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A revision of *Paranaitis* Southern, 1914 (Polychaeta: Phyllodocidae)

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Paranaitis Southern, 1914 (Phyllodocidae, Polychaeta) is revised based on an examination of all available types and newly collected specimens. Redescriptions are provided of the 11 previously described species considered valid: *P. wahlbergi* (Malmgren, 1865), *P. abyssalis* (Hartmann-Schröder, 1975), *P. benthicola* (Knox, 1960), *P. bowersi* (Benham, 1927), *P. caeca* (Moore, 1903), *P. gardineri* Perkins, 1984, *P. inflata* (Hutchings & Murray, 1984), *P. kosteriensis* (Malmgren, 1867), *P. polynoides* (Moore, 1909), *P. speciosa* (Webster, 1879) and *P. uschakovi* Eibye-Jacobsen, 1991. ***Paranaitis misakiensis* sp. nov.**, ***P. moritai* sp. nov.** and ***P. pumila* sp. nov.** are described from Japan. *Anaitis peremptoria* Claparède, 1870; *Anaitis zeylanica* Willey, 1905; *Phyllodoce* (*Anaitis*) *papillosa* Ehlers, 1887; and *Phyllodoce* (*Anaitis*) *rubens* Grube, 1880 are referred to as Phyllodocidae *incertae sedis*, and *P. capensis* (Day, 1960), *P. formosa* (Verrill, 1885) and *P. picta* (Verrill, 1885) to as *Paranaitis incertae sedis*. ***Phyllodoce truncata*** (Hartmann-Schröder, 1965) **comb. nov.** is removed from *Paranaitis*. Some previously unreported characters are introduced, including a series of proboscis characters, morphology of dorsal cirrophores, and symmetry of rostrum of chaetal shaft. Distinguishing characters for all recognized species of *Paranaitis* are provided in a table. In order to assess the position and delineation of *Paranaitis* and the relationships within this taxon, we present a morphology-based parsimony analysis of relationships within the Phyllodocidae. *Paranaitis* is shown to be paraphyletic at the exclusion of *Chaetoparia*, although current support does not allow for any formal synonymy. *Phyllodoce* and the *Eteone*-group appear as consecutive sister taxa to the *Paranaitis-Chaetoparia* clade. The monophyly of Notophyllinae is well supported, but low consensus resolution is obtained for the positions of major taxa such as *Eulalia*, *Eumida*, and the *Mystides*-group. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society,* 2003, **138**, 379–429

ADDITIONAL KEYWORDS: *Anaitis* – Annelida – new species – ***Paranaitis misakiensis* sp. nov.** – ***Paranaitis moritai* sp. nov.** – ***Paranaitis pumila* sp. nov**. – *Phyllodoce truncata* comb. nov. – phylogeny – taxonomy.

INTRODUCTION

Malmgren (1865) described the new genus and new species *Anaitis wahlbergi* for a phyllodocid that was identified by, e.g. having the three first pairs of tentacular cirri arising from the collar (equaling the first segment according to Malmgren, but now considered as segments 1 and 2). Southern (1914) noted that the name *Anaitis* was preoccupied by *Anaitis* Duponchel, 1829 (in Godart & Duponchel, 1829) in Lepidoptera (Insecta), and proposed the replacement name *Paranaitis*. Apparently, Southern's comment passed by unnoticed, since most authors continued to use *Anaitis* for the phyllodocid taxon, treating it as a subgenus of *Phyllodoce* Lamarck, 1818 (e.g. Monro, 1930; Annenkova, 1937; Day, 1960). Not until the publication of Hartman's (1959) catalogue did *Paranaitis* come into current use.

More recently, Pleijel (1991) in a revision of Phyllodocidae, synonymized *Eulalia* (*Euphylla*) Knox, 1960, *Pareteone* Hartmann-Schröder, 1975 and *Compsanaitis* Hutchings & Murray, 1984 with *Paranaitis*. Following Pleijel's (1991) list of phyllodocids, 25 nom-

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*Corresponding author. E-mail: kato@smbl.mbox.media.kyoto-u.ac.jp. Current address: Seto Marine Biological Laboratory, Field Science Education and Research Center, Kyoto University, Shirahama, Nishimuro, Wakayama 649-2211, Japan inal species are currently referred to *Paranaitis*, *Anaitis* or *Phyllodoce* (*Anaitis*).

The Phyllodocid phylogeny has been addressed in three recent studies, Pleijel (1991), Eibye-Jacobsen (1993), and Orrhage & Eibye-Jacobsen (1998). All three yield significant differences in tree topologies, at least in part due to different interpretations of the evolution of the two characters nuchal papilla and distribution of 'tentacular' cirri (see below re. terminology).

The nuchal papilla in phyllodocids is, usually, a small and rounded protuberance which is situated at the dorsal posterior margin of the prostomium, and is generally considered homologous to the median antenna as occurring in, e.g. *Eulalia* Savigny, 1822 and *Eumida* Malmgren, 1865 (cf. Bergström, 1914; Uschakov, 1972; Pleijel, 1991; Orrhage & Eibye-Jacobsen, 1998; but see Eibye-Jacobsen, 1993). A nuchal papilla is present in *Phyllodoce*, in the *Eteone* group (including *Eteone* Savigny, 1822; *Hypereteone* Bergström, 1914 and *Mysta* Malmgren, 1865), in *Paranaitis* and in *Chaetoparia* Malmgren, 1867; although within some taxa in the latter two genera, the shape approaches that of a median antenna.

As to the absence/presence of digitate rather than flattened cirri on the anterior-most 2–3 segments, there are three basic arrangements in phyllodocids: (1), 0+1/1+0/N (representing the three anterior-most segments separated by '+') in the *Eteone* group, (2), 1+1/1+0/N in the *Mystides* group (including *Mystides* Théel, 1879; *Galapagomystides* Blake, 1985; *Pseudomystides* Bergström, 1914; *Hesionura* Hartmann-Schröder, 1958; which together may constitute a grade or a clade) and (3), 1+1/1+1/N in all other phyllodocids. Note that segment 1 in the *Eteone* group is interpreted as being reduced (see Pleijel, 1991 and Orrhage & Eibye-Jacobsen, 1998; for further explanation). This is of importance for the statement that dorsally situated cirri are absent on segment 3 (rather than segment 2) in the *Eteone* group, and this character thus represents a putative homology for the *Eteone* and *Mystides* groups.

In the morphology-based phylogeny of Pleijel (1991), Phyllodocinae Bergström, 1914; was delineated to include *Paranaitis*, *Phyllodoce* and *Chaetoparia*, whereas the *Eteone and Mystides* groups represented a distant, separate clade. The occurrence of a nuchal papilla in Phyllodocinae and in the *Eteone* group appeared as a homoplasy, whereas the reduction of dorsal cirri of segment 3 in the *Eteone and Mystides* groups represented a single event.

Subsequently, two more recent and also morphology-based analyses (Eibye-Jacobsen, 1993; Orrhage & Eibye-Jacobsen, 1998) yielded different topologies and different interpretations of the evolution of these two groups of characters. Eibye-Jacobsen (1993) also supported the monophyly of Phyllodocinae *sensu* Pleijel, but with the *Eteone and Mystides* groups (the latter appearing as a grade also including *Protomystides*) as consecutive sisters to Phyllodocinae. The nuchal papilla in this topology appeared without homoplasy, whereas the cirri on segment 3 were first reduced basally in the *Mystides* grade but then reappeared in both Phyllodocinae and *Protomystides*.

In the study by Orrhage & Eibye-Jacobsen (1998), the *Eteone* group was instead situated within Phyllodocinae as sister to *Phyllodoce*, and the *Mystides* group represented a different clade. Accordingly, also here the nuchal papilla appears without homoplasy, but the reduction of the cirri on segment 3 is different in appearing independently both within Phyllodocinae and in the *Mystides* group.

The position of *Paranaitis* appears to be central in the phyllodocid phylogeny, being one of the taxa of unstable position in previous analyses. In order to assess both the position of *Paranaitis* and the phylogeny within this taxon, we present a cladistic analysis of Phyllodocidae which differs from previous ones in using species, rather than genera, as terminals. On one hand this permits a more precise, specimen-based character scoring, with less a priori assumptions about the monophyletic status of the terminals and their root states. On the other hand, the ingroup includes many hundreds of described species, and the analysis cannot span all known taxa and their variation. In our choice of terminals, we selected a number of species of the more inclusive and morphologically variable taxa such as *Phyllodoce* and the *Eteone* group. Furthermore, some previously unnoticed characters are introduced: direction of paired antennae and palps, size and position of nuchal organs, dorsal elongation of dorsal cirrophores and detailed chaetal morphology (symmetry of rostrum of chaetal shaft and number of main teeth on rostrum). The phylogeny of *Paranaitis* is accompanied by re-descriptions of the taxa and the introduction of two new species. For identification purposes, a summary of diagnostic characters is provided for all species (Table 1).

MATERIAL AND METHODS

MATERIAL FROM THE FOLLOWING MUSEUMS AND INSTITUTIONS WAS EXAMINED

The Australian Museum, Sydney, Australia (AM).
Aikap Museum of Natural History, Akkeshi Marine Station, Hokkaido University, Japan (AMNH).
Akvaplan-niva, Tromsø, Norway.
The Natural History Museum London, UK (BMNH).
Canterbury Museum, Christchurch, New Zealand (CMC).
Coastal Museum of Natural History, Chiba, Japan (CMNH).

Florida Marine Research Institute, St. Petersburg, USA (FSBC).

Muséum national d'Histoire naturelle, Paris, France (MNHN).

National Museum and Galleries of Wales, Cardiff, UK (NMW).

Natural History Museum of Los Angeles County, USA (LACM).

Museum of Comparative Zoology, Harvard, USA (MCZ).

Museum für Naturkunde, Zoologisches Museum, Berlin, Germany (ZMB).

Naturhistorisches Museum, Vienna, Austria (NHMW).

South African Museum, Cape Town, South Africa (SAM).

Swedish Museum of Natural History, Stockholm, Sweden (SMNH).

Smithsonian Institution, Washington, DC, USA (USNM).

Zoological Institute, Hokkaido University (ZIHU).

Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia (ZIR).

Zoological Museum, Hamburg, Germany (HZM).

Zoological Museum, University of Copenhagen, Denmark (ZMUC).

Additional specimens were borrowed from the collections of Torleiv Brattegard (University of Bergen, Norway), Julio Parapar (University of Coruña, Spain), Mary E. Petersen (ZMUC), Eijiro Nishi (Yokohama National University, Japan) and Hiroshi Mukai (Hokkaido University, Japan).

Specimens newly collected by the authors (F.P. & T.K) were relaxed in 7–10% $MgCl_2.6H_2O$, solution, fixed in formalin (10% in seawater) for at least 24 h, rinsed in fresh water and transferred to 70% ethanol for preservation. Specimens for the SEM study were similarly relaxed, preserved for a few hours in 1–2% osmium tetroxide in filtered seawater, rinsed, and stored in distilled water, transferred to ethanol, critical point dried, sputter coated with gold, and examined in a Philips SEM 515 or Hitachi S-520. Most of these specimens, as specified in the text, are deposited at MNHN, SMNH and ZIHU. Drawings were made from preserved specimens with a camera lucida.

Measurements of body width were recorded from the middle of the body, and included neuropodial chaetigerous lobes, but excluded dorsal and ventral cirri and chaetae.

Unless accompanied by references, all information on the distribution of the taxa was based on examined specimens.

Characters for the cladistic analysis were scored in several different ways. Mutually exclusive expressions of a feature ('logically dependent characters' *sensu* Wilkinson, 1995) were scored as a single unordered multistate character (e.g. character 1, frontal antennae and palps: subapically widest/tapering/of equal width). However, for features displaying an absent/present distribution plus informative variation among the taxa scored for presence, the observations were instead expressed as one absent/present character followed by additional subsidiary characters detailing the variation. Taxa lacking the feature were scored with question marks for the subsidiary characters ('C-coding' *sensu* Pleijel, 1995) (e.g. character 3, eyes: absent/present, and character 4, eye position: superficial/deeply sunken). Remaining binary characters were formulated as absent/present (e.g. character 2, prostomial protuberance: absent/present). Parsimony analyses and character state reconstructions were performed with MacClade, version 3.08a (Maddison & Maddison, 1999) and PAUP, version 4.0b8 (Swofford, 1998). Heuristic tree searches were executed with PAUP's default settings, except for the taxon addition sequence which was set to random with 1000 replicates, initial seed 1. The jackknife tree (Farris *et al.*, 1996) was also calculated in PAUP with the following specifications: 35% deletion, emulate Jac resampling, 10 000 replicates, seed 1, fast step-wise addition, and include groups compatible with 50% majority-rule consensus. Bremer support (e.g. Bremer, 1988, 1994) was calculated with TreeRot (Sorensen, 1996).

MORPHOLOGY OF *PARANAITIS*

The shape of the prostomium may be rounded to triangular, although the differences between taxa are gradual and poorly defined. The posterior part of the prostomium is always covered by segment 1. There are two pairs of front appendages of which the dorsal pair is labelled 'paired antennae' and the ventral pair 'palps' (homologous to palps in other Phyllodocida, e.g. Orrhage & Eibye-Jacobsen, 1998). The paired antennae and the palps may be antero-laterally orientated and inserted on a rounded to flat prostomial surface (Fig. 5A, B), or they may be postero-laterally orientated and inserted in lateral prostomial depressions (Fig. 13A). This character is potentially informative, although there are difficulties in discriminating states in some specimens, especially when they are in a poor condition. A single pair of eyes with lenses may be present, or eyes are entirely absent. A single nuchal papilla is situated near the posterior margin of the prostomium in an incision (ligula) surrounded by segment 1, and can be indistinct (e.g. *P. wahlbergi*), short and rounded (e.g. *P. kosteriensis*), or long and pointed and similar to the paired antennae and the palps (e.g. *P. caeca*). The ligula may be deep or shallow.

The proboscis morphology is highly variable in *Paranaitis* and provides a series of characters. It can

Table 1. Characters and character distribution among *Paranaitis* species

					Proboscis		
Species	Direction of antennae	Ligula	Nuchal papilla	Eyes	Division	Proximal part	Distal part
P. wahlbergi	lateral	shallow	indistinct	present	absent	dorsally covered with minute fleshy papillae, lateral row of large papillae on each side, lateral rows absent from proximal-most part	
P. abyssalis	forward	deep	rounded	absent	unknown	proximal-most part covered with minute papillae	
P. benthicola	forward	shallow	conical	absent	unknown	densely covered by large leaf-like papillae	
P. bowersi	lateral	shallow	rounded	absent	absent	6–7 longitudinal rows of large rectangular tubercles	
P. caeca	lateral	shallow	large, antenna-like	absent	absent	lateral row of rounded papillae; dorsally covered with pointed papillae; ventrally with rounded small papillae	
P. gardineri	lateral	deep	rounded	present	gradual	covered with minute chitinous papillae; 2 lateral papillae on each side	5 rows of tubercles; chitinous papillae present
P. inflata	lateral	deep	rounded	present	distinct	covered with minute chitinous papillae; *c*.4 lateral large fleshy papillae on each side	5 rows of tubercles; chitinous papillae absent
P. kosteriensis	lateral	deep	rounded	present	distinct	covered with minute papillae, 4–8 lateral papillae	5 rows of tubercles; chitinous papillae absent
P. misakiensis **sp. nov.**	lateral	deep	rounded	present	gradual	covered with minute papillae, 3–4 lateral papillae	5 rows of tubercles; chitinous papillae present
P. moritai **sp. nov.**	lateral	deep	rounded	present	distinct	covered with minute chitinous papillae; proximal-most part with large chitinous papillae	6 rows of tubercles; chitinous papillae absent
P. polynoides	lateral	deep	rounded	present	distinct	covered with minute chitinous papillae	6 rows of tubercles; chitinous papillae absent
P. pumila **sp. nov.**	forward	deep	rounded	present	absent	entire surface smooth	
P. speciosa	forward	shallow	indistinct	present	absent	dorsally covered with minute fleshy papillae, lateral row of large papillae on each side; lateral rows absent from proximal-most part	
P. uschakovi	forward	deep	rounded	absent	absent	sparsely covered by minute papillae	

First chaetiger	Dorsal cirri		Dorsal cirrophore	Pygidial cirri	Chaetae	Type locality
	Shape	Symmetry				
3	broad cordate; wider than long	outward	small	oval, slightly longer than wide	asymmetrical, 2–3 main teeth	Treurenberg Bay, Spitsbergen
2	almost circular	symmetrical	large, symmetrical	unknown	asymmetrical, single main tooth	off Iberian Peninsula,
2	almost circular	symmetrical	large, symmetrical	unknown	symmetrical, single short main tooth both sides	Chatham Rise, New Zealand
2	reniform; wider than long	symmetrical	large, dorsally elongated	very short, knob-like	asymmetrical, single main tooth	Ross Sea, Antarctic
2	reniform; wider than long	symmetrical	large, dorsally broaden	cylindrical, 2–3 times as long as wide	symmetrical, single short main tooth both sides	Sagami Bay, Kanagawa, Japan
3	broad cordate; wider than long	slightly outward	large, symmetrical	cylindrical, tapered, 6–8 times longer than wide	asymmetrical, single main tooth	off Cape Lookout, North Carolina, USA
3	almost circular	outward	large, symmetrical	cylindrical, twice as long as wide	dorsal: symmetrical, no main tooth ventral asymmetrical, single main tooth	Hawkesbury River, Australia
3	oval; longer than wide	outward	large, symmetrical	cylindrical, 2–5 times as long as wide	dorsal: asymmetrical, smaller main tooth ventral: asymmetrical, larger main tooth	Koster, Sweden
3	oval; longer than wide	outward	large, symmetrical	cylindrical, 2–5 times as long as wide	asymmetrical, single main tooth	Moroiso Bay, Kanagawa, Japan
2 or 3	reniform; wider than long	symmetrical	large, dorsally elongated	cylindrical, *c.* 2.5 times as long as wide	asymmetrical, single main tooth	Otsuchi Bay, Iwate, Japan
2	wider than long	symmetrical	large, dorsally elongated	cylindrical, 3–3.5 times longer than wide	asymmetrical, single main tooth	Monterey Bay, California, USA
2	oval; longer than wide	symmetrical	small	oval, 1.5–2 times as long as wide	asymmetrical, single main tooth	Otsuchi Bay, Iwate, Japan
3	broad cordate; wider than long	outward	small	oval, slightly longer than wide	asymmetrical, single main tooth	Great Egg Harbor, New Jersey, USA
2	reniform; wider than long	symmetrical	large, dorsally broaden	oval, slightly longer than wide	asymmetrical, single main tooth	East of Honshu, Japan

be subdivided into distal and proximal parts (referring to the proboscis in everted state) or not subdivided; in the subdivided proboscis the parts can be sharply delineated or have a gradual transition. In taxa with a subdivided proboscis the distal part is usually covered by six rows of large rounded tubercles, of which the two dorsal rows can merge into a single one. The proximal part lacks tubercles, but is covered by minute chitinous papillae which may also be present on the distal part. These papillae are very small and transparent, and their detection requires examination with a compound microscope. Furthermore, under the epithelium of the proboscis, there are one or a few kinds of rounded structures (Fig. 17B–E) which are possibly secretory glands, and which have frequently been misinterpreted as papillae (e.g. Pleijel, 1993a for *Paranaitis* near *polynoides*). The size and shape of the chitinous papillae are quite variable and related to their position on the proboscis. A group of large papillae may be present in transverse rows on each side of the proximal-most part. In taxa with a nonsubdivided proboscis, the surface may be smooth or covered by tubercles and large or small papillae. A longitudinal lateral row of large papillae may be present on each side.

The nuchal organs in *Paranaitis* have not been detailed in the literature. They are retractile, with horseshoe-shaped bands of cilia, but vary in size and position between species. The nuchal organs can be completely retracted and invisible, and can also be difficult to examine in specimens in poor condition.

Segments 1 and 2 are large, more or less fused to each other, and form a collar around the prostomium. The degree of fusion of these two segments has been thought to be diagnostic for certain species (e.g. *P. polynoides*). Nevertheless, the interpretation of this character is problematic due to the presence of fixation and preservation artefacts.

The cirri of segment 1, the dorsal and ventral cirri of segment 2 and the dorsal cirri of segment 3 differ in shape from the following dorsal and ventral cirri in being long and digitiform rather than rounded and flattened, and are traditionally labelled ‘tentacular cirri’. Although the term is unproblematic within the Phyllodocidae, it is equivocal for a number of other polychaete groups within Phyllodocida (see e.g. Pleijel, 1998), and conflates the actual shape of cirri with other characters, such as a reduction of chaetae and chaetigerous lobes on the anterior segments. Referring to these cirri with a specification of their position (e.g. dorsal cirri of segment 2) and shape (e.g. digitate) increases the precision of the descriptions and eases comparisons between more distant polychaete taxa. For this reason, we avoid here the use of the term ‘tentacular cirri’. The length of the anterior cirri exhibits interspecific differences, although considerable intraspecific variation is present in *P. wahlbergi*. The presence or absence of dorsal aciculae in segments 2 and 3 is potentially informative among *Paranaitis*, although unknown for some rare species (e.g. *P. abyssalis*). The chaetae may be present on segment 2, arising from neuropodial lobes or from the cirrophores of the ventral cirri. From segment 3 and onwards they always emerge from the neuropodial lobes. The number of chaetae varies between species (although not in a very fixed pattern) and is also related to body size. Segment 4 and the following segments are provided with uniramous parapodia with reniform flattened dorsal and ventral cirri. The outline of the dorsal cirri is oval, circular or broadly reniform. The dorsal cirrophores show little intraspecific variation, and are large and distinct in some species and short and indistinct in others. In *P. uschakovi* they carry a ciliary band**.** The dorsal cirrophores may be well developed or indistinct, and when well developed they can be symmetrical around the longitudinal axis (Fig. 13C–F), they can be bilobed with enlarged dorsal lobes (Fig. 8F–I), or they can be thin with dorsal extensions (Fig. 22H–I). The supra-acicular lobes of the neuropodium are longer than the subacicular lobes. The ventral cirri have rounded-to-pointed ends, with the longitudinal axis orientated horizontally. All chaetae are compound in *Paranaitis*. The rostrum of the chaetal shaft is covered by a large number of small teeth, and may have a single to a few additional main teeth on the anterior side, or both on the anterior and posterior sides. When the anterior and posterior sides are similar to each other, the rostrum is labelled as symmetrical; when different it is labelled as asymmetrical. The shape of the chaetae is similar from the dorsal to the ventral part of the fascicles in most species, although gradual changes from asymmetrical to symmetrical are found in *P. inflata* and *P. kosteriensis*. The chaetal blades are always long and slender, and we could not detect any informative variation in them (see also remarks for *P. inflata*).

A pair of pygidial cirri and a single pygidial papilla are present, although unknown for some species. The pygidial cirri may be rounded or cylindrical, and have rounded-to-pointed ends.

The colour and pigmentation pattern of live *Paranaitis*, as in many other phyllodocids, exhibits important interspecific differences. Many species have whitish bodies with a red pigmentation that is unusual (possibly unique except some species of *Mysta*) in phyllodocids, although other pigmentation patterns are also present. In some taxa the pattern may be retained in well-preserved specimens and provide additional information for identification; in others it disappears completely.

TAXONOMY

GENUS *PARANAITIS* SOUTHERN, 1914

Paranaitis Southern, 1914: 66–67.
Anaitis Malmgren, 1865: 94. Junior homonym to *Anaitis* Duponchel, 1829 (in Godart & Duponchel, 1829; Lepidoptera, Insecta).
Eulalia (*Euphylla*) Knox, 1960: 113.
Pareteone Hartmann-Schröder, 1975: 58–59.
Compsanaitis Hutching & Murray, 1984: 24.

Type species
Anaitis wahlbergi Malmgren, 1865: 94, pl. 14, fig. 31A–D, by monotypy.

Description
Prostomium anteriorly rounded, posterior part dorsally covered by first segment. Nuchal papilla may be indistinct, small and rounded, or larger and elongated, situated in posterior part of ligula (incision formed by segment 1). Nuchal organs retractile. Proboscis in some taxa subdivided into proximal and distal parts; lateral rows of papillae absent or present, and dorsal and ventral proboscis surfaces may be covered by chitinous or fleshy papillae and/or large tubercles. Segments 1 and 2 more or less fused, forming collar around prostomium. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Dorsal aciculae of segment 2 and 3 present or absent. Ventral aciculae from segment 2, chaetae from segment 2 or 3. Parapodia uniramous, dorsal cirri with rounded ends. Neuropodial lobes with supra-acicular lobe longer than subacicular. Rostrum of chaetal shafts symmetrical or asymmetrical, covered by many small teeth; single to few large main teeth present or absent. Ventral cirri oval, with rounded ends. Pygidium with single pair of oval or cylindrical pygidial cirri; single median pygidial papilla present.

Remarks
Euphylla was erected by Knox (1960) as a subgenus of *Eulalia* for his new species *Eulalia* (*Euphylla*) *benthicola* and synonymised with *Paranaitis* by Pleijel (1991). The holotype and only known specimen has an unusually long and pointed nuchal papilla, in contrast to the rounded papilla in most *Paranaitis* species. As seen from, e.g. the presence of a collar and a well developed ligula, however, it clearly belongs within *Paranaitis*. A similar nuchal papilla is also found in *P. caeca*, from which it most notably differs in proboscis morphology (with dorsal papillae in *P. caeca*; with rows of tubercles in *P. benthicola*).

Hartmann-Schröder (1975) described a subfamily Pareteoninae and a genus *Pareteone* for her new species *Pareteone abyssalis*, known only by a single specimen. *Pareteone* was considered to be different from *Paranaitis* in having only three pairs of tentacular cirri on first two segments (1/1+1/N). Pleijel (1991) re-examined the holotype, and stated that the first pair of tentacular cirri are not absent but lost due to damage, and synonymized *Pareteone* with *Paranaitis*. Pareteoninae was consequently also synonymised with Phyllodocinae.

Hutching & Murray (1984) described the new genus and species *Compsanaitis inflata*, distinguished from *Paranaitis* by the lack of macropapillae on the proboscis. *Paranaitis* was characterized as having two lateral rows of papillae. Re-examination of Hutching & Murray's specimens, however, shows that *c*. four macropapillae actually do occur on each side of the proximal-most part of the proboscis, and that rows of large tubercles are present on the distal part (their examination was probably based on specimens which did not have the proboscis fully everted). Accordingly, these, or any other observed characters, fail to justify a separation between *Paranaitis* and *Compsanaitis*, and we concur with Pleijel (1991) in regarding the latter name as a junior synonym.

PARANAITIS WAHLBERGI (MALMGREN, 1865)
(FIGS 1–3, 37)

Anaitis wahlbergi Malmgren, 1865: 94, pl. 14, fig. 31A–D; Grube, 1880: 214; Ditlevsen, 1909: 12; Fauvel, 1911: 26; Bergström, 1914: 155–156, fig. 51; Wesenberg-Lund, 1951: 25, 1953: 30.
Paranaitis wahlbergi: Southern, 1914: 67, pl. 8, fig. 16; Hartman, 1959: 158–159, 1965: 62; Uschakov, 1972: 140–141, pl. 7, figs 8 and 9; Pleijel & Dales, 1991: 96, fig. 27A–C; Pleijel, 1993a: 30–32, figs 17,18,19, map 10.

