formed of at least four spines forming a slightly sinuous line (second spine placed a little higher than the three others) posterior to the ocular incision	
		Postrostral	over median line, with at least four spines, located posterior to the rostrum, on the anterior half of cephalic region	NIGPAS-Shen-68, NIGPAS-126346-126347, NIGP-Shen-GM1, sp2, sp19
	Ornamentation	Cephalic area	fine granulation	NIGP-Shen-1-3, NIGP-Shen-5, NIGP-Shen-11, NIGP-Shen-19, NIGP-Shen-32-33, NIGP-Shen-35, NIGP-Shen-39, NIGP-Shen-52, NIGP-Shen-58, NIGP-Shen-62, NIGP-Shen-68, NIGP-Shen-a, NIGP-Shen-GM1, NIGP-Shen-RT132, NIGPAS-126339, NIGPAS-126347, NIGPAS-126366, sp2, sp4, sp8, sp11, sp20, sp23, Tohoku-U-57272
		Branchial area	fine granulation	
		Above branchial area	fine granulation, slightly coarser than elsewhere	
	Gastroliths		circular in outline, relatively flat, one side convex and rounded, other side with a thick rim and a depression in the middle, generally massive, some smaller, probably depending on the growth stage	NIGP-Shen-2-4, NIGP-Shen-12-13, NIGP-Shen-19, NIGP-Shen-26, NIGP-Shen-32-34, NIGP-Shen-38, NIGP-Shen-52, NIGP-Shen-54, NIGP-Shen-a, NIGPAS-126338, NIGPAS-126346, NIGPAS-126353, NIGPAS-126366, sp18

Appendix 1. — Continuation.

			Description	**Observed on specimens**
Cephalothoracic sternites	Epistome		placed between the insertion of antenna and oral area, thick, comprising an arched main part and a subpentagonal cephalic lobe (anterior), dorsal side (toward body cavity) of main part with many holes, a ventral side of main part with a large median pit and a tuberculated carina on each side, extending from the median pit to the lateral margin, subpentagonal cephalic lobe wide (about 30% of epistome width); forming three spines (one pointing forward and two pointing foward and slightly outward), anterior margin slightly oblique, lateral margins poorly preserved and posterior margin (zygomal arch) slightly concave	NIGP-DYH-3, NIGP-Shen-4, NIGP-Shen-14, NIGP-Shen-16, NIGP-Shen-19, NIGP-Shen-22-23, NIGP-Shen-38, NIGP-Shen-40, NIGP-Shen-71, NIGP-Shen-RT145, NIGPAS-126337, NIGPAS-126342-126343, sp5, sp7-10, sp25, Tohoku-U-57254
	Th4-8 sternites		not visible between thoracopods 4 (P1), wider posteriorly, each sternite separated from other by a groove	NIGP-Shen-4, NIGP-Shen-14, NIGP-shen-71, NIGPAS-126342, sp2, sp10, sp14, sp23, sp30, sp31, Tohoku-U-57254
	Annulus ventralis		possibly on th7-8 (P4-5) sternites: appears in the fossil as an inverted Y, possibly where the sternite is folded	NIGP-Shen-16?, NIGPAS-Shen-38, NIGPAS-Shen-66?, NIGPAS-126342
Pleon	Proportions	Lenght	cephalothorax about 1.3 longer than pleon	All specimens except NIGP-Shen-5, 6, 11, 20, 26, 29, 53, 55, 67, GM1, NIGPAS-126338-126339, 126341-126344, 126346-126347, RT141, sp3-4, 6, sp12-14, 15-19, 21-22, 28, 29, Tohoku-U-57267, Tohoku-U-57272
		Width	cephalothorax about 1.4 wider than pleon; Pleon about 1.4 times longer than wide	
		Height	pleon about 2 times longer than high	

Appendix 1. — Continuation.

