

THE LONG TRAIL: A CHIMERA-LIKE FOSSIL CRUSTACEAN INTERPRETED AS DECAPODA, STOMATOPODA, AMPHIPODA AND FINALLY ISOPODA

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Abstract. The process of interpreting and evaluating a fossil is a difficult task. Isopoda is a species-rich group of peracarid eumalacostracans which represent quite a challenge when found as fossils, independent of whether we are working with fragmentary or more complete specimens. Here we describe a new fossil species of crustacean, *Platurpodus odysseus* n. gen. n. sp., from the Irati Formation, Permian of Paraná Basin, Brazil. After misinterpretations, the fossil taxon is recognised here as a representative of Isopoda. The new species presents characters found in Phreatoicidea, Asellota and Oniscidea in a unique combination for the fossil and extant record, such as two pairs of sub-chelate anterior trunk appendages, a short region after the anus and flat uropods. This chimera-like morphology and a morphometric analysis of the sub-chelae indicate convergent evolution in the early diversification of Isopoda. The morphological diversification present in the Palaeozoic and Mesozoic fossil record of Eumalacostraca indicate a “push of the past” effect in different ingroups of Peracarida.

INTRODUCTION

Interpreting a fossil taxon is challenging, and even harder is to make sense of them in the light of evolution. There are many famous cases of misinterpretation of fossils in the history of science (Whittington & Briggs 1985; Davidson 2002; Starr et al. 2016; Foth & Rauhut 2017, among others). Such cases affect and misguide our understanding of evolution and estimations on diversity in the past.

Yet, fossils are still the best clues that we have to comprehend the history of life.

In groups such as Euarthropoda (sensu Maas & Waloszek 2001), which holds enormous morphological and ecological diversity within animals, the misinterpretation of a fossil can lead to the misinterpretation of how several lineages evolved. In such circumstances, morphologically diverse ingroups (where an ingroup is a group of species whose monophyly is established or hypothesised) represent quite a challenge, especially when dealing with fragmented specimens. Among crustaceans, malacostracans, erroneously dubbed “higher crustaceans” (e.g.,

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Abzhanov & Kaufman 2000; Berezina & Petryashev 2012; Štrus et al. 2019), have a rather rich fossil record. Two groups, Isopoda and Amphipoda, are particularly species-rich and form-diverse, each including about one fourth of all formally described extant malacostracan species (Lowry & Myers 2017; Boyko et al. 2020; Horton et al. 2020).

Amphipoda includes aquatic mostly benthic species (Bellan-Santini 2015; Lowry & Myers 2017). Representatives of this group have a laterally compressed body and are differentiated from other representatives of Eumalacostraca by a specialized pleon (posterior six segments of the body) (Bellan-Santini 2015). In most representatives of Eumalacostraca, the anterior five pleon segments carry appendages (pleopods) that are sub-similar, whereas the appendages of segment six are differentiated and therefore received another name, uropod (Kutschera et al. 2012).

In representatives of Amphipoda, the appendages of the anterior three segments differentiated from those of the posterior three. The appendages of the posterior three segments are similar to one another and (unfortunately) also termed uropods (Lowry & Myers 2013). The oldest fossil record of Amphipoda is from the Lower Cretaceous (Jarzembowski et al. 2020), but the group became more common from the Eocene onwards (Coleman & Myers 2000; Jażdżewski & Kupryjanowicz 2010).

Isopoda includes aquatic and terrestrial species, such as the commonly known “pill bugs”. Extant representatives of Isopoda comprise two distinct sister groups, Phreatoicidea and its unnamed sister-group that includes Asellota and Scutocoxifera. This arrangement is supported by morphologic (Wägele 1989; Brusca & Wilson 1991) and molecular phylogenies (Dreyer & Wägele 2002).

Phreatoicidea is often considered to be the oldest lineage of Isopoda (Wilson & Keable 2001) but of course, its sister lineage, which includes the remaining representatives of Isopoda (Wägele 1989; Brusca & Wilson 1991; Wilson & Keable 2001), must be of the same age. With about 90 extant formally described species, they are mainly found in Australia and New Zealand. Yet, some species also occur in South Africa (Gouws 2008) and India (Wilson & Reddy 2011). Phreatoicideans live on the surface vegetation or buried in sediments of freshwater environments, such as streams, ponds,

and mountain lakes. They have limited swimming skills and preferably crawl on the substrate (Wilson & Keable 2001).

Asellotans are small isopodans, in which the pleon segments 3–6 are usually conjoined to the telson. Also, pleopods are sexually dimorphic, specialized for mating. Most asellotans are marine, but some live in freshwater (Dreyer & Wägele 2002). Scutocoxifera includes all the remaining representatives of Isopoda. In this group, the proximal element (coxa) of the anterior seven trunk segments is largely immobilised. It is furthermore strongly flattened (“coxal plates”), and so strongly continuous to the body sclerites that it is often only recognisable as a separate structure by a thin suture line apparent on the tergite (Dreyer & Wägele 2002).

The fossil record of Isopoda includes late Palaeozoic representatives of Phreatoicidea and Scutocoxifera (Schädel et al. 2020), and Triassic Asellota (Selden et al. 2016). As for many groups of Euarthropoda, fossils of Isopoda are often difficult to recognize, as they frequently lack preserved distinct apomorphies.

We present here a new fossil species from the Permian (Cisuralian) of Brazil. The new fossil taxon has a unique mixture of characters, so far unknown in any fossil or extant species, that are found in different ingroups of Eumalacostraca, particularly Phreatoicidea and, to some extent, Amphipoda, characterising a chimera-type morphology, in the sense of the Greek mythical creature composed of body parts of other animals. We discuss the possible phylogenetic affinities of the new taxon, the possible cases of morphological convergence, and the “push of the past” effect present in Isopoda.

MATERIAL AND METHODS

Examined material

The material presented here is housed at the Palaeontology and Stratigraphy Museum “Prof. Dr. Paulo Milton Barbosa Landim” at the Geology Department, Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP), Rio Claro, SP, Brazil, catalogued as URC. AC. 196. This series contains 19 rock slabs with 14 specimens preserved, five of which have a counterpart. An additional part and counterpart specimen used in the description (LPRP/USP 0003 A,B) is deposited in the Palaeontology Collection of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, University of São Paulo (FFCLRP/USP), Ribeirão Preto, SP, Brazil.

The material figured here (Fig. 1) comprises almost all of the fossil specimens of this kind recovered from the above-mentioned collections, with only a few additional samples in the Palaeontology Collection of FFCLRP/USP. Some specimens of the species



Fig. 1 - Overview of the specimens of the new species of eumalacostracan crustacean described in this work. All specimens to the same scale, except the isolated leg element, R. Background filled with virtual matrix.

described here were collected by the authors (PGP, MCL, and RR), others were already deposited in the collections, resulting from decades of collection efforts by several researchers. These fossil specimens are quite rare, especially compared with the occurrence of other eumalacostracan found in the same stratum (Taquaral Member, Irati Formation) and site, the syncarid *Clarkecaris brasiliensis* (Clarke, 1920), with hundreds of remains deposited in different Brazilian collections.

Extant comparative material includes adult males of the amphipodan *Pallaseopsis quadrispinosa* (G.O. Sars, 1867), and of the phreatoicidean *Synamphisopus ambiguus* (Sheard, 1936), both held at the Bavarian State Collection of Zoology (Zoologische Staatssammlung München, ZSM), Munich, Germany. Extant material of the phreatoicidean *Paranphisopus palustris* (Glauert, 1924) is from the Centre of Natural History (Centrum für Naturkunde, CeNak), Hamburg, Germany.

Provenance of the material

All fossil material used in this research comes from a single outcrop, along a secondary farm road about 3 km south-west of the urban area of Rio Claro, São Paulo State, south-eastern Brazil, at UTM coordinates 23K 0228516 7512602, Córrego Alegre datum (Fig. 2). The outcrop exposes part of the Permian beds of the Paraná Basin. The lower part of the outcrop, at the beginning of the road slope, exposes the upper part of the Tatuí Formation. This is covered by a 0.2 m thick coarse sandstone bed, rich in small bone fragments and isolated paleonisciform fish teeth and scales, that may correspond to a basal transgressive lag of the Taquaral Member (Assine et al. 2003; Holz et al. 2010). Above that, the Taquaral Member proper (i.e., the lower unit of the Irati Formation, Passa Dois Group), comprises ca. 6 m-thick pelitic bed, whereas the overlying

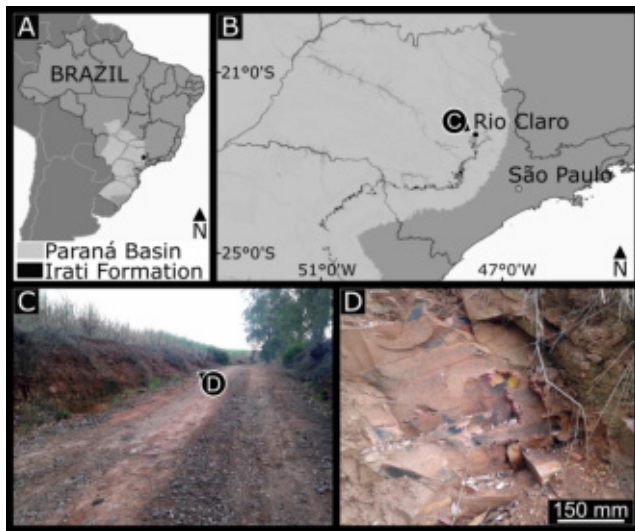


Fig. 2 - Location of studied material. A) Map of Brazil with the location of the Paraná Basin and of São Paulo State. B) Area of outcrops of the Irati Formation in the State and the location of the city of Rio Claro. C) Overview of the outcrop. D) Detail of the rock on site.

