

Revision of *Pseudonereis* (Polychaeta, Nereididae)

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A taxonomic revision of *Pseudonereis* (Polychaeta, Nereididae) shows that some of the described taxa are very similar in most morphological characteristics. The revision includes all ten taxa considered valid, and are redescribed from type material. Lectotypes are designated for *Pseudonereis anomala* Gravier, 1901, *Pseudonereis noodti* (Hartmann-Schröder, 1962) and *Pseudonereis trimaculata* Horst, 1924. The widely geographically distributed and well-known *P. gallapagensis* Kinberg, 1865 and *P. variegata* (Grube, 1857) show striking morphological resemblance to less well-known taxa with similar distribution. Paragnath variation in populations of *P. anomala* is discussed relating to its geographical distribution. *Pseudonereis trimaculata* is recorded from Australia for the first time. Taxa belonging to *Pseudonereis* are predominantly tropical and subtropical. A cladistic analysis using parsimony is included to test for monophyly of *Pseudonereis*. A monophyletic clade including all *Pseudonereis* taxa is given low bootstrap support. This clade is supported by the synapomorphies: presence of paragnaths in closely spaced comb-like rows on the maxillary ring on the pharynx, and presence of p-bar paragnaths in Areas II–IV and VII–VIII. Several of the included taxa share the shield-shaped paragnath in Area VI, which serves to distinguish *Pseudonereis* spp. from *Perinereis* spp. Paragnaths of the type p-bars and shield-shaped bar is described for the first time; the latter character is different from the smooth bar-shaped paragnaths in Area VI as has previously been described in these taxa. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 150, 145–176.

ADDITIONAL KEYWORDS: distribution – parsimony analysis – phylogeny – systematics – taxonomy.

INTRODUCTION

Kinberg (1865) described the new genus *Pseudonereis* including two species from Galapagos and Hawaii, *P. gallapagensis* and *P. formosa*, respectively, characterized by closely spaced conical paragnaths in ‘pectinate-like’ rows on the pharynx, and with elongated dorsal notopodial ligules with terminally attached cirri. These characters were also recognized as unique by Gravier who described a further taxon in this group, *P. anomala* Gravier, 1901. Ehlers (1901) gave a detailed account of South American material of *Nereis variegata* Grube, 1857, which he transferred to *Pseudonereis* and made synonymous with a number of previously described taxa. Hansen (1882) described several new taxa based on material from Rio de Janeiro, Brazil. He did not find any similarities to existing

taxa from South America although he referred to works by Kinberg and Grube; nor did he give any justifications in his descriptions or compare them with other taxa. Several of his new taxa were later found to be synonyms of *Pseudonereis variegata* (Ehlers, 1901; Augener, 1934). It appears that Ehlers (1901) had types of several taxa available for comparison and synonymized many of those Hansen (1882) described with *P. variegata*. Of these taxa only *P. anomala* was briefly mentioned in the literature (Willey, 1904; Fauvel, 1911), until two new taxa were described, *P. rotnnestiana* Augener, 1913 from Western Australia and *P. atopodon* Chamberlin, 1919 from the Tonga Islands in the Pacific, both descriptions drawing attention to similarities with *P. gallapagensis*. Later Fauvel (1932) included the previously described *P. masalacensis* (Grube, 1878) as well as *P. variegata* as synonyms of *P. gallapagensis*, and he also included *Nereis ferox* Hansen, 1882 and *Paranereis elegans* Kinberg, 1865, in accordance with what Ehlers (1901) had stated.

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In addition, several *Neanthes* species are here recognized as belonging to *Pseudonereis*. In previous studies these have often been compared with other *Neanthes* taxa with similar expanded dorsal notopodial ligule in posterior chaetigers. Paragnath pattern and especially the clearly recognizable conical paragnaths in closely spaced comb-shaped rows in Areas II–IV on the maxillary ring have not always been taken into account in this regard. A tendency towards two different schools utilizing different sets of characters in nereidid morphology may be a reason for this. Kinberg (1865) initiated the use of paragnath type, form and number (e.g. Fauvel, 1932), while some authors

followed Malmgren's (1867) scheme of parapodial characters and in large part based their descriptions and comparisons of taxa on parapodial morphology (e.g. Southern, 1921). More recently studies have used all available characters (e.g. Fauchald, 1977; Hutchings & Turvey, 1982; Hylleberg, Natewathana & Bussarawit, 1986).

Recently Bakken & Wilson (2005) provided an emended definition of *Pseudonereis*: presence of paragnaths in Areas II–IV arranged in regular comb-like rows (Fig. 1A–C), and dorsal cirrus terminally attached to dorsal notopodial ligule in posterior chaetigers. The results of phylogenetic analyses (Bakken &

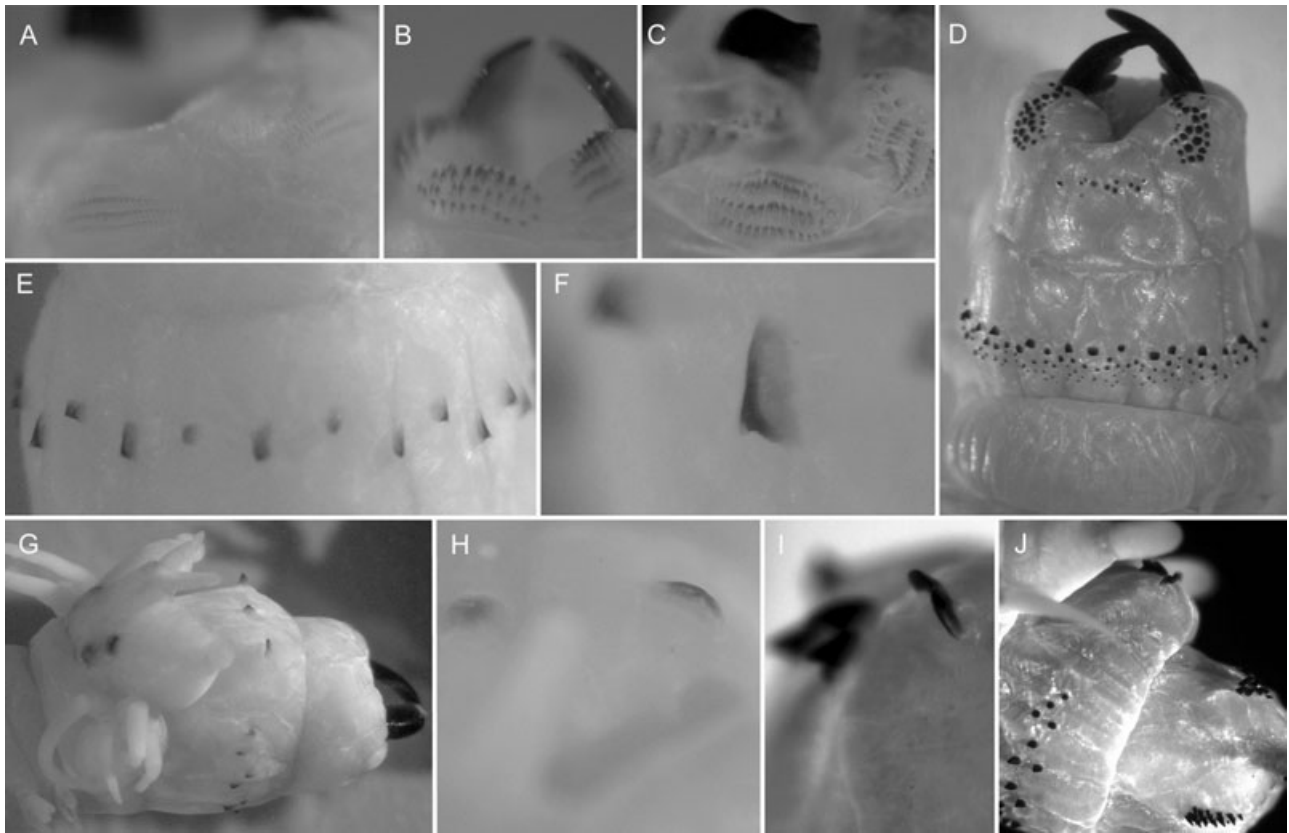


Figure 1. Two new paragnath characters are described as diagnostic characters for *Pseudonereis* spp., p-bars and shield-shaped bars. Additionally, regular comb-like rows are compared with a more common pattern. A–C, paragnaths in typical regular comb-like rows from Area II–IV in *Pseudonereis* spp., observed here are regular rows in Area III and IV for three taxa. D, conical paragnaths are common in all areas in most nereidid taxa with paragnaths, here visualized for Area III and IV, and Area VII–VIII. E, bar-shaped paragnaths (p-bars – pointed bars) interspersed with conical paragnaths in Area VII–VIII. F, bar-shaped paragnath with a point skewed over to one end of the bar (p-bar) from Area VII–VIII. G, a high flattened shield-shaped bar in Area VI protruding from the tissue is different from the smooth bar observed in *Perinereis* spp. H, close up of a shield-shaped bar in Area VI, right side (conical paragnath in Area V to the left). I, a low, smooth bar-shaped paragnath in Area VI typical for *Perinereis* spp. (faded conical paragnaths in Area V to the left). J, smooth bar-shaped paragnath in area VI is low in *Perinereis* spp.; note also the conical paragnaths in Area II, IV, VII–VIII. A, E, F, G and H from a specimen in the syntype series of *Nereis ferox* (= *P. variegata*) ZMUB 2130; B, *Pseudonereis pseudonoodti* (Fauchald, 1977) paratype USNM 53091; C, *Pseudonereis anomala* Gravier, 1901 syntypes MNHN Poly Type-421; D, *Nereis pelagica* Linnaeus, 1758 TB collection; I, J *Perinereis helleri* (Grube, 1878) CG0403 (Chris Glasby).

Wilson, 2005) showed that some taxa should be transferred to *Pseudonereis* from *Neanthes*; *P. cortezi* (Kudenov, 1979), *P. noodti* (Hartmann-Schröder, 1962) and *P. pseudonoodti* (Fauchald, 1977). Their results also showed high levels of homoplasy in Nereididae, suggesting more detailed studies are necessary to answer questions regarding character homology. Examination of specimens of *P. anomala* and *P. gallapagensis* led to examination of type material of taxa assigned to *Pseudonereis* revealing close similarity to several taxa, and indicated a review was necessary.

The main goal of this study is to revise all described taxa in *Pseudonereis* based on examination of type material. All taxa included in *Pseudonereis* that it was possible to obtain material of are redescribed based on type material. One taxon, *P. masalacensis* Grube, was not included as the type material is in poor condition (Hutchings & Glasby, 1985).

MORPHOLOGICAL CHARACTERS

Morphological characters used to describe nereidids, with special emphasis on nereidids with paragnaths, were used in Wilson, Bakken & Glasby (2003) and were described in detail by Bakken & Wilson (2005). Examination of type material in this study warranted inclusion of additional characters which are described below.

PARAGNATHS

Smooth bar-shaped paragnaths in Area VI is a diagnostic feature of *Perinereis* taxa, and numbers of bars in Area VI have been used, in addition to parapodial features, to assign informal groups within *Perinereis* (Hutchings, Reid & Wilson, 1991). Taxa in *Pseudonereis* have also been reported to have bar-shaped paragnaths in Area VI (Kinberg, 1865; Bakken & Wilson, 2005). Examination of type material in this study revealed that most *Pseudonereis* taxa possess a different bar-shaped paragnath in Area VI than the traditionally described low, smooth bar. Instead in *Pseudonereis* taxa it appears as a laterally flattened, high bar (Fig. 1G, H), usually with a pointed tip. The tip is often, but not always, skewed over to one end. This laterally flattened paragnath show resemblance to a shield projecting out from the soft tissue (Figs 1G, H and 14A–C), rather than the smooth, low bar observed in *Perinereis* (Fig. 1I, J). It is included here and termed a ‘shield-shaped’ bar. In some taxa the shield-shaped bar has a pointed tip (see description of *P. cortezi*, Fig. 5A) whereas in others there is a rounded edge. All included taxa examined in this study possess the shield-shaped bar in Area VI, except *P. anomala* and *P. multisetosa* which have cones in

Area VI, and *P. palpata* which has both cones and a bar (see Remarks for *P. palpata*). A thorough evaluation of poorly known *Perinereis* taxa will show if this character is unique to *Pseudonereis*; however, *Perinereis* spp. have usually been described as having smooth bars on Area VI, indicating that shield-shaped bars may be unique to *Pseudonereis* spp.

Paragnaths in most areas on the pharynx are conical (Fig. 1D) in most nereidine taxa (Bakken & Wilson, 2005), but rod-like paragnaths in tight clusters have been described in Areas II–IV (Nateewathana, 1992), and smooth bar-shaped paragnaths in Area IV were described in *Neanthes* spp. by Wilson (1984). The latter have since been observed in several nereidine taxa (Bakken & Wilson, 2005). Paragnaths in closely spaced comb-like rows (Fig. 1A–C) were recognized as being diagnostic for *Pseudonereis* by Bakken & Wilson (2005). Examination of type material in this study showed Area II–IV paragnaths to be low, bar-shaped paragnaths with a pointed tip skewed over to one end, here called a p-bar (pointed bar) (Fig. 1B–C). P-bars may be present alone or in combination with conical paragnaths in Area II–IV, and in Area VII–VIII interspersed with smaller conical paragnaths (Figs 1E, F, 5B, 11B and 14B).

PARAPODIA

Hylleberg *et al.* (1986) highlighted diverse parapodial morphologies in nereidids by reintroducing end-view drawings of parapodia. Their schemes and parapodial terminology have proved to be valuable and have been widely used since (summarized in Bakken & Wilson, 2005). Wilson *et al.* (2003) did not implement a neuropodial superior lobe in their character set, nor did Bakken & Wilson (2005), mainly due to lack of information of this character across taxa. It is, however, included here. Although shown to be present in all *Pseudonereis* taxa (except *P. pseudonoodti* and *P. palpata*) it is not unique, as it is also known to be present in other nereidine taxa (Bakken & Wilson, 2005). Presence of a neuropodial superior lobe and its range along the body (measured in number of chaetigers) should be carefully described when included in descriptions. The neuropodial superior lobe is placed next to the inferior lobe, with the acicula in between the two (Hylleberg *et al.*, 1986; Fig. 1A). The two lobes combined constitute the acicular ligule, often used as a term in descriptions.

In neuropodia a postchaetal lobe is present in many taxa among nereidids. As described in Bakken & Wilson (2005) it may take different shape and extension, and is either restricted to a number of anterior chaetigers or present throughout. In some taxa studied here the neuropodial postchaetal lobe appears somewhat differently than previously reported. If present it

is present throughout but most clearly visible and drawn out to a triangular pointed tip in posterior chaetigers, while in anterior and mid-body chaetigers it is low with no tip. In material examined here some variation is evident in smaller specimens with a body width less than 1 mm, in which cases the postchaetal lobe was difficult to see.

MATERIAL AND METHODS

End-view drawings are often provided accompanying illustrations of parapodia. These are schematic views of a parapodium seen from the tip towards the body wall. End-view drawings follow the scheme suggested by Hylleberg *et al.* (1986; Fig. 1A), and are drawn free hand with the anterior end of the specimen towards the right. Parapodia were drawn in a compound microscope with the aid of a camera lucida. Measurements of body width are measured at chaetiger 10 without parapodia.

Photographs were taken with a JVC GC-X3 digital camera in a Leica MZ APO stereomicroscope and a Leica DMLC compound microscope, picture resolution set to fine at 2032 × 1536.

The following abbreviations for museums and institutions are used: AM (Australian Museum, Sydney, Australia), ZMA (Zoological Museum Amsterdam, the Netherlands), MNHN (Museum National d'Histoire Naturelle, Paris, France), NHMLAC (Natural History Museum of Los Angeles County, Los Angeles, USA), SMNH (Swedish Museum of Natural History, Stockholm, Sweden), USNM (National Museum of Natural History, Smithsonian Institution, Washington DC, USA), ZMUB (Zoological Museum University of Bergen, Norway), ZMUC (Zoological Museum, University of Copenhagen, Denmark), ZMH (Zoological Institute and Zoological Museum, Hamburg, Germany).

TAXONOMY

PSEUDONEREIS KINBERG, 1865

Pseudonereis Kinberg, 1865: 174. – Fauchald, 1977: 90.

Type species. *Pseudonereis gallapagensis* Kinberg, 1865 designated by Hartman (1949).

Diagnosis: Prostomium with entire anterior margin, one pair of antennae, one pair of biarticulated palps with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV **p-bars** and conical paragnaths arranged in regular comb-like rows. Oral ring paragnaths present, Area V conical

paragnaths present or absent; Area VI conical paragnaths present or absent, **shield-shaped bars present or absent**; Area VII–VIII **p-bars** and conical paragnaths present. Dorsal notopodial ligule markedly elongate and markedly broader on posterior chaetigers. Prechaetal notopodial lobe present or absent. Dorsal cirrus terminally attached to dorsal notopodial ligule on posterior chaetigers (subterminally in *P. anomala*). **Neuropodial superior lobe present (absent in *P. palpata* and *P. pseudonoodti*)**. Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers. Notoaciculae absent from chaetigers 1 and 2. Notochaetae homogomph spinigers present, homogomph falcigers present or absent. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent, homogomph spinigers present or absent, heterogomph falcigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers and heterogomph falcigers present.

