

Redescription of *Antipathes dichotoma* Pallas, 1766 (Cnidaria: Anthozoa: Antipatharia)

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Key words: Cnidaria; Anthozoa; Antipatharia; Antipathidae; *Antipathes dichotoma* Pallas; neotype. The type species of the genus *Antipathes*, (*A. dichotoma* Pallas, 1766) is redescribed and a neotype is designated. Differences in the size and shape of the spines, and in the size and density of the polyps are considered key characters in separating related species.

Introduction

The species *Antipathes dichotoma* was established by Pallas in 1766 on the basis of a description given by Marsigli (1725) of a specimen collected in the Mediterranean off the coast of Marseille. Marsigli's specimen (Lithophyte no. 9) was described and illustrated as a loosely dichotomously branched colony with strong spines and a biserial arrangement of polyps, with each polyp appearing to have only two tentacles. Pallas (1766) had no additional specimens on which to expand and clarify the species definition. Brook (1889) was the first worker who provided a more detailed description of the species based on a specimen from the Bay of Naples. Brook's specimen did not closely match Marsigli's illustration in that the branching was more irregular and not so dichotomous. Later workers have followed Brook's diagnosis and, in general, most of the specimens described from the Mediterranean more closely resemble Brook's specimen than Marsigli's illustration.

Brook (1889) designated *Antipathes dichotoma* Pallas as the type species of the genus *Antipathes*. Of the five species originally placed in the genus by Pallas, *A. dichotoma* was the only species of two retained in the genus (the other was *A. foeniculacea* Pallas) for which Brook had a specimen. Brook, however, did not specifically designate his specimen as a neotype. It is unlikely that Marsigli's specimen is still extant, and because of confusion over the identity of this species with others from many different localities, it seemed necessary to describe the species on the basis of modern techniques and to provide sufficient information to help differentiate this species from a number of others which had previously been synonymized with it.

Abbreviations

BMNH = British Museum of Natural History, London, United Kingdom

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA

RMNH = National Museum of Natural History, Leiden, The Netherlands

USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ZSMD = Zoologische Staatssammlung Muenchen, Deutschland

Systematics

Family Antipathidae Ehrenberg, 1834

Genus *Antipathes* Pallas, 1766

Antipathes dichotoma Pallas, 1766

(figs 1-2, 4a, 4d, 5a, 5d)

Lithophyte no. 9 Marsigli, 1725: 105, 108, pl 21, figs 101-103, pl 40, fig 179.

Antipathes dichotoma Pallas, 1766: 216; Lamouroux, 1816: 216; Dana, 1846: 585; Milne Edwards & Haime, 1857: 319; Brook, 1889: 98-100, pl XII, fig. 16, pl XIII, figs 1, 9, pl XIV, figs 1, 5, 6; Gravier, 1918: 227-229; Pax, 1932: 420 (subspecies *dichotoma*); Pax & Müller, 1955: 106-107, fig. 4 (subspecies *dichotoma*).
Not *Antipathes dichotoma*; Gray, 1832: 41; van Pesch, 1914: 52-76; Grigg & Opresko, 1977: 242-261, fig. 9; Zou & Zhou, 1984: 104.

Antipathes? mediterranea Brook, 1889: 104-105.

Antipathes aenea von Koch, 1889: 202-204, fig. 10; Roule, 1905: 66, pl. viii, figs 1-4.

[?] *Antipathes subpinnata*; Pax, 1952: 4-5, figs 1-3.

Material.— Neotype (RMNH Coel. 4891; schizoneotype, USNM 100927), Bay of Naples, G. Stiasny, v.1924; RMNH Coel. 32183, Eastern Atlantic, Morocco, off Cap Blanc du Nord, 33°16'N, 9°10'W, 27.iii.1976, 320 m, Onversaagd Madeira-Marokko Exped., sta 139; MCZ 53537, Bay of Naples, received from G. Bacci, Stat. Zool. Napoli, 25.x.1946; USNM 100084, Mediterranean, Tyrrhenian Sea, no other data; BMNH 1897.4.3.5, Bay of Biscay, Koehler, no other data.

Type locality.— Mediterranean, off Marseille, in 140 fm.

Diagnosis.— Colony tall, up to 1 m or more, sparsely branched with long flexible branches disposed irregularly on all sides of the stem and lower order branches, but occasionally uniseriably arranged with three or four branches in a row. Branch angles variable, but often close to 90°.

Spines on branchlets conical, smooth-surfaced; acute; usually 0.2 mm or more tall (range 0.16 to 0.28 mm); mostly in four to six rows (as seen from one view); 0.5-0.8 mm apart, and with two or three spines per millimeter in each row.

