# Revision of the Antipatharia (Cnidaria: Anthozoa). Part III. Cladopathidae 

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Key words: Cnidaria; Anthozoa; Antipatharia; Cladopathidae; Cladopathinae; Cladopathes Brook; Chrysopathes gen. nov.; Trissopathes gen. nov.; Hexapathinae subfam. nov.; Hexapathes Kinoshita; Heliopathes gen. nov.; Sibopathinae subfam. nov.; Sibopathes van Pesch.
The family of antipatharian corals Cladopathidae (Cnidaria: Anthozoa: Antipatharia) is revised. The family is characterized by polyps 2 mm or more in transverse diameter, six primary mesenteries, and no secondary mesenteries. The family is divided into three subfamilies: Cladopathinae Kinoshita, Hexapathinae subfam. nov. and Sibopathinae subfam. nov. The subfamily Cladopathinae is characterized by a branched pinnulate corallum with three or more rows of primary pinnules, some of which are subpinnulate. Included in the subfamily are the genera Cladopathes Brook (C. plumosa Brook, 1889), Chrysopathes gen. nov. (C. formosa spec. nov. and C. speciosa spec. nov.) and Trissopathes gen. nov. [T. pseudotristicha spec. nov., T. tetracrada spec. nov., and T. tristicha (van Pesch, 1914)]. The subfamily Hexapathinae is characterized by a monopodial or sparsely branched pinnulate corallum, with two rows of simple lateral primary pinnules and one or more rows of simple or subpinnulate anterior primary pinnules. Included in the subfamily are the genera Hexapathes Kinoshita, 1910 and Heliopathes gen. nov. Hexapathes contains the type species H. heterosticha Kinoshita, 1910, as well as H. australiensis spec. nov. Heliopathes contains the type species H. americana, spec. nov. and Antipathes heterorhodzos Cooper, 1909. The subfamily Sibopathinae van Pesch is defined by the absence of an actinopharynx. Species in the single genus Sibopathes [type species S. gephura van Pesch, 1914, and including S. macrospina Opresko, 1993] possess a branched corallum with four to six rows of simple pinnules.

## Introduction

This is the third in a series of papers in which the order Antipatharia (Cnidaria: Anthozoa) is being revised. In the first part of this series the family Myriopathidae and four new genera were established for species related to Antipathes myriophylla Pallas, 1766 (Opresko, 2001). In the second part, the family Schizopathidae was revised and five new genera were established (Opresko, 2002). In this part the family Cladopathidae is revised and three new genera are recognized.

Prior to this series of publications, a clearly defined taxonomic hierarchy at the genus and family level did not exist for the Antipatharia. This was due, in part, to the fact that in the past many species and genera had been described on the basis of incomplete specimens, and often on specimens without polyps. Early classification systems attempted to use the general external morphology of the corallum as the key diagnostic feature of genera (Milne Edwards \& Haime, 1857). Later attempts were made to incorporate information on external polyp morphology as the key generic character with less consideration given to skeletal morphology (Brook, 1889). Examination of numerous species with the polyps intact has led to the realization that the size and morphology of both the polyps and axial spines, when evaluated together,
provide the most useful information to identify relationships among various species groups. This has led to the establishment of new genera and families. Noteworthy, it is the morphology of the corallum that has proven to be the most useful generic character within the recognized family groups.

The holotypes of the new species have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) and/or at the South Australian Museum (SAM), Adelaide, South Australia. Schizoholotypes have also been deposited at the National Museum of Natural History, Leiden, The Netherlands.

Abbreviations<br>BMNH $=$ British Museum of Natural History, London, United Kingdom;<br>RMNH = National Museum of Natural History, Leiden, The Netherlands;<br>SAM = South Australian Museum, Adelaide, South Australia;<br>USNM $=$ Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.;<br>ZMA = Zoological Museum, University of Amsterdam.

## Taxonomic section

## Cladopathidae Kinoshita, 1910

Cladopathinae Kinoshita, 1910: 231.
Diagnosis.- Polyps with six primary mesenteries and no secondary mesenteries. Actinopharynx may be present or absent. Polyps elongated transversely in the direction of the axis; transverse diameter 2 mm or more as measured from distal edge of distal lateral tentacles to proximal edge of proximal lateral tentacles. Corallum monopodial or branched, and pinnulate. Pinnules simple or with one or more orders of subpinnules. Spines conical to acicular, smooth-surfaced, subequal around the circumference of the axis, or taller on one side. Spines equally developed on all pinnules or more strongly developed on anterior pinnules or subpinnules.

Remarks.- The recognition of the family Cladopathidae follows the general classification proposed by Schultze (1896) and supported by Pax (1918). Originally, the genus Cladopathes was included by Brook (1889) in the subfamily Schizopathinae Brook (1889) of the family Antipathidae, together with the genera Schizopathes, Bathypathes, and Taxipathes. Polyps in the latter three genera have ten mesenteries, six primary ones and four secondaries, whereas Cladopathes was described as having six primary mesenteries but no secondary mesenteries.

In 1896, Schultze proposed a new classification of the Antipathidae based on the number of mesenteries. Schultze established a separate subfamily, the Hexamerota for Cladopathes. The subfamily was renamed the Cladopathinae by Kinoshita in 1910, who added to it a new genus Hexapathes. The polyps of Hexapathes heterosticha were described by Kinoshita as having an actinopharynx, six complete primary mesenteries, but no secondary mesenteries. In 1914, van Pesch (1914) created the subfamily Homoeotaeniales to contain both Cladopathes and the new genus Sibopathes van Pesch. Sibopathes is similar to Cladopathes in lacking secondary mesenteries; however, it differs from

Cladopathes, and also from all other known antipatharians, in that the polyps lack an actinopharynx and, consequently, the six primary mesenteries are incomplete. Hexapathes was treated by van Pesch as a synonym of Cladopathes. Thus, van Pesch's Homoeotaeniales is equivalent to the Cladopathinae, and contains those genera having polyps with six mesenteries, but in which an actinopharynx may be present (Cladopathes and Hexapathes) or absent (Sibopathes).

Besides the absence of secondary mesenteries, there are similarities in the morphology of the polyps and sclerenchyme to unite these genera into a higher taxon. In all three genera the polyps are elongated transversely and are greater than 2 mm in transverse diameter. In this regard they are similar to polyps in the family Schizopathidae (see Opresko, 2002). Both Sibopathes and Cladopathes are branched to varying degrees, and in both the corallum is pinnulate, with the pinnules occurring in two or more rows. In Sibopathes the pinnules are simple, whereas in Cladopathes some of the pinnules are subpinnulate. Hexapathes is monopodial, or only very sparsely branched, with two rows of lateral pinnules and one or more irregular rows of anterior pinnules which may be simple or subpinnulate.

In the classification proposed here the Cladopathidae are divided into three subfamilies, the Cladopathinae, containing Cladopathes, Trissopathes gen. nov., and Chrysopathes gen. nov.; the Hexapathinae subfam. nov, containing Hexapathes and Heliopathes gen. nov.; and the Sibopathinae, containing the genus Sibopathes.

## Cladopathinae Kinoshita, 1910

Hexamerota Schuttze, 1896: 12.
Cladopathinae Kinoshita, 1910: 231.
Homoeotaeniales van Pesch, 1914: 21 (in part).
Diagnosis.- Polyps generally 2-4 mm (but up to 6 mm ) in transverse diameter. Corallum bushy or flabellate; pinnulate, and subpinnulate. Primary pinnules arranged in two to six rows and usually also in bilateral groupings. Pinnules in the anteriormost rows (anterior referring to that side of the stem and branches on which the polyps occur) bearing subpinnules; lateral (or posterolateral) and posterior pinnules simple or subpinnulate. Tertiary pinnules present in some species. Spines simple, smooth, deltoid to conical to acicular in lateral view.

Remarks.- The subfamily is divided into three genera: Cladopathes, Chrysopathes gen. nov., and Trissopathes gen. nov. A key to the genera and species is given below. [Note: As in most species of antipatharians, species of the Cladopathinae show considerable variability in many of the taxonomic characters relating to the corallum, particularly when comparing young and old portions of the corallum. The extent of subpinnulation usually increases from the tips of the branches basally. Specific characters, as given in the key below, refer to the most common condition occurring in the more developed portions of the corallum.]

## Key to genera and species of Cladopathinae

1 Primary pinnules irregularly arranged, sometimes in clusters of three (rarely two or four)

Cladopathes (C. plumosa Brook)

- Primary pinnules in four or more regular rows ........................................................................ 2

2 Primary pinnules in four rows; (Trissopathes gen. nov.) ................................................... 3

- Primary pinnules in six rows; (Chrysopathes gen. nov.) ................................................. 5

3 Usually one (sometimes none or two) secondary pinnules on anterior pinnules .......
T. tetracrada spec. nov.

- Two or more (usually subopposite) secondary pinnules on anterior primaries ....... 4

4 One pair of subopposite secondary pinnules on anterior primary pinnules
T. pseudotristicha spec. nov.

- Two or more pairs of subopposite (sometime alternating) secondary pinnules on anterior primary pinnules
T. tristicha (van Pesch)

5 Secondary pinnules, when present, mainly on anterior-most primary pinnules; tertiary pinnules usually absent .....................................................C. formosa spec. nov.

- Secondary pinnules may occur on all primary pinnules, especially on larger branches; tertiary pinnules present
C. speciosa spec. nov.


## Cladopathes Brook, 1889

Type species.-Cladopathes plumosa Brook, 1889.
Diagnosis.- Primary pinnules arranged irregularly in rows; sometimes appearing in clusters of three (rarely two or four). Subpinnules occurring mostly on anterior primary pinnules (sometimes also on lateral/posterolateral ones) and not regularly arranged. Tertiary pinnules present.

Species assigned to Cladopathes.- A single species is currently placed in this genus, Cladopathes plumosa Brook.

Distribution.- Only reported from the southern hemisphere (Indian Ocean, South Atlantic and Australia).

Cladopathes plumosa Brook, 1889
(figs 1-2)

Cladopathes plumosa Brook, 1889: 157-158, pl. 2, figs. 1-4.
Material.— Syntypes (BMNH 90.4.9.26; schizotype, USNM 100406), Indian Ocean, off Prince Edwards Island, $46^{\circ} 41^{\prime} \mathrm{S}, 38^{\circ} 10^{\prime} \mathrm{E}, 310 \mathrm{fm}$ ( 558 m ), 27.xii.1873, HMS "Challenger", sta. 145A, two specimens; BMNH 1889.7.9.9a (part, USNM 100407), south Atlantic, off Ascension Island, HMS "Challenger" Expedition; SAM H-750 (part, USNM 99416), south Australia, Great Australian Bight, 10 nautical miles WSW of Cape Wiles, $135^{\circ} 12^{\prime}$ S, $134^{\circ} 09^{\prime} \mathrm{E}, 1080-977 \mathrm{~m}, 9 . x i .1989, \mathrm{~F} / \mathrm{V}$ "Longva" III, coll. K. Gowlett-Holmes.

