Revision of the Antipatharia (Cnidaria: Anthozoa). Part I. Establishment of a new family, Myriopathidae

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Opresko, D.M. Revision of the Antipatharia (Cnidaria: Anthozoa). Part I. Establishment of a new family, Myriopathidae.
Zool. Med. Leiden 75 (17), 24.xii.2001: 343-370, figs. 1-18.— ISSN 0024-0672.
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Key words: Cnidaria; Anthozoa: Antipatharia; Myriopathidae fam. nov.; *Myriopathes* gen. nov.; *Cupressopathes* gen. nov.; *Plumapathes* gen. nov.; *Antipathella* Brook; *Tanacetipathes* Opresko.
A new family of antipatharian corals, Myriopathidae (Cnidaria: Anthozoa: Antipatharia), is established for *Antipathes myriophylla* Pallas and related species. The family is characterized by polyps 0.5 to 1.0 mm in transverse diameter; short tentacles with a rounded tip; acute, conical to blade-like spines up to 0.3 mm tall on the smallest branchlets or pinnules; and cylindrical, simple, forked or antler-like spines on the larger branches and stem. Genera are differentiated on the basis of morphological features of the corallum. *Myriopathes* gen. nov., type species *Antipathes myriophylla* Pallas, has two rows of primary pinnules, and uniserially arranged secondary pinnules. *Tanacetipathes* Opresko, type species *T. tanacetum* (Pourtalès), has bottle-brush pinnulation with four to six rows of primary pinnules and one or more orders of uniserial (sometimes biserial) subpinnules. *Cupressopathes* gen. nov., type species *Gorgonia abies* Linnaeus, has bottle-brush pinnulation with four very irregular, or quasi-spiral rows of primary pinnules and uniserial, bilateral, or irregularly arranged higher order pinnules. *Plumapathes* gen. nov., type species *Antipathes pennacea* Pallas, has simple pinnules arranged regularly in two rows. *Antipathella* Brook, type species *Antipathes subpinnata* Ellis and Solander, has simple branchlets/pinnules arranged irregularly in one to four rows.

Introduction

The classification of the antipatharian corals has for many years been complicated by: (1) the establishment of numerous species and genera based on limited and often incomplete specimens; (2) the lack of a clearly defined taxonomic hierachy at the genus and family level; and (3) the inclusion of several non-antipatharian groups such as *Gerardia* Lacaze Duthiers (1864) and *Dendrobrachia* Brook (1889). The identification of *Gerardia* as a zooanthid (Carlgren, 1895) and *Dendrobrachia* as an octocoral (Opresko and Bayer, 1991) has resulted in the recognition of the Antipatharia as a rather homogenous group of colonial anthozoans defined by a spiny skeletal axis and polyps with six tentacles, six primary mesenteries, and either zero, four or six secondary mesenteries.

Over the years, several classification schemes have been proposed for the order, including those of Milne Edwards and Haime (1857), Brook (1889), Schultze (1896), Roule (1905) and van Pesch (1914). In one of the last major taxonomic revisions, van Pesch (1914) grouped all species (except *Dendrobrachia fallax* Brook) into a single family, the Antipathidae Ehrenberg (1834). Later workers, however, have recognized three families; the Cladopathidae, Schizopathidae, and Antipathidae (see Pax, 1987), and a fourth family, the Leiopathidae Haeckel (1896) is recognized by Opresko (1998). In the Cladopathidae Brook (1889) [genera *Cladopathes* Brook (1889), *Sibopathes* van Pesch (1914) and *Hexapathes* Kinoshita (1910)], the polyps lack secondary mesenteries, and in the Leiopathidae the polyps contain six secondary mesenteries. The polyps of both Schizopathidae and Antipathidae Ehrenberg (1834) have six primary and four sec-

ondary mesenteries. The Schizopathidae [genera *Schizopathes* Brook (1889), *Bathypathes* Brook (1889) and *Taxipathes* Brook (1889)] is characterized by tranversely elongated polyps, originally described by Brook (1889:45) as 'dimorphic zooids'. The polyps in these genera were reported to be subdivided externally by peristomal folds and internally by meogloeal partitions into three sections, a central one containing the mouth, and two lateral ones, each containing a pair of lateral tentacles and the reproductive tissues (Brook, 1889). These characteristics were specifically identified by Brook for the polyps of *Schizopathes*, but their presence in species of *Bathypathes* and *Taxipathes* has yet to be verified.

The family *Antipathidae* Ehrenberg (1834) contains a very diverse assemblage of forms [A*ntipathes* Pallas (1766), *Aphanipathe*s Brook (1889), *Parantipathes* Brook (1889), *Cirrhipathes* Blainville (1857), and *Stichopathes* Brook (1889), as well as numerous other genera that have been synonomized with *Antipathes*]. Although some genera are morphologically distinct (i.e., the unbranched genera *Cirrhipathes* and *Stichopathes*), most of the others cannot be clearly differentiated, and, as a result, numerous species have been provisionally assigned to *Antipathes*, *sensu lato*.

The examination of a large number of representative species with the polyps intact has revealed that the size and shape of the polyps and the morphology of the axial spines, when considered together, provides a means for grouping species that had previously been referred to the Antipathidae into a number of discrete, family-level taxa. The genera discussed in this paper constitute one such group.

Abbreviations

BMNH = British Museum (Natural History), London, United Kingdom;
RMNH = National Museum of Natural History, Leiden, The Netherlands;
UMML = Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, FL, USA;
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA;
SAM = South Australian Museum, Adelaide, South Australia;
USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Taxonomic section

Myriopathidae fam. nov.

Diagnosis.— Corallum monopodial or branched; branching irregular or pseudodichotomous. Stem and branches usually pinnulate to varying degrees of regularity. Primary pinnules simple or subpinnulate. Pinnular spines relatively large (maximum height of polypar spines at least two times width along the base), acute, conical, or slightly compressed and blade-like; smooth or finely papillose. Polypar spines generally larger than abpolypar spines. Spines increasing in density on larger branches and stem; becoming acicular and often bifid, trifid, or dendritic. Polyps 0.5-1.0 mm (usually 0.6-0.8 mm) in transverse diameter, with distinct interpolypar space 0.2-0.4 mm in width (in preserved material). Tentacles of fully expanded polyps relatively short and rounded at apex.

Remarks.— This family is established on the basis of the size and morphology of the polyps, tentacles and spines, and on the general pinnulation of the corallum. Myriopathidae is closely related to Antipathidae, but differs from that family in that the polyps are smaller (usually 0.5-1 mm vs. 1 mm or greater), and they have relatively shorter tentacles (one to two times the transverse polyp diameter vs. two or more times the transverse diameter). Furthermore, the tips of the tentacles in Myriopathidae usually appear rounded, whereas in *Antipathes sensu stricto* the tentacles appear to narrow gradually to a very fine tip. It should be noted these tentacle differences are usually not apparent in preserved material because the tentacles can be very strongly contracted.

The described differences between the polyps of Myriopathidae and Antipathidae are based on a limited number of photographs of living, fully expanded polyps, and the differential diagnosis may need to be refined as more information becomes available. Because of the small size of the polyps of antipatharians, macrophotography *in situ* is difficult, and informative photographs may only be possible with living specimens maintained in aquaria. However, even in the absence of distinct differences in polyp morphology, there are sufficient differences in sclerenchymal characters to separate the two families. In Myriopathidae the spines are relatively tall and conical (height usually more than twice the width at the base), distinctly unequal, with the polypar spines usually much larger than abpolypar spines, and with the spines increasing in density and becoming more acicular and forked or dendritic on the larger branches and stem. In contrast, in the Antipathidae *sensu stricto* (excluding species of the genus *Aphanipathes*), the spines are triangular, laterally compressed, usually not much taller than they are wide at the base, subequal in size around the circumference of the axis (or only slightly larger on the polyp side), and similar in size, shape and density over most of the corallum (i.e., they do not increase in size or density on the larger branches and stem). The occurrence of forked or dendritic spines on the larger branches and stem in the Myriopathidae is the most consistent and reliable character in separating the two families.

Genera of Myriopathidae are distinctly pinnulated with the exception of the genus *Antipathella* Brook. In species of *Antipathella* the smallest ramifications of the corallum tend to be non-uniform in size and arrangement and they therefore might more appropriately be referred to as branchlets. Genera of Myriopathidae are differentiated primarily on the basis of the morphology of the corallum, and on the number and arrangement of the branchlets/pinnules.

Key to genera of the family Myriopathidae

1. Pinnules/branchlets simple 2
- Pinnules subpinnulate 3
2. Pinnules in two regular rows ..... ***Plumapathes*** gen. nov.
- Pinnules/branchlets in one to four irregular rows ..... ***Antipathella*** Brook
3. Primary pinnules in two rows ..... ***Myriopathes*** gen. nov.
- Primary pinnules in four or more rows. 4
4. Primary pinnules in four irregular rows; higher order pinnules arranged biserially or uniserially, mostly on upper and lower sides of lower order pinnules ..... ***Cupressopathes*** gen. nov.

- Primary pinnules in four to six regular rows and in alternating biserial groups; higher order pinnules usually placed laterally and more extensively developed on abpolypar side of lower order pinnules ..... ***Tanacetipathes*** Opresko

Myriopathes gen. nov.
(figs 1-6)

Antipathes Pallas, 1766: 205 (in part); Brook, 1889: 166 ("Antipathidae myriophylloides"); van Pesch, 1914: 39 (subgenus *Euantipathes*, in part); Pax, 1932: 410.

