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**A revision of the genus *Thouarella* Gray, 1870
(Octocorallia: Primnoidae), including an illustrated dichotomous key,
a new species description, and comments on *Plumarella* Gray, 1870
and *Dasystenella*, Versluys, 1906**

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Abstract

A comprehensive revision of the genus *Thouarella* is presented. Thirty-five holotypes of the 38 nominal *Thouarella* species, two varieties, and one form were examined. The number of original *Thouarella* species has been reduced to 25, mostly through synonymy or new genus combinations. In the process several new species have also been identified, one of which is described here as *Thouarella parachilensis* nov. sp. The genus is split into two groups based on polyp arrangement: Group 1 with isolated polyps and Group 2 with polyps in pairs or whorls. An illustrated dichotomous key and detailed character table of the 25 *Thouarella* species are presented alongside an up-to-date account of all species described in the 19th and 20th centuries and summaries of the few described from 2000 onwards. We propose that *Thouarella longispinosa* is synonymous with *Dasystenella acanthina*, *T. versluysi* with *T. brucei*, and, *T. tenuisquamis*, *T. flabellata*, and *T. carinata* are synonymous with *T. laxa*. Lastly, we propose that *T. bayeri* and *T. undulata* be placed in *Plumarella* and support recent suggestions that *T. alternata*, *T. recta*, *T. superba*, and *T. diadema* are also *Plumarella*.

Key words: Cnidaria, taxonomic revision, sub-Antarctic, octocoral

Introduction

Thouarella Gray, 1870 is a genus of primnoid octocorals within the class Anthozoa. Octocorals usually have small calcium carbonate sclerites over or within their tissue (with a few notable exceptions, discussed in Alderslade & McFadden 2007). Within octocorals there are a wide variety of sclerite shapes and sizes (Bayer et al. 1983) serving different functions, such as limiting adjacent sclerite movement, giving rigidity and support, as well as flexibility (Lewis & Wallis 1991). Primnoids, with the exception of one species of *Mirostenella* Bayer, 1988, which has a jointed axis, have solid continuous, calcified gorgonin axes (Cairns & Bayer 2009). They are found worldwide but are especially common in the Antarctic seas and Southern Ocean (*Thouarella* is no exception) and predominantly occur deeper than 400 m, with the deepest record from 5850 m (although primnoids have been recorded from 8 m depth; Cairns & Bayer 2009).

Thouarella is an architecturally delicate genus in which the majority of species have flower-like, open operculate polyps covered with thin sclerites. Species of *Thouarella* are locally abundant in many areas of the deep sea, especially in the sub-Antarctic, and play an important ecological role, providing habitat for many other animals from a variety of phyla. Although relatively common, little research has focused on species identifications beyond the original type descriptions, many of which are from the turn of last century. Often considered the “bottlebrush” genus, *Thouarella* spp. in fact have a range of branching forms, similar to several other genera, resulting in specimens being frequently misidentified.

Thouarella is a group of very closely related species; their morphology and many characters historically used to separate species and subgenera are variable and the genus is in need of further revision. Having reviewed all available holotypes we present the most thorough review of this ecologically important genus to date. This has resulted in significant changes to the understanding of several species within this genus and the key characters used for species identification.

Abbreviations

NHM—Natural History Museum, London, UK.

NMNH—National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

MNHN—Muséum National d’Histoire Naturelle, Paris, France.

MNHWU—Museum of Natural History, Wrocław University.

SMF—Senckenberg Forschungsinstitut und Museum Frankfurt.

UMUT—University Museum, University of Tokyo.

ZMA—Zoological Museum, University of Amsterdam.

ZMH—Zoological Museum, University of Hamburg.

ZMB—Zoologisches Museum, Berlin.

ZSL—Zoological Society of London, Institute of Zoology.

MYA—million years ago

ZGR—Zapata-Guardiola, Rebeca

SJ—Schleyer, Jon

History of *Thouarella* systematics

The type species of *Thouarella* Gray, 1870 was originally described as a species of *Primnoa* Lamouroux, 1812 by Valenciennes in the report from the 1836–1839 *Venus* expedition (1846). A brief mention of *P. antarctica* appears in Valenciennes (1855a) although merely as a referenced example of one of the five gorgonian forms—“the fifth form consist[ing] of larger or smaller scales, more or less covered with small spines” (taken from the English translation of Valenciennes, 1855b; p. 179). When the classification of gorgonians was reorganised by John Edward Gray in 1857, primnoids were placed under Lithophyta. Two species of *Primnoa* were described in Gray’s 1859 paper: *P. lepadifera* Gray, 1859 (now *P. resedaeformis*) and *P. antarctica* Gray, 1859. These species were separated by their branching morphology with the former described as “tree-like” and the latter with “spreading branches” (p. 483). *Primnoa antarctica* was then listed in Kölliker’s 1865 gorgonian descriptions under Primnoaceae, but it wasn’t until 1870 that *Thouarella* was established by Gray who named the genus after the captain of the *Venus* expeditions, Abel Du Petit-Thouars. At this point the description was of a bottlebrush morphology but the finer details of morphology were unclear as “polyp-cells smooth, bell-shaped, scattered on upper side of branches, covered with four or five series of imbricate scales” (Gray 1870: 45) are listed as defining characters. Gray described and illustrated a new specimen of *Thouarella antarctica* in 1872 (catalogue number NHM1872.4.29.1). It is unclear if he ever sought out the holotype from Paris Museum because, having studied Gray’s 1872 specimen, it appears to be *T. brucei* Thomson & Richie, 1906.

