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Article

First Fossil of Tylidae (Isopoda: Oniscidea) in Kachin Amber, Myanmar, with a List of All Oniscidea Fossil Records

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Abstract: A fossil of Oniscidea, Tylidae gen. et sp. indet. from Kachin amber (Cretaceous Cenomanian), Myanmar, is described here. The convex body, the cephalon with a triangular protrusion between the antennae, and pereonites 2–6 with epimera demarcated from tergites indicate that this specimen belongs to the family Tylidae, but since it is not an adult the identification of the genus and species is uncertain. This specimen has a convex body and shows an ability to conglobate, like all Tylidae. It is the first specimen of Oniscidea with a conglobation ability found in Burmese amber. Up to now, the fossil record of terrestrial isopods has included a total of 20 families and 54 records (36 species and 18 not formally identified species), 20% of which are from the Cretaceous period. These fossil records from the Cretaceous period show that terrestrial isopods were highly diversified as early as in the Cenomanian.

Keywords: Myanmar amber; conglobation ability; fossil; Mesozoic; terrestrial isopods

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1. Introduction

Terrestrial isopods (Oniscidea), also known as woodlice or pill bugs, are the only isopods fully adapted to live on land, occurring in all terrestrial environments from coasts to high mountains, and from forests to deserts [1–5]. The species of Oniscidea evolved to live on land directly from the ocean instead of using freshwater [6]. Like other Peracarida, terrestrial isopods show direct development, involving a marsupial and a postmarsupial phase. After exiting the marsupium the individuals become the first postmarsupial mancas, similar to adults except for the reduced pereonite 7 and seventh pereopods, and the absence of secondary sexual characters [7].

As for many other invertebrate groups, the phylogeny of terrestrial isopods is not yet completely resolved and existing research based on morphological and molecular analyses tends to consider most of the species of Oniscidea as monophyletic, maybe with the exclusion of the genus Ligia Fabricius, 1798 [8–16]. Oniscidea consist of five principal lineages, Diplocheta, Tylida, Microcheta, Synocheta, and Crinocheta [6,17], including almost 4000 species in more than 500 genera and 38 families [2,3,18–22]. Diplocheta and Tylida represent the most basal clades, mainly including semi-terrestrial species [9]. Most species of Diplocheta and Tylida occur in near-shore habitats and are considered the transitional stage of Isopoda conquering the land [5]. Tylida (Tylidae) comprise only two genera: *Helleria* Ebner, 1868 and *Tylos* Audouin, 1826 [16]. *Helleria* comprises only *H. brevicornis* Ebner, 1868, distributed in the woods of the North Tyrrhenian sea [17,22], whereas *Tylos* has a worldwide distribution, occurring on coastal supralittorals [23–26]. Tylidae have a conglobation ability to protect themselves from predators and to reduce water loss [27,28]. *Tylos* juveniles can allow the swash to transport them up the beach by rolling themselves into a ball; although adults have not been observed to show this behaviour, if caught by a wave they flatten themselves against the beach and allow the water to pass over them before moving upshore [24].

Regarding fossils, the earliest Oniscidea fossil record comes from the Cretaceous Albian (105 Ma), but some indications suggest that they could have already appeared on land in the Late Palaeozoic [14,29,30]. Fossil records of Oniscidea are quite scarce and mostly limited to preservation in amber [30]; until recently, they were almost entirely restricted to the Cenozoic. To our knowledge, in the Mesozoic, amber with Oniscidea inclusions is only known from three localities: France, Spain and Myanmar [30]. The formation of Kachin amber is relatively old (Cretaceous, 99 Ma) [31], in the period of intense orogeny in the Mesozoic [32]. Dinosaurs were still in their heyday, and fish and birds were also highly developed [33–35]. At that time, mammals and angiosperms had just appeared [36]. The biodiversity in amber from Myanmar is very high, with a lot of published documents about insects and other terrestrial arthropods [37]. To date, there are only two species in two genera of Oniscidea preserved in Burmese amber [38,39]. The evolutionary history of the Oniscidea is of great significance to better understand the processes of land adaptations in crustaceans. Thus, Oniscidea may also contribute to the reconstruction of the ancient environment near the Early Cenomanian amber-producing forest in northern Myanmar.

In this paper, we describe the first fossil of Tylidae from Kachin amber, Myanmar, and provide an updated catalogue of all fossil species and records of the suborder Oniscidea. This work tries to give an insight into the earliest diversity and history of Oniscidea.

2. Materials and Methods

The amber specimen for our study was collected from Kachin (Hukawng Valley) in northern Myanmar before 2016, at the north end of Noije Bum, which is approximately at 26°15′ N, 96°34′ E and 18 km southwest of the town of Tanai [31]. The age of Kachin amber is attributed to the Early Cenomanian (98.19 $\pm$ 0.62 Ma) [31]. The specimen (NO. BXAM BA-ONI-001) is currently housed in the Institute of Zoology, Chinese Academy of Sciences (for ten years), and will eventually be deposited in the Beijing Xiachong Amber Museum, Beijing, China.

Morphological terminology used in species descriptions is mainly based on Schmidt [40], López-Orozco [21], and Taiti [2]. For setae, scales, and similar structures, we follow the definitions given in Schmidt [40].

The specimen was examined and photographed under a Nikon SMZ25 microscope, coupled to a Nikon DS-Ri2 digital camera system. The line drawings were edited by Adobe Illustrator CC and Adobe Photoshop CC.

With the present paper, we also give a survey of all species of fossil Oniscidea described until today, including all valid names and taxa with uncertain or questionable taxonomic status. The families, genera and species are arranged strictly alphabetically, regardless of their systematic position. The catalogue is mainly based on Schmalfuss, (2003) [17], Schmidt, (2008) [6], and Broly, (2013) [30]. Museums and their Acronyms, with Primary Types

BMNH: British Museum (Natural History), London, United Kingdom.

