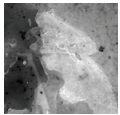


Triassic Isopoda – three new species from Central Europe shed light on the early diversity of the group

MARIO SCHÄDEL, TIMO VAN ELDIJK, HERMAN WINKELHORST, JELLE W.F. REUMER & JOACHIM T. HAUG



Despite its vernacular names (e.g. ‘woodlice’) Isopoda is a group with mostly aquatic species, with most species living in marine environments. The fossil record for isopods compared to other groups of Eucrustacea is relatively sparse. This applies even more for the Triassic. While in the Jurassic Isopoda is relatively well represented by fossils, only eight species have previously been described from the Triassic. In this study three new species of Isopoda are described from two field sites in Europe: *Obtusotelson summesbergeri* sp. nov. and *Discosalaputium aschauerorum* sp. nov. from Polzberg (Gaming, Lower Austria, Austria) and *Gelrincola winterswijkensis* sp. nov. from Winterswijk (Gelderland, Netherlands). All three new species are interpreted as representatives of Scutocoxifera (ingroup of Isopoda). The species *Gelrincola winterswijkensis* sp. nov. is further interpreted to be a representative of Cymothoidea (ingroup of Scutocoxifera). Most of the oldest fossils of Isopoda belong to Phreatoicoidea, which is supposed to be the sistergroup to all remaining Isopoda. Nowadays, Phreatoicoidea is a small relic group, its representatives living in freshwater environments. The new species herein presented contribute to our understanding of the diversity of Isopoda in the Triassic and support the assumption that the transition from a dominance of Phreatoicoidea towards the dominance of the remaining lineages of Isopoda happened quite early (likely prior to the Triassic). • Key words: fossil, morphometry, Scutocoxifera, Polzberg, Winterswijk.

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Mario Schädel, Department of Biology II, Ludwig-Maximilians-Universität Munich, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany; mario.schaedel@palaeo-evo-devo.info • Timo van Eldijk, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Nijenborgh 7, 9747 AG, Groningen, The Netherlands • Herman Winkelhorst, Molenstraat 14, 7122ZW Aalten, The Netherlands • Jelle W.F. Reumer, Stratigraphy and Paleontology, Department of Earth Sciences, Utrecht University, Princetonlaan 8a, 3584 CB Utrecht, The Netherlands • Joachim T. Haug, Department of Biology II, Ludwig-Maximilians-Universität Munich, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany & GeoBio-Center of the LMU Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany

Isopoda is a large ingroup of the crustacean group Peracarida, comprising morphologically diverse representatives that inhabit a variety of ecosystems such as the deep sea, shores, brackish waterbodies, freshwater and one ingroup even managed to inhabit terrestrial ecosystems (Wägele 1989, Brandt & Poore 2003, Broly *et al.* 2013). Even though the majority of representatives of Isopoda can easily be recognised by the organisation of the body and the overall shape, this does not necessarily apply for all groups. One of these groups is Phreatoicoidea. Phreatoicoidea is thought to be the sistergroup to all remaining ingroups of Isopoda and is morphologically distinct in some aspects, including the overall shape (Wägele 1989, Brusca & Wilson 1991). Phreatoicoideans are rather laterally compressed than dorsoventrally compressed, similar to sideswimmers (Amphipoda; Nicholls 1942). Also the the shape of the posteriormost

appendages (uropods) is dissimilar to that in many other lineages of Isopoda by being styliform rather than flat. Extant representatives of Phreatoicoidea are only found in freshwater environments (Wilson & Johnson 1999). Phreatoicoideans are also interesting, as the oldest fossils of Isopoda supposedly are representatives of this group.

The fossil record of the group Isopoda in the Palaeozoic (see Tab. 1 for all described Palaeozoic species) can be denoted as rather scarce compared to the record in the Meso- and Cenozoic. The oldest fossil record of the group (*Hesslerella shermani* Schram, 1970) is from the Middle Pennsylvanian (Upper Carboniferous, about 300 million years old) of Mazon Creek (Illinois, USA) and is interpreted as a representative of Phreatoicoidea (Schram 1970).

Five species have been described from the Middle Permian of Brazil (Paraná Basin, São Paulo State; Mezzalira &

Table 1. Palaeozoic species of Isopoda.

Species	Age	Country & reference
<i>Hesslerella shermani</i> Schram, 1970	late Carboniferous, Moscovian	Illinois, USA (Schram 1970)
<i>Sottiyella montcellensi</i> Racheboeuf <i>et al.</i> , 2009	late Carboniferous, Gzhelian	France (Racheboeuf <i>et al.</i> 2009)
<i>Pseudopalaega granulifera</i> Mezzalira & Martins-Neto, 1992	early Permian, Artinskian	Brazil (Mezzalira & Martins-Neto 1992)
<i>Pseudopalaega microcelata</i> Mezzalira & Martins-Neto, 1992	early Permian, Artinskian	Brazil (Mezzalira & Martins-Neto 1992)
<i>Pseudopalaega iratiensis</i> Martins-Neto, 2001	early Permian, Artinskian	Brazil (Martins-Neto 2001)
<i>Protourda tupiensis</i> Mezzalira & Martins-Neto, 1992	early Permian, Artinskian	Brazil (Mezzalira & Martins-Neto 1992)
<i>Protourda circumscripta</i> Mezzalira & Martins-Neto, 1992	early Permian, Artinskian	Brazil (Mezzalira & Martins-Neto 1992)
<i>Palaeophreatoicus sojanensis</i> Birstein, 1962	middle Permian	Russia (Birstein 1962, Schram 1980)
<i>Protamphisopus reichelti</i> Malzahn, 1962	late Permian, Lopingian	Germany (Glaessner & Malzahn 1962)
<i>Palaeocrangon problematicus</i> (= <i>Prosoponiscus problematicus</i>) (von Schlotheim, 1820)	late Permian, Lopingian	Germany (Schlotheim 1820, Schauroth 1854, Geinitz 1861) & Great Britain (Kirkby 1857)

Martins-Neto 1992, Martins-Neto 2001, Chahud & Petri 2015), which are generally interpreted as representatives of Scutocoxifera. Scutocoxifera is an ingroup of Isopoda, not including Phreatoicidea, which representatives are characterised by having scale-like lateral expansions to the dorsal sclerites of the pereon (postocular segments 7–13) that are part of the proximal leg element (‘coxal plates’) (Dreyer & Wägele 2002). The remainder of the Palaeozoic fossils of Isopoda have all been interpreted as representatives of Phreatoicidea (Glaessner & Malzahn 1962, Schram 1980).

For the Triassic only eight species of Isopoda and one not formally described specimen have been reported so far (Figs 1, 2). *Anhelkocephalon handlirschi* is deliberately not included, see discussion below. Records of the group Isopoda are missing throughout the Early Triassic (Induan and Olenekian).

The earliest Triassic record, so far, is from the early Middle Triassic of France (‘Grès à Voltzia’ Formation, ‘Voltzien-sandstein’, Upper Buntsandstein, Anisian) with *Palaega pumila* Gall & Grauvogel, 1971 (Gall & Grauvogel 1971,

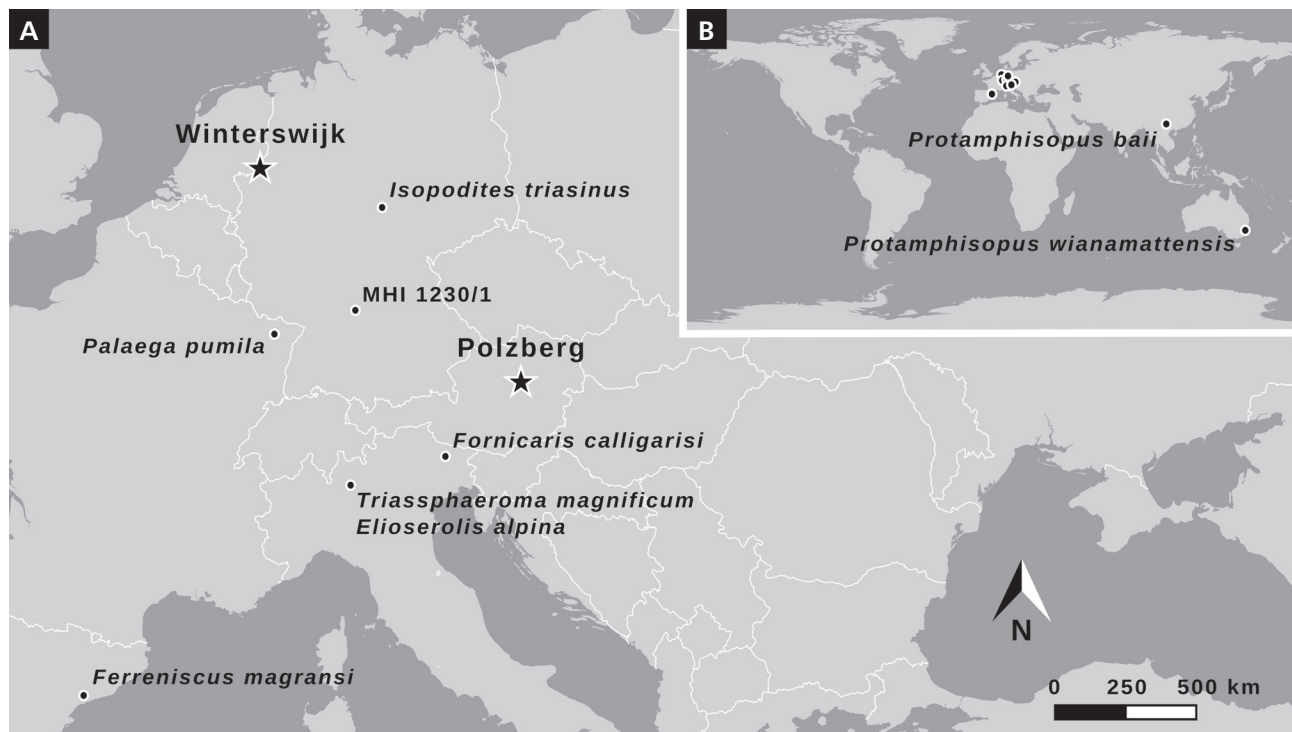


Figure 1. Maps with the field sites of all published findings of Isopoda from the Triassic. • A – map of Europe. • B – world map. Stars denote field sites corresponding to the herein described fossils.