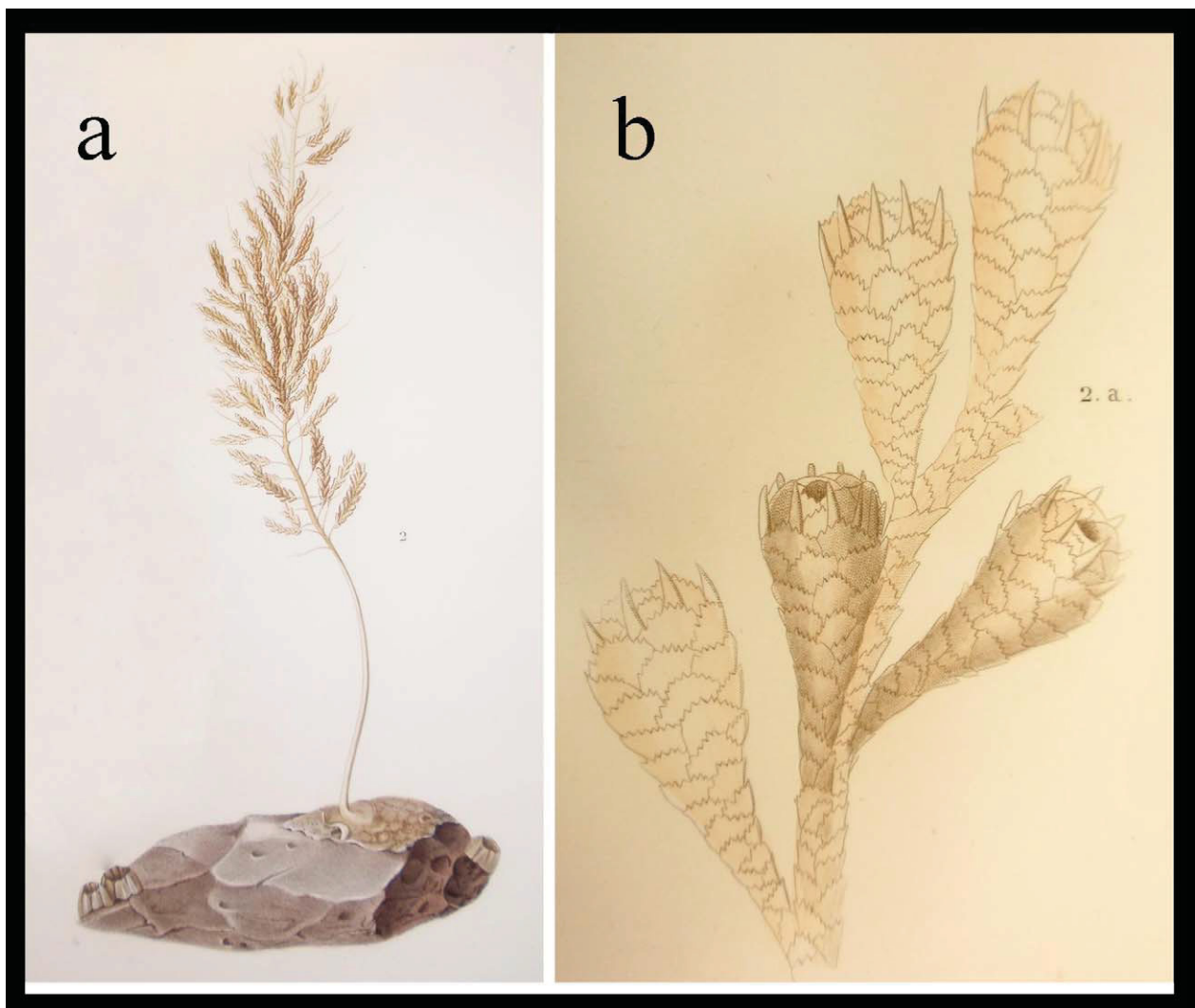


FIGURE 1. First illustration of *Thouarella antarctica* (from Valenciennes 1846): a) full colony; b) close up of polyps.

The next major work concerning *Thouarella* was Wright & Studer (1889) whose descriptions of samples from the H.M.S. *Challenger* expedition included four new species (*T. moseleyi* Wright and Studer, 1889, *T. affinis* Wright and Studer, 1889, *T. koellikeri* Wright and Studer, 1889, and *T. variabilis* Wright and Studer, 1889, the latter including three varieties) and a reclassification of *Plumarella hilgendorfi* Studer, 1878 to *T. hilgendorfi*. They listed a specimen of *Thouarella antarctica*, however, the sclerites (Wright and Studer 1889, pl. 11, fig. 6) of the specimen only loosely resemble those of *T. antarctica* (Figs 4, 5 herein). Versluys (1906: 36) expressed some doubt over Wright and Studer's *T. antarctica* identification, although he still classified the sample as *T. antarctica* putting any physical differences down to depth variation.

Several *Thouarella* species were described from 1906 to 1912: Thomson and Richie (1906) described *T. brucei*; Versluys (1906) described *T. laxa* and *T. tydemani*, and split *Thouarella* into three groups ('Hilgendorfi', 'isolated' and 'Antarctic'); in 1907 Kinoshita described *T. typica*, and in 1908 Roule described *T. pendulina*; Kinoshita (1908a) assessed Primnoidae and subsequently (1908c,d) added two new species, *T. coronata* and *T. parva*, and a new subgenus, *Diplocalyptra*, as well as placing *Amphilaphis biserialis* Nutting, 1912 within *Thouarella* (1908c). Kükenthal began work on *Thouarella* between 1907 and 1915, describing nine new species (see Table 1) and two new subgenera, *Epithouarella* and *Euthouarella* (Kükenthal 1907, 1908, 1912, 1915). Thomson described *T. hicksoni* in 1911 and finally, Nutting (1912) described *T. alternata*, *T. recta*, and *T. superba*.

Thomson and Henderson (1906) published a comparison table for *Thouarella* species, however, it was Kükenthal (1915; 1919; 1924) who wrote the major diagnostic keys for this genus. The subgenera of *Thouarella* in 1915 stood as:

Amphilaphis Studer, 1887—differentiated on dichotomous branching mode;

Euthouarella Kükenthal, 1915—polyps in pairs or whorls of up to four;

Parathouarella Kükenthal, 1915—isolated polyps with spined, leaf-shaped marginals;

Epithouarella Kükenthal, 1915—isolated polyps with marginals lacking a long spine.

Kükenthal did not discuss the subgenus *Diplocalyptra* (species with dichotomous branching), described by Kinoshita (1908a), presumably not knowing of its existence as most of Kinoshita's work was written in Japanese. As *Parathouarella* included the type species *T. antarctica* it was thus redundant and from 1956 *Parathouarella* was simply called *Thouarella* (*Thouarella*) (see Bayer 1956). *Amphilaphis* was removed from *Thouarella* by Kinoshita (1908b), however this removal was not mentioned or followed in later papers by Kükenthal (1912; 1915; 1924). In 1981 Bayer treated *Amphilaphis* as a valid genus on the basis that it has eight full rows of body-wall scales rather than the six rows of body-wall scales plus two reduced adaxial rows, as found in *Thouarella* (Cairns & Bayer 2009). Brito (1993) merged *Amphilaphis* with *Thouarella* based on Bayer's exclusion of the genus in a purported 1988 paper that we cannot locate and is not listed in the references. Thus, although *Amphilaphis* is very similar to *Thouarella* in many respects (discussed in the *Thouarella* genus description), in this study we consider only the so-called 'original' *Thouarella* species and those incorporated into *Thouarella* in peer-review journals up to the end of 2010 (see Table 1). The genus *Amphilaphis* has recently been revised by Zapata-Guardiola & López-González (2012).

Aurivillius (1931) described *T. hilgendorfi* forma *plumatilis* after which there was a 60 year hiatus in *Thouarella* descriptions until Cairns (2006) provided a revised species list and described three new species. Additionally, in the last few years, five new species of *Thouarella* have been described from Antarctica (Zapata-Guardiola & López-González 2010a,b). As exploitation of the deep sea (fisheries, oil and gas production, mining resources etc) and scientific exploration spread to wider geographical locations and depths, there shall likely be more *Thouarella* species described.

