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A new genus and species of terrestrial isopod (Isopoda: Oniscidea) found in Baltic amber

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Abstract. The knowledge of fossil terrestrial isopods is of rudimentary nature and the diversity of terrestrial isopods in the geological past is poorly represented in the current taxonomy of the suborder. Although the number of described fossil species has increased in recent years, many taxa remain undescribed, and several existing species face taxonomic issues due to inadequate or outdated descriptions. No valid representatives of the section Crinocheta, the most diverse section of terrestrial isopods, are currently recognized from Baltic amber. To improve our understanding of the suborder Oniscidea (Latreille, 1802) and its diversity in geological times, we describe the new genus and species *Balticoniscus walterludwigi* gen. et sp. nov. from Eocene Baltic amber.

Keywords. Cenozoic, Crinocheta, Eocene, woodlice.

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Introduction

Terrestrial isopods are a remarkably diverse group characterized by many adaptations for a terrestrial lifestyle (Hornung 2011). In recent times, terrestrial isopods are found on all continents, with the exception of Antarctica, and populate a wide range of ecosystems such as forests, grasslands, coastal areas, caves, urban environments, and even arid desert habitats (Schmalfuss 2003; Schmidt 2008; Hornung 2011). Over 3800 species are described (WoRMS Editorial Board 2024), with an estimated number of up to 3000 species being still undescribed (Sfenthourakis & Taiti 2015). Surprisingly, the fossil record of Oniscidea Latreille, 1802 remains poorly known, with only about sixty records across all families and geological ages, and just 20 described species from the section Crinocheta Legrand, 1946 – six of which are of disputed validity (Schmalfuss 2003; Schmidt 2008; Lu *et al.* 2023; WoRMS Editorial Board 2024). Furthermore, taxonomic issues complicate the record, particularly for species erected before the late 1900s, but also more recently described species face issues, namely *Armadillidium payangadensis* Srivastava, Shukla, Kumar, Kumar & Prakash, 2006, which does not appear to be an isopod at all (Schmidt 2008). Somewhat similar is the case of *Armadillidium molassicum* (Heer, 1865), where it is not possible to confirm the species as a member of Oniscidea (Schmidt 2008). Other species face taxonomic issues of a different nature, such as *Palaeoarmadillo microsoma* Poinar, 2018, which, based on our assessment of its morphology, is not a member of the family Armadillidae Brandt, 1831 but likely belongs to Tylidae Dana, 1852. Recognizably described species from the section Crinocheta comprise one species, *Heraclitus helenae* Sánchez-García, Peñalver, Delclos & Engel, 2021 putatively assigned to the family Detonidae Budde-Lund, 1904 from Cretaceous Spanish amber (Sánchez-García *et al.* 2021), eight species from the families Philosciidae Kinahan, 1857, Stenoniscidae Budde-Lund, 1904, Detonidae Budde-Lund, 1904, Olibrinidae Budde-Lund, 1912 and Scleropactidae Verhoeff, 1938 from Miocene Chiapas amber (Broly *et al.* 2017, 2018), *Protosphaeroniscus tertiaries* Schmalfuss, 1980 and two species of *Pseudarmadillo* Saussure, 1857 from Dominican amber (Schmalfuss 1980, 1984), as well as *Eubelum rusingaense* Morris, 1979 preserved in rock from the Lower Miocene of the Hiwegi Formation, Kenya (Morris 1979). The previously mentioned *Armadillidium molassicum*, as well as the species *Oniscus convexus* Koch & Behrendt, 1854, *Porcellio cyclocephalus* Menge, 1854, *Porcellio granulatus* Menge, 1854 and *Porcellio notatus* Koch & Behrendt, 1854 from Baltic amber are not recognizably described (Schmalfuss 2003; Schmidt 2008; Lu *et al.* 2023). Following this, no valid crinochetan species is known from Baltic amber at present. In addition, there is no reliable evidence to support the identification of fossil specimens as extant species, as pointed out by Weitschat & Wichard (2002) regarding some specimens from Eocene Bitterfeld amber. A complete list of fossil records of Oniscidea is provided by Lu *et al.* (2023).