Diagnosis.— Corallum flabellate or bushy. Stem and branches pinnulate to the second order or more. Primary pinnules arranged biserially and alternately in two lateral or anterolateral rows. Secondary pinnules uniserial at base of primary pinnules, becoming biserial distally. Uniserial secondary pinnules usually projecting out of plane formed by biserial primary pinnules. When present, tertiary pinnules developing on secondary pinnules closest to base of primary pinnule.

Type species.— *Antipathes myriophylla* Pallas, 1766.

Type material.— It is unclear whether Pallas, 1766, described this species on the basis of an Indo-Pacific specimen he himself examined or whether he based it on the pre-Linnaean descriptions he cites (including Rumphius' Erica marina tenuis). Pallas (1766: 210) mentions, however, that he identified the species in various museums in America and gives the American coast as one of the two localities, the other being "Oceanus Indus". The species, as it has been recognized by subsequent investigators, including Brook (1889: 166) and van Pesch (1914: 42) is only known from the Indo-Pacific. Because of the limitations in the original description given by Pallas, and because of the morphological variability associated with this species, the selection of a neotype from the Indo-Pacific appears to be the best approach to resolving the difficulties in identifying the species. Therefore, a specimen collected near Ambon, Indonesia was selected as the neotype. This specimen fits the general description of the species as it has been used since Pallas's publication, and the locality agrees with that of Rumphius.

Neotype.— RMNH Coel. 24064, Indonesia, Moluccas, Ambon, Leitimur, S. coast, Hutumuri, 26.xi.1990, Rumphius Biohistorical Expedition 1990, sta 27, 22-25 m, coll. A. Fortuin & C.L.H.M. Fransen.

Description of the neotype.— The specimen selected as the neotype is about 20 cm tall and 30 cm wide (fig. 1). The basal stem diameter is 3.3 mm. The corallum is branched to the 6th order. The larger branches are up to 9 cm long and tend to form individual fronds separated from each other but overlapping such that in places the flabellate corallum has a thickness of several centimeters. The branches are complexly pinnulate to the third order. The primary pinnules are arranged bilaterally in two rows, as well as alternately along the branches (fig. 2). In each row the primary pinnules are 1.2-2.0 mm apart (mostly 1.4-1.8 mm apart). A maximum of about 12 primary pinnules occur along one centimeter of branch (counting those in both lateral rows). The primary pinnules are up to 7 mm long and 0.15 mm in basal diameter, and they are inclined distally; the distal angle they form with the branch being 60-70°. Three or four secondary pinnules are located on the lowermost portion of each prima-

Fig. 1. *Myriopathes myriophylla* (Pallas), neotype (RMNH Coel. 24064), entire corallum, height about 20 cm.

ry (figs. 2 and 3). They are arranged uniserially, but as the primary pinnule increases in length, more distal secondaries become bilaterial, and the primary pinnule develops into a branch. The uniserial secondaries are at right angles or are inclined distally relative to the primary on which they occur. On each primary pinnule the uniserial secondaries form a plane that is generally perpendicular to the plane containing the branch and the primary on which they occur. The uniserially arranged secondaries have the same orientation from branch to branch, therefore, they all project out of one and the same side of the corallum, giving the corallum a clearly defined anterior and posterior side. The secondary pinnules are up to 2 mm long, with a basal diameter of about 0.1 mm (the longest secondaries occur at the base of the primaries, 0.2-0.8 mm from the branch). As the branches increase in diameter they may overgrow the point of insertion of the secondaries on the primaries. As a result the lowermost secondaries become embedded in the branch sclerenchyme and thus the branch can appear to have four rows of primary pinnules. A single tertiary pinnule may occur on the secondaries, particularly the lowermost of these (fig 3). The tertiaries are mostly 0.8-1.2 mm long and have a basal diameter of about 0.08 mm. They usually occur on the distal or upper side of the secondaries (in the direction of the branch), but they may also project out laterally or even basally.

The spines on the pinnules (fig. 4) are conical to somewhat horn-shaped, slightly compressed, and longer on the polyp side of the axis. On pinnules 0.7 mm in diameter, the polypar spines measure up to 0.11 mm and the abpolypar spines about 0.9 mm. On pinnules 0.12 mm in diameter, the polypar spines may be as much as 0.16 mm and the abpolypar spines 0.14 mm or less, and on branches 0.18 mm in diameter,

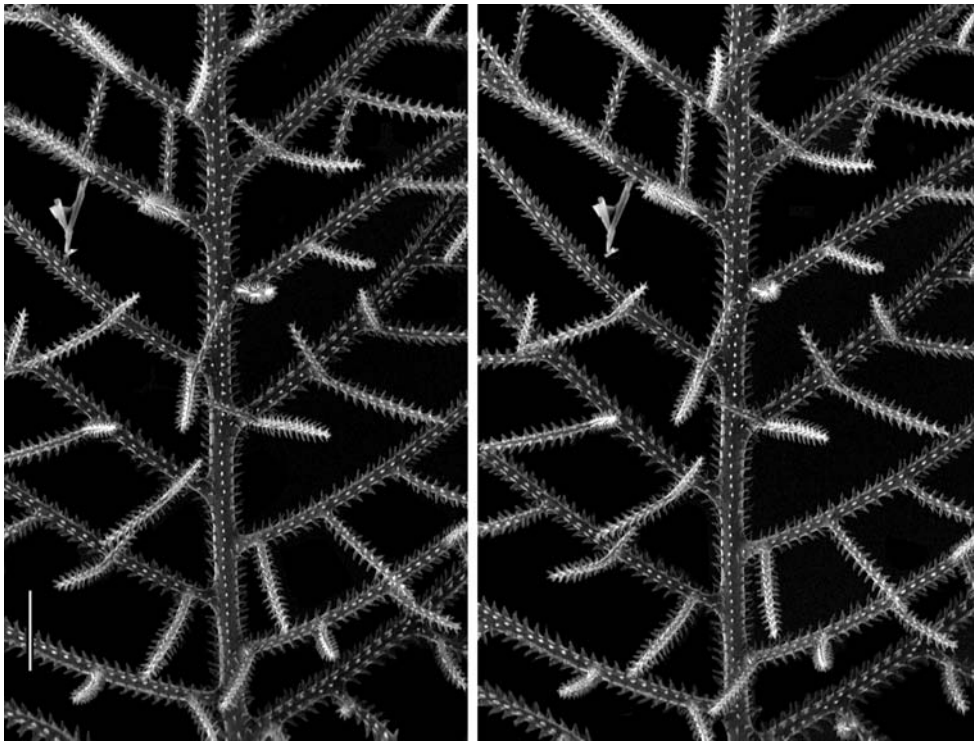

Fig. 2. *Myriopathes myriophylla* (Pallas), neotype (RMNH Coel. 24064), section of branch (frontal view) showing arrangement of pinnules, stereo pair. Scale 1 mm.

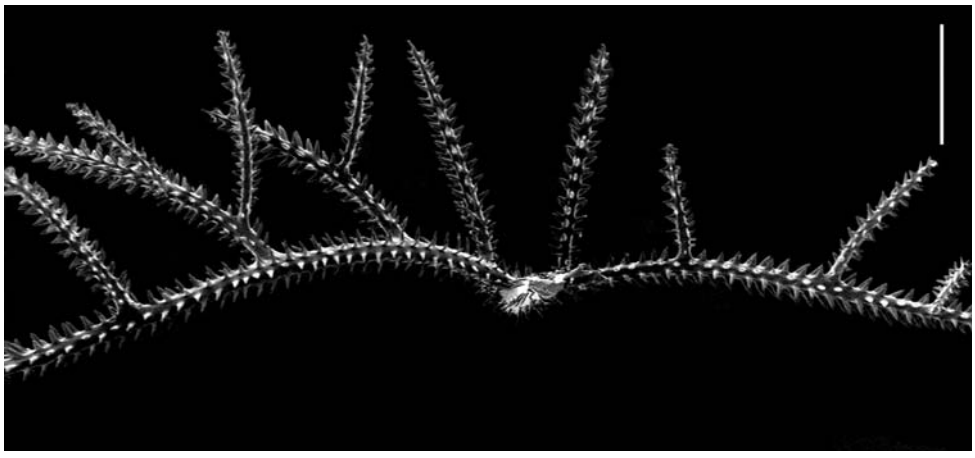

Fig. 3. *Myriopathes myriophylla* (Pallas), neotype (RMNH Coel. 24064), cross section of branch showing arrangement of pinnules. Scale 1 mm.