Assistência Member occurs very weathered, with a thickness of only 3–4 m (instead of the usual 18 m in the region of Rio Claro), due to sectioning by a sub-vertical fault and an associated Cretaceous diabase sill and dike.

The fossil-rich interval of the outcrop corresponds to the Taquaral Member, which usually comprises siltstones and gray to black shales, with abundant pyrite crystals. The fossil specimens occur randomly distributed and dispersed throughout the basal 2 m of that unit. Yet, these are not the typical friable dark pyritic shales which characterize the Taquaral Member at other sections, but they are reddish, almost massive mudstones with oxidized pyrite pseudomorphs. These more compact pelites probably resulted from thermal and hydrothermal influence during the magmatic intrusion and possible later modification by weathering. These alterations likely enhanced preservation, making the outcrop a rich fossil collecting site. The fossil assemblage of this site includes, besides the taxon here described, abundant remains of the syncaridan *Clarkecaris brasiliensis*, as well as teeth, scales, and bones of paleonisciform and actinistian fishes. The crustaceans and several fish remain are preserved as molds coated by iron oxide.

SHRIMP U–Pb zircon geochronology of bentonite laminae of the Assistência Member at PETROBRAS-Six mine (Santos et al. 2006) yielded an age of 278.4 ± 2.2 Ma, matching the Kungurian (Cisuralian) of most recent Permian time scale (Shen et al. 2018). Even though there is a probable unconformity separating both members of the Irati Formation (Holz et al. 2010), the Taquaral Member may be assigned to the beginning of Kungurian or to the underlying stage Artinskian.

Documentation techniques

The fossil specimens were documented with an Olympus® SZ61 stereoscope built-in camera (Model LC20), using its light source. As the material surface is irregular, we took several images at different focal points to obtain the entire depth of field of the specimens. As the specimens were larger than the camera screen, we repeated the process until the entire specimen was documented.

The extant representatives of Phreatoicoidea and Amphipoda used for comparison were respectively documented with a Keyence

VHX-6000 digital microscope and a Keyence BZ9000 fluorescence microscope on the GFP filter (excitation wavelength 470/40nm, emission wavelength 525/50nm), with the same method used for the fossil samples, i.e., taking a series of images at different focal points until the entire depth of field of the specimen was obtained.

The stacks of images were processed into one single fully focused image using Combine ZP. Then, they were stitched together using Photoshop® Elements 11, with the built-in algorithm of Panorama tool. Photoshop® Elements 11 was also used for histogram correction of the images and for artificially adding matrix on some figures. Some details of the fossil specimens were documented with the JEOL scanning electron microscope (model JSM-6010LA). We used uncoated samples to prevent damage to the specimens. Restoration drawings and figures were made with Inkscape. Raw images of specimens used in this study can be found at MorphDBase.

Morphometric analysis

In order to compare the fossil sub-chela shape, we took measurements and performed an outline analysis of sub-chelae of representatives of Isopoda and Amphipoda. For these, we selected images of the first pair of sub-chelate thorax appendages from the literature (Supplement 1), i.e., pereopod 1 in Isopoda and gnathopod 1 in Amphipoda. We used the measurement tool in ImageJ to take length and width of the two most distal parts of the appendages (dactylus and propodus), which compose the sub-chela (Supplement 1). A graphical representation of the taken measurements is presented in Supplement 2.

For the outline analysis, we redrew only the dactyli in Inkscape (Supplement 3), adding an ellipse to its base to minimize interpretation biases in the analysis (cf. Van der Wal & Haug 2020). The drawings of the dactyli were then loaded into SHAPE (Iwata & Ukai 2002), which performed an elliptic Fourier analysis on the outlines of the drawings, transforming the outlines in Elliptical Fourier Descriptors (EDFs), and then performed a Principal Component Analysis (PCA) on the EDFs. The results of the PCA were added to a spreadsheet containing the specimens and the measurements (Supplement 1). The plots were made in R, using R Studio, packages readxl and ggplot2.

RESULTS

Description

Overall morphology. Body composed of three functional units, a functional head (cephalothorax) and a trunk further differentiated into an anterior (free thorax, “pereon”) and posterior (pleon) regions.

Functional head includes the ancestral eumalacostracan head (ocular segment plus post-ocular segments 1–5) and the first thorax segment (post ocular segment 6) dorsally forming a continuous shield (head shield). No visible remains of eyes. Anterior trunk (free thorax) with seven segments (post ocular segments 7–13, also referred to in the literature as pereon or pereion. Pleon with five free segments (post ocular segments 14–18) and the last one (post ocular segment 19, pleon segment

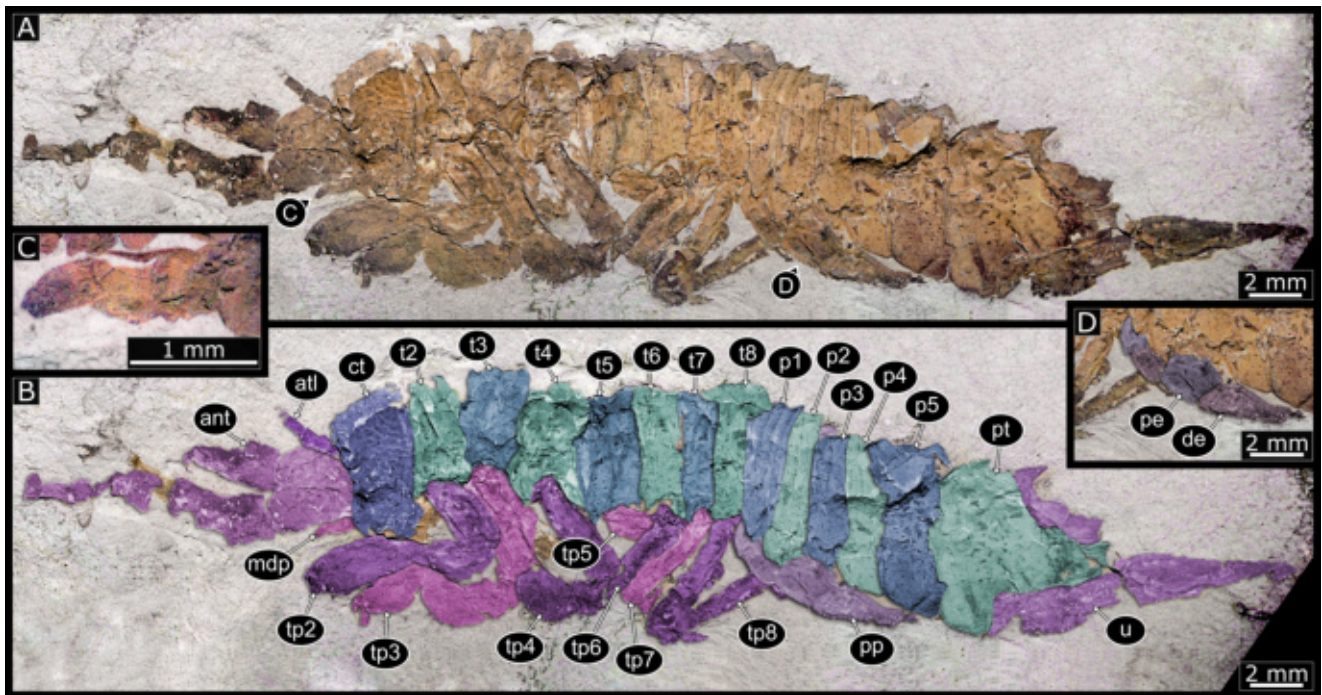


Fig. 3 - A) *Platuropodus odysseus* n. gen. n. sp. from Permian of Brazil (Taquaral Member, Irati Formation, Paraná Basin). B) Colour-coded version of A. Corners of images A and B filled with artificial matrix. C) Detail of maxilliped. D) Detail of the pleopodal exopods, composed of a proximal and a distal element. Abbreviations: ant = antenna; atl = antennula; ct = cephalothorax; de = distal element; mdp = mandibular palp; p1–5 = pleon segments 1–5; pe = proximal element; pp = pleopods; pt = pleotelson; t2–8 = thorax segments 2–8; tp2–8 = thoracopods 2–8; u = uropods.

6) conjoined to the telson, forming a pleotelson. Body longer than wide. Functional head and anterior trunk narrower than pleon in dorsal view, pleon higher than functional head and anterior trunk, in lateral view. Functional head dorsally conjoined to form a shield.

Shield. Antero-posteriorly shorter than trunk; 0.1x in larger specimens (Fig. 1A,B), 0.2x in smaller specimens (Fig. 1P,Q). Roughly square shape (Fig. 3A,B). Surface with many pits. Anterior margin slightly concave. Posterior margin slightly convex. At least two short spines on the lateral margin of shield.

