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A fossil tanaidacean crustacean from the Middle Jurassic of southern Germany

MARIO SCHÄDEL, PAULA G. PAZINATO, SERITA VAN DER WAL & JOACHIM T. HAUG

Abstract

A three-dimensionally preserved fossil tanaidacean is reported from the Middle Jurassic of Southern Germany. The fossil is a fragment of the posterior region of the body. Many morphological details are visible, such as rows of punctures indicating the presence and distribution of setae. A principal component analysis based on measured ratios on the fossil was performed to evaluate the position of the fossil in the morphospace of various malacostracan groups. The analysis could substantiate the interpretation of the fossil as a tanaidacean remain. We furthermore discuss the fossil in comparison to the already known fossil record of tanaidaceans.

Key words: microfossil, morphospace, principal component analysis, Peracarida, Tanaidacea.

1. Introduction

Peracarida is a large group of crustaceans that occurs worldwide in many different habitats, reaching from the deep sea into dry deserts (SHACHAK et al. 1976; DRUMM & BIRD 2016). The group is morphologically very diverse and includes many distinct sub-groups. Some of these are rather small concerning number of species, such as Speleogriphacea and Mictacea. Other ingroups of Peracarida are more species-rich, such as Cumacea, Lophogastrida and Tanaidacea, despite of them not being commonly known among non-experts. Finally, there are well-known and species-rich groups such as Amphipoda, Mysida and Isopoda. The latter is the most well-known one, including forms such as slaters, woodlice and pill bugs.

Most peracaridans are small in size, with a body length of only a few millimetres, yet some are more than 300 millimetres long, the latter are found especially in the deep sea. Representatives of Peracarida inhabit many different environments (terrestrial, marine, freshwater and brackish water). They can also be found living in extreme conditions, such as at hydrothermal vents and polar shelves (BRANDT 1999; LARSEN & KRAPP-SCHICKEL 2007).

Peracarida is considered to be monophyletic, however, there is no consensus about the relationships among the different ingroups (POORE 2005; JENNER et al. 2009; WIRKNER & RICHTER 2010). Autapomorphies characterizing Peracarida are: 1) the presence of a *lacinia mobilis*, a movable spine-like process, in the mandible of the adults; 2) the presence of oostegites (modified epipods) in brooding females (AX 2000; POORE 2005). The peracaridan fossil record dates back at least to the Carboniferous. The autapomorphic and/or diagnostic features of Peracarida are especially difficult to identify in fossils. Hence, it is not surprising that some ingroups have yet no fossil record at all.

Tanaidacea is a peracaridan ingroup with a relatively scarce fossil record, despite their massive abundance at some localities (MALZAHN 1970). Extant tanaidaceans range in size from 1 mm to 77 mm (AX 2000). The great majority of the approximately 1400 formally described species are marine, although there are freshwater and estuarine species (BŁAŻEWICZ-PASZKOWYCZ et al. 2012; ANDERSON & BŁAŻEWICZ-PASZKOWYCZ 2018). Tanaidaceans are benthic organisms that live epifaunal (surface dwellers) or infaunal (burrowing in sediment). A considerable portion of tanaidacean species produce tubes from secreted mucus.

This tube-dwelling lifestyle has been thought to be restricted to a specific tanaidacean ingroup, of which the representatives possess a special gland system (thoracic-gland system; HASSACK & HOLDICH 1987). However, there are two other gland systems (pereopodal- & pleotelsonal-gland system) in tanaidaceans from other lineages, which also allow for the construction of mucus tubes (KAKUI & HIRUTA 2017). This indicates that this special lifestyle has evolved several times independently. Furthermore, some epifaunal living species inhabit empty shells of gastropods and mollusc shells for protection (McSWEENEY 1982). While females of some species never leave their tubes, some male tanaidaceans with well-developed uropods can actively swim over short distances (HASSACK & HOLDICH 1987). Some tanaidacean species are highly sexual dimorphic and some hermaphroditic species even develop up to four distinct male morphotypes, even in different modes, e.g. males that derive directly from juveniles and males that derive from females (SIEG 1983).

Regarding their body organization, tanaidaceans are derived from the eumalacostracan ground pattern. The eumalacostracan ancestor has been reconstructed to have a functional head that comprises the ocular segment plus five post-ocular segments as well as a trunk that is divided

into two functional units (tagmata): the anterior trunk comprising eight segments (the thorax or thorax I sensu WALOSSEK & MÜLLER 1998), and a posterior trunk comprising six segments (the pleon or thorax II sensu WALOSSEK & MÜLLER 1998).

In tanaidaceans, however, the head and the first two segments of the trunk (post-ocular segments 6 and 7) are conjoined and the all these segments dorsally form a continuous shield. The conjoined segments form a longer functional head, which is often referred to as the ‘cephalothorax’. The remaining six free segments of the thorax, the “leftover” of the thorax, is referred to as ‘pereon’, which is not to be confused with the pereon in Isopoda or Decapoda, which involves different segments with different characteristics. The posterior trunk (pleon) comprises five free segments and another segment that bears the uropods and is conjoined with the telson (forming the pleotelson). In some species more pleon segments are conjoined to the pleotelson (SIEG 1983; LARSEN et al. 2015). The appendages of the functional head, i.e. cephalothorax, are: anten-

nula, antenna, mandible, maxillula, maxilla, maxilliped and cheliped, the latter bearing a chela, which is usually enlarged. The six pairs of pereopods (appendages of the pereon) generally lack exopods. The pleopods (appendages of the pleon) can be biramous (bearing endopod and exopod, plesiomorphic condition for eumalacostracans), uniramous (bearing only the endopod), or completely reduced (LARSEN et al. 2015).

Tanaidacea has traditionally been divided into four groups, “Anthracocaridomorpha”, Apseudomorpha, Neotanaidomorpha (herein referred to as Neotanaidae, since Neotanaidomorpha is monotypic) and Tanaidomorpha (SIEG 1983). “Anthracocaridomorpha” includes all Paleozoic species and one Mesozoic species (*Niveotanaeis brunensis* POLZ, 2005). It is most likely not monophyletic, as it is characterised by a plesiomorphic condition (tergite of the sixth pleon segment not conjoined with the telson; SCHRAM et al. 1986). The most recent phylogenetic studies (KAKUI et al. 2011, 2012) also casted severe doubts on the monophyly of Apseudomorpha. The most recent phylogenetic hypoth-

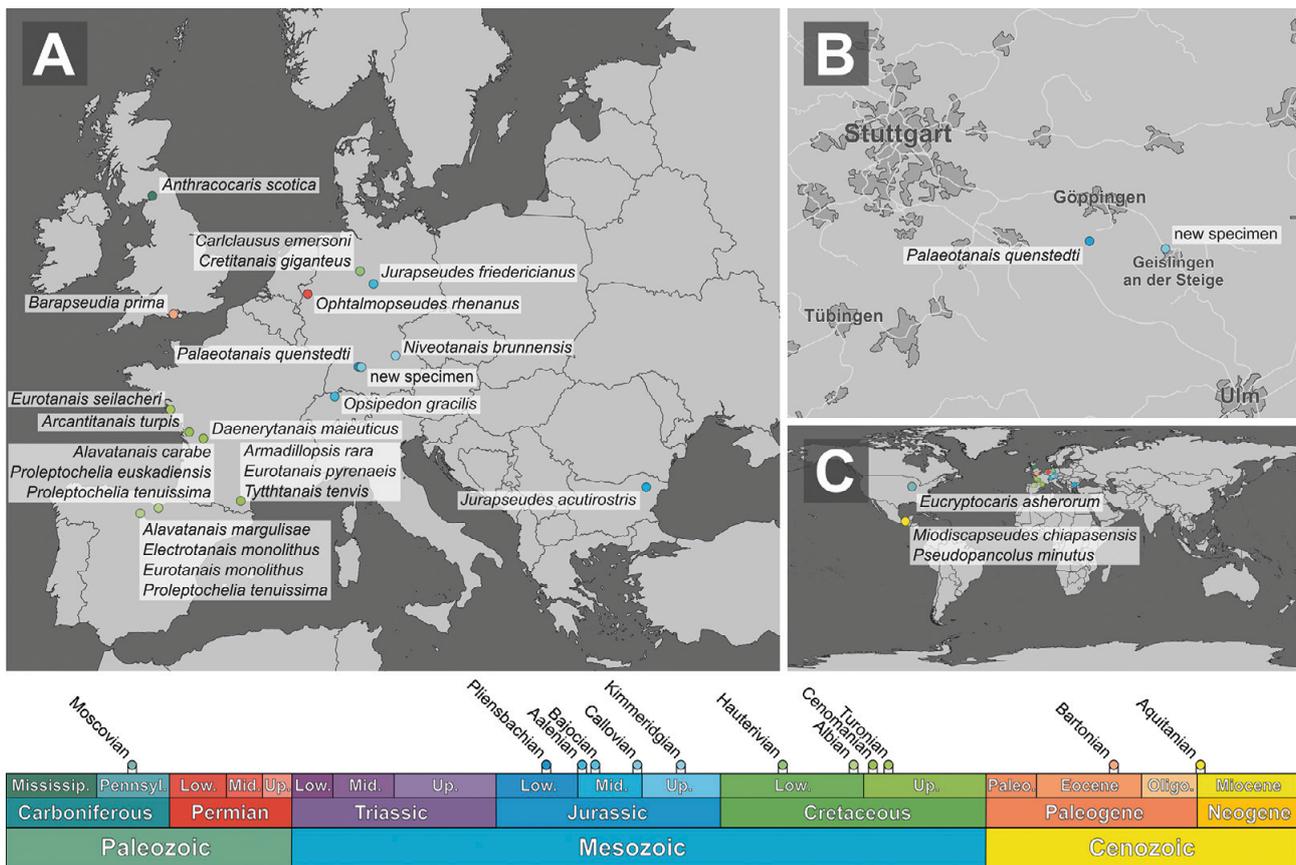


Fig. 1. Maps of different scales (A–C) depicting the geographical occurrence of tanaidacean fossils (described species only). A: Map of Europe; B: map of Southwestern Germany; C: world map; bottom: stratigraphic legend (not to scale). Colours code for different geological ages of the occurrences, colours as suggested by the International Commission on Stratigraphy (ICS). Abbreviations: Low., Lower; Mid., Middle; Mississipp., Mississippian (Lower Carboniferous); Oligo., Oligocene; Paleo., Paleocene; Pennsylv., Pennsylvanian (Upper Carboniferous); Up., Upper.

eses interpret Apseudomorpha (or one of the apseudomorphan lineages) as sistergroup to Tanaidomorpha (DRUMM 2010; KAKUI et al. 2011; LARSEN et al. 2015). The relationship between Tanaidomorpha and Neotanaidomorpha is still vividly debated. Neotanaidae is either interpreted as sistergroup to Tanaidomorpha (LARSEN et al. 2015) or as an ingroup of Tanaidomorpha (KAKUI et al. 2011, 2012). Neotanaids are only found at great water depths and are sexually highly dimorphic regarding their cheliped size and other characters (BŁAŻEWICZ-PASZKOWYCZ et al. 2012).

