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Revision of the Genus *Micronereis* (Polychaeta: Nereididae: Notophycinae)

HANNELORE PAXTON

School of Biological Sciences, Macquarie University,
North Ryde, N.S.W. 2113, Australia.

ABSTRACT. The genus *Quadricirra* Banse, 1977 is not recognized, since its principal diagnostic character, the presence of accessory parapodial cirri, is sexually dimorphic and cannot be correlated with other characters; thus *Micronereis* is the sole genus of the subfamily Notophycinae. A new species, *M. piccola*, is described and *M. siciliensis* and *M. bodegae* are synonymized with *M. variegata* and *M. nanaimoensis* respectively. A key to males and descriptions of all species are provided. The Notophycinae appears to be the most derived subfamily of Nereididae, characterized by a combination of epitokal modifications retained from their nereidid relatives and specializations acquired as members of the meiofauna.

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The polychaete family Nereididae is divided into four subfamilies (Banse, 1977a, b): the Nereidinae, Namanereidinae, Gymnonereidinae and Notophycinae. Banse (1977a) recognized the latter subfamily, originally proposed as Notophycidae by Knox and Cameron (1970) for *Notophycus* only, to include the genera *Micronereis* (and its synonyms *Notophycus* and *Phyllodocella*) and *Quadricirra*. *Quadricirra* Banse, 1977 was erected for *M. halei* Hartman, 1954 from South Australia and an indeterminate species from the Suez Canal that had been reported as an aberrant specimen of *M. variegata* by Fauvel (1927). *Quadricirra* was distinguished from *Micronereis* by the presence of accessory cirri on the lower notopodia and upper neuropodia in the former genus and their absence in the latter. A new species from north-west Australia was described as *Q. bansei* by Hartmann-Schröder (1979). The latter author recognized that the accessory cirri were present only in the males of *Q. bansei* and amended the genus accordingly.

While identifying specimens of Notophycinae I realized that the presence of accessory parapodial cirri is a male epitokal modification. Epitoky is characteristic of the Nereididae; most species metamorphose and swarm for breeding (Clark, 1961). Epitoky in species of Notophycinae has been overlooked, since the changes are relatively minor compared to some other nereidids. However, as Clark (1961:200) pointed out: "The structural modifications associated with epitoky may be no more than an elongation of the chaetae, or it may involve the wholesale reconstruction of the musculature and modification of the sense organs as well as the

enlargement of the parapodia and replacement of the chaetae."

Although notophycines have a wide geographical distribution (Fig. 1), not many specimens have been reported. All known species are small (up to 15 mm) with relatively few segments (up to 26), and are thus members of the meiofauna. The rarity of their collection is attributed to their small size and preferred habitat. Most specimens have been collected in the littoral zone or in lagoons in depths from 0 to 3 m, sometimes by scuba divers with hand-held corers. The deepest record is that of a specimen of *M. eniwetokensis* which was collected from a depth of 30 m (Reish, 1961). The worms are generally associated with algae, which appear to be their main food source.

The morphology and taxonomy of the Notophycinae have been unclear. The aim of this paper is to examine and describe the characteristics of the notophycines in order to distinguish features held in common with other nereidid subfamilies from those that arose as meiofaunal adaptations, and to review their taxonomy and to provide descriptions for all known species.

Materials and Methods

The material examined was loaned by and/or is deposited in the following institutions: Allan Hancock Foundation, University of Southern California, Los Angeles (AHF); Australian Museum, Sydney (AMS); British Museum (Natural History), London (BM); CSIRO Division of Fisheries and Oceanography, Cronulla (CSIRO); Canterbury Museum, Christchurch

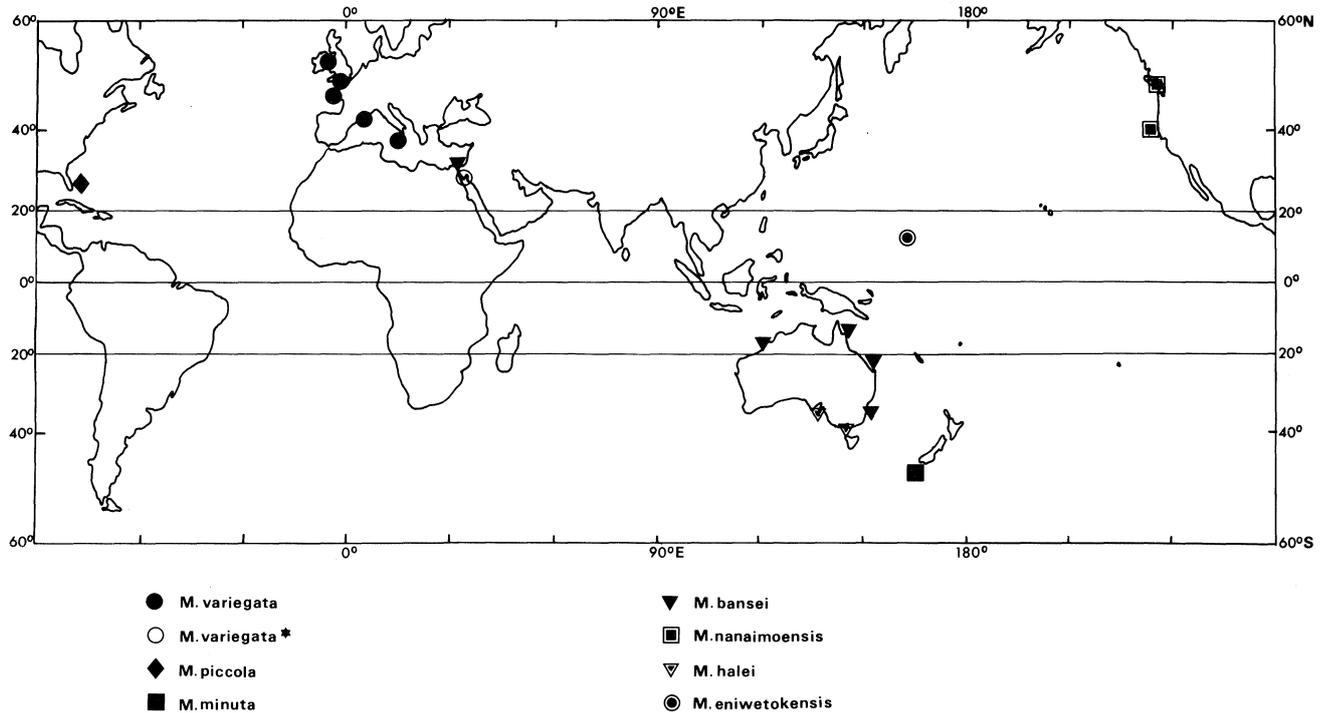


Fig. 1. Geographic distributions of *Micronereis* spp. *Reported as *M. variegata*, but possibly *M. bansei* (see text).

(CM); Istituto Policattedra di Biologia Animale dell' Università di Catania (IPC); National Museum of Victoria, Melbourne (NMV); University of Canterbury, Zoology Department, Christchurch (UC); Smithsonian Institution, Washington (USNM); Western Australian Museum, Perth (WAM).

The specimens were examined with a stereoscopic dissecting microscope or temporarily mounted in 50% (v/v) glycerine and examined with a compound microscope. To examine the jaw apparatus, it was often necessary to make a dorsal incision and dissect out the complete pharynx and buccal tube, which were later permanently mounted. All drawings were prepared with the aid of a camera lucida.

The references listed are extensive but not complete; only those providing new records or information are included.

GENERAL CHARACTERS

The general characters of Notophycinae and information on their life histories are discussed below and compared in Table 1.

General Morphology of Atokes

Prostomium. The prostomium (Figs 3, 14) is round to subquadrate, sometimes weakly bilobed, and about as long as wide. It bears two pairs of eyes; the anterior pair is larger than the posterior pair and has more obvious lenses. The prostomium lacks antennae but bears at the anterior margin a pair of ventrally directed,

rounded protrusions (Figs 15, 28). These structures have been referred to as palps (Berkeley and Berkeley, 1953; Hartman, 1954; Reish, 1961; Cantone, 1971; Hartmann-Schröder, 1979), as upper lips (Rullier, 1954), as frontal lobes (Fauchald and Belman, 1972), and as epidermal lobes (Banse, 1977a). These protrusions were observed as ciliated organs in six-setiger larvae of *Micronereis variegata* (Rullier, 1954), and are similar to the development of the palps of *Nereis diversicolor*, belonging to the nominate subfamily, which begin to develop in four-setiger larvae (Dales, 1950). I therefore follow the majority of authors and term the structures palps. The paired palps are spherical to subconical, small to very small so that they are sometimes difficult to observe. The notophycine palps differ from those of other nereidids in occupying a more central position and lacking palpostyles. The lack of palpostyles, which only develop in *N. diversicolor* when the young worm consists of 18 setigers (Dales, 1950), is perhaps a neotenic character in notophycines, related to their small size.

Peristomium or tentacular segment. The peristomium is very short, forming a distinct apodous segment. It is usually not clearly visible, but may be seen dorsally as a narrow ring (Fig. 14); it is only distinct ventrally when the anterior buccal tube is everted (Fig. 16). There are four pairs of tentacular cirri inserted lateral to the prostomium (Fig. 3). The anterior two pairs, arising in front of the anterior pair of eyes, have been referred to as lateral antennae by some authors. The anterior two pairs of tentacular cirri are shorter than the posterior two pairs which arise from the

peristomium. The fourth pair may be greatly elongated in some species, such as *M. eniwetokensis* and *M. bansei*, where they reach setiger 4–5 in some specimens (Fig. 14). Rullier (1954) has shown that the four pairs of tentacular cirri in *Micronereis variegata* are homologous to those of other nereidids and develop in the same way.

Proboscis. In contrast to those of other nereidids, the notophycine proboscis is not fully eversible. Yet its morphology and armature are closer to the typical nereidid proboscis than has generally been accepted (Fig. 16); terminology follows Dales (1962). The muscular pharynx lies within the anterior three to five segments and contains a pair of jaws. The buccal tube lies between the pharynx and the mouth and like the typical nereidid buccal tube, contains denticles or paragnaths. However, the notophycine buccal tube differs markedly in that it cannot be turned completely inside out: only the anterior part can be protruded. Although the pharyngeal jaws are movable, the pharynx cannot be everted.

