Pseudidotheidae (Crustacea: Isopoda: Valvifera) reviewed with description of a new species, first from Australia

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Abstract

The family Pseudidotheidae, comprising only four species of Pseudidothea, is reviewed. A new highly-ornamented species from south-eastern Australia, Pseudidothea hoplites, is described. A key to species of the genus and family is provided.

Keywords
Isopoda, Valvifera, Pseudidotheidae, Pseudidothea, new species, south-west Pacific, Australia

Introduction
The family Pseudidotheidae Ohlin, 1901 was erected for the east Patagonian genus and species Pseudidothea bonnieri Ohlin, 1901 on the basis of the male first pleopods being modified for a copulatory function, a character never before recorded in the Isopoda. Ohlin also noted that the second to seventh pleopods are of virtually the same size and form. He regarded the Pseudidotheidae as an intermediate link between the Idoteidae Samouelle, 1819 and Arcturidae Dana, 1849. Barnard (1920) noted that the Pseudidotheidae have a flattened body, pereonite 4 never elongate, pereopod 1 prehensile and pleopods 2–4 stout. In Arcturidae the body is cylindrical, pereonite 4 often elongate, pereopod 1 setiferous and pleopods 2–4 slender and setiferous. Nordenstam (1933) added another character: penial processes fused but distally cleft or bilobate.

Pseudidotheidae are distinguished, with other arcturoid valviferans, from Idoteidae and similar families by having the head fused to pereonite 1 (with a few exceptions not so in Idoteidae), penal processes fused but distally cleft, and pleopod 1 with an elongate peduncle and modified exopod in the male. Wägele (1989, 1991) treated the family as one of four subfamilies of Arcturidae, the others being Arcturinae, Xenarcturinae Sheppard, 1957 and Holidoteinae Wägele, 1989. He included Arcturides Studer, 1882 with Pseudidothea in Pseudidotheinae which, he believed, shared the synapomorphy of all pleonites fused and not divided by furrows. This state is true of all arcturoid families, with rare reversals in two genera (Poore, 2001). Arcturididae Poore, 2001 (Arcturides alone), Pseudidotheidae and Xenarcturidae were treated as families by Poore (2001), three members of an unresolved clade. Poore (2001) separated pseudidotheids from other arcturoid families by the uniquely undifferentiated pleopods 2–4, similar to more posterior ambulatory pleopods. While it is true that all limbs are ambulatory and 2–4 do not bear long filtering setae of the arcturid type, pleopods 2 and 3 are more robust than 4–7. In Xenarcturidae, only pleopods 2 and 3 are slender, setose and arcturid-like while pleopods 4–7 are ambulatory. In Arcturidae, pleopods 2–7 are all similar and ambulatory. Holidoteidae was only remotely related in Poore’s (2001) cladogram (see revision by Poore, 2003).

The family contains only Pseudidothea, the type species of which is a junior synonym of an earlier described species, “Idothea Miersii” Studer, 1884, an observation suggested by Ohlin, suspected by later authors, and confirmed here. Microarcturus scutatus Stephensen, 1947 from the South Shetland Islands, was transferred to Pseudidothea by Sheppard (1957). Hurley (1957) described Pseudidothea richardsoni from New Zealand. Here, a fourth species is described from southern Australia.

All limbs are drawn from the left side unless otherwise stated. The following abbreviations are used in figures: A1, A2, antennae 1, 2; MD, mandible; MP, maxilliped; MX1, maxilla 1; MX2, maxilla 2; P1-P7, pleopods 1–7; PL1-PL5, pleopods 1–5; U, uropod; l, left; r, right. Material is lodged at Museum Victoria, Melbourne (NMV); the Canterbury Museum, Christchurch, New Zealand (CMNZ), Museum of New Zealand (Te Papa Tongarewa) (MNZ), Zoological Institute and Museum, Hamburg, and Museum für Naturkunde, Berlin.
Pseudidotheidae Ohlin


