



A remarkably well-preserved terrestrial isopod (Peracarida: Isopoda: Armadillidiidae) from the upper Oligocene of Hungary, with remarks on the oniscidean taphonomy

Matúš Hyžný and Arpád Dávid

ABSTRACT

Isopods rank among the more successful and diverse peracaridan crustaceans, the clade of oniscidean isopods (pill-bugs and wood-lice) being one of the few pancrustacean groups to have successfully invaded terrestrial habitats. Yet, the majority of fossil occurrences of oniscidean isopods stem from amber deposits and only under very special circumstances are they preserved in marine settings; such an occurrence is recorded herein. A single, specifically indeterminate, specimen of *Armadillidium* from upper Oligocene strata at Eger (Hungary) is interpreted as a drowned individual that found itself trapped on a piece of driftwood or was caught by waves while walking on the seashore. The animal was preserved virtually intact and close to a natural posture. A near-perfect preservation of the isopod's cuticular surface indicates their potential to be preserved in marine siliciclastic settings under specific conditions.

Matúš Hyžný. Comenius University, Faculty of Natural Sciences, Department of Geology and Palaeontology, Ilkovičova 6, 842 15 Bratislava, Slovakia; e-mail: hyzny.matus@gmail.com and Department of Geology and Palaeontology, Natural History Museum, Vienna, Burgring 7, 1010 Vienna, Austria

Arpád Dávid. Debrecen University, Department of Mineralogy and Geology, Egyetem tér 1, 4032 Debrecen, Hungary

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INTRODUCTION

Isopods are among the more successful and diverse peracaridan crustaceans to inhabit marine, freshwater and terrestrial habitats alike (Kussakin, 1979; Kensley and Schotte, 1989; Wägele, 1989; Warburg, 1993; Brusca et al., 2007; Wilson, 2008; Poore and Bruce, 2012; Sfenthourakis and Taiti,

2015). In fact, together with several representatives of amphipods and brachyuran decapods, oniscidean isopods are the only pancrustaceans (except for hexapods) to have adapted to terrestrial conditions (e.g., Hornung, 2011; Dunlop et al., 2013). Oniscideans probably originated during the Carboniferous (Broly et al., 2013), although the

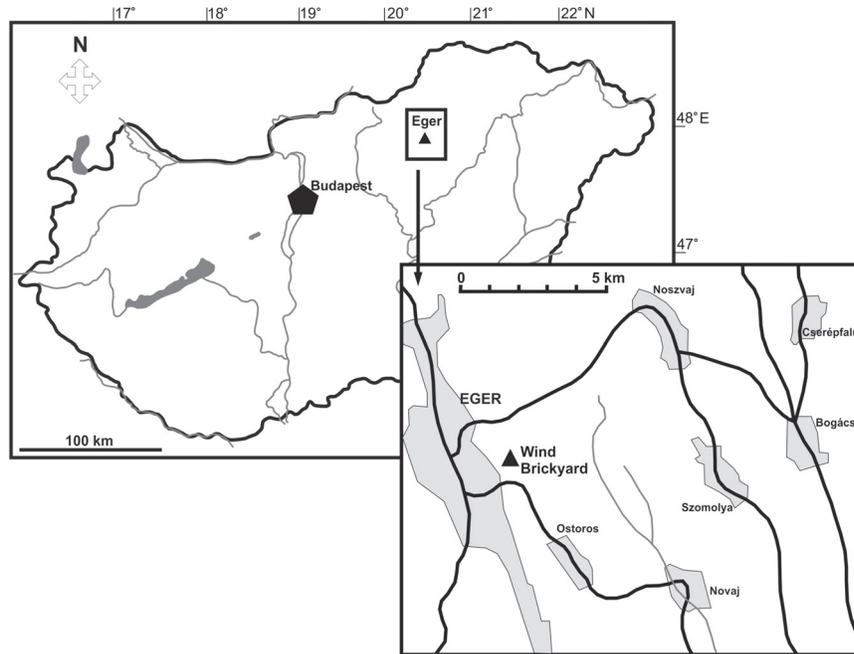


FIGURE 1. Position of the locality studied within Hungary.

oldest verified occurrence of an oniscidean fossil is from the Early Cretaceous (Broly et al., 2015).

