Senckenbergiana biologica 81 | (1/2) | 1–21 15 Figs. Frankfurt am Main, 21.12.2001

Re-descriptions of the antipatharian corals described by E. J. C. Esper with selected English translations of the original German text

(Cnidaria, Anthozoa, Antipatharia)

Dennis M. Opresko & Rosemarie C. Baron-Szabo

Abstract

E. J. C. Esper described seven new species of antipatharian corals (Cnidaria, Anthozoa, Antipatharia). Type specimens of four of these species are present in the collections of the Senckenberg-Museum, those of *Antipathes paniculata*, *Aphanipathes reticulata*, *Leiopathes glaberrima*, *Parantipathes larix*. The current study was undertaken to better understand Esper's species by completing a detailed analysis of the original German descriptions, and by re-examining and re-describing the available type material using modern methods, including scanning electron microscopy. The type species for *Aphanipathes* Brook 1889 is designated: *Aphanipathes sarothamnoides* Brook 1889.

Zusammenfassung

E. J. C. Esper beschrieb 7 neue Arten von Antipatharien (Cnidaria, Anthozoa, Antipatharia). Das Typusmaterial von 4 dieser Arten befindet sich in den Kollektionen des Senckenberg-Museums, Frankfurt am Main: *Antipathes paniculata*, *Aphanipathes reticulata*, *Leiopathes glaberrima* und *Parantipathes larix*. Die vorliegende Arbeit beinhaltet eine detaillierte Analyse der deutschen Originalbeschreibungen sowie korrigierte Diagnosen, basierend auf Untersuchungen mit Hilfe neuester Methoden (unter anderem REM) und soll dazu dienen, einen besseren Einblick und größeres Verständnis dieser Formen zu erhalten. Die Typusart der Gattung *Aphanipathes* Brook 1889 wird festgelegt: *Aphanipathes sarothamnoides* Brook 1889.

Introduction

In his multi-volume work "Die Pflanzenthiere" which was published in parts during the years 1788 to 1830 (see Grasshoff & Scheer 1991 for specific publication dates of text and plates), Eugen Johann Christoph Esper described 110 species of octocorals and antipatharians (see Grasshoff 1991 for a critical review of the species). Under the genus *Antipathes*, Esper discusses 13 species, including one Linnean species, *Antipathes spiralis*, and five species described by Pallas in 1766; i.e., *Antipathes flabellum*, *A. clathrata*, *A. cupressus*, *A. myriophylla*, and *A. foeniculacea*. The remaining seven species (*Antipathes larix*, *A. ligulata*, *A. glaberrima*, *A. reticulata*, *A. compressa*, *A. paniculata*, and *A. virgata*) were described as new species. One of these, *Antipathes ligulata*, has since been identified as the axis of a gorgonian (see Brook 1889, Grasshoff 1991). All of the remaining species have been considered to be true antipatharian corals. Esper based his new species on specimens from private and university collections which he himself examined. Although his descriptions are rather extensive and are considerably enhanced by the excellent illustrations, information on the identity of Esper's species, and their true affinities within the order, have been complicated by difficulties in interpreting the original German descriptions and by the lack of critical details in both the descriptions and illustrations.

Authors' addresses:
Dr. Dennis M. Opresko, Life Sciences Division, Oak Ridge National Laboratory, 1060 Commerce Park (107), Oak Ridge, Tennessee, 37830, USA; email: dmopresko@hotmail.com.
Dr. Rosemarie C. Baron-Szabo, Institute of Paleontology, University of Frankfurt, Postfach 111932, D-60054 Frankfurt am Main, Germany.

The current study was undertaken to better understand ESPER's species by completing a detailed analysis of the original German descriptions and by re-examining and re-describing the available type material using modern methods, including scanning electron microscopy.

Fortunately, in the Senckenberg-Museum, Frankfurt am Main, there are specimens of four species which are considered to be part of material originally examined by ESPER himself. These specimens were transferred to Senckenberg-Museum from the collections of Erlangen University in 1978. The type specimens of two species, *A. virgata* and *A. compressa*, have not been located, and are considered to be permanently lost. The catalogue numbers (SMF) of the specimens discussed in this paper are those for the Senckenberg-Museum. The specimens were kindly made available for study by Dr. M. GRASSHOFF.

Translations of 18th century German descriptions are complicated by the fact that the definition or common usage of some words may have changed over the ensuing time period. This may be particularly significant in the case of units of measurement. In his descriptions of antipatharians ESPER used the following units of measurement: Schuh, Fuß, Zoll, and Linie. While it is difficult to determine exactly what these units are equivalent to, in terms of today's standards, we interpret Schuh and Fuß to mean "foot" and assume they are equivalent to the modern measurement. The word Zoll we assume to mean inch as it is used today, and the word Linie to mean one-twelfth of an inch. Furthermore, some words, such as "Gattung" and "Geschlecht", can have multiple meanings, and it is only in the context of sentence or phrase in which they are used that the most appropriate English equivalent can be determined. In the translations presented in this paper, parenthetical remarks offset by brackets are used to identify words of unclear or variable meaning and to clarify our interpretation of the text.

In the synonymic lists, a question mark (?) refers to a doubtful identification by the author cited, while an asterisk (*) indicates that the specimen(s) described by that particular author had been examined by us.

Systematic part

Order Antipatharia
MILNE EDWARDS & HAIME 857

Remarks: One of the earliest illustrations of an antipatharian coral, that published by MARSIGLI in 1725, included a magnified view of branch which clearly showed the presence of axial spines. In 1766, PALLAS determined that antipatharians, which had previously been placed in the genus *Gorgonia* by LINNAEUS (1758), could be differentiated from gorgonians on the basis of the presence of such axial spines. Surprisingly though, one genus of gorgonians, *Dendrobrachia* BROOK 1889, which for many years was considered to be an antipatharian, has axial spines which are not unlike those in some species of antipatharians (OPRESKO & BAYER 1991). Therefore, the presence of axial spines alone is not a morphological feature defining the *Antipatharia*; instead, it is the fact that the polyps have only six tentacles and six primary mesenteries, that differentiates these corals from all other anthozoans.

Family Antipathidae EHRENBERG 834

Remarks: In 1834 EHRENBERG used the name Antipathina for a family level taxon in the Order Scleropoda of the Class Bryozoa. Although it is likely that EHRENBERG was actually referring to a bryozoan that was encrusting an antipatharian axis, his usage has priority over subsequent designations in which the name was correctly used as a family level taxon for antipatharian corals (GRAY 1840, DANA 1846, VERRILL 1865).

Genus *Antipathes* PALLAS 1766

Type species: *Antipathes dichotoma* PALLAS 1766, by subsequent designation by BROOK (1889: 97).

Diagnosis: Corallum bushy or flabellate, branching irregular, pseudodichotomous or subalternate. Branches straight or curved; simple or pinnulate. Spines laterally compressed and triangular, blade-like or conical; smooth or papillose; subequal around the circumference of the axis or longer on the polyp side. Polyps 0.5 to 2.5 mm in transverse diameter.

Remarks: As it has been treated in the most recent taxonomic monographs of the order (VAN PESCH 1914, PAX 1940), the genus *Antipathes* contains over 100 nominal species representing a very broad spectrum of morphological variability in the growth form of the corallum, in size and shape of the spines, and in the polyps. This arrangement obscures the natural affinities of the species currently placed in this genus. A taxonomic revision of not only the genus *Antipathes*, but of the entire order is currently being undertaken and this will result in many species of *Antipathes* being assigned to different genera, and even different families.

Antipathes paniculata ESPER 1796

[= ?*Antipathes abies* (LINNAEUS 1758)]

(Figs. 1, 2a, 3–7)

1750 "*Cupressus marina altera*" RUMPHIUS: 207, pl. 80, fig. 2.

1758 ?*Gorgonia abies* LINNAEUS: 802.

1758 ?*Gorgonia aenea* LINNAEUS: 802.

1766 ?*Antipathes cupressina* PALLAS: 213.

1786 ?*Antipathes cupressus* ELLIS & SOLANDER: 103.

1788 ?*Antipathes cupressina* – ESPER (Lieferung 1,2 of the Pflanzenthiere 1), pl. 3.

1792 ?*Antipathes cupressina* – ESPER (Pflanzenthiere 2): 143.

1796 **Antipathes paniculata* ESPER (Lieferung 6 of the Fortsetzungen 1), pl. 12.

1797 *Antipathes paniculata* – Esper (Fortsetzungen 1): 184.
1815 ?*Antipathes cupressus* – Lamarck: 474.
1816 ?*Antipathes cupressus* – Lamouroux: 380.
1846 ?*Antipathes cupressus* – Dana: 581.
1857 ?*Antipathes cupressus* – Milne Edwards & Haime: 316.
1858 ?*Antipathes abies* – Gray: 292.
1858 *Antipathes paniculata* – Gray: 294.
1870 non *Arachnopathes paniculata* – Duchassaing: 23.
1889 pars *Antipathes abies* – Brook: 170, pl. 11, fig. 21.
1889 *Antipathes abies* var. *paniculata* – Brook: 171.
1905 *Antipathes abies* – Thomson & Simpson: 97, fig. 4.
1909 *Antipathes abies* var. *paniculata* – Cooper: 43, fig. 9.
1910 *Antipathes abies* – Summers: 279, pl 5, figs. 1 and 6.
1914 pars *Antipathes abies* – van Pesch: 19.
1959 pars *Antipathes abies* – Bayer: 232.
1974 *Antipathes paniculata* – Opresko: 42 and 49.
1991 pars *Antipathes abies* – Grasshoff: 359.

Diagnosis: Corallum monopodial and pinnulate, resulting in bottlebrush appearance. Primary pinnules arranged in 4–6 very irregular rows around circumference of the stem, up to 6 cm long, extending out at nearly right angles to stem. Four to five orders of subpinnules arising primarily from lateral or upper surface of primaries; arranged irregularly, sometimes bilaterial, sometimes uniserial. Spines on pinnules simple, conical and acute or blunt and swollen, and inclined distally to varying degrees. Polypar spines 0.1 to 0.3 mm (from midpoint of base to apex); abpolypar spines 0.07–0.13 mm. Spines arranged in rows extending along length of axis; 5–9 rows visible from one aspect; 10–12 spines per millimeter in each row.

Redescription of the Esper material: The specimen in the Senckenberg-Museum (SMF 5886) is a dry specimen, 22 cm high and 11 cm in diameter across its widest part (Fig. 1). The stem is curved along its length and slightly compressed; at its basal end it is 5 by 7 mm in diameter. The basal plate is missing. The corallum is monopodial, i.e., without distinct branches; however, it is pinnulate. The primary pinnules (or the broken off basal stumps of the pinnules) are present along the entire length of the stem; they extend out in all directions and are extensively subpinnulated, forming quasi-branches (Fig. 2a). They are up to 6 cm long and 2.5 to 3.2 mm in diameter at their base; however, many are not continuous to the outer edges of the corallum. Although they are not uniformly arranged in axial rows, in places they have the appearance of being in 4 or 5 such rows which tend to have a somewhat bilateral arrangement. There are up to 5 primary pinnules per centimeter, counting those on all sides of the stem. Their angle of insertion on the stem is 80–90° and they generally project out horizontally, but can be curved downward as well as somewhat posteriorly on either side of the stem. The primary pinnules possess five or more orders of subpinnules. The pattern of subpinnulation is quite irregular and not consistent from one primary pinnule to the next. The subpinnules often arise from the upper or lateral sides (usually the convex side) of the primary pinnules and they tend to be curved in the same direction as the primary pinnule from which they arise. The distal angle of the secondary pinnules is about

Fig. 1. *Antipathes paniculata* Esper, holotype, SMF 5886; entire corallum, height about 22 cm.

60° and that of the higher order subpinnules 40–60°. The highest order subpinnules can be arranged uniserially with up to 5 per centimeter, or they can be arranged in a somewhat alternate pattern with a very narrow interior angle. None of the pinnules are fused with one another.