BSIP: Bribal Sahni Institute of Palaeobotany, Lucknow, India.

IHNFG: Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Mexico.

MCNA: Museo de Ciencias Naturales de Álava, La Plata, Argentina.

NMS: National Museums Scotland, Edinburgh, United Kingdom.

OSU: Oregon State University, Corvallis, American.

SMNS: Staatliche Museum für Naturkunde Stuttgart, Stuttgart, Germany.

3. Results

3.1. The First Fossil Record of the Family Tylidae from Myanmar

Systematics
Order: Isopoda Latreille, 1817
Suborder: Oniscidea Latreille, 1802
Family: Tylidae Dana, 1852
Genus and species indet.

Materials: One manca specimen (NO. BXAM BA-ONI-001) from Kachin amber from the Hukawng Valley (Myanmar).

Description: Maximum dimensions: 2.9 mm length × 1.7 mm width. Able to roll up into a ball; dorsal surface not distinctly granulated (Figure 1).

Cephalon (Figure 2A,B): triangular frontal process well developed; flat, semi-circular frontal shield above triangular frontal process; eyes consisting of several ommatidia.

Antennula (Figure 2A): short, composed of one or two elements.

Antenna (Figures 1C and 2A–D): five peduncular articles plus flagellum of four articles. Fourth peduncular article longest; fifth peduncular article thickset. Flagellum with three subequal articles and minute terminal article.

Pereon (Figures 1B,C and 2E,F): seven segments. Pereonites 2 to 6 with epimera demarcated by sutures, and pereonite 7 without epimera (manca stage). Pereonite 1 with concave distal margins at sides, posterolateral corners triangular directed backwards; epimera of pereonite 2 trapezoidal, of pereonites 3 and 4 triangular apically rounded, of pereonites 5 and 6 sub-rectangular.

Pereopods (Figure 2G,H): poorly discernible due to conglobating position of the animal. Dactylus and propodus with no setae; carpus longest, twice as long as propodus, covered with many setae, with three swellings on sternal margin, each with two setae; merus and ischium with few setae.

Pleon (Figure 2E,F): consisting of five segments. Pleonites 1 and 2 short and inconspicuous; pleonites 3 and 4 with well-developed epimera directed backwards; pleonite 5 without epimera.

Telson (Figure 2F): sub-rectangular with widely rounded distal margin, about one-and-a-half times as wide as long; in dorsal view, fully covering uropods.

Remarks: The specimen certainly belongs to the family Tylidae, based on the following characteristics: (1) a well-developed frontal process; (2) pereonites with epimera not fused to tergites except pereonite 1; and (3) uropods in a completely ventral position, not visible in dorsal view [24,41]. Even if this specimen is a manca with pereonite 7 not fully developed, it shows a clear difference from both *Tylos* and *Helleria*, i.e., the presence of a flat frontal shield above the frontal process. It differs from *Helleria* also in the pleon tergites not being fused and in the triangular shape of the frontal process. For the latter characteristic, this specimen seems similar to the genus *Tylos*. Due to the manca stage of this specimen, we refrained from establishing a new genus and species for it. More specimens with adult forms are needed to further determine its taxonomic status at genus and species level.

3.2. Catalogue of Oniscidea Fossil Records

The fossil record of Oniscidea comprises 36 species and 17 records with undefined taxon names, including the one new record described herein. Eleven fossil records from Spain, France and Myanmar come from the Mesozoic Era; thirty-nine from the Baltic, Dominican Republic, Ukraine, Kenya, India and Mexico are from the Cenozoic Era, and four have unknown ages (Table 1).

