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A revision of Nereidinae (Polychaeta, Nereididae)

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Preface

A copy of ”*Identification of Annelida Polychaeta from northern European and adjacent Arctic waters*” is a document of personal historic interest. Across the pages are scribbled short annotations beside several polychaete families, and two are circled, Sphaerodoridae and Nereididae. The annotations were made in the office of Torleif Holthe at the Directorate of Nature Management early in 1994, and marked the start of my *cand scient* education a few months later. I have much to thank Torleif for as my supervisor during my *cand scient* and *dr scient* education, he has taught me a lot about polychaetes especially relating to northern areas and a lot about general marine biology, the numerous long discussions we have had, often about completely different topics than polychaetes is much appreciated. He has always been helpful and supportive, and put in a lot of effort when it came to applications and job opportunities. I would like to thank Jon-Arne Sneli for passing along all that marine biology knowledge, not only as my supervisor during the *cand scient* period but also later. I have really appreciated the collaboration we have had, and still have. I am also grateful to Jarle Mork who has been my supervisor during this work, the quick replies of enquires from me have been valuable.

This work would have been something else without the help and support of Robin Wilson. He taught me a lot more than I knew from before about nereidids, everything I know about DELTA, gave valuable insight into biogeography and provided lab space at Museum Victoria in Melbourne. The long discussions about specimens, taxa, methods, analyses, software, theories and projects have been very fruitful, as has those about Australian wine. I stayed two periods at Museum Victoria (MV), five month in 2001/2002 and seven month in 2002/2003 (climatic migration). I would like to thank staff, students and volunteers in the Marine Biology Section at MV for memorable moments and a lot of help. Thanks goes especially to Joanne Taylor for good discussions and valuable help in systematic questions, Gary Poore, Tim O’Hara, Mark Norman, Genefor Walker-Smith, Melissa Storey and Rachael King for sharing their knowledge and always being helpful, Tim also helped during fieldwork as did Jan Watson and David Staples, and Chris Rowley and Tania Bardsley for help in the lab. Janette Norman and Renae Pratt are thanked for their assistance, help and expertise with the molecular work. I would also like to thank Martin Gomon and Dianne Bray, and Les Christidis head of Sciences Department for making the opportunity for me to stay for a whole year in the department. During the time in Australia Chris Glasby were a great host when I visited Darwin, as was Pat Hutchings in Sydney. Pat along with Kate Attwood and Lynda Avery are thanked for a great field trip in northern New South Wales in February 2003. At last, but not least, I would like to thank Rosalind and Barry Poole to let me be a part of their family during my first stay in Melbourne, they taught me a lot about Australia and Australian culture (and heaps of other things).

Librarians Else-Mari Leirvoll and Tore Moen and their colleagues at Gunnerusbiblioteket, NTNU have provided enormous help in finding all the strange, not to mention old, literature I have needed. This work would have been very different without their help and effort.

After the 7th International Polychaete Conference I got the opportunity to participate in the Postconference Course in cladistics held at Sandgerdi, Iceland, for which I am grateful to Elín Sigvaldadottír, Fredrik Pleijel and Greg Rouse for organising and help during the course. I

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Thanks also goes to my parents for being so supportive throughout the years although they have not got a clue what all this has been all about, and to Mona who has been so patient the last few months.

Finally I would like to thank the following persons for access to collections, logistics during visits, and loan of material (institution acronyms are found in Paper III and Paper IV): Kate Attwood, Penny Berents and Pat Hutchings (AM, Sydney), Harry ten Hove (AZM, Amsterdam), Chris Glasby (MAGNT, Darwin), Fredrik Pleijel (NMHN, Paris), Leslie Harris (NHMLAC, Los Angeles), Stefan Lundberg and Sabine Stöhr (SMNH, Stockholm), Anja Schulze and Kristian Fauchald (USNM, Washington DC), Angelika Brandt and Brigitte Hilbig (ZMH, Hamburg), Jon Anders Kongsrud (ZMUB, Bergen), Danny Eibye-Jacobsen (ZMUC, Copenhagen), Cathrine Vollelv (ZMUO, Oslo), Wim Vader (ZMUT, Tromsø).

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Torkild Bakken
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List of papers

I. Bakken, T. 2002. A new species of *Neanthes* (Polychaeta: Nereididae) from southern Australia. *Memoirs of Museum Victoria*, *59*: 327-331.

II. Wilson, R. S., Bakken, T. & Glasby, C. J. 2003. Nereididae (Polychaeta) - A DELTA database of genera, and Australian species. In R. S. Wilson, P. A. Hutchings and C. J. Glasby (Eds), *Polychaetes: An Interactive Identification Guide* (pp. Melbourne: CSIRO Publishing.

III. Bakken, T. & Wilson, R.S. Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. Submitted *Zoologica Scripta*.

IV. Bakken, T. Revision of *Pseudonereis* (Polychaeta, Nereididae) based on type material. *Manuscript*.

These are referred to in the text by the roman numerals.

Abstract

Groups of taxa of the polychaete family Nereididae were studied with the aim of presenting a revision of the subfamily Nereidinae. Detailed description of characters starting with a selected group, *Neanthes*, was extended to include a wider range of species level taxa to include as much variation in morphological characters as possible. Description of morphological characters and taxa were systematised in a database of Nereididae using the DELTA (DEscription Language for TAxonomy) system. Based on this database an interactive key of selected taxa is presented. A dataset of 86 characters for 51 taxa were analysed with parsimony methods to test if heterogeneous large genera like *Nereis*, *Neanthes*, *Ceratonereis* and *Perinereis* were natural groups, and to revise genera in Nereidinae. Although the analyses due to large amounts of homoplasies failed to give results that a complete revision of genera could be provided, they showed that the large genera are not monophyletic groups, and that previous attempts to group species into informal groups based on morphological characters not always are supported. The ingroup could not be grouped as monophyletic, hence suggesting Nereidinae is not a natural group. The results and levels of homoplasy made it impossible to undertake further analyses and provide a revision as such of Nereidinae. Cladistic analyses of a resulting clade from the consensus Nereidinae tree verified the monophyly of *Pseudonereis* including all 11 taxa considered valid, and a revision of the group including redescriptions of all taxa based on type material could be done.

Introduction

Nereididae is a group of polychaete worms that are well known and that were mentioned in pre-Linnaean writing (Fauchald & Rouse 1997). *Nereis pelagica* Linnaeus, 1758 was among the first polychaete species described (Linnaeus 1758), and was later designated to be type species in the genus *Nereis* Linnaeus, 1758, the type genus of the family. Early 19th century authors described several taxa as *Nereis*, which has later been transferred to other families when Nereididae as such was more clearly defined. This is evident from checklists for all families (Hartman 1959a). Nereidids are most common in shallow marine habitats, but they occur in a wide range of environments, from the deep sea to estuaries, freshwater streams and even temporary rainwater puddles in moist terrestrial environments (Wilson 2000).

The family Nereididae is one of the most diverse polychaete families including 43 genera with approximately 535 species (Hutchings et al. 2000). Over the last 10-15 years a few papers treating nereidid phylogeny using phylogenetic methods have been published. Previous classifications of the family have been based on character distribution and similarities among taxa without using specific methods of phylogenetic analyses. Cladistic methods are used in the present work to continue what has been presented recently in this family (Fitzhugh 1987; Glasby 1991; 1993; 1999), addressing questions concerning monophyly of the large genera in one of the subfamilies, Nereidinae.

The large number of described species in the family has led to a high number of available names of species level taxa in some genera. Some of these genera are heterogeneous assemblages of taxa, and has been divided into informal groups based on morphological characters. Fauchald (1972) defined such groups within *Neanthes* Kinberg, 1865 solely based on chaetal and parapodial characteristics and Wilson (1984) updated that system. Hutchings et al. (1991) devised a similar informal subdivision of species within the genus *Perinereis* Kinberg, 1865, based on paragnath and parapodial characters, where the number of smooth bar-shaped paragnaths in Area VI (Figure 2) was a key feature. Another Kinberg genus, *Ceratonereis* Kinberg, 1865, had been widely recognised as representing a heterogeneous grouping of species (Fauchald 1972; Perkins 1980; Hutchings & Turvey 1982), and many species have been assigned to that genus based solely on the absence of oral ring paragnaths. Fauchald (1972) stated this was a catchall genus for species with poorly developed paragnaths. Hartmann-Schröder (1985) reviewed species assigned to *Ceratonereis* and formally erected three subgenera: *Ceratonereis (Ceratonereis)* for species with indented prostomium and distinctive sesquigomph falcigers, *Ceratonereis (Simplisetia)* for species with fused heterogomph falcigers in neuropodial positions, and *Ceratonereis (Composetia)* for remaining species. Khlebovich (1996) elevated these subgenera to full generic status. Groups of species of *Nereis*, with morphological similar characters have been compared in detail (Fauchald 1972; Hutchings & Turvey 1982; Hilbig 1992), although no author has systematically reviewed morphological diversity across this large genus, including more than 150 species.

Fitzhugh (1987) was the first to use phylogenetic analyses on nereidids. He included 38 nereidid genera in his genus level analyses of the family (see below for further details). Based on results from the analyses he suggested a revised classification with three valid subfamilies. Nereidinae was diagnosed to include all taxa with paragnaths on the proboscis. Thus defined, the Nereidinae comprises 18 genera, including the most species-rich and most frequently collected taxa in shallow marine and estuarine waters: *Ceratonereis* Kinberg, 1865; *Hediste* Malmgren, 1867; *Neanthes* Kinberg, 1865; *Nereis* Linnaeus, 1758; *Perinereis* Kinberg, 1865 and *Platynereis* Kinberg, 1865. Since Kinberg (1865), definitions of these genera have relied heavily on the convenient characters provided by the form, number and arrangement of paragnaths (Figure 1). However, in recent decades several studies have reviewed morphological diversity more fully within these large genera, either as an attempt to simplify recognition of species within large genera, or to draw attention to apparently non-monophyletic genera.

The family name

Different forms of the name of the family (Nereides, Nereidæa, Nereidæ, Nereidiens etc.) were used until Johnston (1865) gave the first diagnose and formal description of the family. Even in papers published today two different forms of the family name: Nereidae and Nereididae appear. Pettibone (1971) introduced Nereididae instead of Nereidae with no explanation in her revision of several gymnonereidine taxa. It is beyond doubt that Pettibone was correct when she formed the name Nereididae. The late Dr Carl Støp-Bowitz who was a Latin scholar confirmed this (Støp-Bowitz pers. comm. 1996). According to ”The Code” (article 11.7.2; ICZN 1999) the original user of a vernacular name is to be given as author under some conditions: ”*If a family group name published before 1900, [...], but not in latinised form, it is available with its original author and date only if it has been latinised by later authors and has been generally accepted as valid by authors interested in the group concerned and as dating from that first publication in vernacular form*”.

This has implications for the authorship of Nereididae, which in most publications have Johnston (1865) as author (citations of Johnston 1845 are also observed). Johnston (1865) was the first who latinised the name, as Nereidae, which has been generally accepted and widely used since. The first user of a vernacular form of the name was Lamarck (1818) although in the text he referred to Savigny meaning that a manuscript or something equivalent must have existed.

Family Nereididae – relationships and supra-family classification

Nereididae itself is a monophyletic group (Glasby 1993) by the presence of the autapomorphic characters distinct notopodia, usually with flattened lobes, and notochaetae with compound falcigers and/or spinigers. Nereididae can be diagnosed from other family-level polychaete taxa as follows: ”foregut with one pair of lateral jaws; head discrete and compact, dorsal to mouth; prostomial antennae paired arising anterolaterally; capillary chaetae absent; pygidial appendages present” (Glasby & Fauchald 2002). In his cladistic analyses of a group of families constituting the group Nereidoidea Glasby (1993) and found Nereididae to be an exclusive sister-group to Chrysopetalidae and Hesionidae. These three formed again one clade grouping with a second clade consisting of Pilargidae, Nautiliniellidae and Syllidae. In results from cladistic analyses of polychaetes Rouse & Fauchald (1997) demonstrated different results with Nereididae being sister to a clade including Glyceridae, Goniadidae, Paralacydoniidae, Pisionidae, Lacydonidae and Phyllodocidae. Pleijel & Dahlgren (1998) on the other hand supported Glasby’s (1993), Nereididae grouped with Chrysopetalidae, Hesionidae, a result supported by molecular analyses of the same taxa and data set (Dahlgren et al. 2000).

Classification and Phylogeny of Nereididae – an historic review

Kinberg (1865) established a system where he assigned numbers for different areas on the pharynx to facilitate descriptions of paragnath and papillae distribution. It is obvious that the rich diversity of the nereidid material from the Swedish *Eugenie* around the world expedition 1851-1853, where Kinberg participated himself (Kinberg 1910), made it possible for him to see the variation in pharyngeal armature in nereidids. As a consequence he found it convenient to delineate the pharynx in different Areas. This system has been used since and it is convention to assign these Areas with Roman numerals from I to VIII. Originally Kinberg (1865) used Arabic numerals, which is also indicated in his illustrations (Figure 1) (Kinberg 1910), but he used Roman numerals in a chart he used for delineation of nereidid genera (Figure 2).

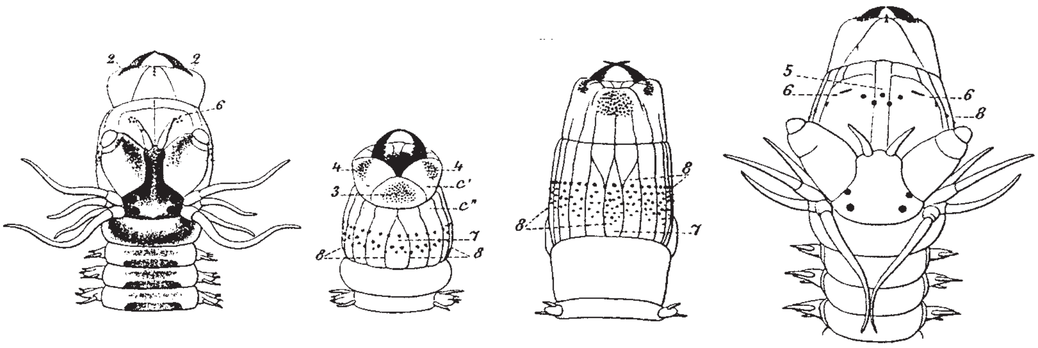


Figure 1. The original illustrations Kinberg (1865) used to delineate Areas to describe pharyngeal armature in nereidids. Area I-IV is placed on the maxillary ring and Area V-VIII on the oral ring. It has been convention to refer to the Areas with roman numbers. Due to the most common distribution pattern of paragnaths Area VII and VIII is usually referred to as one, as Area VII-VIII in descriptions (after Kinberg 1910, plate XX).

Kinberg (1865) used his pharyngeal system to erect new families from nereididform taxa (Figure 3). This was soon to be changed when Malmgren (1867a) published a comprehensive work on North Atlantic polychaetes. Malmgren synonymised Kinberg's new families with Nereididae, and he presented a chart, or a key, with brief diagnosis in Latin to nereidid genera found in the North Atlantic. This was in large based on parapodial features (Fig. 4), but he also used paragnath characters.

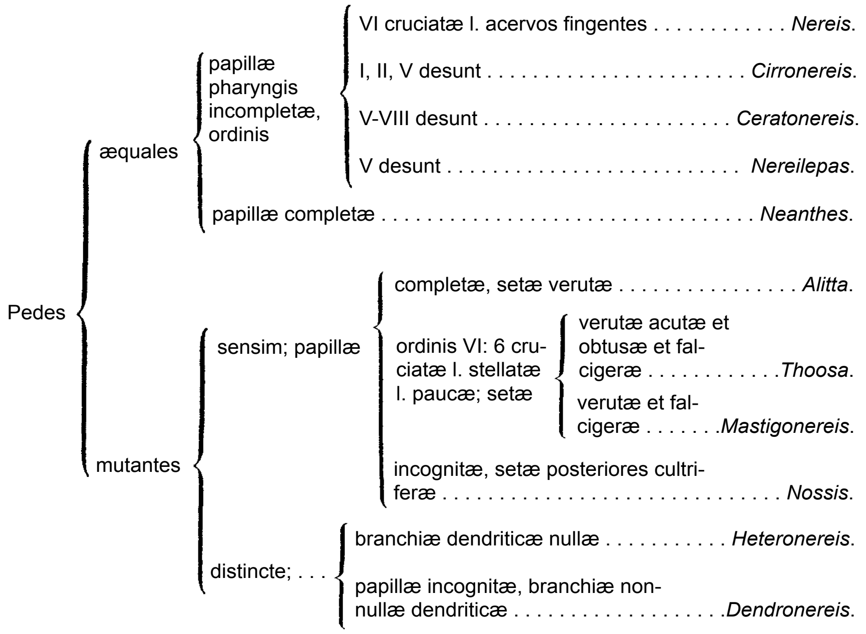


Figure 2. Kinberg (1865) described each Area on the pharynx with using Roman numerals, which has been established as a convention, in this chart of nereidid genera. A detailed description of number, type, form and distribution patterns on each Area with paragnaths or papillae is a necessity in descriptions of nereidids (after Kinberg 1865).

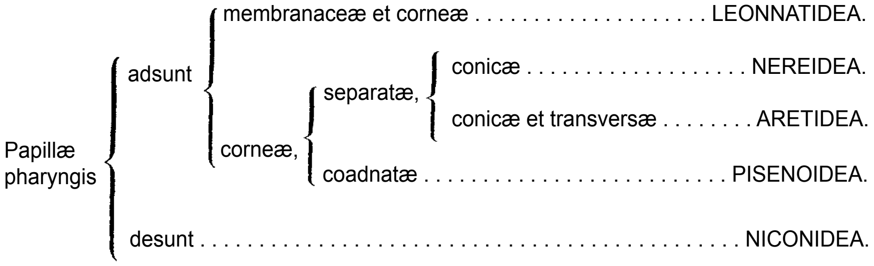
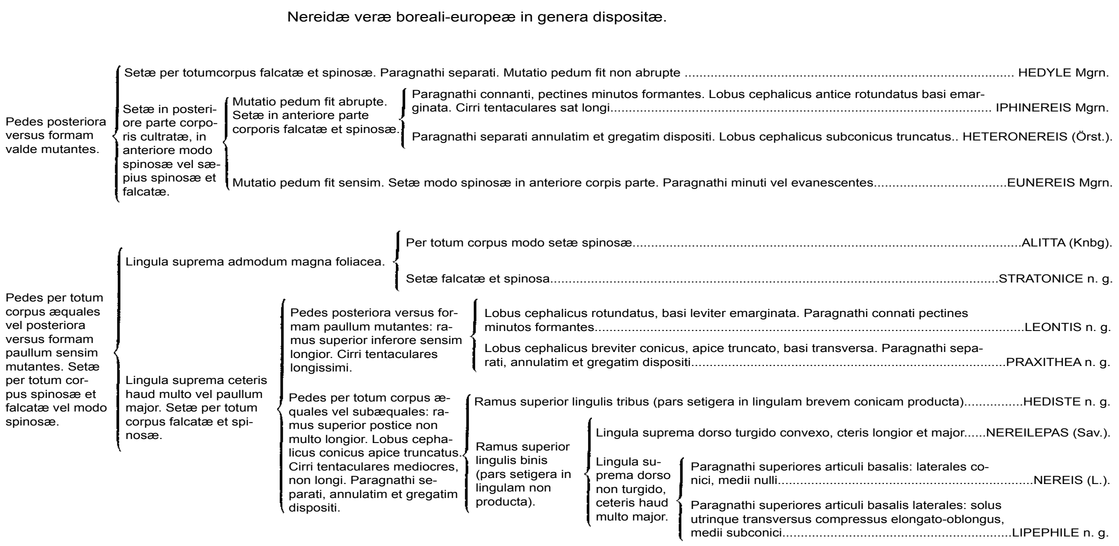


Figure 3. Mainly based on pharyngeal armature Kinberg (1865) erected several families belonging to a group of similar looking taxa. He did not use a specific name for the group as a whole but included them in his paper "Nereidum dispositio nova" (after Kinberg 1865).

Although neither Kinberg nor Malmgren discussed classification of Nereididae as such their contemporary work are interesting because they had contact or at least had each other's papers available upon publication. For example Kinberg (1865) and Malmgren (1865) were published in consecutive pages in the same volume, where Malmgren cited Kinberg's work. Malmgren (1867a) must have studied Kinberg's work in detail, and used the latter author's description of pharyngeal armature although he did not use the numbering system of the pharynx (Figure 4).



Nereidæ veræ boreali-europeæ in genera dispositæ.

- Pedes posteriora versus formam valde mutantes.
  - Setæ per totumcorpus falcatæ et spinosæ. Paragnathi separati. Mutatio pedum fit non abrupte .... HEDYLE Mgrn.
  - Setæ in posteriore parte corporis cultratæ, in anteriore modo spinosæ vel sæpius spinosæ et falcatæ.
    - Mutatio pedum fit abrupte. Setæ in anteriore parte corporis falcatæ et spinosæ.
      - Paragnathi connanti, pectines minutos formantes. Lobus cephalicus antice rotundatus basi emarginata. Cirri tentaculares sat longi........ IPHINEREIS Mgrn.
      - Paragnathi separati annulatim et gregatim dispositi. Lobus cephalicus subconicus truncatus.. HETERONEREIS (Örst.).
    - Mutatio pedum fit sensim. Setæ modo spinosæ in anteriore corpis parte. Paragnathi minuti vel evanescentes........EUNEREIS Mgrn.
- Pedes per totum corpus æquales vel posteriora versus formam paullum sensim mutantes. Setæ per totum corpus spinosæ et falcatæ vel modo spinosæ.
  - Lingula suprema admodum magna foliacea.
    - Per totum corpus modo setæ spinosæ........ALITTA (Knbg).
    - Setæ falcatæ et spinosa........STRATONICE n. g.
  - Lingula suprema ceteris haud multo vel paullum major. Setæ per totum corpus falcatæ et spinosæ.
    - Pedes posteriora versus formam paullum mutantes: ramus superior inferore sensim longior. Cirri tentaculares longissimi.
      - Lobus cephalicus rotundatus, basi leviter emarginata. Paragnathi connati pectines minutos formantes........LEONTIS n. g.
      - Lobus cephalicus breviter conicus, apice truncato, basi transversa. Paragnathi separati, annulatim et gregatim dispositi........PRAXITHEA n. g.
    - Pedes per totum corpus æquales vel subæquales: ramus superior postice non multo longior. Lobus cephalicus conicus apice truncatus. Cirri tentaculares mediocres, non longi. Paragnathi separati, annulatim et gregatim dispositi.
      - Ramus superior lingulis tribus (pars setigera in lingulam brevem conicam producta)........HEDISTE n. g.
      - Ramus superior lingulis binis (pars setigera in lingulam non producta).
        - Lingula suprema dorso turgido convexo, cteris longior et major......NEREILEPAS (Sav.).
        - Lingula suprema dorso non turgido, ceteris haud multo major.
          - Paragnathi superiores articuli basalis: laterales conici, medii nulli........NEREIS (L.).
          - Paragnathi superiores articuli basalis laterales: solus utrinque transversus compressus elongato-oblongus, medii subconici........LIPEPHILE n. g.

Figure 4. An identification scheme for all North European genera of Nereididae mainly based on parapodial characters but also included ”paragnaths” as distinguishing features. The term ”paragnaths” being coined in the presentation (Malmgren 1867a), although it was in another publication Malmgren (1867b) gave a brief explanation (after Malmgren 1867a).

Malmgren published his ”*Annulata polychæta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus congita*” in two different volumes, one edition in the journal of the Royal Swedish Academy of Sciences (Malmgren 1867a) and a second volume as a book (Malmgren 1867b) from a different publisher. Banse (1977a) discussed this topic and found it likely that the book was published before the paper. This has been an important issue in priority of the spelling of Malmgren’s genus *Ceratocephale* (opposed to *Ceratocephala*), showing that the two volumes were type set and printed twice. This is also obvious when Malmgren was writing about nereidids. The starting page for Nereididae has an extra footnote in the book (Malmgren 1867b: 46) where he introduced and explained the term ”paragnathi” (including an explanation in Greek as he usually did when he erected new names). This is not included in the paper (Malmgren 1867a: 163). Hence it seems that it was Malmgren who coined the term ”paragnaths”.

Ehlers (1868) was of the opinion that Kinberg and Malmgren had been too generous recognising the diversity of nereidid morphology and included all genera with paragnaths in *Nereis*. Claparède (1870) compromised and placed species he described in respective subgenera of *Nereis*. Also Saint-Joseph (1898) emended the description for some genera and recognised them as subgenera, while he kept others with rank of genus. Relationship among groups as such was not discussed.

A formal systematic classification delineating nereidid groups did not take place until Corrêa (1948) erected the first subfamily, which he named Lycastinae. Hartman (1959b) reviewed this group, showed that *Lycastis* did not have generic status, redescribed it and gave the group a new name as subfamily Namanereinae placing Lycastinae in synonymy. For taxa included in the subfamily parapodia were central and reduced notopodia a key diagnostic character, along with lack of papillae and paragnaths on the pharynx, (Hartman 1959b). A detailed discussion of genera and species in this context has been presented earlier (Hartman 1959b; Glasby 1999).

Another subfamily was erected for taxa possessing parapodial branchiae and included the genera *Dendronereis* Peters, 1854, *Dendronereides* Southern, 1921, and the newly erected *Tambalagamia* (Pillai 1961). Named Dendronereinae from the type genus, Pillai (1961) argued that these genera should be included in a subfamily of their own due to presence of the aberrant nereidid character notopodial branchiae, hence a synapomorphy for this group. This subfamily was, however, rejected by Banse (1977b) who stated that the branchiae of *Tambalagamia* were expanded notopodial ligules, and thereby the genus rather being related to *Ceratocephale* and *Gymnonereis* Horst, 1919. Based on information from Southern (1921) that resemblance of the branchiae in *Dendronereis* and *Dendronereides* was caused by convergence, Banse (1977b) concluded it would be wrong uniting the two genera in a subfamily based on characters not implying phylogenetic relationship.

Sharing unique characters to define natural groups led Banse (1977a) to erect the subfamily Gymnonereidinae for taxa with bifid neuropodial cirri and possessing very numerous chaetae in anterior chaetigers. He also included other characters in his diagnosis for this group but discussed the homoplasious condition in many of these characters. By this definition Gymnonereidinae (Banse 1977a) included *Ceratocephale*, *Gymnonereis*, *Micronereides* Day, 1963, and *Tambalagamia*. Prior to this Pettibone (1971) had revised a large number of taxa by examination of type material, belonging to a group of nereidids without paragnaths but with or without soft papillae on the pharynx. She did not discuss phylogeny or classification as such but gave a valuable contribution describing in detail parapodial characters. These characters are important in this group with few or no diagnostic pharyngeal characteristics. The group included in Gymnonereidinae by Banse (1977a) consisted of taxa without paragnaths but with complex variation of parapodial lobes and ligules.

Banse (1977b) described a fourth subfamily, Notophycinae, in addition to Nereidinae, Namanereidinae and Gymnonereidinae for minute specimens belonging to *Micronereis* Claparède, 1863 and *Quadricirra* Banse, 1977. *Quadricirra* was later synonymised with *Micronereis* (Paxton 1983), which left *Micronereis* a single genus in Notophycinae. Several unique characters for Nothophycinae were given (Banse 1977b): absence of antennae, pharynx not differentiated in two rings, absence of dorsal cirri in the first two chaetigers and presence of copulatory hooks in males. Banse (1977b) discussed the taxonomic position of *Micronereis* and justified the group of species being nereidids. However, he left the phylogenetic position of the genus within the family open after discussing possible neotenic characters. Absence of antennae may suggest that *Micronereis* represent either the most ancestral or the most derived nereidid group. Relating the presence of antennae in hesionids and syllids, both closely related families, may be convincing towards *Micronereis* being a derived group, but evidence has not been conclusive (Paxton 1983).

Relationship of nereidid taxa was not discussed further until Fitzhugh (1987) published the first analysis using phylogenetic methods on Nereididae. His analyses were a literature study with genera as terminals represented by type species where he took his information from original descriptions. The results gave two trees from the inclusion of two different outgroups (hesionids).

The more parsimonious of the two were used to suggest a new classification of Nereididae, resulting in three monophyletic subfamilies when Notophycinae was synonymised with Nereidinae (Fitzhugh 1987). One subfamily, Gymnonereidinae had to be expanded to include all genera without paragnaths, excluding Namanereidinae that was retained unchanged, giving a rather diverse group of taxa. As mentioned above the taxa included in Gymnonereidinae would then not be a natural group as had been indicated before (Banse 1977a), with the large diversity of parapodial features represented. The suggested classification by Fitzhugh (1987: Fig. 1) indicated monophyletic subgroups of Gymnonereidinae. These were included in another analysis designed to test monophyly of Namanereidinae and investigate phylogeny relating to these subgroups (Glasby 1991). Glasby (1991) suggested Gymnonereidinae was a bit extensive as diagnosed by Fitzhugh (1987), and demonstrated subgroups as indicated in Fitzhugh's results. Some subgroups were supported by synapomorphies. His analyses indicated several homoplasious characters among the included gymnonereidine taxa.

Khlebovich (2001) introduced new characters in an investigation of presence or absence of caecal glands in nereidids in general. He found these to be present in taxa with paragnaths on the maxillary and or oral ring, but absent in taxa with a combination of papillae and paragnaths although he found caecal glands in *Nicon* Kinberg, 1865. Based on presence or absence of caecal glands he erected two tribes in the subfamily Nereidinae. He recognised the original definition of Gymnoereidinae described by Banse (1977a), and left all other taxa in Nereidinae (Khlebovich 1996).

Namanereidinae has been held as a natural group different from other nereidids for a long time (Glasby 1999). This was demonstrated by phylogenetic methods (Fitzhugh 1987). Glasby (1991) found two synapomorphies for Namanereidinae: presence of spherical palpostyles, and dorsal acicula supporting the neuropodia. The monophyly of Namanereidinae was further supported in analyses treating more inclusive groups in the subfamily (Glasby 1999). In addition to the unequivocal support of the synapomorphies he also discussed homoplasious characters supporting the group. Namaereidinae was found to consist of two distinct groups of species level taxa representing the genera *Namalycastis* and *Namanereis* (Glasby 1999).

The widely accepted analyses by Fitzhugh (1987) and his suggested classification are used here, and serve as a basic framework for the present analyses. Khlebovich (1996) allocated some genera to different subfamilies than previous authors, and described tribes within Nereidinae Khlebovich (2001), although neither of these works incorporated phylogenetic analyses.

When it comes to phylogeny and Nereididae all analyses so far are based on morphological characters. The only paper with direct relevance using molecular markers is the one by Dahlgren et al. (2000) who included nereidids in their analyses of sister group relationships in Hesionidae and Chrysopetalidae. There are some papers published on population studies of nereidid taxa, some using allozymes (e.g. Abbiati & Maltagliati 1992; Fong & Garthwaite 1994) and others based on sequences of mitochondrial DNA (e.g. Breton et al. 2003).

Approaches

Morphological characters

The works of Fitzhugh (1987) and Glasby (1991; 1993; 1999) represent the first phylogenetic analyses of Nereididae. Early attempts to deal with classification of Nereididae have been based on comparison of character similarities. Results in the phylogenetic analyses by Fitzhugh (1987) and Glasby (1991) show several characters that are homoplasious across the ingroup. These are issues relevant to the present studies and were taken into account when morphological characters were described in detail (Paper I-II).

Detailed knowledge of characters is a prerequisite for resolved phylogenetic analyses. Ideally as many characters as possible should be included (Kitching et al. 1998) although there may be a limit to what extent they should be included if this mean to introduce more homoplasy in the dataset. In the present analyses this was the case. Pattern of paragnaths in an Area on the pharynx and types of chaetae are examples of homoplasious characters, which were excluded in the parsimony analyses (Paper III), but have been included in other contexts for identification purposes and to make complete descriptions of taxa (Paper II). Other examples are pattern of conical paragnaths in Area V and types of chaetae in neuropodial dorsal fascicle. The latter was included in the neuropodial ventral fascicle (Paper III: Table 1) but not repeated for dorsal fascicle as preliminary analyses showed that it contributed to highlight diversity of characters among nereidid taxa, but introduced a large amount of homoplasies if kept for both fascicles. Generally, some characters, or sets of characters, are better suited in analyses of lower level taxa to resolve morphologically very similar taxa, or polytomies from previous analyses of deeper relationships.

An attempt to include molecular studies

When doing phylogenetic on morphological data on Nereidinae we expected ambiguous results given by a number of most parsimonious trees. This expectation was soon confirmed during preliminary analyses. From a number of most parsimonious trees we hoped to be able to design a set of analyses with molecular markers to test different theories of phylogenetic relationships originating from the morphological work. The idea was to test if it was possible to delineate one group (or more than one) among the shortest length trees from parsimony analyses, with results from molecular analyses. The groups of most parsimonious tree found would be compared with parsimony and maximum likelihood trees from the molecular analyses. Sorting different groups of minimum length trees is possible through MDS plots implemented as a module called Tree Set Visualization (Amenta & Klingner 2002) in the computer software Mesquite (Maddison & Maddison 2003).

As many taxa as possible were processed in the lab depending on available fresh material. Samples were obtained from recently collected specimens from fieldwork in Norway, Denmark and Australia. After DNA extraction and PCR experiments, sequences from 31 specimens representing 17 taxa were obtained (Table 1). All lab work was performed at the Population and Evolutionary Genetics Unit at Museum Victoria, Melbourne. DNA extractions and PCR experiments were done according to Norman et al. (1998). The sequences contained about 600 base pairs from the mitochondrial gene COI. In addition to the 17 taxa one sequence of

Neanthes virens was downloaded from GenBank (sequence from Dahlgren et al. 2000) and aligned with the rest. Initial analyses including sequences of 609 base pairs were done with all sequences and with different subsets of taxa.

Thorough analyses of the data set showed that they could not be used as intended. The main problem was that COI did not give any resolution. Due to this it was not possible to get any support for the clades in the trees obtained. The implication was that no phylogenetic conclusions from trees based on the present COI data were possible. Consequently it was impossible to test the initial theories from the morphological analyses using molecular data.

A likely explanation for problems with no resolution is that this gene, COI, evolves to rapid resulting in multiple changes at sites, and this creates noise in the data, blurring the relationship between sequence differences and time since divergence. The use of COI for phylogenetic studies between distantly related species level taxa should be reassessed. The molecular approach hence took a completely different turn than intended, and the assessment of the utility of COI for investigating relationships in Nereididae will be pursued instead (Norman, Bakken & Wilson in prep).

Table 1. A total of 31 specimens representing 17 taxa collected from different localities in Australia, Denmark and Norway were sequenced for the mitochondrial gene COI. The taxa included represent major clades in the resulting trees from parsimony analyses of morphological characters (see Bakken & Wilson ms, Paper III). Material was also available for *Alitta virens*, *Nereis pelagica*, *Platynereis antipoda* and *Simplisetia limnetica* but failed to give PCR-products for sequencing.

Australonereis ehlersi	*Ceratonereis australia*	*Ceratonereis perkinsi*
Hediste diversicolor	*Neanthes cricognatha*	*Neanthes succinea*
Neanthes vaalii	*Nereis bifida*	*Nereis cockburnensis*
Nereis maxillodentata	*Nereis zonata*	*Perinereis amblyodonta*
Perinereis vallata	*Perinereis variodentata*	*Platynereis dumerilii*
Pseudonereis anomala	*Simplisetia aequisetis*	

Aims and summary of papers

This study was originally intended to be a revision of the large and morphologically heterogeneous genus *Neanthes*, and to assess the phylogenetic relationships of these groups within the subfamily. When characters were studied in detail collecting data for parsimony analyses it soon became clear that working with different taxa across Nereidinae was going to be a more challenging task than anticipated. Paragnaths were known to hold a large amount of information, and also parapodia for that matter. However, when studying *Neanthes* specimens it became apparent that more characters and variation in these could be described. The project had to be redesigned to a phylogeny of the subfamily Nereidinae, implementing an as complete set of characters as possible across the whole family. Molecular work was included from the beginning all the way to be used as supplementary data to the morphological analyses, but resulting sequences proved not to fulfil the aims.

The aims were set to be:

1. Description and assessment of morphological characters
2. Test if the large heterogeneous genera in Nereidinae were monophyletic groups
3. Revise the genera in Nereidinae
4. Phylogenetic relationships of genera in Nereidinae
5. Support morphological phylogenetic analyses with molecular data
6. Phylogenetic analyses of more inclusive clades based on results from analyses of Nereidinae

Species discrimination and character interpretation (Paper I)
Examination of several species level taxa belonging to *Neanthes* revealed that re-interpretation and stronger emphasis of parapodial characters were necessary to be able to distinguish closely related taxa from southern Australia. A stronger emphasis on parapodial characters showed that more detailed descriptions helped in distinguishing morphological similar taxa in a given geographical areas where several morphologically similar taxa occur.

DELTA database of Nereididae (Paper II)
A DELTA (DEscription Language for TAxonomy) database of Nereididae is given as an interactive key. In the present version several Australian, Scandinavian and other selected taxa are available for identification. The Intkey file for identification presented is based on a database including definitions of characters in which the Intkey may be used to identify specimens, to get full descriptions of genus and species level taxa, and to compare morphological similar taxa. The database the Intkey file is made from can be used to present natural language descriptions (as is done in Paper III and Paper IV), create keys, and produce nexus-files for phylogenetic analyses. As demonstrated here it is first of all a valuable resource for interactive identification.

Parsimony analyses of nereidids with paragnaths (Paper III)
Parsimony analyses of a dataset consisting of 86 characters for 51 terminal taxa were undertaken in order to test if the large heterogeneous genera in Nereidinae were monophyletic groups, and to revise the genera of Nereidinae. Terminal taxa were chosen among species

from all genera and subgenera in Nereidinae and from informal groupings in the large genera. The data matrix of 86 binary characters were analysed and reweighted to be able to give interpretable results. Results demonstrated a high level of homoplasy leading to poorly resolved minimum length trees, giving only six clades with significant support. The monophyly of Nereididae had to be rejected, a clade representing *Ceratonereis* and *Solomononereis* were supported, the recently resurrected *Alitta* was confirmed with significant support, and a clade including *Pseudonereis* spp. were given support. The latter resulted in transfer of some species from *Neanthes*, clearly representing misidentified taxa. The included taxa of *Nereis* appeared in two clades in different positions in the consensus tree, as also did groups of *Perinereis*, but lack of support did not warrant taxonomic action such as to describe new genera. This does however demonstrate that further analyses on more inclusive taxa are warranted and should be accompanied with more detailed studies of characters.

Revision of Pseudonereis (Paper IV)

An inclusive clade, *Pseudonereis gallapageneis* and related taxa, came out as a monophyletic clade with bootstrap support from the Nereidinae analyses (Paper III). This was suitable for further analyses as some of its members were poorly known. Type specimens of 11 taxa assigned to this group were examined and redescribed. Further studies of morphological characters resulted in a more detailed description of paragnaths and parapodial characters, where one was included in the data matrix that were used in a cladistic analysis to test monophyly for he group with all taxa included. One of the 11 taxa was left out from the cladistic analysis, *Pseudonereis* spp. was set as ingroup using type specimens as terminal taxa, and three outgroups were selected from other nereidins. A character matrix similar to the one used previously (Paper III) was revised for the included taxa based on examined material. Analyses of a matrix of 87 characters for 13 taxa verified the monophyly of the ingroup, and one taxon was removed from synonymy.

Discussion

Phylogenetic analyses means studying organisms that share characters of common descent. Similar characters are held to be homologous, but characters may be similar and have the same properties without being connected through common descent (Kitching et al. 1998). A thorough study of morphological characters is important in order to get phylogenies that are the most parsimonious solution, and to obtain trees with as few homoplasies as possible. Description of characters was an important task in this study (Paper I, Paper II, Paper III), and has proved to be very valuable for identification purposes (Paper II), for discriminating species level taxa (Paper I) and for phylogenetic analyses (Paper III, Paper IV). However, results from the phylogenetic analyses of nereidids with paragnaths (Paper III) showed that a more detailed study of characters are needed. The level of homoplasies were so high that successive weighting had to be implemented in the analyses, in an attempt to weight characters that obviously were linked in the data matrix.

Characters are important, but so is also character coding and the question of how homology statements should be formulated. Several approaches, advantages and problems with these are discussed in the literature (see e.g. Pleijel 1995; Wilkinson 1995; Kitching et al. 1998). An approach with binary coding was used in this study (Paper III, Paper IV). In the present analyses an approach using e.g. C-coding (Pleijel 1995) would have to involve assessment of character polarity, which could not be justified. Using the method of C-coding would most likely have solved some problems with character linkage or dependent characters, but then *a-priori* weighting would have to be considered to downplay the role of homoplasies. The subject of character coding warrant further studies and should be reassessed when more information on morphological characters are available.

Characters and sets of characters hold more information than implemented in the morphological analyses (Paper III). This is demonstrated in the revision of *Pseudonereis* (Paper IV) where three ”new” characters were described and one of them implemented in the character set. Studies like these need to be carried out to gain more information on characters. In the DELTA database (Paper II) relatively few gymnonereidins have been included compared to nereidine taxa. Especially the more complex parapodial configuration in part of the gymnonereidine taxa (viz. *Ceratocephale*, *Gymnonereis* and *Tambalagamia* (Hylleberg & Nateewathana 1988)), studying homology of these features compared to nereidine and also considering namanereidine taxa (Glasby 1999) is needed.

The results from the morphological analyses of nereidins with paragnaths gave more complex results than anticipated. Although clear indications of high levels of homoplasy were found in preliminary analyses, the results revealed even more problems in this respect. As a result an initial aim, phylogenetic position of groups of taxa or genera, in Nereidinae had to be abandoned. High levels of homoplasy, which also caused clades to change position in the trees when taxa were added or deleted, caused these problems. Again, character homology and inclusion of more characters will help solving resolution and give phylogenetic on phylogenetic relationships. Another initial aim was also not fulfilled in full, the revision of genera in Nereidinae. There was not significant support of the clades in the resulting trees that this goal could be achieved.

An interesting observation from the trees in the parsimony analyses of nereidids with paragnaths (Paper III) is that Nereidinae sensu Fitzhugh (1987) is not monophyletic, as the few gymnonereidins included fell inside the ingroup. Although the analyses were not designed to address this question and the high levels of homoplasy may conceal true relationships, phylogenetic analyses of Nereididae (Rouse & Pleijel 2001) point in the same direction.

New character analyses in more taxa should be done with a view to homology among the characters and to give more details about groups of taxa that appear to be paraphyletic or polyphyletic. Deep branch phylogeny cannot be challenged as long as uncertainties about character homology and development remain. As a consequence more inclusive groups have to be addressed preferably those that have resolution in previous analyses. It is proved here that this serves the purpose when characters can be more diversified (Paper IV) but further work is needed. More molecular work has to be done using different molecular markers as a tool for phylogenetic analyses across Nereididae.

Conclusions and prospects for further work

A main focus in this thesis is the difficulties involving homoplasies that have been shown in the parsimony analyses of morphological data. This calls for a closer attention to detailed studies of characters over a wider range of taxa to in further phylogenetic studies of Nereididae. Although all goals initially aimed at was not fulfilled, major results in this work have been:

- The large genera in Nereidinae are not monophyletic groups
- Informal groups of species level taxa based on morphological characters delineated in previous works does not necessarily constitute monophyletic groups
- Nereidinae could not be rendered monophyletic, hence further analyses are warranted to define subgroups within Nereidinae, suggesting that new analyses of Nereididae as such is needed
- An interactive key of Nereididae for Australian species and for world genera is presented, providing a useful tool for specialists and non-specialists alike
- *Pseudonereis* is a natural group, proved to be monophyletic through phylogenetic analyses
- Analyses of more inclusive clades from phylogeny of nereidids with paragnaths prove that characters can be studied in detail to give further information on character variation in nereidids
- More molecular work should be done, it is necessary to develop adequate markers

When working with the parsimony analyses of nereidins it became clear that it was necessary to reassess one initial aim of the study: character evolution and phylogenetic relationships of the genera or groups of species included. Due to the high level of homoplasies and problems with poorly resolved trees this was impossible. These questions will be readdressed in new analyses representing more taxa and more distantly related taxa with special emphasis with a wider set of characters. Molecular studies will have to be included preferably involving several genes, e.g. both mitochondrial and nuclear genes. Both separate and combined analyses should be attempted.

References

Abbiati M. and Maltagliati F. 1992. Genetic population structure of *Neanthes succinea* (Polychaeta: Nereididae). *Journal of the Marine Biological Association of the United Kingdom* 72: 511-517.

Amenta N. and Klingner J. 2002. Case study: Visualizing sets of evolutionary trees. In *8th IEEE Symposium on Information Visualization (InfoVis 2002)*, pages 71–74.

Banse K. 1977a. Gymnonereidinae new subfamily: the Nereididae (Polychaeta) with bifid parapodial neurocirri. *Journal of Natural History* 11: 609-628.

Banse K. 1977b. A new subfamily, Notophycinae (Polychaeta: Nereididae), for *Micronereis* Claparède and *Quadricirra* new genus. Pp 115-140. In *Essays on polychaetous annelids in memory of Dr Olga Hartman*. Edited by Reish D.J. and Fauchald K. Allan Hancock Found. Los Angeles.

Breton S., Dufresne F., Desrosier G. and Blier, P.U. 2003. Population structure of two northern hemisphere polychaetes, *Neanthes virens* and *Hediste diversicolor* (Nereididae), with different life-history traits. *Marine Biology* 142: 707-715.

Claparède E. 1870. Les annelides chétopodes du Golfe de Naples. 2^{me} partie. *Soc Phys Hist nat Genève Mem* 20: 365-542.

Corrêa D.D. 1948. A polychaete from the Amazon-region. *Bol Faculd Filos Ciênc Let Univ S Paulo Zool* 13: 245-257.

Dahlgren T.G., Lundberg J., Pleijel F. and Sundberg P. 2000. Morphological and molecular evidence of the phylogeny of Nereidiform polychaetes (Annelida). *Journal of Zoological Systematics and Evolutionary Research* 38: 249-253.

Ehlers E. 1868. Die Borstenwürmer (Annelida Chætopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Wilhelm Engelmann, Leipzig. Pp 1-748.

Fauchald K. 1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern pacific ocean. *Allan Hancock Monographs in Marine Biology* 7: 1-575.

Fauchald K. and Rouse G.W. 1997. Polychaete systematics: Past and present. *Zoologica Scripta* 26: 71-138.

Fitzhugh K. 1987. Phylogenetic relationships within the Nereididae (Polychaeta): implications at the subfamily level. *Bulletin of the Biological Society of Washington* 7: 174-183.

Fong P.P. and Garthwaite R.I. 1994. Allozyme electrophoretic analysis of the *Hediste limnocola* - *H. diversicolor* - *H. japonica* species complex (Polychaeta: Nereididae). *Marine*

Biology 118: 463-470.

Glasby C.J. 1991. Phylogenetic relationships in the Nereididae (Annelida: Polychaeta), chiefly in the subfamily Gymnonereidinae, and the monophyly of the Namanereidinae. *Bulletin of Marine Science* 48: 559-573.

Glasby C.J. 1993. Family revision and cladistic analysis of the Nereidoidea (Polychaeta: Phyllodocida). *Invertebrate Taxonomy* 7: 1551-1573.

Glasby C.J. 1999. The Namanereidinae (Polychaeta: Nereididae). Part 1, taxonomy and phylogeny. *Records of the Australian Museum, Supplement* 25: 1-129.

Glasby C.J. and Fauchald K. 2002. POLiKEY. An information system for polychaete families and higher taxa: Version 2: 5 June 2003. http://www.deh.gov.au/biodiversity/abrs/online-resources/polikey/index.html

Hartman O. 1959a. Catalogue of the Polychaetous Annelids of the world. Part 1. *Allan Hancock Foundation Publications Occasional Papers* 23: 1-353

Hartman O. 1959b. Capitellidae and Nereidae (marine annelids) from the gulf side of Florida, with a review of freshwater Nereidae. *Bulletin of Marine Science of the Gulf and Carribean* 9: 153-168.

Hartmann-Schröder G. 1985. Revision der Gattung *Ceratonereis* Kinberg (Nereididae, Polychaeta) (Mit besonderer Berücksichtigung der Arten mit eingeschnittem Prostomium). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 82: 37-59.

Hilbig B. 1992. New polychaetous annelids of the families Nereididae, Hesionidae, and Nephtyidae from the Santa Monica Basin, California, with a rediscription of *Glycera nana* Johnston, 1901. *Proceedings of the Biological Society of Washington* 105: 709-722.

Hutchings P.A., Reid A. and Wilson R.S. 1991. *Perinereis* (Polychaeta, Nereididae) from Australia, with redescription of six additional species. *Records of the Australian Museum* 43: 241-274.

Hutchings P.A. and Turvey S.P. 1982. The Nereididae of South Australia. *Transactions of the Royal Society of South Australia* 106: 93-144.

Hutchings P.A., Wilson R.S., Glasby C.J., Paxton H. and Watson Russell, C. 2000. Appendix 1. In P.L. Beesley, G.J.B. Ross and C.J. Glasby (Eds), *Polychaetes and Allies: the Southern Synthesis* (pp. 242-243). Melbourne: CSIRO Publishing.

Hylleberg J. and Nateewathana A. 1988. Polychaetes of Thailand. Nereididae (part 2): *Ceratocephale* and *Gymnonereis*, with description of two new species and notes on the subfamily Gymnonereidinae. *Phuket Marine Biological Center Research Bulletin* 49: 1-20.

International Commission on Zoological Nomenclature. 1999. International code of Zoological Nomenclature. 4th ed. International Trust for Zoological Nomenclature. London.

Johnston G. 1845. Miscellanea Zoologica. An index to the British annelids. *Ann Mag Natural History* 16: 4-10.

Johnston G. 1865. A catalogue of the British non-parasitical worms in the collection of the British Museum. London.

Khlebovich V.V. 1996. *Polychaetes of the family Nereididae of the Russian seas and the adjacent area. Fauna of Russia and neighbouring countries*. Polychaetous Annelids. 3, ”Nauka” Publishing House, St. Petersburg. Pp 1-223.

Khlebovich V.V. 2001. Caecal glands in Nereididae and a new tribe of the subfamily Nereidinae (Polychaeta, Phyllodocida). *Zoosystematica Rossica* 10: 33-35.

Kinberg J.G.H. 1865. Annulata nova. *Öfversikt af Kongliga Vetenskaps-Akedemiens Förhandlingar* 22: 167-179.

Kinberg J.G.H. 1910. Kongliga svenska fregatten Eugenies resa omkring jorden under befäl af C. A. Virgin åren 1851-1853. Vetenskapliga iakttagelser. II, Zoologi. 3 Annulater. K. Svenska Vetenskapsakademien, Stockholm. Pp 1-78.

Kitching I.J., Forey P.L., Humphries C.J. and Williams D.M. 1998. *Cladistics. 2nd ed. The theory and practice of parsimony analysis.* Oxford: Oxford University Press.

Lamarck J.-B. 1818. Classe Neuviéme. Les Annelides. Histoire naturelle des Animaux sans Vertèbres, préséntant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s’y rapportent; précédée d’une Introduction offrant la Détermination des caractères essentiels de l`Animal, sa distinction du végétal et des autres corps naturels, enfin, l’Exposition des Principes fondamentaux de la Zoologie. 5, Paris. Pp 274-374.

Linnaeus C. 1758. Systema naturæ. Editio decima. Holmiæ. *Facsimile edition British Museum 1956*.