Polyps typically 2.0 to 2.4 mm in transverse diameter (maximum size about 3 mm; minimum size about 1.3 mm), arranged in a single series on the smallest branchlets but in multiple series on the larger branches; 1-1.2 mm apart. Three to four polyps per centimeter on the branchlets.

Description of the neotype.— The neotype is a relatively small specimen (fig. 1a) without a basal holdfast. The main stem is 16 cm long and about 3 mm in diameter at its basal end. The branching is very loose and irregular, with several very long branches up to 40 cm long. A branch 23 cm long is about 0.9 mm in diameter at its basal end. The branches are spaced varying distances apart, mostly 2-3 cm or more. The distal branch angles are 70-90°.

The spines (figs 2a-c) are conical, acute, smooth surfaced, and slightly inclined distally. On branchlets 0.4-0.8 mm in diameter the polypar spines reach a maximum size of about 0.2 mm (as measured from middle of base to apex), and the abpolypar spines are 0.02 to 0.05 mm shorter. Four to six longitudinal rows of spines can be seen in one lateral view (excluding rows in which the spines are only partially visible). Within each row the spines are 0.5-0.7 mm apart, resulting in two to three per millimeter. On the



Fig. 1. *Antipathes dichotoma* Pallas, neotype (RMNH Coel. 4891); a, entire corallum; b, polyps on branchlet; c, polyps on stem. Scale in a, 1 cm; scale in b-c, 0.5 cm.

larger branches and stem the spines become more acicular, but do not increase much in size or density (fig 2d). Spines on the stem are about 0.2 mm tall (fig. 2e), and five rows are visible from one aspect, with two to three spines per millimeter in each row.

The polyps are arranged in a single row on the smallest branches (fig. 1b) but occur on several sides of the axis on the stem (fig. 1c). In the preserved state they measure, on average, about 2 mm in transverse diameter (from the distal side of the base of the distal lateral tentacles to the proximal side of the base of the proximal lateral tentacles), but occasionally a smaller one (1.3 mm in transverse diameter) occurs between two larger ones. The interpolypar space is 1.0 to 1.2 mm, and there are usually three to