			Description	Observed on specimens
	Pleonite 1	Dorsal part	smooth	NIGP-DYH-5, NIGP-Shen-1, NIGP-Shen-4, NIGP-Shen-32, NIGP-Shen-34-35, NIGP-Shen-38-39, NIGP-Shen-42, NIGP-Shen-52, NIGP-Shen-71, NIGP-Shen-a, NIGP-Shen-b, NIGP-Shen-h, NIGP-Shen-RT132, NIGPAS-126346, 126353, sp1-2, sp4, sp8-9, sp11, sp20, sp24, sp30, sp31, Tohoku-U-57254, Tohoku-U-57272
		Axial carina	none	
		Tergopleuron	subquadrate, with a slightly rounded margin, angle slightly acuminate, smaller than the others	
	Pleonite 2	Dorsal part	smooth	
		Axial carina	none	
		Tergopleuron	wide, ovoid, extending over s1 tergopleuron anteriorly and s3 tergopleuron posteriorly	
	Pleonite 3	Dorsal part	smooth	
		Axial carina	none	
		Tergopleuron	subquadrate, with a slightly rounded margin, angle slightly acuminate, larger than s4-s6 tergopleura	
	Pleonite 4	Dorsal part	smooth	
		Axial carina	none	
		Tergopleuron	subquadrate, with a slightly rounded margin, angle slightly acuminate, larger than s5-s6 tergopleura	
	Pleonite 5	Dorsal part	smooth	
		Axial carina	none	
		Tergopleuron	subquadrate, with a slightly rounded margin, angle slightly acuminate, larger than s6 tergopleuron	
	Pleonite 6	Dorsal part	smooth	
		Axial carina	none	
		Tergopleuron	subquadrate, with a slightly rounded margin, angle slightly acuminate	
	Ornamentation		covered in scattered tubercles, coarser between branchiocardiac grooves	
Telson	Outline		subrectangular, with straight lateral margins and slightly curved posterior margin	NIGP-DYH-4-6, NIGP-Shen-14, NIGP-Shen-16-19, NIGP-Shen-38-40, NIGP-Shen-64, NIGP-Shen-66-67, NIGP-Shen-71, NIGP-Shen-f, NIGP-Shen-g, NIGP-Shen-RT132, NIGP-Shen-RT145, NIGPAS-126345, NIGP-126353, NIGPAS-12354, sp1-2, sp5, sp9, sp11, sp16, sp20, sp24, sp26, sp28, sp29, Tohoku-U-57254
	Surface		with a pair of lateral carina, thick and tuberculated anterior to the diaeresis, smooth and thin posterior to diaeresis	
	Diaresis		almost straight, slightly curved laterally, cutting telson at 3/4 of its length	
Eyes	Shape		ovoid, small from 0.62 to 4.1 mm (3-9 % of CL)	NIGP-DYH-5, NIGP-Shen-38, NIG-Shen-40, sp1, sp4, sp11, sp14, sp22
	Ommatidia		square facets each from 14 μm to 61 μm long (side of the square)	
	Setae		none visible	
Cephalic appendages	Antennula a1	Basis	formed of at least three stocky cylindrical podomeres, reaching to the second podomere of antennal endopod, first (proximal) podomere with a dorsal depression leaving room to the eye stalk	NIGP-DYH-4, NIGP-Shen-1, NIGP-Shen-6, NIGP-Shen-12-13, NIGP-Shen-18, NIGP-Shen-20, NIGP-Shen-22, NIGP-Shen-23, NIGP-Shen-26, NIGP-Shen-34, NIGP-Shen-38, NIGP-Shen-71, NIGPAS-126337-126338, NIGPAS-126343, NIGPAS-126353, sp4-5, sp8, sp11, sp20, sp22, sp24-25, sp27, sp29-30, Tohoku-U-57254
		Endopod	short flagellum, slightly shorter and thinner than the exopod	
		Exopod	short flagellum, about 1/3 cephalothorax length	

Appendix 1. — Continuation.