Maddison W. P. and Maddison D.R.. 2003. Mesquite: a modular system for evolutionary analysis. Version 1.0 http://mesquiteproject.org

Malmgren A.J. 1865. Nordiska hafs-annulater. *Öfversikt af Kongliga Vetenskaps-Akedemiens Förhandlingar* 22: 181-192.

Malmgren A.J. 1867a. Annulata polychaeta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus cognita. *Öfversikt af Kongliga Vetenskaps-Akedemiens Förhandlingar* 24: 127-235.

Malmgren A.J. 1867b. Annulata polychaeta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus cognita. Frenckell, Helsingfors. Pp 1-127.

Norman J. Christidis L. Westerman, and M. Hill, F.A.R. 1998. Molecular data confirms the species status of the Christmas Island Hawk-Owl *Ninox natalis*. *Emu* 98: 197-208.

Paxton H. 1983. Revision of the *Micronereis* (Polychaeta: Nereididae: Notophycinae). *Records of the Australian Museum* 35: 1-18.

Perkins T.H. 1980. Review of species previously referred to *Ceratonereis mirabilis*, and descriptions of new species of *Ceratonereis*, *Nephtys*, and *Goniada* (Polychaeta). *Proceedings of the Biological Society of Washington* 93: 1-49.

Pettibone M.H. 1971. Revision of some species referred to *Leptonereis*, *Nicon*, and *Laeonereis* (Polychaeta: Nereididae). *Smithsonian Contributions to Zoology* 104: 1-53.

Pillai T.G. 1961. Annelida Polychaeta of Tambalagam Lake, Ceylon. *Ceylon Journal of Science Biological Sciences* 4: 1-40.

Pleijel F. 1995. On character coding for phylogeny reconstruction. *Cladistics* 11: 309-315.

Pleijel F. and Dahlgren T. 1998. Position and delineation of Crysopetalidae and Hesionidae (Annelida, Polychaeta, Phyllodocida). *Cladistics* 14: 129-150.

Rouse G.W. and Fauchald K. 1997. Cladistics and polychaetes. *Zoologica Scripta* 26: 139-204.

Rouse G.W and Pleijel F. 2001. *Polychaetes*. Oxford University Press. Oxford.

Saint-Joseph A. de. 1898. Les Annélides polychètes des côtes de France (Manche et Océan). *Annales des Science Naturelles* 5: 209-464.

Southern R. 1921. Polychaeta of the Chilka Lake and also of fresh and brackish waters in other parts of India. *Memoirs of the Indian Museum* 5: 563-659.

Wilkinson M. 1995. A comparison of two methods of character construction. *Cladistics* 11: 297-308.

Wilson R.S. 1984. *Neanthes* (Polychaeta: Nereididae) from Victoria with descriptions of two new species. *Proceedings of the Royal Society of Victoria* 96: 209-226.

Wilson R.S. 2000. Family Nereididae. In P. L. Beesley, G. J. B. Ross and C. J. Glasby (Eds), *Polychaetes and Allies: the Southern Synthesis* (pp. 138-141). Melbourne: CSIRO Publishing.

Paper I

Bakken, T. 2002. A new species of *Neanthes* (Polychaeta: Nereididae) from southern Australia.
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Memoirs of the Museum of Victoria 59(2): 327–331 (2002)

A NEW SPECIES OF *NEANTHES* (POLYCHAETA: NEREIDIDAE) FROM SOUTHERN AUSTRALIA

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Abstract

Bakken, T., 2002. A new species of *Neanthes* (Polychaeta: Nereididae) from southern Australia. *Memoirs of Museum Victoria* 59(2): 327–331.

A new species of *Neanthes* from southern Australia is described. Examination of several species of *Neanthes* has resulted in a re-interpretation and stronger emphasis of parapodial characters than is usual in descriptions of nereidid species. These characters are used to describe *Neanthes tasmani* sp. nov. and to distinguishing the new species from the closely related *Neanthes bassi* Wilson, 1984.

Introduction

In an earlier study of *Neanthes* from Victoria, Wilson (1984) found four specimens closely allied to *Neanthes bassi* Wilson, 1984 that possessed characters indicating they belonged to a different species. Re-examination of these four specimens and additional material, as well as more material of *N. bassi*, confirms that this material belongs to a new species.

This study has also resulted in a re-evaluation of parapodial characters used to describe nereidids. The use of detailed descriptions of morphology of parapodia in nereidids was presented by Hylleberg et al. (1986) and Hylleberg and Nateewathana (1988). The importance of these characters is evident in several apparently closely related species of *Neanthes* from southern Australian waters. Parapodial characters tend to vary with specimen size. Wilson (1984) showed that parapodial ligules and lobes tend to occur over a smaller range of chaetigers in specimens with body width less than 1.5 mm than in larger specimens. Parapodial ligules and lobes may be missing altogether in specimens with body width less than 1 mm, especially pre- and postchaetal lobes.

In the present study a distinction is made between a prechaetal or postchaetal lobe and an acicular process. These features are used in the present description to distinguish *N. tasmani* sp. nov. from closely related taxa. My own examination of several nereidine taxa has proved these features to be important characters over a wide range of taxa within the subfamily. In the notopodium a prechaetal lobe is clearly present as a lobe (Fig. 1B) but might be of any size from a small lobe barely evident beyond the dorsal collar to a lobe as long as the dorsal and ventral ligules. An acicular process on the other hand is fused to the ventral notopodial ligule as a ridge on the ligule itself (Fig. 1D). In the neuropodium a clearly identifiable postchaetal lobe is found in many species. This lobe might be digitiform or flattened, a distinction that should be explicit in descriptions. The postchaetal lobe may be reduced in posterior chaetigers, present throughout the body or be absent. If the lobe is absent an acicular process might be present instead, most often seen as an oval process protruding beyond the tip of the aciculum. Pre- and postchaetal lobes and acicular processes can be seen in figures in earlier studies (e.g. Hutchings and Turvey, 1982; Wilson, 1984), but it is important that they are clearly outlined in species descriptions so that otherwise similar species can be distinguished using these characters. To give parapodial characters a stronger emphasise an end-view of parapodia are drawn for *N. tasmani* following the example of Hylleberg and Nateewathana (1986).

The material presented in this work is deposited in Museum Victoria, Melbourne (NMV), Australian Museum, Sydney (AM) and the South Australian Museum, Adelaide (SAM). Measurements of body width are measured without parapodia at about chaetiger 10. This is consistent with earlier studies (e.g. Wilson, 1984) and will be used in future studies as a standard measurement.

Neanthes Kinberg, 1866

Type species. Neanthes vaalii Kinberg, 1866.

Diagnosis. Eversible pharynx with conical paragnaths on both rings, bar-shaped paragnaths in Area IV may be present. Four pairs of tentacular cirri. Parapodia biramous. Notochaetae homogomph spinigers; neurochaetae including homogomph and heterogomph spinigers (after Wilson, 1988).

Neanthes bassi Wilson

Neanthes bassi Wilson, 1984: 210–212, fig. 1.

Material examined. Holotype, NMV F50005. Paratypes, NMV F50006—F50011 (fully location data given in Wilson, 1984).

Additional material. Victoria. NMV F50012–F50017; NMV F50123 (2 specimens); NMV F41866 (referred to as G1866 with full data in Wilson, 1984).

Tasmania. Coles Bay, near boatramp (42°7.0'S 148°17.0'E), 0.5 m, *Zostera* sediment, airlift, 21 Apr 1985, R.S. Wilson (stn TAS 18), NMV F88282.

South Australia. Upper Spencer Gulf (33°16'S 137°51'E), 16 km SW of First Creek, subtidal sand, 12.1 m, T.J. Ward and P.C. Young (stn 795 CG/7), AM W21787; Spencer Gulf, Sir Joseph Banks, Group Reevesby Is, Home Bay South, seagrass bed, upper subtidal, 22 Jan 1986, S.A. Parker, SAM T.E5831 (32 specimens); Pt Lincoln, SAM T.E5859 (1 specimen, epitoke).

Western Australia. Stuart Head, Yacht Club, Princess Royal Harbour (35°04'S, 117°55' E), *Posidonia australis*, 1 m, handheld corer on SCUBA, P. Hutchings, Jan 1988 (site 7), AM W26811; Bramble Point, Princess Royal Harbour (35°02'S, 117°55'E), *Posidonia sinuosa*, 2.5 m, handheld corer on SCUBA, P. Hutchings, Jan 1988 (site 11), AM W26812.

Description. Size range of material examined from 3 mm long, 15 chaetigers and less than 1 mm wide to 22 mm, 70 chaetigers, 1.5 mm wide (complete specimens); from 10 mm, 20 chaetigers, 2 mm wide to 38 mm, 58 chaetigers, 4 mm wide (anterior fragments). Pharynx with conical paragnaths and bars in Area IV, paragnath counts for 29 specimens includes: I = 0–4; II = 6–27; III = 1–14; IV = 1–18, in addition 2–7 bars on each side; V = 0–1; VI = 2–16, usually less than 10; VII–VIII = 5–30. Glandular patches in notopodia present from midbody chaetigers. Prechaetal notopodial lobe (as described by Wilson, 1984) absent but notopodial acicular process present in chaetigers 5–25.

Habitat. Some of the material reported here was collected in the intertidal and upper subtidal, extending the depth-range for this species from intertidal to 51 m. The shallower records are from seagrass-beds including *Posidonia* and *Zostera*.

Distribution. Neanthes bassi is recorded for the first time in Western Australia at Albany and in South Australia from Spencer Gulf. This species is only known from southern Australia, Albany, WA, to off Lakes Entrance, Vic., including north and east coasts of Tasmania.

Remarks. The material examined agrees well with the original description, although parapodial characters are reinterpreted. Numbers of paragnaths are extended for some Areas. Dorsal pigment spots described from the material in the original description are absent in some specimens from Spencer Gulf (SAM T.E5831), and tend to vary in prominence in other specimens.

Neanthes tasmani sp. nov.

Figure 1

Neanthes cf. *bassi* Wilson, 1984: 212.

Material examined. Holotype. Eastern Bass Strait, 100 km off North Point, Flinders I., (31°51.8'S, 148°26.5'E), 130 m, fine sand, Smith-MacIntyre grab, R. Wilson, 15 Nov 1981, RV *Tangaroa* (stn BSS 170-G), NMV F50018.

Paratypes. Eastern Bass Strait, 100 km off North Point, Flinders I. (31°52.6'S, 148°25.2'E), 140 m, WHOI epibenthic sled, R. Wilson, 15 Nov 1981, RV Tangaroa (stn BSS 170-S), NMV F50019–F50021 (3 specimens). Tasmania, E of Maria I. (42°36.0'S, 148°10.0'E), 75 m, fine bryozoa and shell, WHOI epibenthic sled, R.S. Wilson, 23 Apr 1985 (stn TAS 30), AM W27491 (2 specimens).

Description. Holotype, complete specimen 9 mm long for 44 chaetigers, 1.5 mm wide. Body robust, flattened, tapering posteriorly. Colour in alcohol creamy yellow. Prostomium slightly wider than long. Two pairs of dark red to black eyes. One pair of antennae 1.5 times longer than palps. Palps stout with conical palpostyles, wider than long. Four pairs of tentacular cirri, faintly annulated, longest (posterodorsal) pair reaching to chaetiger 9. The first (apodous) segment broadened, enclosing the posterior part of prostomium. Pharynx with translucent yellow to light brown jaws with 7 teeth. Conical paragnaths present on both rings and short bars also present in Area IV, arranged as follows: I = 3 in a longitudinal row; II = 18 (left), 20 (right), 2 rows in an arc; III = 5 in a diamond-shaped group; IV = 15 (left), 7 (right), bars missing on left side, 4 bars on right side; V = 0; VI = 3 (left), 3 (right), in one row; VII–VIII = 8, in single row.

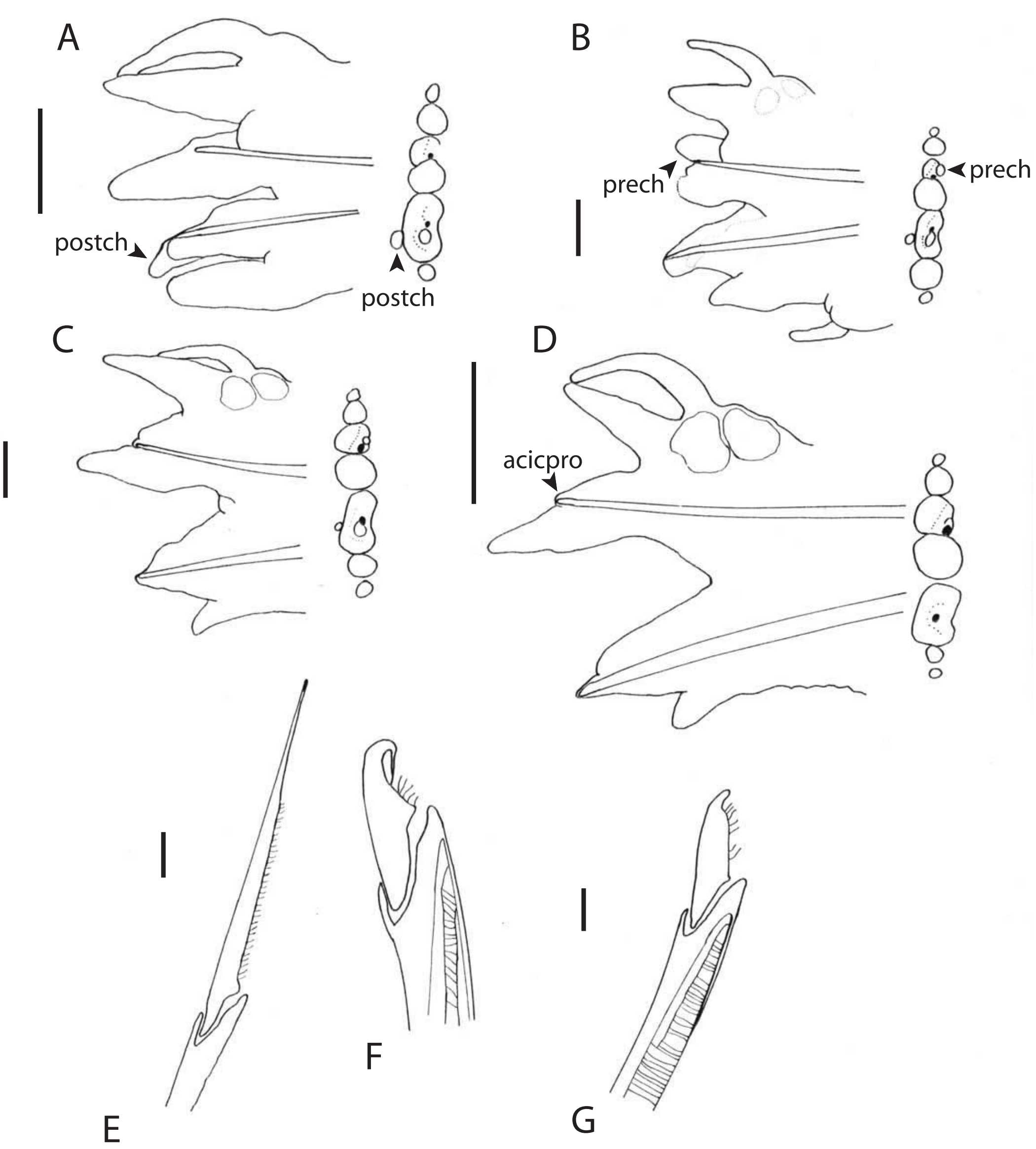

Figure 1. *Neanthes tasmani* sp. nov. Holotype, NMV F50018: a, anterior view of chaetiger 3; b, anterior view of chaetiger 10; c, anterior view of chaetiger 21; d, anterior view of chaetiger 30; g, heterogomph falciger from chaetiger 10.

Paratype, AM W27491: e, heterogomph spiniger with short blade from chaetiger 3; f, heterogomph falciger from chaetiger 30.

Abbreviations: postch = postchaetal lobe, prech = prechaetal lobe, acicpro = acicular process. Scale bars A–D, 0.1 mm; E–G, 0.01 mm. Drawings of the end-view of parapodia are not to scale. End-views are drawn with the anterior end of the specimens to the right.

Dorsal cirrus slightly shorter than ventral notopodial ligule in anterior chaetigers, becoming longer posteriorly up to 1.5 times longer in the few posteriormost chaetigers, basally attached throughout. Dorsal notopodial ligule conical, rounded anteriorly becoming pointed posteriorly; not more than 1.5 times as long as ventral ligule anteriorly, becoming smaller than ventral ligule in posterior chaetigers (Fig. 1D). Ventral ligule conical anteriorly slender and pointed in midbody and posterior chaetigers. Distinct digitiform prechaetal lobe present in chaetigers 5–15 (Fig. 1B). Glandular patches in mid-body and posterior chaetigers.

Neuropodia with prominent inferior lobe in anterior and midbody chaetigers, reduced posteriorly. A distinct digitiform postchaetal lobe present in chaetigers 1–22 (Figs 1A–C). Ventral neuropodial ligule conical, rounded, as long as acicular ligule in anterior chaetigers, smaller, pointed and reduced in posterior chaetigers. Ventral cirri approximately 0.5 times as long as neuropodial acicular ligule, basally attached throughout.

Notochaetae homogomph spinigers, in single straight row between dorsal and ventral ligules. Neurochaetae dorsal fascicle homogomph spinigers and heterogomph falcigers, falcigers with long blades in anterior chaetigers, with short blades in posterior ones (from approximately chaetiger 10). Ventral fascicle heterogomph spinigers with both short and long blades in anterior chaetigers (Fig. 1E), including falcigers (Fig. 1G) from approximately chaetiger 10, in posterior chaetigers heterogomph spinigers (long blades) and heterogomph falcigers (Fig. 1F). Paired cirriform pygidial cirri reaching back 6 chaetigers.

Variation. Variations of 5 paratypes, size range 3 mm long for 14 chaetigers, less than 1 mm wide to 12 mm long for 30 chaetigers, 2 mm wide (anterior fragments), one complete specimen (NMV F88283) 9 mm long for 41 chaetigers, 1 mm wide. Eyes black in paratypes (NMV F88283). Paragnath counts for 5 specimens as follows: I = 2–4; II = 10–25; III = 3–13, in transversal rows; IV = 8–23, also short bars 0-3 on either side; V = 0; VI = 2–8, in circular groups; VII–VIII = 4–7 in a single row. Paragnaths often pale and flattened with large base, including short bars present in Area IV. These might de difficult to distinguish from cones, as the cones are sometimes placed closely together.

Notopodial prechaetal lobe present from chaetiger 5–15. Neuropodial postchaetal lobe present from chaetiger 1 to 18–20.

Remarks. Neanthes tasmani closely resembles *N. bassi* but can be distinguished by the absence of a prechaetal notopodial lobe. Other distinguishing characteristics are given in Table 1. *Neanthes tasmani* also resembles *N. flindersi* Wilson, 1984 as this species has notopodial prechaetal lobes and neuropodial postcheatal lobes in the same range as *N. tasmani*. The two species can be distinguished by length of dorsal parapodial cirri which in *N. flindersi* is 1.5–2.5 times the dorsal notopodial ligule, and by the absence of bars in Area IV in the latter species. *Neanthes kerguelensis* McIntosh, 1885 and *N. nanhaiensis* Wu, Sun and Yang, 1985 both have

Table 1. Comparison of *Neanthes bassi* and *N. tasmani*.

	Neanthes tasmani	*Neanthes bassi*
Area I paragnaths	2–4	0–4
Area II paragnaths	10–25	5–27
Area III paragnaths	3–13	1–14
Area IV (bars) paragnaths	7–23 (0–4)	1–18 (2–7)
Area V paragnaths	0	0–1
Area VI paragnaths	2–8	2–16
Area VII–VIII paragnaths	4–8	5–30
Length of dorsal cirri (times length of dorsal notopodial ligule)	<1–1.5	1
Notopodial dorsal ligule	reduced in posterior chaetigers	as long as notopodial ventral ligule throughout
Notopodial prechatal lobe	present, in chaetigers 3–15	absent, acicular process in chaetigers 5–25
Neuropodial postchaetal lobe	present, in chaetigers 1–21	present, in chaetigers 1–12
Habitat	fine biogenic sand, 75–140 m	sand, shell and mud, seagrass beds, intertidal to 51 m

notopodial prechaetal and neuropodial postchaetal lobes but can be distinguished from *N. tasmani* by the distribution of paragnath numbers and the length and form of the dorsal cirri and dorsal notopodial ligule (Wu et al., 1985; Wilson, 1984).

The reduced size of the dorsal notopodial ligule in the posteriormost chaetigers in *N. tasmani* (observed in the two complete specimens only) is also found in *N. isolata* Hutchings and Turvey, 1982 and *N. uniseriata* Hutchings and Turvey, 1982, but these species can be distinguished from *N. tasmani* by the absence of notopodial prechaetal and neuropodial postchaetal lobes, and by the number of paragnaths (Hutchings and Turvey, 1982; Wilson, 1984).

The faint short bars found in Area IV in *N. tasmani* are different from those present in *N. bassi*, which are very distinct and well developed, even in small specimens with body width less than 1 mm. In contrast, even in the largest specimens of *N. tasmani* the bars are faint and poorly developed, although clearly present. More material is needed to judge if there are further differences between the two species in this respect.

N. tasmani has a deeper depth range than the closely related *N. bassi*. Specimens were found from 75 m to 140 m, while *N. bassi* has a depth range from intertidal to 51 m.

Etymology. The species is named after Abel Tasman who was among the first Europeans to explore the southern seas of Australia and to set foot on Tasmania.

Distribution. Eastern Tasmania (east of Maria Island) and eastern Bass Strait; 75–140 m, fine biogenic sand.

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References

Hutchings, P.A. and Turvey, S.P., 1982. The Nereididae of South Australia. *Transactions of the Royal Society of South Australia* 106: 93–144.

Hylleberg, J. and Nateewathana A., 1988. Polychaetes of Thailand. Nereididae (part 2): *Ceratocephale* and *Gymnonereis*, with description of two new species and notes on the subfamily Gymnonereidinae. *Phuket Marine Biological Center Research Bulletin* 49: 1–20.

Hylleberg, J., Nateewathana A. and Bussarawit S., 1986. Polychaetes of Thailand. Nereididae (part 1): *Perinereis* and *Pseudonereis* with notes on species of commercial value. *Phuket Marine Biological Center Research Bulletin* 43: 1–22.

Wilson, R.S., 1984. *Neanthes* (Polychaeta: Nereididae) from Victoria with descriptions of two new species. *Proceedings of the Royal Society of Victoria* 96: 209–226.

Wilson, R.S., 1988. Synonymy of the genus *Nectoneanthes* Imajima, 1972, with *Neanthes* Kinberg, 1866 (Polychaeta: Nereididae). *Proceedings of the Biological Society of Washington* 101(1): 4–10.

Wu, B., Sun, R. and Yang, D., 1985. *Nereidae (Polychaetous Annelids) of the Chinese Coast.* Springer Verlag: Berlin. 234 pp.

Paper II

Wilson, R. S., Bakken, T. & Glasby, C. J. 2003. Nereididae (Polychaeta) - A DELTA database of genera, and Australian species. In R. S. Wilson, P. A. Hutchings and C. J. Glasby (Eds), *Polychaetes: An Interactive Identification Guide.* Melbourne: CSIRO Publishing.

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Paper III

Bakken, T. & Wilson, R.S. Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths.
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Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths

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Phylogeny of nereidids with paragnaths
T. Bakken & R. S. Wilson

Abstract

Bakken, T. & Wilson, R. S. (0000). Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. *Zoologica Scripta* 00:000-000.

A phylogenetic analysis of nereidids with paragnaths (Nereididae, Nereidinae) was conducted with two goals: to test the monophyly of currently accepted genera, subgenera and informal subgeneric groupings within the Nereidinae; and to revise the genera of Nereidinae. The first goal was realised, but the second was not. Parsimony analyses including 51 terminal taxa from all genera and informal groupings from the large heterogeneous genera *Nereis*, *Ceratonereis*, *Neanthes* and *Perinereis* were undertaken. Analyses of a binary character set of 86 charcaters yielded 5882 most parsimonious trees with a length of 265 steps with consistency index (CI) 0.325 and retention index (RI) 0.643. Reweighting gave 56 characters weight other than 1, and the remaining 30 characters a weight of 1. Reweighting three times resulted in four most parsimonious trees with a length of 57.607, CI = 0.659, RI = 0.786. Many characters widely used in nereidid systematics were found to exhibit high levels of homoplasy, and revision of all Nereidinae based on robust monophyletic clades was not possible. The most parsimonious trees could not be rooted such that the selected ingroup, ”Nereididae with paragnaths”, was monophyletic, causing us to reject the monophyly of the Nereidinae. Among the well supported clades are a large clade with all included taxa except *Namanereis* and *Ceratonereis*-*Solomononereis* based on the presence of notopodial homogomph spinigers and neuropodial dorsal fascicle homogomph spinigers; a clade including *Solomononereis* spp.+*Ceratonereis* spp. defined by the presence of an indented anterior prostomial margin; and dorsal notopodial ligule markedly reduced on posterior chaetigers; a clade with recently resurrected *Alitta* including *Alitta virens* and *A. succinea* new combination defined by the presence of prechaetal notopodial lobe as large as the dorsal notopodial ligule, dorsal notopodial ligule markedly broader on posterior chaetigers; and *Pseudonereis gallapagensis* and related species supported by the synapomorphies presence of paragnaths in Areas II-IV arranged in regular comb-like rows and dorsal cirrus terminally attached to dorsal notopodial ligule in posterior chaetigers. The results indicate that the large genera of Nereidinae, as predicted, do not constitute monophyletic groups. However, further studies are required before a revision of Nereididae with paragnaths can be proposed based on monophyletic groups.

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Introduction

The Nereididae is among the most diverse of polychaete families, comprising over 540 species and 43 genera (Hutchings, et al. 2000). Nereidids are most common in shallow marine habitats, but they occur in a wide range of environments, from the deep sea to estuaries, freshwater streams and even temporary rainwater puddles in moist terrestrial environments (Wilson 2000). The prevalence of nereidids in accessible marine habitats, and their amenability to laboratory culture, has resulted in a variety of species being commercially harvested for fish bait, and used as test organisms in research related to physiology, endocrinology and environmental questions (e.g. Gray 1939; Goerke 1979; Bryan & Gibbs 1979; Olive 1984; Hofmann & Schiedges 1984; Nithart 2000).

Recent phylogenetic studies agree that the Nereididae is monophyletic, with the following synapomorphies: ”presence of distinct notopodia, usually with flattened lobes; notochaetae with compound falcigers and/or spinigers” (Glasby 1993). Nereididae can be diagnosed from other family-level polychaete taxa as follows: ”foregut with one pair of lateral jaws; head discrete and compact, dorsal to mouth; prostomial antennae paired arising anterolaterally; capillary chaetae absent; pygidial appendages present” (Glasby and Fauchald 2002).

Attempts to discover natural groups within the Nereididae using phylogenetic methods have been few and inconclusive. The first such study was that of (Fitzhugh 1987) who recognised three subfamilies: Namanereidinae, Gymnonereidinae and Nereidinae (and synonymised Notophycinae with Nereidinae) (Fig. 1). The parsimony analysis of (Fitzhugh 1987) included 38 genera but was limited by basing character coding on literature descriptions, and by using genera as terminal taxa (represented in each case by the type species). Fitzhugh (1987) himself recognised these limitations and only intended to offer an interim classification, yet his study remains the only attempt to apply parsimony methods across the Nereididae. Glasby (1991) applied parsimony methods to a subset of Nereididae (15 genera) and confirmed the monophyly of the Namanereidinae and Nereidinae but implied that the Gymnonereidinae may be paraphyletic (Fig. 2). Glasby (1999) proceeded to a phylogenetic study of all Namanereidinae, but there have been no further phylogenetic studies of other taxa in the Nereididae.

In this study we apply parsimony methods to another subfamily, the Nereidinae, which comprises all nereidids with hardened scleroprotein structures called paragnaths on the eversible pharynx. Paragnaths are arranged in consistently recognisable Areas denoted conventionally by the Roman numerals I-VIII and distributed on the basal region (”oral ring”) and terminal region (”maxillary ring”) of the pharynx (Fig. 3). Depending on which of two outgroups were used, Fitzhugh (1987) defined the Nereidinae by the synapomorphy conical paragnaths present on oral ring or on maxillary ring. The description of the Nereidinae was:
Prostomium with paired antennae (rarely single or absent). Peristomium with 4 pairs of tentacular cirri. Paragnaths present on oral and/or maxillary rings of pharynx. Pharyngeal papillae absent except on *Leonnates*. Parapodia fully biramous, with superior and inferior notopodial, and inferior neuropodial ligules (all absent on *Micronereis*). Chaetae compound (rarely simple), most commonly comprising noto- and neuropodial homogomph spinigers, and neuropodial heterogomph spinigers and falcigers (derived from Fitzhugh (1987)).

Thus defined, the Nereidinae comprises 18 genera, including the most speciose and most frequently collected taxa in shallow marine and estuarine waters: *Ceratonereis* Kinberg, 1865; *Hediste* Malmgren, 1867; *Neanthes* Kinberg, 1865; *Nereis* Linnaeus, 1758; *Perinereis* Kinberg, 1865 and *Platynereis* Kinberg, 1865. Since Kinberg (1865, 1866) definitions of these genera have relied heavily on the convenient characters provided by the form, number and arrangement of paragnaths. However, in recent decades several studies have more fully reviewed morphological diversity within these large genera, either as an attempt to simplify recognition of species within large genera, or to draw attention to apparently non-monophyletic genera.

Fauchald (1972) defined informal groups within *Neanthes*, solely based on chaetal and parapodial characteristics and Wilson (1984) updated that system. Recent descriptions of species in *Neanthes* suggest that parapodial characters should be given even more emphasis ((Hutchings and Turvey 1982, Bakken 2002), Hutchings et al. (1991) devised a similar informal subdivision of species within the genus *Perinereis*, based on paragnath and parapodial characters, adopting a terminology for parapodial structures proposed by Hylleberg (1986). Another Kinberg genus, *Ceratonereis*, had been widely recognised as representing a heterogeneous grouping of species (Fauchald 1972, Perkins 1980, Hutchings and Turvey 1982), many species having been assigned to that genus based solely on the absence of oral ring paragnaths. Hartmann-Schröder (1985) reviewed species assigned to *Ceratonereis* and formally erected three subgenera: *Ceratonereis (Ceratonereis)* for species with indented prostomium and distinctive sesquigomph falcigers; *Ceratonereis (Simplisetia)* for species with fused heterogomph falcigers in neuropodial positions; and *Ceratonereis (Composetia)* for remaining species. (See discussion below for further explanations of characters). Khlebovich (1996) elevated these subgenera to full generic status. Informal groupings of species of *Nereis* have been proposed by (Fauchald 1972, Hutchings and Turvey 1982, Hilbig 1992), although no author has systematically reviewed morphological diversity across that large genus.

We have used the widely accepted analyses by Fitzhugh (1987) and the suggested classification from this as it uses phylogenetic methods. Khlebovich (1996) allocated some genera to different subfamilies than previous authors, and Khlebovich (2001) described tribes within Nereidinae, although neither of these works incorporated phylogenetic analyses.

Previous phylogenetic studies of nereidids have attempted a classification of genera into subfamilies (Fitzhugh 1987), or an examination of relationships between genera (Glasby 1991, 1999), but these are not our goals. The main aims of this study are to use parsimony methods to:

- test the monophyly of currently accepted genera, subgenera and informal subgeneric groupings within the Nereidinae
- revise the genera of Nereidinae

Material & methods

Material

Source of material is listed for each taxon in the systematic account. The following abbreviations for museums and institutions are used: NHMLAC (Natural History Museum of Los Angeles County, USA), AM (Australian Museum, Sydney, Australia), MV (Museum Victoria, Melbourne, Australia), MAGNT (Museum and Art Galleries of Northern Territory, Darwin, Australia), USNM (National Museum of Natural History, Smithsonian Institution, Washington DC, USA), VM (Museum of Natural History and Archaeology, Norwegian University of Science and Technology, Trondheim, Norway), ZMUC (Zoological Museum, University of Copenhagen, Denmark), ZMUO (Zoological Museum, University of Oslo, Norway), ZMUT (Zoological Museum, University of Tromsø, Norway).

Selection of outgroup taxa

Following Watrous & Wheeler (1981) multiple outgroups were used. Fitzhugh (1987), and Glasby (1991, 1999), showed Namanereidinae to be sistergroup to (Gymnonereidinae + Nereidinae), and Glasby (1991) demonstrated its monophyly. A namanereidin, *Namalycastis quadraticeps*, was included to root the tree. Two gymnonereids, *Australonereis ehlersi, Olganereis edmondsi* were included based on ready availability of material and descriptions, and to represent as much as possible parapodial and chaetal character states seen within the Nereidinae.

Selection of ingroup taxa

For the phylogenetic analysis in this study we have included all possible genera of Nereidinae excepting the monotypic genera *Cirronereis* Kinberg, 1865 *Dawbinia* Benham, 1950, *Laevispinereis* He & Wu, 1989, *Periserrula* Paik, 1977, *Unanereis* Day, 1969 and *Wuinereis* Khlebovich, 1996, for which published descriptions were inadequate and study specimens were not available. Genera such as *Neanthes*, *Ceratonereis s.l.*, *Perinereis* and *Nereis* were represented by several species each, selected to represent morphological diversity within those genera as fully as possible.

Character coding

Characters used are summarised in Table 1 and are discussed below. Homology of character states across taxa was assumed where indistinguishable structures appeared in identical positions, e.g. bar-shaped paragnaths on Area VI; homogomph spinigers in notopodial positions.

Two methods of coding characters were considered: multistate coding and binary coding (Pleijel 1995, Kitching, et al. 1998).

Multistate coding interprets characters as multiple linked states that may be ordered or unordered. Under the multistate coding method, when a character state is scored absent, all dependent characters are scored as inapplicable, yet parsimony programs treat lack of information (?) and inapplicable characters (-) identically (Pleijel 1995). More importantly, since multistate coding makes explicit assumptions about character dependencies, inclusion of states which are incorrectly judged to be homologous will result in incorrect conclusions about cladogram topology and character evolution (Kitching, et al. 1998). Adoption of multistate coding in this analysis would have required assumptions about ordering of characters which we could not justify.

Binary coding divides characters into states that can be considered present or absent (or expressed in an equivalent binary form). Because binary characters can be treated as independent, errors should have less impact on cladogram topology (Kitching, et al. 1998) Binary coding may have the effect of weighting characters which are found to be dependent (Wilkinson 1995). In Nereidinae both paragnath and chaetal characters include apparent dependencies and are subject to this concern but these effects were explored by conducting tree searches with and without successive weighting (see below). Binary coding of characters has the advantage that the same coding can be retained in more inclusive analyses without the need to rescore characters (Pleijel 1995). Use of binary character coding makes fewer assumptions than multistate coding and allows new understandings of character evolution to be discovered through phylogenetic analysis, rather than allowing *a priori* ”understandings” to constrain an analysis Pleijel (1995). Binary coding was adopted in this study.

A data matrix was exported as a nexus file from a DELTA database (Dallwitz, et al. 1993 onwards); of Nereididae (Wilson, et al. 2003); and were edited using the Nexus Data Editor for Windows 0.5.0 (Page 2001). A data matrix of 51 taxa by 86 characters resulted (Table 2). The nereidid DELTA database was also used to generate descriptions of taxa and to explore similarities and differences between sets of taxa (Wilson, et al. 2003). Parsimony analyses were run in PAUP* 4.0b10 (Swofford 2001) using default settings for heuristic searches. Successive weighting were done with the command *reweight*, three times. Bootstrap analyses were set to 100 replicates, and max trees had to be set to 10 000 with *nchuck*=10 *chuckscore*=1 for computational reasons. Trees from the results in PAUP* were examined using the Mesquite: System for Evolutionary Analyses version 0.992-0.994 (Maddison and Maddison 2002). Attempts were made to calculate Bremer support for clades (Bremer 1994) using AutoDecay 5.0 (Eriksson 2001) and PAUP* 4.0b10 (Swofford 2001) but effective search criteria could not be established for computation of optimal trees for all nodes in a practical period of time.

Characters included

There has been little consistency regarding nomenclature of morphological features in nereidids and identical characters have been described using various terms throughout the literature, especially for parapodial characters. Hylleberg, et al. (1986) and Hylleberg and Nateewathana (1988) addressed this issue and presented schematic outlines of parapodial features in nereidids and supplied a detailed terminology. They showed the importance of end-view drawings of parapodia, which they reintroduced from an earlier attempt by (Southern 1921). The terminology of Hylleberg, et al. (1986) and Hylleberg and Nateewathana (1988) has been widely adopted, with minor modifications (Hutchings and Reid 1990, Glasby 1999, Bakken 2002). In this study we use this terminology for parapodial characters, including the implied modifications as they are used in Wilson, et al. (2003). Numbers refers to characters in Table 1.

Antennae. Frontal antennae (1) are absent in *Micronereis* (Paxton 1983) and some namanereidins (Glasby 1999) but are present in all other nereidids as one pair of frontal antennae, or as a single unpaired antenna in *Unanereis* and *Dawbinia*.

Palps. The palpophores in most nereidids possess a transverse groove (2) although it may be faint if palps are extended. In namanereidins a groove is absent. (Glasby 1991, 1993) showed that the spherical palpostyle (3) in namanereidins were evidence of monophyly for this group. *Micronereis* lack palpostyles (Paxton 1983), while in all other nereidids examined the palpostyles are conical (4). Form of the palpostyle may be difficult to interpret, especially in poorly preserved specimens, and they may appear in different conditions over a series of specimens (Bakken in press).

Prostomium. Indented anterior margin of the prostomium (5) (e.g. in *Ceratonereis* spp.) is readily observed. This is not to be confused with a dorsal groove on the anterior part of the prostomium that may be seen in a variety of taxa, perhaps influenced by preservation.

Achaetigerous segment. The length of the achaetigerous segment (6) compared to the chaetigers that follow seems to be consistent within groups of species. In most Nereidinae the achaetous segment is considerably longer than the following chaetigers, while in other Nereidinae (e.g. *Solomononereis*) the achaetous segment might be shorter or as long as following chaetigers. In Namanereidinae the achaetous segment is shorter or as long as than following chaetigers (Glasby 1999).

Tentacular cirri. Distinct cirrophores (7) in the tentacular cirri are present in all nereidids, except *Micronereis*, which lack cirrophores.

Ventral peristomial flap. A large and distinct ventral peristomial flap (8) is present in *Cheilonereis* spp., and in *Laevispinereis fujianensis* (not included here). The figures of *Imajimanereis pacifica* suggest that a ventral peristomial flap may also be present in that species (de León-González and Solís-Weiss 2000 Fig. 2a-b). Whether this structure actually originates from the peristomium as the name indicates, or from the first chaetiger is not considered here.

Pharynx, papillae and paragnaths. A system of numbering different Areas on the pharynx (Fig. 3) for describing paragnath characters was introduced by Kinberg (1865, 1866) and has been universally adopted. Usually, presence or absence, and form of paragnaths have been used to define genera, while paragnath number and form has been used to discriminate species. These Areas are referred to with Roman numerals by convention, and they are distinguishable (9) even if the pharynx is lacking papillae and paragnaths, in all taxa except *Micronereis* and *Dawbinia*.

Papillae may be present or absent on the maxillary ring (10) and if present may be located in one or more of Areas V (21), VI (22) and VII-VIII (23) on the oral ring. We know of no Nereididae with maxillary ring papillae in which discrete maxillary ring Areas can be recognised.

Conical paragnaths are the most common type of scleroprotein paragnaths present on the pharynx in many nereidids. These may be present or absent in the different Areas on the maxillary ring in Areas I-IV, (12, 13, 15, 18) and on the oral ring in Areas V-VIII (26, 27, 32). In Areas II, III and IV small conical paragnaths may be arranged in regular closely spaced comb-like rows (11) in tight triangular very distinctive patterns (Kudenov 1979 Fig. 2b). Minute rod-like paragnaths placed in a compact cluster on the maxillary ring (14, 16, 19) are observed in some taxa (Nateewathana 1992 Fig. 2a-b), clearly with different shape and distribution pattern than conical paragnaths. Smooth bar-shaped paragnaths in Area VI (Hutchings, et al. 1991 Fig. 3a) has been used as a diagnostic character for the genus *Perinereis*. Area VI may have either 1 smooth bar (28), two smooth bars (29) or numerous (more than 3) smooth bars (30), and these conditions were used to recognise informal subgroups within the genus (Hutchings, et al. 1991). Pectinate paragnaths (17, 20, 31, 33) have been used to distinguish species in *Platynereis*. Paragnaths on the oral ring are usually placed in certain patterns, either merged forming a broad band covering Areas V-VIII (25), or present in isolated patches in Area VII-VIII (34) or in lines forming a continuous band (the most common condition; 35). Tiny crown-shaped paragnaths on the oral ring (24) in occur in *Micronereis* species (Paxton 1983 Fig. 4) and do not appear similar to other paragnath types found in other nereidids, although they seem to be used in a similar way and correspond to oral ring paragnaths in other nereidins (Paxton 1983).

Parapodia. There is a great variation in parapodial characters, both among nereidid taxa but also among genera or groups of species. Some gymnonereidins are known to have more complex parapodial structures (Hylleberg and Nateewathana 1988), although an inspection show that several gymnonereidins (e.g. *Nicon*, *Olganereis*, *Rullierinereis*, and *Websterinereis*) have parapodial structures being more similar to most nereidins. Reduction of complexity in namanereidins (Glasby 1999) results in fewer parapodial characters being available in this group. Descriptions of Gymnonereidinae with complex parapodia (viz. *Ceratocephale* and *Gymnonereis*) (Hylleberg and Nateewathana 1988), have used some different terms for seemingly similar features in Nereidinae (Hylleberg, et al. 1986). Homology of parapodial structures, especially, remains problematic throughout the Nereididae. Parapodial characters also vary throughout the body on individual specimens. Reduction of the notopodial dorsal ligule and the neuropodial ventral ligule from anterior to posterior chaetigers is often observed, as well as that pre- and postchaetal lobes may be restricted to a number of anterior chaetigers. Several characters used here require that complete specimens or at least specimens long enough to reflect changes in parapodial morphology can be examined. For this reason species described from heteronereidid specimens only will in many cases have to be regarded as incompletely described and hence cannot be properly assigned systematically.

Notopodia. Namanereidins have strongly reduced parapodia (Glasby 1999) while other nereidids have at least one notopodial ligule (36). Usually more than one notopodial ligule is present. The dorsal notopodial ligule may be absent altogether, may be similar throughout all segments (37), or may be markedly elongated (38), markedly broader (30) or markedly reduced (40) in posterior chaetigers compared to anterior chaetigers. A prechaetal notopodial lobe (if present) is here defined as a digitiform process placed anterior to and between dorsal and ventral notopodial ligules and is not supported by the notopodial acicula (this is called ”superior lobe” by Hylleberg et al. 1986). The prechaetal notopodial lobe, if present, is usually a small lobe (41) less than half the length of the dorsal notopodial ligule; less commonly it is as large as dorsal and ventral notopodial ligules (42); it may be present throughout the body

(43); or may be restricted to anterior chaetigers (44). The notopodial acicular process (45) is different from a prechaetal lobe, and is a small process formed around the tip of the acicula fused to the ventral notopodial ligule (Bakken 2002).

The dorsal cirrus is attached to the dorsal notopodial ligule, and is in most nereidids attached in a basal position to the dorsal notopodial ligule (46), but may be attached to the dorsal edge of the ligule in a sub-terminal (47) or a terminal position (48). The position may vary throughout the specimen, in case usually from a basal or sub-terminal position to a sub-terminal or terminal position posteriorly. In some taxa the dorsal cirrus arises from a basal cirrophore (49), although the most common feature is lack of a cirrophore. Cirrophores are common in several gymnonereidins (Hylleberg and Nateewathana 1988), in some namanereidins (Glasby 1999) and is also observed in some nereidins (*Ceratonereis* species), but in the last case documentation from the literature is often inadequate and needs further study.

Neuropodia. In most nereidins there is no neuropodial superior lobe present, although it exists occasionally. The ”acicular ligule” should be understood to represent superior and inferior lobes combined (or if the inferior lobe only if the superior lobe is missing). The acicular ligule also includes the tissue around the acicula especially in posterior parapodia where this often protrudes from the rest of the neuropodia. An inferior neuropodial lobe is, however, prominent in most taxa at least in anterior chaetigers. Published descriptions usually compare the ventral ligule in length and size relative to the ”acicular ligule”. A neuropodial postchaetal lobe, if present, usually shows great variation in shape and extension compared to the acicular ligule, projecting strongly beyond (50), or as a low rounded lobe level with the acicular ligule (51); it may be digitiform (54) or flattened (55). In the latter case it looks like a flat acicular process covering most of the acicular ligule, while a digitiform lobe is narrow and clearly has shape as a protruding lobe. A postchaetal neuropodial lobe may be present as a protruding tip; it may be restricted to anterior chaetigers (53) or present throughout (52). In most taxa a ventral neuropodial ligule is present (56) but in some Nereidinae it may be smaller on anterior than posterior chaetigers.

Aciculae. Normally aciculae, internal chaetae supporting parapodia, are present in all neuropodia and all notopodia except from the first two chaetigers. However, notoacicula may be present also in chaetigers 1 and/or 2 in some taxa (57); this character is rarely included in published descriptions. Glasby (1999) showed that the position of notoaciculae is an important character in subfamily classification. He found that the ventral position of notoacicula supporting the neuropodia (58) supported monophyly for Namanereidinae. In other nereidids the notoacicula support a notopodial ligule.

Chaetae. Traditionally five or six types of chaetae has been recognised in nereidids (Fauvel 1923, Chambers and Garwood 1992): homogomph spinigers (60), homogomph falcigers (75, 80), heterogomph spinigers (59, 69), heterogomph falcigers (73), fused falcigers (simple chaetae formed by progressive fusion of blade and shaft of heterogomph falcigers (Hutchings and Glasby 1982 Fig. 2d-f); (74)). (Paddle-like chaetae occur in the swarming reproductive phase known as heteronereidids or epitokes (Clark 1961) but their form is unknown for most taxa and heteronereidid characters are not used in this study.) Other chaetal types recognised more recently are sesquigomph falcigers (72, 76) and sesquigomph spinigers (72, 79) (Perkins 1980, Hutchings and Reid 1990). Only one type of chaeta is present in some taxa but more commonly several types of chaetae occur, located in three bundles or fascicles: notopodial fascicle, and dorsal and ventral neuropodial fascicle. Glasby (1999) described four fascicles in the neuropodia in Namanereidinae.

There is significant variability in form within major chaetal types (Fig. 4). Appendages of notopodial homogomph falcigers, when present (62), may take different forms (63, 64, 65), as do homogomph sesquigomph falcigers (66, 67, 68), and heterogomph falcigers, which also vary along the body (81-86).

Other forms of chaetae were not used here but might be informative in analyses inclusive of all Nereididae taxa, for example the form of the shaft and articulation between shaft and blade (Glasby 1999), (Qiu and Qian 2000).

Characters excluded

Caecal glands. Caecal glands have been used to classify genera into tribes within Nereidinae (Khlebovich 2001). This character is not used here, but is worth pursuing in the future when material in quantity is available.

Eyes. Eyes may be absent or present in nereidids. This character was excluded, as eyes were present in all included taxa.

Peristomium. Many authors consider the achaetigerous segment posterior to the prostomium to be the peristomium and term it so in descriptions. It is unclear whether the peristomium is fused to the first segment (Glasby 1993) or if the peristomium is reduced to lips (Rouse and Fauchald 1997). This question will have implications for whether the tentacular cirri origin from the peristomium and/or one or more of the first segments, it will not however, have implications for relationships within Nereididae (Pleijel 2001) and is not discussed further here.

Tentacular cirri. Number of tentacular cirri was not considered in this study, as all included taxa possess four pairs. Some namanereidins have three pairs of tentacular cirri (Glasby 1999); all other nereidids have four pairs.

Neuropodia. Additional variability in form of the ventral neuropodial ligule in anterior chaetigers (other than presence/absence) can be seen in other Nereididae taxa and would need to be considered in analyses of the entire family. However, these characters did not vary within Nereidinae and were not included in this study.

Prechaetal neuropodial lobe as defined by (Hylleberg, et al. 1986) and used by us (Wilson, et al. 2003) seems to be absent in most if not all nereidins. Many authors include features of a ”prechaetal neuropodial lobe” in their descriptions. They do however in most cases refer to the neuropodial inferior lobe (Hylleberg, et al. 1986 Fig. 1A) (*eg* ”conical ligules below acicula on acicular lobes” (Perkins 1980: 9)). We do not consider this character to be present in any of the included taxa, and our descriptions therefore contradict older published descriptions (*eg* of *Leonnates indicus*, *Ceratonereis mirabilis*).

Phylogenetic analysis

Analyses of the binary characters set yielded 5882 most parsimonious trees with a length of 265 steps long with consistency index (CI) 0.325 and retention index (RI) 0.643. Results visualised by a strict consensus tree (Fig. 5) showed low resolution, due to large number of minimal length trees and incongruence. Homoplasies are the main source of incongruence in the tree, and the results showed a high homoplasy index (HI = 0.676). Due to a large amount of homoplasy successive weighting were applied based on the rescaled consistency index (RC) with the *reweight* command in PAUP*, to give characters different weights according to their consistency in the cladogram (Kitching, et al. 1998).

Successive reweighting using the *reweight* command gave 56 characters weight other than 1, and the remaining 30 characters a weight of 1. Reweighting three times resulted in four most parsimonious trees with a length of 57.607, CI = 0.659, RI = 0.786. Character distribution is shown in the apomorphy list (Table 3).

Clades with bootstrap support exceeding 50% are labelled on a strict consensus tree of the four most parsimonious trees after reweighting in Fig. 6. Questions relating to relationships between basal clades are not addressed using these results, nor was this a goal of the study. Tests of the monophyly of existing genera were a goal, as discussed below (”clades with bootstrap support”, and throughout the Systematic Account). With the chosen outgroup the ingroup could not be rooted so as to be monophyletic, a result which questions the monophyly of the Nereidinae *sensu* Fitzhugh (1987). This is also indicated in the Nereididae tree presented by Rouse & Pleijel (2001). These problems can only be addressed by a more comprehensive phylogenetic analysis including all nereidid genera.

The number of characters exhibiting high levels of homoplasy suggests that reassessment of homology of paragnath and chaetae characters based on more detailed morphology, microstructure or chemical composition may be worthwhile in future work. Application of other new information such as molecular sequence data to the problem of Nereididae phylogeny is also a priority for future studies. Some branches in the resulting cladograms were supported by autapomorphic (phylogenetically uninformative) characters, these characters were retained in analyses in order to define and diagnose clades.

The most significant conclusion from these analyses is that the most speciose genera in the Nereididae (*Nereis*, *Neanthes* and *Perinereis*) cannot be considered monophyletic groups. As discussed above, informal groupings of species within these genera have already been proposed, however, based on our parsimony analysis, these may not be monophyletic groups either. Hartmann-Schröder (1985) divided *Ceratonereis s.l.* into three subgenera: *Ceratonereis (Ceratonereis)*, *Ceratonereis (Composetia)*, and *Ceratonereis (Simplisetia)*, later elevated to generic status by Khlebovich (1996). Our analysis confirms that *Ceratonereis s.s.* apparently represent monophyletic taxa, but *Composetia* apparently is not. Further discussion is provided for each genus in the systematic account.