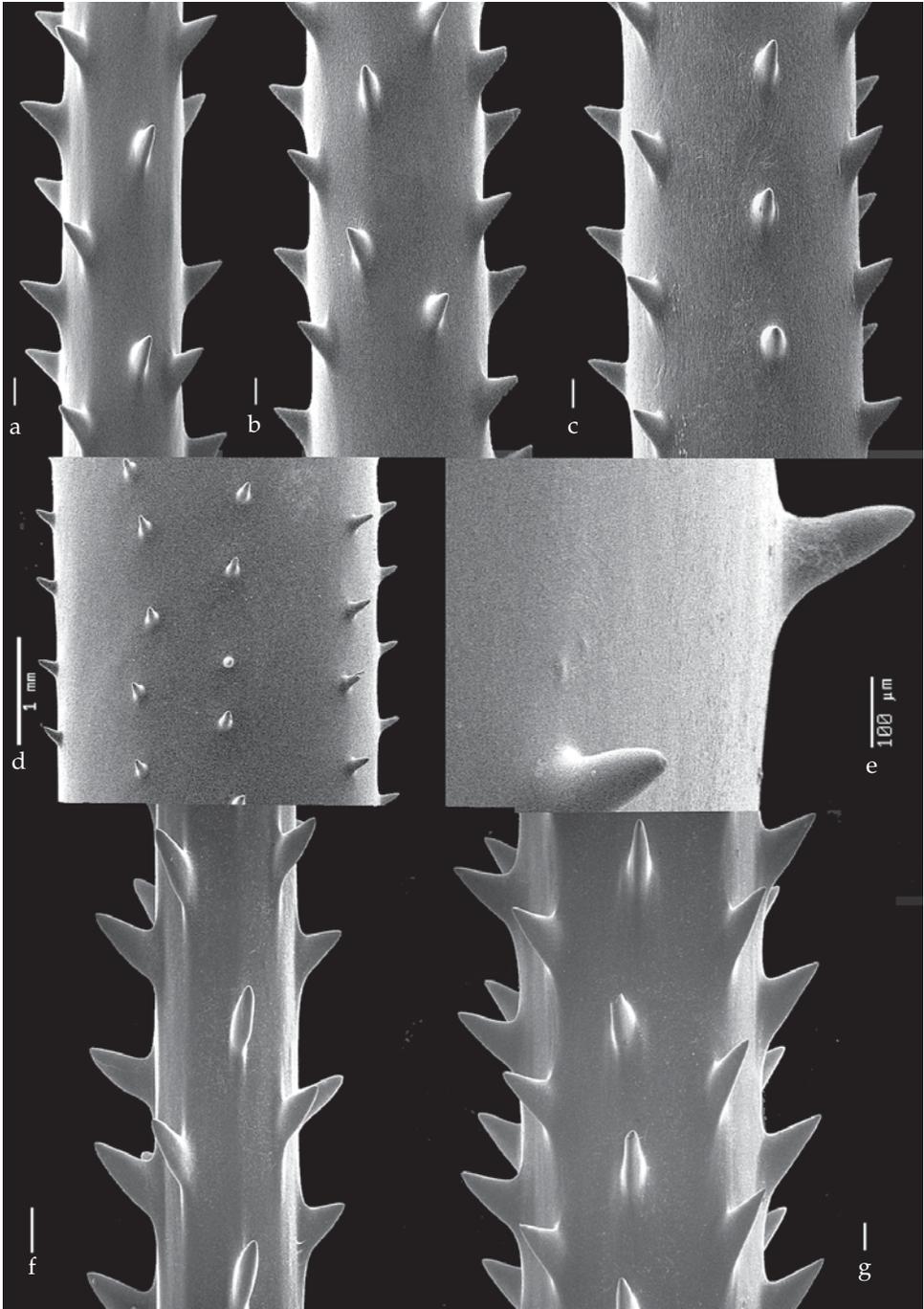


Fig. 2. *Antipathes dichotoma* Pallas, a-e, schizoneotype (USNM 100927), f-g, specimen from MCZ (Catalogue No. 53537). Scale in a-c and in g-f, 0.1 mm.

four polyps per centimeter. The tentacles, in the preserved state, are 5 mm or more in length, the sagittal tentacles often appearing longer than the laterals (fig. 1b).

Intraspecific variation.— Antipatharian species can show considerable variation in morphological characters between specimens, in different parts of the same specimen, and sometimes also in specimens of different size or age. The branching pattern, density of branching, size and shape of the spines, and size of the polyps all vary to some extent. Because species descriptions are by necessity limited to small samples taken from only parts of a colony, any description must be viewed as potentially emendable if other branches of the same specimen are examined, or if a specimen of a different size is studied. Thus, differences in a given character, as reported in the literature, may or may not reflect absolute differences between specimens or even species. The samples of the specimens assigned to *A. dichotoma*, both those described here, as well as those in the literature, differ somewhat in several characters, particularly in the maximum size of the spines; however, in all cases the spines are smooth-surfaced and show no indication of being notched, bifurcated, or multi-knobbed at the apex.

In the MCZ specimen from the Bay of Naples (MCZ 53537) the branches are up to 11 cm long and are spaced at intervals from a few millimeters to as much as 10 cm apart. There is the appearance of groups of branches of varying length and thickness separated by wide distances from other such groups. The spines in this specimen reach a larger size and appear more conical than those in the neotype and the polypar spines are more distinctly larger than the abpolypar spines. On one branchlet 0.34 mm in diameter the polypar spines are 0.18 mm tall (fig. 2f) and the abpolypar spines 0.11 mm. On a branch about 0.8 mm in diameter the spines reach a maximum size of about 0.28 mm (fig. 2g). The polyps in the MCZ specimen are similar in size to those in the neotype, with three to four per centimeter. The British Museum specimen from the Bay of Biscay (BMNH 1897.4.3.5) is 28 cm in height and has a basal stem diameter of 3 mm; its spines measure 0.26-0.28 mm and its polyps are 2.5-3.0 mm in transverse diameter (three or four per centimeter). The RMNH specimen from off Cap Blanc du Nord (RMNH Coel. 32183), closely resembles the neotype in the size of the polyps (2 mm) and in the size of the spines (polypar spines up to about 0.22 mm). In the USNM specimen from the Tyrrhenian Sea (USNM 100084) the spines range in size from 0.17 to 0.24 mm.

The specimen described by Brook (1889) is 29 cm tall with basal stem diameter of 1.3 mm and with branches 3-16 cm in length. Brook reported that the polyps were subequal in size, but with a small one sometimes located between two larger ones. As estimated from the illustrations given by Brook, the spines are up to 0.2 mm tall, and the polyps are about 2 mm in transverse diameter, with three polyps per centimeter. Brook reported as many as four polyps per centimeter.

Brook's type specimen of *Antipathes mediterranea* is 35 cm tall, with a stem diameter of 2 mm, and with branches 4-9 cm apart and up to 10 cm long. The spines (figs. 4d, 5d) are about 0.18 mm tall and spaced about 0.7-0.8 mm apart in each row, and five to six rows can be seen in lateral view. Polyps were not present in this specimen.