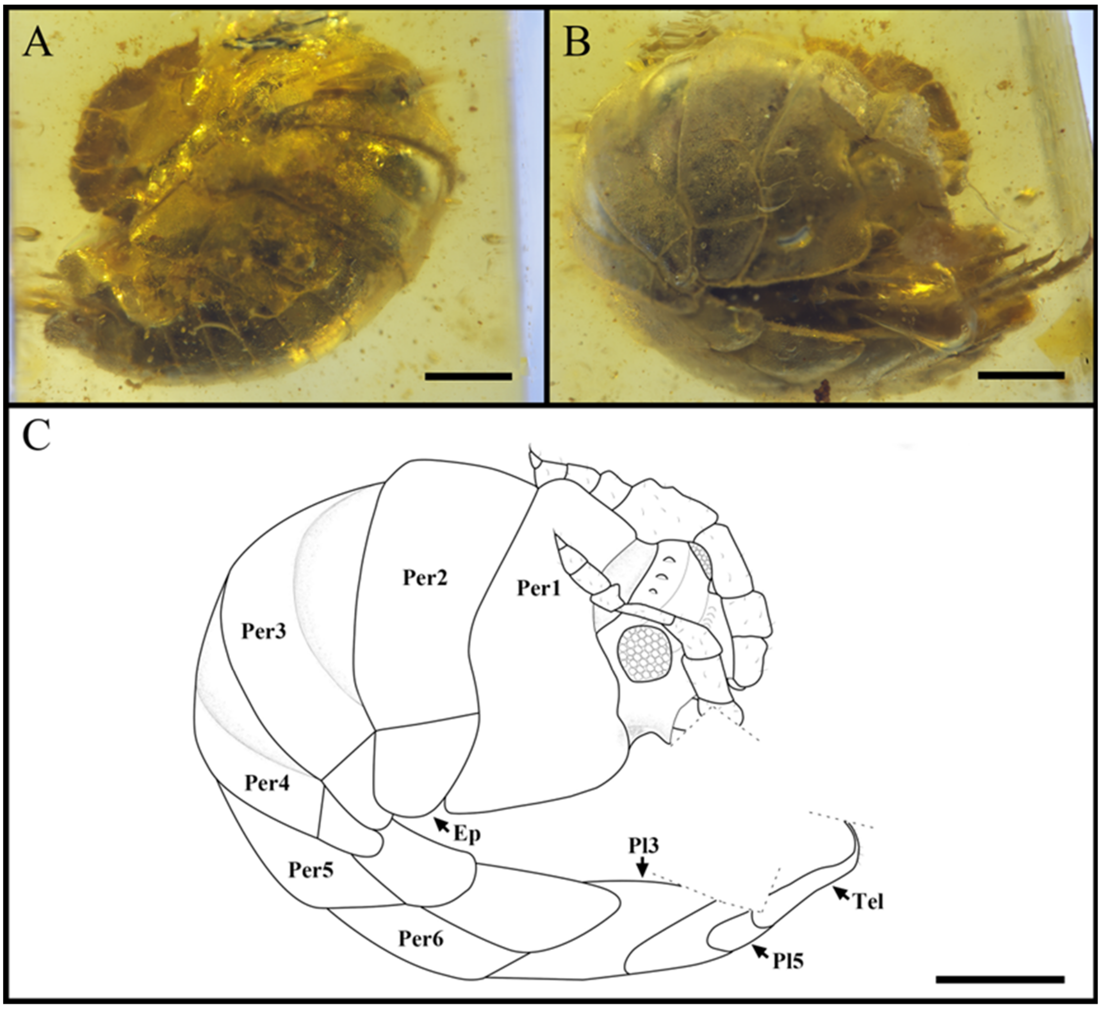

Figure 1. General habitus of specimen. (**A**) Photograph in left lateral view; (**B**) Photograph in right lateral view. (**C**) Line drawing as in B. Per = Pereonite; Ep = Epimeron; Pl = Pleonite; Tel = Telson. Scale bars = 500 µm.

3.2.1. List of Fossil Records of Oniscidea with Definite Taxonomic Status

Family: Agnaridae

Genus: *Protracheoniscus* Verhoeff, 1917

Protracheoniscus Verhoeff, 1917: 167 [42]. Type species: *Porcellio amoenus* C.L. Koch, 1841 (=*Protracheoniscus politus* (C.L. Koch, 1841)) by subsequent designation by Gruner, 1966 [43].

1. *Protracheoniscus politus* (C.L. Koch, 1841)

Porcellio politus C.L. Koch, 1841: 12 [44]. Fossil (rock): Strouhal, 1954 (as *Protracheoniscus* cf. *amoenus*): 53 [45]. Locality: Hundsheim, Austria; Bitterfeld, Germany. Schumann and Wendt, 1989: 37 (list) [46]; Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 220 (catalogue) [17]; Dunlop, 2010: 65 (Figure 5) [48]; Broly et al., 2013: 464 (list) [30].

Age: Chattian, Oligocene, Cenozoic.

Family: Armadillidae

Genus: † *Palaeoarmadillo* Poinar, 2018

Palaeoarmadillo Poinar, 2018: 2 [39] (monotypic). Type species: *Palaeoarmadillo microsoma* Poinar, 2018 by original designation.