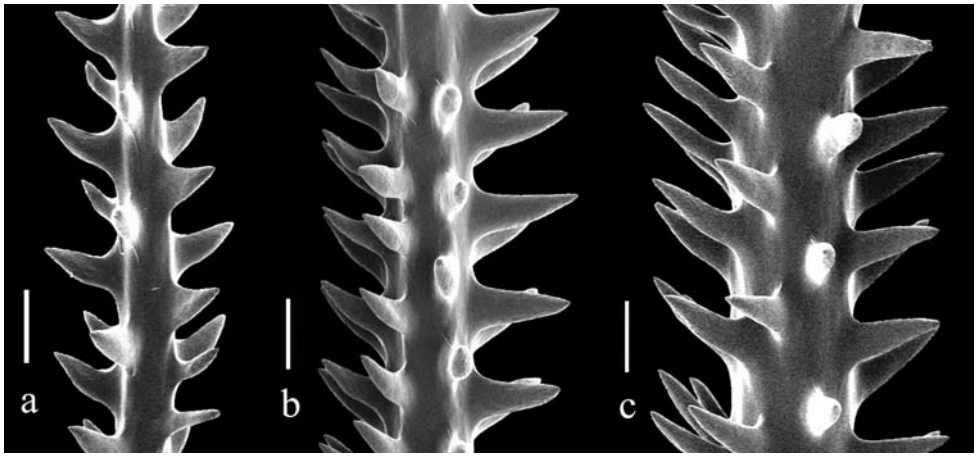

Fig. 4. *Myriopathes myriophylla* (Pallas), neotype (RMNH Coel. 24064); a, section of pinnule 0.07 mm in diameter; b, section of pinnule 0.10 mm in diameter; c, section of pinnule 0.17 mm in diameter. Scale 0.1 mm.

the polypar spines measure 0.17 mm and the abpolypar spines 0.15 mm or less. The spines become more terete and more numerous on the larger branches, and on the stem, where they are about 0.2 mm tall, they are distinctly dendritic.

The polyps are poorly preserved over most of the corallum. However, in places they can be seen to be arranged in a single series on the pinnular side of the branches and primary pinnules (corresponding to the side with the larger spines). Polyps on the secondary pinnules are often confined to the upper (distal) side; therefore, they tend to face towards the more distal polyps on the primary pinnules. The polyps, slightly elongated in the transverse axis, measure 0.6-0.8 mm in transverse diameter. The interpolyp space (between lateral tentacles of adjacent polyps) ranges from 0.2-0.4 mm, and there are about nine polyps per centimeter. In the preserved state the tentacles are knob-like and up to about 0.15 mm long.

Species Assigned to *Myriopathes*.— Nominal species that can be currently assigned to *Myriopathes*, as it is defined above, include *Antipathes ulex* Ellis & Solander, 1786, *Antipathes panamensis* Verrill, 1869, *Hydradendrium spinosum* Carter ,1880, *Antipathes japonica* Brook, 1889, *Antipathes bifaria* Brook, 1889, *Aphanipathes rugosa* Thomson & Simpson, 1905, *Antipathes lata* Silberfeld, 1909, *Aphanipathes stechowi* Pax (1932), and *Antipathes antrocrada* Opresko, 1999. The type specimens of *M. ulex* and *M. lata* were not located, and assignment of these species to *Myriopathes* is based on the descriptions and illustrations given by the original and subsequent authors.

The species of *Myriopathes* listed above can be divided into two subgroups. In one group, represented by the type species, as well as *M. ulex*, *M. panamensis*, *M. stechowi*, *M. spinosa*, and *M. rugosa*, the corallum is generally flabellate (see fig. 1). The second group, containing *M. bifaria*, *M. lata*, *M. japonica*, and *M. antrocrada* (fig. 5) is characterized by a more bushy corallum, although on individual branches the arrangement of the smaller branches and primary pinnules can be somewhat planar.

Within these two subgroups the species are differentiated by the length, density

Fig. 5. *Myriopathes antrocrada* (Opresko), holotype (SAM 746); entire corallum, height about 22 cm.

Fig. 6. Arrangement of pinnules (lateral view) in four species of *Myriopathes*; a, *M. myriophylla* (Pallas), neotype (RMNH Coel. 24064), 1.1×; b, *M. japonica* (Brook), type (BMNH 83.8.29.6), 0.8×; c, *M. bifaria* (Brook), type (BMNH 65.12.15.7), 0.8×; d, *M. antrocrada* (Opresko), holotype (SAM 746), 1.3×.

and orientation of the primary pinnules, the number, length and density of the secondary pinnules and, to a lesser degree, the size and density of the spines. The pinnular arrangement of four species; *M. myriophylla*, *M. japonica*, *M. bifaria*, and *M. antrocrada*, is shown in fig. 6.

Remarks.— In his monograph on the Antipatharia, Brook (1889: 166-170) noted that in the "type of branching" several species (including *A. panamensis*, *A. ulex*, *A. spinosa*, *A. japonica*, and *A. bifaria*) had similarities with *A. myriophylla* Pallas. Brook described these species as belonging to the "Antipathidae Myriophylloides" group.

The genus *Myriopathes* is equivalent to Brook's "Myriophylloides" group.

Myriopathes is very distinct from other genera in the family in that it is the only one in which the primary pinnules are arranged regularly in two rows as well as being subpinnulated. In the general morphology of the corallum, *Myriopathes* resembles *Antipathella* (see below), particularly those species of *Myriopathes* in which the subpinnulation is reduced to not more than a single secondary pinnule on the primary pinnules.

Etymology.— The genus name is derived from the name of the type species "myriophylla" and the commonly used suffix "pathes".

Distribution.— Species of this genus have been reported from the eastern Pacific (*M. panamensis*), Indo-Pacific (*M. myriophylla*, *M. bifaria*, *M. ulex*), Japan (*M. japonica*, *M. stechowi*, *M. lata*), Hawaii (*M. ulex*), Indian Ocean (*M. rugosa*), and Australia (*M. antrocrada*).

***Cupressopathes* gen. nov.**

(figs 7-10)

Gorgonia Linnaeus, 1758: 800 (in part).

Antipathes Pallas, 1766: 205 (in part); Esper, 1796, pl. 12; 1797: 184; Brook, 1889: 170 ("Antipathidae cupressoides"); Milne Edwards & Haime, 1857: 316; van Pesch, 1914: 39 (subgenus *Euantipathes*, in part); Grasshoff, 1991: 359.

Aphanipathes Pax, 1932: 410 (in part).

Diagnosis.— Corallum monopodial or sparsely branched; pinnulate with four or more orders of pinnules. Pinnular and subpinnular pattern not uniform. Primary pinnules arranged in four irregular rows around circumference of stem and branches (sometimes loosely biserial or subspiral); extending out at nearly right angles to stem or slightly inclined distally. Secondary pinnules usually biserial and alternating; sometimes uniserial. Highest order pinnules uniserial or biserial, usually with very narrow interior angle.

Type species.— *Gorgonia abies* Linnaeus, 1758.

Type material.— In his description of *Gorgonia abies* Linnaeus, 1758, does not cite any earlier descriptions of this species. The implication is that he must have had a specimen to examine. If a Linnean type of *G. abies* did at one time exist, it's current whereabouts is unknown. The description given by Linnaeus is rather brief and incomplete, and could apply to any number of antipatharian species. Later workers (Brook, 1889: 170; see also Bayer, 1959: 232 for a review), however, have associated *G. abies* with "Cupressus marina altera" of Rumphius (1750, pl lxxx, fig 2), and have apparently used the illustration given by Rumphius for identifying the Linnean species. The Rumphius illustration appears to be of a relatively young colony in which the subpinnulation is not fully developed. The absence of a Linnean type and the incompleteness of the Rumphius illustration, suggest that the establishment of a neotype would aid considerably in defining this species. Linnaeus reported that the species was found in the Indian Ocean; therefore, selection of a neotype from the Indo-Pacific is considered appropriate.

Neotype.— USNM 76956, Philippines, Sulu Archipelago, Jolo Island, Jolo, Belin Pt., 6°4'20"N, 120°59'20"E, 40 m, 14.ii.1908, R.V. Albatross sta. 5136.

Fig. 7. *Cupressopathes abies* (Linnaeus), neotype (USNM 76956), entire corallum, height about 68 cm.

Fig. 8. *Cupressopathes abies* (Linnaeus), neotype (USNM 76956); a, lateral view of middle of corallum, approx. 1.6×; b, primary pinnule with subpinnules, approx. 1.7 ×.

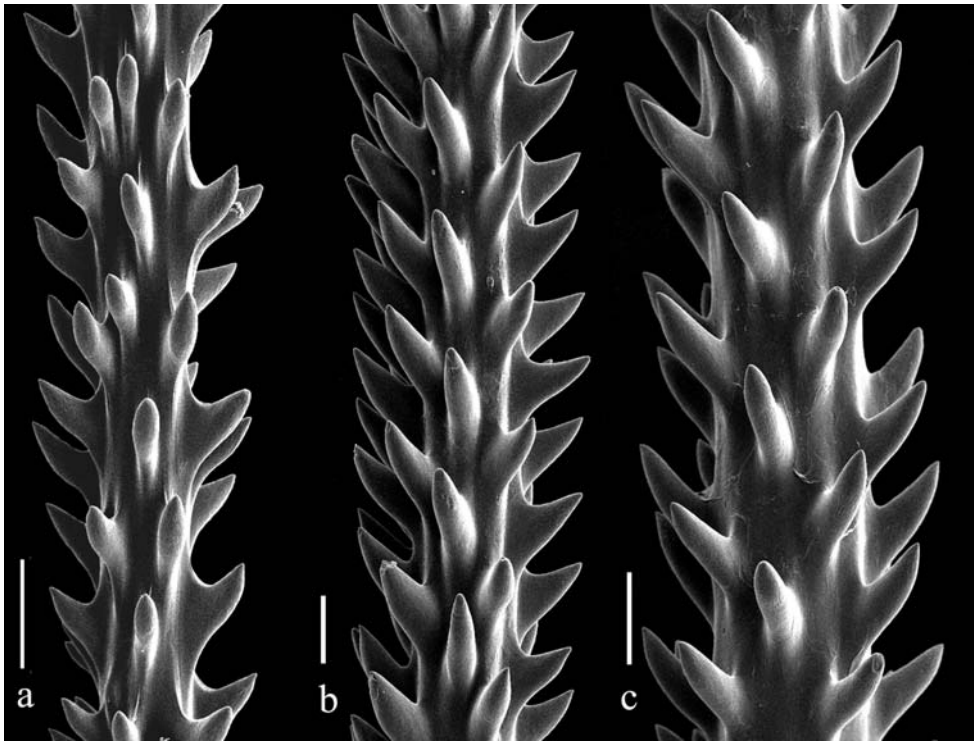

Fig. 9. *Cupressopathes abies* (Linnaeus), neotype (USNM 76956); a, section of pinnule 0.08 mm in diameter; b, section of pinnule 0.14 mm in diameter; c, section of pinnule 0.16 mm in diameter. Scale 0.1 mm.