Von Koch (1889) described under the name *Antipathes aenea* n. sp. a specimen from the Bay of Naples which has subsequently been referred to *A. dichotoma*. The specimen was reported to be 1 m tall with basal stem diameter of 5 mm; with branches up to 20 cm long and 0.1 to 0.15 mm in diameter at the tip, and with spines 0.1 to 0.2 mm tall,

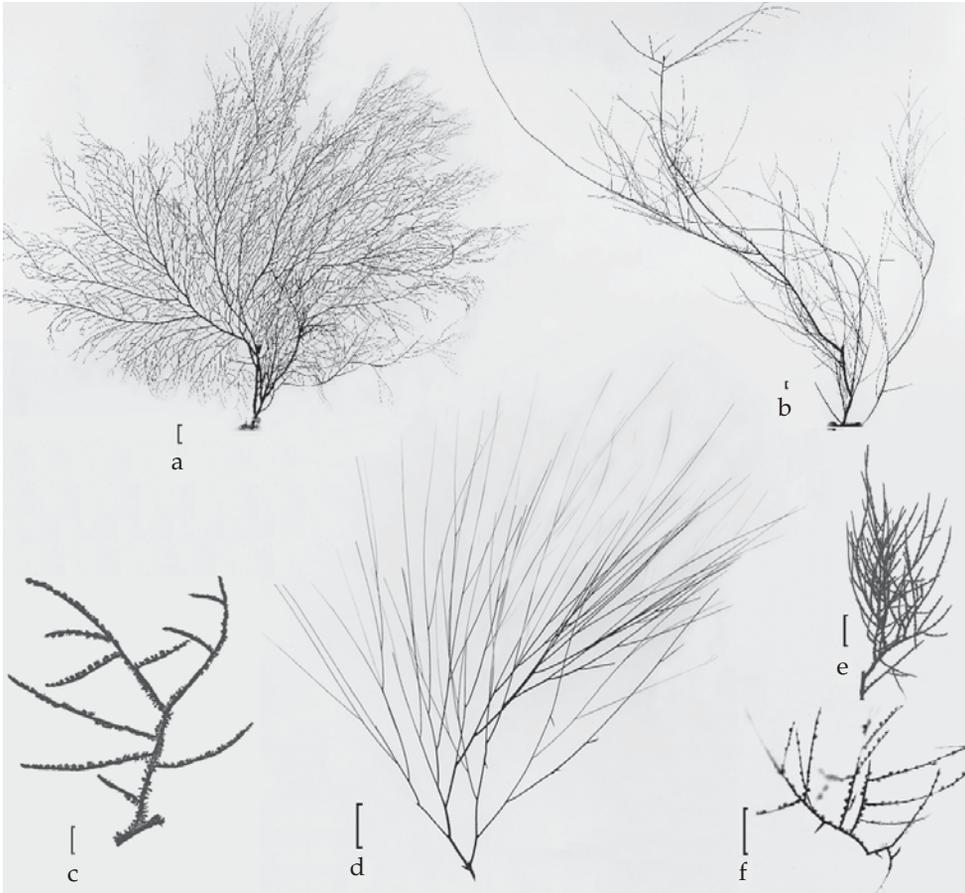


Fig. 3. a, *Antipathes atlantica* Gray, probable syntype (BMNH 1843.2.8.27); b, *A. lentipinna* Brook, part of holotype (BMNH 1973.9.20); c, *A. arborea* Dana, digital scan of the illustration of the type specimen as given by Dana; d, *A. furcata* Gray, holotype (BMNH, probably 1843.2.6 or 8); e, *A. gallensis* Thomson & Simpson, holotype (BMNH 08.2.18.21); f, *A. grandiflora* Silberfeld, holotype (ZSMD No. 507). Scale in a-f, 1 cm.

0.6-0.7 mm apart, and in four to six rows (one view). Von Koch states that 30-35 polyps occur in 10 cm. In the illustrations given by von Koch the spines appear to be about 0.16 mm tall on a branchlet 0.29 mm in diameter, strongly compressed laterally, and flared out along the base in an axial direction; they measure about 0.2 mm on a branchlet 0.4 mm in diameter. [Note: the magnifications given by von Koch for the illustrations of the spines appear to be incorrect by a factor of 10]. The polyps in von Koch's illustration are about 2.5 mm in transverse diameter.

