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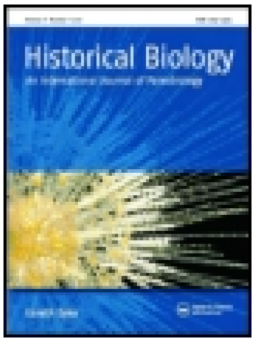
1 author:

George Poinar
Oregon State University



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ARTICLE

A new genus of terrestrial isopods (Crustacea: Oniscidea: Armadillidae) in Myanmar amber

George Poinar Jr.

Department of Integrative Biology, Oregon State University, Corvallis, OR, USA

ABSTRACT
A female terrestrial isopod in amber from Myanmar is described as *Palaeoarmadillo microsoma* gen. et sp. n. (Isopoda: Oniscidea: armadillidae). Placement in the family Armadillidae is based on the 2-segmented flagellum with the flagellum nearly as stout as the basal segments, the head with 2 small medial anterior processes, the fronto-caudally compressed cephalon, the large expanded protopodite with small exopodites dorsally attached and the possibility (based on the shape of the epimera) that the specimen could have formed a global shape. Autapomorphies of the fossil are the shape of the basal antennomeres, flagellum and shape and size of the uropod exopodites. The specimen is parasitized by fly larvae (Diptera) and two mite spermatophores with sperm packets are attached to the dorsum of the isopod.

ARTICLE HISTORY
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KEYWORDS
Terrestrial isopod; Myanmar amber; Armadillidae; mid-Cretaceous

Introduction

The Isopoda is the largest order of crustaceans after the Decapoda. While the great majority of species are marine and freshwater, members of the suborder Oniscidea represent the only group of truly terrestrial crustaceans (Barnes 1963). Commonly called woodlice or pillbugs, terrestrial isopods have indiscriminate feeding habits, which includes consuming dead, dying and decaying animal and plant material, especially the latter. While their fossil record only dates back to the Early Cretaceous, based on phylogenetic and palaeobiogeographic evidence, a pre-Pangaean origin of the Oniscidea in the Late Paleozic has been proposed (Broly et al. 2013).

The bodies of woodlice are well constructed and noticeably dorso-ventrally flattened. They are covered with a series of overlapping, laterally projecting, articulated chitinous plates that provide protection as well as flexibility during movement. The abdominal segments, which may be separate or fused to varying degrees, are usually closely appressed to the thorax, so the two regions may be difficult to clearly demarcate dorsally (Barnes 1963). The above features, as well as the presence of breathing structures located in specialized limbs, make them well adapted for survival (Muchmore 1995).

One well-studied family of these terrestrial isopods is the Armadillidae with over 70 genera with some 590 species. They occur in a range of habitats, from wet tropical to dry forests, savannahs, along the shores of lakes and seas and even in deserts (Taiti et al. 1998). The present study describes a gravid female woodlouse of the family Armadillidae in 100 Mya amber from Myanmar. This is the second fossil isopod described from Myanmar amber. The first representative was a member of the family Styloniscidae (Broly et al. 2015). Based on their present distributions, both the Styloniscidae and Armadillidae can be considered as Gondwanan lineages. This distributional pattern corroborates an earlier proposal that Myanmar amber inclusions represent Gondwanan lineages that were transported to Southeast Asia in the Early Cretaceous (Poinar 2018).

Extant woodlice are attacked by nematode parasites (Poinar 1981), fly parasitoids (Sassaman and Garthwaite 1984) and viral pathogens (Poinar et al. 1985)._ The presence of two fly larvae that had just emerged from the body of the fossil isopod may represent precursors of the Rhinophoridae, a family of flies that today are obligate parasitoids of wood lice. Two mite spermatophores with sperm packets on the dorsum of the fossil shows that it shared its habitat with acarines.

Materials and methods

The amber was recovered from the Noije Bum 2001 Summit Site mine located in the Hukawng Valley southwest of Maingkhwan in Kachin State (26°20´N, 96°36´E) in Myanmar. Based on paleontological evidence, this site was dated to the Upper Albian of the Early-Mid Cretaceous (Cruickshank and Ko 2003), placing the age at 97 to 110 Mya. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma (Shi et al. 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar et al. 2007). Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnification up to 1,000x. Helicon Focus Pro X64 was used to stack photos for better overall clarity and depth of field.