The axial spines (Figs. 3–7) are not perfectly uniform in shape, orientation, or arrangement. (Note: The corallum of this specimen has a thick coating of dust and some spines appear worn and degraded, possibly the result of fungal growth over the years). In general, the spines are relatively large, cylindrical, and often appear swollen, especially on the smallest pinnules. At the tips of pinnules where the diameter of the axis (excluding the spines) is approximately 0.1 mm in diameter, the spines are about 0.1 mm tall and about 0.05 mm in width (Fig. 3). Further away from the tip of the pinnules (axial diameter 0.15 to 0.2 mm), the spines become larger (0.13–0.18 mm) and more cylindrical. They can be rather densely crowded and directed distally (Fig. 4a) or more widely spaced (Fig. 4b). On pinnules greater than 0.3 mm in diameter, the spines appear even more cylindrical and slightly more acute, but they are generally not more than 0.2 mm tall (Fig. 5). Large multi-forked spines, up to 0.28 mm tall, are present on some pinnules, especially on those greater than 0.5 mm in diameter (Figs. 6 and 7), but they can also occur on pinnules as small as 0.25 mm in diameter. They are confined to one side of the axis, probably corresponding to

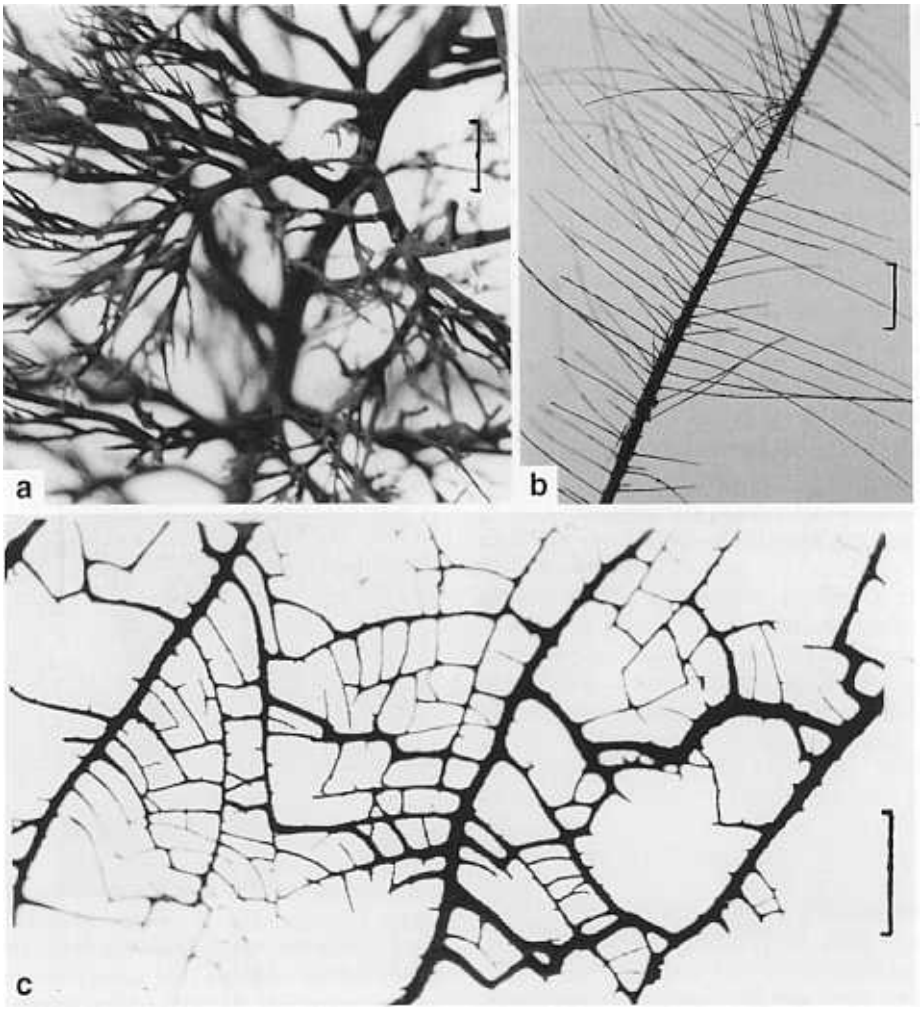

Fig. 2. a) *Antipathes paniculata* Esper, holotype, SMF 5886; close-up view of quasi-branches with subpinnules. b) *Parantipathes larix* (Esper) holotype, SMF 5892; close-up view of pinnules. c) *Aphanipathes reticulata* (Esper), holotype, SMF 5885; close-up view of branchlets. Scale: 1 cm.

the side on which the polyps occur. The spines on the opposite, or abpolypar side of the axis are less than one-half the size of the forked spines. The pinnular spines are arranged in rows along the length of the axis; 5–7 rows are visible in lateral view on pinnules 0.07–0.25 mm in diameter (excluding rows in which spines are only partially visible); and 9 or more rows on pinnules greater than 0.5 mm in diameter. The distance between adjacent spines in each row is usually 0.07–0.11 mm, and there are generally 10–12 spines per millimeter in each row. The central axial canal measures 0.04–0.07 mm. Polyps are not present on the specimen.

Remarks: Esper indicates that he had only one specimen of this species and his description and illustration are in reasonable agreement with the Senckenberg specimen. Esper (1797) describes his specimen as being "some inches larger than shown on the figure. The stem is solid and somewhat compressed, with grooves in its lower part. The wood is as rough and compact as horny material, but has no significant weight; black in colour. Perhaps with age the stems get dissolved out and become spongy, as described by Rumph, because forms of the same species [Gattungen] can be very different in their early growth. The branches irregularly stand off from every part of the stem, forming a dense tuft (*panicula*). They are sinuous [ausgeschweift] and on the branches that are bent downward the twigs only stand on one side, pointing upward."

Esper's illustration shows a monopodial corallum with a curved stem with pseudo-branches standing out on all sides, often curved downward and forming dense tufts with many of the highest order subpinnules arranged uniserially on the upper side of the lower order pinnules. Although the subpinnulation of the specimen in Plate XII is much denser than that in SMF 5886, it is quite likely that some of the smaller, more fragile branchlets were broken off over the years. The uniserial pattern of the higher order pinnules is, however, still evident in many places. Esper (1797) also states that the "whole surface is covered by spiny, densely packed knobs, or very short bristles, which can be identified by touch rather than by sight. They are completely covered by a skinny (cutaneous) layer, which on the stem is thicker than it is on the branches. Because of this coating any roughness is hardly

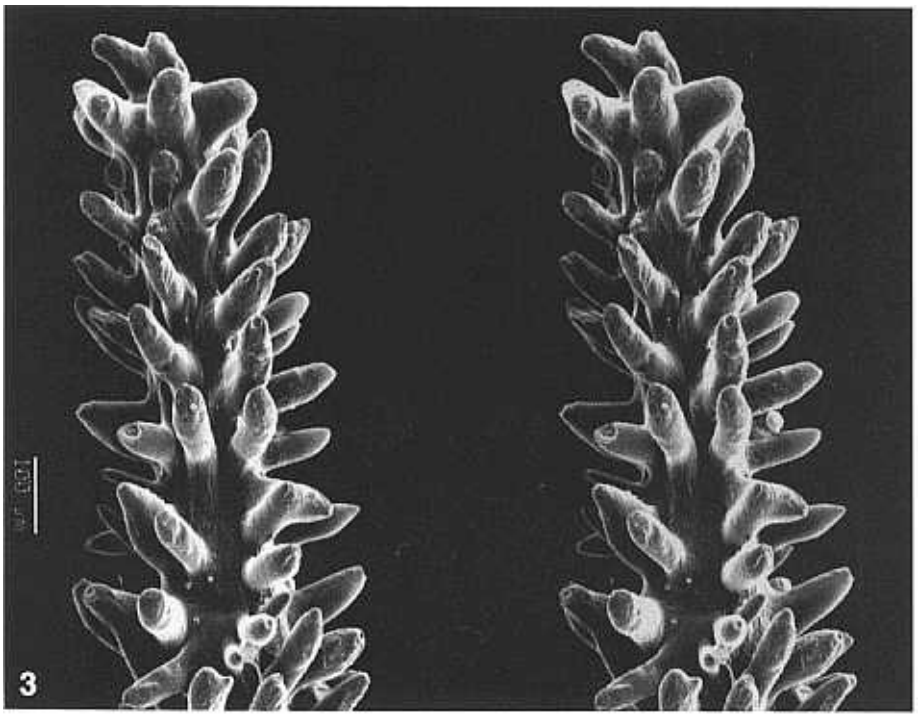

Fig. 3. *Antipathes paniculata* Esper, holotype, SMF 5886; distal end of small subpinnule, axial diameter about 0.12 mm; stereo pair.

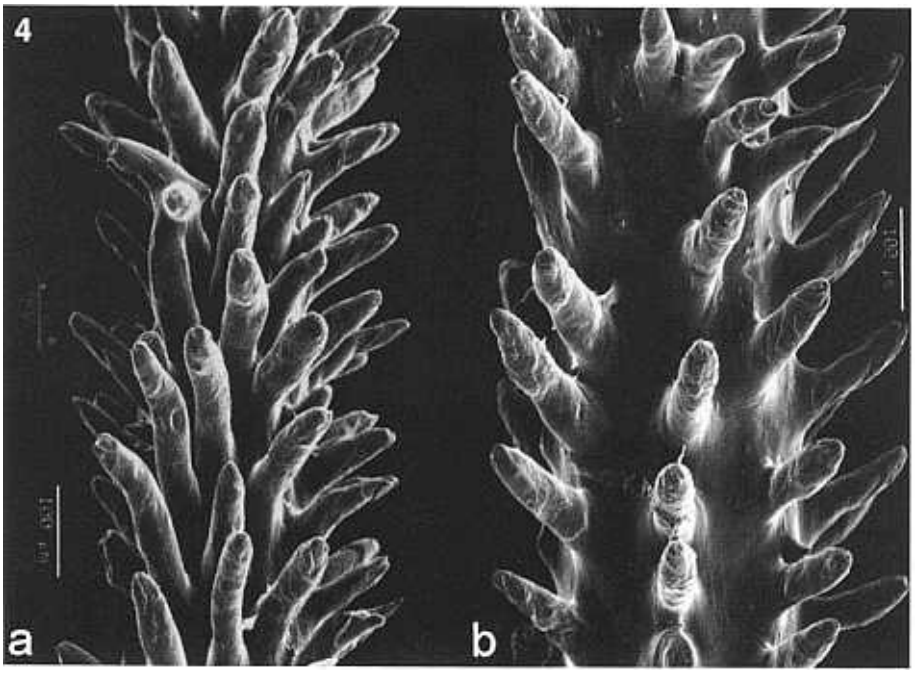

Fig. 4. *Antipathes paniculata* Esper, holotype, SMF 5886. – a) distal section of small pinnule, axial diameter about 0.15 mm. b) midsection of small pinnule, axial diameter about 0.22 mm.

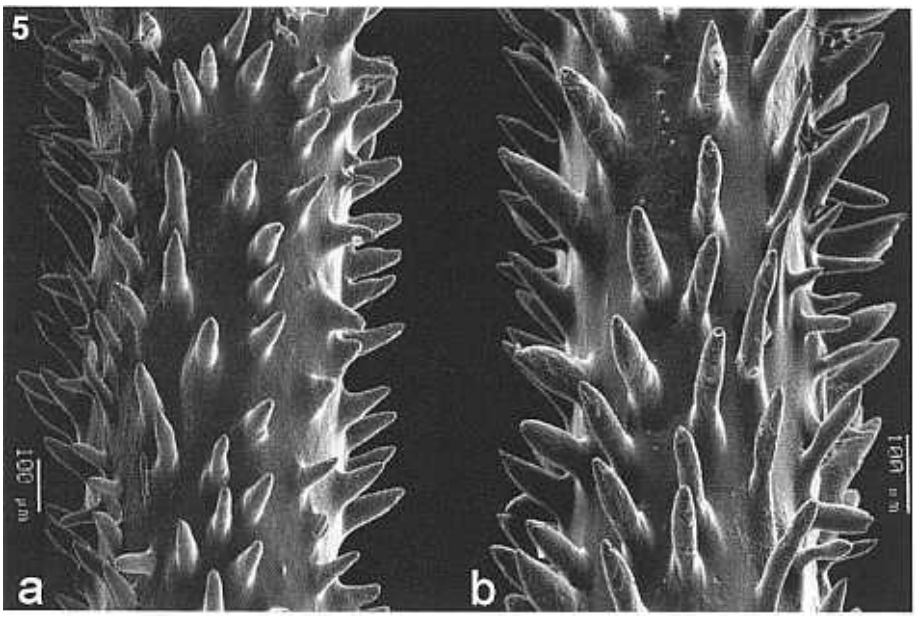

Fig. 5. *Antipathes paniculata* ESPER, holotype, SMF 5886. a) segment of pinnule, axial diameter about 0.32 mm in diameter. b), segment of pinnule, axial diameter about 0.5 mm.