			Description	**Observed on specimens**
	Antenna a2	Basipod	formed of coxa and basipod; coxa wide, with a small short spine in the middle of anterior margin, carrying a small oval nephridiopore ventrally, near posterior margin; basipodite with lateral margin forming a curved spine extending slightly outward anterolaterally, visible dorsally near the eye	NIGP-DYH-3-6, NIGP-Shen-4, NIGP-Shen-6, NIGP-Shen-12-13, NIGP-Shen-16, NIGP-Shen-18, NIGP-Shen-20, NIGP-Shen-22, NIGP-Shen-23, NIGP-Shen-32, NIGP-Shen-34, NIGP-Shen-38, NIGP-Shen-68, NIGP-Shen-71, NIGP-Shen-RT-145, NIGPAS-126337-126338, NIGPAS-126342-126343, NIGPAS-126353, sp1-5, sp8, sp11, sp14-15, sp18-20, sp24-25, sp27, sp29-30, Tohoku-U-57254, Tohoku-U-57272
		Endopod	first three podomeres stocky, 2-3 thicker than flagellum, first podomere with an oblique anterior margin, second podomere longest of the three first podomeres, with a slightly angular, convex, anterior margin, third podomere slightly narrower than the two others and reaching further anteriorly than rostrum, flagellum about 1.5 times longer than cephalothorax and about 3 times thicker than antennular flagella	
		Exopod (scaphocerite)	reaching as far as the base of antennal flagellum, with a thick, acute outer margin with a few small lateral spines, inner margin thin	
	Mandible	Incisor/molar processes	hemicircular, concave dorsally and convex ventrally, oclusal margin straight with a few large, rounded teeth	NIGP-DYH-3, NIGP-DYH-6, NIGP-Shen-1, NIGP-Shen-12-13, NIGP-Shen-18, NIGP-Shen-32-33, NIGP-Shen-35, NIGP-Shen-38, NIGP-Shen-71, NIGP-Shen-RT145, NIGPAS-126337, NIGPAS-126345, NIGPAS-126354, sp5, sp7, sp10, sp30, Tohoku-U-57254
		Palp	short, ending in a distally slightly rounded dactylus	
		Coxal body	as wide (in dorsoventral view) as incisor process, extending obliquely from the incisor process	
	Maxilla 1		not visible / preserved	None
	Maxilla 2		not visible / preserved	None
Thoracic appendages	Thoracopod 1	Maxilliped 1	not visible / preserved	None
	Thoracopod 2	Maxilliped 2	not visible / preserved	None
	Thoracopod 3	Maxilliped 3	leg-like, reaching to the base of first pereiopod propodus, four last podomeres subcylindrical, ischium a little more than 1/3 of 3rd maxilliped total length, subrectangular, slightly flattened, and with a thin row of spines on the inner margin (crista dentata)	NIGP-Shen-29, NIGP-Shen-35, NIGP-Shen-71, NIGP-Shen-a-c, NIGPAS-126337, NIGPAS-126342, NIGPAS-126354, sp2-3, sp8
	Thoracopod 4 = Pereiopod 1	Coxa	poorly preserved in all specimens	None
		Basis	poorly preserved in all specimens	None
		Ischium	a little shorter than merus	NIGPAS-126354
		Merus	wider distally, about as long as palm (propodus excluding index), with an inner/inferior margin fringed with a row of short spines with a slightly larger spine anteriorly; upper margin straight and strengthened by a thin carina	NIGP-Shen-4-5, NIGP-Shen-12, NIGP-Shen-16-17, NIGP-Shen-23, NIGP-Shen-26, NIGP-Shen-32-35, NIGP-Shen-62, NIGP-Shen-66, NIGP-Shen-71, NIGP-Shen-a-c, NIGP-Shen-RT145, NIGPA-126340, NIGPA-126354, sp2-7, sp14, sp20, sp22, sp24, sp25, sp30, sp31, Tohoku-U-57254, Tohoku_U_57272

Appendix 1. — Continuation.