The following clades have bootstrap support (clade numbers in Fig. 6):

1. A large clade with all included taxa except *Namanereis* and *Ceratonereis*-*Solomononereis* has strong bootstrap support (98%), based on the presence of notopodial homogomph spinigers and neuropodial dorsal fascicle homogomph spinigers; absence of notopodial sesquigomph spinigers, notopodial sesquigomph falcigers and of notoaciculae on segments 1 and 2. (Absence of notopodial sesquigomph spinigers and of notoaciculae on segments 1 and 2 occurs homoplasiously in *Ceratonereis perkinsi*; absence of notopodial sesquigomph falcigers occurs homoplasiously in *Solomononereis marauensis*).

2. The clade including *Solomononereis* spp. + *Ceratonereis* spp. has 82% bootstrap support and is defined by the presence of an indented anterior prostomial margin; and dorsal notopodial ligule markedly reduced on posterior chaetigers. Presence of a cirrophore on the dorsal cirrus (49), may also be a synapomorphy for this clade however this character could not be determined for *Solomononereis* spp. from available material.

3. A clade with *Alitta virens* and *A. succinea* new combination has 77% bootstrap support, defined by dorsal notopodial ligule markedly broader on posterior chaetigers (occurs homoplasiously in *Cheilonereis cylclurus* and *Pseudonereis* spp.); dorsal cirrus distally attached to dorsal notopodial ligule on posterior chaetigers (occurs homoplasiously in *Cheilonereis cylclurus*+*Perinereis* spp.+*Pseudonereis* spp.; in *Platynereis antipoda*; *Ceratonereis* spp.; and in *Micronereis bansei*). This clade is equivalent to *Alitta* as resurrected by Khlebovich (1996) and we have used this name for those two species previously placed in *Neanthes*. *Neanthes bongcoi* and *N. cricognatha* form a larger monophyletic clade also including *Alitta*, defined by the presence of prechaetal notopodial lobe as large as the dorsal notopodial ligule (42) (occurs homoplasiously in (*Leonnates indicus* + *L. stephensoni*)).

4*. Pseudonereis gallapagensis* and related species occur in a clade with 88% bootstrap support, sister group to a clade including *Cheilonereis cyclurus* to *Perinereis caeruleis*. This *Pseudonereis* clade is unequivocally supported by the synapomorphies presence of paragnaths in Areas II-IV arranged in regular comb-like rows and dorsal cirrus terminally attached to dorsal notopodial ligule in posterior chaetigers.

5. The monotypic *Australonereis ehlersi* and *Composetia irritabilis* forms a clade with 83% bootstrap support. The clade has unequivocal support by the presence of neuropodial ventral fascicle sesquigomph falcigers; further presence of neuropodial dorsal fascicle sesquigomph spinigers also found in the *Ceratonereis* spp.+*Solomononereies* spp. clade; and presence of neuropodial dorsal fascicle sesquigomph falciger also present in *Ceratonereis mirabilis*.

6. Two *Nereis* species, *N. bifida* and *N. maxillodentata* (69% bootstrap support), formed a clade unequivocally supported by the presence of bidentate notopodial falcigers with equally large distal teeth.

Justification and support for other clades is discussed under the relevant taxon in the systematic account, below.

Systematic Account

Nereididae Lamarck, 1818

Nereides Lamarck, 1818: 310-311.− Savigny 1820: 28.

Nereidae Johnston 1865: 143-145.− Malmgren 1867: 163.− Fauvel 1923: 328-331.− Fauchald 1977a: 85.

Nereididae Banse 1977: 116.− Glasby 1993: 1558.

Lycoridea Grube 1850: 294-296.− Malmgren 1865: 106-107.
Leonnatidea Kinberg, 1865: 167.
Aretidea Kinberg, 1865: 174.
Pisenoidea Kinberg, 1865: 176.
Niconidea Kinberg, 1865: 178.

Remarks. Most workers have cited Johnston (1865) as author for Nereididae. We follow Khlebovich (1986) in using Lamarck (1818) as it according to the nomenclature (ICZN 1999) a family group name published before 1900 not in a latinised form is available if it is later latinised by an author and generally accepted as valid by subsequent authors. The original user of the vernacular name should be used as author.

***Alitta* Kinberg, 1865**

Alitta Kinberg, 1865: 172.− Malmgren 1865: 183.− Khlebovich 1996: 108-109.
Nectoneanthes Imajima, 1972: 113.– Wu *et al*.: 1985: 161.– Khlebovich 1996: 114-115.

Type species. *Nereis virens* Sars, 1835.

Description. Frontal antennae present, 1 pair, subconical or cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular segments fused; a single tentacular segment is present. Four pairs of tentacular cirri present. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge.

Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II, III and IV may be arranged in irregular rows but not in regular comb-like rows. Paragnath counts: Area I conical paragnaths present or absent (only in some specimens of *A. virens*); Area II, conical paragnaths present; Area III, conical paragnaths present; Area IV, conical paragnaths present. Minute rod-like paragnaths in a compact cluster, smooth bar-like paragnaths, and pectinate paragnaths are absent on the maxillary ring. Oral ring papillae absent. Oral ring paragnaths present. Ring of oral ring paragnaths present as irregular rows, not crown-shaped. Area V and VI present as distinct groups. Area V conical paragnaths present or absent; Area VI conical paragnaths present; VII-VIII, conical paragnaths present. Band of conical paragnaths on Areas VII-VIII, present only as a ventral band, arranged in one or more irregular lines forming a continuous band. Minute rod-like paragnaths in a compact cluster, smooth bar-like paragnaths, and pectinate paragnaths are absent on the oral ring.

Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth. Notopodium with at least one distinct ligule or lobe. Branchial filaments absent. Dorsal notopodial ligule present, not markedly elongate on anterior chaetigers; markedly elongate or not on posterior chaetigers; markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, approximately equal to length of dorsal notopodial ligule at least on anterior chaetigers (thus notopodium of 3 similar sized ligules/ lobes), present throughout all chaetigers. Acicular process absent. Ventral notopodial ligule present. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, digitiform. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae of chaetigers 3–4 present. Notochaetae: heterogomph spinigers and sesquigomph absent, homogomph spinigers present, homogomph and sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph and sesquigomph spinigers absent, homogomph spinigers present; heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present or absent; fused falcigers absent, homogomph falcigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers and falcigers present, homogomph and sesquigomph spinigers absent, heterogomph falcigers present, homogomph falcigers absent. Anal cirri cirriform or conical.

Remarks. Kinberg (1865) erected *Alitta* for the single species *A. virens*, emphasising the ”foliose” dorsal ligules of the parapodia, which distinguished this taxon from six other species that he placed in *Neanthes* Kinberg, 1865. In the same year, Malmgren (1865) assigned *A. brandti* to the same genus. Most authors have since treated *A. virens* and *A. brandti* as species of *Neanthes*, hence regarded *Alitta* as a synonym of *Neanthes*. Recently Khlebovich (1996; translation of relevant parts by Khlebovich pers. comm.) resurrected *Alitta* for a group of closely related species; *A. virens*, *A. brandti* and *A. grandis*, a complex of species that need further study and will be discussed elsewhere. In his paper Khlebovich stated that *Alitta* is most closely related to *Nectoneanthes*, only differing in the shape of the dorsal notopodial ligules.

Our analyses support the monophyly of *Alitta* and the genus description is emended above based on the inclusion of *A. succinea*. The type species of *Nectoneanthes*, *N. oxypoda* Marenzeller, 1879, was shown to be synonymous with *A. succinea* by Wilson (1988), on the basis that the expanded dorsal notopodial ligules used by Imajima (1972) to define *Nectoneanthes* were epitokal modifications. Hence is *Nectoneanthes* a junior synonym of *Alitta*. Wilson (1988) also included *Nereis alatopalpis* Wesenberg-Lund, 1949 as a synonym of *A. succinea*. Two other species previously assigned to *Nectoneanthes*; *N. ijimai* (Izuka, 1908) and *N. multignatha* Wu, Sun & Yang, 1981 were referred to *Neanthes* by Wilson (1988), their status is uncertain as they are described from specimens in or approaching epitoky. Khlebovich (1996) retained *Nectoneanthes*, but did not discuss the epitokal characters on which the genus is apparently based.

Our parsimony analyses support by the included species *A. virens* joined in a clade with *A. succinea* new combination Khlebovich (1996). *Alitta* can be diagnosed by the presence of prechaetal notopodial lobe as large as the dorsal notopodial ligule, dorsal notopodial ligule markedly broader on posterior chaetigers and dorsal cirrus distally attached to dorsal notopodial ligule on posterior chaetigers, although each of these states occur as homoplasies in other Nereididae taxa (as discussed above).

Included species. *Alitta brandti* Malmgren, 1867; *A. grandis* (Stimpson, 1853); *A. succinea* (Leuckart, 1847); *A. virens* (Sars, 1835).

Alitta succinea **(Leuckart, 1847) new combination**

Nereis succinea Leuckart, 1847.− Augener 1933: 247.

Nereis (*Neanthes*) *succinea* Hartman 1945: 17-20, pl. 3, figs. 1-2.− Fauvel 1923: 346-347, fig. 135f-m.

Neanthes succinea Imajima 1972: 108-110, fig. 32.− Fauchald 1977b: 29.− Kirkegaard 1983: 228.− Wilson 1984: 218-221, fig. 4; 1988: 5-7.− Wu et al. 1985: 156-159, fig. 88.− de Léon-González et al. 1999: 973; de Léon-González & Solís-Weiss 2000: 556.

Nectoneanthes oxypoda Imajima 1972: 113-117, figs. 35-36.− Wu et al. 1985: 164-167, figs. 92-93.

Nereis alatopalpis Wesenberg-Lund, 1949: 281-283, figs. 15-17.

Nectoneanthes alatopalpis Wu et al. 1985: 168-169, fig. 94.

Material examined. Hirsholm, Denmark, 1978-07-25, surface, ZMUC (10 specimens); Horsens fjord, Vorsø, nord for øen Vejlerne, Denmark, 1972-07-03, coll. E. Rasmussen, ZMUC (24); Isefjord, Vellerup Vig, Denmark, 1962-09-02, depth 0.5 m, coll. E. Rasmussen, ZMUC (69); Limfjorden, øst for Fur st. 25, Denmark, 1979-12-05, coll. Limfjordskomiteen, ZMUC (7); Thisted bredning, Limfjorden st. 5, Denmark, 1979-06-18, coll. Limfjordskomiteen, ZMUC (8); Thisted bredning, Limfjorden st. 3, Denmark, 1979-06-18, coll. Limfjordskomiteen, ZMUC (9); Thisted bredning, Limfjorden st. 11, Denmark, 1979-06-19, coll. Limfjordskomiteen, ZMUC (9); Thisted bredning, Limfjorden st. 12, Denmark, 1979-06-20, coll. Limfjordskomiteen, ZMUC (10); Thisted bredning, Limfjorden st. 0, Denmark, 1979-11-29, coll. Limfjordskomiteen, ZMUC (2); Kristineberg Marinbiologiska station, ”near station”, Sweden, 1975-04-18, coll. R.I. Smith, littoral, ZMUC (3), Kristineberg Marinbiologiska station, ”near station”, Sweden, 1975-04-18, coll. R.I. Smith, littoral , ZMUC (4), Blåbergsholmen, Kristineberg, Sweden, 1975-05-05, coll. R.I. Smith, littoral, ZMUC (2); Colonels Island, Georgia, (Timmons River), USA, 1968-07-17, coll. R. Heard, ZMUC (67); Hobsons Bay, Victoria, Australia (9) (Wilson 1984). Size range of material examined: 12-129 mm long for 51-168 chaetigers, complete specimens; 7-129 mm long for 19-105 chaetigers, anterior fragments. Body width at chaetiger 10, 1.5-4 mm.

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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, with 10–11 teeth.

Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 1-7 cones; Area II = 9-41 cones in arcs with 2-3 rows; Area III =13-47 cones in 3 transverse rows; Area IV = 15-37 cones in diagonal rows, smooth bar-like paragnaths absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V = 0-4 (usually 1–3) in a longitudinal line; VI = 4-19 cones arranged in a roughly circular group; VII-VIII = 40-74, arranged in one or more irregular lines forming a continuous band, similar in size, or irregular mix of large and small paragnaths in a single band 3 rows deep.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Markedly elongate and broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, approximately equal to length of dorsal notopodial ligule at least on anterior chaetigers (thus notopodium of 3 similar sized ligules/lobes), present throughout all chaetigers. Acicular process absent. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 1–1.5 times ventral notopodial ligule at chaetiger 10–20. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, digitiform. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule.

Notochaetae: heterogomph spinigers and sesquigomph absent, homogomph spinigers present, notopodial homogomph falcigers absent. Neurochaetae, dorsal fascicle; heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers and falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers absent. Homogomph falcigers on anterior and posterior chaetigers absent.

Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers and sesquigomph absent. Neuropodial ventral fascicle heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers in of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Homogomph falcigers on anterior and posterior chaetigers absent. Anal cirri cirriform.

Distribution. Widely recorded in Northern and Southern Hemispheres (Wilson 1988).

Alitta virens **(Sars, 1835) (Fig. 7)**

Nereis virens Sars, 1835: 58-60, Tab. 10, fig. 27a-c.– Berkeley & Berkeley 1954: 458.
Nereis (*Neanthes*) *virens* Pettibone 1963: 170-174, fig. 44f.
Neanthes virens Imajima 1972: 110-113, fig. 33.
Alitta virens Malmgren 1865: 183-184.− Khlebovich 1996: 109-112, pl. XIX, figs. 1-6.

Material examined. Norway: Drøbak, Oslofjorden, 1899-04-10, ZMUO (3); Onsø (Engelsviken), 23/1 1902, ZMUO (1); Tønsberg, 1889-04-25, ZMUO (1); Skjærviken, Solsvik, Fjell, Hordaland, 1936-09-18, coll, C. Dons, VM (1); Råkvåg, Stjørna, Trondheimsfjorden, VM (1); Tautra, Trondheimsfjorden, 1935-07-24, VM (1); Tautra, Trondheimsfjorden, 1935-08-16, VM (6); Borgenfjorden, Trondheimsfjorden, C4 B22, 1970-11-24, VM (1); Trondhjem biologiske stasjon, Trondheim, 2000-03-27, coll. T. Bakken, intertidal, VM (2); Stjørdalsfjorden, Trondheimsfjorden, stn SD 1, 1973-10-26, VM (1); Storfosna, Sør-Trøndelag, 1942-05-05, coll. C. Dons, VM (1); Trondheimsfjorden, stn H6, 13/5 1970, VM (2). Denmark: Limfjorden, Kås bredning, 1979-12-04, coll. Limfjordskomiteen, stn 11, ZMUC (23); Isefjord, Vellerup Vig, 1966-04-28, depth 0.75 m, coll. E. Rasmussen & M.E. Petersen, ZMUC (38); Limfjorden, Nibe bredning, stn 36.S, 1979-12-18, coll. Limfjordskomiteen, ZMUC (45); Horsens Fjord, Vorsø, Nord for Vejlerne, 1972-08-03, ZMUC (5). Sweden: Blåbergsholmen, Kristineberg, 1975-07-05, intertidal, ZMUC (1).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 4–5. Jaws with dentate cutting edge, 5–6 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 0–4 conical paragnaths (usually 1–2) present or absent; Area II = 3–13 conical paragnaths present; Area III = 4-18 conical paragnaths; Area IV = 8–30 conical paragnaths present, smooth bar-like paragnaths absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V = 0-3 (usually 0); VI = 0-4 conical paragnaths (usually 1), smooth bars absent, pectinate rows absent; VII-VIII = 9-44 conical paragnaths present, similar in size, arranged in one or more irregular lines forming a continuous band.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Markedly broader on posterior chaetigers (Fig. 7C-D). Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, approximately equal to length of dorsal notopodial ligule at least on anterior chaetigers (thus notopodium of 3 similar sized ligules/lobes) (Fig. 7B-C), present throughout all chaetigers. Acicular process absent. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers (Fig. 7E), not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 1 times ventral notopodial ligule at chaetiger 10–20.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers (Fig. 7E), digitiform. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Notopodial homogomph falcigers absent. Notopodial sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent, falcigers absent, heterogomph falcigers on anterior chaetigers present (Fig. 7F), on posterior chaetigers absent, fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent, heterogomph falcigers present, Type 1 heterogomph falcigers anterior chaetigers present (Fig. 7F), Type 1 heterogomph falcigers of posterior chaetigers present. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent, heterogomph chaetae boss not prolonged. Anal cirri cirriform or conical.

Remarks. As argued by Khlebovich (1996) (see also Khlebovich, et al. (1982)) *A. virens* is morphologically very similar to *A. brandti* and *A. grandis*, but differs in reproduction and life history. This might represent a species complex that needs further study using morphological, reproductive and molecular characters.

Distribution. Type locality Manger near Bergen, Norway (Sars 1835). This species (or species complex) is widely reported from boreal areas in the Northern Hemisphere.

***Australonereis* Hartman, 1954**

Australonereis Hartman, 1954: 19.− Hutchings & Reid 1990: 77.

Type species. *Nereis (Leonnates) ehlersi* Augener, 1913

Description. Frontal antennae present, 1 pair; palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Maxillary ring of pharynx with papillae (sometimes with horny tips), 50–110 papillae, solitary. Maxillary ring of pharynx without paragnaths. Oral ring papillae absent. Oral ring paragnaths absent. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers with rows of papillae connecting with the base of each neuropodium.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, restricted to a limited number of anterior chaetigers. Acicular process absent. Ventral notopodial ligule present. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, digitiform. Ventral neuropodial ligule of anterior chaetigers present. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Notopodial homogomph falcigers absent. Notopodial sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers present, sesquigomph falcigers present, blades serrated. Heterogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent, fascicle fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers present, heterogomph spinigers absent, homogomph spinigers absent, sesquigomph spinigers present. Heterogomph falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent.

Remarks. This monotypic genus is known only from Australia.

Australonereis ehlersi **Augener, 1913**

Australonereis ehlersi Hartman 1954: 19-23, figs. 1-11.− Hutchings & Turvey 1982: 97.− Hartmann-Schröder 1982: 76.− Hartmann-Schröder 1989: 35.− Hartmann-Schröder 1990: 59.− Hutchings & Reid 1990: 77-78, fig. 4.− Qui & Qian 2000: 1141.

Material examined. Australia: New South Wales: Tuross Lake, north shore, 36°2.35'S 150°7.27'E, 0.5 m, MV F94253 (1); Wallagoot Lake, south shore, 36°47.75'S 149°56.46'E, intertidal, MV F91367 (2); Merimbula Top Lake, south shore, 36°53.87'S 149°54.56'E, 0.2-0.5 m, MV F94267 (3).

Description. Frontal antennae present, 1 pair; palpostyles conical. 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 3-4. Jaws with dentate cutting edge, with 5–6 teeth. Maxillary ring of pharynx with papillae (sometimes with horny tips), 50–110 papillae, solitary. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx without paragnaths. Oral ring papillae absent. Oral ring paragnaths absent. Ventrum of anterior chaetigers with rows of papillae connecting with the base of each neuropodium.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, restricted to a limited number of anterior chaetigers. Notopodial prechaetal lobe present on anterior chaetigers, reducing in size posteriorly, last present at about chaetiger 55, acicular process absent. Ventral notopodial ligule present. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 0.2 times ventral notopodial ligule at chaetigers 10–20.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, restricted to a limited number of anterior chaetigers, digitiform, reducing posteriorly, last present on chaetigers 5–7. Ventral neuropodial ligule of anterior chaetigers present. Up to half length of acicular neuropodial ligule, on posterior chaetigers present, up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers present, sesquigomph falcigers present, blades serrated. Heterogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers present, heterogomph spinigers absent, homogomph spinigers absent, sesquigomph spinigers present. Heterogomph falcigers absent. Homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform.

Remarks. Hutchings & Reid (1990) described presence of horny tips on the papillae in some specimens, a feature also reported for *Leonnates indicus* (Qui & Qian 2000). This character was not observed on any of our material and is not used here. *Australonereis ehlersi* possess key chaetae characters found in both the sister taxon *Composetia irritabilis* and in the *Ceratonereis*-*Solomononereis* clade, presence of sesquigomph spinigers and falcigers in neuropodia. The clade with *A. ehlersi* and *C. irritabilis* was unequivocally supported by the presence of neuropodial ventral fascicle sesquigomph falcigers.

Distribution. This taxon is common in estuaries throughout the southern coast of Australia and extending to the northeast and northwest.

Ceratonereis **Kinberg, 1865 emended**

Ceratonereis Kinberg, 1865: 170.– Perkins 1980: 2-3.− Khlebovich 1996: 123.
Ceratonereis (*Ceratonereis*) Hartmann-Schröder 1985: 38.

Type species. *Ceratonereis mirabilis* Kinberg, 1866 designated by Hartman (1948)

Description. Frontal antennae present, 1 pair; palpophore with transverse groove present, palpostyles conical. Prostomium with anterior margin indented. Eyes present, 2 pairs. One apodous anterior segment. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnaths: Area I present or absent, conical or minute rod-like paragnaths in a compact cluster; Area II present, conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area III present, conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV present, conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths absent. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Markedly reduced on posterior chaetigers, or not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent. Acicular process absent. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, arising from basal cirrophore. Basal cirrophore of dorsal cirrus short, at most as long as ventral notopodial ligule or much longer than ventral notopodial ligule, not enlarged and vascularised, cylindrical throughout. Dorsal cirri single.

Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, restricted to a limited number of anterior chaetigers, digitiform or flattened. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule or up to half length of acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae present on segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers absent, sesquigomph spinigers present. Notopodial homogomph falcigers absent. Notopodial sesquigomph falcigers present, blade distally bifid or with a single distal tooth. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers absent. Sesquigomph spinigers present, sesquigomph falcigers absent. Heterogomph falcigers on anterior chaetigers present. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers present, blade distally bifid or with a single distal tooth, heterogomph spinigers present, homogomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth, terminally bifid or with a single terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. Perkins (1980) redescribed some *Ceratonereis* species including the type species, *C. mirabilis*, and highlighted several characters not previously considered describing species within the genus. In his description Perkins (1980) drew attention to the presence of soft cushion-shaped lobes in Area VI. This character apparently only occurs in *Ceratonereis* species and was not used here, but may be useful in assessing relationships between *Ceratonereis* species.

The *Ceratonereis* clade is strongly supported in the parsimony analysis (98% bootstrap support), as is the more inclusive clade (*Ceratonereis*+*Solomonereis*). Morphologically the species in *Ceratonereis* are similar to *Solomononereis* but can be distinguished by the anterior achaetigerous segment being longer than the following segments, the dorsal cirrus being mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers compared to basally in *Solomononereis*, and the presence of conical paragnaths instead of rod-like on the maxillary ring.

Hartmann-Schröder (1985) formalised a solution to morphological heterogeneity within *Ceratonereis s.l.* by erecting three subgenera: *Ceratonereis (Ceratonereis)*, *Ceratonereis (Simplisetia)* and *Ceratonereis (Composetia)*. Khlebovich (1996) elevated each of the three subgenera to the rank of genus. We concur that *Ceratonereis sensu* Khlebovich (1996) (=*Ceratonereis (Ceratonereis)* Hartmann-Schröder 1985) is monophyletic. *Composetia* and *Simplisetia* are discussed below.

Included species. Hartmann-Schröder (1985) included 12 species in her subgenus *Ceratonereis*. She also listed 13 species she could not place in any of the three subgenera, which probably all need to be redescribed until it is possible to give them a correct systematic position (Hartmann-Schröder 1985: 49). Twelve species are assigned to *Ceratonereis*: *C. brockorum* Hartmann-Schröder, 1985; *C. excisa* (Grube, 1874); *C. japonica* Imajima, 1972 (but see comments below for *Solomononereis*); *C. longiceratophora* Hartmann-Shröder, 1985; *C. longicirrata* Perkins, 1980; *C. mirabilis* Kinberg, 1865; *C. perkinsi* Hartmann-Schröder, 1985; *C. singularis* Treadwell, 1929; *C. australis* Hartmann-Schröder, 1985; *C. tentaculata* Kinberg, 1865; *C. tenuipalpata* (Pflugfelder, 1933); *C. ternatensis* Fischli, 1903.

***Ceratonereis mirabilis* Kinberg, 1865**

Ceratonereis mirabilis Kinberg, 1865: 170.− Perkins 1980: 4-11, figs. 1-4.

Remarks. Perkins (1980) examined syntypes of *C. mirabilis* along with additional material and gave a very detailed description. He restricted the distribution previously reported for this species, which has been considered cosmopolitan. He also clarified misidentified material of *C. mirabilis* and related species. Information for this species used here was obtained from Perkins (1980).

Distribution. Type locality is Charles Island, Galapagos Islands (Hartman 1949). Perkins (1980) included material from Bahamas, Barbados, Florida, Gulf of Mexico, Puerto Rico and Brazil in his study.

***Ceratonereis perkinsi* Hartmann-Schröder, 1985**

Ceratonereis perkinsi Hartmann-Schröder, 1985: 43-45, figs. 24-35.

Remarks. The information used here was taken from the original description.

Distribution. Type locality Broome, WA, Australia, known from southern Australia (WA to NSW), and from Tonga and New Guinea (Hartmann-Schröder 1985).

***Cheilonereis* Benham, 1916**

Cheilonereis Benham, 1916: 138.− Fauchald 1977a: 88.

Type species. *Nereis cyclurus* Harrington, 1897.

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap present, covering Area VII-VIII when proboscis everted. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnaths: Area I conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area III present; Area IV conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths absent; VI cones present, arranged in a roughly circular group, smooth bars absent, pectinate rows absent; VII-VIII conical paragnaths present, band of conical paragnaths on Areas VII-VIII discontinuous, present only as a ventral band, arranged in isolated patches, VII-VIII paragnaths differentiated into an anterior band of paragnaths similar in size to elsewhere on the proboscis, and a separate band of minute paragnaths (though not confirmed for *C. peristomialis*). Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Markedly elongate on posterior chaetigers. Markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, restricted to a limited number of anterior chaetigers. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, flattened. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Notopodial homogomph falcigers present, terminal tendon absent, articulated throughout, multidentate, with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth. Notopodial sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers present, Type 1 heterogomph falcigers of posterior chaetigers absent, Type 2 heterogomph falcigers of posterior chaetigers absent. Homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform.

Remarks. *Cheilonereis* was distinguished on the basis of the presence of a ventral peristomial flap, then unique among nereidid genera (Benham, 1916). Subsequently, *Laevispinereis* was described with a very similar structure (He & Wu 1989), however published descriptions were inadequate to score many characters and since no material was available for study *Laevispinereis* was excluded from this analysis. *Paraleonnates bolus* is scored in this study, as having a ventral peristomial flap, but is unrelated to *C. cylurus* based on parsimony analysis. The parsimony analysis places *Cheilonereis* within a clade of *Perinereis* species. Further discussion on the possible synonymy of *Cheilonereis* with *Perinereis* can be found in the *Perinereis* Remarks section, below.

Two species of *Cheilonereis* are recognised: *C. cyclurus* from the east and west coasts of the north Pacific (Imajima 1972; Wu et al. 1985), and *C. peristomialis* from Australian and New Zealand waters. A third species from Japan *Nereis shishidoi* Izuka, 1912 was described but has been treated as a synonym to *C. cyclurus* (Imajima 1972).

Cheilonereis cyclurus **(Harrington, 1897) (Fig. 8)**

Nereis cyclurus Harrington, 1897: 219-220, pl. 16, fig. 3, pl. 17, figs. 1-7.
Cheilonereis cyclurus Imajima 1972: 50-53, fig. 6.− Wu et al. 1985: 79-80, fig. 43a-j.

Material examined. Near Port Townsend, Puget Sound, M.H. Pettibone, 65 m, 8 Aug 1938, USNM 29063 (1); Point Robinson, Puget Sound, 20 fathoms (37 m), sand & gravel, 10 Jul 1940, M.H. Pettibone, USNM 29062 (1); Upright Channel, San Juan Archipelago, with hermit crab, 20 Jun 1935, M.H. Pettibone, USNM 29051 (1); San Juan Archipelago, with hermit crabs, USNM 29066 (7).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 4-8. Ventral peristomial flap present (Fig. 8A), covering Area VII-VIII when proboscis everted. Jaws with dentate cutting edge, with 10 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 2-19 conical paragnaths; Area II = 14-37 conical paragnaths; Area III = 8-30 conical paragnaths; Area IV = 17-48 conical paragnaths, smooth bar-like paragnaths absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths absent; VI = 7-14 conical paragnaths, arranged in a roughly circular group (Fig. 8A), smooth bars absent, pectinate rows absent; VII-VIII = 117-306 conical paragnaths present, arranged in one or more irregular lines forming a continuous band, VII-VIII paragnaths differentiated into an anterior band of paragnaths similar in size to elsewhere on the proboscis, and a separate band of minute paragnaths.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Markedly elongate on posterior chaetigers. Markedly broader on posterior chaetigers (Fig. 8D). Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, restricted to a limited number of anterior chaetigers, reducing in size posteriorly last present at about chaetiger 40–50 (first visible about chaetiger 10 (Fig. 8C), after about 50 a tiny lobe is present only visible in compound microscope), acicular process absent. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers (Fig. 8D), not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 1.5 times ventral notopodial ligule at chaetiger 10-20.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, flattened. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule (Fig. 8 D) (although entire neuropodium is reduced in size compared with notopodium on posterior chaetigers).

Notoaciculae absent from segments 1 and 2 (Fig. 8B). Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Notopodial homogomph falcigers present (Fig. 8H-I), first present at chaetiger 27-29, terminal tendon absent, articulated throughout, multidentate, with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth. Notopodial sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present (Fig. 8E), on posterior chaetigers present, blades serrated, blades having teeth only slightly longer proximally than distally. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present (Fig. 8F), Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers present (Fig. 8G), Type 1 heterogomph falcigers of posterior chaetigers absent, Type 2 heterogomph falcigers of posterior chaetigers absent. Homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform.

Remarks. *Cheilonereis cyclyrus* is placed as a sister group to *P. akuna* and *P. cultrifera*. The clade is defined by presence of a small prechaetal notopodial lobe restricted to anterior chaetigers and presence of type 1 heterogomph falcigers in ventral neuropodial fascicle although each of these characters occurs in other clades. All specimens examined are large and it would be desirable to examine specimens of other size classes to resolve possible differences in some characters.

Reclassification of *Cheilonereis cyclurus* as *Perinereis* will be necessary otherwise *Perinereis* is rendered paraphyletic. However, this will be proposed elsewhere when material of the other *Cheilonereis*, *C. peristomialis*, can be redescribed. See Remarks section for *Perinereis* for further comments.

Distribution. Type locality Puget Sound, Washington, USA. General distribution: east and west coasts of the north Pacific.

***Composetia* Hartmann-Schröder, 1985**

Ceratonereis (*Composetia*) Hartmann-Schröder, 1985: 49.
Composetia Khlebovich 1996: 122.

Type species. *Nereis costae* Grube, 1840 designated by Hartmann-Schröder 1985.

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area II present; Area III present, conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV present, conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths absent. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, present throughout all chaetigers or restricted to a limited number of anterior chaetigers. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers or restricted to a limited number of anterior chaetigers. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent (*contra* Hartmann-Schroder 1985). Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers present or absent, falcigers present or absent. Heterogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers present or absent. Neurochaetae, ventral fascicle: sesquigomph falcigers present or absent, heterogomph spinigers absent, homogomph spinigers present. Heterogomph falcigers present or absent, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present or absent, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers present or absent. Anal cirri cirriform or conical.

Remarks. Hartmann-Schröder (1985) diagnosed *Composetia* as having homogomph falcigers in the notopodia, but this appears to be incorrect, neither *Composetia costae* (Grube 1840) nor any of the remaining species referred to *Composetia* has been described as having notopodial falcigers (Fauvel 1923, Hartman 1948, Day 1967, Fauchald 1972, Imajima 1972) (but adequate descriptions are unavailable for *Ceratonereis vittata* Langerhans 1884). See Hartmann-Schröder (1985) for a list of 29 species nominally assigned to *Composetia*.

Fauchald (1972) stated that *Ceratonereis* was a catch-all genus for species with poorly developed paragnaths. With a more narrowly defined *Ceratonereis*, and with some former *Ceratonereis* species being moved to *Simplisetia*, *Composetia* now seem to serve this purpose. Only two species of *Composetia* could be included in this study, and they are unrelated in our parsimony analysis. Published descriptions of the type species, *Composetia costae* are inadequate, and type material could not be located. Until type material of *Composetia costae* can be redescribed the correct generic placement of other species referred to *Composetia* by Hartmann-Schröder (1985) cannot be reassessed. In the interim, it seems best not to attempt further generic combinations for nominal *Composetia* species. The description provided above is based on descriptions of *C. irritabilis* and *C. scotiae,* however, placement of additional species in *Composetia* would exacerbate the problem.

Included species. *Composetia costae* (type species), *C. irritabilis*, *C. scotiae*. *Composetia costae* and other species referred to *Ceratonereis (Composetia)* by Hartmann-Schröder (1985) require redescription.

Composetia irritabilis **(Webster, 1879)**

Nereis irritabilis Webster, 1879: 31-34, pl. V, s. 56-64, pl. VI, figs. 65-69.
Ceratonereis irritabilis Hartman 1945: 20-21, pl. 3, figs. 7-9.− Fauchald 1977b: 23.
Ceratonereis (*Composetia*) *irritabilis* de Léon-González et al. 1999: 668.

Material examined. Co-type, USNM 531 (2); co-type, USNM 532, Virginia, USA (3); USNM 52934 Banks Channel, Wrightsville Beech, North Carolina, 8 March 1974, S.L. Gardiner coll., intertidal muddy sand (4); USNM 52935 Banks Channel, Wrightsville Beech, North Carolina, 27 Feb 1975, intertidal soft mud mixed with shell (2); USNM 52933 Intracoastal Waterway, Wrightsville Beach, North Carolina, 5 Apr 1974, S.L. Gardiner coll, intertidal muddy sand (2).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 8–11. Ventral peristomial flap absent. Jaws with dentate cutting edge, translucent brow, long and slender, 9 teeth. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 0; Area II = 5-10 conical paragnaths; Area III = 19-34 conical paragnaths; Area IV = 5-13 conical paragnaths, smooth bar-like paragnaths absent. Oral ring paragnaths absent.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, present on anterior chaetigers, reducing in size posteriorly, last present at about chaetiger 5-30 or 40, acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 0.5–1 times ventral notopodial ligule at chaetiger 10–20. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, flattened. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent, sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers present, falcigers present, blades serrated. Heterogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers present. Neurochaetae, ventral fascicle: sesquigomph falcigers present, heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers present. Heterogomph falcigers absent. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers present. Anal cirri cirriform or conical.

Remarks. The labels following the type specimens read ”co-type”, hence they are syntypes. The two specimens in one vial with types (USNM 531) must have been dried out at some point, and it was difficult to get parapodial and chaetal characteristics, the other vial (USNM 532) included epitokes only, most likely those described and illustrated by Webster. The types confirm well with illustrations by Hartman (1945 pl. 3, figs. 7-9), and the additional material examined. *C. irritabilis* is known from Virginia (USA) south to Panama (de Léon-González et al. 1999), Virginia being the type locality.

C. irritabilis has sesquigomph chaetae in anterior and mid-body chaetigers, the sesquigomph falcigers being similar (Hartman 1945) to those found in *Ceratonereis* species. However, placement of *C. irritabilis* with *Ceratonereis* species would be unparsimonious and would halve bootstrap support for the *Ceratonereis* clade.

***Composetia scotiae* (Berkeley & Berkeley, 1956) (Fig. 9)**

Nereis (*Ceratonereis*) *scotiae* Berkeley & Berkeley, 1956: 267, figs. 1-2.

Material examined. Holotype, Mitchell Bay, Nova Scotia, Canada, littoral, 1939-07-18, USNM 328889; paratype Mitchell Bay, Nova Scotia, Canada, littoral, 1939-07-18, USNM 32890 (2).

Description. Frontal antennae present, 1 pair, cirriform. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Longer than wide. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 8–10. Ventral peristomial flap absent. Jaws with dentate cutting edge, with 7 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 1 conical paragnath; Area II = 4-7 conical paragnaths; Area III = 0-5 conical paragnaths present or absent; Area IV = 13-17 conical paragnaths, smooth bar-like paragnaths absent. Oral ring papillae absent. Oral ring paragnaths absent.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule present on anterior chaetigers (Fig. 9B), reducing in size posteriorly, last present at about chaetiger 60–70 (from mid-body fused to ventral ligule, making it look like a bilobed ligule (Fig. 9C)), acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 0.7 times ventral notopodial ligule at chaetigers 10–20.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, digitiform (Fig. 9C). Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers present, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers absent, heterogomph falcigers are replaced by heterogomph spinigers from about chaetiger 30. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present (Fig. 9A), Type 2 heterogomph falcigers of anterior chaetigers absent, falcigers in neuropodial ventral fascicle are absent from about chaetiger 30–40. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent.

Remarks. A small superior lobe in the neuropodium is present making the neuropodial acicular ligule look bilobed (Fig. 9B). This might be difficult to see in the dissecting microscope but is quite evident in the compound microscope. Note the presence of heterogomph spinigers in dorsal neuropodial fascicle in mid-body and posterior chaetigers, where homogomph spinigers are more common in nereidins. It seems that these are replacing the heterogomph falcigers, falcigers are lacking in the posterior part.

Composetia scotiae differs from *C. irritabilis* by the absence of sesquigomph chaetae. It was grouped with *Paraleonnates bolus* in most of our analysis (Fig. 6), but was not given bootstrap support. The most appropriate genus assignment for *C. scotiae* cannot be determined until the type species of *Composetia, C.costae*, has been redescribed. *C. scotiae* is only known from the type material, from Nova Scotia, Canada (Berkeley and Berkeley 1956).

Eunereis **Malmgren, 1867**

Eunereis Malmgren, 1865: 182-183.− Fauchald 1977a: 88-89.

Type species. *Nereis longissima* Johnston, 1840

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring of pharynx without paragnaths. Oral ring papillae absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths present or absent; VI present or absent, arranged in a roughly circular group, cones present or absent, smooth bars present or absent, pectinate rows absent; VII-VIII present or absent, conical paragnaths present or absent, pectinate paragnaths absent or not applicable, arranged in isolated patches or in one or more irregular lines forming a continuous band or not applicable, VII-VIII paragnaths similar in size, or irregular mix of large and small paragnaths in a single band or not applicable. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, if present, usually reduced or absent posteriorly or not applicable, restricted to a limited number of anterior chaetigers. Acicular process present or absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore or arising from basal cirrophore. Not enlarged and vascularised, cylindrical throughout. Dorsal cirri single.

Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule or not, restricted to a limited number of anterior chaetigers or not, digitiform or not. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present or absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle, heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. Several of the characters are in the description recorded as ”present or absent”, mainly due to lack of information from original descriptions of included species rather than true facts considering these characters. As observed by de León-González and Solís-Weiss (2000), *Eunereis* contains species with and species without notopodial homogomph falcigers. The type species, *E. longissima* does have notopodial homogomph falcigers, while the other included species *E. paitillae* does not. According to this parsimony analysis the two included taxa are not related, and *Eunereis*, as represented by *E. longissima* is among the most plesiomorphic of Nereididae genera.

Eunereis longissima **(Johnston, 1840) (Fig. 10)**

Nereis longissima Johnston, 1840: 178-179, Fig. 9.− Augener 1933: 247-248.− Chambers & Garwood 1992: 35-38, fig. 44.
Eunereis longissima Malmgren 1865: 183.− 1867: 172-173, pl. VI, fig. 32.
Nereis (*Eunereis*) *longissima* Hartmann-Schröder 1996: 200-201, fig. 87.− Fauvel 1923: 351, fig. 138a-d.

Material examined. Sweden: Gullmar Fjord, NHMLAC, n565, 3 specimens. England: Devon, Yealm estuary, in silty mud, LWMST, coll. & det. P. Gibbs, 14 Oct 1966, ”000431”, ”BM 1969.19”, NHMLAC (1). Denmark: Vejr Bank, ZMUC (5). North Sea, ZMUC (6).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 2–3. Jaws with dentate cutting edge, with 8 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx without paragnaths. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths absent; VI = 2–7 conical paragnaths, arranged in a roughly circular group (Fig. 10 A); VII-VIII absent. Paragnaths small orange-brown points.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent. Acicular process present on anterior chaetigers first present chaetiger 10 (Fig. 10C), reducing in size posteriorly, last present on chaetiger 25. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 1 times ventral notopodial ligule at chaetigers 10–20 (Fig. 10C).

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present, similar in length to acicular neuropodial ligule (Fig. 10C); on posterior chaetigers present, similar to length of acicular neuropodial ligule (Fig. 10E).

Notoaciculae absent from segments 1 and 2 (Fig. 10B). Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present, first present at chaetiger 45-52, terminal tendon absent, articulated throughout, multidentate with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth (Fig. 10I). Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present (Fig. 10F-G), on posterior chaetigers present, blades serrated, blades having teeth only slightly longer proximally than distally. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present (numerous), in anterior chaetigers with blades finely serrated proximally, in posterior chaetigers with blades finely serrated proximally, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present (only 2–3 per parapodium), Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present (Fig. 10H), Type 2 heterogomph falcigers of posterior chaetigers absent. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical (extend back 8 chaetigers).

Distribution. Type locality is Ireland (Johnston 1840), otherwise known from the North Sea and northern Europe. Habitat marine, inshore, or marine, shelf.

Eunereis paitillae **Fauchald, 1977**

Eunereis paitillae Fauchald, 1977b: 25-26, fig. 5.

Material examined. Holotype (USNM 53086) and paratype (USNM 53087), Paitilla Beach, Panama (Pacific).

Remarks. The holotype is a small specimen with body with of 0.6 mm, and the paratype must has been dry, so that the original description was used to supplement observations of the type material. It was confirmed that, according to the original description, the specimens do not have notopodial falcigers. Fauchald (1977b) noted the bar-shaped paragnaths present, one each in Area VI and three in a ventral position in Area VII-VIII. These look like the smooth bars observed in *Perinereis* spp.

Distribution. Paitilla Beach, Panama (type locality) (Fauchald 1977).

Hediste **Malmgren, 1867**

Hediste Malmgren, 1867: 165.− Fauchald 1977a: 89.– Sato & Nakashima 2003: 405.

Type species. *Nereis diversicolor* O.F.Müller, 1766

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Jaws with dentate cutting edge. Maxillary ring divided into discrete Areas. Maxillary ring papillae absent. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area III conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths absent; VI cones present, arranged in a roughly circular group or in lines or arcs, smooth bars absent, pectinate rows absent; VII-VIII present, conical paragnaths present, pectinate paragnaths absent; arranged in one or more irregular lines forming a continuous band, VII-VIII paragnaths similar in size, or irregular mix of large and small paragnaths in a single band. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, restricted to a limited number of anterior chaetigers. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent.

Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers present. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent.

Remarks. Sato and Nakashima (2003) recently revised an Asian species complex of three *Hediste* species, based on rediscovered type material of *H. japonica*, and description of two new species (see also Sato (1999)). Fused falcigers were not described for *H. kermadeca*, making the placement of this species in *Hediste* doubtful (Kirkegaard, 1995).

Species of *Hediste* are recognised by the presence of a large and stout fused falciger in the dorsal fascicle in posterior parapodia. Species of *Simplisetia* have similar fused falcigers but differ from *Hediste* in lacking oral ring paragnaths. Two species of *Simplisetia* and two species of *Hediste* were included in this study. The parsimony analysis indicates that both taxa may be paraphyletic, but levels of homoplasy (notably in oral ring paragnaths) are such that revision of these taxa is not yet justified.

Included species. *H. atoka* Sato & Nakashima, 2003*, H. diadroma* Sato & Nakashima, 2003*, H. diversicolor* (O. F. Müller, 1776)*, H. japonica* (Izuka, 1908)*, H. kermadeca* Kirkegaard, 1995*, H. limnicola* (Johnson, 1903).

***Hediste diversicolor* O.F. Müller, 1776 (Fig. 11)**

Nereis diversicolor O.F. Müller, 1776: 217.− Fauvel 1923: 344, fig. 133a-f.− Augener 1933: 247.− Chambers & Garwood 1992: 28-31, fig. 41.
Nereis (*Hediste*) *diversicolor* Hartmann-Schröder 1996: 201-204, fig. 88a-c.
Hediste diversicolor Malmgren 1867: 165-166, pl. 28, fig. 28.

Material examined. Norway: Skauga, Rissa, Sør-Trøndelag, 1936-07-11, intertidal, coll. C. Dons, VM (11); Lorvikleiret, Borgenfjorden, Trondheimsfjorden, stn 6-15, 1971-07-16, VM (1); Korsen, Borgenfjorden, Trondheimsfjorden, stn 4-8, VM (1); Devlebukta, Trondheim, 2000-08-19, intertidal, coll. T. Bakken, VM (1); Fauske, Salten, Nordland, 1925-08-28, VM (2); Drøbak, Oslofjorden, stn 8, 1958-11-04, ZMUO (2); Øra, Fredrikstad, depth 15 m, 1968-09-06, ZMUO (4); Øra, Fredrikstad Hestholmen - Gåseskjær, 1967-09-05, ZMUO (6). Denmark: Horsens fjord, Vorsø, 1945-08-22, ZMUC (35); Rønnerne, Fredrikshavn, 1966-07-24, coll. bio course, ZMUC (27); Rønnerne, Fredrikshavn, 1971-08-18, coll. J.B. Kirkegaard, ZMUC (2).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 2–4. Jaws with dentate cutting edge, light brown with 6–7 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 1-5 conical paragnaths; Area II = 7-25 conical paragnaths; Area III = 12-35 conical paragnaths; Area IV = 10–29 conical paragnaths, smooth bar-like paragnaths absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths absent; VI = 1-9 conical paragnaths arranged in a roughly circular group; VII-VIII = 8-55 conical paragnaths, arranged in one or more irregular lines forming a continuous band, similar in size, or irregular mix of large and small paragnaths in a single band.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present from chaetiger 5, smaller than dorsal notopodial ligule on anterior chaetigers (Fig. 11F-G), reducing in size posteriorly, last present at about chaetiger 45, acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 0.5 times ventral notopodial ligule at chaetiger 10–20 (Fig. 11F).

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule (Fig. 11E-F), restricted to a limited number of anterior chaetigers, digitiform, reducing posteriorly, last present on chaetigers about 40. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule (Fig.11 I).

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present (Fig.11 B), sesquigomph spinigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers present (Fig. 11D), first present from chaetiger 40–50. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present (Fig. 11C), in anterior chaetigers with blades finely serrated proximally, in posterior chaetigers with blades finely serrated proximally, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers fascicle of anterior chaetigers present (Fig. 11A), Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Distribution. Northern Europe. Often found in estuarine conditions.

Hediste limnicola **(Johnson, 1903)**

Nereis limnicola Johnson, 1903: 208-210, pl. XVI, figs. 1-10.
Neanthes lighti Hartman, 1938: 80-81, figs. 1-4.

Material examined. USA: *Nereis limnicola* 2 syntypes (USNM 5166), Lake Merced, San Fransico, California: *Neanthes lighti* holotype (USNM 20537), 3 paratypes (USNM 20536) Tomales Creek, California. Lake Merced, San Fransico 1956-10-21, coll. R.I. Smith, USNM 35848 (6).

Remarks. The examined material confirms well with the original descriptions (Johnson 1903; Hartman 1938) and comments on the synonymy by *N. lighti* by Smith (1958).

Imajimainereis **de León-González & Solís-Weiss, 2000**

Imajimainereis de Léon-González & Solís-Weiss, 2000: 552-553.

Type species. *Imajimainereis pacifica* de León-González & Solís-Weiss, 2000

Remarks. Our character coding is based on the original description of the type species (de León-González & Solís-Weiss, 2000). Presence of both paragnaths and soft papillae in Area VII-VIII is unique in Nereidinae, but similar features are reported in Area VI in *Wuinereis simplex* (Qui & Qian 2000; see also Khlebovich 1996). In other respects *I. pacifica* seems similar to species of *Leonnates*.

Leonnates **Kinberg, 1865**

Leonnates Kinberg, 1865: 168.– Hutchings & Reid 1991: 48.– Qui & Qian 2000: 1112-1113.

Type species. *Leonnates indicus* Kinberg, 1865

Description. Eversible pharynx with pair of jaws, soft papillae on oral ring, paragnaths and occasionally soft papillae on maxillary ring. Prostomium with entire anterior margin, one pair of antennae, one pair of biarticulated palps and two pairs of eyes. Four pairs of tentacular cirri. Parapodia biramous, except first two pairs. Notopodia with dorsal and ventral ligule, and often prechaetal lobe present. Neuropodia with postchaetal lobe, and ventral ligule. Notochaetae homogomph spinigers and occasionally homogomph falcigers. Neurochaetae homogomph or heterogomph spinigers and homogomph or heterogomph falcigers. By SEM, ends of the chaetal shafts with a large solitary tooth and a circular fringe of small teeth (modified from Qui & Qian 2000).

Remarks. We have used a generic description modified after Qui & Qian (2000) as they were able to study more taxa than were available to us. Qui & Qian (2000) were apparently not aware of the description of *Wuinereis* (Khlebovich 1996) and included *L. simplex* in their account. Closely related species are found in *Paraleonnates* (Qui & Qian 2000), and in *Laevispinereis* (He and Wu 1989), and also the presence of both paragnaths and papillae on the oral ring in *Imajimainereis* is interesting in this respect. The relationships of these three genera as shown by the parsimony analysis should be considered provisional, pending availability of material of all taxa. In our analyses the *Leonnates* clade has 70% bootstrap support but the characters defining that clade occur as homoplasies in other Nereidinae taxa. In all our analyses *L. indicus* and *L. stephensoni* came out in a clade as sister group to the *A. ehlersi* − *C. irritabilis* clade.

Leonnates indicus **Kinberg, 1865**

Leonnates indicus Kinberg, 1865: 168.− Qui & Qian 2000: 1113-1120, figs. 1-3, Tab. 1.
Leonnates virgatus Grube, 1878: 68.
Nereis (*Leonnates*) *virgata* Grube, 1878: 63-64: pl. 4, fig. 7.
Leonnates jousseaumei Gravier, 1899: 234-237; 1901: 160-164, pl. 11, figs. 34-37, text-figs. 162-165.− Wu et al. 1985: 71-72: fig. 38a-j.− Hutchings & Reid 1991: 52-53.

Remarks. Qui & Qian (2000) synonymised *Lonnates virgatus* Grube, 1878 and *Leonnates jousseaumei* Gravier, 1899 with *L. indicus* based on examination of type material. The information used here is from the description by Qui & Qian (2000).

Distribution. Australia; Indonesia; Singapore, Malaysia; Philippines; Hainan; Maccasar Strait; Bay of Bengal; Arabian Sea; Persian Gulf; Red Sea (Qui & Qian 2000).

Leonnates stephensoni **Rullier, 1965**

Leonnates stephensoni Rullier, 1965.− Hutchings & Murray 1984: 36-37, fig. 11.− Hutchings & Reid 1991: 53-54.

Material examined. Holotype Queensland, Moreton Bay, 27º25’S 153º20’E, 10 Feb. 1961, AM W3790; Queensland, Harvey Bay, Coll. P. Hutchings 1 Jan. 1972, large boulders covered with oysters and barnacles, AM W5388 (1).

Remarks. The present description of the holotype and an additional specimen is in well accordance with the description by Hutchings & Reid (1991) and notes and illustrations by Hutchings & Murray (1984), who studied a large amount of material.

