

# The largest fossil tanaidacean is not a tanaidacean – *Cretitanais giganteus* (Malzahn, 1979) is a junior synonym of *Urda stemmerbergensis* (Malzahn, 1968)

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Tanaidacea and Isopoda are relatively closely related groups of crustaceans. Representatives of both groups can have a quite similar appearance. Extant species of Tanaidacea differ from isopods by their chelipeds, which are appendages with distinctive, often large, chelae. Also, their head is fused with the cheliped-bearing trunk segment and both are covered by a sclerotized shield (carapace). A single fossil from the Lower Cretaceous of Germany – *Cretitanais giganteus* (Malzahn, 1979) – has received much attention in discussions about the fossil record of Tanaidacea and was often described as morphologically aberrant. A  $\mu$ CT scan of a resin cast of the *C. giganteus* holotype was acquired and a high-resolution surface model was constructed. The morphological reinterpretation revealed that, previously, crucial morphological features have been overlooked and misinterpreted. Unlike all known extant tanaidaceans and unlike previously described tanaidacean fossils, *C. giganteus* has not six, but seven pereon tergites and the alleged chela is a merus of a further posterior leg. From this, it is apparent that the fossil is not of a tanaidacean. Instead, the fossil shows a stark resemblance to species of *Urda* Münster, 1840 and is herein interpreted as conspecific with *Urda stemmerbergensis* (Malzahn, 1968), known from the same locality and stratum, making *Cretitanais giganteus* a junior synonym of it.

Cretaceous | Tanaidacea | Isopoda | Scutocoxifera | conspecificity | 3D model

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## Introduction

Tanaidacea is a group of mainly small, benthic peracarid crustaceans with ca. 1600 recognized extant species (Blazewicz-Paszkowycz *et al.*, 2012; WoRMS, 2025). Their body size rarely exceeds 2 mm in length, with the notable exception of the deep-sea species *Gigantapseudes maximus* Gamô, 1984, which measures up to 75 mm in length (Gamô, 1984; Kakui and Fujiwara, 2020). The true number of extant species is likely to be much higher, as the group appears to be massively understudied (Blazewicz-Paszkowycz *et al.*, 2012). Recent phylogenetic studies support the monophyly of Tanaidacea and recover it as the sister group of a clade comprising the sister taxa Isopoda and Cumacea (Kakui *et al.*, 2021; Barta *et al.*, 2025).

Tanaidaceans are usually easily recognizable as such through several aspects of their outer morphology. Their body consists of four tagmata: (1) cephalothorax (post-ocular segments 1–7), encompassed by a sclerotized shield (carapace) with lateral respiratory chambers; (2) pereon (post-ocular segments 8–13), with pereopods (walking appendages); (3) pleon (post-ocular segments 14–18), (usually) with biramous pleopods (some species lack them); (4) pleotelson (post-ocular segment 19 and telson), with (usually biramous) uropods, uropod rami (endo- and exopods) usually multi-articulate (Larsen *et al.*, 2015). The probably most remarkable morphological feature, which sets tanaidaceans apart from their close relatives, is the cheliped (leg of post-ocular segment 7), which, as the name suggests, bears a chela (consisting of propodus and dactylus, sometimes expressed as a subchela) (Larsen *et al.*, 2015). Even in the absence of the characteristic cheliped – such as in some fossils – tanaidaceans can easily be distinguished from isopods, as the carapace-covered cephalothorax is rarely reminiscent of an isopod head. Furthermore, usually, isopods have seven ‘free’

pereon segments (trunk segments not conjoined with head, not encompassed by carapace, and not part of pleon), whereas the pereon of tanaidaceans consists of six segments (Kakui, 2024). However, it should be noted that in Gnathiidae, convergently, the leg of post-ocular segment 7 is conjoined with the head and lacks a ‘free’ tergite (Wilson *et al.*, 2011).

The fossil record of Tanaidacea is rather poor when seen in contrast to the number of extant species (Kakui, 2024) and, like for the extant fauna, appears to be far from being exhaustively discovered, which is reflected by a growing number of species descriptions, especially from amber (e.g. Sánchez-García *et al.*, 2016; Pazinato *et al.*, 2016; Heard *et al.*, 2018; Pazinato *et al.*, 2023), but also from sedimentary deposits (e.g. Heard *et al.*, 2020; Pasini *et al.*, 2022; Wallaard, 2025) – for a recent review of the fossil fauna see Kakui (2024). Among the described extinct species, there is one species, which, compared to others, and despite its relatively young geological age, received disproportionately much attention: *Cretitanais giganteus* (Malzahn, 1979).