The paired jaws are of two types: (1) bulbous proximal area with a distal apex and three to five teeth on the cutting edge of the distal half (Figs 16, 18); or (2) greatly reduced proximal area with a prolongation beyond the distal apex (Fig. 12). The former shortened type of jaw is found in all adult females and in males of four species, while the latter prolonged type of jaw is found in males of the remaining four species (Table 1).

The notophycine paragnaths are very lightly sclerotized and thus difficult to observe; they have not been seen in some species. The anterior part of the buccal tube may contain numerous paragnaths, arranged in regular rows (Fig. 16), which develop from simple cones in juveniles into crown-shaped structures with four to eight cusps in adults (Figs 4, 17). The number of cusps on the crown is of limited taxonomic value (Table 1). The numerous crown-shaped oral paragnaths are reminiscent of mollusc radulae. However, Rullier (1954) has pointed out that their function is different. He found that the gut contents of *M. variegata* were irregular fragments of algae rather than a ground-up pulp and suggested that the oral paragnaths catch and retain algal fragments which are then torn up by the jaws.

The posterior part of the buccal tube contains two to six paragnaths. The most constant of these are the median paragnaths which are found at the junction of the buccal tube and the pharynx and consist of two light yellow bars with two darker, irregularly shaped denticles (Fig. 16). The orientation of the bars changes with pharyngeal movement, so that the bars may lie in a straight line and appear as one (Figs 16, 34), or they may form a V-shape (Fig. 5). Rullier (1954) described up to four additional accessory paragnaths for *M. variegata*; they were associated with the median one but were irregular in shape and varied in number. They have not been observed in any of the other species.

Since the paragnaths of the anterior part of the buccal tube of notophycines correspond to those of the oral ring of typical nereidids and the paragnaths of the

posterior part of the buccal tube correspond to those of the maxillary ring, it is proposed that the conventional nereidid terminology be applied and the crown-shaped paragnaths be referred to as oral, and the median and accessory paragnaths as maxillary paragnaths.

Parapodia. The first two setigerous segments are short and their parapodia are uniramous; the neuropodia have long setal lobes with ventral cirri; dorsal cirri are lacking. The first pair of parapodia is directed strongly anteriorly and ventrally, and the second pair to a lesser degree. The following parapodia are biramous, with notopodia and neuropodia widely separated and directed laterally (Fig. 6). The parapodia are often ciliated (Fig. 22), and have dorsal and ventral cirri, but no ligules. Structures referred to by previous authors as ligules or digitate lobes are considered to be sexually dimorphic accessory cirri (see below).

Each of the parapodial rami is supported by a single yellow aciculum. The setae diverge from the aciculum in fan-shaped bundles. Those of the anterior uniramous setigers are shorter and finer than those of the following ones. The setae are spinigers (Fig. 8); the articulation is generally homogomph but approaches in some cases the hemigomph condition. The shaft of a seta is transparent and the core may have distinct, weak, or no septa. The distal end of the shaft is crenulated, ranging from distinct (Fig. 29) to barely visible. The blades of *M. minuta* are coarsely serrated while those of all other known species are finely serrated. The structure of the serrations is best seen in *M. nanaimoensis* (Fig. 29); each serration ends in a hair-like extension that is twice as long as the serration. The extensions may be present in all species with finely serrated blades but are not always clearly visible.

Segmental eyespots. Small pigment spots on the posterolateral corners of each segment from setiger 4 onwards were observed in some individuals of four species (Table 1). The pigment spots resemble the eye in shade and density and are interpreted as segmental eyespots. The degree of pigmentation differs, so that for a given species the eyespots range from absent to well-developed. They were observed in some males, females and juveniles and cannot be correlated with sex or maturity.

Pygidium. The pygidium is a small lobe with a dorsal anus and a pair of anal cirri.

Sexual Dimorphism and Epitokal Modifications

Modifications common to both sexes. Enlarged eyes are found in both males and females of *M. bansei*; in the females, the enlargement causes the fusion of the anterior and posterior eyes, yet they remain in a dorsal position (Fig. 14); in the males the enlargement proceeds so far that the anterior eyes take up a ventral position (Fig. 15).

Modifications in males. The males of five species (Table 1) have copulatory hooks on the neuropodia of setiger 3 which aid in holding on to the female during

Table 1. Comparison of species of *Micronereis*

Species	<i>M. variegata</i>	<i>M. piccola</i>	<i>M. minuta</i>
Length (mm)	♂ ♂ 2-4 ♀ ♀ 4-8	♂ 1.7 ♀ 2.0*	♂ 3.6 ♀ ♀ up to 5.8
Setigers (number)	♂ ♂ 16-21 ♀ ♀ 21-23	♂ 15 ♀ 16*	♂ 22 ♀ ♀ 24
Oral paragnaths	present	present	present
Number of cusps on crown	4	4	?
Maxillary paragnaths	present	present	present
Median	2 bars	2 bars	2 bars
Accessory	up to 4	not observed	not observed
Segmental eyespots	not observed	present	not observed
Spiniger			
Shaft	no septa	faint septa	no septa
Blade	finely serrated	finely serrated	coarsely serrated
Male characteristics			
Jaws (type)	prolonged	prolonged	prolonged
Accessory parapodial cirri	absent	absent	present
Copulatory hooks on setiger 3	present	present	absent
Number	2	2-3	—
Ornamentation of hook	5-7 spines	4-6 spines	—
Simple setae	absent	absent	present
Other type of setae	absent	falcigers	absent
Female characteristics			
Mucous egg cocoon	present	†	†
Diameter of cocoon (mm)	3-5	†	†
Number of eggs per cocoon	20-80	†	†
Diameter of egg (µm)	240-350	†	†
Colour of eggs	red	†	†
Distribution (Fig. 1)	France; England; Italy; ? Sinai Peninsula	Bahamas	Snares Island, New Zealand

*not fully grown †unknown

coupling. *M. nanaimoensis* has the most elaborate hooks, which have a crest with several spines (Fig. 30), while the hooks of the other four species are distally more or less recurved and bear several spines but no crest (Fig. 9).

Parapodial appendages (Fig. 11) are found on the lower side of the notopodia and the upper side of the neuropodia in males of four species (Table 1). These appendages were regarded as ligules by Fauvel (1927), as cirri by Gravier (1934), as digitate lobes by Hartman (1954) and as accessory cirri by Banse (1977a). Parapodial ligules are typical for members of the nominate subfamily; they are coelomic extensions of the parapodial rami. In contrast, the notophycine structures are attached appendages that can easily separate (Fig. 20). The appendages are thin-walled with a well-developed capillary network; they constitute branchiae or cirri and are referred to herein as accessory cirri. They are absent in young atokous males of *M. halei* and develop at the onset of epitoky.

The males of most species of *Micronereis* undergo some setal changes associated with maturity (Table 1). In its simplest form, the change consists of the addition of slender simple setae, as in *M. nanaimoensis* and *M. minuta*. The change in the setal pattern may involve the transformation of spinigers to compound falcigers, as in *M. halei* (Fig. 32). Partly transformed males possessed some spinigers in which the blades had very fine distal tips which were often bent (Fig. 33). These spinigers become progressively replaced or changed into falcigers. *M. bansei* is the only known species in which spinigers are replaced by simple setae (Fig. 27) and falcigers (Fig. 26).

Modifications in females. Mature females are generally larger than males and consist of a greater number of setigers. The parapodial lobes are enlarged and inflated and have a bulbous area or papilla at the base of the dorsal cirrus (Fig. 23); this presumably serves as a gonopore for the passage of eggs. The dorsal cirri of the median to posterior dorsal cirri may enlarge and

<i>M. bansei</i>	<i>M. nanaimoensis</i>	<i>M. halei</i>	<i>M. eniwetokensis</i>
♂♂ up to 2.1 ♀♀ up to 3.8	♂♂ up to 13 ♀♀ up to 15	♂♂ up to 6.7 ♀ †	♂ 1.7* ♀ 1.8*
♂♂ 20 ♀♀ 22	♂♂ 23 ♀♀ 26	♂♂ 27 ♀ †	♂ 14* ♂ 18*
present 6-8	present 5	not observed —	not observed —
present 2 bars	not observed —	not observed —	present 2 bars
not observed	not observed	not observed	not observed
present	not observed	present	present
faint septa finely serrated	distinct septa serrated	no septa finely serrated	faint septa finely serrated
shortened present	shortened absent	shortened present	shortened absent
present 3	present 5 or more	absent —	absent —
4-6 spines	crested	—	—
present falcigers	present absent	absent falcigers	absent absent
present 1.4-1.6	present 10-20	†	†
150-190	many hundreds	†	†
100	200	†	†
pink	green	†	†
Western Australia, Queensland New South Wales, Australia; Port Said, Egypt	British Columbia, Canada; Washington, California, U.S.A.	South Australia, Victoria Australia	Eniwetak Atoll, Marshall Islands

develop lamellar folds, as in *M. variegata* and *M. bansei* (Fig. 23), or may remain small throughout, as in *M. nanaimoensis*.

TAXONOMY

Family NEREIDIDAE Johnston, 1865

Subfamily NOTOPHYCINAE Knox and Cameron, 1970

Type-genus: *Micronereis* Claparède, 1863.

Micronereis Claparède

Micronereis Claparède, 1863:57. Type-species: *M. variegata* Claparède, 1863, by monotypy. Gender: feminine.

Notophycus Knox and Cameron, 1970:75. Type-species: *N. minutus* Knox and Cameron, 1970, by monotypy and original designation. = *Micronereis minuta*.

Phyllodocella Fauchald and Belman, 1972:107. Type-species: *P. bodegae* Fauchald and Belman, 1972, by monotypy. = *Micronereis nanaimoensis* Berkeley and Berkeley, 1953. *Quadricirra* Banse, 1977a:125. Type-species: *Micronereis halei* Hartman, 1954, by original designation.