Micronereis **Claparède, 1863**

Micronereis Claparède 1863.− Banse 1977: 119-121.− Fauchald 1977a: 89.− Paxton 1983: 5-6.
Notophycus Knox & Cameron, 1970.
Phyllodocella Fauchald & Belman, 1972.
Quadricirra Banse, 1977: 125-126.− Hartmann-Schröder 1979: 121.

Type species. *Micronereis variegata* Claparède, 1863.

Description. Frontal antennae absent; palpophore with transverse groove present, palpostyles spherical or conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment. Tentacular cirri lacking cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring not divided into discrete Areas. Maxillary ring of pharynx with paragnaths. 2 paragnaths in total present on undivided proboscis. Oral ring papillae absent. Oral ring paragnaths present. Ring of oral ring paragnaths present as regular rows of crown-shaped paragnaths. Area V and VI absent, not separated. Area V conical paragnaths absent. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule absent throughout (a single major notopodial acicular ligule present, dorsal cirrus present on an enlarged cirrophore). Prechaetal notopodial lobe absent. Acicular process absent. Ventral notopodial ligule absent. Simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers absent. On posterior chaetigers absent. Ventral cirri single.

Notoaciculae absent from segments 1 and 2 (only confirmed as yet for *M. bansei*). Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Notopodial homogomph falcigers present or absent, Terminal tendon absent, articulated throughout or not. Notopodial sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Neuropodial dorsal fascicle heterogomph falcigers on anterior chaetigers absent. Neuropodial dorsal fascicle fused falcigers absent. Homogomph falcigers on anterior chaetigers present, on posterior chaetigers present, sesquigomph falcigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Neuropodial ventral fascicle heterogomph falcigers absent. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. Sources for information for the genus description is from the DELTA file (Wilson et al. 2003) that includes summary of species where descriptions are coded from Paxton (1983).

Paxton (1983) did an important revision of the genus and included seven species in her review, and three species are described later. *Micronereis* was considered the most highly derived genus within Nereididae (Paxton 1983) and was considered the only genus in the subfamily Notophycine. Fitzhugh (1987) included *Micronereis* in Nereidinae effectively synonymising Notophycinae. Our parsimony analysis suggests instead that *Micronereis* is among the most plesiomorphic of Nereidinae taxa.

Micronereis bansei **(Hartmann-Schröder, 1979)**

Quadricirra bansei Hartmann-Schröder, 1979: 121-122, figs. 227-237.
Quadricirra sp. Banse 1977: 127, pl. 2, fig. c-d.
Micronereis bansei Paxton 1983: 11-12, figs. 14-27.

Remarks. The information used here is taken from Paxton (1983).

Distribution. Australia, Port Said, Egypt (Paxton 1983).

Neanthes **Kinberg, 1865**

Neanthes Kinberg, 1866.− Fauchald 1977a: 89.− Wilson 1984: 210; 1988: 5.− Wu et al. 143-144.

Nectoneanthes Wilson 1988: 5.− Wu et al. 1985: 161.

Type species Neanthes vaalii Kinberg, 1865 by original designation

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area III conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent or; Area IV conical paragnaths present or absent or, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths present or absent, pectinate paragnaths absent or. Oral ring papillae absent. Oral ring paragnaths present, or absent. Area V and VI present as distinct groups, or absent, not separated. Area V conical paragnaths present or absent; VI cones present or absent present, smooth bars or absent, pectinate rows absent; VII-VIII conical paragnaths present or absent, band of conical paragnaths on Areas VII-VIII discontinuous, present only as a ventral band or a ring continuous dorsally and ventrally, pectinate paragnaths absent, arranged in one or more irregular lines forming a continuous band or not, VII-VIII paragnaths similar in size, or irregular mix of large and small paragnaths in a single band or differentiated into an anterior band of paragnaths similar in size to elsewhere on the proboscis, and a separate band of minute paragnaths. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Markedly reduced on posterior chaetigers, or not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly or approximately equal to length of dorsal notopodial ligule at least on anterior chaetigers (thus notopodium of 3 similar sized ligules/lobes), present throughout all chaetigers or restricted to a limited number of anterior chaetigers. Acicular process present or absent, present on anterior chaetigers, reducing in size posteriorly. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers or not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule or a low rounded lobe, not projecting strongly beyond end of acicular ligule, present throughout all chaetigers or restricted to a limited number of anterior chaetigers, digitiform or not. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule or up to half length of acicular neuropodial ligule, on posterior chaetigers present or absent, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule or not applicable. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present or absent. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present or absent, homogomph spinigers present or absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers present or absent, Type 1 heterogomph falcigers of anterior chaetigers present or absent, Type 2 heterogomph falcigers of anterior chaetigers present or absent, Type 0 heterogomph falcigers of posterior chaetigers present or absent, Type 1 heterogomph falcigers of posterior chaetigers present or absent, Type 2 heterogomph falcigers of posterior chaetigers present or absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. *Neanthes* is a large genus in which informal species groups have been proposed for practical purposes (Fauchald 1972; Wilson 1984). Our parsimony analysis indicates that *Neanthes* as presently conceived is polyphyletic. The type species, *N. vaalii*, is grouped with *N. biseriata* in a clade without support identified by highly homoplasious characters. Other species of *Neanthes* are placed in six other clades, each with similar support; the composition of those clades does not match informal groupings proposed by Fauchald (1972) and Wilson (1984). Some *Neanthes* species clearly have been misidentified have been moved to other genera (see discussion for *Alitta* and *Pseudonereis*). Nevertheless, the levels of homoplasy in these data discourage us from making new generic combinations for other morphologically dissimilar species for which names are not already available. Instead an emended description is given based on the species remaining after reidentifications. We are convinced that *Neanthes* as circumscribed here is polyphyletic, but we seek characters showing less homoplasy before describing new genera.

Included species. Based on this parsimony analysis: *Neanthes vaalii* (type species), *N. arenaceodentata*, *N. bassi*, *N. biseriata, N. bongcoi, N. caudata, N. cricognatha, N. flindersi, N. isolata, N. kerguelensis*, *N. unifasciata.* Other *Neanthes* as listed by Wilson (1984) remain unchanged excepting species reidentified here as for *Alitta* and *Pseudonereis*.

***Neanthes biseriata* Hutchings & Turvey, 1982**

Neanthes biseriata Hutchings & Turvey, 1982: 108-110, fig. 6a-d.− Wilson 1984: 212-213.

Material examined. Holotype and paratypes (AM), paratypes (USNM, 9 specimens), additional material from southern Australia is examined (MV) (see Hutchings & Turvey 1982 and Wilson

1994 for details).

Remarks. This species is coded based on the examined type material, and additional specimen. It is thoroughly described in Hutchings & Turbey (1982) and Wilson (1984).

Neanthes bongcoi **Pillai, 1965**

Neanthes bongcoi Pillai, 1965: 142-144, fig. 12a-j.

Material examined. Shirley Island, WA, Australia, 16°17’S 123°26’E, 1988-07-26, mangrove to sand and reef, coll. P.Hutchings, AM W19476 (1); Sandy Cay on Port George, WA, Australia, 15°20’S 124°39’E, 1988-07-12, dredging, coll. P.Hutchings, AM W19478 (1); Calliope River, Qld, Australia, 23°51’S 151°10’E, 1974-1983, Gladstone survey, QLD elec comm, coll. P.Saenger, AM W199365 (31); Bush Bay, WA, Australia, 25°11’S 113°48’E, 1984-01-06, sieved sand from waters edge, coll. H.Stoddart, AM W19867 (1); Mangrove Point, Broome, WA, Australia, stn BR 6/6, depth LSW, 1984-09-30, underside of stones, coll. R.Hanley, MAGNT W2260 (1).

Remarks. A detailed description of this species will be presented elsewhere when type material has been examined. *N. bongcoi* accompanied *N. cricognatha* as a sister group to the *Alitta* clade in all our analyses but failed to show bootstrap support.

Distribution. Dagupan City, Luzon, Philippines (Pillai 1965). Australia: Broome, WA; Darwin Harbour, NT, Calliope River, Qld.

Neanthes cricognatha **Ehlers, 1904**

Neanthes cricognatha Ehlers, 1904.− Augener 1924: 334.− Hutchings & Turvey 1982: 110-111.− Wilson 1984: 213-214.

Nereis (*Neanthes*) *cricognatha* Kott 1951: 106-107.

Remarks. A detailed description and illustrations is available in Wilson (1984), who also commented on synonomies on this species and *N. caudata* and *N. arenaceodentata*. They are separated geographically but are obviously quite similar and might constitute a species complex that warrants further study.

Distribution. Type locality is New Zealand, it is further known from West and South Australia, Victoria, Tasmania and New Zealand (Wilson 1984).

Neanthes flindersi **Wilson, 1984**

Neanthes flindersi Wilson, 1984: 214-216, fig. 2.

Remarks. See Wilson (1984) for details, specimens were re-examined for this study. This species is similar to *N. kerguelensis* as known from southern Australian waters.

Distribution. Bass Strait and Tasmania, Australia (Wilson 1984).

Neanthes isolata **Hutchings & Turvey, 1982**

Neanthes isolata Hutchings & Turvey, 1982: 111-113, fig. 7a-d.

Material examined. Holotype AM W18440; Paratypes AM W18445; AM W18452; AM W18442; AM W18450; AM W18448; USNM 71532 (see Hutchings & Turvey 1982 for details).

Remarks. Information used here is from re-examination of type material.

Distribution. South Australia, Australia (Hutchings & Turvey 1982).

Neanthes kerguelensis **(McIntosh, 1885)**

Nereis kerguelensis McInstosh, 1885: 225-227, Pl. XXXV, figs. 10-12, Pl. XVIA, figs. 17-18.− Augener 1924: 330-333.

Neanthes kerguelensis Hartman 1954: 30.− Hartmann-Schröder 1962: 394-395.− Hartman 1967: 64.− Kirkegaard 1983: 228.− Hutchings & Turvey 1982: 113.− Wilson 1984: 216-218.

Remarks. Wilson (1984) provided a detailed review of material from southern Australia. Specimens were re-examined for this study.

Neanthes unifasciata **(Willey, 1905)**

Nereis unifasciata Willey, 1905: 271-272, pl. IV, figs. 85-88.− Augener 1933: 248-250.− Gibbs 1971: 148.− Wu et al. 1985: 151-153, fig. 85.

Material examined. MAGNT W2468, Coral Bay, Port Essington, NT, CP47/9, 2-5 m, 16.05.1983 (4); MAGNT W2511, Coral Bay, Port Essington, NT, CP47/14, 2-5 m, 16.05.1983 (12); MAGNT W00403, Coral Bay, Port Essington, NT, CP48, 4 m, 17.05.1983 (5); MAGNT W219 Danger Point, Point Bremer, NT, stn CP3A, depth MLN, 30.04.1982, coll. R.Hanley, inside coral rubble (1); MAGNT W00414 New Year Island, NT, stn NY5, depth LWS, 18.10.1087, coll. R.Hanley, reef coral-acorapora (1); MAGNT W00413 New Year Island, NT, stn NY5, depth LWS, 18.10.1087, coll. R.Hanley, reef coral-acorapora (1).

Remarks. The examined material agrees well with the description by Wu et al. (1985).

Distribution. Tropical Indo-west-Pacific (Gibbs 1971). New Caledonia, Philippines, Southern Vietnam, Sri Lanka, India, Suez Canal, Madagascar, Chinese coast (Wu et al. 1985).

Neanthes vaalii **Kinberg, 1865**

Neanthes vaalii Kinberg, 1865: 171.− Augener 1924: 316-317.− Hartman 1954: 27-28, figs. 22-25.− Hutchings & Turvey 1982: 116.− Wilson 1984: 221-222.

Nereis albanyensis Augener 1913: 149-153, pl. II, fig. 6, text fig. 14a-c.

Material examined. Type material (SMNH Type-455) consists of two mid-body fragments, the anterior end is missing, and the material has not any scientific value. Westernport Corinella, Victoria, Australia, MV F50035 (3); additional material re-examined here is listed in Wilson (1984).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 9–10. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 1-4 conical paragnaths; Area II = 7-17 conical paragnaths; Area III = 19-28 conical paragnaths; Area IV = 16-33 conical paragnaths, 1-4 smooth bars present. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths present, (1-)3 conical paragnaths, arranged in a triangular pattern; VI = 3–5 conical paragnaths arranged in a roughly circular group; VII-VIII = 37–59 conical paragnaths present, arranged in one or more irregular lines forming a continuous band, similar in size, or irregular mix of large and small paragnaths in a single band.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present from chaetiger 6, smaller than dorsal notopodial ligule reducing in size posteriorly, last present at about chaetiger 20, acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, 2 times ventral notopodial ligule at chaetiger 10–20.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated, blades having teeth only slightly longer proximally than distally. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, in anterior chaetigers with blades finely serrated proximally, in posterior chaetigers with blades finely serrated proximally, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers present, Type 1 heterogomph falcigers of anterior chaetigers absent, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers absent, Type 2 heterogomph falcigers of posterior chaetigers present. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. The parsimony analysis groups *Neanthes vaalii* and *N. biseriata* in a clade that failed to give bootstrap support based on presence of type 2 heterogomph falcigers in the ventral neuropodial fascicle. This clade came out in most of our analyses.

Distribution. Southern Australia.

Nereis **Linnaeus, 1758**

Nereis Linnaus, 1758.− Fauchald 1977a: 90.

Type species *Nereis pelagica* Linnaeus, 1758 by original designation

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with smooth or slightly crenulate cutting edge or with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I present or absent, conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area II present or absent, conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area III present or absent, conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV present, conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths present or absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths present, or absent. Area V and VI present as distinct groups. Area V conical paragnaths present or absent, arranged in a longitudinal line or arranged in a triangular pattern; VI cones present or absent, smooth bars absent, pectinate rows absent; VII-VIII present or absent, conical paragnaths present, pectinate paragnaths absent, arranged in one or more irregular lines forming a continuous band, VII-VIII paragnaths similar in size, or irregular mix of large and small paragnaths in a single band.

Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth. Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Markedly reduced on posterior chaetigers, or not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present or absent, on posterior chaetigers present. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present or absent, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present or absent, Type 0 heterogomph falcigers of anterior chaetigers present or absent, Type 1 heterogomph falcigers of anterior chaetigers present or absent, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers present or absent, Type 1 heterogomph falcigers of posterior chaetigers present or absent, Type 2 heterogomph falcigers of posterior chaetigers present or absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. *Nereis* is the largest nereidid genus containing about 150 species. There has been no attempt to divide *Nereis* into different groups as is done with the other large genera, although some species with similar morphological features have been compared (Fauchald 1972; Hilbig 1992).

We selected five species of *Nereis* to represent morphological diversity across the genus. The parsimony analysis placed these species in two clades: (*N. pelagica* + *N. zonata*); no bootstrap support and ((*N. bifida* + *N. maxillodentata*) + *N. cockburnenis*); where the least inclusive clade including the former two have bootstrap support (69%). However, for the following reasons we feel that subdivision of *Nereis* is not yet warranted: levels of homoplasy are high; the two *Nereis* clades are placed within an unresolved polytomy, and generic placement of most of the remaining 145 or so species of *Nereis* would be problematic. Homogomph articulation of notopodial falcigers occurs homoplasiously in the two *Nereis* clades in our parsimony analysis but that character can serve to define *Nereis* as above until further characters become available.

There has been no recent attempt to list all *Nereis* taxa other than the catalogue by Hartman (1959), which is still the best source for an overview of described species. Many taxa are insufficiently known as they are described from a single or only a few heteronereidid specimens. This is inclined to cause problems attempting to make a comprehensive list of valid taxa as the description of characters above show important characters highlighting variation in specimens are found in posterior parts leaving heteronereidid specimens impossible to be detailed described.

***Nereis pelagica* Linnaeus, 1758 (Fig. 12)**

Nereis pelagica Linnaeus, 1758.− Augener 1933: 245.− Hartmann-Schröder 1962: 406-407.− Imajima 1972: 142-146, figs. 48-49.− Wu et al. 1985: 120-123, figs. 67-68.− Chambers & Garwood 1992: 38-39, fig. 45.− de Léon-González et al. 1999: 676.

Nereis (*Nereis*) *pelagica* Hartmann-Schröder 1996: 197-199, fig. 86a-f.

Material examined. Norway: Digerud, Drøbak, Oslofjorden, 1953-02-13, coll. M.E. & B.Christiansen, ZMUO (87); Fulehuk-Svenner, 1953-07-27, stn 43, coll. ”G.M. Dannevig”, ZMUO (19); Rammeboen, Hvitsten, 1953-03-10, coll. M.E. & B.Christiansen, ZMUO (41); Tromsøen i sydenden, depth 20-30, 1904-08-08, ZMUO (8); Torungen - Homborsund, stn 51, 1950-07-21, ZMUO (6); Teineboen - Bolærne, Oslofjorden, 1911-06-21, depth 12-16 m, ZMUO (5); Storskjær, Drøbak, 1951-08-13, ZMUO (28); Storskjær, Oslofjorden, 1916-04-09, depth 20 m, ZMUO (5); Sleppet, Honningsvåg, Finnmark, stn 236-56, depth 36-50 m, 1958-08-18, ZMUT (8); Sørfjord Troms, stn 89, depth 14-20, 1958-08-19, ZMUT (9); Sørfjord Troms, stn 28, depth 24 m, 1929-08-03, ZMUT (24); Spitsbergen, stn 514, depth 24 m, 1957-08-24, ZMUT (2); Porsanger Finnmark, stn 232-56, depth 6-10 m, 1921-08-11, ZMUT (15); Borgenfjorden, Strømmen, stn C4 C, depth 2-4 m, 1970-08-15, VM (57). Iceland: Hafranes, 1892-10-01, coll. Lundbeck, ZMUC (13); Onundarfjord, 1935-08-17, coll. Berthelsen, ZMUC (13); Greenland: Davis Strait, depth 100 m, coll. ”Dana”, 1925-06-09, ZMUC (11).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 3–5. Jaws with dentate cutting edge, with 4–5 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 0-3 conical paragnaths (usually 1–2), Area II = 8–23 conical paragnaths; Area III = conical 6-24 paragnaths; Area IV = 12-37 conical paragnaths, 0-4 smooth bars present. Area V and VI present as distinct groups. Area V = 0-2 paragnaths (usually 0), arranged in a longitudinal line; VI = 2–7 conical paragnaths (usually 4 in a cross) arranged in a roughly circular group; VII-VIII = 31-162 conical paragnaths present, arranged in irregular mix of large and small paragnaths in a single band.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, 2–3 times ventral notopodial ligule at chaetigers 10–20.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule (Fig. 12A-B), on posterior chaetigers present, similar to length of acicular neuropodial ligule (Fig. 12C-D).

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present, terminal tendon absent, articulated throughout, multidentate, with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth (Fig. 12G). Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present (Fig. 12F), on posterior chaetigers present, blades serrated, blades having teeth only slightly longer proximally than distally. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present (Fig. 12E), in anterior chaetigers with blades finely serrated proximally, in posterior chaetigers with blades finely serrated proximally, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers present, Type 1 heterogomph falcigers of anterior chaetigers absent, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers absent, Type 2 heterogomph falcigers of posterior chaetigers present. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. *Nereis pelagica* and *N. zonata* are grouped together in the parsimony analysis. There are several morphological differences between these two and the other *Nereis* species included. The shape of the blade in the notopodial homogomph falcigers is different and in the *pelagica-zonata* clade notopodial ligules are similar throughout the specimen. Another difference, which is not consistent to the *bifida-maxillodentata* clade, is presence of paragnaths on both rings. In the latter clade paragnaths are present on both rings on the pharynx in *N. bifida* while the oral ring is bare in *N. maxillodentata*.

N. pelagica is reported to be cosmopolitan, and a number of sub-species have been described (Hartman 1959). Material from different areas should be compared to provide more information. The type locality is unknown.

***Nereis bifida* Hutchings & Turvey, 1982**

Nereis bifida Hutchings & Turvey, 1982: 116-119, fig. 9a-c.− Wilson 1985: 130-132, fig. 2.− Hartmann-Schröder 1990: 60.
Nereis parabifida Hutchings & Turvey, 1982: 132-133, fig. 15a-c.
Nereis jacksoni Kott 1951: 95-98, fig3a-r (in part).− Hartman 1954: 31, figs. 26-29 (in part).

Remarks. This species is adequately described and illustrated in Hutchings & Turvey (1982) and Wilson (1985), specimens listed in their papers were re-examined.

Presence of bidentate notopodial homogomph falcigers and reduced notopodial dorsal ligule in posterior parapodia are diagnostic features for a group of species within *Nereis*, including *N. bifida* and *N. maxillodentata*. The former character is a synapomorphy for this clade, which was given bootstrap support (69%).

***Nereis cockburnensis* Augener, 1913**

Nereis cockburnensis Augener, 1913.− Hartman 1954: 33, figs. 30-32.− Hartmann-Schröder 1982: 78.− Hutchings & Turvey 1982: 121-124, fig. 4b.− Wilson 1985: 132-133.− Hartmann-Schröder 1990: 61.
Nereis (*Neanthes*) *thompsoni* Kott 1951: 103-105, fig. 5a-h.

Remarks. Hutchings & Turvey (1982) gave a detailed description, and further information provided by Wilson (1985), material listed in the latter reference were re-examined.

Distribution. Western Australia, South Australia, Bass Strait, Victoria and New South Wales (Wilson 1985).

Nereis maxillodentata **Hutchings & Turvey, 1982**

Nereis maxillodentata Hutchings & Turvey, 1982: 130-132, fig. 14a-c.− Wilson 1985: 135-136, fig. 1f.

Remarks. Information used here is from Hutchings & Turvey (1982) and Wilson (1985), and re-examined specimens from these references.

Distribution. Victoria, New South Wales, Queensland (Australia) (Wilson 1985).

Nereis zonata **Malmgren, 1867**

Nereis zonata Malmgren, 1867: 164, pl. VI, fig. 34.− Fauvel 1923: 338-339, fig. 130g-n.− Augener 1933: 245-246.− Chambers & Garwood 1992: 44-46, fig. 47.

Material examined. Kara Sea, 73°38’N 63°45’E, stn 38, Jenissej Expedition 1876, depth 146 m, 1876, SMNH (2); Kap Hooker, Jameson Land, East Greenland, stn 346, depth 150m, 1933-07-27, ZMUC (23); Norway: Munkholmen, Trondheimsfjorden, depth 50-100 m, coll. T.Bakken, 2000-05-26, VM (2).

Remarks. A redescription of type material along with additional material throughout the North Atlantic is being prepared and will be presented elsewhere. *N. zonata* is morphologically very similar to *N. pelagica*, the two grouping together in our analyses but failed to show bootstrap support.

Olganereis **Hartmann-Schröder, 1977**

Olganereis Hartmann-Schröder, 1977: 147.− Hutchings & Reid 1990: 90.

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx with papillae, solitary. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx without paragnaths. Oral ring papillae present, solitary. Area V papillae absent; VI papillae present; VII-VIII papillae present. Oral ring paragnaths absent. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Dorsal cirri single.

Neuropodial prechaetal lobe present. Ventral neuropodial ligule of anterior chaetigers present. Up to half length of acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated, blades having teeth only slightly longer proximally than distally. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, in anterior chaetigers with blades finely serrated proximally, in posterior chaetigers with blades finely serrated proximally, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present blade with falcigers with recurved terminal tooth and distinct tendon. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. Hartman (1954) emended the description of *Ceratocephale* to fit the new species *Ceratocephale edmondsi* as it possessed soft papillae on both rings instead of the oral ring only as in *Ceratocephale*. *Olganereis* was later erected for the single species *O. edmondsi* by Hartmann-Schröder (1977) in her treatment of *Ceratocephale*. She based this on presence of papillae on both rings of the pharynx, a single instead of double ventral cirri, and presence of both homo- and heterogomph chaetae instead of homogomph only. This genus is monotypic.

Olganereis has been regarded as a member of Gymnonereidinae and was included here as an outgroup. In all our analyses *O. edmondsi* always came out among the selected ingroup taxa, although in a basal position in the tree.

Olganereis edmondsi **(Hartman, 1954)**

Ceratocephala edmondsi Hartman, 1954: 23-24, figs. 12-17.
Olganereis edmondsi Hartmann-Schröder 1977: 148-149, pl. 2a-e, 3a-c.− Hutchings & Turvey 1982:138-139.− Hutchings & Reid 1990: 90-91.

Remarks. In the parsimony analysis, the branch with *O. edmondsi* is unequivocally supported by presence of the autapomorphic character blade of heterogomph falcigers with recurved tooth and distinct tendon (85). It was not possible to obtain material of this species, hence our description is coded from the literature (Hartman 1954; Hutchings & Reid 1990).

Distribution. This taxon is known from Western Australia to New South Wales (Australia), in intertidal flats (Hutchings & Reid 1990).

Paraleonnates **Khlebovich & Wu, 1962**

Paraleonnates Khlebovich & Wu, 1962.− Wu et al. 1985: 75.

Type species *Paraleonnates uschakovi* Khlebovich & Wu, 1962

Remarks. We have not provided a new description of *Paraleonnates* due to lack of material.

Information used to code *P. bolus* was taken from (Hutchings & Reid 1991), and information from this species only is not sufficient to present an emended genus description. Qui & Qian (2000) examined type and non-type material of *P. uschakovi* but did not present a re-description as such.

Paraleonnates resembles *Leonnates*, but can be distinguished by the presence of spiniger chaetae only (Wu et al. 1985; Qui & Qian 2000). Qui & Qian (2000) also used the presence of both pointed and blunt papillae on the oral ring distinguishing *Paraleonnates*, while there in *Leonnates* are only blunt papillae on the oral ring. There are consistent differences in neuropodial ligules and lobes in representatives in both genera.

Perinereis **Kinberg, 1865 emended**

Perinereis Kinberg, 1865: 175.−Fauchald 1977a: 90.− Hutchings et al. 1991: 245.

Type species *Perinereis novaehollandiae* Kinberg, 1865 (designated by Hartman 1948)

Description. Frontal antennae present, 1 pair, subconical or cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with smooth or slightly crenulate cutting edge or with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent; Area III conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV conical paragnaths present or absent, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths present or absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths present or absent; VI cones present or absent, smooth bars present, pectinate rows absent; VII-VIII conical paragnaths present, pectinate paragnaths absent, arranged in one or more irregular lines forming a continuous band, similar in size, or irregular mix of large and small paragnaths in a single band. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Markedly elongate on posterior chaetigers, or not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers or not, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent or present. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule or up to half length of acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present or absent, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers present or absent, Type 1 heterogomph falcigers of anterior chaetigers present or absent, Type 2 heterogomph falcigers of anterior chaetigers present or absent, Type 0 heterogomph falcigers of posterior chaetigers present or absent, Type 1 heterogomph falcigers of posterior chaetigers present or absent, Type 2 heterogomph falcigers of posterior chaetigers present or absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. The parsimony analysis indicates that *Perinereis* may be polyphyletic. However, five of the eight *Perinereis* species in this analysis are placed in a clade together with *Cheilonereis cyclurus*. Only *P. variodentata*, *P. nuntia* and *P. vallata* are placed outside this clade, the latter two in a clade with support (74%) defined by presence of numerous bars in Area VI, a character occurring homoplasiously in *P. akuna* and *P. caeruleis*. In the larger "*Perinereis*-clade" including. *C. cyclurus*, two least inclusive clades have support: *P. akuna* and *P. cultrifera* (60%) and *P. ablyodonta* and *P. barbara* (94%). Hutchings et al. (1991) proposed informal groups of species within *Perinereis* based on a combination of paragnath and parapodial features, specifically number of smooth bars in Area VI and whether the dorsal notopodial ligule are expanded or not in posterior chaetigers. There are indications in our results that this system has support, but the parsimony analysis, and the level of homoplasy discovered, does not yet justify rejection of the null hypothesis that *Perinereis* is monophyletic. Reclassification of *Cheilonereis cyclurus* as *Perinereis* will be necessary otherwise *Perinereis* is rendered paraphyletic. However, this will be proposed elsewhere when material of the other *Cheilonereis*, *C. peristomialis*, can be redescribed.

Included species. As listed by Hutchings et al. (1991).

***Perinereis akuna* Wilson & Glasby, 1993**

Perinereis akuna Wilson & Glasby, 1993: 259-261, fig 7a-m.

Remarks. The information used here is from the original description by Wilson & Glasby (1993) and re-examined specimens.

Perinereis amblyodonta **(Schmarda, 1861)**

Perinereis novaehollandiae Kinberg, 1865: 175.
Perinereis amblyodonta Hutchings et al. 1991: 247-248, fig 3a-h.

Remarks. Hutchings et al. (1991) described this species based on material from the type locality. In this analysis *P. amblyodonta* is most closely related to *P. barbara*, with 94% bootstrap support.

Distribution. Southern Australia, New Zealand, Philippines.

Perinereis barbara **(Monro, 1926)**

Nereis (*Perinereis*) *barbara* Monro, 1926.
Perinereis barbara Hartmann-Schröder 1989: 37-38; 1990: 62.− Hutchings et al. 1991: 248-250, fig. 4a-g.

Remarks. This species is morphological similar to *P. amblyodonta*. The information used here is from Hutchings et al. (1991).

Distribution. Eastern Australia, India, Singapore.

Perinereis caeruleis **Hoagland, 1920**

Nereis (*Heteronereis*) *caeruleis* Hoagland, 1920: 608-610: pl. 47 figs 13-16, pl 48 figs 1-4.
Perinereis caeruleis Wilson & Glasby 1993: 261-262, Fig. 8a-n.

Remarks. Hutchings et al. (1991) placed this species in the ”*P. nuntia*” species group. In a revision of this group Wilson & Glasby (1993) found *P. caeruleis* to be different from all other species in the group by having a variable indented prostomium and absence of paragnaths in Area II, additional paragnaths present in Area V and VI and possessing distinctive short bladed falcigers. This species warrant further study when more material is available.

Perinereis cultrifera **(Grube, 1840)**

Nereis cultrifera Grube, 1840.
Perinereis cultrifera Gibbs 1971: 149, fig 7.− Imajima 1972: 88-91, fig. 24.− Ben-Eliahu 1975: 181.− Amoureux 1976: 343.− Kirkegaard 1983: 232.− Hutchings et al. 1991: 253-254, fig. 8a-c.− Day 1973: 345.

Material. Hutchings et al. (1991) redescribed what is probably type material of this species. They further noted that this species has been recorded from a wide range of localities throughout the world, originating from the introduction of several varieties (Fauvel 1932). The whole group of varieties is in need of taxonomic revision.

Distribution. Type locality Naples, Italy. Otherwise recorded from Mediterranean Sea, English Channel; more widespread records require verification (Hutchings et al. 1991).

Perinereis nuntia **(Savigny, 1818)**

Perinereis nuntia Wilson & Glasby 1993: 266-268, fig 11a-g.

Remarks. See Wilson & Glasby (1993) for a revision and further information of the *P. nuntia* group.

Perinereis vallata **(Grube, 1858)**

Perinereis vallata Hartman 1954: 35.− Hartmann-Schröder 1962: 412427, figs. 19-43.− Hartmann-Schröder 1965: 148, 298.− Wilson & Glasby 1993: 269-270, fig 12a-l, 13a-g.

Remarks. Our information is from the revision by Wilson & Glasby (1993) and re-examined specimens.

Distribution. Southern Australia, New Zealand, St Paul Island and Chile (Wilson & Glasby 1993).

Perinereis variodentata **(Augener, 1913)**

Nereis (*Perinereis*) *variodentata* Augener, 1913.

Perinereis variodentata Hartman 1954: 35.− Hartmann-Schröder 1982: 79-80; Hartmann-Schröder 1989: 38; Hutchings et al. 1991: 266-268, fig18a-c.

Remarks. Hutchings et al (1991) gave a detailed description and illustrations, where we have the information.

Distribution. Southern Australia.

Platynereis **Kinberg, 1865**

Platynereis Kinberg, 1865: 177.– Wu et al. 1985: 80-81.− Hutchings & Reid 1991: 54.

Uncinereis Chamberlin, 1919: 215-216.

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I absent; Area II absent; Area III conical paragnaths absent, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths present; Area IV conical paragnaths absent, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths present. Oral ring papillae absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths absent; VI cones absent, smooth bars absent, pectinate rows present; VII-VIII conical paragnaths absent, pectinate paragnaths present, arranged in isolated patches or in one or more irregular lines forming a continuous band. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present or absent, with articulation fused on some segments, present as a simple chaeta or articulated throughout, with a single terminal tooth and tendon or simple, not articulated, bifid with terminal tendon or not. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Neuropodial ventral fascicle heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. Presence of pectinate paragnaths are unique to *Platynereis* and reported from all described species. Shape and form of the blade in notopodial homogomph falcigers need to be verified in some of the species.

Platynereis antipoda **Hartman, 1954**

Platynereis dumerilii antipoda Hartman, 1954: 35-36, figs. 33-37.− Hartmann-Schröder 1979: 118.− Hartmann-Schröder 1980: 60.− Wilson 1985: 136-137.− Hutchings & Reid 1991: 55-56.

Material examined. Australia: New South Wales: Tathra, rocks at south end of beach, 36°44'S 149°59'E, 1-2 m, MV F94197 (28); Bittangabee Bay, Green Cape, 37°12.97'S 150°00.89'E, 1-2 m, MV F94225 (1); Victoria: Pope's Eye, 38°16.6'S 144°14.9'E, 5-10 m, MV F93903 (1); Tasmania: Bass Strait, 20 km SSW of Babel Island, 40°06.2'S 148°25.0'E, 22 m, MV F50207 (1).

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 10–12. Jaws with dentate cutting edge, with up to 9 teeth. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I absent; Area II absent; Area III = 1-3 pectinate rows; Area IV = 4-12 pectinate rows. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V paragnaths absent; VI = 2-3 pectinate rows; VII-VIII = 10-15 pectinate row (in 5 transverse groups, each of 2–3 pectinate rows), arranged in isolated patches.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers reducing in size posteriorly, last present at about chaetiger 30, acicular process absent. Dorsal cirrus mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule, present throughout all chaetigers, digitiform. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present, first present at chaetiger 22–30, articulated throughout, with a single terminal tooth and tendon. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fascicle fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, in anterior chaetigers with blades finely serrated proximally, in posterior chaetigers with blades finely serrated proximally, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers absent, Type 1 heterogomph falcigers of posterior chaetigers present, Type 2 heterogomph falcigers of posterior chaetigers absent. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. The branch with *P. antipoda* is supported by several autapomorphies in our results. Most of these are assigned to presence of pectinate paragnaths in different areas on the pharynx (Area III (17), Area IV (20), Area VI (31) Area VII-VIII (33)), but also presence of homogomph notopodial falcigers with blade with distal tendon (63).

Information was mainly taken from the literature (Hutchings & Turvey 1982, Wilson 1985), although some specimens were checked for parapodial and chaetae characters. Many subspecies have been described for *P. dumerilii*, and a survey of these have to be undertaken to resolve the true species identity for many *Platynereis* species.

The Australian material of *P. antipoda* is clearly different from Northern European specimens of *P. dumerilii*, the former is therefore treated with the status of full species. A description of *P. dumerilii* will be given elsewhere.

Pseudonereis **Kinberg, 1865 emended**

Pseudonereis Kinberg, 1865: 174.− Fauchald 1977a: 90.

Type species *Pseudonereis gallapagensis* Kinberg, 1865

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II, III and IV arranged in regular comb-like rows. Paragnath counts: Area I conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, absent; Area III conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths present. Area V and VI present as distinct groups. Area V conical paragnaths present or absent; VI cones present or absent, smooth bars present or absent; VII-VIII conical paragnaths present, pectinate paragnaths absent, paragnaths arranged in one or more irregular lines forming a continuous band, VII-VIII paragnaths similar in size, or irregular mix of large and small paragnaths in a single band. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Markedly elongate on posterior chaetigers. Markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers. Ventral neuropodial ligule of anterior chaetigers present. On posterior chaetigers present, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers present or absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent, homogomph spinigers present or absent. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. The clade with *P. gallapagensis* and related taxa, including three here transferred from *Neanthes*, are unequivocally supported (88%) by the arrangement of conical paragnaths in Areas II-IV, and the terminal position of dorsal cirrus on notopodial dorsal ligule. Further it is support (67%) for the clade including *P. gallapagensis*, *P. noodti* and *P. cortezi*, and for the least inclusive clade of *P. noodti* and *P. cortezi* (67%). A revision of *Pseudonereis* is the subject of a separate analysis, presented elsewhere.

Pseudonereis anomala **Gravier, 1901**

Pseudonereis anomala Gravier, 1901.− Hutchings & Turvey 1982: 141-142.− Hutchings & Glasby 1985: 108-109.− Hylleberg et al. 1986: 13-14, fig. 7.
Nereis nichollsi Kott, 1951: 93-95, fig. 2a-k.

Material examined. Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 1979–03–04, coll. Hutchings & Butler, AM W18310 (98); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 1979–03–04, coll. P. Hutchings W18311 (47); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 1979–03–04, coll. P. Hutchings AM W18312 (6); Mastan Pt. America River, Kangaroo Island, clumps of sponge in fast flowing channel, 1979–03–02, coll. P. Hutchings , AM W18313 (1); Pelsart Group, H. Abrolhos Islands, WA, rock wastings of reef, 1947–09–01, coll. P. Kott, AM W18574 (1).

Remarks. The examined material is in well accordance with descriptions given by Hutchings & Glasby (1982; 1985).

Pseudonereis cortezi **(Kudenov, 1979) new combination**

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

Remarks. Information for this species is from the original description.

Pseudonereis gallapagensis **Kinberg, 1865**

Pseudonereis gallapagensis Kinberg, 1865: 174
Pseudonereis formosa Kinberg, 1865: 174.

Material examined. Syntype, Indifatigable Island, Galapagos, Eugenie Exp. 1851–53, stn 873, SMNH Type-452 (1); Syntype *Pseudonereis formosa*, Honolulu, Hawaii, Eugenie Exp. 1851–53, stn 1081–91, depth 45 m, SMNH Type-5908 (1).

Remarks. A full description and further notes will be given in a revision of *Pseudonereis*.

Pseudonereis noodti **(Hartmann-Schröder, 1962) new combination**

Neanthes noodti Hartmann-Schröder, 1962: 395-398, figs. 7-10.

Remarks. Information is from the original description.

Pseudonereis pseudonoodti **(Fauchald, 1977) new combination**

Neanthes pseudonoodti Fauchald, 1977b: 27-29, fig. 7.

Material examined. Holotype, Paitilla Beach, Panama, Pacific, intertidal, USNM 53090; Paratypes, Paitilla Beach, Panama, Pacific, intertidal, *Telraclita* zone USNM 53091 (4). Additional material: Paitilla Beach, Panama, Pacific, coll. A.A. Reimer, 20.01.1971 USNM 065983 (1); Paitilla Beach, Panama, Pacific, intertidal, coll. A.A. Reimer, 20.01.1971 USNM 065984 (5).

Remarks. This species is coded based on examination of type specimens; a full redescription will be presented in an ongoing revision of *Pseudonereis*.

Simplisetia **Hartmann-Schröder, 1985**

Ceratonereis (*Simplisetia*) Hartmann-Schröder, 1985: 48.
Simplisetia Khlebovich 1996: 121.

Type species *Ceratonereis aequisetis* Augener, 1913 (by original designation)

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I conical paragnaths present or absent (only in *S. transversa*, *S. turveyi*), minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area III conical paragnaths or absent (only in *S. transversa*), minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, smooth bar-like paragnaths absent, pectinate paragnaths absent.

Oral ring papillae absent. Oral ring paragnaths absent. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Acicular process present or absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore. Dorsal cirri single.

Neuropodial postchaetal lobe absent or present, at least on some anterior chaetigers, projecting strongly beyond end of acicular ligule or not applicable, restricted to a limited number of anterior chaetigers or not applicable, digitiform or not applicable. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, similar to length of acicular neuropodial ligule or up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent (only in *S. lizardensis*), homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present. Fused falcigers present. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers present or absent, Type 1 heterogomph falcigers of posterior chaetigers present or absent, Type 2 heterogomph falcigers of posterior chaetigers present or absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent. Anal cirri cirriform or conical.

Remarks. See Remarks for *Hediste*. Hartmann-Schröder (1985) listed 10 species of *Simplisetia*, to which must be added *Simplisetia lizardensis* (Ben-Eliahu, et al. 1984), from Lizard Island in north Queensland, Australia. Six species are from Australia (five from southern Australia), and the remaining five occur elsewhere in the Indo-Pacific. Two species, *S. erythraeensis* and *S. pachychaeta* are also known from Madagascar and South Africa.

Included species. *Simplisetia aequisetis* (Augener, 1913), *S. amphidonta* Hutchings & Turvey, 1982, *S. anchylochaeta* (Horst, 1924), *S. erythraeensis* Fauvel, 1918, *S. limnetica* Hutchings & Glasby, 1982, *S. lizardensis* Ben-Eliahu, Hutchings & Glasby, 1985, *S. pachychaeta* Fauvel, 1918, *S. similisetis* Grube, 1878, *S. transversa* Hutchings & Turvey, 1982, *S. turveyi* Hutchings & Glasby, 1982, *S. vaipekae* Gibbs, 1972.

***Simplisetia aequisetis* (Augener, 1913)**

Ceratonereis aequisetis Hartmann-Schröder 1982: 77.− Hutchings & Glasby 1985: 103-104, Fig. 1.

Ceratonereis (*Simplisetia*) *aequisetis* Hartmann-Schröder 1989: 35-36.– Hartmann-Schröder 1990: 60

Ceratonereis pseudoerythraeensis Hutchings & Turvey, 1982: 98-102, fig. 2a-e.

Description. Frontal antennae present, 1 pair, cirriform; palpostyles conical. 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 5–9. Jaws with dentate cutting edge, (almost invariably right jaw with 9 teeth, left with 6; based on sample of ~100 specimens from SE Australia). Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I = 1-4 conical paragnaths; Area II = 10-36 conical paragnaths; Area III = 17-45 conical paragnaths; Area IV = 12-53 conical paragnaths. Oral ring paragnaths absent.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present, smaller than dorsal notopodial ligule on anterior chaetigers, restricted to a limited number of anterior chaetigers. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers, simple, lacking basal cirrophore, 0.75-1 times ventral notopodial ligule at chaetiger 10-20. Dorsal cirri single.

Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent. Homogomph falcigers absent. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present. Sesquigomph spinigers absent, falcigers absent. Heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present. Fused falcigers present, first present from chaetiger 25–30. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers present, Type 0 heterogomph falcigers of anterior chaetigers absent, Type 1 heterogomph falcigers of anterior chaetigers present, Type 2 heterogomph falcigers of anterior chaetigers absent, Type 0 heterogomph falcigers of posterior chaetigers present, Type 1 heterogomph falcigers of posterior chaetigers absent, Type 2 heterogomph falcigers of posterior chaetigers absent. Neuropodial ventral fascicle homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent.

Remarks. Hutchings & Glasby (1985) redescribed this species including synonymising *C. pseudoerythraeensis* with *C. aequisetis*.

Distribution. This is a widespread species found in most of Australia except the Northern Territory (Hutchings & Glasby (1985)); the type locality is Swan River, Western Australia.

***Simplisetia amphidonta* (Hutchings & Turvey, 1982)**

Ceratonereis amphidonta Hutchings & Turvey, 1982: 97-98, fig. 1a-e.− Hutchings & Glasby 1985: 104.

Material examined. Holotype Maston Point, American River, Kangaroo Island, SA, coll. P. Hutchings 1979-03-02, AM 18397. Australia: Victoria: Western Port, off Crib Point, 38°21.17'S 145°15.13'E, 2 m, MV F50146 (1); Western Port, off Crib Point, 38°21.65'S 145°15.21'E, 2 m, MV F50141 (1); Tasmania: Dover Jetty, 43°19.00'S 147°1.00'E, 1.5 m, MV F50495 (1); Woodbridge, 43°9.50'S 147°14.00'E, intertidal, MV F52558 (14).

Remarks. This species was described based on the holotype only. Additional material examined from Port Phillip Bay confirms the original description, with supplements as coded here.

Type locality. Maston Point, Kangaroo Island, South Australia, Australia.

Distribution. Maston Point and Kangaroo Island, SA and Westernport, Victoria Australia.

***Solomononereis* Gibbs, 1971**

Solomononereis Gibbs, 1971: 151.− Hutchings & Reid 1991: 59.− Nateewathana 1992: 89.

Type species *Solomononereis mauraensis* Gibbs, 1971.

Description. Frontal antennae present, 1 pair, cirriform. Prostomium with anterior margin indented. Eyes present, 2 pairs. One apodous anterior segment. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring divided into discrete Areas. Maxillary ring of pharynx with paragnaths, arranged in discrete areas. Paragnath counts: Area I conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths absent, minute rod-like paragnaths in a compact cluster present; Area III conical paragnaths absent, minute rod-like paragnaths in a compact cluster present, pectinate paragnaths absent; Area IV conical paragnaths absent, minute rod-like paragnaths in a compact cluster present, smooth bar-like paragnaths absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths absent. Transverse dorsal lamellae absent.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Not markedly elongate on posterior chaetigers. Not markedly broader on posterior chaetigers. Markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent. Acicular process absent. Dorsal cirrus not mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers. Dorsal cirri single.

Neuropodial postchaetal lobe absent. Ventral neuropodial ligule of anterior chaetigers present. Similar in length to acicular neuropodial ligule, on posterior chaetigers present, up to half length of acicular neuropodial ligule. Ventral cirri single.

Notoaciculae present on segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers absent, sesquigomph spinigers present. Homogomph falcigers present, terminal tendon absent, articulated throughout, multidentate, with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth. Sesquigomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers absent. Sesquigomph spinigers present, falcigers absent. Heterogomph falcigers on anterior chaetigers absent, on posterior chaetigers present, blades serrated. Fused falcigers absent. Homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent. Heterogomph falcigers absent. Homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent.

Remarks. Minute rod-like paragnaths in Areas II, III and IV are synapomorphic characters for the clade including the two terminal taxa, *S. maurauensis* and *S. phuketensis*. This clade was strongly supported in the resulting trees (96% bootstrap support).

***Solomononereis marauensis* Gibbs, 1971**

Solomononereis marauensis Gibbs, 1971: 152-153, fig 8.− Hutchings & Reid 1991: 59-60.

Remarks. First record of the genus outside the type locality at Solomon Islands in Australia were reported by Hutchings & Reid (1991), from where information on this species was taken, in addition to the original description.

Distribution. Solomon Islands, Northern Australia (Hutchings & Reid 1991).

***Solomononereis phuketensis* Nateewathana, 1992**

Solomononereis phuketensis Nateewathana, 1992: 89-94, figs. 1-3.

Remarks. Nateewathana (1992) suggested that the original material of *Ceratonereis japonica* Imajima, 1972 should be re-examined to see if it should be included in *Solomononereis*. The information used here is taken from the original description.

Distribution. West Coast of Phuket Island, Andaman Sea (Nateewathana 1992).

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References

Amoureux, L. (1976). Une interessante collection de Nereidiens (Annélides Polychètes) des cotes marocaines du detroit de Gibraltar. *Nereis morrocensis*, espece nouvelle pour la Science. *Bulletin du Museum National d'Histoire Naturelle zoologie*, *258*, 337-349.

Augener, H. (1913). Polychaeta I. Errantia. Pp. 65-304, pls 2&3. In W. Michaelsen and R. Hartmeyer (Eds), *Die Fauna Südwest-Australiens*.

Augener, H. (1924). Papers from Dr. T.H. Mortensen's Pacific Expedition 1914-1916. No. 18. Polychaeta II. Polychaeten von Neuseeland I: Errantia. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forenig i Kíbenhavn*, *75*, 241-441.

Augener, H. (1933). Polychaeten aus den Zoologischen Museen von Leiden und Amsterdam. *Zoologische Mededeelingen s'Rijks Museum van Natuurlijke Historie Leiden*, *15*, 177-260.

Bakken, T. (2002). A new species of *Neanthes* (Polychaeta: Nereididae) from southern Australia. *Memoirs of Museum Victoria*, *59*, 327-331.

Bakken, T. (in press). Redescription and resurrection of *Typhlonereis gracilis* Hansen, 1879 (Polychaeta, Nereididae). *Sarsia*,

Banse, K. (1977). A New Subfamily, Notophycinae (Polychaeta: Nereididae) for *Micronereis* Claparède and *Quadricirra* new genus. Pp. 115-140. In D. J. Reish and K. Fauchald (Eds), *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman* (pp. 604). Los Angeles: Allan Hancock Press.

Ben-Eliahu, M. N., Hutchings, P. A. and Glasby, C. J. (1984). *Ceratonereis lizardensis* n. sp. (Polychaeta; Nereididae) and *Malacoceros indicus* (Spionidae), from a Mangrove Habitat at Lizard Island, North Queensland. Pp. 91-97. In P. A. Hutchings (Ed) *Proceedings of* *the First International Polychaete Conference, Sydney, Australia, July 1983* (pp. 483 pp). Sydney: The Linnean Society of New South Wales.

Benham, W. B. (1916). Notes on New Zealand Polychaetes. II. *Transactions and Proceedings of the New Zealand Institute*, *48*, 386-396.

Berkeley, E. and Berkeley, C. (1954). Additions to the polychaete fauna of Canada, with comments on some older records. *Journal of the Fisheries Research Board of Canada*, *11*, 454-471.

Berkeley, E. and Berkeley, C. (1956). A new species and two new records of Polychaeta from Eastern Canada. *Canadian Journal of Zoology*, *34*, 267-271,3figures.

Bremer, K. (1994). Branch support and tree stability. *Cladistics*, *10*, 295-304.

Chamberlin, R. V. (1919). The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology, Harvard*, *48*, 1-514.

Chambers, S. and Garwood, P. (1992). Polychaetes from Scottish waters. A guide to identification: Part 3 Family Nereidae. *Royal Scottish Museum Studies*, *1992*, 1-73.

Claparède, E. (1863). *Beobachtungen ueber Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Kueste von Normandie angestellt*. Leipzig: W. Engelmann.

Clark, R. B. (1961). The origin and formation of the Heteronereis. *Biologial Reviews*, *36*, 199-236.

Dallwitz M.J. Paine TA. Zurcher E.J. (1993 onwards). User's guide to the DELTA system: a general system for processing taxonomic descriptions. 4th edition. http://biodiversity.uno.edu/delta/

Day, J. H. (1967). *A Monograph on the Polychaeta of Southern Africa*. London: Trustees of the British Museum (Natural History).

Day, J. H. (1973). Polychaeta collected by U.D. Gaikwad at Ratnagiri, south of Bombay. *Journal of the Linnean Society of London, Zoology*, *52*, 337-361.

de León-González, J. A. and Solís-Weiss, V. (2000). A review of the polychaete family Nereididae from western Mexico. *Bulletin of Marine Science*, *67*, 549-570.

de León-González, J. A., Solís-Weiss, V. and Rivera, V. O. (1999). Nereidids (Polychaeta) from the Caribbean Sea and adjacent Coral Islands of the southern Gulf of Mexico. *Proceedings of the Biological Society of Washington*, *112*, 667-681.

Ehlers, E. (1904). Neuseeländische Anneliden. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen. Mathematisch-Physikalische Klasse. Neue Folge*, *3*, 1-80, 9 pls.

Eriksson, T. (2001). AutoDecay. 5.0. Available via http://www.bergianska.se/forskning_software.html. Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm.

Fauchald, K. (1972). Benthic polychaetous annelids from deep water off Western Mexico and adjacent areas in the Eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology*, *7*, 1-575.

Fauchald, K. (1977a). The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series*, *28*, 1-188.