As is common for arthropods, terrestrial isopods fossilize very rarely in sediments and seldom in a state that allows a detailed description. Thus, amber inclusions offer great opportunities to study isopod species from geological times. While woodlice are associated with wooded, and thus resin-rich habitats, they remain rare in amber, despite being more frequently encountered than the small number of described species would suggest. This unexpected scarcity may result from taphonomic biases, such as the limited preservation of larger individuals, or possibly a lower isopod biomass in ancient ecosystems. Fortunately, the number of species descriptions has increased over the recent years (e.g., Broly *et al.* 2015, 2017, 2018; Sánchez-García *et al.* 2021), but many taxa are yet to be described. New descriptions are further impeded by oniscidean amber inclusions facing several challenges such as clouding, or the inaccessibility of important characters of the mouthparts, pereopods, and pleopods (Broly *et al.* 2018). Due to this, the evolutionary history of terrestrial isopods is still poorly understood, and their fossil record is almost entirely unknown. To fill these major gaps, a taxonomic foundation is necessary to receive more insights into the diversification, biogeographic distribution and evolutionary history of terrestrial isopods. In this work, a new genus and species are described from Eocene Baltic amber to facilitate future comparative research.

Material and methods

Amber deposit

The present piece of amber with an isopod inclusion was donated to the Paleontological Collection of the University of Tübingen by Walter Ludwig, who acquired it directly from an amber fisherman in the 1960s. The specimen, originating from Jantar in Poland, is considered Baltic amber, which is part of the Prussian Formation from the Eocene. Here, the amber layers are embedded in the 'blue earth' and were either allochthonously deposited with a redeposition during glacial periods (Seyfullah 2018) or a more direct deposition without a major hiatus (Standke 2008). While older depositional periods were once assumed, there is increasing evidence of a late Eocene formation (Alekseev & Alekseev 2016; Sadowski *et al*. 2017; Moser *et al*. 2021). According to chemical analyses (Wolfe *et al*. 2009) and amber inclusions of plant material (Sadowski *et al*. 2016), the possible main producer of the resin that formed the amber is found among the Sciadopityaceae Luerss.

Morphological examination and imaging

No additional preparation of the amber was performed, as the isopod specimen was already very close to the surface, allowing for imaging without further modification. Images in Fig. 1A–B were stacked from multiple photographs taken with a Canon EOS 60D and a Canon EF-S 60 mm f/2.8 Macro USM lens. Photographs were stacked into a single image with Digital Photo Professional ver. 4 (www.canon.de/software/digital-photo-professional). Images in Fig. 1C–D were taken with a SWIFTCAM SC1300 microscope camera mounted on a BMS 74958 stereo microscope. All images were taken in the facilities of the Terrestrial Paleoclimate working group at the University of Tübingen. Illustrations were drawn with GIMP ver. 2.10.38 (www.gimp.org). The µCT-scan was acquired with a Nikon XT H 320 X-ray scanner of the Senckenberg Centre for Human Evolution and Palaeoenvironment and the Eberhard Karls University of Tübingen. Volume rendering was performed with Drishti ver. 3.2 (https://github.com/nci/drishti).

Institutional abbreviation

GPIT = Paleontological Collection of the University of Tübingen, Tübingen, Germany

Results

Class Malacostraca Latreille, 1802
Order Isopoda Latreille, 1816
Suborder Oniscidea Latreille, 1802
Section Crinocheta Legrand, 1946
Family incertae sedis

Balticoniscus gen. nov.
urn:lsid:zoobank.org:act:4338CAC0-D29E-4571-B38D-EF36A222A20C

Type species

Balticoniscus walterludwigi gen. et sp. nov.

Diagnosis

Balticoniscus gen. nov. is characterized by the following unique combination of characters: body strongly convex. Dorsum smooth. Cephalon with frontal shield expanded into wide medial lobe occupying entire space between eyes and protruding over vertex. Anterior margin of cephalon strongly convex in dorsal view. Antennary tubercles present and projecting ventrally, not projecting anteriorly, and not visible in dorsal view of cephalon. Flagellum of antenna two-segmented with distal article three times as long as first. Eyes moderately large, consisting of multiple ocelli. Pereonite epimera without ventral structures for conglobation. Epimera of pereonites II–VII rectangular, anterior corner rounded. Protopodite of uropod cylindrical. Uropod exopodite short and acute, with apex shortly surpassing pleotelson. Endopodites shortly project past posterior tip of pleotelson. Pleotelson triangular, lateral margins weakly concave.

