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# Establishment of a neotype for *Antipathes flabellum* Pallas, 1766 (Anthozoa: Hexacorallia: Antipatharia)

LUCAS TERRANA<sup>1,2\*</sup>, JEREMY HOROWITZ<sup>3,4</sup> & DENNIS M. OPRESKO<sup>3,5</sup>

<sup>1</sup>Natural History Museum & Vivarium, Rue Saint-Martin 42, 7500-Tournai, Belgium.

□ lucas.terrana@tournai.be; bhtps://orcid.org/0000-0001-5767-3220

<sup>2</sup>Biology of Marine Organisms and Biomimetics unit, University of Mons, Avenue du Champ de Mars 6, 7000—Mons, Belgium. <sup>3</sup>Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC, 20013-7012, USA.

<sup>4</sup> HorowitzJ@si.edu; <sup>b</sup> https://orcid.org/0000-0002-2643-5200

<sup>5</sup> dmopresko@hotmail.com; <sup>6</sup> https://orcid.org/0000-0001-9946-1533

\*Corresponding author

# Abstract

A neotype is designated for the antipatharian coral *Antipathes flabellum* Pallas, 1766. The neotype was collected off Madagascar (the original type locality is given as the "*Oceanus Indicus*"). Morphologically, the neotype corresponds closely in corallum shape and skeletal spination to specimens that have traditionally been identified as *Antipathes flabellum*. Another specimen of *A. flabellum* from Madagascar, morphologically almost identical to the neotype and described here, has been sequenced using ultra conserved elements and exon nuclear loci, which showed that it falls within the family currently recognized as Antipathidae.

Key words: Antipatharia, black corals, Antipathes flabellum, neotype

# Introduction

In 1766 Pallas created the genus *Antipathes* (Vermes: Zoophyta) which was differentiated from the genus *Gorgonia* on the basis of the fact that the polyps were gelatinous and lacked calcareous skeletal elements, and the skeletal axis was covered with spines. Pallas (1766) included ten species in the new genus: *A. clathrata* Pallas; *A. cupressina* Pallas; *A. dichotoma* Pallas; *A. ericoides* Pallas; *A. flabellum* Pallas; *A. foeniculacea* Pallas; *A. myriophylla* Pallas; *A. orichalcea* Pallas; *A. pennacea* Pallas; and *A. spiralis* (Linnaeus, 1758). Pallas's generic diagnosis was not specific to any one species nor was a type species assigned. Of the ten species originally placed by Pallas (1766) in *Antipathes*; only two are still in this genus: *A. dichotoma*, for which a neotype has been designated (Opresko, 2003) and *A. flabellum*, for which the type material is lost. The remaining species have been synonymized, assigned to other genera or removed from the Antipatharia (see Table 1).

TABLE 1. Species originally assigned to the genus Antipathes by Pallas (1766) and their current name and family.

Species assigned to	Current accepted name	Authority for the	Current family
Antipathes by Pallas (1766)		transfer/synonymy	
Antipathes clathrata Pallas, 1766	Arachnopathes* clathrata (Pallas, 1766)	Milne-Edwards, 1857	Antipathidae Ehrenberg, 1834
Antipathes cupressina Pallas, 1766	<i>Cupressopathes abies</i> (Pallas, 1766)	Opresko, 2001	Myriopathidae Opresko, 2001
Antipathes dichotoma Pallas, 1766	Antipathes dichotoma Pallas, 1766	-	Antipathidae Ehrenberg, 1834
			Continued on the most marked

