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

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A new family of antipatharian corals, Stylopathidae (Cnidaria: Anthozoa: Antipatharia), is established for Arachnopathes columnaris Duchassaing, 1870, and related species. The family is characterized by small polyps, 1.5 mm or less in transverse diameter; small, conical, smooth spines, often distally directed (especially at the tips of the branchlets and/or pinnules); and by the tendency for the pinnules and branchlets to occur in subopposite pairs or to be arranged in verticils of three or four (rarely five) pinnules. In many species adjacent pinnules or branchlets fuse together or anastomose, resulting in the formation of cylindrical, reticulated worm runs along the stem or branches. Genera are established on the basis of morphological features of the corallum. Stylopathes gen. nov., includes the type species, Arachnopathes columnaris Duchassaing, and is characterized by a monopodial or very sparsely branched corallum. Triadopathes gen. nov. contains only the type species Parantipathes triadocrada Opresko, and has multiple, vertically directed, stem-like primary branches, arising primarily from the lower parts of the corallum. Tylopathes Brook contains the type species T. crispa Brook, and is characterized by a flabel late corallum with short, mostly bilateral branchlets.

Introduction

This is the fifth in a series of publications in which the order Antipatharia is being revised. In the first part the family Myriopathidae was established for Antipathes myriophylla Pallas, 1766, and related species (Opresko, 2001). In the second part, the family Schizopathidae was revised and four new genera were established (Opresko, 2002). In the third part, the family Cladopathidae was revised and three new genera were recognized (Opresko, 2003). In part 4, species related to Aphanipathes sarothamnoides Brook, 1889, were placed in a new family, the Aphanipathidae (Opresko, 2004). In this paper, Arachnopathes columnaris Duchassaing, and related species are placed in the new family Stylopathidae, and two new genera are recognized.

The basis for this revision of the order is the observation that the size and morphology of the polyps, and the morphology of the axial spines, when considered together, provide a means for subdividing the Antipatharia into a number of discrete, family-level taxa. The establishment of these new families hopefully will clarify the natural affinities within the order, and will lead to a more in depth analysis of genera and species.

Holotypes of new species are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Schizoholotypes of some
species have also been deposited at the National Museum of Natural History, Leiden, The Netherlands.

Abbreviations

BMNH = British Museum of Natural History, London, United Kingdom
RMNH = National Museum of Natural History, Leiden, The Netherlands
SAM = South Australian Museum, Adelaide, S. Australia
UMML = Rosenstiel School of Marine and Atmospheric Science (RSMAS), University of Miami, Miami, FL, USA
USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Taxonomic treatment

Stylopathidae fam. nov.

Diagnosis.—Corallum monopodial, branched irregularly, or flabellate. Pinnules or branchlets tending to occur, to varying degrees, in subopposite pairs and/or in verticils. Overlapping branchlets and pinnules sometimes adhering and/or anastomosing. Pinnules and branchlets sometimes forming reticulated, cylindrical worm-runs. Central canal of branchlets/pinnules usually very narrow. Spines smooth, conical, simple, with acute or rounded apex; height generally not much more than about twice the width at the base; subequal in size around the circumference of the axis or slightly longer on the polypar side; inclined distally or extending out at right angles; sometimes directed proximally. Spines on branches and stem, when present, usually appearing narrower and more terete than those on pinnules and branchlets, but often worn away on lower section of stem and on basal plate. Arrangement of spines in rows becoming more irregular on larger branches and stem. Polyps on smallest branchlets/pinnules appearing slightly elongated in axial direction; 0.5 to 1.5 mm in transverse diameter; arranged in a single, although not strictly regular, series and usually separated by a distinct interpolypar space. Tentacles (in preserved material), relatively short, cylindrical, with rounded apex; subequal in size, and generally not longer than the transverse diameter of the polyps.

Remarks.—This family is established on the basis of morphological similarities in the polyps and spines, by the tendency of the branchlets or pinnules to occur in groups of two, three or four, and by the tendency for parts of the corallum to fuse and anastomose. The subopposite or verticillate arrangement of the pinnules and branchlets occurs less frequently in taxa that form flabellate colonies. Although not very large (1.5 mm maximum transverse diameter), the polyps often have the appearance of being elongated along the transverse axis, especially on the narrow branchlets and pinnules. In preserved material, the tentacles are short, and somewhat blunt, and usually stand out from the polyp. The pinnular/branchlet spines are conical and smooth, with a rounded or acute apex. Spines near the distal ends of the branchlets/pinnules tend to be inclined distally; more proximally they stand out at right angles. Occurring sporadically
throughout the corallum are spines that are directed towards the basal end of the branches or pinnules. On the thicker branches and stem, the spines, when present, are similar in size, but appear more terete than those on the pinnules/branchlets. On the lower part of the stem and on the basal plate the spines are frequently worn away. Although the spines are aligned in axial rows, there is a tendency for this arrangement to become distorted. The number of rows of spines on the larger branches and stem can be similar to or greater than that on the pinnules/branchlets, but the arrangement usually becomes much more irregular.

Stylopathidae appears to be intermediate between the Antipathidae and some genera in the Schizopathidae, in particular Parantipathes, and, indeed, some of the species now referred to this family were at one time or another assigned to the genus Parantipathes, mainly because of the apparent elongation of the polyps in the transverse axis. However, in Stylopathidae the polyps are never more than 1.5 mm in transverse diameter and are usually less than 1 mm, whereas in Parantipathes they reach a maximum size of about 2-3 mm. The relatively short, cylindrical tentacles in the polyps of the Stylopathidae are similar to those in polyps of Parantipathes and are quite different from the very elongated, conical and pointed tentacles seen in living, expanded polyps of the Antipathidae; however, it should be noted that no observations have yet been made on the living polyps of any species of stylopathid.

Genera of Stylopathidae vary in external form, some are flabellate and others are columnar and pinnulate. The morphology of the corallum is the basis for dividing the family into the following genera:

**Key to Genera of Stylopathidae**

1a. Corallum flabellate, densely branched; not pinnulate ...................................... *Tylopathes* Brook
1b. Corallum monopodial or branched, and pinnulate .................................................. 2
2a. Corallum monopodial; rarely branched ................................................................. *Stylopathes* gen. nov.
2b. Corallum branched; primarily from near base ..................................................... *Triadopathes* gen. nov.

In addition to the genera listed above, there is the possibility that some taxa similar in external appearance to species of the genus *Arachnopathes* Milne Edwards & Haime, such as *A. ericoides* Pallas, 1766, and *A. clathrata* (Pallas), might eventually prove to be related to the Stylopathidae. These species are characterized by a dense bushy, non-pinnulate corallum and short, curved, anastomosing branchlets, with the branchlets in some cases arising in subopposite pairs or in groups of three. The spines of these species, however, tend to be more similar in morphology to those of the Antipathidae than to the Stylopathidae. Information on the morphology of the polyps of these species is lacking.

*Stylopathes* gen. nov.