Remarks: Both *Notophycus* Knox and Cameron and *Phyllodocella* Fauchald and Belman were referred to *Micronereis* by Banse (1977a). The principal diagnostic character of *Quadricirra*, the presence of accessory parapodial cirri, is found in epitokous males of four species (Table 1), but is absent in atokous males and females. Since this sexually dimorphic character cannot be correlated with other diagnostic characters, e.g. type of jaw and presence of copulatory hooks, it is not considered to be of generic significance. Thus *Quadricirra* is considered to be a junior synonym of *Micronereis*, leaving the latter as the sole genus of the subfamily Notophycinae. *Quadricirra halei* (Hartman, 1954) and *Q. bansei* Hartmann-Schröder, 1979 are referred to *Micronereis*. The specimen from the Suez

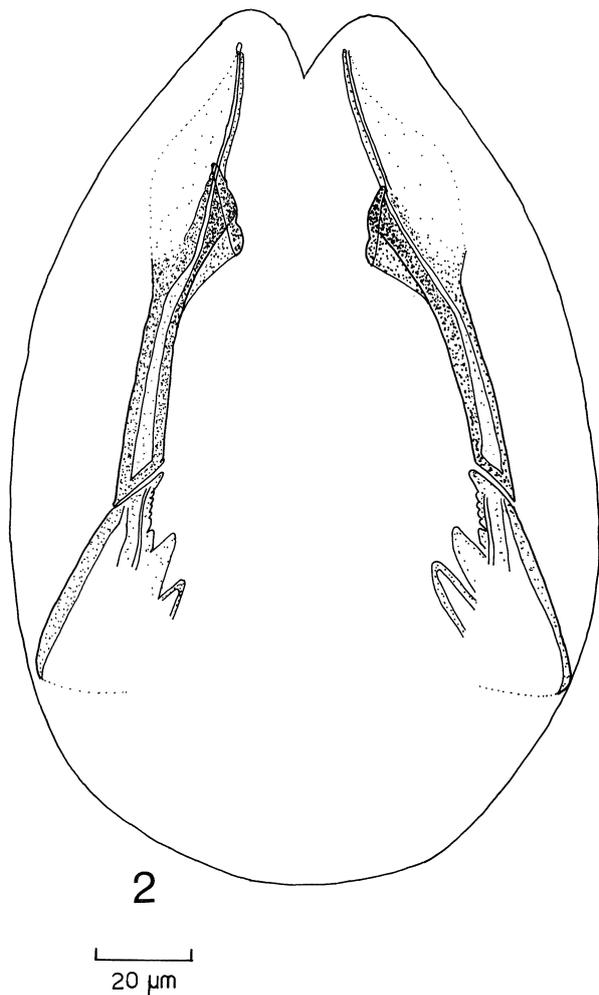


Fig. 2. *Micronereis variegata*, jaws of male (pressure of mounting caused fracture of distal prolongation). (Holotype of *M. siciliensis*, IPC).

Canal reported as *Quadricirra* sp. by Banse (1977a) was found to agree with *M. bansei*.

Micronereis variegata Claparède
Figs 1, 2

Micronereis variegata Claparède, 1863:57 pl. 11:figs 5-7, (Normandy, France); 1864:582, pl. 8:figs 4, 4a.—Quatrefages, 1865:578.—Saint-Joseph, 1888:268.—Racovitza, 1893:1390; 1894:153.—Caullery and Mesnil, 1898:—Fauvel, 1900:315; 1923:332, fig. 128a-f.—Elwes, 1909:350.—McIntosh, 1910:261, fig. 63, pl. 86:fig. 8.—Regnard, 1913:91, figs 3-11.—Herpin, 1925:119.—Rullier, 1954:195, figs 1-43.—Southward, 1956:263.—Reish, 1961:273.—Banse, 1977a:121.—Amoureux *et al.*, 1978:81.
Micronereis siciliensis Cantone, 1971:926, figs 4-9 (Catania, Sicily).—Banse, 1977a:121.

Material examined. *England*: Plymouth—1 ♂ and 1 ♀ (USNM 35680). *Sicily*: Catania, Cannizzaro—♂ HOLOTYPE and ALLOTYPE of *M. siciliensis* (IPC).

Diagnosis. Jaws of males of prolonged type, shortened in adult females. Accessory parapodial cirri absent. Spinous copulatory hooks present in males. Homogomph spinigers; shafts without septa; blades finely serrated.

Description. Length of males 2–4 mm (16–21 setigers), females 4–8 mm (21–23 setigers). Prostomium rounded with pair of ventral palps and 2 pairs of eyes with lenses. Four pairs of short, subulate tentacular cirri. Oral paragnaths crown-shaped with 4 cusps (Rullier, 1954, fig. 13); up to 6 irregularly shaped maxillary paragnaths, of which median ones are most constant (Rullier, 1954, figs 10, 12). Pair of sexually dimorphic jaws (see below). Biramous parapodia sometimes ciliated, with subulate dorsal and ventral cirri; homogomph spinigers: shafts without septa, blades finely serrated. Pygidium with pair of anal cirri.

Male characteristics. Jaws with 3–4 proximal teeth and distal prolongation (Fig. 2). Setiger 3 with 2 neuropodial copulatory hooks each with 5–7 spines. No obvious epitokal changes.

Female characteristics. Jaws of juveniles of prolonged type, jaws of adult females with shortened type with 3–4 teeth.

Biology. Rullier (1954) gave a detailed account of the reproduction and development of *M. variegata*.

Remarks. It was not possible to locate the holotype of *M. variegata* or to obtain specimens from the type locality. However, the specimens from Plymouth agree well with the original description and presumably they are identical.

Cantone (1971) described *M. siciliensis* from Catania, Sicily. She stated that it differed from *M. variegata* in (1) the shape of the male jaw, (2) the presence of palps in the female only, and (3) the copulatory hooks being more recurved. She also mentioned that a capillary seta was found in the posterior segments. Examination of the type material of *M. siciliensis* showed the following: (1) The jaws of the male holotype were figured upside down and misinterpreted by Cantone (1971, fig. 9). The pressure of the slide has fractured the distal prolongation at the point where it breaks off in females, so that the jaw appears to consist of different pieces. When the jaws are viewed in their proper orientation and the weakly sclerotized detail is observed, they are characteristic of *M. variegata* (Fig. 2). (2) Although the palps are more prominent in the female allotype, they are also present in the male holotype. (3) The holotype has only one uniramous segment, while the allotype has the usual two. This condition is considered to be a case of abnormal development. The copulatory hooks are present on the first biramous segment, which in this case is setiger 2 instead of 3. The distal part of the copulatory hook is recurved normally and has about 5 spines, which is within the range of *M. variegata*. No capillary setae were found in the posterior setigers of the complete holotype; the allotype is incomplete.

Banse (1977a) considered the low number of segments, “especially in the male”, as another

distinguishing feature of *M. siciliensis*. The holotype consists of 15 setigers but it lacks setiger 1, so that a normal male would have at least 16 setigers, while the two females were incomplete and the number of setigers is not known. The Mediterranean population of *M. variegata* was reported by Racovitza (1893) as attaining 16–17 setigers in the males.

Based on these observations, it is concluded that the specimens described as *M. siciliensis* agree with *M. variegata* and the former name is considered as a junior synonym of the latter.

Amoureux *et al.*, (1978) reported *M. variegata* from the Sinai Peninsula. The authors stated that the specimens had shortened jaws and lacked accessory parapodial cirri. Unfortunately, the specimens could not be examined during the present study. Since *M. bansei* occurs at Port Said, it is possible that the specimens from the Sinai Peninsula are females of *M. bansei* rather than *M. variegata*.

Distribution: France, England, Italy and questionably Sinai Peninsula (Fig. 1).

Micronereis piccola n. sp.

Figs 1, 3–10

Material examined. *Bahamas:* Cherokee Sound, Abaco, c. 26°N, 77°W, from submerged plastic sponges, Spring 1972, A. Schoener, collector—♂ HOLOTYPE (USNM 54514) and 1 ♂ and 4 ♀ PARATYPES (USNM 60505–8); Bimini, south portion of Bimini Lagoon, c. 25°43'N, 79°16'W, March and April 1970 and January 1971, A. Schoener, collector—1 ♂ and 3 ♀ PARATYPES (USNM 60509–10) and 2 additional specimens (USNM 60511).

Diagnosis. Jaws of males of prolonged type, proximal teeth absent; shortened type in adult females. Accessory parapodial cirri absent. Extended notopodial lobes above dorsal cirrus with several setae. Spinous copulatory hooks present in males. Compound homogomph spinigers with weak septa in shafts; finely serrated blades in females and atokous males; spinigers and falcigers in epitokous males.

Description. Length of male holotype 1.7 mm for 15 setigers; width 0.25 mm without and 0.60 mm with parapodia. Length of young male paratype 1.0 mm for 12 setigers and of female paratypes 0.95–2.0 mm for 14–16 setigers.

Prostomium rounded with pair of small ventral palps and 2 pairs of eyes with lenses, anterior pair larger than posterior pair (Fig. 3). Four pairs of cirriform tentacular cirri; 2 anterior pairs shortest, about 1.5 times length of prostomium, 3rd pair twice length of prostomium, 4th and most posterior pair longest, reaching setiger 4–5. Oral paragnaths crown-shaped with 4 cusps (Fig. 4), maxillary paragnaths 2 light bars (Fig. 5), pair of sexually dimorphic jaws (see below). Biramous parapodia with notopodia and neuropodia each with single aciculum; sparse ciliation observed in young paratypes; notopodia with bulbous extensions above dorsal cirri; long, cirriform dorsal and ventral cirri (Figs 6, 7). Each fascicle with about 10 homogomph spinigers,

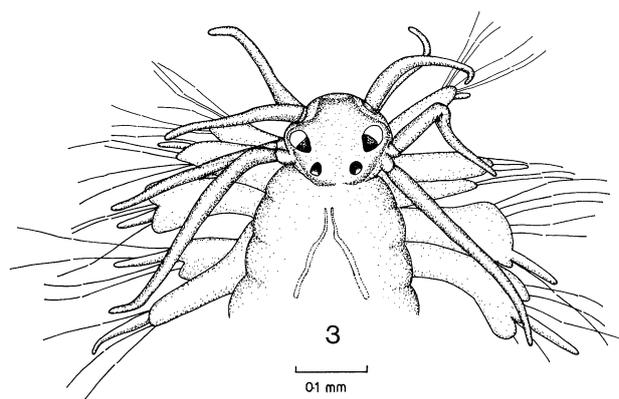


Fig. 3. *Micronereis piccola*, n.sp., anterior end of male, dorsal view. (Holotype, USNM 54514).