Description of the neotype.— The neotype (fig. 7) is a large monopodial colony with bottlebrush pinnulation. The corallum is 68 cm high and about 12 cm wide. The diameter of the stem just above the basal holdfast is about 1 cm. The stem is looped along its length, but this is likely an artifact of preservation due to the specimen having been twisted to fit into a relatively small storage jar.

The primary pinnules (or the broken off basal stumps of the pinnules) are present along most of the stem (the lowermost 4 cm of the stem lacks evidence of ever having pinnules, the next 16 cm has only broken off stumps). In places the primary pinnules are extensively subpinnulated, some forming quasi-branches (fig. 8a). They are up to 7 cm long and 1-1.6 mm in diameter at their base.

Although they are not uniformly arranged in axial rows, in places the primary pinnules have the appearance of being in four such rows, which tend to have a somewhat bilateral arrangement. There are generally five to seven primary pinnules per centimeter, counting those on all sides of the stem. Their angle of insertion on the stem is close to 90° or they can be inclined distally. They generally project out horizontally, but are curved back in opposite directions on either side of the stem and/or sometimes also curved downward. The primary pinnules possess four or more orders of subpinnules (fig. 8b). The pattern of subpinnulation is quite irregular and often a higher order subpinnule may be more extensively subpinnulated than an adjacent

lower order one, creating a complex non-uniform pattern, and sometimes giving the subpinnules on a primary pinnule a tuft-like appearance. Although the subpinnules can appear to be quite irregular in arrangement, the general trend is for them to be alternately biserial and inclined distally (distal angle about 45°). They also tend to be curved in somewhat the same direction as the primary pinnule from which they arise. The secondary pinnules are mostly 3-4 cm in length, and 0.4-1.0 mm in diameter near the base. They are spaced 2-4 mm apart in each row, and there are usually five to seven per centimeter.

The two rows of secondaries may form a relatively wide interior angle (i.e., 120-180°) at the base of the primaries, with the interior angle decreasing more distally on the primary, such that near the tip of the primary the secondaries may have the appearance of being uniserial. However, as noted above, the arrangement is not uniform over the corallum and on some primaries the lowermost secondaries may form a relatively narrow interior angle, or may even appear to be uniserial, and the more distal secondaries may have a wider interior angle.

Tertiary pinnules usually occur on the upper side of the secondaries, and are 2-3 cm long and 0.3-0.5 mm in diameter at the base. The highest order subpinnules (tertiary or quarternary) can be arranged uniserially with up to six to seven per centimeter, or they can be arranged in a somewhat alternate pattern with a very narrow interior angle (i.e., 15° or less).

The spines on the smaller pinnules (fig. 9) are conical to somewhat horn-shaped, slightly compressed, and slightly smaller and more densely arranged on one side of the axis, although this does not always appear to coincide with the polyp side of the axis. On pinnules 0.10-0.12 mm in diameter, the polypar spines are about 0.12 mm tall and the abpolypar spines are nearly the same size. On pinnules 0.15-0.25 mm in diameter, the polypar spines measure 0.14-0.16 mm and the abpolypar spines 0.12-0.14 mm. On pinnules larger than about 0.4 mm, the spines become increasingly cylindrical in shape and up to 0.20 mm tall (fig. 10). There are six to eight longitudinal rows of spines visible in lateral view on pinnules less than 0.4 mm in diameter, and nine to 11 rows on pinnules greater of 0.6-0.8 mm in diameter, with the number increasing with increasing thickness of the axis.

On the stem the spines become more needle-like and dendritic, and appear to be about the same size as the largest pinnular spines, or about 0.20 mm. The spines on the stem are also more densely and irregularly arranged than those on the pinnules.

The polyps are mostly arranged in a single series on the side of pinnules on which the subpinnules arise, or they can be more lateral in position. In a few places, even on some tertiary pinnules, they occur on two sides of the axis. The polyps measure 0.8-0.9 mm in transverse diameter and there are ten to 12 per centimeter on the pinnules. The interpolyp space (between lateral tentacles of adjacent polyps) is generally 0.2 mm or less. In the preserved state the tentacles measure up to 0.7 mm but most are less than 0.4 mm.

Species Assigned to *Cupressopathes*.— In addition to the type species, other nominal species that may be assigned to *Cupressopathes* include *Antipathes pumila* Brook, 1889, *Antipathes paniculata* Esper (1796), and *Antipathes gracilis* Thomson & Simpson, 1905. Although most later investigators have treated *A. paniculata* Esper as synonymous with *A. abies*, Brook (1889: 171) considered it a distinct variety characterized by

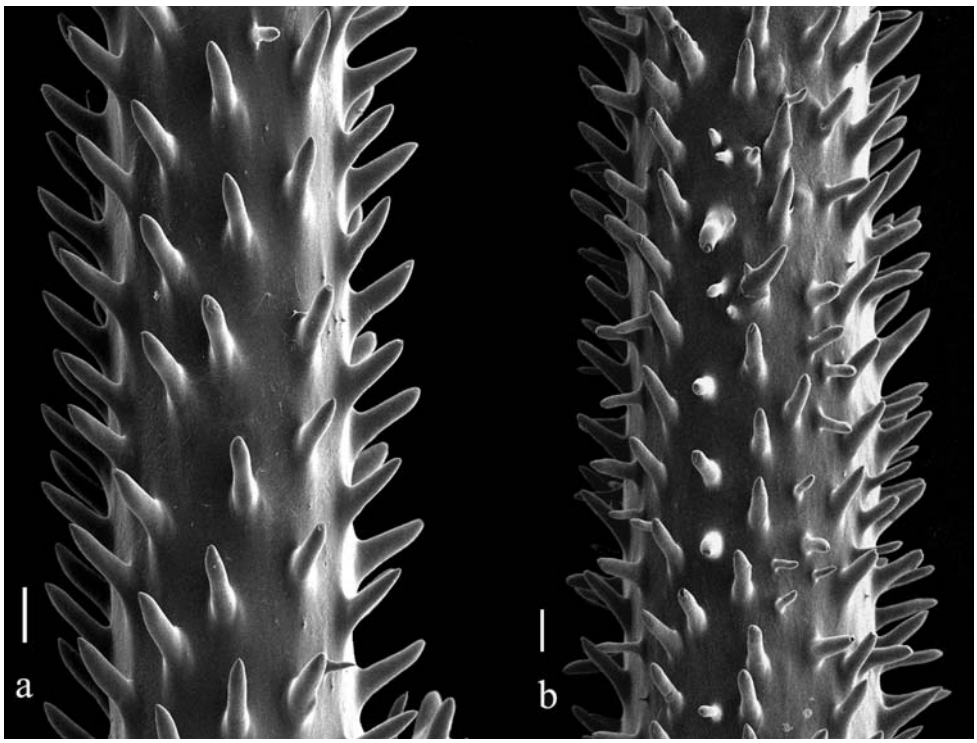

Fig. 10. *Cupressopathes abies* (Linnaeus), neotype (USNM 76956); a, section of pinnule 0.45 mm in diameter; b, section of pinnule 0.61 mm in diameter. Scale 0.1 mm.

elongate branches 8-18 cm in length. Esper (1797: 184) suggested that the branches in *A. paniculata* are much thicker than they are in *A. abies*, but this may simply be the result of differences in age of the specimens (the illustration of *Cupressus marina* given by Rumphius is of a relatively young colony). The type specimen of *A. paniculata* Esper has recently been re-described (Opresko & Baron-Szabo, 2001). Thomson & Simpson, 1905 established *Antipathes gracilis* on the basis of a very small specimen only 6 cm tall, with primary pinnules 3 mm or less in length, and with relatively few secondary pinnules. Further study is needed to determine whether this is a separate species or only a very young colony of *C. abies*.

Cupressopathes pumila (Brook) differs from *C. abies* in having a smaller, more flattened corallum with several of the primary pinnules developing into side branches.

Remarks.— In his monograph on the Antipatharia, Brook (1889: 170) noted that several species had similarities with *Antipathes abies* (Linnaeus) in having a bottlebrush type of branching. Brook described these species as belonging to "Antipathidae Cupressoides". The new genus *Cupressopathes* includes some of the species Brook referred to "Cupressoides".

Etymology.— The genus name is derived from "cupressus", in reference to the general resemblance to trees of the genus *Cupressus*, and the commonly used suffix "pathes".

Distribution.— Species of this genus are known from the western Pacific (*C. abies*, *C. pumila*, *C. paniculata*) and the Indian Ocean (*C. gracilis*, *C. abies*).

Tanacetipathes Opresko, 2001
(figs 11-12)

Antipathes; Pourtalès (1880: 116, in part); Brook, 1889: 160 ("species incertae sedis"); Opresko, 1972: 959 (in part).
*Tanacetipathe*s Opresko, 2001: 349.