Diagnosis.- Corallum (fig. 1c) branched to the $7^{\text {th }}$ order or more, shrub-like or planar. Stem and branches pinnulate and subpinnulate (figs 1d and 2d). Arrangement and spacing of pinnules and subpinnules very variable, especially on larger branches. On smallest branchlets primary pinnules often in clusters of three (rarely two or four), consisting of two anterolateral pinnules and one lateral (or posterolateral or posterior) pinnule. Anterior-most primary pinnules usually with one or two secondary pinnules (range zero to four) (fig. 2d). Secondary pinnules often subopposite when two occur on same primary. Lateral (posterolateral or posterior) primary pinnules usually simple, but sometimes with one or more secondary pinnules, especially on larger branches.


Fig. 1. Cladopathes plumosa Brook, 1889, a-c, digital scans of illustrations of syntype (BMNH 90.4.9.26), from Brook, 1889; a, polyps, $6 \times$; b, spines, $26 \times$; c, corallum, $0.6 \times$; d, schizosyntype (USNM 100406), lateral view of pinnules, scale 5 mm .

Secondary pinnules may be present on primary pinnules even at tips of smallest branchlets. Tertiary pinnules occasionally present on some secondary pinnules on anterior primary pinnules and very rarely on secondary pinnules on posterior (or posterolateral) primary pinnules. Tertiary pinnules often directed basally relative to branch direction. Longest primary pinnules (usually lateral or posterior ones) mostly 0.5 to 1.0 cm long, but some up to 2.5 cm long, and $0.2-0.25 \mathrm{~mm}$ (up to 0.3 mm ) in diameter near the base. Primary pinnules mostly $2-3 \mathrm{~mm}$ apart in each anterior row, with up to 16 pinnules per centimeter in all rows. Primary pinnules generally directed distally (straight and/or curved distally) relative to the branch on which they occur; distal angle of posterior primaries about $60^{\circ}$; distal angle of anterior primary pinnules $60-80^{\circ}$. Secondary pinnules inclined distally relative to the primary pinnule on which they occur. Spines (figs 1 b and $2 \mathrm{a}-\mathrm{c}$ ) on pinnules simple, smooth, acute, usually 0.06 0.08 mm from center of base to apex; arranged in rows, with three or four rows visible (not including spines only partially visible); mostly 0.2 to 0.3 mm apart in each row, with three to less than five spines per millimeter in each row. Central axial canal variable in size; as small as 0.1 mm in diameter at tips of pinnules and up to 0.3 mm in diameter on some branches. Polyps (fig. 1a) mostly 3-4 mm in transverse diameter


Fig. 2. Cladopathes plumosa Brook, 1889, schizoholotype (USNM 100406); a-c, spines on pinnules, scale 0.1 mm ; d, cross-sectional view of pinnules.
with three polyps per centimeters, but sometimes as much as $5-6 \mathrm{~mm}$ in diameter, with only two polyps per centimeter.

Remarks.- In his description of Cladopathes plumosa, Brook (1889) gives no illustration of the pattern of pinnulation or subpinnulation; however, he states that the pinnules are placed in "three or four series showing a subspiral arrangement". He notes that in cases where there are three rows, two generally arise from the anterolateral sides and one from the posterior side of the axis; but at other times two may be lateral, a third anterior, and a fourth posterior. A reexamination of a small portion of the type indicates that the arrangement of the primary pinnules is very variable. On some branchlets the primary pinnules appear to be arranged in groups of two, corresponding to one anterolateral and one posterolateral pinnule. These pinnules are not aligned with those of the more distal or proximal groupings; consequently, a cross-sectional view indicates four rows of primary pinnules. On other branchlets there are three primary pinnules per group, two anterolaterals and one on the posterior or lateral side of the axis. The two anterior-most ones in each group may be aligned with the corresponding anterior-most ones in the more distal or basal groups. The lateral or posterior ones, however, are usually offset; consequently, a cross-sectional view indicates the presence of four rows, but with the spacing of the posterior ones twice that of the anterior ones. On the larger branchlets and branches the arrangement of the pinnules in rows and axial groupings becomes less distinct, and depending on whether the pinnules in these groups are aligned with those of neighbouring groups, they may appear to form more than four rows when viewed in cross-section.

The most typical pattern of subpinnulation consists of one or two secondary pinnules developing $0.4-1.2 \mathrm{~mm}$ from base of each anterior primary pinnule and no secondary pinnules on the lateral (or posterior) primaries. Secondary pinnules are often directed somewhat basally relative to the direction of the branch. Brook referred to the primary pinnules with a single secondary pinnule as a forked pinnule, with the superior arm of the fork up to 2.0 cm long. Not reported by Brook are the numerous cases where, on the same primary pinnule, there are two bilateral secondaries which often arise at nearly the same point (i.e., subopposite). On the larger branches subpinnules may be present on primary pinnules on all sides of the axis.

In the specimen from Ascension Island (BMNH 1889.7.9.9a), the primary pinnules are more evenly spaced apart along the axis, with two or three anterior pinnules between the lateral (or posterolateral) ones. Furthermore, many of the anterior pinnules have two subopposite secondary pinnules and a few even have three secondaries originating from nearly the same point. A few of the secondary pinnules have two subopposite tertiary pinnules. In the specimen from Australia (SAM H-750), the primary pinnules tend to be arranged uniserially, with three or four in a row. There are few subopposite secondary pinnules, but some of the secondary pinnules bear several orders of subpinnules, forming tuft-like branchlets. Fusions occur between neighbouring pinnules and subpinnules. Although the spines in this specimen are similar in shape and size to those in the type ( $0.06-0.08 \mathrm{~mm}$ tall), based on the differences in the pattern of pinnulation and subpinnulation, this specimen may represent a distinct species.

Comparisons.- Based on the number and arrangement of the primary pinnules, this species is closest to Trissopathes tetracrada spec. nov.; however, in the latter
species the pinnules are much more regularly arranged around the axis, and in most cases there is only one secondary pinnule present on the anterior primaries.

Distribution.- Specimens assigned to this species have been collected from off Prince Edward Island, off Ascension Island and from the Great Australian Bight.

## Trissopathes gen. nov.

Type species.- Trissopathes pseudotristicha spec. nov. (see below).
Diagnosis.- Primary pinnules arranged in four regular rows; subequal in size or with lateral/posterolateral primary pinnules longer than anterior ones. Lateral/posterolateral primary pinnules usually without subpinnules; anterior primaries simple or with up to six or more subpinnules. Subpinnules commonly arranged in subopposite pairs (rarely alternating).

Species assigned to Trissopathes.- Three species are assigned to this genus: Trissopathes pseudotristicha spec. nov., Trissopathes tetracrada spec. nov., and Trissopathes tristicha (van Pesch, 1914).

Etymology.- The generic name is derived from the Greek "trissos" (three-fold) and the commonly used suffix "pathes".

Distribution.- Species of this genus have been found in the central and eastern North Pacific, the IndoPacific, the Great Australian Bight, and the eastern North Atlantic.

Trissopathes pseudotristicha spec. nov.
(figs 3-5)

Material.— Holotype (USNM 98848; schizoholotype, RMNH Coel. 32045), eastern Pacific, $19^{\circ} 37.464^{\prime}$ N, $156^{\circ} 02.064^{\prime}$ W, 432 m, 21.ix.1996, "Pisces V" Dive P5-302, sta. HAS-112, spec. HAS 31, coll., S.C. France and E.A. Berntson; paratype (USNM 94488), northeast Pacific, Fieberling Guyot, west of Channel Islands, $32^{\circ} 26.0^{\prime} \mathrm{N}, 127^{\circ} 47.6^{\prime} \mathrm{W}, 490 \mathrm{~m}, 15 . x i i .1990$, "Alvin" dive 2329; paratype (USNM 94489), north Pacific, west of Channel Islands, Fieberling Guyot, $32^{\circ} 26.0^{\prime} \mathrm{N}, 127^{\circ} 47.6^{\prime} \mathrm{W}, 490 \mathrm{~m}, 12 . x .1990$, "Alvin" dive 2292; paratypes (USNM 99925, USNM 99820), north Pacific, Hawaii, Kaena Point, $21^{\circ} 37^{\prime} 12^{\prime \prime}$ N, $158^{\circ} 24^{\prime} 00^{\prime \prime}$ W, 326-447 m, 27.vii.1971, SANGO Expedition XII, R/V "Townsend Cromwell"; paratype (USNM 99809), north Pacific, Hawaii, Kauai Island, Mokolea Point, $22^{\circ} 15^{\prime} 25^{\prime \prime}$ N, $159^{\circ} 23^{\prime} 15^{\prime \prime}$ W, 272-296 fm (495-539 m), 12.vi.1902, R/V "Albatross", sta. 3991.

Diagnosis.- Corallum branched to the fourth order or more; stem and branches generally in a single plane; pinnulate and subpinnulate (fig. 3a). Primary pinnules arranged in four rows, two anterior (or anterolateral) and two posterolateral, and also arranged alternately in bilateral groups containing one anterior and one posterolateral pinnule (figs 3c-d). Posterolateral primary pinnules mostly 1-2 cm long (up to 2.6 cm ) and usually longer than anterior primary pinnules ( $0.5-1 \mathrm{~cm}$ long). Posterolateral primary pinnules directed distally; anterior primary pinnules directed nearly at right angles to direction of branch (fig. 3c). Secondary pinnules on anterior primary pinnules; most often occurring as a single subopposite pair (fig. 4d). Secondary pinnules only rarely found on posterolateral pinnules. Secondary pinnules 0.5 to 1.5 cm long. Tertiary pinnules usually absent. Spines on pinnules (figs 4a-c, 5a-e) simple, smooth, conical, acute; $0.05-0.13 \mathrm{~mm}$ tall (from center of base to apex), and often inclined dis-


Fig. 3. Trissopathes pseudotristicha spec. nov., holotype (USNM 98848); a, part of holotype, scale 1 cm ; b, pinnules with polyps, approx. $2 \times$; c, lateral view of pinnules, scale 5 mm ; d, cross-sectional view of pinnules, scale 5 mm .
tally, especially on the secondary pinnules and near the distal ends of the primary pinnules. Polyps (fig. 3b) 2-4 mm in transverse diameter; arranged uniserially on upper or lateral sides of pinnules and subpinnules, with three or four polyps per centimeter.