# TABLE 1. (Continued)

Species assigned to Antipathes by Pallas (1766)	Current accepted name	Authority for the transfer/synonymy	Current family
Antipathes ericoides Pallas, 1766	Arachnopathes* ericoides (Pallas, 1766)	Milne-Edwards, 1857	Antipathidae Ehrenberg, 1834
Antipathes flabellum Pallas, 1766	Antipathes flabellum Pallas, 1766	-	Antipathidae Ehrenberg, 1834
Antipathes foeniculacea Pallas, 1766	Antipathes dichotoma Pallas, 1766	van Pesch, 1914	Antipathidae Ehrenberg, 1834
Antipathes myriophylla Pallas, 1766	<i>Myriopathes myriophylla</i> (Pallas, 1766)	Opresko, 2001	Myriopathidae Opresko, 2001
Antipathes orichalcea Pallas, 1766	Not an antipatharian	Brook, 1889	-
Antipathes pennacea Pallas, 1766	<i>Plumapathes pennacea</i> (Pallas, 1766)	Opresko, 2001	Myriopathidae Opresko, 2001
Antipathes spiralis (Linnaeus, 1758)	Cirrhipathes spiralis (Linnaeus, 1758)	Blainville, 1834	Antipathidae Ehrenberg, 1834

\*The genus Arachnopathes was not recognized by later workers such as van Pesch (1914) and Pax (1918).



**FIGURE 1.** *In situ* pictures of *Antipathes flabellum*, neotype, specimen NHMT-R2E2064. (**a**, **b**) Lateral views. (**c**) Top view showing two of the folds of colony. (**d**) Close-up view of the polyps.

Pallas (1766) described *Antipathes flabellum* based on a specimen from "*Oceanus Indicus*", and he considered the species to be identical to the pre-Linnean species *Ericae marinae tenuis* (Rumphius, 1750). The specimen described by Pallas, which apparently was in his private collection, is missing and presumed lost. Since the original description, the only detailed reports of *A. flabellum* Pallas are those of Brook (1889), based on a specimen from Madagascar in the Indian Ocean and Schultze (1896), based on a specimen collected in the Moluccas in Indonesia.

Due to the flabellate morphology of *A. flabellum*, the species has been assigned to different genera through time. It was first moved from *Antipathes* to *Rhipidipathes* by Milne-Edwards & Haime (1857). Later, Brook (1889) provisionally assigned the species to the genus *Tylopathes* [i.e., *Tylopathes? flabellum* (Pallas) *non* Esper]; however, Pallas's species was not retained in *Tylopathes* when the genus was later placed in the new family Stylopathidae (Opresko, 2006). A recent description of a specimen belonging to the species has been given in Terrana *et al.* (2020), from a specimen collected in the shallow waters of Toliara (SW Madagascar), and includes plates showing the skeleton spines under SEM.

There are currently 36 nominal species of the genus *Antipathes* that have been described in the Indo-Pacific Ocean, of which 13 lack type material. The purpose of this paper is to designate a neotype for *Antipathes flabellum* Pallas, especially in light of the fact that recent DNA studies indicate that *Antipathes dichotoma* (which is currently the type species of the genus *Antipathes*, the latter being the type genus of the Antipathidae) is more closely related to species in the family Aphanipathidae than to species that have been universally recognized as belonging in the family Antipathidae (Brugler *et al.*, 2013; Bo *et al.*, 2018; Horowitz *et al.*, 2022).

## Designation of the neotype of Antipathes flabellum Pallas, Fig. 1

Antipathes flabellum Pallas 1766, p. 211; Schultze 1896, pp. 28–30. Rhipidipathes flabellum, Milne-Edwards & Haime 1857, p. 321 Tylopathes? flabellum, Brook 1889, p. 137 (see additional citations therein)

#### Material examined

Register number NHMT-R2E2064 of the Natural History Museum & Vivarium of Tournai (Belgium). SEM samples NHMT-R2E2064.1–6. Field data: Collected May 13, 2019, off the North Pass of the Great Reef of Toliara (23°20.978'S, 43°36.885'E), Madagascar, field ID No. M130519, depth 22 m, collected by L. Terrana, SCUBA partner M. Godefroid.