Sphaeromatidea) (Calzada & Urquiola 1994, Calzada *et al.* 2011). Alongside with *Ferrensicus magransi*, Calzada & Urquiola (1994) mentioned the presence of further, likely not conspecific, isopods from the same locality and age (not figured).

From the middle Late Triassic (Norian) there are three species of about the same age (Alaunian to Savatian sub-stage). Two of the species, *Elioserolis alpina* Basso & Tintori, 1994 and *Triassphaeroma magnificum* Basso & Tintori, 1994 have been interpreted as representatives of Sphaeromatidea (Basso & Tintori 1994, Brandt *et al.* 1999). These two species come from the same locality and were found in the ‘Calcare di Zorzino’ limestone near Zogno (Bergamo, Italy). *Elioserolis alpina* has been interpreted as a representative of Serolidae due to the rough similarity in the overall shape (Basso & Tintori 1994); this interpretation has been rejected by Brandt *et al.* (1999) who stated that no interpretation further than Sphaeromatidea is possible.

The other species of similar age, *Fornicaris calligarisi* Wilson & Selden *in* Selden *et al.*, 2016, has also been found in northern Italy (*ca.* 240 km distance, Fig. 1) and is from the ‘Dolomia di Forni’ Formation near Forni di Sotto (Province of Udine). *Fornicaris calligarisi* has been interpreted as a representative of Paramunnidae (ingroup of Janiroidea and Asellota) (Selden *et al.* 2016). Apart from the published specimens there are probably more Triassic asellotans from Italy pending examination (Paolo Schirolli, personal communication, mentioned in Selden *et al.* 2016).

The fossil record for the Jurassic as well as for the Cretaceous and the Cenozoic is far more extensive. For the Jurassic there are more than 35 formally described species (Meyer & Münster 1840; Milne Edwards 1843; Westwood 1854; Ammon 1882; Carter 1889; Woodward 1890; Stolley 1910; Remeš 1912; Van Straelen 1928; Reiff 1936; Frentzen 1937; Bachmayer 1955; Radawanski 1995; Grant-Mackie *et al.* 1996; Polz 1998, 2005a ,b; Guinot *et al.* 2005; Polz *et al.* 2006; Etter 2014; Jones *et al.* 2014; Gašparič *et al.* 2015; Keupp & Mahlow 2017). Already in the Jurassic more ingroups of Isopoda become apparent such as some ingroups of Cymothoidea (Etter 2014, Nagler *et al.* 2017) or Sphaeromatidae (Bachmayer 1955, Radawanski 1995). With the occurrence of fossil-rich amber deposits in the Cretaceous, also terrestrial forms of Isopoda (Oniscoidea) appear in the fossil record (Broly *et al.* 2015).

Modern representatives of Isopoda comprise a large variety of different body shapes, comprising a wide range from long and slender forms such as *e.g.* in Anthuroidea (Wägele 1981) to disc-shaped forms such as *e.g.* in some lineages of Sphaeromatidea (Wägele 1989, Brandt & Poore 2003). Distinct disc-shaped forms are also present in the fossil record (Polz 1998). Also, from an ecological perspective there is much diversity within Isopoda. Their

ecological specialisations range from wood boring (Daniel *et al.* 1991), over burrowing (Matsui *et al.* 2011), herbivory (Salemaa 1987), scavenging (Lowry & Dempsey 2006), and preying (Kaneko & Omori 2003) to parasitism (van der Wal *et al.* 2019). Morphological features that indicate parasitism are also present in the fossil record. Parasitism and the development of true larval forms are also key features for the evolution of certain body shapes such as *e.g.* in Cymothoidea, Epicaridea and Gnathiidae (Smit & Davies 2004, Boyko & Wolff 2014, Nagler *et al.* 2017, Schädel *et al.* 2019). Aside from parasitism, also other ecological factors contributed to the evolution of certain lineages and subsequently also for the evolution of body shapes, such as the colonisation of the deep sea (Lins *et al.* 2012) or interstitial environments (Kim *et al.* 2017).

Here, we present three new fossil forms of Isopoda. All specimens are Triassic in age and come from two field sites in central Europe (Polzberg, Winterswijk). We discuss the preserved morphological features from a phylogenetic perspective. We also summarize the fossil record of the group up until the end of the Triassic and discuss phylogenetic affinities of already described Triassic species. Furthermore, we attempt to analyse the evolution of body shapes based on Triassic and extant specimens.

Material and Methods

Material

Three specimens form the basis of the study. Two originate from the Polzberg locality and one from the Winterswijk locality.

The two specimens from the Polzberg locality were found by Birgitt Aschauer (private collector, Waidhofen an der Ybbs, Austria) and donated to the collection of the Natural History Museum Vienna (Naturhistorisches Museum Wien), accession numbers NHMW 2020/0003/0001 and NHMW 2020/0003/0002. The specimen from the Winterswijk locality was collected by Herman Winkelhorst (private collector, Aalten, Netherlands) and donated to the Museum Naturalis, Leiden, accession number RGM.792591.

Geological setting of the Polzberg locality

The fossil locality Polzberg (after the village near the site and the Polzberg Graben) also known under the alternative name Schindelberg (after the adjoining mountain) is located in the municipality of Gaming, Lower Austria (state), Austria. The Polzberg Graben is surrounded by the mountains Föllbaumberg and Schindelberg. Two scientific excavations have been carried out in 1886 (Stur 1887)

and 1909 (Glaessner 1931). Since then, there have been no further excavations at the original site (underground quarrying). Recently, a new site yielding the same strata has been discovered by amateur palaeontologists Birgitt and Karl Aschauer.

The fossiliferous sediments at the site are dark, organic rich laminated marls of the Reingraben Formation. The stratum in which the fossils were found is also referred to as “Aon Schichten”, “Aon Schiefer” or “Aonoides Schiefer” – referring to the *Trachyceras aon* and/or the *Trachyceras aonoides* ammonite stratigraphic zones (Teller 1891, Glaessner 1931, Hornung & Brandner 2005). The Reingraben shales can be dated to a Julian (Early Carnian, Upper Triassic) age (Hornung & Brandner 2005). The Julian (substage of the Carnian stage) can be correlated with an absolute age of 235.4 to 237 million years (Ogg 2012).

The proximity to the town Lunz am See led to the attribution terms like “Lunz Lagerstätte”. This is problematic, as the Lunz Lagerstätte, which is famous for its abundant plant remains (e.g. Pott & Krings 2010), is of a different age and there is also no close geological connection between the sites (Forchielli & Pervesler 2013).

The fossil remains that have been reported so far from the Polzberg site include ray-finned fishes (Actinopterygia; Abel 1906, Griffith 1977), a lungfish (Dipnoi; Teller 1891), sea urchins (Echinoida; Glaessner 1931), as well as numerous representatives of Mollusca, such as different forms of Cephalopoda (Ammonoidea; Doguzhaeva *et al.* 2007a, and Colleoida; Doguzhaeva *et al.* 2006, 2007b), but also snails (Gastropoda) and clams and relatives (Bivalvia) (including abundant planktic representatives of the group *Halobia*, ‘*Halobia* shale’; Glaessner 1931). Eucrustacean remains include thylacocephalans (Glaessner 1931, Forchielli & Pervesler 2013), paenaeoidean prawns, glypheoideans and polychelidan lobsters (Glaessner 1931). Also rare plant remains have been found from the same sediment (B. Aschauer, personal communication).

Geological setting of the Winterswijk locality

Early Anisian (Middle Triassic) sediments belonging to the Lower Muschelkalk Vossenveld Formation are exposed in the Winterswijk quarry in the easternmost Netherlands (Hagdorn & Simon 2010). These outcrops of finely laminated micritic limestone consist of alternating marly limestones, dolomites, clayey marls and dolomitic clay layers (Borkhataria *et al.* 2006, Klein *et al.* 2015, Maxwell *et al.* 2016). The sediments were deposited near the margin of the epicontinental Germanic Basin and alternately document shallow marine environments and intertidal mudflats with algal laminates and polygonal mudcracks (Klein 2012, Oosterink & Winkelhorst 2013, Klein *et al.* 2015).

The fossil remains that have been so far reported from the Winterswijk site include ray-finned fishes (Actinopterygia; Maxwell *et al.* 2016), sharks (Euselachii; Oosterink 2001) and representatives of Sauropterygia (Klein 2012, Klein *et al.* 2015), as well as brachiopods (Brachiopoda; Oosterink 1986), various representatives of Mollusca, such as snails (Gastropoda), clams and relatives (Bivalvia), and representatives of Cephalopoda (Oosterink 1986) and Scyphozoa (Oosterink & Winkelhorst 2013). Arthropod remains comprise representatives of Xiphosura (Hauschke *et al.* 2009), Decapoda (Klompaker & Fraaije 2011) and Insecta (van Eldijk *et al.* 2017). Remains of plants are mostly represented by palynomorphs (pollen and spores; Hengreen *et al.* 2005b). In addition, numerous ichnofossils have also been identified, including burrowing traces (Knaust 2013), terrestrial track ways (Diedrich 2001) and swimming traces (Schulp *et al.* 2017). An initial stratigraphy of the Winterswijk quarry was published by Oosterink (1986), who identified 39 stratigraphic horizons. Subsequently, additional layers unearthed near the top of the profile were identified by the Working Group Muschelkalk Winterswijk and numbered in accordance with the system of Oosterink (1986) (Maxwell *et al.* 2016). The specimen RGM.792591 described here was found by HW in layer 43, this layer is particularly noteworthy since it has already yielded several insect remains in addition to exquisitely preserved fish fossils (Maxwell *et al.* 2016, van Eldijk *et al.* 2017). There seem to be some unresolved issues regarding the precise dating of the top section of the quarry to which layer 43 belongs (Maxwell *et al.* 2016, van Eldijk *et al.* 2017). Hagdorn & Simon (2010) considered the top section of the stratigraphy to belong to the Illyrian substage of Anisian, based on the occurrence of the bivalve *Neoschizodus orbicularis*. However, they acknowledged that this dating is not compatible with the palynological results obtained by Hengreen *et al.* (2005a, b), which indicate that the top section of the stratigraphy belongs to the Bithynian substage of the Anisian. Regardless, specimen RGM.792591 can thus be correlated with confidence to be Anisian. Although it would seem most probable that layer 43 is of Bithynian age as the palynological date assigned by Hengreen *et al.* (2005a, b) is based on two separate stratigraphic marker species, further stratigraphic studies are required. The Anisian can be correlated with an absolute age of 245.9 to 237 million years (Ogg 2012).