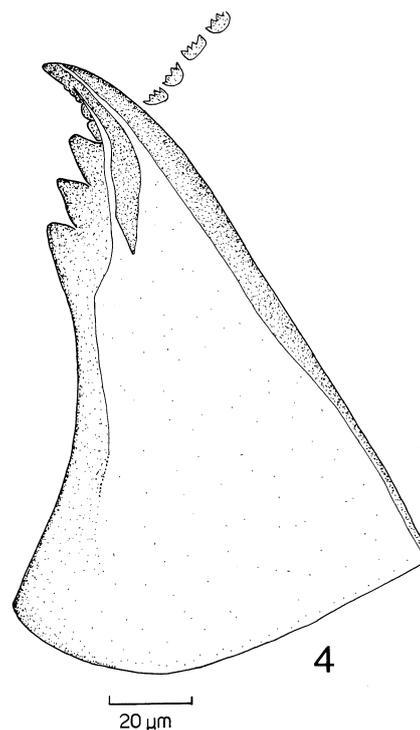


Fig. 4. *Micronereis piccola*, n.sp., jaw and oral paragnaths of adult female. (Paratype 1, USNM 60505).

superior 2–3 projecting above dorsal cirrus; shafts with weak septa (visible with 1000× magnification), blades finely serrated (Fig. 8). Segmental eyespots in some

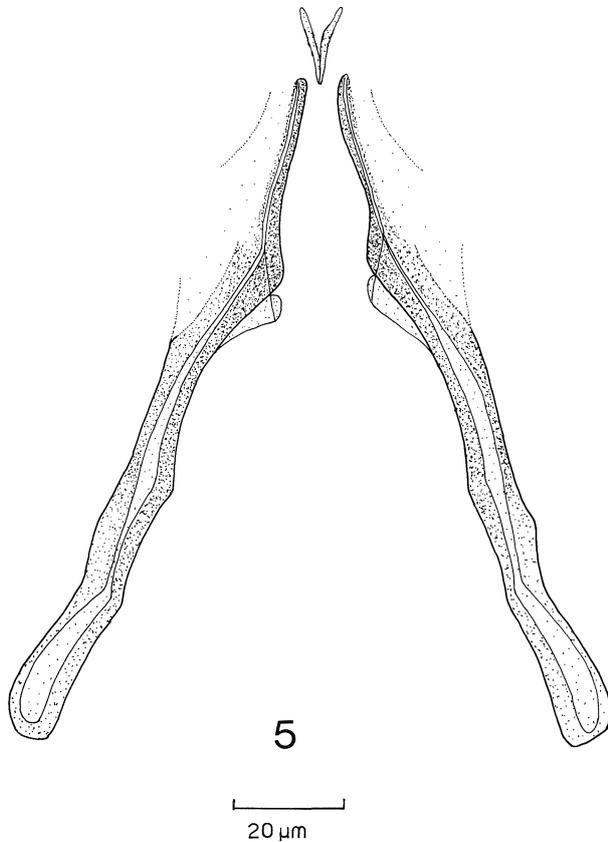


Fig. 5. *Micronereis piccola*, n.sp., jaws and maxillary paragnaths of adult male. (Holotype, USNM 54514).

specimens from setiger 4 onwards. Pygidium with pair of long cirriform anal cirri.

Male characteristics. Jaws of prolonged type, proximal teeth absent (Fig. 5). Setiger 3 with 2–3 neuropodial copulatory hooks, each with 4–6 spines (Fig. 9). Accessory parapodial cirri absent. Spinigers transformed into falcigers during epitoky (Fig. 10).

Female characteristics. Jaws of juveniles with distal prolongation and proximal teeth; adult females with shortened jaws with 3 teeth (Fig. 4).

Biology. The male holotype contained sperm morulae and free spermatozoa. Epitoky was in an early stage, as parapodia 6 and 7 had few falcigers; a less mature male paratype had only compound spinigers. The female paratypes were immature.

Remarks. The presence of prolonged jaws and copulatory hooks in the males links *M. piccola* to *M. variegata*. *M. piccola* differs in having jaws of the males lacking proximal teeth, and in having longer tentacular, dorsal and ventral cirri, more extended lobes above the

dorsal cirri with several notopodial setae, and septa in the shafts of the compound setae.

The name *M. piccola* refers to the small size of this species.

Distribution. Bahamas (Fig. 1).

Micronereis minuta (Knox and Cameron)

Figs 1, 11–13

Notophycus minutus Knox and Cameron, 1970:75, figs 1–5 (Snares Island, New Zealand).

Micronereis minuta.—Banse, 1977a:123, pl. 1:figs e–i.

Material examined. *New Zealand*, Snares Island, Boat Harbour, from red algal washings in *Durvillea* zone, intertidal, 15 January 1967—HOLOTYPE and 2 PARATYPES (CM AQ 3466); Snares Island, Boat Harbour, Senecio Pool, on red algae, 0–2 m, 20 January 1975, C.E. Holmes, collector—1 ♂, 8 ♀♀, 5 juveniles (CM AQ 3505).

Diagnosis. Tentacular cirri with thin terminal article. Jaws of males of prolonged type, shortened type in females. Accessory parapodial cirri present in epitokous male, absent in females. Copulatory hooks absent. Homogomph spinigers lack septa in shafts, blades coarsely serrated; additional capillary simple setae in epitokous male.

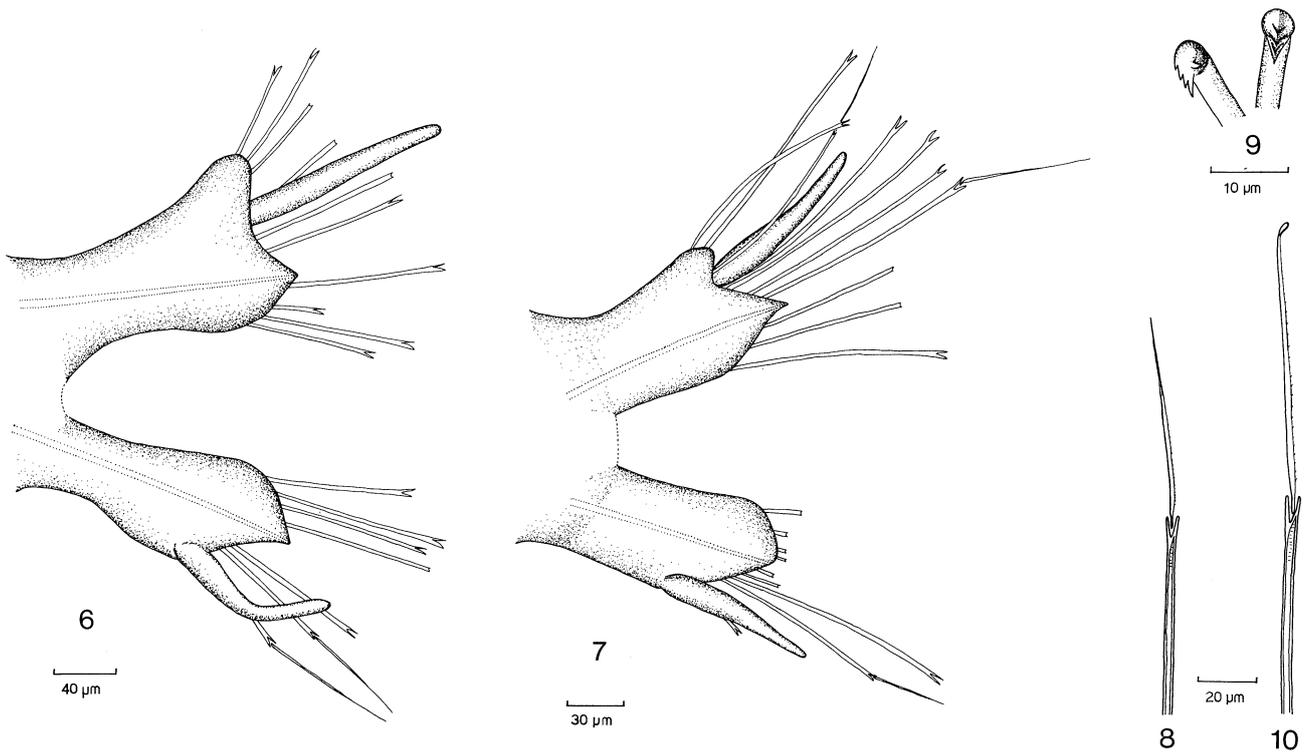
Description. Length of male 3.6 mm (22 setigers), females up to 5.8 mm (24 setigers). Prostomium rounded, with pair of ventral palps and 2 pairs of eyes with lenses. Four pairs of biarticulated tentacular cirri, with diameter of terminal article less than half that of basal; two posterior pairs slightly longer than two anterior pairs, reaching setiger 2–3 (Knox and Cameron, 1970, figs 1–3). Pair of sexually dimorphic jaws (see below). Paragnaths observed only in juvenile; numerous conical oral paragnaths, presumably crown-shaped in adults; maxillary paragnaths consisting of 2 bars, each with a denticle. Biramous parapodia may be ciliated; dorsal cirri larger and inserted more distally than ventral cirri (Fig. 11). Homogomph spinigers, shafts without septa, blades coarsely serrated (Banse, 1977a, pl. 1:figs h, i). Pygidium with pair of subulate anal cirri.

Male characteristics. Jaws of prolonged type with 3 proximal teeth (Fig. 12). No copulatory hooks. Epitokous male with accessory cirri on ventral side of notopodia and dorsal side of neuropodia (Fig. 11), and about 20 homogomph spinigers and 5 simple capillary setae per fascicle.