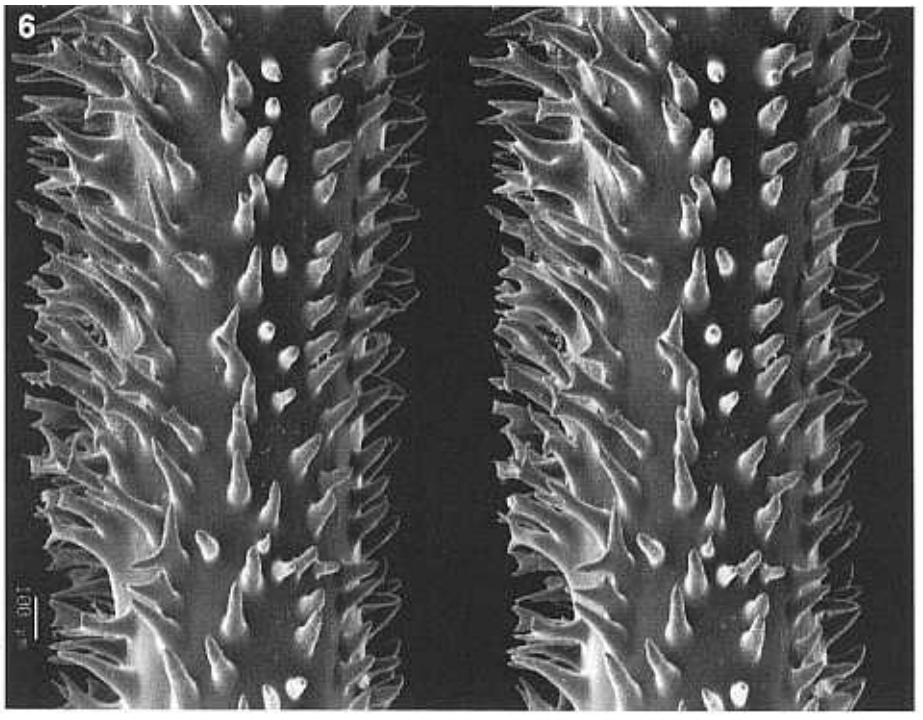

Fig. 6. *Antipathes paniculata* ESPER, holotype, SMF 5886; segment of pinnule with multi-forked spines; stereo pair.

perceptible." Indeed, the spines can be either knobby or bristle-like and they are often very densely crowded, especially on the smaller pinnules.

Comparisons: ESPER (1797) notes that "This spiny coral [*Antipathes paniculata*] very closely resembles *Antipathes cupressina*, which is illustrated on the 3rd plate, and it is likely that Knight PALLAS actually meant this coral [as it is illustrated here]. He [PALLAS] reports that the form *Gorgonia Abies* by LINNÉ may be assigned to his *A. cupressina*, and as represented by the specimen figured on the previously mentioned plate, it appears to

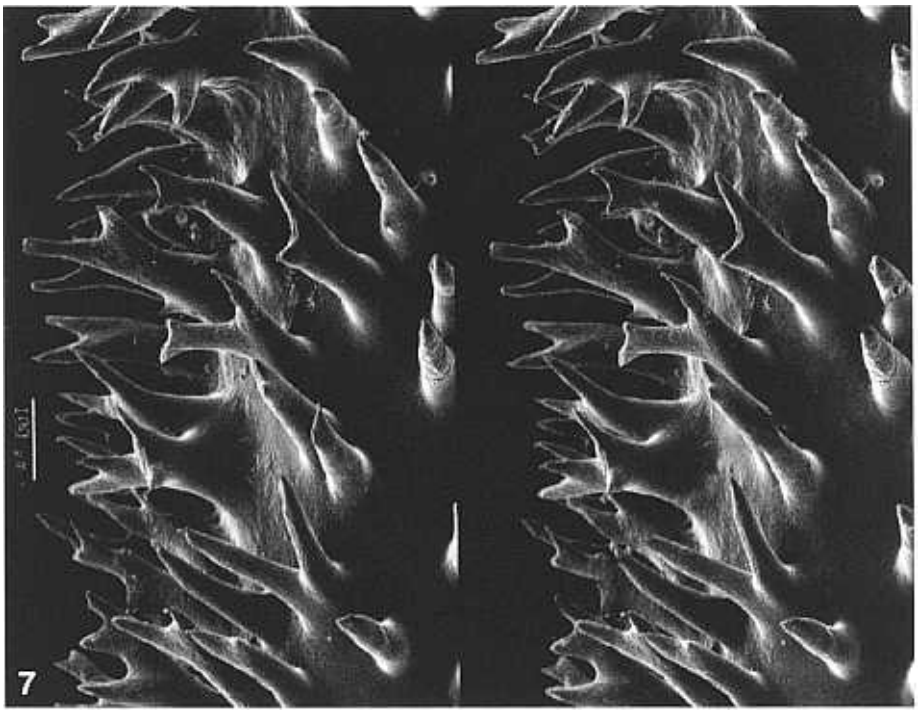

Fig. 7. *Antipathes paniculata* ESPER, holotype, SMF 5886; segment of pinnule with multi-forked spines, enlarged view of Fig. 6; stereo pair.

agree with it in all characters. In addition, he [PALLAS] mentions that RUMPH noted two variations. According to him [RUMPH] the first one is black in colour and covered by a hardly perceptible coating, which is slimy in the living coral. In its growth form the specimen resembles a female cypress, in which, and in addition with other characteristics, it corresponds to the first mentioned species [*A. paniculata*]. His second variation is grey in colour and consists of a spongy substance. It forms a rounded tuft with thinner, softer, and shorter branches. It is reddish brown in colour and in its appearance it resembles a foxtail. Based on this description our herein illustrated coral is very well denoted." ESPER (1797) further notes that "*Antipathes cupressina* is distinguished from this species by having a long, very thin stem, and in the development of shorter nearly pyramidally arranged, widestanding branches. The wood is covered by a hardly perceptible grey coating, embedding spines that are as densely packed, but much more delicate. They correspond to the most delicate bristles and are equal in thickness. The branches are sinuous [ausgeschweift]."

The species described by ESPER (*A. paniculata*) has been considered by most naturalists to be conspecific with *A. abies* (LINNAEUS) and *A. cupressina* PALLAS. However, as noted by ESPER, *Antipathes cupressina* is distinguished from *A. paniculata* by the thinness of the stem and the shorter and more widely spaced branches. BROOK (1889) considered these differences sufficient to recognize ESPER's species as a variety of *A. abies*. As noted by BAYER (1959), *A. abies* has been viewed as being conspecific with another LINNEAN species, *A. aenea*, but it is the latter that was originally associated with the species named "*Cupressus marina*" RUMPHIUS, and it is unclear why *A. abies* was given preference over *A. aenea*. *Antipathes aenea* is also listed before *A. abies* in the 10th edition of the Systema Natura.

Because neither *A. abies* (LINNAEUS), nor *A. cupressina* PALLAS is clearly defined by a detailed description or illustration and because neither is based on a type specimen, the true relationship of these species to *A. paniculata* ESPER cannot be established. It is quite likely, as ESPER notes, that his species can be referred to the first variety of RUMPH's "*Cupressus marina altera*" and that *A. cupressina* PALLAS can be referred to the second. Although it is possible that *A. abies* is only a juvenile form of *A. paniculata*, additional taxonomic studies, including a careful analysis of spine and polyp morphology and size are needed before it can be determined whether the two are conspecific. It is important to note, however, that many of the specimens identified as *A. abies* in the scientific and popular literature very likely refer to *A. paniculata*.

ESPER also compares his species to *Antipathes alopecuroides* ELLIS & SOLANDER 1786 (p. 104, nr. 6, "Foxtail Antipathes", noting that "The description closely agreed with this one [*A. paniculata*], even in the appearance of the grooved lower part of the stem. According to their description, this specimen was brought from South Carolina. It was two feet in length with a flattened basal surface. The stem was a quarter of an inch in thickness, the branches formed a dense, narrow-celled tuft, with a very rough surface. The branches were in the form of a gramineous plant, the foxtail-grass (*Alopecurus* LINNAEUS 1758). The colour of the surface was simply given as greyish." It is unlikely that *A. paniculata* is conspecific with *A. alopecuroides* in that the former species has only been recorded from the Indo-Pacific. The latter spe-

cies was not illustrated by ELLIS & SOLANDER, but from the description, it appears to be related to *A. tanacetum* POURTALES 1880, or some similar species.

Type locality: The specimen belonged to the collection of KLET and was stored in the local university (Erlangen) without any indication of where it had been collected. ESPER (1797) states that according to RUMPH the species is "rarely found, sitting on small rocks in the vicinity of the Uliassar and Bandai Islands" [= probably Saparua Island, East of Ambon, Indonesia; GRASSHOFF, pers. comm.].

Antipathes virgata ESPER 1798

1798 **Antipathes virgata* ESPER (Fortsetzungen 2): 8, pl. 14.
1815 *Antipathes scoparia* LAMARCK: 473.
1816 *Antipathes scoparia* – LAMARCK: 307.
1816 *Antipathes scoparia* – LAMOUROUX: 376.
1846 *Antipathes scoparia* – DANA: 582.
1857 *Antipathes scoparia* – GRAY: 293.
1857 *Antipathes scoparia* – MILNE EDWARDS & HAIME: 319.
1889 *Antipathes virgata* – BROOK: 102, pl. 11, figs. 13–14.
1905 *Antipathes virgata* – ROULE: 78.
1909 *Antipathes virgata* – COOPER: 315, fig. 12.
1909 *Antipathes virgata* – SILBERFELD: 5.
1914 pars *Antipathes dichotoma* PALLAS – VAN PESCH: 52.
1974 *Antipathes virgata* – OPRESKO: 72, figs. 4–5.
1991 *Antipathes virgata* – GRASSHOFF: 362.

Diagnosis: Corallum branched and bushy; branches linear elongate. Spines on branches very crowded. [Note: Because the type specimen is lost, a more complete diagnosis cannot be given unless it is assumed that the specimen described by BROOK is identical to ESPER's species (see Remarks below)].

Remarks: ESPER (1798) states that this species can be "distinguished from any known species by the spreading of its branches and twigs, as well as its growth form. The stem is rounded in outline, black in color, and consists of solid substance, which is typical of these species. The surface is shiny and covered by densely arranged obtuse spines, despite which the surface seems to be smooth; however, by touch a distinct roughness is revealed. The stem expands forming fork-like and widely standing branches that stand off in acute angles. But some of the smaller branches, which can be densely packed, may also originate from the same angle. They lead into thinner twigs, terminating in more delicate prolongations, all of which branch off in the same acute angle, and in high numbers taking a straight upright orientation. Held into the light these thin twigs are transparent and reddish-brown in color. They are covered by densely packed short spines whose forms are only visible in magnification, being arranged in rows of ten or more. As opposed to other species, in this form the spines are not separated from each other but are even more densely developed, forming regular rows. Like others, they too have a transparent yellow color, closely resembling amber."