Remarks: Bakken & Wilson (2005) recently redefined the genus based on phylogenetic analyses of the subfamily Nereidinae. In the description above minor changes are included (highlighted in bold). Position of the dorsal cirrus in *P. anomala* was coded as terminally attached in their analyses. Re-examination of types and additional material examined in this study shows that the position of the dorsal cirrus is subterminal. In *P. multisetosa* the dorsal notopodial ligule is clearly not elongated in posterior chaetigers, a character that should be verified when more material is found, as the single known specimen is probably a juvenile.

Presence of conical paragnaths arranged in regular comb-like rows in Areas II–IV (Fig. 1A–C) is unique to *Pseudonereis* species. Presence of a shield-shaped paragnath in Area VI, here described for the first time, is also shared in *Pseudonereis* species except *P. palpata* (possesses both a bar and conical paragnaths in Area VI), and *P. anomala* and *P. multisetosa* (cones only). A comparison for all taxa is presented in Table 1.

PSEUDONEREIS ANOMALA GRAVIER, 1901 (FIGS 2 AND 3)

Pseudonereis anomala Gravier, 1901: 191–197, TII, pl. XII figs 50,51,52, text figs 194–202. – Hutchings & Turvey 1982: 141–142. – Hutchings & Glasby 1985: 108–109. – Hylleberg *et al.* 1986: 13–14, fig. 7. *Nereis (Pseudonereis) rotnnestiana* Augener, 1913: 184–187, Taf. III, fig. 46, text-fig. 20a–c. *Nereis nichollsi* Kott, 1951: 93–95, fig. 2a–k. *Pseudonereis rotnnestiana* forma *seriodentata* Hartmann-Schröder, 1979: 118–119, figs 216–219. – 1980: 61.

Table 1. Comparison table for taxa in *Pseudonereis* Kinberg, 1865 showing important characters used for identification. *Pseudonereis multisetosa* is easily distinguished by presence of homogomph falcigers in neuropodial dorsal fascicle

Taxon	Paragnathis						Neuropodia				Type locality		
	Area I	Area II	Area III	Area IV	Area V	Area VI	Area VII-VIII	Dorsal cirrus, attached in posterior chaetigers	superior lobe	postchaetal lobe		ventral ligule anterior, × long as acicular ligule	posterior, × long as acicular ligule
<i>P. anomala</i>	1-3	11-31	30-72	20-52	0	3-15, cones	10-24	subterminal	present	present	1	1	Djibouti, Gulf of Aden
<i>P. multisetosa</i>	2	17-18	20	29-33	0	4, cones	8	subterminal	present	present	1	0.5	Rangiroa, French Polynesia
<i>P. palpata</i>	2	39-40	109	108-120	1	1-2, bar + cones	19	terminal	present	absent (?)	1	0.5	Rio de Janeiro, Brazil
<i>P. cortezi</i>	4-6	17-31	33-54	31-55	8-15	1 shield-shaped	62-87	terminal, from c. 50-55	present	absent	0.5	< 0.5, diminishing	Punta La Cholla, Mexico
<i>P. pseudonoodti</i>	4	15-27	28-40	20-61	3	1 shield-shaped	69-100	terminal, from c. 40	absent	present, poorly developed	0.5	< 0.5, reduced	Paitilla, Panama
<i>P. trimaculata</i>	1-2	23-38	51-69	50-78	1-3	1 shield-shaped	20-24	terminal, posterior 1/4	present	present	0.5-0.8	1	Geser, Indonesia
<i>P. atopodon</i>	1	37-49	56	?, 4-5 rows	0-1	1 shield-shaped	14-24	terminal, from c. 60-65	present	present	0.5	0.5	Tonga Islands, Oceania
<i>P. gallapagensis</i>	1	17-20	51-68	38-57	1	1 shield-shaped	17-20	terminal, from c. 15	present	present	1	0.5	Galapagos Islands
<i>P. noodti</i>	1	25-27	64	70-75	1	1 shield-shaped	16-17	terminal, from c. 25	present	present	1	0.5	Chimbote, Peru
<i>P. variegata</i>	1-2	13-34	59-76	63-87	1	1 shield-shaped	18-21	terminal, last few only	present	present	1	1	Valparaiso, Chile

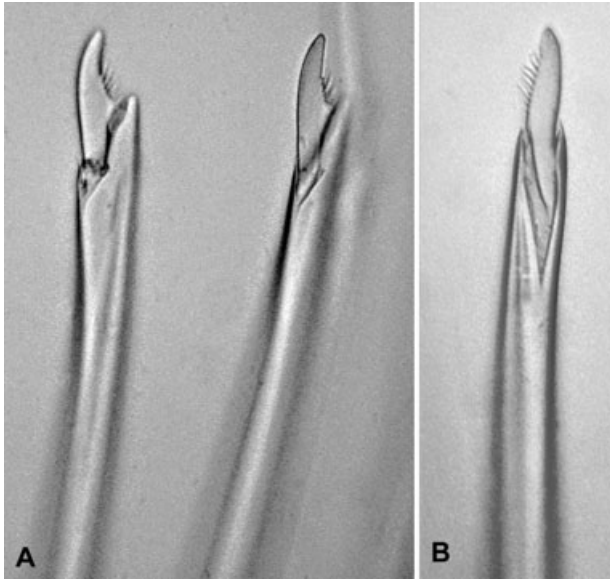


Figure 2. *Pseudonereis anomala* Gravier, 1901 syntypes NMHN POLY TYPE 423. A, heterogomph falcigers neuropodium ventral fascicle from chaetiger 37. B, notopodial homogomph falciger from chaetiger 37.

Material examined: Lectotype MNHN TYPE 1466 (1), paralectotypes, Djibouti 1897 (n29 1897), coll. Coutière, H., MNHN POLY TYPE-423 (12); syntypes, Djibouti 1897, coll. Coutière, H., POLY TYPE-421 (2); Khark, off East side, Iran, 6/3/1937, coll. G. Thorson, ZMUC-POL-1802 (13); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 4.iii.1979, coll. Hutchings & Butler, AM W18310 (98); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 4.iii.1979, coll. P. Hutchings W18311 (47); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 4.iii.1979, coll. P. Hutchings AM W18312 (6); Mastan Pt. America River, Kangaroo Island, clumps of sponge in fast flowing channel, 2.iii.1979, coll. P. Hutchings, AM W18313 (1); Pelsart Group, H. Abrolhos Islands, WA, rock wastings of reef, 1.ix.1947, coll. P. Kott, AM W18574 (1); Plantation Point, NSW 27.vi.1981, AM W25645 (12); North West Solitary Island, coralline algae, 25.vi.1992, coll. P.B. Berents, AM W25646 (1); Broome, probe 6, 9.ix.1975, coll. G. Hartmann-Schröder (5) ZMH P-16564; Port Hedland, probe 34, 30.ix.1975, coll. G. Hartmann-Schröder (1), ZMH P-16565. *Nereis (Pseudonereis) rotnnestiana*, syntype, Rottneest, ZMH V-7929 (1). *Nereis nichollsi*, holotype Rottneest Island, Point Peron, Abrolhos, WA, from weed rock outer edge of reef, coll & id Pat Kott 1946–49, AM W7036 (1); paratypes Rottneest Island, Point Peron, Abrolhos, WA, from weed rock outer edge of reef, coll & id Pat Kott 1946–49, AM W7037 (31). Size range of material examined 48–86 chaetigers

(23–70 incomplete specimens), 10–46 mm long (11–34 incomplete specimens), 1–3.5 mm body width.

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 4–9. Jaws with dentate cutting edge, brown-black, plate-like serrated with 4–5 teeth. Maxillary ring of pharynx with paragnaths arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 1–3 conical paragnaths (4 in two specimens, $n = 39$); Area II = 11–31 p-bar paragnaths in 3–4 rows; Area III = 30–72 p-bar paragnaths in 4 rows; Area IV = 20–52 p-bar paragnaths in 4 rows and additional cones towards the jaws. Area V and VI present as distinct groups. Area V paragnaths absent; VI = 3–15 conical paragnaths, bars absent; VII–VIII = 10–24 conical paragnaths, arranged in one row with similar sized cones, or with two rows where the second row has slightly smaller cones interspersed in the first row or posterior to the first.

Notopodium with dorsal notopodial ligule rounded, as long as ventral notopodial ligule on anterior (Fig. 3A) and mid-body chaetigers (Fig. 3B), markedly elongate and broader on posterior chaetigers (Fig. 3C, D). Prechaetal notopodial lobe absent; acicular process absent. Dorsal cirrus basally attached to dorsal notopodial ligule in anterior chaetigers (Fig. 3A, B), subterminally attached on posterior chaetigers (Fig. 3D). Dorsal cirrus simple, lacking basal cirrophore, 3–4 times as long as ventral notopodial ligule at chaetigers 10–20 (Fig. 3B). Ventral notopodial ligule rounded, slender with a rounded tip in posterior chaetigers.

Neuropodial inferior lobe prominent in anterior chaetigers; a small superior lobe present throughout; neuropodial postchaetal lobe present throughout as a low lobe, not projecting beyond end of acicular ligule, most prominent and drawn out to a triangular tip in posterior chaetigers. Ventral neuropodial ligule similar in length to acicular neuropodial ligule throughout, rounded in anterior chaetigers, slender in posterior. Ventral cirrus similar in length or slightly shorter than acicular ligule.

Notochaetae: homogomph spinigers (Fig. 3F) and falcigers present, falcigers first appear from about chaetiger 30, homogomph falcigers serrated (Figs 2B, 3H). Neurochaetae, dorsal fascicle: homogomph spinigers and heterogomph falcigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present, one or two heterogomph spinigers present from about chaetiger 40 to 50, homogomph spinigers absent, heterogomph falcigers with short blades in anterior and posterior chaetigers present (Figs 2A, 3G).

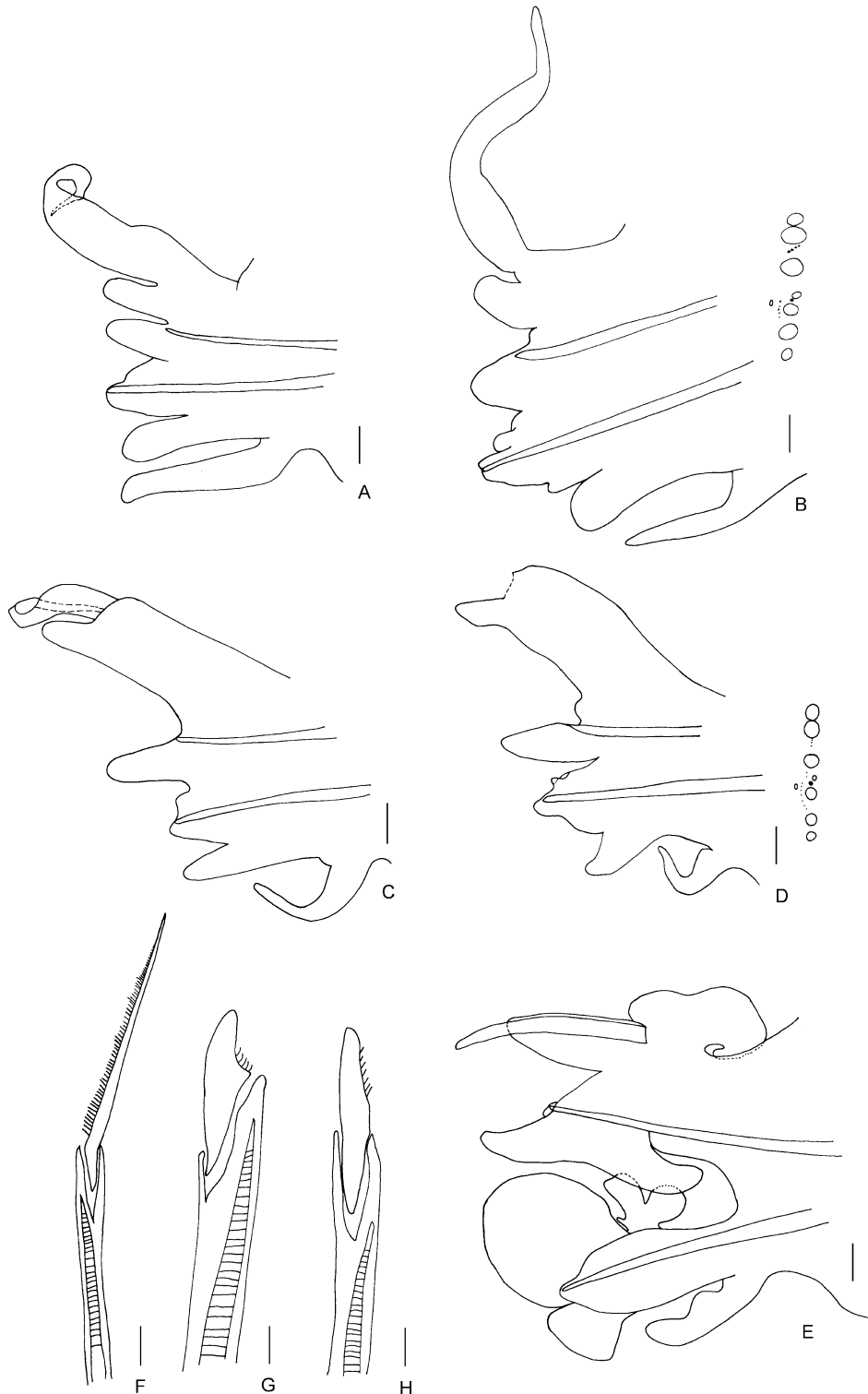


Figure 3. *Pseudonereis anomala* Gravier, 1901 syntypes MNHN Poly Type-423 A–D, F–H; Poly Type 421 E. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 43rd chaetiger anterior view. D, parapodium 60th chaetiger anterior view. E, female heteronereidid, modified parapodium 38th chaetiger anterior view. F, notopodial homogomph spiniger, 20th chaetiger. G, heterogomph falciger neuropodial ventral fascicle, 37th chaetiger. H, notopodial homogomph falciger, 37th chaetiger. End-view drawings of parapodia in B and D are not to scale. Scale bar in A–E 0.1 mm, F and G 0.01 mm. A and B are from one, C from a second and D from a third specimen in the syntype series.

Anal cirri reaching back 8–10 chaetigers. Epitokal modification observed in two specimens (MNHN Poly Type-421), both females filled with large eggs, parapodial modification (Fig. 3E) starting from chaetiger 18.

Remarks: A lectotype is designated from the syntype series (MNHN POLY TYPE-423). The lectotype is a complete specimen measuring 41 mm for 84 chaetigers, 2.5 mm wide. The other 11 specimens from the syntype series are designated paralectotypes. The original description was presented by Gravier (1901) with text figures, but the accompanying figures on plates were printed in an earlier work also on polychaetes from the Red Sea (Gravier, 1900).

The digitiform tip of the dorsal notopodial ligule in posterior chaetigers is obvious and the subterminal position if the dorsal cirrus is very clear. In most specimens the tip of the dorsal ligule is a digitiform protrusion, but this is subject to some variation as it might be a curved tip. This is the case for the syntype of *P. rotnnestiana*, but there is gradual variation over several specimens from the same population (in the paratype series of *Nereis nichollsi*). The protruding tip of the dorsal ligule and the dorsal cirrus in a subterminal position is different from the other taxa in the genus, except *P. multisetosa*, which have the dorsal cirrus in a terminal position. This new information corrects an error in Bakken & Wilson (2005), who coded the dorsal cirrus as terminally attached in posterior chaetigers for this taxon. In the neuropodia a small postchaetal lobe is present. Although it is prominent, typically in posterior chaetigers with a triangular tip, it might be difficult to see especially in smaller specimens (body width < 1 mm).

Pseudonereis anomala differs from other *Pseudonereis* taxa by the presence of notopodial homogomph falcigers and presence of conical paragnaths in Area VI, also present in *P. multisetosa*. *Pseudonereis anomala* can be distinguished from *P. multisetosa* by presence of homogomph falcigers in dorsal fascicle of neuropodia in that the latter.

Pseudonereis rotnnestiana was described from Rottnest Island, Western Australia (Augener, 1913), the same locality from where Kott (1951) described *Nereis nichollsi*. Augener (1913) stated he had two specimens, one small and one larger. The original material was not labelled as types, but according to the measurements given in his description the larger one is identical to a specimen examined here (ZMH V-7929). The specimen is in very good condition but most chaetae are broken; no single notopodial chaeta was observed. Heterogomph spinigers in the neuropodial fascicle were observed in a few posterior chaetigers. Augener (1913) did not include in his description chaetae other than from a 'middle parapodium', did not mention notopodial homogomph falcigers, and he did

not mention chaetae in more posterior chaetigers. Absence of notopodial homogomph falcigers in *P. rotnnestiana* has been given as the only difference between the two similar *P. anomala* and *P. rotnnestiana* (Fauvel, 1932; Hartman, 1954). Augener's only comparison of *P. rotnnestiana* with *P. anomala* was his statement that the two species differed in posterior parapodia, which they indeed do judged from this single specimen. However, there are variations in the shape of the dorsal notopodial ligule in this species, even within a population.