Currently, there are 26 formally described fossil species of tanaidaceans, extending from the Lower Carboniferous to the Eocene (PEACH 1882; CALMAN 1933; QUAYLE 2016; Fig. 1). Fifteen of these species are known from inclusions in amber of the Cretaceous and Neogene (VONK & SCHRAM 2007; SÁNCHEZ-GARCÍA et al. 2015, 2016, 2017; HEARD et al. 2018). The remaining fossils come from non-amber sites. ETTER (2004) suggested that the rather scarce fossil record of tanaidaceans is an artifact, since most tanaidacean fossil remains seem to be destroyed during the standard microfossil sampling procedure, with the exception of the chelae.

As part of the benthos, tanaidaceans are restricted to oxygenated environments, which favour bioturbation. These conditions are highly counterproductive for fossil preservation. Findings of fossil tanaidaceans are therefore usually isolated remains or fragmentary body parts. The identification of isolated parts or fragmentary fossils is challenging in various aspects and many remains of tanaidaceans are probably not recognized as such.

Here we report a new fossil tanaidacean from the Upper Callovian (Middle Jurassic) of southern Germany. Additionally, we present a strategy to deal with the fragmentary nature of such fossils.

2. Material and methods

A single fragmentary specimen stored in a Franke cell (small container for micropalaeontological samples) is presented. The fossil is stored in the palaeontological collection of the University of Tübingen (formerly Geologisch-Paläontologisches Institut Tübingen, GPIT) under the collection number GPIT/NC/07/B/34. Originally, the fossil stems from the collection of KARL FEIFEL (Stuttgart, 1873–1959). The majority of the FEIFEL collection is housed in the State Museum of Natural History in Stuttgart (SMNS). Based on the research focus of K. FEIFEL (biostratigraphy with foraminifers), and judging from the preservation of the fossil it is likely that it was retrieved by sieving sediments for micropalaeontological studies.

Information regarding the geographic and geological context of the described fossil is limited to the short note “Dogger zeta Altenstadt”. The urban district Alten-

stadt of the town Geislingen an der Steige (Göppingen district, Baden-Württemberg, Germany) is the only location that is compatible with the stratigraphic range on the label (Bundesanstalt für Geowissenschaften und Rohstoffe 2018). Within the regional geological context, “Dogger zeta” refers to the Ornatenton Formation. The preservation of the herein described specimen does only match the lithology of the *Peltocoeras athleta* and *Quenstedtoceras lamberti* ammonite zones (G. SCHWEIGERT, pers. comm.). This corresponds to an absolute age time-range of 164.0 to 163.5 million years (OGG et al. 2012).

The fossil was viewed and photographed with the aid of the Keyence VHX-6000 Digital Microscope. To achieve fully focussed images, the implemented focus stacking algorithm of the digital microscope was used. The three-dimensional models (depth from defocus), produced during the focus stacking process, were also saved for later use. For the dorsal and ventral view of the complete specimen, a series of photos were taken by tilting the microscope with the fossil remaining undisturbed.

For high-resolution images of the total specimen, panoramic stitching was performed in Adobe® Photoshop Elements 11. GIMP 2.10 (GNU) was used to adjust the photographs and to create red-cyan stereo anaglyphs from photos taken at different angles. The fragile quality and size of the specimen did not allow for it to be turned, other than into dorsal- and ventral-side up position. To accomplish a lateral image of the specimen, the depth-from-defocus model was turned to the desired projection using the Keyence Communication Software for VHX-6000 / 950F (version 3.0.0). The generated two-dimensional images were then saved. Adobe® Illustrator CS2 was used to create digital illustrations of the fossil. Further illustrations of the specimen and other figures were created in Inkscape (GNU). Virtual rotation models (Suppl. 1, 2) were created using GIMP (by removing background and adjusting images) and ImageJ (SIFT alignment).

The geographical map for the occurrences of fossil tanaidaceans was created in QGIS (GNU) and post-processed in Inkscape.

Measurements: The following distances were measured in the fossil: total length; length of each of the individual body segments along the midline of the animal; maximal width of each body segment; width of the first pleon segment at the joint to the second pleon segment. Where the fossil was partially incomplete, the existing structure was used to reconstruct the opposing body side (see Suppl. 3). A selection of the before mentioned distances (Suppl. 3 and section below) was also measured in drawings and photographs from literature for the following groups of malacostracan crustaceans: Tanaidacea DANA, 1849; Isopoda LATREILLE, 1817; Cumacea KRÖYER, 1846; Spelaeogriphacea GORDON, 1957; Mictacea BOWMAN, GARNER, HESSLER, ILIFFE & SANDERS, 1985; Thermosbaen-

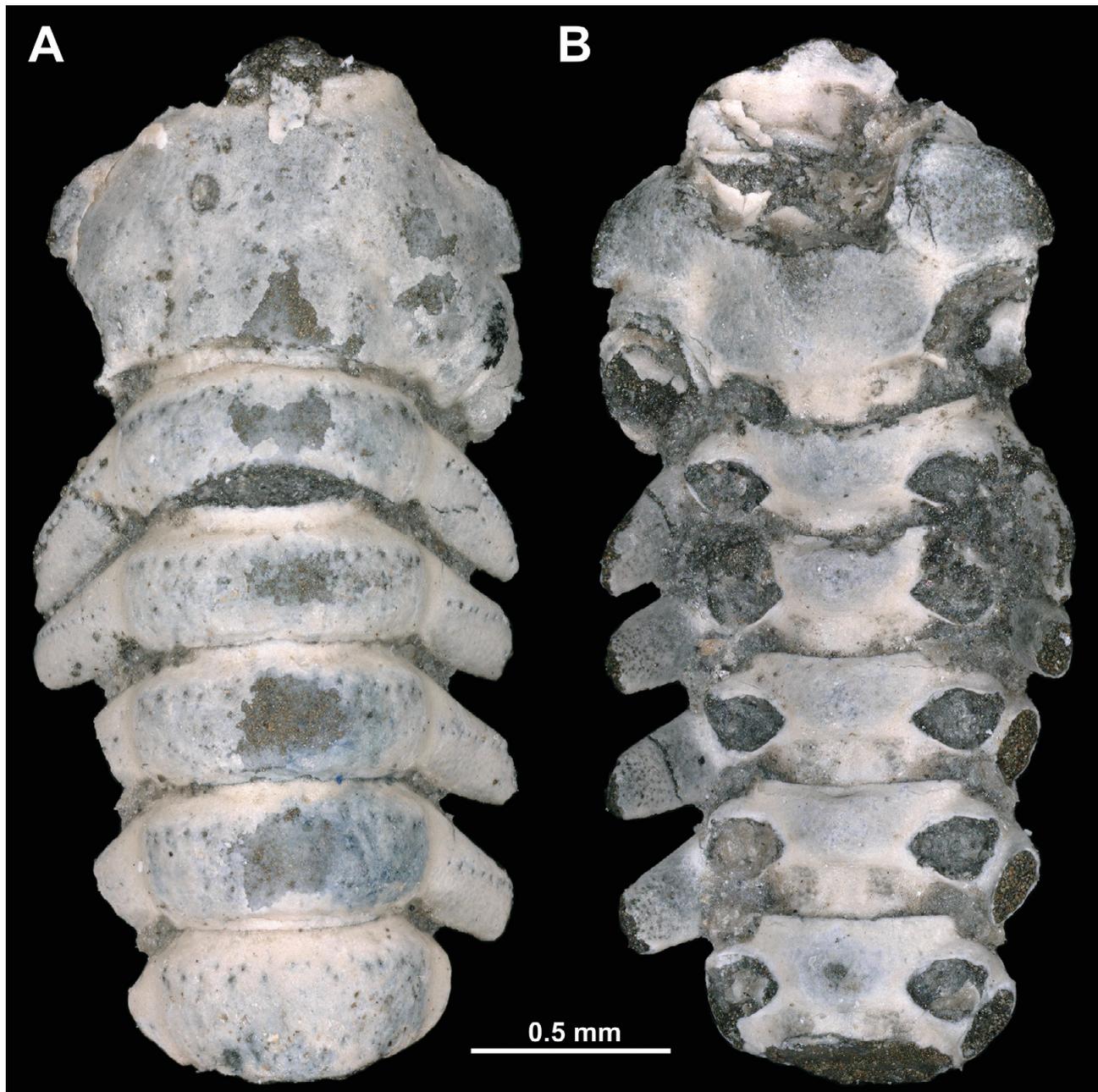


Fig. 2. Photo-micrographs of GPIT/NC/07/B/34. **A:** Dorsal view; **B:** ventral view.

acea MONOD, 1927; Syncarida PACKARD, 1885; Amphipoda LATREILLE, 1816; Mysida BOAS, 1883; and Stomatopoda LATREILLE, 1817 (Suppl. 4, 5). Measurements were done using ImageJ (public domain), Adobe® Acrobat® Reader DC and Adobe® Acrobat® Pro.

