



Zootaxa 4826 (1): 001–062

<https://www.mapress.com/j/zt/>

Copyright © 2020 Magnolia Press

Monograph

ISSN 1175-5326 (print edition)

ZOOTAXA

ISSN 1175-5334 (online edition)

<https://doi.org/10.11646/zootaxa.4826.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:1DC59C31-61D1-4458-897B-29D9CA523634>

ZOOTAXA

4826

Shallow-water black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia) from SW Madagascar

LUCAS TERRANA^{1*}, MARZIA BO², DENNIS M. OPRESKO³ & IGOR EECKHAUT^{1,4}

¹*Biology of Marine Organisms and Biomimetics, University of Mons, Belgium*

²*Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di Genova, Italy*

<https://orcid.org/0000-0001-8400-6722>

³*National Museum of Natural History, Smithsonian Institution, Washington DC, USA*

<https://orcid.org/0000-0001-9946-1533>

⁴<https://orcid.org/0000-0002-8159-1062>

*Corresponding author: [✉ lucas.terrana@umons.ac.be](mailto:lucas.terrana@umons.ac.be); <https://orcid.org/0000-0001-5767-3220>



Magnolia Press
Auckland, New Zealand

Accepted by M. Daly: 16 Jul. 2020; published: 10 Aug. 2020

Licensed under a Creative Commons Attribution 4.0 International License <http://creativecommons.org/licenses/by/4.0/>

LUCAS TERRANA, MARZIA BO, DENNIS M. OPRESKO & IGOR EECKHAUT
Shallow-water black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia) from SW Madagascar
(*Zootaxa* 4826)

62 pp.; 30 cm.

10 Aug. 2020

ISBN 978-1-77688-006-5 (paperback)

ISBN 978-1-77688-007-2 (Online edition)

FIRST PUBLISHED IN 2020 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

<https://www.mapress.com/j/zt>

© 2020 Magnolia Press

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract	3
Introduction	4
Material and methods	4
Results	7
Family Antipathidae Ehrenberg, 1834	8
Genus <i>Antipathes</i> Pallas, 1766	8
<i>Antipathes flabellum</i> Pallas, 1766	8
<i>Antipathes hypnoides</i> (Brook, 1889)	10
<i>Antipathes</i> cf. <i>pseudodichotoma</i> Silberfeld, 1909	16
<i>Antipathes</i> cf. <i>virgata</i> Esper, 1788	18
<i>Antipathes</i> sp.	20
Genus <i>Arachnopathes</i> Milne Edwards, 1857	22
<i>Arachnopathes ericoides</i> (Pallas, 1766)	23
Genus <i>Cirrhopathes</i> de Blainville, 1834	25
<i>Cirrhopathes anguina</i> (Dana, 1846)	25
<i>Cirrhopathes densiflora</i> Silberfeld, 1909	27
<i>Cirrhopathes</i> cf. <i>indica</i> Summers, 1910	30
<i>Cirrhopathes rumphii</i> van Pesch, 1910	33
<i>Cirrhopathes</i> cf. <i>spiralis</i> (Linnaeus, 1758)	37
Genus <i>Stichopathes</i> Brook, 1889	37
<i>Stichopathes</i> cf. <i>diversa</i> (Brook, 1889)	38
<i>Stichopathes</i> cf. <i>maldivensis</i> Forster Cooper, 1903	40
Family Myriopathidae Opresko, 2001	42
Genus <i>Myriopathes</i> Opresko, 2001	42
<i>Myriopathes</i> cf. <i>myriophylla</i> (Pallas, 1766)	42
<i>Myriopathes</i> cf. <i>stechowi</i> (Pax, 1932)	44
<i>Myriopathes</i> cf. <i>ulex</i> (Ellis & Solander, 1786)	46
<i>Myriopathes</i> sp.	48
Genus <i>Cupressopathes</i> Opresko, 2001	50
<i>Cupressopathes abies</i> (Linnaeus, 1758)	50
<i>Cupressopathes</i> cf. <i>pumila</i> (Brook, 1889)	52
<i>Cupressopathes</i> sp. 1	54
<i>Cupressopathes</i> sp. 2	56
Discussion	58
Acknowledgments	58
Literature cited	59

Abstract

Antipatharians, also known as black corals, represent a small group of anthozoan hexacorallians found in all oceans of the world. They are generally considered a deep-water taxon; however, some of the most diverse communities are known from tropical shallow waters. With a few poorly detailed exceptions, shallow-water black corals from the Indian Ocean and especially those from Madagascar are mostly unknown. In this study, we report for the first time a highly diverse black coral assemblage of the Western Indian Ocean thriving in shallow waters and upper mesophotic depths (10–52 m depth) along the SW coast of Madagascar. A total of 22 species belonging to six genera (*Antipathes*, *Arachnopathes*, *Cirrhopathes*, *Cupressopathes*, *Myriopathes* and *Stichopathes*) and two families (Antipathidae and Myriopathidae) are described, of which 20 are found in the northern pass of the Great Reef of Toliara, thus representing the most diverse site of the areas investigated. Most of the shallow-water species from the Indian Ocean were originally described more than a century ago, sometimes without being reported again until now. All the descriptions herein rely solely on morphology and include detailed *in situ* pictures and scanning electron microscope images, in addition to range expansions for many species.

Key words: Antipathidae, Myriopathidae, Indian Ocean, taxonomy, Toliara

Introduction

Antipatharians, also known as black corals, are colonial cnidarians characterized by non-retractile polyps with six unbranched tentacles and a black spiny flexible proteinaceous and chitinous skeleton (Opresko *et al.* 2014). With seven families (Antipathidae, Aphanipathidae, Cladopathidae, Leiopathidae, Myriopathidae, Schizopathidae and Stylopathidae), 46 genera and around 273 species (Brugler *et al.* 2013; Opresko 2019; Molodtsova & Opresko 2020), they represent one of the smallest hexacorallian orders; nonetheless, they still show a wide geographical and bathymetrical distribution as well as large morphological variability (Wagner *et al.* 2012).

The species-level taxonomy of this group is considered very challenging due to the numerous historical descriptions based on incomplete specimens, the lack (or inaccessibility) of many types, and the unclear relationships between morphological and phylogenetic analyses (Bo *et al.* 2012a; Brugler *et al.* 2013). Some parts of the current classification are still polyphyletic pending revisions based on morphological and molecular data (Lapian *et al.* 2007; Lapian 2009; Brugler *et al.* 2013). Nevertheless, since the 1970s, a major effort has been undertaken to revise the taxonomy of the order and to redescribe existing type material. This literature is what is currently adopted for the classification of these taxa. The classification at the familial level is based primarily on internal anatomy (number of mesenteries), polyp morphology (size and shape), and spine morphology, while corallum shape is useful at the generic level (Opresko 1972, 1974, 1976, 1997, 2001, 2002, 2003a, 2003b, 2004, 2006, 2009; Wagner *et al.* 2010; Bo & Opresko 2015).

Antipatharians are generally considered a deep-water taxon, with ~75% of the described species found below 50 m depth (Cairns 2007). However, some of the most diverse communities are known from tropical shallow and mesophotic waters of the Western and Central Indo-Pacific, the Hawaiian Islands and the Caribbean Sea (Opresko & Sanchez 2005; Tazioli *et al.* 2007; Bo *et al.* 2012a, 2019). For instance, the Indonesian Archipelago hosts a rich antipatharian community, with many reported species and undescribed taxa (Tazioli *et al.* 2007; Bo *et al.* 2009, 2012a, 2019), the Caribbean hosts 15 ascertained taxa (Opresko & Sanchez 2005; Bo *et al.* 2019), the Pacific assemblages of Hawai'i are mainly characterized by mesophotic species, with four known from shallow depths (Wagner *et al.* 2015a, b), and the coastal communities of Ecuador account for a few species (Bo *et al.* 2012b).

Descriptions of shallow-water and mesophotic black corals from the Indian Ocean are older than a century and can be found in reports from the Challenger Oceanographic Expedition (Brook 1889) and the Percy Sladen Trust Expedition (Forster Cooper 1909), and from expeditions to the Gulf of Manaar (Thomson & Simpson 1905) and the Mozambique (formerly known as Portuguese East Africa) and the Mergui Archipelago (Summers 1910). Since these original descriptions were published, many species have only been documented a few times, and some not at all. As a result, the biodiversity of the antipatharian fauna in this region is very poorly known, especially for the eastern African coasts including Madagascar. However, the presence of black corals in the shallow waters off the southwestern coast of Madagascar has been documented by several studies including those of Pichon (1972), and more recently Todinanahary *et al.* (2016), Terrana & Eeckhaut (2017, 2019) and Terrana *et al.* (2019). Malagasy black corals have also been collected during recent expeditions of the National Museum of Natural History of Paris to the northwestern coast (100–1200 m, Miriky Expedition in 2009) and the south and southeastern coasts (<30 m, Atimo Vatae Expedition in 2010).

Overall, none of these reports detail the biodiversity and the taxonomic characteristics of the black corals sampled from that region. In this work, we establish the first systematic study using scanning electron microscopy to describe morphologically the diversity of the shallow-water black corals off the southwest coast of Madagascar. We also describe a densely populated black coral bed found in the northern pass of the barrier reef of Toliara that sustains the richest assemblage of the area. This document will form an important foundation for further antipatharian taxonomy studies to resolve knowledge gaps pertaining to species diversity and species ranges in the Indian Ocean and beyond.

Material and methods

Sampling sites and sampling strategy. The study area extends 200 km along the southwest coast of Madagascar (Fig. 1, a), and is bounded by two coastal fishing villages, namely Andavadoaka (22°04.214'S, 43°14.332'E) and Maromena (23°48.476'S, 43°39.477'E) (Fig. 1, b, Table 1). Black corals were collected during expeditions that took

place between December 2014 and December 2019 at 15 sites by SCUBA-diving at depths ranging from 10 to 52 meters (Fig. 1, Table 1).

TABLE 1. Coordinates (WGS84) of the diving locations where black corals were sampled, with the maximum depth.

Number	Station name	Coordinates		Max Depth (m)
1	Nosy Fasy, Andavadoaka	21°58.674'S	43°11.653'E	10
2	Nosy Hao, Andavadoaka	22°04.742'S	43°10.944'E	10
3	Fringing reefs, Andavadoaka	22°00.530'S	43°12.960'E	20
4	Patch reefs, Andavadoaka	22°07.518'S	43°11.886'E	20
5	Ambatomilo	22°30.941'S	43°14.934'E	20
6	Ifaty barrier reef	23°09.089'S	43°33.883'E	25
7	Great reef of Toliara, north channel	23°21.040'S	43°36.944'E	30
8	Great reef of Toliara, north channel	23°21.284'S	43°36.336'E	52
9	Great reef of Toliara, Grande Vasque	23°22.976'S	43°38.152'E	15
10	Great reef of Toliara, south channel	23°30.051'S	43°41.555'E	10
11	Sarodrano reefs	23°29.695'S	43°43.549'E	10
12	Soalara	23°35.197'S	43°42.084'E	15
13	Soalara	23°35.259'S	43°42.531'E	20
14	Anakao	23°39.306'S	43°36.541'E	15
15	Maromena	23°48.113'S	43°38.252'E	25

The sites were chosen based on: (i) previous reports of the presence of black corals in the area (Pichon 1972; Terrana & Eeckhaut 2018, 2019), (ii) reef topography and hydrology, and (iii) past occurrences of coral fishing activities (Todinanahary *et al.* 2016). In the study area, some locations are directly influenced by rivers flowing into the sea. The northernmost site, Andavadoaka, is located 70 km south of the Mangoky delta and is characterized by a series of small fringing reefs all immediately adjacent to the shore (Pichon 1972). The fringing reefs located between Ambatomilo and Ifaty are almost continuous for 80 km. Reefs are fragmented by the Manombo river, which flows into the sea between Ifaty and Tsifota (Fig. 1). The reef off Ifaty is interrupted twice, resulting in two channels where large quantities of water move with the tides. From Toliara to Sarodrano, the reef is a continuous barrier reef 18 km long where the only two links with the open sea are through two channels located at the north and south extremities (Pichon 1972). The north extremity is directly in front of the Fiherenana delta (Fig. 1) while the south extremity is surrounded by small fringing reefs in front of Sarodrano and separated by only 5 km from the Onilahy delta, in the bay of Saint-Augustin (Fig. 1). Finally, south from the Onilahy the fringing reef remains unbroken for almost 100 km (Pichon 1972). In all these places, black corals are commonly found where strong currents and/or high turbidity occur, sometimes in locations characterized by steep slopes, rocky boulders or small caves.

Living colonies were photographed before being sampled; apical subsamples for unbranched species and distal portions for branched species were collected. For several species, whole colonies were sampled. Subsamples were preserved in Bouin's fluid, in 10% formalin buffered with seawater or 70% ethanol for long-term storage. Samples have been deposited at the Royal Belgian Institute of Natural Sciences in Brussels (Belgium) under the general inventory number I.G. 33702, with register numbers INV.131334 to INV.131380.

Specimen descriptions. Scaled pictures of *in vivo* specimens and lab images of full colonies and fragments were used to determine the colony size and branch, pinnule and polyp characteristics. Scanning electron microscope was employed to determine the fine ornamentation and arrangement of the spines. Tissues were carefully removed under a dissection microscope with fine clippers. Residual tissues were cleaned using a 15% bleach solution, immediately rinsed in 70% ethanol to avoid denaturation of the skeleton. This step was repeated until tissues dissolved completely. To remove any remaining pieces of tissue, the skeletons were sonicated. They were then air-dried, mounted on aluminium stubs and coated with pure gold or a mix 60%/40% palladium and gold for three minutes under a 10 mA current in a JEOL JFC-1100E sputter coater. Samples were observed with a JEOL JSM-7200F scanning electron microscope.

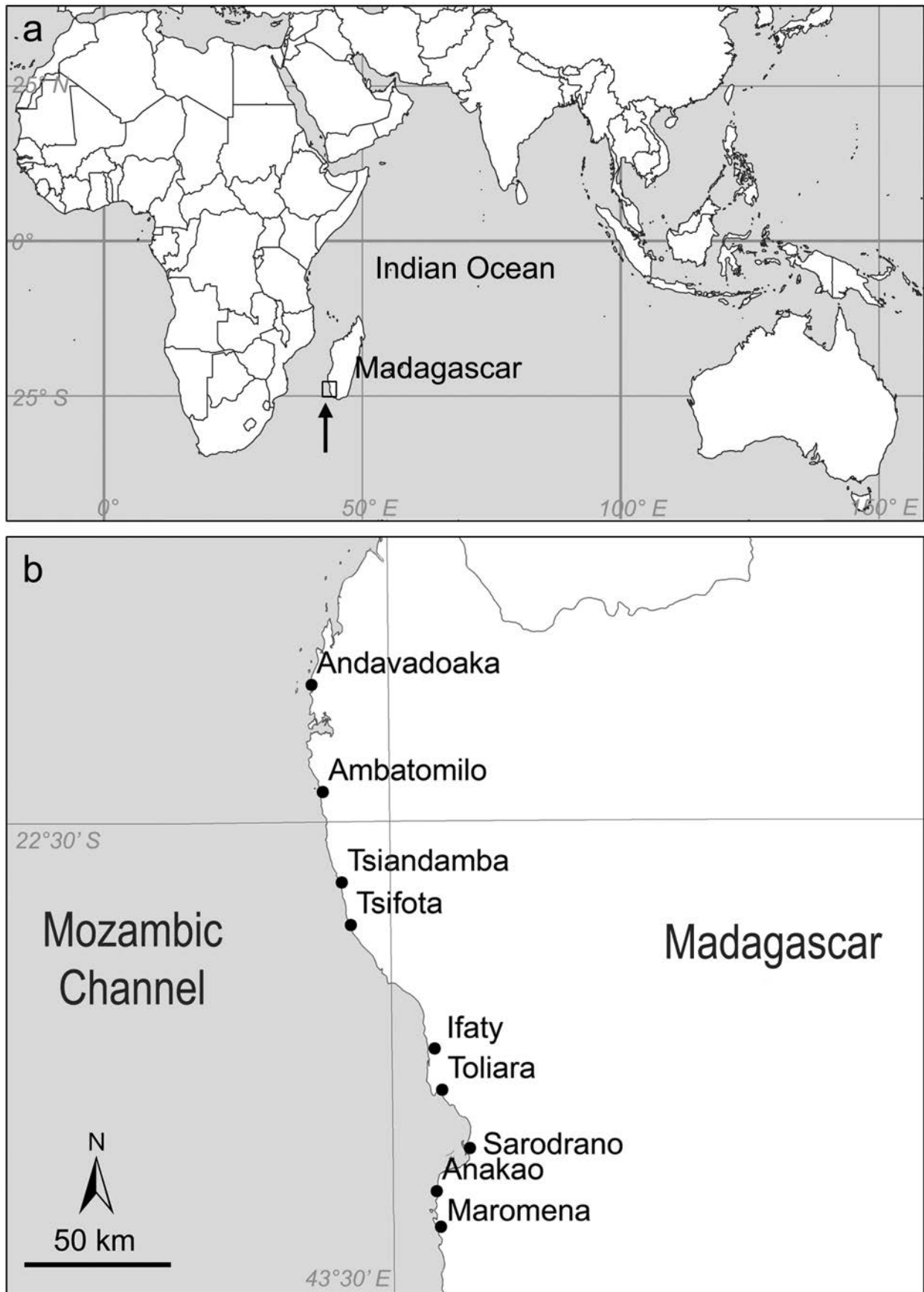


FIGURE 1. (a) Map showing the western position of Madagascar in the Indian Ocean, with the studied sites located off the southwestern coast in the Mozambic Channel. (b) Details of the southwestern coast and the coastal villages near where surveys were performed.

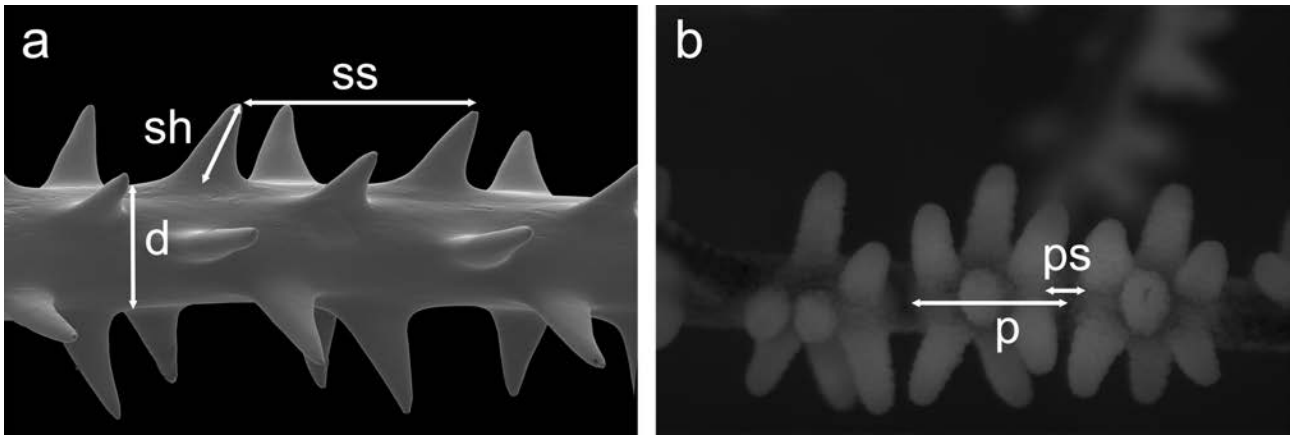


FIGURE 2. (a) Measurements made on the skeleton. (b) Measurements made on the polyps. d—diameter; p—transverse polyp diameter; ps—polyp spacing; sh—spine height; ss—spine spacing.

Measurements detailed below on the spines and polyps were made on fixed fragments following Wagner *et al.* (2010) and Opresko (2001, 2002, 2003b, 2004, 2006) using ImageJ (Schneider *et al.* 2012) or an ocular micrometer using a stereomicroscope. When applicable, the length, density, spacing and angles of insertion of the pinnules were described, as well as the density of branching. Spine height was measured from the apex to the center of the base of the spine (“sh” in Fig. 2a) with the diameter of the branch or pinnule (“d” in Fig. 2a). Spine spacing (also referred to as mutual distance) was measured from the tip of one spine to the tip of an adjacent spine in the same axial row (“ss” in Fig. 2a). Arrangement and number of rows visible in frontal view were also analysed. Polyp size was measured using transversal diameter (“p” in Fig. 2b). Polyp spacing was measured between the edge of the distal lateral tentacles of one polyp and the edge of the proximal lateral tentacles of the adjoining ones (“ps” in Fig. 2b). Density of polyps was expressed as number per cm.

Results

The black corals described here were encountered along the southwestern coast, but most of them can also be found at the north channel of Toliara. At the northern extremity of the Great Reef of Toliara, a large area presents a wide diversity of black corals in the pass. It is found about 1.7 km from the shore, extends for about 500 m in length and 300 m in width with black corals living at depths ranging between 10 to 30 m (Fig. 3). The bed is in front of the mouth of the Fiherenana river. Westward from the bed at depths of 40 to 52 m many black corals are also found.

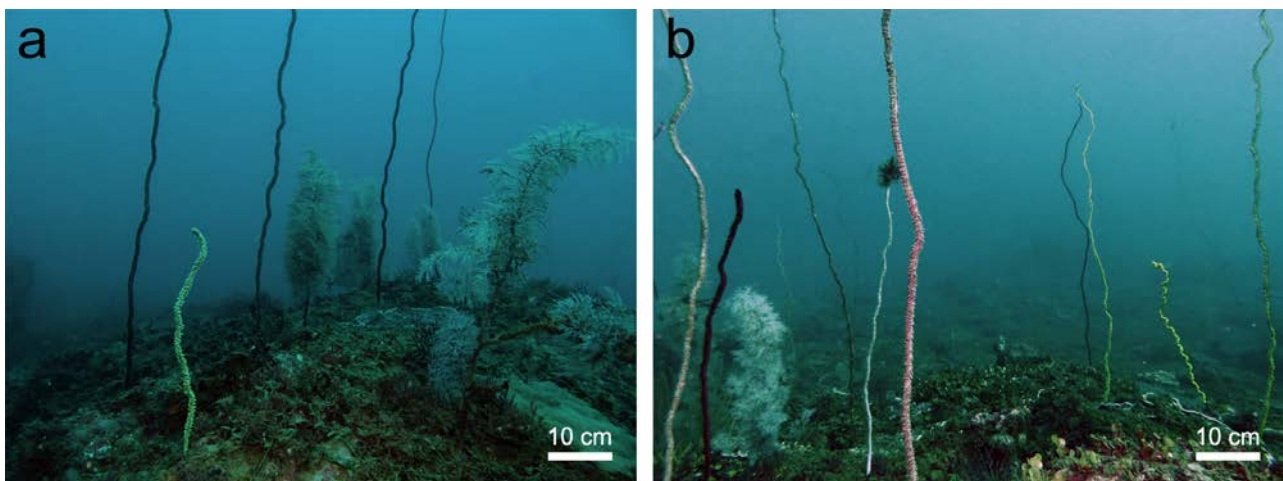


FIGURE 3. (a–b) Different views of the black coral bed in the northern pass of the barrier reef of Toliara showing the abundance of whip and branched colonies.

The morphological analysis resulted in the identification of 22 species belonging to six genera. All of them belong to one of two families: (i) Antipathidae (*Antipathes*, *Arachnopathes*, *Cirrhopathes* and *Stichopathes*) and (ii) Myriopathidae (*Cupressopathes* and *Myriopathes*).

Family Antipathidae Ehrenberg, 1834

This family was the first to be established and contains the highest number of species, with around 130 descriptions (Opresko 1972, 1974; Molodtsova & Opresko 2020). The family is characterized by unbranched species that have a single stem, and branched forms that can be bushy, arborescent, fan-shaped or bramble-like. Clearly defined pinnules are never present, but flabellate species can appear pinnulate because of the bilateral arrangement of the smallest terminal branches. The spines are smooth or papillose and can be simple, forked or multi-lobed. The polyps have ten mesenteries and range from 1 to 3 mm in size (Brugler *et al.* 2013). Polyps are not elongate in the transverse plane and sagittal tentacles are generally longer than the lateral tentacles (Opresko 2005b; Wagner 2015a).

There are currently nine genera within the Antipathidae: *Antipathes*, *Arachnopathes*, *Hillopathes*, *Pteropathes*, *Stichopathes*, *Cirrhopathes*, *Pseudocirrhopathes*, *Allopathes* and *Blastopathes*. Members of this family typically occur at depths less than 200 m, but some species may occur deeper (Opresko 2019). Revisions have been published to clarify the taxonomic position of many antipatharian families (Opresko 2001, 2002, 2003b, 2004, 2005a, 2006), but the family Antipathidae still needs a major revision since colony and skeleton morphologies are very heterogeneous, and genomic studies have identified a number of polyphyletic groups (Bo *et al.* 2012 a; Brugler *et al.* 2013). For example, the type species of the genus *Antipathes*, *Antipathes dichotoma* Pallas, 1766, is more closely related to members of the family Aphanipathidae than to many members of Antipathidae. Future studies gathering molecular and morphological data from large sets of widely distributed specimens will be needed to reassess the current classification of both families (Brugler *et al.* 2013).

Genus *Antipathes* Pallas, 1766

The genus *Antipathes* is the first to have been established (Pallas 1766). It is characterized by colonies that are branched, bramble-like, bushy or fan-shaped (Opresko 1972, 1974). The branches are not pinnulate and the polyps occur in a single row on smaller branches. The spines can be smooth or papillose, simple or forked, multilobed or knobbed at the apex. There are currently about 70 nominal species (Opresko 2019), 36 from the Pacific and Indian Oceans, out of which 13 have their type species lost. New species are still being described, which is why it is difficult to determine the exact number of species belonging in the genus *Antipathes*.

Antipathes flabellum Pallas, 1766

Fig. 4

Antipathes flabellum Pallas 1766, p. 211

Rhipidipathes flabellum Milne-Edwards & Haime 1857, p. 321

Tylopathes? flabellum Brook 1889, p. 137

Material examined. Toliara, 22 m. Fragments from the distal portion of the colony, specimen INV.131354.

Depth range. 15–45 m.

Description. A branched, flabellate and highly anastomosed colony with a brownish color (Fig. 4, a). It measures 45 cm wide and 30 cm high, but larger colonies exist. The general appearance is that of a fan, but with a distinctly horizontal plate-like portion towards the most distal portion of the corallum which extends out perpendicular to the plane of the fan (Fig. 4, a). This plate-like portion is not found on every specimen. The corallum is reticulated; the branches grow almost vertically and bear branchlets which are slightly bent upwards and often fused with the adjacent branchlets (Fig. 4, c). These branchlets measure 1.0–6.0 mm in length and generally have a biserial alternate arrangement, although branchlets can be sub-opposite or opposite to a branchlet on the other side with an average spacing of 1.9 ± 0.9 mm and 7–13 branchlets per cm. Branchlets are inserted on the branches with angles

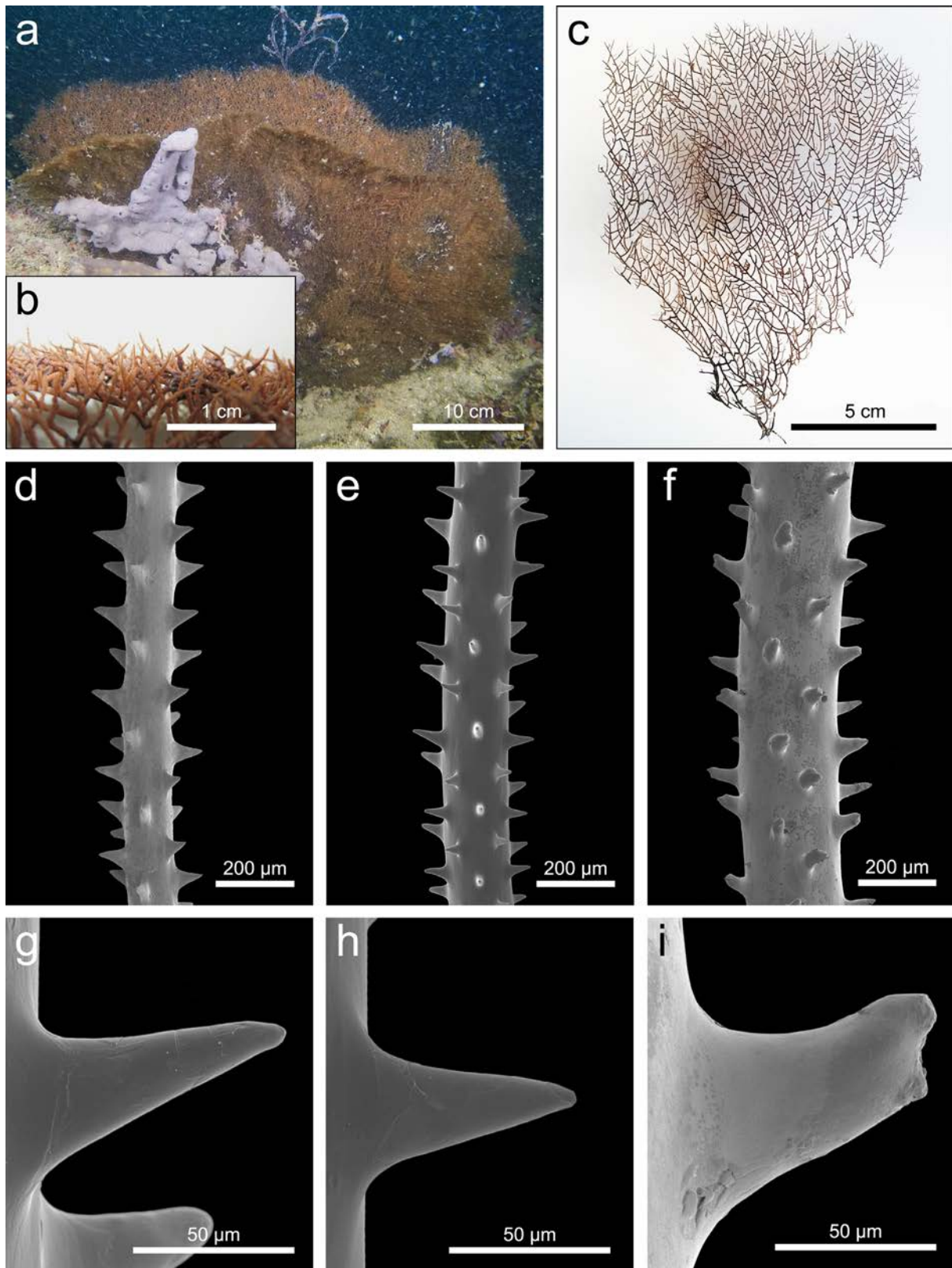


FIGURE 4. *Antipathes flabellum* Pallas, 1766 specimen INV.131354. (a) *In situ* picture of the whole colony showing the flabellate shape. (b) Detailed view of a distal part of the skeleton showing the high number of anastomoses. (c) Section of a branch 0.12 mm in diameter. Polypar side is on the right. (d) Section of a branch 0.17 mm in diameter. Polypar side is on the right. (e) Section of a branch 0.25 mm in diameter. Polypar side is on the right. (f) Polypar spine with distal edge slightly inclined distally on a branch 0.17 mm in diameter. (g) On the same branch, abpolypar spine being straightly inserted on the corallum. (h) Example of an irregularly shaped spine found on larger branches. (i) Another example of an irregularly shaped spine.

varying between 60–100° with an average of $79 \pm 10^\circ$ in a single plane. A third order of branchlets is rarely found, they measure 0.8–2.0 mm in length with a uniserial arrangement. When present, these small branchlets are inserted with angles varying between 60–100° with an average of $85 \pm 15^\circ$. Terminal branchlets which are not fused are sometimes projecting out of the plane of the fan, mostly on one side (Fig. 4, b). The polyps are all located on the same side of the colony, and 9–12 polyps are found per cm. Polyps measure 0.6–0.9 mm in transverse diameter and are spaced 0.06–0.95 mm apart, with an average of 0.32 ± 0.15 mm. Living expanded tentacles seen during the day are small, thick and rounded at the tip. Polyps are arranged in a single row except on the thicker branches where they are less uniform in arrangement and further apart.

The spines are smooth, conical with a sharp apex and generally stand at right angle to the corallum, although sometimes the distal margin is slightly inclined upwards (Fig. 4, d–h). Spines are arranged in 5–6 longitudinal rows. On a branchlet measuring 0.14 mm in diameter, polypar and abpolypar spines have the same size range of 0.06–0.09 mm and are spaced 0.19–0.29 mm and 0.16–0.27 mm apart, respectively. On a branch measuring 0.24 mm in diameter, polypar spines measure 0.07–0.10 mm and are spaced 0.10–0.35 mm apart, while abpolypar spines measure 0.06–0.09 mm and are spaced 0.17–0.30 mm apart. On such branches, some spines show irregular shapes and growths and can be multi-lobed (Fig. 4, f, i).

Taxonomic remarks. Within the Antipathidae, anastomosed colonies are also found within *Arachnopathes* Milne Edwards H., 1857, which shows a distinctly bush-like corallum (Opresko 2006). Similarly, within Stylopathidae, there are species with anastomosed ramifications as well as genera, such as *Tylopathes*, with a similar spine and polyp arrangement; nevertheless, no shallow-water species are known in this family (Opresko 2006).

This species was originally described from the Indian Ocean by Pallas (1766). In the literature, most of the descriptions of this species have been made during the 19th century, with a specimen from Madagascar in the British Museum Collection described by Brook (1889) and very similar to the present specimen. In Brook's specimen, the flattened plate-like portion of the fan is also present. He reports subalternating branchlets measuring 3 to 6 mm, bent upwards and usually fused, as well as free branchlets out of the plane of the fan. Five longitudinal rows of spines can be seen from one aspect. These spines have a sharp apex, most of them being inserted at right angle but some hooked upwards. Schultze (1896) also describes a specimen from Moluccas, Indonesia having very similar features as the present one. His specimen has 3–5 mm long terminal branchlets with numerous fusions, some of the free ones growing out of the plane of the fan as well. 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. On the other hand, the small specimen (10 cm) described by Brito & Ocana (2004) from Canary Islands only shares the size (0.1 mm) and the morphology of the spines, which were reported as being conical. It has longer branchlets (1–10 mm long) and more longitudinal rows of spines (5–8). The photo of the colony presented by these authors reveal a main axis reaching the distal part of the colony, from which numerous thinner branches and branchlets arise, a feature which is not seen in the Malagasy specimen. Considering these differences and the locality (East Atlantic), a reexamination of Brito & Ocana's specimen should be conducted. A neotype should be described for this species, as the type material is lost.