*Arachnopathes* (in part), Duchassaing, 1870: 23.
*Antipathes* (in part); Duchassaing & Michelotti, 1860: 56 (A. americana); 1864: 48 (A. americana); Pourtales, 1874: 46, pl. 9, fig. 8; 1878: 209; 1880: 117, pl. 3, fig. 3.
*Parantipathes* (in part) Brook, 1889: 141; Silberfeld, 1909: 10; van Pesch, 1914: 96.
Type species.— *Arachnopathes columnaris* Duchassaing 1870: 23 (see description of neotype below)

Diagnosis.— Corallum monopodial or very rarely branched. Stem (and branches when present) pinnulate. Primary pinnules simple or subpinnulate; arranged, in varying degrees of regularity, in three, occasionally four rows, and sometimes in quasi-verticillate groupings of three or four. Subpinnules, when present, arranged singly, suboppositely, or in verticils of three or four (rarely five). Spines short, usually not more than 0.1 mm in height on the pinnules and subpinnules; smooth, conical, and inclined distally to varying degrees, especially near the tips of the subpinnules. Polyps 0.6 to 1.3 mm in transverse diameter; arranged uniserially and appearing transversally elongated on the pinnules and subpinnules.

Remarks.— Duchassaing (1870) originally placed his species *columnaris* in the genus *Arachnopathes* which was established by Milne-Edwards in 1857. The primary character that *S. columnaris* has in common with *Arachnopathes ericoides* (Pallas), the type species of the genus *Arachnopathes*, is the tendency for ramifications of the corallum to anastomose. *Arachnopathes ericoides* forms a dense and irregularly branched, bush-like corallum. The validity of the genus *Arachnopathes* was questioned by Brook (1889) who considered the type species to be among the “species incertae sedis”. Later workers, including van Pesch (1914) and Pax & Muller (1955), synonymized the genus with *Antipathes*.

Although Pourtalès (1878) described the polyps of *Antipathes* (*Arachnopathes*) *columnaris* as being very small, Brook (1889) provisionally transferred the species to the genus *Parantipathes*, mainly because of the similarity of the corallum to that of *Parantipathes larix* (Esper). In *Parantipathes*, the maximum size of the polyps is usually greater than 2 mm in transverse diameter, whereas in *S. columnaris* the polyps have never been found to be longer than about 1.5 mm. Although the polyps may appear to be transversely elongated because of the narrowness of the pinnules, this alone is not justification for placing the species in *Parantipathes*. Furthermore, a simple unbranched, but pinnulated corallum is not a character restricted to genus *Parantipathes*.

Species assigned to *Stylopathes*.— In addition to the type species, other nominal species that can be assigned to *Stylopathes* include: *Antipathes americana* Duchassaing & Michelotti, 1860, *Parantipathes tenuispina* Silberfeld, 1909, *S. adinocrada* spec. nov., and *S. litocrada* spec. nov.

Etymology.— The genus name is derived from the Greek, “stylos” (pillar) in reference to the growth form of the corallum, and the commonly used suffix “pathes”.

Distribution.— Species of this genus are known from the western Atlantic (*S. americana, S. columnaris, S. litocrada* and *S. adinocrada*), Japan (*S. tenuispina*), and the Indo-Pacific (*S. columnaris*).

**Stylopathes columnaris** (Duchassaing, 1870) comb. nov. (figs 1-3)

*Arachnopathes columnaris* Duchassaing, 1870: 23.
*Antipathes (Arachnopathes) columnaris*; Pourtalès, 1874: 46, pl. 9, fig. 8; 1878: 209.
*Antipathes columnaris*; Pourtalès, 1880: 117, pl. 3, fig. 3; Opresko, 1974: 101-115 (in part, see fig. 12).
*Parantipathes columnaris*; Brook, 1889: 141 (listed as “Parantipathes?”); Silberfeld, 1909: 28.
*?Parantipathes columnaris*; van Pesch, 1914: 96.
Fig. 1. *Stylopathes columnaris* (Duchassaing), neotype (USNM 77114), entire corallum.

Designation of a neotype.— USNM 77114 (schizotype, RMNH 34020), Caribbean Sea, Rosalind Bank, 16°35'N, 80°55'W, 100 fm (183 m), 24.viii.1957, R/V "Oregon" sta. 1890.

Other material examined.— USNM 10860, Cuba, Straits of Florida, off Havana, 23°10'54"N, 82°17'45"W, 210 m, 17.i.1885, R/V "Albatross" sta. 2322 (1 spec); USNM 75007, Bahamas, west of Wood Cay, 26°41'48"N, 79°01'18"W, 301-231 m, 13.vi.1983, Johnson Sea Link I, sta. 1355; USNM 74823, Gulf of Mexico, 25°44'50"N, 84°21'02"W, 159 m, Continental Shelf Associates, SOFLA sta. 35 (no other data); USNM 10249, Straits of Florida, off Havana, 23°10'40"N, 82°20'15"W, 337 m, 10.i.1885, Albatross sta.
2345; USNM 52536, Barbados, west coast, NR 12-4 ID101, 50-400 m (no other data); USNM 77106, Caribbean Sea, off Aves Island, 15°30’N, 63°38’W, 366-375 m, 8.ix.1964, R/V Oregon sta. 4994 (1 spec.); UMML 7.686, Lesser Antilles, off St. Lucia, 14°05.6’N, 60°51.4’W to 14°07’N, 60°52.2’W, 198-430 m, 7.vii.1969, R/V “Plansby” sta. 890 (1 spec.); UMML 7.744, Off Surinam, 7°28’N, 55°11’W, 75 fm (137 m), 24.iii.1963. R/V “Oregon” sta. 4305 (2 spec.).
Fig. 3. *Stylopathes columnaris*, neotype (USNM 77114): a-f, spines on pinnules, scale 0.1 mm.
Diagnosis.—Corallum monopodial and pinnulated, mostly to the third and fourth order. Primary pinnules on stem arranged primarily in three (rarely four) rows; two lateral and one or two on the anterior side of the stem, and also in verticillate grouping of three or four – one from each row. Lateral primary pinnules longer and more extensively subpinnulated than anterior primaries. Secondary pinnules arranged primarily in verticils of three (rarely four), and sometimes singly or in subopposite pairs. Tertiary and higher order pinnules, when present, occurring singly, in pairs, or in verticils. Cylindrical, reticulated worm run present along posterior side of stem. Subpinnulation of lateral pinnules generally not covering worm run. Tertiary and higher order pinnules usually more extensively developed on outer lateral margins of corallum, especially in older colonies.

Spines small, conical, inclined distally, especially near distal end of the pinnules and subpinnules and becoming less distally inclined towards the proximal end. Spines up to about 0.1 mm tall near the distal end of the pinnules and decreasing to 0.05 mm or less at the proximal end; arranged in irregular rows, with members of each row spaced 0.10-0.25 mm apart. Spines on the side of the axis containing the polyp slightly longer than those on the opposite side.

Polyps 0.6-0.9 mm in transverse diameter; and arranged in a single series (8-10 per centimeter) primarily on the distal or lateral sides of the pinnules.