Imaging

The specimens from the Polzberg locality were photographed using a Canon EOS 70D DSLR camera with a Canon MP-E 65 mm macro objective and MT24 twin flashes. In some cases, a grid of multiple images was recorded to overcome the limit of field of view at higher

magnifications. Stereoscopic images were recorded by tilting the macrophotography setup relative to the specimen.

The specimen from the Winterswijk locality was photographed using a Keyence BZ9000 digital microscope. Incident white light was used to obtain microscopic images and incident fluorescent light was used to obtain epifluorescence microscopic images. For the fluorescence microscopy the fossils were excited by light of 470 nm wavelength (GFP-filter) and 545 nm wavelength (TRITC-filter) (e.g. Metz *et al.* 2015). To overcome the limitations of depth of field and field of view, for both kinds of illumination, a grid of image stacks with images of different levels of focus was recorded (e.g. Haug *et al.* 2011).

Image processing

Images of different levels of focus were combined to overall in-focus images ('focal plane merging') using CombineZP (GPL). Grids of in-focus images were combined to larger images ('panoramic stitching') using TrakEM (ImageJ, GPL). The resulting images were optimised for colour and contrast using GIMP (GPL). Drawings were done using Inkscape (GPL). The map was created using QGIS (GPL) data from naturalearthdata.com (public domain). The map was exported as a vector file and postprocessed using Inkscape (GPL).

Measurements and analysis

Measurements were performed using Adobe Acrobat Reader, ImageJ and Inkscape (using the Bezier tool, the distance between the cursor and the last click is given in the status bar). Measurements (Suppl. files 1, 2) of extant specimens were gathered from Nicholls (1942, 1943) and Richardson (1905); measurements of fossil specimens were gathered from Basso & Tintori (1994), Picard (1858), Schöllmann *et al.* (2015) and Selden *et al.* (2016). Graphs were created using R including the packages readr, ggplot2, ggrepel and gridExtra (Suppl. file 3).

Fossils of *Protamphisopus bairi* and *Protamphisopus wianamattensis*, as well as one of the herein presented fossils, are laterally compressed and thus could not be measured for dorsal/ventral aspect of the body shape. *Ferreniscus magransi* is not included in the analysis, because there appears to be a mismatch between the reconstructive drawing in the original description (Calzada & Urquiola 1994) and a more recent photograph of the specimen (Institut Cartogràfic i Geològic de Catalunya 2018, collection number 52506), that could greatly affect the outcome of the analysis. *Isopodites triasinus* is only figured with an apparently highly stylised, miniature scaled, drawing and the measurement must thus be interpreted with caution.

Results

All new taxonomic names were registered in the ZooBank database (International Commission on Zoological Nomenclature, <http://zoobank.org>) prior to the publication.

Systematic part

Euarthropoda *sensu* Walossek (1999)
Eucrustacea *sensu* Walossek (1999)
Peracarida Calman, 1904
Isopoda Latreille, 1817
Scutocoxifera Dreyer & Wägele, 2002

Obtusotelson gen. nov.

<http://zoobank.org/10472CD8-97E6-4B84-9795-374E63AA05C2>

Type species. – *Obtusotelson summesbergeri* sp. nov. (type and only species).

Etymology. – From Latin *obtusus* (= blunt) and *telson*, referring to the shape of the pleotelson in the holotype of the type species.

Diagnosis. – Not applicable since monotypic.

Remarks. – The name *Obtusotelson* is introduced, exclusively, to allow a representation of the species *summesbergeri* sp. nov. under a Linnean framework (by serving as the generic name of the type species) (e.g. Béthoux 2009). *Obtusotelson* does not represent a monophyletic group of organisms, since only a single species is included (monotypic). Yet, *Obtusotelson* may serve as a 'group name in advance' if, in the future, another species is found to be the sister-species to the type species of *Obtusotelson*.

Obtusotelson summesbergeri sp. nov.

Figure 3A–C

<http://zoobank.org/E449512B-FDF7-45F6-AB88-E41404666FEA>

Types. – Holotype and only type, NHMW 2020/0003/0001, Naturhistorisches Museum Wien (Natural History Museum Vienna), Austria.

Type horizon and locality. – Reingraben Formation, Julian (Carnian), 235.4 to 237 million years (Ogg 2012); Polzberg, Gaming, Lower Austria, Austria.

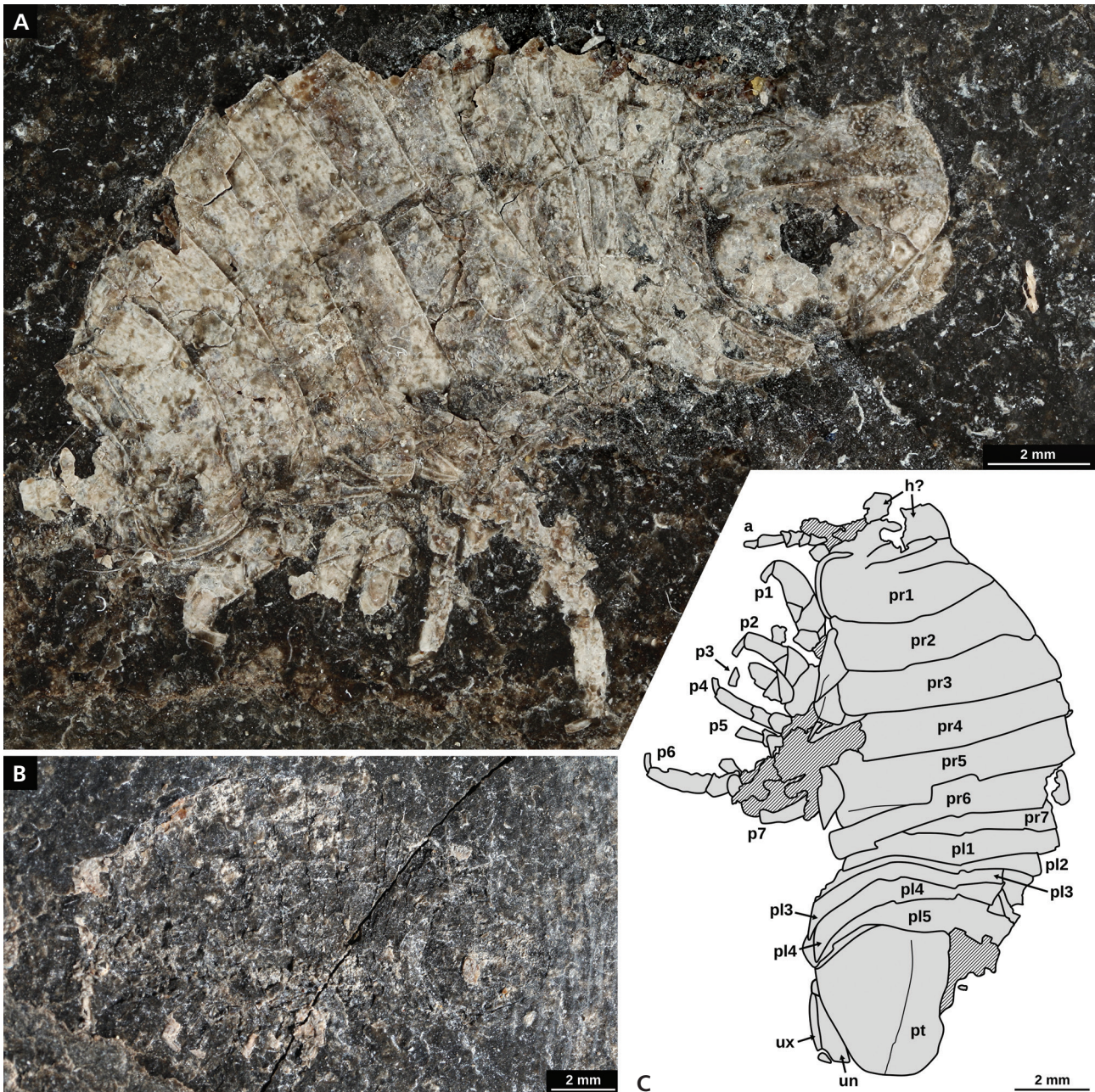


Figure 3. Holotype of *Obtusotelson summesbergeri* sp. nov. (NHMW 2020/0003/0001); A – macroscopic image, positive side (part); B – macroscopic image, negative side (counterpart); C – drawing based on part and counterpart of the holotype. Abbreviations: a – antenna; h? – putative remains of the head; p1–7 – pereopods 1–7; pl1–5 – pleon segments 1–5; pr1–7 – pereon segments 1–7; pt – pleotelson; un – uropod endopod; ux – uropod exopod.

Material. – Holotype only.

Etymology. – After Dr. Herbert Summesberger, retired palaeontologist who worked at the Natural History Museum in Vienna.

Diagnosis. – Body about half as wide as long; coxal plates triangular; dactyli with truncated distal ends; pleon tergites with concave posterior margins and pointed posterolateral

corners; pleotelson with median ridge, posterior margin of pleotelson straight in the median portion (‘truncated’ appearance); uropod posteriorly extending to the level of the posterior margin of the pleotelson, endopod with straight distal margin.

Description. – Preservation of the holotype: Strongly compressed remains of the exoskeleton; specimen accessible in dorsolateral view; remains located on two

corresponding slabs of rock matrix (part and counterpart); counterpart with only few pieces of exoskeleton; head not preserved or represented by inconspicuous fragments; remains of putative antennal elements visible on the counterpart; seven appendages of the pereon (pereopods) preserved on the left side of the body (not all of them might be legs of the left body side).

Description of the holotype: The body is composed of a functional head (ocular segment and postocular segments 1–6, cephalothorax) and a trunk (postocular segments 7–19). The trunk is divided into two tagmata: the pereon (postocular segments 7–13) and the pleon (postocular segments 14–19). The last segment of the pleon is conjoined with the telson, forming a pleotelson. Body longer than wide, about half as wide as long. Measurements are listed in Tab. 2.