Etymology

The name *Balticoniscus* gen. nov. is a reference to the type specimen being preserved in baltic amber, combined with '-oniscus', a suffix traditionally used for members of Oniscidea.

Balticoniscus walterludwigi gen. et sp. nov.

urn:lsid:zoobank.org:act:BD4A386F-22AD-41FD-A7F5-03D7CAACD70F
Figs 1–3

Diagnosis

As for the genus vide supra.

Etymology

The species is named in honor of Walter Ludwig, who generously donated the amber to the Paleontological Collection of the University of Tübingen.

Type material

Holotype

POLAND • ♀; Jantar; 1960s; W. Ludwig leg.; GPIT, GPIT-PV-108383.

Description

Habitus. Maximum body length 4.2 mm. Pereon strongly convex, pleon less convex compared to pereon. Dorsum smooth with weakly rugose muscle spots and covered with small triangular scale setae (Fig. 1D). Scale setae 1.5 times as wide as long.

Cephalon. Cephalon 2.1 times as wide as long. Cephalon with frontal shield developed into wide medial lobe shortly protruding over vertex and occupying entire space between eyes (Fig. 2A–B, D). Antennary tubercles project strictly ventrally (Fig. 1A–B). Shallow transverse groove running along posterior margin of cephalon (Figs 1C, 2D). Eyes moderately large with at least 15 ocelli, half the length of cephalon in lateral view. Antennae short and relatively stout, not reaching posterolateral corner of first pereonite. Length to width ratio of second peduncle of antenna 1.3. Length to with ratio of third and fourth peduncle 1.7. Length to width ratio of fifth peduncle 4.5. Fifth peduncle 2.2 times as long as preceding peduncle and 1.4 times as long as flagellum. Flagellum two-segmented with distal article three times as long as proximal article and five times as long as wide (Fig. 2G).

Pereonites. Pereonites with weakly pronounced muscle spots, almost smooth (Fig. 3C–D). Epimera of pereonite I with convex lateral margin, posterior margin weakly concave. Posterolateral corner of epimera rounded, anterior corner acutely rounded (Fig. 2A). Epimera of pereonites II–VII quadrate with weakly rounded anterolateral corners. Posterior margins of pereonites I–V laterally weakly concave, successively more straight moving posteriorly. Posterior margins of pereonites VI–VII entirely straight (Fig. 2A). All pereonite epimera without ventral articulatory structures.

Pereopods. Carpus of female pereopod 1 with sternal ridge-like projection present along entire length of carpus, reaching its apex at ⅔ of length of carpus (Fig. 2H). Pereopods 1–6 otherwise without particular modifications.

Pleonites. Epimera of pleonites 3–5 quadrate, with weakly pronounced posterolateral corner (Fig. 2A, C, F). Pleonite epimera 3–4 ventrally with transverse ridge to accommodate the succeeding segment. Pleonite epimera 5 with transverse ridge to accommodate uropod protopodite (Fig. 2F).

Pleopods. Exopod of female pleopod 1 subtly triangular with rounded corners, twice as wide as long. Female pleopod exopod 2 subtly triangular with rounded corners, about as wide as long. Female pleopod exopods 3–5 sub-trapezoidal and laterally rounded (Fig. 2E).

