



A review of paragnath morphology in Nereididae (Polychaeta)

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Abstract

The form and arrangement of hardened paragnaths on the pharynx of polychaetes in the family Nereididae has for 150 years been used as a principal system of characters to distinguish species and other taxonomic ranks. Recent studies have shown that phylogenetic relationships based solely on paragnaths give different topologies and clade support than relationships inferred from other character systems. Furthermore, recent revisions and species descriptions continue to increase the range of known paragnath forms. We provide the first comprehensive overview of these important morphological characters, with the aim of encouraging more consistent observation and use of a standardized terminology in future studies. Illustrated descriptions and definitions of all known paragnath types are presented and compared. New terminology is introduced to improve description of paragnath types. Hypotheses are proposed for the chemical composition of paragnaths (scleroprotein), homology between different paragnaths types, and earlier studies implicitly proposing the homology of scleroprotein paragnaths with the more plesiomorphic pharyngeal soft papillae are addressed.

Key words: homology, character evolution, paragnaths, pharyngeal armature

Introduction

Paragnaths are hard denticles that occur in regular patterns on the muscular eversible pharynx of many taxa in the polychaete family Nereididae. The term paragnath was coined by Malmgren (1867) when he used “paragnathi,” including an etymological explanation in Greek, as a part of the diagnosis of *Nereis* L., 1758. However, it was Kinberg (1865) who first instituted a systematic description of the structures now known as paragnaths in Nereididae. Since then, paragnaths and soft papillae (which may occur in place of paragnaths in some taxa) have provided important and readily quantifiable characters for description, classification, and identification of Nereididae. Despite the wide use of paragnaths in systematic studies of the Nereididae, detailed descriptions or definitions of the different paragnath types have never been presented. New forms of paragnaths have usually been described as a part of descriptions of the species in which they were first encountered. Publications synthesizing taxonomic information of Nereididae or a geographical region have sometimes included a short comparative description or a figure of relevant paragnath types (e.g., Day 1967), but there is no complete overview. Phylogenetic analyses (Bakken & Wilson 2005; Fitzhugh 1987; Santos et al. 2005) have given increasing attention to the diversity of forms of paragnaths as a contribution towards an understanding of evolution in the Nereididae. The aim of this paper, then, is to survey the diversity of paragnath forms in the Nereididae and to present definitions of different

paragnath types. We also discuss briefly the soft papillae which occur in place of paragnaths in some nereidid taxa and further develop the hypothesis that scleroprotein paragnaths and soft papillae are homologous structures. This is an idea that surprisingly appears not to have been elucidated previously, although it was implicit in the phylogenetic study of Glasby (1991), and may have been recognized as early as Kinberg (1865) who wrote about pharyngeal armature as hard papillae (paragnaths) and soft papillae.

Classification of Nereididae based on paragnaths. Kinberg (1865) established a system where he assigned numbers for different areas on the pharynx to facilitate descriptions of paragnath and papillae distribution. The high diversity of the nereidid material from the Swedish "*Eugenie* around the world expedition 1851-1853", in which Kinberg participated (Kinberg 1910), made it possible for him to see variation in pharyngeal armature across a greater range of nereidid taxa than had been available to any earlier worker. Kinberg recognized that paragnaths occurred in regular patterns and found it convenient to delineate the pharynx in different Areas designated by the Roman numerals I to VIII. Areas I–IV are located near the jaws and are known as the "maxillary ring" while Areas V–VIII are located near the mouth (when the pharynx is retracted) and are known as the "oral ring." Kinberg's system has been used in all subsequent taxonomic descriptions of Nereididae. It has been convention to refer to the Areas with Roman numerals. Due to the most common distribution pattern of paragnath Areas VII and VIII are usually referred to as one (Area VII–VIII) in descriptions. Originally Kinberg (1865) used Arabic numerals, which is also indicated in his illustrations (Kinberg 1910) (Fig. 1), but he used Roman numerals in a chart for delineation of nereidid genera.