*Cretitanais giganteus* was described by Malzahn (1979) based on multiple specimens that were retrieved by sieving Lower Hauterivian (Lower Cretaceous) clay from a brickyard clay pit near the airport of Langenhagen (Hannover, Germany). In this publication Malzahn described the specimens, which varied tremendously

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in size and were not morphologically consistent with each other, as both *Apseudes giganteus* and *Ophthalmapseudes giganteus* (names used interchangeably throughout the publication). Malzahn designated the largest and most complete specimen of the sample (NHM 1978/1997/1) as the holotype. *Apseudes* is an extant group with more than 200 recognized species (WoRMS, 2025), while *Ophthalmapseudes* is the generic name of a much older, Upper Permian, fossil *Ophthalmapseudes rhenanus* (Malzahn, 1957) (Glaessner and Malzahn, 1962). Soon after, a second specimen (NHM 1979/2057) was published as belonging to *Apseudes giganteus*, which matched the holotype in size (Malzahn and Pockrandt, 1982). The confusing taxonomic situation was later resolved by Schram, Sieg and Malzahn (1986), where only the holotype and the later published specimen (Malzahn and Pockrandt, 1982) were interpreted as conspecific and the generic name was changed to *Cretitanais*, as the fossil appeared not to be closely related to species of *Apseudes* nor with *Ophthalmapseudes rhenanus*. The smaller specimens from the original description (Malzahn, 1979) were described as a separate species, *Carlclausius emersoni* Schram, Sieg and Malzahn, 1986. In this publication, *Cretitanais giganteus* was interpreted as belonging to the major tanaidacean group Tanaidomorpha Sieg, 1980. This interpretation was later challenged by Guțu (2004), who interpreted *Cretitanais giganteus* as belonging to Apseudomorpha Sieg, 1980 – one of two major tanaidacean groups. Owing to this publication, *Cretitanais giganteus* is currently recognized as an apseudomorphan species, not closely related to any extant species, reflected taxonomically by being contained in the monotypic taxa Cretitanaoidea and Cretitanaidae (Heard *et al.*, 2020; Kakui, 2024).

With about 45 mm in length, *Cretitanais giganteus*, as its name hints, is extraordinarily large for a tanaidacean. While there is one extant species that is considerably larger than *Cretitanais giganteus* (*Gigantapseudes maximus* with up to 75 mm in length (Gamô, 1984; Kakui and Fujiwara, 2020)), most extant species are much smaller and usually do not exceed 2 mm in length and the other tanaidacean fossils are also much smaller than the herein discussed fossil (Heard *et al.*, 2020, fig. 6). Heard *et al.* (2020, p.24) expressed some doubts about the phylogenetic affinity of *Cretitanais giganteus*, stating that owing to its “atypical body form” it “may represent a relict clade with non-apseudomorphan progenitors”.

With only a resin cast of the holotype available, it is certainly not possible to provide a comprehensive morphological analysis, which would require a re-examination of the holotype (Malzahn, 1979) and the additional material (Malzahn and Pockrandt, 1982) – all of which is deposited in the collection of the Natural History Museum of Vienna (Geological Palaeontological collection). Instead, the goal of this contribution is to show that *Cretitanais giganteus* is not a tanaidacean, but an isopod of the known species *Urda stemmerbergensis* (Malzahn, 1968) (Malzahn, 1968; Schädel *et al.*, 2023). This report should prevent further discussion of these fossil specimens in the context of the evolutionary history of Tanaidacea, where they otherwise would continue to obstruct the study of the fossil record of the group.

## Materials and methods

The herein described resin cast was imaged using a Bruker SkyScan 1273  $\mu$ CT scanner (Bruker Corporation, Billerica, Massachusetts, USA) at the palaeoanthropology lab at the University of Tübingen. A voltage of 60 kV and a current of 114  $\mu$ A were applied to the source. No filter was used between source and sample (not ideal in

hindsight). The cast was rotated by 206.1° in steps of 0.09° at a distance of 100.8 mm from the source (spot size set to ‘small’) and at a distance of 401.9 mm from the sensor (pixel size 74.800  $\mu$ m). The exposure time was set to 400 ms and neither binning nor frame averaging was applied.

The resulting 16-bit projection images were then processed into a volumetric 3D image using Bruker NRecon v. 2.2.0.6 (proprietary, bundled with scanner). The resulting 16-bit volume had a voxel size of 15.0  $\mu$ m. It was converted into 8-bit format using ImageJ (public domain software, Schneider *et al.* 2012).

Selected slices of the volume were segmented using 3D Slicer (www.slicer.org, extended BSD-style license, Fedorov *et al.* 2012), using the global threshold and level tracing tool in conjunction with the logical operations tool. These semi-manual segmentations were then used to produce a machine-learning segmentation prediction using the smart interpolation tool in Biomedisa (https://biomedisa.in fo/, European Union Public License v. 1.2, Lösel *et al.* 2020) via the Biomedisa extension for 3D Slicer (https://github.com/biomedisa/b iomedisa). This was done to achieve a high-fidelity surface model, which would not work by applying a simple threshold segmentation, mainly due to parts of the cast being in the non-optimal uppermost and lowermost zones of the projection images (partial volume effect), but also due to strongly attenuating small particles within the resin – likely white titanium dioxide (TiO<sub>2</sub>) pigment clots – which caused small-scale ‘starburst’ artefacts (photon starvation) (Barrett and Keat, 2004). After segmentation a 7-by-7-pixel hole filling was performed before the segmentation was exported as a mesh and decimated (edge-collapsing) in Blender (https://www.blender.org, GPL v.2 license) to reduce the file size and memory requirements (no visible decrease in resolution). The surface model is available at 10.5281/zenodo.18097516 under the CC BY-SA 4.0 license.