Distribution. Indian Ocean (type locality, Pallas 1766; Lamarck 1815; Lamouroux 1816; Lamouroux *et al.* 1824; Deshayes & Edwards 1836; Dana 1846; Milne-Edwards & Haime 1857), Indonesia (Schultze 1896), ?Canary Islands (Brito & Ocana 2004), Madagascar (Brook 1889; present study).

Antipathes hypnoides (Brook, 1889)

Figs. 5, 6

Tylopathes? *hypnoides* Brook 1889, p.138, pl. XII, fig. 4

Material examined. Toliara, 31 m. Entire colony, specimen INV.131347.

Depth range. 30–35 m.

Description. A branched, planar and flabellate colony measuring 40 cm in width and 25 cm in height, white in color (Fig. 5, a–c). The basal diameter of the axis is 6 mm and rapidly divides in three branches in the same plane. Some branches grow out of the fan before developing parallel to the plane, giving the appearance of overlaid flabellate parts (Fig. 5, b). The general plane of the colony has anterior and posterior sides, however, the parts growing

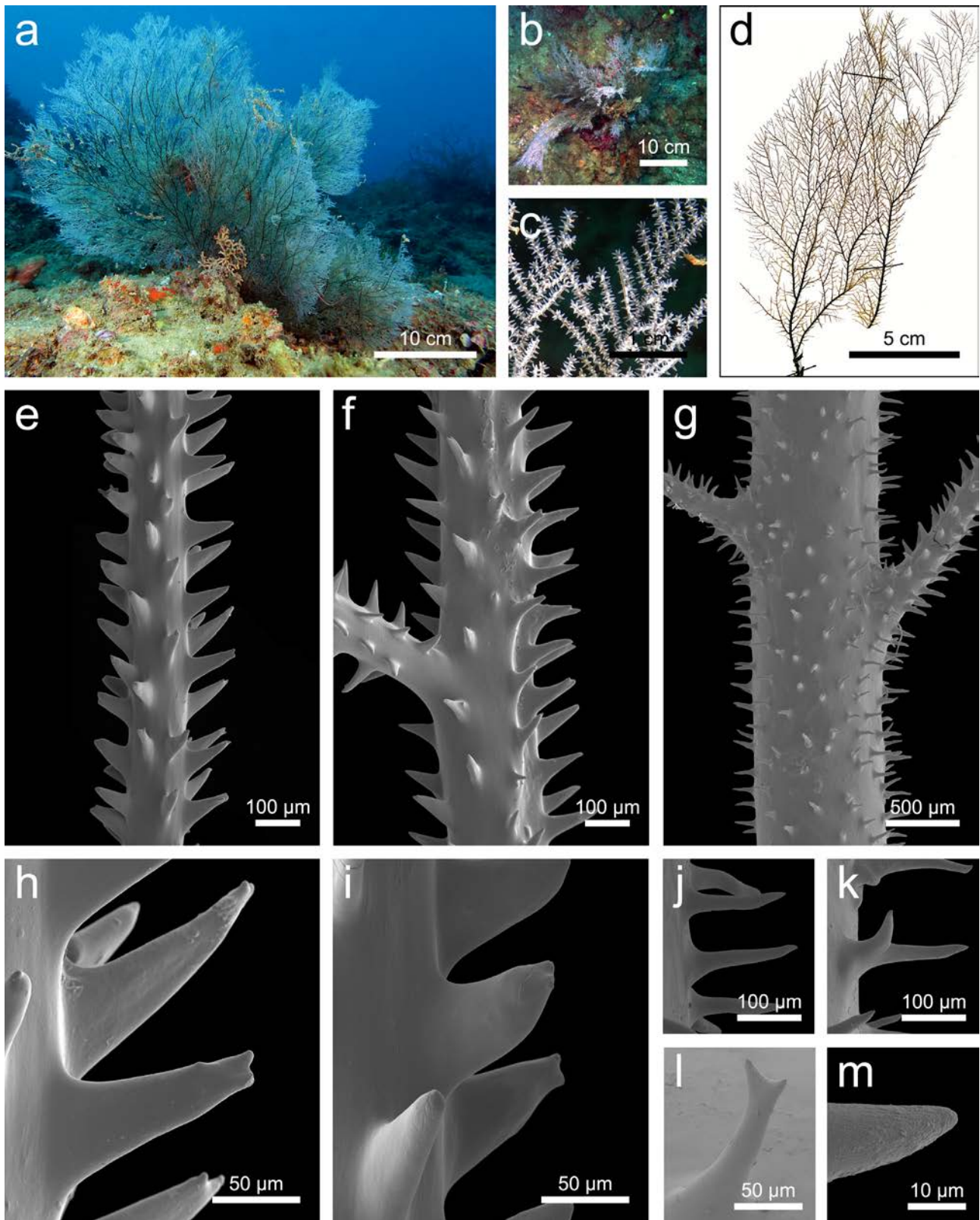


FIGURE 5. *Antipathes hypnoides* (Brook, 1889) specimen INV.131347. (a) Entire colony. (b) Top view of the colony showing some flabellate parts parallel to the plane. (c) Close-up view of expanded polyps. (d) Detailed view of the branching pattern. (e) Section of a branchlet 0.13 mm in diameter. The polypar side is on the right. (f) Section of a branch 0.23 mm in diameter. The polypar side is on the right. (g) Section of a branch 0.90 mm in diameter. (h) Polypar spine on a branch 0.13 mm in diameter. (i) Abpolypar spine on the same branch. (j–l) Needle-like, bifid and forked spines on a 0.90 mm branch. (m) Close-up view of the tip of a spine showing the small papillae.

parallel to the plane can have their anterior side facing the anterior side of the colony. The branchlets are distinctly inserted antero-laterally to the branches, and numerous fusions occur between adjacent ones (Fig. 5, d). The branchlets are not strictly bilateral and alternate as sometimes several branchlets occur on the same side, and rarely opposite or subopposite. At some places they appear nearly as pinnules (Fig. 5, d). Branchlets measure up to 8.5 mm but mostly less than 5 mm in length. Branchlets on the same side of a branch are spaced 1–7 mm, with 7–14 branchlets occurring per cm counting those on both sides (mostly 9–12 per cm). They are inserted on the branches with angles varying between 30–75°, with an average of $55 \pm 10^\circ$. The polyps measure 0.5–0.6 mm in transverse diameter and are spaced 0.2–0.4 mm apart, their tentacles are thick and rounded (Fig. 5, c). They are found in a single row on branchlets but can be irregularly distributed on thicker branches. There are usually 9–12 polyps per cm.

On a branchlet 0.13 mm in diameter, five longitudinal rows of spines can be seen in one aspect, although the longitudinal arrangement is not perfect (Fig. 5, e). On such branch, the polypar spines are tall, conical, generally with an acute tip although some blunt tips are seen (Fig. 5, h). Spines with forked tips are also regularly present (Fig. 5, h). The surface of the tip is finely papillose. Spines measure 0.11–0.13 mm and are spaced 0.10–0.19 mm apart. The abpolypar spines have same morphologies but are shorter, consequently they look stouter (Fig. 5, e, i). Abpolypar spines measure 0.06–0.09 mm and are spaced 0.09–0.16 mm apart. On a branch 0.23 mm in diameter, five longitudinal rows are still seen and the spines have the same morphologies as on thinner branches but they are taller (Fig. 5, f). Abpolypar and polypar spines both reach 0.12 mm and their mutual distance reaches 0.25 mm. On thicker branches, the longitudinal arrangement of the spines is no longer visible (Fig. 5, g). The spines are needle-like and acicular (Fig. 5, g, j), and their tip is distinctly papillose (Fig. 5, m). Bifid and forked spines are also present (Fig. 5, k, l). Their size is 0.11–0.19 mm.

Taxonomic remarks. The spines of the Malagasy specimen share similarities with those of myriopathids by being needle-like, forked or bifid on thicker branches, in addition to having similar size and shape of the polyps. However, on branchlets the spines of the Malagasy specimen are typical of Antipathidae by having apical bifurcations. There is also a difference in the shape of the papillae on the spines: with a few exceptions, in antipathids the papillae are usually round (as in the Malagasy specimen, Fig. 5, m) whereas in the myriopathids the papillae are usually narrow and elongated. Besides there is no true pinnules in the Malagasy specimens, which is a feature of Myriopathidae. However, in some myriopathids such as *Antipathella*, true pinnules are not present and bifurcated needle-like spines can be present on branchlets occasionally (pers. obs. MB).

Originally, this species (Fig. 6) was doubtfully assigned to the genus *Tylopathes* by Brook (1889). In a later study, *T.? hypnoides* and three other species provisionally assigned to *Tylopathes* by Brook (1889), *T.? flabellum*, *T.? dubia* and *T.? elegans*, were excluded from the genus (Opresko 2006). These species most likely should be referred to the genus *Antipathes* based on the morphology of the spines, although their true affiliation is yet to be determined (Opresko 2015). These species, along with *Antipathes craticulata* Opresko, 2015, have in common a flabellate corallum with short, straight or slightly curved terminal branches (Opresko 2015). *Antipathes craticulata* mainly differs from the Malagasy specimen by both the morphology of the spines, which are smooth, conical with an acute tip and up to 0.30 mm, and by the number of branchlets per cm (3–5 per cm). The number of branchlets per cm of the Malagasy specimen (7–14, mostly 9–12) is closer to *An. hypnoides* (12–14) than *An. dubia* (4–6) and *An. elegans* (8–10).

In his description of *Tylopathes? hypnoides*, Brook (1889) reports a fan-like corallum of 23 cm high and 28 cm wide (Fig. 6, a), with branches irregular and spreading, and with frequent fusions (Fig. 6, b). The Malagasy colony is very similar in size and appearance. Brook also reports primary pinnules (*i.e.* branchlets) arranged subalternately and varying in length, many measuring 6 mm (in the present specimen many terminal branchlets are around 5 mm) and some being larger (1.3–2 cm, those bearing branchlets as well). The spines in the type specimen are reported to be subconical and compressed, with the apex often slightly bent upwards. These features can be observed in the present specimen, however, Brook (1889) did not indicate which branch he was analyzing to describe the spines, nor did he report any difference between polypar and abpolypar spines. The size of the spines is reported only as being about three-quarters the diameter of a pinnule, which would be around 0.09 mm for a branchlet measuring 0.13 mm in diameter, which is consistent with the size measured for abpolypar spines in the present specimen. A recent examination of the type (Fig. 6) revealed that the spines are simple, smooth, narrow, with a fairly wide base, and up to 0.15 mm tall (pers. obs. DMO), which falls within the description of the Malagasy specimen. Finally, five longitudinal rows may be counted from one aspect of a branchlet in Brook's specimen, which is also the number of rows reported here for branchlets measuring 0.13–0.23 mm in diameter. Considering these similarities, the close

locality of Brook's specimen to Madagascar (Mauritius) and the detailed picture of the type material (Fig. 6), the present specimen is identified as *An. hypnoides*.

Distribution. Mauritius (type locality, Brook 1889), Madagascar (present study).

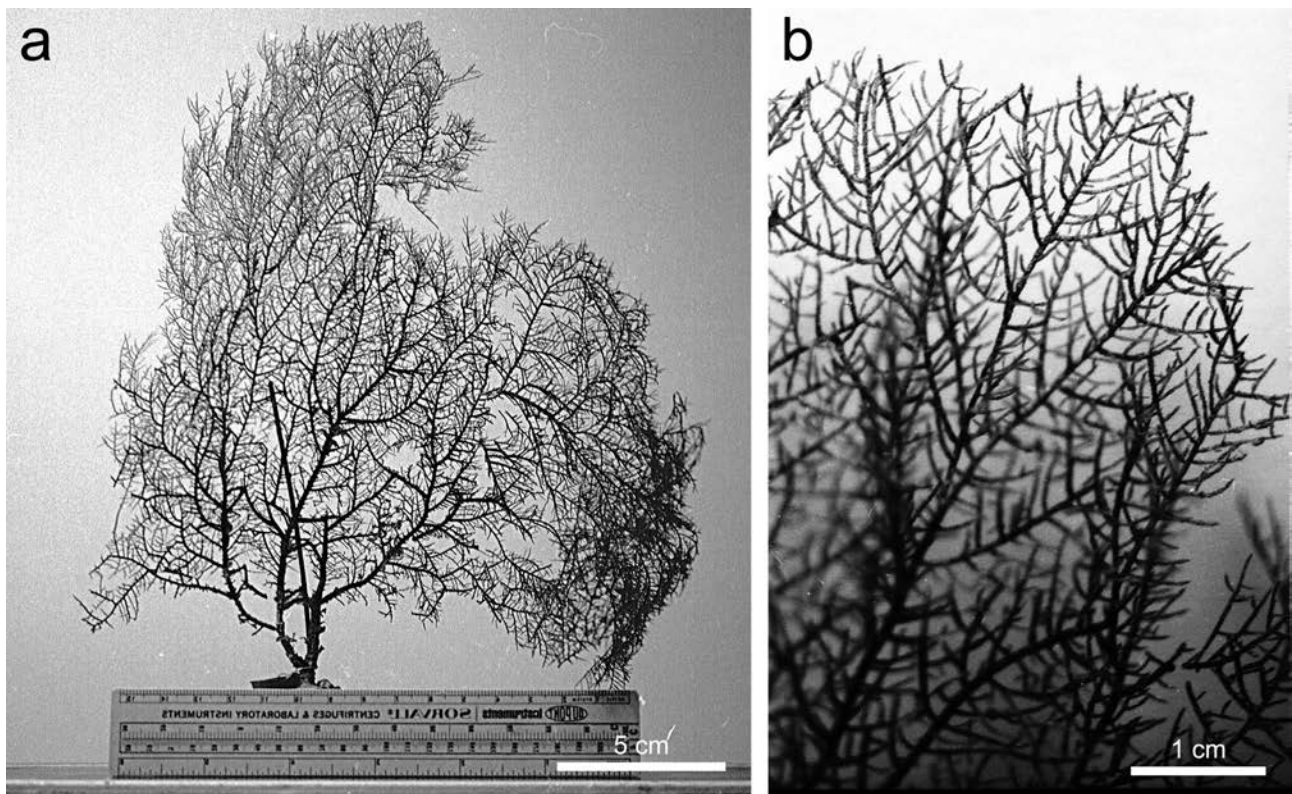


FIGURE 6. (a) *Tylopathes? hypnoides* (Brook, 1889) holotype NHMUK 86.2.8.2 from Mauritius. (b) Close-up view of the schizotype USNM 100356.

Antipathes lentipinna Brook, 1889

Figs. 7, 8

Antipathes lentipinna Brook 1889, p. 103, pl. 9, fig. 19

Material examined. A large branch from one colony, Toliara 35 m specimen INV.131337.

Depth range. 30–50 m.

Description. A branched, bushy colony measuring one meter in width and 60 cm in height, with a reddish color (Fig. 7, a–c). The basal stem is entirely covered by epibionts and divides in two thick axes, each around 1 cm in diameter. The branching pattern tends to be uniserial, with terminal branchlets usually vertically directed, but not everywhere on the colony, some being curved to reach that position (Fig. 7, a–b). The longest branch bearing branchlets in the fragment is 25 cm. Terminal branchlets measure up to 11 cm in length, but usually less than 5 cm. A terminal branchlet measuring 6.3 cm measures 1 mm at the base (measured with tissues). The terminal branchlets are very irregularly spaced, varying from 4 mm to 30 mm. Due to this variability, the number per branchlet per cm cannot be counted, as sometimes there is no branchlet along one cm. The branchlets are mostly inserted 35–45°, but sometimes almost perpendicularly. The polyps are large, with long tentacles and arranged in a single row on the terminal branches (Fig. 7, c). This row is sometimes not perfectly linear. On thicker branches, polyps are irregularly distributed. They measure 0.8–1.3 mm in transverse diameter and are generally close to each other, such as there is no interpolyar space. At places where the row is not continuous and linear, polyps can be spaced up to 0.4 mm apart, and 7–8 polyps are found per cm.

The spines are conical and either slightly inclined towards the distal part of the branch or perpendicularly inserted to the corallum (Fig. 7, d–f). Their surface is papillose on almost their whole surface, with papillae sometimes elongated towards the tip of the spine (Fig. 7, g–i). Their tip is either simple or multiply forked, with a somewhat

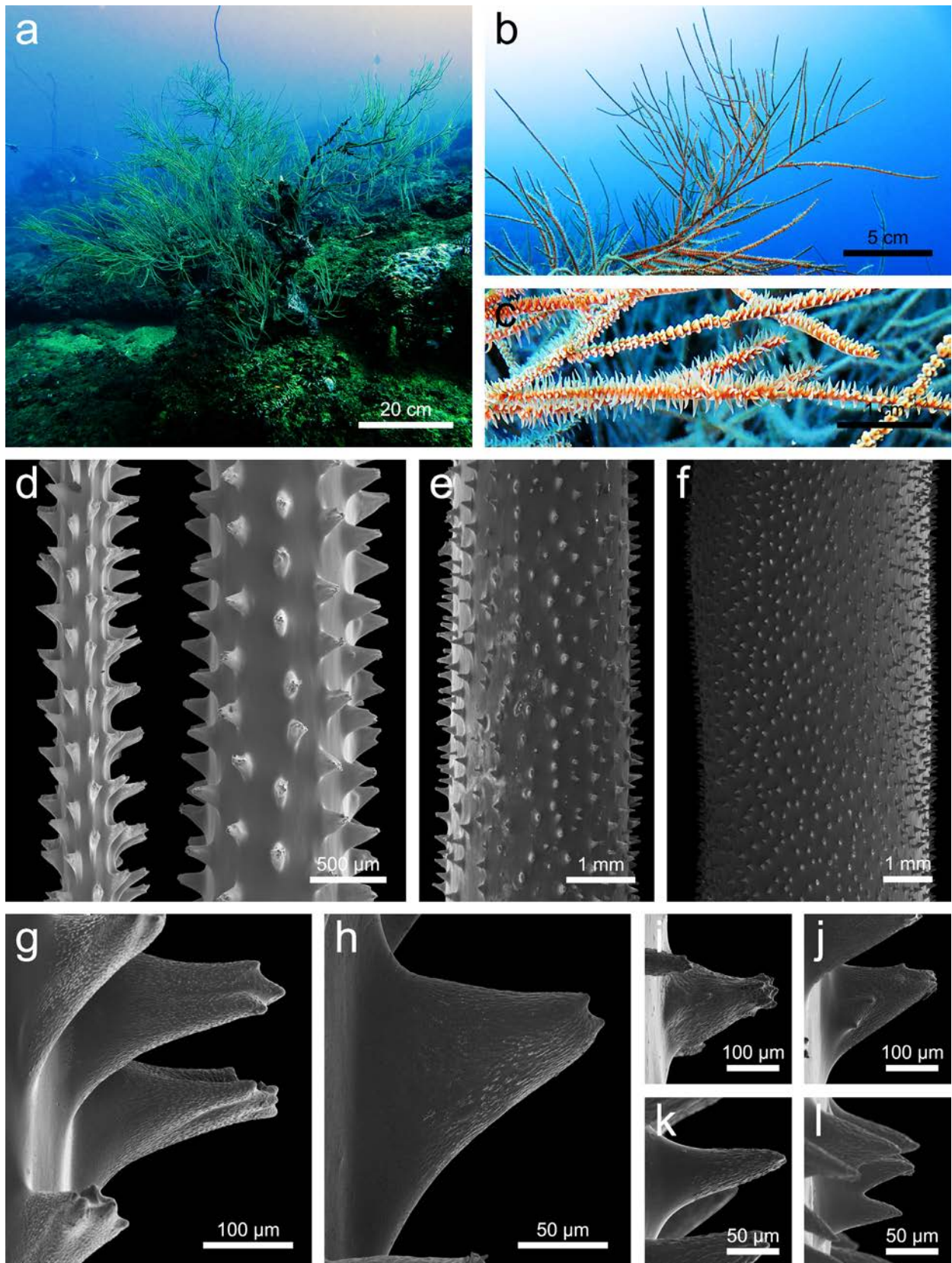


FIGURE 7. *Antipathes lentipinna* Brook, 1889 specimen INV.131337. (a) Entire colony *in situ*. (b) Detailed view of the branching pattern *in situ*. (c) Detailed view of the contracted and expanded polyps *in situ*. (d) Sections of branchlets 0.33 mm and 0.96 mm in diameter, respectively. The polypar side is on the right. (e) Section of a branch 2.65 mm in diameter. (f) Section of a branch 4.6 mm in diameter. (g) Polypar spine on a branch 0.33 mm in diameter. (h) Abpolypar spine on the same branch. (i–l) Different spines found on branches thicker than 1 mm in diameter.

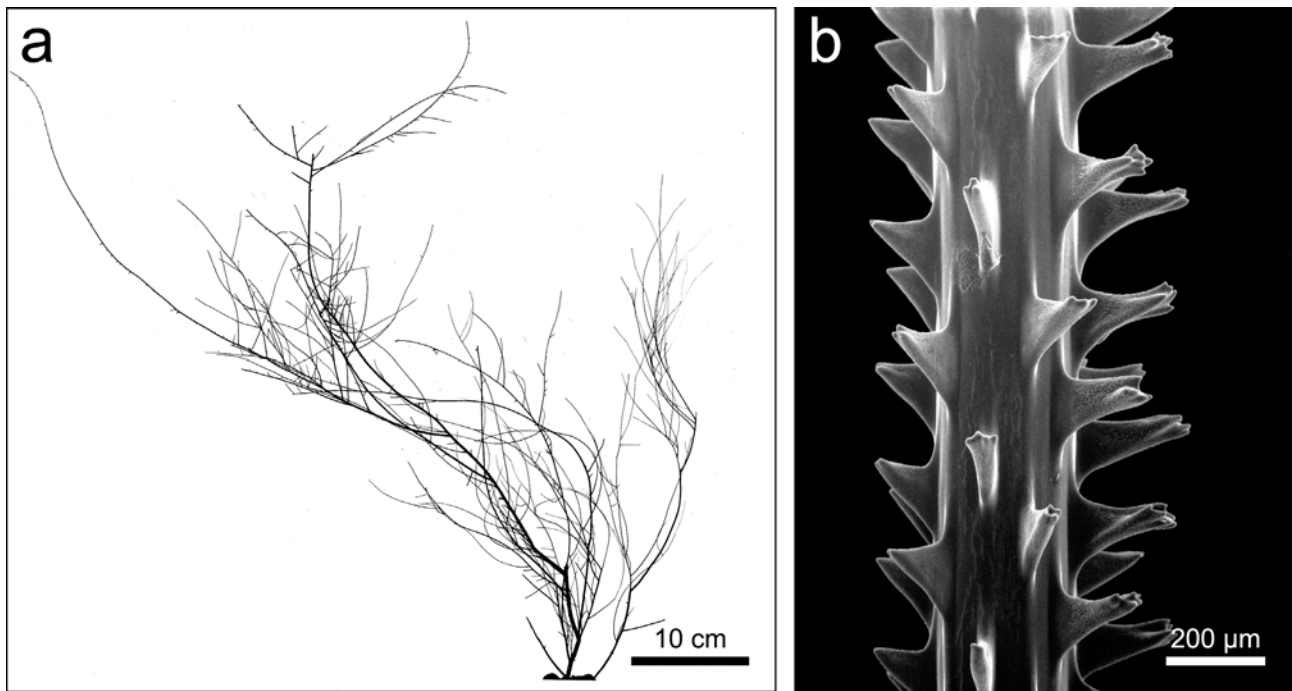


FIGURE 8. *Antipathes lentipinna* Brook, 1889 type specimen. (a) Entire colony, holotype BMNM 1973.9.20. (b) Schizoholotype USNM 100360 showing a section of a branch 0.3 mm in diameter. Photo of Brook's specimen of *A. lentipinna* courtesy of Paul Richens of the NHMUK.

coronate arrangement of the apical lobes (Fig. 7, e, g, i). Sometimes two close spines can fuse at their base (Fig. 7, l). There also may be extra lobes on the lateral sides of the spines (Fig. 7, j). Tall conical spines are only seen on the smallest branchlets, where the difference between abpolypar and polypar spines is also the most marked (Fig. 7, d). Spines tend to be conical on thicker branches (Fig. 7, e–f). On thick branches (*i.e.* 2.6 mm in diameter), some spines are stout (Fig. 7, e–f). On thick branches > 4 mm in diameter, numerous spines are conical with an acute tip (Fig. 7, f). On a branchlet 0.34 mm in diameter, polypar spines measure 0.17–0.24 mm and are spaced 0.27–0.50 mm apart. Abpolypar spines measure 0.12–0.16 mm and are spaced 0.28–0.44 mm apart, 6–7 longitudinal rows can be seen in one aspect. On a branch 0.95 mm in diameter, polypar spines have same sizes as on thinner branches and they are spaced 0.29–0.47 mm apart. The abpolypar spines measure 0.17–0.19 mm and are spaced 0.30–0.46 mm apart, 6–7 longitudinal rows are also seen in one aspect. On a thick branch 4.6 mm in diameter, the rows are no longer visible and the spines measure 0.13–0.17 mm. Secondary spines are scarce and not always present (Fig. 7, e–f), they measure up to 0.05 mm.

Taxonomic remarks. The present specimen shares similar spine morphology with a complex of shrub-like species composed of *Antipathes griggsi* Opresko, 2009, *An. lentipinna* Brook, 1889, *An. spinulosa* (Schultze, 1896), *An. fruticosa* Gray, 1857 and *An. virgata* Esper, 1788 (Opresko 2009). A detailed comparison of these species is given in Opresko (2009). *Antipathes griggsi* is known from the Hawaiian Islands, *An. spinulosa* from Indonesia, *An. fruticosa* from New Zealand, while only *An. lentipinna* and *An. virgata sensu* Brook, 1889, are both from a locality relatively close to Madagascar, the Red Sea. All these species have an irregularly branched corallum and spines with multiple lobes at the apex and papillae or striations on the surface (Opresko 2009). However, only the branching pattern of *An. griggsi*, *An. lentipinna* and *An. fruticosa* is similar to the Malagasy specimen. As highlighted by Opresko (2009), the branching of *An. fruticosa* and *An. griggsi* differ from that of *An. lentipinna* by being more consistently vertically directed. On the other hand, in *An. fruticosa* the apical lobes of the spines tend to be more confined to the apex and, in places, have a more coronate arrangement (which is even more true in *An. spinulosa*) as in *An. lentipinna*, while on the thicker parts, tips of the spines have a more blunt, rounded appearance (Opresko 2009). Examination of the type specimen of *An. lentipinna* by Opresko (2009) revealed similar spines as those observed here (Fig. 8). The coronate arrangement of the apical lobes seen in the holotype (Fig. 8, b) is also seen in the Malagasy specimen (Fig. 7, d, g, i). In his description of *An. lentipinna*, Brook (1889) highlighted the general resemblance of the species with *An. virgata*, from which it differs mostly by more spreading branches (a comparison between the Malagasy branches

and Brook's specimen of *An. virgata* is shown in Fig. 11, c–e). The branchlets of *An. lentipinna* are reported to be 8–15 cm, generally collected together near the upper portion of the branch, and generally uniserial (Brook 1889). The spines are reported to be much longer and more slender than those of *An. virgata*, and simple with no tubercles nor apical lobes in the sample examined by Brook (1889); however, the spine morphology varies from branch to branch in the type (pers. obs. DMO). In addition, Brook did not mention the presence of any secondary spines. In the Malagasy specimen, their presence was scarce and not seen in all branches analyzed. Brook concluded that *An. lentipinna* was distinguished from *A. virgata* by the marked difference in diameter between the branches and branchlets. Later work from Summers (1910) also reported *An. lentipinna* from Mozambique (Portuguese East Africa). Her description was rather vague, and the main features reported were large polyps (2 mm in transverse diameter) and branches on one side only. Considering the slight differences with Brook's description and the similarities in spine ornamentation and shape as described in Opresko (2009), the name *An. lentipinna* is assigned to the present specimen.

Distribution. Red Sea (type locality, Brook 1889), Mozambique (Summers 1910), Madagascar (present study).

Antipathes cf. pseudodichotoma Silberfeld, 1909

Fig. 9

Antipathes pseudodichotoma Silberfeld 1909, p. 27, pl. 2, fig. 4

Material examined. Soalara, 14 m. Fragments collected from the distal portions of the colony, specimen INV.131364.

Depth range. 14–30 m.

Description. A sparsely branched colony measuring about 25 cm in height (Fig. 9, a, b). The colony shows a pseudo-dichotomous arrangement of the branches and these are not restricted to a two-dimensional plane (Fig. 9, a, b). Pinnulation is not present. The angles of the branches measure between 21° and 85°. The basal diameter of the branches is nearly 2 mm tapering upwards. Polyps are light grey (Fig. 9, a, b) and are located on a single side of the branchlets, but on two rows on thicker branches. The polyp line wraps around the branches making it difficult to determine the polypar and abpolypar side. Polyps on the distal branches measure 0.6–1.7 mm in transverse diameter while the interpolypar distance measures up to 0.35 mm on upper branches. There are eight polyps per cm along the examined branches. Four to six longitudinal rows of spines can be seen in one aspect on the upper branches, regardless of the diameter (Fig. 9, c–g). They are triangular, smooth with a pointed tip (Fig. 9, f, g). On a branch 0.26 mm in diameter, the polypar spines have a regular size of 0.12 mm in height and are spaced 0.36–0.40 mm apart while the abpolypar spines measure 0.11–0.14 mm and are spaced 0.31–0.42 mm apart. The spaces between abpolypar spines tend to be more irregular as the branch becomes thicker. On a branch measuring 0.60 mm in diameter, the polypar spines are taller and measure 0.12–0.17 mm and are spaced 0.28–0.41 mm apart. On such branches, the abpolypar spines are multilobed or irregular in shape (Fig. 9, h). They measure 0.10–0.13 mm and are spaced 0.30–0.50 mm apart.

Taxonomic remarks. A comparison of pseudodichotomous colonies is presented in Opresko (2019), where the spines of *Antipathes coronata* Opresko, 2019, *An. elegans* (Thomson & Simpson, 1905), *An. gallensis* Thomson & Simpson, 1905 and *An. sarothrum* Pax, 1932 are discussed. All the latter species are characterized by having spines with apical knobs. The type specimen of *An. pseudodichotoma* is considered to be lost, and the original description is incomplete by lacking information about the spine morphology and the size of the polyps. However, Silberfeld (1909) reported flat (compressed laterally) 0.13 mm high spines (on a branch 0.35 mm in diameter) spaced 0.3–0.4 mm apart, but that author did not mention the presence of any knobs on their apex. Five or six longitudinal rows are seen in lateral view. The polyps have been reported to be spaced of 1–1.5 mm using the distance between oral cones of adjacent polyps, with eight polyps per cm. This diagnosis is similar to the present specimen, but pending the description of a neotype, the missing information about the spine morphology in the original description cannot confirm any further identification. Consequently, the name *An. cf. pseudodichotoma* is used here.

Distribution. Japan (type locality, Silberfeld 1909), North Pacific Ocean (Molodtsova & Opresko 2020), Madagascar (present study).

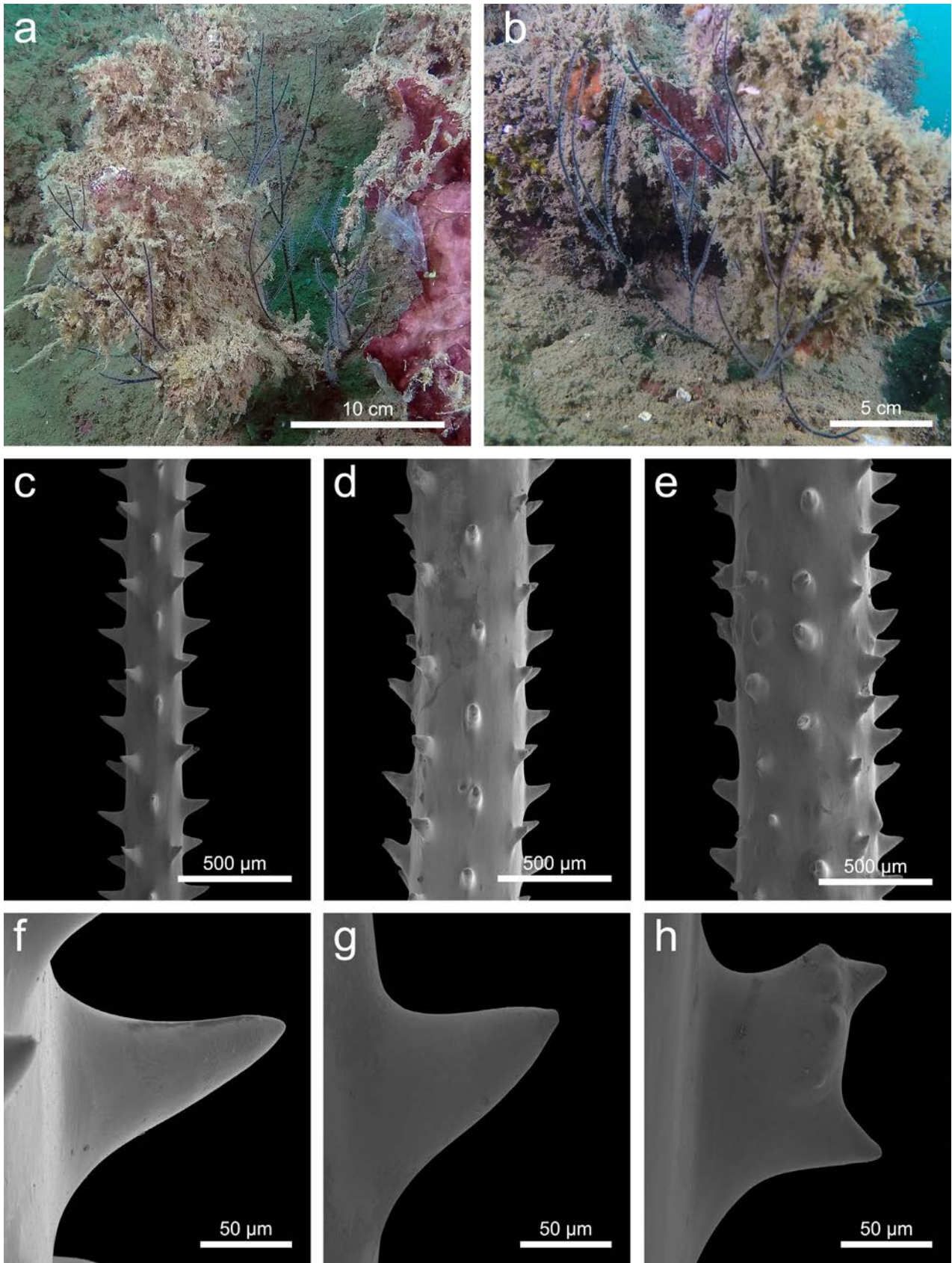


FIGURE 9. *Antipathes cf. pseudodichotoma* Silberfeld, 1909 specimen INV.131364. (a, b) Entire colony measuring about 25 cm in height. (c) Section of a branch 0.24 mm in diameter. The polypar side is on the right. (d) Section of a branch 0.48 mm in diameter. The polypar side is on the right. (e) Section of a branch 0.62 mm in diameter. The polypar side is on the right. (f) Polypar spine on a branch of 0.60 mm in diameter. (g) Abpolypar spine on the same branch. (h) Example of irregular spine.