Description of holotype.- The holotype (USNM 98848) is a complete colony, 34 cm high and about 40 cm wide with a basal stem diameter of $3 \times 4.3 \mathrm{~mm}$ (only a portion of the corallum is shown in fig. 3a). The corallum is branched, mostly to the third or fourth order; however, on one major branch seven orders of smaller branches occur. The overall branching of the corallum is planar with many of the pinnules projecting out of the anterior or polyp side of the corallum. The largest branch is 22 cm long and 2 mm in diameter at its point of insertion on the stem. The lateral primary pinnules are 3-4 mm apart in each row. The anterior primary pinnules are sometimes so closely in line that they appear to form a single row (1.6-1.8 mm apart), in other places they are offset slightly and form an interior angle of about $20^{\circ}$. There are $12-14$ primary pinnules per centimeter, counting pinnules in all rows. The posterolateral pinnules are most frequently about 1 cm long (maximum about 1.5 cm ) and about 0.15 mm in diameter at their base. They are relatively straight, and directed upward (distal angle $50-70^{\circ}$ ). The anterior primary pinnules are $0.5-1.0 \mathrm{~cm}$ long and project out nearly perpendicular to the branch (distal angle $70-80^{\circ}$ ). They are inserted slightly above (distal), at the same level, or slightly below (proximal) the adjacent posterolateral pinnule (fig. 3c). The anterior primary pinnules most commonly have two subopposite secondary pinnules $0.5-1.5 \mathrm{~cm}$ long. Anterior pinnules without subpinnules or with only one subpinnule also occur, particularly at the tips of the branches, but also on other parts of the corallum. The basal-most secondary pinnule arises $0.4-0.6 \mathrm{~mm}$ from the base of the primary on the abpolypar side and the more distal one arises on the polypar side slightly offset from the lowermost one (fig. 4d).

On the largest branches the primary pinnules appear to be arranged in seven or eight rows: however, this is due to the fact that the axis has overgrown the points of insertion of the secondary pinnules.

The spines (figs $4 \mathrm{a}-\mathrm{c}, 5 \mathrm{a}-\mathrm{e}$ ) are triangular to conical, equilateral on the lower (basal) parts of the pinnules, but becoming more distally inclined on the mid and upper sections of the pinnules. Those on the anterior primary pinnules and on the secondary pinnules tend to be more distally inclined than those on the lateral pinnules; the abaxial edge can be two to three times longer than the adaxial edge. The largest spines are commonly found on the distal half of the secondary pinnules, and are up to 0.13 mm tall (from the midpoint of the base to the apex). The spines are arranged in axial rows with three or four rows visible in lateral view (excluding rows in which the spines are only partially visible). The distance between adjacent spines in each row is quite variable, ranging from 0.25 to about 0.4 mm ; however, in general, there are usually about four spines per millimeter in each row.

The polyps (fig. 3b) are arranged uniserially on the upper and lateral sides of the pinnules and subpinnules. Consequently, the corallum has a polypar and abpolypar side with the anterior pinnules projecting out of the polypar side. The polyps are mostly $2-3 \mathrm{~mm}$ in diameter from the distal edge of the distal lateral tentacles to proximal edge of the proximal lateral tentacles. The interpolypar space is about 0.5 mm , with three or four polyps per centimeter. Some of the polyps on the anterior pinnules and subpinnules appear swollen and pinkish, suggesting that they might contain


Fig. 4. Trissopathes pseudotristicha spec. nov., holotype (USNM 98848); a-c, spines on lateral pinnules, scale 0.1 mm ; d, cross-sectional view of pinnules, scale 1 mm .


Fig. 5. Trissopathes pseudotristicha spec. nov., holotype (USNM 98848); a-c, spines on anterior primary pinnules, scale 0.1 mm ; d-e, spines on secondary pinnules, scale 0.1 mm .
eggs. In contrast, none of the polyps on the lateral pinnules have such an appearance.
Remarks.- In one specimen collected from Fieberling Guyot (USNM 94488; height 6.8 cm ) there are 14 primary pinnules per centimeter, the posterolateral pinnules are up to 2.6 cm long, the polyps are up to 4.0 mm in transverse diameter, the secondary pinnules occur as often singly as they do in pairs, and in a few cases a secondary is longer than the anterior primary from which it originates. In another specimen from the same locality (USNM 94489; height 13 cm ), the secondary pinnules are up to 2 cm in length, the pinnular spines are $0.02-0.06 \mathrm{~mm}$ tall, and the polyps are slightly smaller $(2-2.5 \mathrm{~mm})$ than those in the holotype.

Comparisons.- Based on the number and arrangement of subpinnules on the anterior primary pinnules, this species is morphologically intermediate between $T$. tetracrada spec. nov. and T. tristicha (van Pesch). Trissopathes tristicha has two or more subopposite pairs of secondaries, whereas $T$. tetracrada only occasionally has one subopposite pair of secondaries.

Etymology.- The specific name is derived from the Latin "pseudo" (false) and the suffix "tristicha" in reference to similarities to T. tristicha (van Pesch) and to the
fact that while it may appear that there are only three rows of primary pinnules, there are, in fact, actually four.

Distribution.- The species has been collected from the Eastern and Central Pacific.
Trissopathes tetracrada spec. nov.
(figs 6-8)
Material.- Holotype (SAM H-902; schizoholotypes, USNM 99399, RMNH Coel. 32043; paratype, SAM H 1381), Australia, about 125 nautical miles south of Eucla, $33^{\circ}{ }^{\circ} 5^{\prime}$ S, $129^{\circ} 17^{\prime} \mathrm{E}, 999-1110 \mathrm{~m}$, 1.viii.1988, F/V "Adelaide Pearle", coll: K.L. Gowlett Holmes; paratype (SAM H-907), Tasmania, about 36 nautical miles southeast of South East Cape, $44^{\circ} 04.6^{\prime} \mathrm{S}$, $147^{\circ} 23.4^{\prime} \mathrm{E}, 1100-1150 \mathrm{~m}, 9 . \mathrm{ii} .1992$, F/V "Belinda", coll: K.L. Gowlett Holmes; RMNH Coel. 32300, eastern Atlantic, Cape Verde Islands, SE of Boa Vista, $15^{\circ} 46^{\prime} \mathrm{N}, 22^{\circ} 38^{\prime} \mathrm{W}, 1450-2220 \mathrm{~m}, 11 . \mathrm{vi} .1982$, sta. CANCAP 6.055.

Diagnosis.- Corallum bushy to planar (fig. 6a), with overlapping branches; branched to the seventh order or more. Stem and branches pinnulate and subpinnulate. Primary pinnules arranged in four rows of varying regularity, two anterolateral rows and two posterolateral rows (fig. 6c), and also alternately in biserial groups containing one anterolateral and one posterolateral pinnule (fig. 6b). Primary pinnules mostly about 1 cm (rarely up to 2 cm ); with posterolaterals subequal or slightly longer than anterolaterals; spaced evenly around the circumference of the axis near the distal ends of the branchlets, but becoming more lateral in position further down. Anterior primary pinnules simple or with one, sometimes two, secondary pinnules near base (figs 6 c , $7 \mathrm{~d}-\mathrm{e})$. Secondary pinnules usually subopposite when two occur on same primary pinnule. Posterolateral primary pinnules simple. Tertiary pinnules usually absent. Spines on pinnules (figs 7a-c, 8a-c) simple, smooth, acute, mostly 0.08-0.12 mm tall. Polyps 2-3 mm in transverse diameter.

Description of holotype.- The holotype (SAM H 902) is the largest of two specimens collected at the same locality. It is a complete colony, 23 cm high and about 23 cm wide with a basal stem diameter of $3 \times 3.5 \mathrm{~mm}$ (fig. 6a). The corallum is strongly branched, mostly to the sixth or seventh order, but in places there are up to ten orders of branches. Overall, the branching occurs in a thick plane, with overlapping branches and branchlets. The lower 9 mm of the stem is without pinnules. The stem extends vertically 15 cm and some of the larger branches are up to 8 cm in length. The primary pinnules in each row are spaced 2-5 mm (mostly 3-4 mm) apart. On the distal sections of the branchlets the rows are set almost at right angles to one another; however, further down on the branchlets, the anterior rows can be closer together (interior angle 30-60 $)$ and the two posterior rows can be more lateral in position; however, this arrangement is not strictly maintained over the entire corallum. The posterolateral pinnules are mostly $0.5-1 \mathrm{~cm}$ long and $0.15-0.2 \mathrm{~mm}$ in diameter at their base; the larger ones developing into pinnulated branches. They are relatively straight; directed distally (distal angle about $60^{\circ}$ ); spaced $3-4 \mathrm{~mm}$ apart in each row (averaging about four per centimeter), and are arranged alternately. The anterolateral pinnules are positioned at the same level or slightly below (proximal to) the adjacent posterolateral primary pinnules resulting in alternating bilateral groups of two (fig. 6b). The bilateral groups are spaced 1.5 to 2 mm apart, with up to 14 pinnules per centimeter in all rows. The posterolateral pinnules are subequal or slightly longer than the anterolateral pinnules.


Fig. 6. Trissopathes tetracrada spec. nov., a, holotype (SAM H-902), height approx. 23 cm ; b-c schizoholotype (USNM 99399), b, lateral view of pinnules, scale 5 mm ; c, cross-sectional view of pinnules, scale 5 mm .

Rarely an anterolateral is longer than the posterolaterals. The anterolaterals are angled distally in a manner similar to that for the posterolaterals (distal angle $60^{\circ}$ ) or are slightly more horizontally directed. Near the tips of the branchlets, all the primary pinnules tend to be simple; however, further down some of the anterolaterals have one secondary pinnule (sometimes two) arising laterally on either side about 0.4-0.5 mm above the base and extending distally relative to the primary pinnule (fig. 6c). The secondary pinnules are usually no more than 0.5 cm long and about 0.1 mm in diameter at their base. Where two secondary pinnules occur on the same primary pinnule they are usually located laterally and nearly opposite one another (fig. 7d), although in a few cases they occur on the same side. As many as three anterior pinnules in a row may each have two subopposite secondary pinnules, but the predominant condition is a single subpinnule per anterior pinnule (fig. 7e). The posterolateral primary pinnules rarely have subpinnules except when they are in the early stages of developing into branches. Tertiary pinnules are only very rarely found on a secondary pinnule. The anterolateral pinnules and subpinnules generally project out of the front (polyp) side of the corallum.