The mesh was rendered in Blender using the Cycles render engine (ray-trace rendering). The rendered images were adjusted for brightness and contrast in GIMP (https://www.gimp.org/, GPL v.3 license). The drawings and the figure plate design were achieved using Inkscape (https://inkscape.org, GPL v.2 license).

## Results

**Isopoda** Latreille, 1817

**Scutocoxifera** Dreyer & Wägele, 2002

**Anthuridea** Monod, 1922

Remarks. A close relationship between Anthuroidea and Gnathiidae has long been suspected (e.g. Monod, 1922, p.139) on morphological grounds, but has recently been confirmed by a molecular phylogenetic study Thomas Thorpe (2024). A sistergroup or stem-to-crown group relationship between the extinct *Urda* species and Gnathiidae has been shown through comparative morphology Schädel *et al.* (2023). Prior to the publication of Brandt and Poore’s classification 2003, the term Anthuridea has been used for the group that is now referred to as Anthuroidea and has since then fallen out of use. The name Anthuridea is reused here to provide a name for the group that comprises Anthuroidea Leach, 1814, Gnathiidae Leach, 1814 and *Urda* Münster, 1840.

**Urda** Münster, 1840

urn:lsid:zoobank.org:act:A49F2904-5BB7-4EDE-963E-6838F89BA358

1842 *Urda*; zu Münster, p. 21, pl. 1, figs. 2–5

1842 *Reckur*; zu Münster, p. 77, pl. 9, fig. 10

1936 *Palaega*; Reiff, p. 51, p. 67, figs. 1–11, pl. 1–2

1889 *Palaega*; Carter, p. 195, pl. 6 figs. 1–7  
 1968 *Palaega?*; Malzahn, p. 828, pl. 58 figs. 1–2, 4–5  
 1986 *Cretitanais*; Schram, Sieg and Malzahn, p. 139, figs. 9–10;  
**syn. nov.**

***Urda stemmerbergensis*** (Malzahn, 1968)

urn:lsid:zoobank.org:act:41A17936-54FA-4489-BF3E-  
 CB58CB89E242

Figs. 1–2

1968 *Palaega? stemmerbergensis*; Malzahn, p. 828, pl. 58 figs.  
 1–2, 4–5  
 1979 *Ophthalmapseudes giganteus*; Malzahn, p. 70, pl. 1 figs. 1–5,  
 pl. 2 figs. 1–2; **syn. nov.**  
 1979 *Apseudes giganteus*; Malzahn, p. 67; **syn. nov.**  
 1982 *Apseudes* “nov. spec.”[sic]; Malzahn and Pockrandt, p. 58, pl.  
 1 figs. 1–7; **syn. nov.**  
 1986 *Cretitanais giganteus*; Schram, Sieg and Malzahn, p. 140,  
 figs. 9–10; **syn. nov.**  
 2023 *Urda stemmerbergensis*; Schädel, Nagler and Hyžný, p. 45

Type material. Holotype considered lost, no additional type material available (C. Heunisch, 2019, pers. comm.). Holotype retrieved from a drill core (Bohrung Stemmerberg 7, drill core number 493), west of Hannover, near Göxe (Barsinghausen), Lower Saxony, Germany, WGS84 coordinates 52.348669 9.565344, Lower Hauterivian, *Endemoceras noricum* ammonite biostratigraphic zone.

Studied material. Cast of the *Cretitanais giganteus* holotype NHM 1978/1997/1. Original from clay quarry Engelbostel (Langenhagen), Hannover region, Lower Saxony, Germany, WGS84 coordinates 52.463467 9.662451. Clay ironstone concretion, Lower Hauterivian, boundary between *Endemoceras noricum* and *Endemoceras amblygonium* ammonite biostratigraphic zones.

Additional material. NHM 1979/2057, fragmentary remain preserved in a concretion. One end of the specimen has been physically ground to a level plane to obtain a cross section photograph. In this specimen Malzahn and Pockrandt (1982) identified the cephalothorax, which they described as both remarkably short and fragmentary (not consistent with the holotype). What they identified as the head is likely a poorly preserved tergite of the pereon. In close proximity to the grinding surface there appears to be a short tergite (possibly pereonite 1). In terms of size and shape of the tergites, the specimen matches the holotype.