The fossil record of isopods is insufficiently known, mainly because of the delicate nature of their exoskeleton and hence a low fossilisation potential. A direct consequence of this is that there are only a few occurrences in which the morphology of mouthparts or appendages, which are important for isopod systematics and taxonomy, are preserved (e.g., Guinot et al., 2005; Vega et al., 2005; Feldmann, 2009; Wilson et al., 2011; Nagler et al., 2016), including specimens preserved in amber (e.g., Spahr, 1993; Dunlop, 2010; Perkovsky et al., 2010). In view of the fact that oniscidean isopods live in terrestrial habitats, their fossils are scarce and are dominated by amber inclusions (Broly et al., 2013, 2015). Many isopod fossils, except those preserved in amber, are flattened and sometimes distorted due to taphonomical processes. In this respect, the armadillidiid isopod specimen from the Oligocene of Hungary reported herein is remarkable in its three-dimensional preservation.

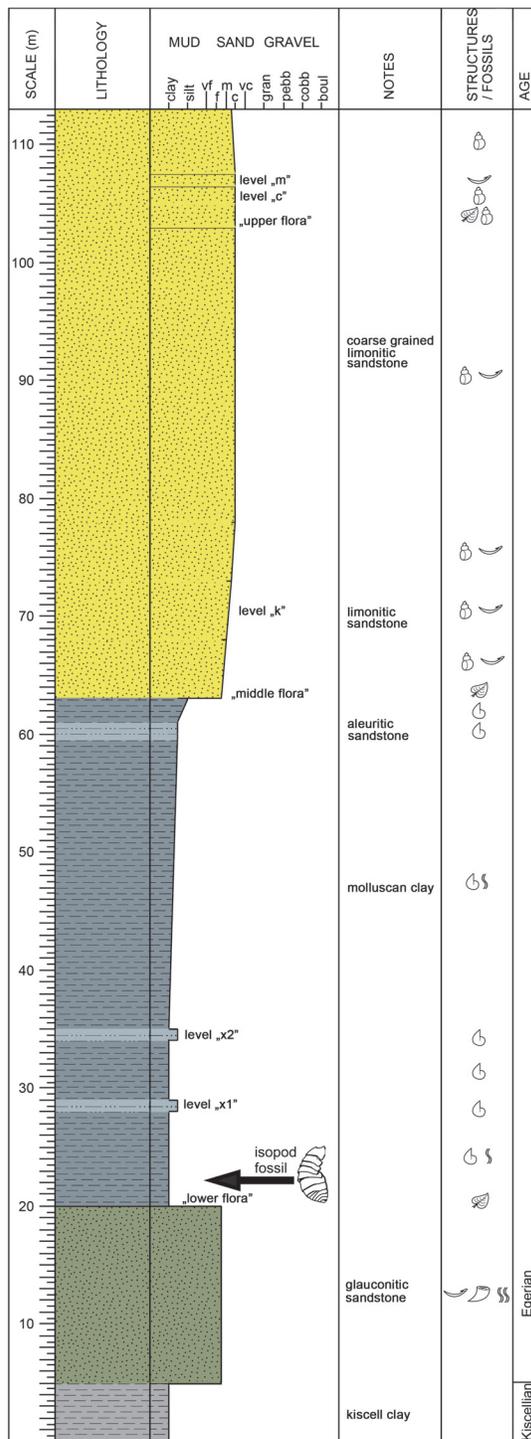
Additionally, the specimen described herein represents the first fossil isopod from Hungary. From neighbouring countries, Mesozoic isopods have been recorded from Austria (Bachmayer, 1949, 1955; see also the review of Jurassic isopods by Etter, 2014) and Cenozoic species from Austria (von Ammon, 1882; Bachmayer, 1947; Tauber, 1950), the Czech Republic (Novák, 1872), Slo-

vakia (Hyžný et al., 2013), Romania (Racovitza and Sevastos, 1910) and Ukraine (Perkovsky et al., 2010). However, nearly all these occurrences involve marine taxa, whereas only the Ukrainian occurrence is based on oniscideans preserved in amber (Perkovsky et al., 2010). Thus, the Hungarian specimen of a terrestrial isopod is a worthwhile addition to the isopod fossil record.