Diagnosis.— Corallum monopodial or branched. Stem and branches columnar (bottlebrush); pinnulate and subpinnulate to the third or fourth order. Primary pinnules arranged in four to six regular rows and in alternating biserial groups of two or three pinnules each. Secondary pinnules primarily on lateral sides of primaries and usually developed more extensively on abpolypar side of primaries. One or more uniserial tertiary pinnules present on the abpolypar side of the lowermost secondary pinnules. Quartenary pinnules present in some species.

Type species.— *Antipathes tanacetum* Pourtalès, 1880 (see Opresko, 2001: 349).

Type material.— Pourtalès' original type series of *Antipathes tanacetum* consisted of numerous specimens from several localities in the Lesser Antilles (see Opresko, 1972). Most of these type specimens are deposited in the Museum of Comparative Zoology (MCZ), Harvard University; however, one syntype is located at the USNM.

Description.— A detailed description of this species is provided by Opresko, 1972. Examination of the syntypes at the MCZ and numerous specimens from the Caribbean and from along the northeast coast of South America in the collections of the Rosenstiel School of Marine and Atmospheric Sciences, U. of Miami, indicate that this species can exhibit considerable variability in both the size of the spines and the degree of subpinnulation of the primary pinnules. The species is characterized by either a monopodial corallum (fig. 11a) or one in which the branching arises primarily from near the base of the stem. The primary pinnules are up to 2.5 cm long, and arranged along the stem in four to six longitudinal rows, and also in alternating groups of two or three pinnules each. There are usually four to six secondary pinnules arranged uniserially on the posterior (abpolypar) side of each primary (fig. 12d). The secondary pinnules nearest the base of the primary are up to 2 cm long; the more distal ones decreasing in size. Tertiary pinnules are common on the abpolypar side of the lowermost secondaries, and occasionally the lowermost of these may bear a quartenary pinnule (fig. 12d). The spines are conical, acute, slightly compressed, up to about 0.3 mm tall, and three to four times taller than they are wide at the base. The polypar spines are usually three or more times larger than the abpolypar spines. The polyps are 0.6-0.8 mm in transverse diameter and arranged in a single series with ten to 13 per centimeter. The polyps occur on the side of the pinnules opposite to the side carrying the subpinnules.

Species Assigned to *Tanacetipathes*.— Nominal species that show strong affinites with *T. tanacetum* (Pourtalès, 1880) include *Antipathes hirta* Gray, 1857, *Antipathes spinescens* Gray, 1857, *Antipathes barbadensis* Brook, 1889, *Antipathes thamnea* Warner, 1981, *T. wirtzi* Opresko (2001), and *T. cavernicola* Opresko (2001). Species in this genus are separated on the basis of the branching pattern of the corallum, the length and

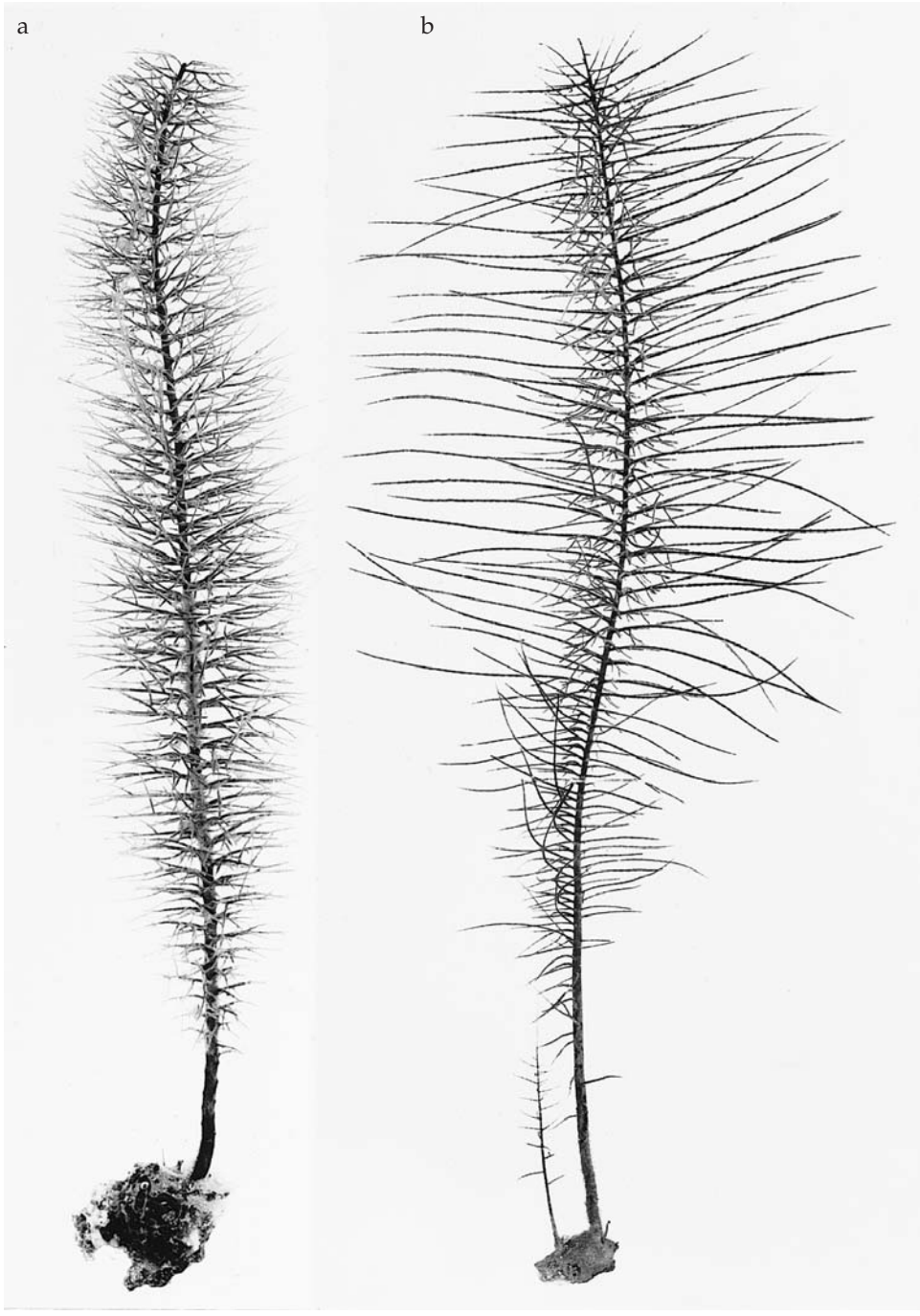

Fig. 11. a, *Tanacetipathes tanacetum* (Pourtalès), UMML 7.1104, entire corallum, height, about 13 cm; b, *Tanacetipathes barbadensis* (Brook), UMML 7.672, entire corallum, height about 14 cm.

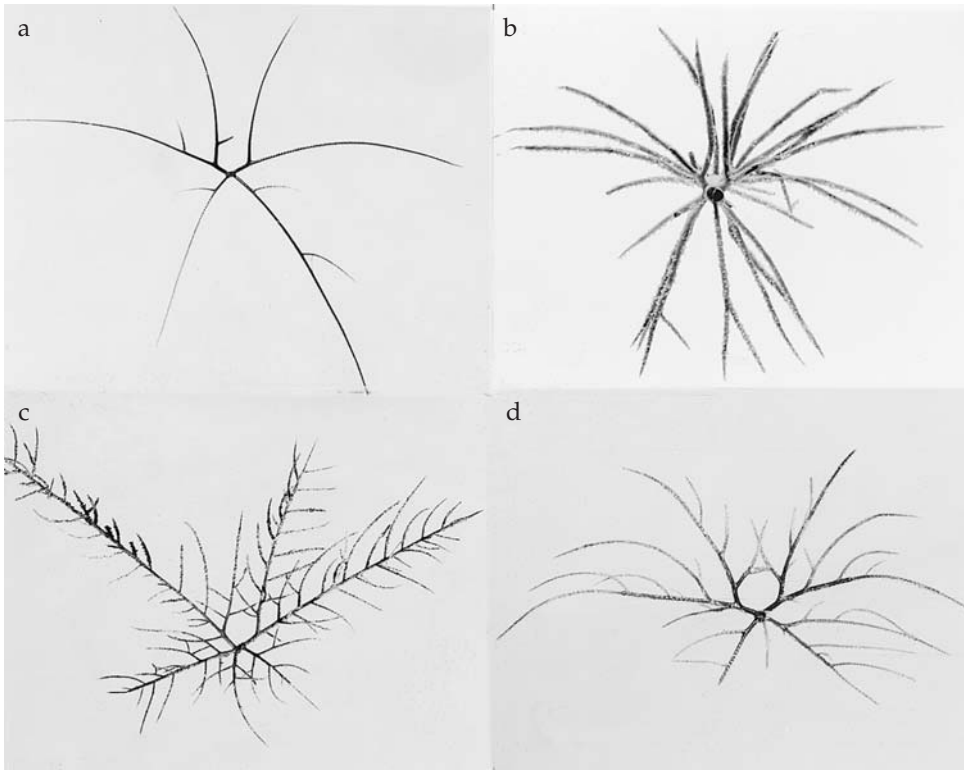

Fig. 12. Arrangement of pinnules (cross sectional view of branch) in four species of *Tanacetipathes*; a, *T. barbadensis* (Brook), UMML 7.946; b, *T. wirtzi* Opresko, USNM 96954: c, *T. thamnea* (Warner), UMML 7.1130; d, *T. tanacetum* (Pourtalès), UMML 7.827.

degree of subpinnulation of the primary and secondary pinnules, and the size of the spines. Both *T. thamnea* and *T. barbadensis* (fig. 11b) form large monopodial or sparsely branched colonies with very long primary pinnules (up to 6 cm). In *T. barbadensis* the primary pinnules have only a few secondary pinnules near the base (fig. 12a). In contrast, in *T. thamnea* numerous secondary pinnules occur along most of the length of both the anterior and posterior primary pinnules (fig. 12c). Both *T. tanacetum* (fig. 12d) and *T. spinescens* have relatively short primary pinnules with extensive subpinnulation on both the anterior and posterior primary pinnules; however, *T. tanacetum* forms mostly monopodial colonies whereas *T. spinescens* is branched. *Tanacetipathes wirtzi* and *T. cavernicola* form small colonies with limited branching, primarily from near the base (see Opresko, 2001), and reduced subpinnulation (fig. 12b). *Tanacetipathes hirta* forms branched colonies with moderately long posterior primary pinnules and only a few secondary pinnules. The arrangement of the pinnules in *T. barbadensis*, *T. wirtzi*, *T. thamnea*, and *T. tanacetum* is shown in fig. 12.