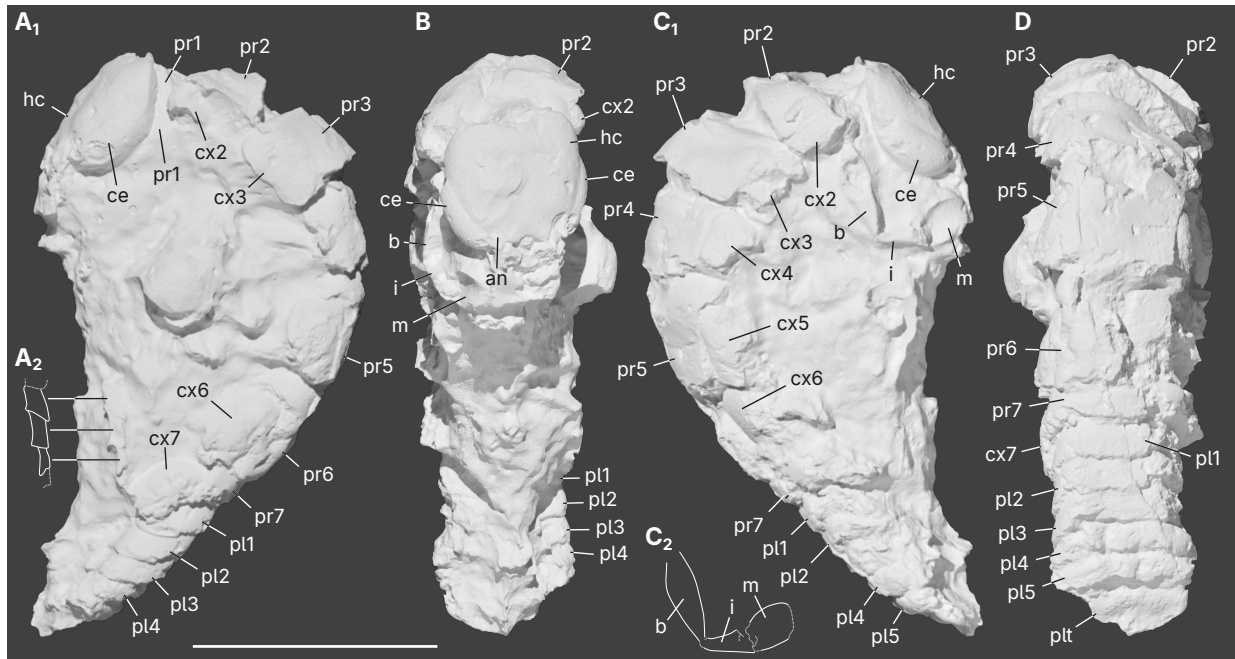
Description of NHM 1978/1997/1. Body slender, much longer than wide. Body consisting of four distinct tagmata along long axis: head (post-ocular segments 1–6), pereon (post-ocular segments 7–13), pleon (post-ocular segments 14–18) and pleotelson (post-ocular segment 19). All tagmata of about equal width in dorsal view (Figure 1B,D).

Head large, dorsoventrally flattened (Figures 1C, 2B), not concealed by subsequent tergites, about as wide as long (Figure 2A). Compound eyes large, located on the lateral sides of the head, stadium-shaped, with semicircular anterior and posterior sides and almost straight dorsal and ventral sides, surface distinctly convex, protruding from head capsule in dorsal view. Anterior margin of compound eye almost meeting the anterior margin of the head, posterior margin well separated from posterior side of head, posterior margin at about two thirds of the length of the head, not extending to the ventral side of the head (Figure 2B). Anterior

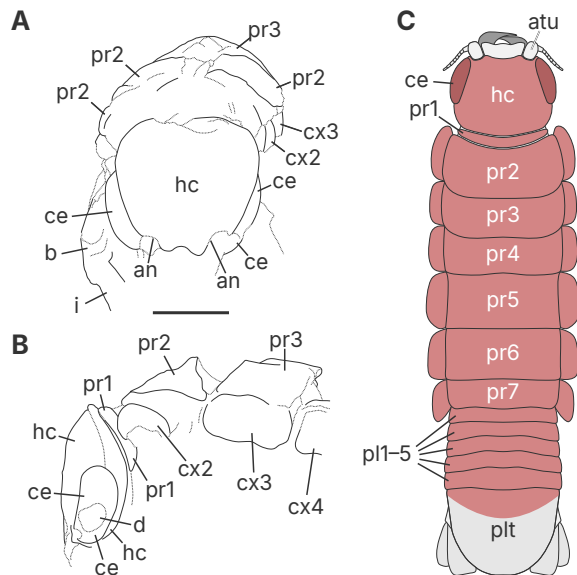
margin of head wide, central part with shallow rounded concavity, deep lateral rounded incisions (antennular notches, occupied by the here-not-apparent first element of the antenna; Figures 1B, 2A). Posterior margin of head in dorsal view about straight or slightly convex (Figures 1A, 2A). Posterior margin of head in lateral view straight and angled towards dorsal surface of head at ca. 45° (Figure 1C).