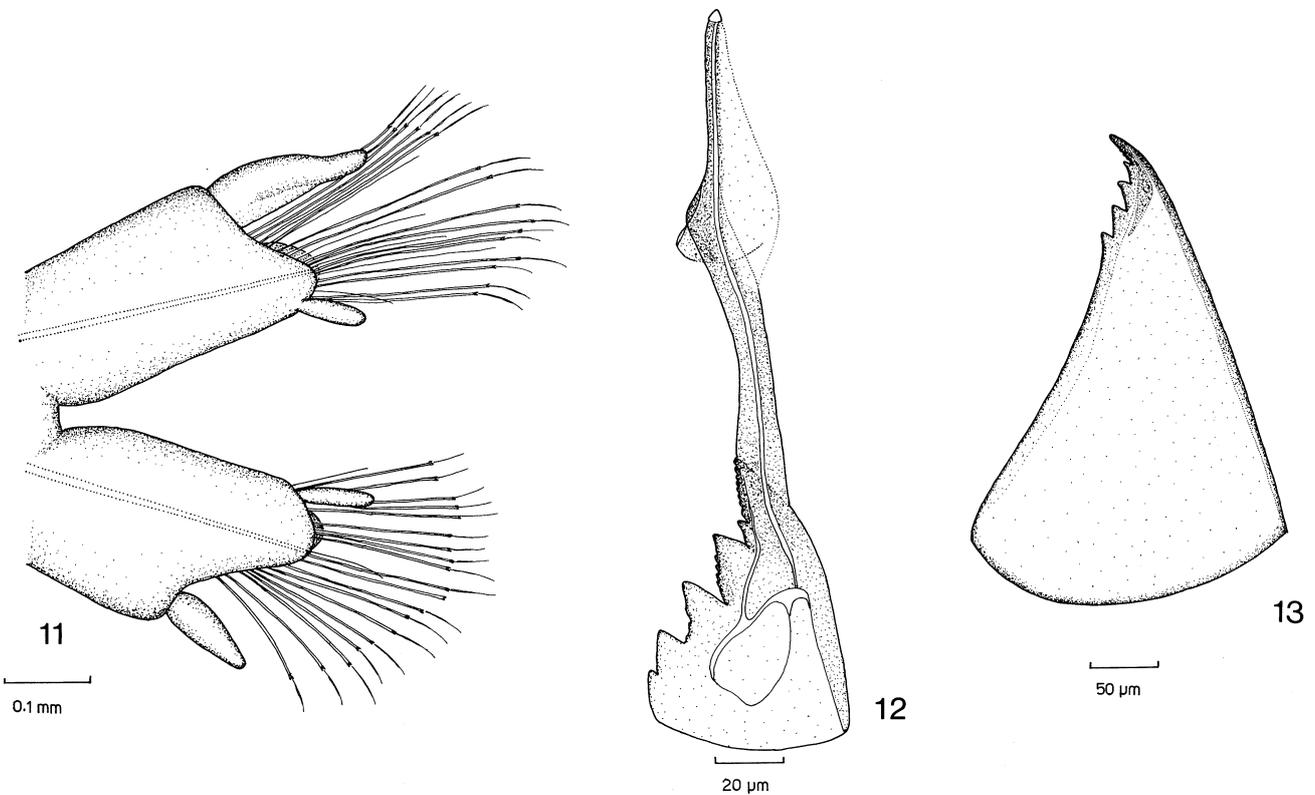
Female characteristics. Jaws of shortened type with 3–4 teeth (Fig. 13). Accessory parapodial cirri absent. About 5–10 homogomph spinigers per fascicle; simple setae absent. Bulbous lobe at base of dorsal cirrus (presumably associated with gonopore).

Biology. The smallest juveniles lacked the anterior two pairs of tentacular cirri and possessed setae associated with the fourth pair as is typical for larval nereidids. The male specimen contained sperm morulae and free spermatozoa.

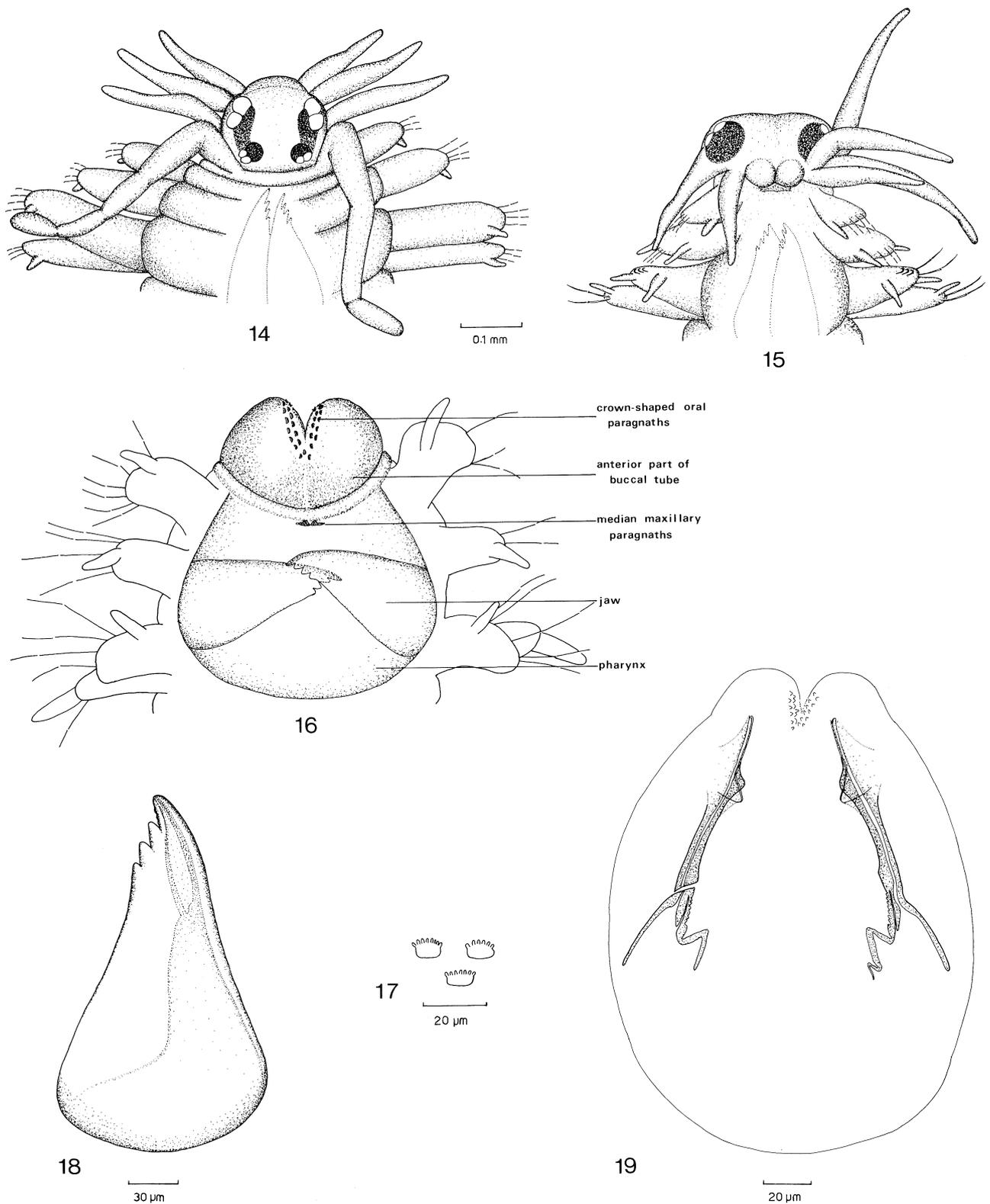
Distribution. Snares Island, New Zealand (Fig. 1).



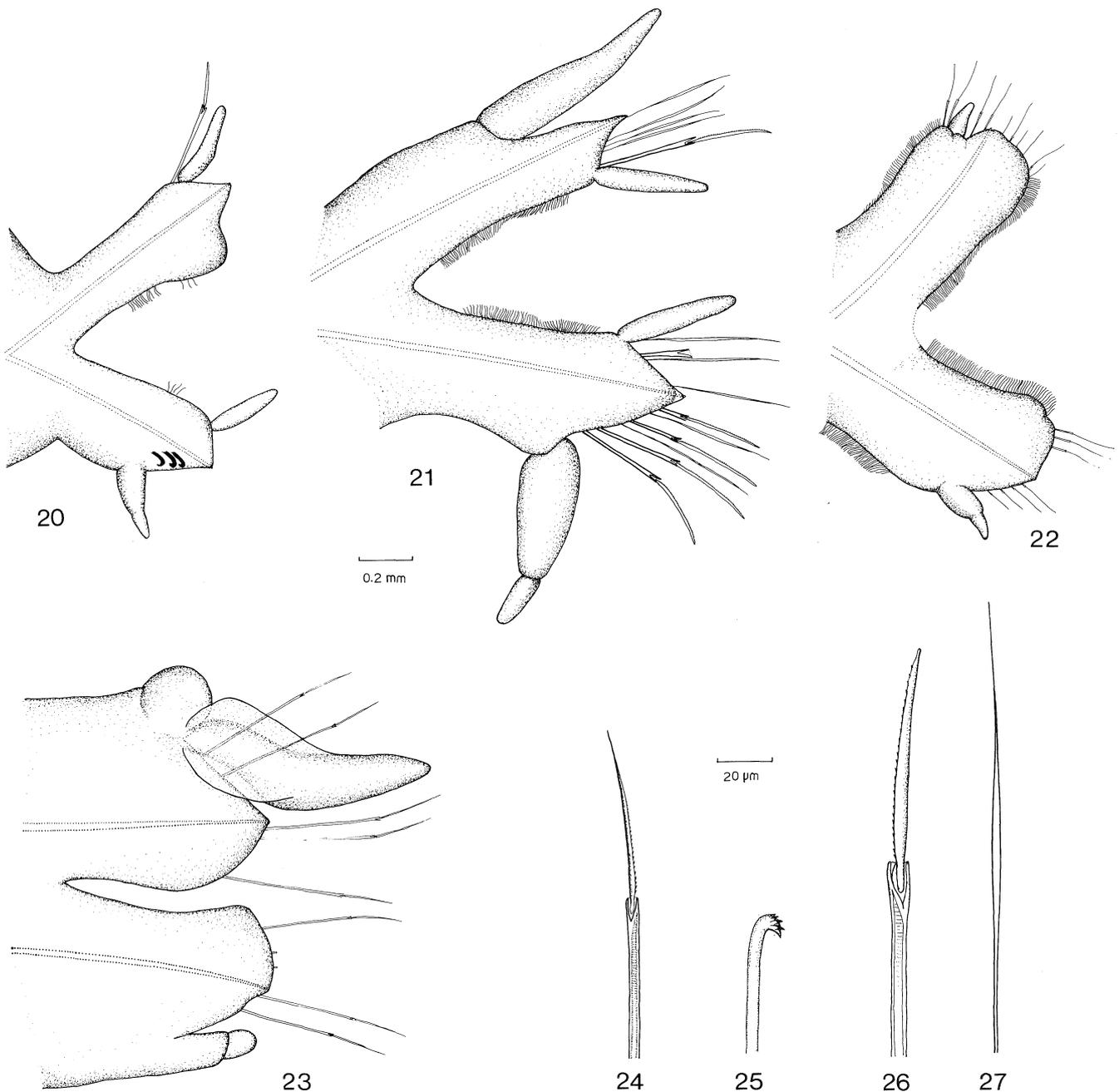
Figs 6-10. *Micronereis piccola*, n.sp. (continued). 6, parapodium of male from setiger 10, anterior view; 7, parapodium of female from setiger 7, anterior view; 8, compound spiniger from setiger 7; 9, copulatory hooks from setiger 3; 10, compound falciger from setiger 7.
[6, 9, 10 holotype (USNM 54514); 7, 8 paratype 1 (USNM 60505).]



