ABYSSIANIRIDAE, A SYNONYM OF PARAMUNNIDAE (CRUSTACEA: ISOPODA: ASELLOTA), WITH TWO NEW SPECIES OF ABYSSIANIRA FROM SOUTH-EASTERN AUSTRALIA

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Abstract


Abyssianira bathyalis sp. nov. and A. tasmaniensis sp. nov. are described from bathyal depths of south-eastern Australia. The history and the concepts of the family name Abyssianiridae Menzies, 1956 are outlined. The antennae and uropods of Abyssianira are shown to be of identical construction to those of the Paramunnidae, those points being the only ones on which Abyssianira has been kept separate from the Paramunnidae in recent studies. On that basis, Abyssianiridae is placed in synonymy of Paramunnidae Vanhöffen, 1914.

Introduction

The janiroidean family Abyssianiridae was created by Menzies (1956) for the new genus and species Abyssianira dentifrons Menzies, 1956. Menzies' diagnosis of the new family did not include any apomorphic attributes to distinguish the new taxon from what he believed to be its closest relatives, the Schistosomatidae Hansen, 1916 (now Mictosomatidae Wolff, 1965, replacement name, homonymy) and the Thambematidae Stebbing, 1913. Both families were then poorly known and Menzies' brief comments are largely irrelevant. In connection with A. dentifrons having the last three pleonites set off from the slightly broader anterior pleonites, Menzies did mention the Munnidae Sars, 1899 (then including the paramunnid genera), but he did not recognize the close similarity in important characters between his new species and the paramunnid Munnidae.

Menzies (1962) described a second species, A. argenteenensis, and presented a slightly modified family diagnosis. He added a new genus and species, Xostylus parallelus, to the family. In the same study Menzies stated that the Abyssianiridae "is closely allied to the Munnidae through the genus Austrosignum, [now in Paramunnidae], which may ultimately have to be transferred to the Abyssianiridae".

Wolff (1962) discussed the placement of several munnid-like genera which had been excluded from the Munnidae s.s. He concluded that Abyssianira belong in the Antiasidae and that the family name Abyssianiridae was a junior synonym of that family. Wolff excluded Xostylus from this new combination as he considered it "a typical janirid, closely related to Ectias Richardson and Caecianiropsis Menzies and Petit".

Sivertsen and Holthuis (1980) showed that the name Antias Richardson, 1906 was preoccupied and the family name Antiasidae (corrected spelling of Antiasidae) invalid. They proposed the replacement name Santia and, following Wolff's analysis (1962), replaced the family name with Abyssianiridae. Following Wilson (1980, see below) the name Antiasidae has recently been replaced by Santiidace Kussakin, 1988.

Wilson (1980) convincingly reintroduced the concept of a separate family Paramunnidae Vanhöffen, 1914 (as Pleurogoniidae by Wilson, but corrected for reasons of priority by Hooker, 1985) distinct from the Munnidae. The main apomorphic characters distinguishing the Paramunnidae are: a covered anus; article 3 of the peduncle of antenna 2 elongate; the male pereopod 1 sagittate; and the penile papillae subcircular. Wilson (1980) discussed the relationships of the Paramunnidae and noted that in most respects Abyssianira is very similar to that family. He stated that Abyssianira can be separated from the Paramunnidae because it has: a short article 3 of antenna 2 and an uropodal protopod. He rejected Wolff's (1962) concept that Abyssianira belong in the Santiiidae because all other species in that family have the anus exposed. He
Figure 1. A, *Paramunna bilobata* G.O. Sars, male, Norway, ident. Sars, (Zoological Museum, Copenhagen); Aa, ventral view of right antennae, arrow: see text; Ab, left uropod, dorsal view; Ac, right uropod, ventral view. B, Paramunniidae, nov. gen. et sp., male, upper slope, south-eastern Australia, (Museum of Victoria, Melbourne); Ba, left mandible; Bb, left uropod, dorsal view. Habitus scales, 1 mm.
concluded that the family Abyssianiridae (sensu Menzies, 1956) should be retained, and followed Wolff (1962) in excluding Xostylus, an opinion which is fully supported by this study. A close relationship between the Paramunnidae and Abyssianiridae was further indicated by Wilson (1987: fig. 8); his view is consistent with that of several other workers (see Wilson, 1987: fig. 7, summary cladograms and references).