Pereon with seven segments with separated tergites (pereonites). Pereonite 1 conspicuously short, not as wide as head, anterior margin evenly shallow concave, lateral corners rounded, posterior margin convex, about parallel to anterior margin. Note that in the fossil this tergite is not in its anatomical position, but displaced towards the left body side. Pereonite 2 considerably longer than preceding tergite, anterior margin distinctly concave and evenly rounded, posterior margin about straight in dorsal view, overall much wider than long, length along midline little more than half the length at lateral sides. Coxal plate 2 separated from tergite by straight deep suture/joint, about as long as tergite, at least half as wide as long. Remain of pereopod (presumably pereopod 2) on right body side of fossil. Proximal-most visible element (presumably basis) much longer than wide, widest in the central part. Second element (presumably ischium) less than half the length of first element, increasing in width towards distal end. Third and distal-most visible element apparent from evenly concave mould distad of second element, much wider than preceding element, one side about straight, other side convex. Distal-most element previously interpreted as the chela (Malzahn, 1979), except for its relatively large size, no indication of a chela-like morphology. Pereonite 3 similar in dimension to preceding tergite, also similar in shape except for about straight anterior margin. Coxal plate 3 as long as corresponding tergite, anterior and posterior margins seemingly rounded, ventral margin with a central concavity, about twice as long as wide (Figure 1A). Pereonite 4 similar to preceding tergite in dimensions and shape. Coxal plate 4 similar to preceding coxal plate, also seemingly with concave lateral margin, anterior margin possibly more straight/less rounded. Pereonite 5 similar in shape to preceding tergite, possibly slightly longer. Coxal plate 5 with straight anterior margin, rounded convex lateral margin, likely with rounded postero-lateral corner (poorly preserved). Pereonite 6 poorly preserved, seemingly similar in dimensions to preceding tergite. Coxal plate 6 with rounded anterior margin, seemingly increasing in width posteriorly, posterior margin poorly preserved, possibly slightly angled in posterior direction. Remain of pereopod 5 or 6 on left body side, presumably merus, carpus and propodus of left pereopod 6; proximal-most visible element elongate, relatively broad, seemingly somewhat flattened; second visible element shorter than preceding element, slightly narrower than preceding element, seemingly flattened; third visible element considerably narrower than preceding element, same length or slightly longer than preceding element, seemingly flattened. Pereonite 7 much shorter than preceding tergite, about one third of length of pereonite 6, lateral aspects bent towards lateral sides (broad u-shaped cross section), posterolateral corner further posterior than posterior-most point along midline, posterior margin straight in central part, concave at lateral sides. Coxal plate 7 similar in shape to preceding coxal plate, overall slightly smaller, lateral margin evenly rounded convex, distinct groove from centre of median side towards posterolateral corner.

Pleon of about same width as pereon, all five tergites very similar in shape and size, of about same length as pereonite 7, lateral aspects bent by ca. 180° towards ventral side, anterolateral



**Figure 1.** *Urda stemmerbergensis* Schädel, Nagler and Hyžný, 2023, surface model of the cast of NHM 1978/1997/1, holotype of the herein synonymised *Cretitanais giganteus*. Light from top/top-left, same scale, 10 mm. **A<sub>1</sub>**, Left body side, lateral view; **A<sub>2</sub>**, Pereopod, same view as **A<sub>1</sub>**; **B**, Head (dorsal view) and pleon (ventral view); **C<sub>1</sub>**, Right body side, lateral view; **C<sub>2</sub>**, Right pereopod, likely of pereon segment 2, same view as **C<sub>1</sub>**; **D**, Pereon and pleon, dorsal view. Abbreviations: **an**, antennular notch; **b**, basis; **ce**, compound eye; **cx2-7**, coxal plates 2-7; **hc**, head capsule; **i**, ischium; **m**, merus; **pr1-7**, pereonites 1-7; **pl1-5**, pleonites 1-5; **plt**, pleotelson;



**Figure 2.** *Urda stemmerbergensis* Schädel, Nagler and Hyžný, 2023. **A,B**, drawings based on the cast of NHM 1978/1997/1, holotype of the herein synonymised *Cretitanais giganteus*, same scale, 3 mm; **A**, Head (dorsal view) and anterior-most pereon segments (frontal view), anterior side of head facing bottom of figure; **B**, Left body side, restricted to the head and the anterior-most pereon segments, lateral view; **C**, Reconstruction of *Urda stemmerbergensis* with body parts preserved in the *Cretitanais giganteus* holotype (and apparent from the cast) marked in red. Abbreviations: **an**, antennular notch; **atu**, antennula; **b**, basis; **ce**, compound eye; **cx2-4**, coxal plates 2-4; **d**, damaged part of compound eye; **hc**, head capsule; **i**, ischium; **pr1-7**, pereonites 1-7; **pl1-5**, pleonites 1-5; **plt**, pleotelson.

margins not apparent from cast (likely rounded), lateral margins not fully apparent from cast (likely straight), posterior margin straight in central part, concave towards lateral sides, convex at lateral-most point (at ca. 90° of the bend), concave towards postero-lateral corner (on ventral side), postero-lateral corner not fully apparent from cast (likely pointed) (Figure 1A, B).

Pleotelson poorly preserved, only anterior margin and anterior-most part of right lateral margin preserved, width at anterior side slightly lesser than width of pereonite 5.

## Discussion

### Non-affinity with Tanaidacea

The fossil of the herein presented cast of NHM 1978/1997/1 (Figures 1,2) was attributed to Tanaidacea despite lacking a preserved chela, which is arguably the most distinctive feature of a tanaidacean. A large well-developed chela separates tanaidaceans from other closely related groups that can be somewhat reminiscent in other aspects of the general appearance (Ax, 2000).

The main reason why the herein discussed fossil was attributed to Tanaidacea despite the lack of apparent chelae is likely its slender body and presence of six 'free' (separated and dorsally visible) pereon tergites. From the perspective of isopods, this means the absence of a seventh tergite. While tanaidaceans typically have a slender body and many representatives of related peracaridean groups have drastically different body shapes, slender bodies occur in several peracaridean lineages outside of Tanaidacea Barta *et al.* (2025), occur in various ingroups of Isopoda and might even be part of the isopod ground pattern Poore and Bruce (2012); Thomas Thorpe (2024).