Morphometric comparison: All measurements were normalized by dividing each distance by the length of the pleon (usually the longest measured distance). Based on the normalized distances, the following

ratios were formed: ratio 1: width of the segment anterior to the first pleon segment divided by the length of that segment (along the midline); ratio 2: width of the broadest pleon segment divided by the length of the pleon (without pleotelson, along the midline); ratio 3: length of the segment anterior to the first pleon segment (along the midline) divided by the length of the pleon (without pleotelson, along the midline); ratio 4: length of the segment anterior to the first pleon segment (along the midline) divided by

the length of the first pleon segment (along the midline); ratio 5: width of the segment anterior to the first pleon segment divided by the width of the broadest pleon segment; ratio 6: width at the posterior end of the broadest pleon segment divided by the width of the same segment. Species that differed in their body organisation in a way that would not allow for a proper comparison to the majority of species (e.g. more pleon segments conjoined with the telson), were excluded from the dataset. A principal component analysis (with and without scaling of the input data)

was performed and visualized in R (GNU) using the packages FactoMineR, and factoextra (Suppl. 6).

3. Description of the specimen

Material: One specimen (Figs. 2–6), consisting of six segments. First preserved segment distinctly differing from the following five, which all have a sub-similar morphology, total length 2.63 mm, total width 1.21 mm.

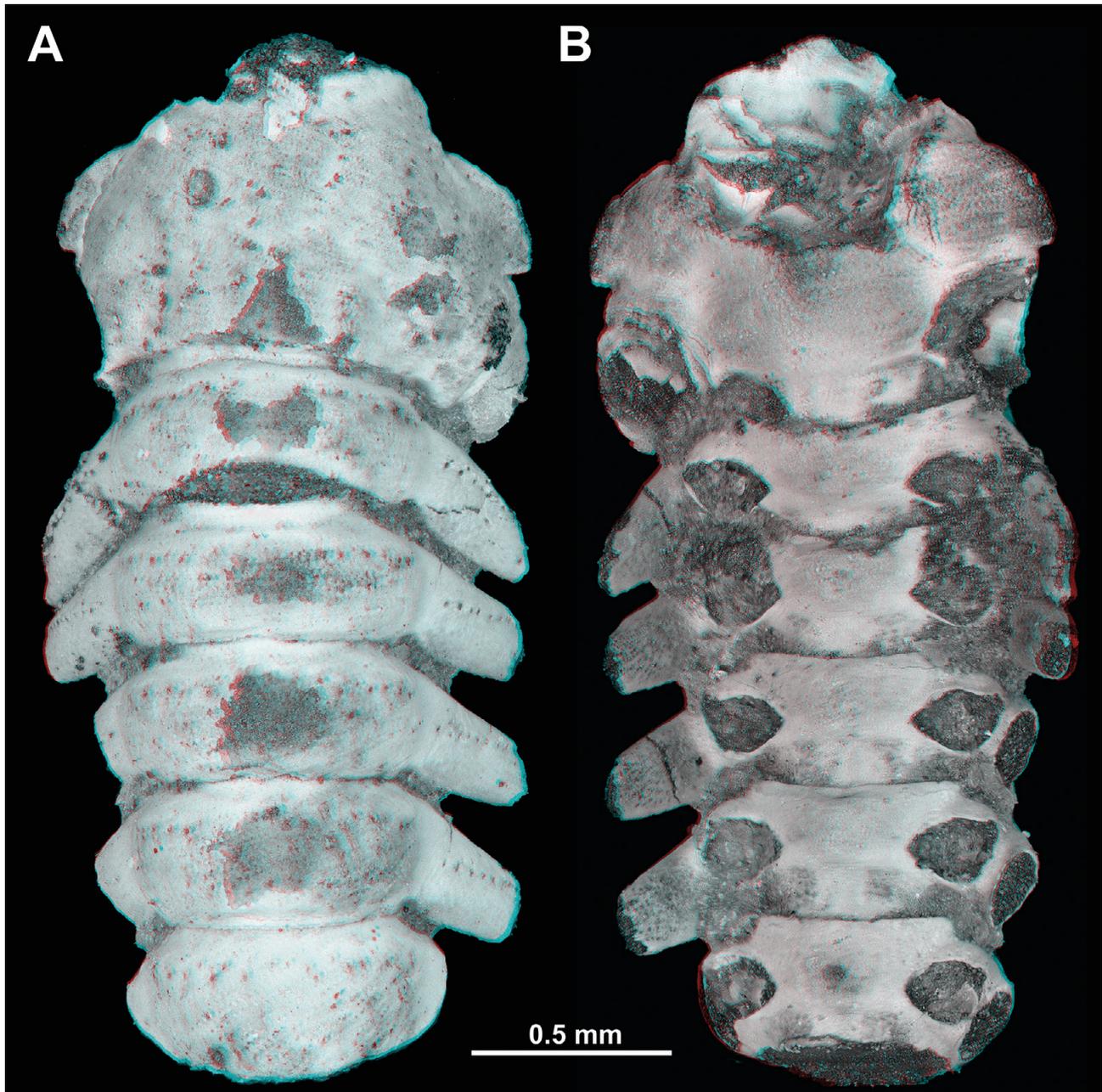


Fig. 3. Red-cyan stereo anaglyphs based on photo-micrographs of GPIT/NC/07/B/34. **A:** Dorsal view; **B:** ventral view.

Repository: University of Tübingen, Palaeontological collection (formerly Geologisch-Paläontologisches Institut Tübingen), collection number GPIT/NC/07/B/34.

Locality: Geislingen an der Steige, Baden-Württemberg, Germany.

Horizon: Upper Callovian, Ornatenton Formation ("Dogger zeta"; 164.0 to 163.5 million years).

Description: Part of a trunk of a sclerotized arthropod. Six free segments, each segment with a distinct dorsal sclerotization (tergite) and ventral sclerotization (sternite). First preserved segments differing distinctly from the following five ones.

First preserved segment 0.62 times as long as wide, with one pair of short and blunt lateral processes arising from the anterolateral part of the segment (dorsal and

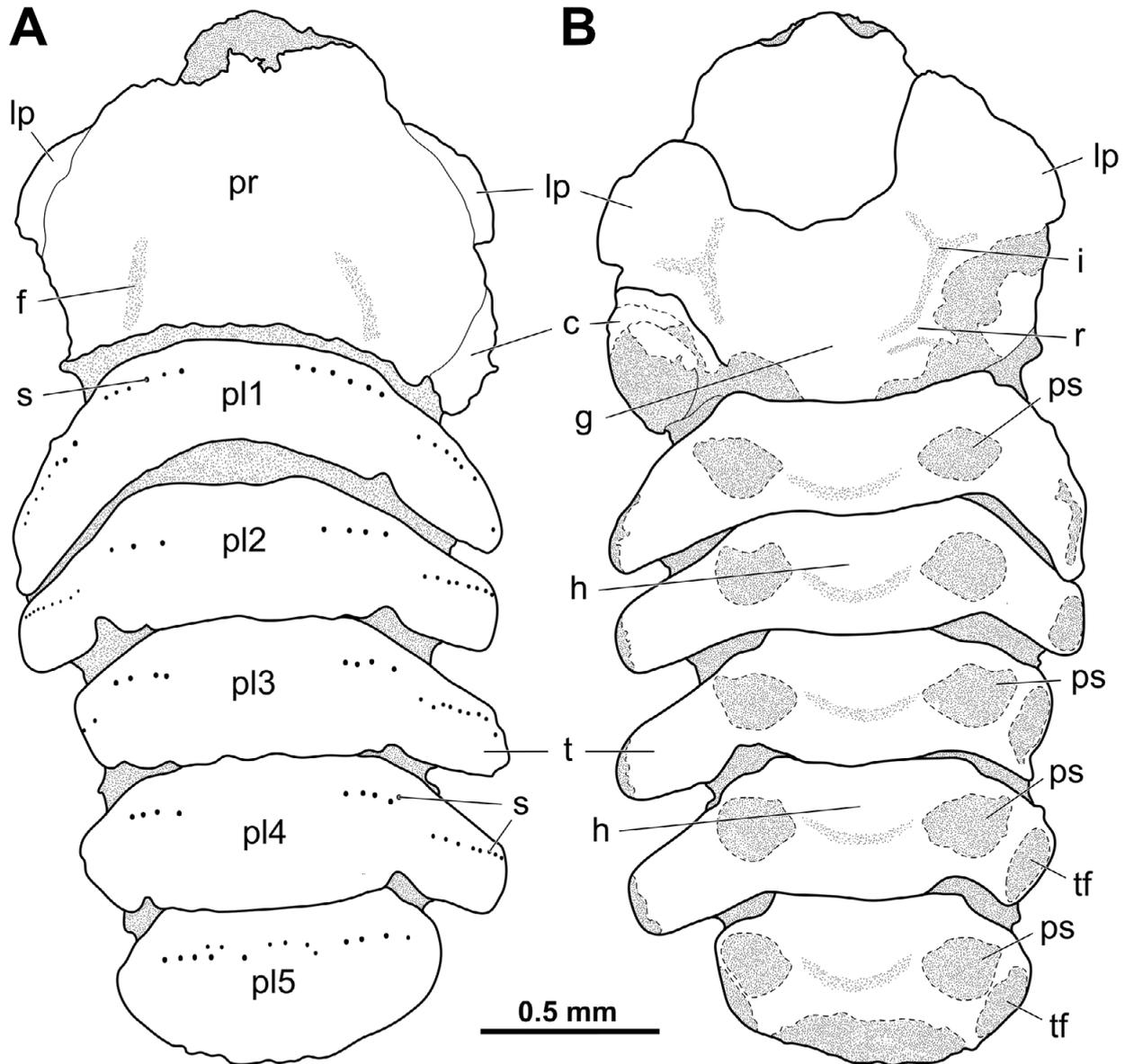


Fig. 4. Drawing of GPIT/NC/07/B/34. **A:** Dorsal view; **B:** ventral view. Abbreviations: c, coxa; f, shallow furrow; g, position of the gonopores in male tanaidaceans (not present here); h, hyposphaenium; i, shallow indent; lp, lateral process; pl1, pleon segment 1; pl2, pleon segment 2; pl3, pleon segment 3; pl4, pleon segment 4; pl5, pleon segment; pr, last pereon segment (post-ocular segment 13); ps, pleopod scars (insertion points); r, crest-like ridge; s, punctures in the tergite, presumably representing setae insertions; t, tergopleuron; tf, tergopleuron fracture surface.

ventral skeletal parts of the segment involved, Figs. 2A, 3A, 6A). Weak oblique furrows on the dorsal side (tergite) protruding from the posterolateral corner of the tergite halfway along the total length of the segment, in a 30° antero-medial direction from the midline (Figs. 3A, 4A). The ventral side is mostly formed by a single sclerite (sternite); no particular structures present in the postero-medial area, such as a genital cone (gonopores; Figs. 2B, 6A).