Antipathes cf. *virgata* Esper, 1788

Figs. 10, 11

Antipathes virgata Esper, 1788, pt. II, p. 8, pl. XIV

Antipathes scoparia Lamarck, t. II, p. 307

Material examined. Toliara, 25 m. Distal branches of different diameters, specimen INV.131349.

Depth range. 25–45 m.

Description. A branched and bushy colony measuring 75 cm in height with a basal diameter of 1.5 cm (Fig. 10, a–c). The branches subdivide pseudo-dichotomously and are vertically elongated and almost parallel, being inserted with an acute angle to the thicker branch (Fig. 10, b, c). On the distal thick branches, smaller branches often originate from the same area and from different sides, giving the colony the general shape of a candelabra (Fig. 10, c). There is no fusion between adjacent branches (Fig. 10, c), but sometimes vertically erected branches can fuse with the main axis when they come in contact. In the upper part of the colony, the terminal branchlets measure up to 9 cm in length. Such branchlets measure around 2 mm in diameter at their base (measured with the tissues), while a shorter branchlet 5.8 cm in length measures 1.2 mm at the base (measured with the tissues). The polyps are generally found in one row, but on branches they are often arranged on both sides giving the appearance of two rows (Fig. 10, c). When they are arranged in a single row, they can twist around the branch. On thicker axes, they are found all around the axis. Polyps appear large with thick and rounded tentacles and measure 1.0–1.7 mm in diameter. The interpolypar space is not uniform; the polyps can be close together or be spaced up to 1 mm apart, and 8–9 polyps are found along one cm. The spines are conical, sometimes slightly hooked upwards on thin branches and inclined distally on thicker branches (Fig. 10, d–i). Spines have papillae on two-thirds of their surface on every side and multiple, rounded knobs at the apex (Fig. 10, g–i). Spines can also be stout with a flattened and knobbed apex on larger branches (Fig. 10, i). The number of longitudinal rows that can be seen from one aspect varies between five and seven. The polypar and abpolypar spines are equivalent in size, regardless of branch thickness. On all branches measuring less than 0.75 mm in diameter, the spines are consistently no more than 0.14 mm tall, whereas on thicker branches they measure 0.11–0.17 mm. The overall mutual distance is consistently within the range of 0.31 to 0.56 mm.

Taxonomic remarks. Historically, there have been several descriptions of *Antipathes virgata* referring to specimens coming from different locations and presenting different states of preservation. The original description of the species was made by Esper (1798, Fig. 11, a) who described a specimen coming from the Indian Ocean that he received as a gift from India. That specimen is lost. In his description, he stated that the specimen could be “distinguished from any known species by the spreading of its branches and twigs, as well as its growth form”. He also reported about a stem expanding in a “fork-like” shape and branches originating from the same angle, but no details were provided regarding the polyps or the morphology of the spines. In the absence of the type specimen and given the lack of information about taxonomical features, his description is inadequate to define the species (Opresko & Baron-Szabo 2001). Other specimens were then described by Brook (1889, from the Persian Gulf, redescribed by Opresko in 1974, see Fig. 11, d–f), Roule (1905, from the Atlantic Ocean) and Forster Cooper (1909, from Saint-Brandon) which have been later compared by Opresko & Baron-Szabo (2001) in their redescription of Esper’s specimens. The latter authors concluded that it was not possible to determine if all these specimens referred to *An. virgata* were identical with the one described by Esper, and that it was questionable whether all three authors were dealing with the same species. In any case, a neotype needs to be designated for the species. Although the spines of the present specimen are similar in shape and size as those described from Brook’s specimen (Brook 1889; Opresko & Baron-Szabo 2001, see Figs. 10, 11), they differ in their fine morphology: the spines of the Malagasy specimen are papillose with many small knobs at their tips, while those of Brook’s specimen are smooth with a few large tubercles at their tips (Figs. 10, 11). The branching pattern also appears to be different (Fig. 11, b, d–f). In Brook’s specimen, the branches are mostly on one side of the axis, and they can be bifurcated before twisting and becoming confluent again (Fig. 11, d–e). These features are not observed here. Forster Cooper (1909) also reported about different morphological features with branches becoming confluent and fusing together at some point, as well as polyps arranged in four rows along the branch and sharp, triangular spines. The original illustration given by Esper (1798, Fig. 11, a) shows a similar branching pattern for the whole colony, however, given all the previous considerations and the different localities, this specimen might be different from those of Brook (1889), Roule (1905) and Forster Cooper (1909), and the name *An. cf. virgata* is used here.

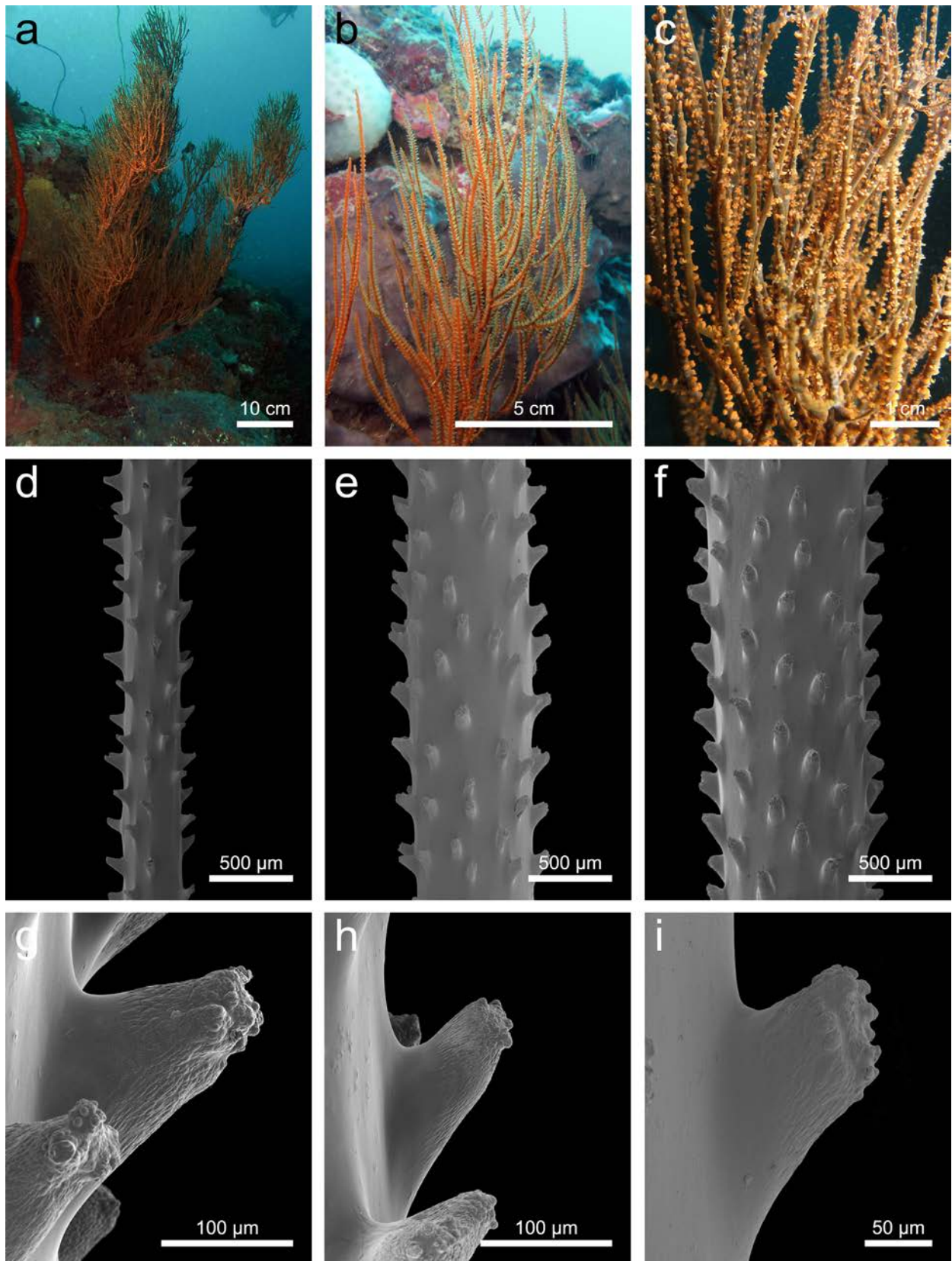


FIGURE 10. *Antipathes cf. virgata sensu Esper, 1788* specimen INV.131349. (a) Entire colony. (b–c) Close-up views of the branching pattern and the polyps. (d) Section of a branch 0.35 mm in diameter. The polypar side is on the right. (e) Section of a branch 0.74 mm in diameter. The polypar side is on the right. (f) Section of a branch 1 mm in diameter. Polyps are found on both sides on this branch. (g) Polypar spine on a branch 0.60 mm in diameter. (h) Abpolypar spine on the same branch. (i) Example of a stout polypar spine on a branch 0.70 mm in diameter.

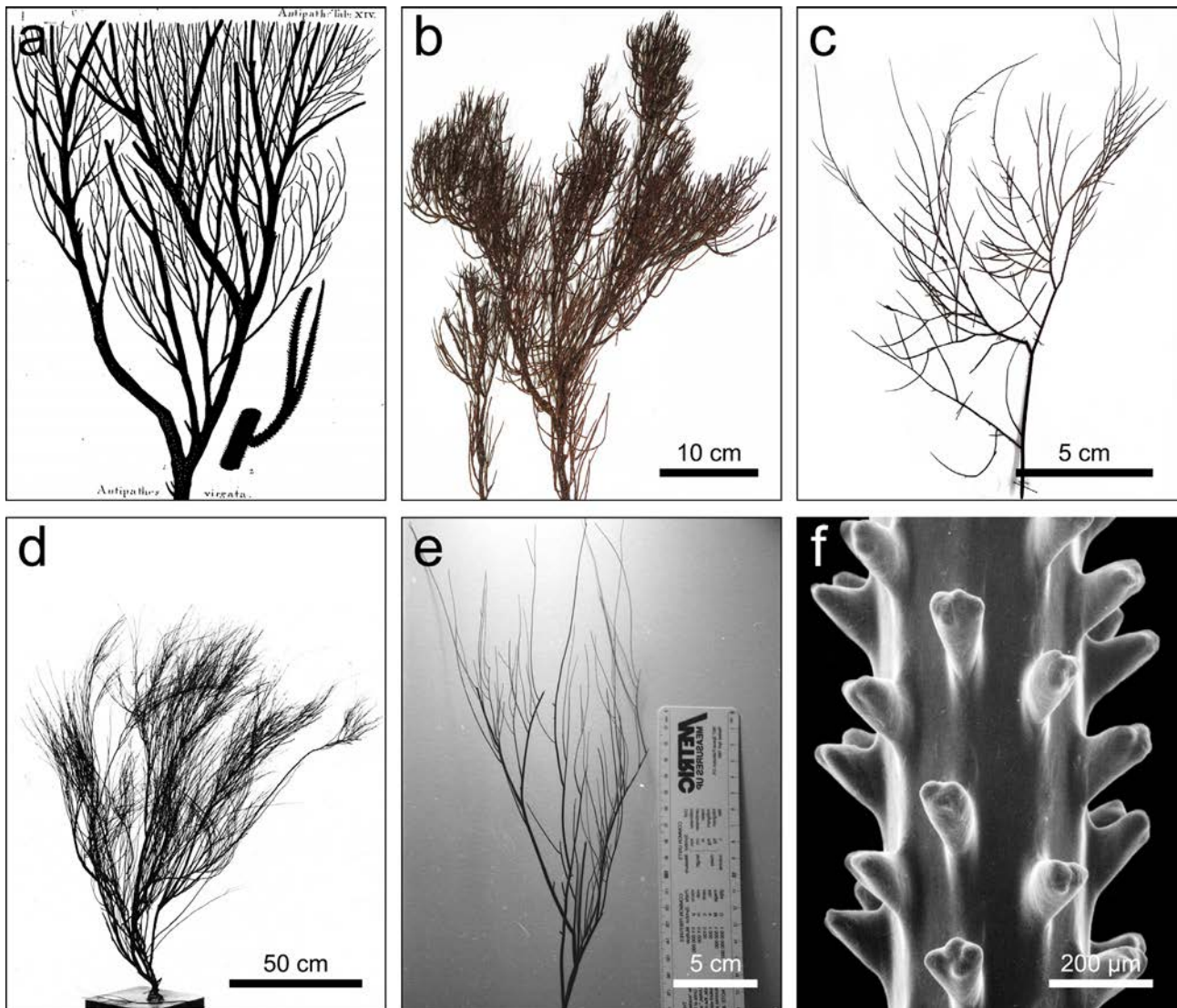


FIGURE 11. Comparison of *Antipathes virgata* Esper, 1788 and related specimens. (a) Original illustration of *An. virgata* by Esper (Esper Fortsetzungen 2, p. 8, pl. 14, 1798) showing the lower portion of the colony. The colony is from the Indian Ocean (gift from India). He reports a colony measuring around 45 cm with no fusion of the branches. (b) A branch of the specimen *An. cf. virgata* INV.131349, from Madagascar. (c) A branch of the specimen *An. cf. lentipinna* INV.131337 from Madagascar showing the same uniserial branching pattern as Brook's specimen of *An. virgata*, but with thick ramifications compared to the latter. (d–f) Views of the entire colony, a branch and a skeletal section of Brook's specimen (Brook 1889) of *An. virgata* from the British Museum. The ramifications are uniserial and thin compared to the specimen from Madagascar. Photo of Brook's specimen of *An. virgata* courtesy of Paul Richens of the NHMUK.

Distribution. Indian Ocean (type locality, Esper 1798), Persian Gulf (Brook 1889), Cargados Carajos (archipelago of Saint-Brandon, Forster Cooper 1909), Azores, Madeira and Cape Verde (Roule 1905), Madagascar (present study).

***Antipathes* sp.**

Fig. 12

Material examined. Soalara, 15 m. Entire colony, specimen INV.131338.

Depth range. 15–30 m.

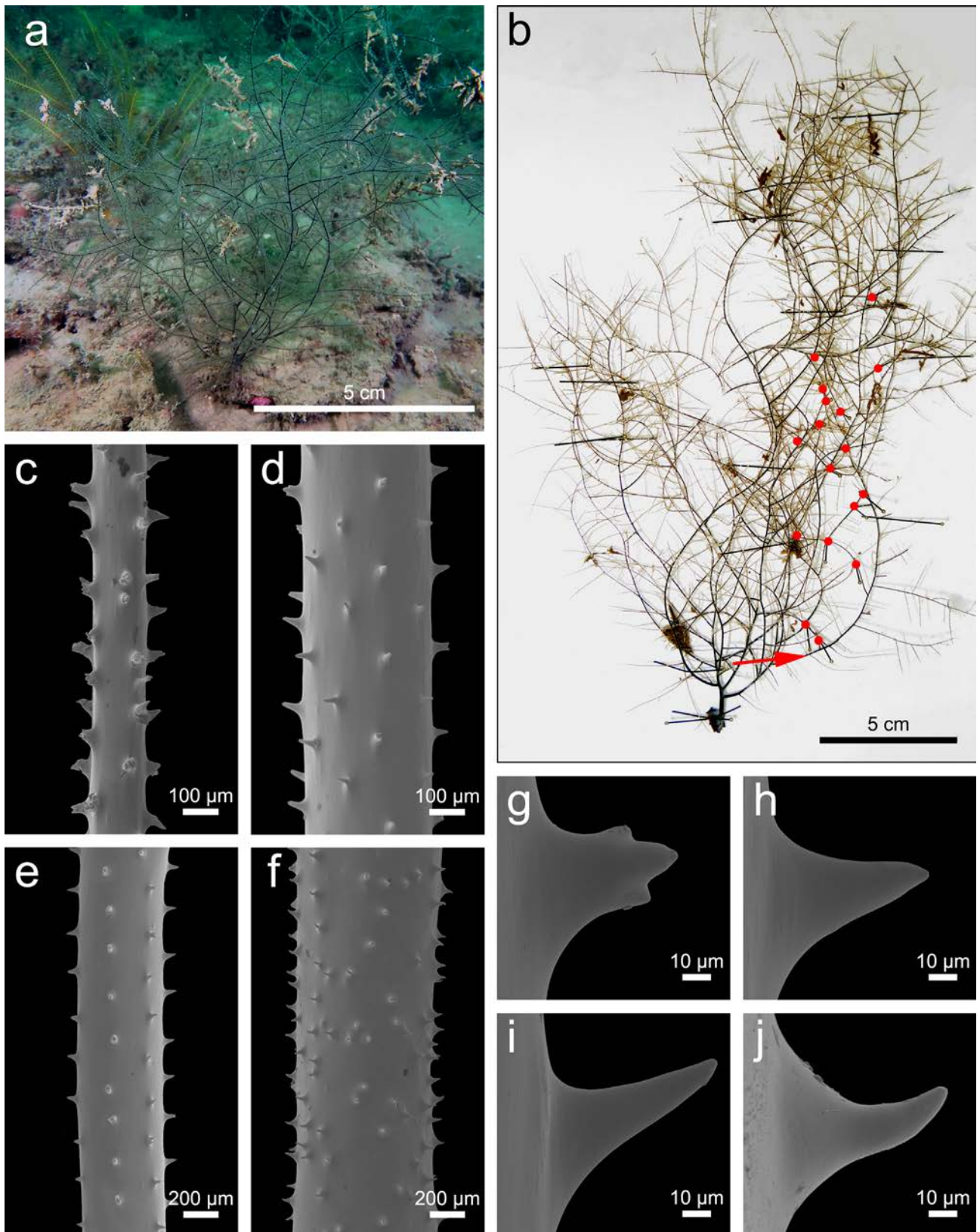


FIGURE 12. *Antipathes* sp. specimen INV.131338. (a) Colony photographed *in situ*. (b) Spread-out colony showing the curved branches and the arrangement of the branchlets. The red dots represent the fusion points of branchlets belonging to the branch indicated by the red arrow. (c) Section of a branch 0.16 mm in diameter. (d) Section of a branch 0.36 mm in diameter. (e) Section of a branch 0.50 mm in diameter. (f) Section of a branch 0.80 mm in diameter. (g–j) Shapes of the spines.

Description. The living colony is bramble-like with the appearance of a mass of entangled and fused branches. It measures 25 cm in height and width *in situ* (Fig. 12, a, b). The terminal branchlets are straight to slightly curved and their end is very thin. Branchlets are inserted almost perpendicular to the next lower order branch, but more often at 70–80°, even if more acute angles are also found (Fig. 12, b). Branchlets are not regularly arranged nor in a single plane. They occur either uniserially or loosely biserially and are irregularly spaced 0.2–11 mm on the same side, with 3–5 branchlets per cm (Fig. 12, b). Terminal branchlets measure up to 5 cm with basal diameter of around 0.6 mm, but more often less than 2.5 cm (Fig. 12, b). Fusions are frequent between adjacent branches and branchlets. For instance, in a branch measuring 8 cm in length, 17 fusions are seen when considering all its branchlets (represented by the red dots in Fig. 12, b). The polyps are located in a single row that can twist around the thin branches but are irregularly spread out on thicker branches. Polyps measure 0.5–0.6 mm in diameter and are spaced 0.2–0.8 mm apart (mostly 0.4–0.5 mm). There are 10–11 polyps per cm.

The spines are widely varying in shape depending on the branch where they sit but are always smooth. On a branch measuring 0.16 mm in diameter, the spines are conical, measure 0.04–0.07 mm, and are spaced 0.13–0.26 mm apart (Fig. 12, c). Most of them show two or more protuberances at the apex without distinction between polypar or abpolypar spines (Fig. 12, c, g). For some spines the protuberances are found close to the base of the spine, consequently the conical shape is no more distinct (Fig. 12, c). On such branches, four longitudinal rows are seen in one aspect (Fig. 12, c). On a branch measuring 0.36 mm in diameter (Fig. 12, d), the spines are either perpendicularly inserted or slightly inclined upward and 6–7 longitudinal rows are seen on lateral view. Most of them are conical (Fig. 12, h), although spines with protuberances are occasionally found (Fig. 12, d). Their size is the same as those of thinner branches, 0.04–0.07 mm, and they are spaced 0.22–0.36 mm apart. On larger branches measuring 0.5 mm (Fig. 12, e), only four longitudinal rows of spines are seen, and all of the spines are almost conical. They are slightly inclined but not in the same direction (Fig. 12, e, i). They measure 0.05–0.09 mm and are regularly spaced 0.19–0.37 mm apart, but often around 0.26 mm, giving the appearance of regular spacing. Finally, on branches measuring 0.80 mm in diameter the arrangement of the spines in longitudinal rows is no more visible (Fig. 12, f). The spines can be conical but most of them are hooked and inclined in different directions (Fig. 12, f, j). Their size remains constant as they measure 0.05–0.09 mm. Because they are not arranged in longitudinal rows, their mutual distance cannot be measured.

Taxonomic remarks. Currently, four valid species are known to be bramble-like: *Antipathes chamaemorus* Pax & Tischbieriek, 1932; *An. lenta* Pourtalès, 1871; *An. polyhedra* Opresko, 2019 and *An. rubusiformis* Warner & Opresko, 2004. Two other species, *An. pauroclema* Pax & Tischbieriek, 1932 and *An. simplex* (Schultze, 1896) could possibly be similar, but both are only known from fragments. *Antipathes simplex* is reported to have laterally compressed spines with rounded tips and inclined towards the end of the branch. They have a height of 0.085 mm on a branch 0.2 mm. Five to six longitudinal rows can be seen on one aspect, which becomes less distinct near the base of the corallum. Polyp transverse diameter has an average of 1 mm. *Antipathes pauroclema* is reported to have variable spine morphologies. On what Pax & Tischbieriek (1932) call the middle part of the skeletal axis, the spines are measuring 0.1 mm on average. On the tip of the branchlets, the spines reach 0.06 mm. In the largest part of the colony they are blunt cone-shaped, on the twig tips they are curved sharply and apically. They are arranged in five longitudinal rows and spaced 0.2–0.25 mm apart. The polyps measure 1.15 mm. Considering the wide variation of the spine morphology, size and arrangement depending on the thickness of the branch seen in the present specimen, as well as the small fragments from which *An. simplex* and *An. pauroclema* have been described, the two latter species cannot be compared confidently. For the remaining bramble-like species, only *An. chamaemorus* and *An. lenta* have triangular, smooth spines, while *An. rubusiformis* has triangular and papillose spines and *An. polyhedra* has tall and narrow spines (Opresko 2019). *Antipathes chamaemorus* differs from the present specimen by being a small colony not exceeding 3 cm in height, and in *An. lenta* no mention is made about the presence of spines with protuberances as seen in the present specimen.

Distribution. Madagascar (present study).

Genus *Arachnopathes* Milne Edwards, 1857

Arachnopathes was established by Milne Edwards (1857) based on the type species *Antipathes ericoides* Pallas, 1766. The genus was later questioned by Brook (1889) before being synonymized with *Antipathes* by van Pesch

(1914) and Pax & Muller (1955) (Opresko 2006). In a more recent work, the species *Arachnopathes columnaris* Duchassaing, 1870 was chosen by Opresko (2006) as the type species of the genus *Stylopathes*. The genus *Arachnopathes* is characterized by branched and bushy colonies with short, straight or curved branchlets fused together into a thick mass (Opresko 2006). The branchlets on the outer edges of the colony may be free or fused. The spines are smooth, triangular to conical to hooked upward, and can be forked.

There are currently five nominal species, of which two are known from the Indian Ocean: *Arachnopathes ericoides* (Pallas, 1766) which is the type species of the genus but for which the type material is lost, and *Ar. clathrata* (Pallas, 1766) for which there is no type. The remaining species, *Ar. aculeata* Brook, 1889, *Ar. indistincta* (van Pesch, 1914) and *Ar. sibogae* (van Pesch, 1914) come from the Pacific Ocean. The latter two were originally assigned to the genus *Aphanipathes*, but they are now provisionally referred to *Arachnopathes* based on similarities in colony form and spine morphology (unpublished observations from co-author DMO). Further DNA analyses on Indian Ocean species might prove that they are related to the Stylopathidae, but based on their spine morphology, they are inferred to be closer to Antipathidae rather than Stylopathidae (Opresko 2006).

Arachnopathes ericoides (Pallas, 1766)

Fig. 13

Antipathes ericoides Pallas, 1766, p.208.

Arachnopathes ericoides Milne-Edwards & Haime, 1857, p.320.

Euantipathes ericoides van Pesch, 1914, p.82., Pl. VIII, fig. 6.

Material examined. Toliara, 23 m. Entire colony, specimen INV.131342.

Depth range. 15–35 m.

Description. A branched, bushy and highly anastomosed colony measuring 25 cm in width and 20 cm in height, with basal diameter of 4 mm (Fig. 13, a), but larger colonies up to 40 cm in height can be found. The colony forms distinct thick masses of branches when seen from the top (Fig. 13, b). When lower thick branches are close to the substrate, they can form new basal plates. The basal part of the colony shows highly anastomosed, curved thick branches that arise from the main stem. Adjacent branches and branchlets tend to fuse together in a flabellate shape, and then the flabellate parts are fused together by the branchlets sitting out of the plane. This branching pattern is less visible in large colonies where the fusions are numerous, but rather seen in young, small colonies. The diameter of the branches and branchlets appears to be similar, the latter only tapering at their end and giving a spiny appearance to the colony (Fig. 13, c). The branchlets are growing in four directions and are inserted at an angle of 60–90°. Branchlets are either straight or slightly curved upwards (Fig. 13, c). The longest measure up to 4 cm and are always curved upwards, 3 to 7 are found per cm counting those on every side (mostly 5–7). Branchlets are irregularly spaced (1–7 mm) and arranged, some being inserted opposite one another (Fig. 13, c, d). This irregular arrangement makes it difficult to determine the length at which a branchlet becomes a branch, as these long branchlets can bear a second order of branchlets. These are usually uniserial, short and straight, but some of them are divided. The polyps are white, thick with rounded tentacles and measure up to 1.2 mm in transverse diameter. They occur in a single row on the branches and branchlets with 9–10 polyps per cm, but on thicker branches they are found all around the axis (Fig. 13, c, d). Smaller polyps occur between larger ones, the mutual distance is irregular: either they sit close to each other, or they are spaced up to 0.8 mm apart (Fig. 13, d).

The spines are varying in size and shape depending on the branch where they occur (Fig. 13, e–j). On a branch measuring 0.23 mm in diameter, the spines are slightly inclined upwards and there is no difference between polypar and abopolypar spines. The spines appear smooth, triangular and some of them are forked at their apex (Fig. 13, e, h), but regardless of the branch and the polypar/abopolypar side, extremely faint striations (Fig. 13, k) or small papillae (Fig. 13, l) are sometimes visible. Four longitudinal rows are seen from one aspect, they measure 0.10–0.12 mm and are spaced 0.21–0.34 mm apart. On larger branches, the spines are smooth, and their morphology is either triangular, conical, hooked or almost cylindrical (Fig. 13, f, g, i, j). Some of them are forked at their apex (Fig. 13, f). They are inclined in different directions (Fig. 13, f, g) and they measure 0.07–0.11 mm in height. On such branches, the longitudinal arrangement is lost, and some bumps are seen on the axial surface, often at the base of the spines (Fig. 13, g, j).

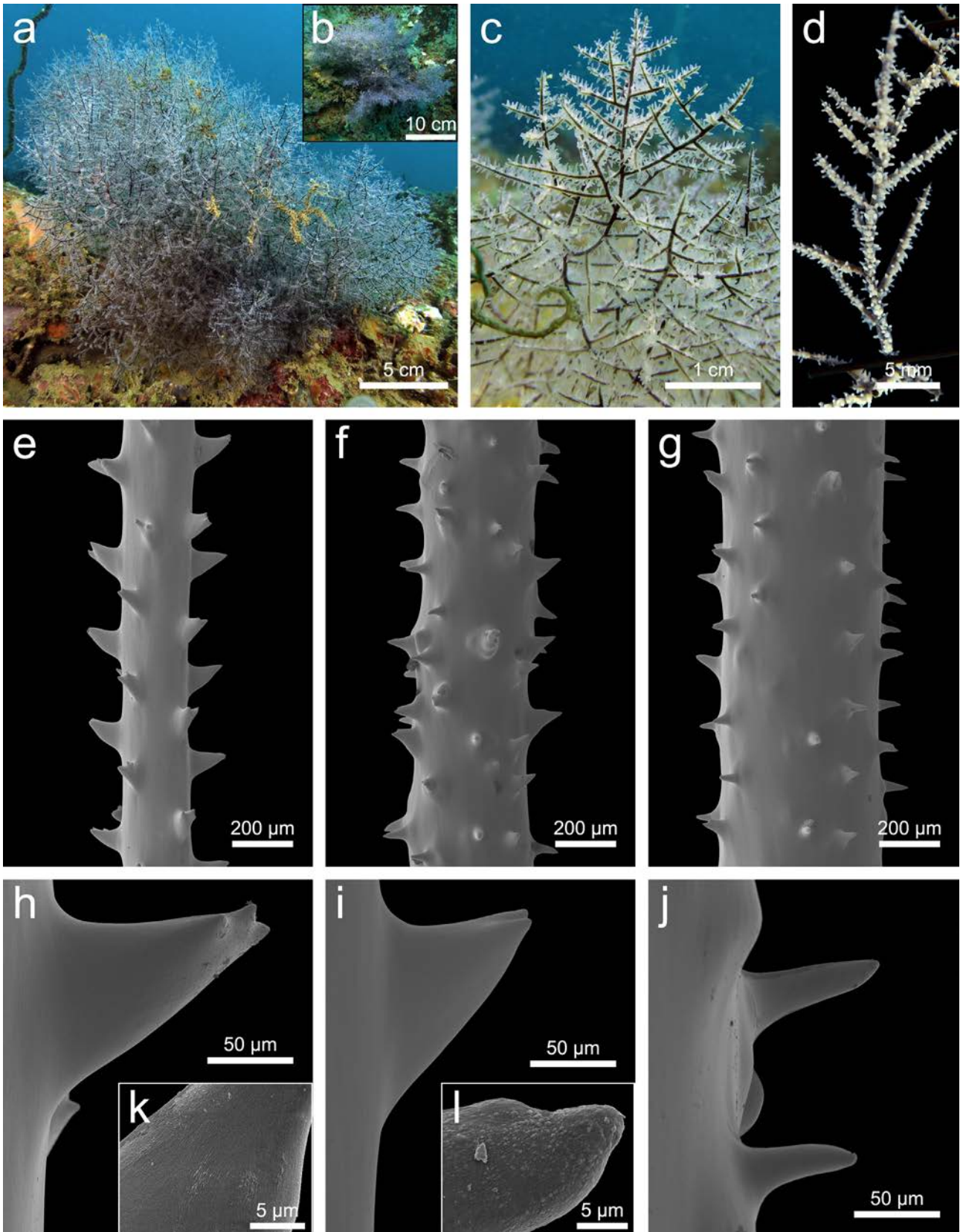


FIGURE 13. *Arachnopathes ericoides* (Pallas, 1766) specimen INV.131342. (a) *In situ* colony in lateral view. (b) The same colony seen from above. (c) Close-up view of the branchlets on a distal branch. (d) Close-up view of the polyps stored in 70% ethanol. (e) Section of a branchlet 0.23 mm in diameter, the polypar side is on the right. (f) Section of a branch 0.38 mm in diameter. (g) Section of a branch 0.55 mm in diameter. (h–j) Different morphologies of the spines.

Taxonomic remarks. The species assigned to the genus *Arachnopathes* are differentiated based on the thickness of the branchlets, the extent of anastomosing and the size and morphology of the spines. Only the features of the spines are well-defined taxonomic traits, and the original descriptions of *Ar. ericoides* and *Ar. clathrata* made by Pallas (1766) lack valuable taxonomic information to clearly separate these two species. To date, only Brook's descriptions of non-type material have enough information to define both, as well as *Ar. aculeata* (Brook 1889). *Arachnopathes aculeata* is characterized branchlets varying in length and density and by spines measuring up to 0.06 mm. Two to four delicate branchlets, measuring 0.5–1.5 cm, are found per cm, but they are longer, thicker and more numerous in the middle of the colony (Brook 1889). *Arachnopathes clathrata* is differentiated from *Ar. ericoides* solely by having a marked contrast between the thickness of the branches and those of the branchlets defined as “needle-like” by Brook (1889), which is not the case for the present specimen. The latter closely matches the descriptions made by Brook (1889) and van Pesch (1914). The only noticeable differences are the spiral arrangement of the branchlets described by Brook (1889), which is not clearly seen in the material from Madagascar, as well as the lack of information regarding which branch he was analyzing when he described the spines as “laterally compressed, ending in a blunt point formed by the lower margin taking a sharp curve upwards to join the upper margin”. Information about the polyps was missing from Brook's description and is given here for the first time.

Distribution. Indian Ocean (type locality, Pallas 1766), Indonesia (van Pesch 1914); Singapore (Pax & Muller 1955); Madagascar (present study).

Genus *Cirripathes* de Blainville, 1834

Cirripathes was established amongst antipatharians by de Blainville (1834). It is characterized by unbranched and unpinnulated corallums, with polyps irregularly found on all sides of the stem. The colonies can be straight, slightly to highly contorted, curved, coiled or forming spirals. The spines on the skeleton are not arranged in verticils (Brook 1889; Bo *et al.* 2009; Wagner 2015a). They can be variously papillose and may be knobbed or lobed at the apex. This genus currently encompasses 16 nominal species, of which four type specimens are lost or missing, including the type of *Cirripathes spiralis* (Linnaeus, 1758). All species have been described from the Indian and Pacific Oceans, except *Cirripathes secchini* Echeverria, 2002 from the SW Atlantic. However, a redescription of the type material is needed for the latter as it might be related to the genus *Stichopathes* rather than *Cirripathes* due to the arrangement of the polyps and the occurrence of secondary spines.

Cirripathes anguina (Dana, 1846)

Fig. 14

Antipathes anguina Dana 1846, p.576

Cirripathes anguina Brook 1889, p.84-85

Cirripathes (Eucirripathes) anguina Van Pesch 1914, p.146-153, figs.203-205, pl.8, figs.3-4, 7

Cirripathes anguinus: Bayer 1959, p.229

Material examined. Distal fragments of different colonies. Toliara 17–20 m specimens INV.131353, INV.131369, INV.131373, INV.131378, INV.131379, INV.131380; Anakao 10–11 m specimens INV.131362, INV.131363; Sarodrano 10 m specimens INV.131358, INV.131359, INV.131360; Maromena 20 m specimen INV.131355.