Biology and reproduction

Octocoral reproduction, environmental/biological cues, and factors affecting reproduction have been studied extensively in shallow water tropical and temperate latitudes but less study has focused on octocoral reproduction in the deep ocean, e.g. Bayer (1996), Brito et al. (1997), Cordes et al. (2001), Slattery and McClintock (1997), Orejas et al. (2002, 2007). Considering only Antarctica, reproductive patterns across many animals are mostly defined by characteristics such as prolonged gametogenesis, delayed maturation, low fecundity, large yolky eggs, and in many cases, predominance of non-pelagic or at least lecithotrophic development, brooding, brood protection, viviparity, slow embryonic development, advanced newly hatched juvenile stages, and slow growth (Pearse et al. 1991). A recent study of three primnoid species suggested that morphology may play a role in

reproductive output, with bottlebrush-shaped *Dasystenella acanthina* (Wright and Studer, 1889) and a *Thouarella* species having over-lapping generations of more than one year, and fan-shaped *Fannyella rossi* Gray, 1872 and *F. spinosa* (Thomson and Rennet, 1931) having annual reproduction (Orejas et al. 2007). A relationship between morphology and reproductive output has also been suggested by studies on gorgonians from lower latitudes (Brazeau & Lasker 1989). These studies, however, represent a very limited sample size and phylogenetic representation. Much more research is required on reproduction, life histories, and molecular ecology of octocorals to help understand patterns of population connectivity and factors effecting reproductive success.

Materials and Methods

We (MT) examined all available type specimens (35 of the 38 holotypes were procured and examined) and hundreds of additional specimens, the majority of which were from the USNM and the SMF. The unseen holotypes are those of: *T. tydemani* Versluys, 1906, which was not seen first hand but detailed images of the remaining three slides of material (taken by ZGR) were examined; the colony *T. parva* Kinoshita, 1908d, is missing from the University of Tokyo museum and unsuccessful attempts were made to locate non-type material, and thus the description relies entirely on original hand drawings of one polyp and sclerites (Kinoshita 1908d); the colony of *T. crenelata* Kükenthal, 1907 was not able to be sent from ZMB, however this species has some distinct and recognisable characters (Kükenthal 1907) so scanning electron microscopy (SEM) images were obtained from voucher specimens held within USNM collections.

Methods

When viewing primnoid polyps under a stereo dissecting light microscope it is useful to dye them using a permanent light-coloured marker pen that highlights sclerite texture and outline. Flattened art clay provides a tacky surface for rolling polyps across so it is possible to view all sides and count the number of scales. To view individual sclerites a polyp was first submerged in ethanol, held gently between tweezers, and a small, soft paintbrush swiped gently over surfaces to remove sand, tissue and other items that may obscure the viewing of sclerites. Polyps were then dissolved in a drop of sodium hypochlorite (bleach). Once free, sclerites were washed with distilled water several times to remove all remnants of bleach. Sclerites were then washed with 70% ethanol and several successively stronger ethanol solutions, up to 95%, before being air-dried. These dried sclerites were placed on stubs for SEM. An eyelash or piece of hair embedded in a lump of art clay on the end of a pencil was useful for manoeuvring individual sclerites onto SEM stubs (similar to methods described in Alderslade 1998). Similarly, a fine-hair brush with all but two hairs removed was equally useful for this task. Modern morphological studies of primnoids rely on SEM images. All images within this publication were taken from stubs coated in gold:palladium 60:40 alloy, to a thickness of between 30–40 nm, at the Smithsonian Institution SEM Laboratory on an Amray 1810 SEM with Lanthanumhexaboride electron source and at Cambridge University Department of Materials, on a JEOL GSM-6340F Field Emission SEM.

Results

Historical summary of the *Thouarella* species groups

Versluys (1906) first grouped *Thouarella* species into the “*Hilgendorfi*-Gruppe” (species with polyps in pairs and whorls), species with isolated polyps (without a group name), and the “*Antarctica*-Gruppe”, which also has isolated polyps.

Kükenthal (1912) again grouped *Thouarella* species (“*Hilgendorfi*-gruppe”, “*Antarctica*-gruppe” and “*Köllikeri*-gruppe”, with the latter having isolated polyps but being differentiated by having a longer marginal scale spine than those remaining in the “*Antarctica*-gruppe”) and later elevated these groups to subgenera (1919). With *Amphilaphis* removed (Kinoshita 1908a; Bayer 1981) and *Diplocalyptra* incorporated (Kinoshita 1908c), *Thouarella* had subgenera separated according to colony branching, polyp placement (whorled, paired, isolated), and the elongation of the distal edge of the marginal scales (Cairns & Bayer 2009).

Antarctica gruppe

Within Group 1 (isolated polyps) there are a number of very closely related species separated by the smallest of variations in characters. In particular the ‘Antarctica-gruppe’ (Versluys 1906) deserves mention because some of these species could be considered a single, variable species. Versluys originally only listed *T. antarctica* (Valenciennes, 1846), *T. affinis* Wright and Studer, 1889, and *T. variabilis* Wright and Studer, 1889, of which we disregard *T. variabilis* as it has very long marginal scales making it distinct from the remaining species. Versluys (1906) grouped these species as they had isolated polyps and a bottlebrush colony arrangement. Kükenthal (1912) considered the ‘Antarctica-gruppe’ to include: *T. antarctica*, *T. affinis*, *T. chilensis* Kükenthal, 1908, and *T. crenelata*. He mentioned that isolated polyp arrangement was a more conservative character than branching arrangement, something with which we agree.

Köllikeri-gruppe

This includes *T. koellikeri* Wright & Studer, 1889, *T. variabilis*, *T. versluysi* Kükenthal, 1907, *T. striata* Kükenthal, 1907, *T. clavata* Kükenthal, 1908, *T. brucei* Thomson and Richie, 1906, and *T. hicksoni*, Thomson, 1911—species with isolated polyps and foliate, elongated marginal scales. In 1919, Kükenthal rearranged the entire genus, moving *T. antarctica* into the ‘Köllikeri group’, as it has relatively tall marginal scales, leaving *T. crenelata*, *T. chilensis*, and *T. affinis* in the ‘Antarctica gruppe’ with isolated polyps and shorter marginal scales. It is this latter group where there are now a number of very similar species.

As described in detail in the species comparisons after the description of *T. antarctica*, there are relatively small, but apparently consistent, differences separating these species and it will be interesting to investigate their genetic relatedness, work that is currently underway.

Hilgendorfi-gruppe

On a species level there are many changes within *Thouarella* in this paper. One deserving special mention is the *Hilgendorfi* complex of species (“*hilgendorfi-gruppe*” sensu, Kükenthal 1912).

In 1906, Versluys placed *T. hilgendorfi* (Studer, 1878), *T. laxa* Versluys, 1906, *T. moseleyi*, and *T. tydemani* into the *T. hilgendorfi* group. In 1912, *T. typica* Kinoshita, 1907, *T. longispinosa* Kükenthal, 1912, *T. carinata* Kükenthal, 1908, *T. tenuisquamis* Kükenthal, 1908, and *T. flabellata* Kükenthal, 1907 were added to this group by Kükenthal. Some 100 years later we find ourselves approaching a similar task in assessing these species whose identifying feature is their paired or whorled polyp arrangement.

Disregarding *T. longispinosa*, which is now considered to be *Dasystenella acanthina* (see species description), this group now looks quite different because of several synonymisations.