Kinberg (1865) used his pharyngeal system to erect new families from nereidiform taxa, but this was soon to be changed by Malmgren (1867). Malmgren synonymized Kinberg's new families with Nereididae, and presented a key with brief diagnoses in Latin to all genera found in the North Atlantic. Ehlers (1868) was of the opinion that Kinberg and Malmgren had been too generous with their recognition of 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*. The concept of using subgenera of *Nereis* is not supported by phylogenetic analyses (Fitzhugh 1987; Bakken & Wilson 2005; Santos et al. 2005).

Classification of Nereididae into subfamilies was introduced by Corrêa (1948) and was later followed by Hartman (1959), Pillai (1961) and Banse (1977), mainly based on groups without paragnaths and papillae, and those with papillae. The nominative subfamily was formally defined phylogenetically by Fitzhugh (1987). Traditionally, taxa with paragnaths have been considered belonging to Nereidinae and taxa with papillae to Gymnonereidinae. This classification has lately been questioned (Bakken & Wilson 2005; Santos et al. 2005).

The arrangement and form of paragnaths have been defined in detail and used to define genera (e.g., Fauchald 1977), and to establish subgroups in obviously heterogeneous genera, combined with other characters. A small set of defined paragnath types is available from this literature, but recent publications have shown that the range of morphological variation in paragnaths is much greater and there is now a need to re-assess the range of paragnath morphology and to provide a standard terminology for descriptions of taxa in Nereididae.

Hardened paragnaths. Despite the occurrence of paragnaths in many Nereididae and their importance in taxonomic descriptions, we are unaware of any published information on the chemical composition of paragnaths or on the physiological basis of their formation. The pharynx of all Nereididae terminates with a pair of jaws (Fig. 1) that, like the paragnaths, are visible only when the pharynx is fully everted (or dissected). In the absence of any published information on the chemistry or genesis of paragnaths, we discuss and extrapolate from studies of the chemistry of the other hard pharyngeal structure in Nereididae, the jaws.

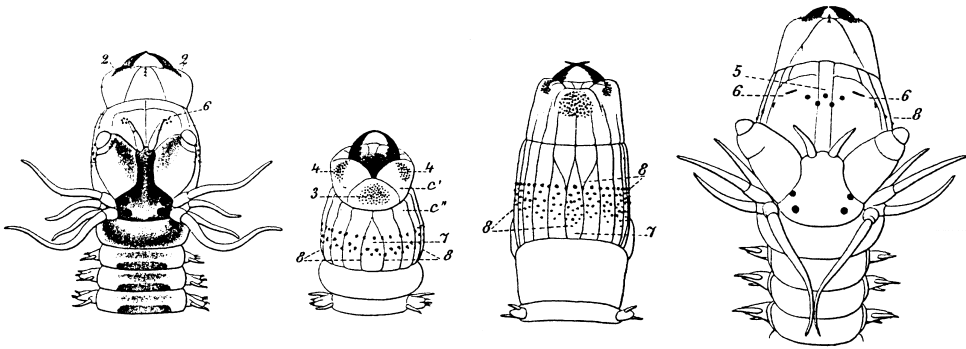


FIGURE 1. The original illustrations Kinberg (1865) used to delineate Areas to describe pharyngeal armature in nereidids. Areas I–IV are placed on the maxillary ring and Areas V–VIII on the oral ring. (after Kinberg 1910, plate XX).

Nereididae jaws and paragnaths (sometimes called “denticles”) are described as chitinous by many invertebrate biology texts (e.g., Marshall & Williams 1972), apparently due to their similarity to insect chitin. However, Voss-Foucart et al. (1973) showed that, at least in *Perinereis cultrifera* (Grube, 1840), there is no chitin present in the jaws, which are instead comprised substantially of scleroprotein. Zinc, a prominent trace metal especially at the tip of the jaws, is actively accumulated from zinc-rich sediments (Bryan & Gibbs 1979; Elfman et al. 1999; Eriksson & Elfman 2000). The scleroprotein composition of nereidid jaws means that they are highly susceptible to chemical oxidation processes occurring in sediments after the death of the worm (Colbath 1986; 1988). Thus polychaete jaws (scolecodonts) attributable to Nereididae are absent, or at least rare, in the fossil record (Fitzhugh 1997; Szaniawski 1974). Epidermal secretion of scleroproteins is widespread in the Polychaeta and occurs during chaetogenesis, and in the production of the sclerotinized cuticular lining of the eversible pharynx of Amphinomidae and Euphrosinidae (Rouse 2000; Rouse & Pleijel 2001). We predict that paragnaths will be found to have similar scleroprotein chemistry to nereidid jaws, perhaps hardened by zinc as a trace metal, especially in species where feeding behavior brings paragnaths in contact with hard substrates.