Depth range. 7–30 m.

Description. The colonies are straight, slightly sinuous, and never form any loop or spiral in their distal parts (Fig. 14, a–g). Juvenile colonies have a thin stem, which can be bent within the first few cms (Fig. 14, h). Adult colonies can reach more than 5 m in length and can be bent at various points along the stem. The basal diameter reaches 1 cm in 3 m-high colonies. The colonies have a lot of different phenotypes with brown, white or grey coenenchymes and black, orange, white, or grey polyps (Fig. 14, a–h). The polyps are large and measure up to 2.9 mm in transverse diameter. Polyps are irregularly distributed around the stem, generally 3–6 polyps are found per cm (as seen in frontal view), with varying interpolypar spaces from 0.6 to 4.0 mm (Fig. 14, a–h), sometimes aggregating to one side of the colony, especially in juvenile colonies where two rows of polyps are found on one side (Fig. 14, h).

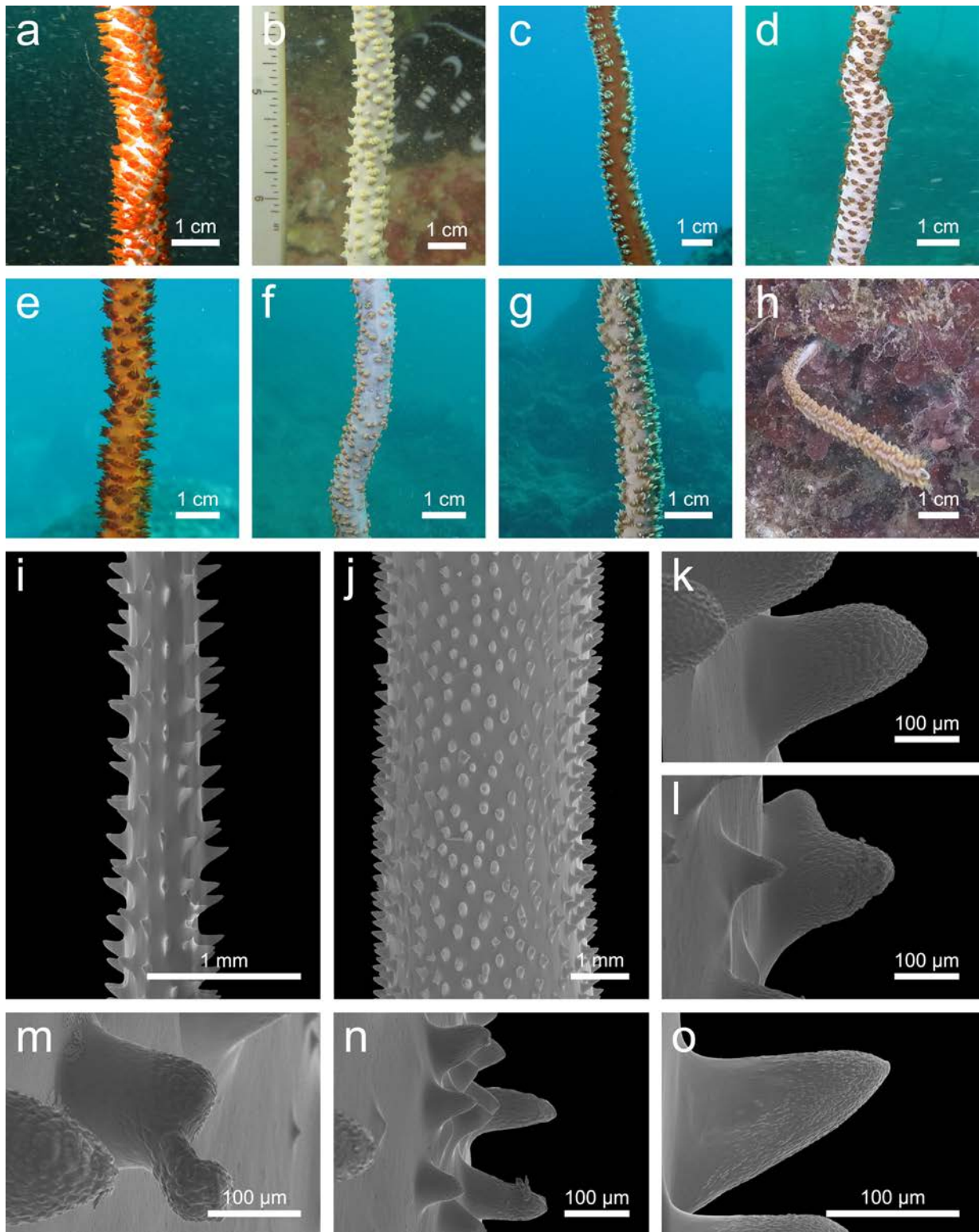


FIGURE 14. *Cirrhipathes anguina* (Dana, 1846) (a–h) *In situ* pictures showing the wide range of phenotypes that the species can present (a—INV.131378; b—INV.131369; c—INV.131373; d—INV.131379; e—INV.131360; f—INV.131359; g—INV.131362; h—INV.131363). All these phenotypes have the same spine morphology. (i) Distal section 0.48 mm in diameter from the 30 cm-long juvenile colony INV.131363. At this stage, regular rows of spines can be seen. (j) Distal section 3.5 mm in diameter of a 2.5 m tall colony INV.131379. The regular rows formed by the spines start to be lost. (k–n) Different spine morphologies seen on distal parts of *Ci. anguina* colonies. The spines are generally stout and papillose but irregular growths are sometimes found, as well as triangular, minute spines or cylindrical, narrow newly formed spines. (o) Triangular, laterally compressed spines from a distal fragment of the juvenile colony INV.131363.

All these phenotypes present the same spine morphology in their distal parts (Fig. 14, j). The spines are highly papillose, mainly stout with a rounded apex (Fig. 14, k), but conical spines can also be found (Fig. 14, o). Adjacent spines can be fused at their base. Irregular growths are sometimes seen on stout spines (Fig. 14, l, m). Newly formed spines are found either with a narrower cylindrical shape, or minute triangular shape (Fig. 14, n, o), but due to their scattered presence they are not ascribable to true secondary spines. All fully formed spines, independent from the occurrence of irregularities, show a distinctly papillose surface (Fig. 14, k–o). The spines of the two different sides of the spines as seen in frontal view measure up to 0.30 mm in height and their mutual distance measures up to 0.70 mm. They either stand at right angles to the corallum or are slightly inclined in different directions (Fig. 14, j). Up to 26 irregular rows can be seen in one aspect on a distal portion 3.5 mm in diameter. On a distal fragment 0.48 mm in diameter from a 30 cm-high young colony, there is a single type of spine. They are triangular and laterally compressed but show a distinct papillose surface (Fig. 14, i, o). They measure 0.11–0.19 mm in height and their mutual distance is 0.20–0.48 mm. The spines are clearly arranged in seven rows, as seen from one aspect.

Taxonomic remarks. The type specimen of this species is lost. In its brief description, Dana (1846) states that this species has polyps “not properly beaked” and measure about 4 mm in diameter. The spines are stout and hardly acute and there are “distinct nodes in the axis every three or four inches towards the upper extremity”. Pending the description of a neotype, the descriptions of *Ci. anguina sensu* Brook 1889 and van Pesch 1910 are used here. Van Pesch (1914) describes blunt and conical spines at right angles to the corallum as well as spines more acute and distally inclined with a rough surface. The spine sizes reported by van Pesch are within the range of those observed for the Malagasy specimens. The spines described by Brook (1889) and van Pesch (1914) differ from the Malagasy specimens in having a different number of rows, which is 12–14 for both authors. However, this number generally tends to vary according to which portion of the colony is analyzed. The mutual distance of the spines of the Malagasy specimens, 0.45 mm, is also similar (van Pesch 1914). Brook (1889) affirms that the stem of *Ci. anguina* is never twisted into regular spirals and the spines are of the same size around the corallum. Indeed, the difference in spines is not as marked as in other species and genera. More simple spines as seen here in the fragment of the young colony depend both on the position on the axis (growing apex with newly forming spines) and the age of the colony. With respect to the polyps, both Brook (1889) and van Pesch (1914) describe polyps arranged all around the colony with varying interpolypar spaces and sizes reaching 4 mm in diameter, which is consistent with the polyps of the Malagasy specimens. Slight differences are perhaps related to intraspecific variation or environmental effects on the shape and size of the colony. The present description is similar to the one given by Wagner (2015a) for Hawaiian specimens identified as *Ci. anguina*.

Distribution. Fiji islands (type locality, Dana 1846), Maldives (Cooper 1903), Red Sea (Cooper 1903), Seychelles (Cooper 1903), Sri Lanka (Cooper 1903), New Guinea (van Pesch 1914), Cape Moreseby (van Pesch 1914), Japan (Okiyama & Tsukamoto 1989), Indonesia (Rumphius, see Bayer 1959), Andaman & Nicobar Islands (Kumar *et al.* 2012), Hawaii (Grigg 2001), Madagascar (present study).

***Cirrhopathes densiflora* Silberfeld, 1909**

Figs. 15, 16

Cirrhopathes densiflora Silberfeld 1909, p.19

Material examined. Distal fragments from four colonies, Toliara 18–24 m specimens INV.131352, INV.131368, INV.131374, INV.131376.

Depth range. 10–30 m.

Description. Single stem colonies which are straight with some crooked parts (Fig. 15, a, b), or sinuous and contorted (Fig. 15, c, d). The apex that can form a small loop (Fig. 15, d, e). They measure up to 170 cm in length. The skeleton is thin and generally tapers from the base to the apex of the colony. The diameter of the stem of the analyzed specimens varies from 2.5 to 8.0 mm at the base, and ranges from 1.5 to 2.5 mm on the distal part of the colonies. The color of the coenenchyme varies from grey to yellow or brown, with the polyps being yellow, white or orange (Fig. 15, b–e). The polyps are located all around the stem in an irregular way, with 3–6 polyps per cm. In contorted colonies, they tend to gather on the same side, leaving one side of the colony partially without any polyps (Fig. 15, e). In the analyzed portions taken at more than 10 cm below the tip of the colony, the polyps measure 1.7–3.9 mm in transverse diameter with a mutual distance of zero when they sit next to each other, up to 6 mm.

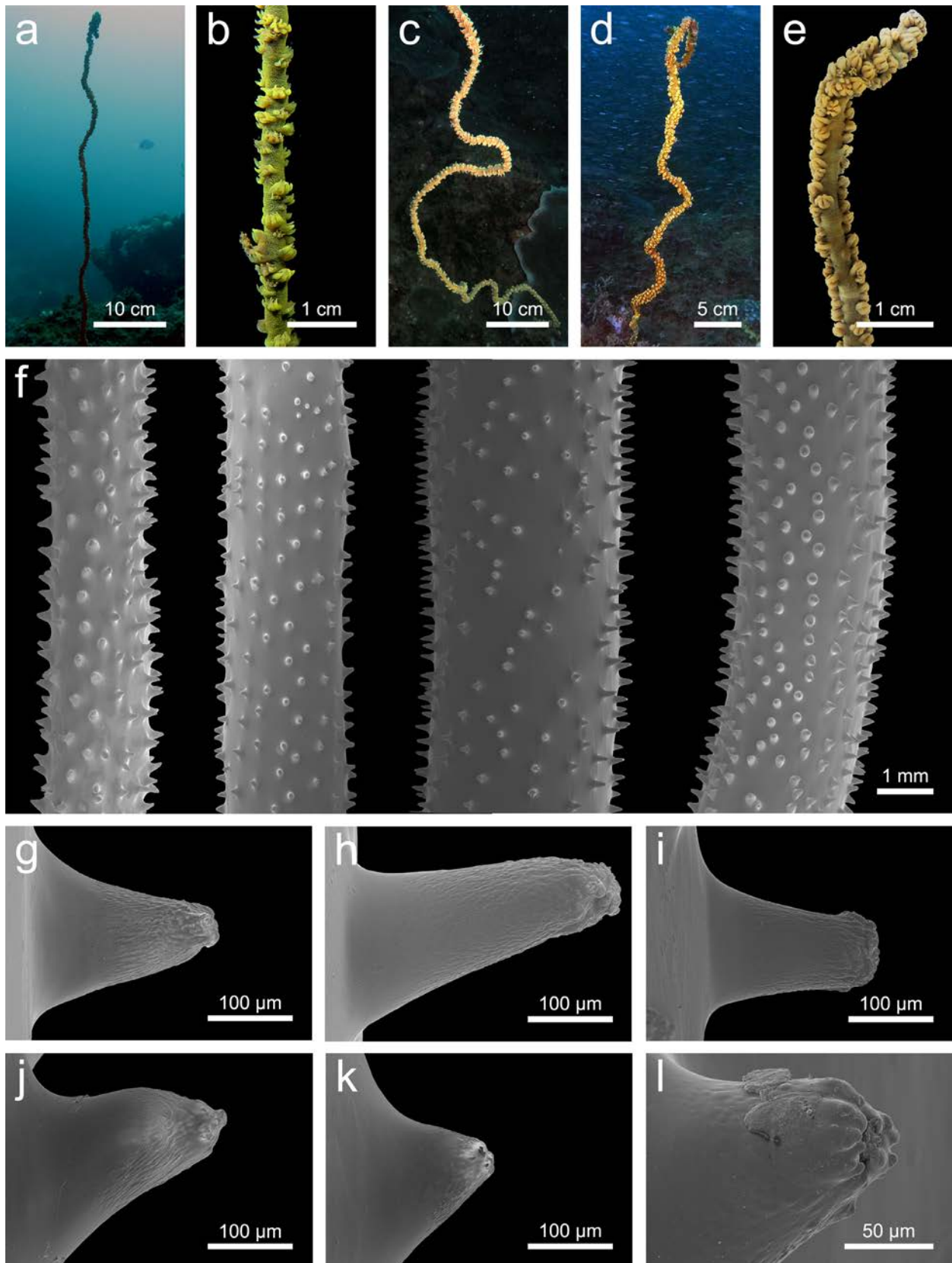


FIGURE 15. *Cirrhipathes densiflora* Silberfeld, 1909. (a–e) *In situ* pictures showing the different phenotypes of the species (a—INV.131368; b—INV.131376; d/e—INV.131374). (f) Sections of the skeleton 1.8 mm in diameter (INV.131352), 2 mm in diameter (INV. 131376), 3.2 mm in diameter (INV.131368) and 2.5 mm in diameter (INV.131374), respectively. (g–i) Spines found on the contorted morphotype (INV.131374, conical polypar spines in (d), cylindrical abpolypar spines in (e, f). (j–k) Spines found on the whip morphotypes (INV.131368, INV.131376). (l) Detailed view of the tubercles at the tip of the spine.

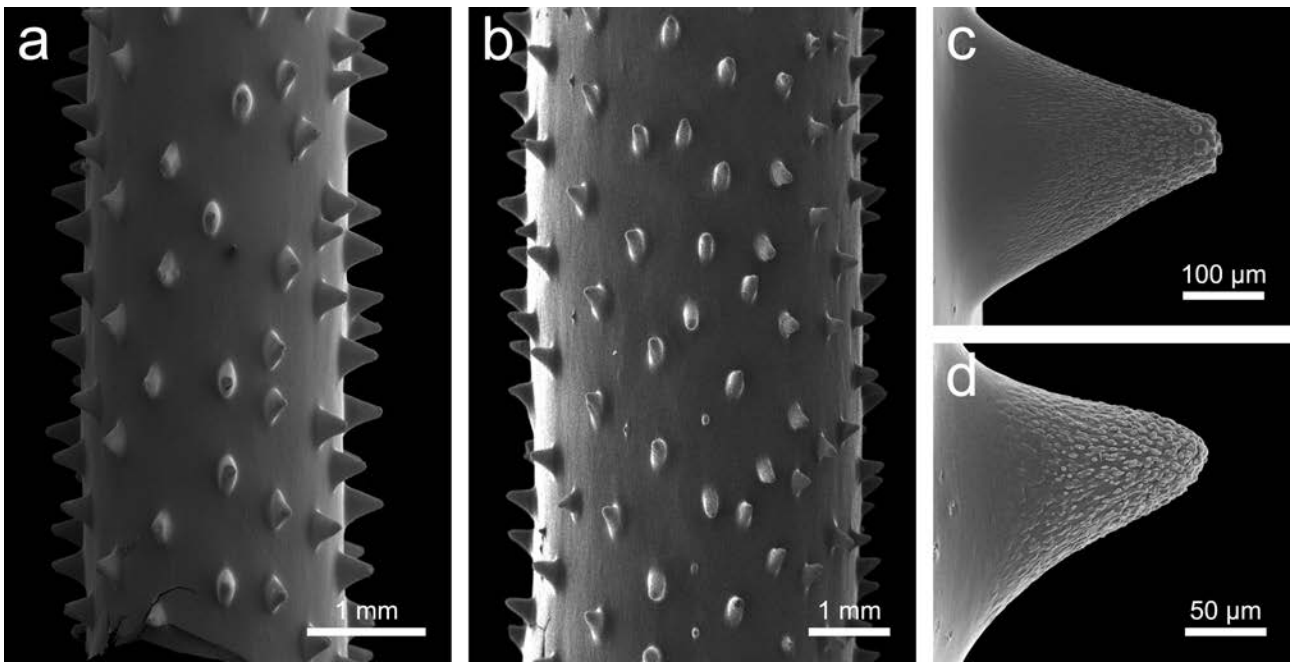


FIGURE 16. (a, c) *Cirrhipathes densiflora* Silberfeld, 1909 type specimen (schizotype USNM 100475) from Japan. (b, d) *Cirrhipathes contorta* van Pesch, 1910 type specimen (schizotype USNM 100414) from Indonesia.

The oral cones are prominent and clearly visible when the polyps are expanded with the mouth appearing like a slit. Longitudinal and cross grooves are usually visible between the polyps (Fig. 15, e). Clusters of nematocysts are distinguished as white spots on the coenenchyme between polyps (Fig. 15, b).

The spines are either at a right angle to the corallum or slightly inclined in different directions (Fig. 15, f). Spines have different shapes, from subtriangular to conical (Fig. 15, g–k), however tall cylindrical spines tend to be more frequent in the polypar side of the contorted colony (Fig. 15, h, i). In any case, the spines are slightly papillose with a knobbed tip more or less defined (Fig. 15, g–l). Growing spines are sometimes visible as they are narrower and cylindrical in shape, or minute and triangular. Adjacent spines are sometimes found fused together at their base. They measure 0.13–0.29 mm and are spaced apart 0.19–0.80 mm. Between seven and ten longitudinal irregular rows of spines can be seen in distal portions of the colony, but the longitudinal arrangement tends to be lost on thicker parts (Fig. 15, f). On the contorted form, the abpolypar spines measure 0.13–0.28 mm and they are spaced 0.19–0.46 mm apart. The polypar spines measure 0.22–0.31 mm and their mutual distance is 0.16–0.72 mm.

Taxonomic remarks. This species was originally described by Silberfeld (1909) who stated that the colony was sinuous, with polyps in multiple rows measuring about 1 mm in diameter and 2 mm in height, rounded spines measuring 0.35 mm in height and inserted at a right angle to the corallum, and having smaller spines with acute tips. He reported seven longitudinal rows of spines seen from one aspect. Since this description, no record of this species has been published. Contorted colonies are typical of *Ci. contorta* van Pesch, 1910. However, in his description van Pesch (1910) states that the colonies are so contorted that a colony measuring 1.5 m in length would fit into a “bottle of 20 cm”. As seen in *Ci. densiflora*, the polyps are also gathered on one side of the axis, 10 to 12 of them found per cm. The spines are triangular, blunt or acute, and measure 0.11–0.15 mm, their mutual distance is around 0.52 mm. They are papillose, but no mention is made about the presence of any knobs at the apex. A reexamination of both type specimens of *Ci. densiflora* Silberfeld, 1909 (USNM 100475, Fig. 16, a, c) and *Ci. contorta* van Pesch, 1910 (USNM 100414, Fig. 15, b, d) confirmed that spines were very similar, but knobs are only found in *Ci. densiflora* (Fig. 16).

In the present case, the Malagasy colony is also generally thicker than typical *Ci. contorta*, and with a more limited contortion of the corallum. In Madagascar, these knobs at the tip of the spines represent one of the main features to differentiate *Ci. densiflora* from *Ci. anguina* as the colonies can be very similar when observed in the field. Regionalization of spine size and ornamentation are common in contorted or spiral species. Contrary to straighter specimens of *Cirrhipathes*, the apical portion might slightly differ from a central or basal one, as well as between straight or looped segments. *Cirrhipathes contorta* has two categories of the size of spines: in loops and curves,

polypar and abpolypar spines are markedly different, which is also the case in the contorted specimen (INV.131374) analyzed here. Examination of entire contorted colonies of non-type material in Indonesia revealed a gradient of spines, from simple to few apical knobs (pers. obs. MB). However, as seen previously, the type does not show distinct knobs –but this has not been analyzed for specimens from all regions. Environmental constraints may contort colonies of *Ci. densiflora*. Monitoring of transplanted colonies in Indonesia suggested that this possibility is not to be excluded (Bo *et al.* 2009). Pending a revision of the *Cirrhopathes* group and the clarification of intra- and inter-specific variability of contorted colonies in the same environments, importance should be given to spines and type material for identifications among genera and species. Therefore, the name *Ci. densiflora* is applied to the different phenotypes observed in Madagascar.

Distribution. Japan (type locality, Silberfeld 1909), Madagascar (present study).

***Cirrhopathes cf. indica* Summers, 1910**

Figs. 17, 18

Cirrhopathes sp. Thomson & Simpson 1905, p.95, pl.1, fig.8

Cirrhopathes indica Summers 1910, p. 274, pl.5, fig.9

Material examined. Two entire colonies, Toliara 45 m specimen INV.131341, and 52 m specimen INV.131348; one distal fragment of a third colony, Toliara 45 m specimen INV.131343.

Depth range. 30–52 m.

Description. The colonies are unbranched and either straight, sinuous or sinuous with a single spiral (Fig. 17, a, Fig. 18, a–c). Colonies without any spiral measure up to 100 cm in height (Fig. 17, a, Fig. 18, a), while the one with the apical spiral measures 80 cm in height. The spiral is around 10 cm in diameter (Fig. 18, b, c). The coenenchyme is brown-greenish with white polyps, and cross grooves are visible (Fig. 17, b, c, Fig. 18, c). The polyps have thick, massive tentacles, which is especially true of the sagittal ones (Fig. 17, b, c), and around three polyps are found along one cm. When expanded, the tentacles are long with rounded tips (Fig. 18, c). At the base of the stem, the polyps are irregularly spread around the axis (Fig. 17, b) but higher up they quickly tend to be gathered on one side without being crowded (Fig. 17, c, Fig. 18, c). Polyps measure up to 3 mm in diameter and their mutual distance varies up to 4.5 mm.

The morphology and arrangement of the spines are dependent on their location along the corallum, and a variability is observed in their arrangement within and among specimens. Three main arrangements are seen from the apical portion to the basal one (Fig. 17, d–f, Fig. 18, d–f). In the growing apical portion (Fig. 17, d, Fig. 18, d), the spines are arranged in verticils, although not always distinctly layered. They are smooth, narrow, conical, slightly hooked with a pointed tip and inclined in different directions (Fig. 17, d, g). They have a few prominent tubercles at their top, not especially gathered on a single side of the spine (Fig. 17, g). In such section 0.63 mm in diameter, they measure 0.15–0.23 mm and are spaced 0.28–0.48 mm apart (Fig. 17, d). However, these spines arranged in verticils are not seen in every colony as illustrated in Fig. 18, e, where the growing part is missing –apical breakages are common in whip corals– and thus the corallum ends with conical, tuberculated spines with a pointed tip and similar sizes as those from the middle parts (Fig. 18, e, g). On an apical part that is 3.1 mm in diameter, the central canal is 0.6 mm in diameter. In the middle portion of the stem (with varying diameters), the spines are either arranged in well defined longitudinal rows or with a slightly irregular arrangement (Fig. 17, e). In a section 3.3 mm in diameter, 11 longitudinal rows are seen. In these middle portions, the spine arrangement and morphology are identical in all specimens analyzed. The spines are conical, narrow to stout, with many tubercles all around their surface (Fig. 17, h, i), arranged in sort of verticils (Fig. 17, i) but this pattern is not regular on all spines. Adjacent spines can fuse together at their bases. There is no difference between polypar and abpolypar spines, both measure 0.19–0.24 mm on a section of corallum 3.3 mm in diameter, and they can reach 0.30 mm on a section 3.9 mm in diameter. They are spaced 0.29–0.62 mm apart. On the basal part just above the anchorage and measuring 6 mm in diameter, the spines are irregularly arranged (Fig. 17, f) and measure 0.14–0.18 mm. They are narrow, conical and have tubercles all around their surface, almost until their insertion (Fig. 17, j). On the basal part of the other specimen examined, and measuring 4.2 mm in diameter, the spines measure 0.11–0.21 mm (Fig. 18, e). Their arrangement does not appear so crowded as in Fig. 16, f, leaving large areas devoid of spines (Fig. 18, f). No spiral arrangement is seen. Their morphology is similar to spines from the middle sections, but at the extreme base they are conical, with a pointed

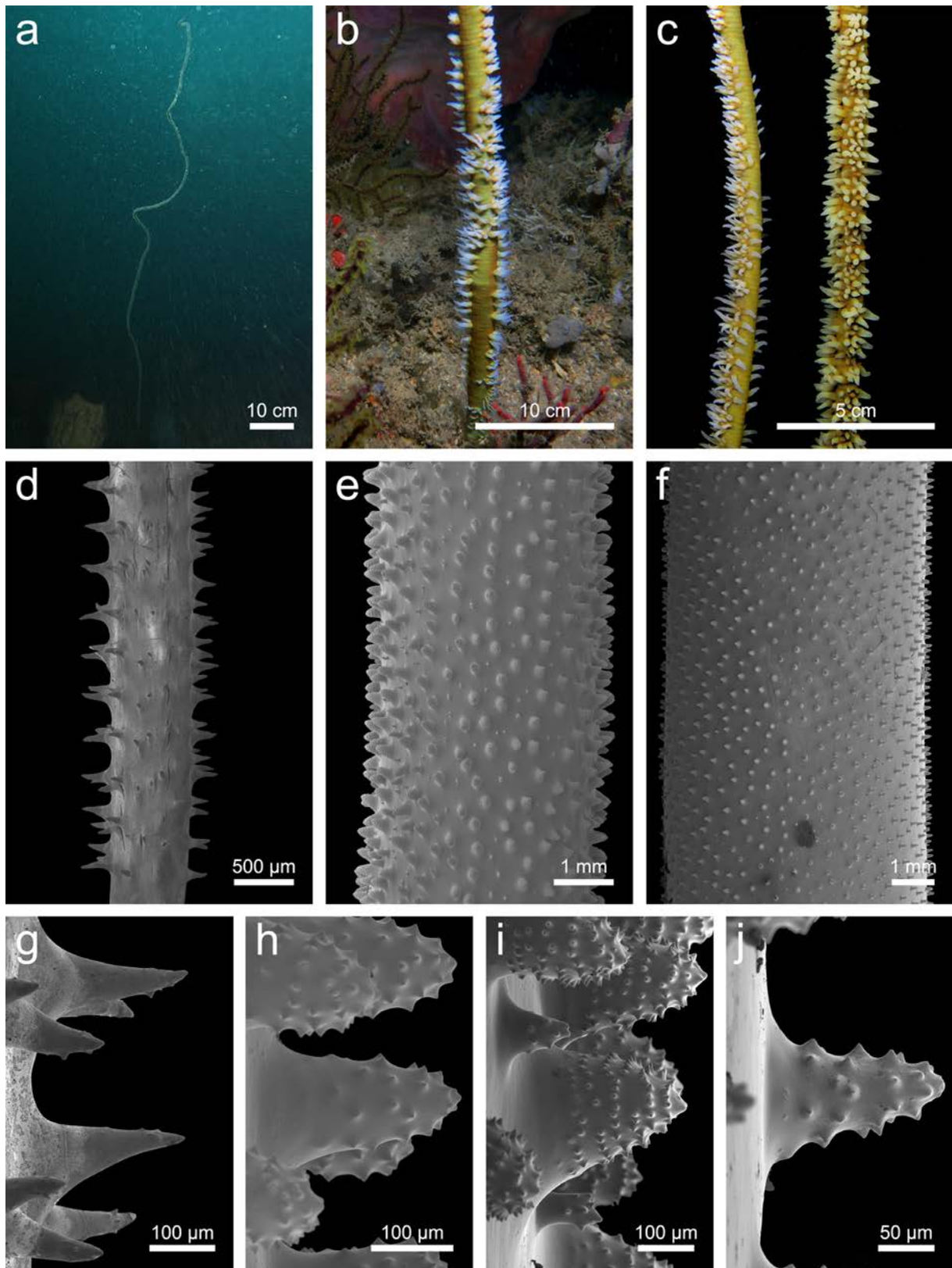


FIGURE 17. *Cirrhipathes* cf. *indica* Summers, 1910 specimen INV.131341. (a) *In situ* picture of the entire colony. (b) Close-up view of the polyp arrangement on the basal part. (c) *In situ* close-up view of the polyp arrangement in the intermediate region showing a side free of polyps. (d) Section of the growing apical region 0.63 mm in diameter and showing irregularly verticillated spines. (e) Section of the intermediate region 3.6 mm in diameter. (f) Section of the basal region just above the basal anchorage measuring 6 mm in diameter. (g) Spines of the apical part. (h–i) Spines of the intermediate region. (j) Spine of the basal region.

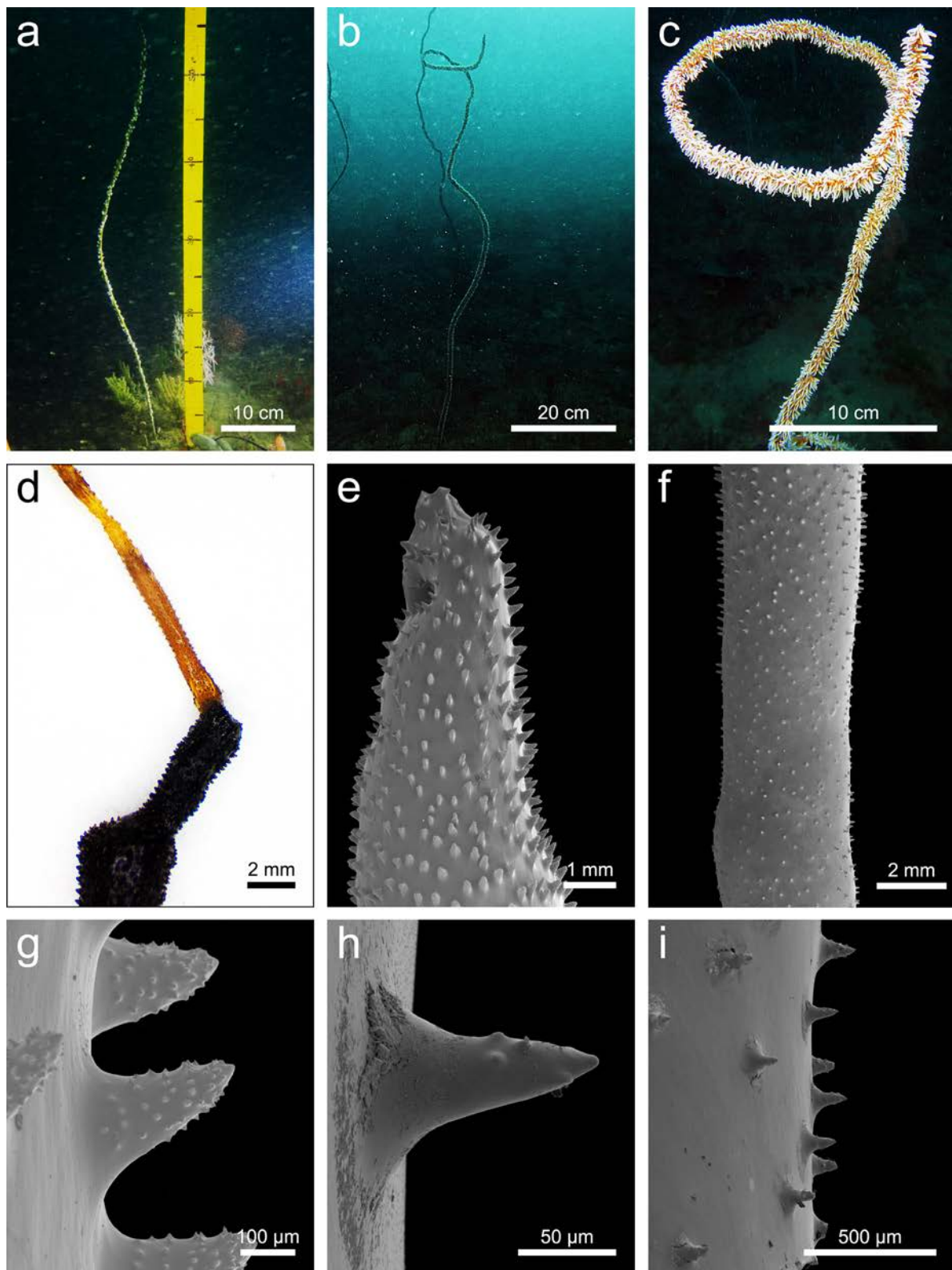


FIGURE 18. *Cirrhipathes cf. indica* Summers, 1910 (a–b) Morphological variations of the species (a—INV.131348, b—INV.131343). (c) Close-up view of the coil in the apical part of the colony INV.131343, with expanded polyps. (d) Detailed view of a growing apical part in INV.131348 where the verticillated spines are found in the bright, narrow part. (e) Detailed view of an apical part lacking the growing skeleton in INV.131343. (f) Section of a basal part in INV.131343 just above the anchorage and measuring 4.2 mm in diameter. (g) Spines of the apical part shown in e). (h) Spine found just above the basal anchorage and showing a few tubercles at the top. (i) Succession of spines near the basal anchorage, where a fully tuberculated one is seen at the top, only 1 mm above the base of the stem.

tip and only a few tubercles on a single side of the spine (Fig. 18, h). Fully tuberculated spines are observed only 1 mm above the basal anchorage (Fig. 18, i).

Taxonomic remarks. Tuberculated spines are found within both genera of whip black corals having more than one row of polyps, *Pseudocirripathes* and *Cirripathes*. To determine which genus the present specimens belong to, it is very important to analyze the polyps and the apical region of the stem. *Pseudocirripathes* polyps are typically not completely contractile, with long sagittal tentacles, and irregularly arranged along the stem leaving wide polyp-free areas. A peculiar large isorhiza is described for the cnidome of this genus. The colonies are characterized by a large hollow central canal and spines triangular or conical with many rounded tubercles at least in a portion of the stem (Bo *et al.* 2009). In the apical portions of the stem, spines are arranged in verticils, a distinctive character. So far, only one species has been described for this genus, *Pseudocirripathes mapia* from the Indo-Pacific area (Bo *et al.* 2009). This species is characterized by a typical tripartition of the spines' arrangement along the stem, spiral a few cms above the basal plate, in regular longitudinal rows in the intermediate region and in clear verticils in the distal portion.