In summary, colonies of *A. dichotoma* can be relatively large, up to 1 m or more in height, sparsely branched, with long branches, 40 cm or more in length; and with large, smooth-surfaced spines and large polyps. The spines are quite variable in size, ranging from 0.16 to as much as 0.28 mm tall, with the polypar spines slightly to

noticeably larger than the abpolypar spines. Significantly, the spines have never been reported to be forked or notched at the apex, nor have they ever been reported to be papillose. Furthermore, the density of the spines and the number of rows does not appear to increase substantially on the larger branches and the stem. Although polyp size is variable, polyps 2 mm or more in transverse diameter are always present, and the density of the polyps on the branchlets is consistently three or four per centimeter. It also appears to be characteristic of the species that on the larger branches and stem the polyps occur on several sides of the axis.

Remarks.— Over the years numerous species have been synonymized with *A. dichotoma*; and this has often been done without any examination of pertinent type specimens. In the Siboga Monograph, van Pesch (1914) placed seventeen species in synonymy with *A. dichotoma*, arguing that there was a complete gradation of forms in terms of morphology of the corallum and the size and shape of the spines and the polyps. Even so, van Pesch proposed dividing the species into seven varieties, for five of which he suggested varietal names (the two others were varieties of *A. furcata* Gray proposed by Schultze in 1902). Following van Pesch's suggestions, Pax (1932) recognized seven subspecies: *A. dichotoma tristis* Duchassaing, 1870; *A. dichotoma furcata* Gray, 1857; *A. dichotoma dichotoma* Pallas, 1766; *A. dichotoma gallensis* Thomson & Simpson, 1905; *A. dichotoma malayensis* Pax, 1932 (for the material described by van Pesch), *A. dichotoma grandiflora* Silberfeld, 1909; and *A. dichotoma arborea* Dana, 1846. These forms are sufficiently different from one another to be maintained as distinct species; brief summaries of their major characteristics are given below:

A. tristis Duchassaing. The type is missing and the original description is rather brief and may apply to any one of several flabellate species from the western Atlantic. The species could easily be identical with the most common Caribbean species, *Antipathes atlantica* Gray (1857). The latter species (fig. 3a) is distinctly flabellate and very densely branched with most of the smallest branchlets being only several centimeters long. The spines are about 0.06 mm tall, and the polyps are only about 1 mm in transverse diameter, resulting in six or seven per centimeter. Therefore, in three key characters this species is distinctly different from *A. dichotoma*.

A. furcata Gray. The type of this species (fig. 3d) consists of a corallum with very thin elongate branches, very narrow branch angles, sub-dichotomous branching, and small spines (0.05-0.10 mm tall). Polyps are not present on the type, but in specimens that can reliably be referred to this species, the polyps are 0.7 to about 1 mm in transverse diameter (six to eight per centimeter). Thus, there can be no confusing this species with *A. dichotoma*.

A. gallensis Thomson & Simpson. The corallum of the type of this species (fig. 3e) is small (8 cm in height) and bushy with relatively short branches that are not more than 2 cm long. The polypar spines are 0.13-0.15 mm tall (based on a re-examination of the holotype), with one or more small knobs at the apex, and the polyps are 0.8-0.9 mm in transverse diameter (eight to nine per centimeter). Therefore, it is unlikely that this species is conspecific with *A. dichotoma*.

A. grandiflora Silberfeld. The type of this species (fig. 3f) has a branching pattern somewhat similar to *A. dichotoma* in that the corallum is sparsely branched with wide branch angles (80-90°); however, the corallum is quite small (about 5 cm in height), and the branches are, at most, 3 cm long. The polypar spines are simple without knobs

or bifurcations and about 0.08 mm tall, and the polyps are not more than 1.2 mm in transverse diameter.

A. dichotoma malayensis Pax. The numerous specimens described by van Pesch from the Siboga Expedition were assigned to this subspecies by Pax (1932). In almost all of van Pesch's material the spines are less than 0.1 mm (in some cases as small as 0.03 mm), and the polyps are about 1 mm or less in transverse diameter. In a few specimens the spines are as much as 0.15 mm, but they are never as large as 0.2 mm. It is unlikely that these specimens are identical with *A. dichotoma*; however, further study is needed to determine if they can be referred to another nominal species.

A. arborea Dana. This species comes closest to *A. dichotoma* in terms of the size of the corallum (up to 1 m) and the pattern of branching, with long branchlets originating from the sides of the lower order branches at varying distances, but with the branch angles most often near 90° (fig. 3c). It differs from *A. dichotoma* in having relatively small, triangular and laterally compressed spines, 0.1-0.12 mm tall (fig. 4c), which can be simple, bifurcated or multiply lobed at the apex, and which have a slightly roughened surface (fig. 5c). In a small piece of Dana's original specimen that is now deposited at the MCZ (MCZ 54087), the polyps are 1.3 mm in transverse diameter, and there are seven to eight polyps per centimeter.