Type material.—Duchassaing’s type material of *Arachnopathes columnaris* has not been located. According to Volpi and Benvenuti (2003), there are no type specimens of this species in the remaining Duchassaing collections in Turin or Florence. Because specimens previously assigned to *A. columnaris* cover a wide range of morphological variability, particularly in the arrangement and degree of subpinnulation (see Opresko, 1974), the establishment of a neotype is necessary to clearly define the species. According to Duchassaing, *Arachnopathes columnaris* was collected in the West Indies (Guadeloupe); therefore, a specimen collected in the Caribbean was selected as the neotype.

Description of the neotype.—The neotype (USNM 77114, fig. 1) is a relatively large colony, 39 cm tall, but only about 3 cm wide, with a basal stem diameter of about 2.7 mm. The lowermost 2 cm of the stem lacks pinnules; the uppermost tip is damaged, possibly as a result of efforts to remove the commensal polychaete. Over most of the corallum, and including the remaining section at the apex of the stem, the primary pinnules are arranged in three rows; two lateral and one on the anterior side of the axis (the side opposite the worm run). Pinnules representing what appears to be a fourth row occur, in places, on the anterior side, but these are not very common. The primary pinnules are generally arranged in verticillate groupings of three (one from each row). The primary pinnules in the two lateral rows are mostly 1 to 1.5 cm in length (up to about 2 cm) and about 0.3-0.4 mm in diameter at their base, and they extend out at a right angle to the stem or are slightly inclined distally (fig. 2a). In each row the pinnules are spaced 2-3 mm apart, with 5-6 per centimeter in one row. Counting all primary pinnules in all rows there are usually 15-18 per centimeter.

The anterior primary pinnules are very short, generally less than 5 mm, and most are simple; however, a few have one or two secondary pinnules and occasionally a whorl of three secondaries.

A worm run 3 mm in diameter is present along the entire length of the stem except for the lowermost 3 cm. The worm run is constructed from the lower section of the lat-
eral primaries and secondary pinnules closest to the stem, as well as numerous small interlinking cross pieces of sclerenchyme (fig. 2a). Also, included in the reticulum are small pseudo-lateral pinnules that connect the stem with the worm run, but usually do not extend beyond the surface of the run. One or two of these small pseudo-laterals occur between each adjacent pair of primary laterals. A few small, mostly simple subpinnules, less than 5 mm in length, arise from the surface of the reticulum.

On each primary pinnule, secondary pinnules (fig. 2b) are arranged mainly in groups of two or three, but sometimes also occur singly or in verticils of four. These groupings occur at intervals of 2-2.5 mm, with four or five (sometimes six) groups per centimeter. The smallest simple secondary pinnules are mostly 3-4 mm in length and 0.2-0.3 mm in basal diameter; some secondaries become elongated and subpinnulated. Tertiary and quaternary pinnules are common, especially on the secondaries at the outer edges of the primary laterals. The tertiary pinnules are mostly 2-3 mm in length and about 0.1-0.2 mm in basal diameter. The tertiary pinnules occur singly, in pairs or in whorls of 3-4 (rarely 5); most extend out nearly at right angles to the axis at their point of insertion, but then curve toward the distal end of the lower order ramification from which they arise (fig. 2b). Adherence and fusions of overlapping subpinnules occur throughout the corallum.

The spines (fig. 3) near the tips of the pinnules and subpinnules are conical, elongated, and distally inclined. They reach a maximum size of about 0.11 mm near the free end of the smallest pinnules. More proximally, the spines become reduced in size and less distally inclined (fig. 3f). On sections of pinnules 0.13-0.16 mm in diameter, the spines are generally 0.06 to 0.08 mm tall. On a section of pinnule 0.25 mm in diameter the spines are as small as 0.05 mm and stand out at right angles to the axis. On the lowest part of the stem most of the spines are worn away; however, a few remain and these are narrow, cylindrical, and about 0.06 mm tall. On the pinnules, the spines are arranged in rows of varying regularity, three to five of which can be seen in lateral view. The spines are spaced 0.11 to 0.19 mm apart in each row, resulting in six to ten per millimeter.

The polyps generally occur in a single row. On the lateral pinnules they are found primarily on the side of the pinnules opposite to that side of the corallum on which the worm run is located. On the subpinnules they occur on the upper (distal) side of the pinnules, but also tend to face out on the side of the corallum as those on the lateral pinnules; therefore the corallum has a noticeable polypar and abpolypar side. On the lateral pinnules the polyps are mostly 0.8 to 0.9 mm in transverse diameter with an estimate of about eight per centimeter. On the subpinnules the polyps appear to be slightly smaller, about 0.6-0.8 mm in transverse diameter, although the poor state of preservation makes estimates of their size imprecise. On the narrower pinnules the polyp tentacles appear to be grouped in pairs with the sagittal pair being closest to the mouth, thereby giving the polyps the appearance of being transversely elongated. The tentacles, in general, are rather small, measuring in one case only 0.15 mm in length. Polyps also occur on the surface of the worm run where the tentacles are often not well-defined, with only the mouths clearly visible.

Remarks.— Other specimens assigned to this species are similar to the neotype in showing the predominantly bilateral pinnulation of the corallum, with the lateral primary pinnules being longer and more developed than the anterior primaries, and with the tertiary pinnules becoming more extensively developed on the outer lateral mar-
gins of the corallum. Although short pinnules may also originate from the worm run, especially in older colonies, these generally do not become subpinnulated. In most colonies the worm run remains visible over most of its length (i.e., is not covered by sub-pinnules from the lateral primary pinnules). On the anterior side of the axis (opposite the worm run) the primary pinnules generally remain small, although in some specimens a few may become almost as large as the laterals. The length of the lateral primary pinnules varies from colony to colony. In some cases (USNM 77106; USNM 10249; USNM 74823; USNM 52536), the corallum is narrower than the holotype (2-2.5 cm wide), the subpinnules are shorter, and the tertiary pinnules develop on secondaries closer to the stem (often on the first or second ones distal to the worm run).

Van Pesch (1914) described from the Indo-Pacific three specimens of “Parantipathes columnaris” having secondary and tertiary pinnules arranged in verticils of three or four, but with the primary pinnules arranged irregularly, and not in verticils. In these specimens the maximum length of the pinnules ranged from 1.4 cm to about 2.75 cm, and the maximum size of the spines ranged from not more than 0.05 mm in two specimens to 0.135 mm in the third.

Comparisons.— *Stylopathes columnaris* is similar to *Stylopathes americana* (see below); in having distinct lateral primary pinnules, with secondary pinnules often occurring primarily in verticils. The two species differ in that *S. americana* generally has shorter secondary pinnules, fewer tertiary and quaternary pinnules, and with the primary pinnules and subpinnules more frequently arranged in verticils of four.

Distribution.— From the northern Bahamas to Brazil, and throughout the Caribbean. Also reported from the Indo-Pacific (van Pesch, 1914).

Bathymetric Range.— 73-567 m in the western Atlantic; 560-984 m in the Indo-Pacific (van Pesch, 1914).

*Stylopathes americana* (Duchassaing & Michelotti, 1860) comb. nov.
(figs 4-5)

Antipathes americana Duchassaing & Michelotti, 1860: 56; 1864: 46.

not Antipathes americana, Opresko, 1972: 975-979 (= Myriopathes? sp., see comment below).