Remarks.— *Tanacetipathes* resembles *Cupressopathes* in its bottlebrush growth form; however, the pattern of pinnulation is different in the two genera. In *Tanacetopathes* the arrangement of the primary pinnules is very uniform in four to six rows, with the subpinnules developing uniserially primarily on the abpolypar side of the

lower order pinnules. In *Cupressopathes* a uniform pattern of pinnulation is usually only apparent in young colonies or on younger portions of older specimens. The primary pinnules occur in four very irregular rows, and the subpinnules tend to be arranged biserially, uniserially or rather irregularly and mostly on the polypar side of the lower order pinnules.

Distribution.— Species of this genus have been reported from the eastern Atlantic (*T. spinescens*, *T. wirtzi* and *T. cavernicola*), and from the western Atlantic (*T. tanacetum*, *T. hirta*, *T. barbadensis*, and *T. thamnea*), but not from the Pacific or Indian Oceans.

***Plumapathes* gen. nov.**

(figs 13-14)

Antipathes Pallas, 1766: 205 (in part); van Pesch, 1914: 85 (subgenus *Aphanipathes*, in part); Opresko, 1974: 82 (in part).
Aphanipathes Brook, 1889: 121 (in part).

Diagnosis.— Corallum sparsely to densely branched and tending to be planar. Stem and branches pinnulate. Primary pinnules simple, relatively uniform in size, and not subpinnulate; arranged in two, very regular bilateral rows; pinnules in each row alternating with those in opposite row.

Type species.— *Antipathes pennacea* Pallas, 1766.

Type material.— Pallas, 1766, based this species on a specimen that he reported came from "Oceanus Indicus" and which he considered to be identical to Rumphius's "Erica marina crassa". Pallas' specimen has not been located. Because of the limitations in the original description, and because of the range of morphological variability that has been reported for this species (see Opresko, 1974), the establishment of a neotype is necessary to clearly define the species.

Neotype.— RMNH Coel.6801, Indian Ocean, Madagascar, Europa Island, 23.xii.1965, P. Vasseur, depth not reported.

Description of the neotype.— The specimen is 12.5 cm high and about 11 cm in width (fig. 13). A basal plate is not present and the specimen may be only a branch from a larger colony. The diameter of the large, stem-like branch is about 2.4 mm at its lower end. The corallum is branched to the third order; mostly in one plane. The stem and branches bear simple filiform pinnules. The largest pinnules are mostly 3-4 cm in length (maximum about 5 cm) and about 0.2 mm in diameter (excluding spines) near the point of insertion on the branch or stem. The pinnules are arranged in two lateral rows with members of each row spaced 1.6-2.0 mm apart. There are six to nine pinnules per centimeter in each row and 13-17 per centimeter for both rows. The spines (fig. 14) are conical, with an acute to rounded apex. Over most of the length of the pinnules the polypar spines are 0.16-0.18 mm tall, and the abpolypar spines are slightly smaller. Near the tip of the pinnules the spines decrease in size to 0.03-0.05 mm, and near the base they are up to 0.24 mm tall. The pinnular spines are arranged in five to six longitudinal rows (lateral view, excluding rows only partially visible), usually with about six spines per millimeter in each row (mutual distance mostly 0.18-0.22 mm). On the branches and stem the spines become more needle-like, but are similar in size to the largest pinnular spines, about 0.24 mm. With increasing

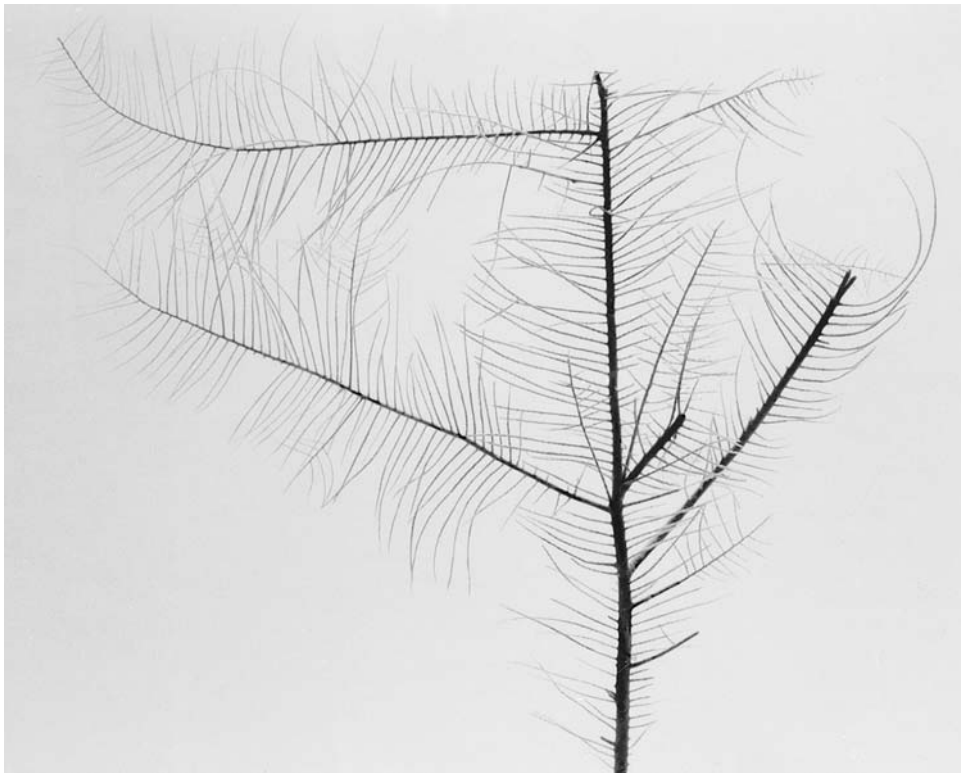

Fig. 13. *Plumapathes pennacea* (Pallas), neotype (RMNH Coel. 6801), entire corallum, height about 12.5 cm.

diameter of the axis, the spines become more densely and more irregularly arranged. On the stem there are 24 or more very irregular rows visible in lateral view.

The polyps are arranged in a single series on the lateral or upper side of pinnules, and on one side of the branches and stem. Consequently, there is a distinct polypar and abpolypar side to the corallum. The polyps measure 0.7-0.8 mm in transverse diameter with a small interpolypar space such that there are 10-14 polyps per centimeter on the pinnules. In the preserved state the tentacles measure up to 0.2 mm long, and have a rounded blunt tip.

Species Assigned to *Plumapathes*.— At present only one other nominal species, *Antipathes fernandezi* Pourtalès, 1874, can be referred to this genus. The pinnules of *P. fernandezi* are not as uniform in size nor are they as regular in arrangement as those in *P. pennacea*.

Although specimens referred to *A. pennacea* are common in the western Atlantic (Caribbean region; Opresko, 1974) and also known from the south Atlantic (St. Helena; Brook, 1889; Opresko, 1974), the species has only rarely been reported from the Indo-Pacific, the type locality. van Pesch, 1914, however, described several specimens from the Philippines under the name *Antipathes pennacea*. These differ from neotype particularly in the maximum size of the axial spines (0.11 mm vs. 0.24 mm). Furthermore, the

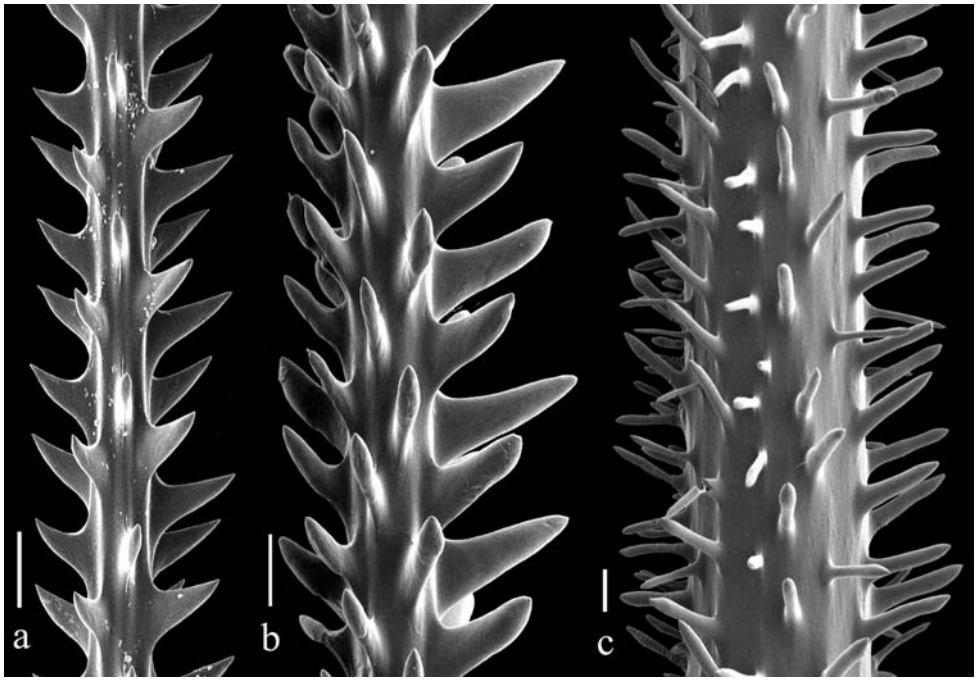

Fig. 14. *Plumapathes pennacea* (Pallas), neotype (RMNH Coel. 6801); a, pinnule 0.9 mm in diameter; b, pinnule 0.13 mm in diameter; c, pinnule 0.42 mm in diameter. Scale 0.1 mm.