Paragnaths are easy to observe and count, except in very small specimens, and they have thus been widely used to quantify variation within and between populations and species of Nereididae. A comprehensive review of this literature is beyond the scope of this paper, but summary of selected studies indicates the range of topics that have used paragnath data. Ecological variation between populations of *Hediste diversicolor* (O.F. Müller, 1776) was investigated by Barnes (1978) and Barnes & Head (1977) who showed that populations from mud sediments have fewer paragnaths than those from coarser sands. Wilson (1993) showed the same phenomenon in *Perinereis vallata*, and Khlebovich and Komendantov (2002) showed that such patterns of intraspecific variation are stable over time. Virgilio et al. (2006) investigated *H. diversicolor* populations using molecular techniques and showed patchiness of populations is at a smaller scale than had been indicated by paragnath data alone. Paragnath data have been quantified and analyzed using multivariate statistics to delimit species (Glasby & Hsieh 2006; Wilson & Glasby 1993) as well as for investigating intraspecific patterns (Maltagliati et al. 2006) and both morphological and allozyme data have been used alongside paragnath counts to provide independent verification of species limits (Fong & Garthwaite 1994; Scaps et al. 2000; Wilson 1984; 1993). In the genus *Platynereis*, however, paragnaths have been shown to be of little or no use in species discrimination (Hutchings & Reid

1991; Read 2007). Understanding of the significance of variation in paragnath numbers generated from these and other studies now give us confidence, and limits, to the use of paragnath counts and morphology in phylogenetic analyses (Bakken & Wilson 2005; Santos et al. 2005).

Biologists presume that the utility of paragnath data in population and systematic studies of nereidid worms reflects the utility of paragnaths to the worms themselves. However, there are few published studies on the functional significance of paragnath morphology, nor is there a convincing demonstration of a strong relationship between paragnath morphology and diet or feeding mode. Those studies that are available offer contrary and unexpected results. Maltagliati et al. (2006) performed a factor analysis of paragnath counts in *H. diversicolor* populations and hypothesized that the two bands of paragnaths forming the oral and maxillary rings operate as separate functional units in feeding; however, this remains untested. Pardo & Dauer (2003) compared the diet of *Neanthes succinea* (Leuckart, 1847) (now *Alitta succinea*) populations; although they did not compare paragnath morphology the populations came from widely differing habitats yet all were found to be deposit feeders with little diet discrimination between habitats. Other studies have shown that variability within species equals or exceeds that seen between species (Goerke 1966; 1971); these observations include switching between filter-feeding and deposit feeding modes by individual specimens of *H. diversicolor*. The grouping of paragnaths denoted by the Areas I–VIII is a regular pattern common to hundreds of species of Nereididae for which we are inclined to seek an adaptive explanation based on functional morphology. However, the available studies suggest that there is no functional significance to lesser variations in paragnath morphology, either between or within species, and the question remains open.

Soft papillae. Many nereidid species have soft papillae in place of paragnaths on the eversible pharynx (a few taxa have both paragnaths and papillae). Small papillae have been observed in juveniles of *Namanereis amboinensis* (Pflugfelder, 1933) (Glasby 1999), but all other species with papillae have traditionally been classified in the subfamily Gymnonereidinae, until recent results by Santos et al. (2005) suggested an alternative classification. As with paragnaths, different forms of papillae have been described, but papillae that are not completely soft and instead have partly sclerotized tips are relevant in the context of this review of paragnath morphology. Taxa with partly sclerotized papillae have been reported in *Leonnates* spp. (Fig. 5B) and *Paraleonnates* spp. (Hutchings & Reid 1991; Qui & Qian 2000), and in *Neanthes glandicincta* (Southern, 1921) (TB & CJG pers.obs.). *Australonereis ehlersi* normally has only soft papillae, but Hutchings & Reid (1990) found some specimens to have partly sclerotized papillae. Partly sclerotized papillae are not well understood, but their existence is consistent with our hypothesis of homology between pharyngeal papillae and paragnaths in Nereididae.