Antipathes columnaris; Opresko, 1974:101-115 (in part, see fig. 13).

Material examined.— UMML 7.692, Virgin Islands, 18°47'N, 64°47'W, 563 m. 23.vii.1969, R/V “Pillsbury” sta. 991 (1 spec.); USNM 77115 (part, RMNH Coel. 34021), Caribbean Sea, Serrana Bank, 13°56'N, 81°56'W, 276 fm (505 m), 14.ix.1957, R/V “Oregon” sta. 1931 (1 spec.); UMML 7.691, Bahamas, off the south coast of Great Inagua, 20°54.5'N, 73°28.2'W, 110-220 m, R/V “Pillsbury” sta. 1143, 13.i.1970 (1 spec.); UMML 7.689, off the south coast of the Dominican Republic, 18°21.4'N, 69°06.6'W to 18°22.8'N, 69°06.6'W, 149 m, 9.vii.1971, R/V “Pillsbury” sta. 1386 (1 spec.); UMML 7.974, Lesser Antilles, off Aniquilla, 18°26.4'N, 63°12.6'W to 18°28'N, 63°11.1'W, 393-451 m, 22.vii.1969. R/V “Pillsbury” sta. 984 (1 spec.); UMML 7.693, 7°28’N, 55°11’W, 75 fm (137 m), 24.iii.1963. R/V “Oregon” sta. 4305; USNM 74828, Gulf of Mexico, off Florida, 25°16’30’’N, 84°14’46’’W, 159 m, 2.viii.1981, Continental Shelf Associates, sta. 38, Field #2/11-38A.

Fig. 4. *Stylopathes americana* (Duchassaing & Michelotti): a, syntype (Turin Coel.78), no scale available, b, section of corallum of the specimen from R/V “Pillsbury” sta. 991 (UMML 7.692), c, secondary pinnules of the specimen from R/V “Pillsbury” sta. 991.
Fig. 5. *Stylopatus americana* (Duchassaing & Michelotti): a-d, spines on pinnules of the specimen from R/V "Pilsbury" sta. 991 (UMML 7.692), scale 0.1 mm.

Diagnosis.—Corallum monopodial and pinnulated, mostly to the second order, sometimes higher. Pinnules and subpinnules over the entire corallum arranged primarily in verticils of three or four. Primary pinnules on stem arranged in two lateral rows and in one or two anterior rows. Lateral primary pinnules usually (but with some exceptions) much longer and more extensively subpinnulated than anterior primaries. Secondary and tertiary pinnules commonly arranged in verticils containing three or four members, although subpinnules may also occur singly or in pairs. Cylindrical reticulated worm run present along posterior side of the stem.

Spines small, conical and inclined distally (especially those at the distal end of the pinnules); 0.06-0.1 mm tall; arranged in four to eight longitudinal rows with the members of each row spaced 0.10-0.25 mm apart. Spines on the side of the axis containing the polyps slightly longer than those on the opposite side.

Polyps small, 0.6-0.7 mm in transverse diameter; and arranged in a single series on the distal and lateral sides of the pinnules, tending to face out on the side of the corallum opposite the one on which the worm run is located.

Type material.—A specimen labeled as *Antipathes americana* Duchassaing & Michelotti is in the Duchassaing & Michelotti collection in the Turin Museum (Coelenterate No. 78). This specimen is considered by Volpi & Benvenuti (2003) to be a syntype of the
species. The specimen, however, does not correspond to the original description which refers to the species as being simple, pinnate with narrow pinnules dichotomizing several times without decreasing much in diameter. A species entirely different from the syntype was identified previously as *A. americana* (see Opresko, 1972); however, in view of the existence of a presumed type specimen, the taxon must be defined on the basis of this syntype. The specimen previously identified as *A. americana* has skeletal characters (e.g., pinnulation pattern) very similar to those of species of *Myriopathes* in the family Myriopathidae (see Opresko, 2001); however, the preserved polyps resemble those of species in the Stylopathidae. Because the morphology of the polyps is considered a higher level taxonomic character than the pinnulation pattern (which can arise independently in different families), it is quite possible that the specimen identified as *A. americana* in 1972 is related to the Stylopathidae. However, because it is also known that the morphology of the polyps can be altered considerably by preservation, the similarity seen in the polyps may not be a reliable indicator of a natural relationship. An evaluation of the morphology of the living expanded polyps, as well as an analysis of molecular data, will be needed to determine the true affinities of this taxon.

Description.—The syntype in the Turin Museum was not available for detailed study; however, a photograph of the specimen is shown in figure 4a. A specimen from the collections of RSMAS (UMML 7.692, “Pillsbury” sta. 991) which appears to conform to the characters of the syntype will be described here.

The specimen from “Pillsbury” sta. 991 is about 18 cm tall (the top of the corallum is missing) and 2.2 cm wide, with a basal stem diameter of 0.9 mm. The lowermost 6 mm of the stem lacks pinnules, the next 2.7 mm shows scars where pinnules had once been. Over most of the corallum the primary pinnules are arranged in three rows; two lateral and one on the anterior side of the axis (the side opposite the worm run). In some places, however, especially on the upper parts of the stem, additional pinnules representing a fourth row are present on the anterior side. The primary pinnules are arranged in irregular groups of three (one from each row), and in places these groups form a distinct verticil. On the upper parts of the stem there are verticils of four primary pinnules. The primary pinnules in the two lateral rows are mostly 1 to 1.5 cm in length and about 0.2 mm in diameter at their base, and extend out at a right angle to the stem. In each row the primaries are spaced 2-2.5 mm apart, with five to six per centimeter. Counting all primary pinnules in all rows, there are usually about 15-18 per centimeter.

The anterior primary pinnules are much smaller than the lateral ones; they are not more than 5 mm long and sometimes have only one group of secondary pinnules which are not regularly orientated or constant in number. These secondary pinnules can arise singly, in pairs or even in verticils of three or four.

Fused along one side of the stem is a worm run about 2.8 mm in diameter. Included in the reticulum are small pseudo-lateral pinnules extending from the stem to other cross sections of the run. There can be one to three of these small pseudo-laterals between each adjacent pair of primary laterals. On each primary pinnule, distal to the worm run, other secondary pinnules are arranged in verticils of mostly four (sometimes three), and these whorls occur at intervals of mostly 1.6-2.0 mm (range 1.2-2.4 mm), with 6-7 whors per centimeter (fig. 4b-c). The secondary pinnules are 1.5-2.5 mm in length and 0.1-0.15 mm in basal diameter. Tertiary pinnules occur, especially on the secondaries on the outer edges of the primary laterals, and on those secondaries on the
lower or upper sides of the lateral primaries (relative to the direction of the stem). The tertiary pinnules are mostly 1-2 mm in length and about 0.1 mm in basal diameter. The secondary and tertiary pinnules are curved toward the distal end of the lower order ramifications from which they arise (fig. 4b-c). Adjacent and overlapping subpinnules may become fused to each other, especially on the lateral margins of the corallum.