St. Helena specimens differ from both the Indo-Pacifc specimens of van Pesch and the western Atlantic material in both the size of the spines (up to 0.32 mm) and in the density of the polyps (see Opresko, 1974, for further discussion). Thus, it is quite likely that more than one species is currently included under the name *P. pennacea*.

Remarks.— The genus *Plumapathes* shows affinities to some species of *Antipathella*, particularly those species in which the pinnules are arranged bilaterally and mostly in two rows. In *Plumapathes*, however, the pinnules are more uniform in both size and arrangement than in any species of *Antipathella*.

Etymology.— The genus name is derived from "pluma" Latin for feather, in reference to the feather-like appearance of the branches, and the commonly used suffix "pathes".

Distribution.— Specimens identified as *P. pennacea* have been reported from the Indo-Pacific, southern Atlantic, and western Atlantic. *Plumapathes fernandezi* is known only from the eastern Pacific.

Antipathella Brook, 1889, emend.

(figs 15-18)

Antipathes; Ellis & Solander, 1786: 101 (in part); van Pesch, 1914: 180 (as subgenus *Euantipathes*, in part); Pax & Müller, 1955: 103.

Antipathella Brook, 1889: 105.

Aphanipathes Brook, 1889: 121 (in part).

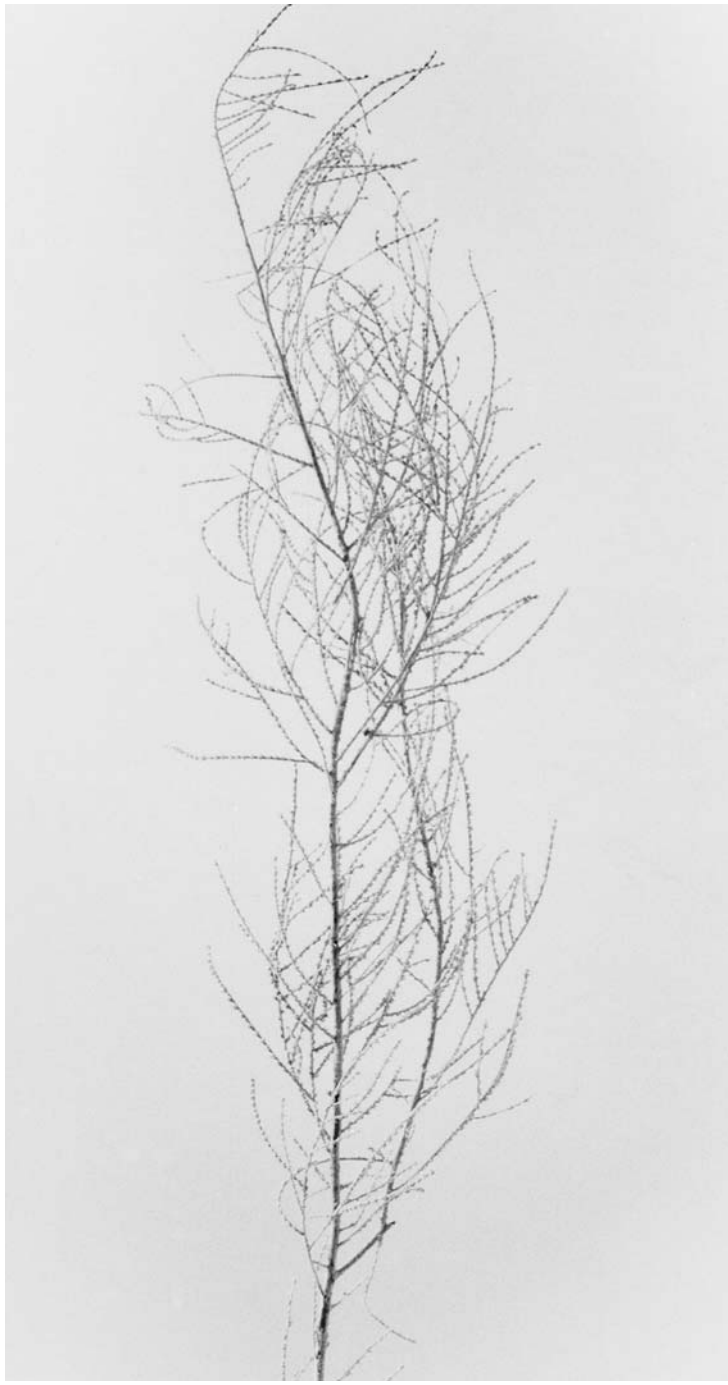

Fig. 15. *Antipathella subpinnata* (Ellis & Solander), neotype (BM 1910-2-10-8), entire corallum, height about 29 cm.

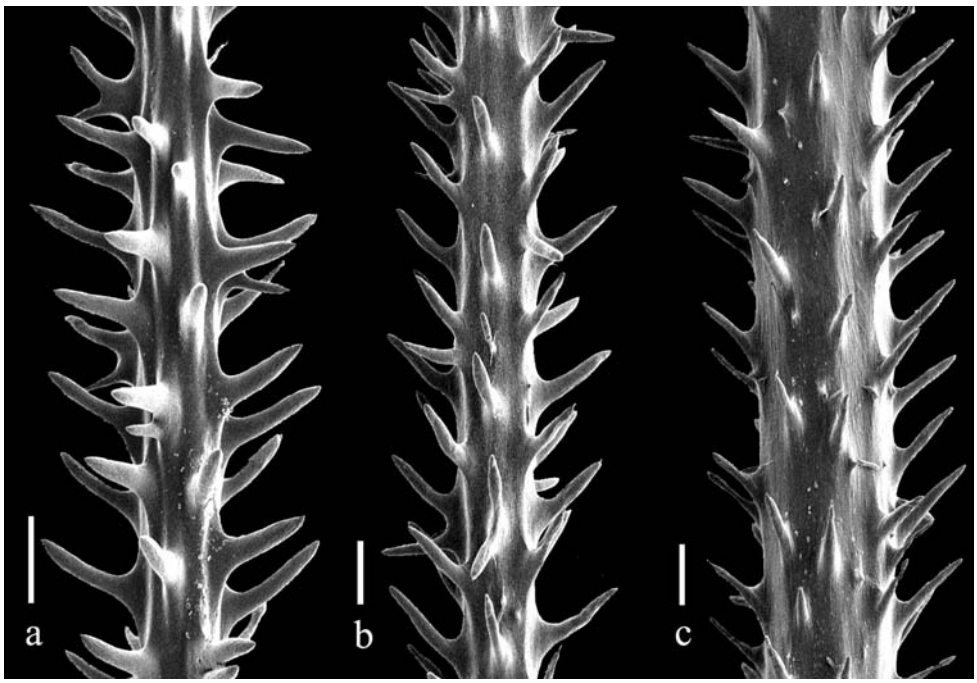

Fig. 16. *Antipathella subpinnata* (Ellis & Solander), neotype (BM 1910-2-10-8); a, branchlet 0.9 mm in diameter; b, branchlet 0.12 mm in diameter; c, branchlet 0.22 mm in diameter. Scale 0.1 mm.

Diagnosis.— Corallum sparsely to densely branched, with simple elongate branchlets or pinnules. Branchlets/pinnules of varying length, and arranged in one to four rows of varying regularity. Branches of corallum usually long and ascending. Branchlets/pinnules generally thin and flexible.

Type species.— *Antipathes subpinnata* Ellis & Solander, 1786, herein designated. In establishing *Antipathella*, Brook, 1889, did not specifically designate *A. subpinnata* as the type species; however, this species was the first of the genus discussed by Brook (1889: 105) and one for which he gives an extensve histological description (Brook, 1889: 192). It is therefore likely that he intended for this species to be the type species of *Antipathella*.