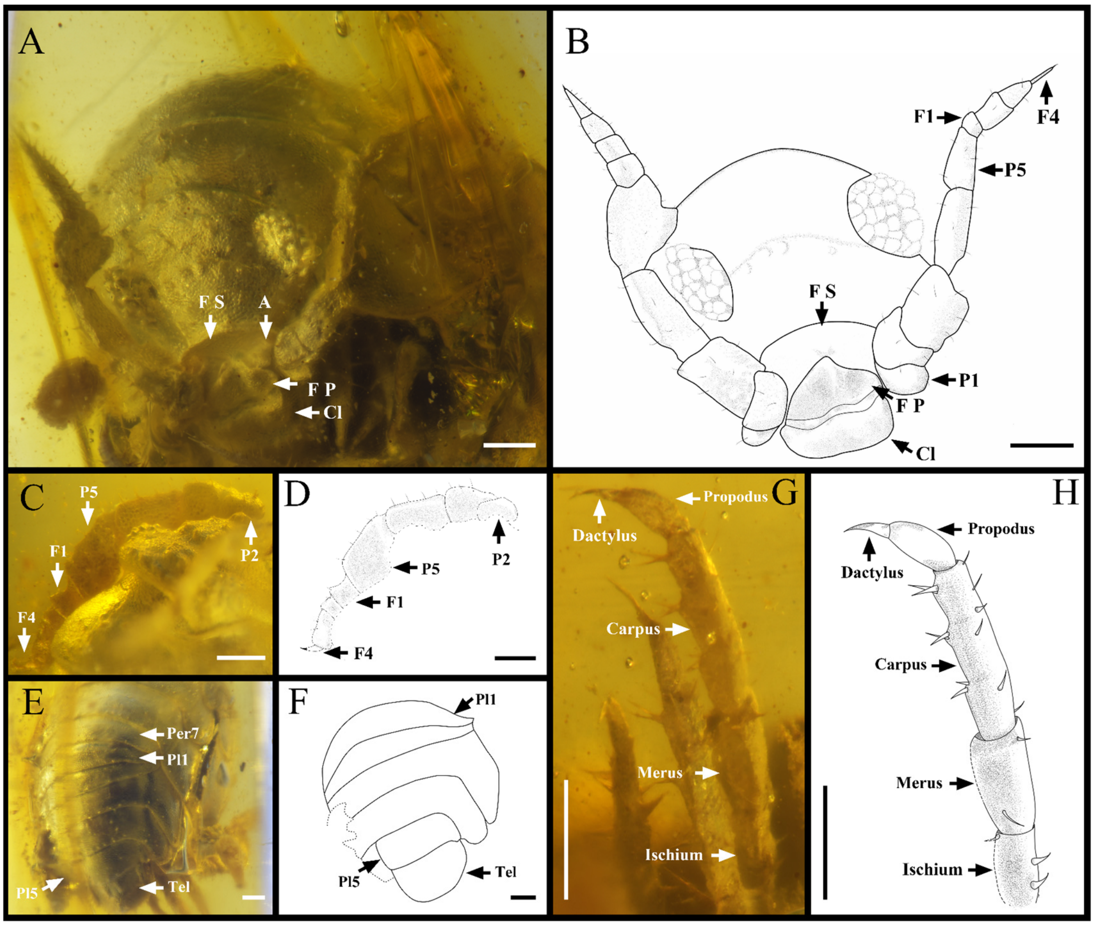

Figure 2. Detailed photographs and interpretative line drawings of Tylidae fossil. (**A**) Photograph of cephalon. (**B**) Line drawing as in A. (**C**) Photograph of antenna. (**D**) Line drawing as in C. (**E**) Photograph of pereonites 6-7, pleon and telson. (**F**) Line drawing as in E. (**G**) Photograph of pereopods. (**H**) Line drawing as in G. A = Antennula; Cl = Clypeus; F1–F4 = Segments of flagellum 1–4; FP = Frontal process; FS = Frontal shield; P1–5 = Segments of peduncle 1–5; Per = Pereonite; Pl = Pleonite; Tel = Telson. Scale bars = 200 µm.

2. † *Palaeoarmadillo microsoma* Poinar, 2018

Palaeoarmadillo microsoma Poinar, 2018: 2 [39] (amber). Locality: Hukawng Valley, Kachin State, Myanmar. Holotype ♀ B-Cr-2 (OSU).

Age: Cretaceous Cenomanian, Mesozoic.

Family: Armadillidiidae

Genus: *Armadillidium* Brandt, 1831

Armadillidium Brandt, 1831: 81 [49]. Type species: *Armadillidium commutatum* Brandt, 1831 (=*Armadillidium vulgare* Latreille, 1804) by subsequent designation by Fowler, 1912 [50].

3. *Armadillidium carniolense* Verhoeff, 1901

Armadillidium carniolense Verhoeff, 1901: 67 [51]. Fossil (rock): Strouhal, 1954: 56 [45]. Locality: Hundsheim, Austria.

Age: Pleistocene, Cenozoic.

4. † *Armadillidium payangadensis* Srivastava, Shukla, Kumar, Kumar & Prakash, 2006

Armadillidium payangadensis Srivastava et al., 2006: 715 [52] (amber). Locality: Payangadi China Clay mine, Cannanore district, Kerala, India. Holotype sex unknown No. 38375 (BSIP). Schmidt, 2008: 220 (comments) [6]; Broly et al., 2013: 464 (list) [30].

Age: Miocene, Cenozoic.

Note: Status uncertain (Schmidt, 2008) [6].

5. *Armadillidium pulchellum* (Zenker, 1798)

Oniscus pulchellum Zenker, 1798: 21 [53]. Fossil (amber): Schumann and Wendt, 1989: 37 (list) [46]. Locality: Germany. Spahr, 1993: 46 (catalogue) [47]; Schmalfuss, 2003: 34 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].

Age: Chattian, Oligocene, Cenozoic.

6. † *Armadillidium molassicum* (Heer, 1865)

Armadillo molassicus Heer, 1865: 622 [54] (rock). Locality: Germany. Schmidt, 2008: 220 (comments) [6]. Schmalfuss, 2003: 43 (nomen dubium) [17]; Broly et al., 2013: 464 (list) [30].

Age: Miocene, Cenozoic.

Note: "not sufficient to recognize whether it is an isopod or a millipede" (Schmidt, 2008) [6].

7. *Armadillidium vulgare* (Latreille, 1804)

Armadillo vulgaris Latreille, 1804: 48 [55]. Subfossil (rock): Dalens and Bouthier, 1985: 85 [56]. Locality: Cosne-sur-Loire, France. Schmalfuss, 2003: 38 (catalogue) [17].

Age: Second century, Cenozoic.

Family: Delatorreiidae

Genus: *Pseudarmadillo* Saussure, 1857

Pseudarmadillo de Saussure, 1857: 308 [57]. Type species: *Pseudarmadillo carinulatus* de Saussure, 1857 by monotypy.

8. † *Pseudarmadillo cristatus* Schmalfuss, 1984

Pseudarmadillo cristatus Schmalfuss, 1984: 4 [58] (amber). Locality: Dominican Republic. Holotype ♂ No. Do-2403-K-1 (SMNS). Paratypes: 1 ♀ No. Do-3881-M-1 (SMNS); six specimens in one piece of amber, No. Do-4612-B (SMNS); 1♂ No. Do-579-K (SMNS); two juveniles (1 mm along) No. Do-457-K (SMNS). Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 222 (catalogue) [17].

Age: Oligocene-Miocene, Cenozoic.

9. † *Pseudarmadillo tuberculatus* Schmalfuss, 1984

Pseudarmadillo tuberculatus Schmalfuss, 1984: 10 [58] (amber). Locality: Dominican Republic. Holotype ♂ No. Do-4157-M-1 (SMNS). Paratypes 1 ♀ No. Do-4156-M-1 (SMNS); two specimens in one piece of amber, No. Do-3349-M (SMNS). Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 222 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].

Age: Oligocene-Miocene, Cenozoic.

Family: Detonidae

Genus: *Armadilloniscus* Uljanin, 1875

Armadilloniscus Uljanin, 1875: 5 [59]. Type species: *Actoniscus ellipticus* Harger, 1878 (=*Armadilloniscus ellipticus* (Harger, 1878)) by subsequent designation by Mulaik, 1960 [60].

10. † *Armadilloniscus miocaenicus* Broly, 2018

Armadilloniscus miocaenicus Broly, 2018 in Broly et al., 2018: 205 [61] (amber). Locality: Chiapas, Mexico. Holotype ♀ IHNFG-4990 (IHNFG).

Age: Lower Miocene, Cenozoic.

Family: Eubelidae

Genus: *Eubelum* Budde-Lund, 1885

Eubelum Budde-Lund, 1885: 291 [62]. Type species: *Eubelum lubricum* Budde-Lund, 1885 by monotypy.