The spines (fig. 5) are smooth and conical with an acute to rounded apex. They reach a maximum size of about 0.08 mm near the free end of the smallest pinnules (fig. 5a). Most are angled to some degree towards the distal end of the pinnule, but nearer the base become reduced in size (about 0.02 mm tall) and more nearly perpendicular to the axis (fig. 5d). The spines are 0.12-0.15 mm apart in each row. Near the distal end of the pinnules about four irregular longitudinal rows of spines can be seen in lateral view; toward the base six to eight rows are visible in lateral view. There is usually a very small area at the point of insertion of the pinnules which lacks spines. On the lower parts of the stem the spines are worn away; at the height of about 3 cm or more they are no more than about 0.04 mm tall and rather narrow, and arranged in four to five rows (seen in lateral view).

The polyps on the corallum are in a rather poor state of preservation. In general, they appear to be arranged in a single row, mostly on the upper or lateral sides of the pinnules (sometimes on the lower side). There is a slight tendency for the polyps to face out the side of the corallum opposite the worm run. The polyps are typically about 0.6 to 0.7 mm in transverse diameter. The number per centimeter could not be determined. The tentacles are very short, only about 0.1 mm in length. On the narrower pinnules the tentacles appear to be grouped in pairs with the sagittal pair being closest to the mouth, thereby giving the polyp the appearance of being transversely elongated.

Remarks.— This species is characterized by the occurrence of the primary and secondary pinnules mostly in verticils containing three and four members. One specimen assigned to this species (USNM 77115) shows a greater development of the lateral primary pinnules (up to 2 cm long) and a greater development of subpinnulation. Similarly, in the colony from R/V "Pillsbury" sta. 1143 (UMML 7.691), the lateral primary pinnules are up to 2 cm long and possess as many as ten whorls of subpinnules. The greatest number of whorls contain four subpinnules, some have only three, but very few have less than three. Only a few of the secondary pinnules, and usually only those in whorls on the distal half of the primary pinnules, are sufficiently long to possess tertiary pinnules and these are also arranged primarily in verticils. Except for the branchlets of the worm-run, there are few fusions of pinnules and subpinnules.

In another specimen referred to this species (UMML 7.974, from "R/V Pillsbury" sta. 984), some of the anterior primary pinnules are as long as the lateral ones and similarly possess whorls of secondary pinnules. This pattern is taken a step further in a specimen from R/V "Pillsbury" sta. 1386 (UMML 7.689) where both the primary pinnules and some of the secondary subpinnules are up to 3 cm long and stand out in all directions from the stem, thus giving the corallum a rather loosely-cylindrical structure.

Comparisons.— As noted above, Stylopathes americana is similar to Stylopathes columnaris but has more distinct lateral pinnules, usually with smaller subpinnules, fewer tertiary pinnules, and a greater tendency for the subpinnules to occur in verticils of four. In its typical form, the corallum tends to have a bilateral configuration due to the stronger development of the lateral primary pinnules; however, exceptions occur in which the anterior pinnules are as long as the laterals.
Distribution.— From the Lesser Antilles to the Bahamas.

Bathymetric Range.— 110-560 m.

Stylopathes adinocrada spec. nov.
(figs 6-7)

Antipathes columnaris; Opresko, 1974:101-115 (in part, see fig. 15).

Type material.— Holotype: USNM 1092612, Lesser Antilles, off Aves Island, 15°30'N, 63°38'W, 360 m. 6.ix.1964, R/V “Oregon” sta. 4994; Paratype: UMML 7.678, Off Surinam, 07°28'N, 55°11'W, 134 m, 24.iii.1964, R/V “Oregon” sta. 4305.

Other material examined.— USNM 5860, Saint Vincent, 13°07'55"N, 61°05'36"W, 124 fm (227 m), 3. iii.1879, USCSS “Blake” sta. 269; USNM 7170, Straits of Florida, off Havana, 708 m, 30.iv.1884, R/V “Albatross” sta. 2152; USNM 76961, Bahamas, Little Bahama Bank, 27°17'36"N, 79°15'36"W, 480 m, 29. iii.1975, R/V “Eastward” sta. 26535 (1 spec.). UMML 7.688, Lesser Antilles, off St. Lucia, 14°05.2’N, 60°50.3’W to 14°07.8’N, 60°50.7’W, 265-567 m, 7.vii.1969, R/V “Pillsbury” sta. 891 (1 spec).

Diagnosis.— Corallum monopodial and densely pinnulated mostly to the third and fourth order. Subpinnules forming a complex mass of anastomosing ramifications on both the anterior and posterior side of corallum. Primary pinnules arranged in three rows and in loose verticils of three, consisting of two laterals and one anterior pinnule. Secondary pinnules in verticils of three, in pairs, or occurring singly. Highest order subpinnules predominantly in pairs or singly. Primary pinnules not easily discernable due to the dense subpinnulation. Cylindrical reticulated worm run extending along the posterior side of the stem.

Spines small, conical, with rounded apex, and slightly inclined distally; mostly 0.03-0.04 mm tall (up to 0.06 mm); arranged in four to five longitudinal rows (in lateral view) with members of each row spaced 0.1-0.2 mm apart.

Polyps 1-1.3 mm in transverse diameter; and arranged in a single series mostly on one side of the pinnules.

Description of the holotype.— The holotype (fig. 6a) is 17.5 cm tall, about 4 cm wide, and 1.5 cm thick, with a basal stem diameter of 1.5 mm. The basal attachment plate is missing. The lowermost 2.7 cm of the stem lacks pinnules but shows scars where pinnules had once been. A reticulated, cylindrical worm run, about 4 mm in diameter, is present on the posterior side of the stem and extends along the entire pinnulated section of the corallum except for the uppermost 1.5 cm. The primary pinnules are difficult to distinguish from the subpinnules due to the density and thickness of the subpinnules. In general, and even at the distal end of the stem above the worm run, the primary pinnules occur in three irregular rows (two lateral and one anterior) and in loose clusters of three, one from each row. In places the clusters clearly define verticils, whereas in others they are quite irregular. Where they follow a regular pattern the clusters are spaced 2.5-3 mm apart, resulting in 12-15 or more primary pinnules per centimeter. The longest lateral primary pinnules are about 2 cm in length and about 0.27 mm in diameter near the base. The anterior primary pinnules occur in a not very straight row, are often offset from the adjacent laterals; and, in places, are missing. Most are not more than about 7 mm long (maximum about 1 cm) and contain two or three clusters of secondary pinnules, some of which carry tertiary pinnules.
Fig. 6. *Stylopathes adinocrada* spec. nov., holotype (USNM 1092612): a, corallum; b, section of corallum; c, primary and secondary pinnules.
The lowermost 2-3 mm of the lateral primary pinnules, and the lowermost section of the secondary pinnules nearest the stem are incorporated into the worm run, together with short interlinking branchlets which form a very close-meshed reticulum (fig. 6b). The secondary pinnules whose basal section is part of the worm run can extend beyond the worm run and become subpinnulated. These secondaries therefore appear to arise from the surface of the worm run. On the distal section of each primary pinnule, the secondary pinnules are frequently arranged in verticils of three, sometimes in offset pairs, and occasionally occur singly (fig. 6c). The clusters of secondaries are spaced irregularly, from less than 1 mm to as much as 4 mm apart, but on average there are usually three or four groups per centimeter. The secondary pinnules are 1.5-2.5 cm in length, and 0.1-0.2 mm in basal diameter. The longest secondaries are generally those originating from the lowermost verticils of the primaries. Tertiary and higher order subpinnules also occur throughout the corallum. Although they can be grouped in verticils, most occur singly or in pairs. The highest order subpinnules on the outer margins of the corallum are mostly 5-7 mm long. The subpinnules can be straight or curved to varying degrees towards the distal end of the pinnule or subpinnule from which they arise. Fusions of adjacent secondary and tertiary pinnules occur throughout the corallum, with the exception of the subpinnules at outermost lateral margins. The result is a plexus of anastomosing subpinnules on both the anterior and posterior sides of the corallum.
The spines (fig. 7) are small and conical, with a rounded apex and a relatively wide base. They reach a maximum size of about 0.06 mm on axial diameters of 0.07-0.12 mm. They are inclined distally slightly. The spines are 0.1-0.2 mm apart in each row and there are five to six rows visible in lateral view. On the thicker pinnules and stem the spines become reduced in size (to about 0.01 mm tall) and extend out more nearly perpendicular to the axis (fig. 7d).