The illustration given by ESPER shows the lower portion of a bushy corallum, with elongate branches, and strong, distally inclined axial spines. ESPER states that the entire specimen is 1½ feet in height and might even reach a significantly larger size. Furthermore, he mentions that even though the branches are crowded together, they are not fused with each other.

BROOK (1889) identified a specimen from the Persian Gulf as this species, although it is unclear as to whether he was describing ESPER's species. BROOK's specimen was reported to be shrub-like, densely branched, and up to 1.5 m tall, with branchlets in the upper portion of the corallum 15 to 50 cm long and mostly on one side of the lower order branches. The spines were described as short, thick, and subcylindrical, with a smooth blunt apex, a rough granular apex, or with irregular wart-like prominences. In re-describing BROOK's specimen, OPRESKO (1979) reported that the spines on the smallest branchlets were either conical and smooth or papillose, or blunt and rugose. They reached a maximum size of about 0.2 mm, were sometimes slightly longer on one side of the axis, and were arranged in about 12 rows with 20–25 spines/cm in each row. On larger branches (2 mm in diameter) the spines were 0.15–0.17 mm and arranged in 20 or more rows.

In the absence of ESPER's type, it is impossible to determine if the specimens referred to this species by BROOK (1889), ROULE (1905), or COOPER (1909) are identical with the specimen described by ESPER, and it is also questionable whether all three authors are dealing with the same species. ESPER's specimen as well as COOPER's came from the Indian Ocean, BROOK's was collected in the Red Sea, and ROULE's was trawled from 528–1384 m off the Azores. Polyps were described by COOPER as being 2.5 mm long and placed in 4 regular lines around the circumference of the smallest branchlets. Polyps were not described by ESPER, nor are they present in BROOK's specimen. In only a few other species have the polyps been reported to be arranged in multiple rows around the axis. One such specimen identified by HAECKEL (1875) as *Antipathes corticata* LAMARCK 1816, was collected in the Red Sea. The type material of *A. corticata*, which apparently lacked polyps, came from the Indian Ocean. Both the type of *A. corticata* and HAECKEL's specimen were reported to be very sparsely branched, and in this regard they differ from both COOPER's specimen and the ones described by BROOK and ESPER. If ESPER's species name is to be retained, a neotype must be designated and although BROOK's specimen is a likely choice, it would be preferable to have a specimen with polyps. COOPER's specimen would be a good alternative; however, that specimen has not been located. It may have been deposited in a museum in India.

Comparisons: ESPER (1798) states that "Various forms of this yet little known species only differ from each other by the growth form than by any essential characteristics. The substance of the wood as well as the rough or spiny coverage of the stem and branches, respectively, can hardly be used to draw any significant characteristics." And indeed this is the case with species of *Antipathes*, *sensu stricto*. The general morphology of the corallum, as shown in ESPER's illustration, *A. virgata* is not unlike that of a number of species described from the Pacific and/or Indian Oceans including *A. sarothrum* PAX 1932 from Japan, *A. pseudodichotoma* SILBERFELD

1909 from Japan, *A. sarothamnoides* BROOK 1889 from New Hebrides, *A. fruticosa* GRAY 1857 from New Zealand and *A. salicoides* SUMMERS 1910 from Portugese East Africa. The species described by SUMMERS was reported to have multiple rows of polyps and relatively strong spines and may be identical to the specimen identified by COOPER as *A. virgata*. Unfortunately, neither COOPER's specimen nor SUMMERS' type material have been located.

Type locality: The locality is given as the Indian Ocean, and ESPER mentions that it was part of a gift from India.

Antipathes compressa ESPER 1797

1797 **Antipathes compressa* ESPER (Fortsetzungen 1): 186, pl. 13, fig. 1.

1857 *Leiopathes compressa* – MILNE EDWARDS & HAIME: 322.

1889 ?[*Antipathes*] *isidis-plocamos* KLUNZINGER – BROOK: 177.

1991 *Antipathes compressa* – GRASSHOFF: 362.

Diagnosis: Because of the lack of detailed information on the branching pattern of the corallum, and on the size and morphology of the spines and polyps, a diagnosis of the species is not possible.

Remarks: According to ESPER (1797), this species is very similar to *Antipathes glaberrima* ESPER 1792, but with "fundamental differences observed when carefully studied." ESPER reported that the stem had "a convex base, is of the same hardness as *Antipathes glaberrima*, and also consists of layers that are one upon another. The surface shows the same smoothness. The color is black or dark brown, and in places there is a metallic or copper-like polish. But the stem and the branches that spread out at obtuse angles are not rounded as they are in that one [*Antipathes glaberrima*] but are flattened out. One notices relicts of small blunt twigs which might have been elongated by only a little. In the deepening of the wide sides a rough surface occurs which is more noticeable by touch than by vision, and has blunt spines which are almost completely eroded. But on single branches of another specimen which I illustrated in the second and third figure the spines were very elongated and arranged in several rows. They formed cone-like points, being unequal in height, and are arranged in 4 rows or, as seen in other specimens, in more than that. These [spines] one will never notice in the previously mentioned spiny coral, also it [*Antipathes glaberrima*] always has a very curved but never flattened stem nor branches."

The illustration given by ESPER shows a corallum almost devoid of branches. The stem and few main branches are curved and sinuous and not unlike that of *Leiopathes glaberrima*; however, ESPER states that there are the remains of eroded spines on the concave side of some of the branches. Although there are some species of *Leiopathes* HAIME 1849, which unlike *L. glaberrima*, have spines on the larger branches, these species have been reported from relatively deep water (OPRESKO 1998) and it is unlikely that ESPER's specimen would have been one of these. ESPER also illustrates magnified views of branches from a different specimen showing rather strong spines, and in the description it is mentioned that the spines are unequal in height, a characteristic of the genus *Antipathes* or *Aphanipathes*, rather than *Leiopathes*. Therefore, it is possible that ESPER had described two different species under the name *compressa*.

Based on the discussion given by BROOK (1889: 7), GRASSHOFF (1991: 36) considered the species to be a nomen dubium. Because the type specimen is missing and ESPER's description and illustration are too incomplete for identification, it is unlikely that the species will ever be correctly identified. ESPER's description of his specimen as having a metallic polish with flattened branches suggests that he may have been describing a specimen of the zoanthid "Savaglia" (= *Gerardia* LACAZE DUTHIERS 1864) which forms a skeletal axis very similar to that of antipatharians.

Type locality: ESPER states that "the Mediterranean Sea was given as the location, but unreliably." The zoanthid "Savaglia" is also found in the Mediterranean.

Genus *Aphanipathes* BROOK 1889

Type species: *Aphanipathes sarothamnoides* BROOK 1889; designated herewith, following the intention of the author (BROOK 1889: 75, 121).

Diagnosis: Corallum bushy or flabellate, branching sparse and irregular, or dense and bushy, pseudodichotomous or subalternate. Branches straight or curved, simple or pinnulate. Spines conical, elongate, smooth or slightly papillose. Polypar spines longer than abpolypar spines. Spines on the polyp side of the axis equal in size or longer in the area of the polyps. Polyps slightly longer in the transverse than sagittal axis, usually 0.5–1.0 mm in transverse diameter.

Remarks: The genus *Aphanipathes* was established by BROOK for species having small, inconspicuous polyps "often obscured by the elongate spines which project through the peristome of many species, in spirit specimens" (BROOK 1889: 43, 121). Other characters mentioned by BROOK include polyps irregularly distributed, not always in a single row, usually with a marked interval between the zooids; tentacles short and projecting little beyond the peristome; and secondary mesenteries reaching nearly to the base of the coelenteron. It is the feature of the spines projecting through the soft tissue, however, that has been used as the primary diagnostic character of the genus, even though there is some question as to what extent this phenomenon is caused by the contraction of the soft tissue upon exposure to air and/or preservation in alcohol. Furthermore, because many species have been described on the basis of skeletal material only, they have often been referred to *Aphanipathes* simply on the basis of the size of the spines and not on evidence of the spines piercing the soft tissues. BROOK states that the spines can be equal in size or longer in the polyp areas, and there are some species currently referred to this genus in which the hypostomal spines are reduced in size or even absent. Thus, species in this genus appear to segregate themselves into three natural groupings; those with subequal polypar spines, those with anisomorphic polypar and unmodified hypostomal spines, and those with anisomorphic polypar spines and atrophied hypostomal spines.

In the "Siboga" monograph, VAN PESCH (1914) treated *Aphanipathes* as a subgenus of *Antipathes*; however, later workers have not followed this taxonomic approach, and have instead retained *Aphanipathes* as a distinct genus (PAX 1918, GRAVIER 1921, PAX 1932, OPRESKO 1972, GRASSHOFF 1985, PAX 1987). This is the approach followed here, but, as noted in the discussion of the genus *Antipathes*, a future taxonomic revision of the order is likely to change many of the current assignments of species to the genus.

Aphanipathes reticulata (ESPER 1795)

(Figs. 2c, 8–11)

1795 **Antipathes reticulata* ESPER (Lieferung 3 of the Fortsetzungen 1), pl. 11.

1797 *Antipathes reticulata* – ESPER (Fortsetzungen 1): 183.

1846 *Antipathes reticulata* – DANA: 579.

1857 *Rhipidipathes reticulata* – MILNE EDWARDS & HAIME: 321.

1858 non *Antipathes reticulata* – GRAY: 291.

1880 non *Antipathes reticulata* – DE POURTALÈS, fig. 22.

1889 *Antipathella reticulata* – BROOK: 117, pl 12, fig. 5.

1914 *Aphanipathes reticulata* VAN PESCH: 90.

1955 *Antipathes reticulata* – PAX & MÜLLER: 108.

1991 *Antipathes reticulata* – GRASSHOFF: 362.

Diagnosis: Corallum flabellate, branched to 10th order or more with extensive anastomosing among branches and branchlets. Major branches distinct, straight or somewhat sinuous. Highest order, unbranched branchlets arranged bilaterally, irregularly alternate or subopposite; straight or slightly curved upward; typically 5–7 mm in length and spaced 1–1.5 mm apart, with 7–10 branchlets per centimeter, on both sides of axis. Spines long, needle-like, acute, sparingly tuberculate and anisomorphic. Polypar spines larger than abpolypar spines, up to 0.31 mm from midpoint of base to apex; abpolypar spines 0.11–0.14 mm. Polypar spines slightly larger on periphery of polyps; hypostomal spines sometimes reduced to 0.03–0.04 mm. Polypar spines with scattered low, rounded tubercles along sides; tubercles sometimes arranged in ring just below apex. Spines on branchlets spaced 0.16–0.39 mm apart (4–5 per millimeter) and arranged in 5–6 rows as seen from one side. Polyps estimated to be up to 0.63 mm in transverse diameter (from proximal side of proximal lateral tentacles to distal side of distal lateral tentacles). Interpolypar space estimated to be 0.36–0.45 mm, with 10–11 polyps per centimeter.

Redescription of the ESPER material: The specimen in the Senckenberg-Museum (SMF 5885, Fig. 8) is approximately 21 cm high and about 13 cm wide, and has two trunks arising from the holdfast; the larger of these has a diameter of about 6 mm just above the basal plate. ESPER notes that the specimen was nearly twice as large as it was possible to illustrate. The general branching of the corallum is flabellate, in a single plane, with the primary branches distinctly thicker than the numerous smaller branchlets which arise in a bilateral, but very irregular fashion. The branchlets are straight or slightly curved upward (towards the branch from which they arise) and they are usually not more than 5–7 mm in length. The branchlets are spaced at varying intervals along the branches, but on average there are usually 7–10 branchlets per centimeter (on both sides of a branch). There are numerous cross fusions and anastomosing of branchlets with those of adjacent branches giving the corallum a distinct reticulate appearance (Fig. 2c). The central canal of the branchlets is about 0.07 mm in diameter.