Appendages of the first preserved segment only partly preserved, represented by the scars of the proximal joints with the trunk and one proximal appendage element on the right side of the body (Figs. 5C–E). Proximal appendage element latero-ventrally inserted in posterior half of first preserved segment; dorsal side of the proximal joint forming a smooth junction to the tergite (scale-like appearance in dorsal view); proximal region of the element laterally 0.37 as wide as the length of the segment along the midline. Element distally extending past tergite posterior margin.

Shallow indentations on the ventral side of the segment antero-medially from the proximal appendage element; three-branched crest-like ridges medially to the element, faintly joined by the median branch; anterolateral and posterolateral branches following the outline of the proximal appendage element.

Preserved segment 2–6 (interpreted as pleon segments 1–5, see below) sub-similar in general morphology. Dorsal sides of the segments (tergites) convex, roughly half-cylindrical, drawn out into lateral processes (tergopleura, often incorrectly addressed to as ‘pleura’/‘pleural processes’). Posterior margins of tergites straight in dorsal view. Reconstructed length-divided-by-width ratios for each of the pleon segments 1–4 are 0.22, 0.30, 0.27 and 0.31 (times as long as wide). Ratio for pleon segment 5 not obtained, as the tergopleura are broken off.

Tergopleura pointing postero-ventrally (35° in posterior direction and 50° in ventral direction). Pleon segments 2 and 4 with tergopleura tips significantly eroded, not representing the true outline. Pleon segments 1–5 each with a transverse row of punctures (presumably, insertion points of setae) along the anterior margin of the tergite, up to 6 punctures in one row preserved, median part eroded in pleon segments 2–4 (Figs. 2A, 4A). Paired rows of punctures on the dorsal side of the tergopleura, extending from the centre of the proximal region of the tergopleuron to the antero-distal-most extent of the tergopleura, up to eight punctures in one row preserved (Figs. 4A, 5A). Distribution of punctures similar in each of the pleon segments.

Sternites with distinct insertion areas of appendages; these are wider than long, with distinct median and anterolateral angles. Three-branched, crest-like ridges medially to the element faintly joined by the median branch; anterolateral and posterolateral branches following the outline of

the proximal appendage element (Figs. 3B, 6B). Anterior to the median branches of the ridges are indistinct protrusions (‘hyposphaeniae’ = ‘hyposphania’), most prominent in pleon segments 2 and 4 (Figs. 3B, 4B).

Morphometric comparison: For a comparative frame ratios of measurements taken of the examined fossil and other malacostracan species were used in a principal component analyses (PCA). Even though only ratios between normalized measurements were included, there are a few isopod species that greatly enlarge the overall morphospace (Fig. 7A). To compensate for this, an analysis with prior scaling of the variables (ratio values) was performed.

In the unscaled PCA, the first principal component (PC1) explains 72.2% of the total variance in the dataset. PC2 explains 18.7% of the total variance. The remaining variance is explained by PC3–6 (Suppl. 7A). PC3 also explained a considerable amount of variance (8.2%). PC1 is dominated by ratio 1 (length vs. width of the last pereon segment), whereas PC2 is strongly affected by ratio 2 (length vs. width of pleon), ratio 3 (length of last pereon segment vs. length of pleon) and ratio 4 (length of last pereon segment vs. length of first pleon segment). Ratios 5–6 are almost negligible concerning their influence on PC1 and PC2.

In the scaled PCA, the first principal component (PC1) explains 36.6% of the total variance in the dataset. PC2 explains 21.8% of the total variance. The remaining variance is explained by PC3–6, where the proportion of variance is more evenly distributed among the principal components as a result of the scaling (Suppl. 7 B). PC1 is most supported by ratio 2 (length vs. width of pleon) and ratio 3 (length of last pereon segment vs. length of pleon), whereas PC2 is mainly affected by ratio 1 (length vs. width of the last pereon segment). Ratios 4, 5 and 6 have a lesser, but still considerable effect on PC1 and PC2.

Once scaled, ratio 1 decreases in its proportional contribution to PC1 (Suppl. 7 C & D). Due to the bundled orientation of ratios 2, 3 and 4 in the multidimensional space, ratio 1 changed from contributing to PC1 (in the unscaled PCA), to contributing to PC2 in the scaled PCA. Yet, ratio 1 still remains the value that contributes the most to PC1 and PC2 combined (Suppl. 7D).

In the unscaled PCA analysis, isopodan species occupy most of the morphospace as they have species that correspond to a high PC1 value (wide last pereon segment) and also species that correspond to a high PC2 value (short but wide pleon). With the exception of one fossil (see discussion below), tanaidaceans are separated from most of the other groups, but not from Isopoda. With few exceptions, species of Mysida, Mictacea, Stomatopoda and Syncarida plot densely together in the area with low PC1 and low PC2 values. Cumaceans plot in the same approximate area but with even lower PC1 values. Fossil and extant tanaid-

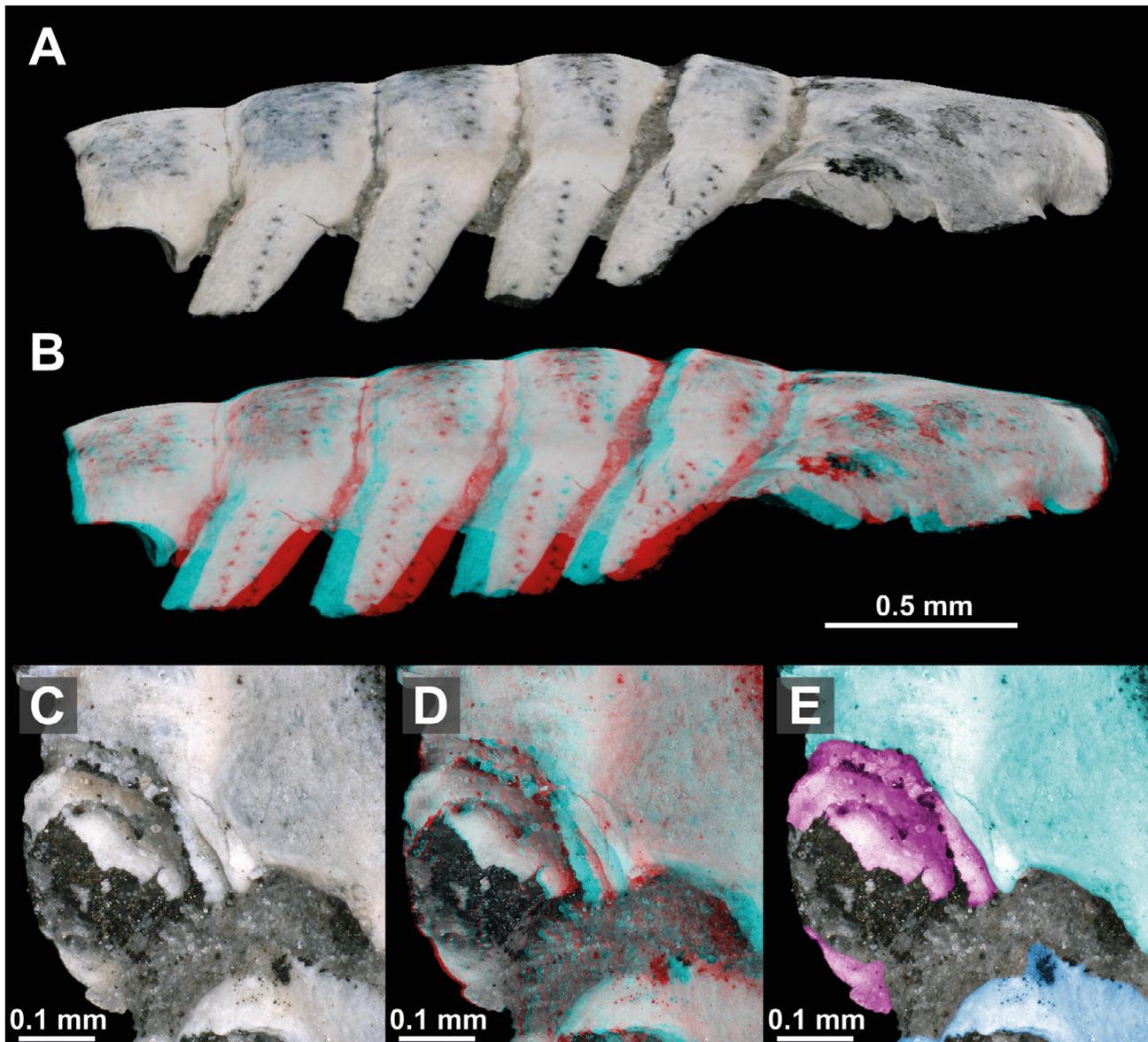


Fig. 5. Lateral view and coxal region of GPIT/NC/07/B/34. **A, B:** Lateral view of the right body side reconstructed based on a 3D depth-from-defocus model; **A:** two-dimensional rendering; **B:** red-cyan stereo anaglyph; **C–E:** photo-micrographs of the right coxa of the last pereon segment; **C:** photo-micrograph, **D:** red-cyan stereo anaglyph, **E:** artificially coloured photo-micrograph. Colouration: cyan, sternite of last pereon segment; blue, sternite of first pleon segment; pink, coxal elements.

aceans do not form separate clusters. The herein described fossil also plots within the tanaidacean cluster.