Diagnosis. Body strongly vaulted. Head and pereonite 1 fused. Pereonite 4 of similar length to pereonite 3. All pleonites fused into pleotelson. Body variously tuberculate or spinose; pleotelson without dorsolateral ridges ending in mediiodorsal posterior spine, never with posterior dorsolateral pair of strong spines; limbs and most of surface covered with fine setae that trap sediment. Dorsal coxal plates 2–7 obsolete, bases of pereopods exposed. Mouthparts and pereopod 1 visible in lateral view. Eyes well developed. Antenna 2 flagellum of 2 or 3 articles plus distal claw. Pereopod 1 a gnathopod, pereopods 2 and 3 differentiated from ambulatory pereopods 4–7. Pereopod 1 dactylus evenly curved along anterior margin, evenly tapering. Pereopods 2 and 3 with propodus able to close on carpus, articles broad and with posterior robust setae; with prominent dactylus, unguis short. Pereopods 4–7 similar and ambulatory. Pereopods of males without dense mat of fine setae. Uropodal exopod (smaller ramus) tapering (with terminal setae only), more than half as long as endopod. Oostegites 1–4 functional, not supported by coxal lobes; oostegite 5 present or absent. Penes fused as a single penial plate, apically simple or barely slit. Pleopod 1 peduncle more elongate than on other pleopods; with marginal setae on rami longer than or equal to length of rami. Pleopod 1 exopod of male thickened and with groove on posterior face, with few simple setae along straight lateral margin; with groove on posterior face of exopod ending on tapering distolateral apical extension. Pleopod 2 of male with appendix masculina about as long as endopod, basally less than half width of endopod.

Remarks. The diagnosis is rephrased from Poore (2001) to better define limb differentiation. We note that the body is covered with fine setae, not illustrated in the new species and indicated or mentioned only in passing for other species by Hurley (1957) and Brandt and Wägele (1990). Such setation is not a typical valviferan characteristic. Poore (2001) defined the family as lacking oostegites on pereopod 5; this is true of three species but not of *P. scutata*. The presence of a fifth pair of oostegites in one species is anomalous among arcturoid families. It is seen elsewhere only in Austracturellidae Poore and Bardsley, 1992 where oostegites 5 are vestigial and act as egg guides rather than as part of the marsupium.

Wägele (1989) considered *Arcturides* a family member but Poore (2001) erected a separate family for this genus.

Pseudidothea Ohlin, 1901


Type species. *Pseudidothea bonnieri* Ohlin, 1901 (by monotypy).

Diagnosis. As for family.

Remarks. Ohlin (1901) was “almost convinced” that *Pseudidothea bonnieri* was identical to *Idotea miersii* Studer, 1884 and noted that “the localities where they were dredged are nearly the same.” He nevertheless, erected his new species. He also expressed his “suspicion” that his new genus was identical to *Arcturides* Studer, 1883. Hale (1946) listed three characters that separated the two genera. In *Arcturides*, the coxae of pereonites 2–7 are distinctly marked off, the antenna 2 flagellum is of three articles and the uropodal exopod as long as endopod. Hale’s view was confirmed by Poore (2001) whose phylogenetic analysis concluded the two genera belong in different families.

Key to species of *Pseudidothea*

1. Pereonites 2 and 3 with forked dorsolateral spines; all pereonites with lateral rows of blade-like ridges, each with anteriorly and posteriorly directed spines; tergites produced laterally over coxae to form a shield with 3 points; .........................................*Pseudidothea hoplites* .......................... 2

   — Peneites with low or high flat tubercles; tergites produced laterally as large tubercles or rounded or flattened laterally; ................................................ 2

2. Pereon with large flat tubercles; pereonite 1 with dorsal pair, pereonites 2–4 with dorsal and lateral pair and pereonites 5–7 with dorsal, dorsolateral and lateral pair; male pleopod 2 with appendix masculina twice as long as rami ............................................. *Pseudidothea scutata* .......................... 3

3. Uropodal exopod with a single strong setae, endopod with 3 pappose setae; antenna 2 peduncle with long fine setae on articles 3–5; pereopods without tubercles; male pleopod 1 endopod with 5 lateral spines proximally, 5 apical plumose setae; exopod with 15 spines on lateral margin, tapering distally to an obtuse apex ................................. *Pseudidothea richardsonii* .......................... 4

   — Uropod rami each with single seta; antenna 2 peduncle with short setae on articles 3–5; pereopods with tubercles; male pleopod 1 endopod with plumose setae marginally; exopod with 16–17 spines laterally, with acute apex bent outwards .......................... *Pseudidothea miersii* .......................... sp. nov.

Pseudidothea hoplites sp. nov.