Head appendages. Antennula (appendage of post-ocular segment 1) with three sub-rectangular elements preserved. Proximal and middle of sub-equal length (0.6 mm) and width (0.4 mm). Distal element slightly longer (0.8 mm), with remains of a single multi-annulated flagellum.

Antenna (appendage of post-ocular segment 2) significantly larger than antennula. Five elements preserved. Proximal element longer than wide (2.0x), longer than subsequent elements (3.0x), anterior margin convex, posterior margins not accessible. Element 2, 3, and 4 shorter than wide (0.7,

0.9, and 0.8x, respectively). Elements 5 (distalmost) at least as long as wide, posterior margin not preserved (Fig. 3A,B). Remains of a single multi-annulated flagellum.

Mandible (appendage of post-ocular segment 3), composed of proximal element, possibly coxa, and three tubular elements, possibly mandibular palp. Possible coxa sub-oval, enlarged, only accessible with SEM (Fig. 4A). Possible mandibular palp with three accessible elements (Fig. 3A–C), proximal and middle elements sub-squared. Middle element slightly smaller than proximal. Distal element the longest, sub-conical, anterior and posterior margins slightly concave. Further mouth parts, maxilla, and maxilliped (appendages of post-ocular segments 4–6) not accessible.

Anterior trunk (free thorax, pereon). Seven free segments, wider than long. Longest region of the body. Trunk segments 1–4 (thorax segments 2–5) wider than 5–7 (thorax segments 6–8) (1.3x), giving the appearance of a waist both in laterally and dorsally preserved specimens. All seven segments of about the same length, anterior and posterior portions are elevated, central portion is concave (Fig. 4B). Anterior and posterior elevated portions more

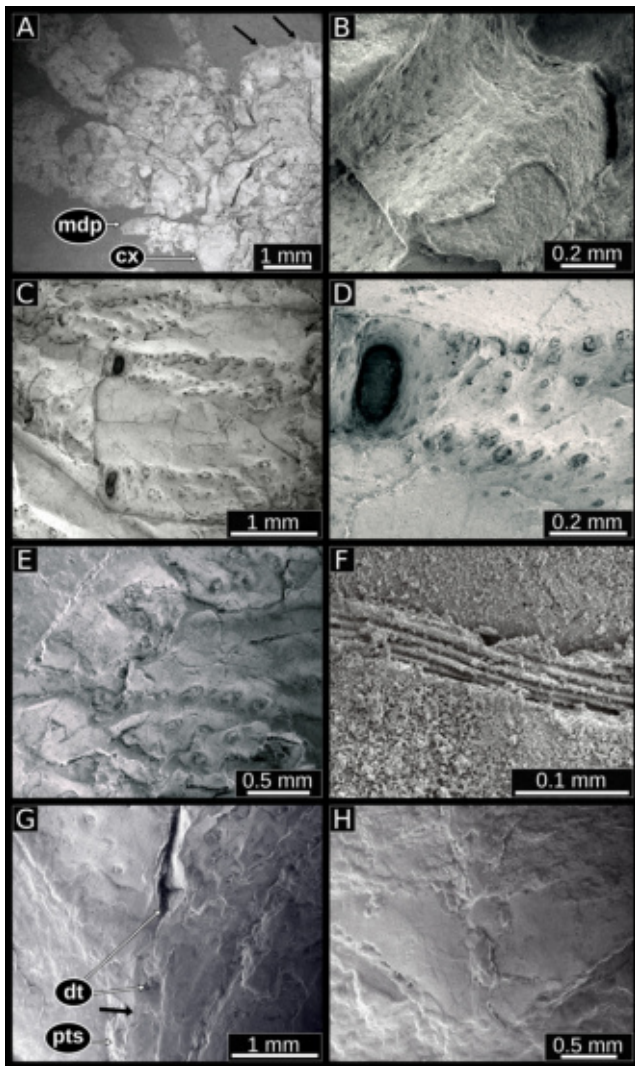


Fig. 4 - Scanning electron microscope images of *Platuropodus odysseus* n. gen. n. sp., A) Anterior portion of cephalothorax and its appendages, antennula, antenna, maxilliped, black arrows show spines on the lateral margin. B) Thorax segment 2 (pereon segment 1), laterally preserved. C) Thorax segments 4 and 5 (pereon segments 3 and 4), dorsally preserved. D) Detail of mid-transversal row of spines and setae of thorax segments, insertion points of spines or setae. E) Lateral portion of pleon segments 1 and 2, dorsally preserved. F) Arthrodistal membrane, between pleon segments 1 and 2. G) Final portion of pleotelson, black arrow indicates suture line of the spine. H) Final portion of pleotelson with spine broken. Abbreviations: cx = coxa; dt = digestive tube; mdp = mandibular palp; pts = pleotelson spine.

or less smooth, concave central portions with a mid-band of somewhat parallel round marks (punctuations), possibly insertion points of setae. The dorso-central portion of each band bears a large oval mark, probably a spine insertion point (Fig. 4B–D).

Anterior trunk appendages (thorax appendages, pereopods, or pereopods). All appear uniramous with coxa, basipod, endopod, no exopod apparent. Trunk appendages 1 and 2 (appendages of thorax segments

2 and 3) larger than the subsequent five appendages (trunk appendages 3–7). Each appendage with seven elements, coxa, basipod and endopod with 5 elements.

Coxa ring-like, basipod of trunk appendages 1 and 2 tubular, elongate; ischium (endopod element 1) tubular, shorter than basipod (3x); merus (endopod element 2) dorsal surface of same length as ischium, ventral surface shorter than dorsal (2x); carpus (endopod element 3) dorsal surface of same length as ischium, ventral surface longer than dorsal (2x), remains of spines on ventral surface. Distal elements (propodus and dactylus, respectively endopod elements 4 and 5) forming a sub-chela (Figs. 5A, B, D–F); propodus and dactylus almost as long as basipod, propodus mid-portion the widest tapering towards anterior portion, dactylus curved towards ventral surface of propodus. Subsequent five trunk appendages 3–7 with ring-like coxa (Fig. 6A, B); subsequent elements tubular, slenderer than those of trunk appendages 1 and 2; long basipod; merus and ischium shorter than basipod (4x); carpus slightly longer than merus (1.5x); propodus almost as long as basipod; dactylus slightly shorter than merus, tapering towards the anterior portion, pointed (Fig. 6C).

Pleon (posterior trunk). Five free segments, sixth segment conjoined to the telson (pleotelson). Free segments 1–4 of about the same length, segment 5 longer than preceding segments (1.5x), segments gradually increasing in width (in dorsal view) and height (in lateral view) (Figs. 5A,C; 7A). Lateral margin of segments anteriorly convex and posteriorly acute (Fig. 4E). Each segment bears a line of rather subparallel punctuations at the posterior margin (Fig. 4E), possibly insertion points of setae. Randomly dispersed punctuations also on the surface of the tergites of the segments (Figs. 5A,C, 4E). Pleotelson with smooth margins, tapering towards the posterior portion, terminating in a long spine (Figs. 7A–C, 4G), possibly articulated – not present in all samples (Figs. 7D, 4H). Posterior margin of the spine rounded. Pleotelson (including terminal spine) almost as long as the five free segments combined. Randomly dispersed punctuations on dorsal surface, possibly insertion points of setae. Telson region funnel-shaped. Spine almost as long as the rest of the pleotelson (Fig. 7B).

Pleopods. Segments 1–5 with remains of appendages, longer in antero-posterior axis than free

Fig. 5 - *Platuropodus odysseus* n. gen. n. sp., A) Thorax (pereon) and pleon, laterally preserved. B) Detail of sub-chela of thorax appendage 3 (pereopod 2), colour-coded. C) Pleon of A, colour-coded. D) Almost complete specimen, lacking some of the appendages, laterally preserved. Black arrow head indicates uropod laterally preserved. E) Detail of thorax appendage 2 (pereopod 1), colour-coded. Black arrows in E, F indicate spines. F) Detail of thorax appendage 3 (pereopod 2), colour-coded. Abbreviations: b = basipod; bu = basipod of uropod; c = carpus; d = dactylus; de = distal element; en = endopod; ex = exopod; i = ischium; m = merus; p = propodus; ps1-5 = pleon segments 1-5; pe = proximal element; pt = pleotelson.