Re-evaluation of Abyssianira

The crucial point in assessing Abyssianira vis a vis the Paramunnidae is the peduncle of antenna 2, which has always been described as having four subequal short proximal articles in Abyssianira (the primitive janiroidean condition). This differs from the situation in Paramunnidae where article 3 is elongate. Furthermore, Wilson (1980) drew attention to the peculiar geniculate antenna 2 of the Paramunnidae: article 3 articulates with the short and compact articles 1 and 2 complex almost at a right angle and points towards the midline. The short article 4 articulates in the opposite way, at a more flexible angle directing the long articles 5 and 6 and the flagellum laterally and upwards. Wilson discussed functional aspects of this arrangement. However, the length of article 3 varies considerably within the family, from being at least three times as long as broad in, e.g., Paramunnia bilobata (type species of the genus, see Fig. 1A) and Austrosignum malmintii Schiecke and Fresi, 1972, to barely longer than broad, e.g., Coulmannia Hodgson, 1910 (Nordenstam, 1933; Kussakin, 1982). More consistent than the elongation of article 3 is its form. In all species of Paramunnidae this article has a distinctive proximolateral bulge carrying a single simple seta. The bulge, which may in addition be ornamented with short cuticular spines or, rarely, stout setae, is set off from the remainder of article 3 by an oblique cuticular line running some way around the ventral and dorsal surfaces of the article (Fig. 1Aa, arrow), occasionally all the way to article 2 (in older specimens of heavily calcified species the line may not be visible without decalcification). There is certainly no flexibility between the bulge and the rest of the article and the derivation of the oblique line cannot be evaluated on the evidence of external morphology alone. Hooker (1985) suggested that in his new species, Muniongonium wilsoni in which the oblique line reaches article 2, the setae-carrying bulge represents a modified antennal scale. It seems, however, to be in the wrong position. Where present, the antennal scale is invariably on the lateroapical margin of article 3 of the peduncle although it may often be displaced proximally. In the Paramunnidae the bulge is at the base of article 3 and the apex of that article has a simple, circular margin.

In Abyssianira, the interesting point is that although article 3 of the peduncle is only slightly longer than broad, a distinct seta-bearing bulge and an oblique line reaching article 2 are present (Fig. 2Aa, Ba), and the various peduncular articles articulate in exactly the way described by Wilson (1980) and above.

The Abyssianira uropods are not as different from those of Paramunnidae as Wilson suggested. The uropodal protopod in species of Abyssianira is at most only marginally longer than in some paramunnids and the two rami are similar in length, proportions, and setation to that of many paramunnids. In the Paramunnidae, the uropodal configuration range from biramous with a small protopod (e.g., Paramunnia bilobata, Fig. 1Ab) to uniramous without a protopod (e.g., several undescribed species from Australia, Fig. 1Bb). Whenever a small protopod is present it is completely or nearly completely inserted into a cuticular fold. The fold may be a thin, hyaline cover very difficult to observe, or, in heavily calcified species, completely opaque, in which case clearing of the cuticle is necessary before the exact uropodal configuration can be observed. In P. bilobata the uropods are inserted on the pleotelson margin; in most other paramunnids the insertion is more or less clearly dorsal. Figs 3 and 6 show that the uropodal protopod in Abyssianira is also inserted dorsally and has a small partly hidden protopod.

With regard to the other diagnostic characters for the Paramunnidae mentioned by Wilson (1980, see above), Abyssianira has a covered anus, and the male pleopod 1 and the internal 'penes' are identical to the Paramunnidae. The mandibular palp of A. dentifrons is similar to that of most paramunnids (e.g., Fig. 1Ba), viz., markedly reduced in length with the short article 3 carrying two small apical setae (Menzies, 1956: fig. 6F). In the new species described below the palp is longer and stouter, and article 3 carries two rather strong apical setae and a number of small stiff grooming setae and setules more posteriorly. However, the palp conforms to Wilson's diagnosis (1980) of the Paramunnidae: "... never longer than body of mandible ... with few setae and cuticular combs." Otherwise the mouthparts, pereopods, and other pleopods in Abyssianira are similar to those of the Paramunnidae. Antenna 1 in Abyssianira is a typical
paramunnid appendage composed of six articles, with article 5 longer than 4 and longer than or equal to 6, and with article 6 carrying a few short and one long apical setae and a single apical aesthetasc. (I have found that pattern to be constant in c. 35 species, new and 'old' in recently collected material from Australian shelves and slopes).

