Marine-like isopod *Heterosphaeroma priscum* from the Late Paleocene freshwater system in Sézanne, France, revisited

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Well-known for its Palaeocene terrestrial flora, the travertine deposit of Sézanne (Marne, Champagne, France) has also yielded a small number of well-preserved crustaceans, including isopods. In 1868, a single specimen of these isopods has been described by the French zoologist Alphonse Milne-Edwards who remarked on its resemblance to the common benthic isopods from the marine littoral (Sphaeromatidae). A few years later, more material of that same species from Sézanne allowed Charles P.E. Munier-Chalmas to place it in his new genus *Heterosphaeroma*, but without figuring the species or proposing many diagnostic features. Recently, more material of this species turned up in the Sorbonne collection allowing for a more complete description. Here, we provide a redescription of the Sézanne isopod species based on rediscovered original material. Systematic features are discussed that confirm its sphaeromid affinity. In light of recent knowledge on incursions of the Thanetian Sea in this area, and associated travertine palaeofauna and flora, we assume a high likelihood for this species to have lived in karstic spring waters and freshwater calcareous streams during the end of the Palaeocene. We finally discuss the ability of some Recent sphaeromatids to live in freshwater conditions, deep inland, and we compare their ecology to those found in the Paris Basin travertine palaeoenvironments.

**Introduction**

Nowadays, the large and predominantly marine isopod genus *Sphaeroma* consists of over a hundred species, of which around half have been placed in other genera over the years (Boyko et al. 2020). A very small portion of those species, however, are true freshwater inhabitants (Wetzer et al. 2018). The terrestrial plants (mostly Paleocene leaves) of Sézanne have been extensively described by De Saporta (1868), who attributed them to undergrowth in a forest-like environment that harboured a calcareous spring. In his prodrome, De Saporta (1868) also reports mollusks, previously identified by D’Orbigny in Duval and Meillet (1842) and also, for the first time, a small number of well-preserved crustaceans. It is probable that a single specimen was given to Alphonse Milne-Edwards when he described *Sphaeroma priscum*. When Charles P.E. Munier-Chalmas proposed in 1872 the new combination *Heterosphaeroma priscum*, he did not specify the number of specimens he examined. Here we re-examined all material now available to elucidate the systematics and the paleoecology of this Palaeocene isopod.
ties) sands. This relationship is important for dating and understanding the actual transgression/regression movements of the Thanetian sea towards Sézanne at the end of the Palaeocene. It has been suggested that these marine sands had been deposited before the Sézanne/Rilly-la-Montagne lacustrine layer (Hébert 1848), but also right after (D’Archiac 1848; Prestwich 1853). Not much later, however, the latter authors agreed that Bracheux sandstone had been deposited prior to the Rilly lacustrine layers, but were actually not present, and therefore unobservable, in Sézanne outcrops.

These sands, present in many localities west and north of Sézanne, provide evidence of the transgression pulse of the Thanetian sea in the Paris Basin, which had not reached Sézanne. Sea movements followed the stages of the emersion of Paris Basin until the early Eocene when it started to gradually subside under the cover of Cenozoic deposits (Hébert 1848). In Sézanne, the spring and resurgence environment relates to a hot and humid climate (De Saporta 1868; De Lapparent 1964; Pentecost 2005) that acted by way of ample water supply on the underlying chalks to form this terrestrial karstic system at the end of the Thanetian.

The material of *Heterosphaeroma priscum* from Sézanne comes mostly from Munier-Chalmas (1872) and reportedly was associated with insects and one decapod crustacean of *Astacus edwardsi* Van Straelen, 1928a. Preserved in similar sediments, both arthropod types apparently show clear freshwater affinities: (i) insects associated to trichopteran and dragonfly larvae (Nel and Blot 1990), and (ii) a decapod crustacean ascribed to a crayfish genus (*Astacus*, Astacoidea). The crayfish constitutes the sole report on the east side of the North-Atlantic in the early Paleogene (*Cambarus primaevus* is known from the Eocene of Wyoming). However, marine influences cannot be totally discarded at this stage. Indeed, it seems some stratigraphic relationships exist between weathering profiles, continental sediments and marine deposits during and in between Thanetian transgressions (see Laurain and Meyer 1986).