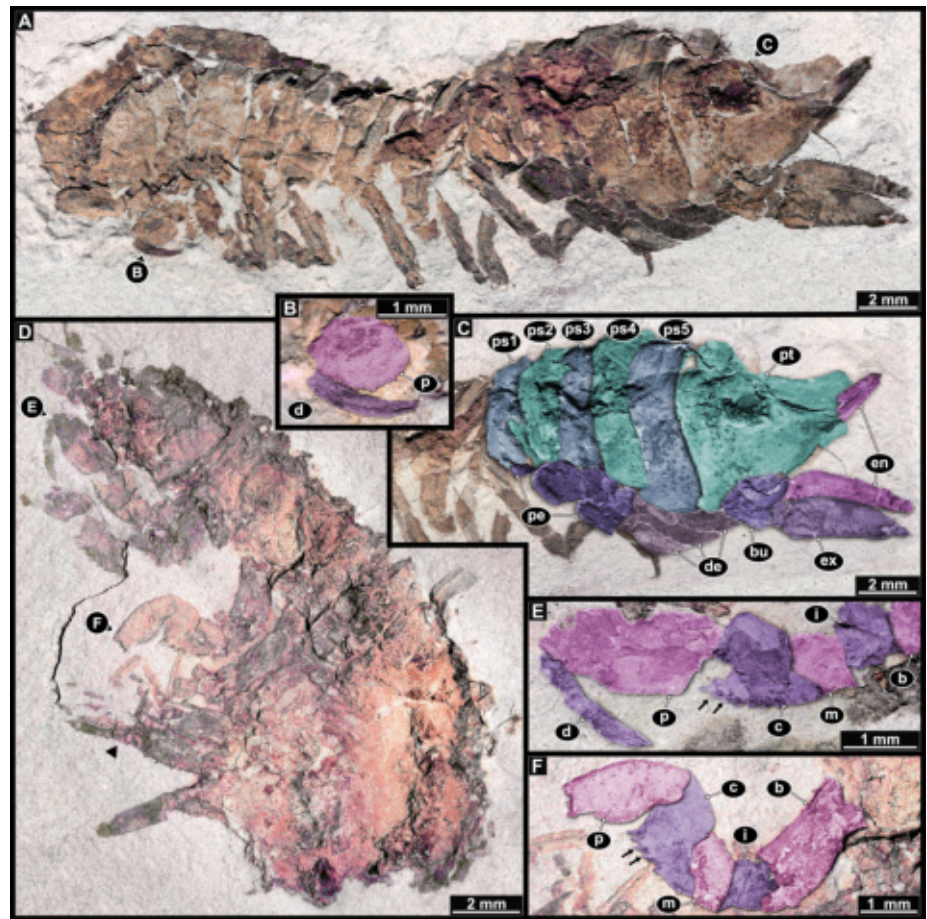
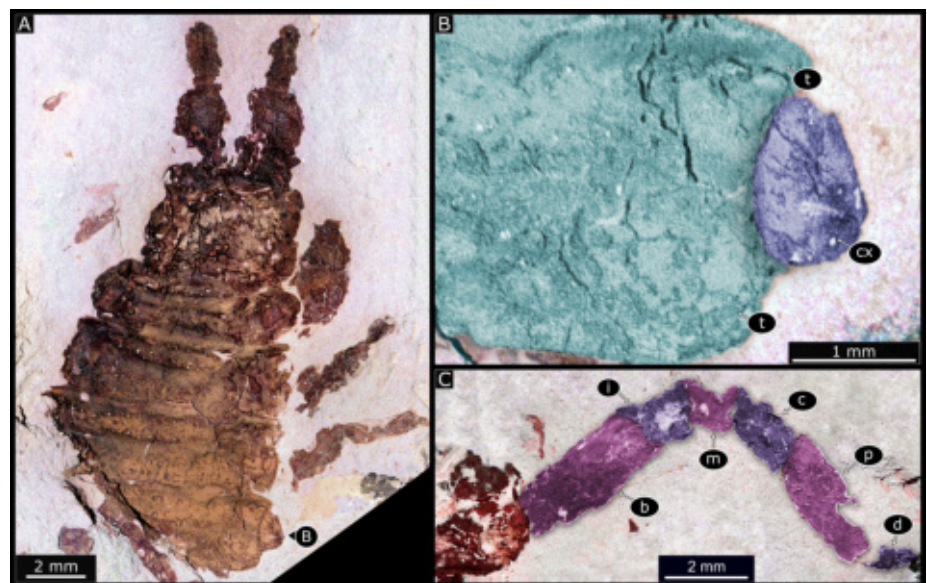


Fig. 6 - *Platuropodus odysseus* n. gen. n. sp., A) Cephalothorax and anterior pereon segments, dorsal view. B) Detail of lateral portion of pereon segment 4, showing the coxa, colour-coded. C) Isolated pointed thorax appendage (pereopod), colour-coded. Abbreviations: b = basipod; c = carpus; cx = coxa; d = dactylus; i = ischium; m = merus; p = propodus; t = telson.



pleon segments (1.5x). Remains shaped like a prolate-ellipse in dorsally preserved specimens (Fig. 8D) and sickled-shaped in laterally preserved ones (Figs. 3A,D, 5A,C,D). Composed of two elements, marked by a transversal suture. Proximal element with anterior portion rounded, posterior portion acute; distal element longer than proximal element

(2.5x), spear-shaped in laterally preserved specimens (Fig. 3D). Margins of distal element setose (Fig. 8D).

Uropods (pleon appendage 6) composed of basipod (proximal element), endopod and exopod. Longer than pleopods (1.5x). Basipod as long as free pleon segment, roughly conical in shape in dorsally

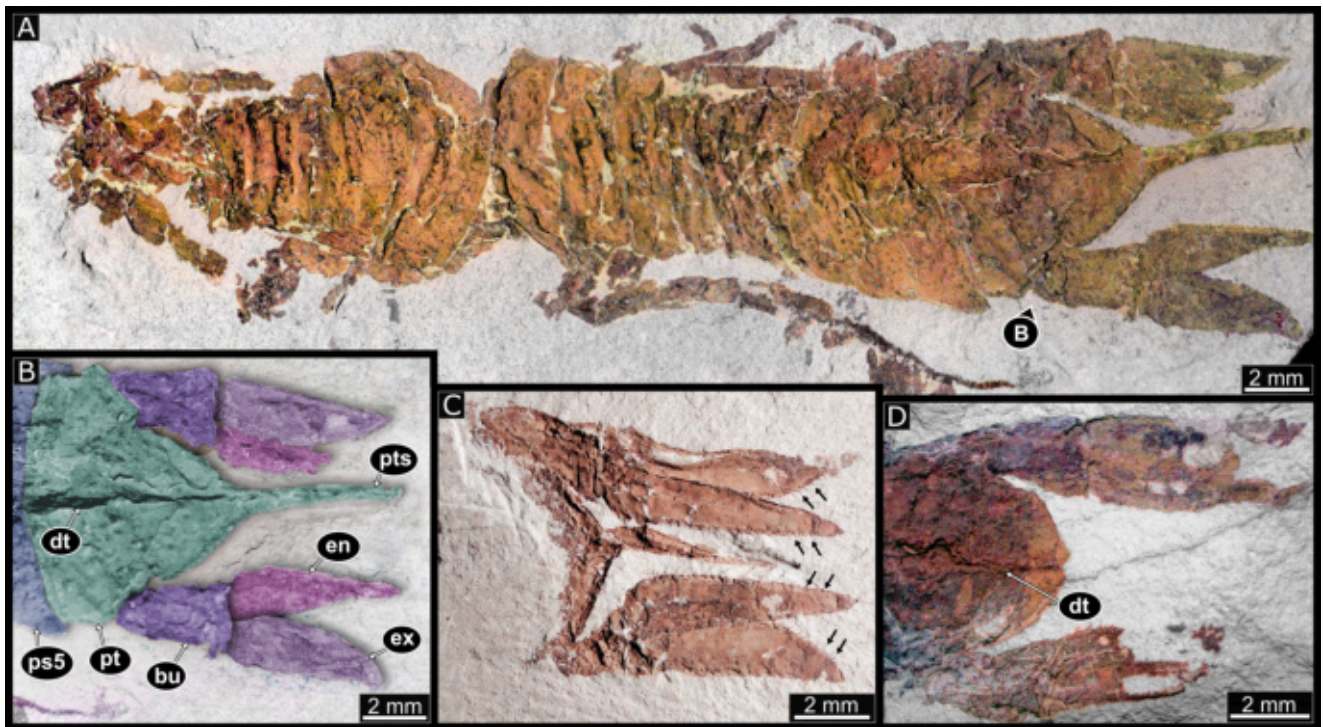


Fig. 7 - *Platuropodus odysseus* n. gen. n. sp. A) Almost complete specimen, dorsally preserved. B) Colour-coded image of pleotelson and uropods of A. C) posterior portion of pleotelson, and uropods, black arrows indicate setae. D) Pleotelson and uropods, pleotelson spine broken-off. Abbreviations: bu = basipod of uropod; dt = digestive tube; en = endopod; ex = exopod; ps5 = pleon segment 5; pt = pleotelson; pts = pleotelson spine.