#### Description of the neotype of Antipathes flabellum Pallas, 1766

The colony is branched to multiple orders, flabellate and irregularly anastomosed (Figs. 1, 2). It measures 26 cm in width, and 20 cm in height and has a brownish color (Figs. 1, 2). At the base, there are several polyp-bearing branches connected to the basal plate, anchored to a piece of rock (Fig. 2, a, b). These stems contact each other and fuse together a few centimeters above the basal plate (Fig. 2, b). They give rise to several branches that will subdivide to form the general appearance of a fan (Fig. 2, a). Directly above the basal plate, the branches have a thickness of ~2.2 mm; which decreases to ~1 mm around 2 cm above the basal plate; and in the middle of the colony the branches measure ~0.54 mm in diameter.

This fan-shaped colony is composed of several folds that grow parallel to each other (Figs. 1, b, c and 2, d). In the middle part of the colony, the terminal branchlets of the extremity of the folds can fuse with the adjacent ones, thus "closing" the fold (Fig. 3, e).

The corallum is reticulated and the branches bear terminal branchlets that are generally slightly bent upwards and extend outside of the plane of the fan (Fig. 2, a, c, d). They randomly fuse with adjacent branches or terminal branchlets to form the anastomosed shape of the colony. The terminal branchlets measure mostly 0.87–4 mm in length (n=50), mean 2.60 ± 0.78 mm, but longer ones have been observed reaching 6 mm. A terminal branchlet measuring 6 mm in length has a basal diameter of 0.16 mm without the tissues and the spines. For comparison, a terminal branchlet measuring 1.7 mm in length has a basal diameter of 0.12 mm without the tissues and the spines. Terminal branchlets of the same side are irregularly spaced 0.38–3.16 mm apart, mean 1.40 ± 0.51 mm (Fig. 2, d). Branchlets do not follow a regular arrangement, as they can be found biserial alternate, sub-opposite or opposite to a terminal branchlet on the other side (Fig. 2, d). There are 5–11 terminal branchlets per cm counting both sides of the branch (Fig. 2, d).



**FIGURE 2.** *Antipathes flabellum* neotype, specimen NHMT-R2E2064. (a) Lateral view of the entire specimen, with the basal plate anchored to a rock. (b) Close-up view of the several basal stems of the colony, all growing from the basal plate. They are covered by polyps. (c) Close-up view of the terminal branchlets that extend outside of the bidimensional plan of the colony. Polyps are found on the outermost side. (d) Close-up view of the branching pattern of the colony, seen by unfolding the colony. The dotted line represents the crease between the two folds. In this case, the polyps of both folds are facing each other in their natural state.

On the terminal branchlets, the polyps are all located on the same side of the colony in a single row, and generally on the outer side (Fig. 2, c). On the branches, they tend to be irregularly distributed on all sides. There are 10-12polyps per cm. They measure 0.42-0.94 mm in diameter and are spaced a maximum of 0.64 mm apart, although they tend to be closer to each other on the terminal branchlets. On living colonies expanded tentacles seen during the day are small, thick and rounded (Fig. 1, d).

On the terminal branchlets, polypar spines are smooth, conical, and extend out at a right angle to the branchlet axis or are slightly inclined upwards (Fig. 3, d, h). On a section measuring 0.14 mm in diameter, polypar spines

measure 0.06-0.08 mm in height and are spaced 0.18-0.27 mm apart (~5–7 spines per mm). On the other side, the abpolypar spines are smooth, triangular, at right angle to the axis or slightly inclined upwards, generally with the distal edge of the spine at right angle to the branchlet axis (Fig. 3, d, i). These abpolypar spines have the same size range as the polypar spines, they measure 0.05-0.09 mm in height and are spaced 0.13-0.29 mm apart (~5–6 spines per mm). There are 4 longitudinal rows of spines visible in one view.