CONTACT George Poinar poinarg@science.oregonstate.edu Department of Integrated Biology, Oregon State University, Corvallis, OR 97331, USA

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Systematic account

Order Isopoda Latreille, 1817
Suborder Oniscidea Latreille, 1802
Family: Armadillidae Brandt, 1831
Palaeoarmadillo gen. n.
LSID- 86E37949-89A5-4381–8339-21A4B5924843
Type species: Palaeoarmadillo microsoma gen. et sp. n.

Generic diagnosis

Two-segmented flagellum with the flagellum nearly as stout as some of the basal segments; compound eyes with between 12 and 14 ocelli; head with 2 small medial anterior processes; fronto-caudally compressed cephalon and large expanded protopodite with small exopodites dorsally attached. Autapomorphies are the shape of the basal antennomeres, shortened flagellum and short, wide, uropod exopodites. The oblique tips of basal antennomeres 3 and 4 and their overlap on the succeeding antennomeres is a unique feature of *Palaeoarmadillo microsoma* gen. et sp. n.

Etymology: The generic name is from the Greek 'palaios' = old and the current family name ' Armadillidae'.

Palaeoarmadillo microsoma gen. et sp. n.
LSID: BD37A073-2B2D-4578–9836-60F2FB2F7B3E
Included species: type species only.
Diagnosis: As for genus (by monotypy)

Etymology

The specific epithet is from the Greek 'micros' = small and the Greek 'soma' = body, in reference to the small size of the fossil.

Type material

Holotype deposited in the Poinar amber collection (accession # B-Cr-2) maintained at Oregon State University, Corvallis, Oregon.

Type locality

Hukawng Valley southwest of Maingkhwan in Kachin State (26°20´N, 96°36´E), Myanmar.

Description

Holotype female. Length, 2.3 mm, greatest width, 1.5 mm. Body complete, light brown, dorsum smooth except for some scattered scale-spines, ventrum with marsupium, (Figures 1–9).

Head (cephalon) (Figures 1–6)

compact, compressed fronto-caudally with a wide frontal shield; with 2 small medial anterior processes; wider that long, width, 440 µm; length, 280 µm; mandible curved, narrowing at tip, 340 µm in length; eyes not protruding from side of head, 49 µm in diameter, composed of 12–14 ommatidia; antennules 3-segmented, length, 210 µm, positioned internal to base of antennae (Figure 4); antennae with 5 basal segments and 2 short, wide flagellar segments nearly as stout as some of the basal segments (Figure 5); antennal shapes and lengths: first basal segment squarish, 62 µm; second basal segment trapezoidal, 42 µm;

Figure 1. Dorsal view of *Palaeoarmadillo microsoma* gen et sp. nov. in Myanmar amber. Scale bar = 0.6 mm.

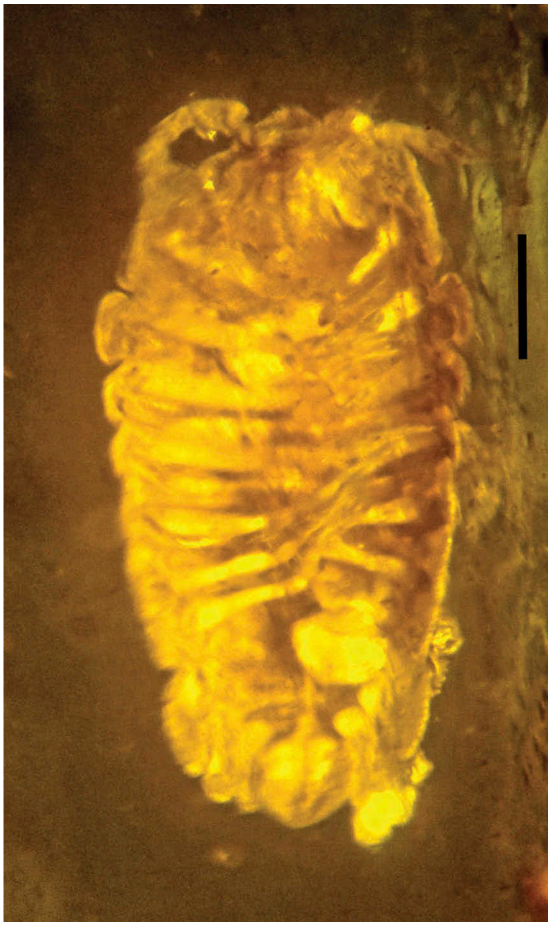

Figure 2. Ventral view of *Palaeoarmadillo microsoma* gen et sp. nov. in Myanmar amber. Scale bar = 0.4 mm.