The spines on the primary pinnules (figs 7a-c) are usually $0.08-0.10 \mathrm{~mm}$ tall (from midpoint of base to apex). The largest and most distally inclined spines are found on the distal half of the secondary pinnules (figs 8a-b). The spines on the upper or distal side of the pinnules (relative to the direction of the branch) tend to extend out more at right angles to the pinnule than those on the lower side which are more inclined distally. The spines on the pinnules are arranged in axial rows, usually with three or four rows visible in lateral view (excluding rows in which the spines are only partially visible). The distance between adjacent spines in each row is 0.2-0.6 mm , and there are on average three to four spines per millimeter in each row. Spines are reduced in size on the larger branches and stem.

The polyps are poorly preserved in the holotype, but appear to be arranged uniserially on the upper sides of the pinnules and subpinnules. In general, the polyps tend to face out of one side of the corallum. The polyps are transversely elongated and $2-3 \mathrm{~mm}$ in diameter as measured from the distal edge of distal lateral tentacles to the proximal edge of the proximal lateral tentacles.

Remarks.- The paratypes exhibit only slight differences from the holotype. In all of them the predominant condition is for the anterior primary pinnules to possess a single secondary pinnule. Where there are two subopposite secondaries, this is more likely to occur on the larger branches and stem. In most cases the posterolateral pinnules are subequal or only slightly longer than the anterior primary pinnules; however, in the specimen from CANCAP 6.055, the posterolateral pinnules are as much as twice as long ( 2 cm vs. about 1 cm ). This specimen also differs from the others in having less dense branching, and the spines appear to be less inclined distally than in the holotype.

Comparisons.- This species is similar to Trissopathes pseudotristicha spec. nov., but differs primarily in the number of secondary pinnules. T. tetracrada usually has only one secondary pinnule on the anterior primary pinnules, whereas in T. pseudotristicha the secondary pinnules consistently occur in one subopposite pair.

Etymology.- The specific name is derived from the Greek "tetra" (four) and "crada" (branch) in reference to the arrangement of the primary pinnules in four distinct rows.


Fig. 7. Trissopathes tetracrada spec. nov., schizoholotype (USNM 99399); a-c, spines on lateral pinnules, scale 0.1 mm ; d-e, cross-sectional view of pinnules, scale 1 mm .


Fig. 8. Trissopathes tetracrada spec. nov., holotype (USNM 99399); a-c, spines on secondary pinnules, scale 0.1 mm .

Distribution.- The species has been collected off the coast of South Australia and Tasmania, and in the eastern Atlantic off Cape Verde.

Trissopathes tristicha (van Pesch, 1914)
(figs 9-10)

Parantipathes (?) tristicha van Pesch, 1914: 99-101.

Material.- Holotype (ZMA Coel. 3005; schizoholotype, USNM 100411), western Pacific, Ceram Sea, $3^{\circ} 27^{\prime} \mathrm{S}$, $131^{\circ} 0.5^{\prime} \mathrm{E}, 567 \mathrm{~m}$, "Siboga" sta. 173; USNM 76953 (part, RMNH Coel. 32042), Philippine Islands, off Sombrero Island, $13^{\circ} 45^{\prime} 15^{\prime \prime} \mathrm{N}, 120^{\circ} 46^{\prime} 30^{\prime \prime} \mathrm{E}, 236 \mathrm{fm}(430 \mathrm{~m})$, 16.i.1908, R/V "Albatross" sta. 5111; SAM H753 (part, USNM 99405), South Australia, Great Australian Bight, 135 nautical miles SSW of Cape Adieu, $34^{\circ} 13^{\prime} \mathrm{S}, 131^{\circ} 30^{\prime} \mathrm{E}, 1122-1330 \mathrm{~m}$, 19.xii.1989, F/V "Longva" III, coll. K. Gowlett-Holmes.

Diagnosis.- Corallum sparsely branched (fig. 9a); pinnulate and subpinnulate (figs $9 b-d$ ). Primary pinnules in four rows; two rows on the anterior side of the axis


Fig. 9. Trissopathes tristicha (van Pesch, 1914), a, USNM 76953, scale 1 cm; b-c, USNM 99405 (from SAM H-753), b, lateral view of pinnules, scale 5 mm ; c, cross-sectional view of pinnules, scale 5 mm ; d, USNM 76953 , oblique lateral view of pinnules.
and two posterolateral rows. Pinnules in anterior rows often aligned such that they appear as a single row when branch is viewed in cross section (figs 9d and 10e). Secondary pinnules present only on anterior primary pinnules, and arranged bilaterally; usually suboppositely, but sometimes offset to varying degrees (figs 9c-d; 10d-e). Two or more pairs of secondary pinnules on each anterior pinnule. Tertiary pinnules absent. Posterolateral primary pinnules mostly 1-1.5 cm long and inclined distally relative to the branch. Anterior primary pinnules mostly 0.5 cm in length, but sometimes as long as posterolaterals. Secondary pinnules lying in the same plane as the anterior primary pinnules on which they occur and of varying length, with basal ones (relative to the direction of the anterior pinnule) longest, and sometimes nearly as long as posterolateral primary pinnules. Pinnular spines (figs 10a-c) simple, smooth, conical to acicular, inclined distally; up to 0.28 mm tall from center of base to apex (largest ones usually on secondary pinnules); arranged in irregular axial rows, three to five of which can be seen in lateral view; with two to three spines per millimeter in each row. Spines reduced in size on branches and stem. Polyps unknown.

Remarks.- The type material of this species consists of one small colony only 9 cm tall. Reexamination of this specimen revealed that as many as six secondary pinnules may be present on an anterior primary pinnule (fig. 10d). These secondary pinnules occur in three subopposite pairs with members of the most distal pair being more offset than the lower ones. The pinnular spines on the type are relatively large, almost acicular in places, distally inclined, and as much as 0.2 mm from the center of the base to the apex (figs $10-\mathrm{a}-\mathrm{c}$ ). The spines on one side of the axis are sometimes slightly taller than those on the opposite side (fig. 10c).

The Albatross material (USNM 76953) consists of several small, branched colonies, none of which has polyps. Although most of the primary pinnules are broken, the few remaining ones suggest that the posterolateral primary pinnules can be as much as 1.3 cm in length and about 0.3 mm in diameter near the base. The anterior primary pinnules are sometimes as long as the posterolaterals. The posterolateral pinnules have a distal angle of about $60^{\circ}$ and the anterior primaries and secondary pinnules have a distal angle of about $80^{\circ}$. As in the type, the pinnules in the two anterior-most rows are positioned such that they appear to form a single row. There are about 10-12 primary pinnules per centimeter (including both anterior and posterolateral ones). In this specimen there are frequently six and sometimes seven secondary pinnules on a single anterior primary pinnule. These are most often arranged subalternately rather than suboppositely. The basal-most secondaries are up to 1 cm long, the distal-most ones are $0.5-0.75 \mathrm{~cm}$ long. The secondaries and the anterior primaries all lie in the same plane. The spines on the primary pinnules are up to 0.2 mm tall; those on the secondary pinnules up to 0.24 mm tall (the largest are found on the distal half of the pinnules). Three to five rows of spines can be seen in one lateral view. In each row the spines are not evenly spaced, but on average there are two or three spines per millimeter in each row.

The specimen from Australia (SAM H753) also has as many as three sets of secondary pinnules on each anterior primary pinnule; however, in this case the secondaries are arranged alternately on some branches, but in subopposite pairs on others. The posterolateral primaries, which are up to 2 cm long and about 0.3 mm in diameter near the base, are more distinctly shifted towards the posterior side of the axis (interior angle on posterior side $110^{\circ}$ to $120^{\circ}$ ). There are 12-14 primary pinnules per centimeter.


Fig. 10. Trissopathes tristicha (van Pesch, 1914), a-d, schizoholotype (USNM 10041); a-c, spines on anterior pinnules, scale 0.1 mm ; d, cross-sectional view of anterior pinnule with subpinnules; e, USNM 76953, cross-sectional view of pinnules.

The anterior primary pinnules are usually less than 0.75 cm , but can be as much as 1 cm long and 0.3 mm in basal diameter. The two rows of anterior primary pinnules are offset such that they form an interior angle about $20^{\circ}$. The distal angle of the anterior primary pinnules is $70-90^{\circ}$. The secondary pinnules lowermost on the anterior primary pinnules are $0.5-0.6 \mathrm{~cm}$ long with a basal diameter of about 0.2 mm . The spines, subequal in size around the circumference of the axis, are $0.2-0.28 \mathrm{~mm}$ tall.

Comparisons.- In this species, as well as in Trissopathes pseudotristicha spec. nov., the primary pinnules in the two anterior rows are usually aligned such that they appear to form a single row, more so in T. tristicha. The two species differ in that there are usually two or three pairs of mostly subopposite (sometimes alternating) subpinnules on the anterior primary pinnules in T. tristicha, whereas in T. pseudotristicha there is usually only one pair, and sometimes only a single subpinnule. Also, the pinnular spines in $T$. tristicha are generally taller and more acicular than those in $T$. pseudotristicha.

Distribution.- The species has been collected from waters off the Philippines and South Australia.

## Chrysopathes gen. nov.

Type species.-Chrysopathes formosa spec. nov. (see below).
Diagnosis.- Primary pinnules arranged in six rows and usually also in alternating biserial groups of three pinnules each. In each grouping of three the anterolateral pinnule is placed slightly below (relative to the direction of the branch) the adjacent lateral/ posterolateral pinnule, and the posterolateral pinnule is placed slightly above the posterior primary pinnule; therefore, the members of a group do not follow a semispiral pattern around the axis. Primary pinnules subequal in length or with laterals longer than those in anterior and posterior rows. Subpinnules confined to the anterior pinnules or present on lateral and posterior pinnules as well. Subpinnules arranged irregularly or alternately, and only rarely in subopposite pairs. Secondary pinnules usually smaller than primary pinnules.

Remarks.- Although the younger parts of colonies may have only four rows of primary pinnules, the typical condition in this genus is six rows. The primary pinnules in the posterior-most rows are usually not very well developed.

Species assigned to Chrysopathes.- Two species are assigned to this genus, Chrysopathes formosa spec. nov. and Chrysopathes speciosa spec. nov.

Etymology.- The generic name is derived from the Greek "chrysos" (gold) and the commonly used suffix "pathes".