Material examined
NORWAY: Holotype (SMNH-Type-233), Treurenberg Bay, Spitsbergen, Svalbard, 79°56′N, 16°50′E, 20–30 fathoms; 6 specimens (SMNH-22502), off Jan Mayen, 69°01′N, 8°24′W, 880 m; 5 specimens, 63°10.0′N, 04°49.0′E, 830 m, 21 March 1981, coll. T. Brattegard; 10 specimens, 63°17.1′N, 04°24.8′E, 1260 m, 22 March 1981, coll. T. Brattegard; 8 specimens, 65°41.8′N, 04°22.9′E, 1211 m, 7 June 1981, coll. T. Brattegard; 2 specimens, 62°33.2′N, 00°58.9′E, 800 m, 16 August 1981, coll. T. Brattegard; 7 specimens, 62°33.6′N, 00°58.9′E, 804 m, 21 January 1982, coll. T. Brattegard; 3 specimens, 63°02.9′N, 00°48.5′E, 1286 m, 15 August 1982, coll. T. Brattegard; 3 specimens, 63°12.8′N, 03°07.3′E, 1003 m, 23 August 1982, coll. T. Brattegard;

5 specimens, 63°10.7′N, 02°45.9′E, 1030 m, 26 November 1982, coll. T. Brattegard; 16 specimens, 62°59.1′N, 03°13.1′E, 804 m, 27 November 1982, coll. T. Brattegard; 1 specimen, 62°07.4′N, 04°34.0′E, 225 m, 27 November 1982, coll. T. Brattegard; 12 specimens, 65°10.1′N, 09°29.6′W, 784 m, 8 June 1983, coll. T. Brattegard; 5 specimens, 62°35.6′N, 01°14.0′E, 781 m, 17 June 1983, coll. T. Brattegard; 12 specimens, 62°35.1′N, 01°47.6′E, 656 m, 23 May 1984, coll. T. Brattegard; 2 specimens, 62°17.6′N, 01°48.7′E, 406 m, 21 November 1984, coll. T. Brattegard; 1 specimen, 62°00.1′N, 02°01.3′E, 374 m, 21 November 1984, coll. T. Brattegard; 23 specimens, 62°31.5′N, 01°26.6′E, 701 m, 8 January 1985, coll. T. Brattegard; 41 specimens, 62°42.4′N, 01°11.2′E, 897 m, 8 January 1985, coll. T. Brattegard; 12 specimens, 62°54.7′N, 00°55.7′E, 1112 m, 8 January 1985, coll. T. Brattegard; 1 specimen, 61°14.4′N, 02°50.2′E, 382 m, 23 March 1985, coll. T. Brattegard; 13 specimens, 60°49.2′N, 05°22.3′E, 81 m, 1 November 1985, coll. T. Brattegard; 2 specimens, 60°49.2′N, 05°22.3′E, 80 m, 1 November 1985, coll. T. Brattegard; 3 specimens, 63°02.7′N, 07°01.7′W, 1022 m, 13 June 1986, coll. T. Brattegard; 3 specimens, 69°01.4′N, 08°24.6′W, 876 m, 25 July 1986, coll. T. Brattegard; 23 specimens, 62°50.6′N, 01°25.9′E, 951 m, 15 August 1986, coll. T. Brattegard; 25 specimens, 62°41.5′N, 01°45.4′E, 750 m, 17 August 1986, coll. T. Brattegard; 2 specimens, 60°49.2′N, 05°22.2′E, 80 m, 17 October 1986, coll. T. Brattegard; 1 specimen, 60°49.3′N, 05°21.6′E, 85 m, 5 December 1986, coll. T. Brattegard. SWEDEN: 10 specimens, Säcken, Bohuslän, 125 m, 4 April 1988, coll. F.P. (mounted for SEM, not kept); 3 specimens (SMNH-23277), SW Y. Vattenholmen, Koster-area, Bohuslän, 160–180 m, 22 July 1988, coll. F.P.; 1 specimen (SMNH-22501), Singlefjord, Bohuslän, 80 m; 1 specimen (ZIHU-2014), Koster area. UNITED KINGDOM: 3 specimens (NMW.Z 1985.023.0021), Scotland, Loch Creran, Argyll, 15–22 m. GREENLAND: 1 specimen (ZUMC-POL-1500), Hurry Fjord, Fame Island, 16 August 1933, 22–24 m.

Description

Holotype complete specimen, 73 mm long, 5.3 mm wide, for 110 segments. Up to 125 mm long, 15 mm wide, for more than 200 segments (Uschakov, 1972); see Figure 3 for measurements of other specimens. Live specimens whitish with clear red colour on dorsum and inner part

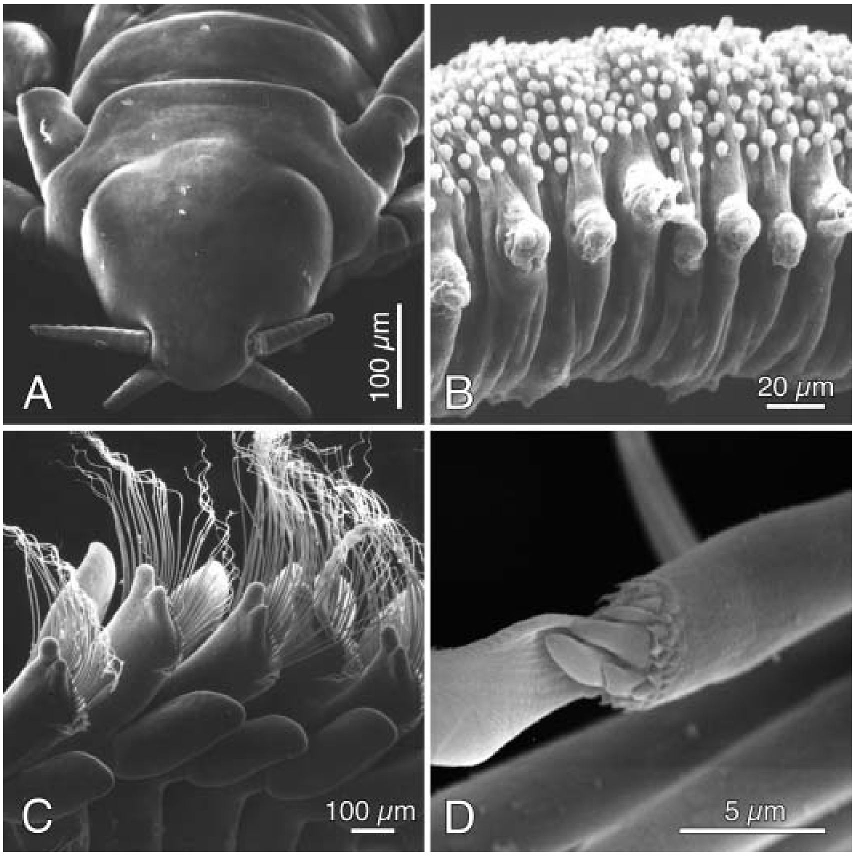

Figure 1. *Paranaitis wahlbergi*, specimens from Koster, Sweden. A, anterior end, dorsal view. B, median part of proboscis, lateral view. C, median parapodia, ventro-lateral view. D, chaetae, anterior view.

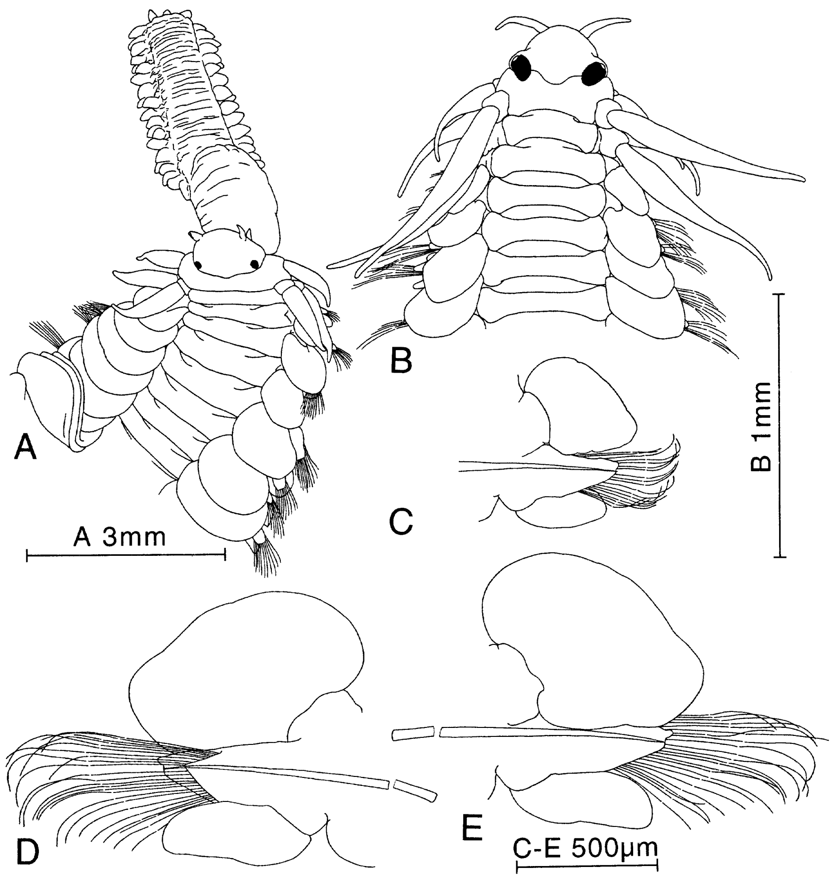

Figure 2. *Paranaitis wahlbergi*, A, specimen from Greenland (ZMUC-POL-1500). B–E, specimen from Norway (SMNH-22502). A, anterior end of large specimen, with partly everted proboscis, dorsal view. B, anterior end of small specimen, dorsal view. C, parapodium of segment 14, anterior view. D, parapodium of segment 33, posterior view. E, same, anterior view.

of dorsal cirri from segments 5–6; eyes red. Preserved specimens whitish, larger specimens iridescent, eyes brownish black. Body dorso-ventrally flattened, almost of uniform width, with tapering posterior end. Prostomium anteriorly rounded, slightly wider than long, posteriorly covered by segment 1, with shallow ligula (Figs 1A, 2A,B). Paired antennae and palps short and narrow, anteriorly to laterally directed. Eyes rounded, with lenses, medium sized in holotype, partly covered by segment 1. Eyes proportionally larger in small specimens. Nuchal papilla indistinct to externally invisible (Fig. 1A; see remarks). Nuchal organs retractile, knob-like, ventro-laterally situated. Proboscis with single lateral row of large fleshy papillae each side; each row with 3–5 merged lines of pointed papillae (Figs 1B, 2A). Terminal ring with large number of indistinct papillae, smaller on dorsal part than on ventral and lateral parts. Paired large papillae present laterally inside ring.

Segments 1 and 2 completely fused dorsally. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered distally. Cirri of segment 1 reaching segment 3–5. Dorsal cirri of segments 2 and 3 reaching *c.* segment 7–9. Ventral cirri of segment 2 reaching segment 4–6. Segment 2 without neuropodial lobes and chaetae. Segment 3 with neuropodial lobes with *c.* 3 chaetae; with small ventral cirri. Dorsal acicula of segments 2 and 3 absent.

Dorsal cirri of median segments oval, asymmetrical, longer than wide (Fig. 2C–E). Dorsal cirrophores short, indistinct. Neuropodial lobes long, with supra-acicular lobes longer than subacicular lobes, with *c.* 75 chaetae in holotype, 20–30 chaetae in Swedish specimens (Fig. 1C); more than 120 chaetae in large Arctic specimens. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with 1–3 short main teeth on anterior side (Figs 1D, 37A). Ventral cirri elongated oval, with rounded ends, about as long as neuropodial lobes (Fig. 2D). Pygidial cirri rounded, small, about as long as wide. Pygidial papilla present.

Habitat

Muddy bottoms, 10–1200 m.

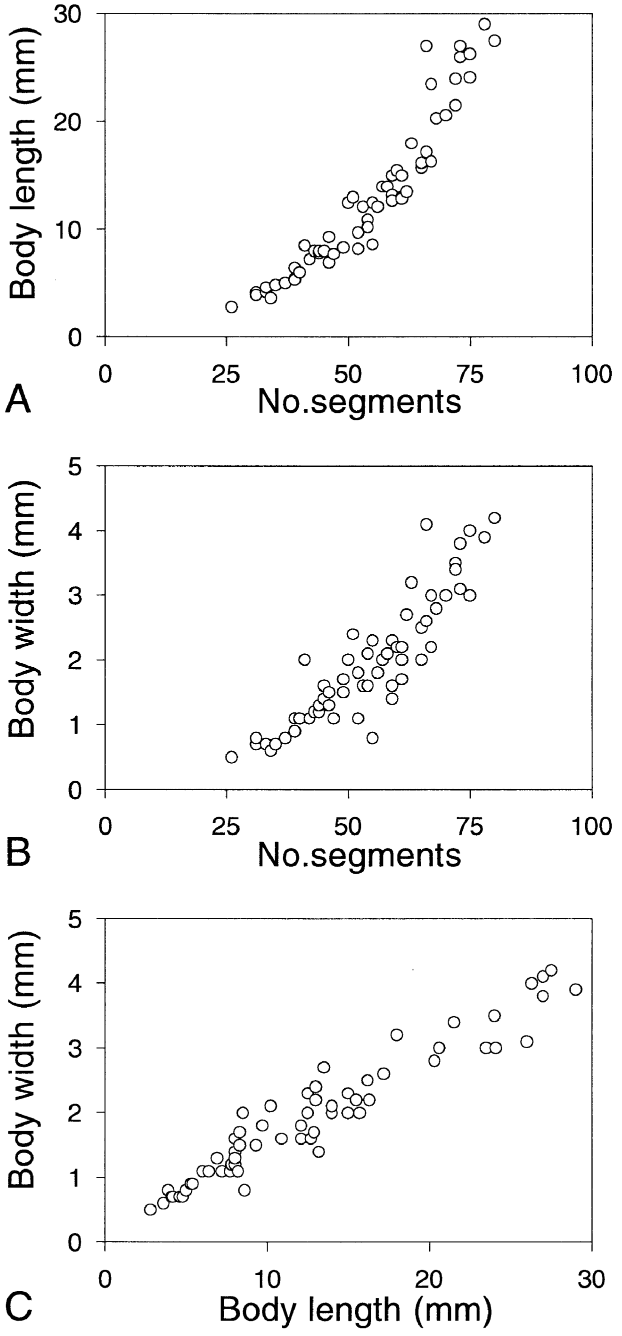

Figure 3. *Paranaitis wahlbergi*, specimens from Norway. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width.

Distribution

Treurenberg Bay, Spitsbergen, Atlantic coast of Norway, Greenland (Wesenberg-Lund, 1953), Goose Fjord, Canada (Ditlevsen, 1909), Kara Sea (Fauvel, 1911), Iceland (Wesenberg-Lund, 1951), Sweden (Pleijel & Dales, 1991), Gibraltar Strait (Pleijel, 1993a), Chukchi Sea.

Remarks

Paranaitis wahlbergi differs from other *Paranaitis* in the character combination proboscis with paired lateral rows of rounded papillae, short and indistinct dorsal cirrophores, and rostrum of chaetal shaft possessing 1–3 short main teeth. It is similar to *P. speciosa* in proboscis and parapodia, but differs in pigmentation and chaetal morphology: *P. speciosa* has a greenish body and a single large main tooth on the rostrum of chaetal shaft.

Paranaitis wahlbergi has been variously reported to have an indistinct nuchal papilla (Uschakov, 1972) or no nuchal papilla (Pleijel & Dales, 1991; Pleijel, 1993a). In their study of the central nervous system of phyllodocids, Orrhage & Eibye-Jacobsen (1998) recorded rudiments of a nuchal papilla, a rhomboid or triangular structure in cross-section situated just behind eyes. It was described as being innervated in the same way as the nuchal papilla of other phyllodocids. From our examination of a large number of specimens, a small indistinct projection was observed in most specimens at the position where a nuchal papilla is situated in other *Paranaitis*, corroborating Orrhage and Eibye-Jacobsen's anatomical observations.

Arctic and more southern specimens exhibit important size differences; whereas the former reach about 10 cm in body length, the latter do not exceed 2 cm. Furthermore, specimens from Sweden tend to have longer digitate cirri on the anterior-most segments, and less numerous chaetae. As both of these characters show a strong relationship to size, we nevertheless treat the Arctic and more southern populations as conspecific.

PARANAITIS ABYSSALIS (HARTMANN-SCHRÖDER, 1975)
(FIG. 4)

Pareteone abyssalis Hartmann-Schröder, 1975: 57–59, figs 19–21.

Paranaitis abyssalis: Pleijel, 1991: 258.

Material examined

Holotype (HZM-P-13605), off Iberian Peninsula, 42°55.4′N, 14°07.9′W, 5260 m.

Description

Holotype lacking posterior end, 15 mm long, 1.3 mm wide, for 52 segments. Body colour of live animals unknown; preserved specimen uniformly pale. Body cylindrical. Prostomium anteriorly rounded, with distinct deep ligula (Fig. 4A). Paired antennae and palps of holotype all lost or damaged. Eyes absent. Nuchal papilla with rounded end, slightly longer than wide, inserted posteriorly in ligula. Paired large, rounded

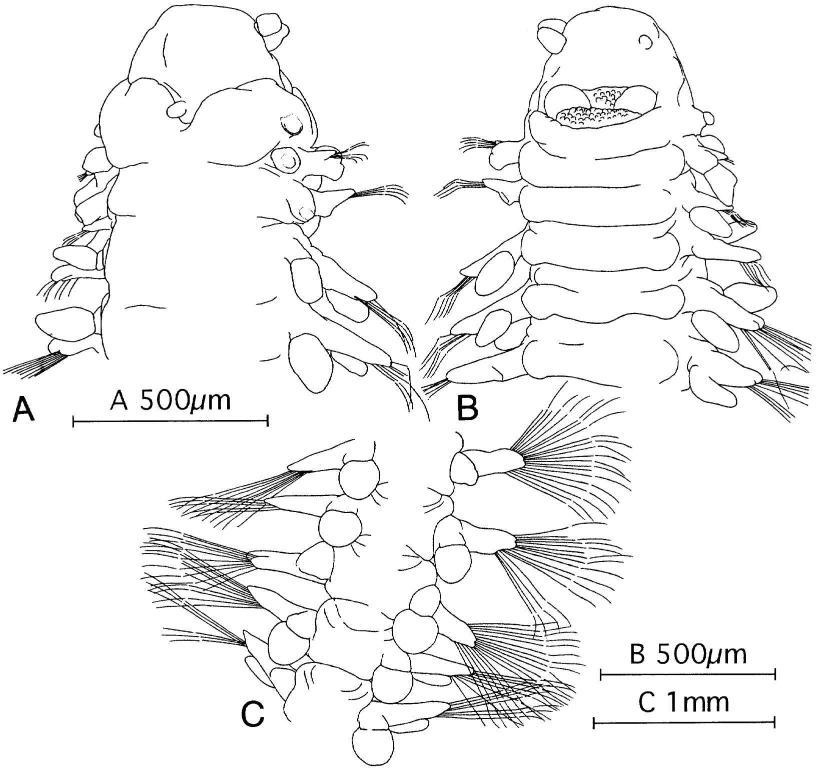

Figure 4. *Paranaitis abyssalis*, holotype. A, anterior end, dorsal view. B, same, with slightly everted proboscis, ventral view. C, median segments, dorsal view.

papillae, situated at lateral margin of mouth (Fig. 4B; see remarks). Proximal-most part of proboscis covered with small rounded papillae; distal part unknown.

Segments 1 and 2 fused. Holotype lacking cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 (ventral one of left side of segment 2 lacking distal part). Segment 2 with *c.* five chaetae arising from small neuropodial lobes fused to ventral cirrophores. Aciculae of segments 2 and 3 unknown.

Dorsal cirri of median segments nearly circular, about as long as wide (Fig. 4C). Dorsal cirrophores distinct, symmetrical. Neuropodial lobes long, with supra-acicular lobes longer than subacicular lobes, with 20–26 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single main tooth almost entirely covered by many small teeth on anterior side, small tooth on posterior side. Ventral cirri oval, *c.* twice as long as wide, with rounded ends. Pygidial cirri and pygidial papilla unknown.

Habitat

5260 m.

Distribution

Known only from the type locality off the Iberian Peninsula.

Remarks

This species is known only from the holotype specimen, which is in poor condition. It differs from other *Paranaitis* in the character combination of nearly circular dorsal cirri, symmetrical dorsal cirrophores, distinct deep ligula of prostomium, and absence of eyes.

We found paired large rounded papillae at the lateral margin of mouth opening (Fig. 4B). It is uncertain whether these represent nuchal organs or proboscis papillae, as the proboscis of the specimen is only slightly everted.

PARANAITIS BENTHICOLA (KNOX, 1960) (FIG. 5)

Eulalia (*Euphylla*) *benthicola* Knox, 1960: 113, figs 137–140.

Paranaitis benthicola: Pleijel, 1991: 258.

Material examined

Holotype (CMC AQ 3461), Chatham Rise, 43°32′S, 178°38′E, 540 m or deeper, 24 January 1954.

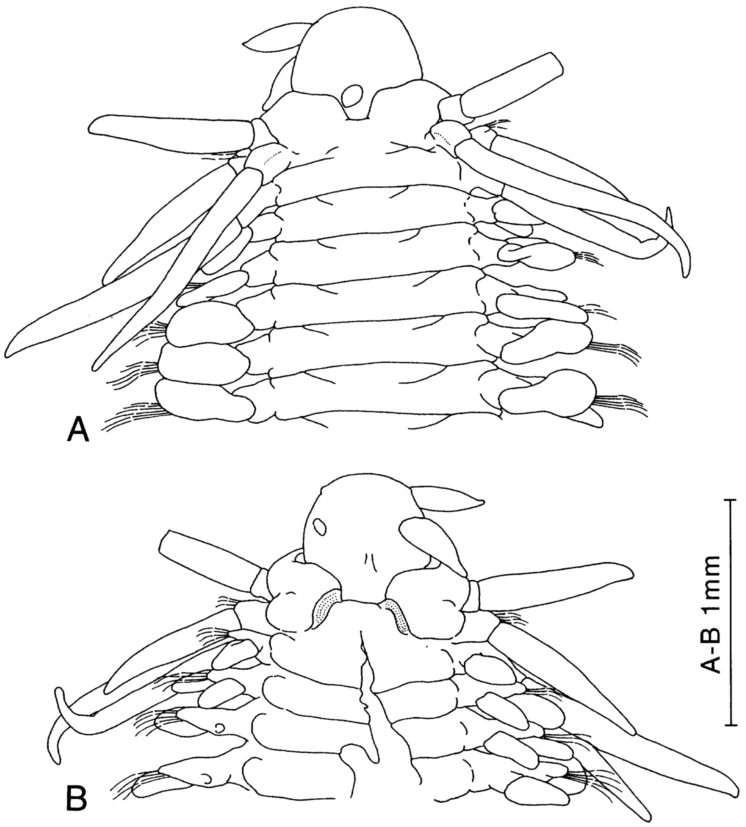

Figure 5. *Paranaitis benthicola*, holotype. A, anterior end, dorsal view. B, same, ventral view.

Description

Holotype lacking posterior end, 33 mm long, 2.3 mm wide, for 107 segments. Body colour of live specimens unknown. Preserved specimen uniformly pale. Body dorso-ventrally flattened. Prostomium anteriorly rounded, slightly wider than long, with distinct deep ligula (Fig. 5A). Paired antennae fusiform, *c.* 2/3 as long as prostomial width. Palps similar in shape to paired antennae, slightly longer. Eyes absent. Nuchal papilla fusiform, *c.* half as long as paired antennae, situated posteriorly in ligula. Nuchal organs retractile, laterally situated (Fig. 5B). Median part of proboscis with six rows of rounded tubercles. Distal most and proximal most part of proboscis, including terminal ring and paired large papillae inside ring, unknown.

Segments 1 and 2 fused dorsally. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 reaching *c.* segment 6. Dorsal cirri of segment 2 reaching *c.* segment 8. Ventral cirri of segment 2 reaching *c.* segment 6. Dorsal cirri of segment 3 reaching *c.* segment 9. Segment 2 with 6–7 chaetae arising from ventral cirrophores (Fig. 5A,B). Segment 3 with small neuropodial lobes with *c.* 10 chaetae. Ventral cirri of segment 3 similar in shape to those on following segments but slightly smaller; anterior cirri gradually increasing in size. Aciculae in segments 2 and 3 unknown.

Dorsal cirri of median segments reniform, wider than long. Dorsal cirrophores distinct, symmetrical. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 23 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft symmetrical, with short single main tooth on anterior and posterior sides. Ventral cirri oval with blunt ends, as long as, or longer than, neuropodia. Pygidial cirri and pygidial papilla unknown.

Habitat

540 m or deeper.

Distribution

Known only from the Chatham Rise, New Zealand.

Remarks

This species is known only from the holotype. It differs from other *Paranaitis* in the character combination long distal part of proboscis (more than 9/10 of total length of proboscis) covered by six rows of large tubercles, and symmetrical rostrum of chaetal shaft with single main tooth on both anterior and posterior side.

PARANAITIS BOWERSI (BENHAM, 1927)

Phyllodoce bowersi Benham, 1927: 77, pl. 1, figs 27–31; Monro, 1936: 111; Hartman, 1959: 160; Wesenberg-Lund, 1962: 40.
Phyllodoce (*Anaitis*) *bowersi*: Monro, 1930: 72–73.
Anaitides bowersi: Hartman, 1964: 49, pl. 15, figs 1, 2.
Anaitis bowersi: Uschakov, 1962: 140–141, pl. 1, figs B–V.
Paranaitis bowersi: Averincev, 1972: 106; Uschakov, 1975: 148, fig. 1.

Material examined

Holotype (BMNH 1928.2.29.13), Ross Sea, 284 m.

Description

Holotype complete specimen, *c.* 60 mm long, 4.7 mm wide, for 117 segments. Preserved specimen uniformly pale; live specimen pale pink (Benham, 1927). Body dorso-ventrally flattened, of uniform width, with tapering posterior end. Prostomium anteriorly rounded, wider than long, with shallow but distinct ligula. Paired antennae and palps short, conical, directed laterally. Eyes absent. Nuchal papilla longer than diameter, situated posteriorly in ligula. Nuchal organs probably fully retracted in holotype, situated in lateral slit between prostomium and segment 1; shape unknown. Distal part of proboscis with six rows of rounded tubercles. Proximal part (less than 1/10 of total length) dorsally smooth, laterally and ventrally with *c.* 30 conical large papillae. Chitinous papillae probably absent. Terminal ring with *c.* 15 rounded well defined papillae. Paired large papillae present laterally inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 and ventral cirri of segment 2 reaching *c.* segment 5. Dorsal cirri of segment 2 reaching *c.* segment 7. Dorsal cirri of segment 3 reaching *c.* segment 8. Segment 2 with small neuropodial lobes with *c.* 7 chaetae, lobes partly fused to ventral cirrophores. Segment 3 with small neuropodia with *c.* ten chaetae, with ventral cirri of similar size and shape as following segments. Aciculae in segments 2 and 3 unknown.

Dorsal cirri of median segments reniform, wider than long. Dorsal cirrophores of median and posterior segments with narrow extension on dorsal side of cirri; extension absent from anterior segments. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 25 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single main tooth on anterior side. Ventral cirri with rounded ends, *c.* 1.5 times as long as wide, slightly shorter than neuropodial lobes. Pygidial cirri cylindrical, with rounded ends, *c.* 1.5 times as long as wide. Pygidial papilla very short, knob-like.

Habitat

219–1837 m.