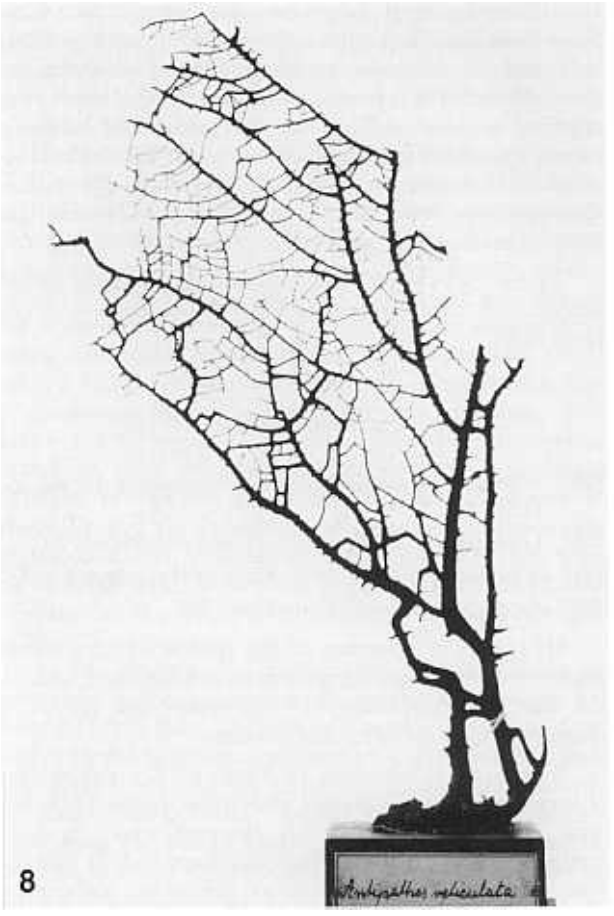

Fig. 8. *Aphanipathes reticulata* (ESPER), holotype, SMF 5885; entire corallum, height about 21 cm.

The spines on the smallest branchlets of the corallum are anisomorphic, with the largest ones occurring on the outer edges of the polyps; slightly smaller ones in the interpolypar areas, and still smaller ones on the abpolypar side of the axis (Fig. 9). In places the hypostomal spines are extremely reduced. All but the hypostomal spines have a distinct accicular or needle-like appearance, with the largest sometimes appearing crooked or bent. The largest polypar spines are up to 0.31 mm (as measured from middle of base to apex), but only 0.03–0.04 mm in diameter at their midpoint; the abpolypar spines are 0.11–0.14 mm tall, and the hypostomal spines can be as small as 0.03 mm. The polypar spines stand out at right angles to the axis or are slightly inclined distally, and have a number of small, rounded, distally inclined tubercles on their surface (Fig. 10). The tubercles are scattered irregularly on the upper half of the spines and they are in some cases arranged in a ring just below apex of the spine

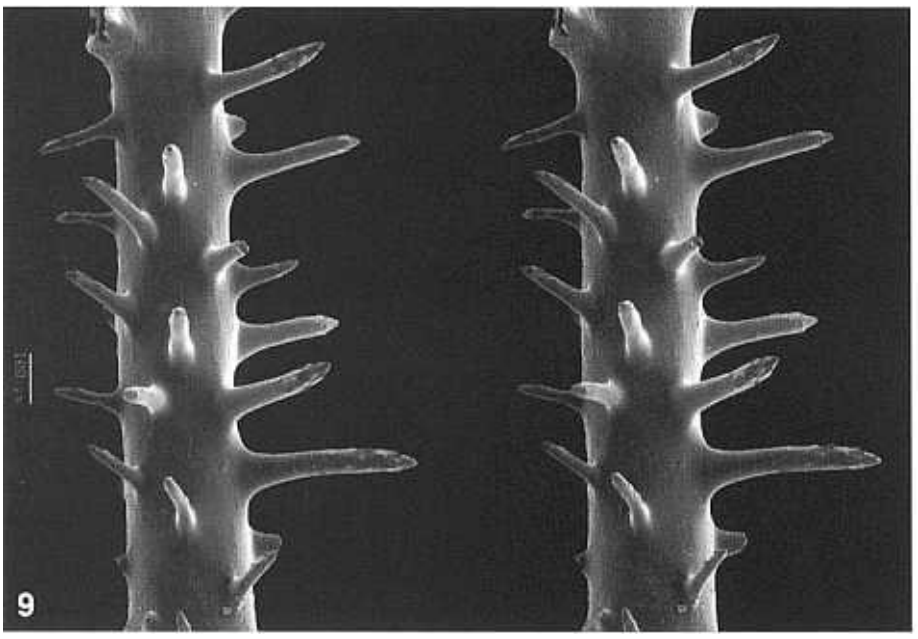

Fig. 9. *Aphanipathes reticulata* (Esper), holotype, SMF 5885; segment of small branchlet, stereo pair.

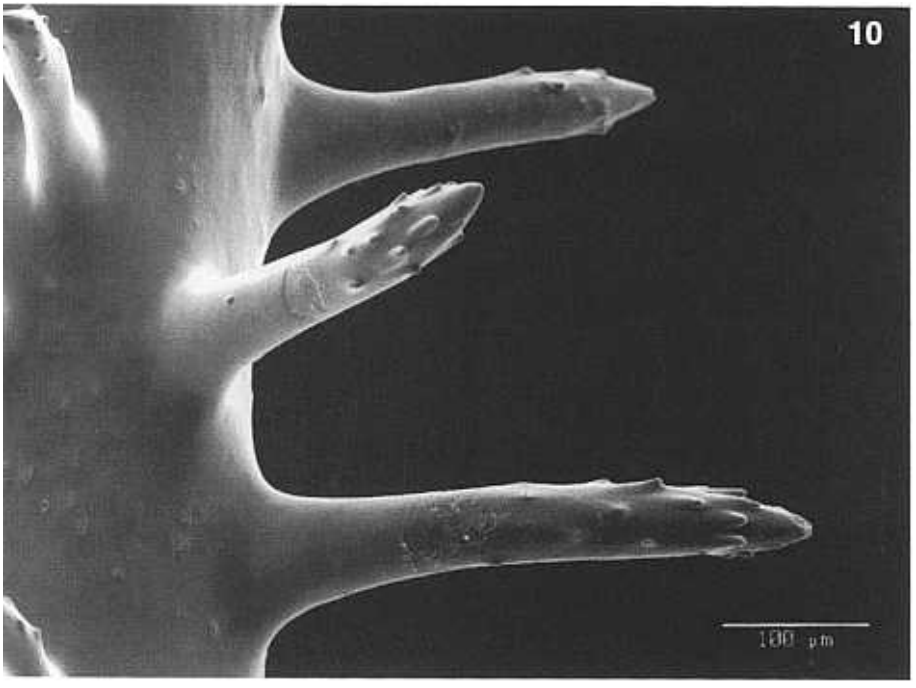

Fig. 10. *Aphanipathes reticulata* (Esper), holotype, SMF 5885; spines with small papillae near apex.

(Fig. 10). The spines on the larger branchlets (Fig. 11) are not as distinctively anisomorphic as those on the smallest branchlets. They are subequal in size, and about 0.25 mm tall. On small and large branchlets the spines are arranged in varying degrees of regularity in 4–6 rows (as seen in lateral view, and excluding those rows in which the base of the spines is not visible) The spacing of the spines within these rows is also very variable, from 0.16–0.39 mm. On average there are 4–5 spines per millimeter in each row.

Remarks: Esper's description is as follows: "The specimen circumscribes a wide plane sheet which, according to the fragments that are found in the vicinity, may have been of a size four times larger than shown in the

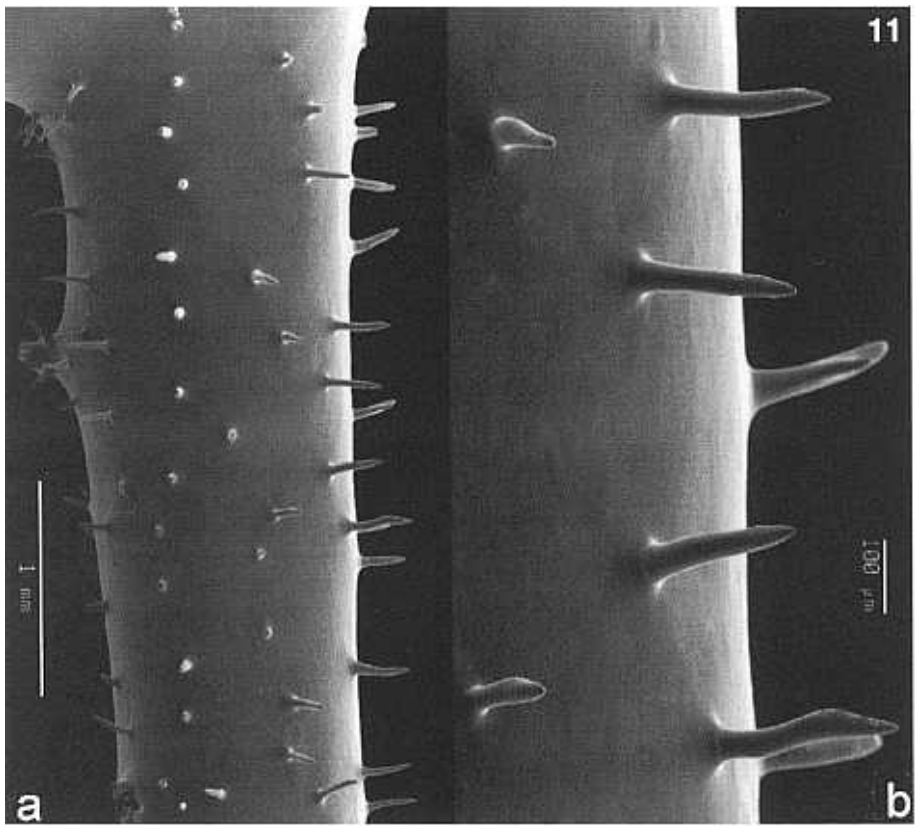

Fig. 11. *Aphanipathes reticulata* (Esper), holotype, SMF 5885; a) spines on higher order branchlet. b) enlarged view of same part of branchlet.

figure. The stems draw through in variable directions; the twigs branch off in angles of every kind. Their distance as well as their joining with the opposing ones is just as variable. The branches are developed in several orders, generally arranged close together, and evenly spaced. They are garnished by small setaceous twigs, which according to this specimen are not always fused completely with the neighboring ones. The wood is very stiff, solid, and fragile. The stems and thicker branches are black-brownish in colour; the twigs are slightly transparent, dark yellow-brownish in colour. The whole specimen is covered by densely packed, blunt, and stiff bristles, which is clearly shown in Figure 2, which represents a close-up view of one of the retiform twigs. These bristles can be bulby or acute, and despite their small size they are very variable in height. In the figures presented by Morison, which in general show very reduced images of the specimens, this spiny coral is introduced as having more wide-standing than reticulated branches, that are arranged in a plane sheet."

Grasshoff (1991) notes that it is likely that the specimen in the Senckenberg-Museum (SMF 5885) is part of the holotype described by Esper. Unfortunately, the illustration given by Esper is not of the entire corallum, but only of the upper part; therefore, the distinct double trunk described above for SMF 5885 is not illustrated by Esper, nor is it described in the text. Furthermore, Esper describes the type as having "short setaceous twigs ... not always completely fused with the neighboring ones," and Esper's Plate 11 does indeed show a specimen with very dense branching, but in which many of the smallest endbranchlets are free. This is somewhat in contrast to the branching pattern of SMF 5885 which is not as dense, but in which many of the smallest branchlets are anastomosing. It is possible, however, that many of the free endbranchlets have been broken off over the years. The most compelling argument for recognizing SMF 5885 as Esper's type is the illustration of the spines which shows that they can be as large as the diameter of the branchlets and are described by Esper as being very variable in height. In the case of SMF 5885, the polypar spines are more than 0.20 mm on branchlets of a similar diameter and are distinctly anisomorphic. SMF 5885 is sufficiently similar to Esper's description and illustration that there is justification for recognizing it as the type of the species.

Comparisons: Esper points out that his species "seems to unite two forms at once ... a variety forming a roomy grating lattice that is larger than one foot in height, and a smaller image that is only half a foot in height, consisting of numerous wide-standing branches."