I conclude that Abyssianira belongs in the Paramunnidae as defined by Wilson (1980). The family name Abyssianiridae Menzies, 1956 thus becomes a synonym of Paramunnidae Vanhöffen, 1914.

I retain Abyssianira as a separate genus for the time being mainly on account of the peculiar and presumably apomorphic structure of the cephalon. Otherwise the four species currently known: A. dentifrons Menzies, 1956, A. argentenensis Menzies, 1962, and the new species Abyssianira bathyalis and A. tasmaniensis described below, appear to possess mainly plesiomorphic paramunnid attributes. Abyssianira shares with several paramunnid genera dorsally visible coxal plates on at least pereopods 5–7 and a more or less clear distinction between the anterior four and posterior three pereonites. The study of a number of new species related to that complex may lead to the recognition of new genera and a redistribution of known species (Just, in preparation). On this background, further discussions of the relationships of Abyssianira and attempts to polarize in more detail the evolutionary direction in characters of the Paramunnidae seem premature.

Paramunnidae Vanhöffen, 1914


Type genus. Paramunna G.O. Sars, 1866.


Abyssianira Menzies, 1956

Diagnosis. Paramunnidae with moderately vaulted body and pleotelson. Pereonites 5–7 set apart from anterior four pereonites, with lateral parts cylindrical, backward pointing. Coxal plates visible in dorsal view on at least pereonites 5–7. Cephalon and pereonite 1 joined along a nearly straight line (cephalon not deeply recessed into pereonite 1 as often found in the family). Eye stalks prominent, broad, barely overreaching pereonite 1. (ocelli have not been observed). Cephalon anteriorly between insertion of antennae 1 dipping steeply downward and curving into thin, horizontal, convex, marginally serrate frontal plate. Antenna 2 article 3 not much longer than broad, as about as long as articles 1 and 2 combined. Mandible with 3-articulate palp, molar cylindrical with truncate apex. Uropods biramous, with distinct protopod about as long as broad. Pleon with two segments; pleotelson with lateral margins serrate.

Type species. Abyssianira dentifrons Menzies, 1956.

Additional species. A. argentenensis Menzies, 1962. A. bathyalis sp. nov. A. tasmaniensis sp. nov.

Abyssianira bathyalis sp. nov.

Figures 2–5

Material examined. Holotype. Bass Strait S of Point Hicks, 38°16.40'S, 149°27.60'E to 38°17.70'S, 149°26.10'E, 800 m, coarse shell and biogenic sediments, WHOI epibenthic sled, RV "Franklin" stn SLOPE-34, 23 Jul 1986, M.F. Gomon et al., Museum of Victoria (NMV) J15772 (male, 25 mm, with 3 slides).

Paratypes (66 specimens in all). Same data as holotype, NMV J15773 (3 males, 2 ovigerous females, 2 preparatory females, 3 young females); Zoological Museum, Copenhagen (1 male, 1 female). Bass Strait S of Point Hicks, 38°19.60'S, 149°24.30'E to 38°19.00'S, 149°27.30'E. 930–951 m, rock, rubble, clay, sand, biogenic sediments, WHOI epibenthic sled, RV "Franklin" stn SLOPE-33, 23 Jul 1986, M.F. Gomon et al., NMV J15774 (2 males, 2 ovigerous females, 5 post breeding females, 2 preparatory females). Bass Strait S of Point Hicks, 38°21.90'S, 149°20.00'E to 38°21.40'S, 149°20.90'E, 1000 m, clay, shell, coarse biogenic sand, WHOI epibenthic sled, RV "Franklin" stn SLOPE-32, 23 Jul 1986, G.C.B. Poore et al., NMV J15775 (3 males, 5 ovigerous females, 5 post breeding females, 3 young females), Eastern Tasmania off Freycinet Peninsula, 42°02.20'S, 148°38.70'E, 800 m, coarse shell, WHOI epibenthic sled, RV "Franklin" stn SLOPE-45, 27 Jul 1986, M.F. Gomon et al., NMV J15776 (1 male, 1 ovigerous female, 3 preparatory females, 1 young female). Eastern Tasmania off Freycinet Peninsula, 41°58.60'S, 148°38.00'E, 500–600 m, coarse shell, large sponges, WHOI epibenthic sled, RV "Franklin" stn SLOPE-47, 27 Jul 1986, M.F. Gomon et al., NMV J15777 (1 male, 3 preparatory females). Eastern Tasmania off Freycinet Peninsula, 41°55.50'S, 148°37.90'E, 400 m, coarse shell, RV "Franklin" stn SLOPE-48, 27 Jul 1986, M.F. Gomon et al., NMV J15778 (1 male, 2 ovigerous females, 4 young females). Eastern Bass Strait slope, 67 km S of Point Hicks, Victoria, 38°23.95'S, 149°17.02'E to 38°23.78'S, 149°15.24'E, 1277–1119 m, fine mud.
Figure 2. Abyssianira bathyalis sp. nov. A, holotype, male; Aa, ventral view of right antennae; Ab, dorsal view of right side of cephalon: 1, frontal plate, 2, spinose ridge, 3, 'brow'; Ac, ventral view of left coxa 1 with spinose projection. B, female paratype, ovigerous, SLOPE-34; Ba, ventral view of right antenna 2 peduncle. Habitus scale, A and B, 1 mm.
Figure 3. Abyssianira bathyalis sp. nov. Mouthparts, holotype: md, mandibles, l and r, left and right; mx1, maxilla 1; mx2, maxilla 2; mp, maxilliped. A, female paratype, see Fig. 2, pleopod 2. B, variant male, see text. SLOPE-32, pereonites 4–7 and pleon.
**Figure 4. Abyssianira bathyalis** sp. nov., holotype, male. pt, pleotelson, ventral view; pl 1–5, pleopods 1–5; d, dorsal view; v, ventral view; ex, exopod of pleopod 4.