Materials and methods

Data on different paragnath types are taken mainly from material referred to in Wilson (1985), Wilson & Glasby (1993), Bakken & Wilson (2005), Glasby & Hsieh (2006), and Bakken (2007). Specimens from these studies have been re-examined when necessary, as well as additional material not previously studied.

The following abbreviations for institutions are used: AM, The Australian Museum, Sydney, Australia; NTM (Museum and Art Gallery of the Northern Territory, Darwin, Australia).

Observations were made using a Nikon SMZ 1500 dissecting microscope and a Nikon Eclipse 80i compound microscope. A QImaging Micropublisher 5.0 MPixel digital camera was used to take image ‘stacks’ which were combined using Helicon Focus software.

Results

Definitions and description of paragnath types. Two main types of paragnaths were recognized according to the dimensions of the base: uniform-base paragnaths have a circular or quadrangular base in a roughly 1:1 breadth/length ratio and rectangular-base paragnaths have a base breadth/length ratio of usually more than 2:1. This distinction is purely utilitarian and does not necessarily reflect character phylogeny. Each of these two main types of paragnaths have several subcategories, which are defined below.

A summary of paragnaths is intended to group different types and together with the definitions and description should help in the identification of each type, and assist with observations of new character information on paragnaths.

Uniform-base paragnaths

Pyramidal paragnaths have a quadrangular base with a pointed apex (Fig. 2A). They were first described in species from the *Perinereis nuntia*-group (Glasby & Hsieh 2006), and resemble conical paragnaths except for the approximately quadrangular base.

Conical paragnaths have a circular base and are tapered towards an apex (Fig. 2B). Size and height is variable and those on the maxillary ring in particular are often skewed in a direction towards a pointed apex. Some appear stout with the apex tipped over, others are small and blunt. Conical paragnaths are the most common paragnath type in nereidids (Bakken & Wilson 2005).

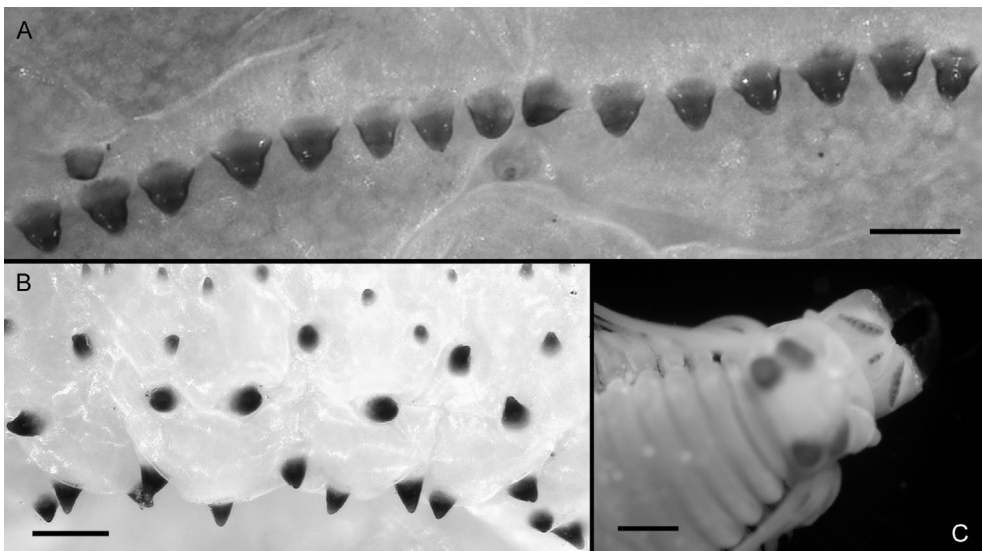


FIGURE 2. A, Pyramidal paragnaths in *Perinereis rhombodonta* (NMT W19038), Areas V and VI; B, conical paragnaths in *Perinereis akuna* (NTM W19028), Areas VII and VIII; C, melted paragnaths as they appear in *Nereis (Ceratonereis) ramosa* (syntype, ZMA VPol909), Areas I and II. Scale bars: A, B = 0.1 mm; C = 0.5 mm. Photos: A. Rose (A, B); C. Glasby (C).