		Description	**Observed on specimens**
	Carpus	short, about half as long as dactylus, narrower proximally, with a pair of thin dorsal carina, inner side of the carpus with two rows of three large spines	NIGP-DYH-3-6, NIGP-Shen-1, NIGP-Shen-4-5, NIGP-Shen-12-13, NIGP-Shen-16, NIGP-Shen-18, NIGP-Shen-23, NIGP-Shen-26, NIGP-Shen-32, NIGP-Shen-35, NIGP-Shen-38, NIGP-Shen-39, NIGP-Shen-40, NIGP-Shen-42, NIGP-Shen-71, NIGP-Shen-a-c, NIGP-Shen-g, NIGP-Shen-RT145, NIGPAS-126337, NIGPAS-126338, NIGPAS-126339, NIGPAS-126342, NIGPAS-126343, NIGPAS-126353-126354, sp1-2, sp5, sp8-9, sp11, sp14, sp18-19, sp30, sp31 (not including distal parts), Tohoku-U-57254, Tohoku-U-57272
	Propodus	about 60% as long as cephalothorax, straight index as long as palm (rest of the propodus) fringed by two rows of small tubercles, palm subrectangular, covered in spines and tubercles, inner side of palm fringed many anthrorse spines, outer side and rest of the palm with tubercles rather than spines	
	Dactylus	straight, about as long as index, with straight occlusal margin fringed by two rows of small tubercles	
Thoracopod 5	Pereiopod 2	about 2/3 of the lenght of first pereiopod, claw a little smaller than half of the first pereiopod claw, straight slightly bent distally, with index (fixed finger arising from propodus) forming a slight angle with propodus, not as the straigt claw of first pereiopod, similar but less bent than the claw of pereiopod 3	NIGP-DYH-6, NIGP-Shen-2-3, NIGP-Shen-12, NIGP-Shen-22, NIGP-Shen-40, NIGP-Shen-42, NIGP-Shen-71, NIGP-Shen-a-c, NIGP-Shen-g, NIGP-Shen-RT141, NIGPAS-126339, NIGPAS-126346, NIGPAS-126354, sp2, sp19, sp24-25, Tohoku-U-57272
Thoracopod 6	Pereiopod 3	slightly longer than second pereiopod, claw with a long palm, forming 3/4 of the total length of the claw, as long and thinner than pereiopod 2 claw, index forming a slight angle (*c.* 25°) with the axis of the palm, stout carpus, a narrower proximally, slightly wider than propodus distally, a little less than 1/3 of the length of propodus, short coxa with the gonopore opening ventrally in females, ischium with a curved spine “hook” on the anterior/mesial side in males	NIGP-DYH-6, NIGP-Shen-2-4, NIGP-Shen-12, NIGP-Shen-32-34, NIGP-Shen-66 (gonopore), NIGP-Shen-68, NIGP-Shen-71, NIGP-Shen-a-c, NIGP-Shen-g, NIGPAS-126337, NIGPAS-126339, NIGPAS-126354, sp2, sp9, sp19, sp30 (gonopore), Tohoku-U-57254, Tohoku-U-57272
Thoracopod 7	Pereiopod 4	about as long as third pereiopod, longer than second pereiopod, achelate, propodus about as long as pereiopod 3 palm, dactylus curved and about as long as pereiopod 3 dactylus, stout carpus, a narrower proximally, slightly wider than propodus distally, a little less than 1/3 of the length of propodus, ischium with a curved spine “hook” on the anterior/mesial side in males	NIGP-Shen-2-3, NIGP-Shen-18, NIGP-Shen-34, NIGP-Shen-68, NIGP-Shen-71, NIGP-Shen-b-c, NIGP-Shen-g, NIGPAS-126337, NIGPAS-126354, sp2, sp5, sp9, sp26
Thoracopod 8	Pereiopod 5	slightly shorter than pereiopod 4, achelate, ornamented with short spines, propodus three times the lenght of carpus, ischium about as long as propodus, ischium about 1/3 as long as carpus and propodus, very short coxa with the gonopode opening ventrally	NIGP-Shen-12, NIGP-Shen-18, NIGP-Shen-32-33, NIGP-Shen-35, NIGP-Shen-68, NIGP-Shen-71, NIGP-Shen-a-c, NIGP-Shen-g, NIGPAS-126337, NIGPAS-126354, sp2, sp5, sp14, sp19, sp26

Appendix 1. — Continuation.