**Description.** Frontal plate strongly convex, coarsely serrate with up to 17–23 marginal teeth visible in dorsal view in mature specimens. Eye-stalks prominent, slightly overreaching peronite 1 in dorsal view, forward pointing at an angle of c. 25° and curving downwards, anterior and posterior margins parallel with small spines, apex rounded or with a few small spines. Antenna 1 inserted under spinose brow-like overhang (Fig. 2Ab3) continuous with anterior margin of eye-stalk. Cephalon with spinose ridge on each side running from median extension of ‘brow’ downwards to lateral margin of frontal plate (Fig. 2Ab2) along medial margin of article 1 of antenna 1.

Peronite 1 with small dorsally visible spinose anterolateral coxal projection. Peronite 1 distinctly longer than succeeding ones, about as long as 2 and half of 3 combined, with small lateral spines. Peronites 2–4 of equal length. 3 the broadest, all with low, rounded, transverse keel dorsally, rounded lateral margins with small scattered spines, especially prominent on slightly projecting, rounded posterior corner of peronite 3; peronite 4 with more or less distinct small spines along entire posterior margin. Peronite 5 shorter than 6 and 7, lateral parts of peronite 7 broader than equal 5 and 6.
Pleon as long as pereonites 2–7 combined (dorsal view, flattened); pleotelson broadest in distal third, with serrate margins faintly convex, nearly parallel, with low, broadly rounded mid-dorsal keel, posteriorly produced into blunt, serrate triangle.

Antenna 1, article 1 with slender spines along medial surface, article 2 as long as 3–5 combined, c. 4 times longer than wide, article 6 two-thirds length of 5. Antenna 2, peduncular articles 1 and 2 of subequal length, article 3 c. 50% longer than greatest width, expanded in distal half, with a few distolateral spines; flagellum with up to 15 articles.

Mouthparts: 3-articulate mandibular palp barely reaching tip of incisor, article 3 short, curved, with 2 long apical, pectinate setae, a subapical row of short setae, and field of fine setules, articles 1 and 2 with a few distal setae; article 2 with distal cuticular combs; long cylindrical molar strongly expanded in distal third, apex truncate with serrate margins, a few setae on dorsoanterior margin, and a strong tooth pointing towards incisor. Maxillipedal epipod slender, oval.

Pereopod 1 slender, article 2 with anterior row of small sharp spines (probably more than shown in Fig. 5), article 3 little more than twice

Figure 5. Abyssianira bathyalis sp. nov., holotype. p1, p2, p7, pereopods 1, 2 (both left), and 7 (right).
as long as wide, article 4 distally expanded, simple, triangular, with 1 posterodistal spine-like seta, article 5 about twice as long as wide, straight, with 2 midposterior spine-like setae, article 6 slightly curved and distally widening, nearly 3 times longer than wide, with 2 posterior spine-like setae, article 7 including unguis about two-thirds length of article 6. Pereopod 2 similar to 3–7 except article 2 with anterior row of small sharp spines (probably more than shown in Fig. 5). Pereopods slightly increasing in length from 2 to 7, articles 5 and 6 with posterior row of spine-like setae.