Fauchald, K. (1977b). Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithsonian Contributions to Zoology*, *221*, 1-81.

Fauchald, K. and Belman, B. W. (1972). A notophycid polychaete from California. *Bulletin of the Southern California Academy of Sciences*, *71*, 107-108.

Fauvel, P. (1923). *Faune de France. Vol 5. Polychètes errantes.* Paris: Paul Lechevalier.

Fauvel, P. (1932) Annelida Polychaeta of the Indian Museum Calcutta. *Memoirs of the Indian Museum* 12: 1-261.

Fitzhugh, K. (1987). Phylogenetic relationships within the Nereididae (Polychaeta): implications at the subfamily level. *Bulletin of the Biological Society of Washington*, *7*, 174-183.

Gibbs, P. E. (1971). The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum of Natural History (Zoology)*, *21*, 101-211.

Glasby, C. J. (1991). Phylogenetic relationships in the Nereididae (Annelida: Polychaeta), chiefly in the subfamily Gymnonereidinae, and the monophyly of the Namanereidinae. Pp 559-573. Third International Polychaete Conference held at California State University, Long Beach California August 6-11, 1989, ed D.J Reish. *48*, 177-596.

Glasby, C. J. (1993). Family revision and cladistic analysis of the Nereidoidea (Polychaeta: Phyllodocida). *Invertebrate Taxonomy*, *7*, 1551-1573.

Glasby, C. J. (1999). The Namanereidinae (Polychaeta: Nereididae). Part 1, Taxonomy and Phylogeny. *Records of the Australian Museum Supplement*, *25*, 1-129.

Gravier, C. (1899). Contribution à l'ètude des annèlides Polychètes de la Mer Rouge. *Bulletin du Musèum National d'Histoire Naturelle, Paris*, *5*, 234-244.

Gravier, C. (1901). Contribution à l'ètude des annèlides Polychètes de la Mer Rouge. *Nouvelles Archives du Museum d'Histoire Naturelle, Paris, series 4*, *3*, 147-268.

Grube, A. E. (1850). Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin*, *16*, 249-364.

Grube, A. E. (1878). Annulata Semperiana. Beiträge zur kenntniss der annelidenfauna der Philippinen nach den von Herrn Prof. Semper mitgebrachten sammlungen. *Mèmoires l'Acadèmie Impèriale des Sciences de St.-Pètersbourg, sèrie 7*, *25*, ix&1-300,15pls.

Harrington, N. R. (1897). On nereids commensal with hermit crabs. *Transactions of the New York Academy of Sciences*, *16*, 214-223,pls16-18.

Hartman, O. (1945). The marine annelids of North Carolina. *Duke University Marine Station Bulletin no.*, *2*, 1-54.

Hartman, O. (1948). The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Arkiv fur Zoologi, Stockholm*, *42A*, 1-137, 18 pls.

Hartman, O. (1954). Australian Nereidae including descriptions of three new species and one genus, together with summaries of previous records and keys to species. *Transactions of the Royal Society of South Australia*, *77*, 1-41.

Hartman, O. (1959). Catalogue of the Polychaetous Annelids of the world. Part 1. *Allan Hancock Foundation Publications Occasional Papers* 23, 1-353.

Hartmann-Schröder, G. (1962). Zur Kenntnis der Nereiden Chiles (Polychaeta errantia), mit Beschreibung epitoker Stadien einiger Arten und der Jugendentwicklung von *Perinereis vallata* (Grube). *Zoologischer Anzeiger*, *168*, 389-441, 47 figures.

Hartmann-Schröder, G. (1965). Die Polychaeten des sublitorals. pp. 59-305. IN: Hartman-Schroeder, Gesa and Gerd Hartmann, Zur Kenntnis des Sublitorals der chilenischen Kuste unter besonderer Berucksichtigung der Polychaeten und Ostracoden. (Mit bemerkungen uber den einflub sauerstoffarmer stromungen auf die besiedlung von marien sedimenten.). *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg, Supplement*, *62*, 1-384.

Hartmann-Schröder, G. (1979). Teil 2. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). *In* Hartmann-Schröder, Gesa & Hartmann, G. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden (Teil 2 und Teil 3). *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg*, *76*, 75-218.

Hartmann-Schröder, G. (1980). Teil 4. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Port Samson im Norden und Exmouth im Süden). *In* Hartmann-Schröder, G. & Hartmann, G. (eds) Zur kenntnis des eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg*, *77*, 41-110.

Hartmann-Schröder, G. (1982). Teil 8. Die Polychaeten der subtropisch-antiborealen Westküste

Australiens (zwischen Cervantes im Norden und Cape Naturaliste im Süden). *In* Hartmann-Schröder, G. & Hartmann, G. (eds) Zur kenntnis des eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg*, *79*, 51-118.

Hartmann-Schröder, G. (1985). Revision der gattung *Ceratonereis* Kinberg (Nereididae, Polychaeta) (mit besonderer beruksichtigung der arten mit eingeschnittenem prostomium). *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg*, *82*, 37-59.

Hartmann-Schröder, G. (1989). Teil 14. Die Polychaeten der antiborealen und subtropisch-tropischen Küste Südost-Australiens zwischen Lakes Entrance (Victoria) im Süden und Maclean (New South Wales) im Norden. *In* Hartmann-Schröder, G. & Hartmann, G. (eds) Zur kenntnis des eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg*, *86*, 11-63.

Hartmann-Schröder, G. (1990). Teil 15. Die Polychaeten der subtropisch-tropischen und tropischen Östküste Australiens zwischen Lake Macquarie (New South Wales) im Süden und Gladstone (Queensland) im Norden. *In* Hartmann-Schröder, G. & Hartmann, G. (eds) Zur kenntnis des eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Zoologischen Institut und Zoologische Museum der Universität Hamburg*, *87*, 41-87.

Hartmann-Schröder, G. (1996). *Annelida, Borstenwürmer, Polychaeta*. Jena: Gustav Fischer.

He, M. and Wu, Q. (1989). A new genus and a new species of Nereidae. *Acta Oceanologica Sinica English Edition*, *8*, 441-443.

Hilbig, B. (1992). New polychaetous annelids of the families Nereididae Hesionidae and Nephtyidae from the Santa Maria Basin, California with a redescription of *Glycera nana* Johnson, 1901. *Proceedings of the Biological Society of Washington*, *105*, 709-722.

Hoagland, R. A. (1920). Polychaetous annelids collected by the United States Fisheries steamer ”Albatross” during the Philippine expedition of 1907-1909. *Bulletin of the United States National Museum*, *100*, 603-634,pls46-51.

Hutchings, P. A. and Glasby, C. J. (1982). Two new species of *Ceratonereis* (Polychaeta: Nereididae) from estuarine areas of New South Wales, Australia. *Proceedings of the Biological Society of Washington*, *95*, 515-521.

Hutchings, P. A. and Glasby, C. J. (1985). Additional nereidids (Polychaeta) from Eastern Australia, together with a redescription of *Namanereis quadraticeps* (Gay) and the synonymising of *Ceratonereis pseudoerythraeensis* Hutchings & Turvey with *C. aequisetis* (Augener). *Records of the Australian Museum*, *37*, 101-110.

Hutchings, P. A. and Murray, A. (1984). Taxonomy of Polychaetes from the Hawkesbury River and the southern estuaries of New South Wales, Australia. *Records of the Australian Museum Supplement*, *3*, 1-118.

Hutchings, P. A. and Reid, A. (1990). The Nereididae (Polychaeta) from Australia - Gymnonereinae *sensu* Fitzhugh, 1987: *Australonereis*, *Ceratocephale*, *Dendronereides*, *Gymnonereis*, *Nicon*, *Olganereis* and *Websterinereis*. *Records of the Australian Museum*, *42*, 69-100.

Hutchings, P. A., Reid, A. and Wilson, R. S. (1991). *Perinereis* from Australia (Polychaeta, Nereididae) from Australia, with redescriptions of six additional species. *Records of the Australian Museum*, *43*, 241-274.

Hutchings, P. A. and Turvey, S. P. (1982). The Nereididae of South Australia. *Transactions of the Royal Society of South Australia*, *106*, 93-144.

Hutchings, P. A., Wilson, R. S., Glasby, C. J., Paxton, H. and Watson Russell, C. (2000). Appendix 1. In P. L. Beesley, G. J. B. Ross and C. J. Glasby (Eds), *Polychaetes and Allies: the Southern Synthesis* (pp. 242-243). Melbourne: CSIRO Publishing.

Hylleberg, J. and Nateewathana, A. (1988). Polychaetes of Thailand. Nereididae (Part 2): *Ceratocephale* and *Gymnonereis*, with description of two new species and notes on the subfamily Gymnonereidinae. *Phuket Marine Biological Center, Research Bulletin*, *49*, 1-20.

Hylleberg, J., Nateewathana, A. and Bussarawit, S. (1986). Polychaetes of Thailand. Nereidae (Part 1); *Perinereis* and *Pseudonereis* with notes on species of commercial value. *Phuket Marine Biological Center, Research Bulletin*, *43*, 1-22.

Imajima, M. (1972). Review of the annelid worms of the family Nereidae of Japan, with descriptions of five new species or subspecies. *Bulletin of the National Science Museum, Tokyo*, *15*, 37-153.

Johnston, G. (1865). A catlogue of the British non-parasitical worms in the collection of the British Museum.

Khlebovich, V. V. (1996). *Fauna of Russia and neighbouring countries. Polychaetous Annelids Volume III. Polychaetes of the family Nereididae of the Russian Seas and the adjacent waters*. St Petersburg: NAUKA publishing house.

Khlebovich, V. V. (2001). Caecal glands in Nereididae and a new tribe of the subfamily Nereidinae (Polychaeta, Phyllodocida).

Khlebovich, V. V., Komendatov, A. and Yakovishina, L. A. (1982). On variation of paragnath number in *Nereis diversicolor*, *N. japonica* and *N. limnicola* (Polychaeta, Nereidae). *Zoologicheskii Zhurnal*, *62*, 1110-1113.

Khlebovich, V. V. and Wu, B.-L. (1962). Polychaetes from the Yellow Sea. Part 5, Additions to the nereid fauna. *Acta Zoologia Sinica*, *14*, 267-274.

Kinberg, J. G. H. (1865). Annulata nova. Nereidum dispositio nova. *Öfversigt af Kongliga Svenska Vetenskaps Akademiens Förhandlingar.*, *22*, 167-179.

Kinberg, J. G. H. (1866). Annulata nova. *Öfversigt af Kongliga Svenska Vetenskaps Akademiens Förhandlingar.*, *22*, 239-258.

Kirkegaard, J. B. (1983). The Polychaeta of West Africa Part II. Errant species 1. Aphroditidae to Nereididae. *Atlantide Report*, *13*, 181-240.

Kirkegaard, J. B. (1995). Bathyal and abyssal polychaetes (errant species). *Galathea Report*, *17*, 7-56.

Kitching, I. J., Forey, P. L., Humphries, C. J. and Williams, D. M. (1998). *Cladistics. 2nd ed. The theory and practice of parsimony analysis.* Oxford: Oxford University Press.

Knox, G. A. and Cameron, D. B. (1970). Polychaeta from the Snares Islands, New Zealand. *Transactions of the Royal Society of New Zealand Biological Sciences*, *12*, 73-85.

Kott, P. (1951). Nereidae and Eunicidae of south Western Australia; also notes on the ecology of Western Australian limestone reefs. *Journal of the Royal Society of Western Australia*, *35*, 85-130.

Kudenov, J. D. (1979). New species and records of polychaetous annelids from the Tetraclita (Cirripedia: Crustacea) zone of the northern Gulf of California, Mexico. *Bulletin of the Southern California Academy of Science*, *78*, 116-121.

Lamarck, J. B. d. (1818). *Histoire Naturelle des animaux sans vertebres, presentant les caracteres generaux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, etla citation des principales especes qui s'y rapportent; precedes d'une Introduction offrant la determination des caracteres essentiels de l`Animal, sa distinction du vegetal et desautres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Tome 5*. Paris: Deterville.

Leuckart, R. S. (1847). Verzeichnis der zur Fauna Helgoland's gehörenden wirbellosen Seethiere. In H. Frey and R. S. Leuckart (Eds), *Beiträge zur Kenntnis Wirbelloser Thiere mit Besonderer Berücksichtigung der Fauna des Norddeutschen Meeres* (pp. Braunschweig: F.Vieweg and Sohn.

Linnaeus, C. (1758). *Systema naturae. Per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Holmiae: Laurentii Salvii.

Maddison, W. P. and Maddison, D. R. (2002). Mesquite: a modular system for evolutionary analysis. 0.992. Available via http://mesquiteproject.org.

Malmgren, A. J. (1865). Nordiska Hafs-Annulater. *Öfversigt af Konglia Vetenskaps-Akademiens Förhandlingar, Stockholm*, *21*, 51-110,181-192, pls 8-15.

Malmgren, A. J. (1867). Annulater polychaeta Spetsbergiae, Gronlandiae, Islandiae et Scandinaviae hactenus cognita. ™*fversigt af Konglia Vetenskaps-Akademiens Förhandlingar, Stockholm*, *24*, 127-235,pls2-15.

McIntosh, W. C. (1885). Report on the Annelida Polychaeta collected by H.M.S. 'Challenger' during the years 1873-76. *Report of the Scientific Results of the Exploring Voyage of H.M.S. Challenger 1873-76*, *12*, 1-554.

Müller, O. F. (1776). *Zoologicae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium*. Copenhaben: Havniae.

Nateewathana, A. (1992). Polychaetes of Thailand. Nereididae (Part 3): *Solomononereis phuketensis* n. sp. From euhaline environments in the Andaman Sea. *Phuket Marine Biological Center, Research Bulletin*, *57*, 89-96.

Page, RDM. (2001). NEXUS Data Editor for Windows. http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html

Paxton, H. (1983). Revision of the genus *Micronereis* Polychaeta Nereididae Notophycinae. *Records of the Australian Museum*, *35*, 1-18.

Perkins, T. H. (1980). Review of species previously referred to *Ceratonereis mirabilis*, and descriptions of new species of *Ceratonereis*, *Nephtys* and *Goniada* (Polychaeta). *Proceedings of the Biological Society of Washington*, *93*, 1-49.

Pettibone, M. H. (1963). Marine polychaete worms of the New England region. 1. Aphroditidae through Trochochaetidae. *Bulletin of the United States National Museum*, *227*, 1-356.

Pillai, T. G. (1965). Annelida polychaeta from the Philippines and Indonesia. *Ceylon Journal of Science*, *5*, 112-177.

Pleijel, F. (1995). On character coding for phylogeny reconstruction. *Cladistics*, *11*, 309-315.

Pleijel, F. (2001). Nereididae Johnston, 1865. In G. W. Rouse and F. Pleijel (Eds), *Polychaetes* (pp. 96-98). Oxford: Oxford University Press.

Qiu, J.-W. and Qian, P.-Y. (2000). Revision of the genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae), with descriptions and comments on other species described in *Leonnates*. *Proceedings of the Biological Society of Washington*, *113*, 1111-1146.

Rouse, G. W. and Fauchald, K. (1997). Cladistics and polychaetes. *Zoologica Scripta*, *26*, 139-204.

Rouse, G. W. and Pleijel, F. (2001). *Polychaetes*. Oxford: Oxford University Press.

Rullier, F. (1965). Contribution à la faune des annèlides polychètes de l'Australie. *University of Queensland Papers. Department of Zoology*, *2*, 163-210.

Sars, M. (1835). *Beskrivelser og Iagttagelser over nogle moerkelige eller nye i Havet ved den Bergenske Kyst levende Dyr af Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort oversigt over de hidtil af Forfatteren sammesteds fundne Arter og deres Forekommen*. Bergen: Thorstein Hallegers Forlag hos Chr. Dahl.

Sato, M. (1999). Divergence of reproductive and developmental characteristics and speciation in *Hediste* species group. *Hydrobiologia*, *402*, 129-143.

Sato, M. and Nakashima, A. (2003). A review of Asian *Hediste* species complex (Nereididae, Polychaeta) with descriptions of two new species and a redescription of *Hediste japonica* (Izuka, 1908). *Zoological Journal of the Linnean Society*, *137*, 403-445.

Savigny, J.-C. (1820). Systeme des annélides, principalement de celles des cotes de l'Egypte et de la Syrie, offrant les caracteres tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Especes.

Southern, R. (1921). Polychaeta of the Chilka Lake and also of fresh and brackish waters in other parts of India. *Memoirs of the Indian Museum Calcutta*, *5*, 563-659,pls19-31.

Swofford, D. L. (2001). PAUP. 4.0b10 for 32 bit Microsoft Windows. Available via http://www.lms.si.edu/PAUP. Sinauer Associates, Inc., Sunderland, Massachusetts.

Watrous, L. E. and Wheeler, Q. D. (1981). The out-group comparison method of character analysis. *Systematic Zoology*, *30*, 1-11.

Webster, H. E. (1879). The Annelida Chaetopoda of the Virginian coast. *Transactions Albany Institute New York*, *9*, 202-269,11 plates.

Wesenberg-Lund, E. (1949). Polychaetes of the Iranian Gulf. *Danish Scientific Investigation in Iran*, *4*, 247-400.

Wilkinson, M. (1995). A comparison of two methods of character construction. *Cladistics*, *11*, 297-308.

Willey, A. (1905). Report on the Polychaeta collected by Professor Herdman, at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, with supplementary reports upon the Marine Biology of Ceylon, by Other Naturalists. Part IV supplementary report*, *30*, 212-324.

Wilson, R. S. (1984). *Neanthes* (Polychaeta: Nereididae) from Victoria with descriptions of two new species. *Proceedings of the Royal Society of Victoria*, *96*, 209-226.

Wilson, R. S. (1985). *Nereis* and *Platynereis* (Polychaeta: Nereididae) from Victoria with description of a new species of *Nereis*. *Proceedings of the Royal Society of Victoria*, *97*, 129-138.

Wilson, R. S. (1988). Synonymy of the genus *Nectoneanthes* Imajima, 1972, with *Neanthes* Kinberg, 1866 (Polychaeta: Nereididae). *Proceedings of the Biological Society of Washington*, *101*, 4-10.

Wilson, R. S. (2000). Family Nereididae. In P. L. Beesley, G. J. B. Ross and C. J. Glasby (Eds), *Polychaetes and Allies: the Southern Synthesis* (pp. 138-141). Melbourne: CSIRO Publishing.

Wilson, R. S., Bakken, T. and Glasby, C. J. (2003). Nereididae (Polychaeta)-A DELTA database of genera, and Australian species. In R. S. Wilson, P. A. Hutchings and C. J. Glasby (Eds), *Polychaetes: An Interactive Identification Guide* (pp. Melbourne: CSIRO Publishing.

Wilson, R. S. and Glasby, C. J. (1993). A revision of the *Perinereis nuntia* species group (Polychaeta: Neridiidae). *Records of the Australian Museum*, *45*, 253-277.

Wu, B., Sun, R. and Yang, D. J. (1985). The nereidae polychaetous annelids of the chinese coast. In W. Baoling, S. Ruiping and D. J. Yang (Eds), *The Nereidae (Polychaetous Annelids) of the Chinese Coast* (pp. VI+234P). Beijing, China. Illus. Maps: Springer-Verlag New York, Inc.: Secaucus, N.J., USA; Berlin, West Germany; China Ocean Press.

Figure legends

Fig. 1 A-B. Cladograms of Fitzhugh (1987) where two different outgroups were used, both belonging to Hesionidae.− A. Outgoup = *Leocratides*, indicating the suggested revised classification that is used today by most authors (the top line labelled 2).− B. Outgoup = *Leocrates*.

Fig. 2. Cladogram of Glasby (1991) where the monophyly of Namanereidinae was demonstrated, and it's sister group position to the remaining genera.

Fig. 3 A−C. Arrangement of paragnaths in a representative nereidine (generalised *Perinereis nuntia* group species).− A. Dorsal view of everted proboscis.− B. Ventral view of everted proboscis.− C. Dorsal view of head with proboscis retracted.

Fig. 4 A−R. Chaetae from representative Nereidinae genera.− A. Homogomph spiniger shaft, *Perinereis vallata*, MV F53971.− B. Heterogomph falciger shaft, *Perinereis vallata*, MV F53971.− C. Sesquigomph falciger shaft, *Ceratonereis mirabilis* redrawn from Perkins (1980 Figure 1C).− D. Type 0 heterogomph falciger, *Namanereis quadraticeps* redrawn from Hutchings & Glasby (1985 Figure 3E) [a < b < 2a].− E. Type 1 heterogomph falciger, *Cheilonereis cyclurus*, USNM 29063, chaetiger 1 [2a < b].− F. Type 2 heterogomph falciger, *Perinereis caeruleis*, MAGNT W1806, chaetiger 10 [a ≈ b].− G. Type 0 falciger, *Perinereis nuntia*), MNHN Bocal A108, ventral neuropodial fascicle, chaetiger 3.− H. Type 0 falciger, *Nereis pelagica*, NHMLAC, ventral neuropodial fascicle, chaetiger 3.− I. Type 1 falciger, *Hediste diversicolor*, NHMLAC, dorsal neuropodial fascicle, chaetiger 10.− J. Type 1 falciger, *Neanthes cricognatha*, MV F5017, ventral neuropodial fascicle, chaetiger 38.− K. Type 2 falciger, *Pseudonereis gallapagensis*, NHMLAC, ventral neuropodial fascicle, chaetiger 1.− L. Type 2 falciger, *Neanthes vaalii*, MV F50189, ventral neuropodial fascicle, chaetiger 71.− M. Fused falciger, *Hediste diversicolor* NHMLAC, dorsal neuropodial fascicle, chaetiger 70.− N. Fused falciger, *Simplisetia aequisetis*, MV F53970, dorsal neuropodial fascicle, chaetiger 40.− O. Homogomph notopodial falciger, *Nereis pelagica*, NHMLAC, chaetiger 68.− P. Homogomph notopodial falciger, *Nereis bifida*, redrawn from Hutchings & Turvey (1982: Figure 14c).− Q. Notopodial homogomph falciger, *Platynereis dumerilii*, MV F50116, chaetiger 66.− R. Notopodial sesquigomph falciger, *Ceratonereis mirabilis*, redrawn from Perkins (1980: Figure 1C), middle chaetiger.

Fig. 5. Strict consensus tree from the parsimony analysis yielded 5882 most parsimonious trees with a length of 265 steps with consistency index (CI) 0.325 and retention index (RI) 0.643.

Fig.. Strict consensus tree of four most parsimonious trees after reweighting three times. Numerals above lines are node numbers referring to Table 3, numerals in *italic* below lines are bootstrap support values, and numbers in large bold font refer to the clades 1-6 discussed in the text.

Fig. 7 A−F. *Alitta virens* (Sars, 1835) Manger, Norway ZMUO C3435. −A. Parapodium 3rd chaetiger anterior view.− B. Parapodium 10th chaetiger anterior view.− C. Parapodium 30th chaetiger anterior view.− D. Parapodium 80th chaetiger anterior view.− E. Parapodium 124th chaetiger anterior view.− F. Porsal fascicle neuropodial heterogomph falciger 10th chaetiger. Scale bar in A-E 0.1 mm, F 0.01 mm. End view drawings in A-E are not to scale.

Fig. 8 A−I. *Cheilonereis cyclurus* (Harrington, 1897) Puget Sound, Washington, USA, USNM 29063. −A. Ventral view of partly everted proboscis.− B. Parapodium 1st chaetiger, anterior view.− C. Parapodium 10th chaetiger, anterior view.− D. Parapodium 65th chaetiger, anterior view.− E. Dorsal fascicle neuropodial falciger, 1st chaetiger.− F. Ventral fascicle neuropodial falciger, 10th chaetiger.− G. Ventral fascicle neuropodial falciger, 65th chaetiger.− H. Notopodial falciger, 40th chaetiger.− I. Notopodial falciger, 65th chaetiger. Scale bars: A: 2.0 mm; B-D: 0.5 mm; E-I: 0.05 mm.

Fig. 9 A−C. *Ceratonereis scotiae* Berkeley & Berkeley, 1956 Nova Scotia, Canada USNM 32890. −A. ventral fascicle neuropodial falciger, chaetiger 11.− B. Parapodium 11th chaetiger anterior view.− C. Parapodium 30th chaetiger anterior view. Scale bars: A: 0.01 mm; B-C: 0.1 mm. End view drawings in B-C are not to scale.

Fig. 10 A−I. *Eunereis longissima* (Johnston, 1840) Yealm Estuary, Devon, United Kingdom, NHMLAC. −A. Dorsal view of everted proboscis.− B. Parapodium 1st chaetiger, anterior view.− C. Parapodium 10th chaetiger, anterior view.− D. Parapodium 50th chaetiger, anterior view.− E. Parapodium 150th chaetiger, anterior view.− F. Dorsal fascicle neuropodial falciger, 1st chaetiger.− G. Dorsal fascicle neuropodial falciger, 10th chaetiger.− H. Ventral fascicle neuropodial falciger, 75th chaetiger.− I. notopodial homogomph falciger, 75th chaetiger. Scale bars: A: 2.0 mm; B-E: 0.5 mm; F-I: 0.05 mm.

Fig. 11 A−I. *Hediste diversicolor* (O.F. Müller, 1776) Rissa, the Trondheimsfjord, Norway. −A. Ventral fascicle neuropodial heterogomph falciger, 25th chaetiger.− B. Notopodial homogomph spiniger, 12th chaetiger.− C. Ventral fascicle neuropodial heterogomph falciger, 69th chaetiger.− D. Dorsal fascicle neuropodial fused falciger, 69th chaetiger.− E. Parapodium 4th chaetiger anterior view.− F. Parapodium 12th chaetiger anterior view.− G. Parapodium 25th chaetiger anterior view.− H. Parapodium 49th chaetiger anterior view; parapodium 64th chaetiger anterior view. Scale bar in A-D 0.01 mm, F-H 0.1 mm. End view drawings in E-H are not to scale.

Fig. 12 A−G. *Nereis pelagica* (Linnaeus, 1758) Loagrunnen, the Trondheimsfjord, Norway. −A. Parapodium 3rd chaetiger anterior view.− B. Parapodium 10th chaetiger anterior view.− C. Parapodium 25th chaetiger anterior view.− D. Parapodium 45th chaetiger anterior view.− E. Ventral fascicle neuropodial heterogomph spiniger, 10th chaetiger.− F. Dorsal fascicle neuropodial heterogomph falciger, 10h chaetiger.− G. Notopodial homogomph falciger, 25th chaetiger. Scale bar in A-D 0.1 mm, E-G 0.01 mm. End view drawings in A-D are not to scale.

Table 1. Character list for 86 binary characters scored as 1 or 2. For a detailed description of characters see text.

1. *One pair of frontal antennae*: (1) present; (2) absent.
2. *Palpophore compact, no transverse groove*: (1) present; (2) absent.
3. *Palpostyle spherical*: (1) present; (2) absent.
4. *Palpostyle conical*: (1) present; (2) absent.
5. *Prostomium, anterior margin*: (1) with entire anterior margin; (2) with anterior margin indented.
6. *Achaetigerous anterior segment, length*: (1) equal to or less than length of chaetiger 1; (2) greater than length of chaetiger 1.
7. *Tentacular cirri, cirrophores*: (1) present; (2) absent.
8. *Ventral peristomial flap*: (1) present; (2) absent.
9. *Pharynx with recognisable Areas*: (1) present; (2) absent.
10. *Maxillary ring papillae*: (1) present; (2) absent.
11. *Paragnaths in Areas II-IV arranged in regular closely spaced comb-like rows*: (1) present; (2) absent.
12. *Area I; paragnaths*: (1) present; (2) absent.
13. *Area II; conical paragnaths*: (1) present; (2) absent.
14. *Area II; minute rod-like paragnaths in a compact cluster*: (1) present; (2) absent.
15. *Area III; conical paragnaths*: (1) present; (2) absent.
16. *Area III; minute rod-like paragnaths in a compact cluster*: (1) present; (2) absent.
17. *Area III; pectinate paragnaths*: (1) present; (2) absent.
18. *Area IV; conical paragnaths*: (1) present; (2) absent.
19. *Area IV; minute rod-like paragnaths in a compact cluster*: (1) present; (2) absent.
20. *Area IV; pectinate paragnaths*: (1) present; (2) absent.
21. *Area V; papillae*: (1) present; (2) absent.
22. *Area VI; papillae*: (1) present; (2) absent.
23. *Area VII-VIII; papillae*: (1) present; (2) absent.
24. *Oral ring; regular rows of crown-shaped paragnaths*: (1) present; (2) absent.
25. *Paragnaths of Areas V-VIII merged forming a continuous band*: (1) present; (2) absent.
26. *Area V; paragnaths*: (1) present; (2) absent.
27. *Area VI; conical paragnaths*: (1) present; (2) absent.
28. *1 smooth bar on Area VI*: (1) present; (2) absent.
29. *2 smooth bars on Area VI*: (1) present; (2) absent.
30. *Numerous (3 or more) smooth bars on Area VI*: (1) present; (2) absent.
31. *Area VI; pectinate paragnaths*: (1) present; (2) absent.
32. *Area VII-VIII; conical paragnaths*: (1) present; (2) absent.
33. *Area VII-VIII; pectinate paragnaths*: (1) present; (2) absent.
34. *Area VII-VIII paragnaths; arranged in isolated patches*: (1) present; (2) absent.
35. *Area VII-VIII paragnaths; arranged in lines forming a continuous band*: (1) present; (2) absent.
36. *Notopodium*: (1) with at least one distinct ligule or lobe; (2) strongly reduced, lacking identifiable ligules or lobes.
37. *Dorsal notopodial ligule similar on anterior and posterior chaetigers*: (1) present; (2) absent.
38. *Dorsal notopodial ligule markedly elongated on posterior chaetigers*: (1) present; (2)

absent.

39. *Dorsal notopodial ligule markedly broader on posterior chaetigers*: (1) present; (2) absent.
40. *Dorsal notopodial ligule markedly reduced on posterior chaetigers*: (1) present; (2) absent.
41. *Prechaetal notopodial lobe; small*: (1) present; (2) absent.
42. *Prechaetal notopodial lobe; as large as dorsal notopodial ligule*: (1) present; (2) absent.
43. *Prechaetal notopodial lobe; present throughout*: (1) present; (2) absent.
44. *Prechaetal notopodial lobe; restricted to anterior chaetigers*: (1) present; (2) absent.
45. *Notopodial acicular process*: (1) present; (2) absent.
46. *Dorsal cirrus; basally attached to dorsal notopodial ligule on posterior chaetigers*: (1) present; (2) absent.
47. *Dorsal cirrus; mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers*: (1) present; (2) absent.
48. *Dorsal cirrus; terminally attached to dorsal notopodial ligule on posterior chaetigers*: (1) present; (2) absent.
49. *Dorsal cirrus with/without cirrophore*: (1) simple, lacking basal cirrophore; (2) arising from basal cirrophore.
50. *Neuropodial postchaetal lobe; projecting beyond acicular ligule*: (1) present; (2) absent.
51. *Neuropodial postchaetal lobe; low rounded lobe not projecting beyond acicular ligule*: (1) present; (2) absent.
52. *Neuropodial postchaetal lobe; present throughout*: (1) present; (2) absent.
53. *Neuropodial postchaetal lobe; restricted to anterior chaetigers*: (1) present; (2) absent.
54. *Neuropodial postchaetal lobe; digitiform*: (1) present; (2) absent.
55. *Neuropodial postchaetal lobe; flattened*: (1) present; (2) absent.
56. *Ventral neuropodial ligule of anterior chaetigers*: (1) present; (2) absent.
57. *Notoaciculae*: (1) present on segments 1 and 2; (2) absent from segments 1 and 2.
58. *Notoacicula, position in parapodia*: (1) supporting notopodia; (2) ventral, supporting neuropodia.
59. *Notopodial heterogomph spinigers*: (1) present; (2) absent.
60. *Notopodial homogomph spinigers*: (1) present; (2) absent.
61. *Notopodial sesquigomph spinigers*: (1) present; (2) absent.
62. *Notopodial falciger homogomph articulation*: (1) present; (2) absent.
63. *Terminal tendon of blade of notopodial falcigers*: (1) present; (2) absent.
64. *Notopodial homogomph falcigers bidentate with large adjacent terminal and subterminal teeth*: (1) present; (2) absent.
65. *Notopodial homogomph falcigers multidentate with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth*: (1) present; (2) absent.
66. *Notopodial falciger sesquigomph articulation*: (1) present; (2) absent.
67. *Notopodial sesquigomph falcigers, blade distally bifid*: (1) present; (2) absent.
68. *Notopodial sesquigomph falcigers, blade with a single distal tooth*: (1) present; (2) absent.
69. *Neurochaetae dorsal fascicle; heterogomph spinigers*: (1) present; (2) absent.

70. *Neuropodial dorsal fascicle; homogomph spinigers*: (1) present; (2) absent.
71. *Neuropodial dorsal fascicle; sesquigomph spinigers*: (1) present; (2) absent.
72. *Neuropodial dorsal fascicle; sesquigomph falcigers*: (1) present; (2) absent.
73. *Neuropodial dorsal fascicle; heterogomph falcigers*: (1) present; (2) absent.
74. *Neuropodial dorsal fascicle fused falcigers*: (1) present; (2) absent.
75. *Neuropodial dorsal fascicle; homogomph falcigers*: (1) present; (2) absent.
76. *Neuropodial ventral fascicle sesquigomph falcigers*: (1) present; (2) absent.
77. *Neurochaetae ventral fascicle; heterogomph spinigers*: (1) present; (2) absent.
78. *Neuropodial ventral fascicle; homogomph spinigers*: (1) present; (2) absent.
79. *Neuropodial ventral fascicle; sesquigomph spinigers*: (1) present; (2) absent.
80. *Neuropodial ventral fascicle; homogomph falcigers*: (1) present; (2) absent.
81. *Ventral neuropodial fascicle heterogomph falciger articulation*: (1) present; (2) absent.
82. *Type 0 heterogomph falcigers in ventral neuropodial fascicle* : (1) present; (2) absent.
83. *Type 1 heterogomph falcigers in ventral neuropodial fascicle*: (1) present; (2) absent.
84. *Type 2 heterogomph falcigers in ventral neuropodial fascicle* : (1) present; (2) absent.
85. *Blade of ventral fascicle heterogomph falcigers with recurved terminal tooth and distinct tendon*: (1) present; (2) absent.
86. *Blade of ventral fascicle heterogomph falcigers terminally bifid*: (1) present; (2) absent.

Table 2. Binary data matrix of 86 characters for 51 taxa.

		20	40	60	80
Namanereis_quadraticeps	1112111212222222222	22222222222222222222	22222212212222222122	21222212212221222222	2112222
Australonereis_ehlersi	1221121211222222222	22222222222222221122	21221212211221121212	12222222221112221221	2222222
Ceratonereis_mirabilis	1221221212221212212	22222222222222221222	12222221222121211112	21222211222112222122	2121221
Ceratonereis_perkinsi	1221221212221212212	22222222222222221222	12222221222121121212	21222212122121222122	2121222
Cheilonereis_cyclurus	1221121112211212212	22222221222212211211	21221221211212211212	12122122221221222122	2111222
Composetia_irritabilis	1221121212221212212	22222222222222221122	21221212211212211212	12222222221112211211	1222222
Composetia_scotiae	1221221212211212212	22222222222222221122	21212212211212121212	12222222211221222122	212122?
Eunereis_longissima	1221121212222222222	22222221222222221122	22222112212222221212	12122122221221222122	2121222
Eunereis_paitillae	1221121212222222222	22222222122212111122	21221212211221121212	12222222221221222122	2111222
Hediste_diversicolor	1221121212211212212	22222221222212211122	21221212211221121212	12222222221221122122	2121222
Hediste_limnicola	1221121212211212212	22222221222212211122	21221212211221121212	12222222221221122112	2121222
Imajimainereis_pacifica	1221121?12221212212	22212221222212211122	212??21221????121212	12222222211221222112	2122222
Leonnates_indicus	1221121211221212212	22112222222222221122	22121212211212121212	12222222221222212221	2222222
Leonnates_stephensoni	1221221212221222212	21112222222222221122	22112212211212121212	12222222221222212212	1222222
Micronereis_bansei	2?22112222222222222	22221222222222221222	22222222212222222212	12222222221222212212	2222222
Neanthes_bassi	1221121212211212212	22222211222212211122	22222112211221121212	12222222211221222122	2121122
Neanthes_biseriata	1221121212211212212	22222211222212211122	21221212212222221212	12222222221221222122	2122122
Neanthes_bongcoi	1221121212211212212	22222221222212211122	22112212211212121212	12222222221221222122	2121222
Neanthes_cortezi	1221121212111212212	22222212122212211122	22222222111221211?12	12222222221221222122	2122122
Neanthes_cricognatha	1221121212211212212	22222111222212221122	22112212211212121212	12222222221221222212	2121222
Neanthes_flindersi	1221121212221212212	22222221222212211122	21221212211221121212	12222222221221222112	2121122
Neanthes_isolata	1221121212211212212	22222211222212211122	22222112212222221212	12222222221221222122	2112122
Neanthes_kerguelensis	1221121212211212212	22222221222212211122	21221212211221121212	12222222221221222112	2111222
Neanthes_pseudonoodti	1221121212111212212	22222211212212211212	22222222112222221212	12222222221221222122	2112222
Neanthes_succinea	1221121212211212212	22222211222212211211	22112221211212121212	12222222221221222122	2121222
Neanthes_unifasciata	1221121212211212212	22222221222212211122	22222212212222221212	12222222221221222122	2111222
Neanthes_vaalii	1221121212211212212	22222211222212211122	21221212212222221212	12222222221221222122	2112122
Neanthes_virens	1221121212211212212	22222211222212211221	22112221211212121212	12222222221221222122	2121222
Nereis_bifida	1221121212221212212	22222221222212211222	12222212212222221212	12121222221221222122	2111222
Nereis_cockburnensis	1221121212211212212	22222211222212211222	12222212212222221212	12122122221221222122	2111222
Nereis_maxillodentata	1221121212221212212	22222222222222221222	12222212212222221212	12121222221221222122	2111222
Nereis_pelagica	1221121212211212212	22222211222212211122	22222212212222221212	12122122221221222122	2112122
Nereis_zonata	1221121212211212212	22222221222212211122	22222212212222221212	12122122221221222122	2112222
Olganereis_edmondsi	1221121211222222222	22112222222222221222	11221212211221121?12	12222222221221222122	2112112
Paraleonnates_bolus	1221121112211212212	22112222222222221122	21221212212112121?11	12222222211222222122	2121222
Perinereis_akuna	1221121212211212212	22222212221212211212	21221221212222221212	12222222221221222122	2121222
Perinereis_amblyodonta	1221121212211212212	22222212122212211212	22222221212112211212	12222222221221222222	2122122
Perinereis_barbara	1221121212211212212	22222211122212211212	22222221212112211212	12222222221221222122	2122122
Perinereis_caeruleis	1221121212212212212	22222211221212211212	22222?21212222221212	12222222221221222122	2122122
Perinereis_cultrifera	1221121212211212212	22222212122212211212	21221221212222221212	12222222221221222122	2111222
Perinereis_nuntia	1221121212211212212	22222212221212211122	22222112212222221212	12222222221221222122	2112222
Perinereis_vallata	1221121212211212212	22222212221212211122	22222112212222221212	12222222221221222122	2121222
Perinereis_variodentata	1221121212211212212	22222211212212211122	21221212211221121212	12222222221221222122	2112222
Platynereis_antipoda	1221121212222222122	12222222222121121122	21221221211212121212	12112222221221222122	2121222
Pseudonereis_anomala	1221121212111212212	22222221222212211211	21221222112222221212	12122122221221222122	2122122
Pseudonereis_gallapagensis	1221121212111212212	22222212122212211211	22222222112222221212	12222222221221222222	2112122
Pseudonereis_noodti	1221121212111212212	22222212122212211211	22222222111221121212	12222222221221222222	2122122
Simplisetia_aequisetis	1221121212211212212	22222222222222221122	21221212212222221212	12222222221221122122	2111222
Simplisetia_amphidonta	1221121212211212212	22222222222222221122	21221212211221121212	12222222221221122122	2121222
Solomonereis_marauensis	1221211212212121221	22222222222222221222	122222122?2222221112	21122122222121222122	2122222
Solomonereis_phuketensis	1221211212212121221	22222222222222221222	122221122?1212121112	21222212122121222122	2121222

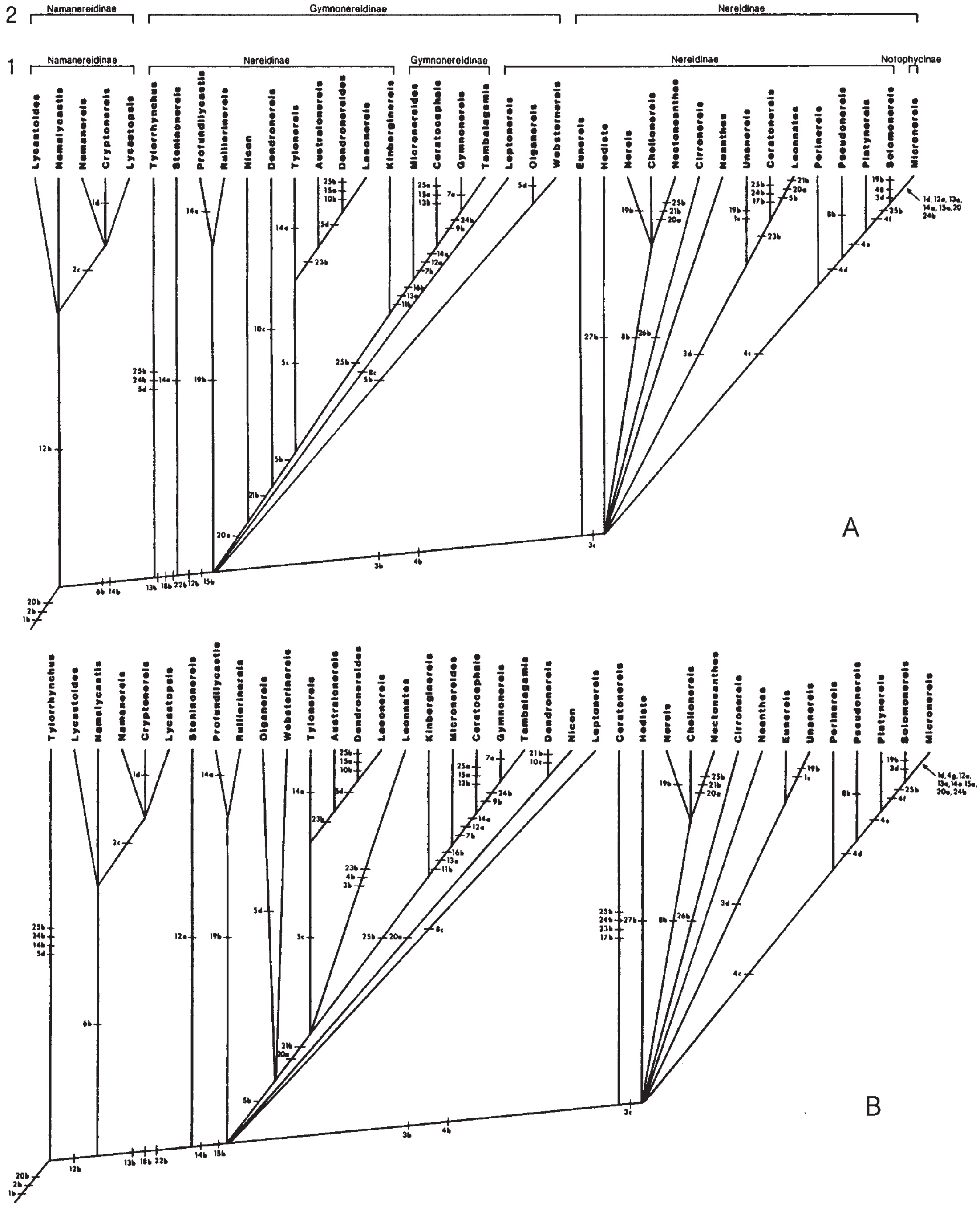
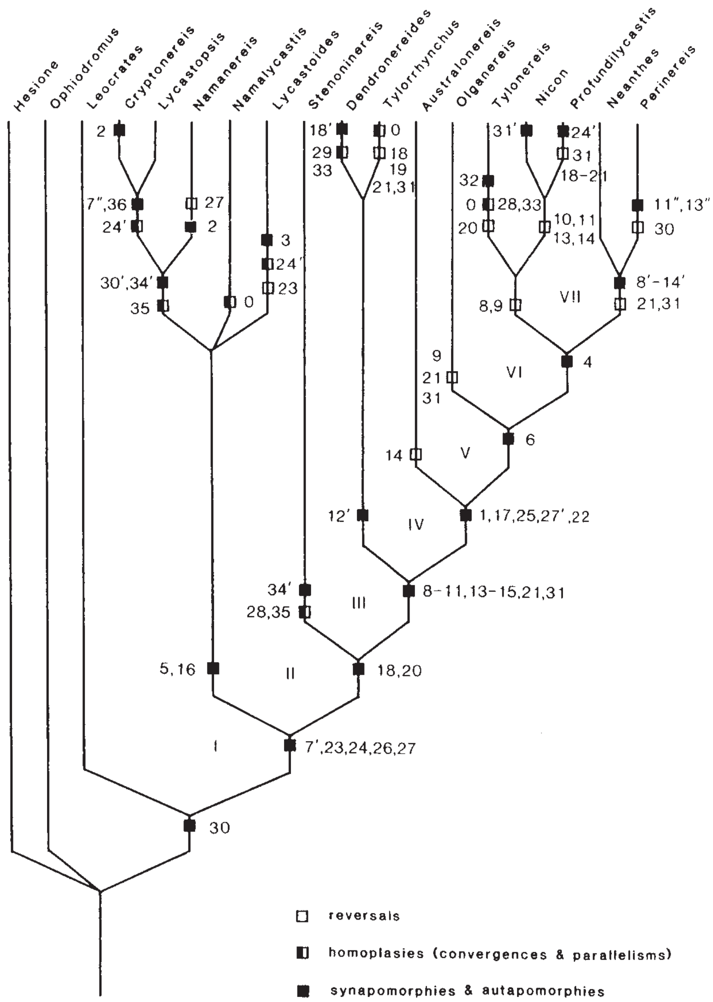

2
Namanereidinae
Gymnonereidinae
Nereidinae
1
Namanereidinae
Nereidinae
Gymnonereidinae
Nereidinae
Notophycinae
Lycastoides
Namalycastis
Namanereis
Cryptonereis
Lycastopsis
Tylorrhynchus
Steninonereis
Profundilycastis
Rullierinereis
Nicon
Dendronereis
Tylonereis
Australonereis
Dendronereides
Laeonereis
Kinberginereis
Micronereides
Ceratocephale
Gymnonereis
Tambalagamia
Leptonereis
Olganereis
Websterinereis
Eunereis
Hediste
Nereis
Cheilonereis
Nectoneanthes
Cirronereis
Neanthes
Unanereis
Ceratonereis
Leonnates
Perinereis
Pseudonereis
Platynereis
Solomonereis
Micronereis
1d, 12a, 13a, 14a, 15a, 20 24b
A
Tylorrhynchus
Lycastoides
Namalycastis
Namanereis
Cryptonereis
Lycastopsis
Steninonereis
Profundilycastis
Rullierinereis
Olganereis
Websterinereis
Tylonereis
Australonereis
Dendronereides
Laeonereis
Leonnates
Kinberginereis
Micronereides
Ceratocephale
Gymnonereis
Tambalagamia
Dendronereis
Nicon
Leptonereis
Ceratonereis
Hediste
Nereis
Cheilonereis
Nectoneanthes
Cirronereis
Neanthes
Eunereis
Unanereis
Perinereis
Pseudonereis
Platynereis
Solomonereis
Micronereis
1d, 4g, 12a, 13a, 14a 15a, 20a, 24b
B

Fig. 1


Hesione
Ophiodromus
Leocrates
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Namanereis
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Australonereis
Olganereis
Tylonereis
Nicon
Profundilycastis
Neanthes
Perinereis
2
7″,36
24′
27
2
30′,34′
35
0
3
24′
23
18′
29
33
0
18
19
21,31
31′
32
0
28,33
20
24′
31
18-21
10,11
13,14
11″,13″
30
8,9
VII
8′-14′
21,31
9
21
31
VI
4
6
14
V
12′
IV
1,17,25,27′,22
34′
28,35
III
8-11,13-15,21,31
5,16
II
18,20
I
7′,23,24,26,27
30
reversals
homoplasies (convergences & parallelisms)
synapomorphies & autapomorphies