**FIGURE 3.** SEM pictures of the skeleton of *Antipathes flabellum* neotype, specimen NHMT-R2E2064. (a) NHMT-R2E2064.5 section of a branch 1.1 mm in diameter. (b) NHMT-R2E2064.6 section of a branch 0.34 mm in diameter. (c) NHMT-R2E2064.6 section of a branch 0.23 mm in diameter. (d) NHMT-R2E2064.4 section of a terminal branchlet 0.15 mm in diameter. (e) NHMT-R2E2064.2 close-up view of a fusion between a terminal branchlet and a branch. (f) NHMT-R2E2064.6 detailed view of blunt and stout spines, sometimes showing two tips. (g) NHMT-R2E2064.5 detailed view of tall, cylindrical spines along with double spines growing from the same base. (h) NHMT-R2E2064.4 polypar spine of a terminal branchlet. (i) NHMT-R2E2064.4 abpolypar spine of a terminal branchlet.

On the section shown in Fig. 3, c, the abpolypar spines are smooth, conical, with a sharp or blunt tip (Fig. 3, g). On this section measuring 0.23 mm in diameter, these spines measure 0.05-0.07 mm in height and are spaced 0.15-0.23 mm apart (~5–8 spines per mm). On the other side, the polypar spines are smooth, conical, inclined in different directions but mostly upwards, with a sharp tip. They measure 0.07-0.11 mm in height and are spaced 0.09-0.30 mm apart (~5–7 spines per mm). There are 4–5 longitudinal rows of spines visible in one view.

On a section of branch measuring 0.34 mm in diameter, the spines measure 0.06-0.09 mm and are spaced 0.27-0.30 mm apart (~4-6 spines per mm). There are 4 longitudinal rows of spines visible in one view. Sometimes, bifid spines are found which can be divided at varying distances from near the tip to the base (Fig. 3, c, f, g). Bifid spines are usually found on the branches and not the terminal branchlets, although some may occasionally occur.

On a section of branch measuring 0.53 mm in diameter, the spines measure 0.05-0.08 mm in height and are spaced 0.18-0.31 mm apart (~5-6 spines per mm). On the branches, the spines are smooth, either conical or cylindrical, and extend out at a right angle to the axis or are inclined in different directions (Fig. 3, a, b, g).

On a section of branch measuring 1 mm in diameter, the spines measure 0.05–0.11 mm in height, and their mutual distance cannot be measured as they are irregularly arranged around the skeleton (Fig. 3, a).

#### Description of the sequenced specimen of Antipathes flabellum, Fig. 4

#### Material examined

Register number NHMT-R2E2063 of the Natural History Museum & Vivarium of Tournai (Belgium). SEM samples NHMT-R2E2063.1–4. Field data: Collected May 11, 2019, off Soalara (South Toliara, 23°35.197'S, 43°42.084'E), Madagascar, field ID No. M110519-[2], depth 17 m, collected by L. Terrana, SCUBA partners M. Godefroid & J.M. Dugauquier. Specimen sequenced with UCEs and included in two phylogenies (see Horowitz *et al.*, 2022 and Quattrini *et al.* 2023).

#### Description

The colony is branched, flabellate, irregularly anastomosed and has epifauna growing on the basal part of the colony (Fig. 4, a, b). It measures 22 cm in width and 28 cm in height (Fig. 4, a, b). The colony has only one stem arising from the basal plate (Fig. 4, b). There are several folds that grow parallel to each other (Figs. 2, b). The terminal branchlets are slightly bent upwards and extend outside of the plane of the corallum (Fig. 2, b). They are randomly fused with adjacent branches or terminal branchlets (Fig. 2, b). The terminal branchlets measure 1.37–4.43 mm in length (n=50), mean 2.80 ± 0.85 mm. Terminal branchlets of the same side are irregularly spaced 0.28–4.0 mm apart, mean 1.51 ± 0.70 mm. Branchlets do not follow a regular arrangement, as they can be biserial and alternate, sub-opposite, or opposite to a terminal branchlet on the other side. There are 7-12 terminal branchlets per cm. On the terminal branchlets, the polyps are located on the same side of the colony in a single row. On the branches, they tend to be irregularly distributed on all sides. There are 10–12 polyps per cm. The polyps measure 0.48–0.94 mm in diameter and are spaced maximum 0.52 mm apart, but they tend to be closer together on the terminal branchlets.