In Tanaidaceans, the seventh post-ocular segment is part of the cephalothorax and does not possess a dorsally visible tergite,

but is covered by the carapace (e.g. Larsen *et al.*, 2015). In most isopods the first pereon tergite is well developed and of similar size to the subsequent ones (e.g. Wetzer *et al.*, 2000). There are, however, exceptions to this rule. In adult representatives of Gnathiidae post-ocular segment seven is at least functionally incorporated into the head (e.g. Ota, 2014, figs. 1,5,3,8,10), whilst in the larvae the tergite is short, but usually still moveable relative to the head (Wilson *et al.*, 2011, figs. 1,2,6). This condition clearly represents a convergence between Gnathiidae and Tanaidacea. On the NHM 1978/1997/1 cast, a short tergite is visible on the left body side. It is displaced from its original position. It neatly fills the gap between the almost straight posterior margin of the head and the deeply concave anterior margin of the second pereon segment. The presence of this previously not recognized tergite undermines the foundation on which the interpretation of the fossil as a tanaidacean resides.

Two legs are preserved and visible on the cast of NHM 1978/1997/1 (Figure 1A<sub>2</sub>, C<sub>2</sub>). While the more posterior leg appears not to be very characteristic, the more anterior leg shows an interesting morphology. In the original description Malzahn (1979) described the more posterior leg on the right body side near the head as a cheliped. However, the chela – the defining feature of the cheliped – was described as partially preserved and lacking its main part. On the cast (Figures 1C, 2B) and in the photographs (Malzahn, 1979, pl. 1, figs. 1,4) of specimen NHM 1978/1997/1 this structure can be easily identified. Two large leg elements and a concave mould of a large third leg element are identifiable on the surface of the fossil. The two positively preserved elements are herein interpreted as the basis and the ischium. Unlike in isopods, in tanaidaceans the ischium is usually absent in the cheliped, while in the pereopods it is usually short and only absent in some lineages (Larsen *et al.*, 2015, figs. 59.7, 59.8, 59.9). If a tanaidacean body plan is assumed, one could therefore argue that the second element is missing or not apparent on the cast and that the second discernible leg element does not represent the ischium. Nevertheless, even then, the morphology seen in NHM 1978/1997/1 is still inconsistent with the previous interpretations of this structure, where it has been identified as the propodus-part of the chela Malzahn (1979); Schram *et al.* (1986). In order to interpret the massive, negatively preserved leg element as the propodus, one would need to argue that the second leg element is either the merus or the carpus and that yet another leg element – either the merus or the carpus – is reduced or too short to be discernible on the cast.

Apart from the lack of a preserved chela, another aspect of this leg should have cast doubt on its interpretation as a cheliped. The elongated proximal leg element seems to originate either from pereon segment 2 – not from what is here described as the head and what was originally described as the carapace. At the moment, its exact segment affinity cannot be determined. This would require a  $\mu$ CT scan of the fossil from which the cast has been made. However, it is clear that if it were a tanaidacean cheliped, the origin of the leg should have been more anterior. Alternatively, a taphonomic dislocation would need to be assumed, which would represent an auxiliary hypothesis that is not necessary if the leg is interpreted as a pereopod.

Heard *et al.* (2020) correctly identified the semicircular incisions on the anterior margin of the dorsal side of the head as antennular notches, as they also occur in Tanaidacea. Prior to this, they have been identified as eye sockets (Gutu, 2004). The probably most crucial misunderstanding present in the literature on this fossil is that

the large compound eyes have been mistaken for “inflated” regions of the cephalothorax (Malzahn, 1979), later termed “branchiostegal portion[s] of [the] carapace” (Schram *et al.*, 1986; Heard *et al.*, 2020). Assuming the fossil was a tanaidacean, it is unlikely that these parts of the fossil would represent inflated areas associated with respiration, because in tanaidaceans the branchial chambers are located in the posterior part of the cephalothorax (Heard *et al.*, 2003, fig. 4). Unlike in tanaidaceans, where large compound eyes are rare and usually limited to the anterior-most part of the cephalothorax, in isopods large eyes are not uncommon, especially in species which actively swim and/or are parasites of fish.

In NHM 1978/1997/1 there are sclerotized plates lateral to the tergites of the pereon, except for the first pereonite. These are herein interpreted as coxal plates a structure that evolved within Isopoda (for phylogenetic implications see discussion below). Similar structures can be found in tanaidaceans where they are referred to as “pleurites” (Schram *et al.*, 1986, p.139) or “pleurae” (Gutu, 2004), which occur in the tanaidacean ingroup Apseudomorpha (Gutu, 2004). However, the sclerites visible in the fossil are separated from the tergite not only by a shallow groove like in the case of apseudomorphan pereonites (e.g. see figures in Błażewicz-Paszkowycz and Bamber, 2007, 2012), but appear to be separated more profoundly – so much so that at pereon segment 2 the left coxal plate has separated from the tergite (Figures 1A, 2B). Also, in Apseudomorpha the pleurites are often expressed more pronouncedly in the anterior pereon segments (e.g. see figures in Błażewicz-Paszkowycz and Bamber, 2007, 2012), while in the herein discussed fossil the coxal plates are well separated in all pereon segments, except for the first, where they are either not present or are conjoined with the tergite as in most isopod species (Dreyer and Wägele, 2002).