Melted paragnaths are considered tentatively as a subtype of conical and are found occasionally in some specimens/species (Fig. 2C). These are here considered to be a sub-category of conical paragnaths because (1) they are often found in epitokes (of various species), and (2) when they have

been observed to be a non-sexually acquired feature they co-occur with "normal" conical paragnaths in the maxillary ring (the maxillary ring usually carries only one type of paragnath.)

Rod-like paragnaths have a circular base and are long and slender, more or less evenly shaped to the apex (Fig. 3A). Rod-like paragnaths were first described by Gibbs (1971) for *Solomononereis* and its type species, *Solomononereis marauensis* Gibbs, 1971. Later, Nateewathana (1992) reported this paragnath type in *S. phuketensis*, where he also described it in more detail. Nateewathana also used the term *cones* in his species description but he pointed specifically to the distinctive difference to the cones reported from *Ceratonereis* species. The rod-like paragnaths were also called *pegs* by Hutchings & Reid (1991). In *Solomononereis* species rods are arranged in dense clusters or in groups (Fig. 3A) (Nateewathana 1992).

It is demonstrated here for the first time that paragnaths in *Platynereis* species also are rods placed in tight lines or rows (Fig. 3B–C). These paragnaths have usually been called "pectinate bars" implying bar-shaped paragnaths with bases of varying length, and with cusps or denticles along the bar, resembling a serrated edge. Being rods in close lines these paragnaths should be described with their proper name (rods), as suggested here, where the lines or rows denote distribution patterns. Rows may be short or long. The appearance of the previously described "pectinate bars" actually being rods in tight rows are in this study confirmed for three species: *Platynereis polyscalma* Chamberlin, 1919 (Fig. 3B), *P. antipoda* Hartman, 1954 (Fig. 3C) and *P. dumerilii* Audouin & Milne-Edwards, 1833.

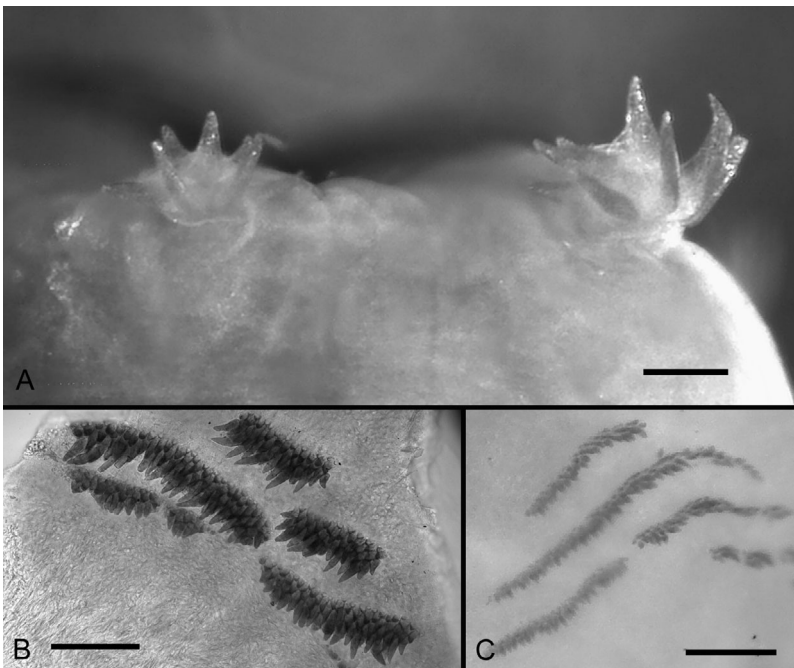


FIGURE 3. A, Rod-like paragnaths in *Solomononereis maurauensis* (NTM W19001), Areas I and II; B, rod-like paragnaths in rows, in *Platynereis polyscalma* (NTM W19031), Area IV; C, rod-like paragnaths in short and long rows in *Platynereis antipoda* NTM W17249, Area IV. Scale bars = 0.1 mm. Photos: A. Rose.