The spines are smooth, either conical or cylindrical, generally at right angle to the axis (Fig. 4, c, d) or inclined in different directions on the larger branches (Fig. 4, c). On a terminal branchlet (Fig. 4, d) measuring 0.14 mm in diameter, polypar spines (Fig. 4, e) measure 0.07-0.11 mm in height and are spaced 0.15-0.28 mm apart (~4–6 spines per mm) while abpolypar spines (Fig. 4, f) measure 0.05-0.07 mm in height and are spaced 0.10-0.28 mm apart (~4–6 spines per mm). There are 4–5 longitudinal rows of spines visible in one view. On a section measuring 0.40 mm in diameter, the spines measure 0.05-0.09 mm in height and are spaced 0.09-0.42 mm apart (~4–6 spines per mm). There are 4 longitudinal rows of spines visible in one view. On a section measuring 0.80 mm in diameter, the spines weat of spines visible in one view. On a section measuring the spines measure 0.06-0.10 mm in height and are mostly irregularly arranged around the axis, but in places where they are arranged in a longitudinal row they are spaced 0.11-0.50 mm apart.

## Discussion

Antipathes flabellum was originally established by Pallas (1766) who briefly described the species as follows: "Antipathes explanata ramosissima subdivisa, ramilis bifariam ramosis, reticulatim cohaerentibus" ("Antipathes spreading and flattened in a plane, very branched, divided into bifurcated branches, reticulately cohering"). Pallas (1766)



FIGURE 4. Antipathes flabellum, sequenced specimen NHMT-R2E2063. (a) In situ picture of the colony, with epifauna growing on the basal part, and a feather star on top. (b) Entire colony photographed in the laboratory showing the epifauna condensed in the basal part. (c) NHMT-R2E2063.1 section of a branch 0.40 mm in diameter. (d) NHMT-R2E2063.4 section of a terminal branchlet 0.12 mm in diameter, with the polypar side on the right. (e) NHMT-R2E2063.4 polypar spine of a terminal branchlet. (f) NHMT-R2E2063.4 abpolypar spine of a terminal branchlet.

further states that his specimen is half a foot in diameter, undulatingly curved and thin; with a short trunk, thinner at the base, and branched in couplets. The branches are described as ascending, divided, very long, thin, and scattered in the plane. Branchlets are setaceous, irregularly alternate, numerous, open, scattered, and the elongations from these converging and coalescing. A parenthetical remark by Pallas suggests that the terminal branchlets project out of one side of the fan. This original description lacks sufficient information on the skeletal spines and polyps for an accurate identification of the species; therefore, it is necessary to establish a neotype consistent with more detailed descriptions given by later authors, mostly during the 19<sup>th</sup> century (see Table 2 for a summary of the intraspecific morphological variation). For example, Brook (1889) described a specimen from Madagascar as being flattened



**FIGURE 5.** Maximum likelihood phylogeny of the Antipatharia based on a 50% complete matrix containing 1,047 loci. Taxon in blue represents *Antipathes flabellum* NHMT-R2E2063.