Hutchings & Glasby (1985) discussed the number of conical paragnaths in Area VI and their arrangement in one or two rows in an arc. Variation in paragnath numbers was also discussed by Hutchings & Turvey (1982) (type specimens of *N. nichollsi*). Although few specimens were examined here, it seems that paragnath numbers are consistent within populations but show minor variations between populations (Table 2). Other morphological differences between the populations are not observed. This is also consistent with two rows of conical paragnaths in Area VI, along with other characters described and illustrated in specimens from Thailand by Hylleberg *et al.* (1986).

Hartmann-Schröder (1979, 1980) reported two different forms, published as '*Pseudonereis rotnnestiana* forma *seriodentata*' and '*Pseudonereis rotnnestiana* forma *costatodentata*'. Describing forms or other infraspecific names is nomenclatorially invalid and does not constitute description of a new taxon (ICZN, 1999). It is likely that this represents an accidental publication of manuscript notes. It is evident from the specimens in question (ZMH P-16564; P-16565) that the form Hartmann-Schröder (1979) described as '*seriodentata*' represents specimens of *P. anomala*, while her form '*costatodentata*' represents specimens of *P. trimaculata* (see remarks for this taxon).

Distribution: Type locality Djibouti, Gulf of Aden, Arabian Sea; known from the Arabian Sea, Persian Gulf, around Australia except in the northern part, Thailand (Hylleberg *et al.*, 1986), Hainan Island and Xisha Island, China (Wu, Sun & Yang, 1985). The depth distribution is intertidal and in shallow water.

PSEUDONEREIS ATOPODON CHAMBERLIN, 1919

(FIG. 4)

Pseudonereis atopodon Chamberlin 1919: 228–229, pl. 35, figs 3–5.

Material examined: Holotype, Nomuka, Tonga Island 12.ii.1899, intertidal, USNM 19467; paratypes, Nomuka, Tonga Island 12.ii.1899, intertidal, USNM 19468 (2). Size range of material examined 87–92 chaetigers, 35–44 mm long, 1 mm wide.

Table 2. Paragnath statistics for *Pseudonereis anomala* from examined specimens of six different localities. Exact location data are given in 'Material examined'. Numbers are given as range and (mean \pm SD) for each area of the pharynx. Specimens from Djibouti represent syntypes from the type series

Locality	n	I	II L	II R	III	IV L	IV R	V	VI L	VI R	VII-VIII
Plantation Point, NSW, Australia	4	1	12-16 (14.0 \pm 1.8)	11-16 (13.5 \pm 2.4)	30-36 (32.3 \pm 3.2)	20-33 (26.0 \pm 6.1)	27-33 (28.8 \pm 2.9)	0	9-13 (11.5 \pm 1.7)	9-15 (11.5 \pm 2.5)	13-15 (13.5 \pm 1.0)
Kangaroo Island, South Australia	9	1-3 (1.2 \pm 0.7)	15-28 (20.8 \pm 4.7)	17-29 (21.8 \pm 3.6)	37-63 (48.2 \pm 8.2)	29-52 (37.9 \pm 6.3)	28-51 (36.9 \pm 6.9)	0	5-9 (6.9 \pm 1.4)	6-9 (6.9 \pm 1.1)	16-19 (17.3 \pm 1.3)
Dampier, Western Australia	7	2-3 (2.1 \pm 0.4)	18-22 (20.1 \pm 1.6)	14-23 (18.7 \pm 3.4)	37-53 (43.1 \pm 5.6)	27-38 (31.3 \pm 4.5)	27-38 (32.6 \pm 4.0)	0	6-12 (8.1 \pm 2.3)	5-10 (7.4 \pm 1.9)	10-16 (13.3 \pm 2.0)
Broome, Western Australia	4	1-4 (2.5 \pm 1.3)	23-26 (25.0 \pm 1.4)	20-26 (23.3 \pm 2.5)	51-72 (60.3 \pm 10.0)	35-49 (41.8 \pm 6.1)	38-48 (44.5 \pm 4.4)	0	7-12 (9.3 \pm 2.2)	7-11 (9.5 \pm 1.7)	14-19 (16.0 \pm 2.2)
Djibouti	9	1-2 (1.7 \pm 0.5)	14-20 (17.2 \pm 2.2)	14-20 (18.0 \pm 2.1)	36-56 (43.6 \pm 6.8)	27-46 (34.3 \pm 6.1)	24-42 (33.0 \pm 6.4)	0	5-7 (5.9 \pm 0.9)	4-9 (5.9 \pm 1.5)	10-17 (14.2 \pm 2.3)
Khark, Iran	5	1-4 (2.2 \pm 1.1)	14-23 (20.0 \pm 3.7)	14-24 (19.2 \pm 4.3)	36-46 (42.0 \pm 4.3)	32-40 (36.2 \pm 3.9)	26-38 (33.6 \pm 4.8)	0	3-6 (4.4 \pm 0.5)	4-5 (4.4 \pm 0.5)	11-14 (13.4 \pm 1.3)

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin, longer than wide. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 4. Jaws with dentate cutting edge, brown, plate-like with 4 teeth. Maxillary ring of pharynx with paragnaths arranged in discrete areas, Areas II-IV arranged in regular comb-like rows. Area I = 1; Area II = 37-49 p-bar paragnaths in 5 rows; Area III = 56 p-bar paragnaths in 5 rows; Area IV = in 4-5 rows, cones towards jaws (impossible to see details due to small size or broken), bar-shaped paragnaths or p-bars not observed. Area V and VI present as distinct groups. Area V = 0-1 conical paragnaths, when present a large cone; Area VI = 1 large shield-shaped bar with a pointed tip (triangular) present; Area VII-VIII = 14-24 paragnaths with an appearance like p-bars, similar in size.

Notopodium with dorsal notopodial ligule short, rounded as long as ventral notopodial ligule in anterior chaetigers (Fig. 4A), markedly elongate and markedly broader on posterior chaetigers (Fig. 4D). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 3 times as long as ventral notopodial ligule at chaetigers 10-20 (Fig. 4B), basally attached to dorsal notopodial ligule in anterior and mid-body chaetigers, terminally attached to dorsal notopodial ligule on posterior chaetigers (Fig. 4D), commencing at about chaetiger 60-65.

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe present; neuropodial postchaetal lobe present throughout (Fig. 4C), a low, rounded, flattened lobe level with acicular ligule or lower. Ventral neuropodial ligule rounded up to half length of acicular neuropodial ligule, similar throughout. Ventral cirri short.

Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers present; heterogomph falcigers present throughout, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 30, heterogomph falcigers with short blade present throughout (Fig. 4E, F).

Anal cirri reaching back 4-5 chaetigers.

Remarks: The neuropodial postchaetal lobe is most prominent in mid-body chaetigers (Fig. 4C). *Pseudonereis atopodon* is very similar to *P. gallapagensis*, the only differences being higher number of paragnaths in Area II in *P. atopodon* (37-49) than in *P. gallapagensis* (17-20), and the length of the ventral neuropodial acicular ligule in *P. atopodon*, compared with as long as acicular ligule in *P. gallapagensis*. *Pseudonereis*

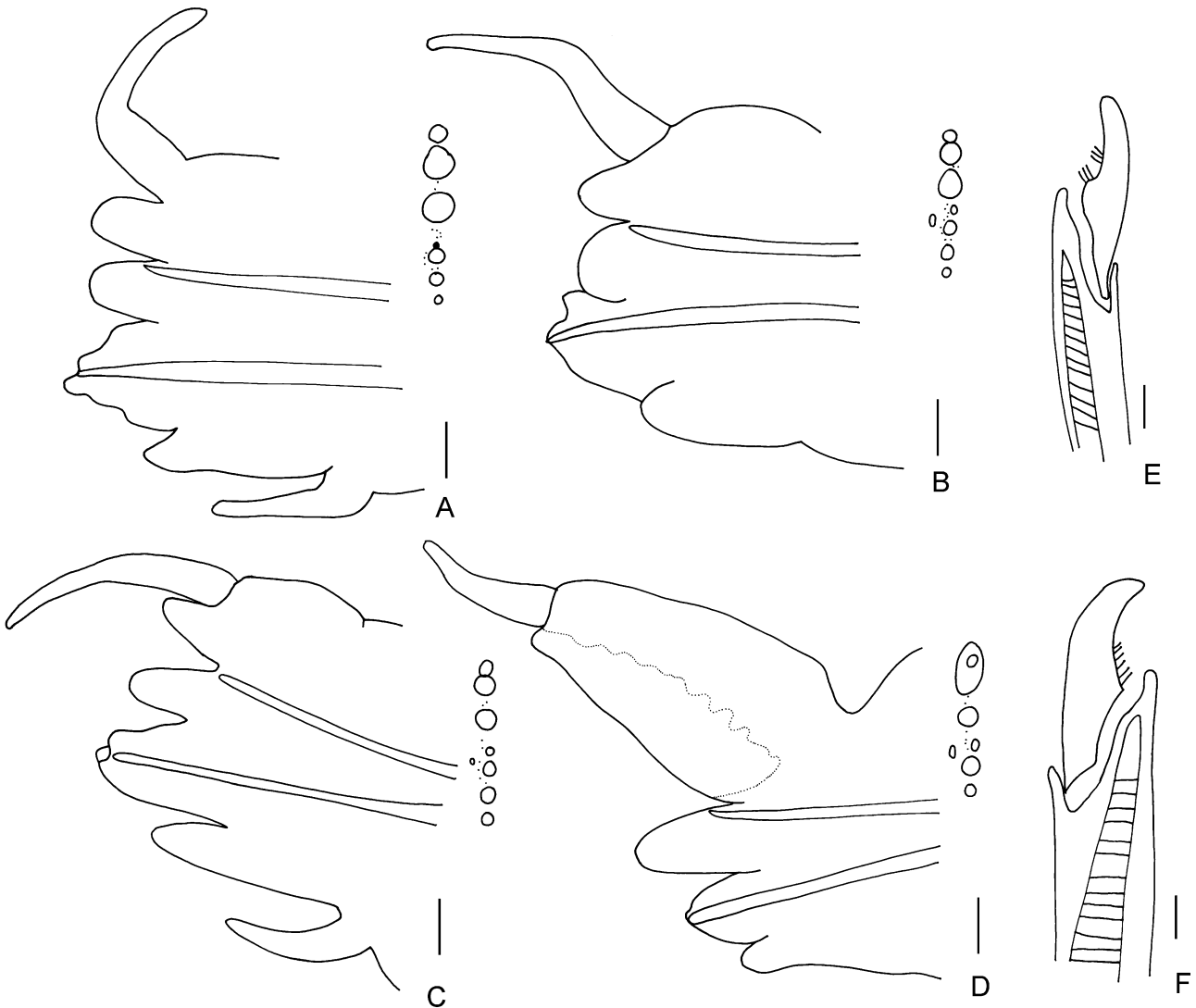


Figure 4. *Pseudonereis atopodon* Chamberlin, 1919 paratypes USNM 19468. A, parapodium 4th chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 70th chaetiger anterior view. E, heterogomph falciger neuropodial ventral fascicle 10th chaetiger. F, heterogomph falciger neuropodial ventral fascicle 60th chaetiger. End-view drawings of parapodia in A–D are not to scale. Scale bar in A–D 0.1 mm, E and F 0.01 mm.

atopodon is also very similar to *P. variegata*, being distinguished by the same relationship of the neuropodial ventral ligule as to *P. gallapagensis*, and in the length of the dorsal cirrus being longer in *P. atopodon* than in *P. variegata* (Table 1).

Obviously *P. atopodon* is very similar to *P. gallapagensis* and *P. variegata* and the identity of the three should be taken into account when more material is available. Differences in paragnath numbers are minor and have not been analysed statistically (more material is required). Of the three specimens examined it was possible in only one to count paragnath numbers for Area III, and none for Area IV.

Chamberlin (1919) stated this taxon was similar to *P. gallapagensis* but did not give a further justification.

Distribution: Nomuka, Tonga Island (type locality), intertidal (Chamberlin, 1919).

PSEUDONEREIS CORTEZI (KUDENOV, 1979)
(FIGS 5, 6)

Neanthes cortezi Kudenov, 1979: 118–120, fig. 2a–h; de León-González & Solís-Weiss 2000: 554–555.

Material examined: Paratypes, Punta La Cholla, Sonora, Mexico, from *Tetraolita squamosa* tests,

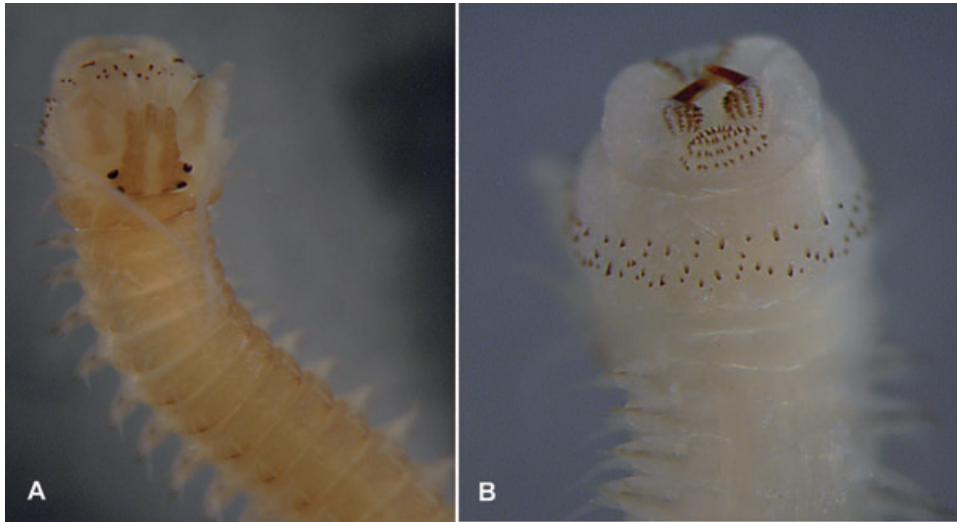


Figure 5. *Pseudonereis cortezi* (Kudenov, 1979) paratype NHMLAC Poly 1344. A, anterior end dorsal view. B, anterior end ventral view. A and B of the same specimen measuring 1 mm body width at chaetiger 10 excluding parapodia.

x.1976, NHMLAC Poly 1344 (23). Size range of material examined 65–90 chaetigers (37–69 incomplete specimens), 10–37 mm long (13–23 incomplete specimens), 0.5–1 mm wide.

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin, longer than wide. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 3–5. Jaws with dentate cutting edge, dark brown with 9–11 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 4–6 conical paragnaths in longitudinal rows; Area II = 17–31 p-bars and conical paragnaths in 4–5 rows in a triangular patch; Area III = 33–54 p-bars and conical paragnaths in 5 rows; Area IV = 31–55 p-bars and conical paragnaths in 4–5 long and 3–4 short rows, shorter rows being closer towards the jaws, and 1–3 p-bars next to the jaws. Area V and VI present as distinct groups. Area V = 8–15 conical paragnaths arranged in a triangular pattern (Fig. 5A); Area VI = 1 large shield-shaped bar present, in some specimens with a distinct pointed tip, cones absent; Area VII–VIII = 62–87 conical paragnaths similar in size forming a broad band, with interspersed p-bars (Fig. 5B).

Notopodium with dorsal notopodial ligule short and rounded as long as ventral notopodial ligule in anterior chaetigers (Fig. 6A, B), markedly elongate and markedly broader on posterior chaetigers, starting from about chaetiger 50–55 (Fig. 6E, F). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2.5 times ven-

tral notopodial ligule at chaetiger 10–20 (Fig. 6B), basally attached to dorsal notopodial ligule in anterior chaetigers, subterminally attached from about chaetiger 35–40 (Fig. 6D), terminally attached from about chaetiger 50–55.

Neuropodial inferior lobe poorly developed; a small superior lobe gives the acicular ligule a bilobed appearance (Fig. 6C), restricted to the first about 40 chaetigers. Neuropodial postchaetal lobe absent. Ventral neuropodial ligule poorly developed, less than 0.5 times as long as acicular ligule, similar to posterior chaetigers, reduced to a papilla (Fig. 6F) in the last about 40 chaetigers. Ventral cirri 0.5 times shorter than ventral ligule.

Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers present; heterogomph falcigers present (Fig. 6G) throughout, blades serrated. Neurochaetae, ventral fascicle: a single heterogomph spiniger present from chaetiger 5–10, heterogomph falcigers with short blade present throughout.

Pygidium with multiple incisions, anal cirri reaching back 3–4 chaetigers. Pigmentation in most specimens part of the palps and the prostomium dark brown, except for a small unpigmented lance-shaped patch in the centre (Fig. 5A; Kudenov, 1979: fig. 2a).