Rectangular-base paragnaths

Also referred to as *bar-shaped* paragnaths, these are long and elongated with a more or less rectangular base. A bar has a base in a length-breadth ratio greater than 1:1 and usually more than 2:1. Length of the bars varies from short to long. Bars of different lengths are often observed in the same Area, but they may also be consistent in size. Different types of bar-shaped paragnaths have been described.

Smooth bars are bars with a flat top (Fig. 4A). They have been described as a characteristic for Area VI paragnaths for species belonging to *Perinereis* (Hutchings et al. 1991). Since we here define different types of bar-shaped paragnaths, the traditional "*Perinereis*-bars" should be referred to as "smooth bars." Smooth bars are also common in Area IV in a range of *Perinereis* and other taxa (Wilson 1984; Bakken & Wilson 2005).

Shield-shaped bars are laterally compressed high bars protruding from the base towards a pointed or a rounded apex (Fig. 4B). This bar shows resemblance to a shield projecting from the tissue. This paragnath type was described by Bakken (2007) for Area VI paragnaths of *Pseudonereis* species; prior to that they were simply referred to as bar-shaped. Shield-shaped bars are also present in the group of *Perinereis* species having a single Area VI paragnaths (CJG pers. obs.).

P-bars (pointed bars) are small bars having a protruding apex in one end of the bar (Fig. 4C), and were observed in most *Pseudonereis* species in Areas II, III, IV and VII-VIII (Bakken 2007). P-bars are observed in variable length, and are often present in combination with conical paragnaths.

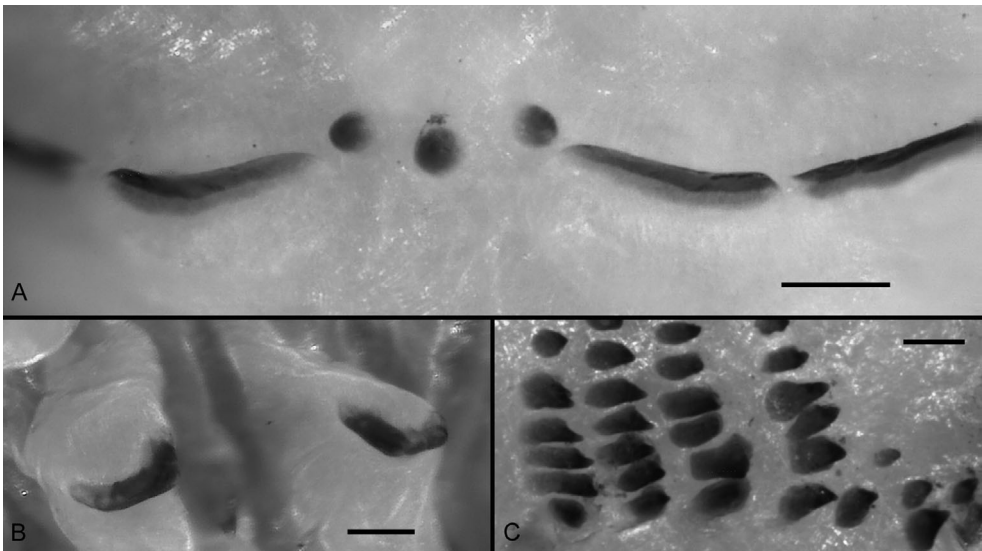


FIGURE 4. A, Smooth bars in *Perinereis vancaurica* (NTM W19000), Areas V and VI; B, shield-shaped bars in *Pseudonereis trimaculata* (NTM W19035), Areas V and VI; C, P-bars of variable length in *Pseudonereis anomala* (NTM W17343), Area IV. Scale bars = 0.1 mm. Photos: A. Rose.

Ambiguous partly sclerotized papillae

Crown-shaped paragnaths are tiny crown-shaped structures with a rectangular base, each crown-shaped paragnath having a number of minute cusps (Paxton 1983). Crown-shaped paragnaths are unique to *Micronereis* species. They are not fully sclerotized. Paxton (1983) reported an ontogenetic

development from small conical paragnaths in juveniles to crown-shaped paragnaths in adults. Based on observations in this study (Fig. 5A) and by colleagues (G. Read pers. comm.), paragnath diversity in *Micronereis* species may encompass more than just one type. Compressed flat paragnaths (Fig. 5A) have never before been observed, and they prove to be different from all other reported paragnath types. Paragnaths in *Micronereis* species alone warrant further study.