**Systematic palaeontology**

**Order Isopoda Latreille, 1817**

**Suborder Sphaeromatidea Wägele, 1989**

**Superfamily Sphaeromatoidea Latreille, 1825**

**Family Sphaeromatidae Latreille, 1825**

**Genus Heterosphaeroma** Munier-Chalmas, 1872

*Type species:* *Sphaeroma priscum* Milne-Edwards, 1868 by original designation, monotypic, La Montagne des Crottes, Sézanne, Marne, France, late Thanetian.

**Heterosphaeroma priscum** (Milne-Edwards, 1868)

Figs. 1–3.

1868 *Sphaeroma priscum*; Milne-Edwards 1868: 426, 2 figures.

1872 *Heterosphaeroma priscum*; Munier-Chalmas 1872: 166.

1928 *Heterosphaeroma priscum*; Van Straelen 1928b: 40.

1969 *Heterosphaeroma priscum*; Moore and Brooks 1969: 377.

1977 *Heterosphaeroma priscum*; Secrétan 1975: 319.

2014 *Heterosphaeroma priscum*; Giuberti et al. 2014: 81.

*Type material:* Holotype: SU.PAL.2017.0.2.61 (Munier-Chalmas old collection), outer mold (Fig. 1A). Despite the existence of several known specimens as early as 1868, it is clear that Alphonse Milne-Edwards had only seen a single specimen when he provided the species description. He writes: “The false abdominal legs of the last pair are lacking in the exemplar I could examine” (Milne-Edwards 1868: 427) leaving no doubt in that matter. Consequently, SU.PAL.2017.0.2.61 is the holotype, which originally consisted of both the outer and inner molds, the latter being now lost. The fossils in Sézanne are preserved as voids in the travertine. Munier-Chalmas recovered these fossils by pouring gypsum/stearine solution and subsequently dissolved the cal-
careous rock in acid leaving moulds for investigations. Consequently, the specimens SU.PAL.2017.0.0.4 and SU.PAL.2017.0.2.4, exist only in the form of casts and the original specimen has been dissolved.

**Type locality:** Sézanne, Marne department, Grand-Est region, France.

**Type horizon:** Upper Thanetian, Palaeocene, Cenozoic.

**Material.**—MNHN.F.B71849, plaster cast of lost SU.PAL.2017.0.2.61 (inner mold, holotype), in dorsal view. B. SU.PAL.2017.0.0.4 (plaster cast), in dorsal view. C. SU.PAL.2017.0.2.4 (C₁, body fossil anterior half; C₂, head close-up), ventral side. Abbreviations: md, mandibular palp; mxp, maxilliped; mx, maxilla; pln, pleonite; prn, pereonite; prp, pereopod. Photographs RV and Rémi Brageu (SU).

Emended diagnosis.—Body oblong to ovoid in dorsal view, length 17 mm, width 10 mm, greatest width at pereonites 4 and 5; cephalon separate from pereonite 1, semi-enclosed by it laterally; pleonites narrow, four in number with first one mostly covered by seventh pereonite, fourth pleonite broadened mid-dorsally, covering or fusing with others at mid-dorsal part; pleotelson regularly rounded with an inflated mid-dorsal section, upper margin with S-form hinge locks on both sides making strong connection to fourth pleonite; uropods with broad and flat, not clearly surpassing in length lower rim of pleotelson, exopod on robust peduncle, much smaller than endopod with apparently smooth outer margin.

Description.—Cephalon semi-ovate and surrounded laterally by the first pereonite. Ophthalmic ridge visible. Eyes with lower half extended posteriorly to the anterior margin of first pereonite (Figs. 1C, 2B). Antennule with robust peduncle segments and much thinner flagellum of which separate segments

Fig. 2. Detailed anatomy of isopod *Heterosphaeroma priscum* (Milne-Edwards, 1868), late Thanetian of Sézanne, Marne, France. A. SU.PAL.2017.0.2.61 (inner mold, holotype), in dorsal view. B. SU.PAL.2017.0.0.4 (plaster cast), in dorsal view. C. SU.PAL.2017.0.2.4 (C₁, body fossil anterior half; C₂, head close-up), ventral side. Abbreviations: md, mandibular palp; mxp, maxilliped; mx, maxilla; pln, pleonite; prn, pereonite; prp, pereopod. Photographs RV and Rémi Brageu (SU).
Concluding remarks

Sphaeromatid isopods occur nowadays mostly in marine habitats where they are benthic and fossorial detritus feeders. Already Milne-Edwards (1868) questioned the marine affinity of Heterosphaeroma when he compared it to species of Sphaeroma while making his short note on this fossil. He mentioned the resemblance of Sphaeroma priscum to common marine isopods. Heterosphaeroma priscum displays a morphology that nowadays is known only in marine taxa, therefore it remains disputable whether it was a true freshwater isopod or if it was a marine/euryhaline species that had been trapped in layers formed under mixed freshwater and marine influences. There are a few other fossil Sphaeromatoidea that have unresolved marine/freshwater affinities (Quaggiotto and De Angeli 2016; Vonk et al. 2015), but also undoubted freshwater taxa such as Archaeosphaeroma frici Novák, 1872 from lower Miocene freshwater chalks in central Europe.