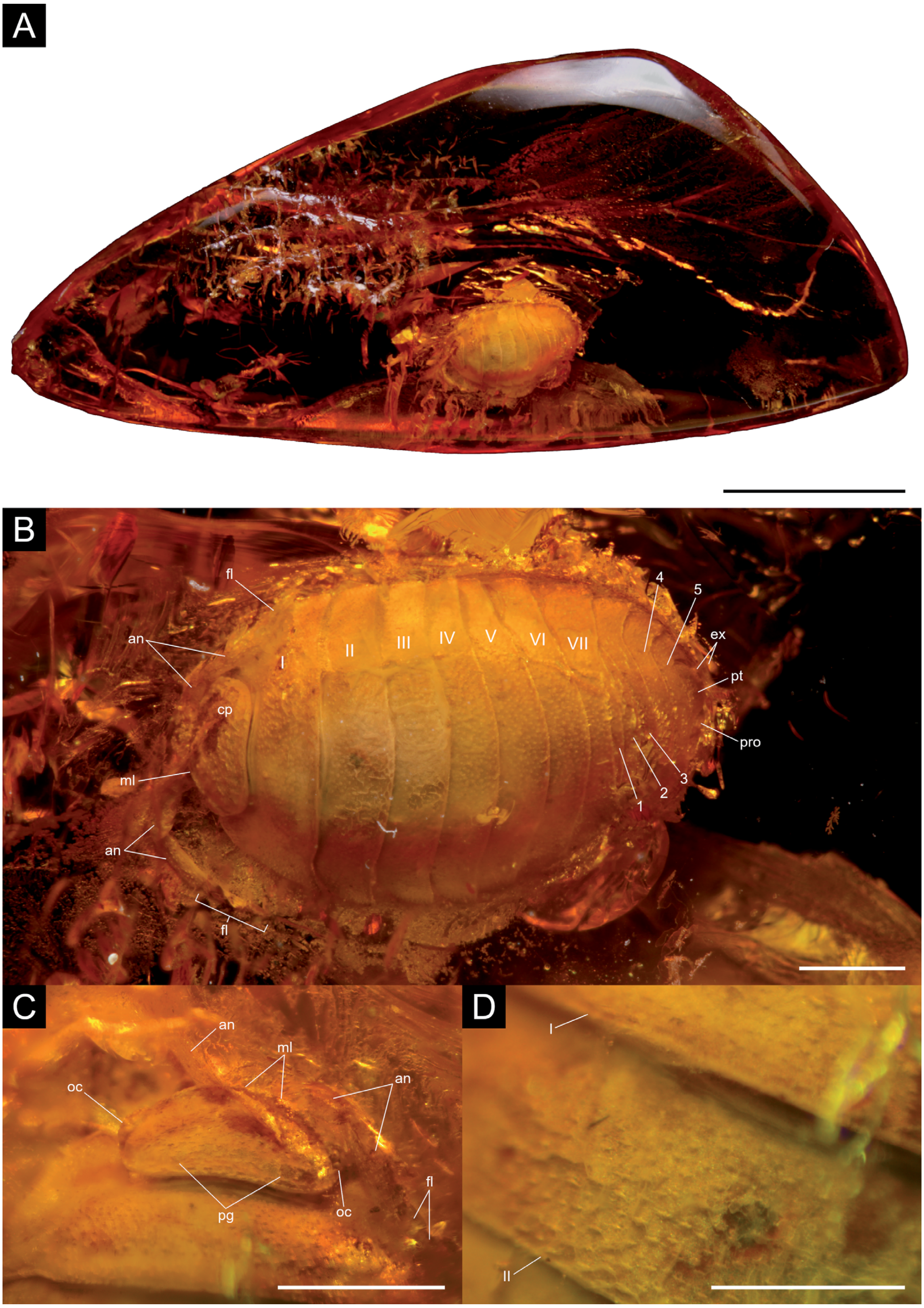

Fig. 1. *Balticoniscus walterludwigi* gen. et sp. nov., holotype, ♀ (GPIT-PV-108383). **A**. Overall view of the amber. **B**. Habitus, dorsal view. **C**. Cephalon, dorsal view. **D**. Scale setae of pereonite I and II. Abbreviations: an = antenna; cp = cephalon; ex = exopodite; fl = flagellum; ml = medial lobe; oc = ocelli/eye; pg = posterior groove of the cephalon; pro = uropod protopodite; pt = pleotelson; I–VII = pereonites; 1–5 = pleonites. Scale bars: A = 5 mm; B–C = 1 mm; D = 0.5 mm.