The polyps are arranged in a single row, mostly on the upper or lateral side of the pinnules, such that they tend to face out the side of the corallum opposite the worm run. The polyps are up to 1.3 mm in transverse diameter. The interpolypar space is about 0.3 mm, and the polyp density is estimated to about eight or nine per centimeter, a more exact measurement is difficult because of the shortness of the segments of the pinnules and subpinnules. The tentacles are about 0.2 mm long in the preserved material.

Remarks.— Several of the specimens assigned to this species (USNM 76961 and USNM 7170) differ from the type in having less dense subpinnulation and thicker pinnules; however, in both cases the subpinnules are developed over the worm run. In the specimen from “Blake” sta. 269 (USNM 5860) the corallum is 5 cm wide.

Comparisons.— *Stylopathes adinocrada* differs from *Stylopathes columnaris* mainly in the pattern of pinnulation of the corallum. In *S. columnaris* the lateral primary pinnules are quite distinct, the subpinnules are often in verticils of three or four, and the subpinnulation is often more dense at the lateral margins of the corallum and does not cover the worm run. In contrast, in *S. adinocrada* the lateral primary pinnules are often indistinct, the higher order subpinnules frequently occur singly and in pairs and not as often in verticils, and the subpinnulation is anastomosing to such an extent that it extends over the worm run. The two species also appear to differ in the size of the polyps. In *S. adinocrada* the polyps are up to 1.3 mm in transverse diameter, whereas in *S. columnaris* they are generally 0.6-0.9 mm in transverse diameter. Young colonies of *S. adinocrada* and *S. columnaris* may be difficult to differentiate on the basis of skeletal features alone, especially if the higher order subpinnules are not yet developed.

Etymology.— From the Greek, “adino” (crowded) and “crada” (twig), in reference to the dense subpinnulation of the corallum.

Distribution.— From Surinam to the Bahamas.

Bathymetric Range.— 134-708 m.

*Stylopathes litocrada* spec. nov.
(figs 8-10)

Type material.— Holotype: USNM 53435 (schizotype, RMNH 34022), Caribbean Sea, “possibly Antilles”, 241 m, 14.II.1902, C.C. Nutting; Paratypes, UMML 7.1173, Lesser Antilles, off Aves Island, 15°30’N, 63°38’W, 360 m, 8.IX.1964, R/V “Oregon” sta. 4994 (2 spec.).

Other material examined.— USNM 100120, Gulf of Mexico, Yucatan Peninsula, NNE of Campeche Bank, 23°56’N, 87°2’W, 293 m, sta. 1184 (no other data); USNM 88334, Gulf of Mexico, off Louisiana, Green Canyon, 27°50’37”N, 91°22’56”W, 274 m, 4.IX.1959, R/V “Silver Bay” sta. 1184; USNM 53439, Gulf of Mexico, SE of Galveston, Texas, 28°00’N, 93°30’W, 91 m, 17.1.1964, R/V “Oregon” sta. 4603; USNM 74831, Gulf of Mexico, off Florida, 25°44’50”N, 84°21’02”W, 159 m, 7.II.1982, Continental Shelf Associates, sta. 35; USNM 88333, Gulf of Mexico, off Louisiana, Green Canyon, 27°44’09”N, 91°07’20”W, 183 m, 6.IX.1989, Johnson Sea Link I DSR/V sta. 2586.
Diagnosis.—Corallum monopodial and pinnulated, mostly to the second order. Pinnules sparsely and irregularly distributed on all sides of corallum. Primary pinnules 2-3 cm long, simple or subpinnulated. Secondary pinnules arranged irregularly (very rarely in verticils); tertiary and quaternary pinnules occurring infrequently. Cylindrical reticulated worm run extending along the posterior side of the stem. Simple or sparsely subpinnulated pinnules also developing from surface of worm run.

Spine small, smooth, conical, up to 0.07 mm tall on the smallest pinnules, but only 0.02 mm tall on the lowermost sections of the largest pinnules; arranged in longitudinal rows of varying regularity, with 4 or 5 rows visible in lateral view. Spines slightly unequal around the circumference of the axis.

Polyps 0.7-0.9 mm in transverse diameter; and arranged in a single series on the pinnules, with 8-10 polyps per centimeter.

Description of the holotype.—The holotype (USNM 53435; fig. 8) is 44 cm tall, and about 4 cm wide, with a basal stem diameter of about 4 mm. The lowermost part of the stem is broken off and the basal plate is absent. Except for the lowest 2 cm and uppermost 1 cm, a reticulated worm run, 4-5 mm in diameter, extends along the length of the stem. The worm run is re-enforced by several pseudo-stems, about half the thickness of the real stem, which are incorporated into the reticulum and follow a course parallel to that of the stem.

The arrangement of the pinnules and subpinnules distal to the worm run is similar to that along the other parts of the stem. Pinnules extend out on all sides of the corallum (fig. 9a). The primary pinnules occur in two lateral rows and also sporadically and irregularly on the anterior side of the stem. The lateral primary pinnules are mostly 1.5-2.2 cm in length and 0.3-0.4 mm in diameter at their proximal end. They are not regularly arranged, a few are subopposite, and some are alternating. Most are 2-3 mm apart, and there are seven to ten or more per centimeter. Many are simple, without subpinnules, but others have one to four secondaries and a few have as many as seven secondaries (fig. 9b). The anterior primary pinnules are similar in size to the laterals and most are simple or have only a few irregularly arranged subpinnules.

One 3 cm long lateral primary has the appearance of developing into a pinnulated branch; it contains about 25 subpinnules which extend out on all sides.