Distribution

Known from Ross Sea and eastern sector of Antarctica (Monro, 1930), and Gulf de Ancud, Chile (Wesenberg-Lund, 1962).

Remarks

Paranaitis bowersi differs from other *Paranaitis* in the character combination dorsally elongated dorsal cirrophores of median and posterior segments, and proboscis with long distal part covered by six rows of tubercles, and with short proximal part with large lateral and ventral papillae.

PARANAITIS CAECA (MOORE, 1903)
(FIGS 6–9, 37)

Eumida caeca Moore, 1903: 426–428, pl. 23, fig. 1 (misspelled as *Eumidia caeca*); Izuka, 1912: 203, pl. 21, fig. 5; Hartman, 1959: 152.
Paranaitis caeca: Eibye-Jacobsen, 1991: 129.

Material examined

Holotype (USNM-15716), Sagami Bay, Japan, 74–78 m; 2 specimens (ZIHU-2015), SW off Miura Peninsula, Sagami Bay, 35°08.13′N, 139°36.21′E, shell sand, 39 m, 12 May 1998, coll. F.P.; 1 specimen (ZIHU-1919), Otsuchi Bay, Iwate Honshu, Japan, 39°20.7′N, 141°57.7′E, sandy mud, 49 m, 7 May 1997, coll. T.K.

Description

Holotype complete ovigerous female, 73 mm long, 3.4 mm wide, for 188 segments; see Figure 9 for measurements of other specimens. Live animal white. Dorsum of segments 8–11 with brown pigmentation, forming transverse band. Dorsum of following segments with brown spot medially on each segment (Fig. 6A), and inner part of dorsal cirri with single large rounded brown spots; medial and lateral spots together forming three longitudinal lines. Colour well retained after preservation. Body long, dorso-ventrally flat-

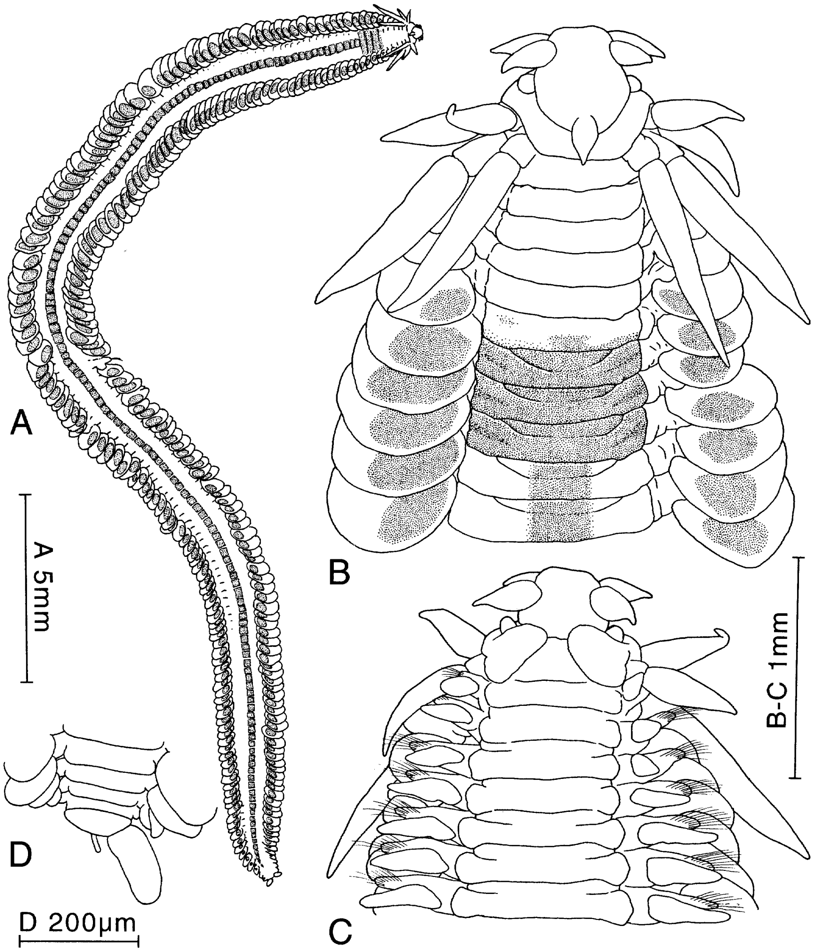

Figure 6. *Paranaitis caeca*. A–C, specimen from Otsuchi Bay, Japan (ZIHU-1919). D, specimen from Sagami Bay, Japan (ZIHU-2015). A, entire animal, dorsal view. B, anterior end, dorsal view. C, same, ventral view. D, posterior end, dorsal view.

tened, anteriorly and posteriorly tapered. Prostomium rounded pentagonal, with shallow but distinct ligula. Paired antennae and palps stout, conical, laterally directed (Fig. 6B, C). Eyes absent. Nuchal papilla large, similar in shape to paired antenna, situated in shallow ligula. Nuchal organs rounded, large, situated laterally between prostomium and segment 1, visible dorsally and ventrally when everted (Fig. 6B, C). Proboscis not divided into proximal and distal parts, with lateral row of rounded papillae each side; dorsal surface entirely covered by pointed papillae, ventral surface by rounded small papillae (Fig. 7). Terminal ring with *c.* 12 papillae. Paired large papillae present laterally inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 stout, cylindrical, distally tapered (Fig. 8A–C). Cirri of segment 1 reaching *c.* segment 5. Dorsal cirri of segment 2 with acicula, reaching *c.* segment 9 (Fig. 8B). Ventral cirri of segment 2 reaching *c.* segment 6. Dorsal cirri of segment 3 with acicula, reaching *c.* segment 10 (Fig. 8C). Segment 2 with dorsal and ventral aciculae, and *c.* 4 chaetae arising from cirrophores of ventral cirri (Fig. 8B). Segment 3 with dorsal aciculae, small neuropodial lobes with ventral aciculae and *c.* ten chaetae, and ventral cirri.

Dorsal cirri of median segments kidney-shaped, wider than long (Fig. 8F–I). Dorsal cirrophores distally enlarged. Neuropodium with supra-acicular lobes longer than subacicular lobes, with 25–30 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft symmetrical, with single short main tooth both sides (Fig. 37B). Ventral cirri oval with rounded to weakly pointed ends, longer than neuropodia (Fig. 8G,I). Pygidial cirri cylindrical, with rounded ends, 2–3 times as long as wide (Fig. 6D). Pygidial papilla present.

Habitat

Sandy mud, 49 m.

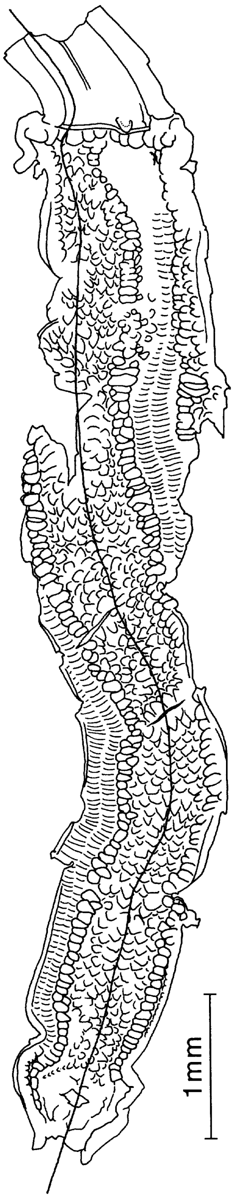

Figure 7. *Paranaitis caeca*, specimen from Japan (ZIHU-1919). Dissected proboscis, ventral view. Dorsal median line is indicated by a curved line.

Distribution

Known from Sagami Bay, Uraga Channel (Izuka, 1912) and Otsuchi Bay, Japan.

Remarks

Paranaitis caeca differs from other *Paranaitis* in the character combination of dorsally papillated proboscis, absence of eyes, elongated and pointed nuchal papilla, symmetrical rostrum of chaetal shaft, and unique pigmentation pattern.

Paranaitis uschakovi and *P. caeca,* two poorly known species from Japan, are similarly in lacking eyes and in having white body with brown pigmentation. Eibye-Jacobsen (1991), based on an examination of the holotype of *P. caeca* and, presumably, the original description of *P. uschakovi*, considered the two species as distinct based on the following differences: (1) shape of prostomium, (2) length of dorsal cirri of segments 2 and 3 (those of segment 3 distinctly longer in *P. uschakovi*, of equal length in *P. caeca*), (3) asymmetrical dorsal cirri in *P. uschakovi* (supposedly considered symmetrical in *P. caeca*), and (4) length of ventral cirri (shorter than neuropodium in *P. uschakovi*, longer in *P. caeca*). We examined the newly collected specimens of both species from Otsuchi Bay, as well as the holotypes of *P. caeca* and *P. uschakovi*, and concluded that most characters above are not suited to differentiate the two taxa. Instead, they may be separated by the following features: (1) shape of nuchal papilla (long and pointed in *P. caeca*; short and rounded in *P. uschakovi*), (2) position of nuchal organs (laterally in *P. caeca*; ventro-laterally in *P. uschakovi*), (3) shape of paired antennae, palps and anterior cirri (narrower paired antennae and palps, and thinner cirri of segments 1–3 in *P. uschakovi*), (4) presence of proboscis papillae in *P. caeca*, (5) presence of ciliated furrows on the dorsal cirrophores of *P. uschakovi*, (6) presence of a dorsal longitudinal line in *P. caeca*, (7) morphology of the rostrum of chaetal shaft (symmetrical without main tooth in *P. caeca*; asymmetrical with single main tooth in *P. uschakovi*), and (8) different growth patterns (Fig. 9).

PARANAITIS GARDINERI PERKINS, 1984
(FIGS 10–12)

Paranaitis gardineri Perkins, 1984: 563–565, fig. 4.

Paranaitis polynoides: Gardiner, 1976: 110, fig. 6m–p; Gathof, 1984: 19-21 to 19-23, figs 19-17 to 19-18. Not *Anaitis polynoides* Moore, 1909.

Material examined

Holotype (USNM-52876), off Cape Lookout, North Carolina, USA; 2 paratypes (USNM-52877), Wrightsville Beach, North Carolina; 1 paratype (HZM-P-17600), Hutchinson Island, Florida, USA; 1 paratype (FSBC I 30424), Hutchinson Island, 27°20.24′N, 80°13.04′W, 10.9 m; 1 paratype (FSBC I 30425), Hutchinson Island, 27°21.23′N, 80°13.24′W, 10 m; 1 paratype (FSBC I 30426), Hutchinson Island, 27°22.08′N, 80°13.46′W, 10.6 m; 1 specimen (mounted for SEM, not kept), Hutchinson Island, 27°21.6′N, 80°13.2′W, 11 m, 4 April 1997, coll. F.P.; 6 specimens (USNM-45527), Tampa Bay, Florida; 1

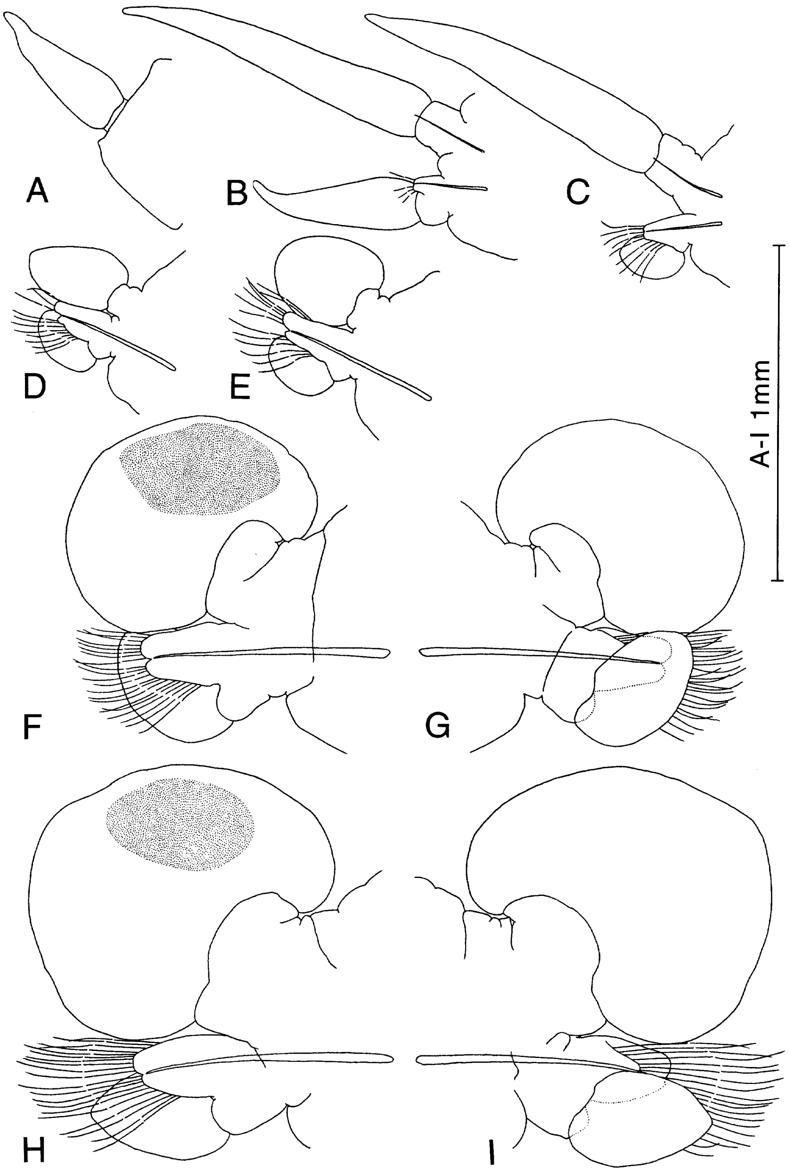

Figure 8. *Paranaitis caeca*, specimen from Japan (ZIHU-1919). A, cirri of segment 1, anterior view. B, parapodium of segment 2, anterior view. C, parapodium of segment 3, anterior view. D, parapodium of segment 4, anterior view. E, parapodium of segment 5, anterior view. F, parapodium of segment 64, anterior view. G, same, posterior view. H, parapodium of segment 106, anterior view. I, same, posterior view.

specimen (USNM-56127), Gulf of Mexico, 29°36′N, 87°48′W, 37 m; 1 specimen (USNM-51022), Beaufort, North Carolina, 34°04′N, 75°25′W, 20 m; 1 specimen (USNM-59331), off Georgia, Gulf of Mexico, USA, 31°01′N, 80°17′W, 40 m; 1 specimen (USNM-59332), off Georgia, 31°01′N, 80°17′W, 40 m; 1 specimen (USNM-59333), off Georgia, 30°57′N, 79°58′W, 183 m; 1 specimen (USNM-59334), off Georgia, 31°03′N, 80°26′W, 34 m; 1 specimen (USNM-75587), off Florida, Gulf of Mexico, 29°34′N, 80°22′W, 44 m; 1 specimen (USNM-59335), Mississippi Sound, Alabama, Gulf of Mexico, 30°03.12′N, 88°14.24′W, 21 m; 1 specimen (USNM-75589), Mississippi Sound, 29°59.20′N, 88°18.49′W, 28.5 m; 1 specimen (USNM-108159), off South Carolina, 31°44.06′N, 80°13.06′W, 33 m.

Description

Holotype complete with regenerated posterior end, proboscis everted, 37.5 mm long (excluding proboscis), 2.7 mm wide, for 101 segments. Up to 89 mm

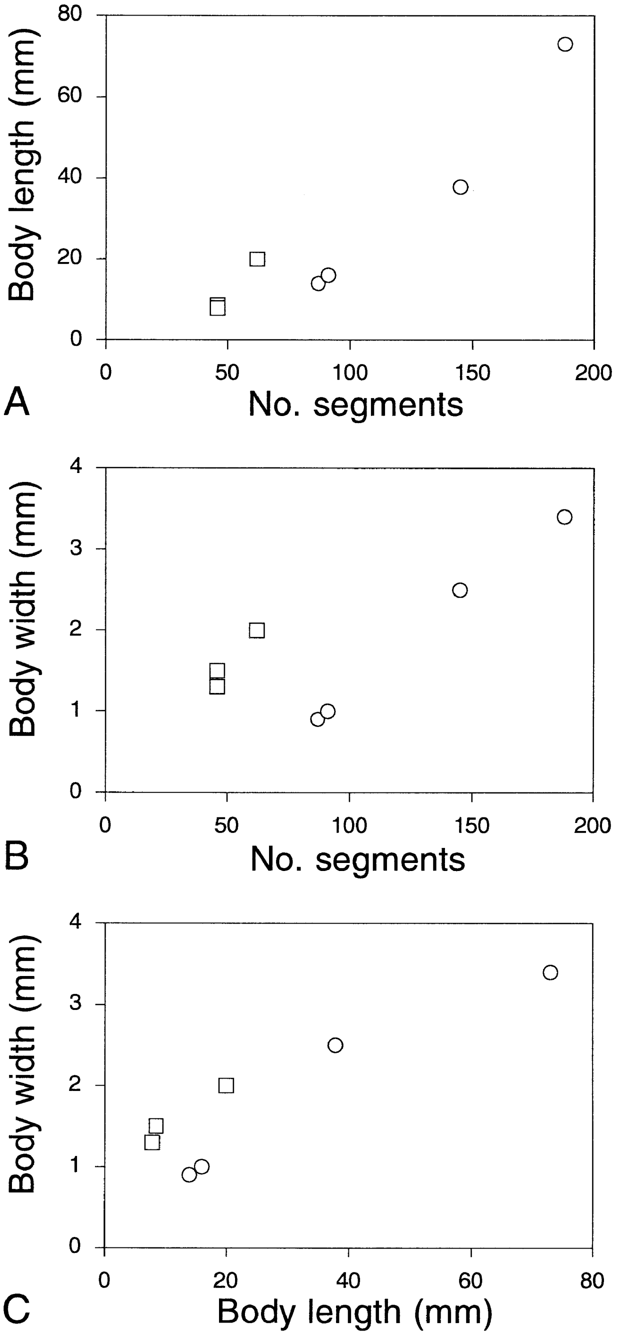

Figure 9. *Paranaitis caeca and P. uschakovi*, specimens from Japan. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width. Circles represent *P. caeca*, and squares *P. uschakovi*.

long, 3.1 mm wide, for 184 segments (paratype, USNM-52877); see Figure 12 for measurements of other specimens. Live animals from North Carolina reported as having diffuse purple spots on dorsum, ventrum, and digitate and flattened dorsal cirri; most animals from Florida lacking colour pattern (Perkins, 1984). Preserved specimens pale yellow with brown spots on dorsum and dorsal cirri. Eyes blackish. Body long and slender, anteriorly and posteriorly tapered. Prostomium anteriorly rounded, with distinct deep ligula (Fig. 10A). Paired antennae and palps conical, antero-laterally to laterally directed. Eyes large, rounded, with lenses, situated at posterior margin of prostomium. Short rounded nuchal papilla inserted posteriorly in ligula, often partly covered by segment 1. Nuchal organs retractile, rounded with horseshoe-shaped bands of cilia, ventro-laterally situated (Fig. 10B). Proximal part of proboscis lacking tubercles, with gradual transition to distal part with tubercles (Fig. 11A). Rounded chitinous papillae covering dorsal, lateral and ventral surfaces of both proximal and distal part (Figs 11A,B). Papillae of terminal ring poorly defined. Paired large papillae present laterally inside ring. Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 reaching *c.* segment 7. Dorsal cirri of segment 2 reaching *c.* segment 9. Ventral cirri of segment 2 reaching *c.* segment 7. Dorsal cirri of segment 3 reaching *c.* segment 11. Segment 2 without neuropodial lobes and chaetae. Segment 3 with small neuropodial lobes with *c.* 7 chaetae and small ventral cirri. Aciculae in segments 2 and 3 unknown. Dorsal cirri of median segments oval, slightly longer than wide in small specimens (Fig. 10C); reniform, wider than long in large specimens. Dorsal cirrophores distinct, wide. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 35 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side (Fig. 10E). Ventral cirri with rounded ends, as long as or slightly shorter than neuropodial lobes (Fig. 10D). Pygidial cirri *c.* 7 times as long as wide, tapering to pointed ends (Fig. 11C). Pygidial papilla present (Fig. 10F).

Habitat

Sand mixed with gravel and shell fragments, muddy sand and coarse calcareous sand, intertidally to 11 m.

Distribution

Known only from south-east US Atlantic coast.

Remarks

Paranaitis gardineri differs from other *Paranaitis* in the character combination proboscis with gradual

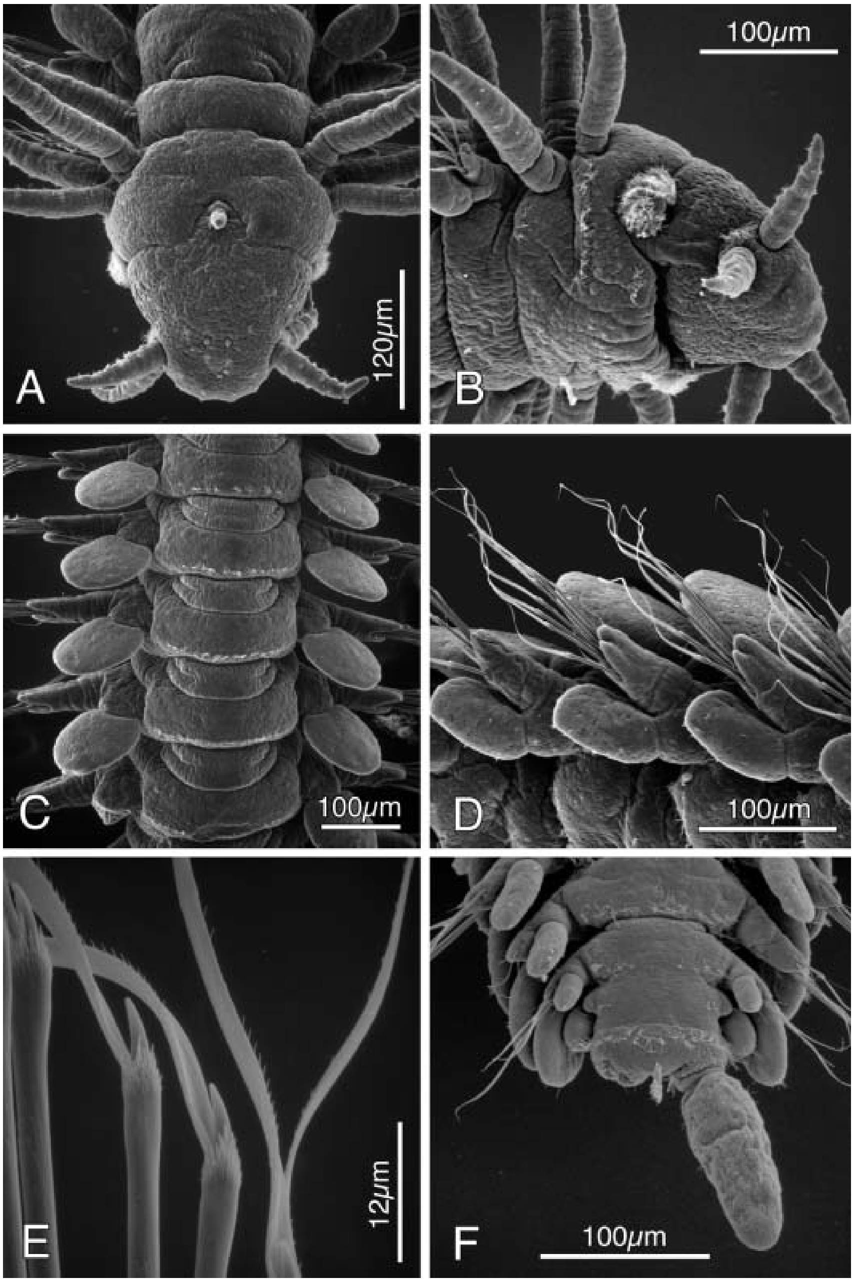

Figure 10. *Paranaitis gardineri*, SEM micrograph of specimen from Florida, USA. A, anterior end, dorsal view. B, same, ventro-lateral view. C, median segments, dorsal view. D, same, ventro-lateral view. E, chaetae, dorsal view. F, pygidium, ventral view (tip of pygidial cirri probably damaged).

transition between proximal and distal parts, long pygidial cirri with pointed ends, and specific body pigmentation. *Paranaitis misakiensis* is similar in proboscis features, but differs in having oval dorsal cirri with narrow dorsal cirrophores, pygidial cirri with rounded ends, and different body pigmentation. Based on re-examination of Gathof's (1984) specimens (USNM-56127), her records of *P. polynoides* from the US Atlantic coast are referred to *P. gardineri*.

PARANAITIS INFLATA (HUTCHINGS & MURRAY, 1984) (FIGS 13–15)

Compsanaitis inflata Hutchings & Murray, 1984: 24–26, fig. 9.1-9. *Paranaitis inflata*: Pleijel, 1991: 258.

Material examined

Holotype (AM W196585), Hawkesbury River, New South Wales, Australia, 2 August 1977; 1 paratype

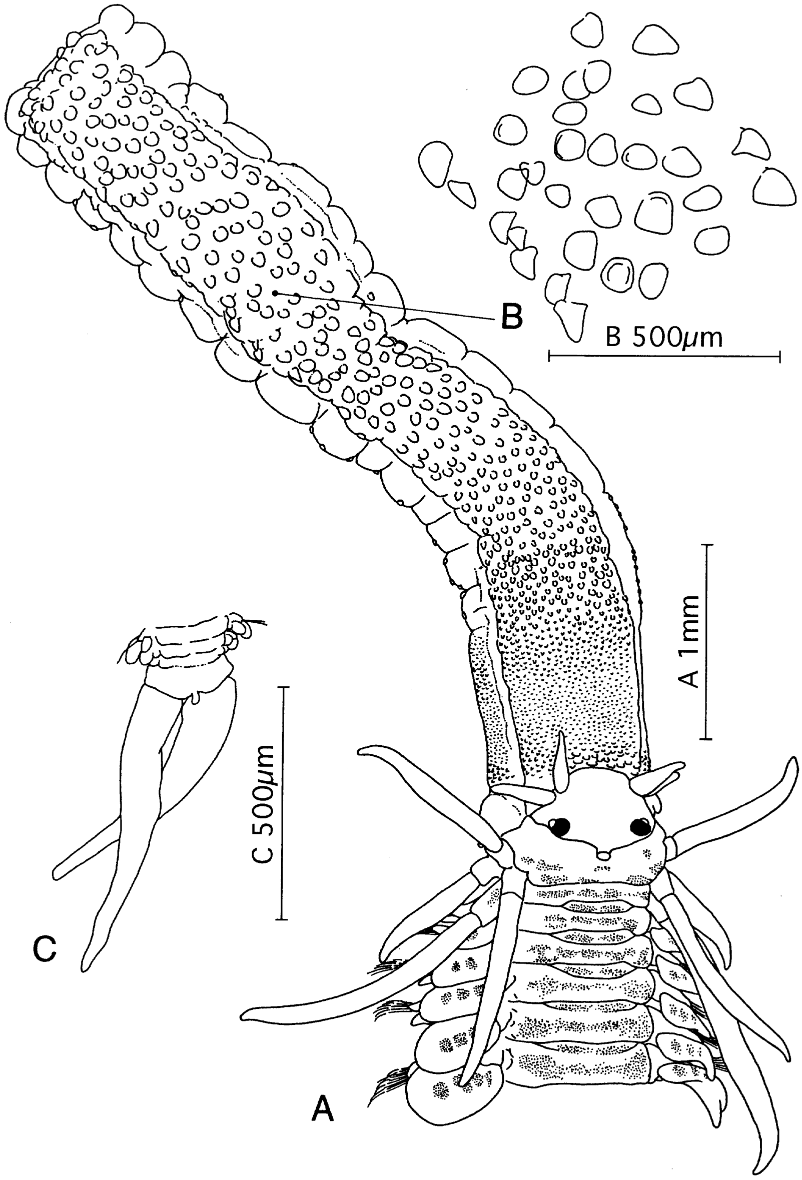

Figure 11. *Paranaitis gardineri*, holotype. A, anterior end, with partly everted proboscis, dorsal view. B, chitinous papillae from dorsal distal part of proboscis. C, posterior end, ventral view.