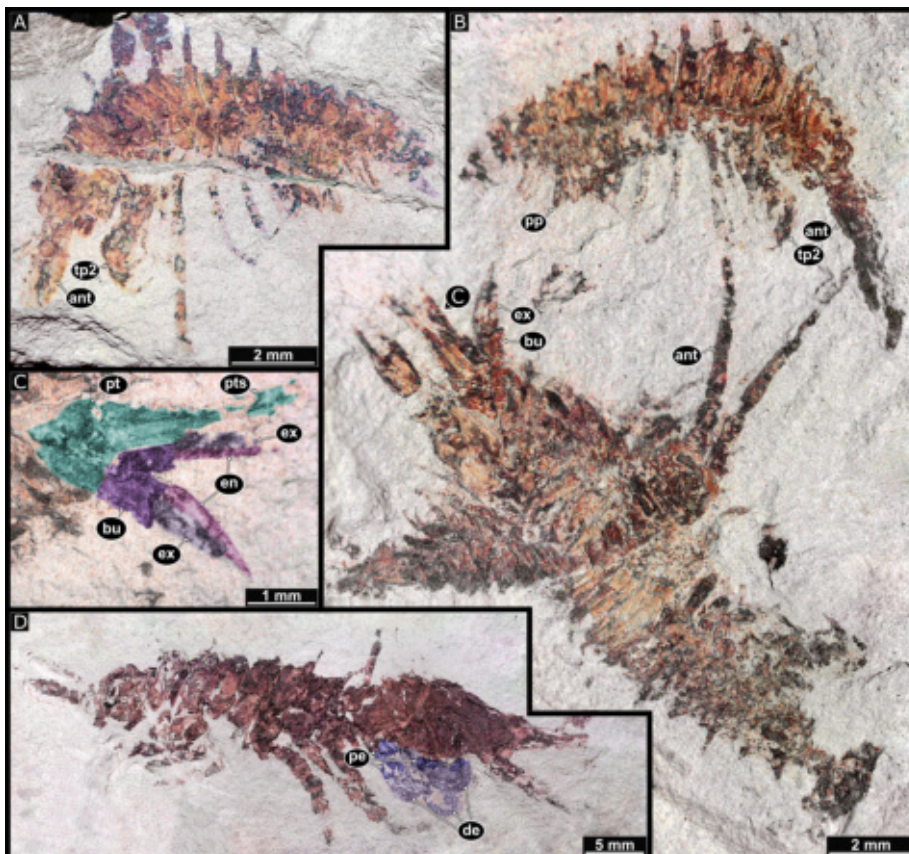


Fig. 8 - *Platuropodus odysseus* n. gen. n. sp., A-C) Juveniles, laterally preserved. C) Detail of posterior portion of pleotelson and uropods of a specimen of B, colour-coded. D) Almost complete specimen, laterally preserved, colour-coded pleopods. Abbreviations: ant = antenna; bu = basipod of uropod; de = distal element; en = endopod; ex = exopod; pe = proximal element; pp = pleopod; pt = pleotelson; pts = pleotelson spine; tp2 = thorax appendage 2 (percepod 2).

preserved specimens, widening toward the posterior margin. Exopod and endopod blade-like, of about the same length, longer than basipod (1.5x). Inner margins setose (Fig. 7C). Exopod slightly wider than endopod in its anterior half (Fig. 5C, 7B,C).

Soft tissue. Some specimens preserve remains of a large cylindrical tube extending through the anterior-posterior mid-line (Fig. 7B,D). Anterior part of digestive tube not accessible, posterior part ending at the most distal part of the telson, before the insertion of the spine (Fig. 4G, 7D). A series of lines extending transversally between pleon segments 1 and 2 is accessible with SEM (Fig. 4E).

Ontogenetic series. Different size groups are present in the samples. The largest specimen (Fig. 3A,B) is 5x times the size of the smallest ones, which are interpreted as juveniles (Fig. 8A–C). The smallest size group are represented by four specimens, in two slabs: three of them preserved closely together on a single rock slab (Fig. 8B). As for the isolate specimen (Fig. 8A), we cannot say if it was originally preserved close or together with the remaining three, but this is a possibility, since the collection date of the two slabs is the same.

Morphometric analysis

The shape analysis performed on the dactylus outline resulted in 7 effective principal components summing up to 96.17% of morphologic variation in the sample; PC1 explains 61.97% and PC2 16.75% of the total variation (Supplement 4), summing up to 78.72%. PC 1 represents the degree of curvature of the dactylus, more strongly to less strongly curved, whereas PC2 is related to dactylus width, broader or thinner median and proximal parts (Supplement 5). The plot of PC1 versus PC2 shows that the new fossil taxon plots closely with representatives of Amphipoda, Asellota, and Phreatoicidea, but far from Cymothoidae, which occupies a different area of the morphospace (Fig. 9A). Representatives of Cymothoidae have a more strongly curved dactyli than representatives of Amphipoda, Asellota, Phreatoicidea and the new fossil taxon, in which the dactylus is less curved. Hence, the dactylus of the new fossil taxon is in this aspect more similar to those of Amphipoda, Asellota, and Phreatoicidea. This pattern of separation was found independently of which PC was plotted.

The regression lines of the measurements (Fig. 9B) show that representatives of Cymothoidae have a longer dactylus in relation to the propodus than the new fossil taxon and representatives of Amphipoda, Asellota, and Phreatoicidea. In these latter groups, the dactylus is almost as long, or shorter than the propodus, whereas in Cymothoidae the dactylus is longer than the propodus, almost two times longer in some cases (Fig. 9B).

When plotting the ratio of dactylus length to propodus length versus PC1 (Fig. 9C), i.e. dactylus curvature, we see that the new fossil taxon, representatives of Amphipoda, Asellota and Phreatoicidea have a less curved and overall shorter sub-chela than representatives of Cymothoidae, due to elongation of dactylus in the latter. When plotting the ratio of dactylus length to propodus length versus PC2 (Fig. 9D), we see that although the new fossil taxon, representatives of Amphipoda, Asellota, and Phreatoicidea have shorter sub-chelae, most of the specimens have dactyli of about the same width, with the exception of a few extremely thin dactyli in Cymothoidae and broader dactyli in Amphipoda and Phreatoicidea (Fig. 9D).

DISCUSSION

Previous interpretations of the fossil specimens

So far, the only fossil taxon of Eumalacostraca formally described from the Taquaral Member was the syncaridan *Clarkecaris brasiliensis*. Fossils of this species are restricted to the Taquaral Member (Chahud & Petri 2013). The overlying Assistência Member has records of a possible scutocoxiferan Isopoda (Mezzalira & Martins-Neto 1992; Martins-Neto 2001) and Pygocephalomorpha (Pinto 1971; Pazinato et al. 2016a), an extinct group of shrimp- to lobster-like peracaridans.

Almost a century later, Foehringer & Langer (2003) reported pleon and pleotelson remains of the crustacean described here. The authors interpreted these specimens as remains of the cephalothorax of a crustacean possibly related to Pleocyemata, an ingroup of Decapoda (Foehringer 2004; Foehringer & Langer 2004).

The same remains reported by Foehringer & Langer (2003) were mentioned by Schram et al. (2013), suggesting that they could be tail-fans of

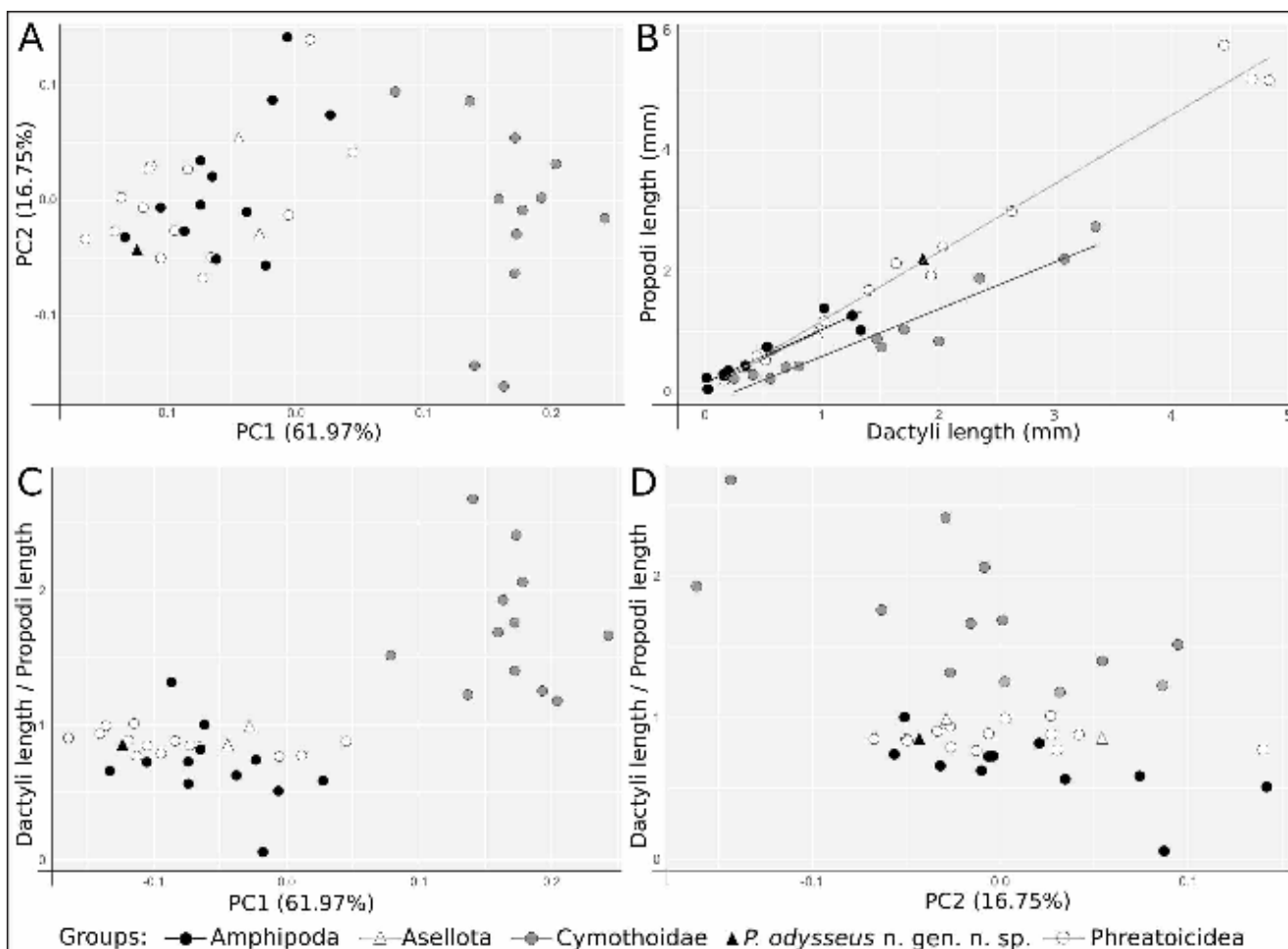


Fig. 9 - Graphical representation of the morphometric analysis of the first thoracic sub-chela of Isopoda and Amphipoda. A) Result of the principal component analysis (PC1 x PC2) of dactyli shape. B) Comparison of length and width of dactyli and propodi. C) Principal component 1 (curvature of dactyli) versus dactyli/propodi lengths. D) Principal component 2 (width of dactyli) versus dactyli/propodi lengths.