Figures 1–3

Material examined. Holotype. Western Bass Strait, 70 km W of Cape Farewell, King Island, Tasmania (39°38.2’S, 143°07.2’E), 127 m, sand, epibenthic sled, R. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 195), NVM J8705 (male, 4.4 mm).

Paratypes. Type locality, NVM J8706 (1 female); 36 km SSW of Stokes Point (40°26.7’S, 143°41.4’E), 85 m, rock dredge, 22 Nov 1981 (stn BSS 198), NVM J8709 (1); 59 km WNW of Cape Farewell (39°28.5’S, 143°17.0’E), 103 m, Smith-McIntyre grab/pipe dredge, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 81), NVM J8703 (1).

Victoria, 80 km SSE of Cape Otway (39°26’5’S, 142°57’E), 113 m, 9 Oct 1980 (stn BSS 67), NVM J8701 (2); NVM J23186 (1 ovigerous female, 5.1 mm, figured); 51 km SSW of Cape Otway, Victoria.
Diagnosis. Head dorsally strongly elevated, with paired double or single spines. Pereonite 1 with 1 pair of small dorsal spines, 2 small lateral spines. Tergites 2–7 each produced laterally in form of a with 3 points, anteriorly, posteriorly and laterally. Pereonites 2 and 3 with small paired middorsal spines, large paired dorsolateral forked spines, and lateral ridges produced acutely anteriorly and posteriorly; pereonite 4–7 with dorsolateral and lateral ridges, finished anteriorly and posteriorly with a small spine. Pereonite 4 with 4 anterodorsal and posterodorsal spines, pereonites 5 and 6 with 3 and pereonite 7 with 2 and a single dorsal denticle.

Sculptrure of pleotelson from anterior to posterior as follows. A central pair of dorsal convexities each with an anteriorly directed spine, lateral to these a series of 3 anteriorly directed spines on each side, followed by large lateral convexities on each side, followed by a pair of central dorsal convexities, remaining pleotelson tapers to an obtuse apex.

Antennae, mouthparts and limbs (from male). Antenna 1 peduncle articles with brush setae, articles rounded and becoming successively smaller; flagellum article 1 very short; article 2 with 6 aesthetascs and setules. Antenna 2 peduncle articles 3–5 with blunt tubercles on lower margin, bearing robust setae, especially on articles 4 and 5; flagellum almost as long as peduncle article 5, articles becoming successively smaller, first with distal robust seta and setules, second with setules, third a short claw.

Mandible incisor with 4 uneven teeth; left lacinia mobilis almost as wide as incisor, with 3 teeth; right lacinia mobilis an unevenly toothed column; left molar process with concave face rimmed by obscure teeth and bearing a setal cluster; right molar process with face ending with row of blunt teeth and bearing setal cluster. Maxilla 1 inner lobe with 2 long pappose setae; outer lobe with 11 apical setae, some obscurely dentate. Maxilla 2 inner lobe oblique margin with 6 pappose setae along posterior edge, 5 setae on anterior edge; middle lobe with 2 longer pappose setae; outer lobe with 3. Maxilliped endite with complex of thin pappose setae and rows of blunt tubercles; palp with tubercles and long setae on mesial margins of articles 2–5; articles 1 and 2 short, 3 and 4 of subequal length, 3 produced mesially, article 5 one-fifth as long as 4, almost as long as wide; epipod apex with small blunt tooth.

Pereopod 1 held close to the mouthparts; merus–propodus with uneven posterior tubercles and stout pectinate setae; propodus almost as wide as long, with rows of mesial pectinate setae along anterodistal margin; proximal part of dactylus linear, about 2.5 times as long as greatest width, complexly setose with mesial pectinate setae, 1 spine on posterior margin, posterodistal corner of dactylus with a spine, seta and 2 setules; unguis a strong claw, less than half length of dactylus.

Pereopod 2 basis–merus short, subequal, carpus–dactylus longer; merus with complex tubercle on lower margin bearing short setae; carpus longer than greatest width, with tubeculate ridge on lower margin bearing 2 long robust setae; propodus robust, about twice as long as wide, with 2 robust setae on lower margin opposing carpus; proximal part of dactylus almost 3 times as long as wide, unguis a short claw. Pereopod 3 similar to pereopod 2. Pereopods 4–7 basis–merus with blunt tubercles on upper margin, most articles with well spaced setae on lower margin; basis about 1.5 times as long as wide; ischiocarps subequal, about as wide as long; propodus about 2.5 times as long as wide, dactylus similar to pereopod 2.