### Systematic affinity within Isopoda

Recognizing the presence of a previously overlooked pereon tergite, the general body organization of the fossil matches the isopod bauplan, in having a head, followed by 7 pereon segments, five pleon segments and a pleotelson (pleon segment 6 conjoined with telson), all of which have separated tergites. The head, the pereon segments and the pleon segments are all at least somewhat flattened, which, despite some isopods deviating from this pattern, is further indicative of an isopod affinity. While this alone would not rule out a position outside of the Isopoda crown group, the affinity with isopod ingroups, which is explained below, convincingly attests a position within Isopoda.

Scutocoxifera is a large, phylogenetically well supported, ingroup of Isopoda, comprising several thousand species (Dreyer and Wägele, 2002; Thomas Thorpe, 2024). Its representatives can be recognized by a sclerite (coxal plate) on the lateral sides of the pereon tergites, which is a conjoined structure of the coxa and the tergite (Dreyer and Wägele, 2002). Coxal plates are present in the herein studied cast (NHM 1978/1997/1) as well as in the specimen reported by Malzahn and Pockrandt (1982, NHM 1979/2057) lateral to all but the first pereon segment, where they are absent in most scutocoxiferan isopods.

In larvae of Gnathiidae, which are micropredators of fish, the compound eyes are located on the lateral sides of the head, span the entire length of the head and, as in the fossil, the margin of the eyes facing the flat dorsal side of the head is often conspicuously straight (Wilson *et al.*, 2011, figs. 1,2,6). Fossils of *Urda* consistently show a very similar eye morphology (for a comparative figure see Schädel *et al.*, 2023, fig. 22).

The shape of these notches, which in combination with the relatively straight broad anterior head margin that separates them, forms a very conspicuous morphology (Figures 1B, 2A), is also seen in larval gnathiids and in *Urda*. It corresponds to flattened first antennular elements and a large upper lip which in larval gnathiids forms the mouth cone, through which the larvae feed on blood and interstitial fluids of fish (Wilson *et al.*, 2011; Schädel *et al.*, 2023). In *Urda* the upper lip does not form a cone, and the curved shape of the mandibles (Schädel *et al.*, 2023, figs. 5,6,7,12,14) suggests a different mode of food uptake.

The NHM 1978/1997/1 cast does not allow for a precise study of the mouthpart region. However, it is possible that some of the mouthparts are preserved in the fossil and could be revealed through carefully applied X-ray tomography (the fossil contains a significant amount of iron; Malzahn, 1979).

The trunk bears a very interesting feature, which is the short first tergite of the pereon and the second pereonite that has a concave anterior margin that fits the form of the first pereonite (Figure 1A, 2B). In Isopoda this constellation is restricted to the larval forms of Gnathiidae – in the adults this segment is completely integrated in the head and the tergite is usually conjoined with the head (Monod, 1926). In fossils of *Urda* this morphology can also be found. While the exact ontogenetic stage of the fossils cannot be determined, the size of the fossils suggests that this was also the case in the adults (Schädel *et al.*, 2023). This morphology corresponds to a functional integration of the first pereon appendages in the feeding apparatus, similar to that seen in larval gnathiids (Monod, 1926; Wilson *et al.*, 2011).

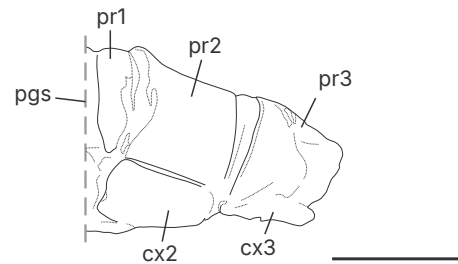
Isopods are usually associated with a dorsoventrally flattened body, whereas the body which produced the herein studied fossils is remarkably slender. However, elongated trunks are widespread within Isopoda and occur in various lineages. One of the groups where slender bodies occur is Gnathiidae. While adults of Gnathiidae are rarely slender, the larval bodies are relatively slender, that is, if the pereon is not (massively) inflated after ingestion of food (e.g. Hadfield *et al.*, 2008). In species of *Urda*, with the exception of *Urda suevica* (Reiff, 1936) also the (presumed) adults have very slender bodies and are relatively large compared to many other isopod species (Schädel *et al.*, 2023).

The morphology of the two pereopods (Figures 1A–C) is very reminiscent of *Urda buechneri* Schädel, Nagler and Hyžný, 2023, for which much of the leg morphology is known owing to a similar preservation of the fossils and the application of  $\mu$ CT. In *U. buechneri* the ischium is also conical in shape and the merus forms a very wide and somewhat flattened leg element (Schädel *et al.*, 2023, fig. 16C–D), that, if it were preserved like in NHM 1978/1997/1 would leave a similar mould on the surface of the fossil bearing nodule.

Another feature of the fossil that points towards an affinity with *Urda* is the shape of the pleonites, of which the lateral aspects are bent ca. 180° towards the ventral side and seem to have pointed posterolateral corners directed towards the pleotelson (Figure 1B). This morphology can also be found in *Urda buechneri* Schädel, Nagler et Hyžný, 2023 (Schädel *et al.*, 2023, fig. 18).