The present Malagasy specimens share all the generic features of *Pseudocirripathes* as well as some features of the type species including (i) similar sizes for the spines and polyps, (ii) regularly arranged longitudinal rows in the intermediate region, and (iii) a typical annular arrangement of tubercles on some spines. However, it differentiates from the type species by (i) not having spirally arranged spines at the base, as they are irregularly arranged, (ii) not presenting spines with a side free of tubercles, (iii) spines from the intermediate region can be stout and blunt rather than conical and narrow, (iv) verticils of spines are not distinctly spaced apart, and (iv) the morphology of the polyps is slightly different, with shorter tentacles.

Among similar *Cirripathes* species, only *Ci. rumphii* is known to have clearly tuberculated spines (even if only few at apex), but no other relatable taxonomic character. *Cirripathes* sp. *sensu* Thomson & Simpson, 1905, described from Sri Lanka (formerly known as Ceylon) at 84 m, was described as having distinctly papillose spines, but their size is only reported for the apical region as being 0.1 mm and their ornamentation is not clear in the drawings provided by these authors. The original description reports a 135 cm long (65 cm in height) whip colony coiled in three spirals of around 10 cm and hollow; no information was given on polyps. It was clearly mentioned that this specimen has spines arranged in distinct verticils at the apex, while they are irregularly arranged in the intermediate and the basal regions of the stem. This latter species has been included in the past in *Cirripathes indica* Summers, 1910 from Mozambique (Portuguese East Africa) by Summers (1910), before being considered closer to *Pseudocirripathes* by Bo *et al.* (2009). In the poorly described species *Ci. indica*, whose type is lost, the colony, showing a hollow canal, is reported to be wound in a large circle of 18 cm in diameter with polyps, badly preserved, distributed all around but gathered together in some parts. The spines are described as being minute and papillose, all alike and equal, irregularly arranged (Summers 1910). It was related to *Cirripathes* sp. *sensu* Thomson & Simpson, 1905 by Summers (1910) but neither the description nor the drawing mentioned verticils. Bo *et al.* (2009) already highlighted that the association of *Cirripathes* sp. Thomson & Simpson with *Pseudocirripathes mapia* was not certain mainly due to the absence of a basal spiral arrangement of the spines, a feature shared with *Ci. indica*. The occurrence of verticils and a distinctly hollow canal, however, were considered features relatable at least at a generic level with *Pseudocirripathes*.

Considering all this information, the species described here shares significant features with those by Thomson & Simpson (1905) and, possibly, Summers (1910). It is plausible that a new *Pseudocirripathes* species, based on *Ci. indica* and including *Cirripathes* sp., should be re-described here.

Distribution. Mozambique (type locality, Summers 1910), Sri Lanka (Thomson & Simpson 1905), Madagascar (present study).

***Cirripathes rumphii* van Pesch, 1910**

Figs. 19, 20

Eucirripathes rumphii van Pesch 1910, p.170–174, figs.245–249

Cirripathes rumphii Zou & Zhou 1982, p.87, pl.15–4, figs. 9–11

Material examined. Distal fragments from two colonies. Ifaty 20 m specimen INV.131361, Andavadoaka 20 m specimen INV.131345.

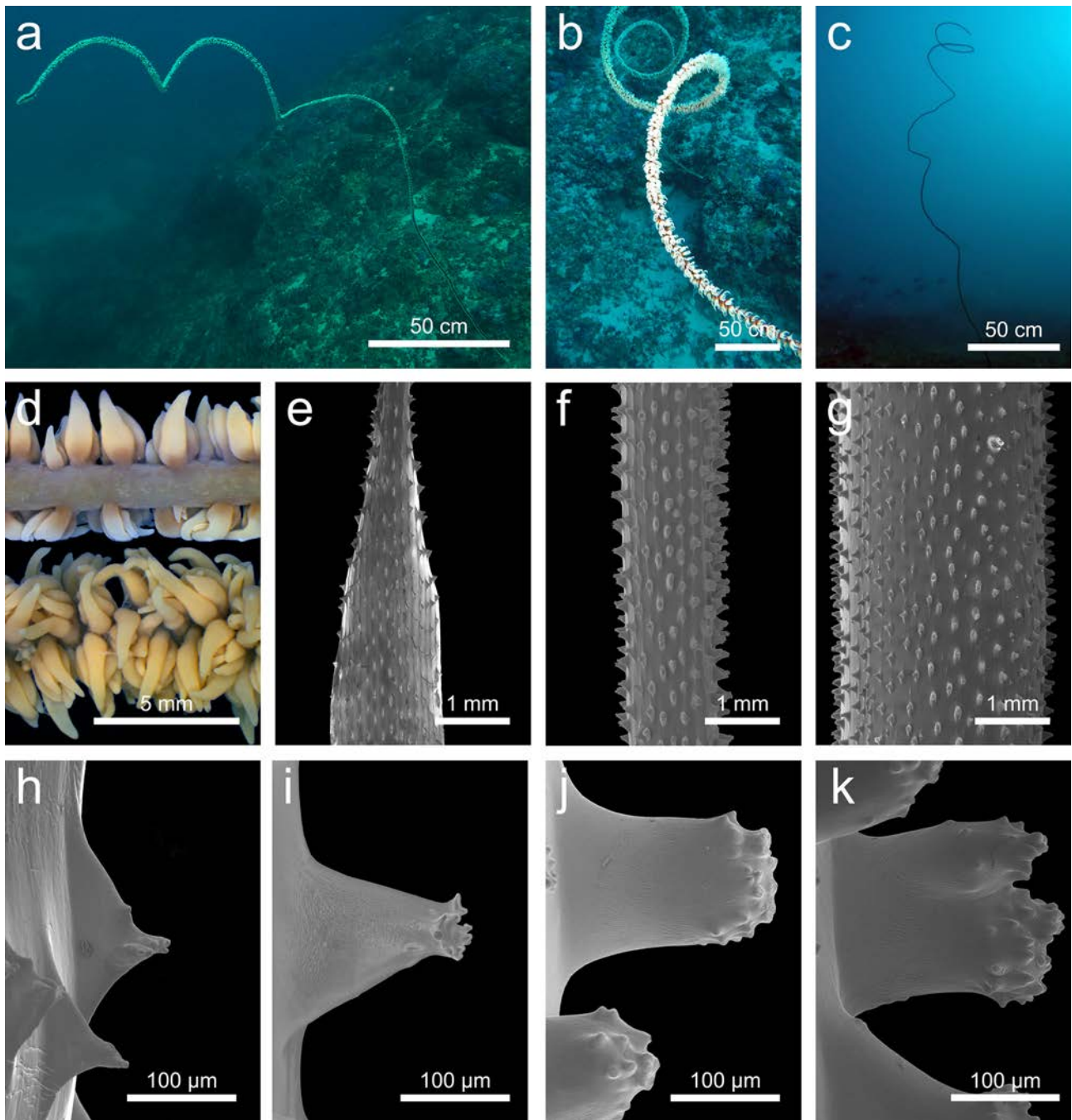


FIGURE 19. *Cirrhipathes rumphii* van Pesch, 1910. (a, b) *In situ* pictures of the specimen INV.131361 with large distal spirals. (c) *In situ* picture of the specimen INV.1312345. with a single distal spiral. (d) Close-up view of the polyp arrangement, leaving one side free of any polyps. (e) Section of the apical growing portion (INV.131345) measuring 1.26 mm in diameter, before tapering. (f) Distal section 1.22 mm in diameter (INV.131361). (g) Distal section 2.76 mm in diameter (INV.131345). (h) Spine found on the growing section shown in (e). (i–k) Spines found on the distal sections shown in (f).

Depth range. 25–45 m.

Description. A thin, single stem colony with the upper part having large dextral coils (Fig. 19, a, b), which can be loose in some colonies. Colonies are growing either horizontally at some point (Fig. 19, a, b) or more vertically (Fig. 19, c). The colonies analyzed reach about 1.8 m in height and starts to coil at about 50 cm from the seafloor. The pitches are about 40 cm and the coils have a diameter of about 20 cm. The skeleton of the basal part is about 2.5 mm in diameter, the one of the distal part is 1.5 mm in diameter. The coral shows a brown coenenchyme with white polyps partially arranged on only one side of the colony, but never in a single row (Fig. 19, d). Polyps measure up to 2.5 mm in transverse diameter and they all sit close to each other so that the coenenchyme between polyps is

sometimes not visible, but their mutual distance can be up to 1.9 mm (Fig. 19, d), with 3-4 found per cm. *In vivo*, the extended tentacles are long with round tips.

On the apical growing portion measuring 1.26 mm in diameter before it tapers, the spines are small, triangular, laterally compressed, smooth, and either simple or with a few distinct knobs at the apex (Fig. 19, e, h). They measure 0.04–0.10 mm and their mutual distance is 0.25–0.52 mm. The spines are arranged in quincunx in the distal part measuring 1.22 mm in diameter (Fig. 19, f) and 11–12 rows can be seen from one aspect. On the polypar side, the spines are conical to cylindrical, have a large base with a roughly blunt apex, and measure 0.15–0.23 mm high (Fig. 19, f, g, j). They are very finely papillose with the tip having many tubercles, and sometimes they can be bifid at the top (Fig. 19, k). The abpolypar spines are papillose, tend to be more conical with a sharper tip having many tubercles as well (Fig. 19, i), with a height of 0.11–0.16 mm. In any case, the spines are laterally compressed (Fig. 19, e–k). The mutual distance between spines varies between 0.15 and 0.51 mm.

Taxonomic remarks. This species was originally described from the Indonesian Archipelago by van Pesch (1910). He did not designate a holotype and based his description on six specimens, of which three are lost and one is missing from the register of the Siboga collection (Bo *et al.* 2009). The two remaining specimens belong to two different species, one belonging to the recently described species *Pseudocirripathes mapia* Bo *et al.*, 2009 (specimen Coel. 02599b from the Zoological Museum of Amsterdam, see Bo *et al.* 2009) and the other belonging to *Cirripathes rumphii* (specimen Coel. 02599a, from the Zoological Museum of Amsterdam, see Bo *et al.* 2009, schizotype USNM 100412, Fig. 20). The most important difference between these two species apart from spine morphology is the spine arrangement in verticils in intermediate and distal parts of *P. mapia*, a feature that *Ci. rumphii* never presents (Bo *et al.* 2009). The description of the present specimen recalls the one originally made pro-parte for Coel. 02599a by van Pesch (1910) and analyzed by Bo *et al.* (2009). The higher level of tuberculation observed here is consistent with an apical-central portion of the stem, while less tubercles and more compressed spines, as observed in Coel. 02599a, are consistent with the tip of the colony. Regionalization and age in this species are very important. Spines in distal portions can be less tuberculated (or not at all) and compressed as in Coel. 02599a, while extremely distal spines do not present any knobs because these are newly formed spines (Fig. 120, b, d). The color of the present specimen matches up with the two phenotypes known for this species, brown and white, or total orange.

Distribution. Indonesia (type locality, van Pesch 1910; Rumphius, see Bayer 1959; Bo *et al.* 2009), South and North Pacific Ocean (Bo *et al.* 2009), Sri Lanka (Thomson & Simpson 1905), China (Zou & Zhou 1982), Madagascar (present study).

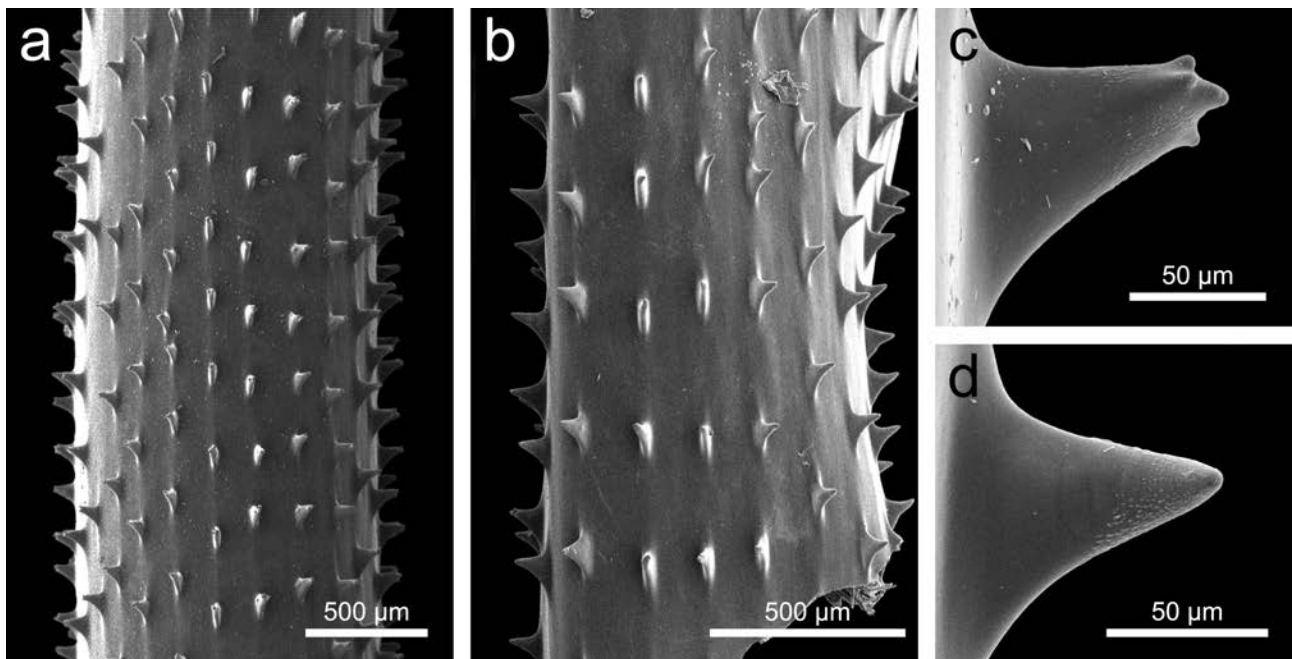


FIGURE 20. *Cirripathes rumphii* van Pesch, 1910 type specimen (schizotype USNM 100412) from Indonesia. (a) Section 1.25 mm in diameter. (b) Section 0.82 mm in diameter. (c) Spine found in the section shown in (a). (d) Spine found in the section shown in (b).

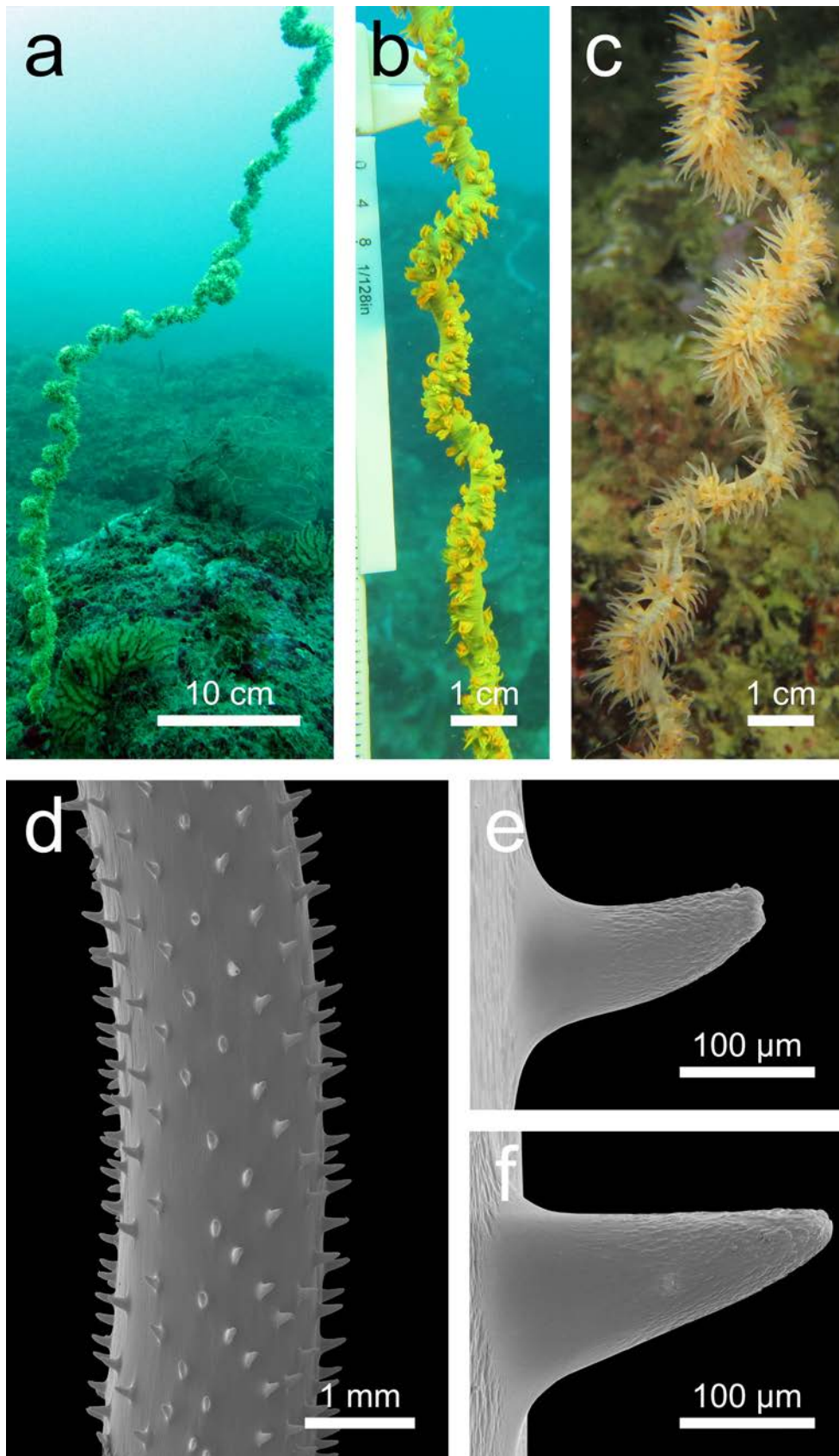


FIGURE 21. *Cirrhipathes cf. spiralis* (Linnaeus, 1758). **(a)** *In situ* picture of the specimen INV.131371 with well-defined coils. **(b–c)** *In situ* pictures of other phenotypes with loose spirals. **(d)** Section 1.9 mm in diameter of the distal part of the colony pictured in (a). **(e)** Inner spines which are papillose, conical with a blunt tip slightly knobbed. **(f)** Longer straight outer spines having the same morphology as the inner spine.

Cirripathes cf. spiralis (Linnaeus, 1758)

Fig. 21

Gorgonia spiralis Linnaeus 1758, p.800

Antipathes spiralis Pallas 1766, p.217

Cirripathes spiralis Brook 1889, p.85, pl.7, fig.10

Cirripathes (Eucirripathes) spiralis van Pesch 1914, p.158, figs 216–241

Cirripathes spiralis Utinomi 1956, p.181, fig.3

Material examined. Toliara, 25 m. Distal fragment, specimen INV.131371.

Depth range. 15–25 m.

Description. The colony has tight dextral helicospirals, which start coiling at about 3 cm from the base before being spaced apart by an average of 1.2 cm (Fig. 21, a). The coils are not always regular and can be slack in some colonies (Fig. 21, b, c). The specimen from which the sample was collected measures about 50 cm in height and the coils are about 1 cm in diameter. The skeleton diameter is about 3 mm at base and tapers slightly at top. The colony is bright or light yellow with yellow to orange polyps (Fig. 21, a–c). The polyps are found all around the stem with the exception of the inner side of the coils (Fig. 21, b, c) and they measure up to 2 mm in transverse diameter. Polyps are irregularly spaced, and the interpolypar distance can reach 3.5 mm, sometimes resulting in large areas of exposed coenenchyme (Fig. 21, b, c). They have a prominent oral cone and the transverse canals are clearly visible (Fig. 21, b). The tentacles appear long and pointed when fully extended (Fig. 21, c). Because of the great variation in the interpolypar distance, the number of polyps per cm is very different across the colony.

The inner and outer spines near the top of the corallum have the same morphology but differ in length. Spines are conical, straight or slightly curved, papillose with a blunt apex which is slightly knobbed (Fig. 21, d–f). They stand either at a right angle to the corallum or are slightly inclined (Fig. 21, d). Spines are arranged in spirals, and up to ten longitudinal rows can be seen on a section 1.9 mm in diameter (Fig. 21, d). The outer spines measure 0.20–0.26 mm in height while the inner spines are 0.16–0.21 mm in height. The spine spacing ranges from 0.15 to 0.7 mm.

Taxonomic remarks. This species was described based on pre-Linnean descriptions, without any type specimen. It was reported as *Acarbarium anguinum* in 1685 and then as *Palmijuncus anguinus* in 1750 by Rumphius (see Bayer 1959) before being mentioned in the 10th edition of the *Systema Naturae* in 1758 by Linnaeus under the name *Gorgonia spiralis* (see Brook 1889). It was latter mentioned under *Antipathes spiralis* by Pallas (1766), before being moved to the new genus *Cirripathes* by Blainville in 1834. It is the type species of *Cirripathes*. The description by Pallas (1766) mentions a distribution in Norway, the Mediterranean Sea and the Indian Ocean. However, as mentioned by Lamouroux (1824), the two first locations might be for other species. Detailed descriptions of this species were made by Brook (1889) and van Pesch (1914). Brook (1889) refers to tall colonies, with a tapering stem and dextral, tight coils, 1.5 cm in diameter. Brooks (1889) notes a somewhat spiral arrangement of spines, forming 10–11 rows, and indicates that spines are conical, blunt, and 0.3 mm long on the polypar side. Van Pesch (1914) gives a more detailed description of polyps and highlights a certain variability in spine size, shape and ornamentation, resulting in four variants, some of which have distinctly tuberculated and papillose tall spines. The present specimen shows a high affinity with Brook's (1889) description but given the lack of a neotype and the limits of the description, it is identified as *Cirripathes cf. spiralis*. It is possible that environmental plasticity, age and region of the stem may cause high variability of the characters.

Distribution. Indian Ocean (Pallas 1766), Indonesia (Ellis & Solander 1786; van Pesch 1914; Wagner *et al.* 2011), Korea (Moon & Song 2008), Hawaii (Clarke *et al.* 2015), Madagascar (present study).

Genus *Stichopathes* Brook, 1889

The genus *Stichopathes* encompasses unbranched corals but they differ from *Cirripathes* in having polyps arranged in a single row on one side of the corallum; the polyp row can sometimes twist around the stem. Even if the homology of this character has been questioned by several authors (Pasternak 1977; Bo *et al.* 2012a), it remains the only character for the distinction of this group. Like *Cirripathes* species, *Stichopathes* species can be straight, slightly to highly contorted, curved or coiled. The spines are smooth, papillose or with tubercles; the presence of

secondary spines is common. To date, this genus encompasses 36 accepted species, of which *Stichopathes pourtalesi* Brook, 1889 from the Caribbean is the type species (Bo & Opresko 2015; Molodtsova & Opresko 2020). The type specimens have been lost for eight of the currently accepted species, and 12 of the currently accepted species were described from the Indian Ocean.

Stichopathes cf. diversa (Brook, 1889)

Fig. 22

Cirrhopathes diversa Brook 1889, p.87, pl.12, fig. 12

Stichopathes diversa Summers 1910, p.275–276

Material examined. Distal parts of two colonies, Toliara 27 m specimen INV.131377, 52 m specimen INV.131375.

Depth range. 30–52 m.

Description. The colony is tightly coiled with dextral helicospirals that are more or less regularly spaced with a pitch of 1–1.9 cm (Fig. 22, a, b). Breaking events can lead to the restart of the coiling process in a different direction (Fig. 22, a). The spirals start to coil at about 3 to 4 cm from the base and have an average diameter of about 1.5 cm. The entire corallum measures 35 to 57 cm in height with a basal diameter of 4–4.4 mm. It slightly tapers towards the apex. The colony appears bright white or brown and the polyps are found in a single row on the outer side of the coils (Fig. 22, c). Smaller polyps are inserted between bigger ones irregularly (Fig. 22, c). Polyps are crowded (5–8 polyps per cm) and sagittally elongated, with no interpolypar spaces since the lateral tentacles of each polyp are touching the adjacent ones (Fig. 22, c). They measure 0.6–1.2 mm in transverse diameter, have a prominent oral cone, and their sagittal tentacles are longer than the lateral ones.

Two kinds of spines are visible, primary and secondary spines (Fig. 22, d–f). The primary spines are taller on the outer side of the coils and disposed at a right angle to the corallum (Fig. 22, e). These spines are either blunt, papillose and knobbed at the apex (Fig. 22, e), or blunt and tuberculated (Fig. 22, f). They correspond to the polypar spines and measure up to 0.4 mm high. The primary spines on the abpolypar side are triangular to conical (Fig. 22, g) or tall and cylindrical (Fig. 22, h) and have large papillae, but no tubercles. They measure up to 0.2 mm high. Secondary spines are interspersed among the primary ones on the entire skeleton (Fig. 22, d–h). They are generally small, smooth and triangular. Up to nine longitudinal rows of primary spines are visible in frontal view in a coiled section 2.1 mm in diameter.

Taxonomic remarks. The description of the present specimens shares some similarities with two species described in the literature for the area as having a coiled corallum, secondary spines and a clear distinction of polypar and abpolypar primary spines. *Cirrhopathes diversa* Brook, 1889, was described from Sri Lanka and successively reported by Forster Cooper (1903) for the Maldives and by Summers (1910) for Mozambique (at 44 m depth). This species, originally described as *Cirrhopathes* due to the lack of polyps, was later synonymized by Summers (1910) as *Stichopathes diversa*. Brook's (1889) type is a 30 cm-tall spiral colony, 1.5 mm in diameter at base and overall quite slender. Usually polyps of thin, coiled *Stichopathes* are not as large, compressed and crowded as in thick coiled *Stichopathes* (or thick straight ones as *S. maldivensis*), but polyps are not available in Brook's type. Examples of thin coiled colonies are given in "Clade A" of Bo *et al.* (2009). In Brook's specimen, the primary spines are stout, cylindrical and with a blunt apex, and are up to 0.35 mm high. Small knobs and a distinctly papillose surface are visible in the type material (pers. obs. DMO). In the drawing, a difference between polypar and abpolypar spines is visible. Forster Cooper (1903) described a specimen 25 cm-tall with a 3 mm basal diameter, tight coils and an overall thick appearance of the stem with a comparable pattern of spines given by the drawings. No information on polyps was given. Summers (1910) described a specimen 15 cm-tall characterized by a tight spiral and compressed, flat polyps; similar to Forster Cooper (1903), she reported a similar pattern of spines but no measures.

Stichopathes alcocki Forster Cooper, 1909 is another species sharing similarities with the specimens considered here. It was originally described from Sri Lanka at 62 m depth, but the type specimen is lost. The 30-cm long fragment described by Forster Cooper (1909) was depicted as a close spiral covered by crowded, flat polyps of 1 mm in diameter, which are consistent with a thick stem (probably 2–3 mm in diameter from the drawing). The spines located on the outer side of the spirals were reported to be blunt, conical and 0.3 mm high, while the inner ones were triangular, hooked upwards and 0.2 mm. No clear tuberculation of the primary spines is obvious from the drawing,

but secondary spines are evident. These primary spines seen in the drawing recall those in Fig. 22, e as tuberculation cannot be always so distinct, and little knobs appear only at high magnification under SEM. Summers (1910) suggested synonymizing *S. alcocki* with *Ci. diversa* based on the characteristic pattern of spines in coils.

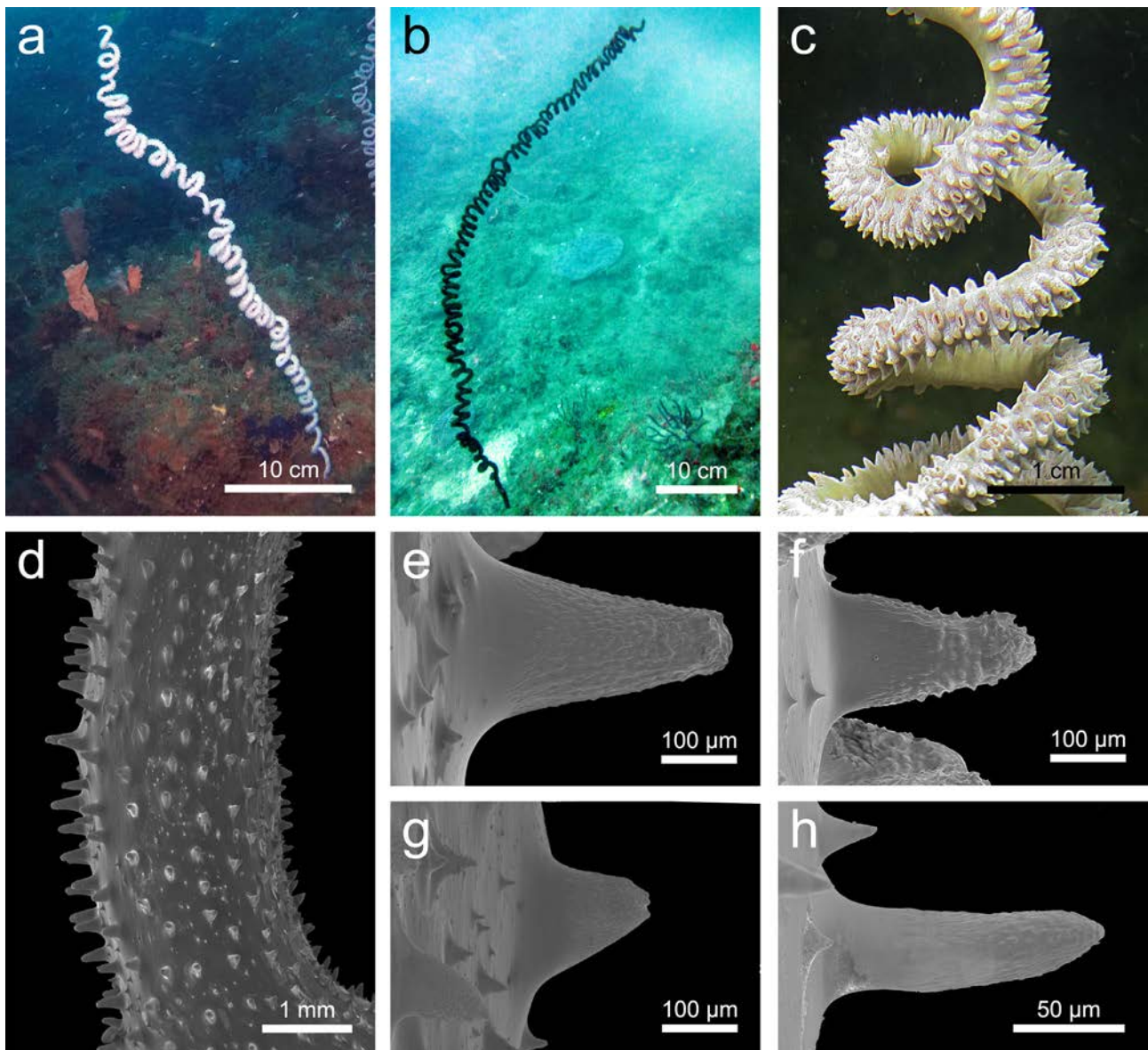


FIGURE 22. *Stichopathes cf. diversa* (Brook, 1889). (a–b) *In situ* pictures of the white (INV.131375) and brown (INV.131377) phenotypes. (c) Close-up view of the sagittally compressed polyps, which are found on the outer side of the coils. (d) SEM view of a 2.1 mm in diameter skeleton of an apical coil (INV.131375). The size difference between polypar spines (the outer ones) and abpolypar spines (the inner ones) is clear. (e–f) Blunt, conical polypar spines showing the variability between papillose and tuberculated surfaces and small tubercles at the tip. Small triangular, secondary spines can be seen all around. (g–h) Variability in abpolypar spines that can be sub-triangular or cylindrical, always showing a papillose surface. Small secondary, triangular spines are seen all around as well.

A few other species can be taken into consideration for comparison as they show secondary spines and a difference in polypar and abpolypar primary spines: *Stichopathes bispinosa* Summers, 1910 from East Africa re-described on Brook's *Cirrhopathes (?) flagellum* from Sri Lanka, and *Stichopathes papillose* Thomson & Simpson, 1905. Summers (1910) described *S. bispinosa*, as having similar flat polyps, but it is a very tall, thick colony with large spirals and very crowded, distinctly papillose and elongated, inclined spines (0.5 mm high polypar, 0.1 mm high abpolypar). Its synonymy with *Cirrhopathes (?) flagellum* is uncertain, given the straight colony and the poor preservation status of polyps of the latter. *Stichopathes papillose* is described as having a stout, spiral corallum (up to 30 cm high) with tight coils and large, flat polyps 1 mm in diameter. Spines are depicted as very cylindrical,

crowded and not particularly different between the two sides (0.3 mm and 0.2 mm, respectively), however knobs are reported (pers. com. DMO). The species variant described by Cooper (1909) from Indonesia is reported as having secondary spines.

In consideration of the fact that a high chance of synonymy is possible between *S. diversa* (at least some of the described specimens), *S. alcocki* and possibly *S. papillosa* (at least the variant), and that the present specimens do show a distinctly tall colony not reported for the discussed taxa, no definitive identification can be made. Pending a revision of the coiled species of *Stichopathes*, the name *S. cf. diversa* is used, based on its early **Description**. The present species recalls the “Clade C” of *Stichopathes* species as described by Bo *et al.* 2012a from Indonesia.

Distribution. Sri Lanka (type locality, Brook, 1889), Maldives (Cooper, 1903), Mozambique (Summers, 1910), Indonesia (Bo *et al.*, 2012a), Madagascar (present study).

Stichopathes cf. maldivensis Forster Cooper, 1903

Fig. 23

Stichopathes maldivensis Forster Cooper 1903, pl. 45, fig. 4

Material examined. Toliara, 17 m, 24 m. Distal fragments of two colonies, specimens INV.131372 and INV.131370.

Depth range. 15–52 m.

Description. Colonies may be either straight and slightly sinuous (Fig. 23, a), may have very loose apical coils or not (up to 1.6 m tall, 7.5 mm in basal diameter; Fig. 23, b, c) or with more evident apical large loops (up to 5 m tall, 8.5 mm in basal diameter). The colonies can show a branched pattern which is the consequence of a breaking event (Fig. 23, b). The coral is white or orange-brownish with the polyps in a single row occasionally twisting around it (Fig. 23, d, e). Polyps are crowded with six polyps per cm and measure 1.5–3.0 mm in transverse diameter, but very small polyps can be found irregularly between the larger ones (Fig. 23, d, e). There is no interpolypar space. The oral cone is prominent, and the tentacles are thick. When they are expanded during the night, they are long and finger-like (Fig. 23, e).