By prior scaling the relative area that isopodans occupy, within the entire morphospace of the dataset, is much smaller. Even so, isopodans still occupy the largest area of the morphospace of all compared groups. The relative position of clusters of the different groups to each other is similar. Species of Mysida, Mictacea, Stomatopoda, Syncarida and Spelaeogriffacea form a dense cluster

in the area with low PC1 values (short last pereon segment and narrow pleon). The tanaidacean cluster is less dense and located in the area with lower PC2 values and higher PC1 values (higher ratios 3 & 4, longer last pereon segment and shorter pleon segments). Fossil and extant tanaidaceans are, like in the unscaled analysis, completely intermixed. The herein described fossil is well within the tanaidacean cluster.

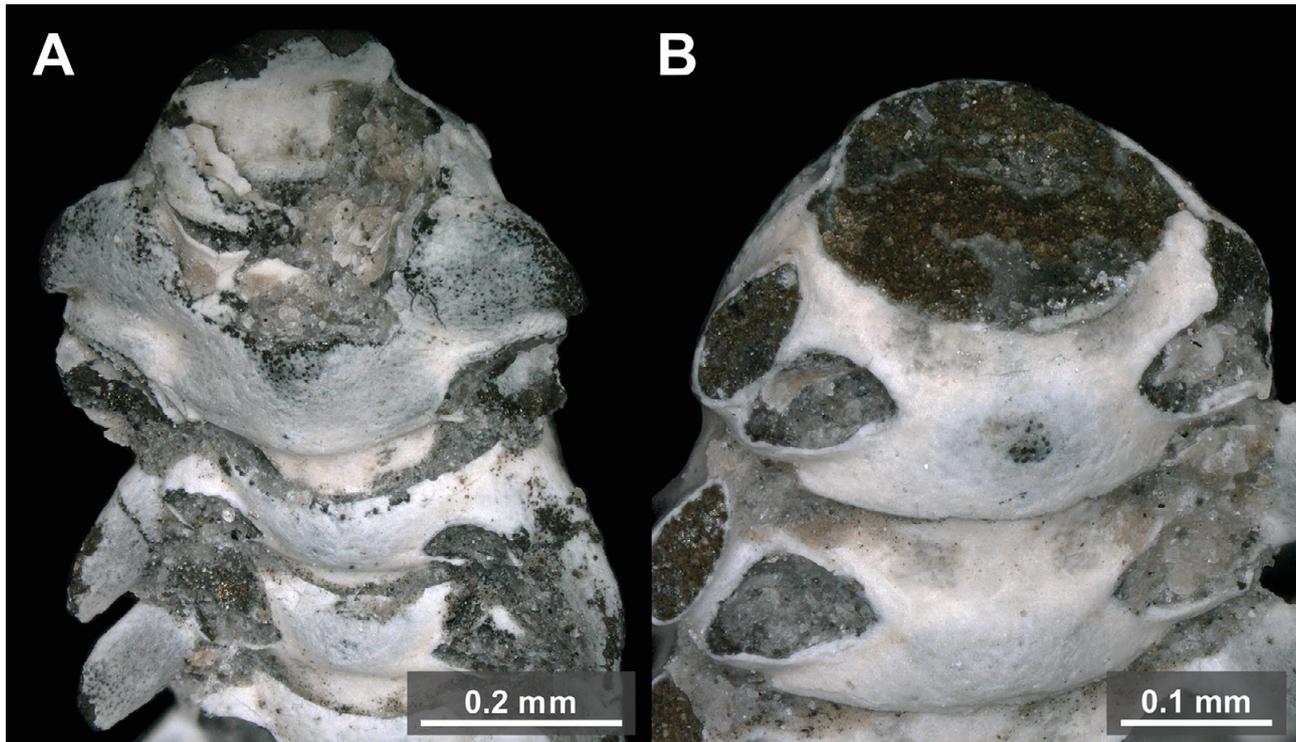


Fig. 6. Photo-micrographs of GPIT/NC/07/B/34. **A:** Anterior region in antero-ventral view; **B:** posterior body region in postero-ventral (slightly lateral) view.

4. Discussion

4.1. Interpretation of the fossil as a tanaidacean

The described fossil has a massively sclerotized exoskeleton, an autapomorphic feature for Arthropoda *sensu stricto* (= Arthropoda s.l. without Onychophora, lobopodians, Tardigrada and possibly Pentastomida; MAAS et al. 2004). The clear morphological distinction between the anteriormost preserved segment and the subsequent segments, is the result of a functional body tagmatization into a tagma consisting of segments bearing distinct appendages of a very rounded cross section, and a tagma consisting of segments that bear appendages with more flattened cross sections. This is best compatible with the tagmatization that is apomorphic for Eumalacostraca (WALOSZEK 1999).

Our morphometric comparison shows that tanaidaceans form a rather discrete cluster within the eumalacostracan morphospace (Fig. 7). The described fossil plots just among the other measured fossil and extant tanaidaceans. Isopodan species occupy a wide space in the overall morphospace, which is to be expected, as they show a great variety of body forms (e.g., Serolidae and Janiridae, BRANDT & POORE 2003). The groups Cumacea, Mysida, Mictacea, Stomapoda and Syncarida occupy only

a smaller part of the complete morphospace. With only few exceptions, representatives of each of the groups form dense clusters themselves. This may be constrained by functional aspects, for example possibly the ability of the tailfan to perform a powerful escape stroke, which seems to be absent in tanaidaceans and isopodans.

Few species of Isopoda plotted within or near to the tanaidacean cluster, in the case of *Acanthastenasellus forficuloides* and *Corallana societensis*. This may be due to the reduced number of pleon segments bearing free tergites (resulting in a shorter pleon). The other isopodans are representatives of the groups Calabozoidea, Tainisopidae and Anthuridae. Calabozoideans can be easily distinguished from the described fossil by the position of the proximal appendage element (coxa) in the last segment of the anterior trunk tagma (pereon). Anthurideans and tainisopids resemble the described fossil by having long pereon segments and distinctly shorter pleon segments (resulting in a shorter pleon). In our analysis, this aspect of similarity is represented by ratios 3 and 4. Species of both groups do not have lateral processes on the last pereon segment and lateral processes of the pleon segments only occur within species of Anthuridea (WÄGELE 1981, 1989), but not of Tainisopidae (WILSON & PONDER 1992; WILSON 2003).

One fossil tanaidacean, *Cretitanais giganteus*, does not plot within the cluster of tanaidaceans, most likely

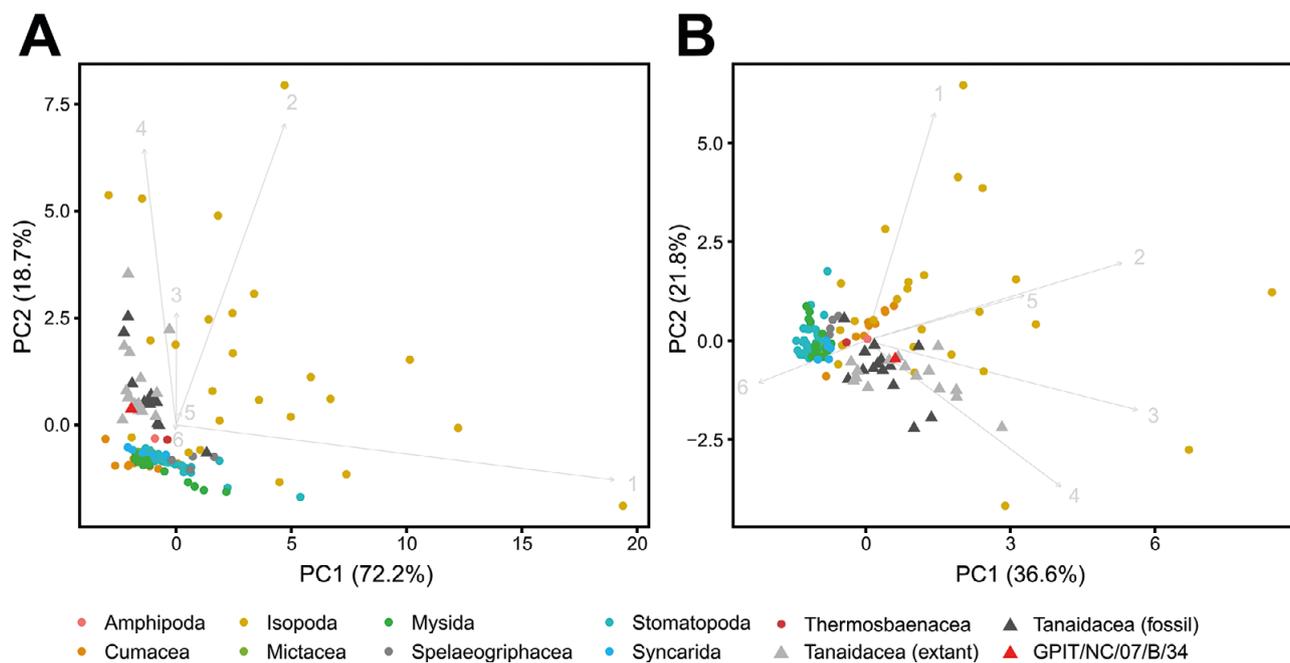


Fig. 7. Principle component analysis of different ratios measured on fossil and extant malacostracan crustaceans. The correlation between variables and the principle components 1 and 2 (x- and y-axis) is depicted by light grey arrows, the corresponding numbers refer to the variables (ratios 1 to 6). **A:** Analysis without logarithmized variables, **B:** analysis with logarithmized variables.

because it has an unusually short last pereon segment. This may represent a neotenuous feature within the species *Cretitanais giganteus*. Early manca stages of tanaidaceans have a much shorter last pereon segment than the previous segment, and lack fully developed pereopods on the last pereon segment (LARSEN 2003; BOYKO & WOLFF 2014). Even though the pereopods of pereon segment 6 are well developed, the longitudinal growth of the last pereon segment could just be ontogenetically suppressed or delayed, which would explain the exceptional morphology in *Cretitanais giganteus*.