The trunk bears one pair of appendages per segment on the ventral side. The appendages of the pereon segments (pereopods) consist of seven elements (from proximal to distal: coxa, basipod, ischium, merus, carpus, propodus, dactylus).

Pereon with all seven segments bearing distinct dorsal sclerites (tergites). Pereon segments 2 to 7 with coxa conjoined with the tergite of the same segment forming a scale-like lateral sclerite (coxal plate). Tergite of pereon segment 1 with rounded lateral margin; posterior margin slightly convex, no coxal plates. Tergite of pereon segment 2 slightly shorter than preceding tergite, about the same width; posterior margin slightly convex; with coxal plate; coxal plate triangular with pointed posterolateral corner, ridge parallel to the anterolateral margin. Tergite of pereon segment 3 about as long as preceding tergite, slightly wider than preceding tergite; posterior margin almost straight; with coxal plate; coxal plate triangular with pointed posterolateral corner, ridge parallel to the anterolateral margin. Tergite of pereon segment 4 about as long as preceding tergite, slightly wider than preceding tergite; posterior margin almost straight; coxal plate not preserved. Tergite of pereon segment 5 about as long as preceding tergite, about the same width as the preceding tergite; coxal plate triangular with pointed posterolateral corner, straight posterior margin. Tergite of pereon segment 6 slightly shorter than the preceding tergite, about the same width as the preceding tergite; posterior margin slightly concave; coxal plate not preserved. Tergite of pereon segment 7 shorter than the preceding tergite; coxal plate not preserved.

Anteriormost preserved leg with merus, carpus, propodus and dactylus preserved; merus with oblique distal margin in accessible view (posterior side); carpus triangular and smaller than the merus; propodus long and with convex dorsal side; dactylus much shorter and narrower than propodus and with truncated distal end. Second preserved leg with merus, carpus, propodus and dactylus preserved; merus triangular in the accessible

Table 2. Measurements of *Obtusotelson summesbergeri* sp. nov. (NHMW 2020/0003/0001).

Body part	Length	Width
complete body	15.29 mm	6.93 mm (preserved part)
pereon segment 1	1.75 mm (along the midline)	not accessible
pereon segment 2	1.26 mm (along the midline)	not accessible
pereon segment 3	1.24 mm (along the midline)	not accessible
pereon segment 4	1.16 mm (along the midline)	not accessible
pereon segment 5	1.02 mm (along the midline)	not accessible
pereon segment 6	0.74 mm (along the midline)	not accessible
pereon segment 7	0.53 mm (along the midline)	not accessible
pleon segment 1	0.81 mm (along the midline)	not accessible
pleon segment 2	0.59 mm (along the midline)	not accessible
pleon segment 3	0.40 mm (along the midline)	not accessible
pleon segment 4	0.67 mm (along the midline)	not accessible
pleon segment 5	0.84 mm (along the midline)	not accessible
pleotelson	3.88 mm	3.75 mm (preserved part)
uropod endopod length	1.80 mm	0.63 mm
uropod exopod	1.53 mm (preserved part)	not accessible

view (posterior side); carpus triangular in the accessible view (posterior side), smaller than the merus; propodus elongated, much longer than wide; dactylus shorter and narrower than propodus, with truncated distal end. Third preserved leg with merus, carpus, propodus and dactylus preserved; sub-similar to the preceding leg; distal part of the propodus not preserved; dactylus with truncated distal end. Fourth preserved leg with merus, carpus, propodus and dactylus preserved; overall much slenderer than the preceding leg; preserved part of the merus short; carpus elongated, longer and slenderer than in the preceding legs; propodus elongated, longer than carpus; dactylus much shorter and narrower than propodus and with truncated distal end. Fifth preserved leg with merus and carpus preserved; merus short; carpus elongated similar to the carpus of the preceding leg. Sixth preserved leg with carpus, propodus and dactylus preserved; carpus elongated; propodus elongated with dorsal side slightly convex, distinctly longer than propodus of leg 4; dactylus much shorter and narrower than propodus and with truncated distal end. Seventh preserved leg with only one elongated element of uncertain affinity (counterpart).

Pleon with all seven segments bearing distinct dorsal sclerites (tergites). Tergite of pleon segment 1 longer than the preceding tergite of pereon segment 7. Tergite of pleon segment 2 longer than the preceding tergite; posterior margin convex or straight in the median part and concave in the lateral parts, posterolateral corner pointed. Tergite of

pleon segment 3 shorter than the tergite of the preceding segment; posterior margin convex or straight in the median part and concave to the lateral side; lateral margin straight; posterolateral corner distinctly pointed. Tergite of pleon segment 4 longer than the preceding tergite, posterior margin straight to slightly convex in the median part and concave to the lateral side; lateral margin straight; posterolateral corner distinctly pointed. Tergite of pleon segment 5 longer than the preceding tergite; posterior margin straight to slightly convex in the median part and concave in the lateral part. Pleotelson roughly trapezoid in dorsal view, with straight lateral margins and straight posterior margin ('truncate' *sensu e.g.* Bruce 1986), anterior side wider than the posterior side, anterior margin with straight median part and concave lateral parts, ridge along the midline, without conspicuous ornamentation.

Appendages of the pleotelson (uropods) consisting of a proximal element (basipod) and two distal elements (endopod, median and exopod, lateral) that both originate from the basipod. Endopod broad, wider in the distal part, with 'truncated tip' (with straight distal margin), median margin slightly convex. Exopod about as long as the endopod or slightly shorter.

Remarks. – The legs that are only present in the anterior part of the body indicate a tagmatisation of the trunk into two functional units (pereon and pleon; autapomorphy of Malacostraca (Walossek 1999). The posteriormost pair of appendages, together with the (pleo-) telson, forms a tail fan (autapomorphy of Eumalacostraca) (Ax 2000). Apomorphic features of Isopoda are often not visible in fossil specimens. Features that are not exclusive for Isopoda but part of the ground pattern of Isopoda are: posteriormost pleon segment conjoined with the telson ('pleotelson') (Wägele 1989, Brusca & Wilson 1991). Head shield forms a capsule, not constituted by postocular segment 7 (postocular segment 7 can constitute to the head shield in some ingroups of Isopoda) (Ax 2000, Haug 2011). A dorsoventral flattened body is often stated as apomorphic for Isopoda (*e.g.* Wägele 1989). However, a dorsoventral flattened body cannot be reconstructed for the ground pattern of Isopoda without assuming convergence in the earliest lineages within Isopoda (Brusca & Wilson 1991, Wilson 1996). Nevertheless, a dorsoventral flattened body can be reconstructed as an apomorphy for an ingroup of Isopoda (Isopoda *nec* Phreatoicidea). In *Obtusotelson summesbergeri* sp. nov. a flattened body shape is not conspicuous, as legs of only one body side are preserved. Yet, in the posterior part of the body, especially in the pleotelson, it is apparent that the outline of the right body side is not constituted by the midline of the body and thus, that the body is indeed dorsoventrally flattened.

In the holotype of *Obtusotelson summesbergeri* sp. nov. the pereon segments 2–5 bear lateral sclerites that are

distinct from the tergites. The distinctness and relative size of these sclerites (about as long or longer than the lateral margin of the corresponding tergite) suggest that these are coxal plates rather than tergopleura or lateral aspects of ring-shaped coxae (*cf.* illustrations in Gruner 1954 and Dreyer & Wägele 2002). Coxal plates are autapomorphic for Scutocoxifera (Dreyer & Wägele 2002). The truncated distal ends of the dactyli indicate the presence of prominent claws. A pair of two claws on the distal end of the dactylus is plesiomorphic for Scutocoxifera (Wägele 1989).

***Discosalaputium* gen. nov.**

<http://zoobank.org/C93F3340-35B0-48FF-8B81-93E4DE43890D>

Type species. – *Discosalaputium aschauerorum* sp. nov. (type and only species).

Etymology. – From Latin *discus* (= disc) and *salaputium* (= manakin), referring to the overall shape and size of the holotype of the type species.

Diagnosis. – Not applicable since monotypic.

Remarks. – The name *Discosalaputium* is introduced, exclusively, to allow a representation of the species *aschauerorum* sp. nov. under a Linnean framework (by serving as the generic name of the type species) (*e.g.* Béthoux 2009). *Discosalaputium* does not represent a monophyletic group of organisms, since only a single species is included (monotypic). Yet, *Discosalaputium* may serve as a 'group name in advance' if, in the future, another species is found to be the sister-species to the type species of *Discosalaputium*.

***Discosalaputium aschauerorum* sp. nov.**

Figure 4A–D

<http://zoobank.org/CD2A1601-94A6-4271-957F-A2658D0EEFBA>

Types. – Holotype and only type, NHMW 2020/0003/0002, Naturhistorisches Museum Wien (Natural History Museum Vienna), Austria.

Type horizon and locality. – Reingraben Formation, Julian (Carnian), 235.4 to 237 million years (Ogg 2012); Polzberg, Gaming, Lower Austria, Austria.

Material. – Holotype only.

Etymology. – In honour of the private collectors and amateur palaeontologists Karl and Birgitt Aschauer, who

provided access to two of the herein presented specimens and donated them to the collection of the Geological Service of Austria.

Diagnosis. – Body with semicircular outline in dorsal view, about as wide as long, dorsoventrally flattened; coxal plates with rounded anterolateral side and angled posterolateral corner; pleon without free (distinct, not conjoined with other sclerites) tergites; pleotelson roughly triangular; uropods large.

Description. – Preservation of the holotype: Strongly compressed remains of the exoskeleton; specimen accessible in dorsal view; remains located on two corresponding slabs of rock matrix (part and counterpart). Head and appendages of the trunk (except for the posteriormost ones) not preserved.

Description of the holotype: The body is composed of a head (ocular segment and postocular segments 1–6, not preserved in the holotype) and a trunk (postocular segments 7–19). The trunk is divided into two functional tagmata: the pereon (postocular segments 7–13) and the pleon (postocular segments 14–19). Body with semicircular outline in dorsal view, about as wide as long. Measurements are listed in Tab. 3.