Pleopod 2 of male, protopod 3 times longer than broad, nearly straight, apex broadly rounded, lateral margin with short setae, endopod rather short, article 2 moderately curved, exopod distally bilobed. Female opereculum ovoid, distally tapering bluntly pointed apex, lateral margins with short setae. Pleopod 3, exopod articles not fully separated, distal article sharply pointed with terminal simple seta, endopod with 3 plumose setae, lateral margin expanded into dorsally (functionally) pointed ear-like lobe, (an ongoing study will show that this is a commonly occurring feature of many paramunnid species). Pleopod 4 with short, bluntly pointed exopod. Uniramous pleopod 5 slightly larger than 4.

Uropods inserted dorsally just inside lateral margin, protopod half hidden, about as long as broad, exopod four-fifths length of endopod, endopod ca. 4 times length of protopod.

Size. Largest female: 3.6 mm; largest male: 3.0 mm; smallest ovigerous female: 2.2 mm.

Distribution. South-eastern Australia; 400–1277 m.

Variation. The frontal plate is often slightly longer than in the holotype. A few specimens have more lateral spines on pereonites, including pereonite 5 (Fig. 3B), than in the holotype.

Remarks. Abyssianira bathyalis differs from the two Atlantic species in its much more strongly convex frontal plate, its straight, nearly laterally pointing eye-stalks, the long pereonite 1 relative to 2 and 3, and the longer more setose mandibular palp. A. dentifrons has strongly convex pleotelson margins and no spines on the posterior projection. A. argentinensis has a more pentagonal pleotelson with a very wide-angled short posterior projection. In A. dentifrons the mandibular molar is nearly unexpanded distally (not known for A. argentinensis). In A. argentinensis article 1 of antenna 1 is expanded distally with a row of medial spines on the expanded part. There are minor differences in the shape and setation of pereopods and uropods, and in the male pleopod 2 in at least A. dentifrons, but the two Atlantic species are still inadequately known.

A. bathyalis differs from A. tasmaniensis below primarily in having the frontal plate more densely serrate, the eyestalks broader and pointing more laterally, cephalic ‘brows’ with spines, antenna 1 with peduncular spines, pereonite 3 with posterolateral spinose lobes, and the mandibular molar more strongly expanded distally.

Abyssianira tasmaniensis sp. nov.

Figures 6, 7

Material examined. Holotype. Eastern Tasmania off Freycinet Peninsula, 41°58.60’S, 148°38.80’E, 500–600 m, coarse shell, large sponges, WHOI epibenthic sled, RV “Franklin” stn SLOPE-47, 27 Jul 1986, M.F. Gomon et al., NMV J15780 (preparatory female, 2.3 mm, with 3 slides).


Description. Frontal plate strongly convex, coarsely serrate with 13–15 marginal teeth visible in dorsal view in mature specimens. Eyestalks slender, not overreaching pereonite 1 in dorsal view, forward pointing at an angle of c. 50° and curving downward, anterior and posterior margins parallel with small spines, apex with irregular spination. Antenna 1 inserted under small, smooth brow-like overhang. Cephalon with spinose ridge on each side running from median extension of ‘brow’ downwards to lateral margin of frontal plate along medial margin of article 1 antenna 1.

Pereonite 1 with anterolateral spinose coxal projection visible in dorsal view, coxa poorly delimited from sternite, pereonite 1 as long as 2 and half of 3 combined, with small midlateral spines. Pereonites 2–4 of equal length, with a few small spines on rounded lateral margins, pereonite 4 with posterior margin smooth between lateral insertion points of pereonite 5. Pereonite
Figure 6. *Abyssanira tasmaniensis* sp. nov., holotype, female. a, ventral view of right side of cephalon; c, ventral view of right coxa I with spinose projection; pl2, plocopod 2; pl3, plocopod 3, dorsal view; up, left uropod, dorsal view. Habitus scale, 1 mm.
Figure 7. Abyssianira tasmaniensis sp. nov., holotype. p1, p2, p7, pereopods 1, 2, and 7 (all left); md, left mandible; mp, maxilliped; mx1, maxilla 1.
5 shorter than 6 and 7, lateral parts of 7 broader than equal 5 and 6.