Some qualitative morphological features of the new fossil further support an interpretation as a tanaidacean. Typical features of tanaidaceans, or tanaidacean ingroups, are: 1) (weakly developed) hyposphaenia on the pleon segments; 2) pronounced lateral processes of pleon tergites (tergopleura); 3) posterolateral position of the coxa on the last pereon segment; 4) transverse rows of setae on the pleon tergites (preserved as punctures in the exoskeleton).

The setal rows present in the described fossil also occur within some extant tanaidomorph tanaidaceans (e.g., *Tanais dulongii*; SARS 1899), but also in non-tanaidomorph tanaidaceans, e.g., *Saltipedis floccus* (GÜTU 1996; BŁAŻEWICZ-PASZKOWYCZ & BAMBER 2007). Pore-like punctures like in the described fossil have also been recorded for the fossil tanaidacean *Cretitanais giganteus*, but there the punctures are on the pereon segments rather than on the pleon segments (MALZAHN 1979).

4.2. Ontogenetic stage

The anteriormost preserved segment in the fossil is interpreted as the last pereon segment (post ocular segment 13). This can be inferred from the morphology of the further posterior segment (typical pleon morphology, not considerably differing from subsequent segments). That the fossil represents a manca stage can be ruled out, because manca stages in tanaidaceans do not have fully developed appendages on the last pereon segment and (at least not in early mancas) the whole segment is shorter than the anterior subsequent (pereon) segments that bear fully developed legs (LARSEN 2003; BOYKO & WOLFF 2014). Consequently, the fossil can only be the remain of a late juvenile (last pereopod with fully developed coxa) or of an adult animal.

4.3. Sex

As in other malacostracans, tanaidacean male gonopores are located medially on the ventral side of the post-ocular segment 13 (thorax segment 8; last pereon segment in tanaidaceans), whereas female gonopores are located at post-ocular segment 11 (thorax segment 6; pereon segment 4 in tanaidaceans). The male gonopores can be closely paired (neotanaidomorphans and most of tanaidomorphans) or conjoined to a single pore (apseudomor-

phans) (LARSEN et al. 2015). In most (or all) tanaidacean species, these male gonopores are somewhat elevated from the sternite surface. Hence, they are often referred to as genital cones (cf. “Monokonophora” & “Dikonophora”, non-monophyletic groups based on gonopore morphology). The area in which the gonopore/-s should be is perfectly preserved in the described fossil, yet there is no sign of genital openings. This leads to the conclusion that the described specimen was most likely a female.

4.4. Systematic challenges within Tanaidacea

As previously stated by SIEG (1983) and SCHRAM (1986), “Anthracocaridomorpha” SIEG, 1980 is only based on plesiomorphic character states. As a result Anthracocaridomorpha is likely to be a non-monophyletic group. According to the most recent literature, “Anthracocaridomorpha” comprises two ingroups: Anthracocarididae BROOKS, 1962 and Niveotanidae POLZ, 2005 (summarized in SCHRAM et al. 1986; SCHRAM 1989; POLZ 2005; ANDERSON 2017). The latter ingroup, Niveotanidae, is monotypic and monospecific, comprising only the species *brunnensis* POLZ, 2005. Anthracocarididae comprises two species, *scotica* PEACH, 1882 and *rhenanus* MALZAHN, 1957 and might represent a natural group, although this is only supported by the presence of a uniramous uropod.

Formerly, another “group” called Cryptocarididae SIEG, 1980 was attributed to “Anthracocaridomorpha” (SCHRAM et al. 1986; SCHRAM 1989). However, Cryptocarididae is monospecific with *Eucryptocaris asherorum* SCHRAM, 1974 (until 1989 referred to as *Cryptocaris hootchi*) as the only species. With flat, bipartite, biramous uropods (SCHRAM et al. 1986; SCHRAM 1989) the species *asherorum* has a plesiomorphic combination of uropod characters for tanaidaceans (as this combination is also a plesiomorphy in the ground pattern of Peracarida). All species of Anthracocarididae together with the species *brunnensis* POLZ, 2005 already have cylindrical uropods as in extant forms. Only species of Anthracocarididae and some (but not all) extant tanaidaceans have uropods consisting of multiple elements (LARSEN et al. 2015). The stem species (“last common ancestor”) of all extant tanaidaceans can be reconstructed as possessing a pleotelson (at least the sixth pleon segment, post-ocular segment 19, is conjoined with the telson), a character absent in Anthracocarididae and in the species *brunnensis* POLZ, 2005.

In contrast to Tanaidomorpha (and Neotanidae, which may be a tanaidomorphan ingroup) Apseudomorpha is characterized by many plesiomorphic character states (SIEG 1983; LARSEN et al. 2015). One phylogenetic study based on morphological characters even pointed out that Apseudomorpha is likely not monophyletic (SIEWING 1953). It is therefore not surprising that molecular phylo-

genetic studies (DRUMM 2010; KAKUI et al. 2011) do not show Apseudomorpha as a monophyletic group.

SCHRAM (1986) proposed the groups Jurapseudidae SCHRAM, 1986 and Jurapseudoidea SCHRAM, 1986. Jurapseudoidea SCHRAM, 1986 is monotypic (= unnecessary in a rankless systematic framework). Jurapseudidae sensu SCHRAM (1986) comprises three species (*friedericianus* MALZAHN, 1965, *acutirostris* SACHARIEWA-KOWATSCHEWA & BACHMAYER, 1965 and *emersoni* SCHRAM, 1986). The diagnosis of Jurapseudidae (“Body slightly dorsoventrally flattened. Males dikonophoric, with strong chelipedes”, SCHRAM 1986: 134) is problematic since all of the character states in it are also found in extant tanaidaceans, and the combination of the character states is not unique for the three species included in the group.

The species *friedericianus* and *acutirostris* were put in the (genus-ranked) group *Jurapseudes* SCHRAM, 1986 (SCHRAM et al. 1986). The diagnosis for *Jurapseudes* (SCHRAM et al. 1986: 134) only contains characters that are not visible in the holotype of *acutirostris* (MALZAHN in BACHMAYER et al. 1965, pl. 5, fig. 3; pl. 6), which is also the only specimen known from this species. The closer relationship between *friedericianus* and *acutirostris* is solely explained by the (not further explained) similarity in the anterior region of the body (SCHRAM et al. 1986: 137). It is thus highly questionable whether Jurapseudidae and *Jurapseudes* represent natural groups.

The remaining Jurassic tanaidacean species have been placed in monotypic (genus-ranked) groups and can simply be referred to by their species names (without generic name) when discussing the possible affinity to the already described species (e.g., LANHAM 1965). All other non-monotypic tanaidacean groups that are only known from fossils are representatives of Tanaidomorpha (VONK & SCHRAM 2007; SÁNCHEZ-GARCÍA et al. 2015, 2016, 2017; HEARD et al. 2018).

Apart from fossil tanaidaceans that were described as species or attributed to an already described species, there are also fossil occurrences of tanaidaceans without species attribution. There are two Triassic records from the Veszprém region in Hungary. One of the occurrences is purely based on fragmentary remains (chela). Thus, the attribution to Tanaidacea is problematic and has also been discussed as such in the original publication (VÉGH & BACHMAYER in BACHMAYER et al. 1965). The other occurrence (HANNIBAL 2003) is also problematic since the only reference is a conference abstract and no photograph or drawing is available to the time of this study. Further, HANNIBAL (2003) attributed his findings to Neotanidae based on characters of the pleon segments. However, no further explanation is given in this regard and the pleon segments of many neotanaids resemble those of apseudomorphans or (other) tanaidomorphans. Judging from illustrations in the literature, we found no features in the pleon

segments (apart from microstructures) that could be diagnostic for neotanaiids.

There are also tanaidaceans from the Lower Cretaceous of Mexico that have not been formally described yet, but have been reported to occur in a very high abundance (VEGA et al. 2003, 2006a, 2006b). VEGA et al. (2006b) tentatively suggested an affinity to the group *Ophthalmapseudes*. Since *Ophthalmapseudes* is currently monospecific, this interpretation could be understood as an affinity to *rhenanus* MALZAHN, 1957.

4.5. Systematic position of the fossil within Tanaidacea

The fifth pleon segment is the posteriormost preserved element of the herein described fossil. Consequently, we lack information about the uropod morphology and the formation of a pleotelson (whether the sixth pleon segment is conjoined with the telson or not). All modern tanaidaceans have a pleotelson. Consequently, their stem species

(“ancestor”) can also be reconstructed as possessing a pleotelson. Due to the preservation of the here presented fossil, we can draw no conclusion whether the fossil is part of the natural group that derived from the stem species of all modern tanaidaceans. This means that a more basal position in the tanaidacean tree is possible (“Anthracocaridomorpha”).

The laterally protruding tergopleura of the pleon in combination with the (although weakly developed) anterolateral processes on the last pereon segment are only seen in extant apseudomorphans, but never in neotanaiids or (other) tanaidomorphans. Representatives of both latter groups have a rather smooth body surface and lack anterolateral processes on the tergites of the pereon. A possible explanation for reduction of this kind of body armature in tanaidomorphans is that they inhabit self-constructed tubes (BŁAZEWICZ-PASZKOWYCZ et al. 2012).