Figs 11-13. *Micronereis minuta*. 11, parapodium of male from setiger 12, anterior view; 12, jaw of male; 13, jaw of female.
[11, 12 specimen 2; 13 specimen 3 (CM AQ3505).]



Figs 14–19. *Micronereis bansei*. 14, anterior end of female, dorsal view (AMS W.17183); 15, same of male, ventral view (AMS W.17186); 16, same of female showing everted anterior buccal tube, ventral view (WAM); 17, oral paragnaths (WAM); 18, jaw of adult (USNM 60512); 19, jaws of juvenile (distal prolongation of one side fractured) (AMS W.17189).



Figs 20-27. *Micronereis bansei* (continued). 20, parapodium of male from setiger 3, anterior view (dorsal accessory cirrus lost); 21, same of male from setiger 12, anterior view; 22, same of female from setiger 3, anterior view; 23, same of female from setiger 12, anterior view; 24, compound spiniger from setiger 12; 25, copulatory hook from setiger 3 of male; 26, compound falciger from setiger 12 of male; 27, simple seta from same. [20, 21 (AMS W.17186); 22 (AMS W. 17183); 23 (AMS W. 17184); 24 (AMS W.17184); 25-27 (AMS W.17186).]

***Micronereis bansei* (Hartmann-Schröder), n. comb.**
Figs 1, 14-27

Micronereis variegata (non Claparède, 1863).—Fauvel, 1927: 433, fig. 107.—Gravier, 1934:351, fig 3.

Quadricirra sp.—Banse, 1977a:127, pl. 2, figs b, d.

Quadricirra bansei Hartmann-Schröder, 1979:121, figs 227-237 (Broome, Western Australia).

Material examined. AUSTRALIA: *Western Australia*: Broome, Gantheaume Point, 24 September 1975, G. Hartmann-Schröder and G. Hartmann, collectors—1 ♂ and 2 ♀♀ (WAM). *Queensland*: Lizard Island, 100 m off E end of Mangrove Beach, 14°40'49"S, 145°28'00"E, sandy bottom with drift algae (*Lyngbya majuscula*) and diatomaceous material, 3 m, 30 September 1978, A. Jones and C. Short, collectors—1 ♂ (AMS W.17179-81) and 4 ♀♀ (AMS W.17182-5, USNM 60512). Lizard Island, 200 m SW off

Freshwater Beach, 14°41'00"S, 145°27'28"E, 3 m, 10 October 1978, A. Jones and C. Short, collectors—1 ♂ (AMS W. 17186) and 1 juvenile (AMS W. 17187–8). Lizard Island, 1.6 km SW off Eagle Island, in sediment from coral fans, rubble and dead coral on reef face and bommies, 4.6–7.6 m, 17 October 1978, J. Lowry and P. Terrill, collectors—1 juvenile ♀ (AMS W. 17189). One Tree Island, 60 m SW from sand spit, Shark Alley, sandy bottom, 1.5 m, 15 October 1979, C. Short and J. Young, collectors—1 ♀ (AMS W. 17190). *New South Wales*: Gunnamatta Bay, Port Hacking, 34°03'25"S, 151°08'53"E, coarse sandy bottom, 1.5 m, 8 January 1975, S. Rainer and A. Bothwell, collectors—1 juvenile ♀ (AMS W. 17191).

EGYPT: *Suez Canal*, Port Said—1 ♂ (BM 1926:11:12:30).

Diagnosis. Jaws of shortened type in adults of both sexes. Spinous copulatory hooks and accessory parapodial cirri present in male epitokes, absent in females. Homogomph spinigers with weak septa in shaft, finely serrated spinigerous blades in females and atokous males, replaced by falcigers and simple setae in epitokous males.

Description. Length of males up to 2.1 mm (20 setigers), females up to 3.8 mm (22 setigers). Prostomium rounded with pair of ventral palps and 2 pairs of eyes with lenses (Figs 14, 15). Four pairs of tentacular cirri, posterior pair longest, reaching setiger 4–5 in some specimens (Fig. 14). Oral paragnaths crown-shaped with 6–8 cusps (Figs 16, 17); maxillary paragnaths 2 bars each with irregularly shaped denticle; pair of jaws with prolonged distal part in juveniles (Fig. 19) and shortened type with 3–4 teeth in adults of both sexes (Figs 16, 18). Parapodia with cilia, simple dorsal cirrus and more or less biarticulated ventral cirrus (Figs 20–22). Slender homogomph spinigers, shafts with weak septa (visible with 1000× magnification), blades finely serrated (Fig. 24). Some specimens with segmental eyespots. Pygidium with pair of anal cirri of varying length.

Male characteristics. Setiger 3 with 3 neuropodial copulatory hooks each with 4–6 spines (Figs 20, 25). Epitokal changes consisting of (1) accessory cirri appearing on ventral side of notopodia and dorsal side of neuropodia (figs 20, 21) and (2) spinigers being replaced by falcigers (fig. 26) and simple setae with widened middle portion (fig. 27).

Female characteristics. Accessory parapodial cirri absent. No obvious change of setae associated with sexual maturity. In mature females dorsal cirri enlarged, with lamellar extensions and bulbous lobe at base (presumably associated with gonopore) (Fig. 22).

Biology. Two of the females were collected inside their mucous cocoons, measuring 1.4 and 1.6 mm in diameter; they contained approximately 150 and 190 pink eggs, 100 µm in diameter.

Remarks. The specimen from Port Said was reported by Fauvel (1927), who remarked that it was obviously a male, having jaws with long appendages and copulatory hooks. He discussed and illustrated the accessory cirri in a middle parapodium and stated that he had not found such cirri on any of the other

specimens in his collection. Although he concluded that the specimen might represent a new species, he chose to report it as *M. variegata* for the time being.

Banse (1977a) re-examined and figured the poorly preserved specimen. He referred it to *Quadricirra* sp. indicating that the features were insufficient for a complete diagnosis. Upon re-examination in the course of the present study, the specimen was identified as *M. bansei*. The jaws were dissected out and found to be of the shortened type, contrary to the statement of Fauvel (1927). The shafts of the compound setae are faintly septate. There are fine atokous spinigers and thicker epitokous falcigers, typical for *M. bansei*. The transformation of this specimen had not yet reached the stage where simple setae appear.

Distribution. Western Australia, Queensland and New South Wales, Australia; Port Said, Egypt (Fig. 1).

Micronereis nanaimoensis Berkeley and Berkeley

Figs 1, 28–30

Micronereis variegata (non Claparède, 1863).—Ramsay, 1914:243, figs 2–5, 7.—Berkeley, 1924:290.—Berkeley and Berkeley, 1948:60, fig. 89.

Micronereis nanaimoensis Berkeley and Berkeley, 1953:85, pls 1, 2 (Departure Bay, British Columbia).—Reish, 1961:276.—Pettibone, 1967:6.—Banse and Hobson, 1974:69, fig. 18h.—Banse, 1977a:122, pl. 1:figs a–d.