Fig. 2

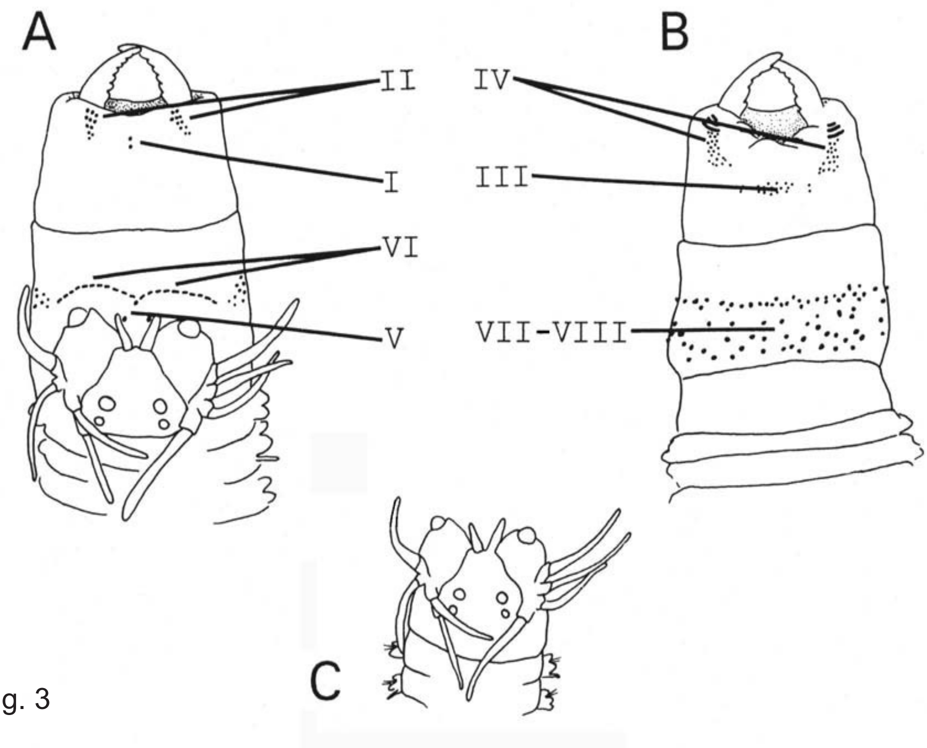

A
II
I
VI
V
B
IV
III
VII-VIII
C

Fig. 3

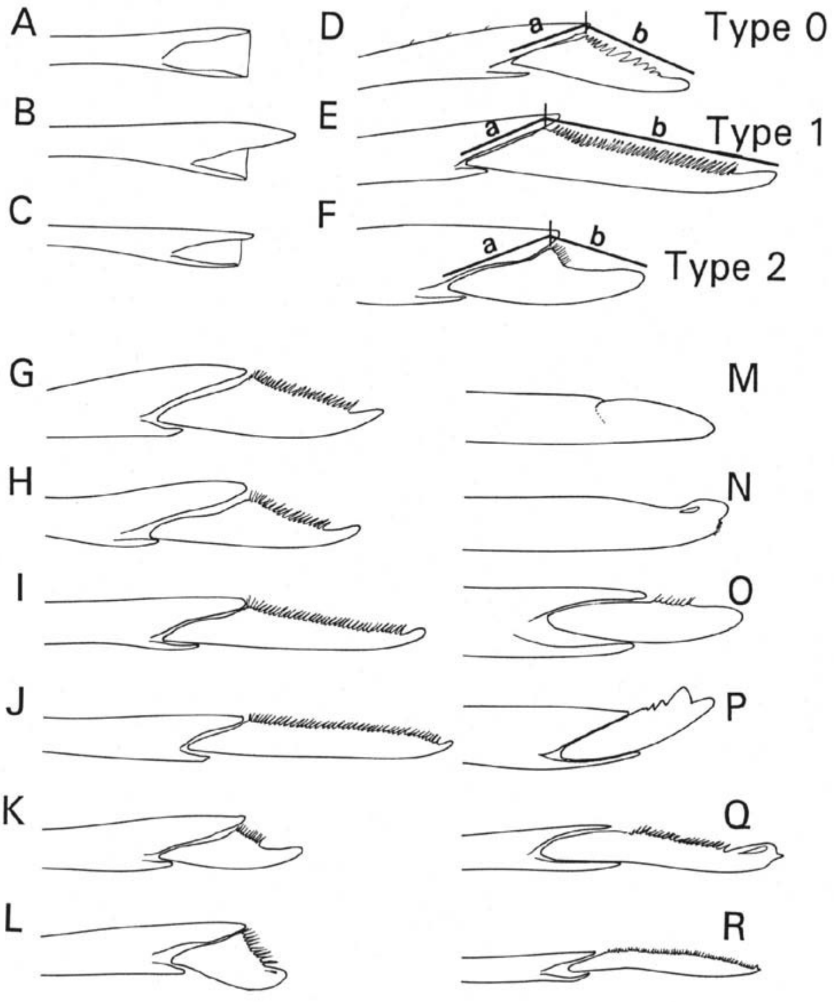
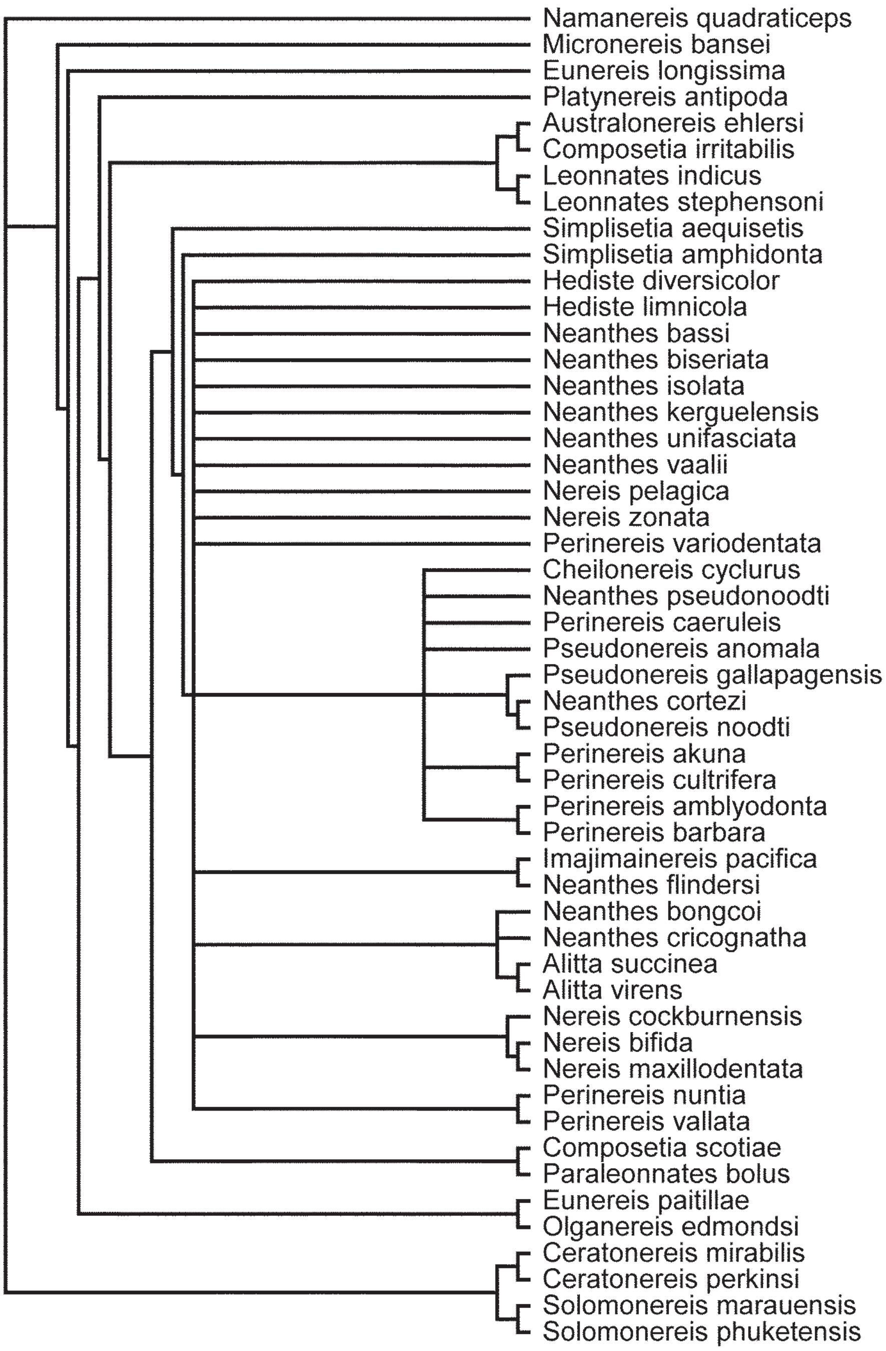


Fig. 4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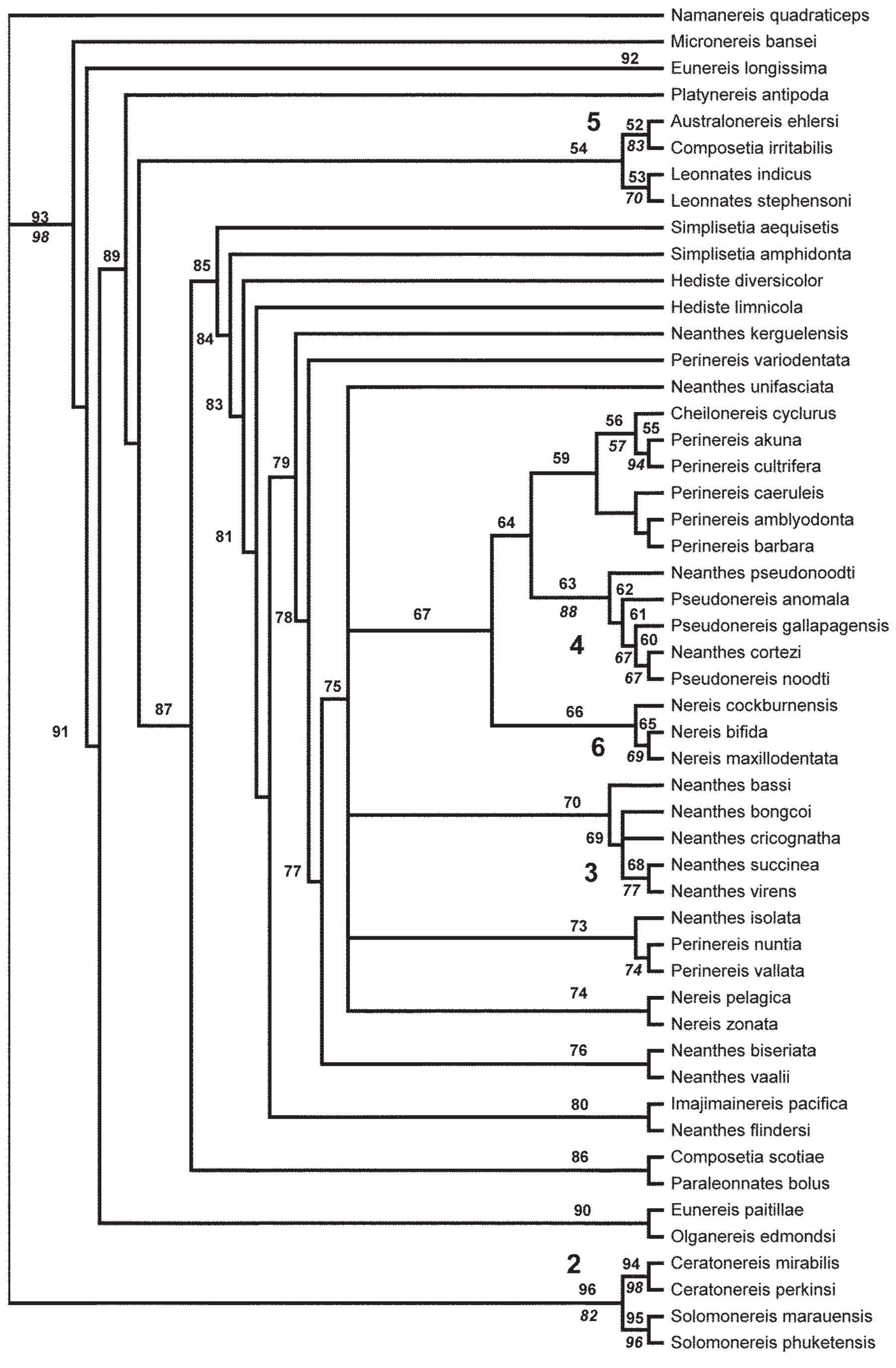
Micronereis bansei
Eunereis longissima
Platynereis antipoda
Australonereis ehlersi
Composetia irritabilis
Leonnates indicus
Leonnates stephensoni
Simplisetia aequisetis
Simplisetia amphidonta
Hediste diversicolor
Hediste limnicola
Neanthes bassi
Neanthes biseriata
Neanthes isolata
Neanthes kerguelensis
Neanthes unifasciata
Neanthes vaalii
Nereis pelagica
Nereis zonata
Perinereis variodentata
Cheilonereis cyclurus
Neanthes pseudonoodti
Perinereis caeruleis
Pseudonereis anomala
Pseudonereis gallapagensis
Neanthes cortezi
Pseudonereis noodti
Perinereis akuna
Perinereis cultrifera
Perinereis amblyodonta
Perinereis barbara
Imajimainereis pacifica
Neanthes flindersi
Neanthes bongcoi
Neanthes cricognatha
Alitta succinea
Alitta virens
Nereis cockburnensis
Nereis bifida
Nereis maxillodentata
Perinereis nuntia
Perinereis vallata
Composetia scotiae
Paraleonnates bolus
Eunereis paitillae
Olganereis edmondsi
Ceratonereis mirabilis
Ceratonereis perkinsi
Solomonereis marauensis
Solomonereis phuketensis

Fig. 5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Micronereis bansei
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Eunereis longissima
Platynereis antipoda
5
52
Australonereis ehlersi
54
83
Composetia irritabilis
53
Leonnates indicus
70
Leonnates stephensoni
93
98
Simplisetia aequisetis
89
85
Simplisetia amphidonta
Hediste diversicolor
84
Hediste limnicola
Neanthes kerguelensis
Perinereis variodentata
83
Neanthes unifasciata
56
Cheilonereis cyclurus
55
57
Perinereis akuna
59
94
Perinereis cultrifera
79
Perinereis caeruleis
64
Perinereis amblyodonta
81
Perinereis barbara
Neanthes pseudonoodti
63
62
Pseudonereis anomala
88
61
78
67
Pseudonereis gallapagensis
4
60
Neanthes cortezi
67
67
Pseudonereis noodti
75
Nereis cockburnensis
66
87
65
Nereis bifida
91
6
69
Nereis maxillodentata
Neanthes bassi
70
Neanthes bongcoi
69
Neanthes cricognatha
68
Neanthes succinea
3
77
77
Neanthes virens
Neanthes isolata
73
Perinereis nuntia
74
Perinereis vallata
74
Nereis pelagica
Nereis zonata
76
Neanthes biseriata
Neanthes vaalii
80
Imajimainereis pacifica
Neanthes flindersi
86
Composetia scotiae
Paraleonnates bolus
90
Eunereis paitillae
Olganereis edmondsi
2
94
Ceratonereis mirabilis
96
98
Ceratonereis perkinsi
82
95
Solomonereis marauensis
96
Solomonereis phuketensis

Fig. 6

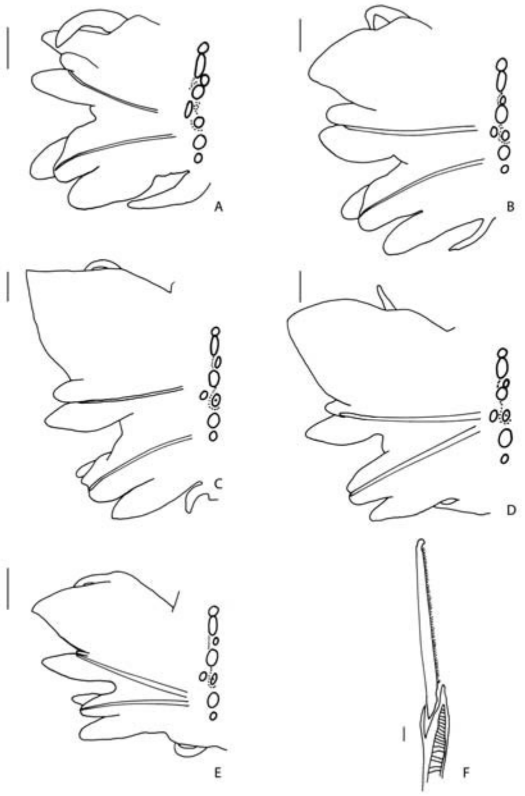

Fig. 7

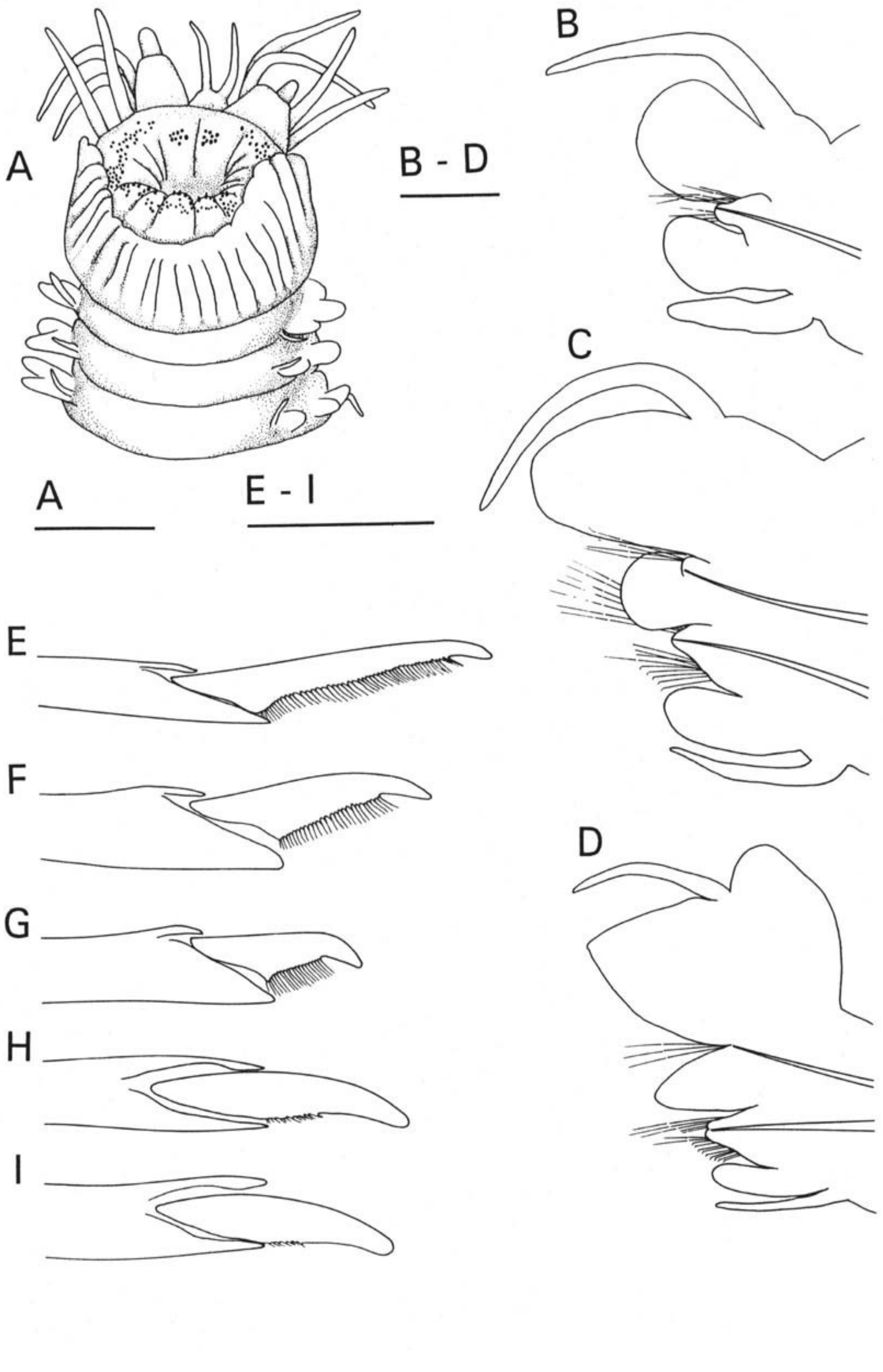

Fig. 8

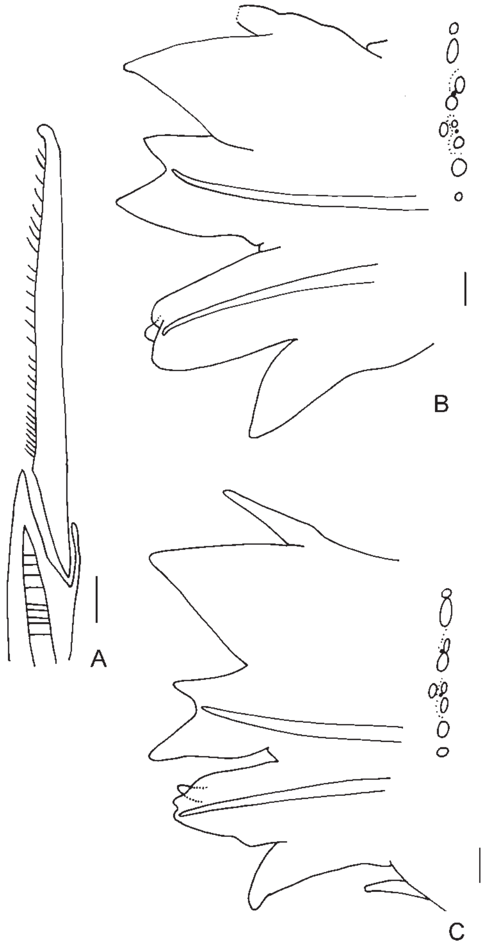

Fig. 9

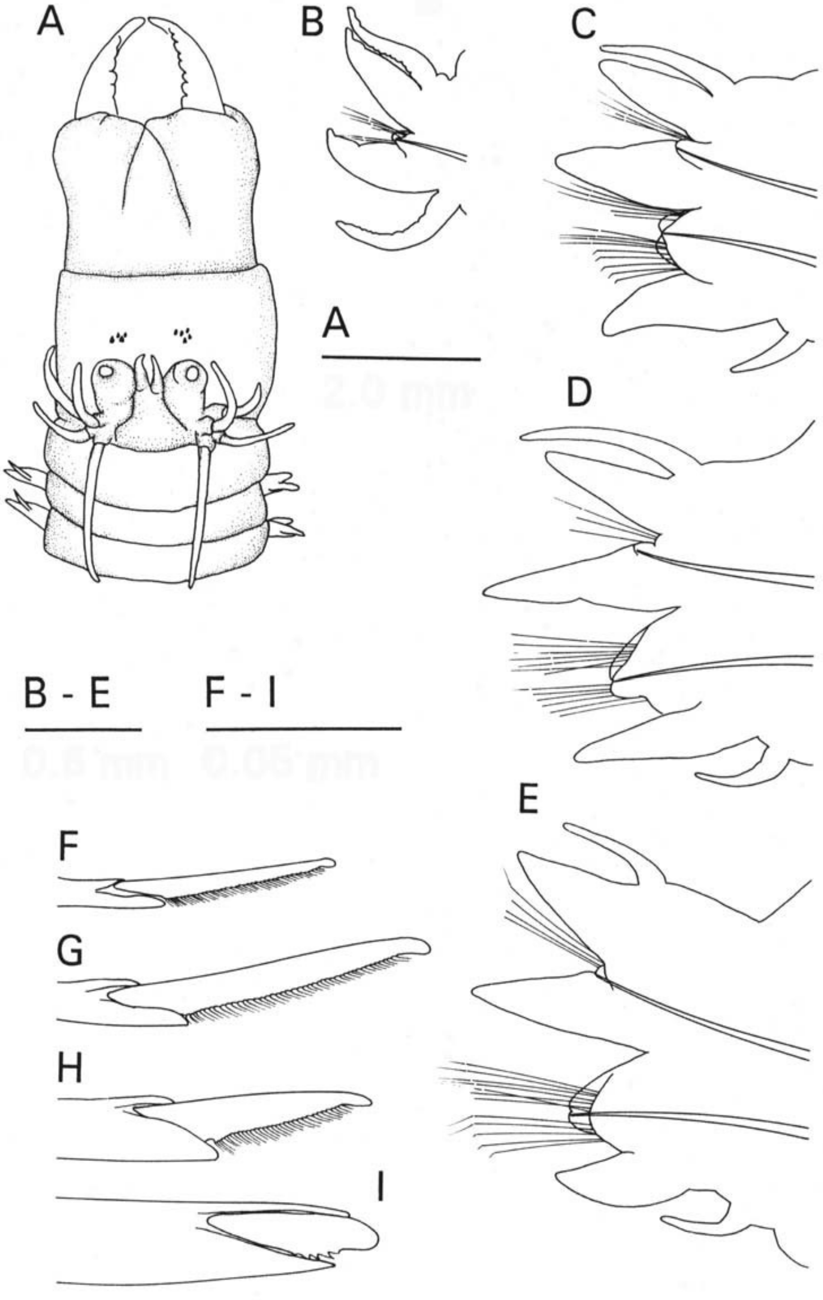

Fig. 10

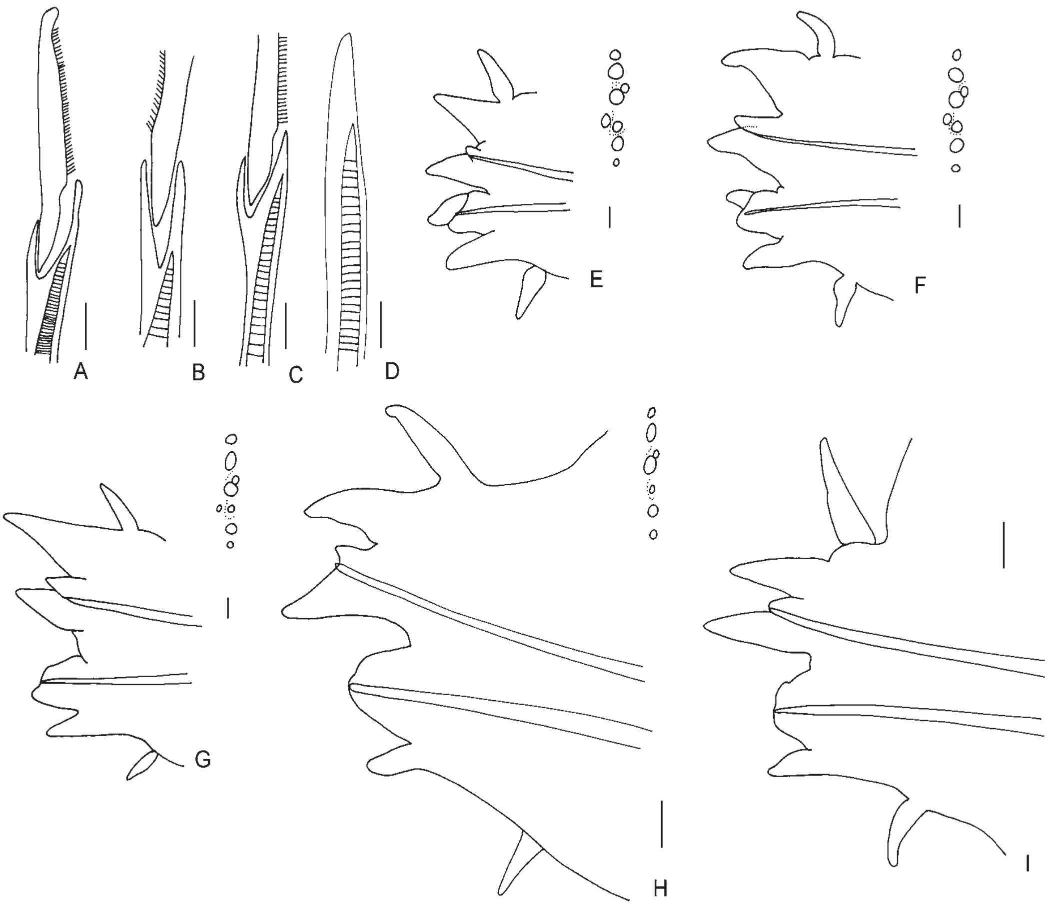

Fig. 11

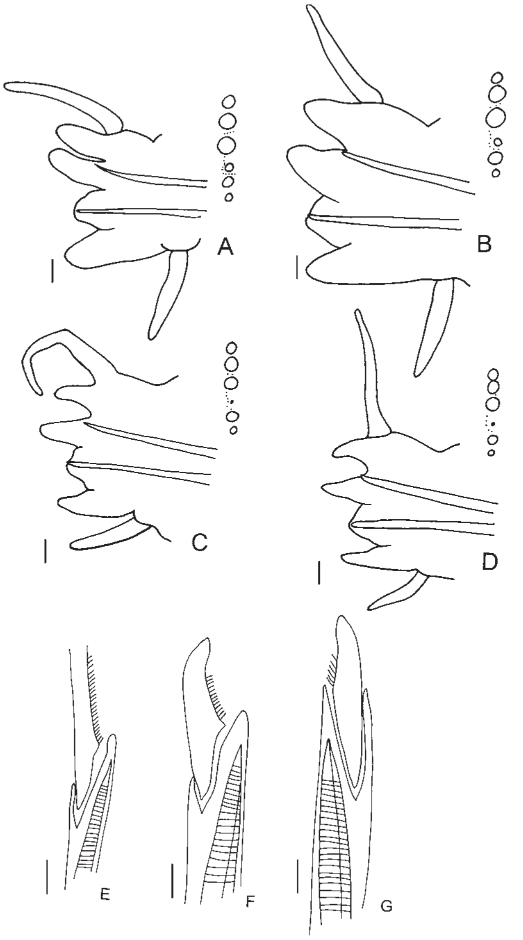

Fig. 12

Paper IV

Bakken, T. Revision of *Pseudonereis* (Polychaeta, Nereididae) based on type material.
Manuscript.

Revision of *Pseudonereis* (Polychaeta, Nereididae) based on type material

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Running head: Revision of *Pseudonereis*

Abstract

A taxonomic revision of *Pseudonereis* (Polychaeta, Nereididae) shows that some of the taxa are very similar in most morphological characteristics. Of 11 taxa belonging to *Pseudonereis* 10 are included and redescribed based on type material. Cladistic analysis using parsimony methods verify previous results that *Pseudonereis* is a monophyletic group defined by the presence of paragnaths in closely shaped comb-like rows on the maxillary ring on the pharynx. Results form the parsimony analyses placed taxa from the ingroup in two major clades, the majority in an unresolved clade defined by two synapomorphies, presence of terminally attached dorsal cirri on notopodial ligules in posterior chaetigers and shield-shaped paragnaths in Area VI, the latter character being described as different from the bars-shaped paragnaths in Area VI. *Pseudonereis anomala* is placed in the second major clade with *P. multisetosa* a taxon showing aberrant characteristics. This clade is defined by presence of notopodial homogomph falcigers and conical paragnaths in Area VI. The widely geographically distributed *P. gallapagensis* and *P. variegata* show striking morphological resemblance to less well known taxa with similar distribution. *P. rottnestiana* is removed from synonymy. Paragnath variation in populations of *P. anomala* is discussed relating to geographical distribution, and a brief discussion of the biogeography of taxa included is given. *Pseudonereis trimaculata* is recorded from Australia for the first time.

Keywords: Nereididae - *Pseudonereis* - taxonomy - systematics, biogeography - Polychaeta

Introduction

Kinberg (1865) described the new genus *Pseudonereis* including two species from Galapagos and Hawaii, *P. gallapagenis* and *P. formosa* respectively, characterised 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 recognised as unique by Gravier who described the next taxon in this group (*P. anomala* Gravier, 1901), and Ehlers (1901) who gave a detailed account of South American material of *Nereis variegata* Grube, 1857 including synonymies of a number of taxa. Other records briefly mentioned *P. anomala* (Willey 1904; Fauvel 1911), until two other taxa were described, *P. rottnestiana* Augener, 1913 from Western Australia and *P. atopodon* Chamberlin, 1919 from the Tonga Islands in the Pacific, both drawing attention to similarities to *P. gallapagensis*. Later Fauvel (1932) included previously described *P. masalacensis* (Grube, 1878) and placed this as well as *P. variegata* as synonymies to *P. gallapagensis* also including *Nereis ferox* Hansen, 1882 and *Paranereis elegans* Kinberg, 1865, in accordance with Ehlers (1901). Hansen (1882) had described several new species from Brazilian material he got the opportunity to examine, but did not find any similarities to existing taxa from South America although he referred to works by Kinberg and Grube, neither did he give any justifications in his descriptions nor compared them to 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 synonymised many of those Hansen (1882) described with *P. variegata*.

Several taxa recognised here included in *Pseudonereis* has originally been assigned to *Neanthes*, and have in the original description often been compared to other *Neanthes* taxa with similar expanded dorsal notopodial ligule in posterior chaetigers. Paragnath pattern and especially the clearly recognisable 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 utilising different sets of characters in nereidid morphology may be a reason for this. Initiated by Kinberg (1865) the use of paragnath types, form and number have been widely used, while some authors followed Malmgren's (1867) scheme of parapodial characters and in large based their descriptions and comparisons of taxa on parapodial morphology. Over the last decades a combination of paragnath and parapodial characters has proved to be a necessity.

Recently Bakken & Wilson (ms) proved *Pseudonereis* to be a monophyletic group (Figure 1) defined by presence of paragnaths in Areas II-IV arranged in regular comb-like rows (Figure 2A) and dorsal cirrus terminally attached to dorsal notopodial ligule in posterior chaetigers. The results of the phylogenetic analyses (Bakken & Wilson ms) showed that some taxa should be transferred to *Pseudonereis* from *Neanthes*. Their results did also show that characters in Nereididae in general are homoplasious, suggesting more detailed studies are necessary over a wide range of taxa within Nereididae to answer questions about character homology and to define monophyletic groups. Proved to be a monophyletic clade *Pseudonereis* was such a candidate. Examination of specimens of *P. anomala* and *P. gallapagensis* lead to examination of type material of most taxa assigned to *Pseudonereis* and showed a review was necessary.

Parsimony analyses were set up to verify the monophyly of the group where all taxa were included. The main aim of this study is to revise described taxa in *Pseudonereis* based on examination of type material. As there are several closely related taxa being morphological very similar it was necessary to redescribe this material to draw attention to their morphology in detail, providing a tool for identification when more material is available The cladistic analysis is not intended to give further answers on the phylogenetic position of *Pseudonereis* in Nereidinae, as it was shown by Bakken & Wilson (ms) that this warrant further analyses over a broad range of taxa.

All taxa included in *Pseudonereis* today that it was possible to get study material of are redescribed based on type material. For this reason one taxon, *P. masalacensis* Grube was not included as the type material is in poor condition (Hutchings & Glasby 1985). *Pseudonereis rottnestiana* was not included in the phylogenetic analyses as the syntype examined turned out to give too many question marks in the data matrix, a redescription is however included below.

Material and Methods

In illustrations of specimens end-view drawings of parapodia are included based on the scheme by Hylleberg et al. (1986: Figure 1A). Measurements of body with 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 2032x1536 - fine.

The following abbreviations for museums and institutions are used: AM (Australian Museum, Sydney, Australia), ZMA (Zoological Museum Amsterdam), 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).

Characters

Characters are described in detail by Bakken & Wilson (ms). A consequence of examination of type material in this study warranted further notes, which are described below. A list of characters used is given in Table 1. Taxa and material used as outgroups are described in Bakken & Wilson (ms). Material used for ingroup taxa are solely examined material and is listed under each taxon in the “Taxonomy” section.

Paragnaths

Smooth bar-shaped paragnaths in Area VI have been a diagnostic feature of taxa in *Perinereis*, and the numbers of bars in Area VI has been used, among parapodial features, to assign informal subgroups based on morphological characteristics within *Perinereis* (Hutchings et al. 1991). Taxa in *Pseudonereis* have also been identified by this character, which was already recognised by Kinberg (1865). Based on examination of type material in this study it is evident that most *Pseudonereis* taxa possess a different bar-shaped paragnath in VI than do most *Perinereis* taxa. In *Pseudonereis* taxa it appears like a laterally flattened and high bar, often with a pointed tip skewed over to one end (but not always). This paragnath show resemblance to a shield projecting out from the soft tissue (Figure 16C), rather than the smooth low bar usually observed in most taxa in *Perinereis*. The character is recorded for all taxa described here but may be inadequately know and in some cases there are variation over specimens whether the shield-shaped bar have a pointed tip or not (see description of *P. cortezi*). All included taxa with bar-shaped paragnaths in Area VI all, except *P. anomala*, *P. multisetosa* and *P. rottnestiana* which have cones in VI and *P. plapata* which have both cones and a bar, possess the shield-shaped paragnath. This character is not used in the character (Table 1) set and data matrix (Table 2) at this point. A thorough evaluation should be done for *Perinereis* taxa to prove if this character is unique to *Pseudonereis* or if it is shared between the groups, if unique to *Pseudonereis* it will enforce the monophyly of the taxon.

Paragnaths in most Areas on the pharynx are usually conical in most nereidine taxa (Bakken & Wilson ms). A bar-shaped paragnath with a pointed tip skewed over to one end, here called a p-bar (pointed bar) (Figure 2B), is also often observed in several taxa especially in Area IV next to the jaws in a position smooth bar-shaped paragnaths have been observed in taxa from *Neanthes*, *Perinereis* and *Nereis* (Wilson 1984; Hutching et al 1991; Bakken & Wilson ms), and in Area VII-VIII interspersed with smaller conical paragnaths (Figure 16B).

Parapodia

Detailed drawings of parapodia show a large diversity in different characters in nereidids. Hylleberg et al. (1986) and Hylleberg & Nateewathana (1988) highlighted this by reintroducing end-view drawings of parapodia. Their schemes and parapodial terminology have proved to be valuable and have been widely used since, with minor updates (Hutchings & Reid 1990; Glasby 1999; Bakken 2002; Wilson et al. 2003). Wilson et al. (2003) did not implement a neuropodial superior lobe in their character set, neither did Bakken & Wilson (ms) mainly due to lack of information of this character across taxa. This character is used here and included in the analyses (Table 1). Although shown to be a common feature in *Pseudonereis* taxa it is not unique, it is known to be present in e.g. *Composetia scotiae* and *Alitta virens* (Bakken & Wilson ms), although it was not described specifically. When present in *Pseudonereis* taxa it is present throughout the body, but this would have to be carefully described for each taxon when included in descriptions.

The neuropodial superior lobe is placed next to and superior the inferior lobe with the acicula in between the two (Hylleberg et al. 1988: Fig. 1A.). The two combined constitutes the acicular ligule often used as a term in descriptions and used to compare the length of the neuropodial ventral ligule and ventral cirrus.

In neuropodia a postchaetal lobe is present in many taxa among nereidids. As described in Bakken & Wilson (ms) it may take different shape and extension, and is usually either restricted to a number of anterior chaetigers or present throughout. In some taxa studied here the neuropodial postchaetal lobe appear somewhat differently than previously reported. If present it is present throughout but only clearly visible and drawn out to a triangular pointed tip in posterior chaetigers, while it in anterior and mid-body chaetigers may look like a ridge behind the acicular ligule and would not been described as a lobe. In material examined this variation is evident in smaller specimens with a body width less than 1 mm. A lobe is a distinctive protrusion, in this case from behind the acicular ligule. The posterior postchaetal lobe is here included in the character list (Table 1).

Fauchald (1977) made a note on the length of the terminally attached dorsal cirrus as a part of the total length of the dorsal notopodial lobe when he compared *P. pseudonoodti* with *P. noodti*. This feature is not used here, but may be a valuable character as long as a quantity of material of each taxon is available. The only problem, as commented below, is that this might be difficult to se either due to preservation or that it may be variable over specimens.

Phylogenetic analyses

Selection of taxa

For the phylogenetic analyses 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 below) and *P. rottnestiana* which was excluded from the parsimony analysis due to lack of information for a range of chaetae characters (see description below).

Bakken & Wilson (ms) in their analyses of nereidids with paragnaths found *Pseudonereis* to be monophyletic with a clade with *Perinereis* spp. and *Cheilonereis cyclurus* as sister group, this whole clade being sister group to a clade including three *Nereis taxa*: *N. cockburnensis*, *N. bifida*, and *N. maxillodentata* (Figure 1). A representative from each of these clades, *P. akuna* and *N. bifida* were selected as outgroups, in addition to a more distantly related taxon *Platynereis antipoda*. Scoring of outgroups (Table 2) are from Bakken & Wilson (ms).

Analyses

A data matrix was exported as a nexus file from a DELTA database (Dalwitz et al. 1993 onwards); of Nereididae (Wilson et al. 2003) and was edited using the Nexus Data Editor for Windows 0.5.0 (Page 2001). The nereidid DELTA database was also used to generate descriptions of taxa and to explore similarities and differences between sets of taxa (Wilson et al. 2003). A data matrix of 13 taxa by 87 characters resulted (Table 2). In both the character list (Table 1) and the data matrix (Table 2) all characters are listed for comparison with the data matrix used by Bakken & Wilson (ms), but constant characters were excluded in the analyses in PAUP* (the *exclude constant* command). Parsimony analyses were run in PAUP* 4.0b10 (Swofford 2001) using default settings for heuristic searches, a bootstrap analyses was performed with 1000 replicates. Trees from results in PAUP* were examined using the Mesquite: System for Evolutionary Analyses version 1.0 (Maddison & Maddison 2003).

In the parsimony analyses all constant characters, 47 in total, were excluded from the data matrix, 20 characters were parsimony informative, and the remaining 20 parsimony uninformative. The analysis resulted in a single most parsimonious tree 53 steps long, CI = 0.7547 and RI = 0.7347, resolved with a monophyletic ingroup with strong bootstrap support (89%) (Figure 3). Within the ingroup there are two clades, one with *P. anomala* and *P. multisetosa* in a clade with good support (86%) being sister group to the remaining taxa (Figure 3). Of the remaining taxa two, *P. cortezi* and *P. palpata* are outside an unresolved polytomy including the remaining taxa, the latter group having bootstrap support although week (59%).

The monophyly of *Pseudonereis* clade demonstrated by Bakken & Wilson (ms) is confirmed, now including more taxa in the ingroup than they had (Figure 3). This clade shows strong bootstrap support (89%) and is unequivocally supported by the presences of paragnaths in Areas II-IV arranged in regular closely spaced comb-like rows (character 11), dorsal notopodial ligule markedly broader on posterior chaetigers (39), presence of Type 2 heterogomph falcigers in ventral neuropodial fascicle (85), absence of Type 1 heterogomph falcigers in ventral neuropodial fascicle (84), and presence of neuropodial superior lobe, the latter with a reversal in *P. pseudonoodti* which lack this character. Presence of paragnaths in Areas II-IV arranged in regular closely spaced comb-like rows is a unique character for *Pseudonereis*. Although shown unequivocal support here the other characters mentioned are known to occur in other taxa in Nereidinae. A broad dorsal notopodial ligule is e.g. found in *Alitta* spp. and *Cheilonereis* spp., neuropodial chaetae Type 1 and 2 falcigers are homoplasious within Nereidinae (Bakken & Wilson ms). Presence of a neuropodial superior lobe is also known to occur in other taxa, as mentioned above. The clade including *P. anomala* and *P. multisetosa* show bootstrap support (86%) and is unequivocally supported by presence of notopodial homogomph falcigers multidentate with two or more small lateral teeth (66), but this character is known to occur in some *Nereis* taxa, not included here. Presence of a homogomph falciger in the neuropodial dorsal fascicle is here an autapomorphic character for *P. multisetosa*. In the analyses demonstrating monophyly for *Pseudonereis* (Bakken & Wilson ms) *P. anomala* was scored for presence of terminally attached dorsal cirrus on posterior dorsal notopodial ligule, which is changed here so that this taxon is scored as dorsal cirrus attached in a subterminal position based on information from material examined. As a consequence *P. anomala* is here positioned in a clade with *P. multisetosa*, which share this character with the outgroup clade including *P. antipoda* and *P. akuna*.

A more inclusive clade within *Pseudonereis* includes *P. palpata* and *P. cortezi*, and the remaining taxa in an unresolved clade. The whole clade show bootstrap support (63%) and is unequivocally supported buy the presence of dorsal cirrus terminally attached to dorsal notopodial ligule on posterior chaetigers (48), and presence of one smooth bar-shaped paragnath in Area VI (28). Bar-shaped paragnaths in Area VI are also known to occur in *Perinereis* taxa, but the type present in all taxa included in the *Pseudonereis* clade is different as discussed above, and enforces the presence of this character as unique to this clade, see above for further comments on the shield-shaped bar in Area VI. The least inclusive clade is a polytomy with the remaining taxa, which are all morphologically very similar as discussed below. This clade has bootstrap support (59%), and is supported by neuropodial postchaetal lobe low (52) and flattened (56), both characters shared by the *P. anomala* - *P. multisetosa* clade. An apomorphy list showing character changes is given in Table 3.

Taxonomy

***Pseudonereis* Kinberg, 1865**

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

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

Description. Frontal antennae present, 1 pair, cirriform; palpophore with transverse groove present, palpostyles conical. Prostomium with entire anterior margin. Eyes present, 2 pairs. One apodous anterior segment, greater than length of chaetiger 1. Tentacular cirri with distinct cirrophores. Ventral peristomial flap absent. Jaws with dentate cutting edge. Maxillary ring of pharynx without papillae. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, Areas II, III and IV arranged in regular comb-like rows. Paragnaths: Area I conical paragnaths present, minute rod-like paragnaths in a compact cluster absent; Area II conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, absent; Area III conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, pectinate paragnaths absent; Area IV conical paragnaths present, minute rod-like paragnaths in a compact cluster absent, bar-like paragnaths (p-bars) present or absent, pectinate paragnaths absent. Oral ring papillae absent. Oral ring paragnaths present, Area V and VI present as distinct groups. Area V conical paragnaths present or absent; VI cones present or absent, shield-shaped bars present or absent; VII-VIII conical paragnaths present, pectinate paragnaths absent, paragnaths arranged in one or more irregular lines forming a continuous band, VII-VIII paragnaths similar in size, or irregular mix of large and small paragnaths in a single band. Transverse dorsal lamellae absent. Ventrum of anterior chaetigers smooth.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present. Markedly elongate on posterior chaetigers (not in *P. multisetosa*). Markedly broader on posterior chaetigers. Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, sub-terminally or terminally attached to dorsal notopodial ligule on posterior chaetigers, not terminally attached throughout all chaetigers. Dorsal cirri single. Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe absent or present. Ventral neuropodial ligule of anterior chaetigers present. Ventral cirri single.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, sesquigomph spinigers absent, sesquigomph falcigers absent, homogomph falcigers present or absent. Neurochaetae, dorsal fascicle: heterogomph spinigers present or absent, homogomph spinigers present or absent, sesquigomph spinigers absent, sesquigomph falcigers absent, fused falcigers absent, homogomph falcigers absent (present in *P. multisetosa*). Neurochaetae, ventral fascicle: sesquigomph falcigers absent, heterogomph spinigers present, homogomph spinigers absent, sesquigomph spinigers absent, heterogomph falcigers present, homogomph falcigers absent. Blade of ventral fascicle heterogomph falcigers lacking distinct tendon on terminal tooth.

Remarks. Bakken & Wilson (ms) recently redefined the genus based on phylogenetic analyses of the subfamily Nereidinae. In the description above minor changes are included. Position of the dorsal cirrus in *P. anomala* was coded as terminally attached in their analyses, based on information from types and additional material examined this was changed in the description of the taxon presented here to a sub-terminal position. In *P. miltusetosa* the dorsal notopodial ligule is clearly not elongated in posterior chaetigers, a character that should be verified in more material for taxon.

Presence of conical paragnaths arranged in regular comb-like rows in Areas II-IV (Figure 2A) is a unique character in *Pseudonereis* taxa. Dorsal cirrus terminally attached on dorsal notopodial ligule is a synapomorphic character in a more inclusive group of nested taxa in *Pseudonereis* excluding *P. anomala* and *P. multisetiosa* (Figure 3). *Pseudonereis rottestiana*, which was not included in the analyses, also belongs in this group being very similar to *P. anomala*. Another character also shared by the more inclusive group is presence of a shield-shaped paragnath in Area VI, except *P. palpata* that possess both a shield-shaped (or bar-shaped) and conical paragnaths in Area VI. The cladogram from the parsimony analyses (Figure 3) shows a polytomy including taxa that are morphologically very similar. In this study information is based on few specimens only from all taxa in this group, indicating that variation over a larger number of specimens may change taxon discrimination. A comparison table for all taxa are presented in Table 4.

Pseudonereis anomala Gravier, 1901 (Figure 4, 5)

Pseudonereis anomala Gravier, 1901.– Hutchings & Turvey 1982: 141-142.– Hutchings & Glasby 1985: 108-109.– Hylleberg et al. 1986: 13-14, fig. 7.

Nereis nichollsi Kott, 1951: 93-95, fig. 2a-k.

Pseudonereis rottnestiana forma *seriodentata* Hartmann-Schröder 1979: 118-119, figs. 216-219.– 1980: 61.

Material examined. Syntypes, 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 (13); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 1979-03-04, coll. Hutchings & Butler, AM W18310 (98); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 1979-03-04, coll. P. Hutchings W18311 (47); Cape de Couedic, Kangaroo Island, SA, algal holdfast, exposed reef, 1979–03–04, coll. P. Hutchings AM W18312 (6); Mastan Pt. America River, Kangaroo Island, clumps of sponge in fast flowing channel, 1979-03-02, coll. P. Hutchings , AM W18313 (1); Pelsart Group, H. Abrolhos Islands, WA, rock wastings of reef, 1947-09-01, coll. P. Kott, AM W18574 (1); Plantation Point, NSW, 1981-06-27, AM W25645 (12); North West Solitary Island, coralline algae, 1992-06-25, coll. P.B. Berents, AM W25646 (1). Broome, probe 6, 1975-09-09, coll. G. Hartmann-Schröder (5) ZMH P-16564; Port Hedland, probe 34, 1975-09-30, coll. G. Hartmann-Schröder (1), ZMH P-16565.Size range of material examined 48-86 chaetigers (23-70 incomplete specimens), 10-46 mm long (11-34 incomplete specimens), 1-3.5 mm wide.

Description. Frontal antennae present, 1 pair, cirriform. 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, III and IV arranged in regular comb-like rows. Area I = 1-3 conical paragnaths (4 in two specimens, n=39); Area II = 11-29 conical paragnaths in 3-4 rows; Area III = 30-72 conical paragnaths in 4 rows; Area IV = 20-52 conical paragnaths including 4 rows and additional cones towards the jaws, bar-like paragnaths present or absent. Area V and VI present as distinct groups. Area V paragnaths absent; VI = 3-15 conical paragnaths, smooth bars absent; VII-VIII = 10-19 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 at least one distinct ligule or lobe. Dorsal notopodial ligule present, rounded, as long as ventral notopodial ligule on anterior (Figure 5A) and mid-body chaetigers (Figure 5B), markedly elongate on posterior chaetigers, markedly broader on posterior chaetigers (Figure 5C-D). Prechaetal notopodial lobe absent; acicular process absent. Dorsal cirrus basally attached to dorsal notopodial ligule in anterior chaetigers (Figure 5A-B), sub-terminally attached on posterior chaetigers (Figure 5D); not terminally attached to dorsal notopodial ligule on posterior chaetigers. Dorsal cirrus simple, lacking basal cirrophore, 3–4 times as long as ventral notopodial ligule at chaetigers 10–20 (Figure 5B). 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 rounded flattened 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 0.5 times as long as acicular ligule.

Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers (Figure 5F) and falcigers present, falcigers first present from about chaetiger 30, homogomph falcigers multidentate, with 2 or more small lateral teeth (Figure 4B, Figure 5H), first and subsequent lateral teeth much smaller than terminal tooth. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present, one or two heterogomph spinigers present from about chaetiger 40–50, homogomph spinigers absent, heterogomph falcigers present, heterogomph falcigers of Type 2 in anterior and posterior chaetigers present (Figure 4A, Figure 5G), homogomph falcigers absent.

Anal cirri, cirriform reaching back 8–10 chaetigers. Epitokal modification observed in two specimens (MNHN Poly Type-421), both females filled with large eggs, parapodial modification (Figure 5E) from chaetiger 18.

Remarks. The digitiform tip of the dorsal notopodial ligule in posterior chaetigers making the dorsal cirrus attached in a sub-terminal position is very clear in all material examined. This is different from the other taxa in the genus, except *P. rottnestiana* and *P. multisetosa,* which have the dorsal cirrus in a terminal position. This is changed from what was described in Bakken & Wilson (ms) 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 with body width less than 1 mm.

Pseudonereis anomala differs from other *Pseudonereis* taxa by the presence of notopodial homogomph falcigers and presence of conical paragnaths in Area VI. These characters are also attributed to *P. multisetosa* and *P. rottnestiana*. It can be distinguished from *P. multisetosa* in that the latter possess homogomph falcigers in dorsal fascicle of neuropodia, and from *P. rottnestiana* by having a finger-like tip on the posterior dorsal notopodial ligules placing the dorsal cirrus in a sub-terminal position. The difference between *P. anomala* and *P. rottnestiana* that *P. rottnestiana* lack notopodial homogomph falcigers (Fauvel 1932; Hartman 1954) are not used here as no complete notopodial chaetae were observed in the type of *P. rottnestiana*.

Hutchings & Turvey (1982) examined the holotype and most paratypes of *Nereis nichollsi* Kott, 1951 and found it to be synonymous with *P. anomala*. Hutchings & Glasby (1985) discussed the number of conical paragnaths in Area VI and how they are arranged in one or two rows in an arc. Some specimens of the same material previously reported from Australia (Hutchings & Turvey 1982; Hutchings & Glasby 1985) were re-examined here. Although the quantity of specimens examined is low it seem that paragnath numbers are consistent within populations but may show minor variations between populations (Table 5). 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's (1979) material of what she described as "*Pseudonereis rottnestiana* forma *seriodentata*" confirms well with the material examined of *P. anomala*. See discussion for *P. rottnestiana* for further details.

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 et al. 1985). The depth distribution is intertidal and in low water.

Pseudonereis atopodon **Chamberlin, 1919 (Figure 6)**

Pseudonereis atopodon Chamberlin, 1919: 228-229, pl. 35, fig. 3-5.