This species appears to be identical to the specimen described by van Pesch (1914) as a new species under the name *Aphanipathes reticulata*. Only a small fragment of van Pesch's type is still in existence. The specimen was described as being flabellate with anisomorphic polypar spines reaching a maximum size of 0.27 mm, about the same as those in *A. reticulata* Esper (maximum 0.31 mm).

Based on VAN PESCH's description and illustration, it would appear that the size and density of the smallest branchlets are also similar. Furthermore, in both species the larger polypar spines are to a slight degree tuberculate, i.e., with small knobs on their surface, and many of the largest polypar spines are crooked or sinuous.

A. reticulata (ESPER) resembles *Aphanipathes colombiana* OPRESKO & Sanchez 1997. Although the spines of both species reach about the same maximum size of 0.3 mm, in *A.* colombiana, the polypar spines are not tuberculate, and only a few appear crooked or sinuous. Another species that is morphologically similar to *A. reticulata* is the Caribbean species *Aphanipathes thyoides* (POURTALÉS 1880; see OPRESKO 1972 for illustration and description). In *A. thyoides*, the corallum is flabellate, but anastomosing branchlets are not common. The spines are smooth and acicular, up to 0.6 mm tall, larger in the area of the polyps, and extremely reduced or absent in the hypostomal region of the polyps.

Type locality: According to ESPER, "localities are not given, but without any doubt they are the East Indian Oceans".

Genus *Parantipathes* BROOK 1889

Type species: *Antipathes larix* ESPER 1790, by original designation (BROOK 1889: 142).

Diagnosis: Corallum monopodial or very sparsely branched, and pinnulate. Pinnules arranged in vertical rows along the length of stem and branches. Pinnules also arranged alternately in groups of three, with pinnules in each group at nearly same height or offset in semispiral pattern. Spines simple, smooth, acute, triangular to conical. Polyps transversely elongated, 1.5 to 2 .5 mm in diameter from proximal side of proximal lateral tentacles to distal side of distal lateral tentacles.

Remarks: The genus *Parantipathes* was established by BROOK (1889) in the subfamily Antipathinae to accommodate species with transversely elongated polyps, but in which the polyps were not subdivided by peristomal folds, the character defining genera in BROOK's subfamily Schizopathinae.

Parantipathes larix (ESPER 1790)

(Figs. 2b, 12–13)

1790 **Antipathes larix* ESPER (Lieferung 5 of the Pflanzenthiere 1), pl. 4.
1792 *Antipathes larix* – ESPER (Pflanzenthiere 2): 147.
1815 *Antipathes larix* – LAMARCK: 474.
1816 *Antipathes larix* – LAMARCK: 308.
1816 *Antipathes larix* – LAMOUROUX: 374.
1821 *Antipathes larix* – LAMOUROUX: 70.
1826 *Antipathes larix* – RISSO: 330.
1834 *Antipathes larix* – DE BLAINVILLE: 551.
1846 *Antipathes larix* – DANA: 577.
1857 *Antipathes larix* – MILNE EDWARDS & HAIME: 315.
1858 *Antipathes larix* – GRAY: 292.
1860 ?*Antipathes larix* – DUCHASSAING & MICHELOTTI: 56.
1865 *Antipathes larix* – LACAZE-DUTHIERS: 49.
1870 ?*Antipathes larix* – DUCHASSAING: 22.
1878 *Antipathes larix* – VON KOCH: 74–78.
1889 *Parantipathes larix* – BROOK: 142–143, pl. 12, fig. 20, pl. 13, fig. 2, pl. 15, fig. 2.
1896 *Parantipathes larix* – ROULE: 313.
1905 *Parantipathes larix* – ROULE: 75.
1907 *Parantipathes larix* – HICKSON: 10.
1914 ?*Parantipathes larix* – VAN PESCH: 102–103.
1918a *Parantipathes larix* – GRAVIER: 1.
1918b *Parantipathes larix* – GRAVIER: 236–238, pl. 12, fig. 1.
1921 *Parantipathes larix* – GRAVIER: 16, pl. 1, figs. 6–8.
1955 *Parantipathes larix* – PAX & MÜLLER: 108.
1991 *Parantipathes larix* – GRASSHOFF: 360.

Diagnosis: Corallum monopodial or very sparsely branched, and pinnulate. Pinnules simple, extending out at nearly right angles to direction of stem and branches, and arranged in up to 6 axial rows. Rows of pinnules spaced evenly around entire axial circumference or arranged bilaterally, with three rows on each side. Pinnules arranged alternately in groups of three, with pinnules in each group at nearly the same height or offset in semispiral pattern. Spines simple, smooth, acute, triangular, at right angles to stem or hooked distally; polypar spines up to 0.11 mm from center of base to apex; apolypar spines smaller than polypar spines, often only 0.03–0.04 mm. Spines arranged in axial rows; 3–4 rows visible in lateral view, with 4–4.5 spines per millimeter in each row. Polyps transversely elongated; transverse diameter 2–2.5 mm (from proximal edge of proximal lateral tentacles to distal edge of distal lateral tentacles). Polyps arranged uniserially on upper side of pinnules, facing towards the distal end of the stem or branches.

Redescription of the ESPER material: The specimen in the Senckenberg-Museum (SMF 5892) is a dry colony without a basal plate (Fig. 12). It is about 60 cm tall and has a small branch originating 9 cm from the top of the corallum. ESPER states that the species may reach 2 to 3 feet in height and that his illustrated specimen is only one-half the natural size. In the Senckenberg specimen the lower half of the stem is compressed such that at its basal end the diameter is 3 mm by 4 mm. Pinnules, or the stumps of pinnules, are present along the entire length of the stem; they are in distinct rows, with each row defining a vertical plane (Fig. 2b). On the lower part of the corallum there are six rows of pinnules; higher up there are only 4 rows. The pinnules are also arranged in alternating groups along the sides of the stem. The members of these groups (two or three pinnules in each) arise from very near the same height on the stem (distance apart about 0.3 mm). The members of each group do not follow a clearly defined semispiral pattern. The groups of pinnules are 3–3.5 mm apart on each side of the stem, such that there are 4 groups per centimeter on one side of the stem and 3 groups per centimeter on the opposite side, for a total of 7 groups containing 21 pinnules along one centimeter of stem.

The pinnules extend out at almost right angles to the stem (distal angle about 90°). The pinnules are all broken off at their distal end. The maximum length of the incomplete pinnules is 6 cm, and the maximum basal diameter is 0.25–0.3 mm.

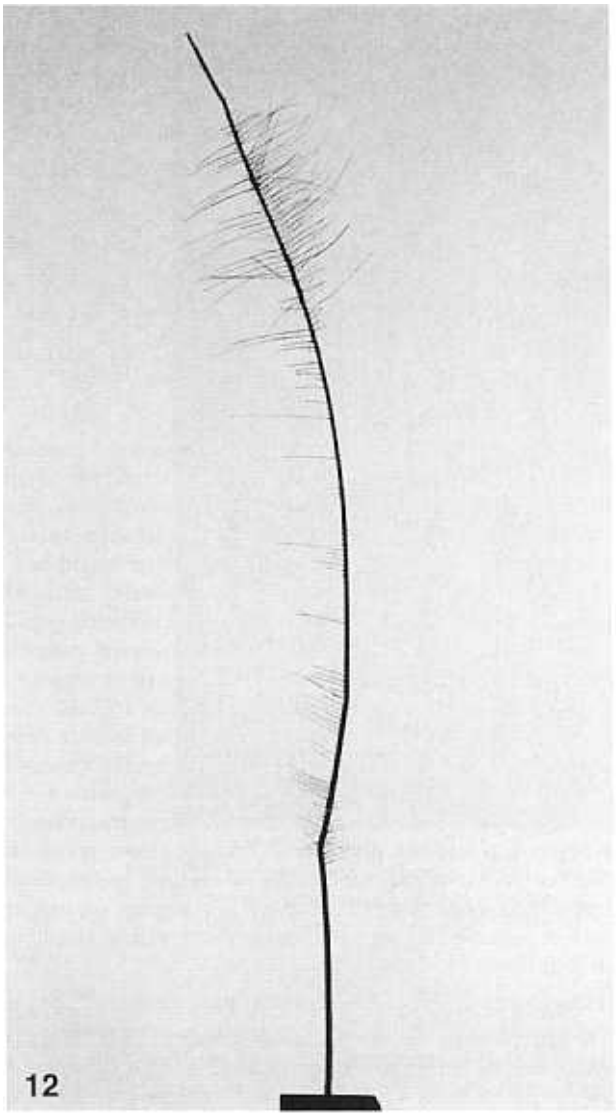

Fig. 12. *Parantipathes larix* (Esper), holotype, SMF 5892; entire corallum, height about 60 cm.

The axial spines (Fig. 13) are simple, smooth, acute, and triangular to horn-shaped in lateral view. The largest spines occur on the upper or distal side of the horizontally extending pinnule. Theses spines, which are assumed to the polypar spines, are up to 0.11 mm tall (as measured from the midpoint of the base to the apex). The abpolypar spines are usually smaller than the polypar spines, and they can be as small as 0.3–0.04 mm. The pinnular spines are arranged in axial rows, 3–4 of which are visible in lateral view (excluding rows in which the spines are only partially visible). The distance between adjacent spines in each row is very variable (0.27–0.52 mm). On average, there are usually 4–4.5 spines per millimeter in each row, but sometimes there can be as few as 3 per millimeter.

The remains of polyps were found on parts of the specimen on the upper side of the pinnules. In one case it was estimated that the distance between two adjacent pairs of tentacles was 1.1 mm. The transverse diameter of that particular polyp was estimated to be about 2.2 mm.

Remarks: One of the earliest pre-Linnaean descriptions of an antipatharian coral that can be identified with a described species appeared in Pona's 1617 work "Monte Baldo descritto ...". Pona's illustration, which is reproduced by Pax (1940: 210) although stylized, accurately depicts the species which Esper named *Antipathes larix*.

The specimen in the Senckenberg-Museum collection is not identical to the specimen illustrated in the Pflanzenthiere (1790, Plate 4). Esper states that in addition to the illustrated specimen which he received from Prof. Hermann (the locality for which was not mentioned), he also had in his possession several larger specimens collected near Naples. The specimen illustrated here (Fig. 12) is likely one of those other specimens. It is probably the only specimen identified by Esper that is still in existence.

Esper's description of the species is as follows: "The basal part is elevated in a cone shaped, with a flattened circumference. From the basal surface one, or rarely several, simple straight stems arise, tapering upward. The stems reach up to about two or three feet in length, with a diameter of two or three twelfths of an inch, on average. The stems are rounded in outline, have a completely smooth surface, and are brownish-black in colour. The wood itself is solid and brittle, dark and shiny black internally. Only one specimen had a bipartite stem. The twigs are as thick as horsehair and stand rectangular to the stem, becoming shorter toward the upper end of the specimen, giving it a pyramidal appearance. In general, the twigs are arranged in two rows lying opposite to each other, but toward the upper part of the stem they tend to form a tuft, which I also noticed in some entire stems. The largest twigs are four to five inches in length, equal in thickness. They are rounded in outline, showing a transparent brownish-yellow colour in magnification. They are covered with very small, wide-standing spines, which appear to be transparent and cone-shaped in high magnification. In places relicts of the jelly coating are present. Now and then these delicate twigs are covered by small leaf-like [batterförmigen: possibly a misprint and meant to be blätterförmigen] dark brown bodies, which may also occur as irregularly shaped clusters, that form a viscous gel when dissolved in water."

Esper's description and illustration are sufficiently detailed to leave no question as to the identity of this species. In particular, the description of the pinnules as being simple, up to 5 inches long (10–12 cm), and arranged bilaterally on the lower part of the corallum and in tufts on the upper part of the corallum is very characteristic. A very extensive species description is also given by Brook (1889). Brook notes that the pinnules in each bilateral grouping can be arranged in a semispiral pattern, a condition which is not clearly defined in the type. Esper notes that the largest specimens he examined were 2–3 feet in length; Brook (1889) describes a specimen 1.3 m long with pinnules 12 cm in length and another 0.5 m long with pinnules only 3.5 cm in length. Further study is needed to determine whether Mediterranean specimens with shorter pinnules are indeed *P. larix* or whether they represent a separate species.