GEOLOGICAL SETTING

The described specimen originates from the Wind Brickyard, situated in the southeastern part of Eger, Hungary (GPS co-ordinates: 47°53'47.55" N, 20°23'52.20" E; see Figure 1). This outcrop represents the stratotype of the Egerian Regional Stage of the Central Paratethys (Báldi and Seneš, 1975; for a correlation with the Mediterranean scale, see Piller et al., 2007). The sequence exposed belongs to nanoplankton zone NP 25 and the *Paragloborotalia opima opima* Biozone, corresponding to the Chattian (late Oligocene).

The Wind Brickyard section (Figure 2) exposes the lower part of the Eger Formation (Báldi and Seneš, 1975). Several marine facies (shallow bathyal, sublittoral, littoral and lagoonal) can be observed here, with diverse flora and fauna (e.g., Báldi, 1973; Kvaček and Hably, 1991; Dávid, 1993, 1999; Fodor, 2001; and references therein). Strata assigned to the Eger Formation rest conformably on the lower Oligocene Kiscell Clay For-



Legend:

	Plant material		Shells		limonitic sandstone
	Solitary corals		Minor bioturbation		clay
	Bivalves		Moderate bioturbation		aleuritic sandstone
	Gastropods				glauconitic sandstone

FIGURE 2. Section exposed at the Wind Brickyard in Eger, Hungary. See text for comments.

mation (Báldi, 1983). Higher in the section, glauconitic tuffaceous sandstones are exposed, and above follows the so-called molluscan clay (thickness 35–40 m), which contains a rich and diverse microfauna with foraminifera, small molluscs and teleost otoliths. Higher up, the 5.0–5.5 m thick sequence of sandy clay (called “middle flora”) is exposed, followed by approximately 2 m of limonitic sandstones containing a varied, excellently preserved molluscan fauna. This level is referred to as the “k” layer (from “kövületes” for fossiliferous, in Hungarian). The succession continues with brackish, shallow-marine sands, the so-called “m” layer (from “mytilitic”). Finally, there is a 4–5 m thick level of limonitic sand on the top of the succession.

The isopod specimen was found in the molluscan clay, which was deposited in a deep sublittoral–shallow bathyal environment (Báldi, 1973, 1998). Gastropod, bivalve and dentaliid taxa belong to the *Hinia–Cadulus* community. The upper levels formed in shallow sublittoral (*Pitar polytropa* community) and littoral (*Tympanotonus-Pirenella* and *Mytilus aquitanicus* communities) settings. The occurrence of pieces of driftwood in the molluscan clay, bioeroded by teredinid bivalves (Dávid, 2004), illustrates that different trunks could be transported by currents to great distances from the coast prior to settlement and final burial.

SYSTEMATIC PALAEOLOGY

Order ISOPODA Latreille, 1817

Suborder ONISCIDEA Latreille, 1802

Section CRINOCHEETA Legrand, 1946

Family ARMADILLIDIIDAE Brandt, 1833

Remarks. Apparently, the Hungarian specimen was able to roll up into a ball, thus, it belongs to conglobating isopods. The general habitus of the specimen in question may fit to several oniscidean families, including Armadillidae, Armadillidiidae, or Eubelidae. One of the autapomorphies of the Eubelidae is sulcus arcuatus, a longitudinal groove on the first coxal plate (Taiti et al., 1991; Schmidt, 2003). The studied specimen does not possess this character, and hence its potential attribution to Eubelidae is disputed. The uropods of armadillidiids differ from the uropods of other conglobating Oniscidea: their exopodite is plate-like, truncate posteriorly. The exopodite fills out the gap between the pleotelson and the pleon-epimera 5, and their truncate apical margin is part of the body outline (Schmidt, 2003). Unfortunately, the Hungarian specimen does not retain uropods. The pleotelson, however, is partly preserved and its outline is undoubtedly triangular, as it is typical for armadilli-

TABLE 1. Fossil occurrences of the family Armadillidiidae.