Distribution.- Species of this genus are known only from the eastern Pacific.
Chrysopathes formosa spec. nov.
(figs 11-12)

Material.— Holotype (USNM 83566; schizoholotype, RMNH Coel. 32041), northeast Pacific, Jasper Seamount, $30^{\circ} 25^{\prime}$ N, $122^{\circ} 45^{\prime}$ W, depth not reported, 20.x.1984, R/V "Atlantis", coll. L. Levin; paratype (USNM 83568), northeast Pacific, Jasper Seamount, $30^{\circ} 25^{\prime} 36^{\prime \prime} \mathrm{N}, 122^{\circ} 43^{\prime} 42^{\prime \prime} \mathrm{W}, 950-840 \mathrm{~m}$, 1.xi.1986, Seatomado Expedition, coll. A. Genin; USNM 53434, east Pacific, off Equador, $00^{\circ} 37^{\prime} 00^{\prime \prime} \mathrm{S}, 81^{\circ} 00^{\prime} \mathrm{W}, 733$ m, 2.iii.1888, R/V "Albatross" sta. 2792.


Fig. 11. Chrysopathes formosa spec. nov., holotype (USNM 83566); a, entire corallum, scale 1 cm ; b, lateral view of branchlet with pinnules, scale 1 cm ; c, cross-sectional view of pinnules, scale 5 mm .

Diagnosis.- Corallum (fig. 11a) branched primarily in a single plane, with five or more orders of branches. Stem and branches pinnulate and subpinnulate (figs 11b-c). Primary pinnules arranged in up to six rows and in biserial groups of two or three pinnules each consisting of one anterolateral, one lateral (or posterolateral), and one posterior pinnule. Pinnules spaced 3-4 mm apart in each row, with 15-18 primary pinnules per centimeter (total for all rows). Lateral primary pinnules mostly 1.5 cm or less in length (rarely as much as 2 cm ) and generally less than 0.2 mm in basal diameter. Branches develop from lateral pinnules. Anterior primary pinnules generally less than 1 cm long, and posterior primaries (when present) mostly 0.5 cm or less. Anterior-most
primary pinnules simple or with one secondary pinnule arising near base, and usually only on abpolypar side of axis (figs 11c, 12e). Lateral primary pinnules occasionally with a single secondary pinnule; posterior primary pinnules simple. Tertiary pinnules absent. Spines (figs 12a-d) simple, smooth, mostly $0.08-0.12 \mathrm{~mm}$ tall (from middle of base to apex), but up to 0.16 mm . Spines near base of pinnules triangular in lateral view, those on the middle to distal sections of pinnules inclined distally to varying degrees. Spines on anterior pinnules and subpinnules generally more inclined distally than those on lateral and posterior pinnules. Spines reduced in size on branches and stem; not more than 0.05 mm . Spines on pinnules arranged in rows extending along length of axis, three or four rows visible in lateral view, with four to less than six spines per millimeter in each row. Polyps ranging from about 1.8 to 3 mm in transverse diameter from proximal edge of proximal lateral tentacles to distal edge of distal lateral tentacles; arranged in a single row on one side of the pinnules and subpinnules.

Description of the holotype.- The holotype (USNM 83566) is about 9 cm high and 15 cm wide (fig. 11a). The "stem" has broken off pinnules near its basal end indicating that the specimen was only part of a larger colony. The lower end of the "stem" is about 1.6 mm in diameter. The corallum is branched mostly to the third and fourth order. The larger branches are relatively straight, up to about 8 cm long with a basal diameter of about 1.2 mm ; they extend upward at about the same angle as the lateral pinnules (branch angles of $60-70^{\circ}$ ). The branches are mostly $1-3 \mathrm{~cm}$ apart on each side of the lower order ramifications. The overall branching pattern of the corallum is planar with smaller branches arising from the sides of lower order branches.

The primary pinnules are generally straight and stiff, and they project out on all sides of the axis (figs $11 \mathrm{~b}-\mathrm{c}$ ). With the exception of the distal sections of the smaller branchlets which carry only four rows of simple pinnules (in bilateral and alternating groupings of two pinnules each), the arrangement of the primary pinnules on most of the branches is biserial and in alternating groups of three pinnules each, one anterolateral, one lateral (or posterolateral), and one posterior, resulting in six rows when viewed in cross-section (fig. 11c). In some cases the pinnules in the two posterior rows are so close together that they appear to form a single row with double the number of pinnules as the other rows; in other cases the interior angle of the two posterior rows is $15-30^{\circ}$. The pinnules are $3-4 \mathrm{~mm}$ apart in each row and, counting the primary pinnules in all rows, there are up to 18 pinnules per centimeter. The primary pinnules in the lateral rows are usually 1 cm or less in length, although a few are as long as 1.5 cm and up to 0.2 mm in diameter near the base. The anterior primary pinnules are usually not more than 1 cm long and the posterior primaries are mostly 0.5 cm in length. The lateral and posterior primary pinnules are inclined distally (distal angle $60-70^{\circ}$ ); the anterior ones to a lesser degree. The typical pattern of subpinnulation is a single secondary pinnule on each of the anterior primary pinnules (fig. 12e) and no secondaries on the lateral or posterior primary pinnules; however, in a few cases a single secondary is also found on the lateral primary pinnules, but usually not on the posterior ones. The secondary pinnules are $0.5-0.7 \mathrm{~cm}$ long.

The spines (figs 12a-d) are triangular to conical in lateral view, acute and slightly inclined distally, especially on the distal sections of the anterior pinnules and subpinnules. They are generally not more than 0.12 mm tall (from midpoint of base to apex) on the primary pinnules; however, on some of the secondary pinnules spines as tall as


Fig. 12. Chrysopathes formosa spec. nov., holotype (USNM 83566); a-d, spines on pinnules, scale 0.1 mm ; e, cross-sectional view of pinnules, scale 1 mm .
0.16 mm can be found, and these appear to be subequal in size around the circumference of the axis. The spines on stem and larger branches are rarely more than about 0.05 mm . The spines on the pinnules are arranged in axial rows, three or four of which can be seen in lateral view (excluding rows in which the spines are only partially visible). The distance between adjacent spines in each row ranges from about 0.2 mm to 0.3 mm ; overall, there are four to about six spines per millimeter in each row.

The polyps are very poorly preserved on the type. They appear to be $1.8-3 \mathrm{~mm}$ in transverse diameter (from the distal edge of distal lateral tentacles to proximal edge of proximal lateral tentacles). Their density (number per centimeter) could not be determined.

Remarks.- One of the paratypes (USNM 83568) is a flabellate colony 53 cm tall and about 25 cm wide. The largest branch is 13 cm long and 1.5 mm in basal diameter. The branches are spaced $1-3 \mathrm{~cm}$ apart as in the holotype. In this specimen the pinnules tend to be curved distally, and in places the lateral primary pinnules are up to 2 cm and distinctly longer than the anterior primaries. This specimen demonstrates that even in large colonies subpinnulation is largely limited to a single secondary pinnule on each of the anterolateral primary pinnules. The specimen from Albatross sta. 2792 (USNM 53434) is a small colony ( 12 cm high) with secondary pinnules common on the lateral primaries as well as on the anterior ones. This specimen also differs from the holotype in having smaller spines (not more than 0.06 mm ).

Comparisons.- This species is very similar to Chrysopathes speciosa spec. nov., but differs from that species in having fewer secondary pinnules on the anterolateral primaries; secondaries only rarely on the lateral primary pinnules, and no tertiary pinnules. Furthermore, in C. formosa the spines are not as strongly inclined distally as in C. speciosa spec. nov., the primary pinnules are spaced further apart, and the polyps appear to be slightly smaller.

Etymology.- The specific name is derived from the Latin "formosa" for beautiful.
Distribution.- The species has been collected from the eastern Pacific.
Chrysopathes speciosa spec. nov.
(figs 13-14)

Material.— Holotype (USNM 76958; schizoholotype, RMNH Coel. 32040), northeast Pacific, off Oregon, $46^{\circ} 03^{\prime} \mathrm{N}, 124^{\circ} 38^{\prime} \mathrm{W}, 400 \mathrm{fm}(728 \mathrm{~m})$, R/V "Commando"; paratype (USNM 92590), Alaska, W of Dall Island, 914-1462 m, 1991, coll. F. and C. Athorp; paratype (USNM 89366), Off California/Oregon coast, 1000-1200 m, xi.1990, coll. R. Baxter

Diagnosis.- Corallum (fig. 13a) branched, usually planar, but sometimes somewhat bushy. Stem and branches pinnulate and subpinnulate (figs 13b-d). Primary pinnules arranged equidistantly around the axis in four rows near tips of branchlets, increasing to six rows on lower sections of branchlets, and in bilateral groups of two or three pinnules, one from each row; 18-27 pinnules per centimeter for all rows. Primary pinnules usually not more than about 1 centimeter long; subequal or with laterals slightly longer than anterior and posterior ones. Primary pinnules near tips of branchlets mostly simple or with one secondary pinnule on anterior primaries only; becoming increasingly subpinnulate on the lower parts of the branches (figs 13c-d, $14 \mathrm{e})$, with one or more secondary pinnules occurring on anterior and lateral primary


Fig. 13. Chrysopathes speciosa spec. nov., holotype (USNM 76958); a, upper part of corallum, approx. 0.6 $\times$; b, lateral view of pinnules, scale 5 mm ; c, cross-sectional view of branchlet with pinnules, scale 5 mm ; d, oblique lateral view of pinnules, scale 1 mm .
pinnules, but only infrequently on posterior primary pinnules. Up to four secondary pinnules on some primary pinnules. Arrangement and spacing of secondary pinnules very variable, either alternate, uniserial, subopposite, or irregular. Secondary pinnules inclined distally relative to the direction of the primary pinnule, and projecting laterally or somewhat distally or basally (fig. 13d). Tertiary pinnules present on some secondaries. Spines on pinnules (figs 14a-d) simple, smooth, acute; inclined or curved distally; mostly $0.06-0.12 \mathrm{~mm}$ tall from center of base to apex; arranged in axial rows, three or four of which visible in lateral view; spaced $0.2-0.3 \mathrm{~mm}$ apart, resulting in 4 to 6 spines per millimeter in each row. Spines on branchlets and stem reduced in size, usually not larger than about 0.05 mm . Polyps $2.0-3.3 \mathrm{~mm}$ in transverse diameter from proximal edge of proximal lateral tentacles to distal edge of distal lateral tentacles; arranged in single row, with three to four polyps per centimeter.