Crucial arguments against freshwater origin of Heterosphaeroma priscum come from better understanding of the Mezo-Cenozoic Champagne stratigraphy as presented by Laurain and Meyer (1986) who improved the resolution of the upper Thanetian transgression-regression cycles thanks to new key field observations. They identified the relationships between (i) altered chalk facies, (ii) concretion-type facies and (iii) detrital facies. They demonstrated that the Thanetian

Fig. 3. Appendage views of isopod Heterosphaeroma priscum (Milne-Edwards, 1868), late Thanetian of Sézanne, Marne, France. A. SU.PAL.2017.0.2.12 (plaster cast). B. SU.PAL.2017.0.2.3.2-2. Abbreviations: pl, pleonite; prn, pereonite; prp, pereopod. Photographs RV and Rémi Brageu (SU).
transgression had a larger extension towards the south-east (i.e., up to Sézanne, where beach pebbles cover the chalk surface) than previously known, and connect the travertine deposits to two different subfacies: terrestrial and stromatolitic. The latter usually display a thin stratification, encompassing darker filaments when seen at high magnification. Correlated to the activity of cyanobacteria, the formation of this part of the travertines in Champagne may be linked to shallow-water sea conditions, as confirmed by perforations ascribed to marine borers (gastrochaenid mollusces, Laurain and Meyer 1986: 122–123, pl. 2: 6). In Sézanne, no stromatolite travertine were reported by the authors: only terrestrial travertines laying over the reworked Cretaceous pebbles, marking the end of the transgression (Laurain and Meyer 1986).

We compared the preservation of *Heterosphaeroma priscum* and the sedimentary matrix it is hosted in, with that of the other arthropods described from Sézanne. The travertine pieces display a high concretional density with dot-like structures, which are in all aspects similar to the matrix hosting insects figured by Nel and Blot (1990). These travertines, bearing adult true bugs (Hemiptera) but mostly dragonfly/trichopteran larvae, had to form close to or in the same freshwater streams. Isopod preservation is also comparable to that of *Astacus edwardsi* Munier-Chalmas, 1872 likely originating from the same locality; and described by Van Straelen (1928a) as an European representative of freshwater Astacoidea. SU.PAL.2017.0.2.3.2-1 (Fig. 4B) evidences the synlocation of the isopods with the plant/leaf-rich travertine of Sézanne, showing on the same surface a complete isopod and the leaf of the woody vine *Cissus cissoides* (De Saporta, 1868) Hollick, 1936. Considering the above arguments, it is plausible to propose a freshwater/waterspring environment for *Heterosphaeroma priscum* in the Thanetian of Champagne rather than any admixture of marine/brackish waters from a tidal creek in the karstic surface system.

Freshwater species related to *Sphaeroma* form probably independent lineage that made the transition from the marine environment to inland waters on several times, as was concluded by Wetzer et al. (2018) based on molecular studies of *Gnorimosphaeroma* Menzies, 1954, *Lekanesphaera* Verhoff, 1942, and *Thermosphaeroma* Cole and Bane, 1978. Recent sphaeromids living in hot springs that provide calcifying conditions are known from the genus *Thermosphaeroma*, with seven species. Most of these forms are omnivorous, as implied by the scarce (vegetation) food supply of hot spring environments. The species of *Thermosphaeroma* have never been observed to prey on aquatic insects living in the same springs (Shuster 1981). Some species are even known to have cannibalistic behaviour. On the other hand, the springwaters usually completely exclude fish and avian predation risks, possibly permitting high densities of these isopods and decreasing the risks associated with male mate-searching behaviour of reproduction (Shuster 1981). The absence of modern sphaeromids in more common epigean freshwater systems, such as streams, ponds, rivers and lakes, has been attributed to failure in escaping predaceous aquatic insects and competition with several species of larval insects (Bowman 1981; Shuster 1981). In Sézanne, the preservation and lithology of the fossil predaceous insects (adults and larvae) indicate spring/streams habitats shared with *Heterosphaeroma priscum*.