The secondary pinnules are not regularly arranged on the primaries; they often extend out on all sides (fig. 9b) only infrequently occur in verticils or in subopposite pairs. In places the arrangement appears to follow a somewhat alternating pattern but this is not consistent throughout the corallum. The secondary pinnules are of varying sizes, with some reaching 1.7 cm in length with a basal diameter of about 0.25 mm. Secondary pinnules similar in size to the primary pinnules also develop directly from the surface of the worm run. The combined density of both these secondaries and the primaries was estimated to be about 12-15 per centimeter. The subpinnules arising from the worm run can be simple or sparsely subpinnulated. Tertiary pinnules occur on some secondaries, but are not common; these are up to 1.6 cm long with a diameter of 0.2 mm at the proximal end. Quaternary pinnules occur very rarely.

The axial spines (fig. 10) are small and conical, with a relatively acute apex. They are 0.03 mm or less in height near the tips of the pinnules (fig. 10a; axial diameter 0.03 mm), and 0.05-0.07 mm over most of the mid-section of the pinnules (fig. 10b-f; axial diameter 0.05-0.15 mm), but become reduced to only 0.02 mm on the most basal sections of the
larger pinnules (fig. 10g; axial diameter 0.2 mm or greater). In general, the size, orientation and arrangement of the spines on the pinnules and subpinnules varies in regularity. Many are slightly inclined distally, but others stand out at right angles to the axis,
Fig. 9. *Stylopathes Utocrada* spec. nov., holotype (USNM 53435): a, section of corallum; b, primary and secondary pinnules.

and a few are angled downward towards the base of the pinnule or subpinnule. The spines are 0.17-0.23 mm apart in one row, resulting in 5-7 per millimeter in each row, and there are 4-5 rows visible in lateral view.

The polyps on the pinnules are arranged in a single row, mostly on the upper or lateral sides. The polyps are up to about 0.8-0.9 mm in transverse diameter, the inter-polypar space is up to 0.4 mm, and there are 8-10 polyps per centimeter. The tentacles are subequal and about 0.25 mm long.

Remarks.—The specimens assigned to this species are all similar to the holotype in having simple or sparsely and irregularly subpinnulated primary pinnules, with secondary pinnules also arising from the surface of the worm run, thus giving the corallum a loose bottlebrush appearance. The extent of subpinnulation varies from colony to colony, and in some specimens most of the lateral primary pinnules are simple. Smaller, younger specimens generally have shorter primary pinnules. In a few specimens such as USNM 88333, the subpinnules occur more frequently in verticils of three to four, but this is far from common. In the latter specimen the primary pinnules are up to 3 cm long, and the polyps are about 0.7 mm in transverse diameter, with 9-10 polyps per centimeter.

Comparisons.—*Stylopathes litocrada* very closely resembles *Stylopathes tenuispina* (Silberfeld). In both species the primary pinnules are simple or only sparsely subpinnulated and extend out at right angles on all sides of the stem. The two species differ, however, in several ways. According to Silberfeld, the primary pinnules in *S. tenuispina* are up to 4 cm long, and possess only two or three subpinnules which form with the primary pinnules narrow distal angles. In contrast, in *S. litocrada*, the pinnules are not more than 3 cm long; there can be up to seven subpinnules on a primary, and many of
Fig. 10. *Stylopathes litocrada* spec. nov., holotype (USNM 53435): a-g, spines on pinnules, scale 0.1 mm.
the subpinnules form rather wide distal angles with the primary. Both species have relatively small spines, but those in *S. tenuispina* can reach up to 0.1 mm, whereas those in *S. litocrada* are generally not more than 0.07 mm.

Another species described by Brook (1889), *Antipathes cylindrica*, which has long been thought to be related to *S. tenuispina*, is not included here in *Stylopathes*. *A. cylindrica* has a simple bottle-brush type of corallum, but lacks a typical reticulated worm-run; instead it usually possesses one or more horny polychaete tubes that lie closely affixed to the stem. In addition, the pinnules and subpinnules are often in subopposite pairs and arranged in four rows, Unpublished observations by T. Molodtsova (pers. commun.) indicate that *A. cylindrica* or related species possess multi-forked spines on the basal holdfast, a characteristic of the family Myriopathidae. Therefore, it is quite possible that *A. cylindrica* is related to *Cupressophores* or *Tanacetipathes* in the Myriopathidae.

**Etymology.** From the Greek, "litos" (sparse) and "erada" (twigs), in reference to typical pinnulation of the corallum.

**Distribution.** From the Lesser Antilles to the northern Gulf of Mexico.

**Bathymetric Range.** 91-380 m.

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**Genus Triadopathes gen. nov.**

(figs 11-12)

*Parantipathes;* Opresko, 1999: 1550 (in part).

**Type Species.** *Parantipathes triadocrada* Opresko, 1999: 1550-1545, figs 7-9.

**Type material.** Holotype (SAM H-908; schizoholotypes USNM 99410, RMNH 34024), off Tasmania, about 46.5 nautical miles SSE of South East Cape, 44°22.7'S, 147°07.3'E, 1060-1170 m, F/V "Belinda", 12.ii.1992, coll: K. Gowlett Holmes; paratype (SAM H 759), South Australia, Great Australian Bight, about 80 nautical miles WSW of Pearson Id, in Investigator Group, 34°1'TS, 132°38'E, 160 m, F/V "Comet", 14.iv.1979, coll: K. Gowlett Holmes; paratype (SAM H-760), South Australia, Great Australian Bight, about 90 nautical miles W of Cape Wiles, 38°04'S, 133°59'E, 625-890 m, F/V "Longa" III, 9.xi.1989, coll: K. Gowlett Holmes.

**Diagnosis.** Corallum branched, larger branches arising mostly from near the base and ascending. Branches pinnulate. Pinnules arranged primarily, but not exclusively, in three axial rows, as well as in subverticillate groupings containing one pinnule from each row. Secondary and higher order subpinnules arranged in similar pattern. Multiple orders of subpinnules arising on the lateral primary pinnules, but not uniformly developed from branch to branch. Branches, pinnules and subpinnules adhering and fusing. Spines simple, conical, smooth, with acute to rounded apex; usually 0.06-0.08 mm tall. Spines 0.16-0.30 mm apart in each row, with five to six spines per millimeter. Polyps not more than 1.2 mm in transverse diameter; with seven to eight polyps per centimeter.