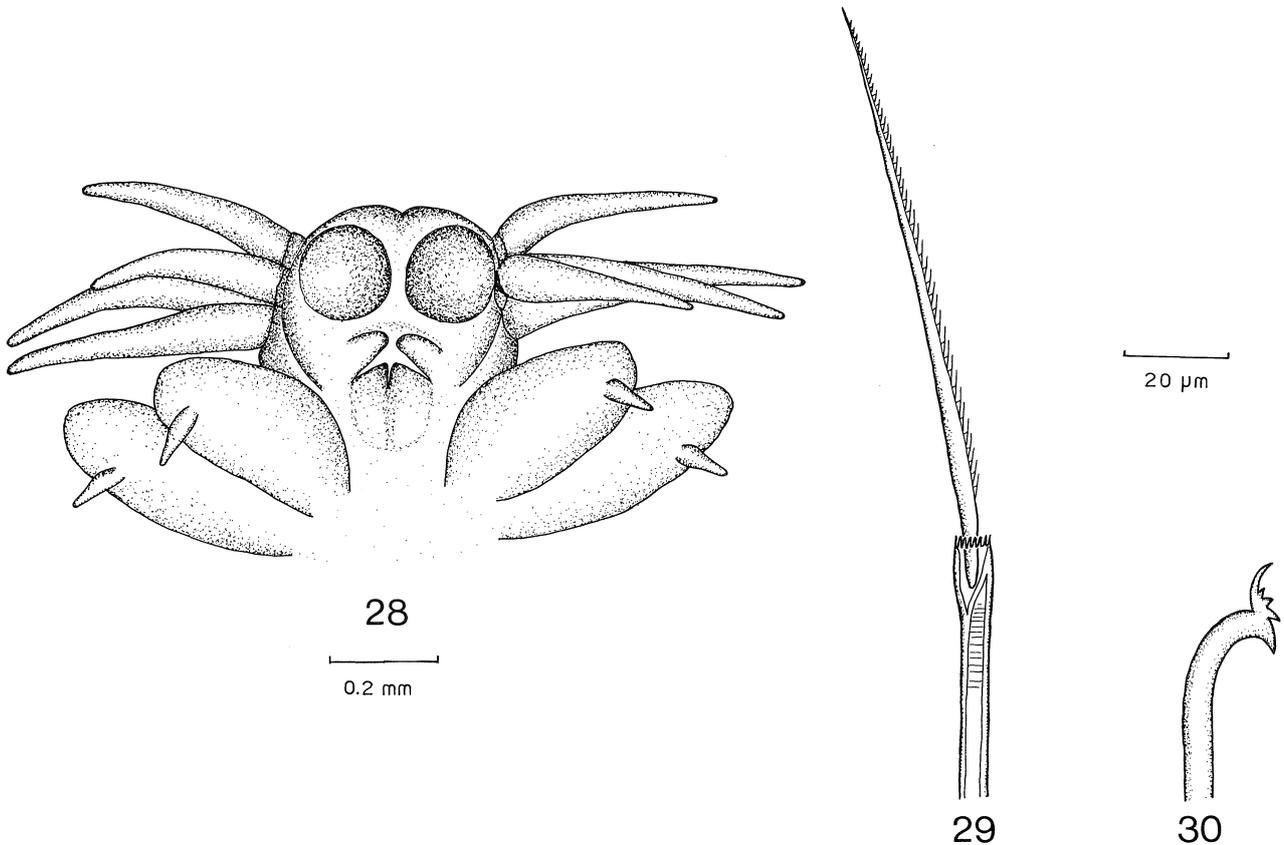
Phyllococella bodegae Fauchald and Belman, 1972:107, figs 1, 2 (Bodega Bay, California).—Banse, 1977a:124.

Material examined. CANADA: British Columbia, Departure Bay, 23 April to 23 May 1947, E. and C. Berkeley, collectors—1 ♂ and 3 ♀ SYNTYPES (AMS W.17175–8, from USNM 32855–6).

Diagnosis. Jaws of shortened type in both sexes. Accessory parapodial cirri absent. Mouth with conical lateral lips. Crested copulatory hooks present in males. Homogomph spinigers; shafts with distinct septa, serrated blades, epitokous males with additional simple setae.

Description. Length of males up to 13 mm (23 setigers), females up to 15 mm (26 setigers). Prostomium rounded to quadrate with pair of ventral palps and 2 pairs of eyes with lenses. Four pairs of short, subulate tentacular cirri. Mouth with conical lateral lips (Fig. 28). Oral paragnaths crown-shaped with 5 cusps (Banse, 1977a, pl. 1:fig. a); maxillary paragnaths not observed; pair of jaws of shortened type in both sexes with 3–4 teeth (Berkeley and Berkeley, 1953, pl. 1:fig. 3). Parapodia strongly ciliated, biramous from setiger 3, with small dorsal and ventral cirri; homogomph spinigers; shafts with distinct septa and distally crenulated; blades serrated, each serration ending in distinct hair-like extension (Fig. 29). Pygidium with pair of anal cirri.

Male characteristics. Setiger 3 with 5 or more crested neuropodial copulatory hooks (fig. 30). Setae of epitokes include spinigers and additional simple setae with widened middle portion.



Figs 28–30. *Micronereis nanaimoensis*. **28**, anterior end, setae omitted, ventral view; **29**, compound spiniger from setiger 11; **30**, copulatory hook from setiger 3.
[28 (AMS W.17175); 29, 30 (AMS W.17178).]

Female characteristics. Parapodia greatly inflated but dorsal cirri small throughout length of body. Bulbous lobe at base of dorsal cirrus (presumably associated with gonopore). No obvious change of setae associated with sexual maturity.

Biology. Reproduction and development of *M. nanaimoensis* has been described by Berkeley and Berkeley (1953).

Remarks. Fauchald and Belman (1972) described *Phyllodocella bodegae* from Bodega Harbor, California on the basis of a single female found in a mucous cocoon. Banse (1977a) referred the species to *Micronereis*. It is relatively large (8 mm for 24 setigers) and has conical lateral lips, inflated parapodia with small dorsal and ventral cirri, and homogomph spinigers that have distally crenulated, septate shafts and serrated blades with hair-like extensions (Fauchald and Belman, 1972, figs 1, 2). All these characters agree with *M. nanaimoensis*. Although the type specimen of *M. bodegae* cannot be located (Kudenov, pers. comm.), the information available is sufficient to demonstrate that *M. bodegae* is a junior synonym of *M. nanaimoensis*.

Distribution. British Columbia, Canada; Washington and California, U.S.A. (Fig. 1).

***Micronereis halei* Hartman** Figs 1, 31–33

Micronereis halei Hartman, 1954:25, figs 18–21 (South Australia).—Reish, 1961:276.

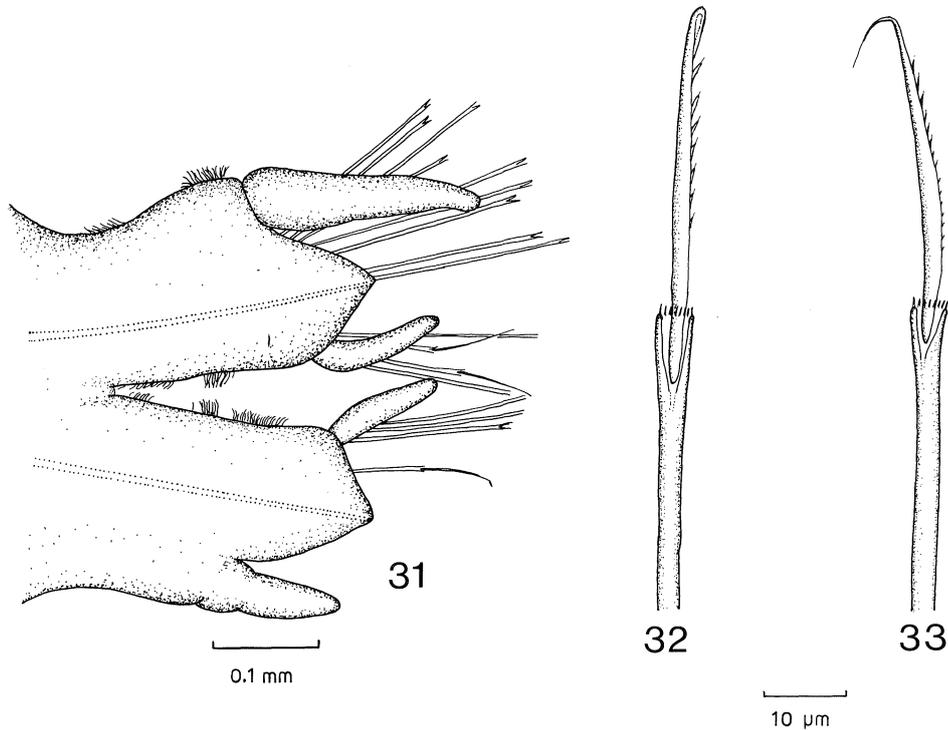
Micronereis sp. 1 Poore *et al.* 1975:27, 50.

Quadricirra halei.—Banse, 1977a:126, pl. 2:figs a, c.

Material examined. AUSTRALIA: *South Australia*: Sellick Beach, at outer edge of reef, from stones on rock pools, 16 January 1936, H.M. Hale and K. Sheard, collectors—10 SYNTYPES (1 ♂ AHF Poly 843; 3 ♂♂ AHF Poly 844; 2 ♂♂ and 1 juvenile AHF n 1008; 2 ♂♂ AHF n 7645; 1 juvenile AHF n 7647). *Victoria*: Port Phillip Bay, c. 38°21'S, 144°51'E, PPBES sta. 985, 9 m, 9 December 1971—1 juvenile (NMV 8164).

Diagnosis. Jaws of males, and presumably females, of shortened type. Male epitokes with accessory parapodial cirri, without copulatory hooks. Homogomph spinigers; shafts without septa; blades finely serrated in male atokes; spinigers and falcigers in male epitokes.

Description. Length of males up to 6.7 mm (27 setigers). Prostomium rounded, with pair of ventral palps and 2 pairs of eyes with lenses (Hartman, 1954, fig. 18). Four pairs of weakly biarticulated tentacular



Figs 31–33. *Micronereis halei*. 31, parapodium of male from setiger 12, anterior view; 32, compound falciger from setiger 12 of male; 33, compound spiniger with fine distal tip from setiger 12 of male. [31 (AHF n 1008); 32, 33 (AHF Poly 0844).]

cirri; anterior 2 pairs shorter, posterior 2 pairs reaching setiger 3. Oral and maxillary paragnaths not observed; pair of jaws of shortened type in both sexes with 4–5 teeth (Hartman, 1954, fig. 19). Parapodia may be ciliated; dorsal cirri of biramous parapodia larger than ventral cirri (Fig. 31). Homogomph spinigers, shafts without septa, blades finely serrated, of varying length. Segmental eyespots present in one specimen (NMV 8164). Pygidium with pair of anal cirri.

Male characteristics. No copulatory hooks. Accessory cirri attached ventrally on notopodia and dorsally on neuropodia (= digitate lobes in Hartman, 1954, fig. 20). Setae of epitokes consisting mostly of falcigers (Fig. 32) and some spinigers with fine distal tips, often bent (Fig. 33); serrations on blades stronger than in atokes.

Female characteristics. No adult females were available for examination.