an ancient form of mantis shrimps (Stomatopoda). More precisely, they assigned the fossil specimens to Perimecturidae, an early branch of Stomatopoda, only more distantly related to modern day mantis shrimps (Verunipeltata; Haug et al. 2010). Known representatives of Perimecturidae indeed have a tail-fan with a long spine on the telson and large uropods, similar to the specimens described herein.

During a review of the fossil material from the Taquaral Member, the senior author (Pazinato et al. 2016b; Pazinato 2017), at first followed their interpretation as a mantis shrimp, due to the presence of prominent sub-chelate appendages and a telson with a long spine. However, their short functional head and the morphology of the sub-chelate appendages differs from those of mantis shrimps (Haug et al. 2012), hampering their assignment to that group.

Narrowing down: the fossil taxon is a representative of Peracarida

The body organisation of the fossil specimens described here is quite intriguing and presents a mixture of characters found in different eumalacostracan groups. There is a functional head including thorax segment 1 (cephalothorax). There are seven free anterior trunk segments (thorax segments 2–8, pereon segments 1–7) with uniramous appendages. Thoracic appendages 2 and 3 (pereopods 1 and 2) have distal elements forming a sub-chela. Thoracic appendages 4–8 (pereopods 3–7) have pointed distal elements (“walking limbs”). Finally, there are six pleon segments with biramous appendages, the sixth segment is conjoined to the telson, forming a pleotelson (Fig. 10).

Among living representatives of Eumalacostraca, that unique arrangement of anterior body traits, including a short cephalothorax and

Fig. 10 - *Platuropodus odysseus* n. gen. n. sp., A) Drawing of digital image of holotype, URC.AC.196.1. B) Restoration of the same specimen as A and restoration of a juvenile, B₁, to the same scale, laterally preserved. C) Restoration of paratype, URC.AC.196.2, dorsally preserved.

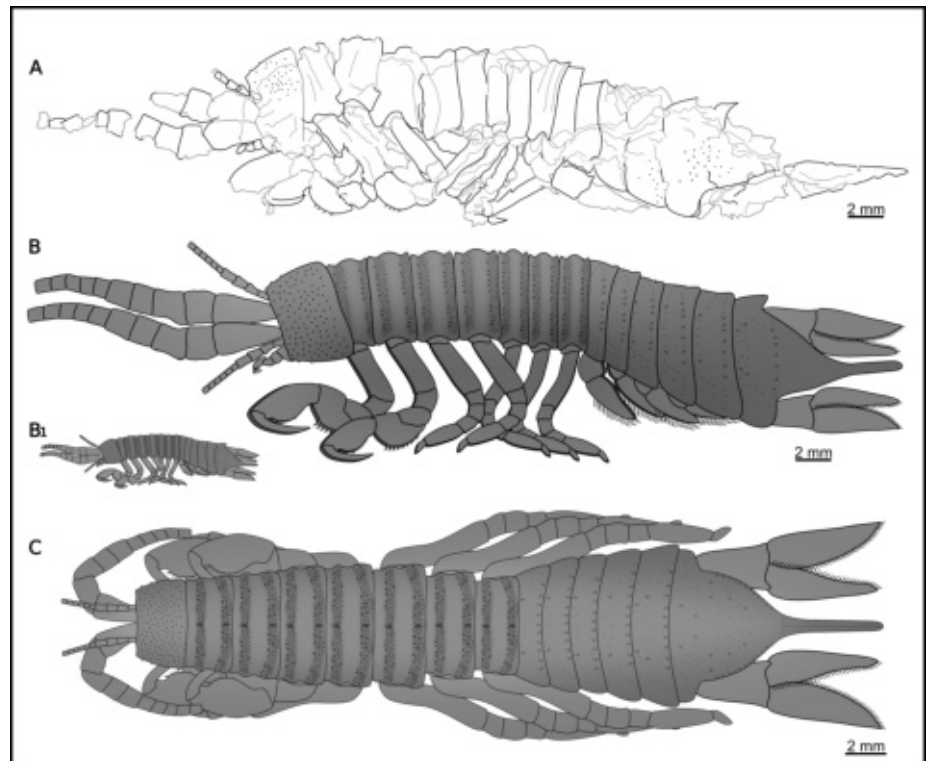
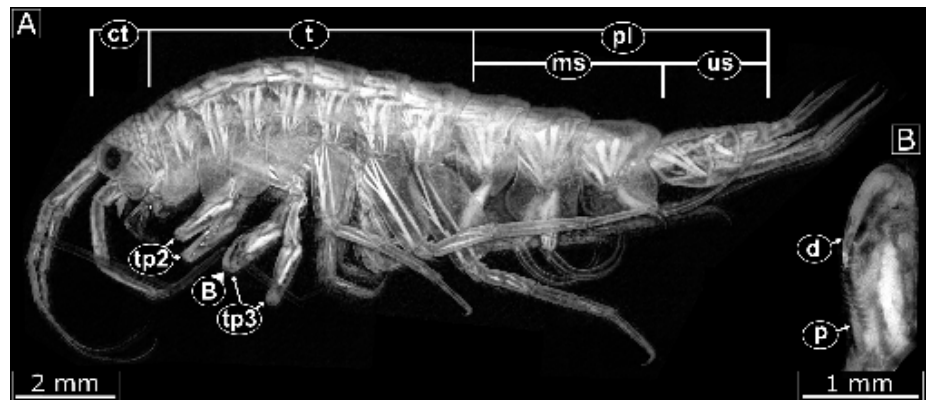


Fig. 11 - Fluorescence microscope image of *Pallaseopsis quadrispinosa*, a representative of Amphipoda. A) Complete specimen, lateral view. B) Detail of thoracic appendage 2 (gnathopod 1), lateral view. Abbreviations: ct = cephalothorax; d = dactylus; ms = metasome; p = propodus; pl = pleon; t = thorax; tp2-3 = thoracopods 2-3; us = urosome.



two sub-chelate appendages in the anterior trunk is found together only in Amphipoda (Fig. 11), what led us at the time to believe it could be an early representative of that group (Pazinato et al. 2019a,b).

Despite their young fossil record, dating back to the Cretaceous (~130 Ma; Jarzembowski et al. 2020) there is no consensus as to when the lineage towards Amphipoda split off from other peracaridan groups. This may have happened in the late Palaeozoic, or much later, only in the Cretaceous (Schram 1986; Lowry & Myers 2013) from which the oldest fossil specimens of Amphipoda are known so far (Jarzembowski et al. 2020). A late Palaeozoic origin can be expected because other peracaridan lineages (Jenner et al. 2009) have Carboniferous or Permian fossils, as in the case of Tanaidacea (Calman 1933),

Isopoda (Schram 1970) and the extinct group Pygocephalomorpha (Schram 1986).

All amphipodans that retain a pleon have that element highly modified. It is differentiated into two distinct morphological units: pleon segments 1–3 with natatory pleopods (“metasoma”, a term with quite a different meaning in other groups) and pleon segments 4–6 with fusiform uropod-like appendages (“urosoma”; Fig. 11A). In some amphipodans, the pleon is extremely reduced (e.g., *Caprella*, the group of skeleton shrimps).

However, the pleon arrangement of the fossil taxon differs greatly from that in Amphipoda. Within Eumalacostraca, a pleotelson is found in larvae of Stomatopoda and Decapoda and in adults of five lineages, Brachyura, Thermosbaenacea,

Cumacea, Isopoda, and its sister-group Tanaidacea. Four of these lineages, as well as Amphipoda, are ingroups of the monophyletic group Neocarida (Thermosbaenacea + Peracarida in Richter & Scholtz 2005, = Pancarida in Ax 2000 and Jenner et al. 2009). Hence, we can safely infer that the fossil taxon is part of the neocaridan fossil record.