Careful study of the types of the other species synonymized with *A. dichotoma* by van Pesch is needed before it can be determined whether any of these is the same as Pallas's species. It should be noted, however, that many of these species have been described as having much smaller spines and polyps than those in *A. dichotoma*, and in several cases the growth form of the corallum is quite different. That is not to say that some species may eventually be shown to have overlapping characters with *A. dichotoma*. In many species groups of antipatharians, an intergrading of characters is often apparent when a sufficiently large suite of specimens is examined. This is most likely due to the fact that most taxonomic characters at the species level are non-disjunct, inherently variable, and possibly also subject to alteration by external environmental factors. In addition, there also exists the possibility of hybridization among closely related species, as has been shown in other colonial anthozoan groups. Therefore, the occurrence of intermediate forms of well-defined species can be expected, and perhaps can only be treated as such.

Comparisons to related species.— As noted above, *A. arborea* Dana (type locality: Fiji) resembles *A. dichotoma* Pallas in the general form of the corallum, but differs in having smaller polyps and relatively small spines which, on some parts of the corallum, can be bifurcate or multiply lobed at the apex, and with varying degrees of fine surface sculpturing (figs 4c, 5c). Several other species, including *A. galapagensis* Deichmann (1941) from the eastern Pacific; *A. curvata* van Pesch (1914) and *A. spinulosa* Schultze (1896) from the Indo-Pacific; and *A. lentipinna* Brook (1889) from the Red Sea, have a similar growth form. These species also differ from *A. dichotoma* in the size and morphology of the spines and/or in the size of the polyps. In *A. galapagensis* the spines (fig. 4b) are conical, acute or with a slightly rounded apex, directed distally, mostly 0.14-0.16 mm tall, some with a slight indication of a bifurcation at the apex, and covered on parts of their surface with very fine irregularities (fig. 5b). The polyps were reported by Deichmann (1941) to be about 2 mm; however, a re-examination of type material in the USNM revealed that they are about 1 mm in transverse diameter with an inter-

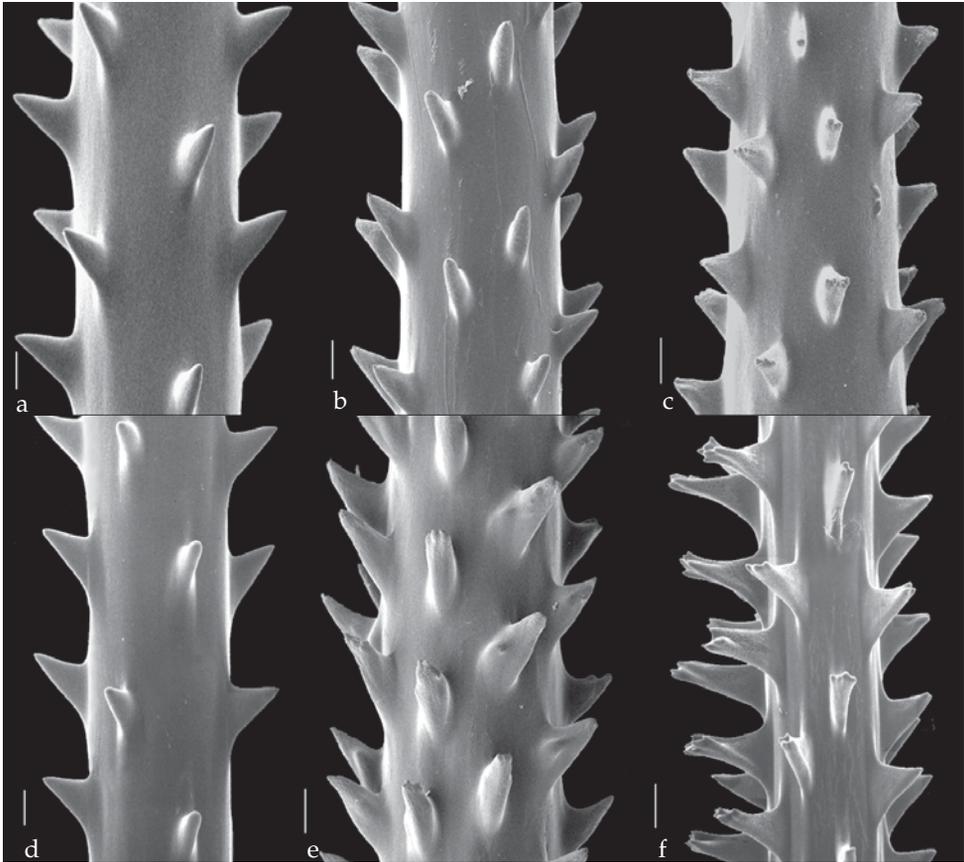


Fig. 4. Spines: a, *Antipathes dichotoma* Pallas, schizoneotype (USNM 100927); b, *A. galapagensis* Deichmann, holotype (USNM 43443); c, *A. arborea* Dana, holotype (USNM 701); d, *A. mediterranea* Brook, schizoholotype (USNM 94483.); e, *A. curvata* van Pesch, schizoholotype (USNM 100416); f, *A. lentipinna* Brook, schizoholotype (USNM 100360). Scale in a-f, 0.1 mm.