11. † *Eubelum rusingaense* Morris, 1979

Eubelum rusingaense Morris, 1979: 72 [63] (rock). Locality: between Hiwegi Hill and the east coast of Rusinga Island, Lake Victoria, Kenya. Holotype sex unknown BM(NH) In. 61025 (BMNH). Broly et al., 2013: 464 (list) [30].

Age: Lower Miocene, Cenozoic.

Family: Ligiidae

Genus: † *Eoligiiscus* Sánchez-García, Peñalver, Delclos & Engel, 2021

Eoligiiscus Sánchez-García et al., 2021: 5 [29] (monotypic). Type species: *Eoligiiscus tarraconensis* Sánchez-García, Peñalver, Delclos and Engel, 2021 by original designation.

12. † *Eoligiiscus tarraconensis* Sánchez-García, Peñalver, Delclos *et* Engel, 2021

Eoligiiscus tarraconensis Sánchez-Garcíaet al., 2021: 5 [29] (amber). Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Holotype sex unknown MCNA 9751 (MCNA).

Age: Albian, Cretaceous, Mesozoic.

Genus: *Ligidium* Brandt, 1833

Ligidium Brandt, 1833: 173 [64]. Type species: *Ligidium persoonii* Brandt, 1833 (=*Ligidium hypnorum*) by monotypy.

13. † *Ligidium splendidum* Strouhal, 1940

Ligidium splendidum Strouhal, 1940 ? (amber). Keilbach, 1982: 198 (catalogue) [65]. Locality: Baltic, northern Europe. Spahr, 1993: 46 (catalogue) [47]; Broly et al., 2013: 464 (list) [30].

Age: Eocene, Paleogene, Cenozoic.

Family: Olibrinidae

Genus: † *Palaeolibrinus* Broly, 2018

Palaeolibrinus Broly, 2018: 204 [61] (monotypic). Type species: *Palaeolibrinus spinicornis* Broly, 2018 by original designation.

14. † *Palaeolibrinus spinicornis* Broly, 2018

Palaeolibrinus spinicornis Broly, 2018 in: Broly et al., 2018: 204 [61] (amber). Locality: Campo La Granja mine, near Simojovel, Chiapas, Mexico. Holotype ♂ IHNFG-4984 (IHNFG).

Age: Early Miocene, Cenozoic.

Family: Oniscidae

Genus: *Oniscus* Linnaeus, 1758

Oniscus Linnaeus, 1758: 824 [66]. Type species: *Oniscus asellus* Linnaeus, 1758 by subsequent designation by Audouin, 1823 [67].

15. † *Oniscus convexus* Koch & Behrendt, 1854

Oniscus convexus Koch & Behrendt, 1854: 2 [68] (amber). Locality: Baltic, northern Europe. Keilbach, 1982: 199 (catalogue) [65]; Spahr, 1993: 46 (catalogue) [47]; Schmalfuss, 2003: 162 (nomen dubium) [17]; Broly et al., 2013: 464 (list) [30].

Age: Eocene, Paleogene, Cenozoic.

16. *Oniscus asellus* Linnaeus, 1758

Oniscus asellus Linneaus, 1758: 637 [66]. Subfossil (rock): Dalens and Bouthier, 1985: 86 [56]. Locality: Cosne-sur-Loire, France.

Age: Second century, Cenozoic.

Family: Philosciidae

Genus: † *Aquitanoscia* Broly, Serrano-Sáchez, Rodríguez-García & Vega, 2017

Aquitanoscia Broly et al., 2017: 2 [69]. Type species: *Aquitanoscia chiapasensis* Broly, Serrano-Sáchez, Rodríguez-García & Vega, 2017 by original designation.

17. † *Aquitanoscia chiapasensis* Broly, Serrano-Sáchez, Rodríguez-García & Vega, 2017

Aquitanoscia chiapasensis Broly et al., 2017: 3 [69] (amber). Locality: Los Pocitos mine, near Simojovel, Chiapas, Mexico. Holotype ♀ IHNFG-5016 (IHNFG).

Age: Early Miocene, Cenozoic.

18. † *Aquitanoscia materna* Broly, Serrano-Sáchez, Rodríguez-García & Vega, 2017

Aquitanoscia maternus Broly et al., 2017: 6 [69] (amber). Locality: Los Pocitos mine, near Simojovel, Chiapas, Mexico. Holotype ♀ IHNFG-5017 (IHNFG).

Note: The name *maternus* (masculine adjective) given by Broly et al. (2017) to this species has to be changed to *materna* (feminine adjective) since the genus name *Aquitanoscia* is feminine [69].

Age: Early Miocene, Cenozoic.

Family: Porcellionidae

Genus: *Porcellio* Latreille, 1804

Porcellio Latreille, 1804: 45 [55]. Type species: *Porcellio scaber* Latreille, 1804 by subsequent designation by Gruner, 1966 [43].

19. *Porcellio gallicus* Dollfus, 1904

Porcellio gallicus Dollfus, 1904: 45 [70]. Subfossil (rock): Dalens and Bouthier, 1985: 86 [56]. Locality: Cosne-sur-Loire, France.

Age: Second century, Cenozoic.

20. *Porcellio scaber* Latreille, 1804

Porcellio scaber Latreille, 1804: 45 [55]. Fossil (rock): Strouhal, 1954: 52 [45]. Locality: Hundsheim, Austria. Subfossil: Dalens and Bouthier, 1985: 86 [56]. Locality: Cosne-sur-Loire, France. Schmalfuss, 2003: 205 (catalogue) [17].

Age: Pleistocene, Cenozoic.

21. † *Porcellio cyclocephalus* Menge, 1854

Porcellio cyclocephalus Menge, 1854 in Koch and Behrendt, 1854: 10 [68] (amber). Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Keilbach, 1982: 199 (catalogue) [65]; Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 194 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].