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**Fig. 4.** Detailed anatomy of isopod *Heterosphaeroma priscum* (Milne-Edwards, 1868), late Thanetian of Sézanne, Marne, France. A. SU.PAL.2017.0.2.3.1, ventral view. B. SU.PAL.2017.0.2.3.2-1, dorsal view and leaf co-occurrence (dashed), isopod individuals (arrows). C. SU.PAL.2017.0.2.3.2-2, dorsal view. Abbreviations: pln, pleonite; plp, pleopod; prn, pereonite; prp, pereopod. Photographs RV and Rémi Brageu (SU).
References
Bowman, T. E. 1!81. Thermosphaeroma milleri and T. smithi, new sphaeromatid isopod crustaceans from hot springs in Chihuahua, Mexico, with a review of the genus. Journal of Crustacean Biology 1: 105–122.

Boyko, C. B., Bruce, N. L., Hadfield, K. A., Merrin, K. L., Ota, Y., Poore, G. C. B., Taiti, S., Schotte, M., and Wilson, G. D. F. (eds.) 2020. World Marine, Freshwater and Terrestrial Isopod Crustaceans Database. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=257071 on 2020-02-10

Brökeland, W., Wägele, J. W., and Bruce, N. L. 2001. Pararivireia holdichi n. sp., an enigmatic isopod crustacean from the Canary Islands with affinities to species from New Zealand. Organisms Diversity & Evolution 1: 83–98.

Bruce, N. 2005. New sphaeromatids (Crustacea: Isopoda: Sphaeromatidea) from coastal and freshwater habitats in New Zealand. Zootaxa 1002: 1–20.

Chilton, C. 1925. Some Amphipoda and Isopoda from the Chatham islands. Records of the Canterbury Museum 2: 317–320.

Cole, G. A. and Bane, C. A. 1978. Thermosphaeroma subequalulum, n. gen., n. sp. (Crustacea: Isopoda) from Big Bend National Park, Texas. Hydrobiologia 59: 223–228.

D’Archiac, E. J. A. 1848. Histoire des progrés de la géologie. Tome II, Part 2. 600 pp. Société Géologique de France, Paris.

De Saporta, G. 1868. Prodrome d’une flore fossile des travertins anciens de Sénance. Mémoires de la Société Géologique de France 3: 1–436.

De Lapparent, A. F. 1964. Région de Paris. Excursions géologiques et voyages pédagogiques. 2nd edition. 196 pp. Hermann, Paris.

Duval, G. and Meillet, C. 1842. Coupe des terrains des environs de Sénance. Bulletin de la Société Géologique de France 1: 100–104.

Hébert, E. 1848. Notice sur les dépôts situés dans le bassin de Paris, entre la craie blanche et le calcaire grossier. Bulletin de la Société Géologique de France 2: 388–410.

Hollick, C. A. 1936. The tertiary floras of Alaska. U.S. Geological Survey Professional Paper 182: 1–185.

Giusberti, L., Fornasiero, M., and Zorzin, R. 2014. The Pesciara-Monte Bolca (Italy) revisited. Mémoires de la Société Géologique de France 2: 3–6.

Van Straelen, V. 1928b. Contribution à l’étude des isopodes méso- et céno-zoiques. Mémoires de l’Académie Royale de Belgique. Classe scientifique Série 2: 1–66.

Verhoeff, K. W. 1942. Sphaeromidien – Studien und buchnerillo N.G. 83. Isopoden-aufsatz. Zeitschrift für Morphologie der Tiere und Ökologie der Tiere 39: 153–175.

Vonk, R., Lapella, L., and Zorzin, R. 2015. Eocene isopods of Pesciara di Bolca (Italy) revisited. Journal of Crustacean Biology 35: 540–546.

Wägele, 1889. Evolution und phylogenetisches System der Isopoda: Stand der Forschung und neue Erkenntnisse. Zoologica 140: 1–262.

Wegmann, C.-E. 1842. Séance du 21 Novembre 1842. Bulletin de la Société Géologique de France 1 (14): 70.

Wetzer, R., Bruce, N., and Pêrez-Losada, M. 2018. Relationships of the Sphaeromatidae genera (Peracarida: Isopoda) inferred from 18S rDNA and 16S rDNA genes. Arthropod Systematics and Phylogeny 76: 1–30.

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