**Description of the holotype.** A detailed description of the holotype has been given previously (Opresko, 1999); and only a brief summary is presented here. The holotype is about 25 cm tall, with several, vertically extending, branches up to 20 cm in length (fig. 11a). The primary pinnules (fig. 11a) are frequently arranged in three rows and also in clusters of three; however, they may also occur singly and in pairs, and rarely in clusters of four. Where they occur in three rows, two of the rows are bilateral in posi-
Fig. 11. *Triadopathes triadocrada* (Opresko), holotype (SAM H-908): a, entire corallum, height about 22 cm; b, primary and secondary pinnules; c, cross section of branch; d, polyps.

tion, and the third is on the posterior side of the stem and branches. The pinnules in the two lateral rows are usually much more higher developed (complexly subpinnulate) than those in the posterior row (fig. 11c). The lateral pinnules have four or more orders of subpinnules; the posterior primary pinnules have only one or two. The subpinnules develop in the same manner as the primary pinnules, most often in clusters of three. Any one of the subpinnules can, in turn, have similar subpinnules, and this pattern can
be repeated over several higher orders of subpinnules. The subpinnules do not develop to the same extent from pinnule to pinnule; therefore the pattern of subpinnulation is not symmetrical. The largest unpinnulated pinnules or subpinnules are rarely more than about 7 mm in length and have a basal diameter of 0.14-0.16 mm (excluding spines). Fusions of overlapping pinnules and subpinnules occur frequently, resulting in a dense mass of anastomosing subpinnules, several centimeters thick, spreading out laterally and sometimes also on the front side of the stem and branches.

The spines (fig. 12) are simple, smooth, and conical with a relatively acute apex; generally 0.06-0.08 mm tall, but as much as 0.12 mm near the base of the larger pinnules. They are subequal to as much as twice as tall on one side. The majority of spines project out at right angles to the axis or are inclined distally, especially near the distal end of the pinnule, however, a few are directed downward towards the base of the pinnule. The distance between adjacent spines in each row varies from about 0.16 to 0.30 mm; on average there are 5-6 spines per millimeter in each row. Spines on the larger branches are relatively narrow and acicular, but few are more than 0.06 mm tall.

The polyps (fig. 12d) are distributed uniserially on the upper or anterolateral sides of the subpinnules and pinnules, and the corallum has a distinct polypar side. The polyps are 0.8-1.1 mm in transverse diameter, with seven to eight polyps per centimeter.

Remarks.—This genus is close to some species of *Stylopathes* in having the pinnules grouped together in quasi verticils. It differs from *Stylopathes* in being branched, and in only rarely having more than three pinnules or subpinnules per group. Although spe-
cies of *Stylopaths* occasionally develop branches, these tend to be identical to the stem in the terms of the pattern of pinnulation and subpinnulation. In contrast, in *Triadopathes* the branches are much more irregular in development and appear to represent a step toward a more distinctly branched corallum. In this regard the genus is intermediate in development between *Stylopaths* and the flabellate genus *Tylopaths* (see below).

Species assigned to *Triadopathes*.— Only the type species is currently assigned to this genus.

Distribution.— The type species was found off the coast of Tasmania (holotype) and off the southern coast of Australia (paratypes).

Bathymetric Range.— 160-1170 m.

Genus *Tylopaths* Brook, 1889
(figs 13-14)

*Tylopaths* Brook, 1889: 134.

Type Species.— *Tylopaths crispa* Brook, 1889: 135-136, pl. 3, figs 1-4.

Type material.— Holotype (BMNM 90.4.9.8; schizotypes USNM 100378, RMNH 34023), Off Chile, Sarmiento Channel, 51°27’30”S, 74°3’0”W, 400 fm (732 m), 10.i.1876, HMS “Challenger” sta. 310.

Diagnosis.— Corallum flabellate, but often with overlapping branches; smallest branchlets arising laterally or irregularly on all sides of branches. Branches developing predominantly from lateral or anterolateral branchlets. Corallum sometimes with cylindrical, reticulated worm runs formed by smallest branchlets. Spines small, subtriangular to conical, smooth; up to 0.11 mm tall. Polyps about 1 mm in transverse diameter.

Description of the holotype.— According to Brook (1889:135), the type material consists of a number of “fronds, depressed in the center and having the majority of the branches and pinnules directed inwards.” One of these fronds was reported to be 14 cm long and 22 cm broad. The illustration given by Brook of one of the specimens in the type series is shown in fig. 13a. Brook (1889) refers to the smallest branchlets (figs 13b-c) as pinnules, although they are not nearly as regular in size and arrangement as true pinnules. They arise uniserially or bilaterally, sometimes they are subopposite, and very rarely three arise from very nearly the same point. Brook (1889) reported about 70 “pinnules” along a 5.5 cm branch, or about 12 per centimeter. In several places on the corallum the branchlets closest to the branch from which they arise are bent and curved and fused together in such a manner as to form a cylindrical worm run.

The spines (fig. 14) on the branchlets are short, smooth, generally conical, and have a sharp apex. The upper margin is mostly straight, and most spines are inclined distally to some degree, but not uniformly, and a few are even inclined towards the base of the branchlet. The largest spines are up to about 0.11 mm tall (on a branchlet about 0.18 mm in diameter) and about 0.7 mm wide at the base. There is a slight difference in the size of the spines around the circumference of the axis, with the abpolypar spines being about 0.02-0.03 mm shorter than the polypar spines. The spines occur in not very regular rows, with four or five rows visible in lateral view. The spines are spaced at varying distances apart (0.20-0.26 mm), but on average there are about five spines per millimeter in each row.
Fig. 13. *Tylopathes crispa* Brook: a, syntype (BMNH 90.4.9.8), entire corallum, digital scan of illustration given by Brook (1889); b-d, schizosyntype (USNM 100378); b, section of corallum with worm run; c, branchlets at edge of colony; d, polyps, approx. 12x.
Fig. 14. Tylopathes crispa Brook, schizosyntype (USNM 100378), spines on branchlets, scale 0.1 mm.
The polyps (fig. 13d) appear elongated in the transverse axis, and are about twice as long transversely as they are wide along the sagittal axis. They measure 0.8 to 1.0 mm from the distal side of the distal lateral tentacles to the proximal side of the proximal lateral tentacles. There are nine to ten polyps per centimeter along the axis. The polyps on the smallest branchlets tend to be arranged in a single, but not very regular row, whereas those on the thicker branches often occur in two rows, on opposite sides of the axis. On the older portions of the corallum the polyp tentacles become atrophied and/or reabsorbed; first the sagittal ones and then the lateral ones, so that in places only the mouth remains visible.

Remarks.— In species referred to this genus the smallest branchlets are mostly bilateral and offset, but some are subopposite and in a few cases they occur in groups of three. The relationship of this genus to others in the family is established by morphology of the polyps, the tendency of the branchlets to anastomose and to form cylindrical worm runs (in some species), and by the morphology, and not always uniform orientation and arrangement of the spines. Additional information is needed on the morphology of the living polyps.

Species assigned to *Tylopathes*.— In addition to the type species, one other nominal species, *Antipathella contorta* Brook (1889), is provisionally assigned to this genus. This species forms a more flabellate corallum with denser and more bilateral branchlets. As reported by Brook (1889), it has worm runs similar to those occurring in *T. crispa*, and was collected from the same general locality. Another species which may belong in this genus is *Antipathes glutinata* Totton (1923) from New Zealand. It is known only from a small fragment and the overall growth form of the corallum is unknown; however, the distally directed spines, the irregular, but sometimes subopposite branchlets, and the coalescing of adjacent branchlets, suggest an affinity to Tylopathes.

Distribution.— Species of this genus have been reported from the southern tip of South America (*T. crispa, T. contorta*), and possibly from New Zealand (*A. glutinata*).

Bathymetric Range.— 319-729 m.

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