Description of the holotype.- The holotype (USNM 76958) is about 25 cm high and about 15 cm wide (fig. 13a). A holdfast is not present, and the basal part of stem is about 2.5 mm in diameter. The corallum is branched sparsely up to the fifth order with the larger branches 12 cm long and $1-3 \mathrm{~cm}$ apart (on either side of axis). The branches and branchlets are generally straight and directed distally (distal branch angle about $70^{\circ}$ ). The overall branching of corallum is planar, but several of the branches overlap. The branches arise primarily from the lateral primary pinnules.

The primary pinnules tend to be straight and stiff, relatively uniform in size and directed upward (distal angle $60-80^{\circ}$ ). They are arranged in four to six rows and also in groups of two or three which are most often spaced 1.2 to 1.6 mm apart, resulting in about 21-24 pinnules per centimeter (for all rows). The primary pinnules tend to be nearly equal in length, although in places the laterals are slightly longer than the anterior or posterior ones. The longest primary pinnules are $0.8-1.0 \mathrm{~cm}$ in length and about 0.2 mm in diameter near the base. The width across an individual branchlet (including pinnules) is as much as 1.5 cm . Up to four secondary pinnules are present on some primary pinnules; however, on the smallest branchlets, only the anterior pinnules possess subpinnules, and these usually have no more than one. The lowermost secondary pinnule is inserted $0.5-0.6 \mathrm{~mm}$ from the base of the primary. The spacing and arrangement of subsequent (more distal) secondary pinnules is very irregular; they may be subopposite, somewhat uniserial, or irregularly alternating (fig. 14e). The secondary pinnules lie in same plane as the primary pinnule or are directed distally or basally, relative to the direction of the branch on which they occur. Secondary pinnules also occur on the lateral primary pinnules, but are only rarely present on the posterior primaries. Tertiary pinnules are present on some secondaries, but they are not numerous. They occur primarily on the secondaries on the anterior primary pinnules, and, like the secondaries, they are not arranged regularly.

The axial spines (figs 14a-d) are mostly 0.06 to 0.12 mm (from the midpoint of the base to the apex), but some are up to 0.18 mm tall, and they can be inclined or curved distally. They can be hooked upward with the distal edge concave and the proximal edge convex in outline. The spines are subequal in size around circumference of axis; however, they appear to be slightly more distally inclined on the abpolypar side of the pinnules and slightly more at right angles to the axis on the polypar side. The spines on the pinnules are arranged in rows along length of the axis; three to four rows are visible in lateral view (excluding rows in which spines are only partially visible). The


Fig. 14. Chrysopathes speciosa spec. nov., holotype (USNM 76958); a-d, spines on pinnules, scale 0.1 mm ; e, cross-sectional view of pinnules, scale 1 mm .
distance between adjacent spines in each row is $0.2-0.3 \mathrm{~mm}$; resulting in four to six spines per millimeter in each row.

The polyps are elongated along the transverse axis; the distance from the distal edge of distal lateral tentacles to proximal edge of the proximal lateral tentacles ranges from 2.0 to about 3.3 mm (two to three per centimeter). On the pinnules the polyps are arranged in a row on one side of the axis such that those on the pinnules in the two posterior rows face away from each other, and those on the pinnules in the two anterior rows face toward each other.

Remarks.- The specimens assigned to this species are similar to the holotype in being subflabellate with the primary pinnules arranged in a maximum of six rows, and with the subpinnulation becoming more extensive on the larger branchlets and branches. The spacing between adjacent primary pinnules and also the position of the primaries around the circumference of the axis is variable, and in places the pinnules are more distinctly arranged in bilateral groups. In one paratype (USNM 92590) the pinnules are slightly more crowded, resulting in as many as 27 primary pinnules per centimeter, whereas in another (USNM 89366) the pinnules can be further apart, with only 18 pinnules per centimeter.

Comparisons.- This species differs from C. formosa spec. nov. in having more numerous subpinnules, including more secondary pinnules on the anterior and lateral primary pinnules, and also more tertiary pinnules. These differences can only be observed in comparing large colonies, and small or young colonies of the two species may be difficult to tell apart. Furthermore, in C. speciosa the spines are more typically inclined or curved distally than in C. formosa spec. nov., the primary pinnules are spaced closer together, and the polyps appear to be slightly larger in transverse diameter.

Etymology.- The specific name is derived from the Latin "speciosa", beautiful.
Distribution.- The species has been collected in the northeast Pacific, off the coasts of Alaska, Oregon and California.

## Sibopathinae subfam. nov.

Homoeotaeniales van Pesch, 1914: 21 (in part).
Diagnosis.- Polyps mostly 2-3 mm in transverse diameter; with six incomplete mesenteries, and lacking an actinopharynx. Corallum branched and pinnulate. Pinnules simple, arranged in four (rarely five or six) rows and usually in biserial groupings. Spines simple, smooth, acute, usually triangular in lateral view.

Remarks.- The subfamily contains the single genus Sibopathes. Based on skeletal morphology and size of the polyps, species in this subfamily bear a strong resemblance to species of the subfamily Parantipathinae in the family Schizopathidae (see Opresko, 2002). In both cases the corallum consists of simple elongate pinnules arranged in multiple, usually biserial, rows, and the polyps are generally $2-3 \mathrm{~mm}$ in transverse diameter. The main difference between the two subfamilies is in the absence of secondary mesenteries and an actinopharynx in Sibopathes. It is quite possible that these structures were secondarily lost from a parantipathinid ancestor, and that Sibopathes is more closely related to the Parantipathinae than to the Cladopathidae. However, because convergence of skeletal characters appears to be not uncommon in antipatharians, it seems
more appropriate to retain Sibopathes in the Cladopathidae until more data are available. This may be a case where molecular techniques would be helpful in resolving the issue.

Sibopathes van Pesch, 1914
(fig. 15)
Type species.— Sibopathes gephura van Pesch, 1914: 203-205, pl. VI, figs. 3, 5-6, 15; pl. VII, fig. 3.

Diagnosis.- As for the subfamily.
Holotype.- ZMA Coel. 3283. IndoPacific, east of Timor, Indonesia, $8^{\circ} 17.4^{\prime} \mathrm{S}, 127^{\circ} 30.7^{\prime} \mathrm{E}, 1224 \mathrm{~m}$, "Siboga" sta. 280.

Description of the type species.- Corallum branched and pinnulate (fig. 15a); pinnules simple, up to 2 cm long; arranged predominantly in four rows (fig. 15c). Van Pesch (1914) described the position of the rows as two lateral, one anterior, and one posterior; however, reexamination of the type revealed that in places the rows can also be arranged biserially, that is, with two rows on the right and two on the left. In such cases the pinnules are placed in alternating pairs with the front or anterolateral pinnule of each pair located slightly below the adjacent lateral (as viewed from the front or polyp-side of the corallum). Additional pinnules representing a fifth row occur infrequently on parts of the corallum. These are located in front of and slightly below the adjacent anterolateral pinnules such that the group of three pinnules forms a descending series going from the side to the front of the branch (as viewed from the polyp-side of the corallum). The pinnules tend to be curved distally relative to the branch on which they occur. The spines (fig. 15b) are simple, triangular, not more than 0.04 mm tall; arranged in three to four longitudinal rows, with five to seven spines per millimeter in each row. Abpolypar spines are nearly equal in size to the polypar spines. The polyps are $2-2.5 \mathrm{~mm}$ in transverse diameter, and are arranged in a single row with three to four polyps per centimeter.

Species assigned to Sibopathes.- Besides the type species, one other species is assigned to this genus: Sibopathes macrospina (Opresko, 1993). The latter species differs from $S$. gephura in having larger spines ( $0.07-0.12 \mathrm{~mm}$ vs. 0.04 mm ), and a slightly different arrangement of the pinnules (see Opresko, 1993).

Distribution.- The type species was collected in the IndoPacific; the second known species is from the Gulf of Mexico.

## Hexapathinae subfam. nov.

Homoeotaeniales van Pesch, 1914: 21 (in part).
Diagnosis.- Polyps 3-9 mm in transverse diameter; with an actinopharynx and six complete mesenteries. Corallum monopodial or very sparsely branched, and pinnulate. Pinnules arranged in two lateral (sometimes anterolateral or posterolateral) rows and in one or more anterior rows. Lateral pinnules simple; anterior pinnules simple or subpinnulated. Spines conical to subcylindrical, subequal or larger on the anterior pinnules and subpinnules.


Fig. 15. Sibopathes gephura van Pesch (1914), holotype (ZMA Coel. 3283); a, entire corallum, height approx. 10 cm ; b, spines on pinnule, scale 0.1 mm ; c, lateral view of pinnules, scale 1 mm .

Remarks.- The subfamily contains two genera, Hexapathes Kinoshita and Heliopathes gen. nov. In Hexapathes, the anterior pinnules may be nearly as long as the lateral pinnules, and the spines on anterior pinnules and subpinnules are similar in size and morphology to those on the lateral pinnules. In Heliopathes, the anterior pinnules are usually much shorter than the lateral pinnules, and the spines on the anterior pinnules and subpinnules are much more developed than those on the lateral pinnules.

Observations made on a limited number of specimens assigned to this subfamily suggest that the reproductive tissues may be confined to the polyps located at the base of the anterior pinnules and subpinnules. In several instances egg-like masses were observed in the soft tissues in this area of the corallum but not in other parts of the corallum. The tissues of these specimens were in various stages of disintegration, so it cannot be said with certainty whether specialized reproductive polyps were present; however, if true, then it might partially explain why in species of Heliopathes the spines on the anterior pinnules are much larger than those on the lateral pinnules. Polyps with eggs or sperm were not described by Kinoshita (1910) for the type of Hexapathes heterosticha.

Comparisons.- Some species of this subfamily resemble those of the genus Abyssopathes in the family Schizopathidae (see Opresko, 2002) in having a monopodial corallum with two rows of lateral pinnules and an additional single or multiple series of pinnules on the anterior side of the stem. Abyssopathes is currently assigned to the family Schizopathidae on the presumption that the polyps possess secondary mesenteries; however, this has not been verified (see Opresko, 2002 for discussion). Although similar in general morphology, the stem of Abyssopathes is curved such that it apparently extends parallel to the substrate and the "anterior" pinnules project down from the stem towards the substrate (see description in Pasternak, 1964). These pinnules are very short and curved distally (relative to the direction of the stem). The lateral pinnules, on the other hand, curve upward away from the substrate, with those on one side of the stem curving towards the tips of the lateral pinnules from the opposite side to form a funnel or basket-like structure. In contrast, in the monopodial species of the Hexapathinae the corallum is generally upright (or slightly inclined forward), the lateral pinnules project out to the sides of the stem and then curve upward, and the anterior pinnules project at right angles to the stem (or are also curved distally). Until additional histological studies are conducted on the polyps of Abyssopathes, the true affinities of these two genera will be unclear.