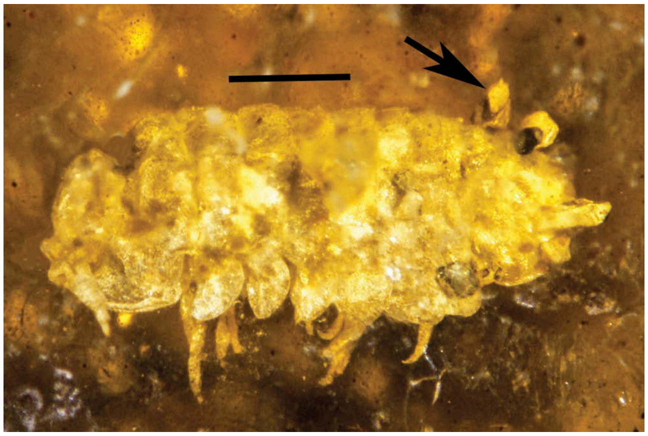

Figure 3. Lateral view of *Palaeoarmadilo microsoma* gen et sp. nov. in Myanmar amber. Arrow shows one of the mite spermatophores. Scale bar = 0.5 mm.

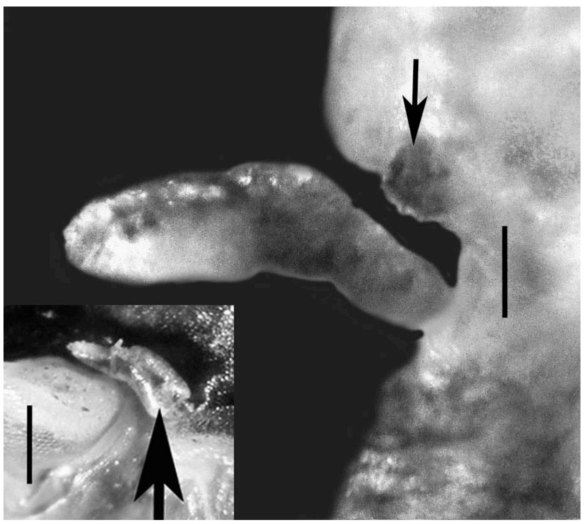

Figure 4. Antennule of *Palaeoarmadillo microsoma* gen et sp. nov. in Myanmar amber. Arrow shows eye with ommatidia. Scale bar = 50 µm. Insert shows antennule (arrow) of extant *Armadillidium vulgare* (Latreille, 1804). Scale bar = 205 µm.

third basal segment cone- shaped, 195 µm; fourth basal segment trapezoidal, 113 µm; fifth basal segment trapezoidal, slightly curved, 83 µm; flagellum straight, 136 µm; with distal sensilla on apical flagellar article almost as long as terminal segment.

Thorax (pereion)(Figures 1–3, 6)

Seven-segmented with each segment bearing a pair of walking legs (pereiopods); ends of thoracic tergites with expanded epimera having rounded to truncate margins. At the base of several pereiopods, ventrally, is a marsupium positioned along one side of the thorax. Some newly hatched juveniles are present.

Abdomen (pleon)(Figures 1–3, 8)

Length, 440 µm; with six pleonites, the 3rd, 4th and 5th of which possess epimera that extend posterolaterally over the pleon; basal margin of protopodite rounded; uropod exopodites minute, attached dorsally, not reaching distal margin of protopodite.