Thouarella laxa was described from Japan by Versluys (1906). The following year Kükenthal (1907) described *T. flabellata* from Somalia, and *T. tenuisquamis* (originally described as *Thouarella regularis* Kükenthal, 1907) from Nicobar, northwest of Sumatra, briefly stating the latter could be similar to *T. laxa*. Kükenthal did not specifically compare these species to each other or *T. laxa*, perhaps because of the large distance between their type localities. In 1908, Kükenthal described *T. carinata* from Okinawa and subsequently remarked that it differed from *T. laxa* in having branchlets and polyp whorls that were more densely placed, as well as different sclerite shapes (Kükenthal 1919). The differences seen between these species in this study are very minor (as discussed in species descriptions) and for this reason we conclude that these species (*T. laxa*, *T. tenuisquamis*, *T. flabellata*, and *T. carinata*) are conspecific and propose their synonymisation under the senior synonym *T. laxa*.

Kükenthal (1924) separated *T. tydemani* and *T. laxa* based on the number of whorls per cm (4–6), which is a variable character, but polyps of *T. laxa* (Fig. 32c) look very similar to those of *T. tydemani* (see Zapata-Guardiola & López-González 2010a). A recent paper (Zapata-Guardiola & López-González 2010a) shows that *T. tydemani* polyps have toothed ridges on the inner surface of body-wall scales; these are absent in *T. laxa*. *Thouarella moseleyi* has similar body-wall scale morphology, however, the reduced height of marginal scales and the clavate polyp shape make *T. moseleyi* distinct from both *T. tydemani* and *T. laxa*. *Thouarella laxa* has bottlebrush-shaped colonies and colonies of *T. tydemani* are pinnate. The former has polyps that are more inclined to the branchlet than the latter species (whose polyps are almost perpendicular to the branchlet) that also has longer, more flexible branchlets, and less pairs/whorls per cm, making these distinct species.

The sclerites, number of whorls per cm, and number of polyps per whorl of *T. hilgendorfi* and *T. typica* are nearly identical, and as these character differences can vary widely within colonies and species, we agree with Cairns (2010) that these two species should also be synonymised.

The “*hilgendorfi*” group thus includes:

- *T. hilgendorfi* (synonym: *T. typica*)
- *T. laxa* (synonyms: *T. tenuisquamis*, originally described as *T. regularis*, *T. flabellata*, *T. carinata*)
- *T. moseleyi*
- *T. tydemani*

In essence, the polyps and sclerites of all of “Hilgendorfi” species (with the exception of *T. moseleyi*, whose polyps are clavate) have nearly identical shapes and sizes. It is astounding that species looking so similar are found from Hawaii (*T. hilgendorfi*) to east Africa (*T. laxa*, formerly *T. flabellata*). We have kept these species separate based on branching structure but would be interested to see if genetic studies support this distinction; this research is currently underway.

New *Thouarella* species groups

As already mentioned, before this revision *Thouarella* had subgenera separated according to colony branching (*Diplocalyptra*), polyp placement (whorled and paired—*Hilgendorfi* group, isolated—*Antarctica* and *Köllikeri* groups), and the elongation of marginal scale distal edges (with the *Köllikeri* group having longer marginals than *Antarctica* group species; Cairns & Bayer 2009). We query the reliability of two of these characters as colony branching can vary within a species (*Thouarella* seems particularly variable in this respect, making this character unsuitable for subgeneric separation), and the entire spectrum of elongation of the distal edge of marginal scales, from rounded to spinose, can be found in *Thouarella* making this character also a poor choice for assigning species to subgenera. Polyp placement, however, is a more reliable character; species with isolated polyps are easily distinguished from those with paired or whorled polyps and, although some species with paired polyps infrequently have whorls of three and even four polyps, this is very rare in species with isolated polyps. Consequently, given that *Thouarella* species are very closely related, we acknowledge this close relationship by splitting *Thouarella* into species groups rather than subgenera. Furthermore, as discussed above, the most reliable character available to group *Thouarella* species is polyp placement and it is on this character that we, as partially done by Versluys (1906), base our species group delineations (Table 1): Group 1—species with isolated polyps and Group 2—species with polyps in pairs or whorls. Group 1 would thus include both *Antarctica* and *Köllikeri* groups. The *Hilgendorfi* group is now in Group 2.

Within Group 1 the number of abaxial body-wall scales, polyp size, number of polyps per cm, and polyp shape are equally important when determining species. Group 2 species have very similar polyps and differentiation is based primarily on branching arrangement and branchlet rigidity. See Table 3 for more details.

Thouarella morphology and characters

Branching structure

The most common *Thouarella* branching structure is a **bottlebrush** form, with branchlets arranged on all sides of the main stem in at least three directions. *Thouarella* species are also **pinnate** (featherlike branching with branchlets on each side of branch), **pinnate to bipinnate** (pinnate branching where branchlets are also pinnately branched), **dichotomous** (repeated bifurcation of branching; Bayer et al. 1983) and **bilateral to bottlebrush** (where branchlets occur in at least three directions, and are thus technically bottlebrush, however branchlets can curve into one plane creating a bilateral appearance). Part of the colony of *T. coronata* is also considered to be **sympodially** branched (the main axis being formed by the basal sections of lateral branches, often forming a zigzag). In some instances, overall colony structure can be one shape and branching structure different, for example, *T. hilgendorfi* has a uniplanar, flabellate colony shape yet individual bottlebrush branches and branchlets.

The complex morphological structure of *Thouarella* makes these octocorals ideal habitat for many species of epifauna. In this study specimens of *Thouarella* were often found harbouring polychaetes along their stem between branchlet planes, brittlestars clinging to branchlet tips, amphipods wedged between polyps, and egg cases and ascidians attached to stems and branchlets (Fig. 2).

TABLE 1. *Thouarella* species—Groups 1 and 2.

	Species	Synonym(s)	Distribution
Group 1— Isolated polyps	1. <i>T. antarctica</i> (Valenciennes, 1846)		Falkland Islands, SW Atlantic
	2. <i>T. variabilis</i> Wright and Studer, 1889	<i>T. variabilis</i> var. <i>gracilis</i> Wright and Studer, 1889	Circum-Antarctic
	3. <i>T. brevispinosa</i> Wright and Studer, 1889		SW Atlan., S. Indian Ocean
	4. <i>T. affinis</i> Wright and Studer, 1889		SW to S. Atlantic
	5. <i>T. koellikeri</i> Wright and Studer, 1889		SE Pacific, SW Atlan. Antarctic Peninsula
	6. <i>T. brucei</i> Thomson and Richie, 1906	<i>T. versluysi</i> Kükenthal, 1907	Mid-S. Atlan., SE Pacific, Antarctic Peninsula
	7. <i>T. striata</i> Kükenthal, 1907		Bouvet Isl., SW Atlan., Patagonian shelf
	8. <i>T. crenelata</i> Kükenthal, 1907		Circum sub-Antarctic
	9. <i>T. clavata</i> Kükenthal, 1907		South Africa
	10. <i>T. pendulina</i> (Roule, 1908)		Circum-Antarctic
	11. <i>T. chilensis</i> Kükenthal, 1908		Chile, S/SW Atlantic, S. Indian Ocean, Antarctic Peninsula
	12. <i>T. hicksoni</i> Thomson, 1911		South Africa
	13. <i>T. bipinnata</i> Cairns, 2006		SW Atlantic
	14. <i>T. viridis</i> Zapata-Guardiola and López-González, 2010		South Georgia Island, Patagonian shelf
	15. <i>T. minuta</i> Zapata-Guardiola and López-González, 2010		Circum-Antarctica
	16. <i>T. andeep</i> Zapata-Guardiola and López-González, 2010		SW Atlan., circum-Antarctica
	17. <i>T. parachilensis</i> nov. sp.		South Georgia Island, Antarctic Peninsula
Group 2— Paired or / whorled polyps	18. <i>T. hilgendorfi</i> (Studer, 1878)	<i>T. typica</i> Kinoshita, 1907	Hawaii, Indonesia, Indian Ocean, Japan
	19. <i>T. moseleyi</i> Wright and Studer, 1889		Kermadec, New Zealand, and Indonesia
	20. <i>T. laxa</i> Versluys, 1906	<i>T. tenuisquamis</i> Kükenthal, 1908 <i>T. flabellata</i> Kükenthal, 1907 <i>T. carinata</i> Kükenthal, 1908 <i>T. regularis</i> Kükenthal, 1907	East Africa to east Asia
	21. <i>T. tydemani</i> Versluys, 1906	? <i>Hookerella pulchella</i> Gray, 1870	Indonesia
	22. <i>T. coronata</i> Kinoshita,		Japan
	23. <i>T. parva</i> Kinoshita, 1908		Japan
	24. <i>T. biserialis</i> (Nutting, 1912)	<i>Amphilaphis biserialis</i>	Hawaii
	25. <i>T. grasshoffi</i> Cairns, 2006		N. Atlantic