Pleon as long as peronites 2–6 combined (dorsal view, flattened); pleotelson broadest proximally, with serrate margins faintly convex, posteriorly produced into rounded serrate triangle; pleotelson with evenly curved dorsal surface in transverse section.

Antenna 1 article 1 without spines, article 2 about as long as 3–5 combined, nearly 6 times longer than wide, article 6 two-thirds length of 5. Antenna 2 peduncular articles 1 and 2 joined at strongly oblique articulation (Fig. 6a), 2 longer than 1, article 3 without spines, about one-fifth longer than wide, about two-thirds length of article 2 (ventral view).

Mouthparts similar to A. bathyalis, except mandibular molar less strongly expanded distally and maxillipedal epipod with rounded, angular lateral margin.

Pereopods similar to A. bathyalis, but pereopod 1 more slender, articles 3 and 5 nearly 3 times longer than wide, article 6 with 3 posterior spine-like setae. Pereopods 1 and 2 article 2 with row of small fragile spines along entire anterior margin and proximoposterior group of similar spines. Pereopods 3–4 with short midanterior row of similar spines and proximoposterior group of spines.

Female operculum ovoid, distally tapering towards bluntly pointed apex, with short marginal setae. Male pleopods 1–2 as in A. bathyalis. Pleopods 3–5 as in A. bathyalis.

Uropods inserted dorsally just inside lateral margin, protopod half hidden, about as long as broad, endopod 3 times longer than protopod, exopod about three-fifths length of endopod.

Size. Largest male: 3.6 mm; largest female: 4.0 mm; smallest ovigerous female: 2.4 mm.

**Distribution.** South-eastern Australia: 400–1770 m.

**Remarks.** Abyssianira tasmaniensis differs from the two Atlantic species in the same way as A. bathyalis (see above), except for its forward pointing eyestalks which are similar to those of A. argentinensis although more slender. The main differences between A. tasmaniensis and A. bathyalis were discussed in the remarks on the latter species.

**Discussion**

The two Atlantic species of Abyssianira have been found at abyssal depths only (A. dentifrons: 4618–5293 m, Central and South Atlantic; A. argentinensis: 2681 m, South Atlantic). In contrast, the two Australian species are from upper to mid-bathyal depths (A. bathyalis: 400–1277 m; A. tasmaniensis: 400–1770 m). In spite of extensive sampling over many years the genus has never been reported from the Antarctic. The two Australian species have similar plesiomorphic mandibular palps compared to the reduced, more typical paramunniid palp in at least A. dentifrons, (Menzies, 1962 did not note any deviation from A. dentifrons in this character in his very brief description of A. argentinensis).

Taken together, these distributional and morphological data suggest that ancestral Abyssianira evolved in cold water, but not of present day polar temperatures, at moderate depths of the upper bathyal, perhaps even the lower shelf. The occurrence in the deep central and southern Atlantic as well as in more shallow water of the south-eastern Australian slope indicates that the origin of the genus should be sought in the southern hemisphere, and more specifically in the cold-water Weddellian Province of late Cretaceous or early Tertiary Gondwanan. If that scenario is correct, it is entirely likely that additional species of Abyssianira may be discovered on the mid to upper slopes of South America and New Zealand.

It is not possible at present to evaluate whether or not ancestral Abyssianira had functional eyes. One positive indication is the presence, at least in some preserved specimens of A. bathyalis, of scattered dark matter (?)pigment in the eye stalks (Fig. 2Aa). If the above hypothesis of a shallow water origin of the genus is correct, functional eyes were most likely present and species with a few functional ocelli may still be in existence. (Paramunniidae with eyes typically have a few ocelli only). The discovery of such species would lend support to the shallow water origin hypothesis as against the alternative, an abyssal-deep bathyal origin with subsequent emergence into shallower depths. In this case one would suppose Abyssianira evolved from a paramunniid stock which had already lost functional eyes.

The shallow water hypothesis invokes vicariance through continental drift, with subsequent local dispersal into deep water. in cases from the eastern South American slope into the Atlantic abyss. The alternative scenario includes no vicariance element and relies solely on an unspecified centre of origin and unlimited horizontal and vertical dispersal, which for paramunniids in general means walking.

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References