Remarks: The original description (Kudenov, 1979) stated that a single conical paragnath was present in Area VI. This is, however, a large, laterally flattened, high and triangular shield-shaped bar as in most other *Pseudonereis* species. In some specimens this bar has a distinct point skewed towards one side. In Area III the conical paragnaths are more spaced (Fig. 5B) as is usual in other species with comb-shaped

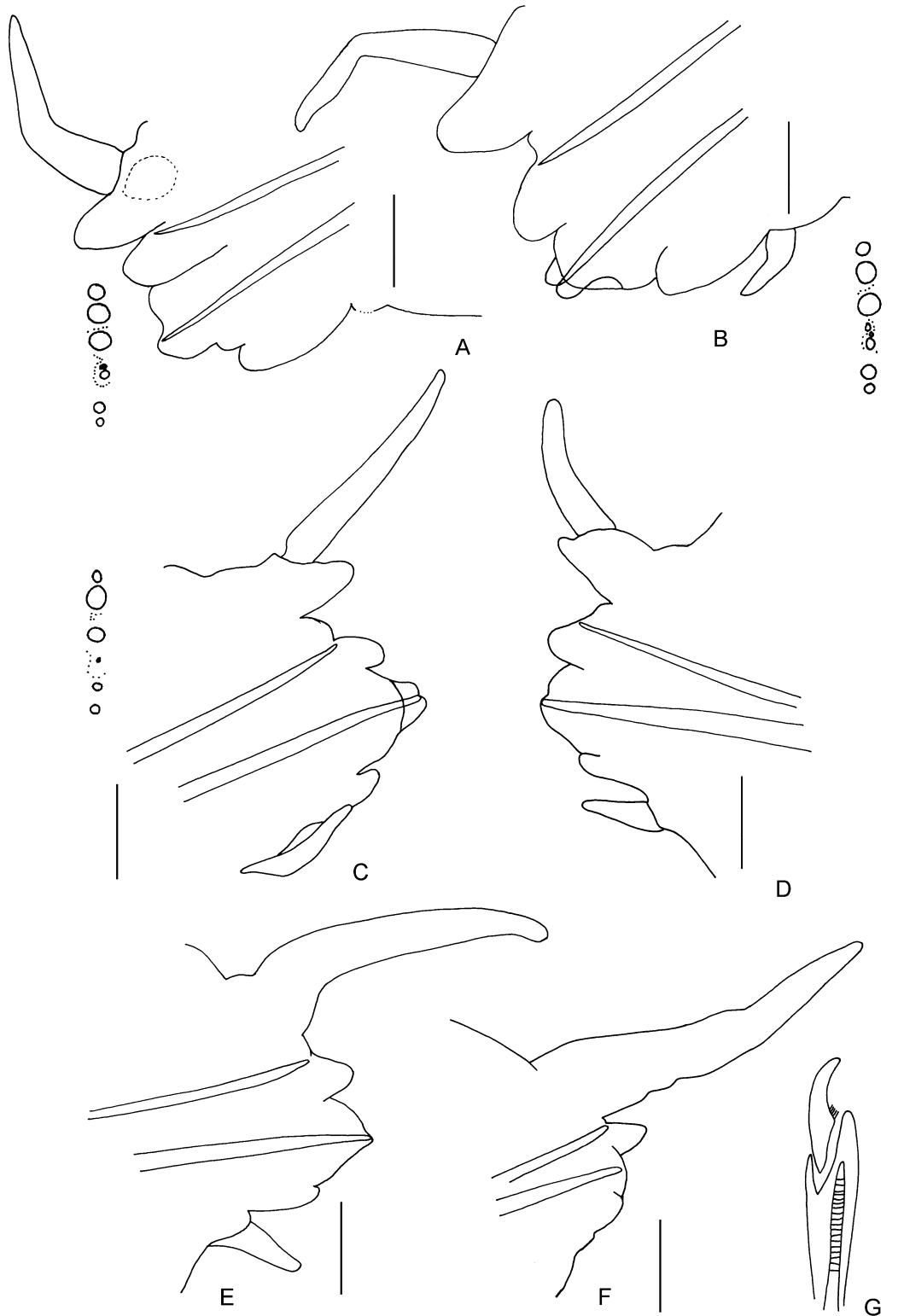


Figure 6. *Pseudonereis cortezi* (Kudenov, 1979) paratype NHMLAC Poly 1344. A, parapodium 3rd chaetiger anterior view. B, parapodium 11th chaetiger anterior view. C, parapodium 30th chaetiger posterior view. D, parapodium 50th chaetiger anterior view. E, parapodium 65th chaetiger posterior view. F, parapodium 80th chaetiger posterior view. G, heterogomph falciger neuropodial dorsal fascicle. End-view drawings of parapodia in A–C are not to scale. Scale bar in A–F 0.1 mm, G 0.01 mm.

rows, although still tight rows. In Areas II and IV the closely comb-shaped rows appear as commonly observed in *Pseudonereis* species. It is very difficult to see in the specimens examined here where the notopodial dorsal ligule ends and where the dorsal cirrus starts, and it is likely the expansion in breadth and length of the dorsal ligule is quite small so that the cirrus is rather long and has a wide base. In most other taxa the dorsal cirrus is attached to the tip of the dorsal ligule and is usually 1/4–1/6 of the length of the ligule. In this taxon it appears that the dorsal cirrus comes to a major part of the dorsal ligule. This question must be left unanswered until more material, preferably live, is available.

Pseudonereis cortezi is distinguished from the other taxa by the absence of a neuropodial postchaetal lobe, which is usually prominent in posterior chaetigers, and by the high number of paragnaths in Area V (8–15) (Fig. 5A) while the other taxa have 0–3. *Pseudonereis cortezi* most closely resembles *P. pseudonoodti* but can be distinguished from the latter by presence of a neuropodial superior lobe in anterior and mid-body chaetigers.

Distribution: Type locality Bahia Cholla, Puerto Peñascola, northern Gulf of California

PSEUDONEREIS GALLAPAGENSIS KINBERG, 1865
(FIG. 7)

Pseudonereis gallapagensis Kinberg, 1865: 174. – Hartman 1949: 68–69. – Hartmann-Schröder 1962b: 432–434. – Fauchald 1977: 32–33.

Pseudonereis formosa Kinberg, 1865: 174.

Material examined: Syntype, Indifatigable Island, Galapagos, Eugenie Exp. 1851–53, stn 873, SMNH Type-452 (1); Valparaiso, Chile, Eugenie Exp. 1851–53, stn 500, SMNH 37896 (1); Chinchá Island, Peru, Eugenie Exp. 1851–53, stn 531, SMNH 37897 (1); Chinchá Island, Peru, Eugenie Exp. 1851–53, stn 531, SMNH 37898 (1); Syntype *Pseudonereis formosa*, Honolulu, Hawaii, Eugenie Exp. 1851–53, stn 1081–91, depth 45 m, SMNH Type-5908 (1). Size range of material examined 43–73 chaetigers (incomplete specimens), 26–47 mm long, 2–2.5 mm wide.

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin, wider than long. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 3–4. Jaws with dentate cutting edge, dark brown, with 4–5 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas; Areas II–IV arranged in regular comb-like rows. Area I = 1 conical paragnath; Area II = 17–20 p-

bar paragnaths in four rows; Area III = 51–68 p-bar paragnaths in 4 rows; Area IV = 38–57 including p-bar paragnaths in 4 rows, around 15 cones towards jaws and 2–4 p-bars next to the jaws. Oral ring paragnaths present, Area V and VI present as distinct groups. Area V = 1 conical paragnath, Area VI = 1 large triangular shield-shaped bar present, cones absent; Area VII–VIII = 17–20 in two rows, anterior row with cones, posterior with p-bars, forming a single band of paragnaths.

Notopodium with dorsal notopodial ligule short and rounded (Fig. 7A, B) markedly elongate and markedly broader on posterior chaetigers (Fig. 7C–E), expansion from about chaetiger 15. Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 3 times ventral notopodial ligule at chaetiger 10–20 (Fig. 7B), basally attached in anterior chaetigers, terminally attached to dorsal notopodial ligule on posterior chaetigers, commencing at about chaetiger 15. Ventral notopodial ligule rounded as long as neuropodial acicular ligule in anterior chaetigers, longer than, protruding, posteriorly.

Neuropodial inferior lobe prominent in anterior-most chaetigers only, a small superior lobe present (Fig. 7A, B). Neuropodial postchaetal lobe present throughout, projecting level with acicular ligule as a low rounded flattened lobe, with a pointed tip in posterior chaetigers. Ventral neuropodial ligule of anterior chaetigers similar in length to acicular neuropodial ligule, up to half length of acicular neuropodial ligule in posterior chaetigers. Ventral cirri as long as acicular ligule throughout.

Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers present; heterogomph falcigers present on anterior (Fig. 7F) and posterior chaetigers, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers, usually a single, present in posterior chaetigers, heterogomph falcigers with short blade present throughout.

Pygidium with multiple, ventral incisions, anal cirri reaching back 4–5 chaetigers (observed in one specimen).

Remarks: The description above is based on the syntype of *P. gallapagensis* (SMNH Type-452) and the syntype of *P. formosa* (SMNH Type-5908), the latter being the more complete specimen, which is also used for illustrations (Fig. 7). The type of *P. gallapagensis* consists of one anterior end and three other fragments from the same specimen in poor condition. It is very difficult to get details from the different pieces, as they are flattened and the parapodia are a little deformed. Patterns of paragnaths in the different areas of the pharynx are possible to see but it is not possible to count numbers. One heterogomph spiniger was observed in ventral fascicle in mid-body and posterior

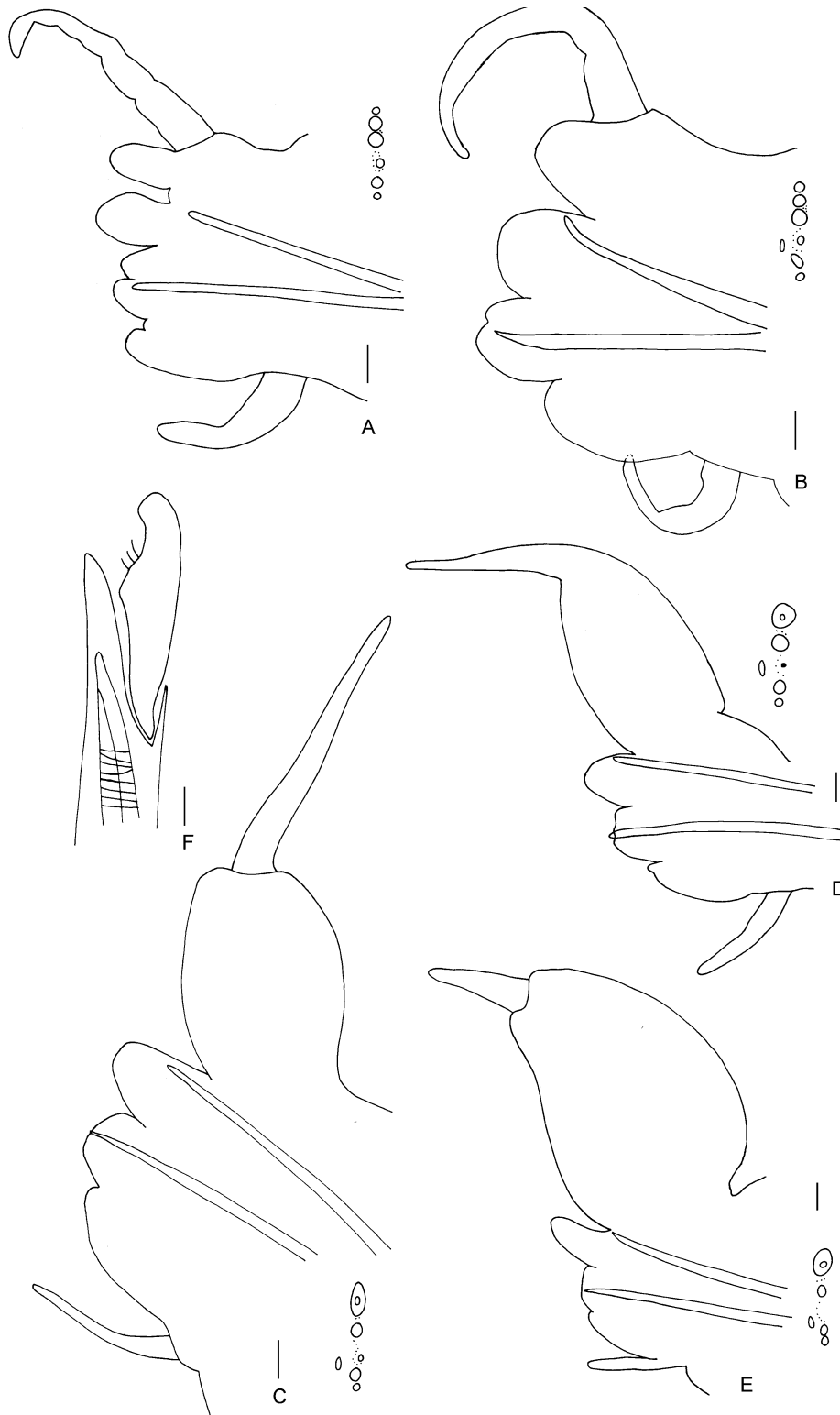


Figure 7. *Pseudonereis gallapagensis* Kinberg, 1865 syntype of *Pseudonereis formosa* Kinberg, 1865 SMNH Type-5908. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 50th chaetiger anterior view. E, parapodium 70th chaetiger anterior view. F, heterogomph falciger neuropodial dorsal fascicle, 3rd chaetiger. End-view drawings of parapodia in A–E are not to scale. Scale bar in A–E 0.1 mm, F 0.01 mm.

chaetigers; heterogomph spinigers were not observed in the type specimen of *P. formosa*. Otherwise these specimens are very similar and are judged to be conspecific. Hartman (1949) stated *P. formosa* was a synonym of *P. gallapagensis* after examining type material of both specimens and the material was labelled accordingly. Re-examination of the material for this study revealed an original label in the vial with the specimens from Honolulu reading *P. formosa* in faded yellow ink. This specimen is clearly the type specimen of *P. formosa* (SMNH Type-5908).

No differences were observed in the material examined from Galapagos, Hawaii, Peru and Chile listed above, but specimens are not in good condition. Hartman (1949) concluded that the specimens identified as *Neanthes variegata* by Kinberg (1865) (SMNH 37897, SMNH 37898) can be referred to *P. gallapagensis* and I agree.

Pseudonereis gallapagensis is most similar to *P. variegata* and *P. atopodon*, and can be distinguished from *P. variegata* by the longer dorsal cirrus, ventral neuropodial ligule up to half as long as acicular ligule in posterior chaetigers compared with as long as in *P. variegata*, and by having fewer paragnaths in Area IV. In the literature (e.g. Hartmann-Schröder, 1962b; Fauchald, 1977) the position of the dorsal cirrus on the dorsal notopodial ligule has been used to distinguish these species. In *P. gallapagensis* the dorsal cirrus is attached terminally from anterior chaetigers (from about chaetiger 15), while in *P. variegata* it is terminally attached in posteriormost chaetigers only. *Pseudonereis gallapagensis* can be distinguished from *P. atopodon* by ventral neuropodial ligule as long as acicular ligule in anterior chaetigers compared with up to half as long as in *P. atopodon*, and having fewer paragnaths in Area II than *P. atopodon* (Table 1).

Fauchald (1977) noted that *P. gallapagensis* has frequently been confused with other taxa. For this reason the synonymies given above are not extensive but restricted to material examined.

Hartman (1949: 69) examined what she thought to be Kinberg's specimens of *Neanthes variegata*, and referred them to *P. variegata* (Grube, 1857), which she obviously considered to be a different species (Hartman, 1959). This must have been based on a misunderstanding. Kinberg (1865: 172) clearly assigned his specimens to Grube's species as '*N[eanthes] variegata* (Grube)'. Kinberg never described a species under the name *Neanthes variegata*.

Distribution: Indefatigable Island, Galapagos (type locality); South America, Pacific coast; Hawaii.

PSEUDONEREIS MASALACENSIS (GRUBE, 1878)

Remarks: Hutchings & Glasby (1985) examined the type material and found it to be in too poor condition

to redescribe. They suggested this taxon should be regarded as indeterminable until material could be obtained from the type locality, especially due to lack of complete chaetae. They commented that no enlargement of dorsal notopodial lobes was observed in the holotype of *P. masalacensis*, suggesting that this species does not belong to *Pseudonereis*.

Type locality is Masolac, Philippines.

PSEUDONEREIS MULTISETOSA

HARTMANN-SCHRÖDER, 1992

(FIG. 8)

Pseudonereis multisetosa Hartmann-Schröder, 1992: 64–65, figs 42–52.

Material examined: Holotype, Rangiroa, French Polynesia, sample 9, 11.ix.1982, ZMH P-20706 (1). Size range of material examined 67 chaetigers, 10 mm long, 0.7 mm wide.

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin, longer than wide. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 5. Jaws with dentate cutting edge, translucent yellow-brown, 11–12 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 2 conical paragnaths; Area II = 17–18 conical paragnaths in 3 rows; Area III = 20 conical paragnaths in 2 rows; Area IV = 29–33 including conical paragnaths in 3 rows and a patch of cones towards jaws. Oral ring paragnaths present, Area V and VI present as distinct groups. Area V = 0; VI = 4 conical paragnaths arranged in transverse lines, bar-shaped paragnaths absent; VII–VIII = 8 conical paragnaths in a single row, present only as a ventral band.

Notopodium with dorsal notopodial ligule rounded, shorter than ventral notopodial ligule in anterior 10–12 chaetigers (Fig. 8A), as long as posteriorly, not markedly elongate on posterior chaetigers, markedly broader on last about 10 posterior chaetigers (Fig. 8D). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore but basis somewhat inflated anteriorly (Fig. 8A), 3–4 times length of ventral notopodial ligule at chaetigers 10–20 (Fig. 8B), basally attached to dorsal notopodial ligule on anterior and mid-body chaetigers, subterminally attached on posterior chaetigers (Fig. 8D).