As mentioned above, transverse rows of setae on the pleon tergites occur in both Apseudomorpha and Tanaidomorpha (including Neotanaiidae). Dense transverse rows on the first pleon segment are characteristic for the apseu-

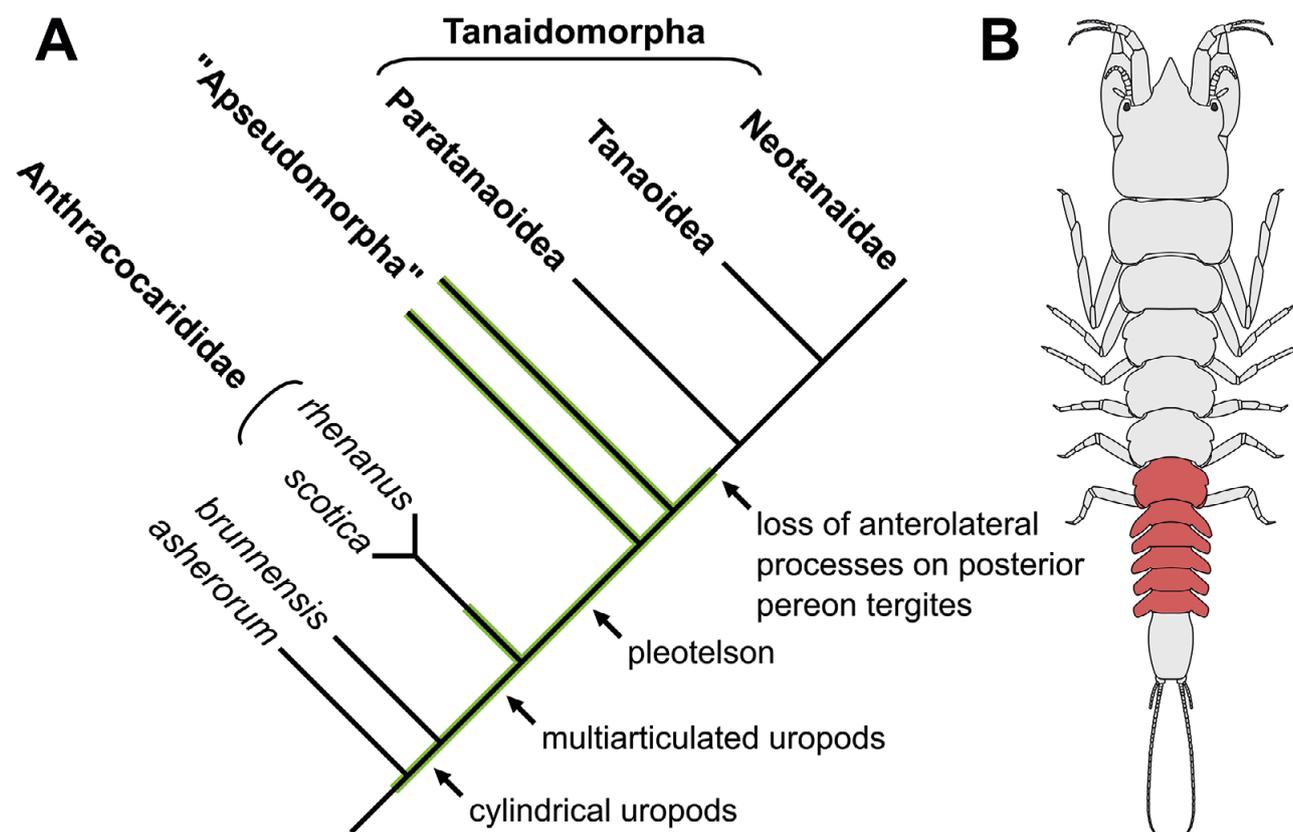


Fig. 8. A: Phylogenetic interpretation of GPIT/NC/07/B/34 based on morphological features (green, possible position within the tree); natural groups in fat letters. Arrows depict the occurrence of derived features. Topology based on KAKUI et al. (2011) (plus independent evaluation of fossil morphology) and nomenclature from ANDERSON (2017); B: Reconstruction of GPIT/NC/07/B/34. Colouration: red, preserved body region; grey, not preserved in the studied specimen.

domorphan group Parapseudini GÜTU, 1981 (= Parapseudinae). Pseudohalmyrapseudes LARSEN & HANSKNECHT, 2004 and Halmyrapseudes BACESCU & GÜTU, 1974 are ingroups of Parapseudini and are both characterised by additional rows of setae on the remainder pleon tergites (GÜTU 2008). Some neotanaid species (e.g., *Carololangua mirabunda* GARDINER, 1975) have rows of setae on the pleon tergites. In *Neotanais pfaffi*, just like in the described fossil, rows of setae on the dorsal side of well-developed tergopleura are present.

Consequently, we find setal rows on the dorsal surface of the pleon to be a problematic character for systematic research on higher groups of tanaidaceans. There is also no clear character for identifying a “row” in this aspect. For example, other non-Parapseudini apseudomorphan have setae on the pleon tergites that are somewhat arranged in rows, with three setae in each “row” (e.g., *Aapseudes quasimodo* BŁĄŻEWICZ-PASZKOWYCZ & BAMBER, 2012). Species descriptions often lack drawings or photographs of tergite structures, making it even more difficult to trace these characters in the literature (see HYŽNÝ & KLOMPMAKER 2015 for a discussion). Further, the disposal of setae in rows could be constrained by the position of nerves beneath the tergites.

The described fossil cannot easily be identified as a representative of a specific monophyletic ingroup of Tanaidacea. However, there are morphological features in the new fossil (anterolateral processes of posterior pereon segments) that allow to exclude some tanaidacean ingroups from the phylogenetic interpretation. This results in a “non-monophyletic” expression of the potential phylogenetic position (Fig. 8). Our phylogenetic interpretation of the here described specimen is:

Tanaidacea nec Tanaidomorpha & Neotanaidae

This expression neglects the presence of monotypic group names such as Neotanaidomorpha or Neotanaoidea. If these groups should become non-monotypic, this expression might have to be modified. Depending on the phylogenetic hypothesis this expression also contains redundant information (Neotanaidae as an ingroup of Tanaidomorpha).

4.6. Species delimitation

With respect to the assumed impermanence of biological species over time, we focus on the Jurassic species for comparison:

Species *quenstedti* REIFF, 1936: *Palaeotanais quenstedti* REIFF, 1936 is the only published fossil tanaidacean in close geographical proximity to the here described fossil (Fig. 1B). Being Early Jurassic in age there is a temporal distance of more than 25 million years between the herein described fossil and the holotype of *quen-*

edti REIFF, 1936. The specimen described herein and the holotype of *quenstedti* REIFF are about equal in size (no scale-bars or well-defined measurements in the figures of REIFF 1936). The type material of *quenstedti* REIFF is said to be lost (SCHRAM et al. 1986). This statement was erroneous (G. SCHWEIGERT, pers. observation 07.03.2019), however, the preservation of the specimen and the patterns of destruction due to pyrite decay as described by REIFF (1936) and ETTER (2004) does not allow further analysis.

Species *brunnensis* POLZ 2005: There is a 10 million years minimal temporal distance between the examined fossil and the type specimens of *Niveotanais brunnesis* POLZ, 2005. Another specimen assigned to *brunnensis* comes from the Middle Jurassic Monte Fallano Formation in Italy, but its preservation (completely compressed) makes comparative studies very difficult. If the Middle Jurassic specimen from Monte Fallano (JONES et al. 2014) is indeed a representative of *brunnensis*, then there is a minimal time distance of 2.1 million years (Fig. 9). The only morphological difference between the herein described fossil and the *brunnensis* specimens is the size. The *brunnensis* type specimens are slightly smaller (2.22 mm vs. 2.63 mm), whereas the Monte Fallano specimen is much smaller (0.83 mm vs. 2.63 mm), when compared to fossil described in this study, in terms of the preserved body region. Although some of the type specimens of *brunnensis* are quite complete, the mode of preservation does not allow for comparison at a very detailed level. For example, punctures in the exoskeleton caused by the former presence of setae cannot be expected to be preserved and visible in the type material of *brunnensis*, due to the calcification of the fossils. Also, only the rough three-dimensional shape of structures can be compared as the *brunnensis* types are moderately compressed. There could be morphological differences between the here described fossil and *brunnensis* that are just not evident from the described material.

Species *gracilis* HEER, 1865: When compared to the type specimen of *Opsipeton gracilis* HEER, 1865, there is an 8.2 million years minimal temporal distance to the herein described fossil (Fig. 9). Morphological differences include: 1) lateral spines on last pereon segment projecting anterolaterally in *gracilis*; 2) distinct furrows on the lateral processes of the pleon tergites of *gracilis* that are not present on the new fossil; 3) the fifth pleon segment that is distinctly longer than the anterior ones in *gracilis*, while in the described fossil the fifth pleon segment is subequal in size to the anterior ones. Curiously, the tergopleura of *gracilis* reminded FRIEDRICH V. HUENE (famous vertebrate palaeontologist from Tübingen) of lateral processes of vertebrae. This led to the erroneous description of the “urodelan” *Boomgaardia salamandriformis*, later recognized as a specimen of *gracilis* (SCHWEIGERT & ETTER 2008).