## Hexapathes Kinoshita, 1910

Type species.- Hexapathes heterosticha Kinoshita 1910: 231-234.
Type locality.- Japan, Bay of Tokyo.
Diagnosis.- Corallum simple or very sparsely branched, and pinnulate. Pinnules in two lateral rows and in one or two anterior rows. Lateral pinnules simple; anterior pinnules simple or subpinnulate. Lateral pinnules generally do not extend beyond the top of the stem; anterior primary pinnules and subpinnules sometimes nearly as long as lateral pinnules. Spines subequal in size on primary and secondary pinnules. Polyps 3 to 9 mm in transverse diameter.

Description of the type species.-Kinoshita (1910) reported that the type specimen
was 20 cm tall with a basal stem diameter of 2 mm . The lateral pinnules were described as being 14 cm in maximum length, 0.65 mm in maximum thickness, and spaced $2.5-6$ mm apart. The anterior pinnules were described as being directed horizontally, very densely set and reaching a maximum length of 10 cm , "but the majority remaining quite short". Kinoshita (1910) makes no mention of the anterior pinnules bearing subpinnules and, in general, he refers to the corallum as having "numerous simple branchlets". This statement can be interpreted to mean that the anterior pinnules are not subpinnulated, although it is also quite possible that he had overlooked the presence of subpinnules. The spines were reported to be $0.05-0.10 \mathrm{~mm}$ tall on the polyp side of the axis and not more than 0.07 mm on the abpolypar side. The polyps were reported to be $5-9 \mathrm{~mm}$ (usually 7 mm ) in size, and were described by Kinoshita as having an actinopharynx, six complete primary mesenteries, and no secondary mesenteries.

Remarks.- Although Kinoshita's description implies that the anterior pinnules are simple, the type description was not accompanied by a photo or illustration of the corallum. Consequently, this assumption needs to be confirmed by reexamination of the type. Inquires to the University Museum in Tokyo were unsuccessful in locating Kinoshita's type collection.

Species assigned to Hexapathes.- One other species, H. australiensis spec. nov., is assigned to this genus. The two species are differentiated primarily on the basis of the presence or absence of subpinnules on the anterior primary pinnules.

Distribution.- Species of this genus are known from Japan (H. heterosticha) and from off Tasmania (H. australiensis).

Hexapathes australiensis spec. nov.
(figs 16-17)

Material.— Holotype (SAM H-742; schizoholotype USNM 99397), off Tasmania, $41^{\circ} \mathrm{S}, 144^{\circ} 08^{\prime} \mathrm{E}, 25$ nautical miles west of Richardson Point, 520 m, xii.20.1984, R/V "Soela" sta 51, coll. W. Zeidler.

Diagnosis.- Corallum (fig. 16a) very sparsely branched, and pinnulate. Pinnules (fig. 16b) arranged, with varying degrees of regularity, in two lateral or posterolateral rows and one or two anterior rows. Lateral pinnules simple, elongate, inclined distally, and arranged alternately. Anterior pinnules simple or with one secondary pinnule on upper or lateral side; of varying length, sometimes as long as lateral pinnules. Spines (figs 17a-c) on pinnules small, triangular to conical in lateral view; and mostly $0.08-0.12 \mathrm{~mm}$ tall. Polyps estimated to be $3-4 \mathrm{~mm}$ in transverse diameter.

Description of holotype.- The holotype (SAM H-742; fig. 16a) is about 25 cm tall (two pieces) and has a width of about 7 cm . The corallum is broken 3 cm above the basal plate and also at the top where the diameter of the stem is about 0.4 mm . The stem is 0.8 $\times 0.9 \mathrm{~mm}$ in diameter just above the basal plate. The lowermost 2.8 cm of the stem lacks pinnules. At a point beginning about 1.5 cm above the basal plate and extending for 1.3 cm , the surface of the stem is modified into a series of axial grooves and ridges (eight or nine ridges and the same number of grooves are visible in one view). Small spines occur along the crest of some of the ridges. The ridges and grooves extend upward on the stem to the point where the lowermost pair of lateral pinnules is located.


Fig. 16. Hexapathes australiensis spec. nov., holotype (SAM H-742): a, entire corallum, height approx. 25 $\mathrm{cm} ; \mathrm{b}$, close-up lateral view of stem showing anterior pinnules and subpinnules, approx. $2.5 \times$.

The number, arrangement and relative position of the pinnules is not consistent throughout the corallum, and in places some pinnules are missing altogether. In general, there are two lateral or posterolateral rows and one or two anterior rows. On the lowermost part of the pinnulated section of the stem, the two lateral rows are nearly in the same plane (i.e., the interior angle formed by the two rows is about $180^{\circ}$ ); however, at higher points on the corallum the interior angle becomes more obtuse (and the lateral pinnules are therefore more posterolateral in position), and near the top, the angle is about $270^{\circ}$. The most regular pattern seen on the specimen is one in which there are two rows of posterolateral pinnules, whose members are arranged alternately along the stem, and two rows of anterior pinnules whose members are
placed slightly below the adjacent posterolateral pinnules. The two lowermost lateral pinnules on the stem are nearly opposite one another (the pinnule on the right is slightly lower than the one on the opposite side when viewing the side of the corallum with the anterior pinnules). On the lower part of the stem the general appearance is of only three rows of simple pinnules, two lateral and one anterior; the lateral pinnules being up to 5 cm long (broken at the tip) and 0.5 mm in diameter near the base, and the anterior pinnules being only 2 cm long and 0.5 mm in diameter at the base. In each lateral row, the pinnules are spaced $4-11 \mathrm{~mm}$ apart (generally, there are two per centimeter; however, they may also be absent). Many of the lateral pinnules are broken; the largest remaining one is 10.5 cm long, slightly less than half the total height of the corallum. The lowermost lateral pinnules are $0.3-0.4 \mathrm{~mm}$ in diameter near their base. The lateral pinnules are generally inclined distally (distal angle formed with the stem is about $60^{\circ}$ ). The third lateral pinnule from the bottom of the corallum on the right side is developed into a pinnulated branch; the basal 1.5 cm of this branch is unpinnulated followed by ten pinnules (total for all rows) in about 18 mm . Most of the pinnules on this branch are $5-6 \mathrm{~mm}$ long; however, one is 2.6 cm long. Several of these branch pinnules have a single secondary pinnule.

Anterior pinnules are not found on the part of the corallum next to the three lowermost pairs of lateral pinnules. Above this point, there are usually two anterior pinnules (sometimes only one) associated with each pair of lateral/posterolateral pinnules. On the lower half of the corallum the anterior pinnules are $2-3 \mathrm{~cm}$ long, about 0.4 mm in diameter near their base, and they are spaced 2-4.5 mm apart (resulting in three to four per centimeter). In the middle of the corallum (about 13 cm above the base), the anterior pinnules are more crowded (spaced 1.7-2.7 mm apart with five to six per centimeter) and many are up to 6 cm long. Over most of their length, the anterior pinnules are inclined distally (at about the same angle as the lateral pinnules); however, at their point of insertion on the stem, the distal angle that they form with the stem is close to $90^{\circ}$ for those on the lower part of the corallum and $70-80^{\circ}$ for those on the upper part.

Subpinnules do not occur on the lateral pinnules, but they are present on some of the anterior pinnules, particularly those in the middle of the corallum; i.e., higher than about 10 cm above the basal plate. However, even in the middle of the corallum they are not found on every anterior pinnule, and there is never more than one secondary pinnule on an anterior primary. The secondary pinnules originate $0.8-1.0 \mathrm{~mm}$ from the base of the anterior pinnules and they are usually located on the distal or lateral sides of the anterior primary pinnules. Over short distances the subpinnules on adjacent primary anterior pinnules have the same orientation; i.e., they may all originate on the distal side of the primary pinnule or they may all originate on the inner side in which case those on opposite primaries are directed inward toward each other (rarely they both occur on the outer side and therefore extend away from each other). Secondary pinnules are present near the top of the corallum where the stem diameter is 0.4 mm (all pinnules broken off).

The spines (figs 17a-c) on the lateral pinnules are small, triangular to conical in lateral view (flared out distally and proximally at their base) and perpendicular to the axis or somewhat inclined distally. They are mostly 0.08 to 0.12 mm tall (up to 0.14 mm ) as measured from the center of the base to the apex; the largest of these often


Fig. 17. Hexapathes australiensis spec. nov., holotype (SAM H-742): a-c spines on pinnules, scale 0.1 mm .
appear to occur on the upper side of the pinnules. Three to five very irregular rows of spines are visible in one lateral view of the pinnules, and within each row there are three to four spines per millimeter. The spines on the anterior pinnules are about the same size as those on the lateral pinnules (up to 0.12 mm ). The largest of these are usually located near the base of the anterior pinnules and some are directed downward (proximally relative to the axis of the pinnule). Spines at the tips of the lateral pinnules (axis 0.3 mm ) are very small, only $0.03-0.04 \mathrm{~mm}$. Spines on the stem are reduced in size, only about 0.06 mm , and they are not regularly arranged in rows. The central canal on the stem and pinnules is relatively large, about 0.3 mm in diameter.

Polyps are in a poor state of preservation on the holotype; however, they are estimated to be $3-4 \mathrm{~mm}$ in transverse diameter (from the distal side of the distal lateral tentacles to proximal side of proximal lateral tentacles). Masses of tissue containing what appear to be eggs and mesenteric filaments are present at the base of some of the secondary pinnules.

Remarks.- It is likely that the holotype is a mature colony as suggested by the presence of eggs in the tissues at the base of the secondary pinnules. The unique features of this specimen are the very irregular arrangement of the pinnules, the very
obtuse interior angle formed by the two rows of lateral pinnules in the upper part of the corallum, and the non-uniform growth form of the corallum.

Young colonies of this species are likely to appear very different from the holotype. Those smaller than 4 cm are not likely to have anterior pinnules and those smaller than 10 cm are not likely to have secondary pinnules. Such colonies might easily be identified as a different species.

Comparisons.- Although Hexapathes australiensis resembles H. heterosticha in having relatively long anterior pinnules and spines that are not significantly larger on the anterior pinnules, it can be differentiated from $H$. heterosticha by the presence of secondary pinnules and by its smaller polyps.

Distribution.- Known only from off Tasmania.

## Heliopathes gen. nov.

Diagnosis.- Corallum monopodial and pinnulate. Pinnules in two lateral rows and in one or more anterior rows. Lateral pinnules simple; anterior pinnules subpinnulate; Lateral pinnules curved upward, and often extending up to or above the top of the stem. Spines on anterior pinnules and subpinnules larger than those on lateral pinnules. Polyps 5 to 6 mm in transverse diameter.