Species	Age	Country	Setting	Reference
<i>Armadillidium vulgare</i>	Pleistocene	France	clastics	Dalens and Bouthier (1985)
<i>Eoarmadillidium granulatum</i>	Pleistocene	France	clastics	Dollfus (1904)
gen. et sp. indet	early Miocene	Mexico	amber	Serrano et al. (2007)
<i>Armadillidium pulchellum</i>	late Oligocene	Germany	amber	Spahr (1993)
<i>Armadillidium</i> sp.	late Oligocene	Hungary	clastics	herein
gen. et sp. indet	Eocene	Northern Europe	amber	Weitschat and Wichard (2010)
Disputed by Schmidt (2008)				
<i>Armadillidium molassicum</i>	middle Miocene	Germany	clastics	Heer (1865)
<i>Armadillidium payangadensis</i>	?Miocene	India	amber	Srivastava et al. (2006)

diids (Schmidt, 2003), rather than quadrangular, which is typical for armadiliids (Schmidt, 2003). As a conclusion, the Hungarian specimen is assigned to the family Armadillidiidae. Up to now, only a handful of veritable occurrences of this family are known from the fossil record (Table 1).

Genus ARMADILLIDIUM Brandt, 1833

Type species. *Armadillo vulgaris* Latreille, 1804, by original designation.

Diagnosis. See Sars (1899, p. 188) and Richardson (1905, p. 665); see also Schmalfuss (2013, p. 13).

Remarks. Armadillidiids constitute a well-founded monophyletic group (Schmidt, 2008) that comprises about 300 species. The most speciose genus is *Armadillidium* Brandt, 1833, with nearly 200 described forms (Schmalfuss, 2003), including *A. vulgare* (Latreille, 1804), the “most extensively investigated species of terrestrial isopods,” as noted by Schmalfuss (2003, p. 2). According to Schmalfuss (2013), the genus is defined by: 1) ability to roll up into a closed ball, which may have a lemon-like shape; 2) lungs with multiple spiracles in 1st and 2nd pleopod-exopodite; 3) uropod-exopodite flattened and truncated, filling the space between epimeron of pleonite 5 and telson; 4) frontal part of head with a triangular shield (which seems to be a modified supra-antennal line) reaching the level of the upper head surface or surpassing this level; 5) lateral parts of inter-ocular line present. Unfortunately, the Hungarian specimen does not possess a head, which precludes a confident generic assignment. However, we argue that based on various clues discussed below it is reasonable to assign the specimen to *Armadillidium*.

The pereonite-epimeron I does not have a notch (schisma), which is characteristic for many genera, i.e., *Alloschizidium* Verhoeff, 1919; *Ballo-*

dillium Vandel, 1961; *Eluma* Budde-Lund, 1885; *Paraschizidium* Verhoeff, 1918; and *Schizidium* Verhoeff, 1901. Thus, the assignment of the Hungarian specimen to these genera can be excluded. Also, based on the smooth cuticular surface, the assignment to genera with tuberculated representatives, i.e., *Cyphodillidium* Verhoeff, 1939; *Echinarmadillidium* Verhoeff, 1901; *Paxodillidium* Schmalfuss, 1985; and *Platanosphaera* Strouhal, 1956, can be excluded. *Cristarmadillidium* Arcangeli, 1935; *Eleoniscus* Racovitza, 1907; *Trichodillidium* Schmalfuss, 1989; *Troglarmadillidium* Verhoeff, 1900; and *Typhlarmadillidium* Verhoeff, 1900, are known only from a few species, and their distribution is rather limited. For instance, representatives of *Trichodillidium* are so far known only from Greece, including Crete and adjacent islands (Schmalfuss, 1989, 2003), whereas monotypic *Eleoniscus* is restricted to southeastern Spain (Racovitza, 1907; Schmalfuss, 2003). A vast majority of all species of the family Armadillidiidae belong to the genus *Armadillidium* (Schmidt, 2003); therefore it is the most parsimonious course of action to interpret the Hungarian specimen as a representative of this genus. In addition, the autochthonous European distribution of *Armadillidium* (Schmalfuss, 2000, 2013) strengthens the argument in favour of attributing the Hungarian specimen to that genus.

Armadillidium sp.

Figures 3.1-6, 4.1-3, 5.1

Material. The specimen studied (MM 2015.513.1; collections of the Matra Museum of Hungarian Natural History Museum at Gyöngyös, Hungary) comes from the molluscan clay of the Wind Brickyard section at Eger (Figures 1-2). It is preserved three-dimensionally in poorly lithified sand; no