Biology. Eight of the 10 syntypes examined contained male gametes. Accessory parapodial cirri were absent in the smaller specimens; one syntype (AHF Poly 844, measuring 4.1 mm in length for 23 setigers) with very short accessory cirri and few falcigers was thought to be in the early stages of epitoky.

Distribution. South Australia and Victoria, Australia (Fig. 1).

Micronereis eniwetokensis Reish

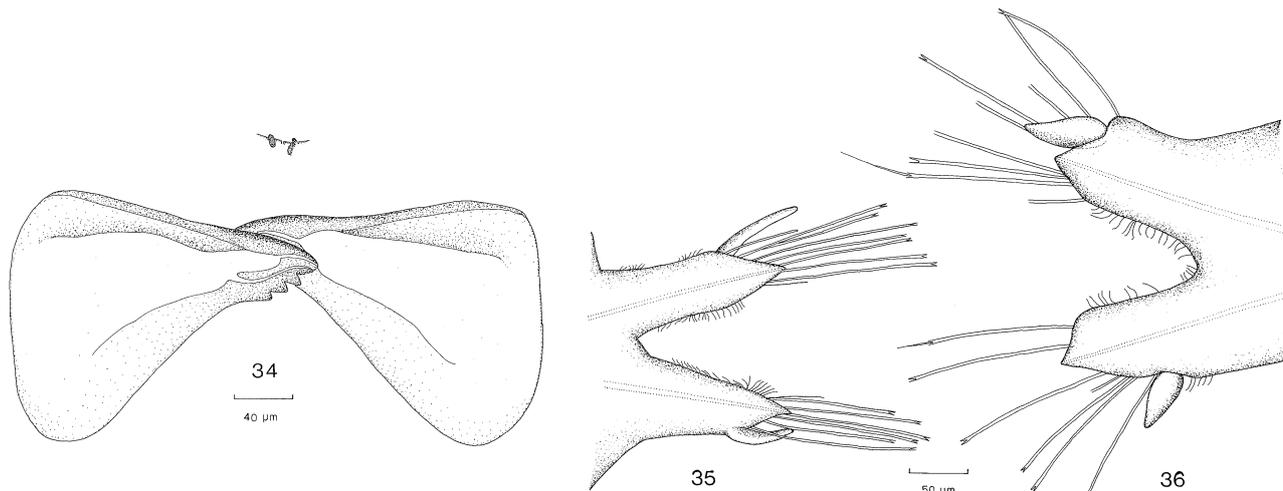
Figs 1, 34–36

Micronereis eniwetokensis Reish, 1961: 273, figs 2–6 (Eniwetak Atoll, Marshall Is).—Banse, 1977a:122.

Material examined. *Marshall Islands:* Eniwetak Atoll: Aaraanbiru I., intertidal, 4 September 1956, D.J. Reish, collector—♀ HOLOTYPE (USNM 30404) and 1 ♀ PARATYPE (USNM 30405). Igurin I., 27 August 1956, D.J. Reish, collector—1 ♀ (USNM 30406). Parry I., 30 m, 14 September 1957, M. Chamberlain, collector—1 ♂ (USNM 30407).

Diagnosis. Jaws of shortened type in both sexes. Accessory parapodial cirri and copulatory hooks absent. Homogomph spinigers with septate shafts, blades finely serrated.

Description. Length of female 1.8 mm (18 setigers), male 1.7 mm (14 setigers). Prostomium rounded, with pair of ventral palps and 2 pairs of eyes with lenses, posterior pair smaller and lenses not as obvious as in anterior pair. Four pairs of subulate tentacular cirri, short in female specimens, longer in male, reaching to end of setiger 3. Oral paragnaths not observed; median maxillary paragnaths consisting of 2 light bars, each with dark, irregularly shaped denticle; paired jaws of shortened type in both sexes, with 3 teeth and bulbous basal part (Fig. 34). Biramous parapodia with notopodia and neuropodia each with single yellow aciculum (not black, as stated by Reish, 1961); heavy ciliated; weakly subulate dorsal and ventral cirri (Figs 35, 36).



Figs 34–36. *Micronereis eniwetokensis*. **34**, jaws and median maxillary paragnaths; **35**, parapodium of male from setiger 6, anterior view; **36**, parapodium of presumed female from setiger 8., anterior view. [34, 36 paratype (USNM 30405); 35 (USNM 30407).]

Homogomph spinigers, shafts with weak septa, blades finely serrated. One specimen (USNM 30407) with segmental eyespots.

Male characteristics. Male slender, with few setigers; no epitokal changes observed.

Female characteristics. More inflated appearance and higher number of setigers.

Distribution. Eniwetak Atoll, Marshall Islands (Fig.1).

Key to the Species of *Micronereis* (Males only)

1. Males with prolonged type of jaws (Fig. 2) 2
 - Males with shortened type of jaws (Fig. 18) 4
2. Males without copulatory hooks on neuropodia of setiger 3; epitokous males with accessory cirri on lower part of notopodia and upper part of neuropodia (Fig. 11) *M. minuta*
 - Males with copulatory hooks (Fig. 9); epitokous males without accessory parapodial cirri (Fig. 6) 3
3. Shafts of spinigers with septa (Fig. 8); prolonged male jaws without proximal teeth (Fig. 5) *M. piccola*, n.sp.
 - Shafts of spinigers without septa; prolonged male jaws with proximal teeth (Fig. 2) *M. variegata*
4. Males with copulatory hooks on neuropodia of setiger 3 (Figs 25, 30); epitokous males with simple setae (Fig. 27) 5
 - Males without copulatory hooks; epitokous males without simple setae 6
5. Epitokous males with accessory cirri on lower part of notopodia and upper part of neuropodia (Fig. 21); copulatory hooks with spines (Fig. 18) *M. bansei*
 - Epitokous males without accessory parapodial cirri; copulatory hooks crested (Fig. 30) *M. nanaimoensis*
6. Epitokous males with accessory cirri on lower part of notopodia and upper part of neuropodia (Fig. 31) and some falcigers (Fig. 32) *M. halei*
 - Epitokous males without accessory parapodial cirri (Fig. 35) and only spinigers *M. eniwetokensis*

DISCUSSION

The Nereididae is one of the most uniform polychaete families. Of the four subfamilies, the Notophycinae departs most widely from the basic nereidid plan. Banse (1977a) discussed the taxonomic position of the Notophycinae and concluded that, although they are the most aberrant, they belong to the Nereididae. He considered the seta, particularly the internal septa and the structure of the distal end of the shaft, as the strongest evidence. Notophycines were regarded as primitive nereidids (Ramsay, 1914), but Banse (1977a: 132) stated that "the evidence which has become available since his study has not provided unambiguous evidence".

The notophycines display a curious mixture of epitokous characters retained from their nereidid relatives, and specializations acquired as members of the meiofauna. The epitokal modifications in females consist only of enlargement of eyes, parapodia and dorsal and ventral cirri. Male modifications range from enlarged eyes in *Micronereis variegata* to the possession of accessory parapodial cirri and the addition and replacement of spinigers by simple setae and falcigers as in *M. bansei*.

Reproductive adaptations common to the meiofauna in general are related to the relatively small number of gametes that small animals can produce, and include copulation, hermaphroditism, the formation of egg cocoons and brood protection (Swedmark, 1971). Reproduction and development have been studied in detail for two species of *Micronereis*: *M. nanaimoensis* by Berkeley and Berkeley (1953) and *M. variegata* by Racovitza (1893) and Rullier (1954). Both species undergo an extended courtship and spawning behaviour. The meiofaunal specializations consist of copulatory hooks in the male, a slightly larger body in the female, relatively large and few eggs, construction of a mucous cocoon, brood protection and care by the female, and direct development of the young. The combination of more developed epitokal modifications in the males and the reproductive meiofaunal adaptations has led to a pronounced sexual dimorphism.

Antennae are absent in Notophycinae at all stages of development. Antennae are present in all other subfamilies and develop early in the 3-setiger larva of *N. diversicolor* (Dales, 1950). The absence of antennae in Notophycinae is a unique character among the Nereididae, suggesting that the notophycines represent either the most ancestral or the most derived subfamily. In view of the fact that the most closely related families, the Hesionidae and Syllidae (Dales, 1962) are characterized by the possession of antennae, it is probable that their absence in the Notophycinae

represents a derived state and that they are the most derived subfamily of Nereididae.

The species of *Micronereis* display a mosaic of characters (Table 1). The prolonged type of jaw is found in males of *M. variegata*, *M. piccola*, and *M. minuta*, while the males of the remaining four species, *M. bansei*, *M. nanaimoensis*, *M. halei* and *M. eniwetokensis*, have jaws of the shortened type. Rullier (1954) has shown that the prolonged jaw of *M. variegata* develops in young male and female individuals. When the females reach about 16 setigers, the prolongation breaks off at a predestined place (Fig. 2) and the jaw enlarges proximally, while the males retain the distal prolongation. The prolonged jaws were observed in juvenile females of *M. minuta* and *M. piccola*. An interesting find was the presence of prolonged jaws in a juvenile specimen of *M. bansei* (Fig. 19), which belongs to the group of species where both adult males and females have the shortened type of jaws. This indicates that the prolonged type develops first in both groups of species and the shortened jaw of both sexes is a derived condition.

Accessory parapodial cirri are found in mature males of *M. bansei*, *M. minuta* and *M. halei*, while they are absent in the remaining four species. The males of four species have copulatory hooks; their shape is similar in *M. variegata*, *M. piccola*, and *M. bansei*, but more elaborate in *M. nanaimoensis*.

The type of jaw and presence or absence of accessory parapodial cirri and copulatory hooks cannot be correlated and thus cannot be used to divide the genus into species groups. It appears that the transformation from the prolonged to the shortened type of jaw occurred primitively only in females, but may have been adopted by males more than once independently. It is presumed that accessory cirri and copulatory hooks evolved only once in *Micronereis* and thus their absence should represent the ancestral, and their presence the derived, character state. However, both characters may have been lost independently more than once, and the relationships within *Micronereis* are unclear.

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While this paper has been in press, *Micronereis ochotensis* Buzhinskaya has been described from the Sea of Okhotsk, U.S.S.R.

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