Material examined. Holotype, Nomuka, Tonga Island, 1899-02-12, intertidal, USNM 19467; paratypes, Nomuka, Tonga Island, 1899-02-12, intertidal, USNM 19468 (2). Size range of material examined 87-92 chaetigers, 35-44 mm long, 1 mm wide.

Description. Frontal antennae present, 1 pair, cirriform. 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, platelike with 4 teeth. Maxillary ring of pharynx with paragnaths arranged in discrete areas, Areas II, III and IV arranged in regular comb-like rows. Area I = 1; Area II = 37-49 conical paragnaths in 5 rows; Area III = 56 conical paragnaths in 5 rows; Area IV = in 4-5 rows, cones towards jaws (impossible to see details due to small size or broken), smooth bar-like paragnaths not observed. Area V and VI present as distinct groups. Area V = 0-1 conical paragnaths, when present a large cone; Area VI = 1 a large bar-shaped paragnath flattened with a pointed tip (triangular), cones absent; Area VII-VIII = 14-24 paragnaths with an appearance like p-bars, similar in size.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, short rounded as long as ventral notopodial ligule in anterior chaetigers (Figure 6A), markedly elongate and markedly broader on posterior chaetigers (Figure 6D). 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 (Figure 6B), basally attached to dorsal notopodial ligule in anterior and mid-body chaetigers, terminally attached to dorsal notopodial ligule on posterior chaetigers (Figure 6D), commencing at about chaetiger 60-65.

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe present; neuropodial postchaetal lobe present throughout (Figure 6C), 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.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, heterogomph falcigers present throughout, blades serrated, homogomph falcigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 30, homogomph spinigers absent, heterogomph falcigers present Type 2 throughout (Figure 6E-F), homogomph falcigers absent.

Anal cirri cirriform, reaching back 4–5 chaetigers.

Remarks. The neuropodial postchaetal ligule was observed as most prominent in mid-body chaetigers (Figure 6C)), but the appearance of this character should be re-evaluated when more material is available. *P. 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 ligule being up to 0.5 times as long as neuropodial acicular ligule in *P. atopodon*, compared to as long as acicular ligule in *P. gallapagensis*. It 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*.

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 e.g. paragnath numbers are small and might just as well be overlapping when more material is included. Of the three specimens examined it was possible in only one to count paragnath numbers for Area III, and none for Area IV, a weakness in the description given above.

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

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

***Pseudonereis cortezi* (Kudenov, 1979) (Figure 7, 8)**

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, Oct 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, cirriform. 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, III and IV arranged in regular comb-like rows. Area I = 4-6 conical paragnaths in longitudinal rows; Area II = 17-31 conical paragnaths in 4-5 rows in a triangular patch; Area III = 33-54 conical paragnaths in 5 rows; Area IV = 31-55 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 (Figure 7A); Area VI = 1 large high and laterally flattened triangular 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 (Figure 7B).

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, short and rounded as long as ventral notopodial ligule in anterior chaetigers (Figure 8A-B), markedly elongate and markedly broader on posterior chaetigers, starting from about chaetiger 50-55 (Figure 8E-F). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2.5 times ventral notopodial ligule at chaetiger 10–20 (Figure 8B), basally attached to dorsal notopodial ligule in anterior chaetigers, sub-terminally attached from about chaetiger 35-40 (Figure 8D), terminally attached from about chaetiger 50-55.

Neuropodial inferior lobe poorly developed; a superior lobe present as a bilobed part of the acicular ligule (Figure 8C), 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 (Figure 8F) in the last about 40 chaetigers.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, heterogomph falcigers present (Figure 8G) throughout, blades serrated, homogomph falcigers absent. Neurochaetae, ventral fascicle: a single heterogomph spiniger present from chaetiger 5–10, homogomph spinigers absent, heterogomph falcigers Type 2 present throughout, homogomph falcigers absent.

Pygidium multi-incised ventral incision, anal cirri cirriform reaching back 3-4 chaetigers. Pigmentation pattern observed in most specimens as the part of the palps and the prostomium pigmented dark brown, except for a small lance shaped patch in the centre (Figure 7A; Kudenov 1979: Fig. 2a).

Remarks. The original description (Kudenov 1979) included presence of a single conical paragnath in Area VI. This is however a typical large laterally flattened, high and triangular bar as in most other *Pseudonereis* species, in some specimens this bar comes with a distinct point skewed towards one side, a p-bar. In Area III the conical paragnaths are more spaced (Figure 7B) as is usual in other species with comb-shaped rows, although still tight rows, in II and IV the closely comb-shaped row appear as commonly observed in *Pseudonereis*. It is very difficult to see in the specimens examined where the notopodial dorsal ligule ends and where the dorsal cirrus starts, or how these are attached together, 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 usually come to 1/4-1/6 the length of the ligule. In this taxon it looks like the dorsal cirrus comes to a major part of the dorsal ligule. This question must be left unanswered until more material, preferably fresh, 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) (Figure 7A) while the other taxa have 0-3. It most closely resembles *P. pseudonoodti* by the two characters mentioned but can be distinguished from it by the presence of a neuropodial superior lobe in anterior and mid-body chaetigers.

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

Pseudonereis gallapagensis **Kinberg, 1865 (Figure 9)**

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); Chincha Island, Peru, Eugenie Exp. 1851-53, stn 531, SMNH 37897 (1); Chincha 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, cirriform. 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, III and IV arranged in regular comb-like rows. Area I = 1 conical paragnath; Area II = 17-20 conical in four rows; Area III = 51-68 conical paragnaths in 4 rows; Area IV = 38-57 including conical 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 flattened bar present, cones absent; Area VII-VIII = 17-20 in two rows, anterior row with cones, posterior with p-bars, forming a band of paragnaths.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present short and rounded (Figure 9A-B) markedly elongate and markedly broader on posterior chaetigers (Figure 9C-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 (Figure 9B), 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 anteriormost chaetigers only, a small superior lobe present (Figure 9A-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.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, heterogomph falcigers on anterior chaetigers present (Figure 9F), on posterior chaetigers present, blades serrated, homogomph falcigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers, usually a single, present in posterior chaetigers, homogomph spinigers absent, heterogomph falcigers Type 2 present of anterior and posterior chaetigers present, homogomph falcigers absent.

Pygidium multi-incised, ventral incision, cirri cirriform, reaching back 4–5 chaetigers (observed in one specimen).

Remarks. The description given above is made from a combination of 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 (Figure 9). 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 bit deformed due to this. 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 is observed in ventral fascicle in mid-body and posterior chaetigers, heterogomph spinigers was not observed in the type specimen of *P. formosa*. Otherwise these specimens are in well accordance to each other. 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-examining 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* and has been assigned a new registration number (SMNH Type-5908).

It is not possible to see any differences in the material examined from Galapagos, Hawaii, Peru and Chile listed above, but the material is not in very good condition. Hartman (1949) concluded that the specimens identified as *Neanthes variegata* by Kinberg (1865) (SMNH 37897, SMNH 37898) belonged to *P. gallapagensis* to which must be agreed. It should be remarked that the material is in poor condition.

Pseudonereis gallapagensis is most similar to *P. variegata* and *P. atopodon*. It 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 to 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 as a difference, which is demonstrated in the material examined. 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. From *P. atopodon P. gallapagensis* can be distinguished by ventral neuropodial ligule as long as acicular ligule in anterior chaetigers compared to up to half as long as in *P. atopodon*, and having fewer paragnaths in Area II than *P. atopodon* (Table 4).

Hartman (1949: 69) treated *Neanthes variegata* as described by Kinberg, and after examination of these specimens she referred them to *P. variegata* (Grube, 1857), which she 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. Type locality Indifatigable Island, Galapagos, South America, Pacific coast.

***Pseudonereis masalacensis* (Grube, 1878)**

Remarks. Hutchings & Glasby (1985) examined the type material and found it to be in too poor condition that it was possible to make a redescription. They suggested this taxon should be regarded indeterminable until material could be obtained from the type locality, especially due to lack of complete chaetae. Type locality is Masolac, Philippines.

***Pseudonereis multisetosa* Hartmann-Schröder, 1992 (Figure 10)**

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

Material examined. Holotype, Rangiroa, French Polynesia, sample 9, 1982-09-11, ZMH P-20706 (1). Size range of material examined 67 chaetigers, 10 mm long, 0.7 mm wide.

Description. Frontal antennae present, 1 pair, cirriform. 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, III and 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, smooth bars absent; VII-VIII = 8 conical paragnaths in a single row, present only as a ventral band.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, rounded, shorter than ventral notopodial ligule in anterior 10-12 chaetigers (Figure 10A), as long as posteriorly, not markedly elongate on posterior chaetigers, markedly broader on last about 10 posterior chaetigers (Figure 10D). Not markedly reduced on posterior chaetigers. Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus Simple, lacking basal cirrophore but basis somewhat inflated anteriorly (Figure 10A), 3-4 times ventral notopodial ligule at chaetigers 10–20 (Figure 10B), basally attached to dorsal notopodial ligule on anterior and mid-body chaetigers, sub-terminally attached on posterior chaetigers (Figure 10D).

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe present throughout (Figure 10C). Neuropodial postchaetal lobe present throughout, a low rounded lobe, projecting level with end of acicular ligule. Ventral neuropodial ligule of 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.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent; homogomph spinigers present, in mid-body chaetigers (about 20-40) with short very pointed blades and very broad proximally (Figure 10H); notopodial homogomph falcigers present (in posterior chaetigers), first present in chaetiger 40–50; notopodial homogomph falcigers multidentate, with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth; notopodial homogomph spinigers replaced by homogomph falcigers in posterior chaetigers. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, heterogomph falcigers on anterior chaetigers present(Figure 10F), on posterior chaetigers present, blades serrated, homogomph falcigers (Figure 10E) on anterior chaetigers present to about chaetiger 15, on posterior chaetigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers present; homogomph spinigers absent; heterogomph falcigers Type 2 present throughout (Figure 10G), homogomph falcigers absent.

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

Remarks. This taxon is known from a single specimen only (Hartmann-Schröder 1992), the holotype being in good condition. Paragnath numbers presented here are different from those in the original description, which stated that the pharynx was not dissected.

Pseudonereis multisetosa is different from all other *Pseudonereis* taxa by the presence of a homogomph falciger in the neuropodial dorsal fascicle, which is a rare feature among nereidins in general, but present in *Leonnates* and show resemblance to 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 special representing a different kind of spinigers (Figure

10H) only illustrated before in *Leonnates jousseaumei* (Gravier 1899), which was in turn synonymised with *L. indicus* (Qui & Qian 2000). This chaeta is here called a spiniger due to its thin whip-like tip, being the usual condition in spinigers. Hartmann-Schröder (1992) described it as having both spiniger and falciger characteristics.

Hartmann-Schröder (1992) stated that due to 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*. This is only one feature pointing towards a placement in *Pseudonereis* another is the expansion in breadth and length of the dorsal notopodial ligule in posterior chaetigers. There are indications of this expansion in the type specimen as well, but it is only expanded in breadth and only in the last about 10 chaetigers, and the expansion is not well expressed.

As there are several distinctive morphological features pointing in different directions, further analyses including this taxon should be undertaken when more material become available. Questions about the dorsal parapodial ligules in posterior chaetigers should in that case be readdressed as well as the types and distribution of chaetae. The single known specimen may be a juvenile or at least a small specimen.

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

Pseudonereis noodti **(Hartmann-Schröder, 1962) (Figure 11)**

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. Syntypes, Chimbote, Peru, 1956–04–25, coll. Noodt, ZMH P-14380 (2). Size range of material examined 13-31 chaetigers (incomplete specimens), 12 mm long (incomplete), 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, III and IV arranged in regular comb-like rows. Area I = 1 conical paragnath; Area II = 25-27 conical paragnaths in 3 diagonal rows; Area III = 64 conical paragnaths in 4 rows; Area IV = 70-75 including conical paragnaths in four comb-shaped rows, additional cones and p-bars towards the jaws. Oral ring paragnaths present, Area V and VI present as distinct groups. Area V = 1, a large cone; Area VI = 1, a large triangular bar present, cones absent; Area VII-VIII = 16-17, two alternating rows of similar sized paragnaths.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule short and rounded as long as ventral notopodial ligule (Figure 11A-B), markedly elongate and markedly broader on posterior chaetigers (Figure 11C-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 ventral notopodial ligule at chaetiger 10–20 (Figure 11B), basally attached in anterior chaetigers, terminally attached to dorsal notopodial ligule on posterior chaetigers commencing from chaetiger about 25. Ventral notopodial ligule short and rounded, similar throughout.

Prominent inferior lobe in anterior chaetigers, a small superior lobe present give the acicular ligule a bilobed appearance (Figure 11B-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.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present (Figure 11H), heterogomph falcigers on anterior chaetigers present (Figure 11F), on posterior chaetigers present (Figure 11G), blades serrated, homogomph falcigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers absent; homogomph spinigers absent; heterogomph falcigers Type 2 in anterior and posterior chaetigers present, homogomph falcigers absent.

Anal cirri cirriform.

Remarks. The type material consists of two anterior and two posterior ends, which due to the size of the specimens is possible to match together. The smaller specimen has a complete posterior end. It was only possible to count paragnaths on the oral ring in the larger specimen.

Pseudonereis noodti is most similar to *P. gallapagensis* and almost indistinguishable. 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* compared to 70-75 in *P. noodti*), and that in *P. noodti* the dorsal cirrus become terminally attached about chaetiger 25 while it is about chaetiger 15 in *P. gallapagensis*. These are all minor differences that might be within the range of variation if more material will be available. The low number of specimens examined does not warrant placing *P. noodti* in synonymy with *P. gallapagensis*. Heterogomph spinigers in neuropodial ventral fascicle was not observed in the two specimens examined, in which it differs from *P. gallapagensis*. Due to that only two specimens are examined, it will have to be verified in additional specimens if this is a true feature in this species. Lack of heterogomph falcigers in the neuropodial ventral fascicle was also noted in the original description (Hartmann-Schröder 1962a).

The striking similarity to *P. gallapagensis* was not recognised 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. Found along the South-American Pacific coast from Chimbote Peru (type locality) in the north and south along the Chilean coast to Puerto Montt (Hartmann-Schröder 1962b). It has been found intertidally and in rockpools.

Pseudonereis palpata (Treadwell, 1923)

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

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

Remarks. A redescription of this species based on a quantity of material, including type material, will be presented elsewhere (Santos, Steiner & Bakken ms). The information for coding used here is from the paratype examined. This specimen was not complete and in poor condition. In the data matrix the neuropodial postchaetal lobe is scored as absent, but due to the poor condition of the single specimen examined, this character would have to be verified from the redescription of more material.

This taxon is unique among *Pseudonereis* as it possesses both bar-shaped and conical paragnaths in Area VI. The type or shape in the bar-shaped paragnath was not recorded from the paratype and will have to be verified from additional material. In the parsimony analysis *P. palpata* falls outside the more inclusive clade that possess a single shield-shaped paragnath in Area VI.

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

Pseudonereis pseudonoodti (Fauchald, 1977) (Figure 12, 13)

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

Material examined. Holotype, Paitilla Beach, Panama, Pacific, intertidal, USNM 53090; Paratypes, Paitilla Beach, Panama, Pacific, intertidal, *Telraclita* zone USNM 53091 (4). Additional material: Paitilla Beach, Panama, Pacific, coll. A.A. Reimer, 20.01.1971 USNM 065983 (1); Paitilla Beach, Panama, Pacific, intertidal, coll. A.A. Reimer, 20.01.1971 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, cirriform; 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, III and 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 conical paragnaths in 4 rows in a triangular patch; Area III = 28-40 conical paragnaths in 4 rows; Area IV = 20-61 conical paragnaths in 4-5 rows, additional and bar-like 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 (Figure 12A); Area VI = 1 bar, a high laterally flattened and pointed triangular bars present, cones absent; Area VII-VIII = 69-100, in 2-3 rows with similar sized conical paragnaths, with larger p-bars interspersed (Figure 12B).

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, digitiform rounded in anterior chaetigers (Figure 13A-B), markedly elongate on posterior chaetigers (Figure 13D-E), markedly broader on posterior chaetigers (Figure 13E), expansion commencing at about chaetiger 30-35. Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2–3 times ventral notopodial ligule at chaetiger 10–20 (Figure 13B), basally to mid-dorsally attached to dorsal notopodial ligule on anterior chaetigers (Figure 13B), terminally attached to dorsal notopodial ligule on posterior chaetigers, from about chaetiger 40 (Figure 13D-E).

Neuropodial inferior lobe prominent in anteriormost 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 (Figure 13D-E). Ventral neuropodial ligule of anterior chaetigers up to half length of acicular neuropodial ligule, on posterior chaetigers reduced (Figure 13E).

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present, heterogomph falcigers on anterior chaetigers present (Figure 13F), on posterior chaetigers present, blades serrated, fused falcigers absent, homogomph falcigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers present commencing in chaetiger about 5–10, homogomph spinigers absent, heterogomph falcigers Type 2 present throughout (Figure 13G), homogomph falcigers absent.

Remarks. A neuropodial postchaetal lobe is present, being of similar shape and form as in the other species; a rounded lobe level with or lower than the acicular ligule. As in most other *Pseudonereis* species it is most prominent in posterior chaetigers. The postchaetal lobe was only clearly visible in the larger specimens, and very difficult to detect in the smaller ones making this character unreliable when only small specimens, <1 mm body with, are available. 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 (Figure 12A). The paragnaths in Area VI are high, flat and pointed triangular bars as seen in most other *Pseudonereis*-species.

The vial with the paratypes (USNM 53091) included 9 specimens where five belonged to *Nereis riisei*. The remaining four specimens were sorted out and included in the description.

In many respects this species is very similar to *P. cortezi*. The paragnaths in Area III are more widely spaced (Figure 12B) 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 there 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 rottnestiana **Augener, 1913 (Figure 14)**

Nereis (*Pseudonereis*) *rottnestiana* Augener, 1913: 184-187, Taf. III, Fig. 46, text-fig. 20a-c.

Material examined. Syntype, Rottnest, ZMH V-7929 (1 specimen). Size range of material examined 68 chaetigers, 33 mm long, 3 mm wide.

Description. Frontal antennae present, 1 pair, cirriform. 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 7. Jaws with dentate cutting edge. Maxillary ring of pharynx with paragnaths arranged in discrete areas, Areas II, III and IV arranged in regular comb-like rows. Area I = 0; Area II = 28-31 conical paragnaths in 5 rows; Area III = 79 conical paragnaths in 5 rows; Area IV = 49-58 conical paragnaths including 5 rows and additional towards jaws, smooth bar-like paragnaths absent. Area V and VI present as distinct groups. Area V paragnaths absent; VI = 8-9 conical paragnaths, smooth bars absent; VII-VIII = 24 in one row with large, and a posterior row with smaller conical paragnaths.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, digitiform rounded, 1.5 times as long as ventral notopodial ligule in anterior chaetigers (Figure 14A), markedly elongate and markedly broader on posterior chaetigers, in the last 1/3 of the body (Figure 14E). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus basally attached on anterior (Figure 14A-B) and sub-terminally attached to dorsal notopodial ligule on posterior chaetigers (Figure 14D-E), not terminally attached to dorsal notopodial ligule on posterior chaetigers. Dorsal cirrus simple, lacking basal cirrophore, 3 times as long as ventral notopodial ligule at chaetiger 10–20 (Figure 14B). Ventral notopodial ligule large stout rounded, similar throughout.

Neuropodial inferior lobe prominent in anterior chaetigers; a small superior lobe present from chaetiger 5-6 (Figure 14C). Neuropodial postchaetal lobe present throughout, a low rounded flattened lobe, not projecting beyond end of acicular ligule, lower than acicular ligule, level with in the posterior 1/3 of the body (Figure 14D). Ventral neuropodial ligule well developed, rounded digitiform, slightly shorter than acicular ligule throughout. Ventral cirri as long as acicular ligule in anterior chaetigers, posteriorly 1-1.5 times as long as acicular ligule.

Notoaciculae absent from segments 1 and 2. Notochaetae: all chaetae broken in the type specimen. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present (Figure 14F), heterogomph falcigers on anterior present, posterior chaetigers present, blades serrated. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 50–60 (Figure 14H), homogomph spinigers absent, heterogomph falcigers Type 2 present in anterior and posterior chaetigers (Figure 14G), homogomph falcigers absent.

Anal cirri cirriform.

Remarks. 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 is identical to the specimen examined (ZMH V-7929), hence this is a syntype. The specimen is in very good condition but most chaetae are broken, not a single notopodial chaeta was observed. Heterogomph spinigers in the neuropodial fascicle was observed in a few posterior chaetigers. Augener (1913) did not include in his description other chaetae 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 has been given as the only difference between *P. anomala* and *P. rottnestiana* (Fauvel 1932; Hartman 1954). Augener did not justify his description of *P. rottnestiana* compared to *P. anomala* only stated that the two species differed in posterior parapodia, which they indeed do judged from this single specimen.

The syntype is large and has a somewhat flattened posterior end, like it is damaged although parapodia and the pygidium are intact. Compared to *P. anomala* the type specimen differ in the outline of posterior dorsal notopodial ligules as it does not have a digitiform protrusion from the ligule below the cirrus but merely a squared outline with a blunt pointed tip (Figure 14E). In specimens examined of *P. anomala* the digitiform end of the dorsal notopodial ligule is quite prominent. Another difference is the length of the ventral cirrus, in the syntype of *P. rottnestiana* it is 1.5 times as long as the acicular ligule throughout while in the *P. anomala* specimens examined it is slightly shorter than the acicular ligule in anterior chaetigers and as long as in posterior chaetigers. The syntype specimen lack paragnaths in Area I and has a higher number of paragnaths in most other Areas than in the *P. anomala* specimens although these differences are small. Due to the differences listed, although they are observed in a single specimen only, *P. rottnestiana* is here removed from synonymy and should be kept as a valid taxon until more material may reveal its true identity.

Hartmann-Schröder (1979 (see also Hartmann-Schröder 1980)) reported two different forms, published as *Pseudonereis rottnestiana* forma *seriodentata* and *Pseudonereis rottnestiana* forma *costatodentata*. She did not refer to specific specimens (types or similar), and examination of the material she assigned showed it was inadequately labelled as such. The names must have been given in preparation of the publication (Hartmann-Schröder 1979). This exercise of describing forms or other infrasubspecific names is nomenclatorial invalid and is not to be regarded as a description or naming of a new taxon (ICZN 1999).

It is evident from the specimens examined that the form Hartmann-Schröder (1979) described as “*seriodentata*” represents specimens of *P. anomala*, while her form “*costatodentata*” represents specimens of *P. trimaculata* (see this for further comments).

Distribution. Type locality Green Island, Rottnest, WA, Australia, from the intertidal.

Pseudonereis trimaculata Horst, 1924 (Figure 15)

Nereis (*Pseudonereis*) *trimaculata* Horst, 1924: 187-188, Pl. XXXVI, figs. 8-9.

Pseudonereis rottnestiana 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, 9/9 1975, 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, 2000-07-27 (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, 2000-07-26 (2). Size range of material examined 60-91 chaetigers for 17-41 mm long, 1-2 mm wide.

Description. Frontal antennae present, 1 pair, cirriform. 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, III and IV arranged in regular comb-like rows. Area I = 1-2 conical paragnaths, in a longitudinal row when 2; Area II = 23-38 conical paragnaths in 4 rows; Area III = 51-69 conical paragnaths in 4 rows; Area IV = 50-78 including conical 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 = a single large laterally flattened bar, cones absent; Area VII-VIII = 20-24 large conical paragnaths of similar size present in two alternating rows.

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, digitiform rounded as long as ventral neuropodial ligule in anterior chaetigers (Figure 15A-B), markedly elongate on posterior chaetigers commencing about chaetiger 55-60, markedly broader on posterior chaetigers commencing about chaetiger 50-55 (Figure 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 (Figure 15B), basally attached in anterior chaetigers, sub-terminally attached in mid-body chaetigers (Figure 15D), and terminally attached to dorsal notopodial ligule on posterior chaetigers in the last 1/4 of the body (Figure 15E).

Neuropodial inferior lobe prominent in anterior chaetigers, a small superior lobe present (Figure 15A), 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 (Figure 15D). 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.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present (Figure 15I), homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present (Figure 15H), heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present (Figure 15G), blades serrated, fused falcigers absent, homogomph falcigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 30 (Figure 15F), homogomph spinigers absent, heterogomph falcigers Type 2 present in anterior and posterior chaetigers present, homogomph falcigers absent.

Pygidial cirri cirriform, reaching back about 10 chaetigers.

Remarks. The original material (ZMA V-pol 954) labelled as “type” and given as syntype in the record (ZMA) consisted of two specimens, not three as stated in the original description. Of the two specimens one was a *Platynereis* sp. and the other a specimen that confirmed to be an original compared to the original description. The syntype confirmed well with the Australian material examined and illustrated (Figure 15).

Pseudonereis trimaculata belongs morphologically in a group with *P. gallapagensis*/*N. ferox*/*P. noodti*/*P. pseudonoodti* (Figure 3) where it most closely resembles *P. pseudonoodti* (Table 4). 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 there are individual differences in paragnath numbers in the different Areas, the length of dorsal cirrus and development and length of the ventral neuropodial ligule distinguishing the two (Table 4).

Horst (1924) did only give a brief description but included illustrations of two parapodia, one anterior and the other what 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 justify difference to other described *Pseudonereis* taxa. These spots are glands often observed in parapodia of nereidids, but only vaguely visible now.

Hartmann-Schröder (1979) described specimens from this taxon as a variety of *P. rottnestiana*, using the term “form”. The label with these specimens (HZM P-16567) did not have name as such but a comment was added to distinguish the specimens as separate from *P. rottnestiana* (see this taxon 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.

Pseudonereis variegata (Grube, 1857) (Figure 16, 17)

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.
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 (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, cirriform. Prostomium with entire anterior margin, longer than wide. Eyes present, 2 pairs (Figure 16A). 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, III and IV arranged in regular comb-like rows. Area I = 1-2 conical paragnaths; Area II = 13-34 conical paragnaths in three rows; Area III = 59-76 conical paragnaths in four rows, anteriormost row half as long as the others; Area IV = 63-87 conical paragnaths, 4-5 rows, additional cones towards jaws present, 2-4 p-bars present. Area V and VI present as distinct groups. Area V = 1 conical paragnath. Area VI = 1 bar, large triangular flattened (shield-shaped) (Figure 16B-C); Area VII-VIII = 18-21, conical paragnaths and large p-bars in two alternating rows, p-bars being more posteriorly placed (Figure 16B).

Notopodium with at least one distinct ligule or lobe. Dorsal notopodial ligule present, stout rounded as long as ventral notopodial ligule in anterior chaetigers (Figure 17A-B), markedly elongate and markedly broader on posterior chaetigers, expanded in breadth from about chaetiger 30 (Figure 17C), in length from about chaetiger 40 (Figure 17D-E). Prechaetal notopodial lobe absent, acicular process absent. Dorsal cirrus simple, lacking basal cirrophore, 2 times ventral notopodial ligule at chaetiger 10–20, basally attached in anterior chaetigers (Figure 17B), sub-terminally attached from about chaetiger 30 (Figure 17D-E), terminally attached to dorsal notopodial ligule on posteriormost chaetigers (Figure 17F). Ventral notopodial ligule stout rounded, in posterior chaetigers digitiform.

Neuropodial inferior lobe prominent in anterior chaetigers; small superior lobe present throughout (Figure 17E-F). Neuropodial postchaetal lobe present throughout low rounded not projecting beyond end of acicular ligule, in posterior chaetigers with a small triangular tip (Figure 17D-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 ling as neuropodial acicular ligule.

Notoaciculae absent from segments 1 and 2. Notochaetae: heterogomph spinigers absent, homogomph spinigers present, homogomph falcigers absent. Neurochaetae, dorsal fascicle: heterogomph spinigers absent, homogomph spinigers present (Figure 17G); heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present, blades serrated; homogomph falcigers on anterior chaetigers absent, on posterior chaetigers absent. Neurochaetae, ventral fascicle: heterogomph spinigers present from about chaetiger 40, with blades finely serrated; homogomph spinigers absent; Type 2 heterogomph falcigers present (Figure 17H) throughout; homogomph falcigers on anterior chaetigers absent, posterior chaetigers absent.

Pygidium multi-incised, ventral incision, anal cirri cirriform reaching back five chaetigers.

Remarks. Description and illustrations presented here are based on the syntypes of *Nereis ferox* and variation given from additional material listed. Type material of *Nereilepas variegata* Grube was not available for study. *N. ferox* has been synonymised in the literature by Ehlers (1901) and Augener (1934). It appears that Ehlers examined the types of *N. ferox* and found it to be identical to *P. variegata*.

Pseudonereis variegata most resembles *P. gallapagensis* (Table 4) but is distinguished by the length of ventral neuropodial ligule, which in *P. variegata* is of similar length as acicular ligule but up to half as long in *P. gallapagensis*; and by the number of conical paragnaths in Area IV where *P. variegata* has more (68-87) than *P. gallapagensis* (38-57). The length of the dorsal cirrus in anterior chaetigers is also different being longer in *P. gallapagensis*. *P. variegata* has generally higher number of paragnaths in all Areas than *P. gallapagensis*, although these differences are small and as there are only few specimens counted these differences may be even smaller when more material is examined. Similarities to *P. atopodon* is also noted (Table 4), see this taxon for further comments.

Paragnaths in Area VII-VIII in several rows has been used as a diagnostic feature to distinguish *P. variegata* from *P. gallapagensis* (Hartmann-Schröder 1962b; Fauchald 1977). Based on the examined material only this is not a very confident character as there are similarities and the variation is low. The same sources also used the attachment of the dorsal cirrus on the dorsal notopodial ligule in posterior chaetigers as another distinctive feature, and has 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 owing to complete specimens to be observed, while in *P. gallapagenis* 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 several taxa Hansen (1882) described from Brazil later examined by Ehlers (1901) and Augener (1934) who found them to be identical with *P. variegata*; *Nereis coerulea*, *Nereis obscura*, and *Phyllonereis benedeni*. They did not mention *P. gallapagensis*. Hartman (1949) placed *Paranaereis elegans* Kinberg, 1865 in synonymy with *P. variegeta* 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, hence it is not included in the material examined above. Extensive synonymies are listed in Ehlers (1901) (see also Augener 1934), those included above represents specimens examined.

Distribution. Type locality of *Nereis ferox* is Rio de Janeiro, Brazil. South America, Atlantic coast. Habitat marine, inshore, or marine, shelf.

Discussion

This revision has showed that there are minor details distinguishing some of the taxa. For example the difference between *P. gallapagensis* and *P. noodti* are miniscule, except for number of paragnaths in Area III and IV all characters are overlapping (Table 4). Placing *P. noodti* into synonymy with *P. gallapagensis* is not warranted at this stage due to lack of material, but this should be looked into when a large number of specimens are available. The similarity of *P. gallapagensis* to *P. atopodon* is striking although a character separating the two; size and distribution of the ventral neuropodial ligule throughout the body usually is a stable feature showing minor or no variation within a taxon in other groups of nereidins (own observations). Number of paragnaths in Area II is also different being higher in *P. atopodon* than *P. gallapagensis*. Again more material is needed.

Two other taxa being very similar in most characters are *P. cortezi* and *P. pseudonoodti*, although the different number of paragnaths in Area V is quite convincing (Table 4). A striking feature in these two is the absence or poor development of the neuropodial postchaetal lobe, this being different from all other taxa (with a possible exception in *P. palpata*).

Hylleberg et al (1986) and Hutchings & Glasby (1985) commented on differences in paragnath numbers of different populations of *P. anomala* but could not find other differences in the material available to them. It is demonstrated here from the material examined that such variations within *P. anomala* falls within the range of variation of paragnath numbers for this taxon (Table 5), and it is not possible to detect other morphological differences, in accordance with Hylleberg et al. (1986) and Hutchings & Glasby (1985).

The distribution of the taxa belonging to *Pseudonereis* is predominantly tropical and subtropical, although there are found specimens rather far south on the Pacific side of South America (Ehlers 1901; Hartmann-Schröder (1962b). A majority are described from Central and South America and the Indo-Pacific region. For some of these taxa only a few specimens are known, some only from the type specimens, which at present questions the identity of a couple of taxa. Upon availability of more material from all taxa from this area it should be possible to designate whether these are genuine taxa or that some of them are synonymous. The vertical distribution is also interesting in this group, all taxa are known from the intertidal only a few also from shallow waters.

Fauchald (1977) noted that *P. gallapagensis* has been frequently been confused with other taxa. This notification should be kept in mind when synonymies in older works are considered in a biogeographical context. For this reason synonymies give above are not extensive but restricted to material examined.

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References

Augener H. 1913. Polychaeta I, Errantia. Pp 63-304. In *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905*. Edited by Michaelsen W. and Hartmeyer R. 4, Gustav Fischer, Jena.

Augener H. 1934. Polychaeten aus den zoologischen Museen von Leiden und Amsterdam, IV (schluss). *Zoologische Mededeelingen, Leiden* 17: 67-160.

Bakken T. 2002. A new species of *Neanthes* (Polychaeta: Nereididae) from southern Australia. *Memoirs of Museum Victoria* 59: 327-331.

Dallwitz M.J. Paine TA. Zurcher E.J. (1993 onwards). User's guide to the DELTA system: a general system for processing taxonomic descriptions. 4th edition. http://biodiversity.uno.edu/delta/

de León-González JA. Solís-Weiss V. 2000. A review of the polychaete family Nereididae from western Mexico. *Bull Marine Sci* 67: 549-569.

Ehlers, E. 1901. Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. *Festschrift zur Feier des Hundertfünfzigjährigen Bestehens der Königlichen Gesellschaft der Wissenschaften zu Göttingen. Abhandlung der Mathematisch-Physikalischen Klasse*: 1-232.

Fauchald K. 1977. Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithsonian Contributions to Zoology* 221: 1-81.

Fauvel P. 1911. Annélides polychètes du Golfe Persique recueillies par M. N. Bogoyawlensky. *Archives de Zoologie Experimentale et Generale* 6: 353-439.

Fauvel P. 1932. Annelida Polychaeta of the Indian Museum Calcutta. *Memoirs of the Indian Museum* 12: 1-261.

Glasby CJ. 1999. The Namanereidinae (Polychaeta: Nereididae). Part 1, taxonomy and phylogeny. *Records of the Australian Museum, Supplement* 25: 1-129.

Gravier C. 1899. Contribution à l'étude des Annélides Polychètes de la Mer Rouge. *Bulletin du Musèum National d'Histoire Naturelle, Paris* 5: 234-244.

Grube AE. 1857. Annulata Örstediana. Enumeratio Annulatorum, quac in itinere per Indiam occidentalem et Americam centralem annis 1845-1848 suscepto legit cl. A. S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinere ad Americam meridionalem collectis. *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn*: 158-186.

Hansen GA. 1882. Recherches sur les annélides receueillies par M. le professeur Édouard van Benedon pendant son vuyage au Brésil et à la Plata. *Memoires Couronnes et Memoires des Savants Etrangers publies par L'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 44: 1-29.

Hartman O. 1949. The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Arkiv för Zoologi* 42: 1-136.

Hartman O. 1954. Australian Nereidae including descriptions of three new species and one genus, together with summaries of previous records and keys to species. *Transactions of the Royal Society of South Australia* 77: 1-41.

Hartman, O. (1959). Catalogue of the Polychaetous Annelids of the world. Part 1. *Allan Hancock Foundation Publications Occasional Papers* 23: 1-353.

Hartmann-Schröder G. 1962a. Zweiter Beitrag zur polychaetenfauna von Peru. *Kieler Meeresforschungen* 18: 109-147.

Hartmann-Schröder G. 1962b. Zur Kenntnis der Nereiden Chiles (Polychaeta errantia), mit Beschreibung epitoker Stadien einiger Arten und der Jugendentwicklung von *Perinereis vallata* (Grube). *Zoologischer Anzeiger* 168: 389-441.

Hartmann-Schröder G. 1979. In Hartmann-Schröder, G. & Hartmann, G. Zur kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 2. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 76: 75-218.

Hartmann-Schröder G. 1980. In Hartmann-Schröder, G. & Hartmann, G. Zur kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 4. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Port Samson im Norden und Exmouth im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 77: 41-110.

Hartmann-Schröder G. 1992. Zur Polychaetenfauna der Polynesischen Inseln Huahiné (Gesellschaftsinseln) und Rangiroa (Tuamotu-Inseln). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 89: 49-84.

Horst R. 1924. Polychaeta errantia of the Siboga Expedition. Part III Nereidae and Hesionidae. *Siboga Expeditie* 24: 145-169.

Hutchings PA. Glasby CJ. 1985. Additional nereidids (Polychaeta) from eastern Australia, together with a redescription of *Namanereis quadraticeps* (Gay) and the synonymising of *Ceratonereis pseudoerythraeensis* Hutchngs & Turvey with *C. aequisetis* (Augener). *Records of the Australian Museum* 37: 101-110.

Hutchings PA. Reid A. 1990. The Nereididae (Polychaeta) from Australia - Gymnonereidinae sensu Fitzhugh, 1987: *Australonereis*, *Ceratocephale*, *Dendronereides*, *Gymnonereis*, *Nicon*, *Olganereis* and *Websterinereis*. *Records of the Australian Museum* 42: 69-100.

Hutchings PA. Reid A. Wilson RS. 1991. *Perinereis* (Polychaeta, Nereididae) from Australia, with redescription of six additional species. *Records of the Australian Museum* 43: 241-274.

Hutchings PA. Turvey SP. 1982. The Nereididae of South Australia. *Transactions of the Royal Society of South Australia* 106: 93-144.

Hylleberg J. Nateewathana A. 1988. Polychaetes of Thailand. Nereididae (part 2): *Ceratocephale* and *Gymnonereis*, with description of two new species and notes on the subfamily Gymnonereidinae. *Phuket Marine Biological Center Research Bulletin* 49: 1-20.

Hylleberg J. Nateewathana A. Bussarawit S. 1986. Polychaetes of Thailand. Nereididae (part 1): *Perinereis* and *Pseudonereis* with notes on species of commercial value. *Phuket Marine Biological Center Research Bulletin* 43: 1-22.

International Commission on Zoological Nomenclature. 1999. International code of Zoological Nomenclature. 4th ed. London: International Trust for Zoological Nomenclature.

Kinberg JGH. 1865. Annulata nova. *Öfversikt af Kongliga Vetenskaps-Akedemiens Förhandlingar* 22: 167-179.

Kott P. 1951. Nereididae and Eunicidae of South Western Australia: Also notes on the ecology of western Australian limestone reefs. *Roy Soc West Australia Jour* 35: 85-130.

Kudenov JD. 1979. New species and records of polychaetous annelids from the *Tetraclita* (Cirripedia: Crustacea) zone of the Northern Gulf of California. *Bulletin of the Southern California Academy of Sciences* 78: 116-121.

Maddison WP. Maddison DR. 2003. Mesquite: a modular system for evolutionary analysis.

Version 1.0 http://mesquiteproject.org

Malmgren AJ. 1867. Annulata polychaeta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus cognita. *Öfversikt af Kongliga Vetenskaps-Akedemiens Förhandlingar* 24: 127-235.

Page RDM. 2001. NEXUS Data Editor for Windows. http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html

Qui J-W. and Qian P-Y. 2000. Revision of the genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae), with descriptions and comments on other species described in *Leonnates*. *Proceedings of the Biological Society of Washington* 113: 1111-1146.

Swofford DL. 2001. PAUP. 4.0b10 for 32 bit Microsoft Windows. Available via http://www.lms.si.edu/PAUP. Sunderland, Massachusetts: Sinauer Associates, Inc.

Treadwell AL. 1923. Two new species of polychaetous annelids of the genus *Nereis* from Brazil. *Revista do Museu Paulista* 13: 1-10.

Willey A. 1904. Littoral Polychaeta from the Cape of Good Hope. *Transactions of the Liennean Society of London, Zoology* 9: 255-268.

Wilson RS. 1984. *Neanthes* (Polychaeta: Nereididae) from Victoria with descriptions of two new species. *Proceedings of the Royal Society of Victoria* 96: 209-226.

Wilson RS. Bakken T. Glasby CJ. (2003). Nereididae (Polychaeta)-A DELTA database of genera, and Australian species. In Wilson RS, Hutchings PA, Glasby CJ. (Eds), *Polychaetes: An Interactive Identification Guide*. Melbourne: CSIRO Publishing.

Wu B. Sun R. Yang, DJ. 1985. The Nereidae (Polychaetous Annelids) of the Chinese coast. Berlin: Springer Verlag.

Figures

Figure 1. The tree represents a clade from a tree showing the monophyletic *Pseudonereis* clade, taken from a tree in Bakken & Wilson (ms). The two neighbouring clades show the closest relatives in their highly homoplasious strict consensus tree, where outgroups in the analysis of *Pseudonereis* is taken from.

Figure 2. Paragnaths from a specimen in the syntype series of *Nereis ferox* (=*P. variegata*) ZMUB 2130. A, paragnaths in typical regular comb-like rows from Area III, a synapomorphy for *Pseudonereis* representing paragnath pattern found in Areas II-IV on the pharynx. B, bar-shaped paragnaths with a point skewed over to one end of the bar (p-bar) from Area VII-VIII, appears to be common in *Pseudonereis* taxa.

Figure 3. The single most parsimonious tree from the analysis of 13 taxa for 87 characters, three outgroup and 10 ingroup taxa. Constant characters were excluded in the analyses retaining 20 parsimony un-informative and 20 parsimony informative characters. Tree statistics are: length 53 steps, CI = 0.7547, RI = 0.77347. Numbers above line are node numbers, numbers below lines bootstrap support.

Figure 4. *Pseudonereis anomala* Gravier , 1901 syntypes NMHN POLY TYPE 423. A, heterogomph falcigers ventral fascicle from chaetiger 37. B, notopodial homogomph falciger from chaetiger 37.

Figure 5. *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-G 0.01 mm. A and B are from one, C from a second and D from a third specimen in the syntype series.

Figure 6. *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, hetergomph 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-F 0.01 mm.

Figure 7. *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.

Figure 8. *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.

Figure 9. *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.

Figure 10. *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).

Figure 11. *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.

Figure 12. *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 13. *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-G 0.01 mm.

Figure 14. *Pseudonereis rottnestiana* Augener, 1913 syntype ZMH V7929. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 27chaetiger anterior view. D, parapodium 40th chaetiger. E, parapodium 61st chaetiger anterior view. E, homogomph spiniger neuropodial dorsal fascicle 27th chaetiger. F, heterogomph falciger neuropodial ventral fascicle 61st chaetiger. G, heterogomph spiniger neuropodial ventral fascicle 61st chaetiger. End-view drawings of parapodia in A-D are not to scale. Scale bar in A-B, E 0.1 mm, C-D 0.5 mm, F-G 0.01 mm.

Figure 15. *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.

Figure 16. *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 is demonstrated in C. A-C of the same specimen measuring 3 mm body width at chaetiger 10 excluding parapodia.

Figure 17. *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-H 0.01 mm.

Tables

Table 1. Character list showing all characters used in the phylogenetic analyses. This list is the same as the one used by Bakken & Wilson (ms) in analyses of Nereidinae except that the character “neuropodial superior lobe (here listed as character 50) is included.

1. One pair of frontal antennae: (1) present; (2) absent.
2. Palpophore compact, no transverse groove: (1) present; (2) absent.
3. Palpostyle spherical: (1) present; (2) absent.
4. Palpostyle conical: (1) present; (2) absent.
5. Prostomium, anterior margin: (1) with entire anterior margin; (2) with anterior margin indented.
6. Achaetigerous anterior segment, length: (1) equal to or less than length of chaetiger 1; (2) greater than length of chaetiger 1.
7. Tentacular cirri, cirrophores: (1) present; (2) absent.
8. Ventral peristomial flap: (1) present; (2) absent.
9. Pharynx with recognisable Areas: (1) present; (2) absent.
10. Maxillary ring papillae: (1) present; (2) absent.
11. Paragnaths in Areas II-IV arranged in regular closely spaced comb-like rows: (1) present; (2) absent.
12. Area I; paragnaths: (1) present; (2) absent.
13. Area II; conical paragnaths: (1) present; (2) absent.
14. Area II; minute rod-like paragnaths in a compact cluster: (1) present; (2) absent.
15. Area III; conical paragnaths: (1) present; (2) absent.

16. Area III; minute rod-like paragnaths in a compact cluster: (1) present; (2) absent.
17. Area III; pectinate paragnaths: (1) present; (2) absent.
18. Area IV; conical paragnaths: (1) present; (2) absent.
19. Area IV; minute rod-like paragnaths in a compact cluster: (1) present; (2) absent.
20. Area IV; pectinate paragnaths: (1) present; (2) absent.
21. Area V; papillae: (1) present; (2) absent.
22. Area VI; papillae: (1) present; (2) absent.
23. Area VII-VIII; papillae: (1) present; (2) absent.
24. Oral ring; regular rows of crown-shaped paragnaths: (1) present; (2) absent.
25. Paragnaths of Areas V-VIII merged forming a continuous band: (1) present; (2) absent.
26. Area V; paragnaths: (1) present; (2) absent.
27. Area VI; conical paragnaths: (1) present; (2) absent.
28. 1 smooth bar on Area VI: (1) present; (2) absent.
29. 2 smooth bars on Area VI: (1) present; (2) absent.
30. Numerous (3 or more) smooth bars on Area VI: (1) present; (2) absent.
31. Area VI; pectinate paragnaths: (1) present; (2) absent.
32. Area VII-VIII; conical paragnaths: (1) present; (2) absent.
33. Area VII-VIII; pectinate paragnaths: (1) present; (2) absent.
34. Area VII-VIII paragnaths; arranged in isolated patches: (1) present; (2) absent.
35. Area VII-VIII paragnaths; arranged in lines forming a continuous band: (1) present; (2) absent.
36. Notopodium: (1) with at least one distinct ligule or lobe; (2) strongly reduced, lacking identifiable ligules or lobes.
37. Dorsal notopodial ligule similar on anterior and posterior chaetigers: (1) present; (2) absent.
38. Dorsal notopodial ligule markedly elongated on posterior chaetigers: (1) present; (2) absent.
39. Dorsal notopodial ligule markedly broader on posterior chaetigers: (1) present; (2) absent.
40. Dorsal notopodial ligule markedly reduced on posterior chaetigers: (1) present; (2) absent.
41. Prechaetal notopodial lobe; small: (1) present; (2) absent.
42. Prechaetal notopodial lobe; as large as dorsal notopodial ligule: (1) present; (2) absent.
43. Prechaetal notopodial lobe; present throughout: (1) present; (2) absent.
44. Prechaetal notopodial lobe; restricted to anterior chaetigers: (1) present; (2) absent.
45. Notopodial acicular process: (1) present; (2) absent.
46. Dorsal cirrus; basally attached to dorsal notopodial ligule on posterior chaetigers: (1) present; (2) absent.
47. Dorsal cirrus; mid-dorsally to sub-terminally attached to dorsal notopodial ligule on posterior chaetigers: (1) present; (2) absent.
48. Dorsal cirrus; terminally attached to dorsal notopodial ligule on posterior chaetigers:
(1) present; (2) absent.
49. Dorsal cirrus with/without cirrophore: (1) simple, lacking basal cirrophore; (2) arising from basal cirrophore.
50. Neuropodial superior lobe: (1) present; (2) absent.

51. Neuropodial postchaetal lobe; projecting beyond acicular ligule: (1) present; (2) absent.
52. Neuropodial postchaetal lobe; low rounded lobe not projecting beyond acicular ligule: (1) present; (2) absent.
53. Neuropodial postchaetal lobe; present throughout: (1) present; (2) absent.
54. Neuropodial postchaetal lobe; restricted to anterior chaetigers: (1) present; (2) absent.
55. Neuropodial postchaetal lobe; digitiform: (1) present; (2) absent.
56. Neuropodial postchaetal lobe; flattened: (1) present; (2) absent.
57. Ventral neuropodial ligule of anterior chaetigers: (1) present; (2) absent.
58. Notoaciculae: (1) present on segments 1 and 2; (2) absent from segments 1 and 2.
59. Notoacicula, position in parapodia: (1) supporting notopodia; (2) ventral, supporting neuropodia.
60. Notopodial heterogomph spinigers: (1) present; (2) absent.
61. Notopodial homogomph spinigers: (1) present; (2) absent.
62. Notopodial sesquigomph spinigers: (1) present; (2) absent.
63. Notopodial falciger homogomph articulation: (1) present; (2) absent.
64. Terminal tendon of blade of notopodial falcigers: (1) present; (2) absent.
65. Notopodial homogomph falcigers bidentate with large adjacent terminal and subterminal teeth: (1) present; (2) absent.
66. Notopodial homogomph falcigers multidentate with 2 or more small lateral teeth, first and subsequent lateral teeth much smaller than terminal tooth: (1) present; (2) absent.
67. Notopodial falciger sesquigomph articulation: (1) present; (2) absent.
68. Notopodial sesquigomph falcigers, blade distally bifid: (1) present; (2) absent.
69. Notopodial sesquigomph falcigers, blade with a single distal tooth: (1) present; (2) absent.
70. Neurochaetae dorsal fascicle; heterogomph spinigers: (1) present; (2) absent.
71. Neuropodial dorsal fascicle; homogomph spinigers: (1) present; (2) absent.
72. Neuropodial dorsal fascicle; sesquigomph spinigers: (1) present; (2) absent.
73. Neuropodial dorsal fascicle; sesquigomph falcigers: (1) present; (2) absent.
74. Neuropodial dorsal fascicle; heterogomph falcigers: (1) present; (2) absent.
75. Neuropodial dorsal fascicle fused falcigers: (1) present; (2) absent.
76. Neuropodial dorsal fascicle; homogomph falcigers: (1) present; (2) absent.
77. Neuropodial ventral fascicle sesquigomph falcigers: (1) present; (2) absent.
78. Neurochaetae ventral fascicle; heterogomph spinigers: (1) present; (2) absent.
79. Neuropodial ventral fascicle; homogomph spinigers: (1) present; (2) absent.
80. Neuropodial ventral fascicle; sesquigomph spinigers: (1) present; (2) absent.
81. Neuropodial ventral fascicle; homogomph falcigers: (1) present; (2) absent.
82. Ventral neuropodial fascicle heterogomph falciger articulation: (1) present; (2) absent.
83. Type 0 heterogomph falcigers in ventral neuropodial fascicle: (1) present; (2) absent.
84. Type 1 heterogomph falcigers in ventral neuropodial fascicle: (1) present; (2) absent.
85. Type 2 heterogomph falcigers in ventral neuropodial fascicle: (1) present; (2) absent.
86. Blade of ventral fascicle heterogomph falcigers with recurved terminal tooth and distinct tendon: (1) present; (2) absent.
87. Blade of ventral fascicle heterogomph falcigers terminally bifid: (1) present; (2) absent.

Table 3. List of apomorphies for the cladogram in Fig. 3. All character changes in the apomorphy list are given. Character numbers refer to characters in Table 1.