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe present throughout (Fig. 8C). Neuropodial postchaetal lobe present throughout, a low rounded lobe, projecting level with end of acicular ligule. Ventral neuropodial ligule of

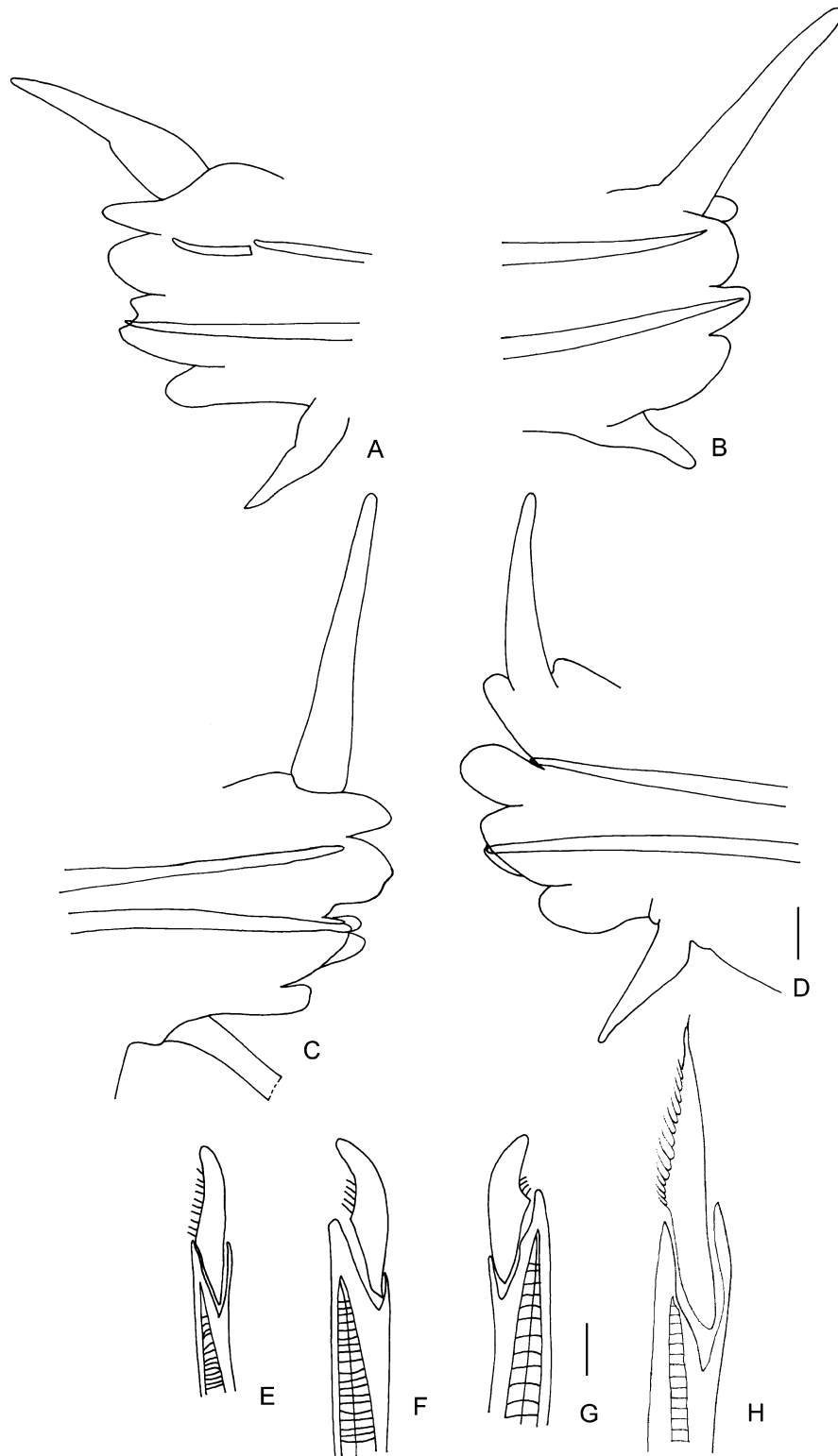


Figure 8. *Pseudonereis multisetosa* Hartmann-Schröder, 1992 holotype ZMH P-20706. A, parapodium 5th chaetiger anterior view. B, parapodium 12th chaetiger anterior view. C, parapodium 20th chaetiger posterior view. D, parapodium 56th chaetiger posterior view. E, homogomph falciger neuropodial dorsal fascicle 12th chaetiger. F, heterogomph falciger dorsal fascicle 12th chaetiger. G, heterogomph falciger ventral fascicle 56th chaetiger. H, notopodial homogomph spiniger 42nd chaetiger. Scale bar in A–D 0.1 mm, E–G 0.01 mm. H is taken from Hartmann-Schröder (1992).

anterior chaetigers present, short and rounded, similar in length to or slightly shorter than acicular neuropodial ligule, on posterior chaetigers up to half length of acicular neuropodial ligule.

Notochaetae: homogomph spinigers present, in mid-body chaetigers (about 20–40) with short very pointed blades and very broad proximally (Fig. 8H); notopodial homogomph falcigers present first present in chaetiger 40–50, notopodial homogomph falcigers serrated; notopodial homogomph spinigers replaced by homogomph falcigers in posterior chaetigers. Neurochaetae, dorsal fascicle: homogomph spinigers and heterogomph falcigers present on anterior (Fig. 8F) and posterior chaetigers, blades serrated, homogomph falcigers (Fig. 8E) on anterior chaetigers present to about chaetiger 15, on posterior chaetigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers present, heterogomph falcigers with short blades present throughout (Fig. 8G).

Pygidium ventrally incised, anal cirri cirriform reaching back 6 chaetigers.

Remarks: This taxon is known only from the holotype, which is in good condition, but may be a juvenile. Paragnath numbers presented here are different from those in the original description, as the pharynx had not been dissected.

Pseudonereis multisetosa differs from all other *Pseudonereis* taxa by the presence of a homogomph falciger in the neuropodial dorsal fascicle, which is rare feature in Nereidinae, but occurs in *Leonnates* and resembles those described for *L. indicus* (Qui & Qian, 2000). The short, very pointed spiniger with broad lower part observed in mid-body chaetigers (~20–40) is a different kind of spiniger (Fig. 8H) only illustrated before in *Leonnates jousseaumei* (Gravier, 1899), which was in turn synonymized with *L. indicus* (Qui & Qian, 2000). This chaeta is here called a spiniger due to its thin whip-like tip. Hartmann-Schröder (1992) described it as having both spiniger and falciger characteristics.

Hartmann-Schröder (1992) stated that the presence of paragnaths in regular comb-shaped rows (termed pectinate in the original description) on the maxillary ring and the conical paragnaths on the oral ring justified the placement of this taxon in *Pseudonereis*. Another character pointing to a placement in *Pseudonereis* is the expansion in breadth of the dorsal notopodial ligule in posterior chaetigers. There are indications of this expansion in the type specimen as well, but it is only slightly expanded in breadth and only in the last about ten chaetigers.

As there are several distinctive morphological features pointing in different directions, further analyses including this taxon should be undertaken when more material becomes available. The form of the dorsal

parapodial ligules in posterior chaetigers should in that case be redescribed as well as the types and distribution of chaetae.

Distribution: Rangiroa, Tuamoto Islands, French Polynesia (type locality).

PSEUDONEREIS NOODTI
(HARTMANN-SCHRÖDER, 1962)
(FIG. 9)

Neanthes noodti Hartmann-Schröder, 1962a: 129–130, pl. 11, figs 65, 66, pl. 12, fig. 68, pl. 20, fig. 67. – 1962b: 395–398, figs 7–10.

Material examined: Lectotype, Chimbote, Peru 25.iv.1956, coll. Noodt, ZMH P-24716 (1); Paralectotype ZMH P-14380 (1). Size range: lectotype 13 chaetiger anterior fragment +38 chaetigers posterior fragment; paralectotype 31 chaetigers anterior fragment +37 chaetigers posterior fragment. Both specimens 1.5 mm wide.

Description: Frontal antennae present, 1 pair, cirriform; palpostyles conical. Prostomium with entire anterior margin, longer than wide. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 2–3. Jaws with dentate cutting edge, brown/black with 6 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 1 conical paragnath; Area II = 25–27 p-bar paragnaths in 3 diagonal rows; Area III = 64 p-bar and conical paragnaths in 4 rows; Area IV = 70–75 including p-bar paragnaths in four comb-shaped rows, additional cones and p-bars towards the jaws. Area V and VI present as distinct groups. Area V = 1, a large cone; Area VI = 1, a large triangular shield-shaped bar present, cones absent; Area VII–VIII = 16–17, two alternating rows of similar sized paragnaths, cones and p-bars interspersed.

Notopodium with dorsal notopodial ligule short and rounded as long as ventral notopodial ligule (Fig. 9A, B), markedly elongate and markedly broader on posterior chaetigers (Fig. 9C, D), merging to dorsal cirrus over chaetigers 15–20. Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2–3 times length of ventral notopodial ligule at chaetigers 10–20 (Fig. 9B), basally attached in anterior chaetigers, terminally attached to dorsal notopodial ligule on posterior chaetigers commencing from about chaetiger 25. Ventral notopodial ligule short and rounded, similar throughout.

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe gives the acicular ligule a

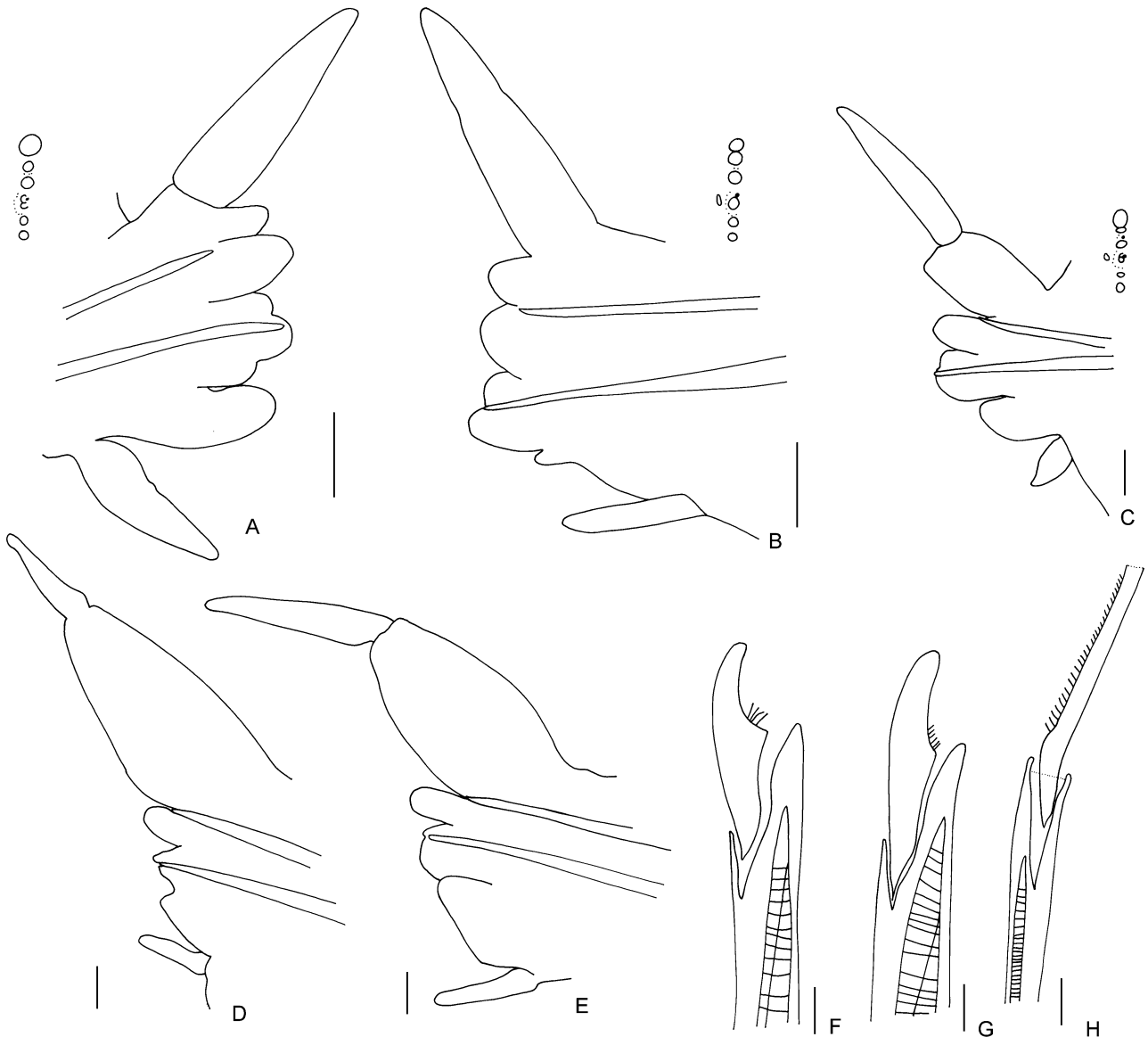


Figure 9. *Pseudonereis noodti* (Hartmann-Schröder, 1962) holotype HZM P-14380. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 20th chaetiger anterior view. D, parapodium 58th chaetiger anterior view. E, parapodium 42nd chaetiger posterior view. F, heterogomph falciger neuropodial dorsal fascicle 10th chaetiger. G, heterogomph falciger neuropodial dorsal fascicle 58th chaetiger. H, homogomph spiniger neuropodial dorsal fascicle 58th chaetiger. End-view drawings of parapodia in A–C are not to scale. Scale bar in A–E 0.1 mm, F–H 0.01 mm.

bilobed appearance (Fig. 9B–D). Neuropodial postchaetal lobe present throughout as a low rounded flattened lobe, not projecting beyond end of acicular ligule, level with or lower than the acicular ligule. Ventral neuropodial ligule of anterior chaetigers present, short rounded, similar in length to acicular neuropodial ligule; on posterior chaetigers present up to half length of acicular neuropodial ligule. Ventral cirri almost as long as acicular ligule throughout.

Notochaetae: homogomph spinigers. **Neurochaetae,** dorsal fascicle: homogomph spinigers present

(Fig. 9H), heterogomph falcigers on anterior (Fig. 9F) and posterior chaetigers (Fig. 9G) present, blades serrated. **Neurochaetae,** ventral fascicle: heterogomph spinigers absent, heterogomph falcigers with short blades in anterior and posterior chaetigers present.

Anal cirri present.

Remarks: The type material consists of two anterior and two posterior ends, which due to the size of the specimens is possible to match; the smaller specimen has a complete posterior end. It was only

possible to count paragnaths on the oral ring in the larger specimen. The larger specimen (anterior fragment and adjoining posterior fragment) is designated lectotype, and the smaller specimen as paralectotype.

Pseudonereis noodti is most similar to *P. gallapagensis*. They can be separated by *P. noodti* having a higher number of paragnaths in Area II and in Area IV (38–57 in *P. gallapagensis* vs. 70–75 in *P. noodti*). Also in *P. noodti* the dorsal cirrus becomes terminally attached about chaetiger 25 as opposed to about chaetiger 15 in *P. gallapagensis*. Heterogomph spinigers in neuropodial ventral fascicle were not observed in the two specimens examined in *P. noodti*, but they are present in *P. gallapagensis*. Absence of heterogomph spinigers in the neuropodial ventral fascicle was also noted in the original description (Hartmann-Schröder, 1962a).

The striking similarity of *P. noodti* to *P. gallapagensis* was not recognized by Hartmann-Schröder (1962a,b) who examined several specimens and gave a detailed description including of epitokes and reproductive modes (Hartmann-Schröder, 1962b). The additional specimens included in the original treatment of this species (Hartmann-Schröder, 1962a,b) were unavailable for study.

Distribution: South American Pacific coast from Chimbote Peru (type locality) in the north and south along the Chilean coast to Puerto Montt (Hartmann-Schröder, 1962b). Intertidally and in rockpools.

PSEUDONEREIS PALPATA (TREADWELL, 1923)

(FIG. 10)

Nereis (Neanthes) palpata Treadwell, 1923: 1239–1243, figs 6–15.

Material examined: Paratype, Ilha dos Alcatrazes, Sao Paulo, Brazil, USNM 19031 (1). Size range of material examined 67 chaetigers (incomplete), 75 mm long, 4 mm wide.

Description: Frontal antennae present, 1 pair, cirri-form, as long as palps. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 4. Jaws with dentate cutting edge, brown to black, plate-like finely serrated at proximal end, no distinct teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 2, conical paragnaths; Area II = 39–40 in transverse rows; Area III = 109 in four transverse rows; Area IV = 108–120 in four diagonal lines, additional towards the jaws. Area V and VI present as distinct groups. Area V = 1 conical; VI = 1 conical and 1 bar present (one bar on left and right side, one cone on right side); VII–VIII = 19 paragnaths.