polypar space of 0.7-0.8 mm, and with six to seven polyps per centimeter. The spines in *A. curvata*, although reported by van Pesch to be about 0.12 mm; are up to 0.18 mm tall on some branchlets of the holotype (fig. 4e). They are triangular in shape on the smallest branchlets but become more conical and more inclined distally on the larger branchlets. Some are bifurcated or multiply lobed at the apex and they also have very small papillae or striations on the distal part of their surface (fig. 5e). The type of *A. curvata* is a dry specimen and polyps were not described by van Pesch; however, in re-examining the type, the remains of a few polyps were found suggesting that they are about 1.3 mm in transverse diameter. In specimens deposited in the RMNH, which were collected from the general area of the type locality and which appear to be referable to *A. curvata*, the polyps are 1.0 to 1.2 mm in transverse diameter, with six to eight polyps per centimeter (sometimes as many as 12 per centimeter when they occur in multiple rows on the larger branches). In *A. lentipinna* the spines are very variable

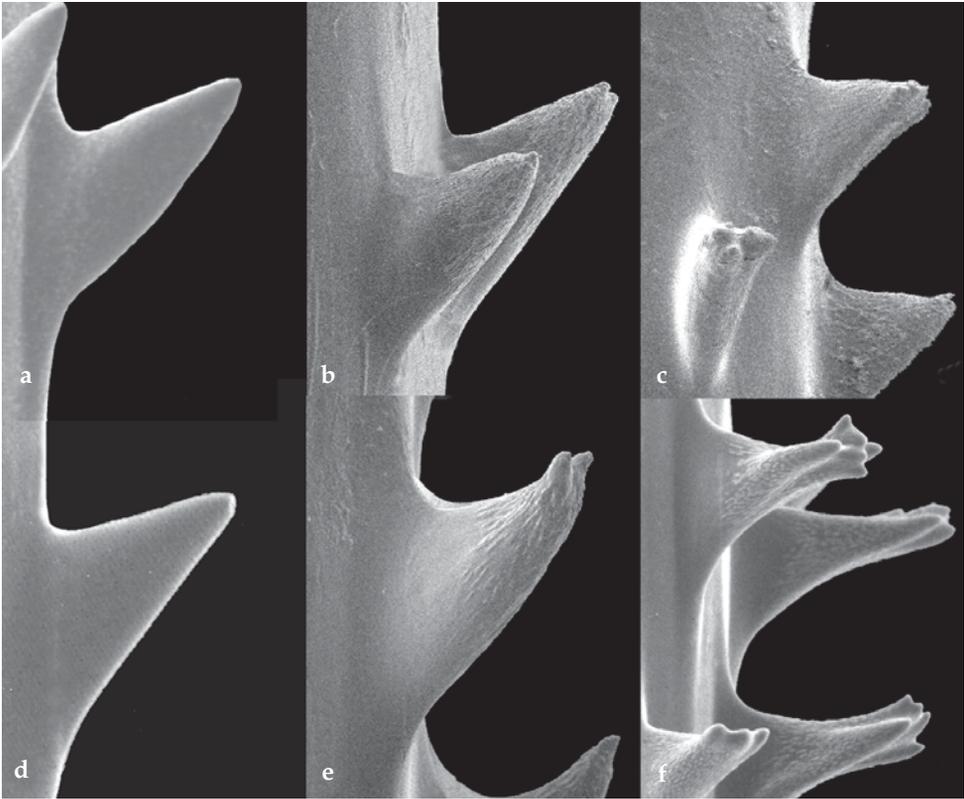


Fig. 5. Enlarged view of spines: a, *Antipathes dichotoma* Pallas, schizoneotype (USNM 100927); b, *A. galapagensis* Deichmann, holotype (USNM 43443); c, *A. arborea* Dana, holotype (USNM 701); d, *A. mediterranea* Brook, schizoholotype (USNM 94483); e, *A. curvata* van Pesch, schizoholotype (USNM 100416); f, *A. lentipinna* Brook, schizoholotype (USNM 100360).

in size, with some as large as those in *A. dichotoma* (up to 0.24 mm tall). They can be simple or multiply lobed at the apex (figs 4f, 5f), with the apical lobes sometimes becoming enlarged to give the spines a coronate appearance. A similar type of coronate spine is also found in *Antipathes spinulosa* (Schultze, 1896). The spines in *A. spinulosa* are up to 0.285 mm tall. In both species the spines are also very finely papillose over their surface (fig. 5f). Bifurcate, multi-lobed or coronate spines were not reported by Brook in the original description of *A. lentipinna*, and, indeed, on many parts of the type specimen only simple spines are present. Polyps are not present on the type of *A. lentipinna*, but in a specimen assigned to this species by Summers (1910), the polyps were reported to be 2 mm. Summers' specimen came from waters off Mozambique. In *A. spinulosa* the polyps range in size from 0.9 to 1.6 mm.