Comparisons: According to Esper, "This species seems to closely correspond to *Antipathes pennacea*

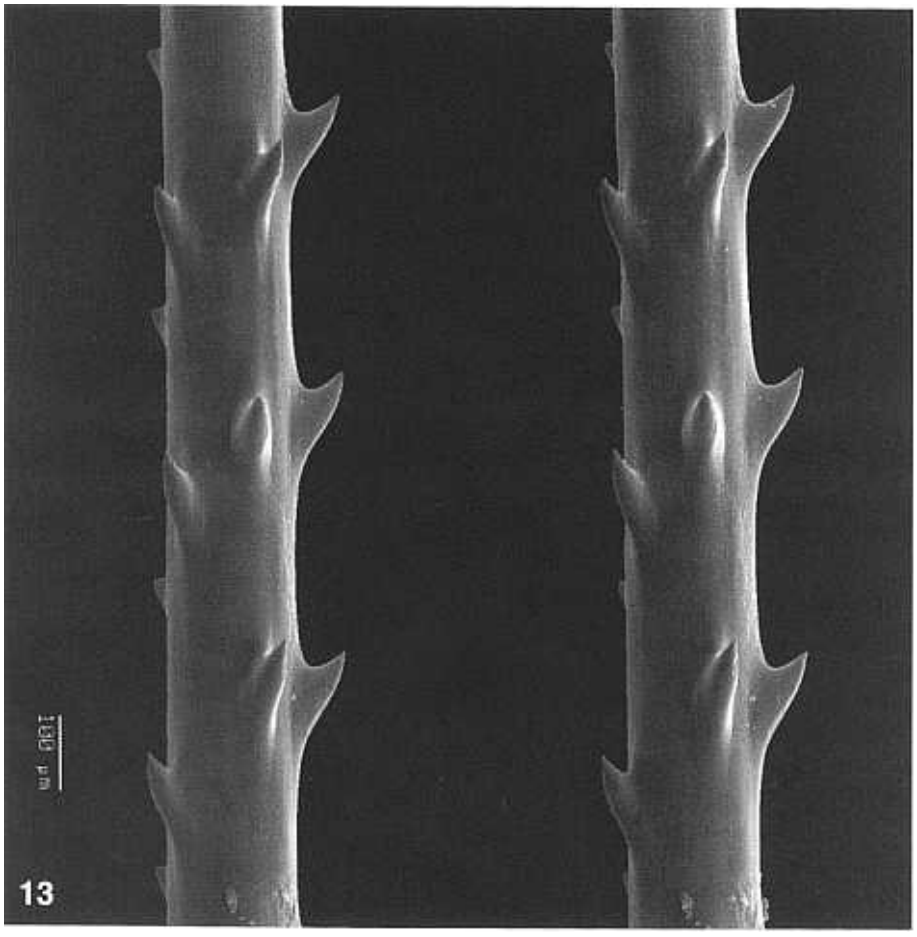

Fig. 13. *Parantipathes larix* (ESPER), holotype, SMF 5892; segment of pinnule, stereo pair.

PALLAS, but is distinguished from it by the lack of a soft woolly covering, a characteristic which does not connect it to this form, unless a variable nature applies, yet in its younger stages it resembles a feather." ESPER further states that *A. pennacea* PALLAS 1766 is closely related to *A. subpinnata* ELLIS & SOLANDER 1786. In *A. pennacea*, the pinnules are arranged pinnately and never in more than two rows, and in *A. subpinnata* they are arranged very irregularly in four rows. Neither species is affiliated with the genus *Parantipathes*.

Parantipathes larix (ESPER) is related to *P. tetrasticha* (DE POURTALÈS 1868) and *P. helicosticha* (OPRESKO 1999). The three species are similar in general appearance of the corallum, but differ in the length or number of pinnules or in the size of the spines or polyps. *P. larix* has a maximum of 6 rows of pinnules and, according to BROOK (1889), the pinnules can be as much as 12 cm in length. In the specimen described here the pinnules are a minimum of 6 cm long and ESPER reported that the largest were 4–5 inches (10–12 cm) long. In *P. tetrasticha*, there are up to 8 rows of pinnules and the pinnules are only 4 cm in length. In *P. helicosticha* there are usually 6–8 rows (maximum of 10), and the pinnules are rarely more than 2 cm in length. The polypar spines of *P. larix* are smaller than those in *P. helicosticha* (0.11 mm vs 0.20 mm), but slightly larger than those of *P. tetrasticha* (0.04–0.08 mm). The polyps of *P. larix* are about 2.0 mm in transverse diameter whereas those in *P. helicosticha* are usually 1.6–1.8 mm, and those in *P. tetrasticha* are up to 2.5 mm

Type locality: ESPER (1792) does not indicate where his illustrated specimen was collected, however, he states that the larger specimens that were given to him were found in the "ocean near Naples." Therefore, the Bay of Naples must be considered the type locality. The species is known only from the Mediterranean and eastern Atlantic. Although it has also been reported from the Indo-Pacific by VAN PESCH (1914), that specimen appears to more closely resemble *P. helicosticha* than *P. larix*.

Family Leiopathidae HAECKEL 896 (emended)

Diagnosis: Polyps with six primary and six secondary mesenteries. Primary (pm) and secondary mesenteries (sm) complete, attached to both inner wall of oral cone and actinopharynx. Secondary mesenteries located between transverse primary mesenteries (tpm) and sagittal primary mesenteries (spm); two on one side and four on opposite side of transverse axis, with one-half of each complement occurring on each side of sagittal axis; clockwise pattern described by sequence tpm–sm–spm–spm–

sm–tpm–sm–sm–spm–spm–sm–sm. New polyps developing from coenenchymal surface between older polyps, as well as at distal end of branchlets.

Remarks: In 1896 SCHULTZE proposed a reclassification of the *Antipatharia* based on the number of mesenteries in the polyps. The family Antipathidae was divided into three subfamilies, the Dodekamerota with 12 mesenteries, the Dekamerota with 10 mesenteries, and the Hexamerota with six mesenteries. The Dodekamerota contained the single genus *Leiopathes*. HAECKEL (1896, as cited in CARLGREN 1908) was the first naturalist to treat the Dodekamerota as a suborder of the *Antipatharia* and to elevate *Leiopathes* to the family rank using the name "Liopathida". This taxon, with the correctly emended name Leiopathidae, was subsequently recognized by BOURNE (1905), ROULE (1905), and HICKSON (1906). However, in his study of the *Antipatharia* of the "Siboga" Expedition VAN PESCH (1914) discovered a species of *Cirrhipathes* (*C. contorta*) whose polyps also possessed six secondary mesenteries. This led VAN PESCH to conclude that the number of secondary mesenteries was not as significant a taxonomic character as SCHULTZE had assumed. He therefore created a new taxon, the "Heterotaeniales" to contain both the Dekamerota and the Dodekamerota. The "Heterotaeniales" was treated by VAN PESCH as a subtribe of the Antipathidae and included all species possessing both primary and secondary mesenteries, regardless of the number. In the last major revision of the order, PAX (1918) renamed the "Heterotaeniales" the "Pleiomerota", and elevated the taxon to the rank equivalent to superfamily. Within the Pleiomerota, PAX placed the families Antipathidae and Schizopathidae. *Leiopathes* was included in the Antipathidae (synonomized with *Antipathes*). The submergence of the "Dodekamerota" by VAN PESCH (1914) was based solely on his finding that *C. contorta* had six secondary mesenteries. However, VAN PESCH (1914) states that the additional fifth and sixth secondary mesenteries in *C. contorta* are incomplete, meaning that they extend from the body wall but do not reach to the actinopharynx. In contrast, in *Leiopathes* all the secondary mesenteries are complete. Furthermore, according to VAN PESCH, the two incomplete mesenteries in *C. contorta* do not reach to the upper end of the oral cone nor do they occupy the same relative position as those in *Leiopathes*. In *C. contorta* they are located between the anterior secondary mesenteries and the primary sagittal mesenteries (VAN PESCH 1914), whereas in *Leiopathes* they occur between the anterior secondaries and the primary transverse ones (BROOK 1889). These differences indicate that the two incomplete mesenteries in *C. contorta* are not homologous to those in *Leiopathes*. Consequently, *Leiopathes* can be viewed as a distinct and homogenous group meriting recognition at the family level (OPRESKO 1998).

Genus *Leiopathes* HAIME 1849

Type species: *Antipathes glaberrima* ESPER 1792, by original designation (HAIME 1849: 224).

Diagnosis: Corallum irregularly sympodial; branching multi-directional or flabellate. Branchlets arranged irregularly; loosely bilateral or uniserial; pinnules not present. Spines poorly developed; small, simple, smooth surfaced; conical, deltoid, or hemispherical in shape; reduced in size or absent on larger branches and stem. Polyps very variable in size and spacing; equally wide in sagittal and transverse diameters, or slightly longer along sagittal axis; uniserially arranged on smallest branches, irregularly distributed on all sides of axis on larger branches and stem.

Remarks: The genus name *Leiopathes* was first used by GRAY in 1840 in a listing of the collections of the British Museum of Natural History; however, the name was not accompanied by a description, illustration or reference to a previously described species; therefore, it must be considered a *nomen nudum*. The name appeared in subsequent editions of the Synopsis of the British Museum, but also without a designated type species (GRAY 1842). There is no evidence that GRAY published a detailed description of *Leiopathes* until 1857. However, in 1849 HAIME published a description of *Leiopathes lamarcki* and in that publication he specifically states that the type of *Leiopathes* is ESPER's species *Antipathes glaberrima*. Even though HAIME refers to *Leiopathes* as GRAY's genus, HAIME must be considered the author of *Leiopathes*. In 1857 GRAY reported that the species he had previously described in 1832 (as *Antipathes dichotoma* PALLAS 1766) "has been separated from others in the genus because the surface of the axis is smooth and not covered with a number of minute, uniform cylindrical spines like the true *Antipathes*" (GRAY 1857). In another paper appearing in the next year, GRAY defines the genus as follows: "Axis smooth, polished, branched, forked. Bark soft, deciduous, deliquescent, sometimes forming (when dry) smooth, transparent masses at the fork of the branches" (GRAY 1858). It is in this second publication that GRAY places *Antipathes glaberrima* ESPER in the new genus, and he further suggests that *Antipathes dichotoma* PALLAS might be synonymous with *A. glaberrima*. Observations made by LACAZE DUTHIERS (1865) revealed that *L. glaberrima* possessed axial spines. Even though these spines are restricted to the smallest branchlets, their presence essentially eliminated the primary generic character used by GRAY. However, BROOK (1889) demonstrated that the polyps of *L. glaberrima* have 12 complete mesenteries, not ten as in other species of the genus *Antipathes*, and for this reason he advocated that the genus be maintained. Thus, *Leiopathes* is currently recognized not on the original diagnostic characters given by GRAY, but solely on the secondary description given by BROOK.

Leiopathes glaberrima (ESPER 1792)

(Figs. 14–15)

1766 ?*Antipathes clathrata* – PALLAS: 212.

1788 ?*Antipathes clathrata* – ESPER (Lieferung 1–2 of the Pflanzenthiere 1), pl. 2.

1792 ?*Antipathes clathrata* – ESPER (Pflanzenthiere 2): 141.

1792 **Antipathes glaberrima* ESPER (Pflanzenthiere 2): 160, pl. 9, figs. 1–5.

1815 *Antipathes glaberrima* – LAMARCK: 471.

1815 ?*Antipathes clathrata* – LAMARCK: 475.

1816 *Antipathes glaberrima* – LAMARCK: 306.