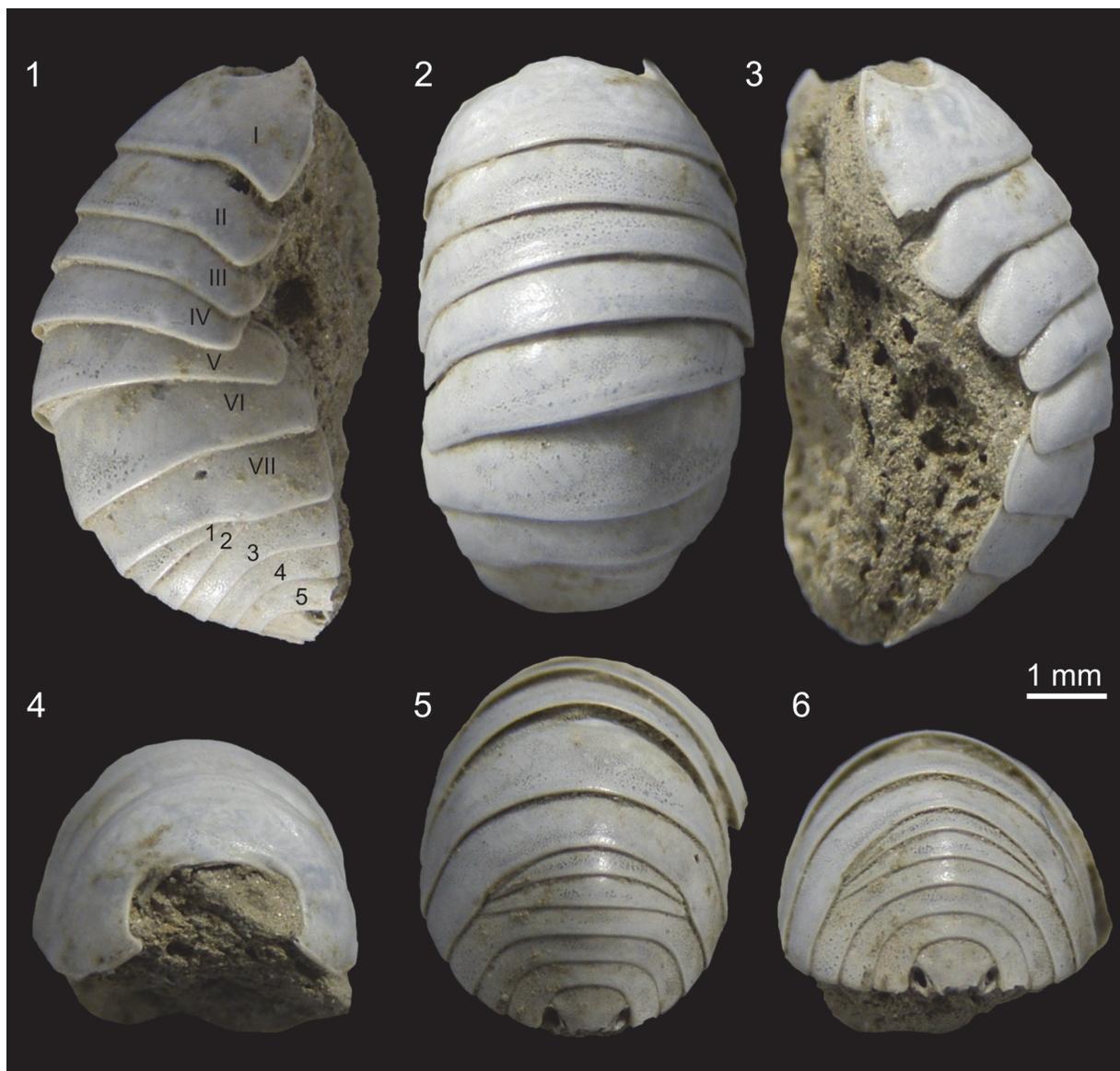


FIGURE 3. *Armadillidium* sp. from the upper Oligocene of Eger, Hungary (MM 2015.513.1). 1. Lateral (right) view. 2. Dorsal view. 3. Lateral (left) view. 4. Anterior view; note the missing cephalon. 5. Postero-dorsal view. 6. Posterior view. Roman numerals indicate pereonites; Arabic numerals refer to pleonites.

deformation is observed (Figures 3.1-6, 5.1). All cuticular surfaces are preserved.