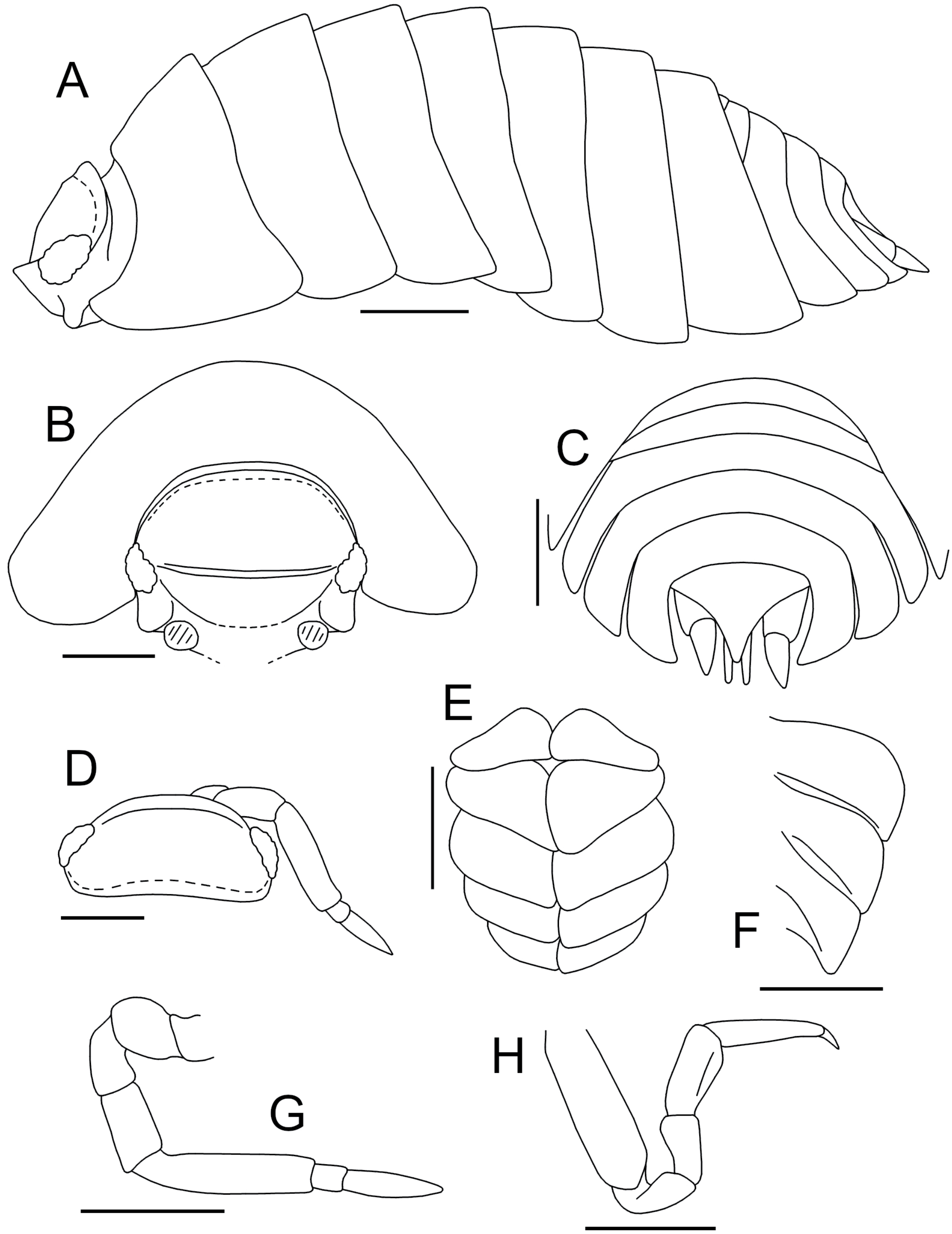

Fig. 2. *Balticoniscus walterludwigi* gen. et sp. nov., holotype, ♀ (GPIT-PV-108383). **A**. Habitus, lateral view. **B**. Cephalon and pereonite I, anterior view. **C**. Pleon, dorsal view. **D**. Cephalon, dorsal view. **E**. Female pleopods, ventral view. **F**. Pleonite epimera 3–5, ventral view. **G**. Right antenna, ventral view. **H**. Pereopod 1, posterior view. Scale bars = 0.5 mm.