Pereon segment 1 with concave anterior margin and convex posterior margin, lateral part not distinct from median part (no coxal plate). Lateral margin anterolaterally projected and straight to slightly convex. Pereon segment 2 distinctly wider than preceding segment, with concave anterior margin, posterior margin overall straight with concave part in the median part; lateral expansions distinct from the (rest of) the tergite by a notch on the posterior margin (possibly representing coxal plates); lateral expansions with slightly convex lateral margin, anterolateral corner rounded,

curved ridge on the expansion from centre of the base of the expansion to the posterolateral corner, posteromedian corner with distinct angle. Pereon segment 3 wider than preceding segment, shape similar to preceding segment but anterior margin overall straight with convex proportion in the centre. Pereon segment 4 about as wide as preceding segment, shape similar to preceding segment. Pereon segment 5 about as wide as preceding segment, shape similar to preceding segment but without concave portion in the posterior margin. Pereon segment 6 narrower than the preceding segment, anterior margin evenly convex, posterior margin strongly concave, lateral expansion narrower than in preceding segments and pointing posterolaterally. Pereon segment 7 narrower than the preceding segment, shape similar to preceding segment but with strongly convex anterior margin, lateral expansion narrow and pointing more posteriorly than in the preceding segment.

Pleon segments 1–5 not discernible in the holotype. Pleon segment 6 conjoined with the telson forming the pleotelson. Pleotelson roughly triangular in dorsal view, anterior margin straight in the median part, anterior margin oblique (anteromedian to posterolateral) in the lateral part.

Uropod large, located lateral to the posterolateral margin of the pleotelson, anterolateral corner close to the lateral expansion of pereon segment 7; elements of the uropod (basipod, endopod and exopod) not discernible.

Remarks. – The posteriormost pair of appendages, together with the (pleo-) telson, forms a tail fan (autapomorphy of Eumalacostraca; Ax 2000). Although the low relief preservation of the holotype does not allow to estimate the exact dorsoventral aspect of the living animal, due to the positioning of the holotype, it can be concluded that *Discosalaputium aschauerorum* sp. nov. was wider than high. A dorsoventrally flattened body can be seen as apomorphic for a monophyletic ingroup of Isopoda (Isopoda *nec* Phreatoicoidea; see discussion above). The lateral expansions in the pereon are distinct from the tergite by a notch on the posterior margin. Also, the shape of the expansion and the shape and position of the ridge on the dorsal side of the expansion resembles much that of representatives of Scutocoxifera, indicating that the expansion is likely a coxal plate, which is autapomorphic for Scutocoxifera (Dreyer & Wägele 2002). However, this would imply that the coxal plate is conjoined with the tergite, as it is *e.g.* in most adult land-living isopods (Oniscoidea; Gruner 1954). To test this assumption it would be necessary to inspect the coxal area on the ventral side of the body. All dorsal sclerites in the holotype of *Discosalaputium aschauerorum* sp. nov. can be identified as parts of the pereon, due to the likely presence of coxal plates. This implies that aside from the pleotelson, all dorsal sclerites of the pleon are reduced or conjoined with the pleotelson. A reduction in the number of free

Table 3. Measurements of *Discosalaputium aschauerorum* sp. nov. (NHMW 2020/0003/0002).

Body part	Length	Width
complete body	7.67 mm (preserved part)	8.30 mm (reconstructed from one body side)
pereon segment 1	not accessible	6.13 mm
pereon segment 2	0.52 mm	7.98 mm
pereon segment 3	0.64 mm	4.19 mm
pereon segment 4	0.63 mm	8.38 mm (reconstructed from one body side)
pereon segment 5	0.59 mm	8.28 mm (reconstructed from one body side)
pereon segment 6	0.53 mm	8.18 mm (reconstructed from one body side)
pereon segment 7	0.48 mm	3.95 mm
pleotelson	2.40 mm	3.68 mm

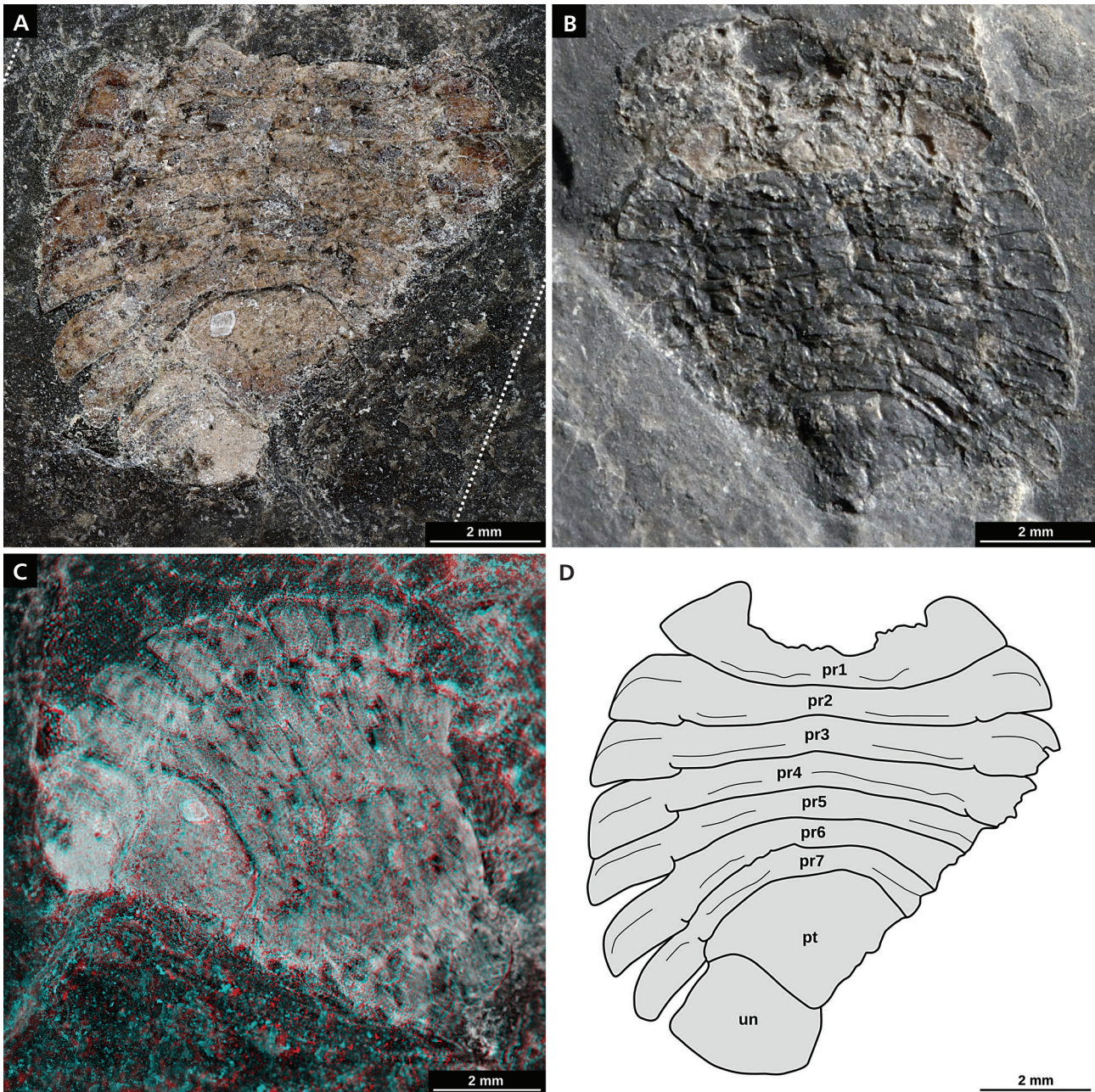


Figure 4. Holotype of *Discosalaputium aschauerorum* sp. nov. (NHMW 2020/0003/0002); A – macroscopic image, positive side (part), dotted lines mark areas where artificial matrix has been added digitally for aesthetic reasons; B – macroscopic image, negative side (counterpart); C – red-cyan stereo anaglyph based on macroscopic images, positive side (part); D – drawing based on part and counterpart of the holotype. Abbreviations: pr1–7 – pereon segments 1–7; pt – pleotelson; un – uropod endopod.

pleon segments, in combination with a semicircular body outline, can be seen in various lineages of Sphaeromatidea (e.g. Plakarthriidae, Bathynataliidae and some lineages of Sphaeromatidae) (Wägele 1989, Brusca & Wilson 1991, Brandt & Poore 2003). Yet, conditions where not even one pleon tergite is distinct from the telson are extremely rare (e.g. *Ancinus belizensis* Kensley & Schotte, 1987).

Very wide uropods, in combination with a semicircular outline of the body, like in the holotype of *Discosalaputium*

aschauerorum sp. nov., do only occur in Sphaeromatoidea Brandt & Poore 2003 (see Fig. 5A–B, D–E). The absence of free dorsal pleon sclerites could be interpreted as apomorphic for Sphaeromatoidea. Yet, because no other apomorphic features are visible in the holotype, we suggest to be careful with a possible affinity of *Discosalaputium aschauerorum* sp. nov. with Sphaeromatoidea.

The morphology of the lateral aspect of the tergites (or the coxal plates) in *Discosalaputium aschauerorum* sp.

nov. is very similar to that in *Elioserolis alpina*. Yet, in the reconstruction of *Elioserolis alpina* by Basso & Tintori (1994) there are two free pleon tergites (the photograph is of bad quality and the specimen should be restudied as some parts of the dorsal morphology are unclear). Also there is an age gap of 18 million years between the occurrences of both species, making it unlikely that they are conspecific in the sense of a biological species concept.

Cymothoidea Wägele, 1989

***Gelrincola* gen. nov.**

<http://zoobank.org/F7EA70DD-56B0-411C-AE07-0EE68107E515>

Type species. – *Gelrincola winterswijkensis* sp. nov. (type and only species).

Etymology. – From Latin *Gelria* (= Gelderland, province of the Netherlands where the field site is located) and *incola* (= inhabitant), referring to the field site of the holotype of the type species.

Diagnosis. – Not applicable since monotypic.