Age: Eocene, Paleogene, Cenozoic.
Note: "Unrecognizably described from Baltic amber" (Schmalfuss, 2003) [17].

22. † *Porcellio granulatus* Menge, 1854

Porcellio cyclocephalus Menge, 1854 in: Koch and Behrendt, 1854: 10 [68] (amber). Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Keilbach, 1982: 199 (catalogue); Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 197 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].
Age: Eocene, Paleogene, Cenozoic.
Note: "Unrecognizably described from Baltic amber" (Schmalfuss, 2003) [17].

23. † *Porcellio notatus* C.L. Koch, 1854

Porcellio notatus Koch, 1854 in Koch and Behrendt, 1854: 10 [68] (amber). Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Keilbach, 1982: 199 (catalogue); Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 202 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].
Age: Eocene, Paleogene, Cenozoic.
Note: "Unrecognizably described from Baltic amber" (Schmalfuss, 2003) [17].

Genus: *Porcellionides* Miers, 1877

***Porcellionides* Miers, 1877: 668** [71]. Type species: Porcellio (*Porcellionides) jelskii* Miers, 1877 (=*Porcellionides pruinosus* (Brandt, 1833)) by subsequent designation by Schmalfuss and Ferrara, 1978 [41].

24. *Porcellionides pruinosus* (Brandt, 1833)

Porcellio pruinosus Brandt, 1833: 181 [64]. Fossil (rock): Baas, 1982: 119 [72]. Locality: Nidderau Germany. Schmalfuss, 2003: 212 (catalogue) [17].
Age: unknown.

Family: Scleropactidae
Genus: † *Palaeospherarmadillo* Broly, 2018

Palaeospherarmadillo Broly, 2018: 207 [61]. Type species: *Palaeospherarmadillo mazanticus* Broly, 2018 by original designation.

25. † *Palaeospherarmadillo mazanticus* Broly, 2018

Palaeospherarmadillo mazanticus Broly, 2018 in Broly et al., 2018: 207 [61] (amber). Locality: Campo La Granja mine, near Simojovel, Chiapas, Mexico. Holotype ♂ IHNFG-4997 (IHNFG). Paratype ♂ IHNFG-4998 (IHNFG).
Age: Early Miocene, Cenozoic.

26. † *Palaeospherarmadillo rotundus* Broly, 2018

Palaeospherarmadillo rotundus Broly, 2018 in Broly et al., 2018: 208 [61] (amber). Locality: Campo La Granja mine, near Simojovel, Chiapas, Mexico. Holotype sex unknown IHNFG-5302 (IHNFG).
Age: Early Miocene, Cenozoic.

Genus: † *Protosphaeroniscus* Schmalfuss, 1980

Protosphaeroniscus Schmalfuss, 1980: 4 [69] (monotypic). Type species: *Protosphaeroniscus tertiarius* Schmalfuss, 1980 by original designation.

27. † *Protosphaeroniscus tertiarius* Schmalfuss, 1980

Protosphaeroniscus tertiarius Schmalfuss, 1980: 4 [73] (amber). Locality: Dominican Republic. Holotype ♂ Do 1494-K-1 (SMNS). Paratype: ♂ Do 1503-K-1 (SMNS). Keilbach, 1982: 199 (catalogue); Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 217 (catalogue) [17]; Schmidt, 2007: 74 [74]; Broly et al., 2013: 464 (list) [30].

Age: Oligocene Miocene, Cenozoic.

Family: Stenoniscidae

Genus: †*Archeostenoniscus* Broly, 2018

Archeostenoniscus Broly, 2018: 209 [61]. Type species: *Archeostenoniscus robustus* Broly, 2018 by original designation.

28. † *Archeostenoniscus robustus*, Broly, 2018

Archeostenoniscus robustus Broly, 2018 in Broly et al., 2018: 209 [61] (amber). Locality: Campo La Granja mine, near Simojovel, Chiapas, Mexico. Holotype ♀ IHNFG-4988/A (IHNFG).

Age: Early Miocene, Cenozoic.

29. † *Archeostenoniscus mexicanus* Broly, 2018

Archeostenoniscus mexicanus Broly, 2018 in Broly et al., 2018: 210 [61] (amber). Locality: Campo La Granja mine, near Simojovel, Chiapas, Mexico. Holotype sex unknown IHNFG-4996 (IHNFG).

Age: Early Miocene, Cenozoic.

Family: Trachelipodidae

Genus: *Trachelipus* Budde-Lund, 1908

Trachelipus Budde-Lund, 1908: 281 [75]. Type species: *Porcellio rathkii* Brandt, 1833 (=*Trachelipus rathkii* (Brandt, 1833)) by original designation and monotypy.

30. *Trachelipus rathkii* (Brandt, 1833)

Porcellio rathkii Brandt, 1833: 177 [68]. Fossil (rock): Baas, 1982: 119 [72]. Locality: Turkey. Schmalfuss, 2003: 261 (catalogue) [17].

Age: unknown.

Family: Trichoniscidae

Genus: † *Autrigoniscus* Sánchez-García, Peñalver, Delclos & Engel, 2021

Autrigoniscus Sánchez-García, Peñalver, Delclos & Engel, 2021: 13 [29] (monotypic). Type species: *Autrigoniscus resinicola* Sánchez-García, Peñalver, Delclos & Engel, 2021, by original designation.

31. † *Autrigoniscus resinicola* Sánchez-García, Peñalver, Delclos &Engel, 2021

Autrigoniscus resinicola Sánchez-García et al., 2021: 13 [29] (amber). Locality: Peñacerrada I amber site [Peñacerrada I = Moraza], eastern margin of the Basque-Cantabrian Basin, Burgos, northern Spain. Holotype ♂ MCNA 12522 (MCNA).

Age: Albian, Cretaceous, Mesozoic.

Genus: *Trichoniscus* Brandt, 1833

Trichoniscus Brandt, 1833: 174 [64]. Type species: *Trichoniscus pusillus* Brandt, 1833 by monotypy.