Notopodium with dorsal notopodial ligule rounded as long as ventral ligule (Fig. 10A), markedly elongate and broader on posterior chaetigers (Fig. 10B). Prechaetal notopodial lobe absent; acicular process

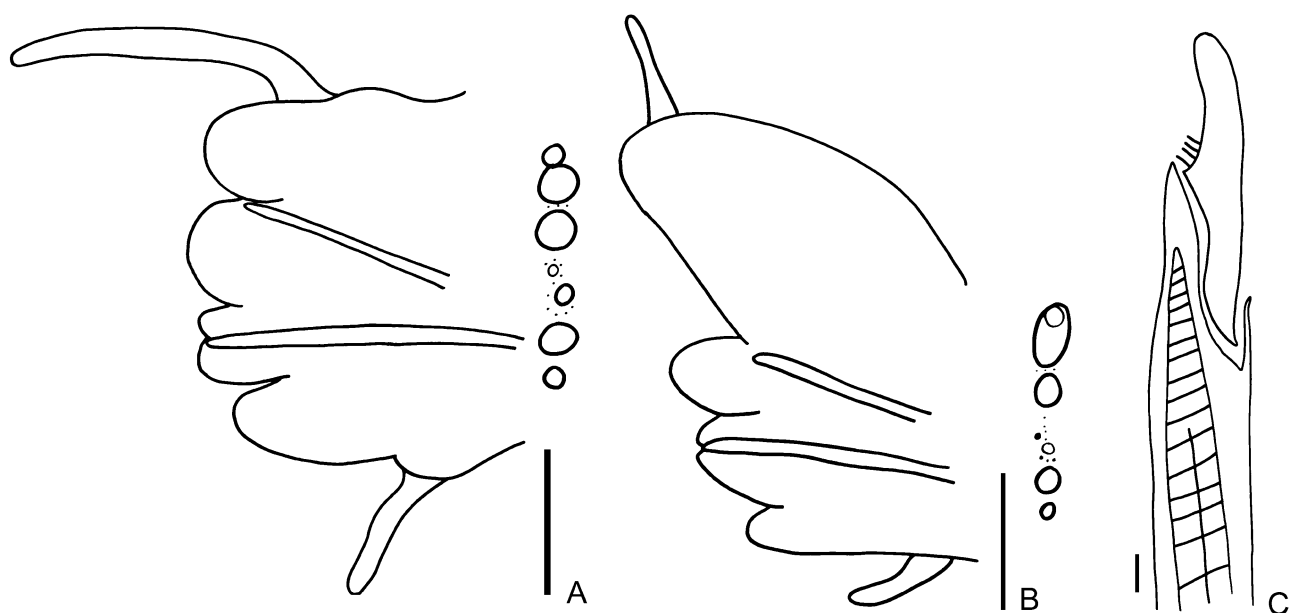


Figure 10. *Pseudonereis palpata* (Treadwell, 1923) paratype USNM 19031. A, parapodium 10th chaetiger anterior view. B, parapodium 65th chaetiger anterior view. C. Heterogomph falciger neuropodial dorsal fascicle 41st chaetiger. Scale bar in A and B 0.5 mm, C 0.01 mm. End-view drawings of parapodia in A and B are not to scale.

absent. Dorsal cirrus basally attached to dorsal notopodial ligule on anterior and mid-body chaetigers, terminally attached on posterior chaetigers, 3–4 times as long as ventral notopodial ligule at chaetiger 10–20. Ventral notopodial ligule rounded.

Neuropodial inferior lobe rounded distinct throughout; a small superior lobe present throughout; neuropodial postchaetal lobe absent. Ventral neuropodial ligule up to half as long as acicular neuropodial ligule throughout. Ventral cirrus as long as acicular ligule in anterior chaetigers, becoming shorter, 0.5 times as long in posterior chaetigers.

Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers and heterogomph falcigers (Fig. 10C) present, blades serrated, blades having teeth only slightly longer proximally than distally. Neurochaetae, ventral fascicle: heterogomph spinigers present, with blades finely serrated proximally, homogomph spinigers absent; heterogomph falcigers with short blades present.

Remarks: The description presented here is based on a single specimen in poor quality. A more detailed

redescription of this species based on a quantity of material from Brazil is being prepared and will be presented elsewhere. In the data matrix (Table 3) the neuropodial postchaetal lobe is scored as absent, but due to the poor condition of the single specimen examined, this character should be verified from additional material.

This taxon is unique among *Pseudonereis* in possessing both bar-shaped and conical paragnaths in Area VI. The type or shape in bar-shaped paragnaths presented as new characters here was not recorded from the paratype and will have to be verified from additional material.

Distribution: South America, Atlantic coast, type locality: Estado de S. Paulo, Brazil.

PSEUDONEREIS PSEUDONOODTI (FAUCHALD, 1977)
(FIGS 11, 12)

Neanthes pseudonoodti Fauchald, 1977: 27–29, fig. 7.

Material examined: Holotype, Paitilla Beach, Panama, Pacific, intertidal, USNM 53090; Paratypes, Paitilla

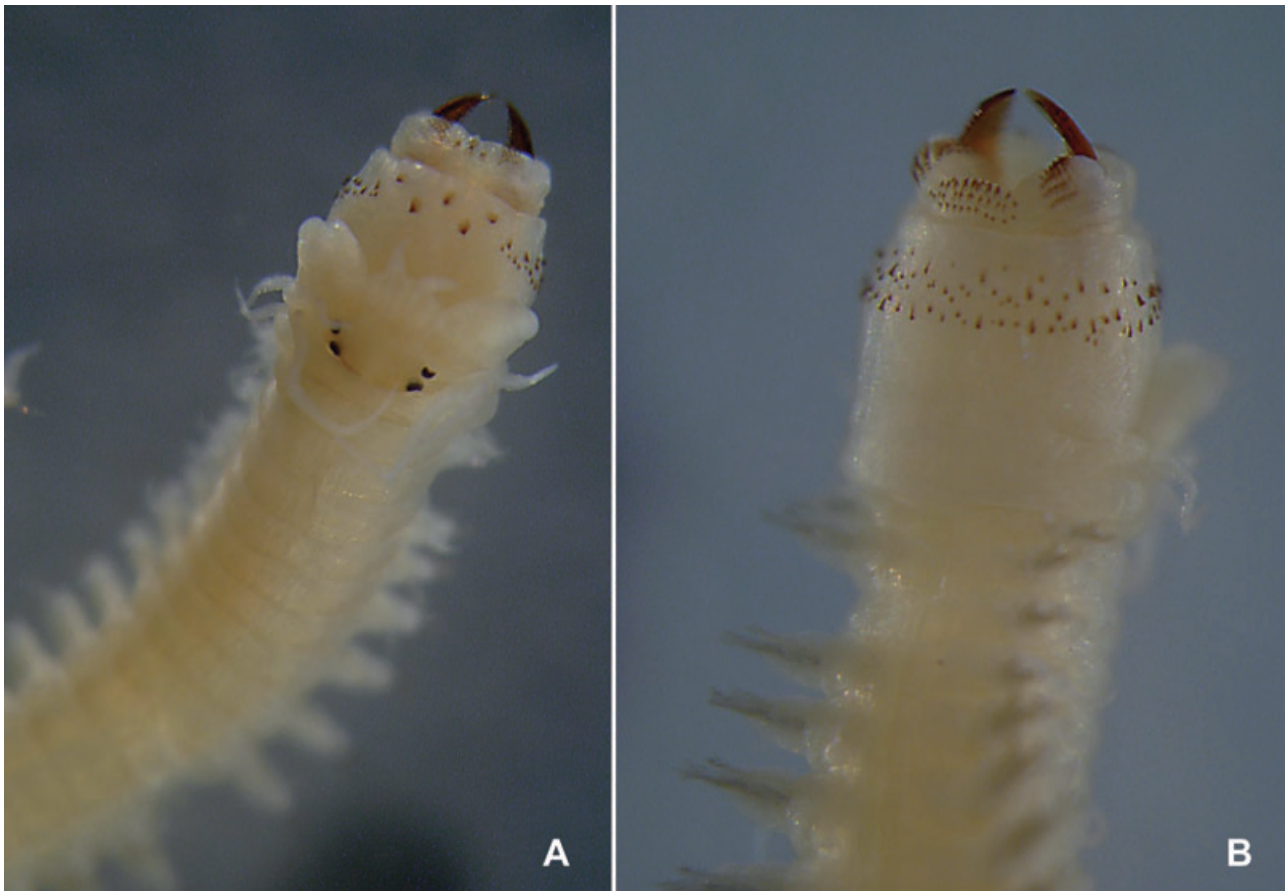


Figure 11. *Pseudonereis pseudonoodti* (Fauchald, 1977) paratype USNM 53091. A, anterior end dorsal view. B, anterior end ventral view. A and B are of the same specimen measuring 0.8 mm body width at chaetiger 10 excluding parapodia.

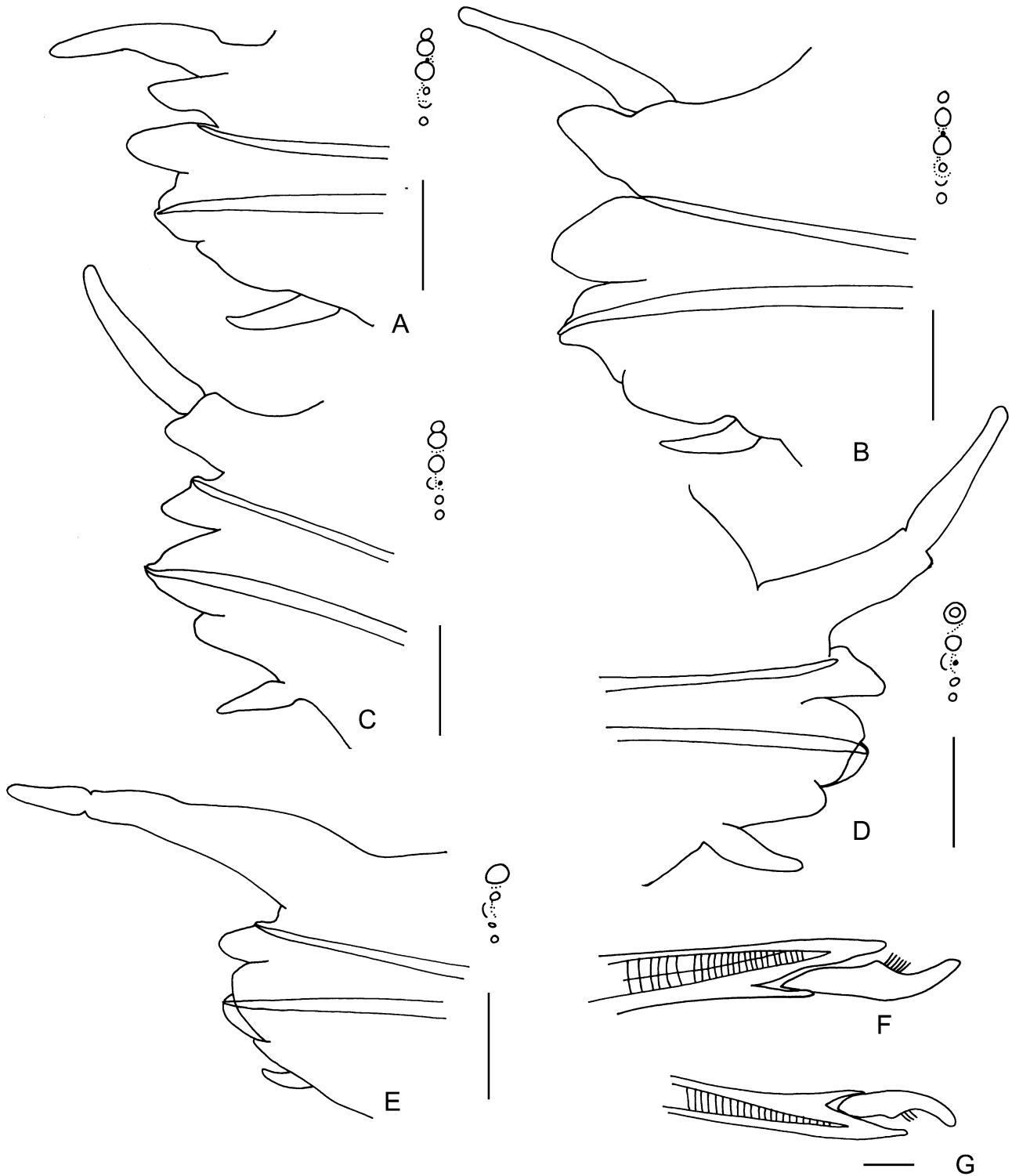


Figure 12. *Pseudonereis pseudonoodti* (Fauchald, 1977) paratype USNM 53091. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 40th chaetiger posterior chaetiger. E, parapodium 50th chaetiger anterior view. F, heterogomph falciger neuropodial dorsal fascicle 50th chaetiger. G, heterogomph falciger neuropodial ventral fascicle 30th chaetiger. End-view drawings of parapodia in A–E are not to scale. Scale bar in A–E 0.1 mm, F and G 0.01 mm.

Beach, Panama, Pacific, intertidal, *Tetraclita* zone USNM 53091 (4). Additional material: Paitilla Beach, Panama, Pacific, coll. A.A. Reimer, 20.i.1971 USNM 065983 (1); Paitilla Beach, Panama, Pacific, intertidal, coll. A.A. Reimer, 20.i.1971 USNM 065984 (5). Size range of material examined 29–74 chaetigers (only one specimen complete), 4–18 mm long, 0.5–1 mm wide.

Description: Frontal antennae present, 1 pair, cirri-form; palpostyles conical. Prostomium with entire anterior margin, wide as long. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 3–4. Jaws with dentate cutting edge, translucent brown, with 8 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 4 conical paragnaths, one in front of a transverse row of 3; Area II = 15–27 p-bar paragnaths in 4 rows in a triangular patch; Area III = 28–40 p-bar and conical paragnaths in 4 rows; Area IV = 20–61 p-bar and conical paragnaths in 4–5 rows, additional cones and p-bar paragnaths towards the jaws absent. Oral ring paragnaths present, Area V and VI present as distinct groups. Area V = 3 conical paragnaths present arranged in a triangular pattern (Fig. 11A); Area VI = 1 shield-shaped bar with pointed tip present, cones absent; Area VII–VIII = 69–100, in 2–3 rows with similar sized conical paragnaths, with larger p-bars interspersed (Fig. 11B).

Notopodium with dorsal notopodial ligule digitiform rounded in anterior chaetigers (Fig. 12A, B), markedly elongate on posterior chaetigers (Fig. 12D, E), markedly broader on posterior chaetigers (Fig. 12E), expansion commencing at about chaetiger 30–35. Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2–3 times length of ventral notopodial ligule at chaetiger 10–20 (Fig. 12B), basally to mid-dorsally attached to dorsal notopodial ligule on anterior chaetigers (Fig. 12B), terminally attached to dorsal notopodial ligule on posterior chaetigers, from about chaetiger 40 (Fig. 12D, E).

Neuropodial inferior lobe prominent in anterior-most chaetigers only; superior lobe absent. Neuropodial postchaetal lobe present throughout, a low rounded lobe projecting level with or lower than end of acicular ligule, most prominent in posterior chaetigers (Fig. 12D, E). Ventral neuropodial ligule of anterior chaetigers up to half length of acicular neuropodial ligule, on posterior chaetigers reduced (Fig. 12E).

Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers present; hetero-

gomph falcigers on anterior (Fig. 12F), and posterior chaetigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present commencing in chaetiger about 5–10, heterogomph falcigers with short blades present throughout (Fig. 12G).

Remarks: The vial with the paratypes (USNM 53091) with nine specimens included five specimens of *Nereis riisei*. The description is based on the remaining four specimens.

The neuropodial postchaetal lobe was difficult to detect in the smaller specimens examined (< 1 mm body width). Fauchald (1977) stated in the original description that there was a single large paragnath in Area V and two in each of Area VI. This is reinterpreted here to be three widely spread cones in Area V in a triangular pattern, and a single in Area VI (Fig. 12A). The paragnaths in Area VI are high, flat and pointed triangular bars (shield-shaped) as seen in most other *Pseudonereis* species.

Pseudonereis pseudonoodti is very similar to *P. cortezi*, but can be distinguished by absence of the neuropodial superior lobe, which is present in *P. cortezi*, and the number of paragnaths in Area V. In *P. pseudonoodti* the paragnaths in Area III are more widely spaced (Fig. 11B) than in other species, although still in tight regular rows, the notopodial dorsal ligule is greatly expanded in length but not so much in breadth, and it is almost impossible to see clearly where the dorsal cirrus starts on the expansion from the notopodial ligule.

Distribution: Type locality Paitilla Beach (Pacific), Panama, intertidal rocky substrates (Fauchald, 1977).

PSEUDONEREIS TRIMACULATA HORST, 1924

(FIG. 13)

Nereis (Pseudonereis) trimaculata Horst, 1924: 187–188, pl. XXXVI, figs 8, 9.

Pseudonereis rotnestiana forma *costatodentata* Hartmann-Schröder, 1979: 119, figs 220–222.

Material examined: Syntype, between Gisser and Ceram, Indonesia, Siboga Expedition, stn 172, reef exploration, ZMA Vpol-954 (1); Broome, WA, probe 6, 9/91975, HZM P-16567 (7); south-west tip of West Lewis Island, Western Australia, Australia, 20°36.38'S 116°36.06'E, WA624, intertidal, coll. P.Hutchings & L. Avery 27.vii.2000, AM W29016 (1); North-west of West Lewis Island, Western Australia, Australia, 20°33.52'S 116°38.21'E, WA621, under boulders and in crevices, depth 0 m, coll. P.Hutchings & L. Avery 26.vii.2000, AM W29017 (2). Size range of material examined 60–94 chaetigers for 17–41 mm long, 1–2 mm wide.