Type species.- Heliopathes americana spec. nov. (see below)
Species assigned to Heliopathes.- One other species, Antipathes heterorhodzos Cooper (1909), is assigned to this genus. The two species are differentiated primarily on the basis of the extent of subpinnulation of the anterior primary pinnules and the size of the spines.

Etymology.- The generic name is derived from the Greek "helios" (sun) and the commonly used suffix "pathes".

Distribution.- One species (H. americana) is from the western Atlantic, and the second (H. heterorhodzos) was collected in the Indian Ocean.

Heliopathes americana spec. nov.
(figs 18-19)

Material.— Holotype (USNM 92591), Caribbean Sea, off Jamaica, Grappler Bank, $18^{\circ} \mathrm{N}, 75^{\circ} \mathrm{W}$, coll. C. Cutress; paratype (USNM 100111), northwestern Atlantic: off Georgia, from the wreck of the S.S. "Central America", $32^{\circ} \mathrm{N}, 77^{\circ} \mathrm{W}, 2200 \mathrm{~m}$, coll. C.E. Herdendorf.

Diagnosis.- Corallum (fig. 18a) monopodial and pinnulate; pinnules arranged in two lateral rows and one or two irregular anterior rows. Lateral pinnules simple, elongate, arranged alternately and inclined and curved distally and extending to the top of the corallum; anterior pinnules short, subpinnulate, and extending out nearly perpendicular to the plane containing the stem and lateral pinnules. Anterior pinnules with one to three secondary pinnules, the lowermost two usually arranged bilaterally. Secondary pinnules may be subpinnulate, with the tertiary pinnules usually arising from upper and/or lower surface of secondaries. Spines on lateral pinnules small (about 0.05 mm or less), triangular, acute, compressed. Spines on anterior pinnules larger on one side of axis (up to 0.13 mm ) and inclined distally. Polyps $5-6 \mathrm{~mm}$ in transverse


Fig. 18. Heliopathes americana spec. nov., a-c, holotype (USNM 92591): a, entire corallum, scale 1 cm ; b, close up frontal view of anterior pinnules, approx. $3 \times$; c, cross-sectional view of pinnules, approx. 4 $\times$; d, paratype (USNM 100111), polyp, approx. $5 \times$.
diameter (from distal edge of distal lateral tentacles to the proximal edge of the proximal lateral tentacles).

Description of the holotype.- The holotype (USNM 92591) is about 10 cm high (including pinnules) and about 8 cm wide (fig. 18a). The stem extends to the top of the corallum. Viewed from the side, the stem has a somewhat s-shaped curvature with the top of the corallum titled forward. Near the base, the stem is $0.5 \times 0.7 \mathrm{~mm}$ in diameter, but a maximum thickness of 0.8 mm is reached at a height of about 2 mm . The surface of the stem is smooth for a distance of about 2 mm above the basal plate; higher up it is fluted with 12-14 narrow grooves and ridges visible in one view. These grooves and ridges extend upward to a point beyond where the lateral pinnules start. Fine ridges also occur along the more basal part of most of the lateral pinnules and these correspond to the rows of pinnular spines. The lower 2 cm of the stem lacks pinnules; the following 1 cm contains the lateral and anterior pinnules; and the upper 7 cm is without pinnules.

Except for the lowermost pair of lateral pinnules which are nearly opposite, all the lateral pinnules are arranged alternately, six on each side. Those on the right side arise from points on the stem slightly higher than the adjacent lateral pinnules on the left side. In each lateral row the pinnules are spaced $1.7-2.3 \mathrm{~mm}$ apart (six per centimeter). All the lateral pinnules are broken at their tip; the remaining sections are 7 to 9 cm long and about 0.4 mm in diameter near their base. The lower lateral pinnules initially extend out at right angles from the stem, but then curve upward. The lateral pinnules near the top of the stem are more vertically directed (distal angle $30^{\circ}$ ). The interior angle formed by the two planes containing the lateral pinnules is about $120^{\circ}$ for the lowermost pairs and $150^{\circ}$ for the higher ones.

The anterior pinnules (figs $18 \mathrm{~b}-\mathrm{c}$ ) are $6-8 \mathrm{~mm}$ long, up to 0.16 mm in diameter near their base, and they are spaced 0.9 to 1.0 mm apart in a single irregular row (nine are present over a distance of 8 mm ). They occur only on that part of the stem distal to the point of insertion of the second lowermost pair of lateral pinnules, and they extend out at right angles to the stem or are slightly inclined upward (distal angle about 70$80^{\circ}$ ). There are one or two orders of subpinnules on the anterior pinnules. The number and arrangement of the subpinnules is not strictly regular from pinnule to pinnule. One and sometimes two secondary pinnules occur on each anterior primary pinnules, and a secondary pinnule, in turn, may have one (rarely two) tertiary pinnules. The lowermost secondary pinnules arise near the base of the anterior pinnules; they are generally arranged laterally and not quite opposite and are inclined and curved distally relative to the direction of the anterior pinnule on which they are located. The tertiary subpinnules arise mostly on the upper and/or lower sides of secondary subpinnules. They are also inclined and curved distally relative to the secondary pinnule.

The spines on the lateral pinnules are small, triangular, compressed and slightly distally inclined (fig. 19c). They are mostly about 0.03 mm tall (from the apex to the center of the base), but can be as much as 0.05 mm at the base of the pinnules. Five to eight longitudinal rows can be seen in one lateral view, and within each row the spines are usually spaced about $0.13-0.18 \mathrm{~mm}$ apart (about $5-8$ spines $/ \mathrm{mm}$ ). The spines on the anterior pinnules and subpinnules (figs 19a-b) are larger than those on the lateral pinnules and they also vary in size depending on their location. Those on the outer or convex sides of the subpinnules are up to 0.13 mm tall and strongly inclined distally.


Fig. 19. Heliopathes americana spec. nov., holotype (USNM 92591): a-b, spines on anterior pinnules; c, spines on lateral pinnule, scale 0.1 mm .

Those on the opposite or concave side of the subpinnules are small and triangular and not more than 0.05 mm .

Polyps are not present on the specimen; however, the remains of soft tissue are visible on the inner/concave sides of some of the anterior subpinnules, and in a few places this tissue appears to contain eggs.

Remarks.- The holotype is probably a mature colony as suggested by the thickness and length of the pinnules and by the apparent presence of eggs in the remains of the soft tissue.

The paratype (USNM 100111) is similar to the holotype in size ( 10.5 cm high and about 9 cm wide) and in general appearance. In this specimen a third secondary pinnule sometimes occurs on an anterior primary pinnule. When present, this secondary pinnule is inserted on the top or bottom of the primary and distal to the first two secondaries. The spines in this specimen are similar to those in the holotype in that those on the lateral pinnules are not more than 0.05 mm and those on the anterior pinnules are up to 0.12 mm . In this specimen, however, the spines on the anterior pinnules are more subequal in size around the circumference of the axis. Spines up to about 0.04 mm tall
occur along the crest of some of the ridges on the lower part of the stem. Polyps are present in only a few places and they are in a very poor state of preservation; however, it was possible to estimate their transverse diameter to be $5-6 \mathrm{~mm}$ and the length of the interpolypar space to be about 2 mm (fig. 18d). The tentacles are about 4 mm in length, and there are no indications of the polyps being subdivided by peristomal folds.

Although there are some morphological differences between the holotype and the paratype, most of these are considered to be due to presumed differences in the age of the colonies. There is evidence, particularly in the narrowness of the pinnules and the smaller number of subpinnules, to suggest that the paratype is a younger colony. Although the paratype is similar in size to the holotype and has the same number of lateral pinnules (six on each side), the maximum diameter of the stem is only 0.5 mm (vs. 0.8 mm in the holotype), and the lateral pinnules are narrower (diameter 0.2 mm vs. 0.4 mm in the holotype) and more thin-walled. Furthermore, the lower sections of the lateral pinnules do not have the fine ridges and grooves that are seen in the holotype, and there are, in general, fewer tertiary pinnules present on the secondary pinnules. This specimen also differs from the holotype in having more widely spaced pinnules. The interpinnular distance of the lateral pinnules is $4.0-6.7 \mathrm{~mm}$ vs. $1.7-2.3$ mm in the holotype. The interpinnular distance of the anterior pinnules is $1.7-2.1 \mathrm{~mm}$ (eleven occur over a distance of 1.9 cm , resulting in a density of about six per centimeter) vs. $0.9-1.0 \mathrm{~mm}$ (about 11 per centimeter) in the holotype.

Comparisons.- A species described by Cooper (1909) as Antipathes heterorhodzos is here referred to the genus Heliopathes. Cooper's species differs from H. americana primarily in having five to six, relatively long secondary pinnules, all arising from about the same point on the anterior primary pinnules. Furthermore, if Cooper's illustration is accurate, there are no tertiary pinnules on any of the secondary pinnules. The whereabouts of the type specimen of H. heterorhodzos is unknown; consequently, the characteristic features of the species, as presented in Cooper's description and illustrations, can not be verified.

A specimen collected from off Cuba and provisionally referred to Cooper's species by Opresko (1974), is more similar to H. americana in that it has tertiary as well as secondary pinnules. There are some indications that this specimen might represent a larger and older colony of H. americana. Even though the size of the Cuban specimen ( 8 cm in height) is less than that of the type of H. americana $(10 \mathrm{~cm}$ ), the true size cannot be determined because both the tip of the stem, as well as the tips of the lateral primary pinnnules, are all broken off. In this specimen the primary pinnules occur over a greater length of the stem ( 4.5 cm vs. 1 cm in the type of H. americana), and the anterior primary pinnules and subpinnules are up to 1.5 cm long whereas in the type of H . americana they are not more than 8 mm long. Furthermore, there are up to four secondary pinnules per anterior primary and up to two tertiary pinnules per secondary. These are all characteristics that might be expected in an older colony. There are, however, features in the type of H. americana, such as the thickness and uniform length of the pinnules, the presence of ridges and grooves at the base of the lateral pinnules, the absence of any sign of newly forming pinnules, and the apparent presence of eggs in the tissue, which would suggest that the type is a mature colony at its maximum size. The examination of a larger number of specimens might help resolve the issue.

Etymology.- From "america", a reference to the site at which the paratype was
collected (the wreck of the SS. "Central America"), and also to the general geographic area where the species has been found

Distribution.- The holotype and paratype came from the northwestern Atlantic.

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