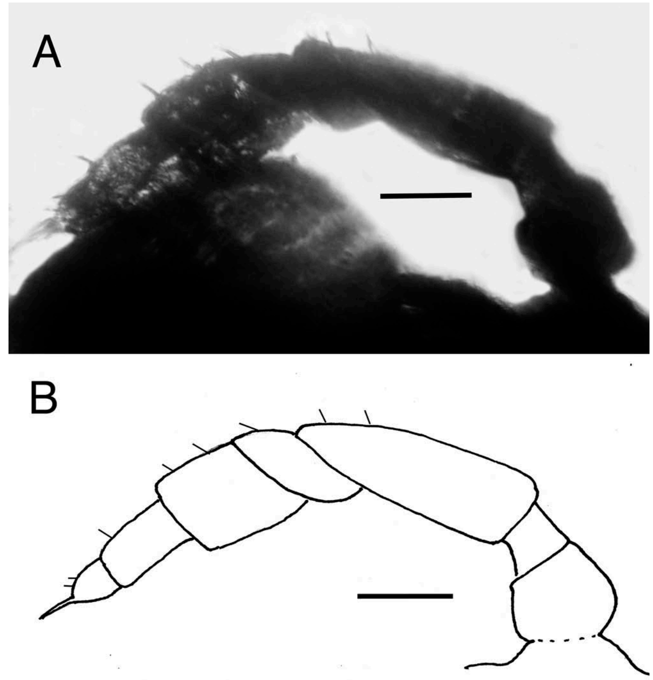

Figure 5. *Palaeoarmadillo microsoma* gen et sp. nov. in Myanmar amber. A. Photo of dorsal view of antenna. Scale bar = 78 µm. B. Drawing of dorsal view of antenna showing outline of segments. Scale bar = 78 µm.

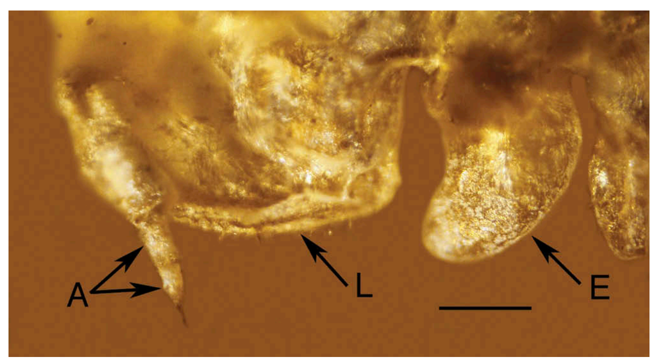

Figure 6. Dorsal view of left side of anterior body portion of *Palaeoarmadillo microsoma* gen et sp. nov. in Myanmar amber. A = 2 segments of flagellum. L = anterior leg. E = epimeron of pereonite. Scale bar = 76 µm.

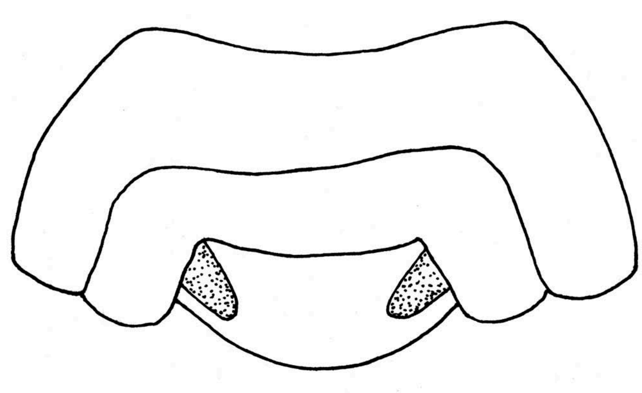

Figure 7. Sketch of dorsal view of pleon with exposed uropods exopodites (stippled) of *Palaeoarmadillo microsoma* gen. et sp. nov. in Myanmar amber. Scale bar = 123 µm.