(USNM-81484), Hawkesbury River; 1 specimen (AM W196572), Hawkesbury River, 2 August 1979; 1 specimen (AM W196569), Hawkesbury River, 3 August 1977.

Description

Holotype complete specimen with partly everted proboscis, 15 mm long, and 0.7 mm wide, for 117 segments. Up to 25 mm long, 1.0 mm wide, for 151 segments (paratype, USNM-81484). Live animals not observed. Body dorso-ventrally flattened, anteriorly and posteriorly tapered. Prostomium anteriorly rounded, with distinct deep ligula (Fig. 13A). Paired antennae and palps conical, *c.* one-third as long as prostomial width. Eyes large, rounded, with lenses, situated at posterior margin of prostomium, often partly covered by segment 1. Rounded nuchal papilla posteriorly in ligula. Nuchal organs retractile, rounded, ventro-laterally situated. Proboscis with distinct division separating proximal and distal part (Fig. 14A). Proximal part covered by numerous rounded chitinous papillae, 10–30 µm in diameter (Fig. 14B–E), and with three pairs of large, pointed papillae. Distal part with five rows of tubercles. Terminal ring with *c.* ten poorly delineated papillae. Paired large papillae laterally inside ring. Segments 1

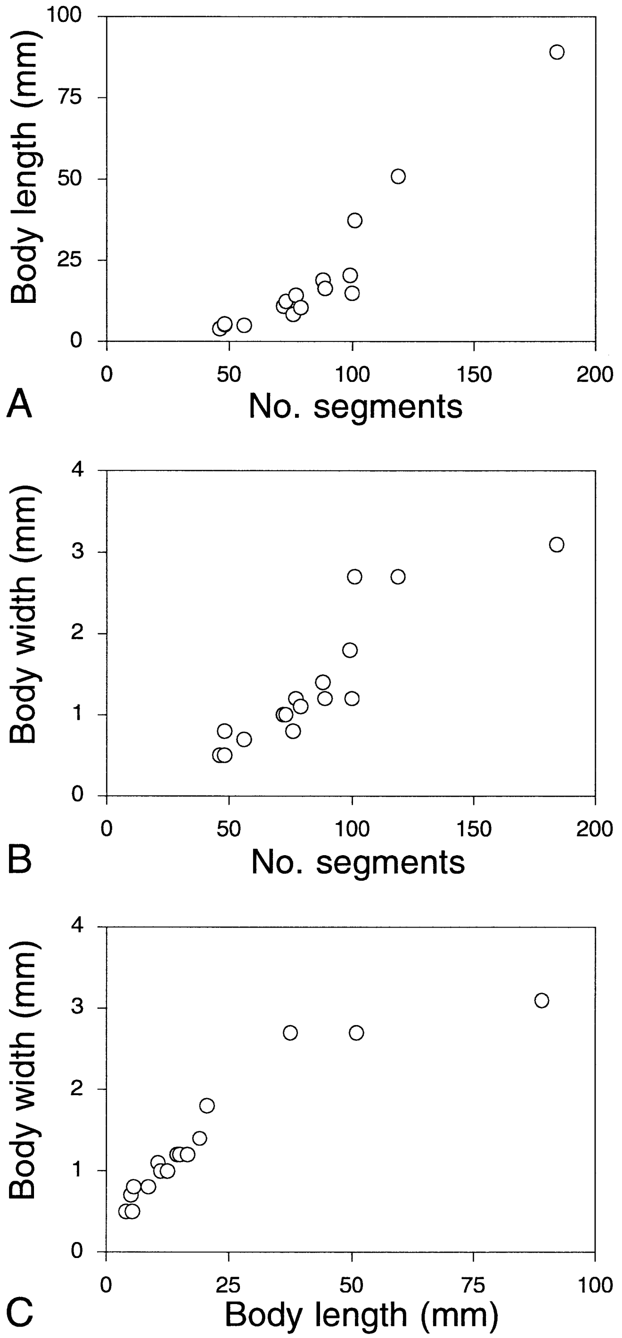

Figure 12. *Paranaitis gardineri*, specimens from USA. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width.

and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 reaching *c.* segment 6. Dorsal cirri of segment 2 reaching *c.* segment 10. Ventral cirri of segment 2 reaching *c.* segment 5. Dorsal cirri of segment 3 reaching *c.* segment 10. Segment 2 without neuropodial lobes and chaetae. Segment 3 with neuropodial lobes with *c.* five chaetae, and small ventral cirri. Aciculae in segments 2 and 3 unknown. Dorsal cirri of median segments oval, slightly longer than wide (Fig. 13C–F). Dorsal cirrophores distinct, short. Neuropodium with supra-acicular lobes longer than subacicular lobes, with 9–13 chaetae. Morphology of rostrum of chaetal shaft gradually changing from dorsal to ventral within single fascicle (Fig. 15). Dorsal chaetae from part symmetrical, lacking main tooth; ventral chaetae asymmetrical, with single large main tooth on anterior side, smaller main tooth on posterior side. Ventral cirri with rounded ends, *c.* twice as long as wide, shorter than neuropodial lobes (Fig. 13D,F). Pygidial cirri cylindrical, with rounded ends, *c.* twice as long as wide (Fig. 13B). Pygidial papilla present.

Habitat

Muddy sand and sandy mud, 4–12 m.

Distribution

Known only from Hawkesbury River, Australia.

Remarks

Hutchings & Murray (1984) described the proboscis of *Paranaitis inflata* as lacking any macropapillae, but being entirely covered by minute micropapillae, based on a paratype specimen with everted proboscis (AM W196598). Their interpretation is probably based on specimens which only had part of the proboscis everted. Re-examination and dissection of the proboscis of one of their specimens (AM W196572) showed that the distal part of proboscis was covered by rows of large tubercles, and that *c.* three large pointed papillae are present on each side on the proximal-most part. Hutchings & Murray (1984) also recorded that the dorsal and ventral chaetae differed within a single fascicle, and that the rostrum of the ventral chaetae is less ornamented than that of the dorsal chaetae. Our examination confirmed the differences between the dorsal and the ventral chaetae; the dorsal chaetae are symmetrical and lack the main tooth, whereas the ventral chaetae are asymmetrical and provided with a single main tooth. The different degrees of ornamentation recognized by Hutchings & Murray may correspond to the absence/presence of a main tooth when examined at lower magnification. We could not confirm their reported difference of longer dorsal than ventral blades on segment 10. *Paranaitis inflata* is similar to *P. kosteriensis*, differing mainly in chaetal morphology, body size and pigmentation.

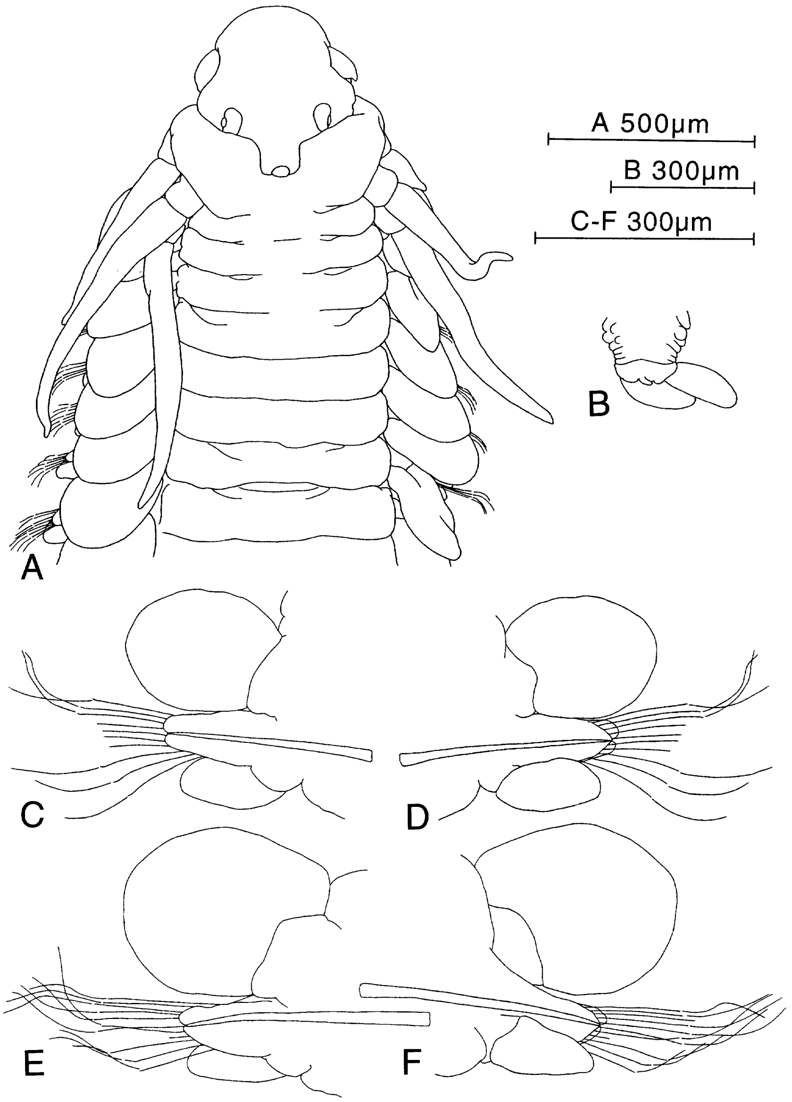

Figure 13. *Paranaitis inflata*. A, paratype (USNM-81484). B, holotype. C–F, specimen from Hawkesbury River, Australia (AM W196572). A, anterior end, dorsal view. B, posterior end, ventral view. C, parapodium of segment 11, anterior view. D, same, posterior view. E, parapodium of segment 87, anterior view. F, same, posterior view.

PARANAITIS KOSTERIENSIS (MALMGREN, 1867)
(FIGS 16, 17, 37)

Anaitis kosteriensis Malmgren, 1867: 142; Bergström, 1914: 156, textfig. 52, pl. 1, fig. 2.

Paranaitis kosteriensis: Fauvel, 1923: 157–158, fig. 56; Hartman, 1959: 158; Eliason, 1962: 234–235; Pleijel & Dales, 1991: 94, fig. 26A–C; Pleijel 1993a: 24–25, figs 13, 14, map 7; Parapar *et al.*, 1993: 415–417, fig. 3c.

Mystides lizziae McIntosh, 1908: 110–111, pl. 58, fig. 11, pl. 69, figs 11 and 12, pl. 77, fig. 20.

Not *Paranaitis kosteriensis*: Pettibone, 1963: 77, fig. 17d (= *Paranaitis* sp.).

Material examined

SWEDEN: holotype (SMNH-Type-2402), Koster, Bohuslän, 237 m; 3 specimens (SMNH-22547), Gullmaren, Bohuslän; *c.* 25 specimens (F.P. collection), various localities in northern Bohuslän. NORWAY: 1 specimen (SMNH-4786), Trondheim, Rødberg; 1 specimen (Akvaplan-niva), North Sea, Glitne Field (UTM ED50, Zone 31; N: E) 6510980.0: 423197.0, sand, *c.* 110 m; 1 specimen (Akvaplan-niva), North Sea, Glitne Field (UTM ED50, Zone 31; N: E) 6508923.0: 423342.0, sand, *c.* 110 m; 2 specimens, western Norway, Bergen area (ZMB 34013, 34195). UNITED KINGDOM: 1 specimen, holotype of *Mystides lizziae*

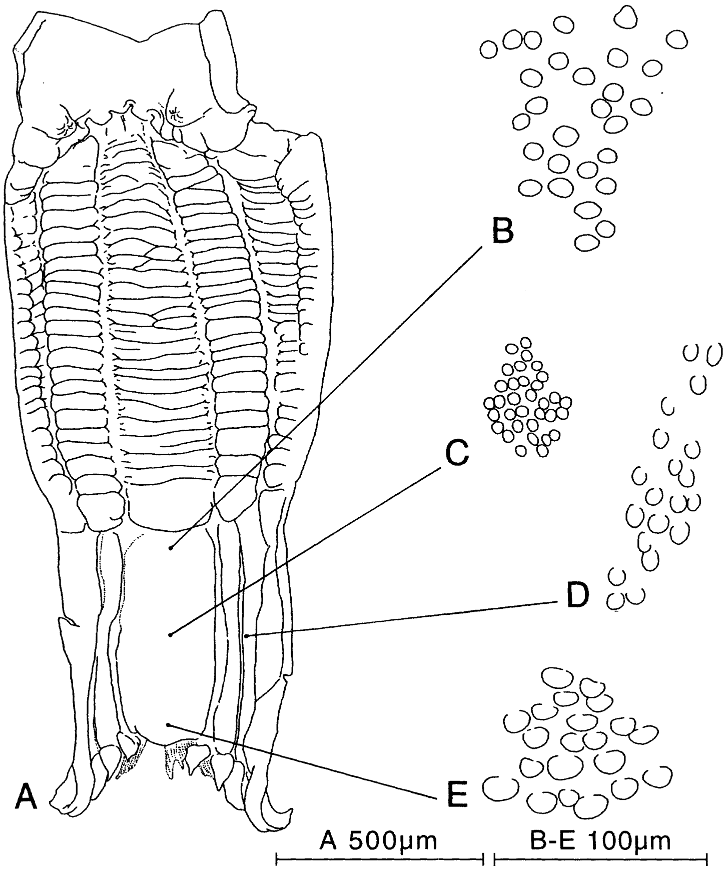

Figure 14. *Paranaitis inflata*, specimen from Hawkesbury River, Australia (AM W196572). A, dissected proboscis, ventral view (median area corresponds to dorsal part). B–E, chitinous papillae.

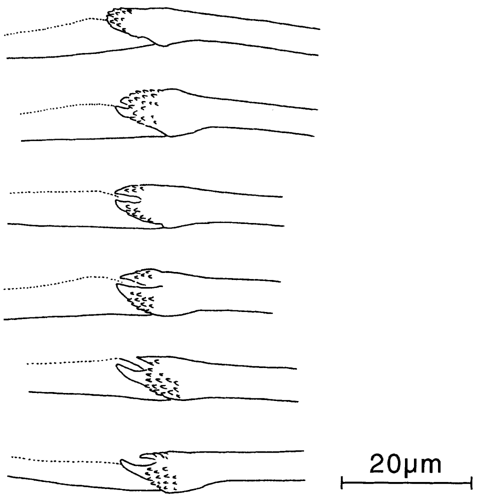

Figure 15. *Paranaitis inflata*, specimens from Australia (AM W196572). Chaetae from a single fascicle of right parapodium of segment 87. Top to bottom correspond to dorsal to ventral.

(BMNH 1921 : 5 : 1 : 1062), St Andrews, Scotland; Plymouth, The Sound, Duke Rock, 12 m, 9 June 1986, coll. F.P.. SPAIN: 5 specimens (Julio Parapar collection), La Coruña and Ares Bay, Galicia. ITALY: 3 specimens (SMNH-22595, 22597), Brucoli, Sicily, Italy, 37°17′N, 15°11′E, 40 m.

Description

Holotype ovigerous female, lacking posterior end, 19.5 mm long, 2.1 mm wide, for 69 segments. Up to 80 mm long, for 155 segments (Nelson-Smith *et al.* 1990); for further length-segment measurements, see fig. 14 of Pleijel (1993a). Live specimens white, with reddish brown transverse bands across dorsum. Proximal part of dorsal cirri with similar pigmentation. Eyes red. Preserved specimens similar to live ones, but eyes black. Body slender, dorso-ventrally flattened, anteriorly and posteriorly tapered. Prostomium rounded trapezoidal, with distinct deep ligula (Fig. 16A). Paired antennae and palps conical, laterally to postero-laterally directed. Eyes large, rounded, with lenses, situated at posterior margin of

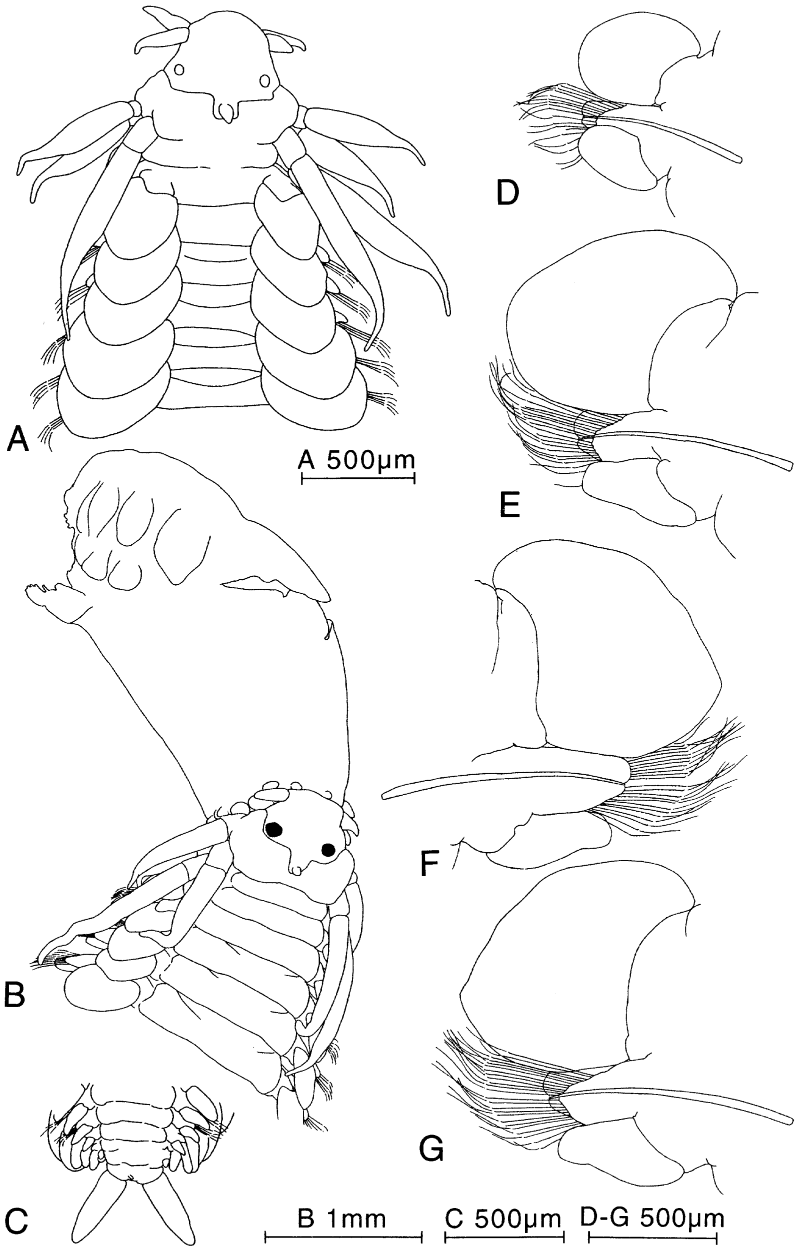

Figure 16. *Paranaitis kosteriensis*. A, holotype; B, D–G specimens from Sweden (SMNH-22547). C, specimen from Norway. A, anterior end, dorsal view. B, same with partly everted and damaged proboscis, dorsal view; C, posterior end, ventral view. D, parapodium of segment 9, posterior view. E, parapodium of segment 41, posterior view. F, parapodium of segment 60, anterior view. G, same, posterior view.

prostomium, often partly covered by segment 1. Nuchal papilla slightly longer than wide, with rounded tip, inserted posteriorly in ligula. Nuchal organs not observed. Proboscis with distinct division separating proximal and distal parts (Fig. 17A). Proximal part covered with minute chitinous papillae (Fig. 17B-E), and with 4–5 large papillae in transverse row basally each side (Fig. 16B). Distal part with rounded tubercles in five rows. Terminal ring with *c.* ten papillae; lateral papillae larger than dorsal and ventral ones. Paired large papillae present laterally inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 reaching *c.* segment 6. Dorsal cirri of segment 2 reaching segment 8–9. Ventral cirri of segment 2 short, reaching *c.* segment 5. Dorsal cirri of segment 3

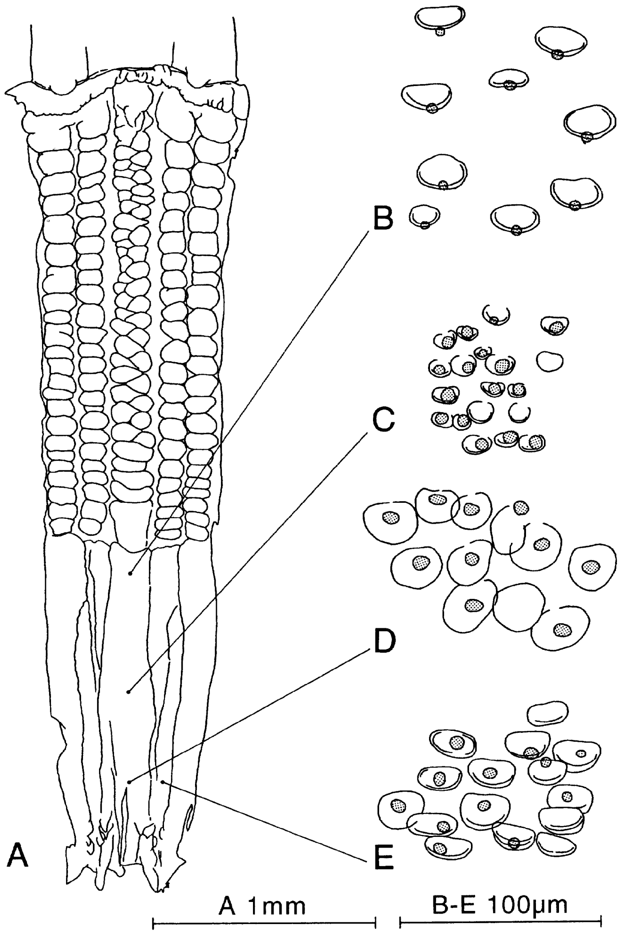

Figure 17. *Paranaitis kosteriensis*. A, specimen from Sicily, Italy (SMNH-22595). B–E, specimen from Sweden (SMNH-22547). A, dissected proboscis, ventral view (median area corresponds to dorsal part). B–E, chitinous papillae.

reaching *c.* segment 10. Segment 2 lacking neuropodia and chaetae. Segment 3 with neuropodia with *c.* six chaetae, and small ventral cirri. Dorsal aciculae of segment 2 and 3 absent.

Dorsal cirri of median segments oval, asymmetrical and slightly longer than wide (Fig. 16D–G). Dorsal cirrophores distinct, symmetrical. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 20 chaetae. Morphology of rostrum of chaetal shaft gradually changing from dorsal to ventral within single fascicle. Chaetae from dorsal part asymmetrical, main tooth on anterior and posterior sides almost equal in size (Fig. 37C). Chaetae from ventral part asymmetrical, with tooth on anterior side distinctly larger than on posterior side (Fig. 37D). Ventral cirri elongated, with rounded end. Pygidial cirri cylindrical, 2–5 times as long as wide (Fig. 16C). Pygidial papillae present.

Habitat

Muddy sand or mixed sediment with mud, sand, shell and stones, 10–230 m.

Distribution

Sweden, Western Norway, Denmark, British Isles, Spain and Portugal; Gibraltar Strait; Sicily (Pleijel, 1993a).

Remarks

Paranaitis kosteriensis is identified by the character combination presence of eyes, deep ligula, distinctly subdivided proboscis, dorsal cirrophores as wide as long, and absence of chaetae on segment 2. These features are also present in *P. inflata*, which, however, differs in having symmetrical chaetae in the dorsalmost part of the fascicles, and a smaller maximum body size. *Paranaitis kosteriensis* is also similar to *P. misakiensis* which differs in having indistinctly subdivided proboscis and chaetae with a long main tooth.

The specimen (USNM-27029) from 2320 m off the US east coast which was recorded by Pettibone (1963) does not belong to *P. kosteriensis*, as seen from the circular dorsal cirri, and the chaetae on segment 2. In the absence of information on a series of characters, we prefer to leave this single specimen undescribed.

***PARANAITIS MISAKIENSIS* SP. NOV.**

(FIGS 18–21, 37)

Material examined

Holotype (ZIHU-1380), 2 paratypes (ZIHU-1381), Moroiso Bay, Misaki, Kanagawa, Honshu, Japan, sand, 5 m, 35°09.1′N, 139°36.5′E, 21 May 1996, coll. T.K.; 1 paratype (ZIHU-1382), Aburatsubo, Misaki, intertidal, mud, 20 May 1996, coll. T.K.; 1 paratype (ZIHU-1977), Koajiro Bay, Misaki, mud, 8 m, 21 May 1996, coll. T.K.; 1 paratype (MNHN POLY TYPE 1381), Moroiso Bay, sand, 9 m, 35°09.1′N, 139°36.4′E, 21 May 1996, coll. T.K.; 1 paratype (MNHN POLY TYPE 1382), Koajiro Bay, sand, 15–20 m, 22 June 1994, coll. T.K.; 2 paratypes (ZIHU-1383), off U-ze, Amakusa, Kumamoto, Kyushu, Japan, shell sand, 30 m, 11 November 1994, coll. T.K.; 1 paratype (MNHN POLY TYPE 1380), Odawa Bay, Kanagawa, 5 m, 22 April 1978, coll. H. Mukai; 1 paratype (ZIHU-1384), Odawa Bay, 5 m, 17 June 1978, coll. H. Mukai; 1 paratype (ZIHU-1385), Odawa Bay, 3 m, 17 June 1978, coll. H. Mukai; 1 paratype (AMNH z46-00015-1), Odawa Bay, 4 m, 22 July 1978, coll. H. Mukai; 1 paratype (AMNH z46–00015–2), Odawa Bay, 3 m, October 1978, coll. H. Mukai; 1 paratype (CMNH-ZW-836), off Manazuru Port, Sagami Bay, Kanagawa, Japan, sandy mud, 30–40 m, 17 July 2000, coll. Nishi; 1 specimen (ZIHU-1924), Tsukumo Bay, Noto, Ish-

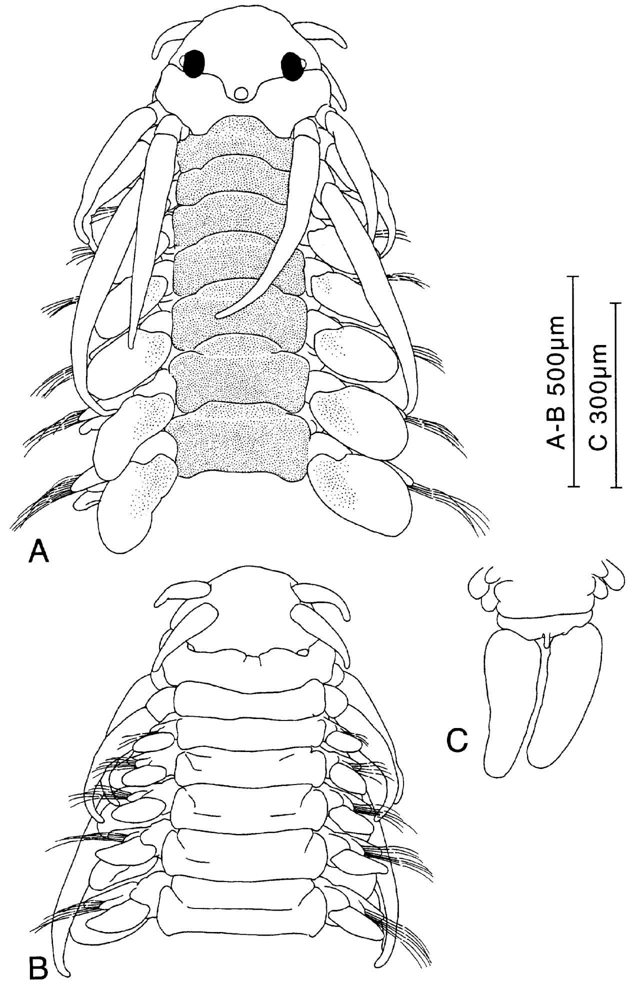

Figure 18. ***Paranaitis misakiensis* sp. nov.**, holotype. A, anterior end, dorsal view. B, same, ventral view. C, posterior end, ventral view.