Male pleon peduncle twice as long as wide, with 4 coupling hooks; endopod lamellar with 6 apical plumose setae;...
Figure 1. *Pseudodothea hoplites*. Paratype female, NMV J23186. Dorsal and lateral views. Scale bar 2 mm.
exopod longer than endopod with 8 spinules on lateral margin, tapering distally, thickened and folded laterally to partially cover a groove that runs to the apex. Male pleopod 2 rami apically flattened, endopod with 9 apical plumose setae; exopod with 21 marginal plumose setae; appendix masculina styliform, slightly longer than endopod. Pleopods 3–5 becoming successively larger, rami apically rounded with single simple seta on endopod.

Uropod unarmed, rounded anteriorly, tapering posteriorly; exopod about two-thirds as long as endopod, conical, with apical seta; endopod broader, apically rounded with 4 distal setae and 3 lateral setae.

Sexual differentiation. Female differs from male in broader body, especially of pereonites 2–4; ornamentation more developed; antenna 1 flagellum with 3 clusters of aesthetascs on article 2; pereopods 1–4 with oostegites, pereopod 5 without oostegite; penial process absent; pleopods 1 and 2 without male modifications. Male with ventral terga separate on pereonites 1–4 and fused across midline of pereonites 5–7.

Etymology. Hoplites (Gr.), man in armour, in reference to the elaborate spines and ridges.

Distribution. South-eastern Australia (Victoria and Tasmania), 4–127 m depth.

Remarks. Pseudidothea hoplites is distinguished from other species of Pseudidothea by the complex ornamentation of the

Figure 2. Pseudidothea hoplites. Holotype male, NMV J8705. Left and right mandibles, maxillae 1 and 2, maxilliped with detail of anterior face of endite. Pleopods 1–5; penial process; uropod with detail of rami.
Figure 3. *Pseudidothea hoplites*. Holotype male, NMV J8705. Antennae 1 (not all aesthetasc drawn) and antenna 2; left pereopod 1 with detail of dactylus; inner face of right pereopod 1 propodus. Pereopods 2, 4 and 7, with details of dactyli.
Isopods of the family Pseudothoidea

Pseudothoidea miersii (Studer)

Studer (1884: 17, pl. 1 fig. 5. (lapsus for Idotea)
Pseudothoidea bonnieri Ohlin, 1901: 276–281, fig. 6.—Nordenstam, 1933: 114, fig. 27.—Sheppard, 1957: 175–176.
Arcturides miersii.—Nierstrasz, 1941: 262.

**Diagnosis.** Head dorsally convex; pereon with irregular minute tubercles. Pleotelson with blunt anterolateral processes, dorsally smooth, tapering to broadly truncate and slightly upturned apex. Male antenna 1 flagellum with about 6 clusters of aesthetascs. Antennae and pereopods without tubercles. Antenna 2 peduncle with short setae on articles 3–5. Pereopods minutely setose and with tubercles. Male pleopod 1 endopod about 1.5 times as long as peduncle with marginal plumose setae; exopod longer, 16–17 spinules on lateral margin, tapering distally, to acute apex bent outwards, with oblique furrow opening at apex. Male pleopod 2 appendix masculina tapering to acute point, slightly longer than endopod. Uropodal exopod with strong apical setae, endopod with 1 short seta; exopod about two-thirds as long as endopod (Ohlin, 1901). Oostegite absent from pereopod 5 (Sheppard, 1957).

**Distribution.** East Patagonia, Falkland Islands, 115–500 m depth.

**Remarks.** Studer (1884) based his new species *Idotea miersii* on a specimen 9 mm long, collected by the *Gazelle* Expedition off the east coast of South America at 47°1′6″S, 63°29′6″W at 63 fathoms (110 m). In the same paper he redescribed his earlier named species, *Arcturides cornutus*. Ohlin (1901) based *Pseudothoidea bonnieri* on two males, 9 mm long, in the Hamburg Museum. When Ohlin (1901) described *P. bonnieri* he was almost convinced that his specimens were identical with *Idotea miersii* (Studer) and in a footnote reported how he had tried to borrow Studer’s material from the Museum für Naturkunde in Berlin but “got the reply that, as there were only two of them, it would be against the regulations to send them away from the Museum.” Angelika Brandt compared material from the museums in Hamburg and Berlin on our behalf:

- from Hamburg, a 4 mm manca and a 6.4 mm male (ZMH K-1877) labelled and catalogued “*Pseudothoidea bonnieri*, Pisagua, Chile, 19°27′S, 70°10′W, K. Kophamel 1877–1889”; and

Brandt (pers. comm.) could find no differences between the specimens and concluded that one of Ohlin’s two males had been donated to the museum in Berlin. This seems certain. The locality recorded by the two museums, but not the coordinates and collecting date of the Berlin specimen, is at odds with the type locality and more recent records of the species and is clearly wrong. Ohlin must have included antennae in his total length of 9 mm while Brandt’s measurements of 6.2 and 6.4 mm do not. The manca was not mentioned by Ohlin. Studer’s material can not now be found although Ohlin’s footnote tells that it existed in 1901. It is tempting to speculate that, being unable to borrow Studer’s material and convinced of the synonymy of his species *bonnieri* with Studer’s *miersii*, Ohlin sent one of his syntypes to Berlin for comparison. This may explain why the Berlin male has two species names but whoever concluded this remains a mystery.

Sheppard (1957) examined many specimens from the Falklands region, reported them as *Pseudothoidea bonnieri* but thought too that *I. miersii* was a synonym. Kussakin (1967) also illustrated a species using the older species name, as *Pseudothoidea miersii*, and noted that *P. bonnieri* is probably a synonym. He observed that slight differences exist: in *P. bonnieri* the second article of the peduncle of antenna 1 bears a rounded tubercle with four setae (referring to Sheppard, 1957); in Kussakin’s specimens there is a slight swelling with five setae. The epipod of the maxilliped in Sheppard’s illustration of *P. bonnieri* has slightly concave lateral margins, while in Kussakin’s specimens it has a regular oval form with convex lateral margins. We consider that these minor differences can be attributed to intraspecific variation or mounting.

To add to the confusion, Nierstrasz (1941) synonymised Studer’s two species, *Pseudothoidea bonnieri* and *Arcturides cornutus*, without explanation. It seems improbable that Studer could confuse his own two species in one paper and specimens of *A. cornutus* in our possession look nothing like a pseudothoidea; in fact, Poore (2001) placed the two species in different families.

We conclude, with Kussakin (1967), that *P. bonnieri* should be treated as a junior synonym of *I. miersii*. We treat as additional evidence the observation that all authors have reported only one species like this off eastern South America; the only other in the genus in the region, *P. scutata* Stephenson, 1947 is quite different.

*Pseudothoidea richardsoni* Hurley

**Figure 4**


**Material examined.** New Zealand, Banks Peninsula region. Off Lyttelton, 4 fm [7.3 m], H. Suter, CMNZ (4 females, 5.1–6.1 mm; 4 males, 4.8–5.1 mm, 1 figured); NMV J47116 (1 female, 1 male). Big Bay, mud bottom, 12 m, MNZ CR-9846 (2). Beacon Rock, mud bottom, 10–12 m, MNZ CR-9850 (1). E side of Port Levy, mud bottom, MNZ CR-9855 (1).

**Diagnosis.** Head with anterior margin vaguely tuberculate, dorsally with tubercles, pereon finely setose and vaguely tuberculate; tergites slightly laterally produced. Pleotelson with blunt anterolateral processes, laterally tuberculate, dorsally...
smooth, tapering to a blunt apex. Male antenna 1 flagellum with about 7 clusters of aesthetascs. Antennae and pereopods without tubercles. Pereopods finely setose. Antenna 2 peduncle with long, fine setae on articles 3–5. Male pleopod 1 endopod about as long as peduncle, with plumose setae laterally and apically; exopod longer than endopod, with diagonal groove, apically tapering, bent outwards and terminating in an acute tooth, proximal half of lateral margin with short setae, distal half with longer, plumose setae. Male pleopod 2 appendix masculina acutely bent, about twice as long as rami (Stephensen, 1947). Uropodal exopod about two-thirds as long as endopod, each ramus with single seta (Sheppard, 1957). Oostegite present on pereopod 5.

**Distribution.** Cook Strait and Lyttelton Harbour, New Zealand, 7–146 m depth.

**Remarks.** Hurley (1957) observed that *P. richardsoni* is close to “*P. bonnieri* Ohlin” (=*P. miersii*) but he considered there are sufficient differences to warrant a separate species; these include uropodal endopod with three pappose setae, lack of tubercles on the pereopods and antenna 2 peduncle with long fine setae on articles 3–5.