Branch	Character
node_20 - bifida	12(1-2); 38(1-2); 40(2-1); 46(2-1); 47(1-2); 65(2-1); 83(2-1)
node_20- node_14	27(1-2); 41(2-1); 44(2-1)
node_14 - *akuna*	26(2-1); 30(2-1); 63(1-2)
node_14 - *antipoda*	12(1-2); 13(1-2); 15(1-2); 17(2-1); 18(1-2); 20(2-1); 31(2-1); 32(1-2); 33(2-1); 34(2-1); 35(1-2); 37(2-1); 38(1-2); 51(2-1); 53(2-1); 55(2-1); 64(2-1)
node_20 - node_19	11(2-1); 39(2-1); 50(2-1); 84(1-2); 85(2-1)
node_19 - node_15	52(2-1); 53(2-1); 56(2-1); 66(2-1)
node_15 - *multisetosa*	38(1-2); 76(2-1)
node_19 - node_18	26(2-1); 28(2-1); 47(1-2); 48(2-1); 63(1-2)
node_18 - node_17	27(1-2)
node_17 - node_16	52(2-1); 53(2-1); 56(2-1)
node_16 - *atopodon*	51(2-1)
node_16 - *noodti*	78(1-2)
node_16 - *pseudonoodti*	50(1-2)

Table 2. Character matrix of 87 characters used in parsimony analyses of 10 *Pseudonereis* taxa and three outgroups. All characters listed in Table 1 are shown, but constant characters were excluded from the analyses in PAUP*.

		2 0	4 0	6 0	8 0
bifida	1221121212221212212	22222221222212211222	12222212212222222121	21212122222122122212	22111222
akuna	1221121212211212212	22222212221212211212	21221221212222222121	21222222222122122212	22121222
antipoda	1221121212222222122	12222222222121121122	21221221212121212121	21211222222122122212	22121222
anomala	1221121212111212212	22222221222212211211	22222221211211221121	21212212222122122212	22122122
atopodon	1221121212111212212	22222212122212211211	22222222111111221121	21222222222122122212	22122122
cortezi	1221121212111212212	22222212122212211211	22222222111222222121	21222222222122122212	22122122
trimaculata	1221121212111212212	22222212122212211211	22222222111211221121	21222222222122122212	22122122
gallapagensis	1221121212111212212	22222212122212211211	22222222111211221121	21222222222122122212	22122122
noodti	1221121212111212212	22222212122212211211	22222222111211221121	21222222222122122222	22122122
palpata	1221121212111212212	22222211122212211211	22222222111222222121	21222222222122122212	22122122
pseudonoodti	1221121212111212212	22222212122212211211	22222222112211221121	21222222222122122212	22122122
ferox	1221121212111212212	22222212122212211211	22222222111211221121	21222222222122122212	22122122
multisetosa	1221121212111212212	22222221222212211221	22222221211211221121	21212212222122121212	22122122

Table 5. Paragnath statistics are presented for *Pseudonereis anomala* from five different localities. Exact location data are given in "material examined". Numbers are given as range and (mean ± sd) for each Area.

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

Table 4. Comparison table for taxa in *Pseudonereis* Kinberg, 1865 showing important characters used for identification. *P. multisetosa* is easily distinguished by presence of homogomph falcigers in neuropodial dorsal fascicle.

	Paragnaths								Neuropodia			
										ventral ligule		
Taxon	Area I	Area II	Area III	Area IV	Area V	Area VI	Area VII-VIII	Dorsal cirrus, attached in posterior chaetigers	postchaetal lobe	anterior, x long as acicular ligule	posterior, x long as acicular ligule	Type locality
P. anomala	1-3	11-29	30-72	20-52	0	3-15, cones	10-19	sub-terminal	present	1	1	Djibouti, Gulf of Aden
P. rottnestiana	0	28-31	79	49-58	0	8-9, cones	24	sub-terminal	present	1	1	Rottnest Island Western Australia
P. multisetosa	2	17-18	20	29-33	0	4, cones	8	sub-terminal	present	1	0.5	Rangiroa, French Polynesia
P. palpata	2	39-40	109	108-120	1	1-2, bar + cones	19	terminal	absent (?)	1	0.5	Rio de Janeiro, Brazil
P. cortezi	4-6	17-31	33-54	31-55	8-15	1 shield-shaped	62-87	terminal, from c. 50-55	absent	0.5	<0.5, diminishing	Punta La Cholla, Mexico
P. pseudonoodti	4	15-27	28-40	20-61	3	1 shield-shaped	69-100	terminal, from c. 40	present, poorly developed	0.5	<0.5, reduced	Paitilla, Panama
P. trimaculata	1-2	23-38	51-69	50-78	1-3	1 shield-shaped	20-24	terminal, posterior 1/4	present	0.5-0.8	1	Dampier, Western Australia
P. atopodon	1	37-49	56	?, 4-5 rows	0-1	1 shield-shaped	14-24	terminal, from c. 60-65	present	0.5	0.5	Tonga Islands, Oceania
P. gallapagensis	1	17-20	51-68	38-57	1	1 shield-shaped	17-20	terminal, from c. 15	present	1	0.5	Galapagos Islands
P. noodti	1	25-27	64	70-75	1	1 shield-shaped	16-17	terminal, from c. 25	present	1	0.5	Chimbote, Peru
P. variegata	1-2	13-34	59-76	63-87	1	1 shield-shaped	18-21	terminal, last few only	present	1	1	Valparaiso, Chile

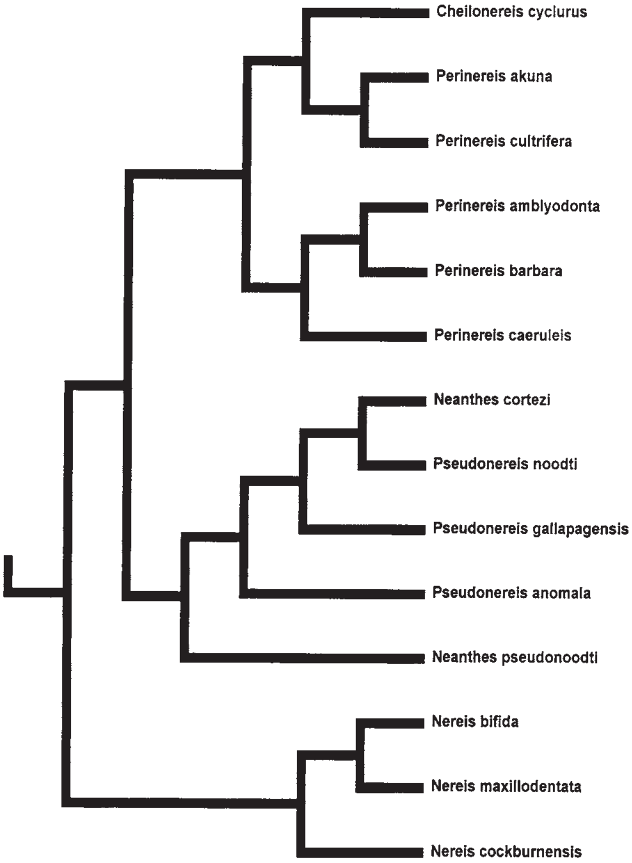

Figure 1. The tree represents a clade from a tree showing the monophyletic *Pseudonereis* clade, taken from a tree in Bakken & Wilson (ms). The two neighbouring clades show the closest relatives in their highly homoplasious strict consensus tree, where outgroups in the analysis of *Pseudonereis* is taken from.

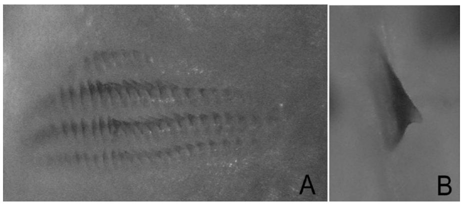

Figure 2. Paragnaths from a specimen in the syntype series of *Nereis ferox* (=*P. variegata*) ZMUB 2130. A, paragnaths in typical regular comb-like rows from Area III, a synapomorphy for *Pseudonereis* representing paragnath pattern found in Areas II-IV on the pharynx. B, bar-shaped paragnaths with a point skewed over to one end of the bar (p-bar) from Area VII-VIII, appears to be common in *Pseudonereis* taxa.

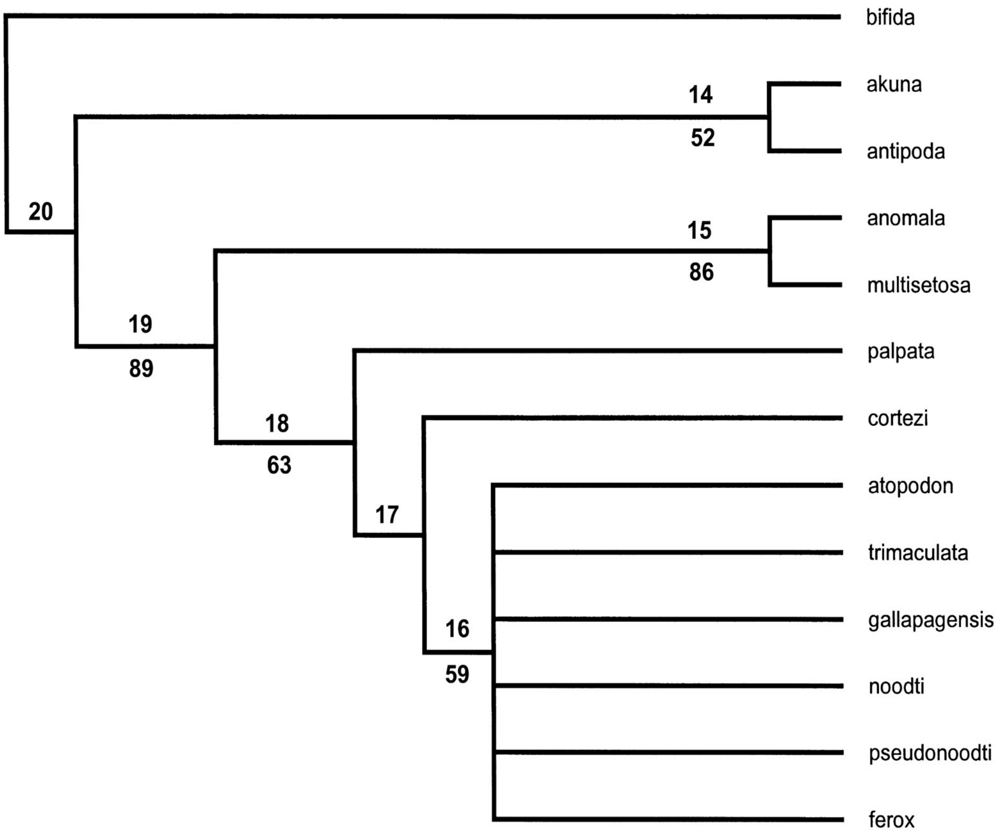

Figure 3. The single most parsimonious tree from the analysis of 13 taxa for 87 characters, three outgroup and 10 ingroup taxa. Constant characters were excluded in the analyses retaining 20 parsimony un-informative and 20 parsimony informative characters. Tree statistics are: length 53 steps, CI = 0.7547, RI = 0.77347. Numbers above line are node numbers, numbers below lines bootstrap support.

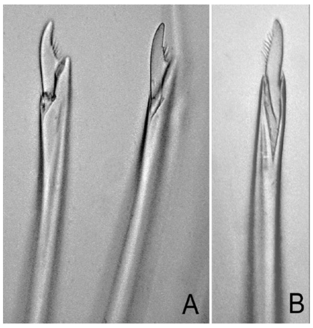

Figure 4. *Pseudonereis anomala* Gravier , 1901 syntypes NMHN POLY TYPE 423. A, heterogomph falcigers ventral fascicle from chaetiger 37. B, notopodial homogomph falciger from chaetiger 37.

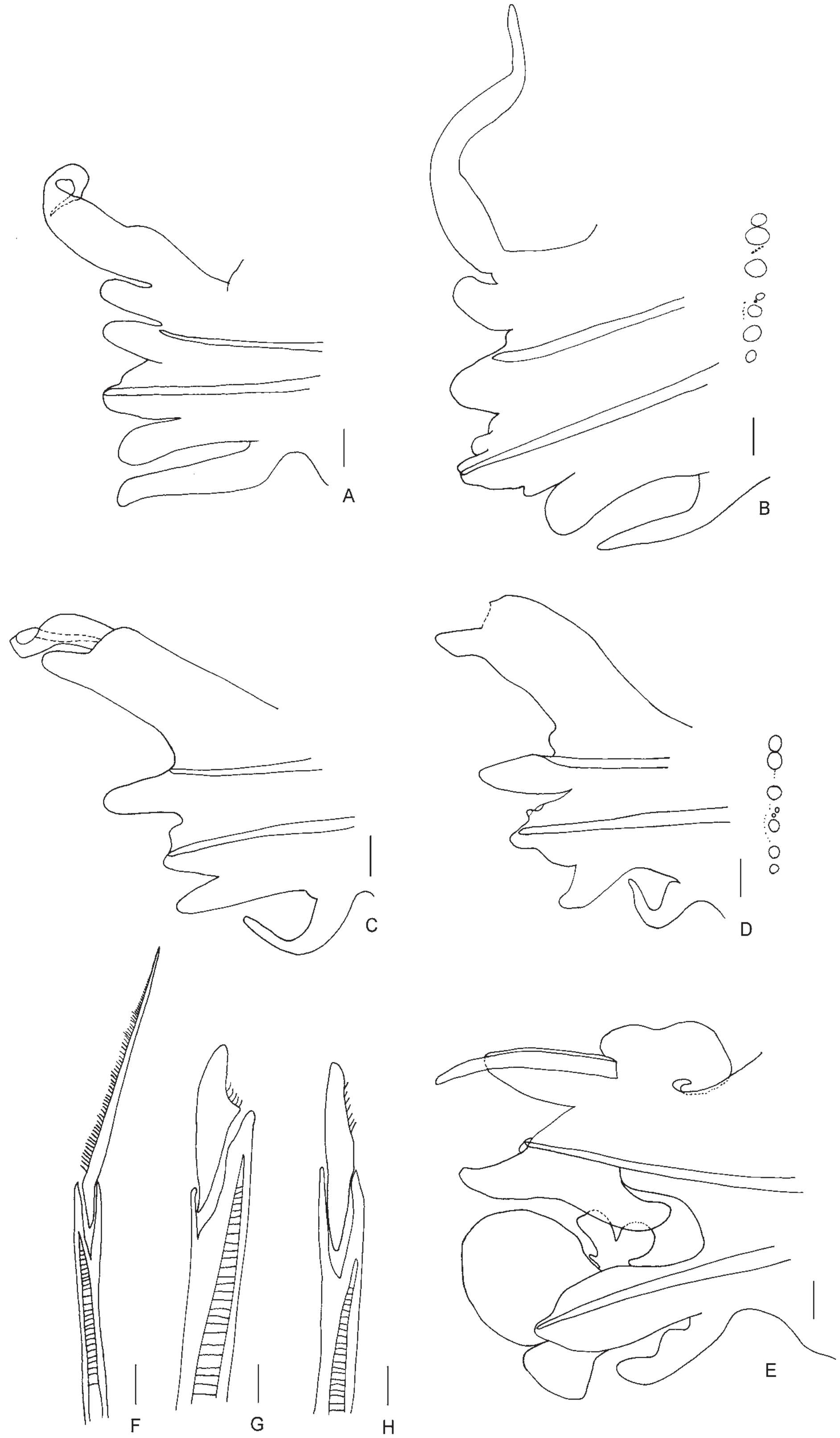

Figure 5. *Pseudonereis anomala* Gravier , 1901 syntypes MNHN Poly-Type-423 A-D, F-H; Poly-Type 421 E. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 43rd chaetiger anterior view. D, parapodium 60th chaetiger anterior view. E, female heteronereidid, 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-G 0.01 mm. A and B are from one, C from a second and D from a third specimen in the syntype series.

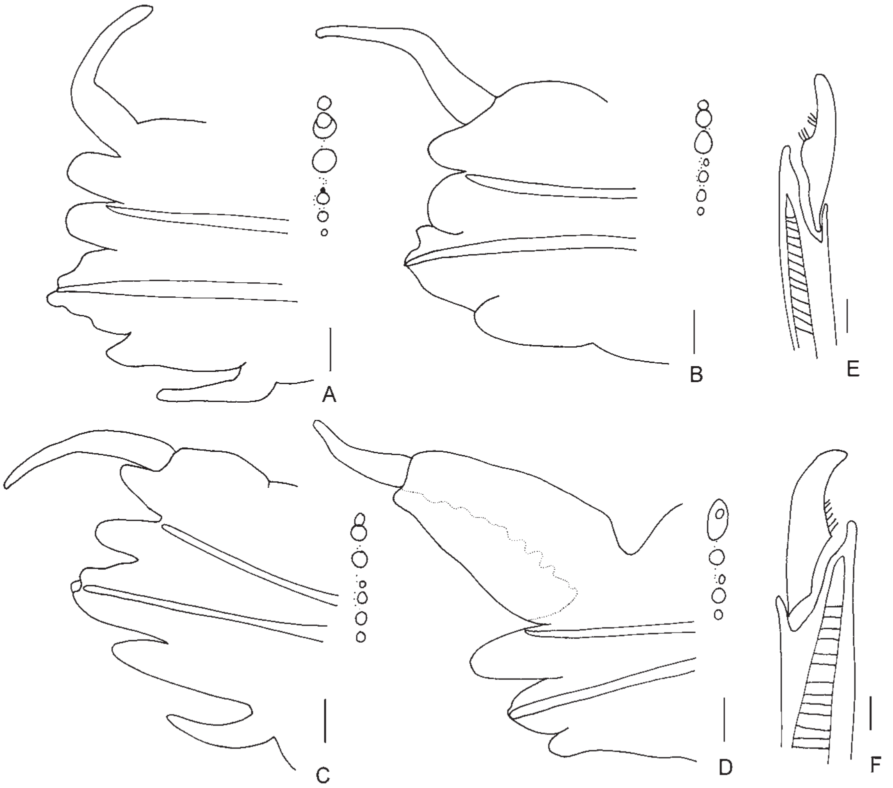

Figure 6. *Pseudonereis atopodon* Chamberlin, 1919 paratypes USNM 19468. A, parapodium 4th chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 70th chaetiger anterior view. E, heterogomph falciger neuropodial ventral fascicle 10th chaetiger. F, hetergomph 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-F 0.01 mm.

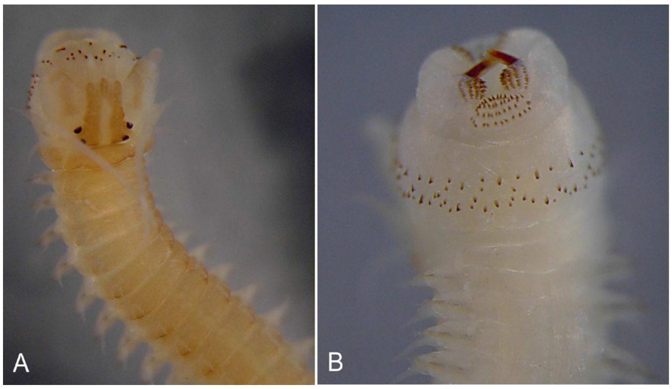

Figure 7. *Pseudonereis cortezi* (Kudenov, 1979) paratype NHMLAC Poly-1344. A, Anterior end dorsal view. B, anterior end ventral view. A and B of the same specimen measuring 1 mm body width at chaetiger 10 excluding parapodia.

Figure 12. *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.

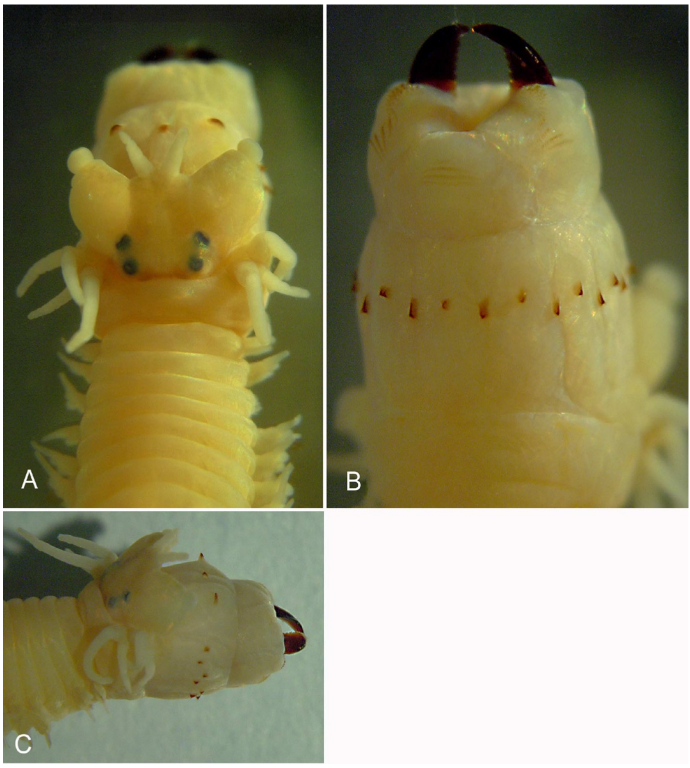

Figure 16. *Pseudonereis variegata* (Grube, 1857) syntypes of *Nereis ferox* Hansen, 1882 ZMUB 2130. A, anterior end dorsal view. B, anterior end ventral view. C, anterior end lateral view. The laterally flattened shield-shaped paragnaths protruding from the tissue is demonstrated in C. A-C of the same specimen measuring 3 mm body width at chaetiger 10 excluding parapodia.

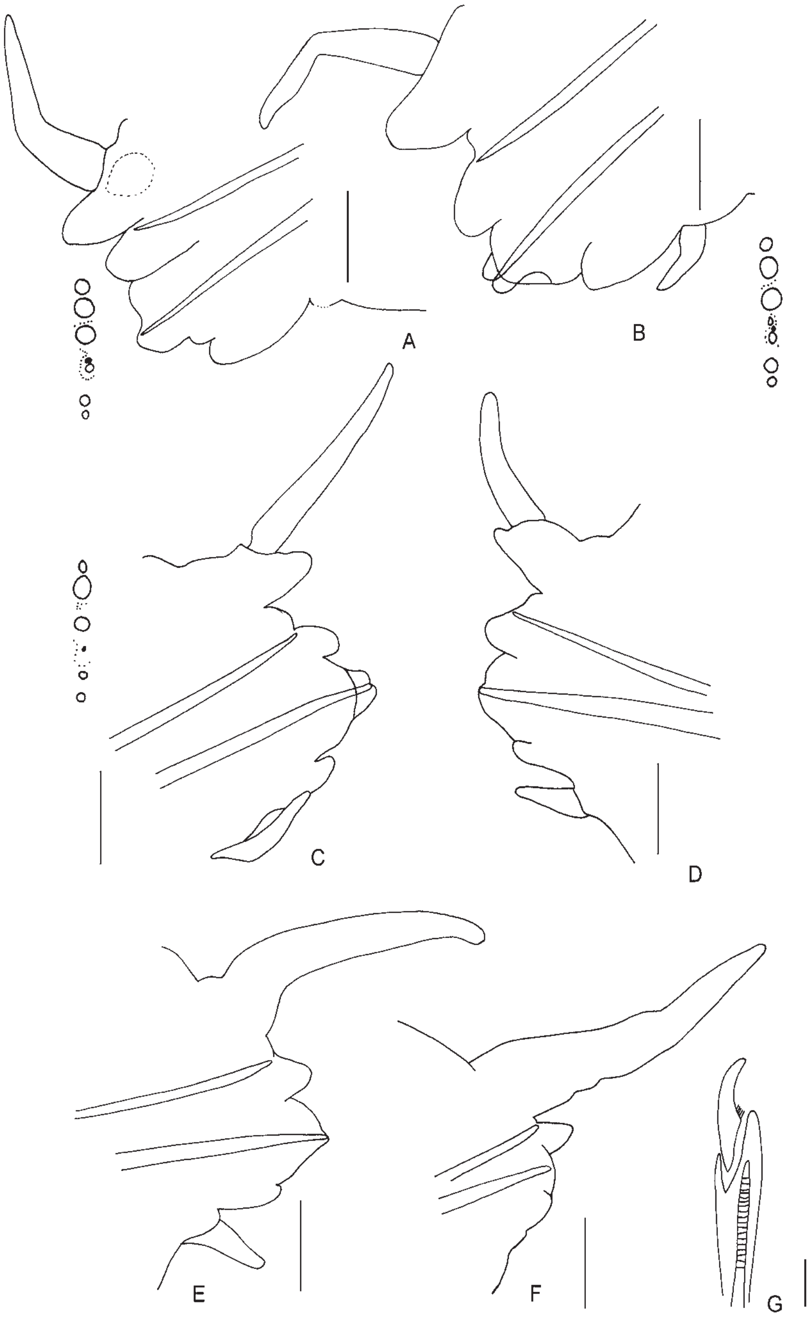

Figure 8. *Pseudonereis cortezi* (Kudenov, 1979) paratype NHMLAC Poly-1344. A, parapodium 3rd chaetiger anterior view. B, parapodium 11th chaetiger anterior view. C, parapodium 30th chaetiger posterior view. D, parapodium 50th chaetiger anterior view. E, parapodium 65th chaetiger posterior view. F, parapodium 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.

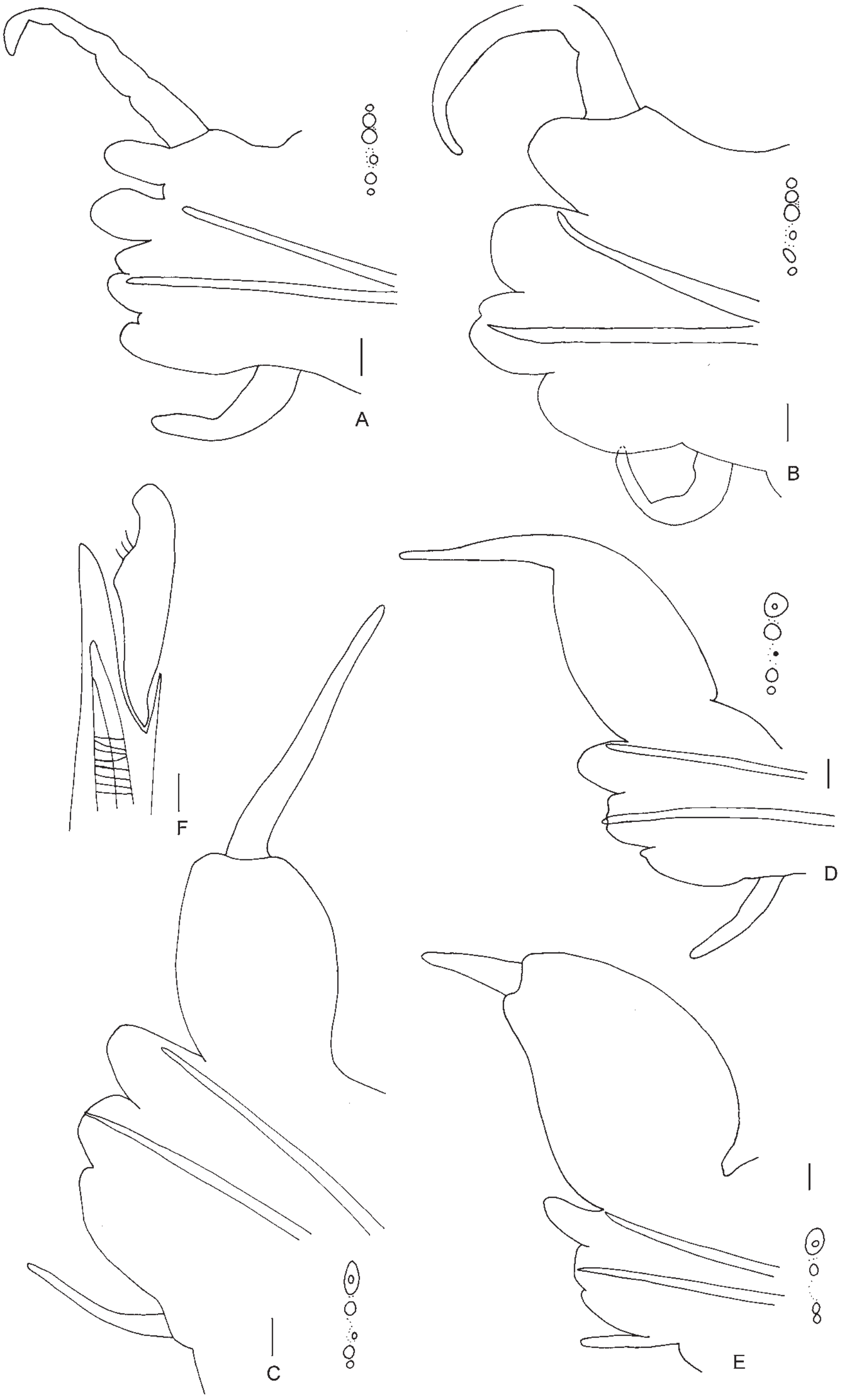

Figure 9. *Pseudonereis gallapagensis* Kinberg, 1865 syntype of *Pseudonereis formosa* Kinberg, 1865 SMNH Type-5908. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 50th chaetiger anterior view. E, parapodium 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.

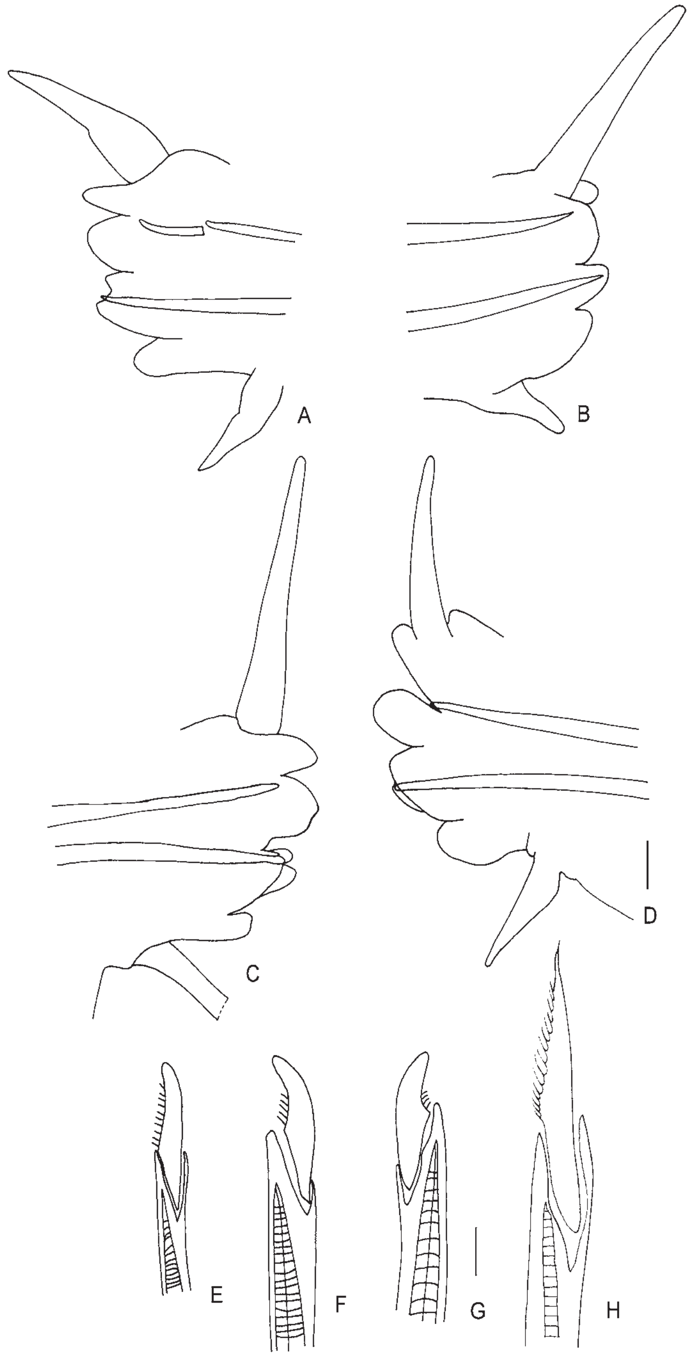

Figure 10. *Pseudonereis multisetosa* Hartmann-Schröder, 1992 holotype ZMH P-20706. A, parapodium 5th chaetiger anterior view. B, parapodium 12th chaetiger anterior view. C, parapodium 20th chaetiger posterior view. D, parapodium 56th chaetiger posterior view. E, homogomph falciger neuropodial dorsal 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).

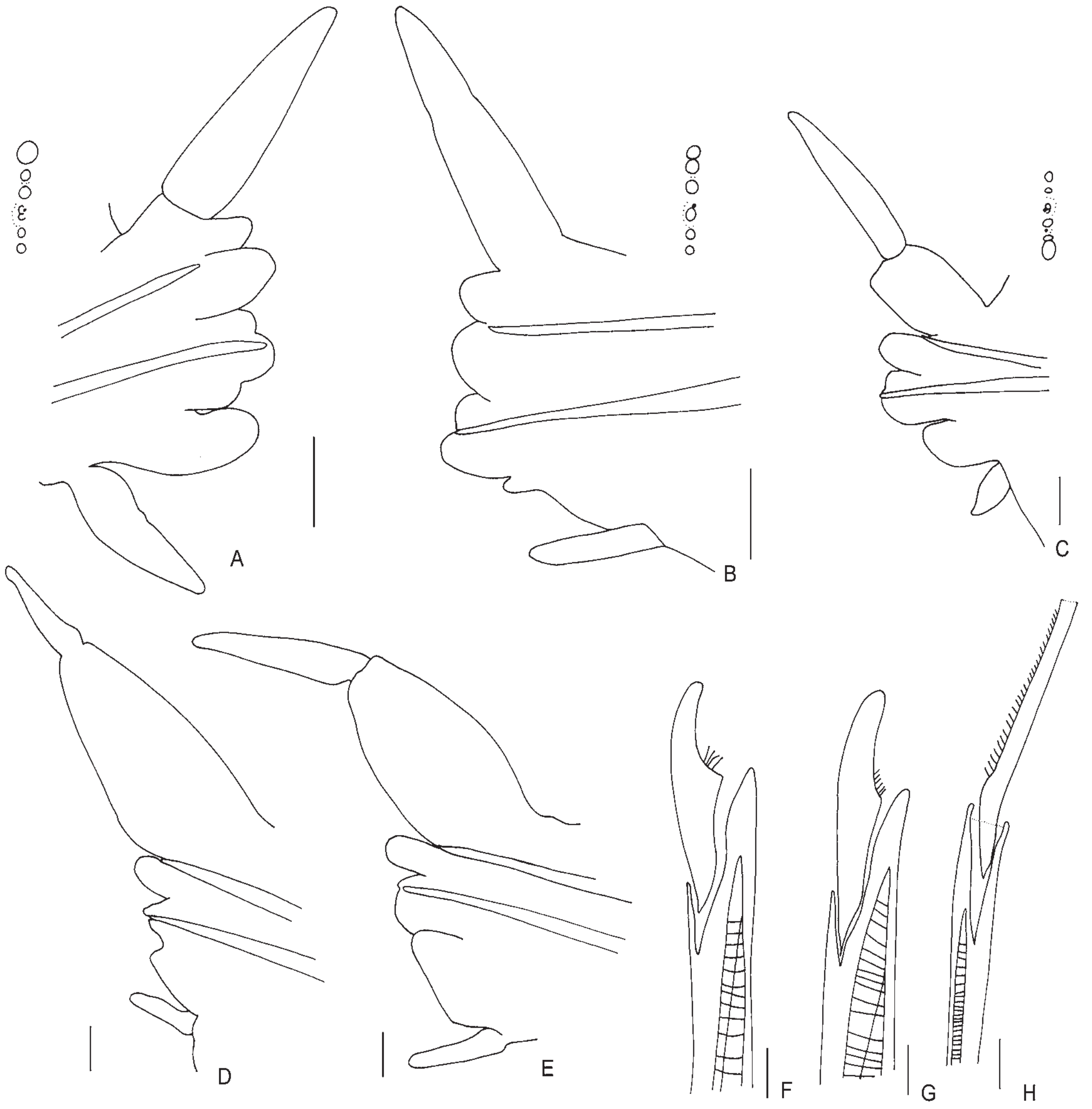

Figure 11. *Pseudonereis noodti* (Hartmann-Schröder, 1962) holotype HZM P-14380. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 20th chaetiger anterior view. D, parapodium 58th chaetiger anterior view. E, parapodium 42nd chaetiger posterior view. 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.

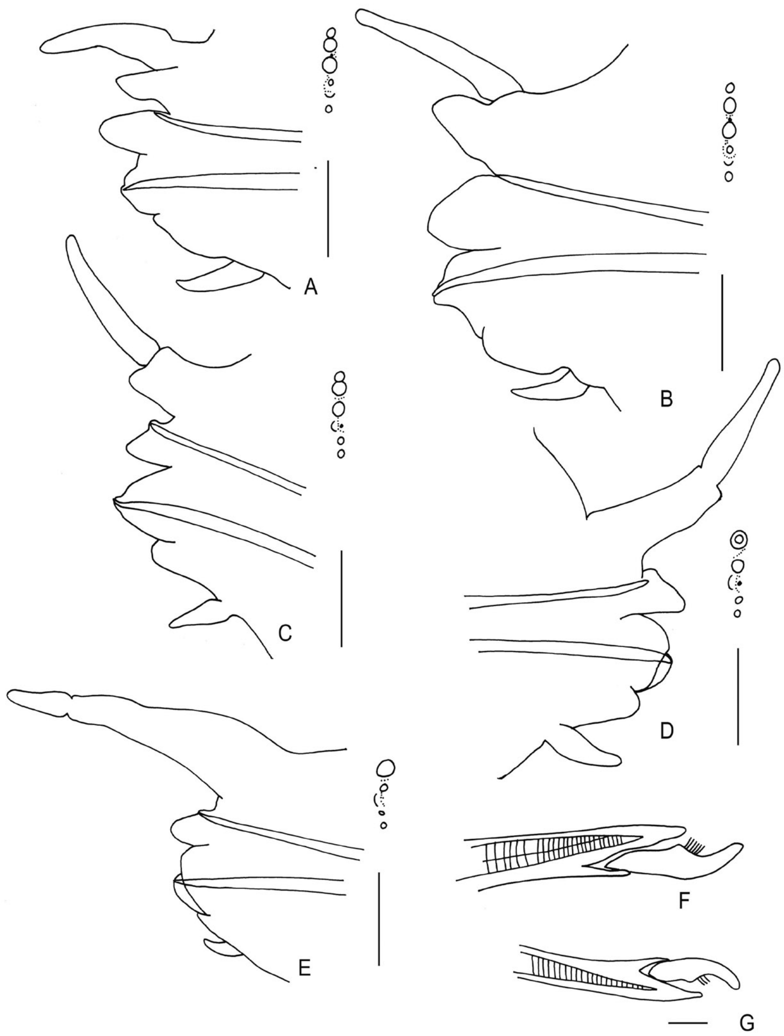

Figure 13. *Pseudonereis pseudonoodti* (Fauchald, 1977) paratype USNM 53091. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 40th chaetiger posterior chaetiger. E, parapodium 50th chaetiger anterior view. 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-G 0.01 mm.

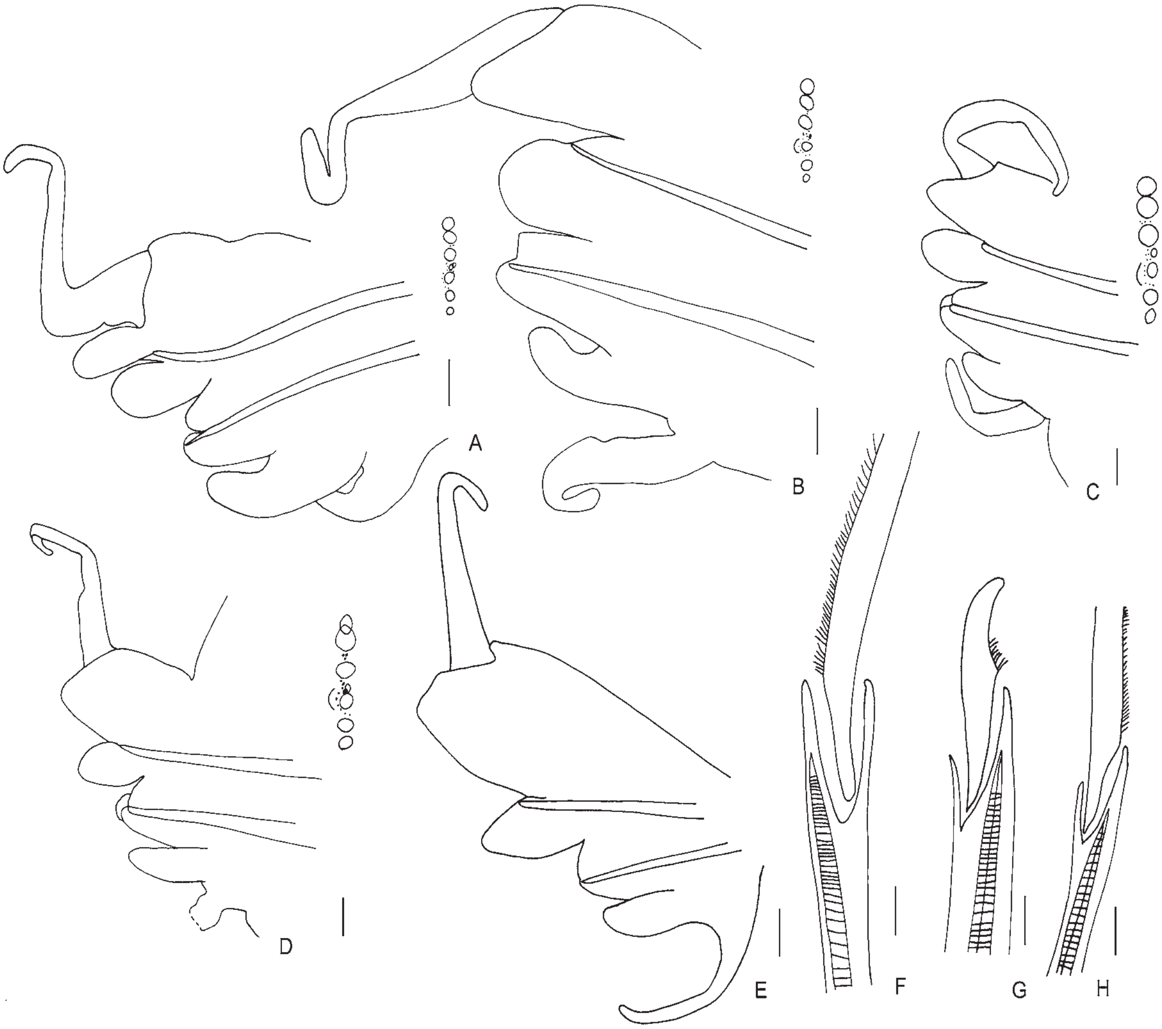

Figure 14. *Pseudonereis rottnestiana* Augener, 1913 syntype ZMH V7929. A, parapodium 3rd chaetiger anterior view. B, parapodium 10th chaetiger anterior view. C, parapodium 27chaetiger anterior view. D, parapodium 40th chaetiger. E, parapodium 61st chaetiger anterior view. E, homogomph spiniger neuropodial dorsal fascicle 27th chaetiger. F, heterogomph falciger neuropodial ventral fascicle 61st chaetiger. G, heterogomph spiniger neuropodial ventral fascicle 61st chaetiger. End-view drawings of parapodia in A-D are not to scale. Scale bar in A-B, E 0.1 mm, C-D 0.5 mm, F-G 0.01 mm.

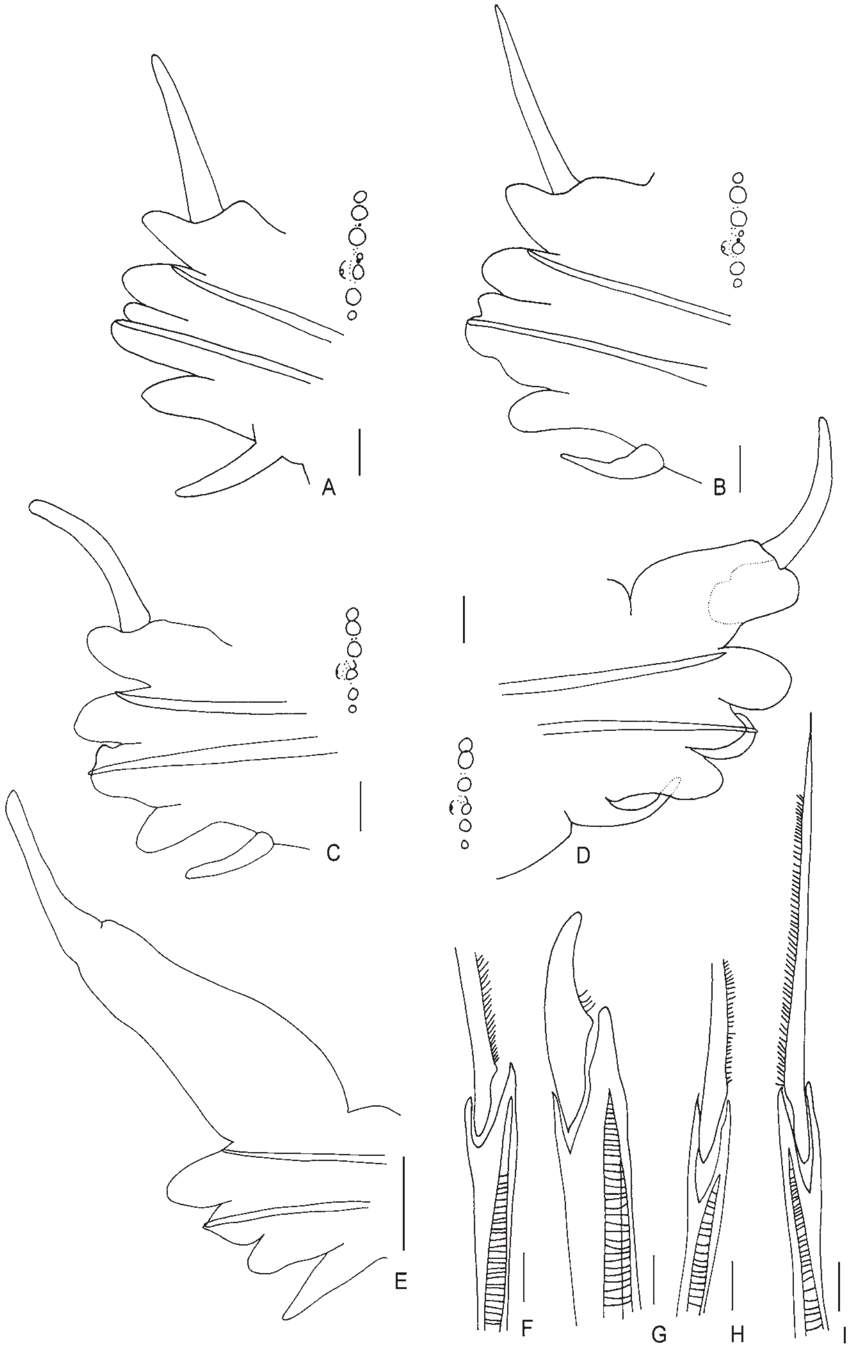

Figure 15. *Pseudonereis trimaculata* Horst, 1924 ZMH P-16567. A, parapodium 3rd chaetiger anterior view. B, parapodium 11th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 50th chaetiger posterior view. E, parapodium 65th chaetiger anterior view. F, heterogomph spiniger 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.

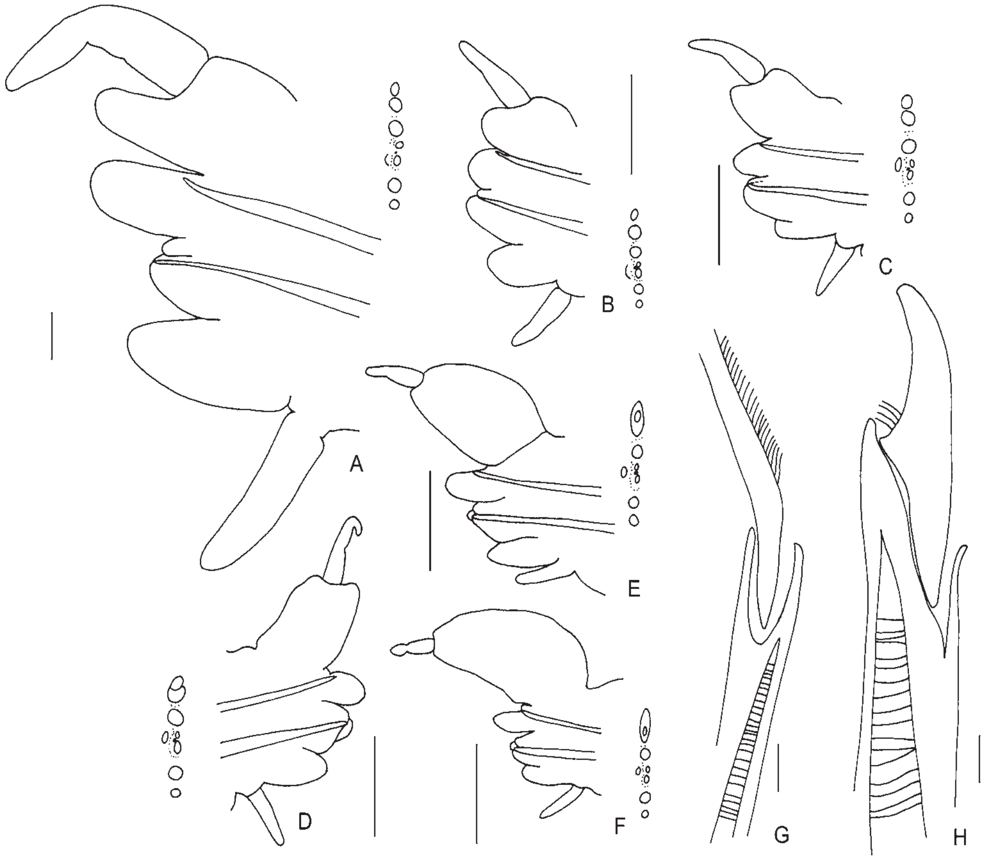

Figure 17. *Pseudonereis variegata* (Grube, 1857) syntypes of *Nereis ferox* Hansen, 1882 ZMUB 2130. A, parapodium 3rd chaetiger anterior view. B, parapodium 11th chaetiger anterior view. C, parapodium 30th chaetiger anterior view. D, parapodium 40th chaetiger posterior view. E, parapodium 56th chaetiger 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-H 0.01 mm.

Doctoral theses in Biology
Norwegian University of Science and Technology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of Pisum sativum and Arabidopsis thaliana
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (Triturus, Amphibia) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook Corvus frugilegus.
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984		Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (Trichoptera) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders Oweniimorpha and Terebellomorpha, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit Parus montanus.
1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of Nicotiana sanderae and Chrysanthemum morifolium
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (Salmo salar): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (Mytilus edulis).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (Salmo salar L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose Alces alces.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose Alces alces, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (Salmo salar) and brown trout (Salmo trutta): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie Pica pica.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (Lynx lynx) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout Salmo trutta and roach Rutilus rutilus in particular.

1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera Coregonus and Salvelinus: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (Phleum pratense L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins Fratercula arctica
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, Salmo salar L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter Lutra lutra.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (Gallinago media): Male mating success and female behaviour at the lek.

1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant Phalacrocorax carbo carbo.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (Rubus idaeus L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, Vulpes vulpes.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss Dicranum majus Sm. as influenced by nitrogen supply
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter Lutra lutra distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink Mustela vision.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel Thalassoica antarctica; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of Mysis relicta and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the Schistidium apocarpum complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (Salmo salar) and Arctic charr (Salvelinus alpinus): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.

1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of Mytilus edulis and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal Halichoerus grypus and Harbour seal Phoca vitulina in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer Brachionus plicatilis quality in early first feeding of turbot Scophtalmus maximus L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper Cinclus cinclus in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (Hylobius abietis), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in Acinetobacter calcoacetius.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (Salvelinus alpinus (L.)) and brown trout (Salmo trutta L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (Salmo salar) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
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