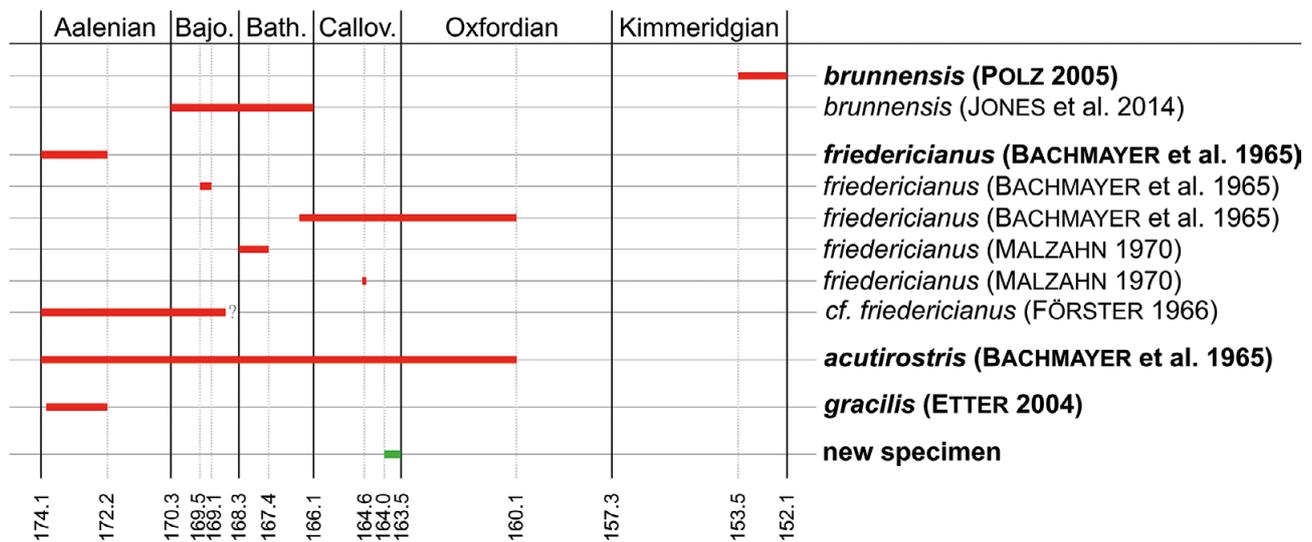


Fig. 9. Temporal occurrences of Middle and Late Jurassic tanaidaceans based on literature information. The depicted time-spans (horizontal red and green lines) do not refer to the longevity of the species but to the temporal uncertainty of each occurrence. Different occurrences of the same species are depicted separately. The question mark accentuates an undefined geological timespan (in this case: “Lower Dogger”). Abbreviations: Bajo, Bajocian; Bath, Bathonian; Callov., Callovian.

Species *acutirostris* SACHARIEWA-KOWATSCHWA & BACHMAYER, 1965: When compared to *Jurapseudes acutirostris* SACHARIEWA-KOWATSCHWA & BACHMAYER, 1965, there is no minimal temporal distance to the described fossil, as the geological reference of the types of *acutirostris* is very unprecise (Fig. 9). The holotype of *acutirostris* (which is also the only fossil ascribed to this species) suggests that *acutirostris* was much larger than the animal that produced the herein described fossil remain. Although there is no overlap regarding the preserved body regions for the two fossils this can be roughly reconstructed. The cephalothoracic region in *acutirostris* is 6 mm long, whereas the herein described fossil has a total length of only 2.6 mm. As the cephalothoracic region in tanaidaceans is (usually?) no longer than the combined lengths of the pleon and last pereon segment, we can estimate that *acutirostris* was by far larger than the fossil described in this study. However, the reasons for the size difference could also be attributed to ontogeny or sexual dimorphism/polymorphism (e.g., SIEG 1983: 151, fig. 7C). Other morphological comparisons are not possible because only the anterior part of the *acutirostris* body is preserved in the holotype, meaning that there is no overlap with the described fossil.

Species *friedericianus* MALZAHN, 1965: Between the type specimens of *Jurapseudes friedericianus* and the examined fossil the minimal temporal distance is of 8.2 million years, but again, if other occurrences are included the minimal temporal distance is eliminated (Fig. 9). The holotype of *friedericianus* MALZAHN, 1965

is an arbitrary composite of three isolated remains of tanaidaceans from the same geological context. According to MALZAHN (1965), the size of these pieces together is 1.2 mm (anterior rim of head to telson). Just as the specimen described in this study, some type specimens of *friedericianus* also show rows of indents (setae insertion points) on the tergopleura of the pleon segments. Differences in morphologies between *friedericianus* MALZAHN, 1965 and the examined fossil include: 1) the shape of the anterolateral processes on the last pereon segment, which are distinctly spine shaped in *friedericianus* but rather blunt in the described fossil; 2) the hyposphaenia in *friedericianus* are more distinctly developed than in the herein examined fossil. The relative length of the pleon segments compared to the pereon segments in *friedericianus* is given as one third of the length of the pereon segment. However, there are depicted type specimens (MALZAHN in BACHMAYER et al. 1965) that are clearly in conflict to this description (MALZAHN in BACHMAYER et al. 1965, pl. 2, fig. 6). Overall, some pleon-region type specimens differ distinctly from the corresponding holotype fragments (cf. MALZAHN in BACHMAYER et al. 1965, pl. 1, fig. 3; pl. 2, fig. 6). Considering the amount and stratigraphical distribution of non-type specimens (7.6 million year minimal time range for the species) and the discussion above, the validity of *friedericianus* MALZAHN, 1965 as a natural species is questionable.

All Middle Jurassic species come from Central or Southeastern Europe (Fig. 1). Thus, (palaeo-)geographical aspects cannot be used to support species delimitation.

Due to the different preservation of comparable fossils and potential sexual dimorphism, a conspecificity with one (or more) described Middle Jurassic species (*acutirostris*, *friedericianus*, *brunnensis*, and *gracilis*) cannot be excluded. It is not unlikely that the fossil belongs to a new species that has not yet been described. However, we refrain from formally describing a new species based on the new specimen. This is especially with respect to the fragmentary preservation of the specimen, which would result in a holotype that is difficult to compare to future findings.

Due to the morphological similarity to some published specimens of *friedericianus* MALZAHN, 1965 (MALZAHN in BACHMAYER et al. 1965, table 2, fig. 6; MALZAHN 1970, table 1, fig. 4) the specimen is suggested to be referred to as:

cf. *friedericianus* MALZAHN, 1965

The prefix “cf.” should not be understood as a final taxonomic statement, but rather as a call for further comparative studies. Many more, well-dated, additional specimens could be available in micropalaeontological samples in museum collections. Also, less destructive fieldwork (compared to sieving) could deliver more complete three-dimensionally preserved tanaidacean fossils from non-amber sites.

4.7. Taphonomy

The type of preservation seen in the described fossil seems to be rather common for three-dimensionally preserved specimens that were retrieved by sieving. This type of preservation (connected pleon segments with or without some thoracic segments and pleotelson attached) is found in many fossil tanaidaceans (BACHMAYER et al. 1965, pl. 1, fig. 3; pl. 2, figs. 6, 7; GLAESSNER & MALZAHN 1962, pl. 2, figs. 6–13; pl. 3, figs. 1, 2, 5, 6, 10, 11; pl. 4, figs. 2, 3; MALZAHN 1970, pl. 1, figs. 2, 4; MALZAHN 1979, pl. 1, figs. 6–9; SCHRAM et al. 1986, figs. 7B, 8C, D, 10C, D). This is most likely not only a result of the preservation potential of this specific body area, but also the result of the mechanical and chemical stress during the sieving process.

As all known tanaidaceans share a benthic lifestyle and many species live infaunal, they inhabit an environment that is prone to bioturbation or they contribute to bioturbation themselves. Bioturbation is one of the main driving forces that prevent fossilization by oxygenating deeper layers of sediments. ETTER (2004) suggested a stable dysoxic (low-oxygen level), but not anoxic environment for the preservation of three-dimensionally preserved tanaidaceans, as higher oxygen levels favour bioturbation. Permanently or temporary lower (anoxic) conditions would

not allow for tanaidaceans to live in a benthic environment. The upper part of the Ornatenton Formation, where the here presented fossil was found, is characterised by bioturbated mudstones with a relatively low diversity of benthic life (mainly nuculid bivalves and solitary corals; G. SCHWEIGERT, pers. comm.). With respect to lithology and paleoecology, the presence of tanaidaceans within the Ornatenton Formation fits well into model predicted by ETTER (2004), that the preservation of tanaidaceans as fossils is dependent on dysoxic benthic oxygen levels.

All fossil tanaidomorph species (according to GÜTU 2004, *Cretitanais giganteus* is not a tanaidomorph) have been found in amber. Yet, only one apseudomorph species has been recorded from amber deposits. This record differs from the known fossil apseudomorphs as it is less than one millimetre in total length and probably represents non-adult animal (HEARD et al. 2018). There may be multiple reasons for this systematic-taphonomic distribution of tanaidaceans in the fossil record. Most geologically younger Lagerstätten yielding tanaidaceans are amber deposits. This is surely not linked to the geological age only, as for example, the youngest fossil occurrence of tanaidaceans is an apseudomorph from a non-amber Lagerstätte (QUAYLE 2016). Also, taphonomical aspects could have triggered this distribution.

5. Conclusions

Despite the fragmentary nature of the single specimen described here, we can draw the following general conclusions:

- The presence of distinct rows of setae in tanaidaceans on the pleon tergites, and the corresponding tergopleura, can now be dated to a Middle Jurassic age (ca. 160 million years ago).
- The new fossil is most likely a representative of Tanaidacea, but not of the tanaidacean ingroup Tanaidomorpha.
- An analysis of the morphospace of various malacostracan groups helped to substantiate the interpretation as a tanaidacean, despite the absence of relevant apomorphic character states preserved in the fossil.
- Many more tanaidacean fossils should be available by new fieldwork or the study of previously collected fossils or sediment samples. Well-documented, more complete specimens could especially advance the scientific progress in systematic research on this group. Due to their special ecological role, tanaidaceans could also serve as important facies indicators.

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List of supplementary electronic files

Suppl. 1: Rotation model dorsal.

Suppl. 2: Rotation model ventral.

Suppl. 3: Graphical representation of the ratios used for the principal component analysis.

Suppl. 4: Spreadsheet file containing the measurements and the calculation of the ratios used in the PCA analysis.

Suppl. 5: Supplementary references (corresponding to the references in Suppl. 4).

Suppl. 6: R script (Principal component analysis).

Suppl. 7: Additional information on the principal component analysis (PCA). **A:** proportion of overall-variance explained by each principal component (PC) for the unscaled PCA; **B:** proportion of overall-variance explained by each principal component (PC) for the scaled PCA; **C:** proportional contribution of each ratio to PC1 and PC2 combined for the unscaled PCA; **D:** proportional contribution of each ratio to PC1 and PC2 combined for the scaled PCA.