32. † *Trichoniscus asper* Menge, 1854

Trichoniscus asper Menge, 1854 in Koch and Behrendt, 1854: 10 [68] (amber). Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Keilbach, 1982: 199 (catalogue); Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 266 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].

Age: Eocene, Paleogene, Cenozoic.

Genus: *Hyloniscus* Verhoeff, 1908

Hyloniscus Verhoeff, 1908: 176 [76]. Type species: *Itea riparia* C.L. Koch, 1838 (=*Hyloniscus riparius* (C.L. Koch, 1938)) by original designation.

33. *Hyloniscus riparius* (C.L. Koch, 1838).

Itea riparia C.L. Koch, 1838: 17 [77]. Fossil (amber): Schumann and Wendt, 1989: 37 [46]. Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Spahr, 1993: 47 (catalogue) [47]; Schmalfuss, 2003: 113 (catalogue) [17]; Broly et al., 2013: 464 (list) [30].

Age: Eocene, Paleogene, Cenozoic.

Family: Tylidae
Genus: *Tylos* Audouin, 1826

Tylos Audouin, 1826: 96 [67]. Type species: *Tylos latreillii* Audouin, 1826, by monotypy.

34. *Tylos granulatus* Krauss, 1843

Tylos granulatus Krauss, 1843: 64 [78]. Fossil (rock): Haughton, 1931: 27 [79]. Locality: west coast of South Africa.

Age: late Tertiary, Cenozoic.

Family: Detonidae?
Genus: † *Heraclitus* Sánchez-García, Peñalver, Delclos & Engel, 2021

Heraclitus Sánchez-García, Peñalver, Delclos & Engel, 2021: 19 [29] (monotypic). Type species: *Heraclitus helenae*, Sánchez-García, Peñalver, Delclos & Engel, 2021 by original designation.

35. † *Heraclitus helenae* Sánchez-García, Peñalver, Delclos & Engel, 2021

Heraclitus helenae Sánchez-García, Peñalver, Delclos & Engel, 2021: 21 [29] (amber). Locality: Basque-Cantabrian Basin, Burgos, northern Spain. Holotype sex unknown MCNA 12546 (MCNA).

Age: Albian, Cretaceous, Mesozoic.

Family: Styloniscidae?
Genus: † *Myanmariscus* Broly, Maillet & Ross, 2015

Myanmariscus Broly, Maillet & Ross, 2015: 221 [38] (monotypic). Type species: *Myanmariscus deboiseae* Broly, Maillet & Ross, 2015 by original designation.

36. † *Myanmariscus deboiseae* Broly, Maillet & Ross, 2015

Myanmariscus deboiseae Broly et al., 2015: 221 [38] (amber). Locality: Hukawng Valley, Kachin State, Myanmar. Holotype ♀ NMS G.2010.20.42 (NMS).

Age: Cenomanian, Cretaceous, Mesozoic.

3.2.2. List of Fossil Records of Oniscidea with Unidentified Taxonomic Status

Family: Uncertain
Genus: Uncertain

Four specimens, species uncertain.

Reference: Alonso et al., 2000 [80] (amber); Delclos et al., 2007 [81] (amber); Perrichot, 2004 [82] (amber); Ross et al., 2010 [83] (amber).
Age: Albian, Cretaceous, Mesozoic.
Fossil locality: Spain; Spain; France; Myanmar.

Family: Uncertain
Genus: † *Eoarmadillidium* Dollfus, 1904
Eoarmadillidium Dollfus, 1904: 146 (monotypic). Type species: *Eoarmadillidium granulatum* Dollfus, 1904 by original designation.

† *Eoarmadillidium granulatum* Dollfus, 1904
Eoarmadillidium granulatum Dollfus, 1904: 146 [70] (amber). Locality: Cette, France. Schmalfuss, 2003: 94 (catalogue) [17].
Age: unknown.

Family: Armadillidiidae
Genus: Uncertain
Two specimens, species uncertain.
Reference: Serrano et al., 2007 [84] (amber); Weitschat and Wichard, 2010 [85] (amber).
Age: Lower Miocene, Cenozoic; Paleogene Eocene, Cenozoic.
Fossil locality: Mexico; Baltic, northern Europe.

Genus: *Armadillidium* Brandt
One specimen, species uncertain.
Reference: Hyžný and Dávid, 2017 [86] (rock).
Age: Upper Oligocene, Cenozoic.
Fossil locality: Hungary.

Family: Ligiidae
Genus: *Ligia* Fabricius, 1798
Two specimens, species uncertain.
Reference: Néraudeau, 2008 [87] (amber); Spahr, 1993 [47] (amber).
Age: Albian, Cretaceous, Mesozoic; Eocene, Paleogene Cenozoic.
Fossil locality: France; Baltic, northern Europe.

Family: Philosciidae
Genus: Uncertain
One specimen, species uncertain.
Reference: Schmalfuss, 1984 [58] (amber).
Age: Oligocene-Miocene, Cenozoic.
Fossil locality: Dominican Republic.

Family: Platyarthridae
Genus: *Trichorhina* Budde-Lund, 1908
One specimen, species uncertain.
Reference: Schmalfuss, 1984 [58] (amber).
Age: Oligocene Miocene.
Fossil locality: Dominican Republic.

Family: Porcellionidae
Genus: Uncertain
One specimen, species uncertain.
Reference: Perkovsky et al., 2010 [88] (amber).
Age: Oligocene-Miocene, Cenozoic.
Fossil locality: Ukraine.

Family: Styloniscidae or Trichoniscidae
Genus: Unccertain
One specimen, species uncertain.
Reference: Schmalfuss, 1984 [58] (amber).
Age: Oligocene-Miocene, Cenozoic.
Fossil locality: Dominican Republic.