Two types of spines are found (Fig. 23, f–j). On a distal fragment measuring 4.45 mm in diameter, about 10–11 longitudinal rows of primary spines are visible from one aspect (Fig. 23, f). The primary spines are tall, cylindrical and disposed at a right angle to the stem on the polypar side (Fig. 23, f, g). They measure 0.80–1.00 mm and are spaced 0.45–0.80 mm apart. On the abpolypar side, these primary spines are smaller, conical and slightly inclined (Fig. 23, h, i). They measure 0.45–0.63 mm and are spaced 0.49–0.83 mm apart. On both sides the primary spines are papillose as well as tuberculated (Fig. 23, g–i), occasionally only on one side of the spine (Fig. 23, i). The secondary spines, interspersed between the primary spines, are small and very irregular in their shape and ornamentation (Fig. 23, j). They are either cylindrical, conical or triangular, smooth or with tubercles only at the tip or on their whole surface (Fig. 23, j).

Taxonomic remarks. Bo *et al.* (2012a) characterized the problematic genus *Stichopathes* for which they identified different phylogenetic clades. This species falls in “Clade D” of the groups described by these authors (Bo *et al.* 2012a), where they tentatively identify the clade as *Stichopathes cf. maldivensis*. It also corresponds to the description of *Stichopathes?* sp. made by Wagner (2015a) in Hawaii. The type specimen of this species is lost and was originally described from the Maldives at 67 m by Forster Cooper (1903). It was succinctly described as a straight colony (85 cm tall with a thick stem 4 mm in basal diameter) with two types of spines, where the primary ones were stout, conical and blunt with a papillose surface and knobs at the tip and the secondary spines were mostly triangular and irregularly distributed. No measures are given in the description, but an estimation from the drawing suggests that the height of primary spines in the type material (unknown region) is around 0.25 mm with an overall less crowded arrangement than in the present specimens and a lower density of tuberculation. However, this species, one of the most common in shallow-water Indo-Pacific assemblages (Clade D), presents a wide range of spine measures, shape and density of tuberculation depending on the considered region as well as the age of the colony (Bo *et al.* 2012a). No other described straight *Stichopathes* species with thick stem matches the spine pattern of *S. maldivensis*. However, the synonymy of *Cirrhopathes (?) flagellum* Brook, 1889 with *S. bispinosa* is doubtful. Brook described a very long (3.5 m), thick straight and scarcely sinuous colony, with similarities in habit and size of this species with *Cirrhopathes anguina*, something also seen in SW Madagascar where they are usually found together at same depths

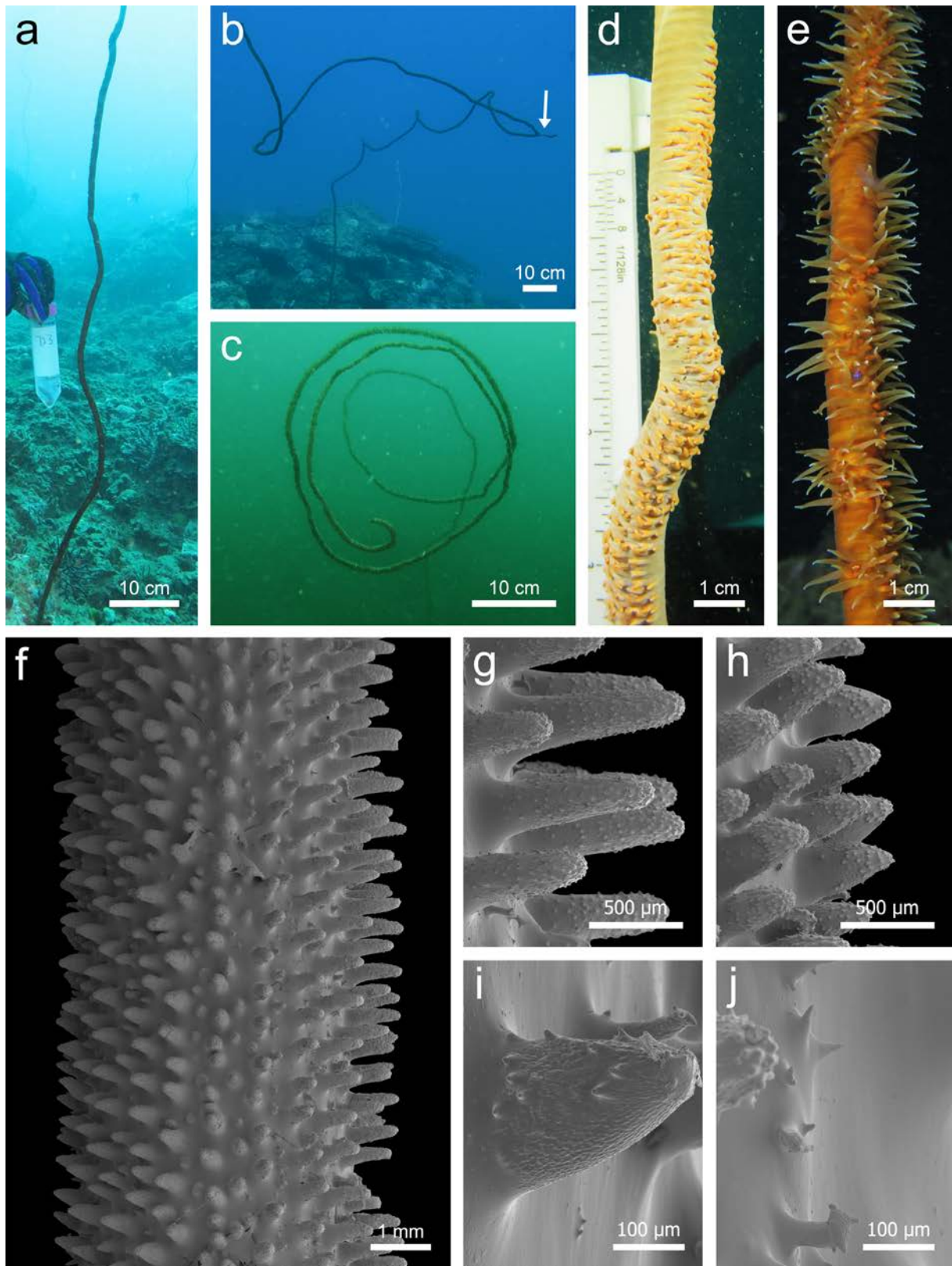


FIGURE 23. *Stichopathes* cf. *maldivensis* Forster Cooper, 1903. (a–c) *In situ* pictures showing the different morphologies that this species displays. A branched appearance is sometimes seen as a consequence of a breaking event, as shown by the white arrow. (d) White phenotype (INV.131372) with contracted polyps. (e) Brown-orange phenotype (INV.151020) with expanded polyps. The polyp row is twisting around the stem. (f) Section of a distal fragment measuring 4.5 mm in diameter (INV.131370). Polypar side is on the right. (g) Tall cylindrical polypar spines. (h) Conical abpolypar spines. (i) Close-up view of an abpolypar spine showing the tuberculation occurring on only one side. (j) Secondary spines.

and locations and with similar sizes. Brook's specimen presents much elongated primary spines (0.5 mm tall) with small rounded prominences at their apex, and slender and elongate secondary spines. In addition, usually secondary spines are reported as triangular and small, while in *Cirrhopathes* (?) *flagellum* they are distinctly reported as slender and elongated, as it happens with the present Malagasy specimen and some Indonesian ones. Its attribution to the genus *Cirrhopathes* depends on poorly preserved polyps and therefore is questionable; consequently *Cirrhopathes* (?) *flagellum* might be related to the present one.

Distribution. Maldives (type locality, Cooper 1903), Indonesia (Bo *et al.* 2012a), Hawaii (Wagner 2015a), Madagascar (present study).

Family Myriopathidae Opresko, 2001

This family was established to differentiate from the Antipathidae a sub-group of branched black corals which showed peculiar morphological features and subsequently proved to cluster separately from the Antipathidae in phylogenetic studies (Opresko 2001, Lapian *et al.* 2007, Brugler *et al.* 2013). The group is characterized by polyps having ten mesenteries and measuring 0.5 to 1 mm in transverse diameter. They have short tentacles with a rounded tip, and acute, conical to blade-like spines up to 0.3 mm tall on the smallest branchlets or pinnules, and cylindrical, simple, forked or antler-like spines on the larger branches and stem (Opresko 2001). In this family, colony morphology and pinnulation pattern represent the most important identification criteria to distinguish the different genera. There are currently five genera within the family: *Antipathella*, *Cupressopathes*, *Myriopathes*, *Plumapathes* and *Tanacetipathes*. They typically occur between 10 and 200 meters and are usually found in shallow waters in association with species from the family Antipathidae.

Genus *Myriopathes* Opresko, 2001

The genus was erected as a family, the Myriopathidae, by Opresko (2001). The type species *Antipathes myriophylla* Pallas, 1766, and a neotype has been described from Ambon, Indonesia by Opresko (2001). Species from this genus are characterized by a flabellate or bushy corallum, the stem and the branches are pinnulate to the second order or more with the primary pinnules arranged biserially and alternately in two lateral or anterolateral rows. The secondary pinnules are uniserial at the base of primary pinnules but become biserial distally. The uniserial secondary pinnules usually project out of plane formed by the biserial primary pinnules (Opresko 2001). Some species also have tertiary pinnules on the secondary pinnules. There are currently 11 nominal species within this genus, for which four type specimens are lost, and only four are described using modern techniques, including the neotype.

Myriopathes cf. *myriophylla* (Pallas, 1766)

Fig. 24

Antipathes myriophylla Pallas 1766, p. 205

Euantipathes myriophylla van Pesch 1914, p. 39

Myriopathes myriophylla Opresko 2001, p. 346–352, figs. 1–6

Material examined. Toliara, 45 m. Entire colony, specimen INV.131334.

Depth range. 30–45 m.

Description. The colony is branched and measures around 35 cm in width and 20 cm in height, with a basal diameter of 3 mm (Fig. 24, a). The branching pattern is planar and flabellate, and the colony is white colored (Fig. 24, a). It is branched up to the 6th order with branches measuring up to 15 cm in length (Fig. 24, a). The branches tend to form individual fronds separated from each other but overlapping (Fig. 24, a). The primary pinnules are biserial alternate and measure 2.5–11.5 mm, but average 7 mm (Fig. 24, b). They are inclined 30–60° to the branch, with an average of 45° (Fig. 24, b). In each row the primary pinnules are spaced 1.0–3.0 mm apart, with an average of 1.7 mm (Fig. 24, b). There are generally 7–8 primary pinnules occurring along one cm of a branch, counting those in both lateral rows (Fig. 24, b). Secondary pinnules measure up to 3 mm in length with an average of 2 mm and are

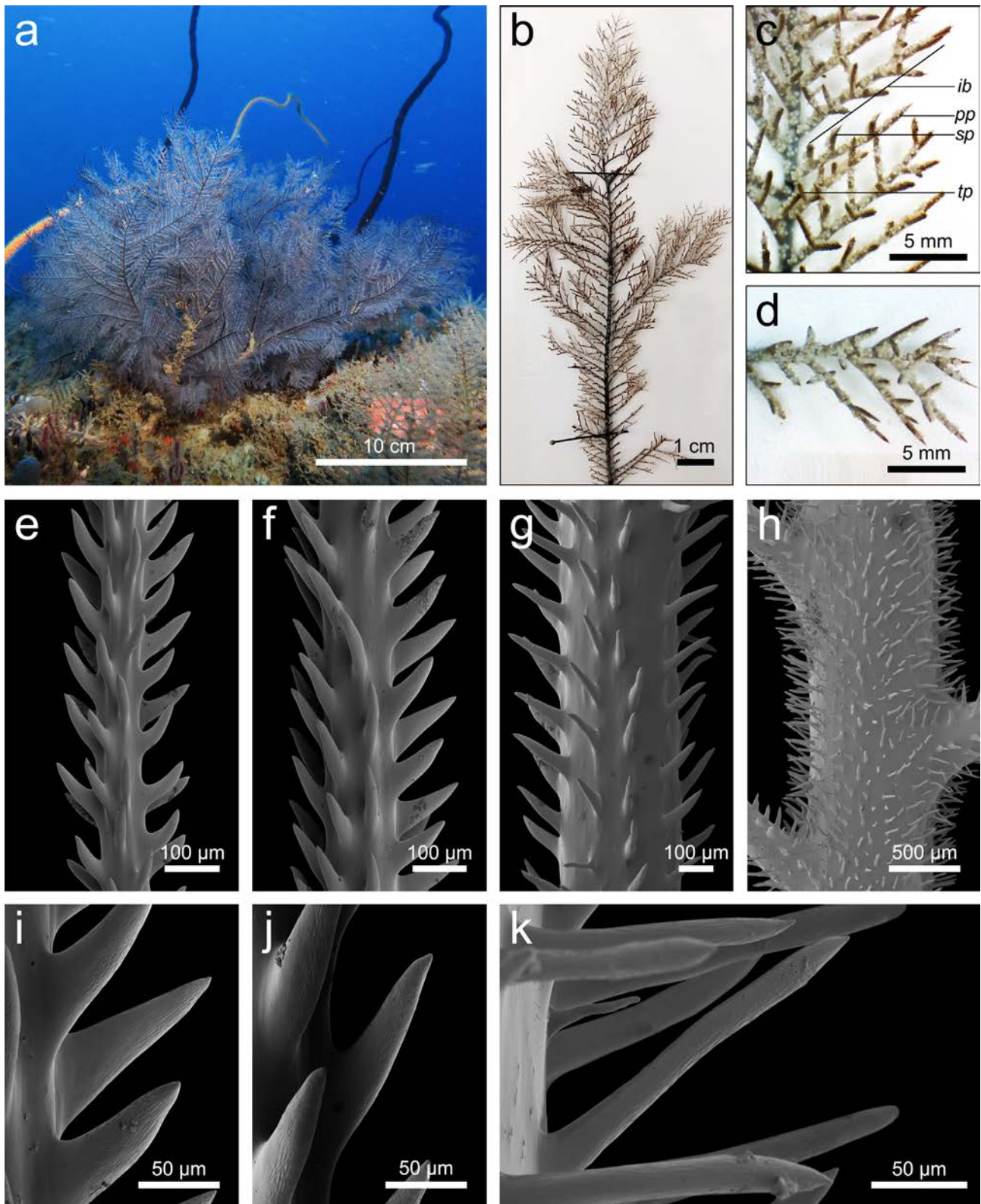


FIGURE 24. *Myriopathes cf. myriophylla* (Pallas, 1766) INV.131334. (a) *In situ* picture of the entire colony. (b) Detailed view of a branch and its pinnulation. (c) Close-up view of incipient branches and primary pinnules (*ib*—incipient branches; *pp*—primary pinnules; *sp*—secondary pinnules; *tp*—tertiary pinnules). (d) An incipient branch with bilateral primary pinnules with up to four uniserial secondary pinnules. (e) Section of a subpinnule 0.09 mm in diameter, the polypar side is on the right. (f) Section of a primary pinnule 0.14 mm in diameter, the polypar side is on the right. (g–h) Branches of different diameter showing the spine arrangement and morphology. (i) Polypar spine of a primary pinnule. (j) Abpolypar spine of a primary pinnule. (k) Tall, needle-like spines of a branch.

always present (Fig. 24, b–d). The first secondary pinnule is generally inserted around 1 mm above the base of the primary pinnule, but sometimes further away. They are also inserted out of the plane formed by the primary pinnules (Fig. 24, c, d). Up to four uniserial secondaries are found on primaries, afterwards they tend to be biserial on the distal part of the primaries when they become incipient branches (Fig. 24 b–d). Short single tertiary pinnules are also present, but not on all secondary pinnules (Fig. 24, c, d). The polyps are located on a single side of the pinnules, but on thicker branches they can be spaced irregularly all around the axis. Polyps measure up to 1 mm and are spaced up to 0.7 mm apart, for about 10–12 polyps per cm.

The spines on the pinnules are tall, conical and either straight or slightly horn-shaped, and they are inclined upwards (Fig. 24, e, f). They are slightly papillose on two-thirds of their surface, with papillae slightly elongated towards the tip of the spines (Fig. 24, i, j). On a subpinnule measuring 0.09 mm in diameter, five longitudinal rows of spines are seen, and there are no differences in the size of the polypar and abpolypar spines which measure 0.08–0.12 mm and are spaced 0.09–0.16 mm apart, except on polypar side where the mutual distance reaches up to 0.18 mm (Fig. 24, e). On a primary pinnule 0.14 mm in diameter, there are also no differences in the size of the polypar and abpolypar spines, which measure 0.10–0.14 mm. The abpolypar spines are spaced 0.10–0.18 mm apart, and the polypar spines up to 0.23 mm apart (Fig. 24, f). However, the inclination of abpolypar spines is more pronounced than the polypar spines (Fig. 24, f). The spines become more numerous and taller, narrower and needle-like as the axis gets thicker, with the longitudinal rows being lost (Fig. 24, g, h). On thick branches about 1 mm in diameter, their inclination is no longer very regular, and some are inclined basally as well as distally and others are perpendicular to the axis (Fig. 24, h). On such branches, the spines are needle-like and still slightly papillose, with the papillae elongated towards the tip of the spine (Fig. 24, k). Bifid spines are almost absent (Fig. 24, g). On these branches there is no distinction between polypar and abpolypar spines. They measure 0.14–0.22 mm in height on a branch 0.9 mm in diameter, and the mutual distance cannot be calculated as the longitudinal arrangement is lost.

Taxonomic remarks. Among the *Myriopathes* species with a flabellate corallum, which encompasses *M. ulex*, *M. panamensis*, *M. stechowi*, *M. spinosa*, *M. rugosa* and *M. myriophylla* (see Opresko 2001), only *M. myriophylla* has a pinnulation pattern similar to that of the Malagasy specimen and only *M. myriophylla* has tertiary pinnules. In the type specimen, the primary pinnules are up to 7 mm long and the secondary pinnules 2 mm long. These lengths are similar to those seen in the Malagasy specimen. The secondary pinnules of the latter specimen do not have the tendency to be on the lowermost portion of each primary as much as in *M. myriophylla* (Opresko 2001), as they are generally found 1 mm from the base of the primary. Additionally, a single tertiary pinnule occurs in the present specimen as seen in the neotype of *M. myriophylla* described by Opresko (2001). Therefore, the present specimen is assigned to *M. cf. myriophylla* and the slight differences (seen in angles of insertions of the pinnules, their number per cm or the maximum length of the pinnules for instance) are considered here as small variations.

Distribution. Indian Ocean (type locality, Pallas 1766), Indonesia (Ellis & Solander 1786; van Pesch 1914; Opresko 2001), Madagascar (present study).

Myriopathes cf. stechowi (Pax, 1932)

Fig. 25

Aphanipathes? stechowi Pax 1932, p.436–441, figs.16–18

Myriopathes stechowi Opresko 2001, p.349

Material examined. Soalara 17 m, branches from one colony, specimen INV.131335.

Depth range. 15–25 m.

Description. The colony is branched and measures around 50 cm in width and height (Fig. 25, a). The branching pattern is planar, with long branches measuring up to 30 cm in length, the whole colony appears red except for thick, dark and black branches (Fig. 25, a). The branches do not tend to overlap, but rather grow by forming almost perpendicular angles to the lower order branches bearing them (Fig. 25, a, b). The primary pinnules are biserial alternate and measure 0.5–1.7 cm, but mostly around 1 cm (Fig. 25, c). Primary pinnules are inserted 60–80° to the branch with an average of 70° and are slightly directed towards the posterior side of the colony (Fig. 25, b, c). In each row the primary pinnules are spaced 1.3–2.0 mm apart, with an average of 1.6 mm (Fig. 25, c). There are generally 10–11 primary pinnules occurring along one cm of a branch, counting those in both lateral rows (Fig. 25, b, c). Secondary pinnules are present but not on every primary (Fig. 25, c). Secondary pinnules measure up to 5 mm in length,

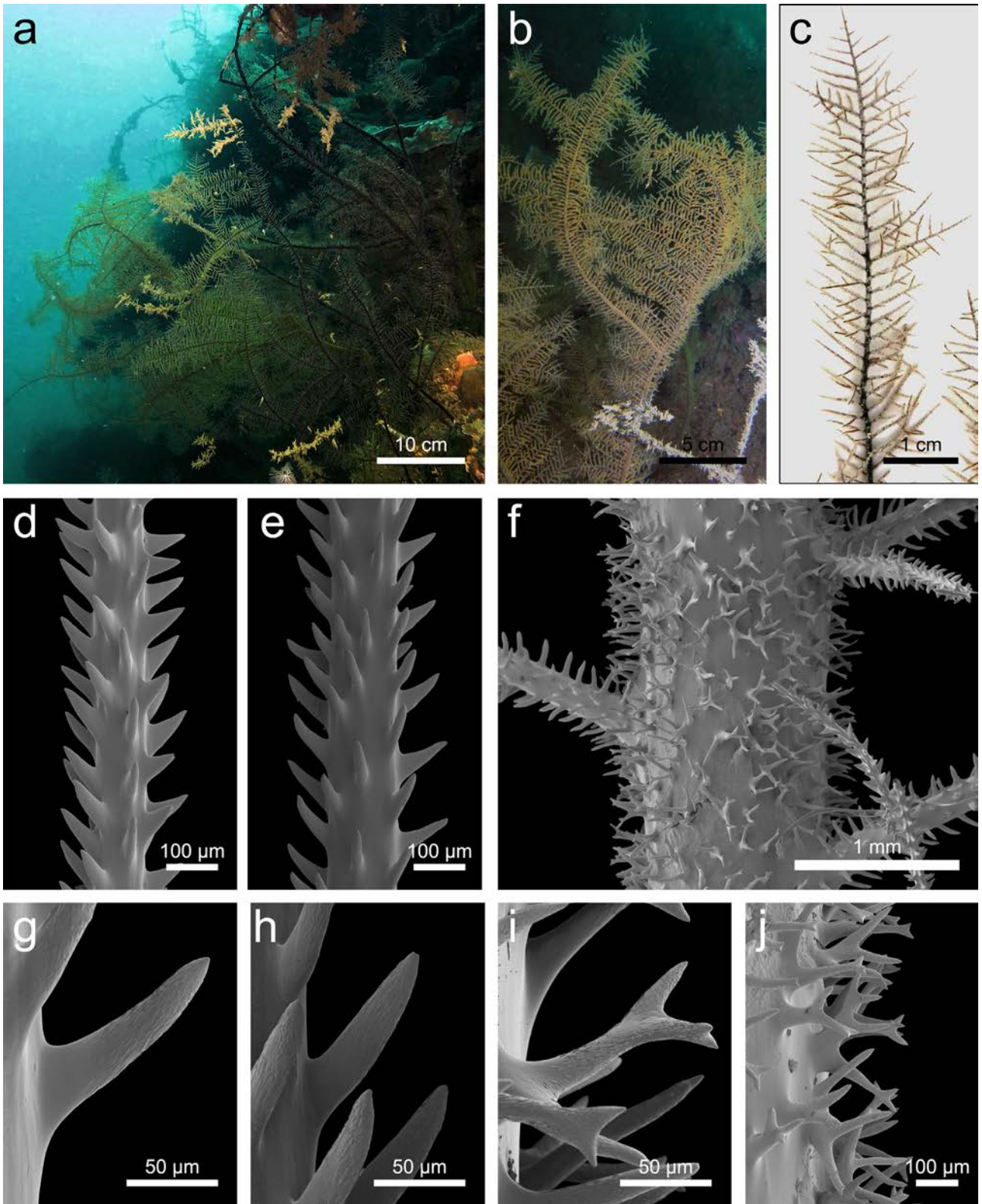


FIGURE 25. *Myriopathes* cf. *stehowi* (Pax, 1932) INV.131335. (a) Entire colony *in situ*. (b) Close-up view of the branching pattern *in situ*. (c) Detailed view of the pinnulation. (d) Section of subpinnule 0.1 mm in diameter, polypar side is on the right. (e) Section of primary pinnule 0.14 mm in diameter, polypar side is on the right. (f) Section of a branch 1.1 mm in diameter, showing numerous antler-shaped spines. (g) Polypar spine on primary pinnule. (h) Abpolypar spine on primary pinnule. (i) Antler-shaped spine on a branch. (j) Detailed view of the numerous bifid and antler-spines of a branch.

but mostly 2.0–3.0 mm (Fig. 25, c). They are inserted out of the plane and in some places, especially on thick branches, they emerge very close to the base of the primaries, giving the appearance that they are inserted at the same point on the branch. There are usually up to three uniserial secondaries on the primaries, with a maximum of five after which they become biserial and transform into a branch (Fig. 25, c). Tertiaries pinnules are rare, but when present only a single one is found on a secondary. The polyps are located on a single side of the pinnules, but on thicker branches they can be irregularly all around the axis. Polyps measure 0.6–0.8 mm and are spaced up to 0.4 mm apart, for about 10–12 polyps per cm.

The spines on the pinnules are conical and either straight-sided or slightly horn-shaped (Fig. 25, d, e). They are inclined upwards, but the inclination is greater on the abpolypar side (Fig. 25, d, e). Their surface is clearly papillose, with papillae elongated towards the tip of the spines (Fig. 25, g, h, i). On a subpinnule measuring 0.10 mm in diameter, 5–6 longitudinal rows are seen in one aspect. Polypar spines measure 0.06–0.09 mm and abpolypar spines measure 0.08–0.10 mm, and their mutual distance is 0.09–0.16 mm. On a primary pinnule measuring 0.14 mm in diameter, polypar spines measure 0.08–0.13 mm and are spaced 0.10–0.15 mm apart, while abpolypar spines measure 0.08–0.10 mm and are spaced 0.07–0.16 mm apart. The spines become more numerous and taller, narrower and very often antler-shaped or bifid on thick branches (Fig. 25, f). The bifurcation can occur at the base or near the tip of the spine (Fig. 25, i, j). They are no longer inclined regularly upwards on such branches (Fig. 25, f), and the longitudinal arrangement is lost. On these branches there is no distinction between polypar and abpolypar spines. They measure 0.18–0.26 mm in height on a branch 1.1 mm in diameter, and the mutual distance cannot be calculated as the longitudinal arrangement is lost.

Taxonomic remarks. Planar and flabellate myriopathids are represented by *M. ulex*, *M. panamensis*, *M. stechowi*, *M. spinosa* and *M. rugosa* (Opresko 2001). Amongst the three latter species, *M. spinosa* (Carter, 1880) reported by Brook (1889) from Sri Lanka at 120 m is described as having only one to three uniserial secondaries, which is different from the present species. The pinnulation is too poorly described by Brook (1889) to compare other morphological features. *Myriopathes rugosa* (Thomson & Simpson, 1905), originally reported from Sri Lanka, described as having an angular branching pattern of the main branches as seen in the present specimen, with similar angles of insertion of the primary pinnules. Again, the pinnulation is too poorly described to be confident with this identification. Finally, *M. stechowi* (Pax, 1932) originally described from Japan is the closest species to the present one. They share a similar pinnulation pattern as well as pinnules and spines of similar sizes, and both have numerous antler-shaped spines. This species could be related to *M. stechowi*, however Pax (1932) reported smooth spines for this species. Therefore, the Malagasy specimen is at this time assigned to *M. cf. stechowi*.

Distribution. Japan (type locality, Pax 1932), Madagascar (present study).

***Myriopathes cf. ulex* (Ellis & Solander, 1786)**

Fig. 26

Antipathes ulex Ellis & Solander 1786, p. 100, figs. 7–8

Euantipathes ulex van Pesch 1914, p. 79, fig. 62

Myriopathes ulex Opresko 2001, p. 349

Material examined. Toliara, 19 m. Distal branches, specimen INV.131356.

Depth range. 15–30 m.

Description. The colony is branched and measures about 50 cm in height (Fig. 26, a). The individual fronds of the colony are planar and flabellate, and the colony appears dark brown (Fig. 26, a, b). The primary pinnules measure up to 1 cm, after which they become incipient branches, and are regularly inclined 30–45° to the branch; they are mainly biserial alternate (Fig. 26, b, c). In each row the primary pinnules are 1.0–2.0 mm apart, with an average of 1.5 mm. There are generally 10–12 primary pinnules occurring along one cm of branch, counting those in both lateral rows. Up to four secondary pinnules can be found but not on all primary pinnules. Secondary pinnules are usually uniserial but a biserial arrangement is sometimes found (Fig. 25, c). They measure 1.5–4.0 mm long and are inclined 30–45° with respect to the primary pinnule bearing them. Tertiary pinnules are usually not present, but one can be rarely found. The polyps are located on a single side of the pinnules, but on thicker branches they can be spaced irregularly all around the axis. Polyps are slightly elongated in transversal direction and measure 0.4–0.9 mm in transverse diameter. Polyps are spaced 0.08–0.44 mm apart for about 10–12 per cm. The tentacles are short, thick

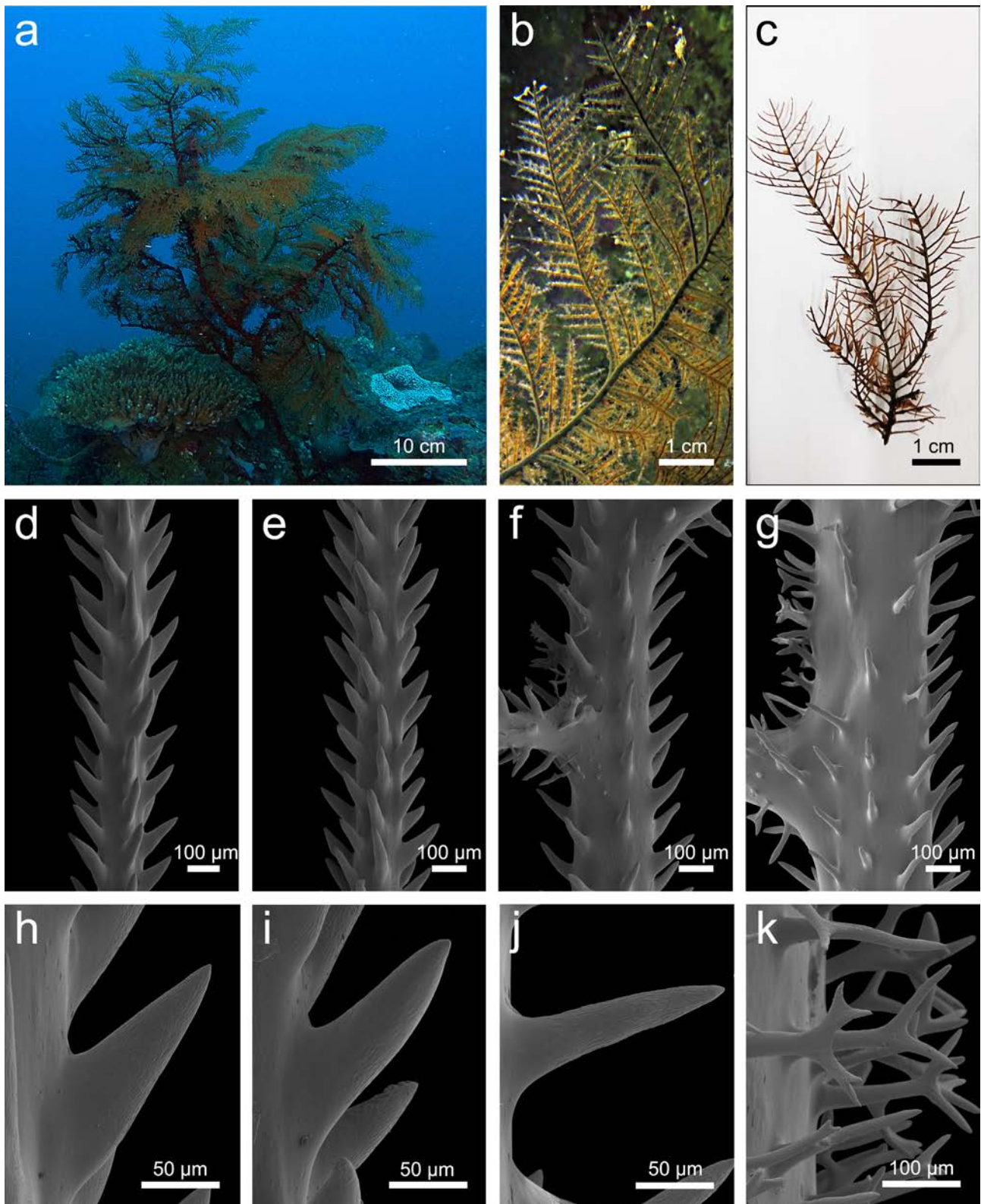


FIGURE 26. *Myriopathes* cf. *ulex* (Ellis & Solander, 1786) INV.131356. (a) *In situ* picture of the entire colony. (b) *In situ* close-up view of a branch and the primary pinnules. (c) Close-up view showing the pinnulation in details. (d) Section of secondary pinnule 0.12 mm in diameter. The polypar side is on the right. (e) Section of primary pinnule 0.14 mm in diameter. The polypar side is on the right. (f) Section of distal fragment of the main branch bearing primary pinnules and measuring 0.25 mm in diameter. (g) Section of thicker branch 0.34 mm in diameter and bearing primary pinnules. (h) Polypar spine from secondary pinnule. (i) Polypar spine from primary pinnule. (j) Tall, needle-like spine of a branch. (k) Branched, bifid or antler-like spines occurring on a branch measuring 1.8 mm in diameter.

and rounded at the apex. The spines on the pinnules are conical to horn-shaped, slightly papillose with the papillae elongated towards the tip of the spine (Fig. 26, d–f). They are longer on the polypar side although it is not always the case on small subpinnules. On a secondary pinnule measuring 0.12 mm in diameter, 3–4 longitudinal rows of spines are seen (Fig. 26, d). The polypar and abpolypar spines are not differing in size on such pinnules (Fig. 26, h), both measuring up to 0.17 mm in height with mutual distances of 0.1–0.19 mm and 0.1–0.22 mm, respectively. On a primary pinnule measuring 0.14 mm (Fig. 26, e), 4–5 longitudinal rows are seen where the polypar spines measure up to 0.17 mm (Fig. 26, i) and the abpolypar spines up to 0.16 mm, with mutual distances of 0.1–0.19 mm and 0.1–0.26 mm, respectively. All these spines are inclined upwards. The spines become more numerous and cylindrical as the axis gets thicker, with the longitudinal rows being lost (Fig. 26, f, g, j). They tend to become perpendicular to the corallum. On branches with diameters of 0.34–1.8 mm the spines are needle-like and slightly papillose, with the papillae elongated towards the tip of the spine (Fig. 26, j). Bifid or antler-shaped spines are also found (Fig. 26, k). On these branches there is no distinction between polypar and abpolypar spines. They measure 0.1–0.26 mm in height, and the mutual distance cannot be calculated as the arrangement in longitudinal rows is lost.