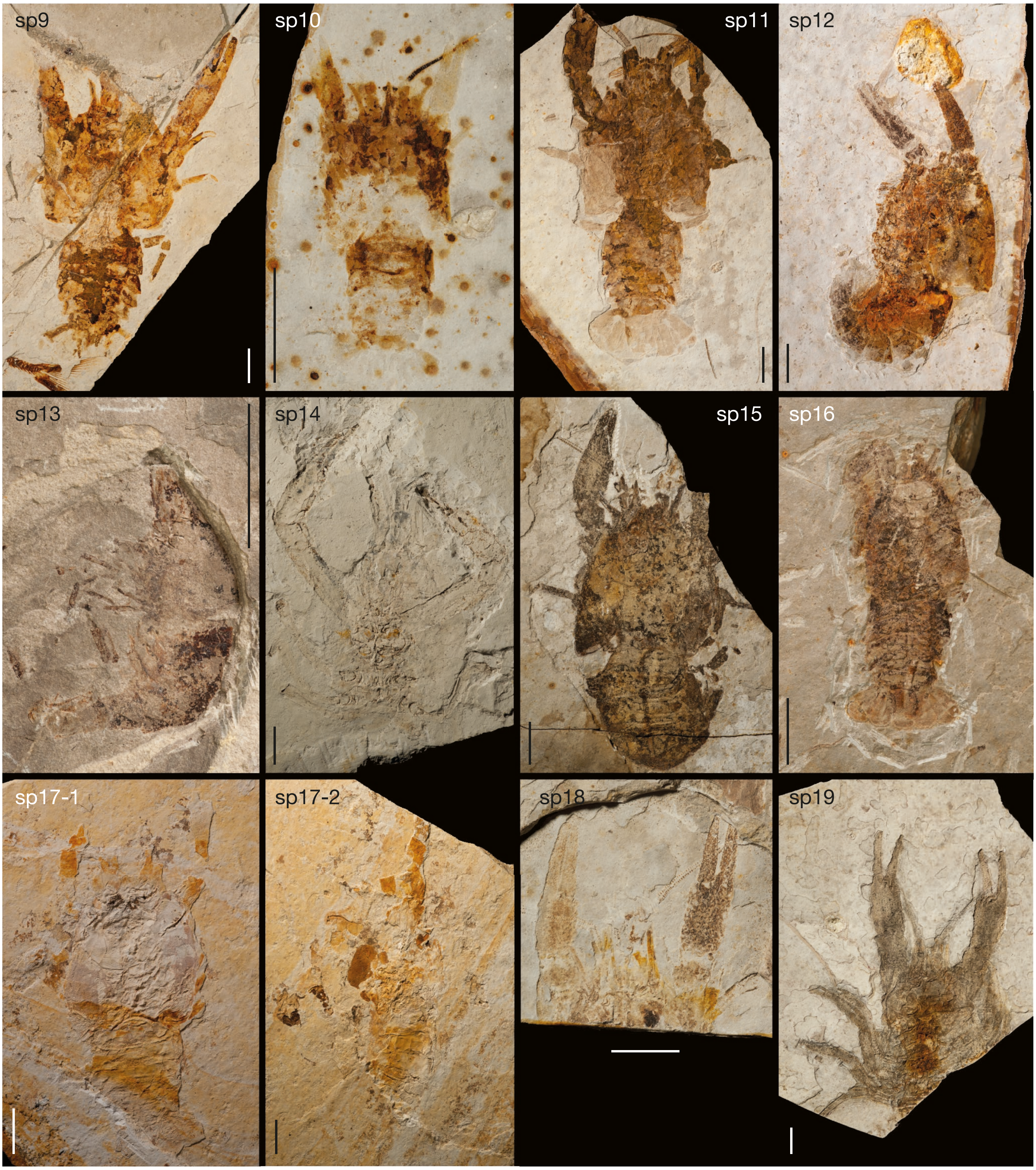
			Description	**Observed on specimens**
Pleonal appendages	Pleopod 1 & 2	Female (pleopod 1)	with two flagella?	NIGP-Shen-38?, NIGP-Shen-66
		Female (pleopod 2)	with two flagella	NIGP-Shen-12, NIGP-Shen-38, NIGP-Shen-66, NIGP-Shen-71
		Male (Gonopod 1)	short basal podomere connected to a longer, styliform podomere	NIGP-Shen-1-3, NIGP-Shen-5, NIGP-Shen-22, NIGP-Shen-29, NIGP-Shen-32-33, NIGP-Shen-h, NIGPAS-126337, NIGPAS-126354, sp4, sp9, sp30, Tohoku-U-57254
		Male (Gonopod 2)	as wide as P5, composed of at least three parts, proximal part short, median part twice as long as proximal part, distal part soft, curving anteriorly, possibly sudivided	
	Pleopod 3		ovoid basipodite strengthened by a longitudinal carina, two flagella, about 1/2 as long as pleonite heigth	NIGP-Shen-2-3, NIGP-Shen-66, NIGP-Shen-71, NIGP-Shen-b-c, NIGP-Shen-g, NIGP-Shen-h, NIGPAS-126340, sp2, sp22
	Pleopod 4		with two flagella, about 1/2 as long as pleonite heigth	NIGP-Shen-2-3, NIGP-Shen-66, NIGP-Shen-b-c, NIGP-Shen-g, NIGP-Shen-h, NIGPAS-126340, sp2, sp22
	Pleopod 5		with two flagella, about 1/2 as long as pleonite heigth	NIGP-Shen-2-3, sp22
	Pleopod 6 (uropod)	Basipod	short, reniform, with a deep rounded articulation near the outer margin	NIGP-DYH-6, NIGP-Shen-2-3, NIGP-Shen-12, NIGP-Shen-14, NIGP-Shen-16-19, NIGP-Shen-23, NIGP-Shen-32-35, NIGP-Shen-38-40, NIGP-Shen-51-52, NIGP-Shen-64, NIGP-Shen-66-68, NIGP-Shen-71, NIGP-Shen-a-c, NIGP-Shen-f, NIGP-Shen-g-h, NIGP-Shen-RT141, NIGPAS-126340, NIGPAS-126344-126345, NIGPAS-126353-126354, sp2, sp4-6, sp9, sp11, sp16, sp22, sp24, sp26-27, sp30, sp31, NIGPAS-126354, NIGPAS-126372