Remarks. – The name *Gelrincola* is introduced, exclusively, to allow a representation of the species *winterswijkensis* sp. nov. under a Linnean framework (by serving as the generic name of the type species) (e.g. Béthoux 2009). *Gelrincola*

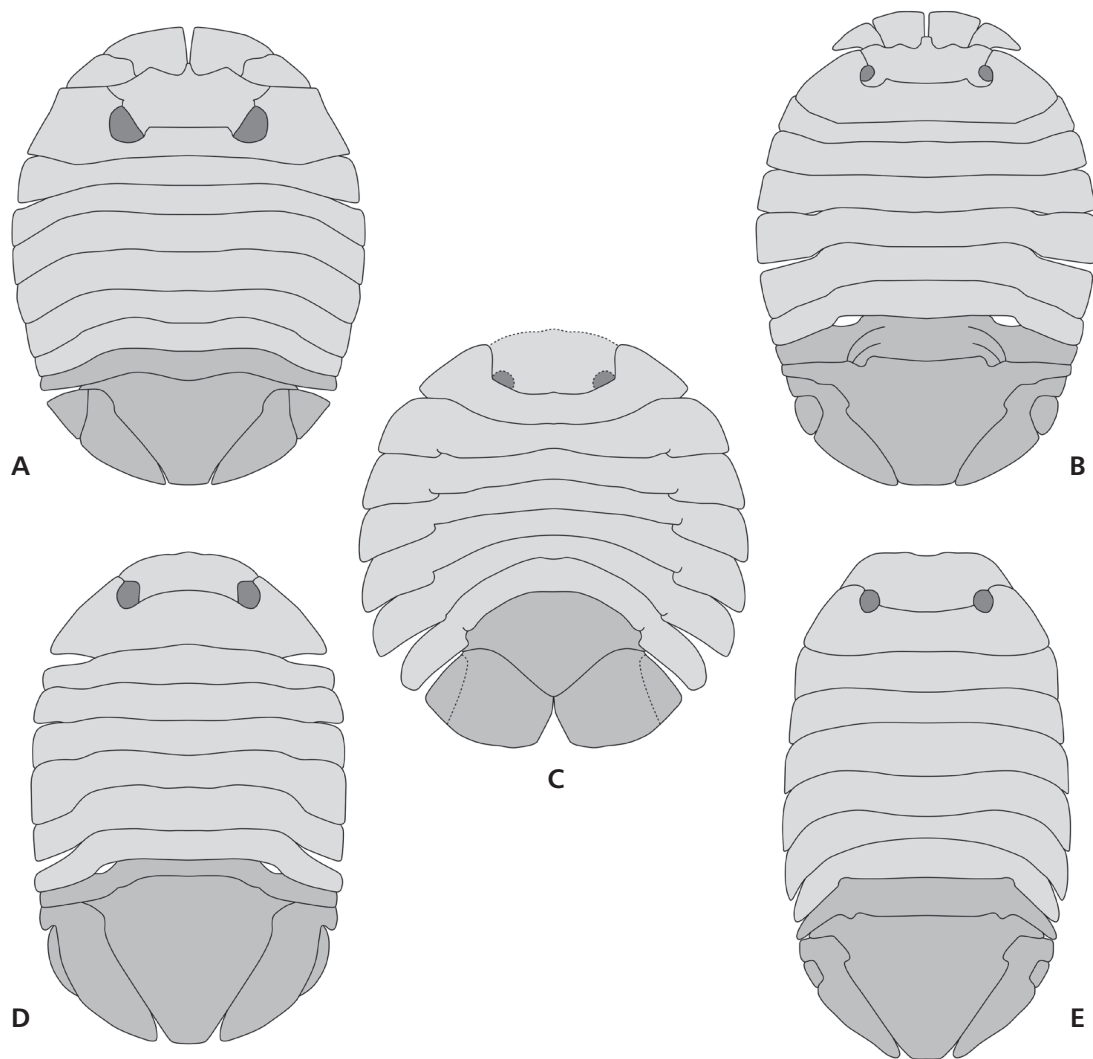


Figure 5. Habitus of different representatives of Sphaeromatidae, pleon and telson region marked with a darker shade of grey. • A – *Platusphaera membranata*, redrawn from Bruce 1994. • B – *Discidina banawarra*, redrawn from Bruce 1994. • C – *Discosalaputium aschauerorum* sp. nov., reconstruction, dotted lines mark body parts which are not preserved in the holotype. • D – *Apemosphaera naranagi*, redrawn from Bruce 1994. • E – *Cassidinidea clarkae*, redrawn from Schotte & Kensley 2005.

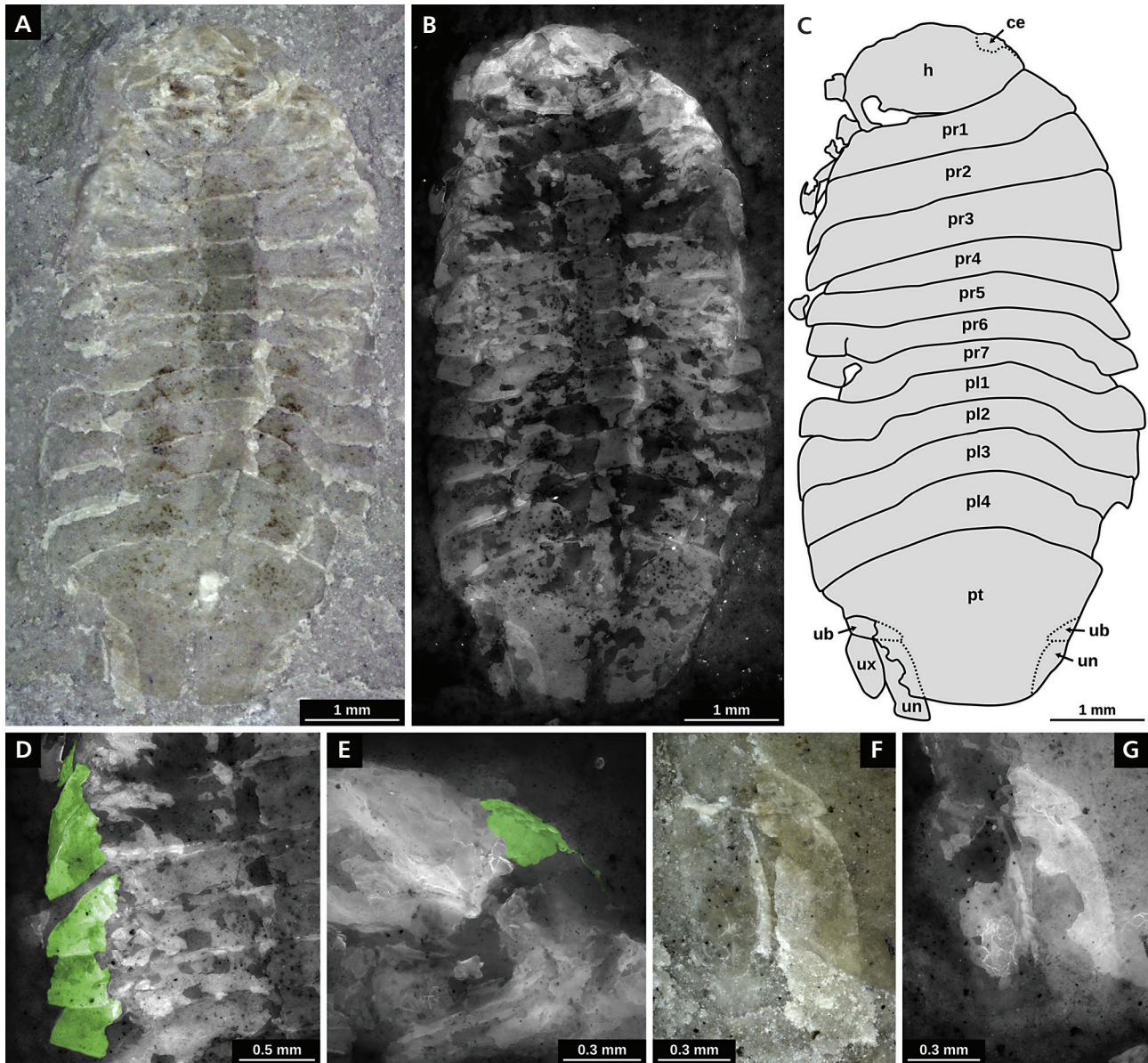


Figure 6. Holotype of *Gelrincola winterswijkensis* sp. nov. (RGM.792591); A – microscopic image, white light microscopy; B – microscopic image, epifluorescence microscopy; C – drawing based on multiple microscopic images; D – detail of the left lateral side of the pereon, (green – coxal plates); E – detail of the lateral head region, epifluorescence microscopy, (green – compound eye); F – detail of the left uropod, white light microscopy; G – detail of the left uropod, epifluorescence microscopy. Abbreviations: ce – compound eye; h – head; pl1–4 – pleon segments 1–4; pr1–7 – pereon segments 1–7; pt – pleotelson; ub – uropod basipod; un – uropod endopod; ux – uropod exopod.

does not represent a monophyletic group of organisms, since only a single species is included (monotypic). Yet, *Gelrincola* may serve as a ‘group name in advance’ if, in the future, another species is found to be the sister-species to the type species of *Gelrincola*.

***Gelrincola winterswijkensis* sp. nov.**

Figure 6A–G

<http://zoobank.org/534AEBC1-F99E-43D1-B09D-6030A3A0185C>

Types. – Holotype and only type, RGM.792591, Museum Naturalis, Leiden, Netherlands.

Type horizon and locality. – Lower Muschelkalk Vossenveld Formation, Anisian, 245.9 to 237 million years (Ogg 2012); Winterswijk, Gelderland, Netherlands.

Material. – Holotype only.

Etymology. – After the name of the town ‘Winterswijk’, the field site where the holotype was found.

Diagnosis. – Body obround in dorsal view, about half as wide as long; head more than twice as long as the subsequent pereon tergite; pleon segment 5 without free tergite; pleotelson wider than long; uropod basipod triangular with median angle located ventral to the pleotelson; uropod endopod posteriorly protruding beyond the posterior margin of the pleotelson.

Description. – Preservation of the holotype: Strongly compressed remains of the exoskeleton; specimen accessible in dorsal view.

Description of the holotype: The body is composed of a head (ocular segment and postocular segments 1–6) and a trunk (postocular segments 7–19). The trunk is divided into two functional tagmata: the pereon (postocular segments 7–13) and the pleon (postocular segments 14–19, dorsal sclerite of one segment missing in the holotype). Pleon segment 6 conjoined with the telson forming the pleotelson. Body in dorsal view with straight lateral sides and rounded anterior and posterior side, about half as wide as long. Measurements are listed in Tab. 4.