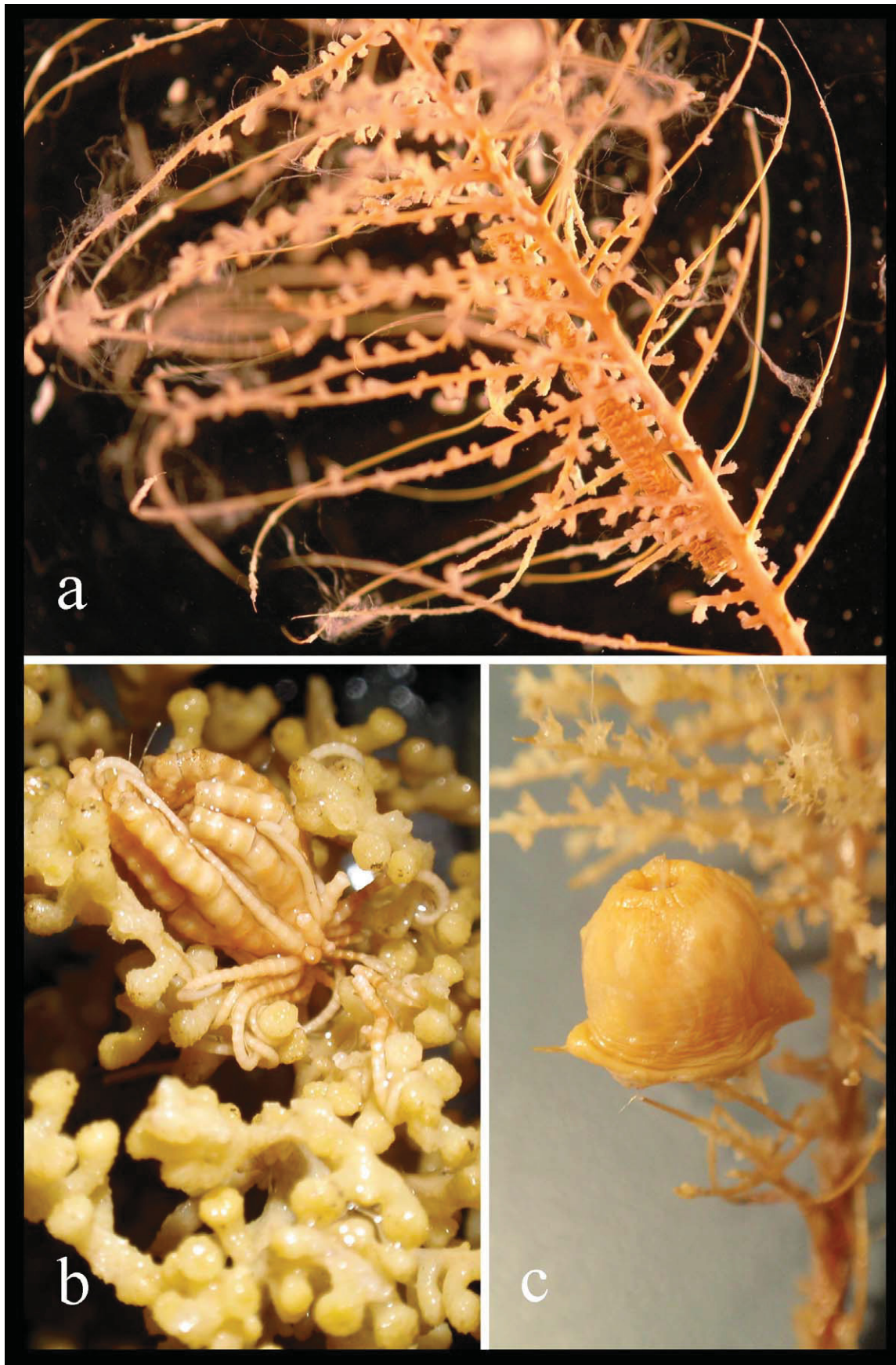


FIGURE 2. Animals found within the branchlets of *Thouarella* specimens: a) Polychaete found along stem of the holotype of *T. affinis*; b) crinoid arboreal cup in branchlets of *T. crenelata* (ZSL AE57); c) anemone attached to branchlet of specimen of *T. variabilis* (SMF, MD42, sta. 22).

Polyp shape, arrangement, and distribution

Polyps of *Thouarella* are generally **flared distally** (this ranges from modest to widely flared) or **clavate** (having a tall, rounded operculum, visible from side view e.g., *T. koellikeri*, Fig. 12c, or a rounded polyp where the operculum is beneath encasing marginals and thus not visible, e.g., *T. parachilensis* nov. sp, Fig. 28c). Polyps open widely to take in food and this function, and the associated change in polyp shape, should be remembered when undertaking species identifications; polyps are not fixed in shape when alive.

Thouarella polyps occur individually (**isolated**, e.g. *T. crenelata*, Fig. 18b), in **pairs** (e.g. *T. laxa*, Fig. 32c; *T. laxa* polyps also occur in whorls), or in **whorls** (e.g. *T. coronata*, Fig. 34c) of up to five.

The density of polyps (**number of polyps per cm**) is often related, in some degree, to polyp size; there will be more 1 mm long polyps per cm than those 2.5 mm long. This is an important point to consider and the reason why we did not use the number of polyps/pairs/whorls per cm in the dichotomous key. However, this is still sometimes a useful factor in species identifications and can be useful as long as the polyp length in the species description is indicated. **Polyp length** is the length measured abaxially from polyp tip to base.