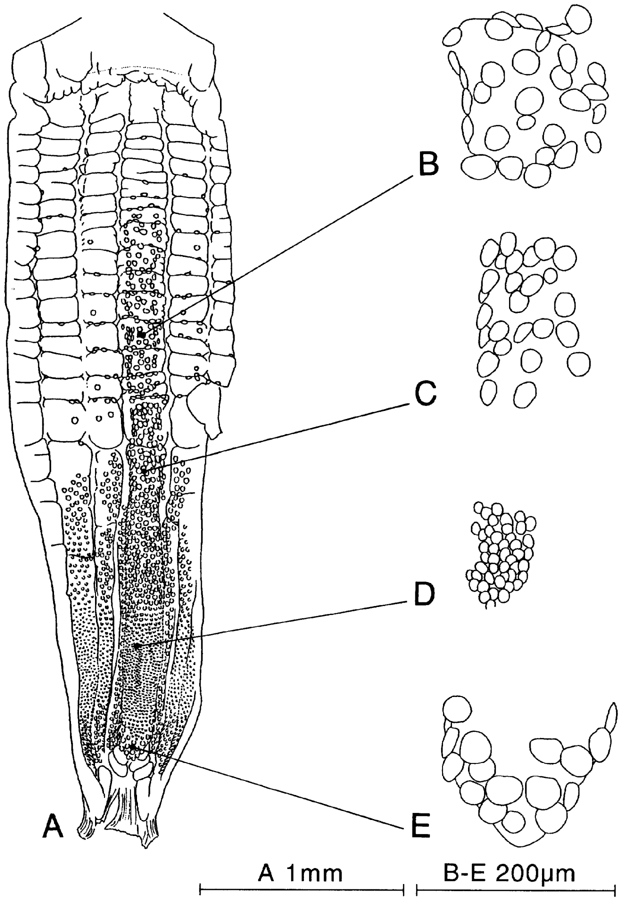

Figure 19. ***Paranaitis misakiensis* sp. nov.**, paratype (ZIHU-1381). A, dissected proboscis, ventral view (median area corresponds to dorsal part). B–E, chitinous papillae.

ikawa, Honshu, sandy mud, 30 m, 16 May 1995, coll. T.K.; 1 specimen (CMNH-ZW-1440),Odawa Bay, October 2001, coll. T. Kudo.

Description

Holotype complete specimen, 14.7 mm long, 1.0 mm wide, for 82 segments. Largest examined specimen, from Amakusa, 33.2 mm long, 1.4 mm wide, with 110 of segments (ZIHU-1383) See Figure 21 for measurements of other specimens.

Live animals transparent white, with reddish brown transverse bands across dorsum on each segment. Eyes red. Preserved specimens similar to live ones; eyes blackish. Body dorso-ventrally flattened, anteriorly and posteriorly tapered. Prostomium anteriorly rounded, wider than long, with a distinct deep ligula (Fig. 18A). Paired antennae and palps conical, laterally to posteriorly directed. Eyes large, rounded, with lenses, situated at posterior margin of prostomium, often partly covered by segment 1. Nuchal papilla situated posteriorly in ligula. Nuchal organs small, ventro-laterally situated (Fig. 18B). Proximal part of proboscis lacking tubercles, with gradual transition to distal part with tubercles (examined by dissection, Fig. 19A). Distal part with five rows of tubercles. Rounded chitinous papillae present on both proximal and distal parts (Fig. 19B–E). Papillae of terminal ring partly merged. Paired large papillae present laterally inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered (Fig. 20A-C). Cirri of segment 1 reaching *c.* segment 6. Dorsal cirri of segment 2 reaching *c.* segment 8. Ventral cirri of segment 2 reaching *c.* segment 6. Dorsal cirri of segment 3 reaching *c.* segment 9. Segment 2 with ventral aciculae, but lacking neuropodial lobes and chaetae (Fig. 20B). Segment 3 with small neuropodial lobes

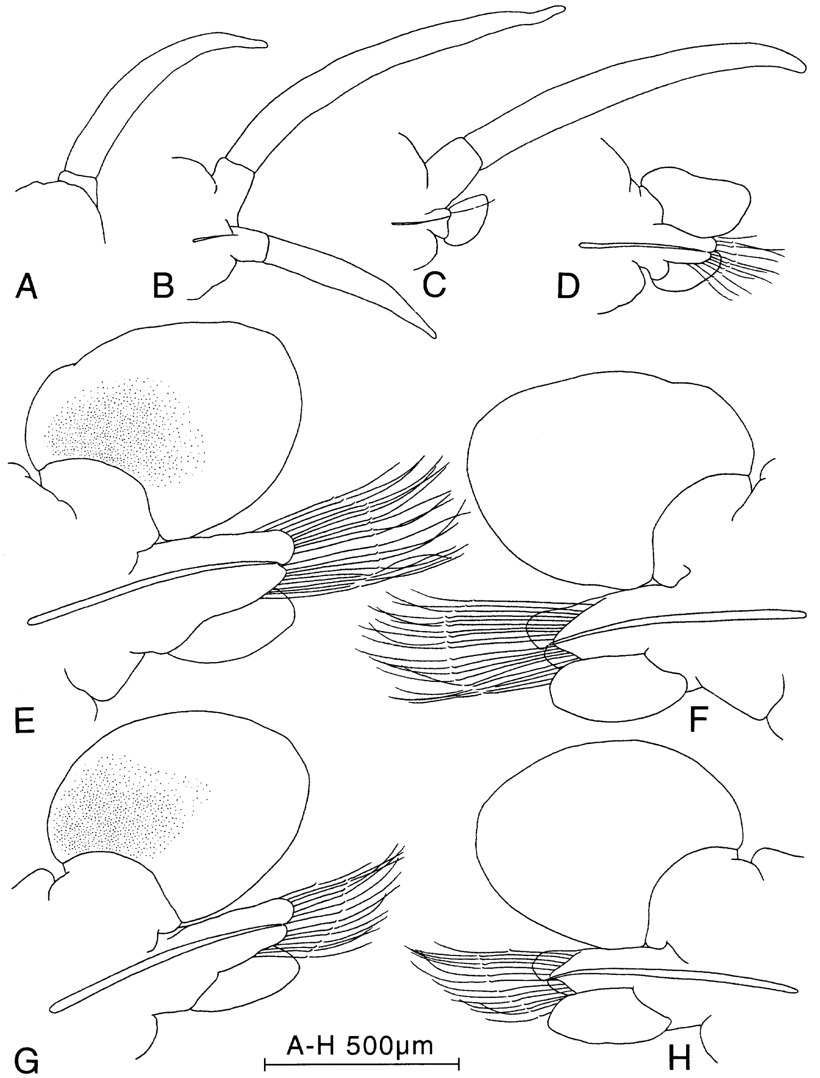

Figure 20. ***Paranaitis misakiensis*** **sp. nov.**, paratype (ZIHU-1381). A, cirri of segment 1, anterior view. B, parapodium of segment 2, anterior view. C, parapodium of segment 3, anterior view. D, parapodium of segment 5, anterior view. E, parapodium of segment 33, anterior view. F, same, posterior view. G, parapodium of segment 75, anterior view. H, same, posterior view.

with aciculae, 1–3 chaetae, and ventral cirri (Fig. 20C). Dorsal aciculae of segments 2 and 3 absent.

Dorsal cirri of median segments oval, asymmetrical, longer than wide (Fig. 20D–H). Dorsal cirrophores short, distinct. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 20 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side (Fig. 37E). Ventral cirri with rounded ends, *c.* twice as long as wide, slightly shorter than neuropodial lobes (Fig. 20F,H). Pygidial cirri cylindrical, with rounded ends, 2–5 times as long as wide (Fig. 18C). Pygidial papilla present.

Habitat

Usually on bottoms with shell sand and sand, but also on mud, intertidally to 30 m.

Distribution

Known only from south Japan.

Remarks

Paranaitis misakiensis **sp. nov.** is similar to *P. kosteriensis* in, e.g. presence of eyes, deep ligula, oval dorsal cirri with symmetrical cirrophores, and cylindrical pygidial cirri with rounded ends. It differs in proboscis and chaetal characters. In contrast to

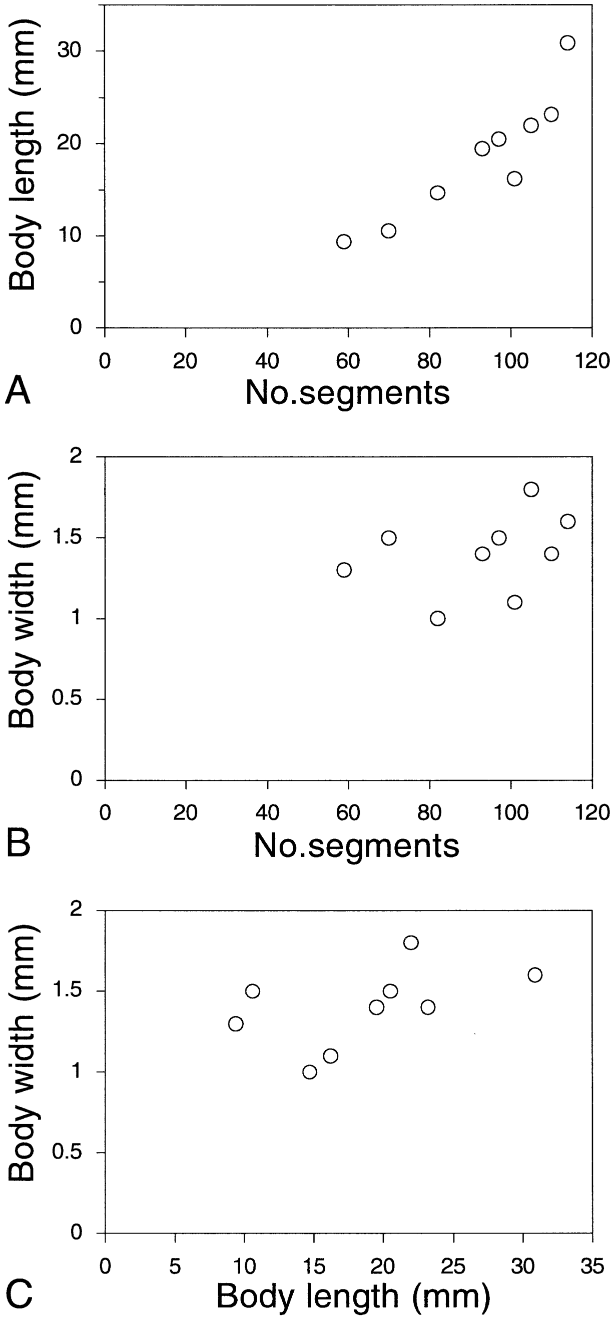

Figure 21. ***Paranaitis misakiensis* sp. nov.**, specimens from Japan. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width.

P. kosteriensis, which has a distinct proboscis division, the distal and proximal parts of *P. misakiensis* are separated by a gradual transition. Furthermore, the chitinous papillae appear on both the proximal and distal parts in *P. misakiensis*, whereas in *P. kosteriensis* the papillae occur only on the proximal part. As for differences in chaetal morphology, the main tooth on the rostrum in *P. misakiensis* is distinctly larger than that of *P. kosteriensis*.

Paranaitis misakiensis instead resembles *P. gardineri* in proboscis and chaetal characters, but differs in parapodial and pygidial morphology and in pigmentation. The dorsal cirrophores of *P. gardineri* are large and very wide, and the dorsal cirri are wider than long in median segments. The dorsal cirrophores of *P. misakiensis* are thinner, and the dorsal cirri are longer than wide in median segments. The pygidial cirri of *P. gardineri* are about seven times as long as wide and have pointed ends, whereas those of *P. misakiensis* are shorter, 2–5 times as long as wide, and have rounded ends. The pigmentation is purple in *P. gardineri*, whereas in *P. misakiensis* it is reddish brown.

Etymology

This species is named for Misaki, the type locality.

***PARANAITIS MORITAI* SP. NOV.**

(FIGS 22, 23)

Material examined

Holotype (ZIHU-1925), Otsuchi Bay, Iwate, Honshu, Japan, 39°21.01′N, 141°58.51′E, shell sand, 59 m, 7 May 1997, coll. T.K.; 1 paratype (ZIHU-2291), Shimoda, Shizuoka, Honshu, Japan, 34°38.404′N, 138°56.915′E, 39–45 m, 18 August 1999.

Description

Holotype complete with regenerated caudal end, 31.8 mm long, 2.9 mm wide, for 99 segments. Paratype complete, 31 mm long, 2.7 mm wide, for 92 segments. Preserved specimen pale with brown pigmentation dorsally. Dorsal part of collar and following segments brown. Dorsal cirri with few to several brown spots, which frequently fuse to each other and form irregular-shaped pigmentation. Body dorso-ventrally flattened, anteriorly and posteriorly tapered. Prostomium anteriorly rounded, wider than long, posteriorly with distinct deep ligula (Figs 22A, 23B). Paired antennae and palps conical, laterally directed. Eyes large, rounded, with lenses, situated at posterior margin of prostomium. Nuchal papilla small, rounded, inserted posteriorly in ligula. Nuchal organs small, rounded, ventro-laterally situated. Proximal part of proboscis dorsally covered with small conical papillae, ventrally with larger conical papillae (examined by dissection; holotype and paratype; Fig. 22B). Distal part with five rows of large tubercles, without chitinous papillae. Terminal ring with *c.* 12 papillae. Two large lateral papillae present inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of seg-

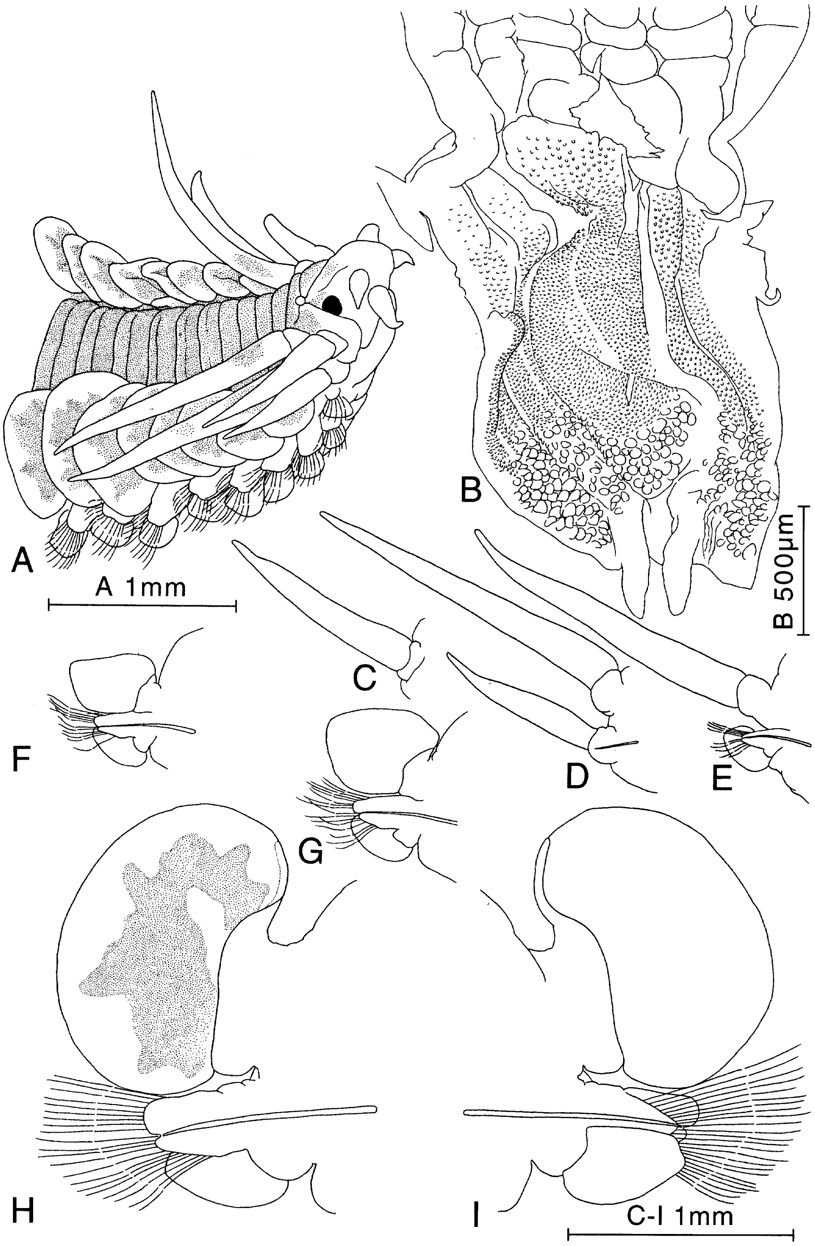

Figure 22. ***Paranaitis moritai* sp. nov.**, holotype (ZIHU-1925). A, anterior end, dorso-lateral view. B, proximal part of dissected proboscis, ventral view. C, cirri of segment 1, anterior view. D, parapodium of segment 2, anterior view. E, parapodium of segment 3, anterior view. F, parapodium of segment 4, anterior view. G, parapodium of segment 5, anterior view. H, parapodium of segment 43, anterior view. I, same, posterior view.

ment 3 cylindrical, long and tapered (Figs 22C–E, 23C). Cirri of segment 1 short, reaching *c.* segment 5. Dorsal cirri of segment 2 reaching *c.* segment 11. Ventral cirri of segment 2 reaching *c.* segment 5. Dorsal cirri of segment 3 reaching *c.* segment 10. Segment 2 with ventral aciculae and 0–5 chaetae, without neuropodia (Figs 22D, 23C). Segment 3 with small neuropodia with ventral aciculae and *c.* nine chaetae and ventral cirri. Dorsal aciculae of segment 2 and 3 absent.

Dorsal cirri of anterior segments cordate (Figs 22F, G); those of middle segments reniform, wider than long (Figs 22H, I). Dorsal cirrophores slightly prolonged dorsally. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 30 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side. Ventral cirri oval with rounded end, slightly shorter than neuropodia.

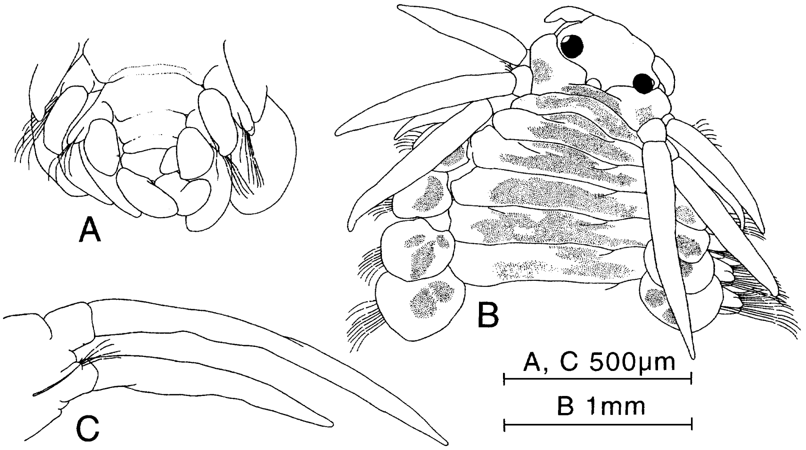

Figure 23. ***Paranaitis moritai* sp. nov.** A, holotype (ZIHU-1925). B, paratype (ZIHU-2291). A, posterior end, ventral view. B, anterior end, dorsal view. C, parapodium of segment 2, anterior view.

Pygidial cirri cylindrical with rounded end, about 2.5 times as long as wide (Fig. 23A). Pygidial papilla not observed.

Habitat

Shell sand, 55–59 m.

Distribution

Known only from east Japan.

Remarks

The present new species shares a deep ligula, presence of eyes, presence of chaetae on segment 2, chaetal morphology, and dorsally elongated dorsal cirrophores, with *P. polynoides*. It differs in having the proximal part of proboscis covered by large, as well as small, chitinous papillae (small only in *P. polynoides*). The pigmentation on the dorsal cirri also differs from *P. polynoides*, having a few to several spots, which are frequently fused to each other and form irregular asterisk-shaped marks, as compared to single rounded ones in *P. polynoides*.

Etymology

This species is named for Mr Koichi Morita of Otsuchi Marine Research Center, in recognition of his vast knowledge of marine life.

PARANAITIS POLYNOIDES (MOORE, 1909)
(FIGS 24–26, 37)

Anaitis polynoides Moore, 1909: 339–342, pl. 16, figs 19–21; Berkeley, 1924: 287; Zachs, 1933: 127 (misspelled as *Anaites polynoides*).

Paranaitis polynoides: Hartman, 1936: 117; 1959: 158; 1968: 291, figs 1–3; Hartman & Reish, 1950; 12; Uschakov, 1972: 1141–142, pl. 7, figs 1–4; Blake, 1994: 164–165, fig. 4.22.

Phyllodoce (*Anaitis*) *polynoides*: Annenkova, 1937: 156.

Not *Paranaitis polynoides*: Fauchald, 1972: 52 (= *Paranaitis* sp.); Gathof, 1984: 19-21 to 19-23, figs 19-17, 18a–e (= *Paranaitis gardineri*).

Material examined

Holotype (USNM-17267), Monterey Bay, California, 83 m; 1 specimen (USNM-123242), off California, 38°16.14′N, 123°24.18′W, 184 m; 1 specimen (USNM-26839), off Apple Cove, Puget sound, Washington, shell, fine gravel and mud, 27 m; 1 specimen (USNM-32461), South Gedney Island, Puget Sound, Washington, 108 m; 1 specimen (ZIHU-2016), Palos Verdes shelf, Santa Monica Bay, California, 33°43.14′N, 118°24.66′W, olive green silt, 307 m, 15 January 1997, coll. F.P.

Description

Holotype complete specimen, 40 mm long, 3.4 mm wide, for 88 segments; see Figure 24 for measurements of other specimens. Preserved specimen white to yellow, with reddish brown pigmentation dorsally from *c.* segment 7. Single large rounded reddish brown spot present on inside of dorsal cirri. Body stout, dorsoventrally flattened, anteriorly and posteriorly tapered. Prostomium rounded, wider than long, with distinct deep ligula (Fig. 24A). Paired antennae and palps conical, directed laterally. Eyes large, rounded, with lenses, situated at posterior margin of prostomium, often partly covered by segment 1. Nuchal papilla small, rounded, situated posteriorly in ligula. Nuchal

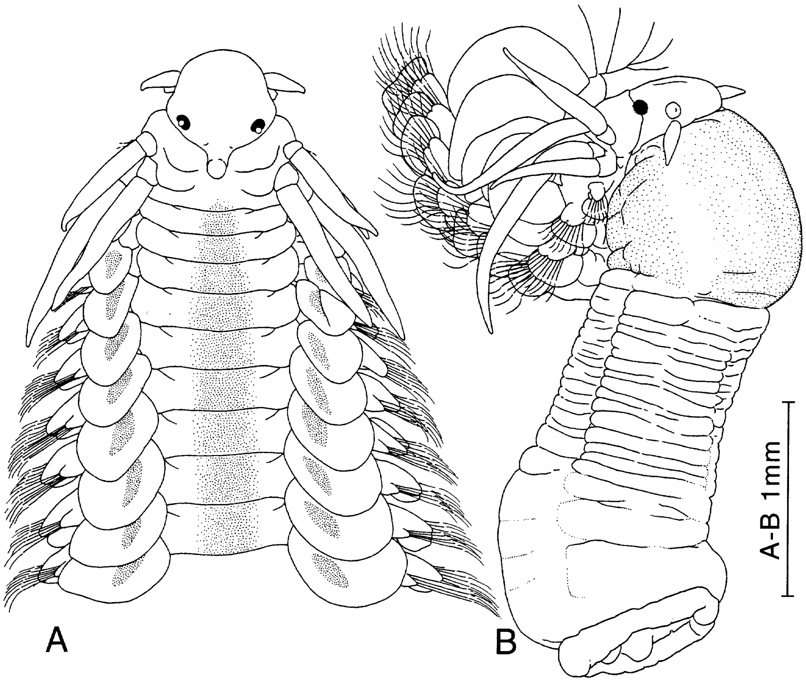

Figure 24. *Paranaitis polynoides*. A, specimen from Washington, USA (USNM-32461). B, specimen from Santa Monica Bay, California (ZIHU-2016). A, anterior end, dorsal view. B, anterior end with fully everted proboscis, lateral view.

organs small, rounded, ventro-laterally situated. Proboscis with distinct division separating proximal and distal parts (Fig. 24B). Proximal part entirely covered by diffusely distributed minute and conical chitinous papillae; size and shape of papillae similar on whole proximal part. Proximal-most part with 1–2 large conical papillae each side. Distal part with six indistinct longitudinal rows of tubercles, conical papillae absent. Terminal ring with *c.* 20 poorly delineated papillae. Paired large papillae present laterally inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered (Fig. 25A–C). Cirri of segment 1 short, reaching about anterior margin of segment 4. Dorsal cirri of segment 2 reaching *c.* segment 7. Ventral cirri of segment 2 reaching *c.* segment 5. Dorsal cirri of segment 3 reaching *c.* segment 8. Segment 2 with small neuropodial lobes fusing to ventral cirrophores, with ventral aciculae and *c.* three chaetae. Segment 3 with neuropodia with ventral aciculae and *c.* eight chaetae, and ventral cirri of similar size and shape as following segments. Dorsal aciculae of segment 2 and 3 absent.

Dorsal cirri of median segments reniform, symmetrical, *c.* twice as wide as long. Dorsal cirrophores asymmetrical, with narrow extensions on dorsal side of cirri (Fig. 25F). Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 20 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side (Fig. 37F). Ventral cirri oval with rounded ends (Fig. 25G). Pygidial cirri cylindrical with rounded ends, 3–3.5 times as long as wide (Fig. 25H). Pygidial papilla present.

Habitat

Sand, mud, and rocks, intertidally to 286 m.

Distribution

Pacific coast of Canada (Berkeley, 1924) to southern California.

Remarks

Paranaitis polynoides differs from other *Paranaitis* in the character combination wide reniform dorsal cirri with dorsally elongated dorsal cirrophores, and proboscis with distinct division separating proximal and distal parts.

We consider Uschakov's (1972) record from the north-west Pacific as doubtful, based on his description of lateral rows of papillae on the proximal part of proboscis.

Paranaitis polynoides has been reported both from the Atlantic and the Pacific coasts of USA and Canada.