Description. Body oblong-ovate, approximately twice as long as wide, lateral outlines subparallel, dorsal surface strongly vaulted and smooth. Cephalon not preserved, but presumed to have been wider than long (based on the slit in pereonite I). Pereonites distinctly wider than long, subequal, each being approximately 1.5 mm in length. No epimera separated on any pereonite. Epimera of pereonite I with acute posterior corner, without schisma. Pleon as wide as pereon. Pleonites 1 and 2 covered at sides by pereonite VII. Terminal seg-

ment of pleon (pleotelson) trapezoidal or triangular in shape, apparently tapering posteriorly, with broken posterior margin and probably not extending beyond epimera of pleonite 5. Uropods broken.

Remarks. The specimen is very well preserved; however, it lacks head and appendages, which are crucial for the taxonomy of oniscidean isopods as discussed by Schmidt (2002). Based on the comparisons discussed above it is assigned to the Armadillidiidae and identified tentatively as a representative of *Armadillidium*. The studied specimen shows overall similarity to *Armadillidium vulgare* (e.g., Sars, 1899, p. 189, pl. 81; Richardson, 1905,

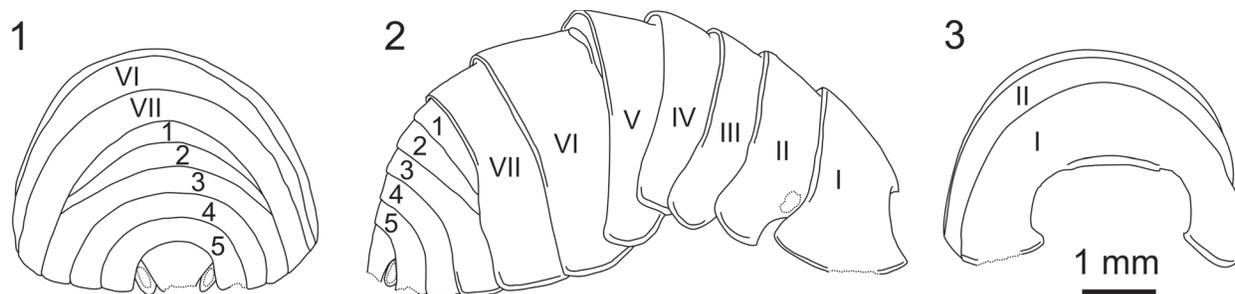


FIGURE 4. *Armadillidium* sp. from the upper Oligocene of Eger, Hungary (MM 2015.513.1), interpretative line drawings. 1. Posterior view. 2. Lateral (right) view. 3. Anterior view. Roman numerals indicate pereonites; Arabic numerals refer to pleonites.

p. 666, figure 706; Van Name, 1936, p. 276, figures 157-158; Frankenberger, 1959, plate 2, figure 11; Hegna, 2010, figures 2A-B) and related species such as *A. pulchellum* (Zenker, 1798) (e.g., Sars, 1899, p. 191, plate 83, figure 4). Close comparison, however, is not possible. Despite the fact that the chance of discovery of additional specimens is minimal, we refrain from erecting a new species based on the present material because of lack of sufficient number of distinguishing characters.

DISCUSSION

Terrestrial Isopods as Fossils

Because the cuticle of terrestrial isopods contains only minor amounts of materials resistant to chemical and physical degradation (Neues et al., 2007), the probability of burial and fossilization in terrestrial environments is low. In most cases, extinct oniscideans are preserved as amber inclusions (Spahr, 1993; Schmalzfuss, 2003; Dunlop, 2010; Broly et al., 2013, 2015). In view of this, reports of such animals from other settings are worth noting. In fact, there are only a few reports on fossil oniscideans that are not contained in amber. Based on a single specimen of an oniscidean isopod from the Pleistocene clastic sediments of France, Dollfus (1904) described a new genus and species, *Eoarmadillidium granulatum*. Dallens and Bouthier (1985) reported *A. vulgare* from the Pleistocene of France. Heer (1865) described a new species, *A. molassicum*, from the middle Miocene clastic sediments of Germany. Schmidt (2008), however, disputed the attribution of the Heer's specimen to isopods; a millipede would be a more fitting identification. Contrary to these instances when only a single specimen was recovered, *Eubelum rusingaense* Morris, 1979 was described from numerous specimens from the lower Miocene lacustrine sediments of Rusinga

Island, Lake Victoria, Kenya. As far as the preservation is concerned, the Hungarian specimen seems to surpass most of the occurrences discussed above. Its cuticle is preserved virtually intact, which is usually not the case in arthropod fossils, which are tens of millions years old. In fact, *Armadillidium* sp. from Eger is the oldest armadillidiid isopod reported from siliciclastic sediments (Table 1). It documents that the cuticular surfaces of oniscoidean isopods may be very well preserved under specific conditions in siliciclastic settings; better preservation is documented only from amber inclusions.