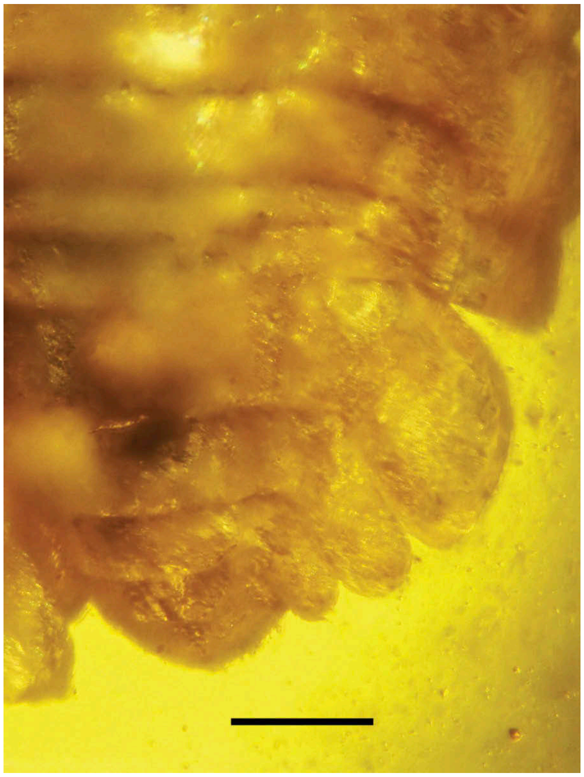

Figure 8. Dorsal view of pleon and abdominal segments of *Palaeoarmadillo microsoma* gen. et sp. nov. in Myanmar amber. Scale bar = 220 μm.

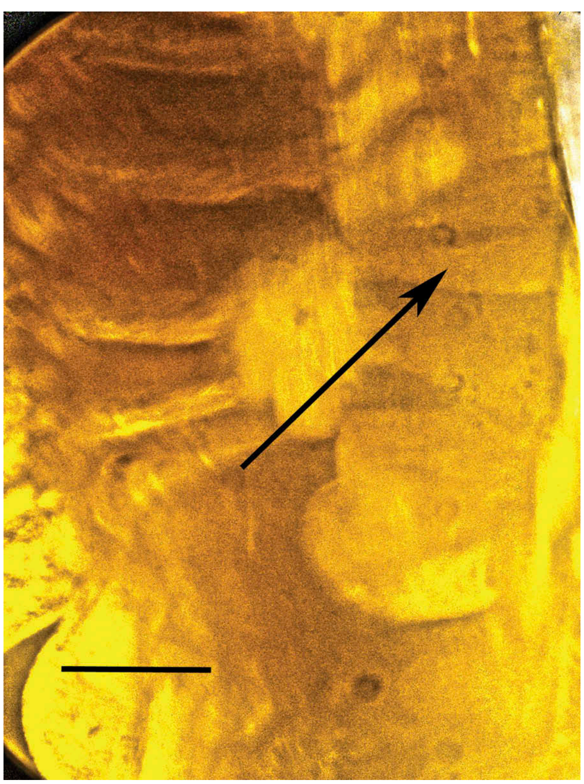

Figure 9. Ventral view of marsupium (arrow) of *Palaeoarmadillo microsoma* gen. et sp. nov. in Myanmar amber. Scale bar = 204 μm.

Comments: Placement in the family Armadillidae is based on the 2-segmented flagellum with the flagellum nearly as stout as the basal segments, the head with 2 small medial anterior processes, the fronto-caudally compressed cephalon, the large expanded protopodite with small exopodites dorsally attached and the possibility (based on the shape of the epimera) that the specimen could have formed a global shape. Autapomorphies of the fossil are the shape of the basal antennomeres, flagellum and shape and size of the uropod exopodites. While the specimen is small, the body length of armadillids can be as short as 2.0 mm (Taiti et al. 1998). Other members of the Oniscoidea also have small bodies. For example, some females of the porcellionid, *Agabiformius lentus* Bubbe-Lund from Bermuda are only 2.0 mm in length (Schultz 1972). Based on its features, the fossil falls within the Crinocheta group that includes those families most adapted to a terrestrial existence (P. Broly, personal communication).

Discussion

One of the characters of most armadillids is their ability to roll up in a convex shape to protect their softer underparts. This was probably the case with the fossil since it possesses a rounded lobe on the second pereon epimeron, a feature known to occur in extant armadillids, including members of the genus *Armadillo*, that can form a ball (Taiti et al. 1998). Additional epimera of the fossil also may have been adapted to accommodate a rolling-up behavior (Figure 1). The uropodal ptotopodite is flattened and the configuration of the protopodite is similar to that of the specimen referred to as Armadillidae genus 1 sp. 1 characterized by Judd and Perina (2013, pg.190) from Western Australia. In this species, the protopodite is rounded and the dorsal uropod exopodites do not extend to the distal margin of the protopodite. A similar configuration occurs on the fossil as well as on other members of Australian Armadillidae (Lewis 1998; Judd and Perina 2013).