Sclerites

The variation and differences of size, shape, and arrangement of sclerites is used in species diagnosis. Review of the original literature pertaining to the identification of *Thouarella* indicated that the terms “opercular”, “circumopercular” and “marginal” have been used in different ways at different times. To avoid confusion, all sclerite categories are defined below:

Operculars (Fig. 3f–i) fulfill the functional role of covering and thus protecting the polyp head. There are eight operculars in *Thouarella* and they can be arrowhead-shaped (with a dented proximal edge, Fig. 3h,i), acute isosceles triangle/lanceolate-shaped (Fig. 3f) or tongue-shaped (rounded distal edge, Fig. 3g). They may or may not have a distinctive keel on their inner face.

Accessory operculars (Fig. 3a–e) have been found in several *Thouarella* species. Originally noted by Kinoshita (1908b, pl. 5), they are smaller (250–500 µm) than operculars, often of a similar shape, and usually adhere to the inner surface of typical operculars (and against the polyp body/tentacle-base); they tend to be found in one ring, although two rings have been described in *Plumarella* (formerly *Thouarella*) *bayeri* (Zapata-Guardiola & López-González, 2010), and are often less than eight in number. Similar small operculars are found in *Convexella* Bayer, 1996 and *Digitogorgia* Zapata-Guardiola & López-González, 2010.

Marginals (Fig. 3j–l), or circumoperculars, are the transverse circle of scales most proximal to the operculars and tend to be the same size or larger than the operculars and usually fold over the operculars, forming a protective cone when the polyp contracts. There are eight marginals and the inner surface is keeled. These keels are diagnostic at the genus level; their presence is the only character that separates *Thouarella* from *Plumarella* (Cairns, 2010).

Submarginals (Fig. 3m–o) are the next most proximal transverse circle of scales below the marginals. They are sometimes differentiated from body-wall scales in having a more pointed distal edge and occasionally a reduced keel on the inner surface and are thus often specifically included in species descriptions.

Body-wall scales (Fig. 3p–s) generally form the majority of scales covering the polyp body in longitudinal rows beneath the submarginals to the polyp base. Body-wall scales usually progressively reduce in size from the abaxial side of a polyp to adaxial. Body-wall scales have tubercles covering the inner surface, as is common for the proximal third to two-thirds of most sclerites. From the marginals to the polyp base the number of scales in each transverse circle often decreases as the polyp diameter attenuates.

Coenenchymal scales form one or two layers along branches. Most sclerites within the categories described above are generally the same shape however, in contrast, coenenchymal scales are often a range of shapes: circular, oval and elliptical, possibly because all edges are free to grow.

Other commonly used terms and structures include:

Keels are an important characteristic in *Thouarella* species. They are found on the inner surface of the operculars, marginals, and sometimes submarginals. *Plumarella* and *Thouarella* may look very similar but the presence of a keel on the marginals determines that a species is in the genus *Thouarella*, not *Plumarella* (Cairns 2010). Within *Thouarella* there are simple keels (Fig. 3k), complex multi-keels (Fig. 3l), channelled keels (Fig. 3j), keels with lateral projections (visible from the outer surface e.g. Fig. 5h), and, unsurprisingly with the high level of variability in *Thouarella*, there are specimens that can span two of these forms. The text below is provided to enable the reader to understand our descriptions of keeled marginals (although operculars and submarginals also bear keels):

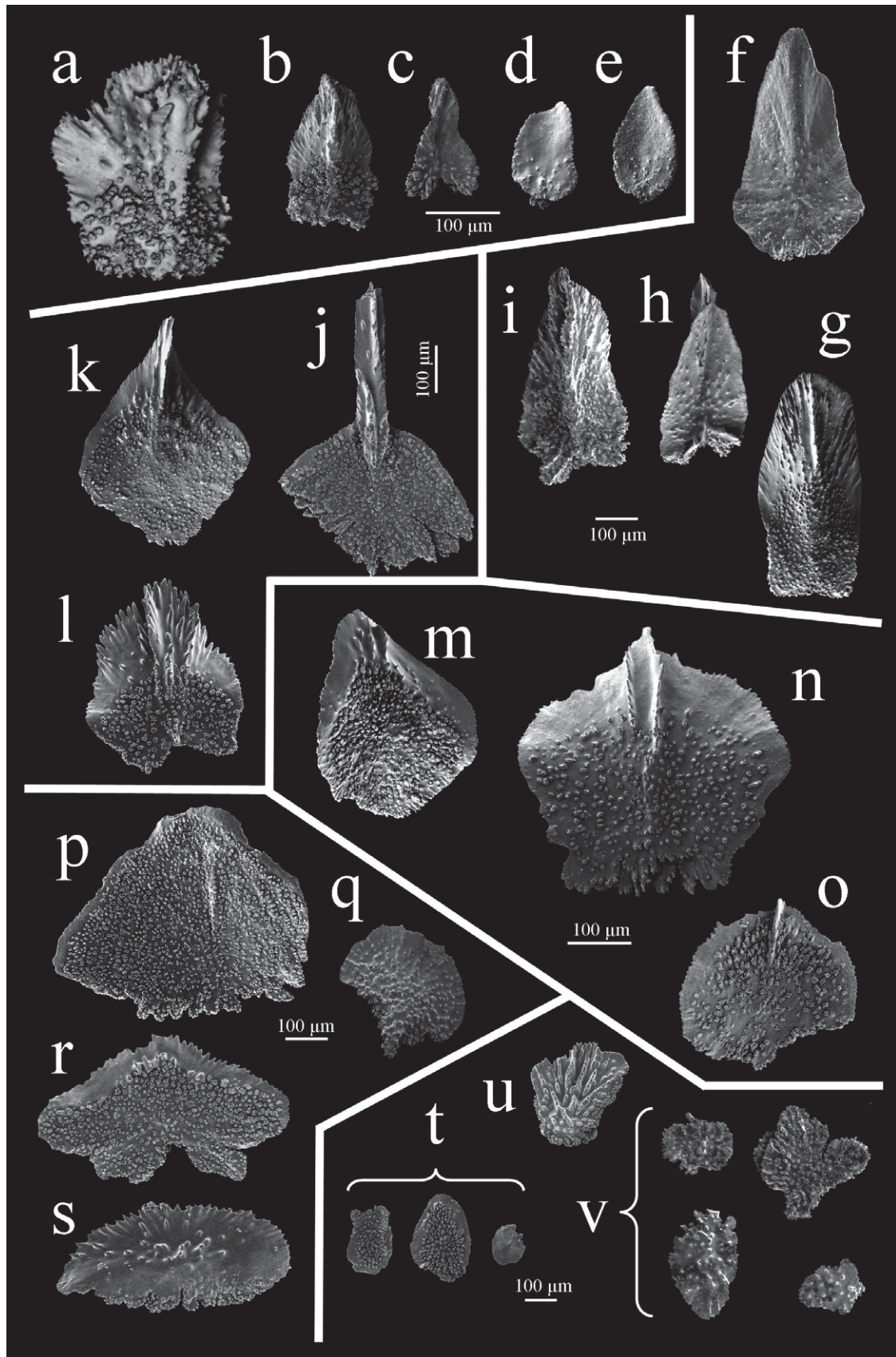


FIGURE 3. Examples of sclerite categories. Accessory operculars: a) *Thouarella chilensis*; b,c) *T. hicksoni*; d,e) *T. coronata*. Operculars: f) *T. clavata*; g) *T. affinis*; h) *T. koellikeri*; i) *T. antarctica*. Marginals: j) *T. variabilis*; k) *T. affinis*; l) *T. crenelata*. Submarginals: m) *T. coronata*; n) *T. koellikeri*; o) *T. hicksoni*. Body-wall scales: p) *T. clavata*; q) *T. hicksoni*; r,s) *T. parachilensis* sp. nov. Coenenchymal scales: t) *T. laxa*; u) *T. crenelata*; v) *T. antarctica*.