From the Land to the Sea

The specimen of *Armadillidium* sp. from the Wind Brickyard at Eger is preserved in a marine setting. Similar to many crinochetan isopods, *Armadillidium* possesses fairly complex "lungs" in the pleopod exopodites (e.g., Frankenberger, 1959; Wägele, 1989; Hornung, 2011) and is, therefore, adapted to subaerial habitats. The aquatic life habit of a number of Crinocheta evolved secondarily (Tabacaru, 1999; Schmidt, 2008), but this is not the case for *Armadillidium*, which is a fully terrestrial animal. Thus, the marine setting of the present isopod fossil occurrence was not its natural habitat. The fossil apparently does not represent a moult, which typically consists of two parts and is shed biphasically (Schöbl, 1880; Tait, 1917; Vernet and Charmantier-Daures, 1994; Charmantier-Daures and Vernet, 2004; Hornung, 2011). Moreover, freshly moulted individuals of terrestrial isopods often consume their exuvia to regain mineral content (Steel, 1993; Hornung, 2011, figure 3C). In short, the Eger fossil is interpreted as a corpse. *Post-mortem* transport could have damaged delicate joints between segments of the exoskeleton, especially over longer distances, which would be required for a terrestrial isopod to land into a

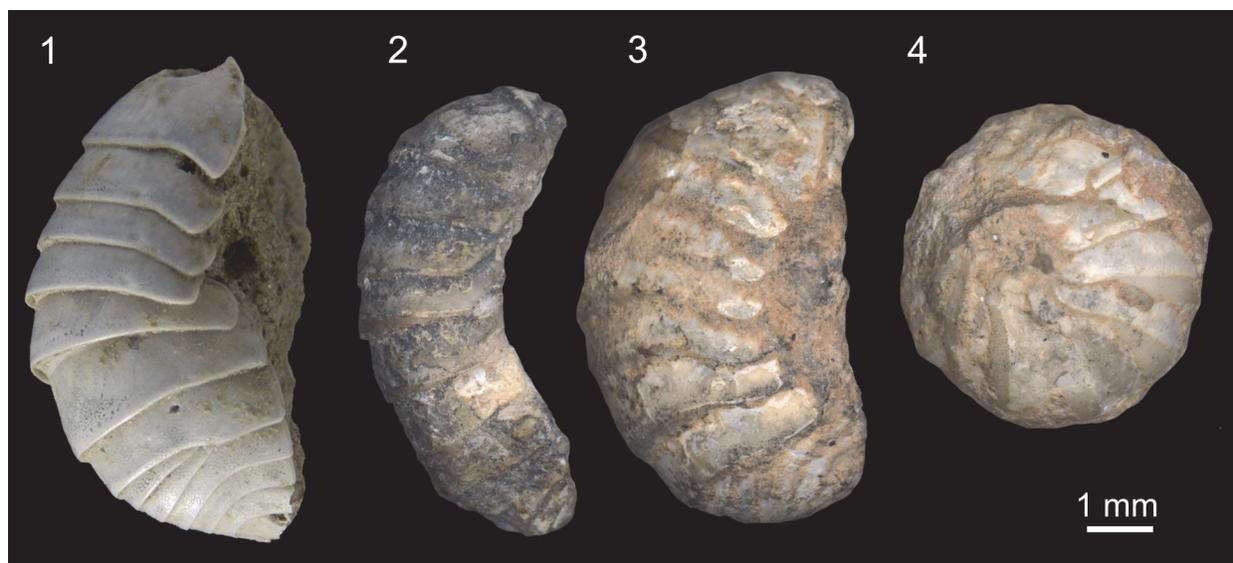


FIGURE 5. Fossil oniscidean isopods preserved in natural posture. **1.** *Armadillidium* sp., upper Oligocene of Hungary (MM 2015.513.1). **2-4.** *Eubelum rusingaense* Morris, 1979, lower Miocene of Kenya, deposited in the collections of the Natural History Museum, London. **2.** BMNH In. 61035. **3.** BMNH In. 61036. **4.** BMNH In. 61037 (fully enrolled specimen).

marine depositional setting. It is reasonable to assume that the animal was introduced into marine waters when alive and then died almost instantly as a result of high salinity. Rapid burial must have occurred to ensure preservation of the delicate exoskeleton.