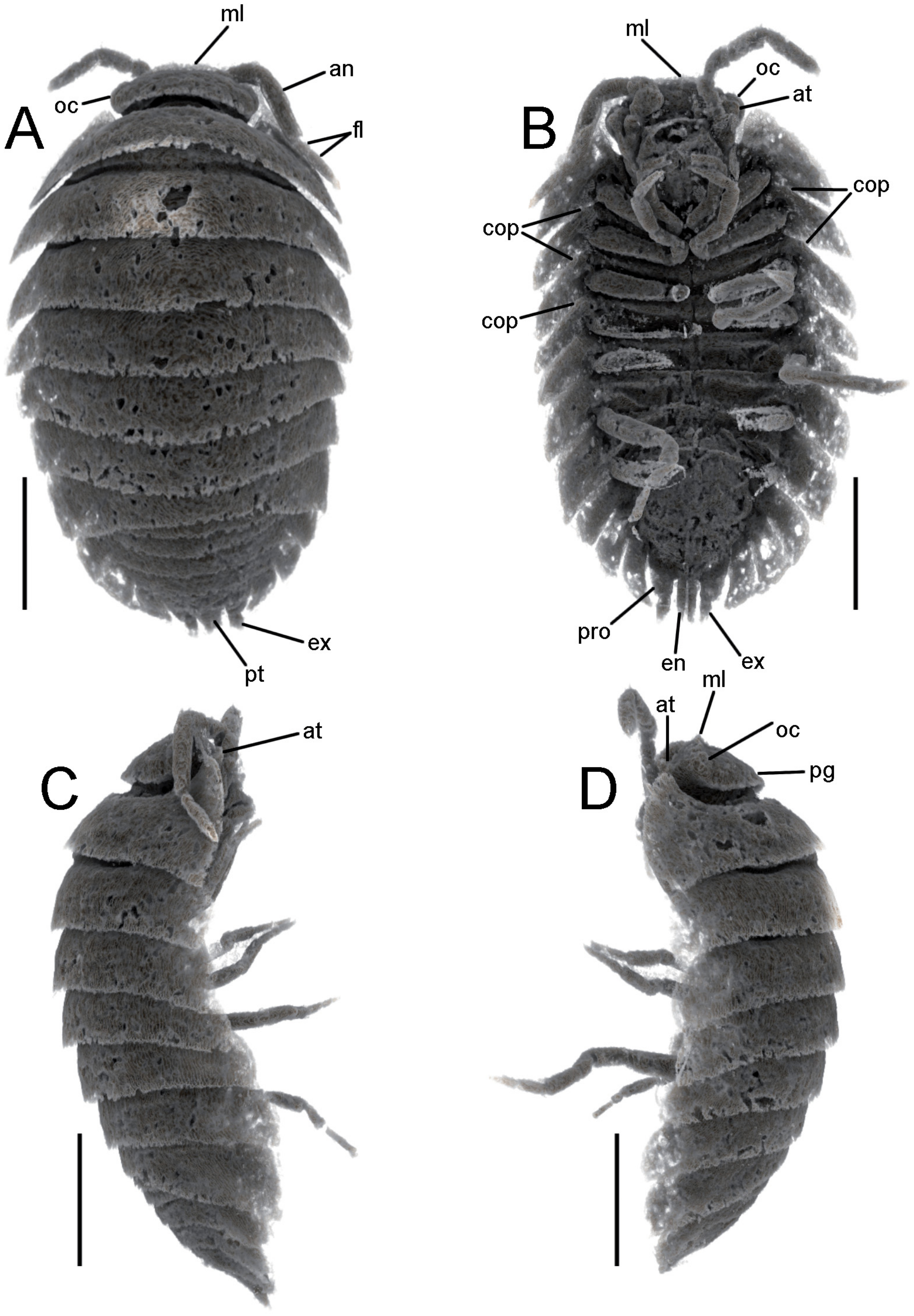

Fig. 3. Volumetric rendering of *Balticoniscus walterludwigi* gen. et sp. nov., holotype, ♀ (GPIT-PV-108383). **A**. Dorsal view. **B**. Ventral view. **C**. Right lateral view. **D**. Left lateral view. Abbreviations: an = antenna; at = antennary tubercle: cop = conoid process; en = uropod endopodite; ex = uropod exopodite; fl = flagellum; ml = medial lobe; oc = ocelli/eye; pg = posterior groove of the cephalon; pro = uropod protopodite; pt = pleotelson. Scale bars = 1 mm.

PLEOTELSON. Pleotelson triangular, as wide as long, with weakly concave lateral margins and not surpassing pleonite 5 posteriorly. Pleotelson strongly acute.

UROPODS. Uropod protopodite cylindrical and short, not exceeding past posterior tip of pleotelson. Uropod endopodite moderately sized, 1.3 times as long as protopodite. Uropod exopodite small and conoid, 0.75 times as long as protopodite. Uropod endopodite and exopodite shortly protruding past posterior tip of pleotelson (Fig. 2C).