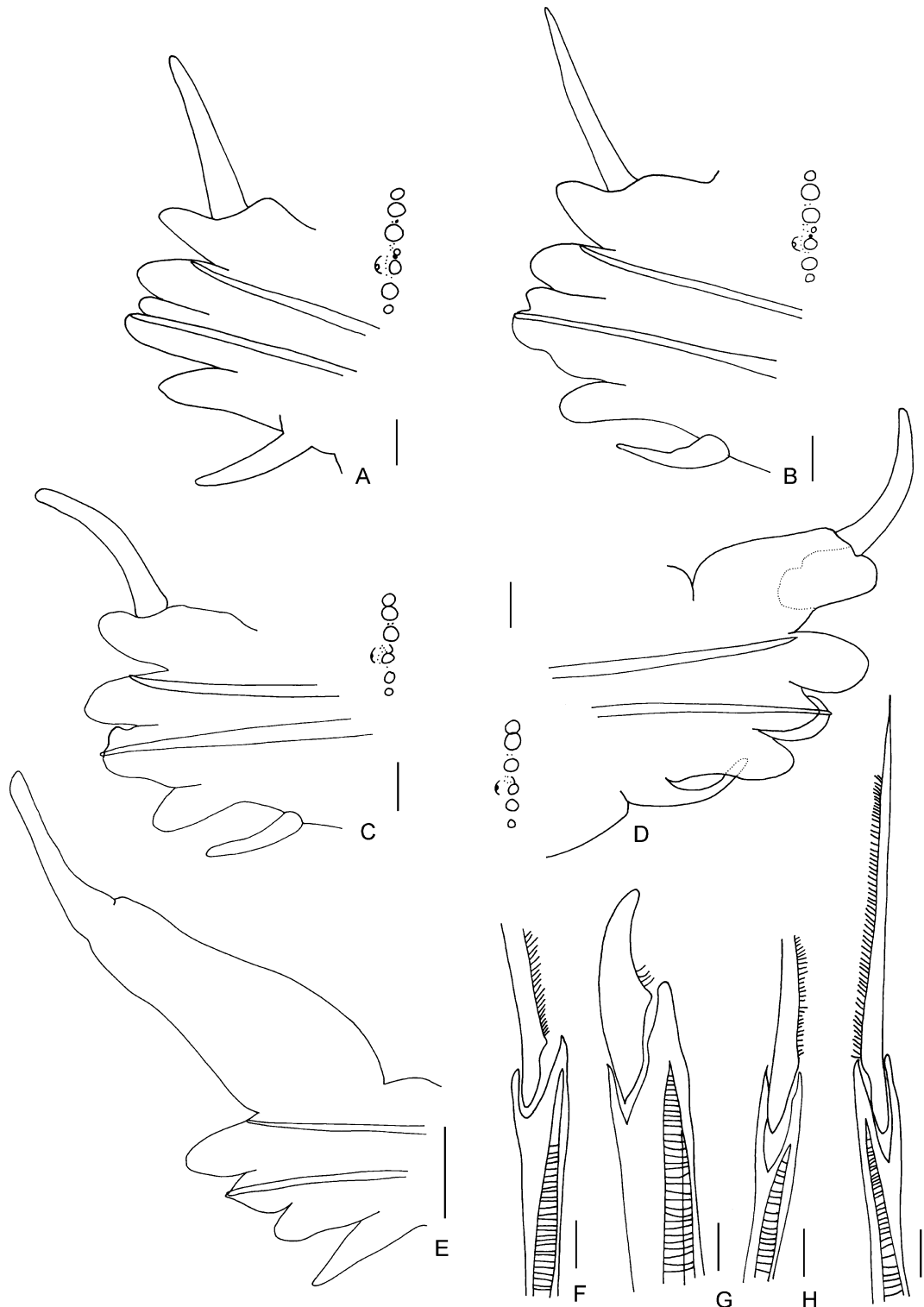


Figure 13. *Pseudonereis trimaculata* Horst, 1924 ZMH P-16567. A, parapodium 3rd chaetiger anterior view. B, parapodium 11th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 50th chaetiger posterior view. E, parapodium 65th chaetiger anterior view. F, heterogomph spiniger neuropodial ventral fascicle 30th chaetiger. G, heterogomph falciger neuropodial dorsal fascicle 30th chaetiger. H, homogomph spiniger neuropodial dorsal fascicle 30th chaetiger. I, homogomph spiniger notopodium 3rd chaetiger. End-view drawings of parapodia in A–D are not to scale. Scale bar in A–E 0.1 mm, F–I 0.01 mm.

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 5–7. Jaws with dentate cutting edge, brown, with 5–6 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II–IV arranged in regular comb-like rows. Area I = 1–2 conical paragnaths, in a longitudinal row when 2; Area II = 23–38 p-bar paragnaths in 4 rows; Area III = 51–69 p-bar paragnaths in 4 rows; Area IV = 50–78 including p-bar paragnaths in 4 rows additional cones and 2–4 p-bars towards jaws. Oral ring paragnaths present, Area V and VI present as distinct groups. Area V = 1–3 large conical paragnaths present, arranged in a triangular pattern when 3; Area VI = 1 shield-shaped bar present, cones absent; Area VII–VIII = 20–24 large conical paragnaths of similar size and interspersed p-bars present in two alternating rows.

Notopodium with dorsal notopodial ligule digitiform rounded as long as ventral neuropodial ligule in anterior chaetigers (Fig. 13A, B), markedly elongate on posterior chaetigers commencing about chaetiger 55–60, markedly broader on posterior chaetigers commencing about chaetiger 50–55 (Fig. 13D, E). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2 times length of ventral notopodial ligule at chaetiger 10–20 (Fig. 13B), basally attached in anterior chaetigers, subterminally attached in mid-body chaetigers (Fig. 13D), and terminally attached to dorsal notopodial ligule on posterior chaetigers in the last quarter of the body (Fig. 13E).

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe present (Fig. 13A), less developed from mid-body chaetigers, visible throughout. Neuropodial postchaetal lobe present throughout, a low rounded lobe with a small pointed tip, projecting level with the end of acicular ligule (Fig. 13D). Ventral neuropodial ligule rounded, well developed throughout, up to half length of acicular neuropodial ligule on anterior chaetigers, on posterior chaetigers similar to length of acicular neuropodial ligule. Ventral cirri 0.5 times as long as neuropodial acicular ligule.

Notochaetae: homogomph spinigers present (Fig. 13I). Neurochaetae, dorsal fascicle: homogomph spinigers present (Fig. 13H), heterogomph falcigers on anterior and posterior (Fig. 13G) chaetigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 30 (Fig. 13F), heterogomph falcigers with short blades present throughout.

Anal cirri reaching back about 10 chaetigers.

Remarks: The original material (ZMA V-pol 954) labelled as ‘type’ and given as syntype in the museum record (ZMA) consisted of two specimens, not three as stated in the original description. Of the two specimens the smaller one is a *Platynereis* sp. and the other was used to prepare the original description. This specimen is designated as lectotype, and confirmed well with the Australian material examined and illustrated (Fig. 13). The lectotype is a complete specimen and measures 41 mm in length for 94 chaetigers, 2 mm wide. Paragnaths were not possible to count except in Area I = 1; Area VI = 1/1; Area VII–VIII = 20.

Pseudonereis trimaculata is similar to *P. gallapagensis*, *P. variegata*, *P. noodti* and *P. pseudonoodti*; it most closely resembles *P. pseudonoodti* (Table 1). The other taxa in this group have a large single conical paragnath in Area V while *P. pseudonoodti* and *P. trimaculata* have three. Apart from this character there are differences in paragnath numbers, length of dorsal cirrus and development and length of the ventral neuropodial ligule separating these species (Table 1).

Horst (1924) gave only a brief description but included illustrations of two parapodia, one anterior and the other which appears to be from a mid-body chaetiger, although the figure legend stated it was from a posterior parapodium. He drew attention to black spots on the parapodia that he used to distinguish his new taxon from other described *Pseudonereis* taxa. These spots are glands often observed in parapodia of nereidids, but now only vaguely visible in the lectotype.

Hartmann-Schröder (1979) described specimens representing this taxon as a variety of *P. rotnestiana*, using the term ‘form’ (*Pseudonereis rotnestiana* forma *costatodentata*). The label with these specimens (HZM P-16567) did not have the name as such but a comment was added to distinguish the specimens as separate from *P. rotnestiana* (see *P. anomala* for further comments).

Distribution: Type locality Geser, Indonesia, known from the type locality and Western Australia. This is the first record of this taxon from Australia. All records are from intertidal and low littoral environments.

PSEUDONEREIS VARIEGATA (GRUBE, 1857)
(FIGS 14, 15)

Nereilepas variegata Grube, 1857: 164–165.

Nereis ferox Hansen, 1882: 14, pl. IV, figs 34–39. – Augener 1934: 133.

Nereis variegata Ehlers, 1901: 112–11118, pl. XIV, figs 1–21.

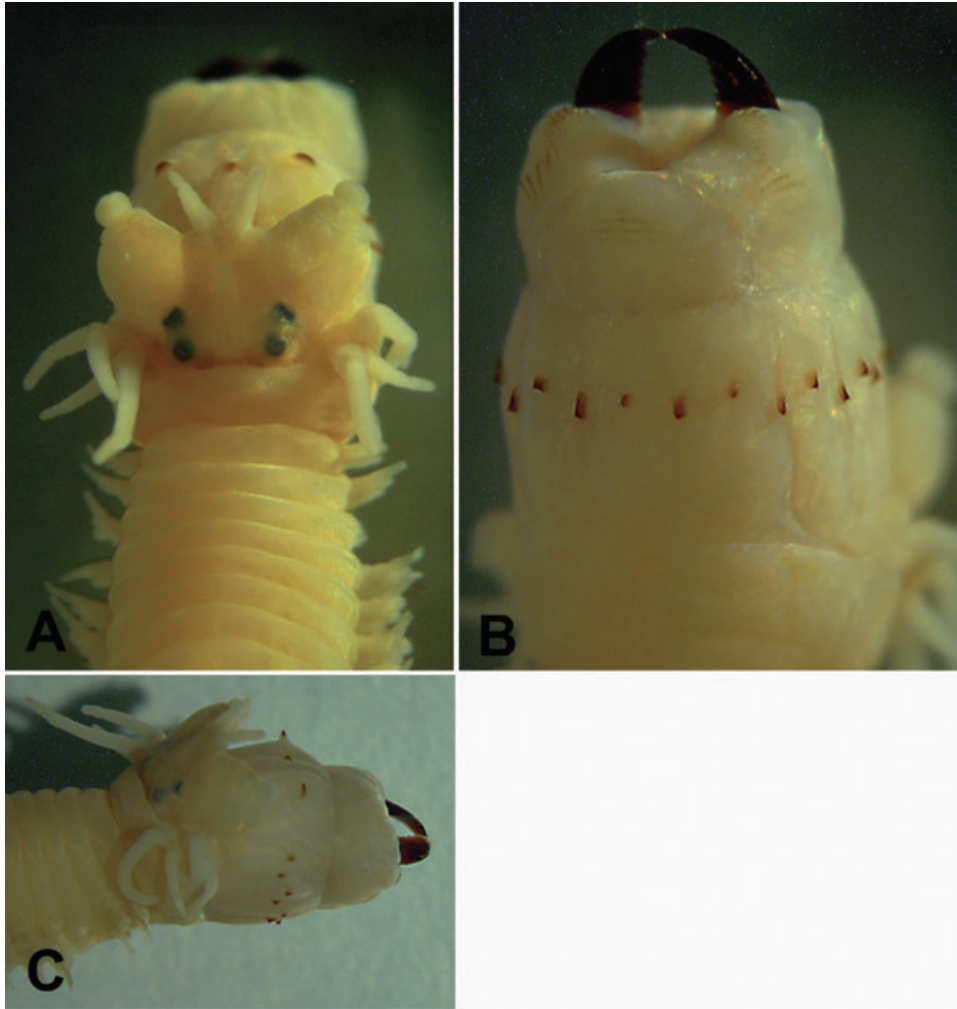


Figure 14. *Pseudonereis variegata* (Grube, 1857) syntypes of *Nereis ferox* Hansen, 1882 ZMUB 2130. A, anterior end dorsal view. B, anterior end ventral view. C, anterior end lateral view. The laterally flattened shield-shaped paragnaths protruding from the tissue are demonstrated in C. A–C are of the same specimen measuring 3 mm body width at chaetiger 10 excluding parapodia.

Pseudonereis variegata Hartman, 1949: 69–70. – Hartmann-Schröder 1962b: 434–435. – Fauchald 1977: 33, fig. 9d–e.

Material examined: Syntypes *Nereis ferox* Hansen, 1882, Rio de Janeiro, ZMUB 2130 (3); Rio de Janeiro, v. Beneden, ZMUC-POL-1804 (2). Size range of material examined 64–94 chaetigers (62 incomplete specimen), 26–46 mm long (35 incomplete specimen), 1.5–3 mm wide.

Description: Frontal antennae present, 1 pair, cirri-form. Prostomium with entire anterior margin, longer than wide. Eyes present, 2 pairs (Fig. 14A). One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 3–5. Jaws with dentate cutting edge, black/brown platelike

serrated with 4–5 teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Areas II–IV arranged in regular comb-like rows. Area I = 1–2 conical paragnaths; Area II = 13–34 p-bar paragnaths in three rows; Area III = 59–76 p-bar paragnaths in four rows, anteriormost row half as long as the others; Area IV = 63–87 p-bar paragnaths in 4–5 rows, additional cones and 2–4 p-bars towards jaws. Area V and VI present as distinct groups. Area V = 1 conical paragnath. Area VI = 1 large shield-shaped bar present (Fig. 14B, C); Area VII–VIII = 18–21, conical paragnaths and large p-bars in two alternating rows, p-bars being more posteriorly placed (Fig. 14B).

Notopodium with dorsal notopodial ligule stout rounded as long as ventral notopodial ligule in anterior chaetigers (Fig. 15A, B), markedly elongate and markedly broader on posterior chaetigers, expanded

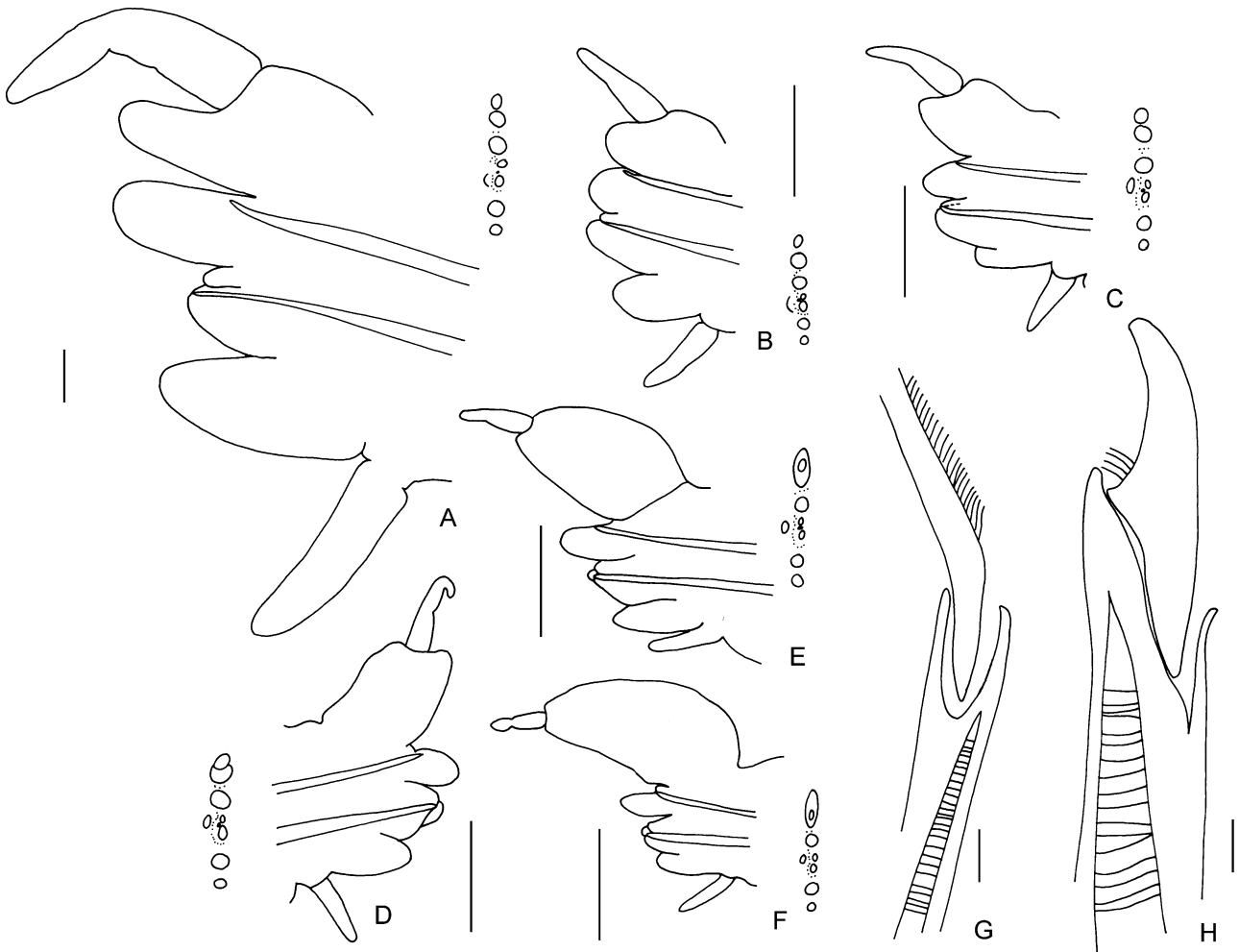


Figure 15. *Pseudonereis variegata* (Grube, 1857) syntypes of *Nereis ferox* Hansen, 1882 ZMUB 2130. A, parapodium 3rd chaetiger anterior view. B, parapodium 11th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 40th chaetiger posterior view. E, parapodium 56th chaetiger anterior view. F, parapodium 78th chaetiger anterior view. G, homogomph spiniger neuropodial dorsal fascicle 11th chaetiger. H, heterogomph falciger neuropodial ventral fascicle 11th chaetiger. End-view drawings of parapodia in A–F are not to scale. Scale bar in A 0.01 mm, B–F 0.5 mm, G and H 0.01 mm.

in breadth from about chaetiger 30 (Fig. 15C), in length from about chaetiger 40 (Fig. 15D, E). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2 times length of ventral notopodial ligule at chaetiger 10–20, basally attached in anterior chaetigers (Fig. 15B), subterminally attached from about chaetiger 30 (Fig. 15D, E), terminally attached to dorsal notopodial ligule on posteriormost chaetigers (Fig. 15F). Ventral notopodial ligule stout rounded, in posterior chaetigers digitiform.