Taxonomic remarks. The type specimen originally described by Ellis & Sollander (1786) is lost. It was very succinctly described as being “very much branched, with loose, spread, very rough and pointed branches”. The drawings show small primary pinnules, with sparse small single secondaries pinnules. Later descriptions were made by Brook (1889) and van Pesch (1914). Brook (1889) stated that the pinnules were subalternate, directed anteriorly, occasionally simple but usually alternately pinnate or bipinnate, and measuring 1.8 to 2.5 cm in length. Van Pesch (1914) reported branches from 0.5 to 2.5 cm long inserted with an angle of 60°. Tertiary pinnules are absent and fusions do not occur. Based on the recent revision of Opresko (2001), this species groups in the flabellate *Myriopathes*, together with *M. ulex*, *M. panamensis*, *M. stechowi*, *M. spinosa*, *M. rugosa* and *M. myriophylla*. It can be provisionally separated from the other species, based on a less dense pinnulation due to a lower number of subpinnules with a more planar arrangement. In the typical *M. ulex*, secondary pinnules are rather sparse and usually only one is found per primary pinnule, while there are usually no tertiaries. Due to the differences in the number of secondaries, the name *M. cf. ulex* is attributed here.

Distribution. Indonesia (type locality, Ellis & Solander 1786), Indian Ocean (Lamouroux 1816), Philippines (Gray 1857), Korea (Moon & Song 2008), Hawaii (Wagner 2015a), Madagascar (present study).

Myriopathes sp.

Fig. 27

Material examined. Branches of one colony, Soalara 15 m specimen INV.131336.

Depth range. 15–30 m.

Description. The colony is branched and measures around 35 cm in width and 25 cm in height (Fig. 27, a). Branches are not inserted in a single plane which can result in a general bushy shape of the colony, with branches overlapping (Fig. 27, a). However, each branch is planar and measures up to 10 cm in length (Fig. 27, a, b). The colony is white but the contrast with the dark skeleton is clearly visible (Fig. 27, a, b). The primary pinnules are biserial, alternate, short and slightly inclined towards the anterior side of the colony, they measure up to 1 cm (Fig. 27, a, b). Primary pinnules are inserted 45–75° to the branch, with an average of 60° (Fig. 27, b). In each row the primary pinnules are spaced 1–3 mm apart, mostly 1.3–1.4 mm (Fig. 27, b, c). There are generally 11–12 primary pinnules occurring along one cm of a branch, counting those in both lateral rows (Fig. 27, b). When secondary pinnules are present, up to three uniserial ones can be found on a primary, after which they become biserial and alternate and the primary pinnules become a branch (Fig. 27, b, c). Secondary pinnules measure up to 3 mm in length, but mostly around 1.5 mm (Fig. 27, b, c). They are usually inserted out of the plane formed by the primaries (Fig. 27, b, c) but some fuse with overlapping pinnules (Fig. 27, g). There are no tertiary pinnules. The polyps are located on a single side of the pinnules, except on thicker branches where they can occur irregularly on all sides of the axis. Polyps measure 0.5–0.6 mm and are spaced up to 0.7 mm apart, for 11–12 polyps per cm.

The spines on the pinnules are conical and either straight or slightly horn-shaped (Fig. 27, d, e). They are inclined upwards, but the inclination is greater on abpolypar side (Fig. 27, d, e). Their surface is clearly papillose, with papillae elongated towards the tip of the spines (Fig. 27, h–k). On a subpinnule measuring 0.10 mm in diameter, 5–6 longitudinal rows are seen (Fig. 27, d). There are no differences in size between polypar and abpolypar spines,

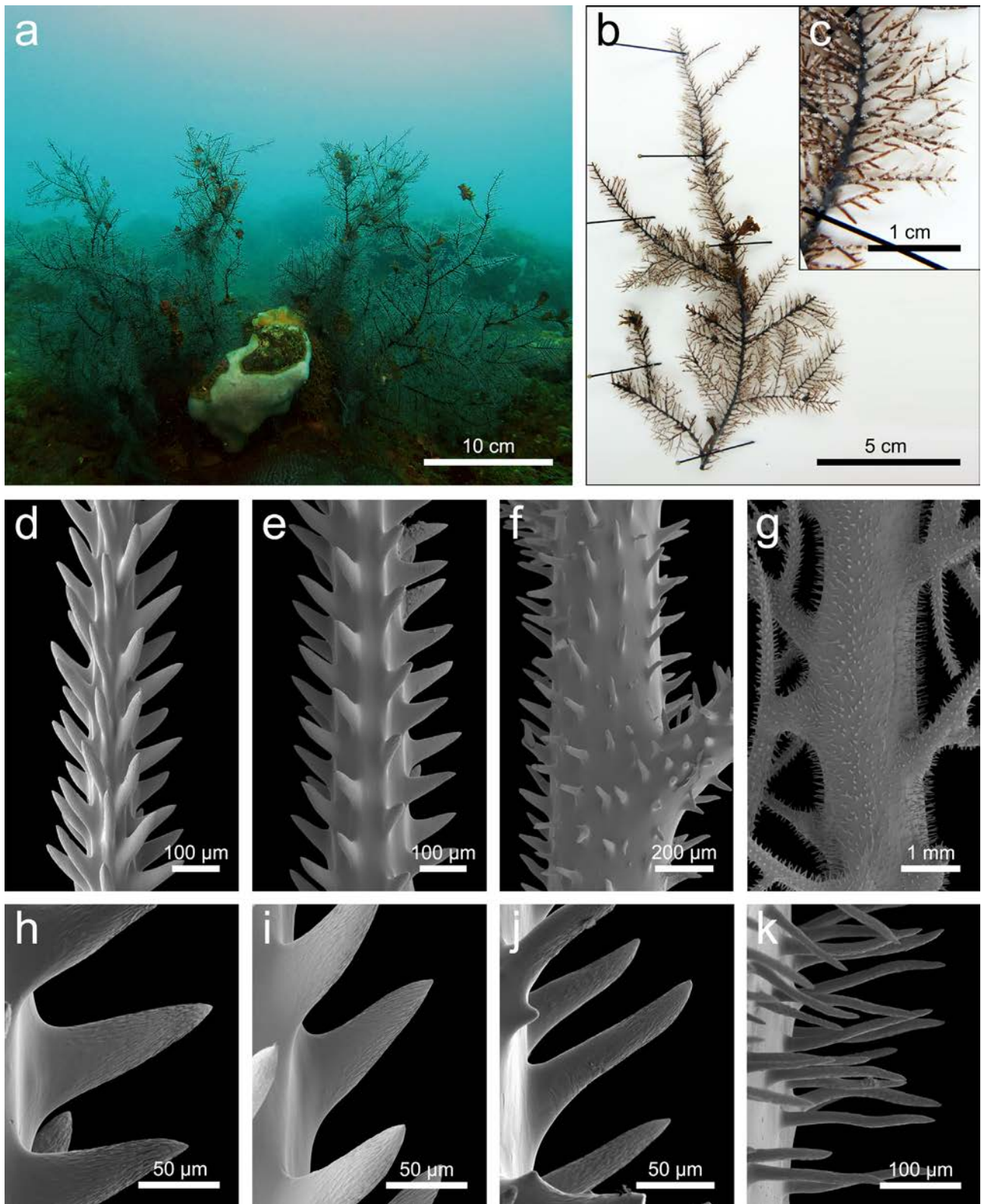


FIGURE 27. *Myriopathes* sp. INV.131336. (a) *In situ* picture of the entire colony. (b) Close-up view of a branch and the pinnules. (c) Close-up view showing the pinnulation in details. (d) Section of subpinnule 0.10 mm in diameter, polypar side is on the right. (e) Section of primary pinnule 0.18 mm in diameter, polypar side is on the right. (f) Section of primary pinnule 0.41 mm in diameter, polypar side is on the right. (g) Section of branch 1.8 mm in diameter. (h) Polypar spine of a subpinnule. (i) Abpolypar spine of a subpinnule. (j) Tall, cylindrical spine on a primary pinnule. (k) Needle-like spines of a branch.

they measure 0.10–0.13 mm and their mutual distance is 0.11–0.20 mm. On a primary pinnule measuring 0.36 mm in diameter, polypar and abpolypar spines have similar sizes, they measure 0.10–0.14 mm and are spaced 0.07–0.20 mm (Fig. 27, f). The spines become more numerous and taller, narrower and needle-like on thicker branches (Fig. 27, g). Bifid spines are almost never found, and the longitudinal arrangement is lost (Fig. 27, g). On these branches there is no distinction between polypar and abpolypar spines. They measure 0.12–0.22 mm in height on a branch 1.8 mm in diameter, and the mutual distance cannot be calculated as the longitudinal arrangement is lost.

Taxonomic remarks. The most important features of this species are the short length of the primary pinnules, the uniserial secondary pinnules, the absence of tertiary pinnules and the fusions occurring between adjacent pinnules. Species without tertiary pinnules are represented by *M. ulex*, *M. panamensis*, and *M. spinosa* while the pinnulation of *M. rugosa* is too poorly described to be compared. In *M. spinosa* it is reported that up to three uniserial secondaries are present, but the description lacks details to be confident with the identification. Therefore, the present specimen is not assigned to a nominal species.

Genus *Cupressopathes* Opresko, 2001

This genus is characterized by a bottle-brush pinnulation with four very irregular or quasi-spiral rows of primary pinnules, and uniserial, bilateral or irregularly arranged higher order pinnules. The type species *Cupressopathes abies* (Linnaeus, 1758) has been redescribed by Opresko (2001) while establishing the family Myriopathidae. There are currently five nominal species: *Cu. abies* (Linnaeus, 1758), *Cu. pumila* (Brook, 1889), *Cu. paniculata* (Esper, 1796), *Cu. gracilis* (Thomson & Simpson, 1905) known throughout the Indo-Pacific, and the recently described *Cu. simplex* Opresko, 2019 from New Zealand (Opresko 2019).

Cupressopathes abies (Linnaeus, 1758)

Fig. 28

Gorgonia abies Linnaeus, 1758, p.1290.

Antipathes cupressina Pallas, 1766, p.213.

Antipathes cupressus Ellis & Solander, 1786, p.103.

Antipathes abies Gray, 1857, p.292.

Euantipathes abies van Pesch, 1914, p.39–42, figs.12–14.

Cupressopathes abies Opresko 2001, p.352–358, figs.8–10.

Material examined. Distal fragments from two colonies, Toliara 25 m specimens INV.131367 and INV.131357.

Depth range. 15–52 m.

Description. Usually a monopodial colony with a bottlebrush shape, measuring up to 70 cm high (Fig. 28, a, b); however, some colonies have up to five main branches, each one having a regular width of about 10 cm considering the axis and the pinnules (Fig. 28, b). Each stem bears primary pinnules which are arranged pluriserially in about four rows that measure up to 5 cm in length (Fig. 28, c). Between five and seven primary pinnules are found along one cm, counting those on all sides of the branch (Fig. 28, c). Primary pinnules are inserted at nearly 90° on the stem and branches, then they extend horizontally and are naturally curved downward. Up to six orders of subpinnules are found on the primary ones (Fig. 28, c, d). These subpinnules are always on the same side of the primary pinnules, most of the time they are biserial and distally inclined but uniserial ones can also be found (Fig. 28, d). Subpinnules always grow upwards. Secondary pinnules measure up to 3 cm while tertiaries measure up to 2.5 cm. Higher orders of subpinnules are irregular and rarely measure more than 2.5 cm. The polyps are monoserial and are arranged on the same side of the ramification. Their colors are white or brown (Fig. 28, a, b). Sometimes two rows of polyps can be seen, especially on thicker lateral branches. On the stem and thick branches, the polyps can be distributed all around the axis. Polyps measure 0.3–0.9 mm in transverse diameter. Their mutual distance goes from zero when they sit next to each other to 0.6 mm. There are 12 polyps per cm on the pinnules and subpinnules.

The morphology of the spines on the pinnules and subpinnules follow gradual changes with the diameter of the ramification, from sub-conical to acicular, sharp needle-like, as in other myriopathids (Fig. 28, e–l). Their surface is slightly papillose on two-thirds of their height with papillae elongated towards the tip of the spine. They are inclined upwards,

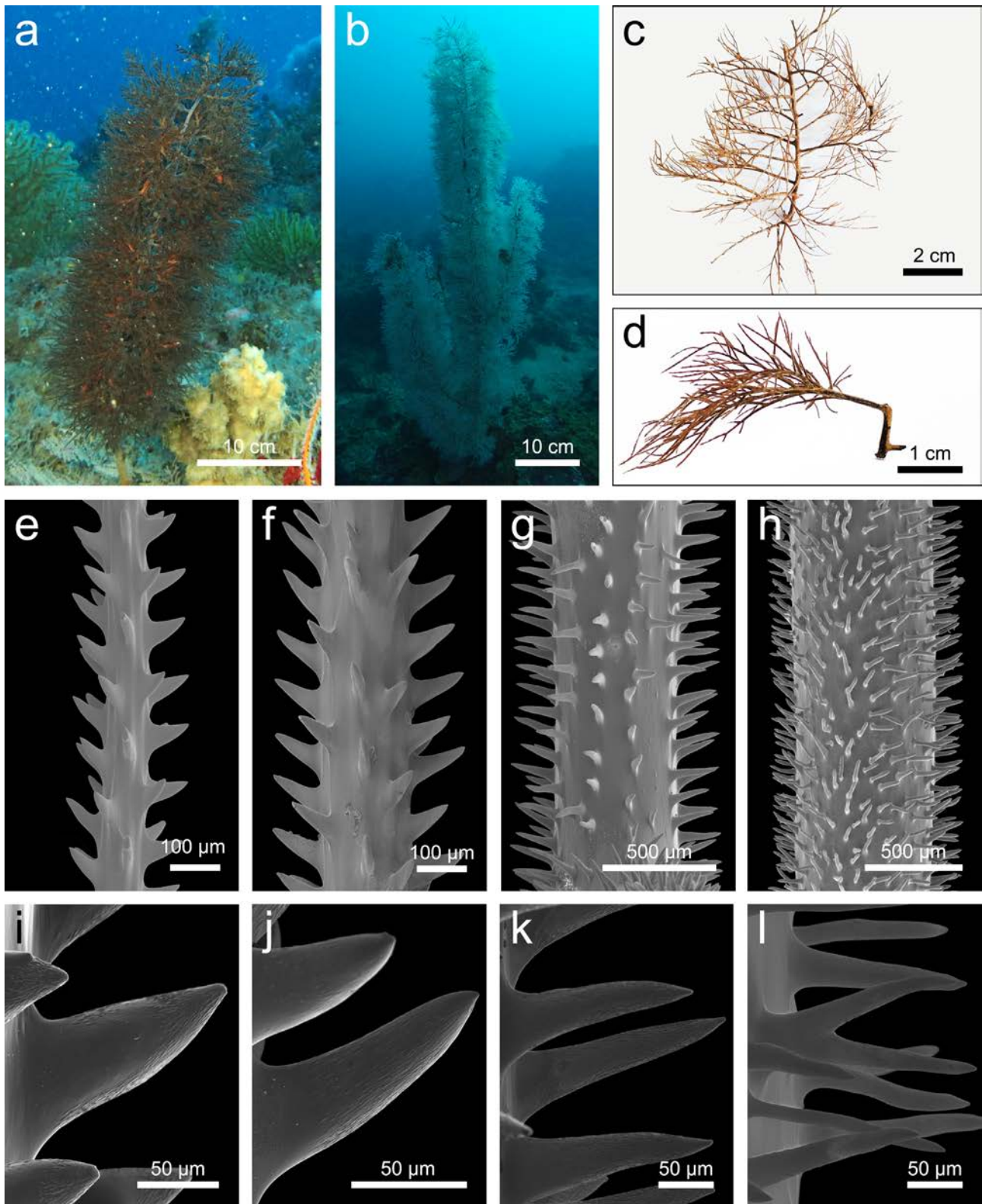


FIGURE 28. *Cupressopathes abies* (Linnaeus, 1758). (a–b) *In situ* pictures of a single-stem (INV.131367) and a branched colony (INV.131357). (c) Lateral view of the arrangement of the primary pinnules on a distal part of a colony. (d) Lateral detailed view of the subpinnules on a primary pinnule. (e) Section of subpinnule 0.09 mm in diameter, polypar side is on the right. (f) Section of subpinnule 0.18 mm in diameter, polypar side is on the right. (g) Section of primary pinnule 0.54 mm in diameter, polypar side on the right. (h) Section of main distal branch 0.70 mm in diameter. (i) Polypar spine of a subpinnule. (j) Abpolypar spine of subpinnule. (k) Tall, acicular spine occurring on thick primary pinnule. (l) Bifid spine occurring on branches.

and this is more distinct on the abpolypar spines (Fig. 28, e–g). On thicker branches the inclination is not regular (Fig. 28, h). On a subpinnule 0.11 mm in diameter, the spines are arranged in five longitudinal rows as seen from one aspect. The polypar spines measure 0.07–0.1 mm with a mutual distance of 0.16–0.24 mm and the abpolypar spines 0.06–0.09 mm with a mutual distance of 0.1–0.22 mm. On subpinnules of 0.35 mm, eight longitudinal rows can be seen. Both polypar and abpolypar spines reach 0.13 mm, with mutual distances of 0.11–0.21 mm and 0.11–0.24 mm, respectively. On a primary pinnule of 0.65 mm in diameter, the longitudinal arrangement is lost, and the spines are not consistently inclined upwards anymore but project out in various directions. Polypar spines measure 0.9–0.17 mm and abpolypar spines 0.15 mm. On the main distal branch measuring 1 mm in diameter, the arrangement and inclination is irregular in the same way as on the primary pinnules. The spines measure up to 0.24 mm in height, they are tall and more densely arranged, sometimes bifid either from the base or only at the top (Fig. 28, l).

Taxonomic remarks. This species was previously described in the western Pacific and the Indian Ocean. The present diagnosis closely matches the description of the neotype made by Opresko (2001) from the Philippines and collected at 40 m depth.

Distribution. Philippines (neotype locality, Opresko 2001), Sri Lanka (Thomson & Simpson 1905), Seychelles (Cooper 1903), Mozambique (Summers 1910), Indonesia (van Pesch 1914), Madagascar (present study).

***Cupressopathes cf. pumila* (Brook, 1889)**

Figs. 29, 30

Antipathes pumila Brook 1889, pl. XI, fig. 17

Cupressopathes pumila Opresko 2001, p. 356–358.

Material examined. Entire colony, Toliara 24 m INV.131366.

Depth range. 20–30 m.

Description. The colony is branched and measures about 40 cm high and 25 cm wide with a basal diameter of 6.5 mm (Fig. 29, a). Each branch bears four irregular rows of primary pinnules that reach up to 5 cm in length (Fig. 29, b, c). Primary pinnules are inserted at an angle slightly less than 90° to the branch. The arrangement of primary pinnules does not give the typical overall bottle-brush appearance but rather a plumose aspect (Fig. 29, a). There are five to seven primary pinnules along one cm of the axis, counting those on all sides (Fig. 29, c). These primary pinnules can be pinnulated to 4th order, some can be more densely pinnulated than the others (Fig. 29, d–f). The subpinnules are mostly biserial but they can also be uniserial (Fig. 29, e, f). Subpinnules are inserted at an acute angle to the primary pinnules with a general tendency to grow upwards, but this is not the case in many places (Fig. 29, c–f). Secondary pinnules are generally less than 2.5 cm in length, but at some places they reach lengths up to 5 cm (Fig. 29, e, f). Higher order pinnules are less than 1.5 cm long (Fig. 29, c–f). The polyps are slightly elongated transversally; they measure 0.4–1.0 mm in transverse diameter and are spaced 0.15–0.35 mm apart, with ten polyps along one cm. Polyps are located on a single side of the branches, but they can twist around it. On thicker branches, polyps are irregularly distributed.

The spines on pinnules and subpinnules follow the general gradual change seen within this genus, from conical and horn-shaped to acicular, sharp and needle-like (Fig. 29, g–n). They are finely papillose over two thirds of their height, with the papillae elongated towards the tip of the spines (Fig. 29, m, n). On the subpinnules these papillae tend to appear as faint striations and the spines almost appear smooth (Fig. 29, k, l). The spines are inclined upwards, which is more pronounced on abpolypar side, although on thicker branches this inclination is irregular (Fig. 29, g–j). On a subpinnule 0.13 mm in diameter, the spines are arranged in five longitudinal rows. The polypar spines measure 0.08–0.10 mm in height and are spaced 0.12–0.20 mm apart, while the abpolypar spines measure 0.07–0.09 mm and are spaced 0.11–0.18 mm apart. On a primary pinnule of 0.28 mm, six longitudinal rows of spines can be seen. The polypar and abpolypar spines measure 0.10–0.14 mm and 0.09–0.13 mm, respectively, and they are spaced 0.10–0.19 mm and 0.10–0.18 mm, respectively. On a thick branch of 1.3 mm in diameter, the longitudinal arrangement is lost, and the spines measure up to 0.26 mm. Bifid spines can also be found on such branches.

Taxonomic remarks. The present species differs from *Cupressopathes abies* in having a smaller, more flattened corallum with several of the primary pinnules developing into side branches (Brook 1889, Opresko 2001, Fig. 30 a). The typical bottle-brushed shape of *Cu. abies* is not found in this species (Fig. 30, a), as there is a tendency for its primary pinnules to have more irregular lengths along the corallum than those of *Cu. abies*. In general, compared to *Cu. abies*,

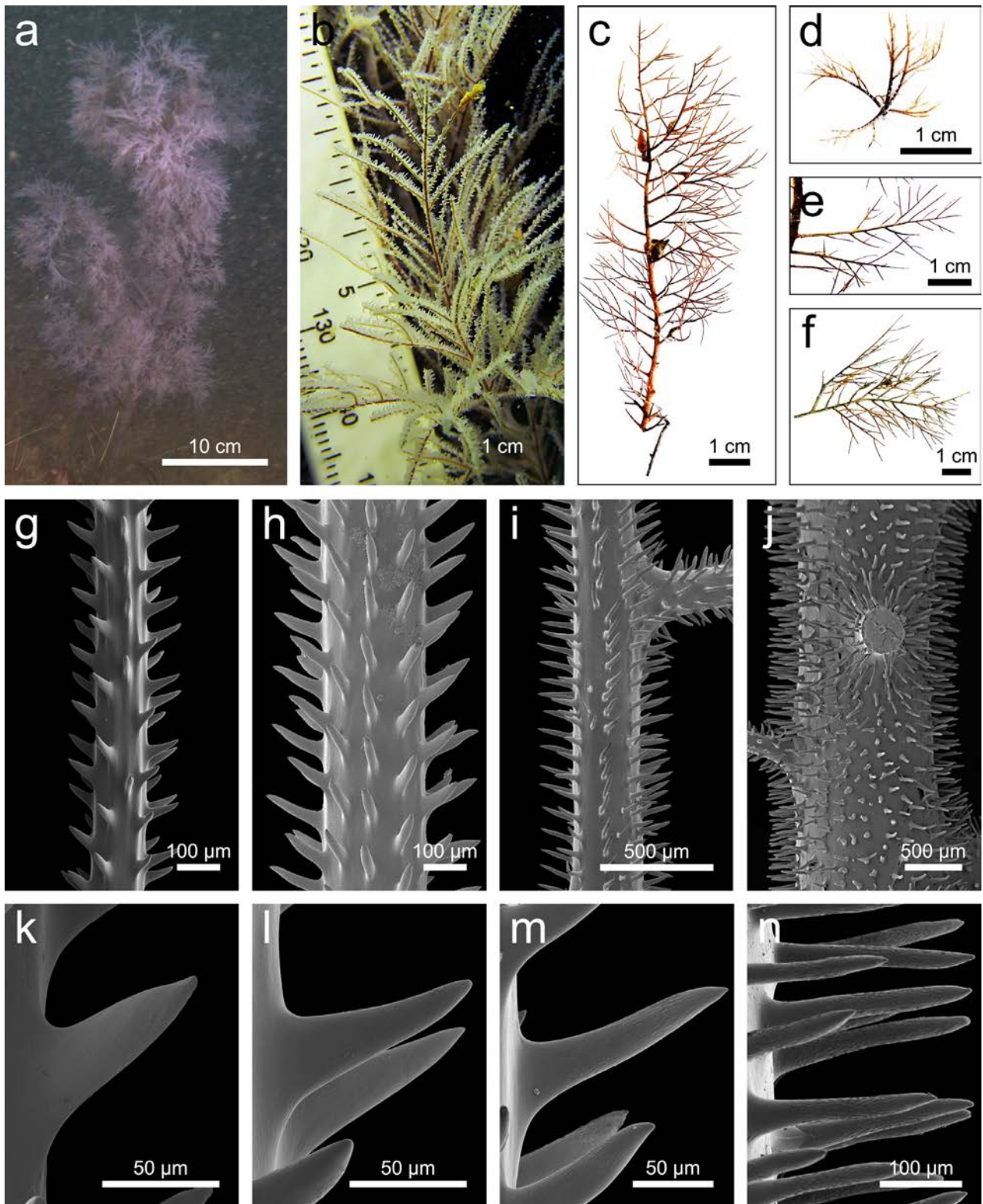


FIGURE 29. *Cupressopathes* cf. *pumila* INV.131366. (a) *In situ* pictures of the whole colony (b) *In situ* close-up view of a primary pinnule. (c) Detailed view of the branching pattern and the pinnulation of a distal branch. (d) Cross section of a distal branch showing the arrangement of the primary pinnules in four irregular rows. (e–f) Detailed top views of the pinnulation of two primary pinnules showing the biserial arrangement of the subpinnules and the variation in their density. (g) Section of subpinnule 0.13 mm in diameter, polypar side is on the right. (h) Section of primary pinnule 0.25 mm in diameter, polypar side is on the right. (i–j) Sections of two branches 0.30 mm and 1.30 mm in diameter, respectively. (k) Abpolypar spine of subpinnule. (l) Polypar spine of subpinnule. (m) Polypar spine on primary pinnule. (n) Tall, acicular and needle-like spines occurring on thick branch.

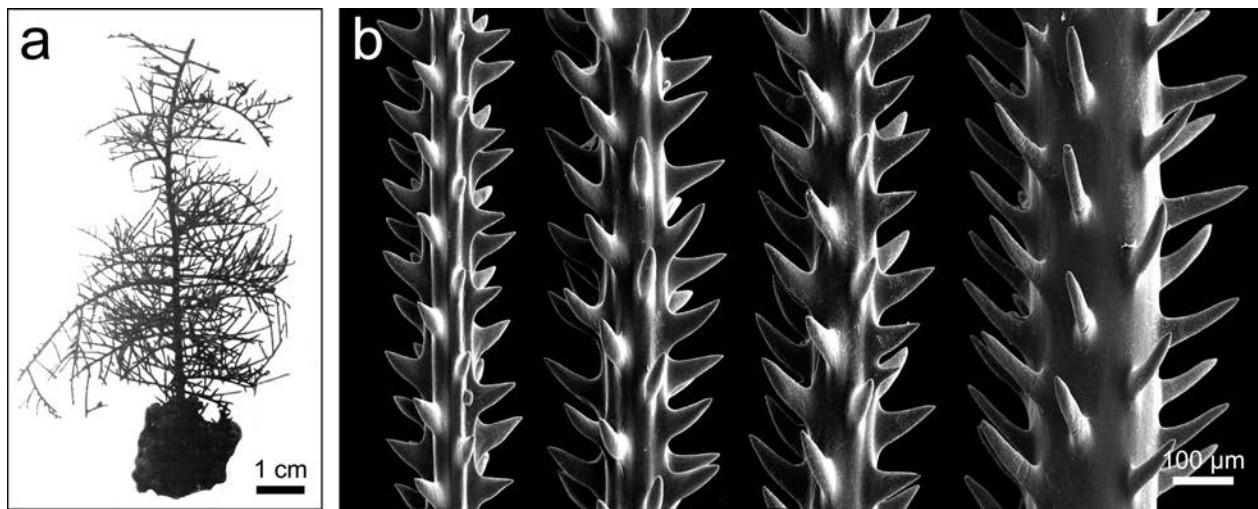


FIGURE 30. *Cupressopathes pumila* (Brook, 1889) type specimen. (a) Entire colony, holotype Brit. Mus. 83.9.13.15. (b) Schizoholotype USNM 100355 showing different sections of 0.08, 0.11, 0.12 and 0.22 mm in diameter, respectively.

Cu. pumila has more branches and a longer, less dense pinnulation, with a greater tendency for the subpinnules to be bilateral. Spines are similar to those of myriopathids (Fig. 30, b).

Distribution. India (type locality, Brook 1889), western Pacific (Opresko 2001), Madagascar (present study).

Cupressopathes sp. 1

Fig. 31

Material examined. Distal fragments of one colony, Soalara 13 m INV.131365.

Depth range. 10–20 m.

Description. The colony has a bushy general appearance, it is branched, pinnulate but not flabellate and is about 40 cm high and 40 cm wide (Fig. 31, a). There are four irregular rows of primary pinnules inserted at right angles to the branch (Fig. 31, b, c). Primary pinnules measure up to 2 cm in length and extend horizontally with an angle of insertion varying from 70° to 90°, giving a slight distal inclination (Fig. 31, b, c). Four to six primary pinnules are found along one cm, counting those on all sides of the branch (Fig. 31, b). Subpinnulation is sparse and irregular, up to six subpinnules can be found on a primary (Fig. 31, b–d). Secondary pinnules are mostly uniserial, but they can be biserial on the distal part of the primary pinnules (Fig. 31, c, d). These subpinnules are inclined distally but they are not always growing upwards. Some of them are straight while others can be slightly curved (Fig. 31, b–d). Secondary pinnules measure up to 1 cm while other subpinnules always measure less than 1 cm. The polyps are white and generally arranged in a single row on the pinnules, but they can twist around the latter on thicker primary pinnules. On branches, polyps are irregularly distributed all around. Polyps measure 0.4–0.9 mm in transverse diameter. Their mutual distance goes from zero when they sit next to each other to 0.50 mm. There are 9–12 polyps per cm on the pinnules and subpinnules.

The morphology of spines on pinnules and subpinnules gradually change as the axis gets thicker, from conical and horn-shaped to acicular, sharp and needle-like, as in other myriopathids (Fig. 31, e–h). They are very finely papillose, with the papillae elongated towards the tip (Fig. 31, i–k). On some spines the papillae are almost not distinguishable, and many appear as faint striations (Fig. 31, i–k). These papillae are on the upper part of the spine on the distal and proximal sides (Fig. 31, i–k). The spines are inclined upwards, especially on abpolypar sides, although on thicker branches this inclination is irregular (Fig. 31, e–h). On a subpinnule of 0.1 mm in diameter, the spines are arranged in five longitudinal rows. The polypar spines measure 0.08–0.09 mm with a mutual distance of 0.13–0.15 mm. The abpolypar spines measure 0.07–0.09 mm and are spaced 0.11–0.16 mm apart. On a pinnule of 0.21 mm in diameter, the spines are arranged in six longitudinal rows. The polypar spines measure 0.1–0.15 mm and are spaced 0.1–0.19 mm apart. The abpolypar spines measure 0.1–0.12 mm and are spaced 0.1–0.2 mm apart. On the main branch of 1 mm in diameter, the longitudinal arrangement is lost, and the spines measure up to 0.21 mm. Bifid spines can also be found on the thick branches (Fig. 31, l).

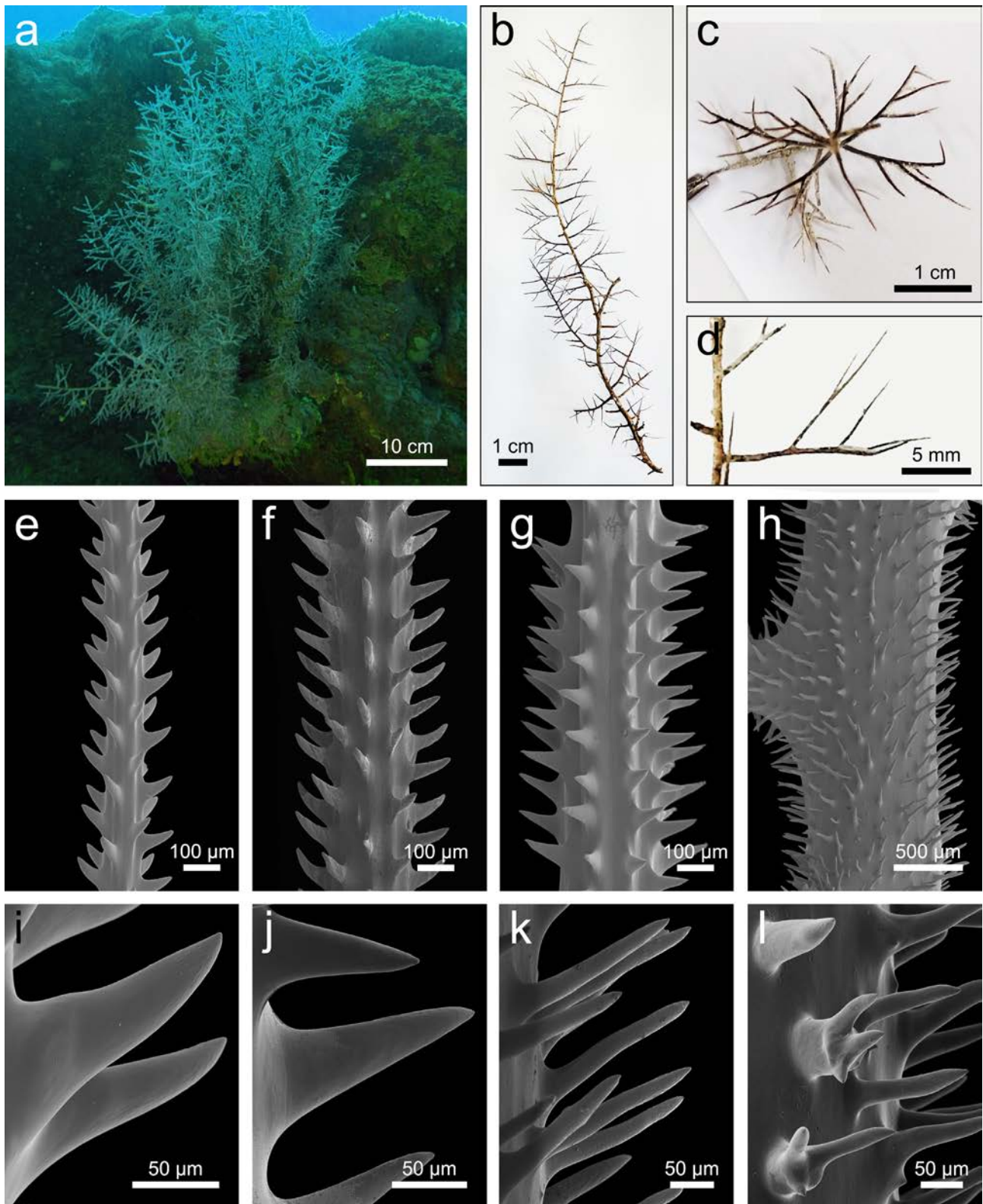


FIGURE 31. *Cupressopathes* sp. 1, INV.131365. (a) *In situ* picture of the whole colony. (b) Detailed view of the pinnulation on a distal branch. (c) Cross section of a pinnulated branch showing the arrangement in irregular rows. (d) Lateral view of the scarce subpinnulation of a primary pinnule. (e) Section of subpinnule 0.1 mm in diameter, polypar side is on the right. (f) Section of primary pinnule 0.22 mm in diameter, polypar side is on the right. (g) Section of distal branch 0.27 mm in diameter. (h) Section of branch 1.10 mm in diameter. (i) Abpolypar spine of a subpinnule. (j) Polypar spine of subpinnule. (k) Tall, acicular needle-like spines occurring on thick branches. (l) Bifid spines occurring on a branch.