Remarks

The entire ventral side, the pleotelson, and the uropods are surrounded by numerous deep cracks, particles, as well as clouding, and could therefore only be examined via µCT-scan. Right pereopods 3–5 and 7, as well as left pereopods 6–7 appear to be preserved only basally, missing the majority of the leg (Fig. 3B). Even though most of the area surrounding the cephalon is obstructed as well, major parts of the antennae are visible (Fig. 1B–C). Some structures that are visible with light microscopy could not be retrieved in the volumetric rendering, notably the flagellum of the left antenna, as well as many small portions of the pereonites and pleonites, which resulted in small holes in the surface of the visualized specimen (compare: Figs 1 and 3). Due to this, it is possible that more of the pereopods is present than could be observed with the volumetric rendering.

The preserved individual appears to be female, as no genital papilla and no pleopod endopodites are present. Given that the seventh pereonite is well-developed and the seventh leg, though only basally preserved, appears to have been well-formed and functional, the preserved individual had progressed beyond the postmarsupial manca stages. It was not possible to determine whether the individual was sexually mature.

Syninclusions

Two Nematocera Latreille, 1825, likely belonging to the family Sciaridae Billberg, 1820, are preserved in the amber as well (Fig. 1A). A more precise identification, or whether these individuals belong to an already described species, is not known at present.

Discussion

Phylogenetic placement of *Balticoniscus* gen. nov.

Unfortunately, as is common with fossil species, not all characters of generic and phylogenetic importance could be examined, such as the mouthparts, the number of pseudotracheae and the lung type. Only a comparison with recent taxa is possible at present, as previously described fossil crinochetan species are either not sufficiently described and of questionable validity or are placed in families which *Balticoniscus walterludwigi* gen. et sp. nov. certainly does not belong to. This comprises namely the crinochetan families Philosciidae Kinahan, 1857, Detonidae Budde-Lund, 1904, Eubelidae Budde-Lund, 1899, Olibrinidae Budde-Lund, 1912, Scleropactidae Verhoeff, 1938, Delatorreiidae Verhoeff, 1938 and, due to the faulty placement of *Palaeoarmadillo* Poinar, 2018, the family Armadillidae (Morris 1979; Schmalfuss 1980, 1984; Broly *et al.* 2017, 2018; Poinar 2018; Sánchez-García *et al.* 2021). Many oniscidean families are currently not defined by autapomorphies (Schmidt 2008), but the familial placement of *Balticoniscus* gen. nov. can only be discussed by comparisons with the few known autapomorphies, as well as the general morphotypes found within the different families and genera of Oniscidea. The character most helpful to assess the familial placement of *Balticoniscus* is the presence of rudimentary conoid processes on the anterior margins of pereonite epimera 2–4. According to Schmidt (2008) these processes, although present here only as subtle protuberances, place *Balticoniscus* inside an unnamed group of Crinocheta that includes the families Bathytropidae Vandel, 1952, Tendosphaeridae Verhoeff, 1930, Oniscidae Latreille, 1802, Trachelipodidae Strouhal, 1953, Cylisticidae Verhoeff, 1949, Agnaridae Schmidt, 2003, Porcellionidae Brandt, 1831 and Armadillidiidae Brandt, 1833. Unfortunately, most of these families are problematic and some likely not monophyletic, which results in unreliable or a lack of unique defining characteristics (Schmidt 2008). *Balticoniscus* cannot be placed in any of these families with certainty, as the new genus differs significantly from the known genera of these families by the small and strictly ventrally projecting antennary tubercles, which do not contribute to the anterior outline of the cephalon, unlike the large anteriorly projecting lateral lobes typically seen in most genera contained in this unnamed group. While this modification of the cephalon appears to be unique for the new genus, it is not present in any other genus and therefore does not indicate a close relationship to any of the known species.

Furthermore, based on the respective groundpattern and apomorphies proposed by Schmidt (2003, 2008), the families Tendosphaeridae Verhoeff, 1930, Oniscidae, Bathytropidae, Cylisticidae and Armadillidiidae can be ruled out. Thus, Porcellionidae, Agnaridae, and Trachelipodidae are the remaining candidates. Although Schmidt (2003) questioned the monophyly of the Porcellionidae – characterized by monospiracular lungs on the first two pleopod exopods – molecular analyses support it as monophyletic (Mattern 2003; Schmidt 2008). Trachelipodidae is regarded as paraphyletic and characterized by 'Trachelipus-type' lungs, from which the monophyletic Agnaridae was split off to accommodate species with 'Porcellio-type' lungs (Schmidt 2008). The lung type in *Balticoniscus* gen. nov. remains undetermined due to the examination of such key internal characters typically requiring dissection. Following this, its placement within this group of families is uncertain.