From these four lineages, only Thermosbaenacea and Isopoda present an overall body arrangement that resembles that of the fossil taxon, where the head is conjoined to thorax segment 1, there are 7 free thorax segments and the pleotelson is formed by 5 free segments, plus pleon segment 6 conjoined to telson. In tanaidaceans and cumaceans the head is conjoined to the first two trunk segments. Like the fossil taxon, representatives of Isopoda have uniramous anterior trunk appendages, whereas those of thermosbaenaceans are biramous. Hence, the fossil taxon is most likely part of the early diversification of Isopoda.

A morphologic comparison with representatives of Isopoda

Normally when we think of isopodans the dorso-ventrally flattened body shape of “pill bugs” comes to mind. However, as already quantitatively demonstrated, the group has diverse body arrangements (Schädel et al. 2019; Schädel et al. 2020). A putative autapomorphy of the group Isopoda is the biphasic moulting, a moult in two steps with some time interval between, e.g., one to two days in the case of *Armadillo officinalis* (Montesanto & Cividini 2017). Such autapomorphy is, however, hard to infer from the fossil record. Therefore, to further explore possible relationships of the fossil taxon, we briefly discuss a few characters that are supposed to be apomorphies for different ingroups of Isopoda.

Body shape

Within Isopoda, there is a large variety of body shapes. Representatives of Asellota range from almost cylindrical to dorso-ventrally flattened crustaceans (Poore & Lew Ton 2002). Although most representatives of Scutocoxifera have dorso-ventrally flattened bodies, some ingroups are sub-cylindrical (e.g., Anthuridea). Phreatoicideans appear to have a laterally compressed body, the pleon segments are higher than anterior trunk segments in lateral view (Fig. 12), and this is considered to be a autapomorphy of Phreatoicidea by some au-

thors (Wägele 1989; Wilson & Keable 2001), whereas other suggest their body shape is instead more cylindrical (Nicholls 1943, 1944; Brusca & Wilson 1991). Body shape is best seen in fossils that are three-dimensionally preserved. For other cases, such as the specimens described here, it is more difficult to assess. These were preserved both laterally and dorsally compressed, what makes it difficult to recover the actual shape of body segments. We can safely say that the posterior pleon segments (4, 5 and 6) are broader than the more anterior trunk segments, including those of the pleon (1–3) in dorsal view (Fig. 7A), resembling the phreatoicidean body shape in lateral view (e.g. Fig. 5A,D).

Pleotelson: short or elongate region after anus and uropods

Within Isopoda, the position of the anus and uropods varies along the antero-posterior axis of the pleotelson. Hence, depending on the group, there will be a shorter or longer region posterior to the anus and uropods. In Scutocoxifera, except for Oniscidea (Scutocoxifera *nec* Oniscidea), uropods and anus are located far anterior on the pleotelson, with an elongate region extending beyond the anus aperture. In contrast, in Oniscidea, Asellota and most representatives of Phreatoicidea the anus and uropods are posteriorly located, leaving a very short region beyond it. Brusca & Wilson (1991) suggested that a short region behind the anus and uropods is plesiomorphic within Isopoda, this condition is also present in its sister-group Tanaidacea. The fossil taxon described here, however, displays a third type of arrangement, in which the uropods are located more anteriorly, like those of Scutocoxifera, but the anus aperture is far posterior, positioned immediately anterior to the prominent spine, like in some phreatoicideans and asellotans (Fig. 7A,B).

Coxae of anterior trunk appendages

Representatives of Scutocoxifera are promptly recognized by the coxae of the anterior trunk appendages. These have dorso-ventrally flattened expansions, positioned laterally to the tergites (‘coxal plates’; Dreyer & Wägele 2002). The presence of such coxal plates is a synapomorphic character for Scutocoxifera. The plesiomorphic condition, found in extant Phreatoicidea and Asellota, is a ring-like coxa not seen in dorsal view, like the condition in the fossil taxon.

Fig. 12 - Extant phreatoicideans *Synamphisopus ambiguus*, A) and *Paramphisopus palustris*, A₁) specimen in lateral view. B) Detail of telson portion of pleotelson, showing short terminal spine (white arrow) surrounded by spine-like setae (arrow heads), dorsal view. C) Thorax appendage 2 (pereopod 1) with dactylus and propodus forming a sub-chela. D) Detail of telson portion of pleotelson, showing short terminal spine (white arrow) surrounded by spine-like setae (arrow heads), lateral view. Abbreviations: b = basipod; c = carpus; cx = coxa; d = dactylus; i = ischium; m = merus; p = propodus.



Shape of uropods

Representatives of Isopoda have uropods with flat or styliiform endo- and exopods (Wägele 1989; Brusca & Wilson 1991; Wilson 1996). Asellota, Phreatoicidea, and Oniscidea are groups with representatives with styliiform uropod endo- and exopods. Scutocoxifera *nec* Oniscidea have been considered to have representatives with flat uropod endo- and exopods. The latter are usually dorso-ventrally flattened, giving the appearance of a “well-developed tail-fan” (Brusca & Wilson 1991, p. 192). In the case of the new fossil specimens, both uropod rami are broad and blade-shaped in dorsal (Fig. 7) and lateral (Fig. 5A) views, suggesting the uropod is dorso-ventrally flattened. The fossil specimens therefore seem to possess flat uropod endo- and exopods, today found only in representatives of Scutocoxifera.

The ground pattern condition of uropods in Isopoda has been debated (Wägele 1989; Brusca & Wilson 1991; Wilson 1996). Wägele (1989) considered styliiform uropods as independent apomorphies of Phreatoicidea and Oniscidea (sister-group to the remaining groups of Scutocoxifera, namely Valvi-

fera, Spheromatidea, Anthuridea and Cymothoida). This would indicate that flat uropod endo- and exopods would represent the ancestral condition. Quite the opposite, Brusca & Wilson (1991) suggested flat uropod endo- and exopods as an apomorphy for Scutocoxifera *nec* Oniscidea. Styliiform uropod endo- and exopods is a ground pattern condition for Isopoda in this reconstruction. This latter view is supported by observations of the sister-group of Isopoda, Tanaidacea, which have styliiform uropod endo- and exopods (Kutschera et al. 2012). Hence, flat uropod endo- and exopods, as seen in the fossil specimens described here, seem indeed to have evolved within Scutocoxifera (Brusca & Wilson 1991; Schädel et al. 2020).

Telson spine

A prominent terminal spine like that found in the fossil taxon (Fig. 7A–C) is not present in any known isopodan lineages. However, some species of Phreatoicidea present a prolongation of the pleotelson (what Nicholls, 1944 called a ‘stump’). In the case of phreatoicideans, the prolongation is less than half the length of the pleotelson, and its poste-

rior region is ornamented with spines (Fig. 12A, B, D). In the fossil taxon, the prolongation (terminal spine) is as long as the pleotelson and its margins are smooth.

Sub-chelate trunk appendages

Grasping structures seem like a successful and recurrent adaptation that evolved independently through deep time in many lineages of Euarthropoda (Haug et al. accepted; Pazinato et al. 2021). The fossil taxon described here bears two pairs of anterior trunk appendages with sub-chelate distal tips (pereopods 1–2, thoracopods 2–3). In the case of Isopoda, representatives of Phreatoicidea, Asellota and parasitic forms of Cymothoidea (Cymothoidea *nec* Cirolanidae) possess sub-chelate trunk appendages, but not in the combination (number and position) presented in the fossil. In Phreatoicidea, the first pair of free trunk appendages (pereopod 1, thoracopod 2) is sub-chelate, and usually the males have a larger sub-chela than females (Nicholls 1943, 1944). Phreatoicideans use this appendage for moving food from the freshwater substrate, lifting particles by moving the dactyli while crawling (Chopra & Tiwari 1951). However, in some cases the grasping appendages do not seem to move at all during feeding (e.g. *Paramphisopus palustris* in Nicholls 1943). Like phreatoicideans, most representatives of Asellota possess the first free trunk appendages with a sub-chela. These are also used for digging up food resources or to actively hold on to food while eating and grooming (Hessler & Strömberg 1989). The Cymothoidea lineage of Scutocoxifera includes forms with sub-chelate appendages. As in phreatoicideans, representatives of Corallanidae possess the first free trunk appendages (pereopod 1, thoracopod 2) with sub-chelae. The monophyletic unnamed group including Aegidae, Cymothoidea and Epicaridea have at least three pairs of sub-chelate anterior trunk appendages (pereopods 1–3, thoracopods 2–4). Cymothoidea and Epicaridea, as well as certain larval stages of Gnathiidae, have six pairs of sub-chelae (all pereopods: 1–6, all thoracopods: 2–7) (Nagler et al. 2017). In all of these groups, the sub-chelae are more or less hook-shaped and used to grasp onto a host. Cymothooids present quite a lot of morphologic variation during ontogeny and also regarding attachment site (Van der Wal & Haug 2020), but when compared to other isopodans they form a distinct cluster, due to the degree of curvature and relative length of the dactylus