T. brucei marginals have a multi-keel (Fig. 15f), the most common type amongst *Thouarella* species, often with small lateral projections visible from the outer surface, as with the marginals of *T. antarctica* (Fig. 5h).

T. affinis has marginals with a simple, single keel (Fig. 11h).

T. variabilis has marginals that are spinose but flat, with a channelled keel (Fig. 3j).

Plumarella diadema (Cairns 2006) (formerly *Thouarella diadema*) has a long spine (circular in cross-section), which is unkeeled but has longitudinal parallel channels (a bifurcate example of which is seen in Fig. 36d).

The term **serrated** is often applied to the distal edge of sclerites (see distal edges of *T. brucei*, Fig. 15g). In *Thouarella* most sclerite edges are actually **finely serrate** (see Figs 3g,n,o).

Coarsely or roughly lobate (e.g. Fig. 3j,p,r) has been used to describe the uneven, sometimes tuberculate proximal edges of most *Thouarella* sclerites.

Pectinate is truly comb-like and only found in *Plumarella recta* (Nutting, 1912) and *P. alternata* (Nutting, 1912), which were both formerly placed in *Thouarella*.

Species synonymisations and removals

As of 2010, we consider there to be 25 species within *Thouarella* (Table 1). In the dichotomous key, scale bars are included and are usually the same within each couplet (e.g. 6a and 6b). This was not possible with colony images as their size differed enormously, thus colony/branchlet lengths are listed.

Several species of *Thouarella* are proposed for synonymisation within this study. *Thouarella laxa* Versluys, 1906, *T. tenuisquamis* Kükenthal, 1908, *T. flabellata* Kükenthal, 1915 and *T. carinata* Kükenthal, 1915 are proposed as conspecific and thus synonymised with the senior synonym *T. laxa*. In addition, *Thouarella variabilis* var. *a* Wright and Studer, 1889 and *T. variabilis* var. *gracilis* Wright and Studer, 1889 are proposed as synonymised under *T. variabilis*, and *T. variabilis* var. *brevispinosa* Wright and Studer, 1889 raised to species level (*T. brevispinosa*). We also propose that *Thouarella versluysi* Kükenthal, 1907 is synonymised with *T. brucei* Thomson and Ritchie, 1906.

Plumarella sardana (formerly *Thouarella sardana*) (Zapata-Guardiola & López-González, 2010) and *P. diadema* (formerly *T. diadema*) (Cairns, 2006) are conspecific and thus synonymised as *P. diadema*; in agreement with Cairns (2011).

Lastly, mostly as a result of the clarification of the difference between *Plumarella* and *Thouarella* (Cairns 2010), the species listed in Table 2 have been removed from *Thouarella*.

TABLE 2. Species removed from *Thouarella* genus.

Old combination/ name	New combination / synonym
<i>T. diadema</i> Cairns, 2006	<i>Plumarella diadema</i>
<i>T. recta</i> Nutting, 1912	<i>Plumarella recta</i>
<i>T. alternata</i> Nutting, 1912	<i>Plumarella alternata</i>
<i>T. superba</i> Nutting, 1912	<i>Plumarella superba</i>
<i>T. bayeri</i> Zapata-Guardiola and López-González, 2010b	<i>Plumarella bayeri</i> n. comb.
<i>T. undulata</i> Zapata-Guardiola and López-González, 2010b	<i>Plumarella undulata</i> n. comb.
<i>T. longispinosa</i> Kükenthal, 1912	<i>Dasystenella acanthina</i> (Wright and Studer, 1889)

Reliability of some of the morphological characters

Kükenthal created his last key for *Thouarella* species in 1924. In it the number of abaxial scales and whorls of polyps per cm are used to differentiate between the many species. We believe that these characters are far from fixed and can vary substantially within a colony making Kükenthal's key unreliable, as he did not allow for ranges within these characters. That said, the number of polyps per cm is still important in species identification with the consideration that this value can be modestly variable.

Colony formation can be altered by the presence of annelid commensals that induce branchlets to flatten and curve to form tube-like tunnels along axes (Brito 1993); this must be considered when looking at specimens. However, by examining where branchlets depart the stem, the arrangement can be recognised. Colonies of *Thouarella* encapsulate a range of forms including: pinnate, dichotomous, bottlebrush, bottlebrush but appearing

planar. This range of variation is unusual in just one octocoral genus (Bayer 1956; 1981). We consider polyp morphology (usually distally flared with 8 operculars and 8 keeled marginals) as the defining character for this genus.

The range in number of abaxial polyp scales given in the species descriptions of *Thouarella* is necessary because polyps enlarge as they brood and coenenchymal scales at the polyp base appear to become part of the lower polyp body. Without this consideration, brooding specimens could be regularly misconstrued as different or new species. We suggested that many polyps of a colony, from the tip to the base of branchlets and from the tip to the base of the colony, be examined in species identification as variability within a colony is common.

Generally, polyp placement (isolated, paired, whorled), the number of abaxial scales (which usually has a small range), the number of polyps per cm, and the colony form are the most important characters in identifying *Thouarella* species as they are relatively fixed and thus reliable. Beyond this, marginal scale shape, including the elongation of marginal distal edges, and average polyp size are also informative.

A character that is considered less important within this study is the outer surface texture of sclerites. Around commensal tubes, polyps tend to have thicker, calcified sclerites (Brito 1993), as is commonly noted in other primnoids (Bayer 1964; Eckelbarger et al. 2005). Therefore, making use of sclerite texture alone for the purposes of taxonomy is ill-advised.

Did *Thouarella* originate in the Antarctic?

Several authors have discussed primnoid character evolution (Kinoshita 1908a; Versluys 1906; Cairns & Bayer 2009). Both Versluys (1906) and Kinoshita (1908a) thought it evolutionary advantageous for there to be fewer and larger scales on polyps, and this holds true in recent primnoid morphological studies. For instance, *Primnoeides*, with its simple opercular and numerous small body-wall scales not arranged in rows, is considered basal to all other primnoid genera (see Cairns 2006; Cairns & Bayer 2009). Many genera compared to *Thouarella* in this revision are unsurprisingly from within the same grouping in the phylogenetic analysis of morphological characters undertaken in Cairns and Bayer (2009). Most genera within this grouping occur in Antarctica, where the earliest clade within the Primnoidae, according to morphological analysis, also occurs, suggesting Antarctica could be the origin of the family (Cairns & Bayer 2009). Antarctica cooled around *c.* 42 MYA in the Eocene with a permanent ice sheet established from around 34 MYA (Tripathi et al. 2005). These low temperatures and the break-up of the former supercontinent of Gondwana created an isolation that has made Antarctica's present-day marine biota the world's most distinctive and one of three centres of species origin globally (Briggs 2003). Prehistoric dispersals from Antarctica to other ocean basins and trenches have been proposed for other invertebrates, e.g. holothurians (Gebruk 1990, noted in Briggs 2003) and cephalopods (Strugnell et al. 2008). However, molecular phylogenetic analyses are required to confirm the origins of Primnoidae. It is noteworthy that population fragmentation and isolation in times of glacial maxima could have been important mechanisms for allopatric speciation in Antarctic fauna, increasing taxonomic diversity (Clarke & Crame 1989; 2010; Rogers 2007, 2012). Seventeen species of *Thouarella* are found in the Antarctic, sub-Antarctic and south Atlantic waters whereas just nine are known from the rest of the world (three from Japan, one from Asia to the Pacific, another from Asia to East Africa, one each from the North Atlantic, Indonesia, Hawai'i and South Africa). With high numbers of species from high latitudes of the southern hemisphere one could speculate that this region is the centre for radiation of *Thouarella*, however, as already mentioned, genetic studies are required to clarify this.