Family: Trachelipodidae
Genus: Uncertain
Two specimens, species uncertain
Reference: Weitschat and Wichard, 2010 [85] (amber); Perkovsky et al., 2010 [88] (amber).
Age: Paleogene-Eocene, Cenozoic; Upper Eocene, Cenozoic.
Fossil locality: Baltic, northern Europe. Ukraine.

Family: Tylidae
Genus: Uncertain
One specimen, species uncertain
Reference: This study (amber).
Age: Cenomanian, Cretaceous Mesozoic.
Fossil locality: Myanmar.

Table 1. Species of fossil terrestrial isopod per family and geological era.

Family	Mesozoic	Cenozoic
Agnaridae	-	1 species [45]
Armadillidae	1 species [39]	-
Armadillidiidae	-	5 species and 3 records, status uncertain [45,46,52,54,56,84–86]
Delatorreiidae	-	2 species [58]
Detonidae	-	1 species [61]
Eubelidae	-	1 species [63]
Ligiidae	1 species and 1 record, status uncertain [29,87]	1 species and 1 record, status uncertain [47,65]
Olibrinidae	-	1 species [61]
Oniscidae	-	2 species [56,68]
Philosciidae	-	2 species and 1 record, status uncertain [58,69]
Platyarthridae	-	1 record, status uncertain [58]
Porcellionidae	-	6 species (1 species, age unknown) and 1 record, status uncertain [45,56,68,72,88]

Table 1. *Cont.*

Family	Mesozoic	Cenozoic
Scleropactidae	-	3 species [61,73]
Stenoniscidae	-	2 species [61]
Trachelipodidae	-	1 species (age unknown) and 2 records, status uncertain [72,85,88]
Trichoniscidae	1 species [29]	2 species and 1 record, status uncertain [46,68,77]
Detonidae?	1 species [29]	-
Styloniscidae?	1 species [38]	-
Styloniscidae or Trichoniscidae	-	1 record, status uncertain [58]
Tylidae	1 record, status uncertain (this study)	1 species [79]
Unclear	4 records, status uncertain [80–83]	1 record status, uncertain (1 species ages unknown) [70]
total	5 species and 6 records, status uncertain	31 species (3 species ages unknown) and 12 records, status uncertain (1 species ages unknown)

4. Discussion

The specimen described above is the second fossil record of the family Tylidae, the first of this family for Kachin amber (Late Cretaceous) [31]. As all the other taxa in this family, this specimen is able to roll up into a ball [17,41]. Conglobation ability is common, in mammals, such as in hedgehogs, armadillos, and pangolins; and in arthropods, such as pill millipedes (Glomerida) [89], beetles (Ceratocanthinae) [90], cockroaches (Blaberidae) [91], and pill bugs (Oniscidea). In terrestrial isopods, there are many groups (e.g., Armadillidae; Armadillidiidae) with the conglobation ability. The conglobation ability has appeared several times independently within the Oniscidea [40].

The fossil records of Oniscidea are rare. While the earliest fossil record of Oniscidea only dates back to the Early Cretaceous, based on phylogenetic studies and the palaeobiogeographic context of fossil specimens an origin of Oniscidea in the Late Paleozoic has been proposed [14,30]. To date, there are 54 terrestrial isopod fossil records within 20 families [Table 1]. The classification position of some groups is not clear due to the lack of detailed morphological characteristics [see list]. Among them, the earliest fossil records are from Spanish amber (Cretaceous Albian, 105 Ma) [29,92].

Forty-one records of terrestrial isopods have been reported from the Cenozoic deposits of the Baltic, Dominican Republic, Ukraine, Kenya, India, and Mexico. All the major modern families of woodlice were already present and widely distributed geographically at that time. Twelve records of terrestrial isopods come from the Mesozoic (Cretaceous), mainly from Spain, France, and Myanmar [Table 1]. It seems unlikely to find inclusions of oniscideans in amber older than Cretaceous because the amber-producing plants, although recorded from Carboniferous, did not produce enough sap to trap macroscopic invertebrates until the Late Jurassic [57]. The fossils belong to four out of five major groups of Oniscidea: Diplocheta and Tylida, which are the earliest diverged clades, and Synocheta and Crinocheta, at the higher phylogenetic level [93].

Among crustaceans, three major groups have invaded terrestrial environments: the peracarid orders Amphipoda. Isopoda, and Decapoda [94]. In Isopoda, except for Oniscidea, species in other suborders either live in the ocean or in fresh water. Terrestrial isopods (Oniscidea) are the only isopods fully adapted to live on land (except a few species that have become secondarily adapted and returned to aquatic habitats [5]). It is widely believed that the invasion of terrestrial environments from the sea by isopods has involved a transitional step within the supralittoral, instead of using freshwater [95].

The two earliest diverged families, Ligiidae and Tylidae, successfully colonised the supralittoral [5,26,96]. The evolution of terrestrial isopods from ancestral marine isopods was proposed to have proceeded from a *Ligia*-like ancestor [95]. This statement has been recently questioned with molecular evidence [13,16] that showed *Ligia* to be related to marine isopods and not to the rest of Oniscidea. All the extant species of *Tylos* live in intertidal and supralittoral areas, and a large number of marine taxa are found in Burmese amber [37]. These data confirm the paleogeographic reconstruction of the area with the Burmese amber indicating the influence of a marine environment [96]. This could mean that the Tylidae also lived near the sea during the Cretaceous.

5. Conclusions

In this paper, we report the first fossil record of a terrestrial isopods with conglobation ability from amber of Kachin State, which is the second fossil record of Tylidae. To date, a total of 54 records of isopod fossils from 20 families have been reported. The fossils of Oniscidea are largely biased toward preservation in amber and, until recently, most terrestrial isopod fossils dated from the Cenozoic period. Due to the manca stage of the specimen described, its precise taxonomic position at genus and species level cannot be established. However, the morphological characteristics of the specimen show that it is undoubtedly a member of Tylidae, morphologically close to the genus *Tylos.*

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