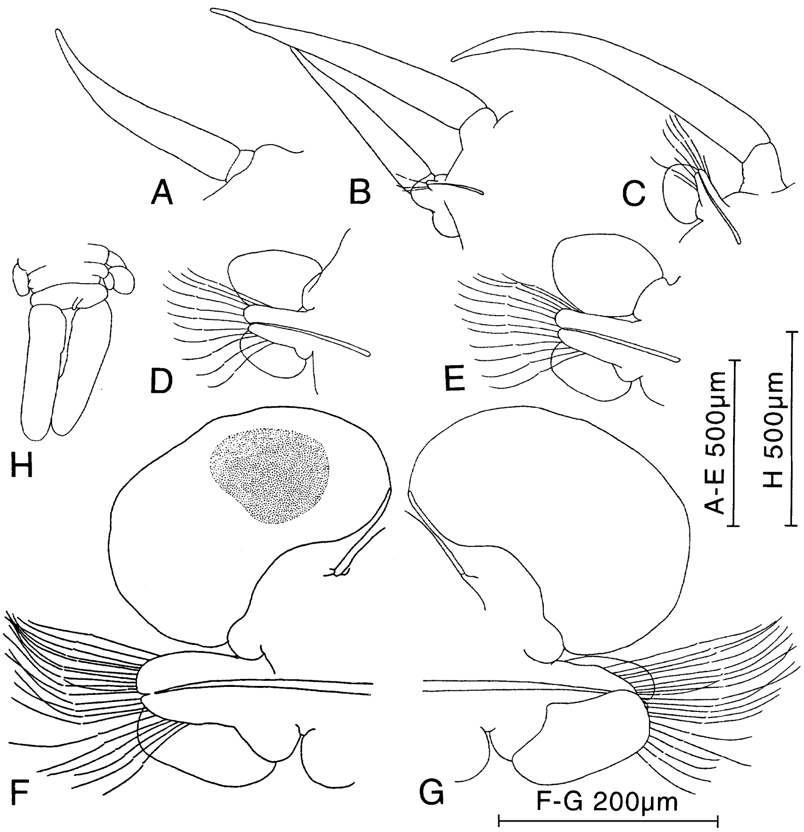

Figure 25. *Paranaitis polynoides*, specimen from Santa Monica Bay, California (ZIHU-2016). A, cirri of segment 1, anterior view. B, parapodium of segment 2, anterior view. C, parapodium of segment 3, anterior view. D, parapodium of segment 4, anterior view. E, parapodium of segment 5, anterior view. F, parapodium of segment 21, anterior view. G, same, posterior view. H, posterior end of body, ventral view.

We examined all specimens (13 lots) identified as *P. polynoides* and deposited in USNM, and found that only the Pacific specimens actually conform to *P. polynoides*. The Atlantic specimens, including Gathof's material (USNM-56127), were re-identified as *P. gardineri*.

Fauchald (1972) reported this species from deep waters (2401–2480 m) off California. The specimen (LACM Vel. 7231) has a retracted proboscis, but differs from *P. polynoides* in having long oval dorsal cirri and symmetrical dorsal cirrophore, and probably belongs to an undescribed species of *Paranaitis*. However, in the absence of information on a series of characters, we prefer to leave this single specimen undescribed.

PARANAITIS PUMILA SP. NOV.

(FIGS 27–29, 37)

Material examined

Holotype (ZIHU-1378), 21 paratypes (ZIHU-1379), 18 paratypes (MNHN POLY TYPE 1379), Otsuchi Bay, Iwate, Honshu, Japan, 39°23.1′N, 141°58.8′E, shell sand, 67 m, 11 August 1998, coll. T.K. 11 specimens (ZIHU-1968), Otsuchi Bay, 39°21.0′N 141°58.5′E, shell sand, 58.7 m, 7 May 1997, coll. T.K.; 17 specimens (ZIHU-1969), Otsuchi Bay, 39°20.5′N, 141°57.5′E, shell sand, 45.3 m, 25 May 1998, coll. T.K.; 60 specimens (ZIHU-1970), Otsuchi Bay, 39°23.2′N, 141°58.8′E, shell sand, 62.5 m, 26 May 1998, coll. T.K.; 24 specimens (ZIHU-1971), Otsuchi Bay, 39°20.8′N, 141°58.4′E, shell sand, 53 m, 10 August 1998, coll. T.K.; 10 specimens (ZIHU-1972), Otsuchi Bay, 39°21.0′N, 141°58.4′E, shell sand, 59 m, 10 August 1998, coll. T.K.; 1 specimen (ZIHU-1973), Otsuchi Bay, 39°22.0′N, 142°00.8′E, sand, 98.9 m, 27 September 2000, coll. T.K.; 12 specimens (ZIHU-1974), Otsuchi Bay, 39°23.3′N, 141°59.7′E, sand, 80.6 m, 27 September 2000, coll. T.K.; 28 specimens (ZIHU-1975), Otsuchi Bay, 39°23.4′N, 141°59.0′E, shell sand, 64.0 m, 27 September 2000, coll. T.K.; 1 specimen (ZIHU-1976), Otsuchi Bay, 39°21.4′N, 141°59.1′E, shell sand, 70.3 m, 27 September 2000, coll. T.K.; 1 specimen (CMNH-ZW-832), Otsuchi Bay, 39°22.16 N, 141°59.97E, 87 m, 14 October 1996.

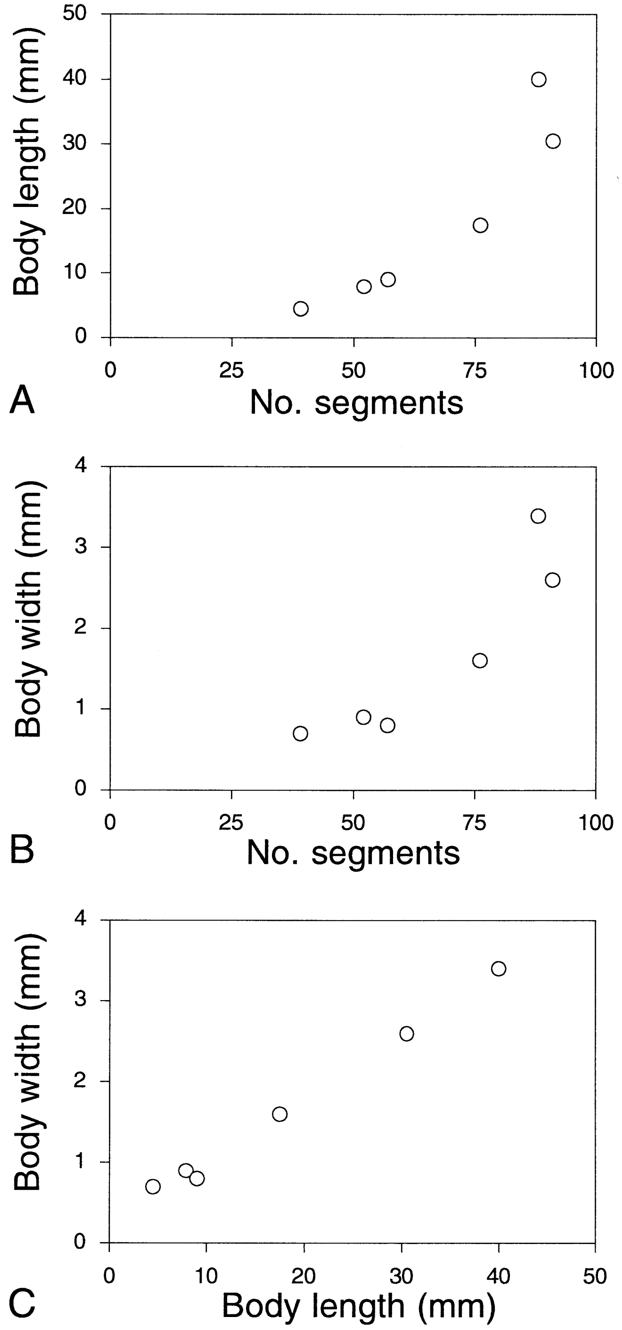

Figure 26. *Paranaitis polynoides*, specimens from USA. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width.

Description

Holotype complete ovigerous female, 8.5 mm long, 0.8 mm wide, for 52 segments; see Figure 29 for measurements of other specimens. Live animals white with reddish brown pigmentation on each side of dorsum, forming two longitudinal lines (Fig. 27D). Median part of dorsum pale yellow. Yellow pigmentation lost in preserved specimens, but longitudinal lines retained. Eyes brown. Body of uniform width. Prostomium anteriorly rounded, wider than long, posteriorly with distinct deep ligula (Fig. 27A). Paired antennae and palps narrow, anteriorly directed. Eyes large, rounded, with lenses, situated at posterior margin of prostomium, often partly covered by segment 1. Nuchal papilla rounded, situated posteriorly in ligula. Nuchal organs oval, ventro-laterally situated. Proboscis short, not divided into proximal and distal parts, lacking papillae or tubercles (Fig. 27B, C). Terminal ring with *c.* 17 papillae. Paired large papillae present laterally inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered (Fig. 28A–C). Cirri of segment 1 reaching *c.* segment 5. Dorsal cirri of segments 2 and 3 reaching *c.* segment 7. Ventral cirri of segment 2 reaching *c.* segment 5. Segment 2 with well-developed neuropodia near cirrophores of ventral cirri, with ventral aciculae and *c.* six chaetae. Segment 3 with neuropodial lobes with ventral aciculae and *c.* six chaetae, with ventral cirri of almost same shape and size as on following ones. Dorsal aciculae of segments 2 and 3 absent.

Dorsal cirri of median segments rounded cordate, symmetrical, about as long as wide (Fig. 28D–H). Dorsal cirrophores small, dorsally indistinct. Neuropodium with supra-acicular lobes longer than subacicular lobes, with 12–15 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side (Fig. 37G). Ventral cirri oval, slightly shorter than neuropodia. Pygidial cirri oval 1.5–2 times as long as wide (Fig. 27E). Pygidial papilla present.

Habitat

Shell sand, 45–67 m.

Distribution

Known only from Otsuchi Bay, Japan.

Biology

Mature males and females collected in August at Otsuchi Bay.

Remarks

***Paranaitis pumila* sp. nov.** differs from other *Paranaitis* in the character combination presence of eyes, anteriorly directed narrow paired antennae and palps, deep ligula, neuropodial lobes with chaetae on

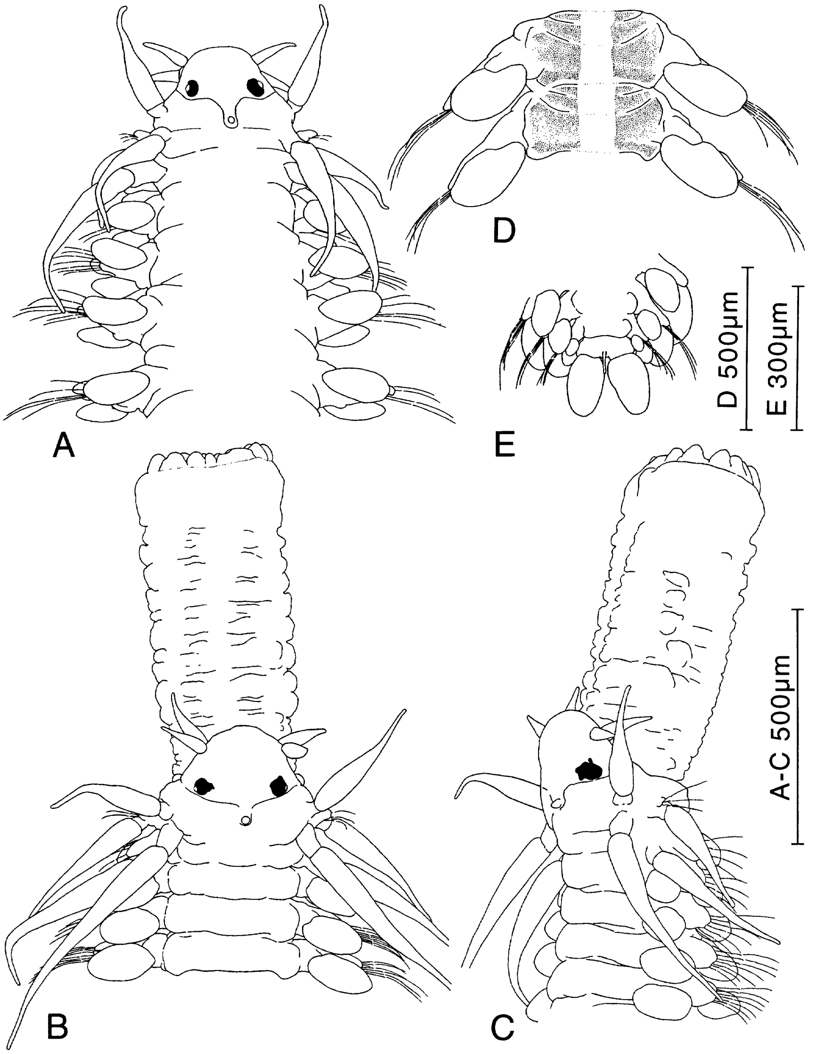

Figure 27. ***Paranaitis pumila* sp. nov.** A, D, E, holotype; B, C, specimen from Otsuchi Bay, Japan (ZIHU-1974). A, anterior end, dorsal view. B, anterior end with fully everted proboscis. C, same, lateral view. D, median segments, dorsal view. E, posterior end, ventral view.

segment 2, and undivided proboscis lacking chitinous papillae.

Etymology

The new species is named for its small body size, '*pumila*' being Latin for dwarf.

PARANAITIS SPECIOSA (WEBSTER, 1879)
(FIGS 30–33, 37)

Anaitis speciosa Webster, 1879: 131–132, pl. 1, figs 8, 9; Webster & Benedict, 1884: 702, 1887: 710.

Paranaitis speciosa: Hartman, 1959: 158; Pettibone, 1963: 75–77, fig. 17a; Day, 1973: 22; Gathof, 1984: 19-23 to 19-25, figs 19-19, 20a–e.

Material examined

USA: 4 syntypes (USNM-380), Great Egg Harbor, New Jersey; 4 specimens (USNM-485), Provincetown, Massachusetts; 3 specimens (USNM-26972), Great Egg Harbor, New Jersey; 1 specimen (USNM-75588), Gulf of Mexico, Alabama, off Mobile Bay, 29°43.29′N, 87°54.30′W, 35 m; 1 specimen (USNM-89977), Gulf of Mexico, Mississippi, Mississippi Sound, 30°04.54′N, 88°49.54′W, 12.2 m; 1 specimen, Beaufort, North Carolina, shell sand, 12 m, 4 May 1972, coll. M.E. Petersen; 7 specimens, Bogue Banks, Morehead, North Carolina, 28 February 1965, coll. M.E. Petersen. JAPAN: 1 specimen (ZIHU-1920), Otsuchi Bay, Iwate, Honshu, 39°20.5′N, 141°58.4′E, sandy mud, 41 m, 25 May 1998, coll. T.K.; 1 specimen (ZIHU-1921),

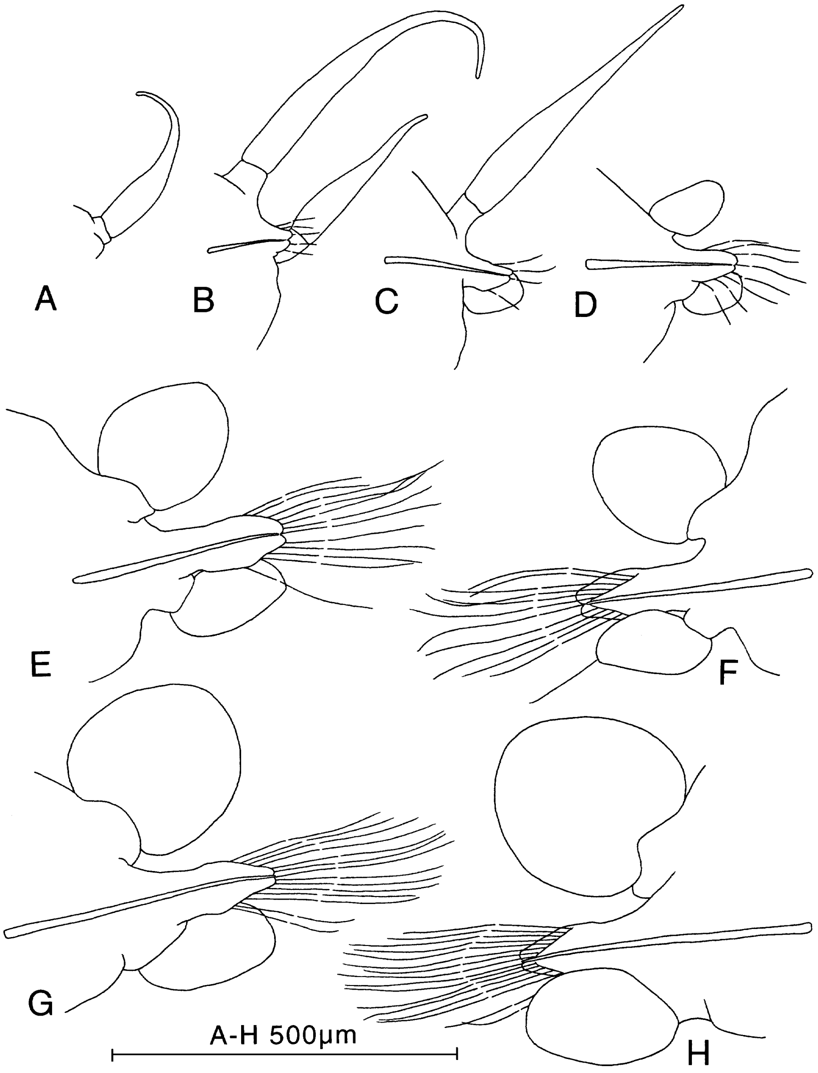

Figure 28. ***Paranaitis pumila* sp. nov.**, paratype (ZIHU-1379). A, cirri of segment 1, anterior view. B, parapodium of segment 2, anterior view. C, parapodium of segment 3, anterior view. D, parapodium of segment 4, anterior view. E, parapodium of segment 17, anterior view. F, same, posterior view. G, parapodium of segment 44, anterior view. F, same, posterior view.

39°20.8′N, 141°57.9′E, Otsuchi Bay, sand, 48 m, 10 August 1998, coll. T.K.

Description

Largest syntype complete, whole mounted specimen, 4.5 mm long, 1.0 mm wide, for 35 segments larger specimen with regenerated caudal end 12.0 mm long, 1.6 mm wide, for 51 segments (ZIHU-1920). See Figure 33 for measurements of other specimens. Live animals reddish yellow to very dark brown with darker transverse band on segments 8 and 9 (Webster, 1879; new observations on Japanese specimens). Preserved specimens pale.

Body stout, dorso-ventrally flattened, anteriorly and posteriorly tapered (Fig. 30A). Prostomium rounded, wider than long. Indistinct but deep ligula present in syntypes (Fig. 30B); absent in larger specimens (Figs 31A, 32A, ZIHU-1920, 1921). Paired antennae short and narrow, anteriorly to postero-laterally directed, *c.* one-third as long as wide of prostomium. Palps similar to paired antennae in length, slightly wider. Eyes medium sized, rounded, with lenses, situated at posterior margin of prostomium. Nuchal papilla indistinct, small, rounded, inserted posteriorly in ligula in syntypes; not detected in larger specimens (specimens from North Carolina, ZIHU-1920, 1921). Nuchal organs elongated oval, laterally situated

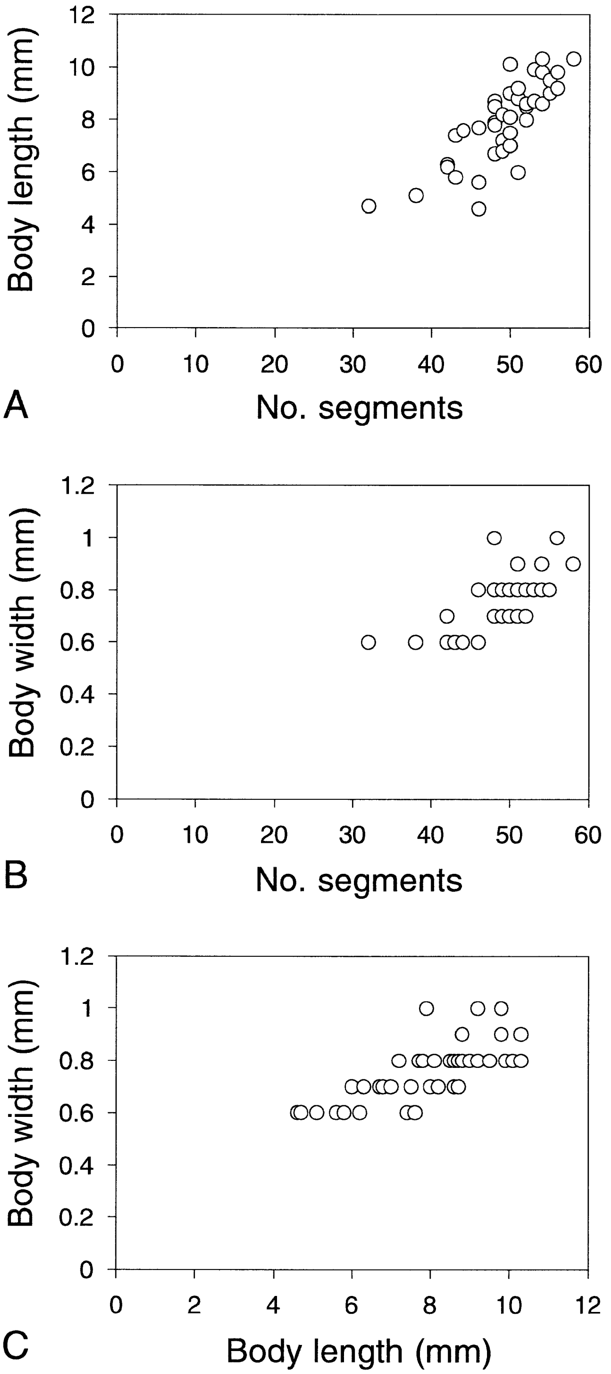

Figure 29. ***Paranaitis pumila* sp. nov.**, type series. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width.

(Fig. 31B). Proboscis dorsally covered with minute rounded papillae, with single lateral rows of large rounded papillae each side (Figs 32B,C). Terminal ring with about 30 papillae. Paired large lateral papillae present inside ring.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 short, reaching about anterior margin of segment 4. Dorsal and ventral cirri of segment 2 reaching about middle of segment 5. Dorsal cirri of segment 3 reaching about middle of segment 6. Chaetae absent on segment 2. Distribution of aciculae in segments 2 and 3 unknown.

Dorsal cirri of median segments broad cordiform, with rounded ends (Figs 30C,D, 31C,D, 32D,E). Dorsal cirrophores short and indistinct. Neuropodium with supra-acicular lobes longer than subacicular lobes, with *c.* 50 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side (Figs 37H,I). Ventral cirri reniform with rounded ends, shorter than neuropodial lobes. Pygidial cirri oval with rounded ends. Pygidial papilla present.

Habitat

Found in *Mytilus* beds, in tubes of *Diopatra cuprea*, in sand, mud, silt, clay and shell bottom, intertidally to 185 m.

Distribution

Maine to North Carolina; Gulf of Mexico (Gathof, 1984).

Remarks

Paranaitis speciosa differs from other *Paranaitis* in the character combination indistinct nuchal papilla, proboscis with lateral row of large papillae on each side, and rostrum of chaetal shaft with single large main tooth. It is similar to *P. wahlbergi* in the indistinct nuchal papillae (at least in large specimens), and in the parapodia with small indistinct dorsal cirrophores, but differs in the morphology of the rostrum of the chaetal shaft. These two species can also be distinguished by pigmentation: live European *P. wahlbergi* have a clear red dorsum, whereas *P. speciosa* has a dark green, yellow, or yellow brown dorsum with a transverse dark dorsal band on segments 8 and 9.

In large specimens of *P. speciosa* from USA and Japan (ZIHU-1920, 1921) the ligula is shallow and the nuchal papilla invisible. In the syntypes, which are small, whole mounted specimens, both ligula and nuchal papilla may be present, although not very distinct and the observations are admittedly somewhat uncertain. We here tentatively treat the syntypes and

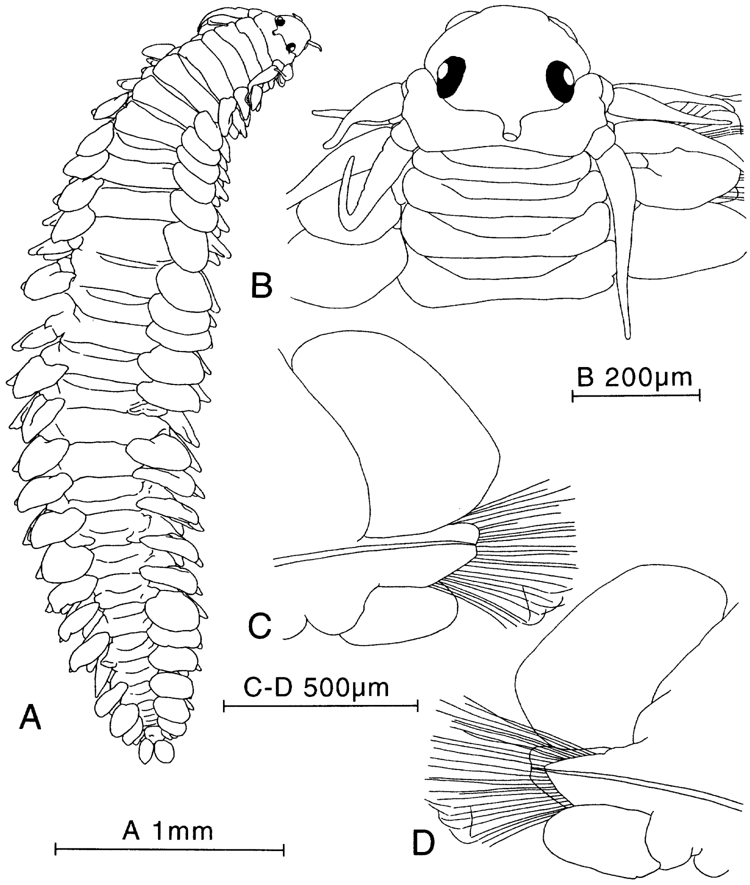

Figure 30. *Paranaitis speciosa*, syntype (USNM-380). A, entire animal, dorsal view. B, anterior end, dorsal view. C, parapodium of median segment, anterior view. D, same, posterior view.

the other specimens as conspecific; collection and examination of topotypes of various sizes would clearly be of great value.

Two Japanese specimens (ZIHU-1920, 1921) are herein referred to *P. speciosa*, and share, e.g. the poorly defined nuchal papilla, the undivided proboscis with lateral rows of large papillae, the short dorsal cirrophores, and the presence of large single main tooth on the rostrum of the chaetal shaft. Nevertheless, common Pacific and Atlantic distributions is unusual, and examination of further specimens from a large range of localities are needed.

PARANAITIS USCHAKOVI EIBYE-JACOBSEN, 1991
(FIGS 9, 34, 35, 37)

Paranaitis uschakovi Eibye-Jacobsen, 1991: 129. (replacement name for *Paranaitis caecum* Uschakov, 1972.

Paranaitis caecum Uschakov, 1972: 142–143, pl. 7, figs 5–7. Junior homonym to *Paranaitis caeca* (Moore, 1903).