Head half circular in dorsal view, posterior margin slightly convex; compound eyes at the lateral side of the head, touching the lateral outline in dorsal projection. Pereon segment 1 about half of the length of the head, much wider than long, distinctly broader than the head,

posteriorly increasing in width, anterior margin slightly concave, posterior margin straight, lateral margin anterolaterally projected and straight to slightly convex. Pereon segment 2 wider than preceding segment, anterior margin straight, posterior margin straight throughout most of the width and concave at the lateral-most part. Pereon segment 3 similar to preceding segment but posterior margin slightly concave. Pereon segment 4 shorter than the preceding segment, narrower or about as wide as preceding segment. Pereon segment 5 about as long as preceding segment, wider than preceding segment, anterior margin convex, posterior margin concave, lateral margins rounded. Pereon segment 6 similar to preceding segment. Pereon segment 7 similar to preceding segment. Pleon segment 1 longer and wider than the preceding segment, anterior margin convex in the median part and concave in the lateral part, posterior margin concave in the median part and convex in the lateral part, anterolateral corner rounded, posterolateral corner angled. Pleon segment 2 similar to preceding segment but slightly narrower. Pleon segment 3 longer and narrower than preceding segment, anterior margin convex in the median part and slightly concave (less than in the preceding segments) in the lateral part, anterolateral corner rounded, posterolateral corner angled. Pleon segment 4 longer and narrower than preceding segment, anterior margin convex in the median part and slightly concave in the lateral part, posterior margin concave.

Pleotelson narrower and about three times longer than preceding segment, about one and a half times wider than long, anterior margin convex; posterior margin trapezoid to semi-circular in dorsal view, posterior side ‘truncated’ (median portion of the posterior margin almost straight. Uropods inserting laterally on the pleotelson at about mid-length of the pleotelson, about 60% as long as the pleotelson; basipod short and wide, triangular in shape, proximal margin straight, distal margin slightly convex, lateral margin straight, median side angled; endopod parallelogram-shaped, much longer than wide, distal end ‘truncated’ (straight distal margin), lateral margins straight, median margin with weak denticulate pattern in the proximal part; exopod about as wide as the endopod, preserved part much shorter than the endopod, median margin slightly convex. It should be noted that, to our knowledge, this specimen constitutes the oldest known isopod fossil from the Netherlands.

Remarks. – The posteriormost pair of appendages, together with the (pleo-) telson, forms a tail fan (autapomorphy of Eumalacostraca, Ax 2000). Although the low relief preservation of the holotype does not allow to estimate the exact dorsoventral aspect of the living animal, due to the positioning of the holotype, it can be concluded that *Gelrincola winterswijkensis* sp. nov. was wider than high. A dorsoventrally flattened body can be seen as apomorphic

Table 4. Measurements of *Gelrincola winterswijkensis* sp. nov. (RGM.792591).

Body part	Length	Width
complete body	7.30 mm	3.65 mm (pleon segment 1)
head	0.99 mm	1.92 mm
pereon segment 1	0.42 mm (along the midline)	2.72 mm
pereon segment 2	0.47 mm (along the midline)	3.29 mm
pereon segment 3	0.51 mm (along the midline)	3.40 mm
pereon segment 4	0.37 mm (along the midline)	3.12 mm
pereon segment 5	0.37 mm (along the midline)	3.50 mm
pereon segment 6	0.32 mm (along the midline)	3.50 mm
pereon segment 7	0.29 mm (along the midline)	3.24 mm
pleon segment 1	0.34 mm (along the midline)	3.65 mm
pleon segment 2	0.34 mm (along the midline)	3.61 mm
pleon segment 3	0.44 mm (along the midline)	3.48 mm
pleon segment 4	0.61 mm (along the midline)	3.78 mm (reconstructed from one body side)
pleotelson	1.90 mm	2.95 mm
uropod basipod	0.21 mm	0.63 mm
uropod endopod	0.95 mm	0.35 mm
uropod exopod	0.68 mm	0.32 mm

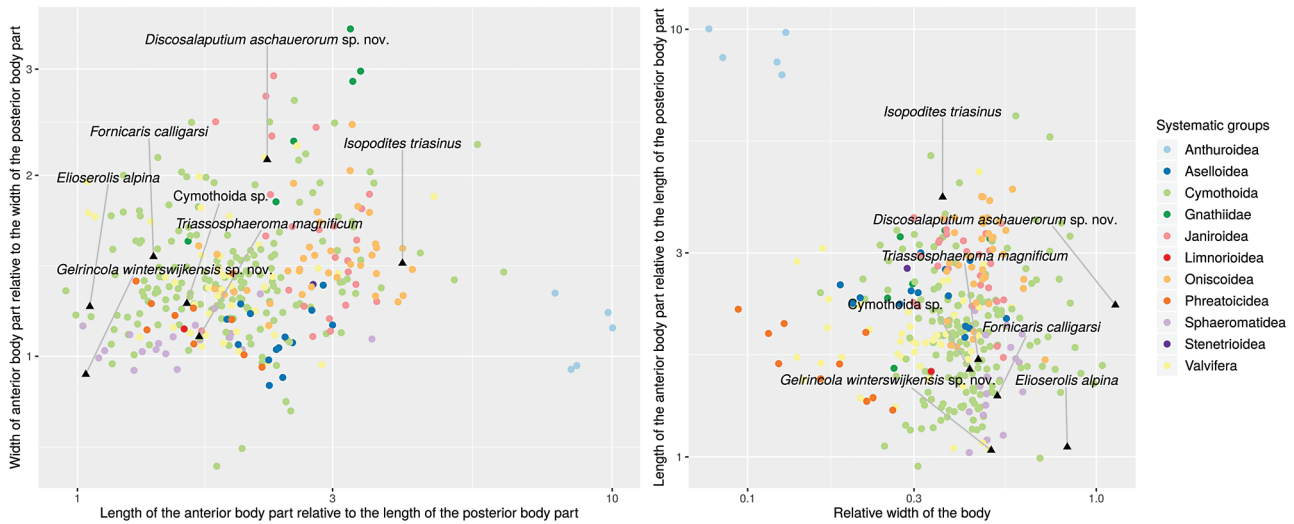


Figure 7. Scatter plots, showing ratios of morphometric measurements of extant and Triassic representatives of Isopoda. Triassic fossils marked by black triangles; extant specimens marked by small circles, both plots correspond to the legend on the right side.

for a monophyletic ingroup of Isopoda (*Isopoda nec Phreatoicoidea*; see discussion above). The posteriormost pleon segment is conjoined with the telson (‘pleotelson’) and the head shield is not constituted by postocular segment 7 (pereon segment 1). Both of those features are present in the ground pattern of Isopoda (Wägele 1989, Brusca & Wilson 1991, Ax 2000). The presence of coxal plates (Fig. 6D) is autapomorphic for Scutocoxifera (Dreyer & Wägele 2002). The basipod of the uropod is triangular and the median angle is located ventral to the pleotelson (Fig. 6F, G). This condition is apomorphic for Cymothoidea (Wägele 1989).

Morphological comparison of the fossils to extant representatives of Isopoda

For this morphological inspection which is graphically represented by Fig. 7, the morphology of the isopod body is drastically simplified. Only the length and width of two regions of the body are considered: anterior region (head capsule and pereon), posterior region (pleon and telson). Some ingroups of Isopoda with extant representatives (based on arbitrary samples of extant representatives) have little variance in the observed variables, resulting in relatively dense point clouds in the plots (Fig. 7, e.g. Asselloidea, Oniscoidea and Phreatoicoidea). Other groups such as Valvifera and Cymothoidea have relatively more variance in those variables, resulting in less dense point clouds in the plots. Anthuroidea is the only isopod ingroup which is graphically distinctly separated from the remainder groups (Fig. 7). This is a result of a unique body shape. Anthuroideans have a long and slender body with a very short pleon. There is no such body shape known

from the Triassic fossil record. Some phreatoicoideans have equally slender bodies, however their pleon and telson region is proportionally longer (Fig. 7, right plot). There is a reconstruction of the dorsal view of *Protamphisopus wianamattensis* in Nicholls (1942). Yet, due to the incompleteness of this reconstruction, we decided not to include measurements from it. However, it can be assumed that *Protamphisopus wianamattensis* falls within the same range as the included extant specimens (we tried to cover as much of the morphological diversity as possible).

All of the Triassic specimens fall within the range of extant forms of Isopoda and do not plot in areas that are dominated by a single ingroup of Isopoda. Consequently, no indications of relationships can be drawn from this analysis. The posterior body region of *Gelrincola winterswijkensis* sp. nov. is wide compared to the majority of measured specimens. This might be a preservational artefact, as the specimen is a compression fossil and the lateral aspect of the anterior body part (coxal plates) may have behaved differently from the lateral aspect of the posterior body region (tergopleura of the pleon). The relative width of the complete body in *Discosalaputium aschauerorum* sp. nov. is quite extreme. This is partly also a result of the missing head in the holotype (measurements were performed, assuming a short head that does not extend beyond the anteriormost part of the first pereon tergite). In *Isopodites triasinus* the number of free pleon tergites is strongly reduced (likely only one free pleon tergite). This results in a comparably short posterior body region, though it is by far not as short as in Anthuroidea. The species *Obtusotelson summesbergeri* sp. nov. was not included in this analysis because, due to the preservation of the holotype, it was not possible to reconstruct the aspects by which the other species are compared.

Discussion

Diagnoses

It is very likely, that the herein provided diagnoses are not sufficient to distinguish the herein described species from all known fossil and extant species. However, they are sufficient to separate them from all other Triassic species and also from the Palaeozoic species. There is an age gap between the youngest herein described species and the beginning of the Jurassic of at least 34.1 million years (Fig. 2). This time interval is large enough to assume that, if there were fossils with a very similar morphology in the Jurassic, the herein described species are not conspecific to any already described species.