The first male pleopods are also different from those of *P. miersii*. *Pseudidothea miersii* has a male pleopod 1 peduncle with 6–7 coupling hooks, endopod with plumose setae marginally, exopod with 16 or 17 spinules laterally and with an acute apex bent outwards, almost at right angles. In contrast, *P. richardsoni* has a peduncle with eight coupling hooks, an endopod with five lateral spinules proximally and five apical plumose setae, and an exopod with 15 spinules on its lateral margin, tapering distally to an obtuse apex.

**Pseudidothea scutata** (Stephensen)

*Microarcturus scutatus* Stephensen, 1947: 15–17, figs 5, 6.


*Pseudidothea scutatus*—Brandt and Wägele, 1990: 97–105, figs 1–3 (lapsus)

**Material examined.** Antarctica, Western Weddell Sea, A. Brandt on RV *Polarstern*, Jan–Feb 2002 (ANDEEP stns): 61°09.82'S, 54°33.40'W, 302–306 m, NMV J47401 (1 male); 61°11.94'S, 54°37.37'W, 302–306 m, NMV J47402 (1 male); 61°20.51'S, 55°28.66'W, 159–117 m, NMV J47403 (1 female); 61°44.88'S, 58°1.54'W, 256–295 m, NMV J47404 (1 male); 59°52.21'S, 59°58.75'W), 3643–3622 m, NMV J47405 (1 specimen).

**Diagnosis.** Head smooth, pereonites with large, high, flat tubercles: pereonite 1 with 1 pair of dorsal tubercles and 3 pairs of shorter lateral processes; pereonites 2–4 with 1 pair of dorsal and 1 pair of lateral tubercles and 1 or 2 pairs of shorter dorsolateral processes; pereonites 5–7 with 1 pair each of dorsal, dorsolateral and lateral tubercles. Pleotelson with sub-acute anterolateral processes, 3 pairs of mediadorsal spines and shorter and more irregular processes, apically acute and bent dorsally. Male antenna 1 flagellum with about 25 clusters of aesthetascs. Antenna 2 and pereopods 2 and 3 with tubercles. Antenna 2 peduncle with long, fine setae on articles 3–5. Male pleopod 2 appendix masculina acutely bent, about twice as long as rami (Stephensen, 1947). Uropodal exopod about two-thirds as long as endopod, each ramus with single seta (Sheppard, 1957). Oostegite present on pereopod 5.

**Distribution.** South Shetland Islands, Antarctic Peninsula, 159–3622 m depth.

**Remarks.** Sheppard (1957) included Stephensen’s *Microarcturus scutatus* in the synonymy of what she called “*Pseudidothea scutatus* sp. n.”. She admitted that Stephensen’s “species appears to be identical with my specimens” and that she received Stephensen’s paper after making her own descriptions and figures. Her intention would appear to...
have been be to make a new combination rather than a new species.

The species differs from all other species of *Pseudidothea* in the presence of well developed oostegites on pereopods 5 (Sheppard’s 1947 observation confirmed in new material). Although the pair of fifth oostegites meet in the middle, they are flat and do not help in enclosing the eggs.

The dorsal and lateral pereonal tubercles of the holotype, a 20-mm long male, are separated by gaps smaller than the tubercle diameters. In the same-sized female described by Brandt and Wägele (1990) the tubercles are relatively smaller and separated by gaps equal to their diameters. The uropodal rami of the two specimens also differ: the endopod of the male being shorter and narrower than the exopod while the two are subequal in the female. In the absence of other material, we assume these differences are sexual rather than specific. The new material collected during the 2002 ANDEEP cruise is typical of this well-described species. The individual dredged from 3643–3622 m depth, much deeper than the usual depths of a few hundred metres, could not be distinguished from the rest.

**Acknowledgements**

This contribution was made possible through a grant from the Australian Biological Resources Study. We are grateful to Graham Milledge who inked the figures. We thank Angelika Brandt, Zoological Institute and Museum, Hamburg, for examining type material and for the donation of material from the ANDEEP cruise. We also thank her and Oliver Coleman, Museum für Naturkunde, Berlin, for discussion about the type status of material in their museums. We thank the Canterbury Museum, New Zealand, and the Museum of New Zealand (Te Papa Tongarewa) for the loan of material.

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