Material examined

Holotype (ZIR 16140), east of Honshu, 38°38′N, 141°53′E, 239 m; 1 specimen (ZIHU-1922), Otsuchi Bay, Iwate Honshu, Japan, 39°20.9 N 141°58.5′E, shell sand, 56 m, 25 May 1998, coll. T.K.; 1 specimen (ZIHU-1923), Otsuchi Bay, 39°20.5′N, 141°57.4′E, sandy mud, 45 m, 25 May 1998, coll. T.K.

Description

Holotype, largest known specimen, 20 mm long, 2 mm wide, for 62 segments (Uschakov, 1972); see Figure 9 for measurements of other specimens. Live animals white, with single large rounded brown spots on inner parts of dorsal cirri, forming two longitudinal dorsal lines. Pigmentation disappears following preservation. Body short, dorso-ventrally flattened, posteriorly tapered. Prostomium rounded triangular, with shallow ligula (Fig. 34A). Paired antennae and palps narrow, anteriorly directed. Eyes absent. Nuchal papilla small, rounded (Fig. 34B). Nuchal organs rounded, rather large, situated ventrally, not dorsally visible.

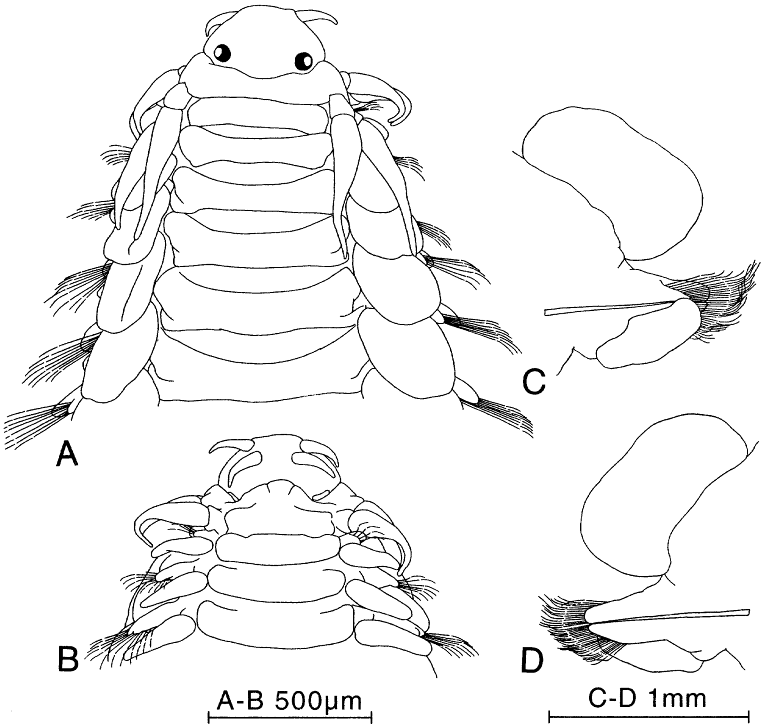

Figure 31. *Paranaitis speciosa*, specimen from North Carolina, USA (Mary Petersen's personal collection). A, anterior end, dorsal view. B, same, ventral view. C, parapodium of segment 18, posterior view. D, same, anterior view.

Proboscis lacking distinct papillae (examined by dissection; ZIHU-1923). Terminal ring with large number of poorly defined papillae. Inside of proboscis covered by small rounded, flat papillae. Paired large papillae present laterally inside ring.

Segments 1 and 2 indistinctly separated dorsally and ventrally. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 reaching *c.* segment 5. Dorsal cirri of segments 2 and 3 reaching *c.* segment 8. Ventral cirri of segment 2 reaching *c.* segment 6. Segment 2 with ventral aciculae and *c.* six chaetae arising from small neuropodial lobes fused to ventral cirrophores. Segment 3 with neuropodial lobes with ventral aciculae and *c.* seven chaetae, with ventral cirri. Ventral aciculae present from segment 2. Dorsal aciculae of segment 2 and 3 absent.

Dorsal cirri of median segments kidney-shaped, symmetrical, wider than long (Fig. 35A–D). Dorsal cirrophores dorsally prolonged, with weakly developed ciliary bands. Neuropodial lobes long, with supra-acicular lobes longer than subacicular lobes, with *c.* 25 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, with single large main tooth on anterior side (Fig. 37J). Ventral cirri oval, slightly pointed, about as long as neuropodia in median segments, slightly longer in posterior segments. Pygidial cirri short, oval (Fig. 34C). Pygidial papilla present.

Habitat

Sandy bottom, 45–598 m.

Distribution

Known from east of Honshu, Japan.

Remarks

Paranaitis uschakovi was originally described as *Paranaitis caecum* by Uschakov (1972). In his revision of *Eumida*, Eibye-Jacobsen (1991) transferred *Eumida caeca*, Moore, 1903; to *Paranaitis*. Since *Paranaitis caecum* Uschakov, 1972 thereby became a junior homonym of *Paranaitis caecum* (Moore, 1903), Eibye-Jacobsen introduced the new name *Paranaitis uschakovi* for Uschakov's species.

The examined specimens conform to *P. uschakovi* and are characterized by the following unique combination of characters: absence of eyes, shallow but distinct ligula, neuropodial lobes with chaetae on segment 2, and white body with dark spots on inner part of dorsal cirri.

There has been some confusion regarding differences between the present species and *P. caeca*. We

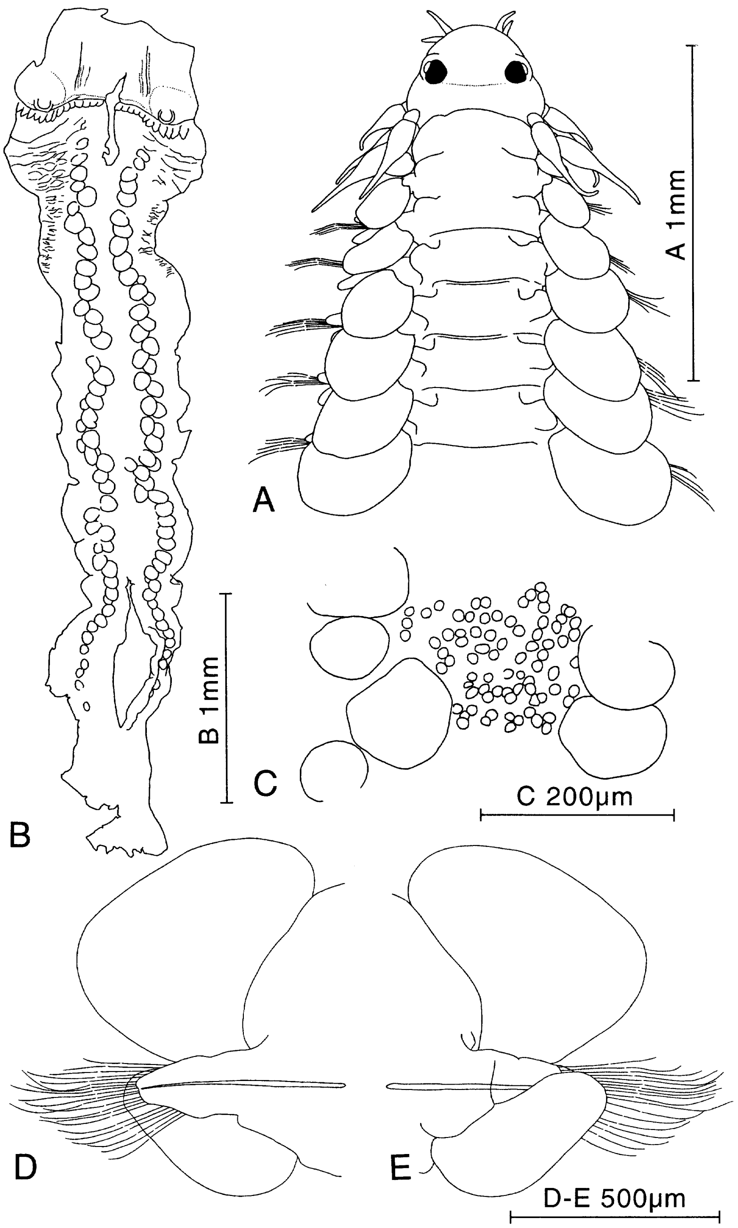

Figure 32. *Paranaitis speciosa*. Specimen from Japan (ZIHU-1921). A, anterior end, dorsal view. B, dissected proboscis, ventral view (median area corresponds to dorsal part). C, proboscis papillae. D, parapodium of segment 32, anterior view. E, same, posterior view.

suggest that they may be separated by a number of morphological differences; see remarks for *P. caeca* for further information.

PARANAITIS INCERTAE SEDIS
PARANAITIS CAPENSIS (DAY, 1960)
(FIG. 36)

Phyllodoce (*Anaitis*) *capensis* Day, 1960: 298, fig. 5a–c.
Phyllodoce (*Paranaites*) *capensis* (sic): Day, 1967: 148, fig. 5.2q–s.
Paranaitis capensis: Pleijel, 1991: 258.

Material examined

Holotype (SAM-A20265), False Bay, South Africa, 34°09.6′S, 18°29.3′E, 31 m.

Description

Holotype complete specimen, 33 mm long, 1.8 mm wide, for 105 segments. Body colour of live specimens

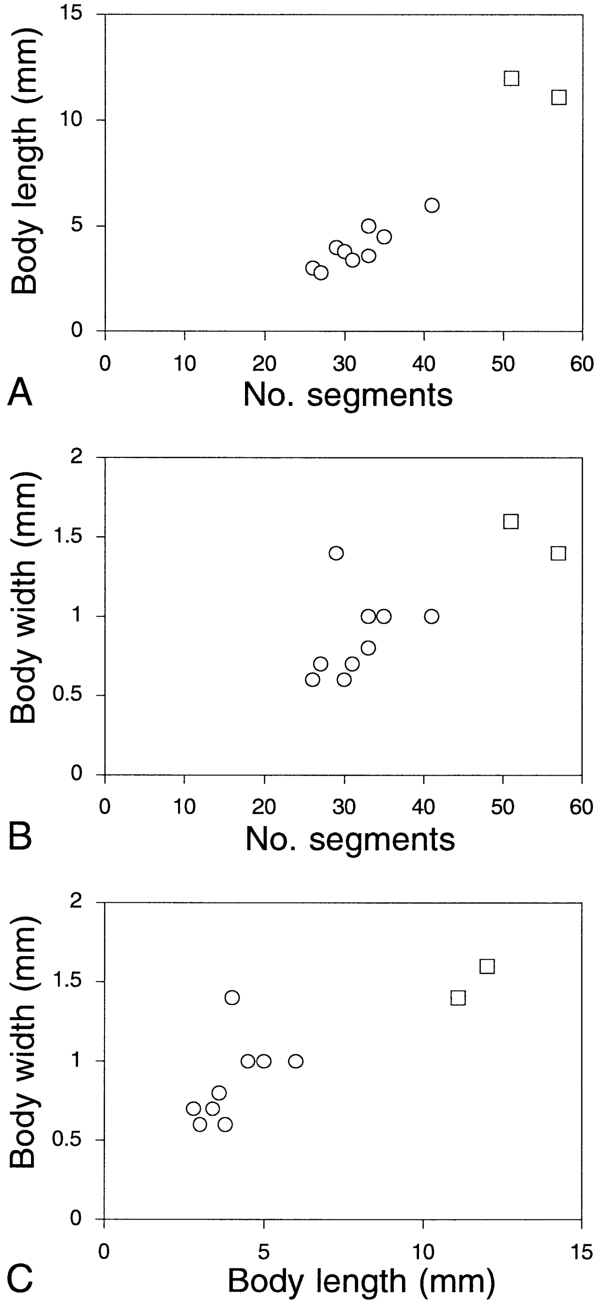

Figure 33. *Paranaitis speciosa*, specimens from USA and Japan. Relationships between A, number of segments and body length, B, number of segments and body width, and C, body length and body width. Circles represent specimens from USA, squares, Japan.

unknown. Preserved specimen uniformly creamy white. Body dorso-ventrally flattened, posteriorly tapered. Prostomium anteriorly rounded, *c.* 1.5 times as wide as long, with deep ligula (Fig. 36A). Paired antennae and palps conical, laterally to posteriorly directed. Eyes medium-sized, rounded, with lenses, situated near posterior margin of prostomium. Nuchal papilla short, rounded, posteriorly situated in ligula. Nuchal organs not observed. Proboscis (probably dissected by Day) in poor condition, with distinct division separating proximal and distal part; proximal part covered with wide oval chitinous papillae, distal part with 5–6 rows of rounded tubercles. Terminal ring indistinct.

Segments 1 and 2 fused. Cirri of segment 1, dorsal and ventral cirri of segment 2, and dorsal cirri of segment 3 cylindrical, long and tapered. Cirri of segment 1 reaching *c.* segment 5. Dorsal cirri of segments 2 and 3 reaching *c.* segment 7. Ventral cirri of segment 2 reaching *c.* segment 5. Segment 2 without neuropodial lobes and chaetae. Segment 3 with small neuropodial lobes with *c.* six chaetae, with ventral cirri of similar shape and size as following segments. Aciculae of segments 2 and 3 unknown.

Dorsal cirri of median segments oval, longer than wide. Dorsal cirrophores short, distinct, symmetrical. Neuropodium with supra-acicular lobes longer than subacicular lobes, with 15–20 chaetae. Dorsal and ventral chaetae similar within single fascicle. Rostrum of chaetal shaft asymmetrical, single main tooth on anterior side, smaller tooth on posterior side. Ventral cirri with rounded ends, as long as neuropodial lobes. Pygidial cirri cylindrical with rounded ends, *c.* three times as long as wide (Fig. 36B). Pygidial papilla present.

Habitat

Sand, shell and rocks, 55 m.

Distribution

Known only from False Bay and Cape (Day, 1967), South Africa.

Remarks

Following Day, 1960, *P. capensis* differs from *P. kosteriensis* in the following characters: (1) more developed collar, (2) different proboscis, (3) longer dorsal cirri, and (4) different morphology of chaetal shafts. However, we cannot confirm any of these differences from examination of the holotype. In view of the poor condition of this specimen, of the lack of additional material, and of the distribution of the taxa, we avoid to synonymize *P. capensis* with *P. kosteriensis*. Further investigation based on newly collected South African specimens are required.

*P*ARANAITIS FORMOSA (VERRILL, 1885)

Anaitis formosa Verrill, 1885: 433; Verrill in Hartman, 1944: 337, pl. 23, fig. 8.
Paranaitis formosa: Hartman, 1959: 158.
[type locality: Massachusetts]

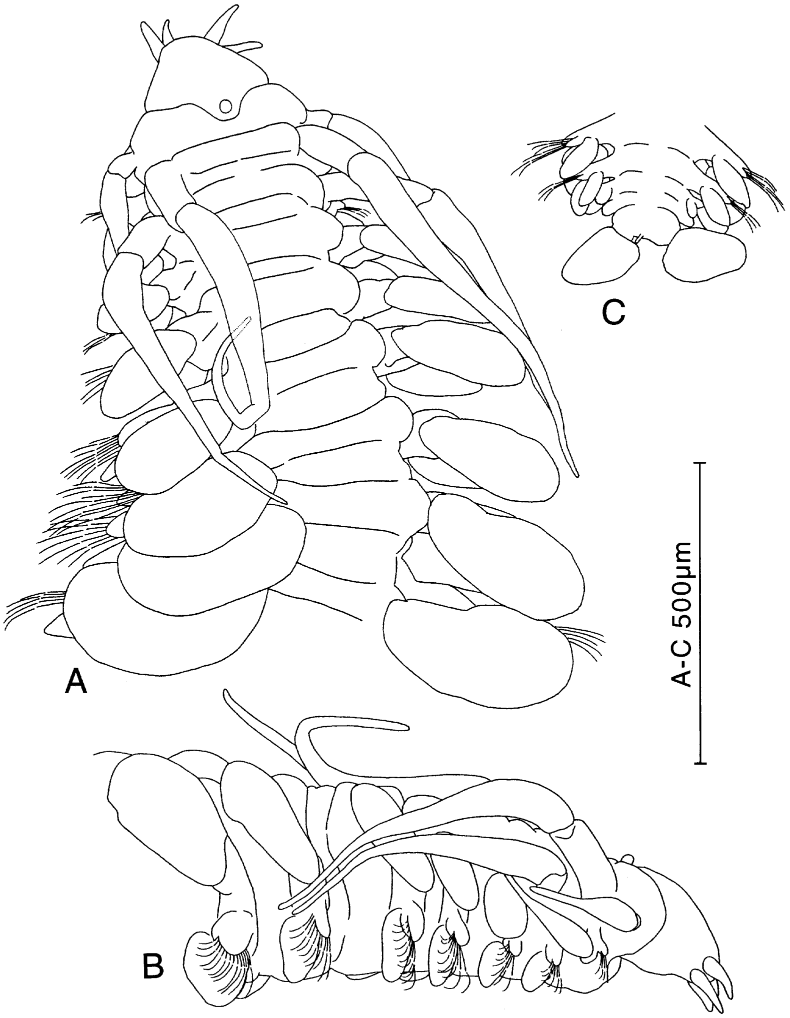

Figure 34. *Paranaitis uschakovi*, specimen from Otsuchi Bay, Japan (ZIHU-1923). A, anterior end, dorsal view. B, same, lateral view. C, posterior end, ventral view.

No type material exists. Judging from the original description, *P. formosa* closely resembles *P. speciosa*, having a proboscis with lateral rows of papillae, no nuchal papillae, short anterior cirri, and dorsal dark bands on segments 7 and 8 (segments 9 and 10 on the plate of Verrill in Hartman, 1944). *Paranaitis formosa* presumably represents a junior synonym of *P. speciosa*.

PARANAITIS IMBRICATA (EHLERS, 1875)

Eulalia imbricata Ehlers, 1874: 294; 1875: 43–44, pl. 2, fig. 15; McIntosh, 1908: 64–66, fig. 42.

[type locality: 'Porcupine' expedition station 23, 56°9′N, 14°10′W, North Atlantic]

Type material seems to be missing. Judging from the original description, this species appears to belong to *Paranaitis*, in having posteriorly inserted nuchal papilla (described as an antenna in Ehlers, 1875), broadly ovoid dorsal cirri, and the first segment partly covering the posterior margin of prostomium (judging from the drawing). However, due to the absence of type or any other materials, we treat this species as *Paranaitis* insertae sedis.

PARANAITIS PICTA (VERRILL, 1885)

Anaitis picta Verrill, 1885: 433; Verrill in Hartman, 1944: 338, pl. 14, fig. 1.

Paranaitis picta: Hartman, 1959: 158.

[type locality: Massachusetts]

No type material exists. According to the original description, this species is closely related to *P. speciosa*, but is distinguished by more slender bodyshape, heart-shaped head, longer and narrower dorsal cirri, and different pigmentation. However, these minor differences do not exclude the possibility that *P. picta* is a junior synonym of *P. speciosa*.

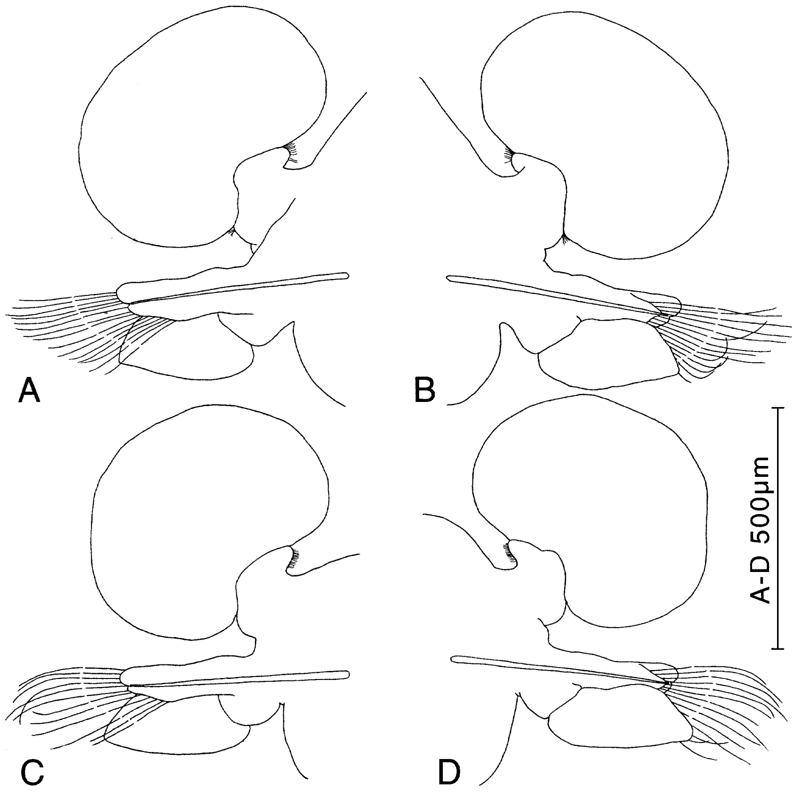

Figure 35. *Paranaitis uschakovi*, specimen from Otsuchi Bay, Japan (ZIHU-1923). A, parapodium of segment 22, anterior view. B, same, posterior view. C, parapodium of segment 32, anterior view. D, same, posterior view.

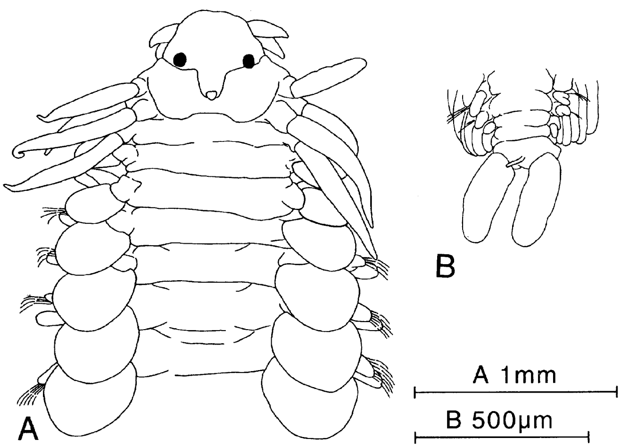

Figure 36. *Paranaitis capensis*, holotype. A, anterior end, dorsal view. B, posterior end, ventral view.

PHYLLODOCIDAE INCERTAE SEDIS

ANAITIS PEREMPTORIA CLAPARÈDE, 1870

Anaitis peremptoria Claparède, 1870: 459–460, pl. 9, fig. 6.
[type locality: Naples, Italy]

No type material exists. Judging from the original description, this species belongs to Phyllodocidae, although any more specific allocation is uncertain due to lack of information.

ANAITIS ZEYLANICA WILLEY, 1905

Anaitis zeylanica Willey, 1905: 262, plate 3, figs 57–60.
Paranaitis zeylanica: Hartman, 1959: 159; Gallardo, 1968: 58, pl. 11, figs 2, 3.
[type locality: Ceylon, India]

Type material is lacking and the original description is not very detailed. However, all reported characters suggest that this species belongs to *Phyllodoce*, rather than to *Anaitis* (= *Paranaitis*). Gallardo (1968) redescribed the species from specimens collected in Viet Nam. Although clearly also belonging to *Phyllodoce*, we are unable to state if they are conspecific to Willey's animals.

PHYLLODOCE (*ANAITIS*) *PAPILLOSA* EHLERS, 1887

Phyllodoce (*Anaitis*) *papillosa* Ehlers, 1887: 140–142, plate 40, figs 7–9.
Paranaitis papillosa: Hartman, 1959: 158.

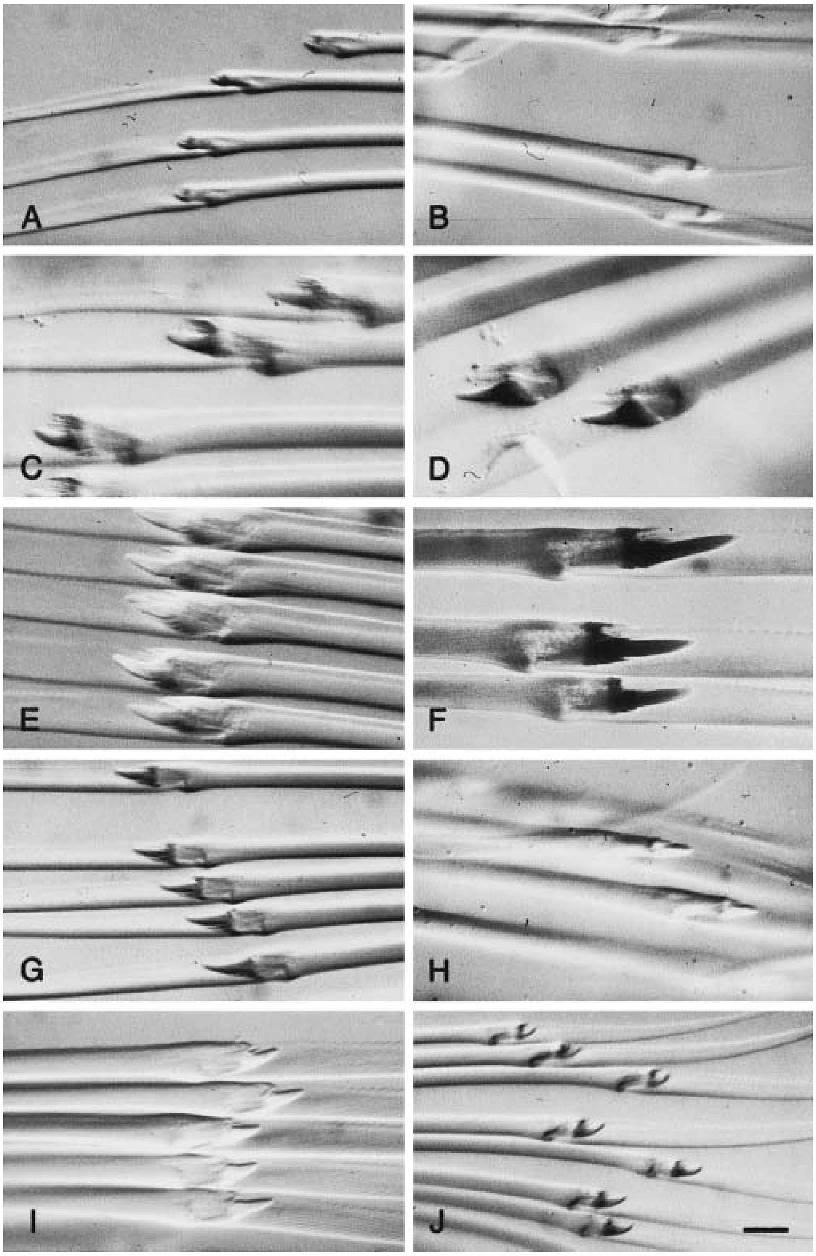

Figure 37. Chaetae of species of *Paranaitis*. A, *P. wahlbergi*, specimen from Sweden, ZIHU-2014. B, *P. caeca*, specimen from Japan, ZIHU-1919. C, *P. kosteriensis*, specimen from Sweden, SMNH-22547, dorsal chaetae. D, *P. kosteriensis*, same specimen, ventral chaetae. E, ***P. misakiensis* sp. nov.**, paratype, ZIHU-1381. F, *P. polynoides*, ZIHU-2016. G, ***P. pumila* sp. nov.**, paratype, ZIHU-1379. H, *P. speciosa*, syntype USNM 380. I, *P. speciosa*, specimen from Japan, ZIHU-1921. J, *P. uschakovi*, specimen from Japan, ZIHU-1923.

Material examined

Holotype (MCZ 839), Florida, Key West, USA, 2–4 m, expedition 'Blake' 1877–78.