The five species, *A. arborea*, *A. lentipinna*, *A. curvata*, *A. galapagensis*, and *A. spinulosa* are more similar to each other than to *A. dichotoma* in that they all show a tendency, at least on parts of the corallum, for the spines to have notches, bifurcations or multiple lobes at the apex. They are also alike in having fine surface sculpturing in the form of

irregular, rounded or elongated papillae or striations (mostly on the upper third of the surface near the apex). That is not to say that simple spines more like those in *A. dichotoma* do not occur in these species. Spines near the tips of the smallest branches are more likely to be simple, and simple spines may also occur on other parts of the corallum, especially on the abpolypar side of the axis. Four of the species, *A. arborea*, *A. curvata*, *A. spinulosa*, and *A. galapagensis* differ from *A. dichotoma* in having smaller polyps (from about 1 mm to 1.6 mm). Based on information given in the literature, *A. lentipinna*, has polyps of a size similar to those in *A. dichotoma* (about 2 mm).

Comments on the species synonymy.— The specimen originally identified by Gray in 1832 as *A. dichotoma*, was later referred by Gray (1857: 290) to *Leiopathes glaberrima* (Esper, 1792). As noted above, almost all of the *Siboga* specimens described by van Pesch (1914) as *A. dichotoma* (later named *A. dichotoma malayensis* by Pax, 1932), differ from the true *A. dichotoma* in having smaller spines and smaller polyps. Additional study is needed to determine if these specimens can be referred to other nominal species. Specimens assigned by Zou & Zhou (1984) to *A. dichotoma* were described as having spines at the ends of the branchlets that are conical with a blunt apex, bifurcated or swollen, nipple-like, and 160 to 190 μm tall. The illustration suggests that they are also papillose. Spines in the middle of the branchlets were reported to be smooth, slightly compressed, and 114-125 μm tall. The size of the polyps was not reported.

The specimens from Hawaii identified by Grigg & Opresko (1977) as *A. dichotoma* were described as having spines that were faintly papillose or with small knobs at the apex and with seven to eight polyps per centimeter (the size of individual polyps being 1.0 to 1.3 mm). Grigg & Opresko (1977) noted that the spines more closely resembled those of *A. lentipinna* Brook than *A. dichotoma*. However, at that time of publication of that report, Mediterranean material of the true *A. dichotoma* was not available for comparison, and the Hawaiian specimens were referred to *A. dichotoma* based on the fact that van Pesch (1914) had synonymized *A. lentipinna* with *A. dichotoma*. As indicated above, the approach taken by van Pesch is not supported by the available information, and the Hawaiian specimens must be considered as being distinct from *A. dichotoma*. Whether they can be referred to *A. lentipinna* or another nominal species is a subject for further study. If Summer's observation that the polyps of *A. lentipinna* are 2 mm in size is verified, this would argue for the Hawaiian species, which have polyps only 1.0-1.3 mm in transverse diameter, being more closely related to *A. curvata*, *A. arborea*, or *A. spinulosa*. In the Hawaiian species the spines range in size from 0.18 to 0.28 mm; larger than those in *A. curvata* (0.12-0.18 mm) and *A. arborea* (0.10-0.12 mm), but slightly smaller, on average, than those reported for *A. spinulosa* (0.285 mm). The preliminary evidence suggests that the Hawaiian form may be a distinct and separate species.

Distribution.— Known from the Mediterranean, off Marseilles, in the Bay of Biscay, Tyrrhenian Sea, and in the Bay of Naples. Roules' specimen was collected outside the Mediterranean, off the Spanish coast, in the Gulf of Gascogne, and the specimen in the RMNH was collected off the coast of Morocco. No specimen has yet been described in the literature from the western Atlantic or the Indo-Pacific that can conclusively be identified as *A. dichotoma*.

Bathymetric range.— Marsigli (1725) reported that his specimen came from 140 fm, Brook's specimen came from 110 fm, and Roule's from 300 m. The type of *A. mediterranea* Brook was collected in 32-54 fm.

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