The body of the described specimen is slightly bent and recalls the preservation state of *Eubelum rusingaense*. Morris (1979, p. 74, figures 1-11; see also Figures 5.2-4 here) described and figured several specimens of this terrestrial isopod from lacustrine deposits in “many degrees of enrollment, from a flat to a relaxed arched condition; six specimens show a nearly complete enrollment with only a slight gap between the frontal line and the pleotelson.” Apparently, the animals displayed defensive behaviour, i.e., enrollment, when entering the water, although without much effect. The Hungarian specimen described herein may illustrate a similar phenomenon, although it is far from being completely rolled up. It, however, has a curved shape and shows an ability to conglobation when alive.

Yet, how does a fully terrestrial arthropod become introduced undamaged into a marine setting? Oniscidean isopods usually live under stones and logs and are often found inside rotting tree trunks. The molluscan clay at Wind Brickyard contains fossilised driftwood fragments (Dávid, 2004), which apparently were taken far away from the coast prior to final settlement and burial. Most

probably the isopod crept out of a crevice and was washed into the sea, since it was not buried within the driftwood as would be expected if the log had sunk with the occupant inside. In fact, soil-dwelling arthropods are often associated with driftwood (e.g., Coulson et al., 2002, and references therein) and rafting has even been suggested to be a dispersal agent (Donlan and Nelson, 2003). Nevertheless, terrestrial invertebrates occupying crevices in the wood could easily be washed out into the sea. Marine conditions, however, were lethal for them (but see Coulson et al., 2002). The specimen of *Armadillidium* recorded herein is considered to be one of such “unhappy travellers.” Alternatively, the animal could have been caught by waves while crawling on the seashore. Since representatives of the Armadillidiidae occur in a wide range of habitats and some *Armadillidium* species live close to the seashore, e.g., *A. album* or *A. fallax* (Holthuis, 1945; Vandel, 1962; Warburg, 1993), such scenario would be equally possible.

Distribution of *Armadillidium*

As far as European distribution is concerned, armadillidiids are autochthonous to the Mediterranean area (Schmaffuss, 2000, 2013; Schmidt, 2003), which they have occupied at least since the Paleogene, as documented by the present report and previously published occurrences (for a review see Broly et al., 2013; Table 1). *Armadillidium* has a radiation centre in the northeastern Mediterra-

nean area (Schmalfuss, 2000, 2013). The dating of the origin of the group is unknown at present, but the late Oligocene material from Germany (Spahr, 1993) and the roughly coeval Hungarian specimen reported herein suggest that it is at least 26 million years old. The genus *Armadillidium*, however, may well be paraphyletic (Schmalfuss, 2013); therefore, any conclusions made at the present state of knowledge are premature. Today, *Armadillidium* exhibits cosmopolitan distribution due to introducing some species (e.g., *A. vulgare*) to other areas (e.g., the New World) by humans (Van Name, 1936; Garthwaite et al., 1995; Jass and Klausmeier, 2000).

CONCLUSION

Despite the extreme scarcity of fossil terrestrial isopods in marine siliciclastic sediments, a uniquely preserved specimen of Oniscidea is reported from the upper Oligocene strata of the Wind Brickyard in Eger (Hungary). Although it does not preserve a cephalon or appendages, it is attributed to unidentified species of *Armadillidium*, a widespread genus which today occurs in a most of Europe. Its occurrence in the late Oligocene of Hungary together with roughly coeval record from Germany suggests that the genus is at least 26 million years old. The specimen from Wind Brickyard is remarkable in the near-perfect preservation of its cuticular surfaces, suggesting that rather soft and fragile cuticle of terrestrial isopods may be very well preserved under specific conditions in siliciclastic marine settings. Better preservation is documented only from amber inclusions. The specimen is interpreted as a drowned individual that found itself either trapped on a piece of driftwood or caught by waves while on the seashore. It is likely that rotting logs, now preserved as fossils at the Wind Brickyard contained some passengers, isopods in particular, before they were washed out to sea.

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