According to the original description the holotype and the only known specimen lacks a median antenna. Close examination of this specimen, however, revealed a scar between the eyes which indicates a lost antenna. Segment 1 is dorsally limited and does not form a collar together with segment 2, and the dorsal cirri are pointed and not rounded as in *Paranaitis*. Genus uncertain, possibly an *Eumida*.

PHYLLODOCE (*ANAITIS*) *RUBENS* GRUBE, 1880

Phyllodoce (*Anaitis*) *rubens* Grube, 1880: 229.
Paranaitis rubens: Hartman, 1959: 158.

[type locality: Japan]

The type for *Phyllodoce* (*Anaitis*) *rubens* has been lost (Hartwich, 1993). All that remains for examination is a microscope slide with a single parapodium in poor condition which lacks dorsal and ventral cirri (ZMB 3759). Although the rostrum of the chaetal shaft of the specimen show similarities to *Paranaitis*, we can only conclude that the generic affinity is uncertain.

SPECIES REFERRED TO OTHER GENERA

PHYLLODOCE JEFFREYSII (MCINTOSH, 1908)

Anaitis jeffreysii McIntosh, 1908: 73.

Treated as a junior synonym of *Anaitides longipes* Kinberg, 1866 by Parker (1987), based on an examination of type material. See also *Phyllodoce longipes* in Pleijel (1988, 1993a)

PHYLLODOCE LINEATA (CLAPARÈDE, 1870)

Anaitis lineata Claparède, 1870: 458–459, pl. 9, fig. 4.
Phyllodoce lineata: Fauvel, 1923: 147, fig. 51h–l.

No type material exists. Transferred to *Phyllodoce* by Fauvel (1923). A redescription and taxonomical remarks based on newly collected specimens were provided by Pleijel (1988).

NEREIPHYLLA PUSILLA (CLAPARÈDE, 1870)

Anaitis pusilla Claparède, 1870: 460–461, pl. 9, fig. 5.
Nereiphylla pusilla: Pleijel & Mackie, 1993: 155–160, figs 1–3.

Belongs to *Nereiphylla*. See Pleijel & Mackie (1993) for a redescription.

PHYLLODOCE ROSEA (MCINTOSH, 1877)

Anaitis rosea McIntosh, 1877: 215–216.
Anaitides rosea: O'Conner, 1987: 311–313, fig. 1, pl. 7.
Phyllodoce rosea: Pleijel, 1988:151–152, figs 8 and 9.

Transferred to *Phyllodoce* by Pleijel (1988).

***PHYLLODOCE TRUNCATA* (HARTMANN-SCHRÖDER, 1965) COMB. NOV.**

Paranaitis truncata Hartmann-Schröder, 1965: 102–104, figs 59–62.

Examination of three paratypes (HZM P 14111) confirms Pleijel's (1991) suggestion that this species belongs within *Phyllodoce*.

PHYLLODOCE CHALYBEIA GRUBE, 1880

Phyllodoce (*Anaitis*) *chalybeia* Grube, 1880: 215.
Paranaitis chalybeia: Hartman, 1959: 158.
Phyllodoce chalybeia: Pleijel, 1991: 258.

Belongs to *Phyllodoce* judging from the examination of type specimens (1 syntype, ZMB 4689).

PHYLLODOCE MADEIRENSIS LANGERHANS, 1880

Phyllodoce (*Anaitis*) *madeirensis* Langerhans, 1880: 307–308.

Belongs to *Phyllodoce* judging from the original description and the examination of probable type material (NHMW Inv. 2462) collected by Langerhans from Madeira.

PHYLLODOCE SANCTAEVINCENTIS MCINTOSH, 1885

Phyllodoce (*Anaitis*?) *sanctaevincentis* McIntosh, 1885: 166–167.

Belongs to *Phyllodoce* judging from examination of the type specimen (BMNH 1885.12.1.130). May be a junior synonym of *Phyllodoce madeirensis* Langerhans, 1880 (Pleijel, 1991).

PHYLOGENY

The parsimony analysis yielded 125 equally parsimonious trees, 132 steps trees, with a CI of 0.41 (excluding uninformative characters) and a RI of 0.70. The strict consensus tree is shown in Figure 38, and one of 125 equally parsimonious trees is selected to illustrate the character transformation and jackknife values in Figure 39. Jackknife values are presented only for the clades with a value over 50%. In the strict consensus tree the Notophyllinae, including *Notophyllum*, *Austrophyllum*, *Nereiphylla* and *Clavadoce*, is monophyletic, and have an identical composition to previous analyses (Pleijel, 1991; Eibye-Jacobsen, 1993; Orrhage & Eibye-Jacobsen, 1998), although there is some variation relating to the resolution within that clade. The monophyly of Notophyllinae is supported by the following four characters: antennae and palps broadest subproximally, nuchal organs laterally projecting, dorsal cirrophores well-defined, and ventral cirri obliquely orientated. A second clade (here, for simplicity labelled 'A') is represented by all remaining the phyllodocids, except *Mystides*, *Pseudomystides*, *Hesionura* and *Galapagomystides*, which appear in a basal polytomy (Fig. 38). Considering the putative apomorphy absence of dorsal cirri on segment 3, this may be surprising, but the group is obviously heterogeneous in a series of other characters. Furthermore, this character also appears independently in the *Eteone* group. Clade A is without precedence in the literature, although several of the various subgroups have been suggested. The resolution within *Phyllodoce* agrees with Pleijel (1993b), although *P. violacea* is collapsed in our consensus tree. Of more interest for the current study, the *Eteone* group is sister to a clade

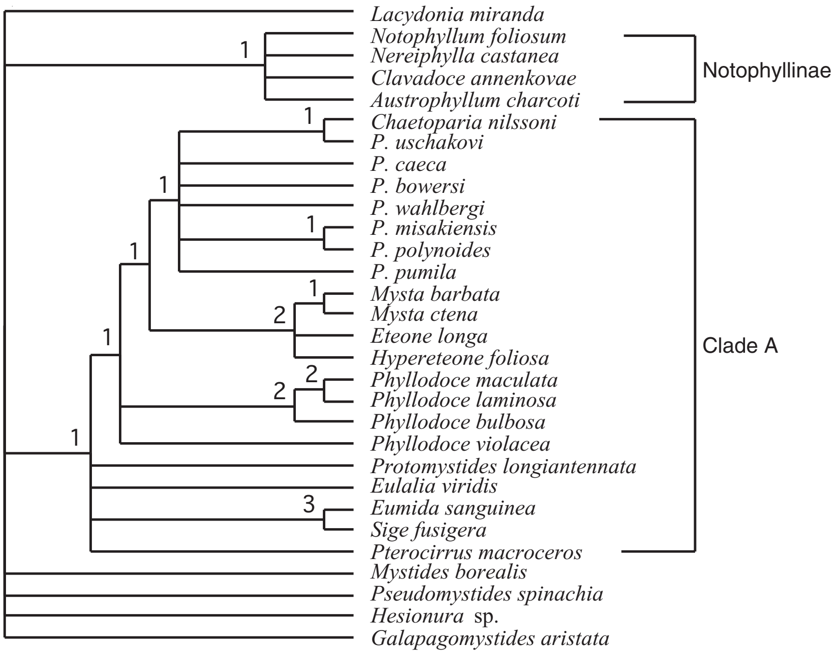

Figure 38. Strict consensus tree of the 125 equally parsimonious cladograms. Numerals above lines represent the Bremer support values.

consisting of *Paranaitis* plus *Chaetoparia*, a result which contradicts the topology of Pleijel (1991) who joined *Phyllodoce* and *Paranaitis*, but judged *Eteone* to be distant from these. However, this is in agreement with Eibye-Jacobsen (1993) and, in part, with Orrhage & Eibye-Jacobsen (1998), and there are certainly a number of striking and unique similarities between the members of *Eteone* and of *Paranaitis*. *Chaetoparia*, in our analysis, forms a subgroup within *Paranaitis*, a hypothesis which has not previously been evaluated, in that other studies employed genera as terminals. In all these, though, *Paranaitis* and *Chaetoparia* are either sister taxa or neighbours in a grade. We are currently not confident enough in this result to propose a formal synonymy of *Paranaitis* with *Chaetoparia*, but suggest that the matter warrants further investigation. Within *Paranaitis* there is otherwise no resolution in the consensus tree, except the sister group relation between *Paranaitis polynoides* and the new species *P. misakiensis*. The clade including *Phyllodoce*, the *Eteone* group, *Paranaitis* and *Chaetoparia* is supported by five apomorphies: a very short median antenna (i.e. a nuchal papilla), knob-like and retractile nuchal organs, cylindrical ventral cirri on segment 2 (i.e. not flattened as in *Eumida* or *Eulalia*), dorsal cirri with rounded ends, and well-defined dorsal cirrophores. The clade consisting of the *Eteone* group, *Paranaitis* and *Chaetoparia*, is supported by three apomorphies: proboscis lacking macropapillae, the presence of paired large papillae inside proboscis, and asymmetrical rostrum of chaetal shaft. The clade consisting of *Paranaitis* and *Chaetoparia* is supported by six characters: presence of a prostomial ligula, segment 1 covering the dorso-posterior part of the proboscis, incomplete terminal ring of proboscis papillae, dorsal fusion of segments 1 and 2, presence of pygidial papilla, and a white body colouration with additional red pigmentation.

The support based on the jackknife and Bremer values indicates a low stability in many clades. Reasonably well-supported groups include *Paranaitis misakiensis* and *P. polynoides*, the *Eteone*-group, *Phyllodoce* and *Eumida-Sige*. Clearly, resolution of the relationships between the major groups of Phyllodocidae is not easily obtained and will demand additional characters and studies and more extensive taxon sampling. At present, the monophyly of Notophyllinae seems well corroborated, as do the clades including *Chaetoparia*, *Eteone*, *Paranaitis* and *Phyllodoce*. The position of the *Mystides* group, if indeed it is a group, remains highly uncertain, and this is also the case for the positions of the species-rich genera *Eumida* and *Sige*.

ACKNOWLEDGEMENTS

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Table 2. Summary of characters. Character numbers correspond to Table 3 and Fig. 39

1. Paired antennae and palps: subproximally widest 0; basally widest 1; of equal width 2.
2. Prostomial protuberance: indistinct 0; well-defined 1.
3. Eyes: absent 0; present 1.
4. Position of eyes: superficial 0; deeply sunken 1.
5. Median antenna or nuchal papilla: absent 0; present 1.
6. Length of median antenna/nuchal papilla: papilliform 0; shorter than paired antennae 1; as long as or longer than paired antennae 2.
7. Prostomium with dorsal posterior incision: absent 0; present 1.
8. Ligula: absent 0; present 1.
9. Extension of ligula: shallow 0; deep 1.
10. Segment 1 covering postero-dorsal part of prostomium: absent 0; present 1.
11. Shape of nuchal organs: ridge-like 0; knob-like; retractile 1; laterally projecting 2; forming posterio-dorsal outgrowths on prostomium 3.
12. Proboscis division in two distinct parts: absent 0; present 1.
13. Proboscis with lateral rows of papillae: absent 0; present 1.
14. Distal part of proboscis with six rows of tubercles: absent 0; present 1.
15. Proboscis covered with micropapillae: absent 0; present 1.
16. Proboscis covered with macropapillae: absent 0; present 1.
17. Proximalmost part of proboscis with large papillae: absent 0; present 1.
18. Proboscis with chitinous papillae: absent 0; present 1.
19. Proboscis with thorny papillae: absent 0; present 1.
20. Terminal ring of papillae: absent 0; present 1.
21. Condition terminal ring of papillae: complete 0; incomplete 1.
22. Terminal ring of papillae with micropapillae: absent 0; present 1.
23. Paired large papillae inside proboscis: absent 0; present 1.
24. Dorsum segment 1: large 0; small 1.
25. Dorsal fusion of segment 1 and 2: absent 0; present 1.
26. Cirri of segment 1: absent 0; present 1.
27. Cirri of segment 2: dorsal pair as long as ventral pair 0; dorsal pair longer than ventral pair 1; ventral pair longer than dorsal pair 2.
28. Flattened ventral cirri segment 2: absent 0; present 1.
29. Dorsal cirri segment 3: absent 0; present 1.
30. Shape of dorsal cirri segment 3: normal 0; digitate 1.
31. Chaetae segment 2: absent 0; present 1.
32. Chaetae segment 3: absent 0; present 1.
33. Dorsal aciculae segment 2: absent 0; present 1.
34. Ventral aciculae segment 2: absent 0; present 1.
35. Dorsal aciculae segment 3: absent 0; present 1.
36. Dorsal aciculae median segments: absent 0; present 1.
37. Dorsal capillaries median segments: absent 0; present 1.
38. Dorsal cirri with pointed ends: absent 0; present 1.
39. Dorsal cirrophores: indistinct 0; well-defined 1.
40. Shape dorsal cirrophores: symmetrical 0; asymmetrical 1.
41. Ciliated furrow on dorsal cirrophore or dorsal cirri: absent 0; present 1.
42. Dorsal part of neuropodial lobe: as large as ventral part 0; larger than ventral part 1.
43. Orientation of ventral cirri: horizontal 0; oblique 1.
44. Distal end of pygidial cirri: pointed 0; rounded 1.
45. Pygidial papilla: absent 0; present 1.
46. Rostrum of chaetal shafts: symmetrical 0; asymmetrical 1.
47. Pigmentation: uniform colour 0; white body with red pigmentation 1; dark spots on intersegmental areas 2; white body with dark spots 3.

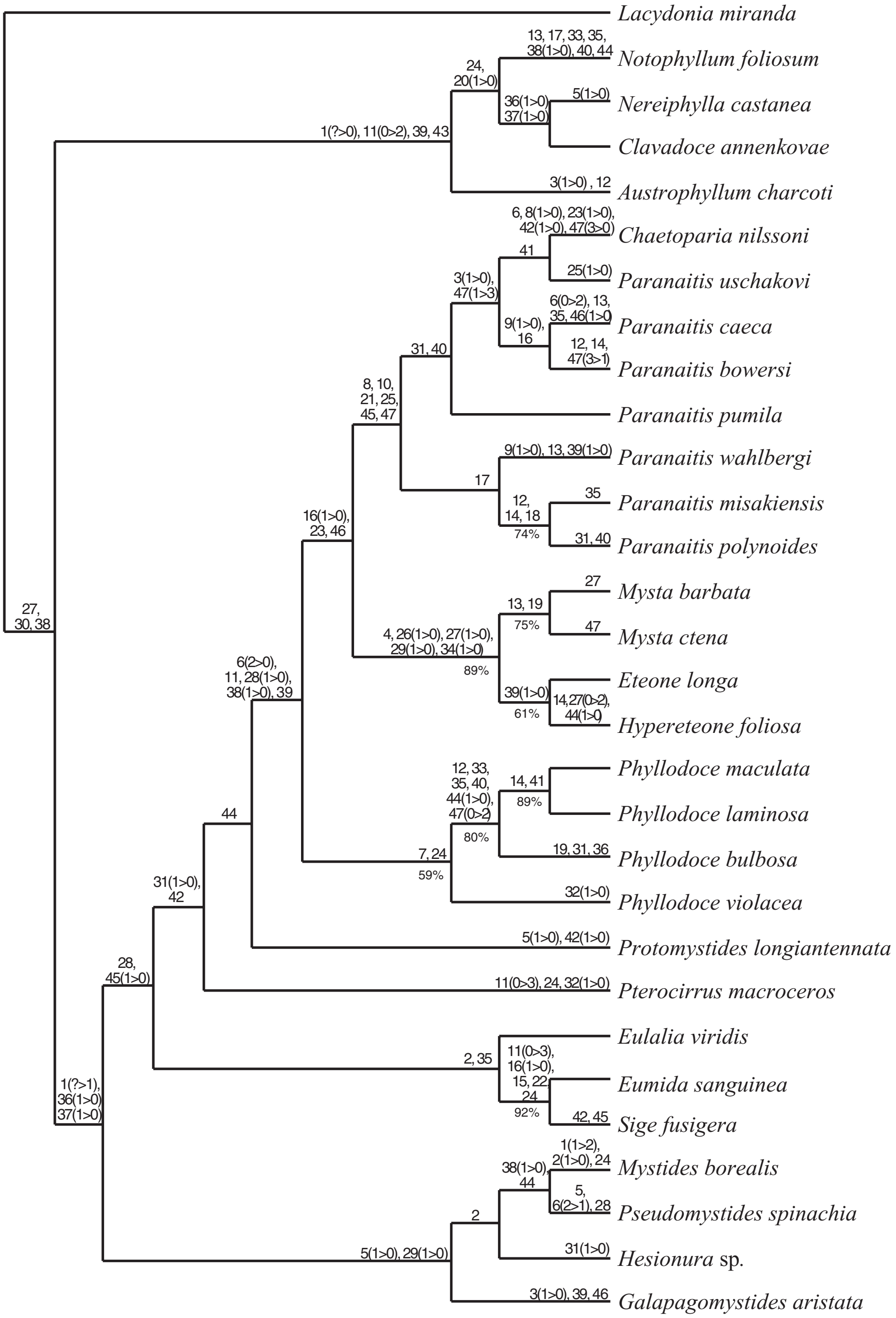

Figure 39. One of the 125 most parsimonious cladograms, based on the characters in Table 2 and matrix in Table 3. Numerals above lines represent character transformations optimized with ACCTRAN; when not noted, the transformations are from character state 0–1. Numerals below lines represent jackknife values.

Marine Biological Laboratory. Loans of specimens were kindly arranged by Penny Berents (AM), Angelika Brandt and Gisela Wegener (HZM), Torleiv Brattegard (University of Bergen), Sabine Cochrane (Akvaplan-niva), Danny Eibye-Jacobsen and Mary Petersen, ZMUC, Sandra Farrington (FSBC), Kristian Fauchald, Paul Greenhall, Chad Walter and Linda Ward (USNM), Leslie Harris (LACM), Elizabeth Hoensen and Michelle van der Merwe (SAM), Ardis B. Johnston (MCZ), Miranda Lowe and Alex Muir

Table 3. Character matrix. Character numbers correspond to Table 2 and Fig. 39. '?' denotes unknown or inapplicable states, and '/' polymorphism. *Lacydonia* is an outgroup

	Characters																																													
									1										2										3										4							
Species	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Lacydonia miranda	?	0	1	?	1	2	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1	?	0
Notophyllum foliosum	0	0	1	0	1	2	0	0	?	0	2	0	1	0	0	1	1	0	0	0	?	?	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0
Nereiphylla castanea	0	0	1	0	0	?	0	0	?	0	2	0	0	0	0	1	0	0	0	0	?	?	0	1	0	1	1	0	1	1	1	1	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0
Clavadoce annenkovae	0	0	1	0	1	2	0	0	?	0	2	0	0	0	0	1	0	0	0	0	?	?	0	1	0	1	1	0	1	1	1	1	0	1	0	0	0	1	1	0	0	0	1	?	?	0	0
Austrophyllum charcoti	0	0	0	?	1	2	0	0	?	0	2	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	?	?	?	1	1	1	1	0	0	0	1	0	?	0	0
Chaetoparia nilssoni	1	0	0	?	1	1	0	0	?	?	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	1	1	1	0	0	0	1	1	0
Phyllodoce maculata	1	0	1	0	1	0	1	0	?	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	2
Phyllodoce violacea	1	0	1	0	1	0	1	0	?	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	1	1	0	0	?	?	?	0	0	0	1	0	0	1	0	1	0	0	?
Phyllodoce laminosa	1	0	1	0	1	0	1	0	?	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	2
Phyllodoce bulbosa	1	0	1	0	1	0	1	0	?	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	2
Paranaitis uschakovi	1	0	0	?	1	0	?	1	?	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	1	1	1	1	0	1	1	1	3
Paranaitis caeca	1	0	0	?	1	2	?	1	0	1	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	1	1	0	0	0	1	1	0	1	0	1	1	0	3
Paranaitis bowersi	1	0	0	?	1	0	?	1	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1	1	?	?	?	0	0	0	1	1	0	1	0	1	?	1	1
Paranaitis wahlbergi	1	0	1	0	1	?	?	1	0	1	1	0	1	0	0	0	1	0	0	1	1	0	1	0	1	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1
Paranaitis misakiensis	1	0	1	0	1	0	?	1	1	1	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	0	0	1	0	1	1	1	1
Paranaitis polynoides	1	0	1	0	1	0	?	1	1	1	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	1	1
Paranaitis pumila	1	0	1	0	1	0	?	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	1	0	0	1	0	1	1	1	1
Mysta barbata	1	0	1	1	1	0	0	0	?	?	1	0	1	0	0	0	0	0	1	1	1	0	1	?	?	0	1	0	0	?	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0
Mysta ctena	1	0	1	1	1	0	0	0	?	?	1	0	1	0	0	0	0	0	1	1	1	0	1	?	?	0	0	0	0	?	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1
Eteone longa	1	0	1	1	1	0	0	0	?	?	1	0	0	0	0	0	0	0	0	1	0	0	1	?	?	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Hypereteone foliosa	1	0	1	1	1	0	0	0	?	?	1	0	0	1	0	0	0	0	0	1	0	0	1	?	?	0	2	0	0	?	0	0/1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Mystides borealis	2	0	1	0	0	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	0	0	?	1	1	?	1	?	0	0	0	0	0	0	0	0	1	1	0	0
Pseudomystides spinachia	1	1	1	0	1	1	0	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	?	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Hesionura sp.	1	1	1	0	0	?	0	0	?	0	0	0	0	0	0	1	0	0	0	?	?	?	?	0	0	1	1	0	0	?	0	1	0	1	0	0	0	1	0	0	0	0	0	0	?	0	0
Galapagomystides aristata	1	0	0	?	0	?	0	0	?	0	?	0	0	0	0	1	0	0	0	0	?	?	0	0	0	1	1	0	0	?	1	1	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0
Protomystides longiantennata	1	0	1	0	0	?	0	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Eulalia viridis	1	1	1	0	1	2	0	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0/1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Eumida sanguinea	1	1	1	0	1	2	0	0	?	0	3	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Sige fusigera	1	1	1	0	1	2	0	0	?	0	3	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0
Pterocirrus macroceros	1	0	1	0	1	2	0	0	?	0	3	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0

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APPENDIX

NOMENCLATURAL SYNOPSIS OF *PARANAITIS*

1865. Malmgren (1865: 94, pl. 14, fig. 31) described the genus *Anaitis* for the new species *A. wahlbergi*.

1867. Malmgren (1867: 20) described *Anaitis kosteriensis*.

1870. Claparède (1870: 458–461, pl. 9, figs 4–6) described *Anaitis lineata*, *A. peremptoria* and *A. pusilla*.

1874. Ehlers (1874: 294) described *Eulalia imbricata*.

1877. McIntosh (1877: 215–216) described *Anaitis rosea*.

1879. Webster (1879: 131–132, pl. 1, figs 8, 9) described *Anaitis speciosa*.

1880. Grube (1880: 215, 229) described *Phyllodoce* (*Anaitis*) *chalybeia and P.* (*A.*) *rubens*.

1880. Langerhans (1880: 307–308) described *Phyllodoce* (*Anaitis*) *madeirensis*.

1885. Verrill (1885: 433–434) described *Anaitis formosa* and *A. picta*.

1885. McIntosh (1885: 166–167) described *Phyllodoce* (*Anaitis*) *sanctaevincentis*.

1887. Ehlers (1887: 140–142, pl. 40, figs 7–9) described *Phyllodoce* (*Anaitis*) *papillosa*.

1903. Moore (1903: 426–428, pl. 23, fig. 1, 1a) described *Eumida caeca*.

1905. Willey (1905: 262, pl. 3, figs 57–60) described *Anaitis zeylanica*.

1908. McIntosh (1908: 73, 110–111, pl. 58, fig. 11, pl. 69, figs 11–12, pl. 77, fig. 20) described *Anaitis jeffreysii* and *Mystides lizziae*.

1909. Moore (1909: 339–342, pl. 16, figs 19–21) described *Anaitis polynoides*.

1914. Bergström (1914: 156–158, textfig. 52, pl. 1, fig. 1) synonymized *M. lizziae* with *A. kosteriensis*.

1914. Southern (1914: 66–68) pointed out that *Anaitis* was preoccupied by *Anaitis* Duponchel, 1829 (in Godart & Duponchel, 1829) for a group of geometrid moths, and proposed the replacement name *Paranaitis*. He also transferred *A. jeffreysii* to *Paranaitis*.

1923. Fauvel (1923: 157–158, fig. 56a–c) transferred *A. kosteriensis* and *A. lineata* to *Phyllodoce*.

1927. Benham (1927: 77–78, pl. 1, figs 27–31) described *Phyllodoce bowersi*.

1930. Monro (1930: 72–73) transferred *P. bowersi* to *Phyllodoce* (*Anaitis*).

1936. Hartman (1936: 117) transferred *A. polynoides* to *Paranaitis*.

1959. Hartman (1959: 158–159) transferred *P.* (*A.*) *chalybeia*, *A. formosa*, *A. jeffreysii*, *A. lineata*, *P.* (*A.*) *papillosa*, *A. picta*, *A. pusilla*, *A. speciosa*, *P.* (*A.*) *rubens*, *A. rosea* and *A. zeylanica* to *Paranaitis*.

1960. Day (1960: 298, fig. 5a–c) described *Phyllodoce* (*Anaitis*) *capensis*.

1960. Knox (1960: 113, figs 137–140) described new subgenus *Eulalia* (*Euphylla*) for the new species *E.* (*E.*) *benthicola*.

1962. Eliason (1962: 234–235) transferred *A. kosteriensis* to *Paranaitis*.

1962. Uschakov (1962: 140–141, pl. 1, fig. B) transferred *P.* (*A.*) *bowersi* to *Anaitis*.

1963. Pettibone (1963: 75–77, fig. 17a) synonymized *A. formosa* and *A. picta* with *P. speciosa*.

1964. Hartman (1964: 49, pl. 15, figs 1, 2) transferred *A. bowersi* to *Anaitides*.

1965. Hartmann-Schröder (1965: 102–104, figs 59–62) described *Paranaitis truncata*.

1967. Day (1967: 148, fig. 5.2.q–s) transferred *P.* (*A.*) *capensis* to *Phyllodoce* (*Paranaitis*).

1972. Averincev (1972: 106) transferred *A. bowersi* to *Paranaitis*.

1972. Uschakov (1972: 142–143, pl. 7, figs 5–7) described *Paranaitis caecum*.

1975. Hartmann-Schröder (1975: 57–59, figs 19–21) described subfamily Paraeteoninae and genus *Paraeteone* for the new species *P. abyssalis*.

1984. Hutchings & Murray (1984: 24–26, fig. 9) described genus *Compsanaitis* for new species *C. inflata*.

1984. Perkins (1984: 563–565, fig. 4) described *Paranaitis gardineri*.

1987. O'Connor (1987: 311–313, fig. 1, pl. 7) transferred *Anaitis rosea* to *Anaitides*.

1988. Pleijel (1988: 151–152) transferred *Anaitis rosea* to *Phyllodoce*.

1991. Eibye-Jacobsen (1991: 129) transferred *E. caeca* to *Paranaitis*. Thereby *Paranaitis caecum* Uschakov, 1972 became a junior homonym to Moore's species, and Eibye-Jacobsen introduced the replacement name *P. uschakovi* for Uschakov's species.

1991. Pleijel (1991: 237–238) synonymized *Euphylla*, *Compsanaitis* and *Pareteone* with *Paranaitis*, and Pareteoninae with Phyllodocinae. He also transferred *P.* (*A.*) *capensis* to *Paranaitis*.

1993. Pleijel & Mackie (1993: 155–160, figs 1–3) transferred *P. pusilla* to *Nereiphylla* and designated neotype material.