Conglobation in *Balticoniscus* gen. nov.

Conglobation is a common antipredatory strategy and allows terrestrial isopods to conserve moisture (Smigel & Gibbs 2008; Hornung 2011; Tuf & Ďurajková 2022). This ability evolved multiple times within Oniscidea (Gruner 1953; Schmidt 2008) and can be found in many different families, such as Cylisticidae, Armadillidae, Armadillidiidae, Scleropactidae, Delatorreiidae, Eubelidae Budde-Lund, 1899 or Pudeoniscidae Lemos de Castro, 1973.

The strongly convex dorsum of *Balticoniscus walterludwigi* gen. et sp. nov. is reminiscent of extant conglobating genera such as *Cylisticus* Schnitzler, 1853 and *Porcellium* Dahl, 1916, or the genera contained in the family Armadillidiidae. While these similarities are not indicative of a close relation to any of these genera, it strongly suggests that *Balticoniscus walterludwigi* was capable of conglobation. While the epimera are not as steeply angled as is seen in conglobating species such as *Armadillidium vulgare* (Latreille, 1804) or *A. pulchellum* (Zenker, 1799), they display a steepness similar to many other conglobating taxa like *A. nasatum* Budde-Lund, 1885 or *Cylisticus convexus* (De Geer, 1778). The small uropods, protruding only shortly past the posterior margin of the pleonites and pleotelson, reinforce the likeliness of *Balticoniscus* gen. nov. being a conglobating genus (Gruner 1953). Additionally, the short antennae and position of the small antennary tubercles suggest endoantennal conglobation, as they likely allowed the antennae to fold inward and be enclosed within the rolled-up body.

While the ability to conglobate is likely, it cannot be entirely ruled out that *Balticoniscus* gen. nov. was a non-conglobating clinger or runner, as non-conglobating species with a convex dorsum are known as well, such as *Porcellio gallicus* Dollfus, 1904. However, runner type taxa are usually characterized by shorter epimera and relatively longer legs, and clinger type taxa feature a much flatter dorsum and nearly horizontally oriented epimera. The lack of ventral articulating structures, which are present in many genera of Armadillidae and Armadillidiidae (Gruner 1953; Taiti *et al.* 1998), might indicate limited or facultative conglobation but is not conclusive, as these structures are not obligatory for conglobating isopods. In conclusion, *Balticoniscus* gen. nov. shows several characteristics indicative of a conglobating taxon, but is lacking adaptions seen in dedicated conglobators. Therefore, the new genus may be comparable to the extant genus *Cylisticus*, which shows a similar degree of adaption to conglobation, but is more inclined to flee from potential threats than to make use of its ability to conglobate (Gruner 1953). Future discoveries of *Balticoniscus* may provide additional evidence for the ability to conglobate, as such a defensive behavior may also be employed in response to environmental hazards, which potentially includes the events that resulted in an entrapment in amber.

Ecological considerations

Baltic amber is one of three major Late Eocene amber deposits in Europe, alongside Rovno and Bitterfeld amber. It is distinct in having a lower δ^2H signature, which indicates relatively cooler climatic conditions. Notably, Baltic amber exhibits high isotopic variability, which may reflect a broad catchment area or an extended period of resin deposition (Mänd *et al*. 2018). The likely catchment area was situated to the north, toward present-day Scandinavia, with average temperatures around 17°C. However, some amber specimens yield isotope values that indicate average temperatures below 15°C, unique among European amber deposits, while others reflect more tropical conditions (Wolfe *et al*. 2016). Without isotope analysis of the specific amber piece containing *Balticoniscus* gen. nov., a wide range of temperature and precipitation regimes is possible. Overall, beetle and plant species indicate a humid, thermophilic and polydominant forest in a flat to hilly landscape with primarily oligotrophic waters that can be interpreted as sea lowlands (Alekseev & Alekseev 2016). Comparable conditions can be found in the modern warm-temperate zonobiomes of East Asia and North America (Sadowski 2017).

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