the spines is g place where s <sub>l</sub>	given with t pecimens w	heir maximu	um range of var d.	iation, as well	as the mutual (	distance and	the number	of longitudinal row	's of spines.	The locality	y correspone	ls to the original
Reference	Height (cm)	Width (cm)	Length branchlets (mm)	Branchlet spacing (mm)	Number of branchlets per cm	Number polyps per cm	Polyp size (mm)	Typical spine shape and orna- mentation	Spine size (mm)	Mutual distance (mm)	Number of rows	Locality
Brook (1889)	Not reported	Not reported	3-6	4-10	Not reported	Not re- ported	Not reported	Sharp tip, mostly at a right angle to the axis, but certain hooked upwards	0.11 (estim.)	0.16-0.20 (estim.)	2 V	Off Madagas- car
Schultze (1896)	16	18	3-5	Not re- ported	Not reported	~10	0.75	Smooth, narrow, at right angle to the axis, rounded or sharp tip	0.095	Not reported	56	Moluccas, Indonesia
Terrana <i>et al.</i> (2020)	30	45	1–6	1.9 (mean)	7-13	9–12	6.0-9.0	Smooth, conical, sharp tip, gener- ally at right angle to the corallum	0.06-0.1	0.16-0.35	5-6	Toliara, SW Madagascar
Neotype NHMT- R2E2064	20	26	1–6	0.4-3.2	5-11	10–12	0.4-0.95	Smooth, conical, sharp tip, gener- ally at right angle to the corallum	0.05-0.11	0.13-0.30	4-5	Toliara, SW Madagascar
Sequenced specimen NHMT- R2E2063	28	22	1.4-4.4	0.28-4	7-12	10–12	0.48-0.94	Smooth, conical, sharp tip, gener- ally at right angle to the corallum	0.05-	0.09–0.5	4-5	Soalara (South Toliara), SW Madagascar

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and trellis-like with a flattened plate-like section coming off at right angles; the lower branches arising irregularly and fused together by "bridges of sclerenchyme". In the upper part of the colony the branches extend vertically and possess subalternately arranged pinnules which are 3 to 6 mm long and fused to adjoining pinnules. These pinnules were reported to have secondary pinnules that arise from the anterolateral margins and are usually free. With the exception of these free small secondary pinnules, the whole of the corallum is fused into a close reticulum. The spines are described as moderately long and twice as tall as wide at the base, and tapering to a moderately sharp point. As estimated from the figure given, the spines are approximately 0.11 mm tall (Brook, 1889, Plate XI, fig. 18). Most of the spines are said to form a right angle to the axis but some are hooked upward. Polyps were not described.

Schultze (1896) described a specimen from Moluccas (Indonesia) with terminal branchlets measuring 3–5 mm long and numerous fusions, some of them growing out of the plan. The spines are conical and narrow, smooth with rounded or sharp tips, and inserted at right angle to the corallum. They measure 0.095 mm and five to six rows can be seen from one aspect. The transverse diameter of the polyps measures 0.75 mm and ten are found per cm. These values are considered in the variation range of the species (Table 2).

Schultze reported unusual spines on a branch of 0.04mm with spines "heavy form and irregular arrangement, either dense and sparse", which differs "very noticeably from the usual condition". Schultze stated that "Such findings are rare and are without value for species differentiation."

In Terrana *et al.* (2020), a specimen of *A. flabellum* (RBINS, INV.131354, field ID M041215-M017) was collected in the same site and depth as that of the neotype described here, in the North Pass of the Great Reef of Toliara (SW Madagascar). The specimen INV.131354, which is a fragment of a colony, shares the same morphological traits than the neotype NHMT-R2E2064 described here regarding the branching pattern, the general shape of the colony, polyp size and spacing, and skeleton features (spine arrangement, shape, ornamentation, size and spacing, Table 2).

The specimen NHMT-R2E2063, morphologically described here, was sequenced in Horowitz *et al.* (2022) using ultra conserved elements and exon nuclear loci (Fig. 5), which showed that it falls within the family currently recognized as Antipathidae. See Materials and Methods in Horowitz *et al.* 2022 for details about molecular analyses. The morphological features of NHMT-R2E2063 closely matches the neotype, and the slight differences in size or mutual spacing of the spines are considered as morphological intraspecific variation, therefore the genetic sequence of NHMT-R2E2063 can be considered as representative of the species for which the neotype is the specimen NHMT-R2E2064.

In conclusion, in regards to the colony growth form; size and density of the branchlets; size, shape and ornamentation of the spines; and size and density of the polyps (summarized in Table 2), the neotype is considered representative of the species as it has been recognized for the past 150 years for Indo-Pacific specimens.

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