Partly sclerotized papillae are soft papillae with a hard sclerotized tip, and are not considered to be paragnaths, as mentioned above.



FIGURE 5. A, Paragnaths in *Micronereis halei* (AM W31042), ?Areas VII and VIII. B, partly sclerotized papillae from *Leonnates* cf. *indicus* (NTM W212), Areas I and II. Scale bars: A = 20 μ m; B = 0.1 mm. Photos: C. Glasby (A); A. Rose (B).

Discussion

Both paragnaths and papillae have been assumed to be used in feeding, but we are unaware of any study that has observed how these structures function during feeding. If the worm grasps food with the jaws, then retracts the pharynx, the maxillary paragnaths, or papillae, presumably provide an increasingly secure grasp of the food item as the pharynx retracts. This function was pointed out by Barnes & Head (1977) in their study of *Hediste diversicolor* but is likely to hold for all species of Nereididae that feed in this way. However, paragnaths, at least, are also used in burrowing, and Dales (1963), again studying *Hediste diversicolor*, observed that the pharynx is only everted far enough to expose the oral ring during burrowing. One prediction arising from this observation is that paragnath numbers on the oral ring should vary independently of those on the maxillary ring, and this was found to be so by Barnes & Head (1977).

If the functional difference between the oral and maxillary rings of the pharynx is a general phenomenon in Nereididae, then those functions should be best differentiated in taxa which show the greatest morphological divergence between oral and maxillary rings. Such taxa are those that have both papillae and paragnaths on the pharynx. In species belonging to *Leonnates* and *Periserrula*, it is usual that papillae are found on the oral ring and paragnaths on the maxillary ring, but in some *Leonnates* species paragnaths and papillae co-occur on the maxillary ring (Qui & Qian 2000). *Imajimainereis pacifica* was described having paragnaths on both rings and also papillae in Areas VII–VIII on the oral ring (de León-González & Solís-Weiss 2000). These taxa would be interesting candidates for studies of the functional basis of feeding and burrowing behavior in relation to pharynx morphology.

The hypothesis that scleroprotein paragnaths and soft papillae are homologous structures could be tested by seeking observations of serial homology (development during ontogeny of paragnaths to papillae or vice versa), or by congruence in a parsimony analysis, since homology is effectively a statement of synapomorphy (de Pinna 1991; Patterson 1982). Phylogenetic analyses by Fitzhugh (1987) and Glasby (1991) indicate the following serial homology for pharynx characters: pharynx lacking papillae and paragnaths → pharynx with papillae → pharynx with paragnaths. Glasby's (1993) analysis included only a few taxa with paragnaths and did not focus on investigating phylogeny within the family. Further phylogenetic analyses by Bakken & Wilson (2005) and Santos et al. (2005) did not support the polarity demonstrated by Fitzhugh (1987) and Glasby (1991), but both analyses were inconclusive with regard to this question due to large amounts of homoplasies. The transformation series from bare pharynx to papillae to paragnaths remains the best available hypothesis on pharyngeal armature in Nereididae but is open to testing in future analyses.

Based on previous results mentioned here we can suggest some hypotheses on homology and character evolution in papillae and paragnaths as pharyngeal armature in nereidids:

- Paragnaths and papillae are homologous
- Papillae is plesiomorphic relative to paragnaths

Many clades or genera of Nereididae appear not to be definable on the basis of paragnath type alone. Exceptions are *Pseudonereis*, which is the only taxon having P-bars, and *Micronereis*, the only taxon having crown-shaped paragnaths. Of course this probably reflects the inadequacy of the current classification of the group as much as the value of paragnath type as a phylogenetic character.

Nevertheless, with paragnath types now explicitly formulated, recognition and documentation for both taxonomic and phylogenetic purposes should be easier. We predict that future phylogenetic studies will find more clades having paragnath synapomorphies and will then provide more knowledge for homology assessments and studies of character evolution. In this way the suggested hypotheses can be tested, including that at least some of the different shaped paragnaths have evolved from sclerotization of similarly-shaped papillae.

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