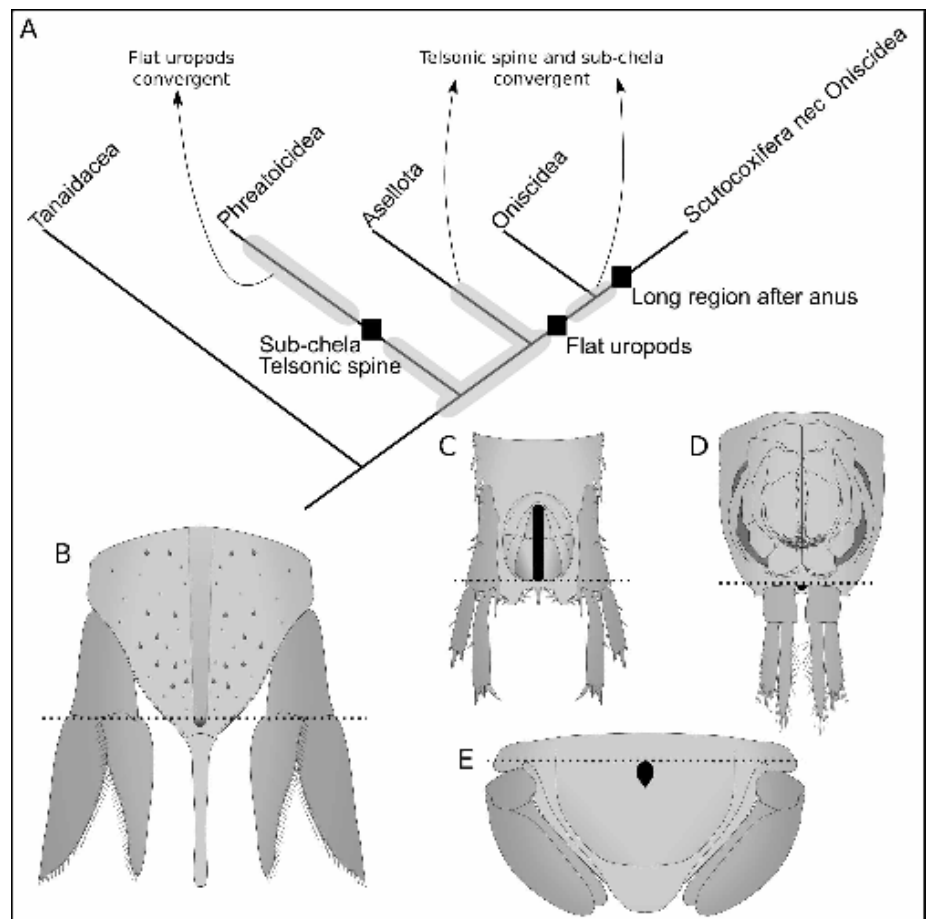
(Fig. 9). Our morphometric analysis shows that the sub-chela of the new fossil taxon is more similar to those of Phreatoicidea, Asellota, and Amphipoda. They group together, separating from cymothooids, and are characterized by less curved dactyli and longer propodi in relation to dactyli (Fig. 9). Like asellotans and phreatoicideans, amphipodans use their sub-chelate appendages for feeding (reason why they are termed ‘gnathopods’ among specialists of the group) – creating water current, manipulating detritus or predated (Coleman 1989). There are also observations of the sub-chelate appendages being used in burrowing, grooming and mating (Coleman 1989; Holmquist 1982). The similarity between dactylus and relative size of propodi among these groups is possibly related to a burrowing and digging habit, especially among the isopodan lineages, since both phreatoicideans and asellotans are detritivores and have the habit of digging up food. Although we cannot objectively infer the supposed functions of the sub-chelate appendages of the fossil taxon, the morphology and relative size of dactylus and propodus, compared to extant species, are compatible with a detritivorous lifestyle.

Chimera-like Isopoda

The fossil specimens possess plesiomorphic characters of Isopoda such as a sub-cylindrical body shape, ring-like coxa, and a short region posterior to the anus, but also have a mixture of characters that characterize different ingroups of Isopoda, in a unique combination within both the fossil and extant record. Such a chimera-like morphology, in the sense of the Greek mythical creature composed of body parts of other animals, is not unusual in the fossil record and may illustrate the evolutionary phenomena currently understood as convergence (Haug et al. 2019; Luque et al. 2019).

The shape of the sub-chelate trunk appendages and the long telson spine support the interpretation of the fossil taxon as part of Phreatoicidea. Following this interpretation, we would have to assume that the flat uropods are convergent with Scutocoxifera and that they may have reappeared twice within Isopoda, since flat uropods seems to be the plesiomorphic condition in Peracarida (Kutschera et al. 2012). Yet, we also could consider the fossil taxon as representative of an early lineage of Isopoda, or of Asellota or Scutocoxifera within it; and in all these cases the telson spine and sub-chelae would

Fig. 13 - A) Scheme of three possible systematic positions of the new fossil within Isopoda. Light-grey areas of the branches represent putative positions of the fossil taxon and which convergent characters need to be assumed for each position. B) Pleotelson of *Platuropodus odysseus* n. gen. n. sp. dorsal view. C) Pleotelson of *Platuropodus odysseus* n. gen. n. sp. ventral view. D) Pleotelson of *Synamphisopus doggi* Wilson & Keable, 2002, Phreatoicidea (based on Wilson & Keable 2002, their fig. 25a), ventral view. E) Pleotelson of *Janaïra platyoura* Doti & Wilson, 2010, Asellota (based on Doti & Wilson 2010, their fig. 19e), ventral view. F) Pleotelson of *Zuzara venosa* (Stebbing, 1876), Scutocoxifera nec Oniscidea (based on Brandt & Poore 2003, their fig. 3b), ventral view.



be convergent to Phreatoicidea (Fig. 13). Either way, independent of our phylogenetic interpretation, the fossil taxon indicates convergent evolution in the early diversification of Isopoda.

Although the evolutionary phenomena leading to convergence and to the species with unique combination of traits present in separate groups (chimeric morphology) are not completely understood, the ‘experimental’ morphology of this new taxon may be illustrative of a “push of the past effect” within Isopoda. Such effect can be seen in almost every long-living evolutionary lineage, that survived until the present, and predicts bursts of morphological diversity at the beginning of radiation and after mass extinctions (Budd & Mann 2018). A “push of the past effect” is compatible with the fossil record of Peracarida during the late Palaeozoic and Mesozoic, when there are high early rates of morphological change in Isopoda (Nagler et al. 2017; Schädel et al. 2020) and also in other peracaridan lineages, such as Lophogastrida (Pazinato et al. 2021). Following this line of thought, this fossil taxon and its new morphological combination is yet another example of the burst of initial diversification of Isopoda during the Cisuralian.

SYSTEMATIC PALAEOLOGY

EUARTHROPODA (sensu Maas & Waloszek, 2001)

Eucrustacea (sensu Waloszek, 1999)

Peracarida Calman, 1904

Isopoda Latreille, 1817

Platuropodus n. gen.

Type species: *Platuropodus odysseus* n. sp.

Etymology: From the Greek, “plat” (= flat) + “ur” (= tail), “podo” (= foot), referring to the flat uropods.

Diagnosis: Due to monotypy, the diagnosis of the genus is the same as the diagnosis of the type species.

Platuropodus odysseus n. sp.

Figs. 1, 3-8, 15

Synonyms: 2013 Indeterminate crustacean - Chahud & Petri, p.123, fig.3.

v 2014 decápode reptântio - Fochringer, p.39-44, figs.8-12.

v 2017 Morfotipo 1 - Pazinato, p.61-65, figs.32-42, p.71, figs.47a,c,e-g

Types: Holotype: URC.AC.196.1A, B, part and counterpart of almost complete specimen, lateral view.

Paratypes: URC.AC. 196.2, almost complete specimen, dorsal view; and LPRP/USP 0003A,B, part and counterpart of thorax, pleon and respective appendages, lateral view.

Type locality: Outcrop at a secondary road about 3 km south-west of the urban area of Rio Claro, São Paulo, Brazil. Coordinates: 22° 28' 16" S, 47° 38' 16" W.

Type stratum and age: Taquaral Member, Irati Formation, Permian (Cisuralian, Kungurian), between 272.95 ±0.11 and 283.5 ±0.6 million years (Santos et al. 2006).

Etymology: Specific epithet refers to the long journey of interpretations of this fossil.

Diagnosis: Body longer than wide; cephalothorax and thorax shorter than pleon in lateral view; thorax segments with indented mid-transversal row of spines and setae; thorax appendages 2 and 3 sub-chelate; uropods with flat endopod and exopod; pleotelson with postero-ventrally anus and long mid-spine, almost as long as the pleotelson.

CONCLUSIONS

The described fossil specimens represent a new species of Isopoda, *Platuropodus odysseus*, from the Permian (Cisuralian, Kungurian) of São Paulo state, Brazil, with a unique combination of characters unknown for any fossil or extant representative of Eumalacostraca. This chimera-like morphology and the morphometric analysis of the sub-chelae indicate convergent evolution in the diversification of Isopoda. Additionally, the fossil record of Isopoda, and peracarids, demonstrates a “push of the past” effect during the Palaeozoic and Mesozoic evolution of the group.

Misinterpretations of this fossil raises the issue of how arbitrary taxonomy is, especially when it comes to establishment of species in palaeontology. When possible, revisions of doubtful fossils species should precede studies on species richness. If incorrect, taxonomic interpretations may under- or overestimate richness of groups and mislead our understating of biodiversity through geological time.

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