### Non-type material from Malzahn and Pockrandt 1982

Malzahn and Pockrandt (1982) described a second fossil attributed to Tanaidacea from the locality that yielded “*Apseudes giganteus*” (NHM 1979/2057, Fig. 3). Like the “*Apseudes giganteus*” holotype, the fossil was preserved within a clay-iron concretion, showing a similar preservation; however, it was far more fragmentary in nature,



**Figure 3.** Drawing of the later published additional specimen NHM 1979/2057 (herein treated as *Urda stemmerbergensis*), redrawn from photograph (Malzahn and Pockrandt, 1982, pl. 1 fig. 6). Note that the specimen has been physically ground to a level plane (dashed line) for photographic purposes and what is labelled here as pr3 has originally been interpreted as partial cephalothorax by Malzahn and Pockrandt (1982), scale ca. 5 mm. Abbreviations: **cx2–3**, coxal plates, likely 2–3; **pgs**, physical grinding surface; **pr1–3**, pereonites, likely 1–3.

preserving only few sclerotized remains. They interpreted these remains as the carapace and two pereonites of a tanaidacean.

Shortly after, in 1986, Schram *et al.* identified this specimen as not belonging to a tanaidacean but as being a fragmentary remain of a decapod crustacean. They also highlighted some of the problems in its original documentation, where the arbitrary removal of sediment matrix from the photographs (analog background removal procedure) falsely hinted at a tanaidacean affinity.

Ironically, based on the herein presented assessment, both the originally proposed close affinity of the fossil with the “*Apseudes giganteus*” type and the non-affinity with Tanaidacea held true. The main flaw in Malzahn & Pockrandt’s (1982) interpretation was that they confused a poorly preserved pereonite as the carapace and did not notice that there is an apparently fully preserved short tergite close to the side of the fossil that they ground to a level plane for further inspection. This short tergite appears to be pereonite 1 – they confused the anterior with the posterior end of the fragmentary fossil. On either side of the presumed pereonite 2 there are well separated sclerites, which unmistakably are coxal plates of an isopod. They appear to be missing due to taphonomic reasons or due to preparation at the subsequent pereon segment.

### Conspecificity with *Urda stemmerbergensis*

The holotype of *Urda stemmerbergensis* (Niedersächsisches Landesamt für Bodenforschung, Hannover, no accession number) appears to have been lost (C. Heunisch, 2019, pers. comm.) and, according to Malzahn (1968), was already in a state of decay when the fossil was described due to severe pyrite decay. The damage is apparent as inflations caused by the increased volume of the pyrite decay products in the photographs of the original description (Malzahn, 1968, pl. 58, fig. 4). Unfortunately, the specimen was only figured in dorsal view, thus not allowing an inspection of the lateral sides of the specimen.

The measurements of the *Urda stemmerbergensis* holotype reported by Malzahn (1968) suggest that its holotype was either as long or slightly shorter than the animal that formed the herein examined cast (NHM 1978/1997/1). This comparison is not trivial, since the animal from the cast has fossilized in a distinctly curved posture that leads to a greater length measured along the convex dorsal midline. Both fossils are about equal in width and the ratio between the lengths of pleon and pereon are about equal as well.

Whilst the morphological evidence for a conspecificity is weak due to incomplete knowledge of the morphology of the *U. stem-*

*merbergensis* type, there are no apparent differences between the two fossils that would argue against them stemming from the same species. However, the fact that both fossils were excavated from the same quarry and from the same rock formation – both fossils were extracted from rocks attributed to the *Endemoceras noricum* ammonite stratigraphic zone – provides a convincing argument for the conspecificity of the two fossils.

## Conclusions

The holotype of *Cretitanais giganteus* (NHM 1978/1997/1) is not, as had long been assumed, a fossil remain of a tanaidacean but one of an isopod. The morphology of the herein studied cast of the holotype suggests that the animal is closely related to extinct isopod species of the (possibly paraphyletic) group *Urda* Münster, 1840. Following the herein presented interpretation of the fossil morphology, a striking similarity between the remains formerly identified as tanaidacean fossils (NHM 1978/1997/1 and NHM 1979/2057) and the holotype of *Urda stemmerbergensis* becomes apparent. Given that all so far reported remains attributed to *Cretitanais giganteus* (Malzahn, 1979) and the holotype of *Urda stemmerbergensis* (Malzahn, 1968) stem from the same fossil site and layer of rock, there is little doubt that they represent remains of the same species, making *Cretitanais giganteus* (Malzahn, 1979) a junior synonym of *Urda stemmerbergensis* (Malzahn, 1968).

The recognition of the former *Cretitanais giganteus* material as isopod remains adds to the scarce but growing knowledge about the extinct species assemblage *Urda*, which either forms the sistergroup or the stem group of Gnathiidae – a species-rich group of micropredators that prey on fish. However, and most importantly, the new interpretation of the fossils that have long been thought to stem from tanaidaceans removes one of the most iconic species from the fossil record of Tanaidacea. The omission of *Cretitanais giganteus* from the study of the tanaidacean evolutionary history, which it had influenced for nearly six decades, should make way for a fresh view on this research area.

## Data availability

A high-resolution digital surface model of the cast is available through the Zenodo repository under the following link: <http://dx.doi.org/10.5281/zenodo.18097516>

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## Competing interests

The author declares no competing interests.

## Ethics and AI use

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