1816 ?*Antipathes clathrata* – LAMARCK: 309.
1816 ?*Antipathes boscii* LAMOUROUX: 375, pl. 14, fig. 5.
1816 ?*Antipathes clathrata* – LAMOUROUX: 382.
1832 ?*Antipathes dichotoma* – GRAY: 41.
1846 ?*Antipathes boscii* – DANA: 584.
1846 *Antipathes glaberrima* – DANA: 585.
1849 *Leiopathes glaberrima*– HAIME: 284–287.
1858 *Leiopathes glaberrima* – GRAY: 290.
1858 ?*Leiopathes boscii* – GRAY: 290.
1857 ?*Antipathes boscii* – MILNE EDWARDS & HAIME: 318.
1857 ?*Arachnopathes clathrata* – MILNE EDWARDS & HAIME: 320.
1857 *Leiopathes glaberrima* – MILNE EDWARDS & HAIME: 322.
1864 ?*Antipathes dissecta* – DUCHASSAING & MICHELOTTI: 142.
1871 *Antipathes dissecta* – DE POURTALÈS: 53.
1880 *Antipathes glaberrima* – DE POURTALÈS: 118, pl. 3, figs. 2, 28.
1889 ?*Arachnopathes clathrata* – BROOK: 164.
1889 *Leiopathes glaberrima* – BROOK: 95, pl. 4, figs. 8–9, pl. 12, figs. 21–22, pl. 15, figs.3–5.
1889 *Antipathes glaberrima* – VON KOCH: 194, fig. 2.
1899 non *Leiopathes glaberrima* – JOHNSON: 817.
1914 *Antipathes glaberrima* – VAN PESCH: 76.
1918a *Leiopathes glaberrima* – GRAVIER: 343.
1918b *Leiopathes glaberrima* – GRAVIER: 225.
1921 *Leiopathes glaberrima* – GRAVIER: 14.
1955 *Antipathes glaberrima* – PAX & MÜLLER: 107.
1962 *Antipathes glaberrima* – PAX & MÜLLER: 104.
1974 *Leiopathes glaberrima* – OPRESKO: 116, figs. 16–17.
1977 *Leiopathes glaberrima* – GRIGG & OPRESKO: 244.
1985 *Antipathes glaberrima* – GRASSHOFF: 73.
1988 *Leiopathes glaberrima* – GRASSHOFF: 124.
1989 *Leiopathes glaberrima* – GRASSHOFF: 215.
1991 *Leiopathes glaberrima* – GRASSHOFF: 361.

Diagnosis: Corallum large, irregularly branched, with long crooked branches. Highest order branchlets 1–2 cm long, 0.5–0.7 mm in diameter, 1–2 cm apart, and usually extending out at right angles to the branchlets from which they arise. Spines small, simple, smooth surfaced, conical; 0.02–0.06 mm high; absent on larger branches and stem. Polyps variable in size and spacing, up to 1.0 mm in transverse diameter; equally wide in sagittal and transverse diameters, or slightly longer along sagittal axis; 4–6 per centimeter. [Note: Because the specimen in the Senckenberg-Museum is incomplete, the diagnosis given above is based, in part, on the description given by BROOK (1889: 95) of a specimen from the Bay of Naples].

Redescription of the ESPER material: The holotype (SMF 5887) is a dry specimen, 28 cm high with only the stumps of branches remaining (Fig. 14). A basal plate is present. The diameter of the stem just above the basal plate is 6 by 9 mm. The distance between the branch stumps ranges from 3 to 6 cm. The distal branch angles range from about 80° to greater than 90°. Spines are not noticeable on the outer surface of the sclerenchyme; however, when the outer layers were removed leaving a fragment only 0.5 mm in diameter, minute spines, less than 0.02 millimeters in height could be observed (Fig. 15). These spines are arranged irregularly around the

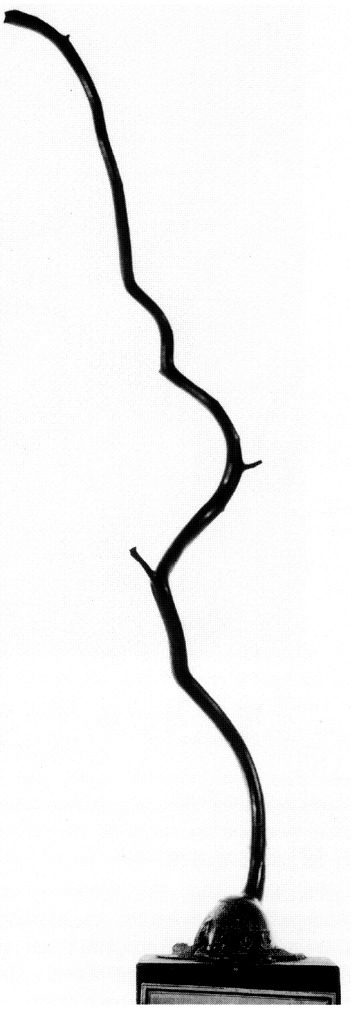

Fig. 14. *Leiopathes glaberrima* (ESPER), holotype, SMF 5887; entire corallum, height about 28 cm.

circumference of the axis and spaced about 0.6 mm apart. Polyps are not present on the corallum. No other information on the branching pattern of the corallum or the size or arrangement of the smallest branchlets could be determined from the specimen. However, the central axial canal was found to be 0.05 mm, indicating that the smallest branchlets were at least this size.

Remarks: Part of ESPER's description of the species is as follows: "The form of the basal plate almost completely corresponds to that of *Antipathes spiralis*; it is cone-shaped or vaulted, and on solid substrate it extends out forming a thin membrane. Its outer surface shows the same smoothness, but internally it is very cracked and filled with layers of milleporans or with pebbles. The simple stem rises with bendings or rarely straight upwards. In intervals it forms either spiral windings or elongated, arching, very irregular torsions. The bendings occur in various degrees and are circular or form angles. Commonly, the top is forked, at least, as I have noticed on several branches. Every now and again various tips of small branches, hardly being a few twelfths of an inch [Linien] in length, can be observed on the surface,

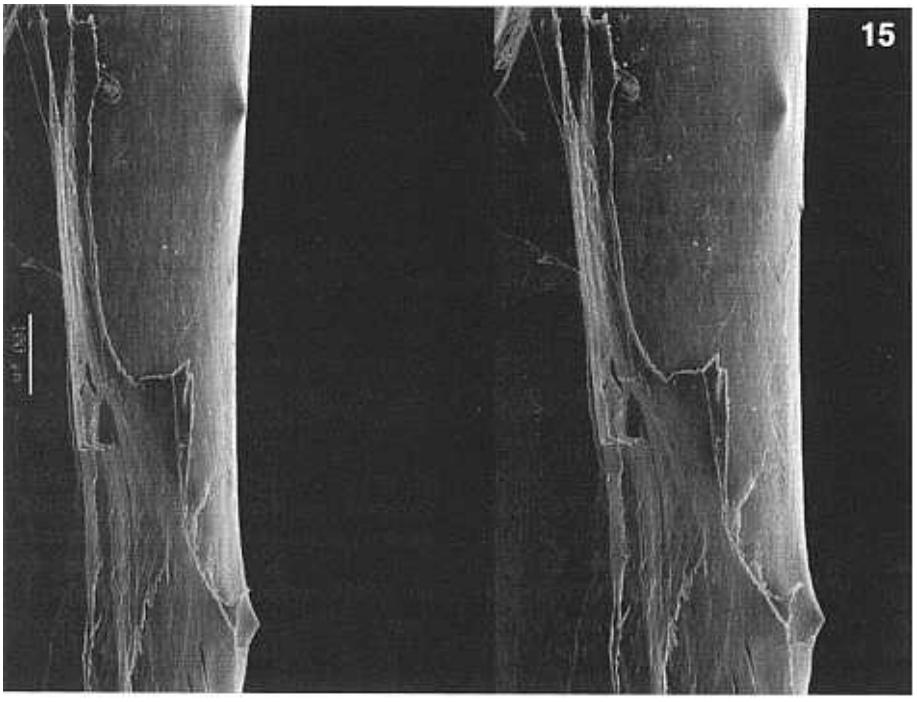

Fig. 15. *Leiopathes glaberrima* (ESPER), holotype, SMF 5887; segment of stem with outer axial layers removed to show spines, stereo pair.

standing one or two inches apart from each other, or can also be closer or more distant than that. In its transverse cut next to the basal part the wood is stretched [ablangrund; a misspelling?], whereas its remaining parts are flattened and windy in different kinds of ways. At the most this in itself smooth surface reveals flat deepenings and angular elevations that draw out, thus increasing the shiny polish when hit by light. However, this already distinguishes this coral from *Antipathes spiralis* which has a roundish wood."

ESPER expresses the opinion that his species might be identical with the ones described by IMPERATO (1599) and BONANNI (1709) under the name "Savaglia", by LINNAEUS under the name *Gorgonia Antipathes*, by PALLAS (1766) under the name *Antipathes orichalcea*, and by KNORR (1767) who described it simply as a "black coral". "Savaglia" (= *Gerardia*) has since been identified as a zoanthid (see PAX 1940 for a review of this genus); *Gorgonia antipathes* has been placed in the gorgonian genus *Rumphella* BAYER 1955 (see BAYER 1959, for discussion), and *Antipathes orichalcea* PALLAS 1766 is thought to be an unidentifiable species of gorgonian (BROOK 1889).

In differentiating his species from *Antipathes spiralis*, ESPER emphasizes the fact that the surface of the axis in *A. glaberrima* is smooth and that the axis consists of concentric lamellae, but lacks the hollow core characteristic of the axis of *A. spiralis*. It is unlikely that ESPER could have observed the central canal of *L. glaberrima* because of its small size, and because his specimen lacked the fine branchlets, he would not have seen the axial spines near the tip of the branchlets. LAMARCK (1815: 306) was one of the first naturalists to point out that spines are present in this species, but that they can only be seen at the tips of the smallest branches. DANA (1846), however, thought that ESPER's specimen might be a decorticated gorgonian, and he also pointed out the similarity of ESPER's figure of *A. glaberrima* and ESPER's illustration of *A. compressa*.

Comparisons: The branching pattern of *Leiopathes glaberrima* (ESPER) is similar to that of *L. acanthophora* OPRESKO 1998. Both species have relatively long irregularly arranged branchlets. Based on descriptions given in the literature, the branchlets in *L. glaberrima* are thicker than those in *L. acanthophora*. BROOK (1889) reported that the ultimate branchlets in the specimen of *L. glaberrima* that he examined were 0.5–0.7 mm in diameter, whereas those in *L. acanthophora* are only 0.2–0.3 mm. The spines of *L. glaberrima* are significantly smaller than those of *L. acanthophora*. As determined from ESPER's type, the spines are no more than 0.02 mm high. An illustration given by BROOK (1889), suggests a spine size of 0.04–0.06 mm. In comparison, spines in *L. acanthophora* are 0.10–14 mm. Furthermore, in *L. glaberrima* the larger branches are devoid of spines, but this is not the case in *L. acanthophora*. BROOK (1889) also reported that the polyps in his specimen of *L. glaberrima* were about 1.0 mm in maximum diameter. In contrast, the polyps in *L. acanthophora* are as much as 2 mm in diameter.

Type locality: ESPER notes that "The Mediterranean Sea is the only known dwelling place of this coral." he further states that specimens had been collected in the Sea of Naples and also off the coasts of Regusa. The species has also been reported from other locations in the Atlantic as well as from the Pacific; however, these determinations require further verification.

Acknowledgements

The authors wish to thank Dr. Manfred GRASSHOFF and Ulrike SCHREIBER of the Senckenberg-Museum, Frankfurt am Main for their kind hospitality and assistance during our visit. Dr. S. CAIRNS of the Smithsonian Institution provided research space at the USNM and S. BRADEN of the Smithsonian's SEM laboratory prepared the samples for electron microscopy. The editorial assistance of Drs. Wolfgang NÄSSIG and Manfred GRASSHOFF is greatly appreciated. The authors, as Research Associates of the U.S. National Museum of Natural History, would like to express their deep appreciation for the continuing support of the Smithsonian Institution. Additional support was provided by Oak Ridge National Laboratory, Oak Ridge, TN.

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Received: 16. x. 2000, 21. vi. 2001, accepted: 19. vii. 2001