Taxonomic remarks. The Soalara specimen does not match any *Cupressopathes* species described to date. The most important features of this specimen are the significant branching, giving the colony a bushy appearance; the very sparse subpinnulation; and the spines being finely papillose, giving the appearance of an almost smooth surface.

Cupressopathes sp. 2

Fig. 32

Material examined. Entire colony, Toliara 22 m, INV.131340.

Depth range. 20–25 m.

Description. The colony is monopodial with a bottle-brush shape, it measures 40 cm in height and 8 cm in width (Fig. 32, a), with a branch growing near the apex (Fig. 32, b). Primary pinnules are irregularly arranged in about four rows around the stem (Fig. 32, b, c), sometimes two successive primaries are inserted on the same side. These primary pinnules are found around 13 cm above the basal anchorage, but the previous presence of primaries around 4 cm above the plate is clearly seen, indicating that they had been broken off. Primary pinnules are thick and measure up to 5 cm in length, but there is an asymmetry in their length as they do not exceed 3 cm in length on one side (Fig. 32, a, b). However, this asymmetry could be due to breaking events as many primary pinnules are not tapering and have a blunt end. Primary pinnules are almost perpendicularly inserted to the branch or slightly inclined upwards (Fig. 32, a, b). Between five and seven primary pinnules are found along one cm, counting those on all sides of the branch. The primary pinnules are branched to the 5th order, and more than six secondary subpinnules can be found on one primary (Fig. 32, c–e). The secondary pinnules are always on the same side of the primary pinnules and growing upwards (Fig. 32, b, d). Secondary pinnules are mostly biserial but on some primaries a few uniserial secondaries can be found. Secondary pinnules measure up to 3 cm while tertiaries measure up to 1.5 cm. Higher orders of subpinnules are irregular and usually shorter than the tertiary pinnules. The polyps are monoserial and are arranged on the same side of the pinnules. However, on primary pinnules and thick secondary pinnules the row of polyps is not regular, and on thicker branches they can be found irregularly arranged all around the axis. Polyps are white and measure 0.4–0.6 mm. On primary and thick secondary pinnules they are widely spaced, up to 1 mm apart. On subpinnules, their mutual distance is 0.2–0.6 mm. There are 10–14 polyps per cm on the pinnules and subpinnules.

The spines vary in shape; from conical and inclined upwards on the subpinnules, to tall, cylindrical and needle-like spines on the branches (Fig. 32, f–i). On primary and secondary pinnules they are not as acicular as in other myriopathids, but rather have a stout, thick conical shape, sometimes with a blunt apex, and inclined in different directions (Fig. 32, g, h). Moreover, spines on the primaries and secondaries may present grooves on one or several sides of their surfaces (Fig. 32, g, h). The spines are finely papillose on their proximal and distal sides, with papillae elongated towards the tip of the spines and almost looking like faint striations (Fig. 32, j–m). On branches, the spines can be bifid, very often divided near the tip of the spine rather than the base (Fig. 32, m). Individual spines can often be missing in the regular longitudinal rows. On a subpinnule 0.15 mm in diameter, four longitudinal rows are seen from one aspect (Fig. 32, f). Abpolypar and polypar spines have a similar size, measuring 0.08–0.11 mm, and are spaced 0.09–0.23 mm apart. On a secondary pinnule 0.36 mm in diameter, six longitudinal rows are seen, and polypar and abpolypar spines have similar sizes, measuring 0.10–0.14 mm and spaced 0.12–0.28 mm apart. On a primary pinnule 0.85 mm in diameter, the longitudinal arrangement is lost, the spines reach 0.17 mm while on a branch 2.2 mm in diameter, they measure 0.20–0.26 mm.

Taxonomic remarks. This specimen presents the typical bottle-brush shape of *Cu. abies*. Pinnule sizes are also close to those of *Cu. abies*, except for their diameter as primary and secondary pinnules are particularly thick for this specimen. Such a narrow, cylindrical shape has already been described in *Cu. cylindrica* by Brook (1889), but he reported a colony 32 cm tall and 4 cm in diameter, meaning that the maximum length of a primary pinnule would be less than 2 cm, which is less than half the length of the longest primary pinnules observed here. Brook also reported fusions between adjacent pinnules which were not seen in the present specimens. In *Cu. abies*, the bottle-brush shape is symmetrical as the primary pinnules have a consistent length across the colony. The asymmetry seen here might be due to prevailing current or the presence of symbiotic polychaete, as they are known to induce skeletal modifications (Molodtsova & Budaeva 2007), or possibly due to localized breakage as some primaries were not tapering but showing a blunt end. In addition, spines were regularly missing from a longitudinal row on the secondary

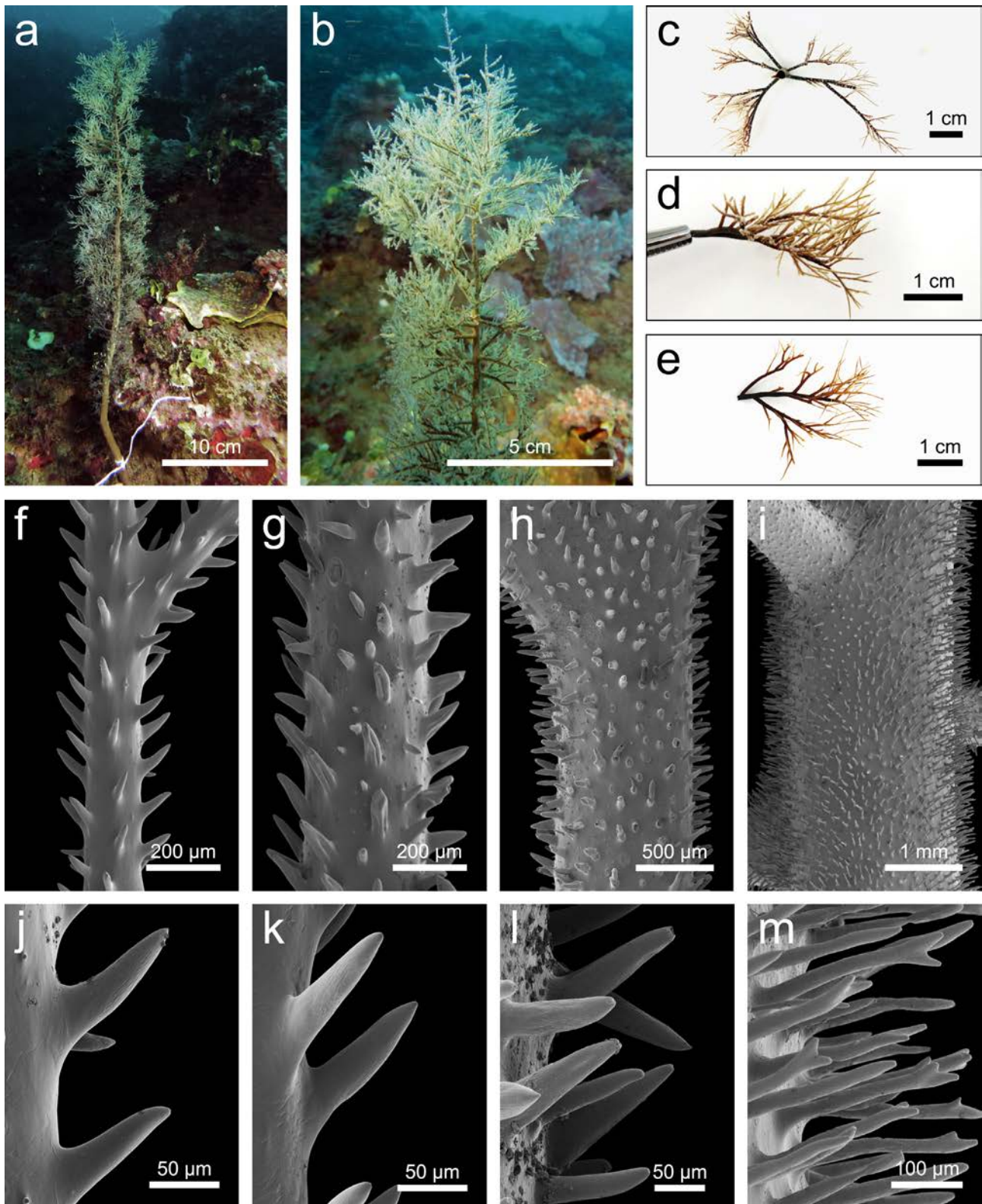


FIGURE 32. *Cupressopathes* sp. 2, INV.131340. (a) *In situ* picture of the entire colony showing the asymmetry in the cylindrical shape. (b) Close-up view of the distal part of the colony where a branch is growing. (c) Cross section showing the irregular arrangement of the primary pinnules. (d) Lateral view of the pinnulation on a primary pinnule. (e) Top view of the pinnulation of a primary pinnule. (f) Section of subpinnule 0.15 mm in diameter, polypar side is on the right. (g) Section of secondary pinnule 0.34 mm in diameter, polypar side is on the right. (h) Section of primary pinnule 0.85 mm in diameter. (i) Section of branch 2.2 mm in diameter. (j) Polypar spine of subpinnule. (k) Abpolypar spine of subpinnule. (l) Polypar spine of primary pinnule. (m) Needle-like and bifid spines of a branch.

and primary pinnules. Furthermore, some spines show a peculiar groove on their surface. Despite these particular skeletal modifications, the present specimen recall *Cu. abies*. Similar colonies are found in areas of moderate currents, which might explain the thickness of ramifications as well as the absence of large lateral branches and the overall cylindrical appearance. The asymmetrical pinnulation might be environmentally-determined depending on the prevailing current direction.

Discussion

On the west coast of Madagascar, coral reefs are well represented in the North-West and South-West areas, especially between the Mangoky delta and Androka (Pichon 1972; Nadon *et al.* 2005; McClanahan *et al.* 2009; Todinahary *et al.* 2016). Our study area, from Andavadoaka to Maromena, represents more than 200 km of shoreline, with a heterogeneous reef complex composed of fringing, barrier and patch reefs (Pichon 1972; Nadon *et al.* 2005; McClanahan *et al.* 2009). Black corals were always found in places where currents are strong, or turbidity is high, as in the northern pass of the Great Reef of Toliara where 20 out of the 22 species described in this report were observed. Shallow-water black coral assemblages have been found elsewhere in the world, *i.e.* in Indonesia (Tazioli *et al.* 2007), Hawaiian Islands (Wagner 2015a), Caribbean (Opresko & Sanchez 2005), Ecuador (Bo *et al.* 2012b) and the Azores (de Matos *et al.* 2014). In regard to geographic distribution patterns, there is a general trend of decreasing shallow-water species richness from the Indonesian hotspot (Bo *et al.* 2019), where a recent study of black corals revealed around 30 species (personal communication of co-author MB). In comparison, the shallow waters of Hawaii down to 150 m deep present only eight species from six genera and three families (Wagner 2015a, Bo *et al.* 2019). However, this trend in decreasing species richness appears to be not so pronounced across the Indian Ocean towards the East African coasts, as 22 species from six genera and two families were found in Madagascar. The species identified in this study support the generally accepted depth distribution of black coral families, where in shallow waters the most common species belong to the families Antipathidae and Myriopathidae (Bo *et al.* 2019). However, future work may lead to the discovery of other species around the island, as well as in deeper waters.

To try and solve the taxonomic issues within antipatharians, suitable genes for studying phylogenetic relationships have already been tested by several authors in the past (Lapian *et al.* 2007; Lapian 2009; Wagner *et al.* 2010; Bo *et al.* 2009, 2012a; Brugler *et al.* 2013; MacIsaac *et al.* 2013). However, these studies have revealed that mitochondrial genes do not always contain enough variation to discriminate between putatively different species, and the nuclear genes that have been used, such as ITS, do not always discriminate species within the same genus because of the high intra-species variation. Genes from the nuclear ribosomal cistron (18S and 28S) have an intra-individual variation due to the large number of copies within the nuclear genome (Vollmer & Palumbi 2004), which leads to the existence of different haplotype for the same species and heterozygous ITS sequences. Lapian *et al.* (2007) also suggested a high rate of hybridization among species within the Myriopathidae, and particularly between *Myriopathes* and *Cupressopathes* species. Such a high range of morphological variability of the colonies has already been observed in *Cupressopathes*-like specimens (Lapian 2009) and could be valid for other genera such as *Cirrhopathes*. In addition, recent phylogenetic analyses have questioned the monophyly of whip black corals suggesting that branched and unbranched species may have evolved multiple times and may form polyphyletic groups, hence changing the current systematic position of many species (Bo *et al.* 2012a; Brugler *et al.* 2013).

The taxonomic study presented here using updated knowledge about antipatharians fills one of the large gaps existing in the taxonomy of shallow-water black corals from the Western Indian Ocean. The occurrence of potentially new species seen in Madagascar highlights the need for the future designation of neotypes, for which genetic data should be compulsory. New insights into shallow-water black corals from the Indian Ocean, especially from the central region, may solve some still doubtful species, synonyms and extend species distributions.

Acknowledgments

We thank the reviewers Mercer Brugler and Jeremy Horowitz for their remarks and suggestions. We also thank the editor Marymegan Daly for the copyediting of the manuscript. Many thanks to the Institut Halieutique et des

Sciences Marines from the University of Toliara (Madagascar) for their help in providing facilities and logistics. Thanks to Emily Claereboudt, José Randrianandrasana, Mathilde Godefroid and Malagasy students for their help during the dives. LT travels and expeditions were funded by a FNRS grant, a Fédération Wallonie-Bruxelles grant, a Fonds Léopold III pour l'Exploration et la Conservation de la Nature grant, and the University of Mons. LT was funded by a PhD grant from the FRIA-FNRS MCF/XH/FC-16755. This work was supported by the FNRS project PDR/OL T.0084.18.

Literature cited

- Bayer, F.M. (1959) The Alcyonarian and Black Corals (Anthozoa: Octocorallia and Antipatharia) described and figured by G.E. Rumphius. In: de Wit, H.C.D. (Eds.), *Rumphius Memorial Volume*. Baarn, Hollandia, pp. 225–247.
- Blainville, H.M.D. de (1834) Manuel d'Actinologie ou de Zoophytologie. Levrault F.G., Paris, viii, 694 pp.
<https://doi.org/10.5962/bhl.title.8768>
- Bo, M., Barucca, M., Biscotti, M.A., Canapa, A., Lapan, H.F.N., Olmo, E. & Bavestrello, G. (2009) Description of *Pseudocirripathes* (Cnidaria: Anthozoa: Hexacorallia: Antipathidae), a new genus of whip black corals from the Indo-Pacific. *Italian Journal of Zoology*, 76 (4), 392–402.
<https://doi.org/10.1080/11250000802684104>
- Bo, M., Bavestrello, G., Barucca, M., Makapedua, D.M., Polisenio, A., Forconi, M., Olmo, E. & Canapa, A. (2012a) Morphological and molecular characterization of the problematic whip black coral genus *Stichopathes* (Hexacorallia: Antipatharia) from Indonesia (North Sulawesi, Celebes Sea). *Zoological Journal of the Linnean Society*, 166, 1–13.
<https://doi.org/10.1111/j.1096-3642.2012.00834.x>
- Bo, M., Lavorato, A., Di Camillo, C.G., Polisenio, A., Baquero, A., Bavestrello, G., Irei Y. & Reimer, J.D. (2012b) Black coral assemblages from Machalilla National Park (Ecuador). *Pacific Science*, 66 (1), 63–82.
<https://doi.org/10.2984/66.1.4>
- Bo, M. & Opresko, D.M. (2015) Redescription of *Stichopathes pourtalesi* Brook, 1889 (Cnidaria: Anthozoa: Antipatharia: Antipathidae). *Breviora*, 540 (1), 1–18.
<https://doi.org/10.3099/MCZ16.1>
- Bo, M., Montgomery, A.D., Opresko, D.M., Wagner, D. & Bavestrello, G. (2019) Antipatharians of the mesophotic zone: four case studies. In: Loya, Y., Puglise, K.A. & Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*, Springer, New-York, pp. 683–708.
https://doi.org/10.1007/978-3-319-92735-0_37
- Brito, A. & Ocaña, Ó. (2004) Corals of the Canary Islands. In: Lemus, F. (Ed), *Skeleton Anthozoa of the Littoral and Deep Bottoms*. La Laguna, Spain, pp. 428–431.
- Brook, G. (1889) Report on the Antipatharia collected by HMS Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage of HMS Challenger During the Years 1873–76*, Zoology, 32 (1), 1–222.
<https://doi.org/10.5962/bhl.title.6513>
- Brugler, M.R., Opresko, D.M. & France, S.C. (2013) The evolutionary history of the order Antipatharia (Cnidaria: Anthozoa: Hexacorallia) as inferred from mitochondrial and nuclear DNA: implications for black coral taxonomy and systematics. *Zoological Journal of the Linnean Society*, 169 (2), 312–361.
<https://doi.org/10.1111/zoj.12060>
- Cairns, S.D. (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of marine Science*, 81 (3), pp. 311–322.
- Carter, H.J. (1880) XXXVI.—On the Antipatharia (Milne Edwards), with reference to *Hydradendrium spinosum*. *Annals and Magazine of Natural History*, 6 (34), 304–305.
<https://doi.org/10.1080/00222938009458941>
- Clarke, M.E., Whitmire, C.E. & Yoklavich, M.M. (2015) State of Deep-Sea Coral and Sponge Ecosystems of the U.S. West Coast: 2015. In: Hourigan, T.F., Etnoyer, P.J. & Cairns S.D. (Eds.), *The State of Deep-Sea Coral and Sponge Ecosystems of the United States*, NOAA Technical Memorandum, Silver Spring, Maryland, pp. 1–42.
- Cooper, C.F. (1903) Antipatharia. In: Gardiner, J.S. (Ed.), *Fauna and Geography of the Maldive and Laccadive Archipelagos*. Cambridge University Press, Cambridge, pp. 791–796.
- Cooper, C.F. (1909) Reports of the Percy Sladen Trust expedition on the Indian Ocean, 1905. Antipatharia. *Transactions of the Linnean Society of London*, 12 (4), 301–321.
<https://doi.org/10.1111/j.1096-3642.1909.tb00144.x>
- Dana, J.D. (1846) Zoophytes. In: Sherman, C. (Ed.), *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N.*, Lea & Blanchard, Philadelphia, pp. (1–7) + 1–740.
<https://doi.org/10.5962/bhl.title.70845>
- de Matos, V., Gomes-Pereira, J.N., Tempera, F., Ribeiro, P.A., Braga-Henriques, A. & Porteiro, F. (2014) First record of *Antipathella subpinnata* (Anthozoa, Antipatharia) in the Azores (NE Atlantic), with description of the first monotypic garden for this species. *Deep Sea Research Part II: Topical Studies in Oceanography*, 99, 113–121.

<https://doi.org/10.1016/j.dsr2.2013.07.003>

- Deshayes, G.P. & Milne-Edwards, H. (1836) *Histoire naturelle des animaux sans vertèbres, par JBPA de Lamarck*. J.B. Baillière, Paris, 440 pp.
<https://doi.org/10.5962/bhl.title.63986>
- Duchassaing, P. (1870) *Revue des Zoophytes et des Spongiaires des Antilles*. Masson, Paris, 52 pp.
- Echeverría, C.A. (2002) Black corals (Cnidaria: Anthozoa: Antipatharia): first records and a new species from the Brazilian coast. *Revista de biología tropical*, 50 (3–4), 1067–1077.
- Ellis, J. & Solander, D. (1786) *The natural history of many curious and uncommon zoophytes collected by the late John Ellis, systematically arranged and described by the late Daniel Solander*. White, B. & Son, London, 208 pp.
<https://doi.org/10.5962/bhl.title.2145>
- Esper, E.J.C. (1798) *Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. Theilen 1–3 (Lieferungen 1–17)*. Raspe, Nürnberg, 320 + 303 + 230 pp.
- Gray, J.E. (1857) On the animal and bark of Antipathes. *Proceedings of the Zoological Society of London*, 1857, 1–113.
<https://doi.org/10.1111/j.1096-3642.1857.tb01211.x>
- Grigg, R.W. (2001) Black coral: History of a sustainable fishery in Hawai'i. *Pacific Science*, 55, 291–299.
<https://doi.org/10.1353/psc.2001.0022>
- Kumar, J.Y., Raghunathan, C. & Venkataramani, K. (2012) Studies on newly recorded Antipatharian corals from Andaman and Nicobar Islands. *Records of the Zoological Survey of India*, 112 (1), 1–10.
- Lamarck, J.B. (1815) Sur les Polypiers corticifères. *Mémoires du Muséum d'Histoire Naturelle, Paris*, 1, 401–476.
- Lamouroux, J.V.F. (1816) *Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes*. Imprimerie de Poisson, Caen, pp. 560.
<https://doi.org/10.5962/bhl.title.11172>
- Lamouroux, J.V.F., Bory de Saint-Vincent & Deslongchamps, J.A.E. (1824) Histoire Naturelle des Zoophytes ou Animaux rayonnés. *Encyclopédie Méthodique, Paris*, 2, 1–819.
- Lapian, H.F.N. (2009) Biodiversity study of black coral (Order: Antipatharia) collected from Manado, Indonesia based on rDNA Internal Transcribed Spacer (ITS) sequences analysis. *Biodiversitas*, 10 (1), 1–5.
<https://doi.org/10.13057/biodiv/d100101>
- Lapian, H.F.N., Barucca, M., Bavestrello, G., Biscotti, M.A., Bo, M., Canapa, A., Tazioli, S. & Olmo, E. (2007) A systematic study of some black coral species (Antipatharia, Hexacorallia) based on rDNA internal transcribed spacers sequences. *Marine Biology*, 151, 785–792.
<https://doi.org/10.1007/s00227-006-0525-8>
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio Decima, reformata*. Laurentii Salvii, Holmiae, Stockholm, 824 pp.
- MacIsaac, K.G., Best, M., Brugler, M.R., Kenchington, E.L.R., Anstey, L.J., Jordan, T. (2013) *Telopathes magna* gen. nov., spec. nov. (Cnidaria: Anthozoa: Antipatharia: Schizopathidae) from deep waters off Atlantic Canada and the first molecular phylogeny of the deep-sea family Schizopathidae. *Zootaxa*, 3700 (2), 237–258.
<https://doi.org/10.11646/zootaxa.3700.2.3>
- McClanahan, T.R., Graham, N.A.J., Wilson, S.K., Letourneur, Y. & Fisher, R. (2009) Effects of fisheries closure size, age, and history of compliance on coral reef fish communities in the western Indian Ocean. *Marine Ecology Progress Series*, 369, 99–109.
<https://doi.org/10.3354/meps08279>
- Milne Edwards, H & Haimés, J. (1857) *Histoire Naturelle des Coralliaires ou Polypes Proprement Dits*. La Librairie Encyclopédique de Roret, Paris, 326 pp.
<https://doi.org/10.5962/bhl.title.11911>
- Molodtsova, T. & Budaeva, N. (2007) Modifications of corallum morphology in black corals as an effect of associated fauna. *Bulletin of Marine Science*, 81 (3), 469–480.
- Molodtsova, T. & Opresko, D. (2020) World List of Antipatharia. Antipatharia. Accessed through: World Register of Marine Species. Available from: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=22549> (accessed 7 July 2020)
- Moon, H.W. & Song, J.I. (2008) Taxonomy of the black coral family Myriopathidae (Anthozoa: Antipatharia) from Korea. *Korean Journal of Systematic Zoology*, 24, 251–263.
<https://doi.org/10.5635/kjsz.2008.24.3.251>
- Nadon, M.-O., Griffiths, D. & Doherty, E. (2005) *The coral reefs of Andavadaoaka, southwest Madagascar*. Blue Ventures, London, 29 pp.
- Okuyama, M. & Tsukamoto, Y. (1989) Sea whip goby, *Bryaninops yongei*, collected from outer shelf off Miyakojima, East China Sea. *Japanese Journal of Ichthyology*, 36 (3), 369–370.
<https://doi.org/10.11369/jji1950.36.369>
- Opresko, D.M. (1972) Redescriptions and reevaluations of the antipatharians described by L.F. de Pourtales. *Bulletin of Marine Science*, 22, 950–1017.
- Opresko, D.M. (1974) *A study of the classification of the Antipatharia (Coelenterata: Anthozoa) with redescriptions of eleven species*. Ph.D. Dissertation, University of Miami, Miami, 193 pp.
- Opresko, D.M. (1976) Redescription of *Antipathes panamensis* Verrill (Coelenterata, Antipatharia). *Pacific Science*, 30 (3),

235–240.

- Opresko, D.M. (1997) Review of the genus *Schizopathes* (Cnidaria: Antipatharia: Schizopathidae) with a description of new species from the Indian Ocean. *Proceedings of the Biological Society of Washington*, 110 (2), 157–166.
- Opresko, D.M. (2001) Revision of the Antipatharia (Cnidaria: Anthozoa). Part I. Establishment of a new family, Myriopathidae. *Zoologische Mededelingen*, 75, 343–370.
- Opresko, D.M. (2002) Revision of the Antipatharia (Cnidaria: Anthozoa). Part II. Schizopathidae. *Zoologische Mededelingen*, 76, 411–442.
- Opresko, D.M. (2003a) Redescription of *Antipathes dichotoma* Pallas, 1766 (Cnidaria: Anthozoa: Antipatharia). *Zoologische Mededelingen*, 77, 481–493.
- Opresko, D.M. (2003b) Revision of the Antipatharia (Cnidaria: Anthozoa). Part III. Cladopathidae. *Zoologische Mededelingen*, 77, 495–536.
- Opresko, D.M. (2004) Revision of the Antipatharia (Cnidaria: Anthozoa). Part IV. Establishment of a new family, Aphanipathidae. *Zoologische Mededelingen*, 78, 209–240.
- Opresko, D.M. (2006) Revision of the Antipatharia (Cnidaria: Anthozoa). Part V. Establishment of a new family, Stylopathidae. *Zoologische Mededelingen*, 80-4, 109–138.
- Opresko, D.M. (2009) A New Name for the Hawaiian antipatharian coral formerly known as *Antipathes dichotoma* (Cnidaria: Anthozoa: Antipatharia). *Pacific Science*, 63 (2), 277–291.
<https://doi.org/10.2984/049.063.0209>
- Opresko, D.M. (2019) New species of black corals (Cnidaria: Anthozoa: Antipatharia) from the New Zealand region, part 2. *New Zealand Journal of Zoology*, 47 (3), 149–186.
<https://doi.org/10.1080/03014223.2019.1650783>
- Opresko, D.M. & Baron-Szabo, R.C. (2001) Re-descriptions of the antipatharian coral described by EJC Esper with select English translations of the original German text. *Senckenbergiana biologica*, 81, 1–21.
- Opresko, D.M. & Sanchez, J.A. (2005) Caribbean shallow-water black corals (Cnidaria: Anthozoa: Antipatharia). *Caribbean Journal of Science*, 41 (3), 492–507.
- Opresko, D.M., Tracey, D. & Mackay, E. (2014) Antipatharia (black corals) for the New Zealand region. A field guide of commonly sampled New Zealand black corals including illustrations highlighting technical terms and black coral morphology. *New Zealand Aquatic Environment and Biodiversity Report*, No. 131, 1–20.
- Pallas, P.S. (1766) *Elenchus Zoophytorum Sistens Generum Adumbrationes Generaliores et Specierum Cognitarum Succinctas Descriptiones Cum Selectis Auctorum Synonymis*. Hagae—Comitum, Frankfurt, 451 pp.
<https://doi.org/10.5962/bhl.title.6595>
- Pasternak, F.A. (1977) Antipatharia. Galathea Report. *Scientific Results of the Danish Deep-Sea Expedition around the world 1950-52*, 14, 157–164.
- Pax, F. (1932) Beiträge zur Kenntnis der Japanischen Dörnchenkorallen. *Zoologische Jahrbucher* 9 (63), 407–450.
- Pax, F. & Müller, I. (1955) Gli antozoi del Museo Civico di Storia Naturale di Trieste Parte I: Antipatharia, Ceriantharia, Zoantharia, Actiniaria, Alcyonaria, e Pennatularia. *Atti del Museo Civico di Storia Naturale Trieste*, 20, 103–129.
- Pichon, M. (1972) The coral reefs of Madagascar. In: Battistini, R. & Richard-Vindard, G. (Eds.), *Biogeography and Ecology in Madagascar*. Springer, Dordrecht, pp. 367–410.
https://doi.org/10.1007/978-94-015-7159-3_11
- Pourtalès, L.F. de (1871) Deep-sea corals. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 2, 4.
<https://doi.org/10.5962/bhl.title.13636>
- Roule, L. (1905) Description des Antipathaires et Cérianthaires recueillis par SAS le Prince de Monaco dans l'Atlantique nord. *Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert Ier Prince de Monaco*, 30, 1–100.
<https://doi.org/10.5962/bhl.title.59328>
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, 9 (7), 671–675.
<https://doi.org/10.1038/nmeth.2089>
- Schultze, L.S. (1896) Beitrag zur Systematik der Antipatharien. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 23, 1–40.
- Silberfeld, E. (1909) Japanische Antipatharien. *Abhandlungen der math.—phys. Klasse der K. Bayer. Akademie der Wissenschaften*, I (Supplement—BD 7. Abhandlg.), 1–30.
- Summers, S.L. (1910) VIII.—Antipatharians from the Indian Ocean. *Journal of the Royal Microscopical Society*, 30 (3), 273–281.
<https://doi.org/10.1111/j.1365-2818.1910.tb01715.x>
- Tazioli, S., Bo, M., Boyer, M., Rotinsulu, H. & Bavestrello, G. (2007) Ecological observations of some common antipatharian corals in the Marine Park of Bunaken (North Sulawesi, Indonesia). *Zoological Studies*, 46 (2), 227–241.
- Terrana, L. & Eeckhaut, I. (2017) Taxonomic description and 3D modelling of a new species of myzostomid (Annelida, Myzostomida) associated with black corals from Madagascar. *Zootaxa*, 4244 (2), 277–295.
<https://doi.org/10.11646/zootaxa.4244.2.9>
- Terrana, L. & Eeckhaut, I. (2019) Sexual reproduction of the shallow-water black coral *Cirrhopathes anguina* (Dana, 1846) from Madagascar. *Marine Biology Research*, 2019, 1–14.

<https://doi.org/10.1080/17451000.2019.1662444>

- Terrana, L., Lepoint, G. & Eeckhaut, I. (2019). Assessing trophic relationships between black coral and their symbionts using stable isotopes. *Belgian Journal of Zoology*, 149 (1), 107–1021.
<https://doi.org/10.26496/bjz.2019.33>
- Thomson, J.A. & Simpson, J.J. (1905) Report of the Antipatharia collected by Prof. Herdman at Ceylon, 1902. *Ceylon Pearl Oyster Report*, 4, 93–106.
- Todinanahary, G., Terrana, L., Lavitra, T. & Eeckhaut, I. (2016) First records of illegal harvesting and trading of black corals (Antipatharia) in Madagascar. *Madagascar Conservation & Development*, 11 (1), 6–11.
<https://doi.org/10.4314/mcd.v11i1.5>
- van Pesch, A.J. (1910) Beiträge zur Kenntnis der Gattung *Cirrhopathes*. Leiden, 96 pp.
- van Pesch, A.J. (1914) The Antipatharia of the Siboga Expedition. *Siboga Expeditie Monographie*, 17, 1–258.
- Vollmer, S.V. & Palumbi, S.R. (2004) Testing the utility of internally transcribed spacer sequences in coral phylogenetics. *Molecular Ecology*, 13, 2763–2772.
<https://doi.org/10.1111/j.1365-294X.2004.02265.x>
- Wagner, D. (2015a) A taxonomic survey of the shallow—water (< 150 m) black corals (Cnidaria: Antipatharia) of the Hawaiian Islands. *Frontiers in Marine Science*, 2, 24.
<https://doi.org/10.3389/fmars.2015.00024>
- Wagner, D. (2015b) The spatial distribution of shallow—water (< 150 m) black corals (Cnidaria: Antipatharia) in the Hawaiian Archipelago. *Marine Biodiversity Records*, 8, e54.
<https://doi.org/10.1017/s1755267215000202>
- Wagner, D., Brugler, M.R., Opresko, D.M., France, S.C., Montgomery, A.D. & Toonen, R.J. (2010) Using morphometrics, *in situ* observations and genetic characters to distinguish among commercially valuable Hawaiian black coral species; a redescription of *Antipathes grandis* Verrill, 1928 (Antipatharia: Antipathidae). *Invertebrate Systematics*, 24 (3), 271–290.
<https://doi.org/10.1071/IS10004>
- Wagner, D., Waller, R.G. & Toonen, R.J. (2011) Sexual reproduction of Hawaiian black corals, with a review of reproduction of antipatharians (Cnidaria: Anthozoa: Hexacorallia). *Invertebrate Biology*, 130, 211–225.
<https://doi.org/10.1111/j.1744-7410.2011.00233.x>
- Wagner, D., Luck, D.G. & Toonen, R.J. (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). *Advances in Marine Biology*, 63, 67–132.
<https://doi.org/10.1016/b978-0-12-394282-1.00002-8>
- Warner, G.F. & Opresko, D.M. (2004) A new black coral (Anthozoa: Antipatharia) from a reef wall environment in Jamaica. *Bulletin of Marine Science*, 74 (1), 169–174.
- Zou, R. & Zhou, J. (1982) Studies on the antipatharians of China. I. The genus *Cirrhopathes* with the description of a new species. *Tropic Oceanology*, 1, 82–91.