Palaeoarmadillo microsoma gen. et sp. n. is the second terrestrial isopod described from Myanmar amber. The first species, *Myanmariscus deboiseae* Broly et al. (2015), was tentatively placed in the family Styloniscidae within the Synocheta group and can be easily distinguished from *Palaeoarmadillo microsoma* gen. et sp. n. by its 6 flagellar segments and lack of eyes (Broly et al. 2015).

The presence of two putative mite spermatophores (length = 30 μm) with sperm packets on the dorsum of the fossil shows that the fossil shared its habitat with acarines (Figure 10). The lower stalk portion is the spermatophore and the globular top portion the sperm packet. The shapes of extant mite spermatophores, including some similar to those on the back of the fossil isopod, are depicted in Krantz (1978).

Also of interest are two fly larvae (Diptera) that are adjacent to the fossil isopod (Figure 11). It is typical for parasites, especially if they are near the end of their larval stage, to leave the body of their host when the latter falls in resin. Larvae of the family Rhinophoridae (Oestroidea: Diptera) are isopod parasitoids in North America (Sassaman and Garthwaite 1984), Great Britain (Bedding 1973) and other parts of the globe. All members of this family are obligate parasites of terrestrial isopods and are the only known Diptera to parasitize this host group (Crosskey 1978). It is possible that these fossil larvae are precursors of this group of flies, however in the mid-Cretaceous, other fly lineages also could have been parasitizing terrestrial isopods.

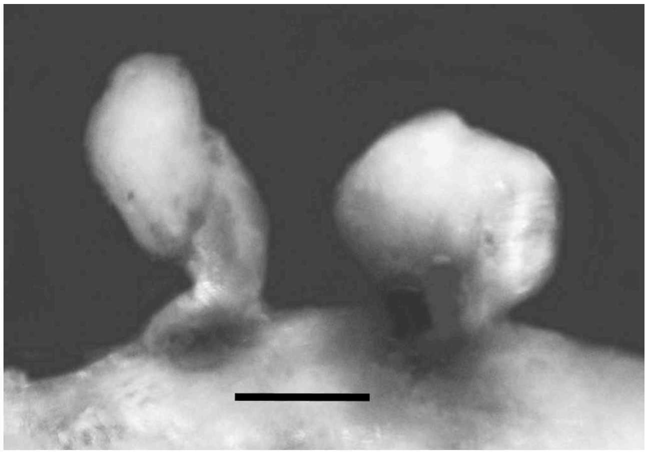

Figure 10. Lateral view of two mite spermatophores on the dorsum of *Palaeoarmadillo microsoma* gen et sp. nov. in Myanmar amber. Scale bar = 14 μm.

Figure 11. Dorsal left hind margin of *Palaeoarmadillo microsoma* gen. et sp. nov. in Myanmar amber showing two fly larvae (arrows) adjacent to their isopod host. Scale bar = 210 μm.

Marine isopods date back to the Pennsylvanian of the Upper Carboniferous (Schram 1970) and a number of terrestrial fossils have been reported from Baltic and Dominican amber (Poinar 1992). An analysis of fossil isopods was provided by Schmidt (2008), who at that time concluded that the oldest known fossil terrestrial isopods were in Baltic amber. A more extensive, updated review of the fossil Oniscidea was presented by Broly et al. (2013) followed by Lins et al. (2017). The latter authors concluded that of the 10,000 described isopods, 3,600 species are from the terrestrial suborder Oniscidea. At present, the oldest terrestrial fossil isopods are those from Myanmar amber.

It is interesting that a Gondwanan origin was proposed for both the Styloniscidae (Isopoda: Oniscidea) (Broly et al. 2015) and the Armadillidae (Taiti et al. 1998) based on their extant distributions. Both Myanmar amber isopods corroborate the proposal that Myanmar amber fossils originated in Gondwana and rafted to Southeast Asia in the Early Cretaceous (Poinar 2018).

Acknowledgments

Thanks are extended to Helmut Schmalfuss for first indicating to the author that the fossil belonged to the family Armadillidae and to Barry O Connor, Gerald Krantz and Evert Linquist for concurring that the structures on the back of the fossil resemble mite spermatophores. The author is grateful to P. Broly and an anonymous reviewer whose comments greatly improved the paper.

Disclosure statement

No potential conflict of interest was reported by the author.

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