Type material.— Brook's, 1889, description of *Antipathes subpinnata* differs in several ways from the description and illustration given by Ellis & Solander. The illustration provided by Ellis & Solander shows the relatively regular placement of the smallest branchlets on all sides of a lower order branch, giving the branchlets the general appearance of pinnules; however, most later workers, including Brook, 1889, have referred specimens to this species whose smallest branchlets are much less uniform in size and which are not always placed in well-defined rows (Brook, 1889; Pax & Müller, 1955: 103). In these specimens the smallest branchlets may be arranged either uniserially, bilaterally or irregularly on all sides of the axis. Because these "pinnules" are not uniform in size or arrangement, the term pinnules is not quite accurate. Brook, 1889, however, based *Antipathella* on such a specimen, which was collected near

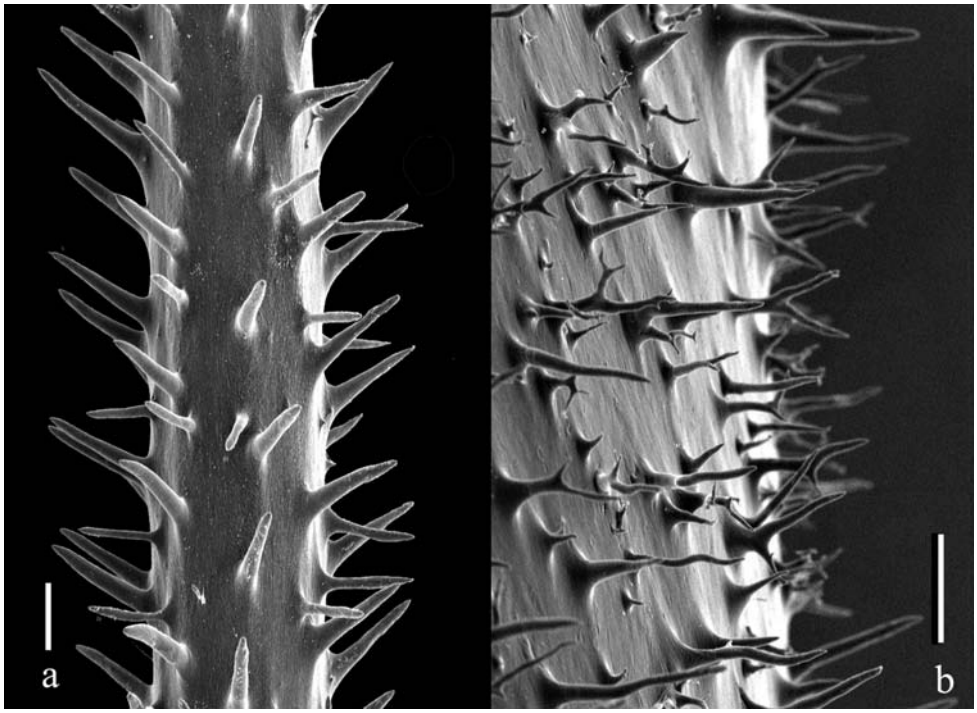

Fig. 17. *Antipathella subpinnata* (Ellis & Solander), neotype (BM 1910-2-10-8); a, branch 0.27 mm in diameter; b, lower part of stem; Scale 0.1 mm.

Naples (Ellis & Solander's material came from near Gibraltar). Ellis & Solander's type is lost; therefore, it is appropriate to designate as a neotype of *A. subpinnata* a specimen that agrees with Brook's definition of the genus and one that was collected in the same geographic area.

Neotype.— BMNH 1910-2-10-8. Locality: Naples, Norton Collection (no other data).

Description of the neotype.— The specimen (fig. 15) is a small colony 29 cm high, and about 7 cm in width. The diameter of the stem at its basal end is 2.5 mm. The corallum consists of several elongate branches arising vertically, and nearly parallel to each other. The longest branch is 13 cm with a basal diameter of about 1.1 mm. Branchlets arise at various points along the stem and lower order branches. They are not uniform in size and are not arranged in any regular pattern. Some are bilateral, but they are not always arranged alternately. In several places they follow a uniserial pattern over short distances. Rarely, branchlets extend out from three or all four sides of the branches. Most of the longer of these branchlets are 1.5 to 3.0 cm in length; a few are up to 4.0 cm long and about 0.4 mm in diameter at the base. Brook, 1889, reported that the "pinnules" of his specimen were up to 5 cm in length. On the neotype the branchlets are for the most part directed distally, with the distal angle varying from about 30° to 75°. Over most of the corallum there are three to four branchlets per centimeter of axis, occasionally five and rarely six per centimeter (counting those on all sides of the axis).

Fig. 18. *Antipathella subpinnata* (Ellis & Solander), neotype (BM 1910-2-10-8); branchlets with polyps, approx. 4 ×.

The spines on the branchlets (fig. 16) are subcylindrical, acute, usually inclined distally, although sometimes directed horizontally, and occasionally even basally. On branchlets 0.08-0.12 mm in diameter the polypar spines are 0.10-0.16 mm tall; on branchlets 0.22-0.26 mm in diameter the polypar spines measure 0.16-0.18 mm. The abpolypar spines are generally only slightly smaller than the polypar spines (0.1-0.2 mm). The spines are arranged in five to six rows (viewed from one aspect, and excluding rows in which the spines are only partially visible), and within each row they are spaced 0.18-0.24 mm apart, resulting in about five to six spines per millimeter.

The spines become more needle-like in appearance and more densely crowded on the branches and stem (fig. 17). They are up to 0.16 mm tall and some are forked at their apex (fig. 17b).

The polyps (fig. 18) have the appearance of being transversely elongated; however, they are only about 1 mm in transverse diameter. Small polyps are interspersed among the larger ones, but not in a regular pattern and only on parts of the corallum. The polyps are arranged uniserially, with 7-9 polyps per centimeter along the axis. Brook, 1889, reported 30 polyps along 4 centimeters of axis (about 7.5 per centimeter). On the neotype the polyps do not have the same orientation from branch to branch; therefore, the corallum does not have a polypar and abpolypar side. In the preserved material the tentacles appear short, up to 0.6 mm long, and have a blunt, rounded apex. The interpolypar space is very variable, 0.1-0.5 mm in length.

Species Assigned to *Antipathella*.— The following species are considered to be cogeneric with *Antipathella subpinnata*: *Antipathes wollastoni* Gray, 1857, *Antipathes strigosa* Brook, 1889, *Antipathes aperta* Totton, 1923, and *Antipathes fiordensis* Grange, 1990.

All the species referred to *Antipathella* are similar in that the size and arrangement of the branchlets/pinnules are not uniform throughout the corallum, although in most of these species the branchlets tend to be more uniform in size and arrangement than in *A. subpinnata*, and, therefore, are more like true pinnules. These pinnules are usually arranged in two to four irregular rows, which at times may appear bilateral, or may follow a somewhat spiral pattern. In *A. subpinnata* the branchlets/pinnules tend to be thicker and stand out more obliquely than in the other species where the pinnules tend to be more slender and directly upwards. In *A. strigosa*, the pinnules are mostly in two rows (three to 11 per centimeter). In *A. wollastoni* the pinnules frequently occur in four rows with a total of 14-20 pinnules per centimeter. *Antipathella aperta* has relatively short pinnules, but the species was based on a very small, and possibly incomplete specimen. The spines on the larger branches and stem of *A. wollastoni*, *A. aperta*, and *A. fiordensis* are strongly dendritic, whereas those in *A. strigosa* and *A. subpinnata* tend to be simple or only forked (large specimens of *A. subpinnata* have not been examined for this character). *Antipathella fiordensis* has very distinct secondary spines on the larger branches.

Remarks.— The genus *Antipathella* was established by Brook, 1889, for species having polyps which differed from the polyps of *Antipathes sensu stricto* by being smaller, more oval, and with the tentacles disposed in two rows of three each so that the polyps were somewhat longer in the transverse axis (Brook, 1889: 81, 105). This slight transverse elongation of the polyps is a very subtle morphological difference from *Antipathes*, and many later workers considered it to be insufficient to recognize as a generic character. However, when considered together with differences in the morphology and size of the spines, the differences between *Antipathella* and *Antipathes* become more apparent. The spines of *Antipathes*, *sensu stricto*, are triangular and laterally compressed, whereas those of *Antipathella* are conical to subcylindrical, and distinctly forked or dendritic on the larger branches and stem.

Of all the genera placed in Myriopathidae, *Antipathella* has the most lax pinnulation pattern, and in this regard, the genus approaches *Antipathes sensu stricto* in the general morphology of the corallum. Within the Myriopathidae, *Antipathella* resembles those species of *Myriopathes* having only a small number of secondary pinnules (i.e., *M. ulex*).

Distribution.— Species of *Antipathella* are known from the Mediterranean (*A. subpinnata*), northeastern Atlantic (*A. wollastoni*) and from New Zealand (*A. aperta*, *A. strigosa*, *A. fiordensis*).

Acknowledgements

For their hospitality and helpfulness during visits to their respective museums, the author wishes to thank B.W. Hoeksema and M. Slierings of the RMNH, S. Halsey and P. Cornelius of the British Museum, and S. Cairns of the USNM. Thanks also to S. Cairns for reviewing the manuscript, and to L.P. van Ofwegen of the RMNH for his editorial help. S. Braden of the USNM kindly prepared samples for examination with the scanning electron microscope (SEM). A special note of thanks to Rosemarie Baron-Szabo for her support and encouragement.

This work was supported in part by the National Museum of Natural History, Leiden; the National Musuem of Natural History of the Smithsonian Institution,

Washington, DC, and by Oak Ridge National Laboratory, Oak Ridge, TN.

This paper is dedicated to the memory of Koos den Hartog, a friend and fellow cnidarian worker who was very supportive of my work on antipatharians.

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Received: 22.iii.2001
Accepted: 31.vii.2001
Edited: L.P. van Ofwegen