		Endopod	petaliform, distall margin rounded, distal margin fringed by setae, strengthened by a thin median longitudinal carina, covered with thin tubercles	
		Exopod	petaliform, distall margin rounded and fringed by setae, outer lateral margin straight, strengthened by a thin median longitudinal carina, diaeresis located in the posterior third part of the exopod, diaeresis marked by a row of small spines anterior to the diaeresis , outer spine ornamenting the diaeresis slightly larger	

APPENDIX 2. — List of specimens used in this study and cited in other studies, with notes on the preservation, some characters observed and measurements used in the statistical analysis. Values on a light orange background could not be precisely measured because of preservation. Values on a beige background are automatically calculated from other, measured values. https://doi.org/10.5852/geodiversitas2023v45a24_s2

APPENDIX 3. — 3D model obtained by photogrammetry of specimen NIGP-Shen-GM1. To visualize the model, extract all content of the archive in a folder, then open the file "NIGP_GM1.obj" with the 3D software of your choice, for instance Meshlab. https://doi.org/10.5852/geodiversitas2023v45a24_s3

APPENDIX 4. — Specimens without registration numbers used in the study. Continued in next two figures. Scale bars: 10 mm.

Appendix 5. — Specimens without registration numbers used in the study, continued from previous figure. Scale bars: 10 mm.



APPENDIX 6. — Specimens without registration numbers used in the study, continued from previous figures. Scale bars: 10 mm.