Interpretation of *Anhelkocephalon handlirschi* Bill, 1914

From the same locality as *Palaega pumila*, another species has been described, *Anhelkocephalon handlirschi* Bill, 1914, also interpreted as a representative of Isopoda. The holotype and a single paratype (both have never been figured) have presumably been destroyed during a fire (Schwebel *et al.* 1983). Further material from the same site, that matched the diagnosis given by Bill (1914), has been assigned as the neotype and paraneotype of the species by Schwebel *et al.* (1983). The morphology that is apparent in the two available types does not provide convincing features that would allow for an interpretation as a representative of Isopoda. The character states listed by Schwebel *et al.* (1983) for their systematic interpretation can hardly be considered autapomorphic for Isopoda. Brandt *et al.* (1999) raised doubts about the interpretation of *Anhelkocephalon handlirschi* as a representative of Isopoda. In our view, there are features in the posterior part of the body that strongly resemble that of representatives of the enigmatic group Cycloida rather than those of Isopoda (*cf.* drawings and reconstructions in Dzik 2008). Further examination of the types will be needed to further compare the fossils of *Anhelkocephalon handlirschi* to Cycloida.

Interpretation of *Ferrensicus magransi* Calzada & Urquiola, 1994

Parts of the reconstruction and the subsequent systematic interpretation of *Ferrensicus magransi* appear doubtful, as there are discrepancies between the reconstruction drawing and a photograph provided in the holotype database of the corresponding museum collection (Institut Cartogràfic i Geològic de Catalunya 2018, collection number 52506).

A redescription and restudy of *Ferrensicus magransi* could be interesting from a systematic viewpoint, as *Ferrensicus magransi* is suggested to be a sister-taxon to the group Archaeoniscus (Calzada & Urquiola 1994, Calzada *et al.* 2011); yet this interpretation could be the result of arbitrary systematic practice (*e.g.* arbitrary allocation of diagnostic characters to species and monotypic taxa) that is persisting throughout the literature.

Uropods

There has been much dispute about the uropod morphology in the ground pattern of Isopoda. Wägele (1989, 1994) reconstructed the ground pattern of Isopoda with flat uropod endo- and exopods. In contrast, Brusca & Wilson (1991) reconstructed the ground pattern of Isopoda with styliform uropod endo- and exopods. A comparison with suitable outgroups (representatives of Tanaidacea and Cumacea have styliform uropod endo- and exopods) suggests that styliform uropods have been present in the stem species of Isopoda (Kutschera *et al.* 2012). This is also consistent with the fossil record – the oldest fossils of the group have styliform uropod endo- and exopods (Schram 1970, Racheboeuf *et al.* 2009).

The reconstruction of the ground pattern of Isopoda for this character is of major concern for the interpretation of fossils of the group. If styliform uropod endo- and exopods are reconstructed for the ground pattern of Isopoda, then the most parsimonious conclusion is that the styliform uropod endo- and exopods of many lineages (*e.g.* Phreatoicidea and Asellota) are plesiomorphic and the flat uropod endo- and exopods evolved within Scutocoxifera (Wilson 1996, *cf.* Dreyer & Wägele 2002). Thus, fossils of Isopoda with flat uropods could be interpreted as scutocoxiferans, even if the coxal plates are not preserved or not distinctly separated from the tergite.

Both Scutocoxifera and its ingroup Cymothoidea have a fossil record older than the herein presented fossils. The earliest record of scutocoxiferans is from the Early Permian (Mezzalana & Martins-Neto 1992, Martins-Neto 2001). The earliest record of a representative of Cymothoidea is *Palaega pumila* (Gall & Grauvogel 1971), which is likely a bit older than *Gelrincola winterswijkii* sp. nov. (see Fig. 2 and ‘Geological setting of the Winterswijk locality’).

Above, we mentioned the possibility that *Discosalaputium aschauerorum* sp. nov. might be a representative of Sphaeromatidea. If this is true, *Discosalaputium aschauerorum* sp. nov. would indeed be the earliest fossil record of this group. Yet, to further support this assumption, the examination of further specimens is needed. Especially, the structure of the uropods could be helpful for a more precise systematic interpretation.

Decrease of phreatoicideans

The relative abundance of phreatoicideans compared to representatives of its sistergroup (all remaining lineages of Isopoda) has rapidly decreased since the Carboniferous. In the Carboniferous both of the two formally described species are phreatoicideans (100% phreatoicideans) (Schram 1970, Racheboeuf *et al.* 2009). In the Permian three out of five formally described species are phreatoicideans (60% phreatoicideans) (Schlotheim 1820, Schauroth 1854, Kirkby 1857, Geinitz 1861, Glaessner & Malzahn 1962, Mezzalana & Martins-Neto 1992, Martins-Neto 2001). In the Triassic two out of twelve formally described species (and two not formally described species, including the herein described species) are phreatoicideans (16.7% phreatoicideans) (Picard 1858, Chilton 1918, Gall & Grauvogel 1971, Basso & Tintori 1994, Wilson & Edgecombe 2003, Fu *et al.* 2010, Schöllmann *et al.* 2015, Selden *et al.* 2016). In the Jurassic there are at least 35 formally described species of Isopoda which are not representatives of Phreatoicidea (Meyer & Münster 1840; Milne Edwards 1843; Westwood 1854; Ammon 1882; Woodward 1890; Carter 1889; Stolley 1910; Remeš 1912; Van Straelen 1928; Reiff 1936; Frentzen 1937; Bachmayer 1955; Radawanski 1995; Grant-Mackie *et al.* 1996; Polz 1998, 2005a, b; Guinot *et al.* 2005; Polz *et al.* 2006; Etter 2014; Jones *et al.* 2014; Gašparič *et al.* 2015; Keupp & Mahlow 2017). This is in contrast to one, not formally described, phreatoicidean from Antarctica (Borns *et al.* 1972) (0.3% phreatoicideans). Also, phreatoicideans disappeared from marine sediments and have their youngest marine record in the Middle Triassic (Fu *et al.* 2010) and the youngest (freshwater) record in the Jurassic (Borns *et al.* 1972).

The proportional decrease in phreatoicideans does not only reflect the systematic aspect but also a morphological aspect, as phreatoicideans are rather limited in their body shape (*cf.* figures in Nicholls 1942, 1943 and Fig. 7), whereas within its sistergroup a wide variety of body shapes evolved (*e.g.* figures in Brandt & Poore 2003 and Fig. 7).

Systematic bias towards scutocoxiferans in the fossil record

It is noteworthy that all of the herein described species, and all but one previously described Triassic species, are scutocoxiferans. The one other species has been interpreted as a representative of Asellota (Selden *et al.* 2016). The Triassic record of Asellota (Selden *et al.* 2016) is also the only formally described or figured one of the group, up to date (see personal communication in Selden *et al.* 2016 for further putative occurrences). The scarcity of fossils of Isopoda that are neither representatives of Phreatoicidea nor Scutocoxifera might be an indication that they lived

in areas which are not ideal for the fossilisation of their remains (*e.g.* deep sea, fluviatile freshwater environments, etc.) or that their preservation potential is poor (see also discussion in Selden *et al.* 2016).

Conclusions

Three new species of Isopoda can be added to the seven already formally described species of Isopoda from the Triassic. All of the here described species are representatives of Scutocoxifera and one of them – *Gelrincola winterswijkii* sp.nov. – is also a representative of the scutocoxiferan ingroup Cymothoidea. These fossils substantially increase our knowledge about the morphological diversity of isopods in the Triassic. The herein described species *Discosalaputium aschauerorum* sp. nov. adds a further disc-shaped form with strongly reduced pleon to the Triassic fossil record and might be the oldest fossil record of Sphaeromatidea; however, the affinity is partly ambiguous and the same overall-morphology could also have evolved in other lineages.

There are still large stratigraphic gaps for the fossil record of Isopoda within the Triassic (*e.g.* in the Early Triassic and in the Late Triassic during the Carnian and the Norian and in the Rhaetian). Also, certain body shapes are still lacking in the Triassic fossil record, that occur later on in the Jurassic, such as slender, not laterally compressed isopods (*e.g.* *Urda rostrata* Münster in Meyer & Münster, 1940). Perhaps future discoveries of Triassic isopod fossils will reveal new body shapes. Furthermore, it will be interesting to see if future findings might be able to close the aforementioned stratigraphic gap

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Appendix

Translation of the original description of *Isopodites triasinus* Picard, 1858: "Before I close this communication, I have to mention an animal belonging to the family of crustaceans ['Kruster' in the original], which will not of no interest with respect to the scarcity of this class of animal. *Sphaeroma triasina* nov. sp. fig. 11. This interesting finding from the limestone banks of our Keuper transitions, which I provisionally attributed to the pill-bugs, is located on the shell of *Ammonites nodosus*. The body organisation and namely the structure of the antennae points toward a placement within the pill-bugs – which is why decided to do so. The characterisation I will give in the following.

Antennae: two pairs of which the longer ones point to the front and the shorter ones to the rear. The front antennae consist of two pairs, a peduncle-like proximal element and a flagellum with multiple elements, which gave the flagellum movability. The length of this large antennae is 4 mm of which one half is made up by the peduncle and the other half is made up by the flagellum. The length of the complete body is 13 mm and the width is less than 4 mm. The body is vaulted except for the shield-like tail shield [= pleotelson], which consists of a single piece and is ornamented by a median carina. The head shield is pushed in, as are the body shields [= tergites] but like those it is

completely preserved; of the latter [= tergites] 7 are preserved. Aside from those and the tail shields [= pleotelson and uropods], which probably acted like a fin, it seems that there have been one or two rings, which belong to the latter [probably the pleotelson is meant here]. However, those are so heavily damaged that they cannot be discerned properly. Of the lateral legs there are only two, barely, visible on the left side. While the posterior legs [= uropods] are scissor-like forked and are located to both sides of the tail shield [= pleotelson]. One, a bit longer second distal element pair [likely a posterior pereopod] has been present of which there is a rudiment visible on the left side. On the right side nothing of this kind is visible."

Supplementary File 1. Graphical representation of the measurements used for Fig. 7 exemplified on a drawing of *Cirolana harfordi* (based on a photograph, © Peter J. Bryant). Red rectangles represent the measurements performed on the literature specimens. Upper rectangle, length and width of head and pereon combined; lower rectangle, length and width of head and pleon combined.

Supplementary File 2. Measurements used for Fig. 7.

Supplementary File 3. R code used to create Fig. 7.