Neuropodial inferior lobe prominent in anterior chaetigers; small superior lobe present throughout (Fig. 15E, F). Neuropodial postchaetal lobe present throughout, low rounded not projecting beyond end of

acicular ligule, in posterior chaetigers with a small triangular tip (Fig. 15D, F). Ventral neuropodial ligule of anterior chaetigers present, well developed, similar in length to acicular neuropodial ligule throughout. Ventral cirrus 0.5–1 times as long as neuropodial acicular ligule.

Notochaetae: homogomph spinigers. Neurochaetae, dorsal fascicle: homogomph spinigers (Fig. 15G) and heterogomph falcigers present throughout, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 40, with blades finely serrated; heterogomph falcigers with short blades (Fig. 15H) present throughout.

Pygidium with multiple ventral incisions, anal cirri reaching back five chaetigers.

Remarks: Description and illustrations presented here are based on the syntypes of *Nereis ferox* and variation given from additional material examined. Type material of *Nereilepas variegata* Grube was not available for study. *Nereis ferox* has been synonymized in the literature by Ehlers (1901) and Augener (1934). Ehlers apparently examined the types of *N. ferox* which he found to be identical to *P. variegata*. Type specimens of *N. ferox* and *P. variegata* should be compared but could not be located in this study.

Pseudonereis variegata resembles most closely *P. gallapagensis* (Table 1) but is distinguished by the length of the ventral neuropodial ligule, which in *P. variegata* is of similar length to the acicular ligule but up to half as long in *P. gallapagensis*; and by the number of conical paragnaths in Area IV (68–87 in *P. variegata*; 38–57 in *P. gallapagensis*). The length of the dorsal cirrus in anterior chaetigers is also different being longer in *P. gallapagensis*. *Pseudonereis variegata* has generally a higher number of paragnaths in all areas than *P. gallapagensis*, although these differences are small and may be insignificant when more material is examined. Similarities to *P. atopodon* are also noted (Table 1; see this taxon for further comments).

Paragnaths in Area VII–VIII in several rows have been used as a diagnostic feature to distinguish *P. variegata* from *P. gallapagensis* (Hartmann-Schröder, 1962b; Fauchald, 1977). The material examined here indicates this character is not useful. The same sources also used the attachment of the dorsal cirrus on the dorsal notopodial ligule in posterior chaetigers as another distinctive feature, and have been given as distally attached in posterior chaetigers in *P. gallapagensis* and subdistally in *P. variegata*. In the data matrix the dorsal cirrus is coded as terminally attached in both taxa, but the distinction may be applied in identifications, especially when anterior fragments only are available or at least not complete specimens. In *P. variegata* the dorsal cirrus is terminally attached only in the posteriormost chaetigers, while in *P. gallapagensis* the dorsal cirrus is terminally attached from anterior chaetigers, from about chaetiger 15.

Other taxa mentioned in the literature in association with *P. variegata* are three taxa (*Nereis coerulea*, *Nereis obscura*, and *Phyllonereis benedeni*) Hansen (1882) described from Brazil and later examined by Ehlers (1901) and Augener (1934) who found them to be identical with *P. variegata*. They did not mention *P. gallapagensis*. The material collected by van Beneden in Rio de Janeiro, Brazil, and examined by Hansen is obviously split between different museums, and part of this material could not be located and examined.

Hartman (1949) placed *Paranereis elegans* Kinberg, 1865 in synonymy with *P. variegata* although she stated the single specimen was damaged. The same specimen has been examined (SMNH Type-459) and the fragment left is found to be of no scientific value, and hence is not included in the material examined above. Extensive synonymies are listed in Ehlers (1901) (see also Augener, 1934); those included above represent only those specimens examined by me.

Distribution: Type locality of *Nereis ferox* is Rio de Janeiro, Brazil. South America, Atlantic coast. Habitat is inshore and shelf. According to Grube (1857) specimens he used to describe *Nereilepas variegata* were collected by Kröyer in Valparaiso (Chile) and Callao (probably Peru).

PHYLOGENY

SELECTION OF TAXA

For the phylogenetic analysis, type specimens and additional material of all taxa where material was available for study were included. This includes all described taxa in *Pseudonereis*, except *P. masalacensis* for which type material is in poor condition (see above).

Bakken & Wilson (2005) found support for *Pseudonereis gallapagensis* and related taxa with paragnaths in Areas II–IV in comb-shaped rows, and presence of a bar-shaped paragnath in Area VI. This clade was nested as sister group to several taxa from *Perinereis*. *Pseudonereis anomala*, which has cones in Area VI and possesses notopodial homogomph falcigers, a character absent in the *P. gallapagensis* clade, was nested basally in a clade including *Perinereis* spp. and the *Pseudonereis* clade, and again *Cheilonereis cyclurus* was in a basal branch. Representatives from the paraphyletic *Perinereis* and *C. cyclurus* were selected to be included in the analysis. In addition the more distantly related taxa *Platynereis antipoda*, *Neanthes vaalii*, *Nereis pelagica*, *Simplisetia aquisetis* and *Namanereis quadraticeps* were included to reflect character diversity. No outgroups were defined in the analysis.

The purpose of this analysis is to include new data (characters and taxa) and to test if *Pseudonereis* represents a monophyletic group of species.

ANALYSIS AND RESULTS

A data matrix was edited using the Nexus Data Editor for Windows 0.5.0 (Page, 2001) based on information from a DELTA database (Dallwitz, Paine & Zurcher, 1993 onwards) of Nereididae (Wilson *et al.*, 2003) and the nereidid DELTA database was also used to generate descriptions of taxa and to explore similarities and

Table 3. Character matrix of 19 parsimony-informative characters for 19 taxa

	5					1					1								
	0					0					5								
<i>Namanereis quadraticeps</i>	0	0	0	-	-	0	0	-	0	-	0	-	0	0	-	0	1	0	0
<i>Cheilonereis cyclurus</i>	0	1	1	0	0	0	1	0	1	?	1	1	0	1	0	1	0	1	0
<i>Neanthes vaalii</i>	0	1	1	0	0	1	1	0	1	0	1	0	0	0	-	0	0	1	2
<i>Nereis pelagica</i>	0	1	1	0	0	0	1	0	1	0	0	0	0	0	-	1	0	1	2
<i>Perinereis amblyodonta</i>	0	1	1	0	0	1	1	1	1	1	0	1	0	0	-	0	0	0	2
<i>Perinereis nuntia</i>	0	1	1	0	0	0	1	3	1	0	0	0	0	0	-	0	0	1	0
<i>Perinereis variodentata</i>	0	1	1	0	0	1	1	?	1	0	0	0	0	0	-	0	0	1	0
<i>Platynereis antipoda</i>	0	0	0	-	2	0	1	5	1	0	1	1	0	1	0	1	0	1	1
<i>Pseudonereis anomala</i>	1	1	1	2	3	0	1	0	1	?	0	1	1	1	1	1	0	1	2
<i>Pseudonereis atopodon</i>	1	1	1	2	3	1	1	4	1	?	0	2	1	1	1	0	0	1	2
<i>Pseudonereis cortezi</i>	1	1	1	?	?	1	1	4	1	?	0	2	1	0	-	0	0	1	2
<i>Pseudonereis gallapagensis</i>	1	1	1	2	3	1	1	4	1	?	0	2	1	1	1	0	0	1	2
<i>Pseudonereis multisetosa</i>	1	1	1	2	3	0	1	0	1	2	0	1	1	1	1	1	1	1	2
<i>Pseudonereis noodti</i>	1	1	1	2	?	1	1	4	1	?	0	2	1	1	1	0	0	0	2
<i>Pseudonereis palpata</i>	1	1	1	0	0	1	1	?	1	?	0	2	1	0	-	0	0	1	2
<i>Pseudonereis pseudonoodti</i>	1	1	1	2	?	1	1	4	1	?	0	2	0	1	1	0	0	1	2
<i>Pseudonereis trimaculata</i>	1	1	1	2	3	1	1	4	1	?	0	2	1	1	1	0	0	1	2
<i>Pseudonereis variegata</i>	1	1	1	2	3	1	1	4	1	?	0	2	1	1	1	0	0	1	2
<i>Simplisetia aequisetis</i>	0	1	1	0	0	0	0	-	0	0	1	0	0	0	-	0	0	1	0

Table 4. Character list for 19 parsimony-informative characters. For details see text

1. Paragnaths in Areas II–IV arranged in regular closely spaced comb-like rows: (0) absent; (1) present.
2. Area I; paragnaths: (0) absent; (1) present.
3. Area II; paragnaths: (0) absent; (1) present.
4. Area II; paragnath types: (0) conical; (1) minute rod-like in compact cluster; (2) p-bars.
5. Area III; paragnath type: (0) conical; (1) minute rod-like in a compact cluster; (2) pectinate; (3) p-bars.
6. Area V; paragnaths: (0) absent; (1) present.
7. Area VI; paragnaths: (0) absent; (1) present.
8. Area VI; paragnath type: (0) conical; (1) 1 smooth bar; (2) 2 smooth bars; (3) numerous (3 or more) smooth bars; (4) shield-shaped; (5) pectinate.
9. Area VII–VIII; paragnaths a/p: (0) absent; (1) present.
10. Dorsal notopodial ligule; feature on posterior chaetigers: (0) similar to anterior chaetigers; (1) markedly elongated on posterior chaetigers; (2) markedly broader on posterior chaetigers; (3) markedly reduced on posterior chaetigers.
11. Prechaetal notopodial lobe; a/p: (0) absent; (1) present.
12. Dorsal cirrus attachment to dorsal notopodial ligule on posterior chaetigers: (0) basal; (1) mid-dorsal to subterminal; (2) terminal.
13. Neuropodial superior lobe: (0) absent; (1) present.
14. Neuropodial postchaetal lobe; a/p: (0) absent; (1) present.
15. Neuropodial postchaetal lobe; size: (0) projecting beyond acicular ligule; (1) lower than or level with acicular ligule.
16. Notopodial falciger homogomph articulation: (0) absent; (1) present.
17. Neuropodial dorsal fascicle; homogomph falcigers: (0) absent; (1) present.
18. Neurochaetae ventral fascicle; heterogomph spinigers: (0) absent; (1) present.
19. Ventral neuropodial fascicle heterogomph falcigers; length of blade: (0) Type medium; (1) Type long; (2) Type short.

differences between sets of taxa (Wilson *et al.*, 2003). Scoring of taxa was taken from the data matrix in Bakken & Wilson (2005: appendix 3) and updated with characters as described above, and the new *Pseudonereis* taxa included. A data matrix of 19 taxa and 40

characters resulted, of which 19 characters were parsimony-informative (Table 3). Parsimony-informative characters are listed in Table 4.

Parsimony analyses were run in PAUP* 4.0b10 (Swofford, 2001) using default settings for heuristic

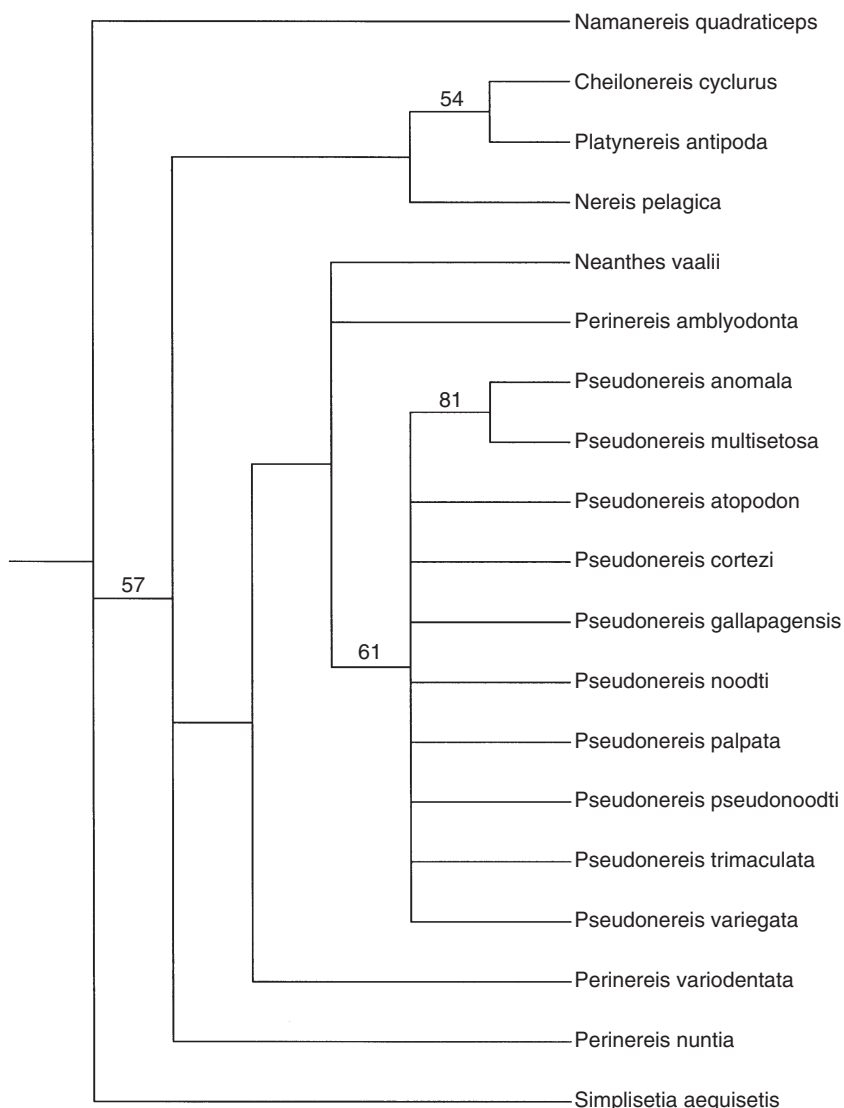


Figure 16. A strict consensus tree of 14 127 most parsimonious trees from analysis of 19 taxa for 19 parsimony-informative characters, including all valid *Pseudonereis* taxa; tree length 42 steps, CI = 0.6190 and RI = 0.8025. Numbers above lines show bootstrap support.

searches, with TBR branch swapping, addition sequence random 100 replicates, collapsed branches and 'MulTrees' options in effect. All characters were unordered, and uninformative characters were excluded. A bootstrap analysis was performed with 100 replicates, max trees set to 15 000. Trees from PAUP* results were examined using the Mesquite: System for Evolutionary Analyses, version 1.05 (Maddison & Maddison, 2004).

The analysis resulted in 14 127 most parsimonious trees, 42 steps, CI = 0.6190 and RI = 0.8025, resolved with a monophyletic ingroup of *Pseudonereis* spp. with bootstrap support (61%) (Fig. 16). Within this group the majority of taxa were unresolved, but containing a

clade consisting of *P. anomala* and *P. multisetosa* with good support (81%).

Based on all taxa considered valid, the monophyly of *Pseudonereis* is demonstrated, although with low bootstrap support (61%). An unresolved clade containing all terminals is unequivocally supported by the presence of paragnaths in Areas II–IV arranged in regular closely spaced comb-like rows, presence of p-bars in Areas II and IV, with a reversal in *P. palpata*. Furthermore, it is supported by the presence of dorsal cirrus terminally attached to dorsal notopodial ligule on posterior chaetigers, and presence of one shield-shaped paragnath in Area VI, with a reversal in *P. palpata*, which has cones and smooth bar(s). Other characters

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