Interestingly, all non-sub-Antarctic/Antarctic/southern Atlantic species, with the exception of *T. hicksoni* (from South Africa), fall within Group 2 (species with polyps in pairs/whorls). Polyps of Group 2 species look very similar, with species differing mostly in branching morphology (this is a tentative comment on branching morphology, as such small fragments of some holotypes remain). Group 2 species, as already mentioned, occur from East Africa to Hawaii, crossing the Indian and Pacific Oceans. It remains to be seen how important branching structure is in the evolution of *Thouarella*. Within primnoids at least, it does not appear to be very informative in determining phylogeny (Cairns & Bayer 2009).

Key to *Thouarella* species

Group 1 – species having isolated polyps

1a. Most polyps with 5 scales or less in abaxial row: 2

1b. Most polyps with 5 scales or more in abaxial row: 9

2a. Polyps less than 1.5mm long: 3

2b. Polyps larger than 1.5mm long: 5

3a. Polyps less than 1mm long. *T. minuta*

3b. Polyps 1–1.5mm long: 4

4a. Polyps appressed to branchlet, pointed operculars, marginals with simple keel. *T. pendulina*, see figs. 22, 23

4b. Polyps inclined at 30° to appressed against branchlet, operculars tongue-shaped, marginals with ridged, complex keel. *T. hicksoni*, see figs. 26, 27

5a. Colony pinnate to bipinnate, polyps clavate and orientate toward one face of the colony. *T. bipinnata* (see Cairns, 2006)

5b. Colony bushy/ bilaterally bottlebrush or bottlebrush shaped, polyps distally flared and isolated: 6

6a. Marginals elongated, spinose.

T. variabilis, see figs. 6, 7

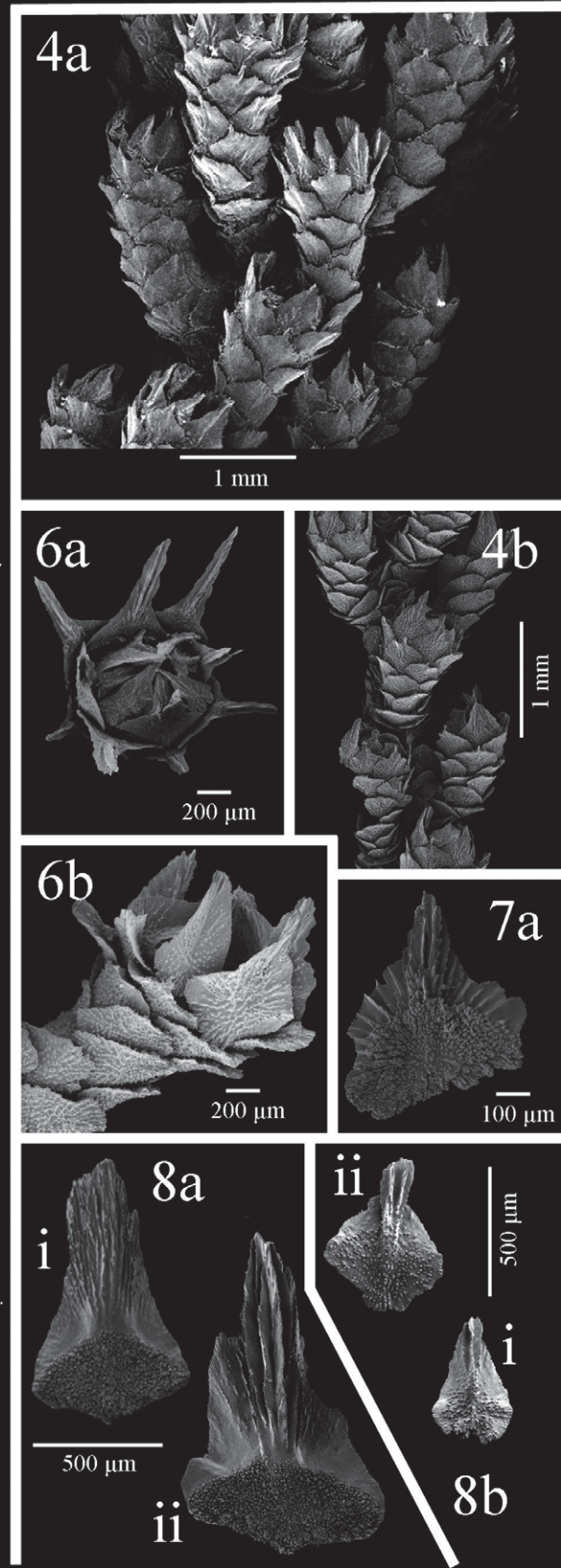
6b. Marginals triangular or with triangular distal edge: 7

7a. Marginals with heavily ridged inner surfaces. *T. striata*, see figs. 16, 17

7b. Marginals with relatively smooth inner surfaces, sometimes with small ridges adjacent to keel: 8

8a. Opercular scales triangular, inner surface ridged (i), marginals with dense tubercles (ii). *T. andeep*

8b. Opercular scales triangular with pointed distal edge, inner surface with keel (i), marginals with sparse tubercles (ii and polyp in 6b). *T. brucei*, see figs 14, 15



9a. Polyps clavate (see 12 a): 10

9b. Polyps distally flared: 13

10a. Polyps with tall operculum (9a, 11b): 11

10b. Polyps with low operculum mostly hidden in side view (e.g. 12a,b): 12

11a. Heavily ridged inner distal edge of marginals and submarginals, 6–7 abaxial scales. *T. viridis* (see 9a)

11b. Pointed marginals and submarginals with small keels on inner surface, 7–10 abaxial scales. *T. koellikeri*, figs. 12, 13

12a. 6–10 abaxial scales, polyps clavate, evenly spaced along branchlets, operculum fully visible from anterior. *T. crenelata*, figs. 18, 19

12b. 7–11 abaxial scales, polyps bulbous, in dense clusters at branchlet tip, operculum encased by marginals. *T. parachilensis*, figs. 28, 29

13a. Most marginals tall triangular, some abaxial marginals widely triangular: 16

13b. Most marginals widely triangular to diamond shaped: 14

14a. Tongue-shaped operculars. *T. affinis*, figs. 10, 11

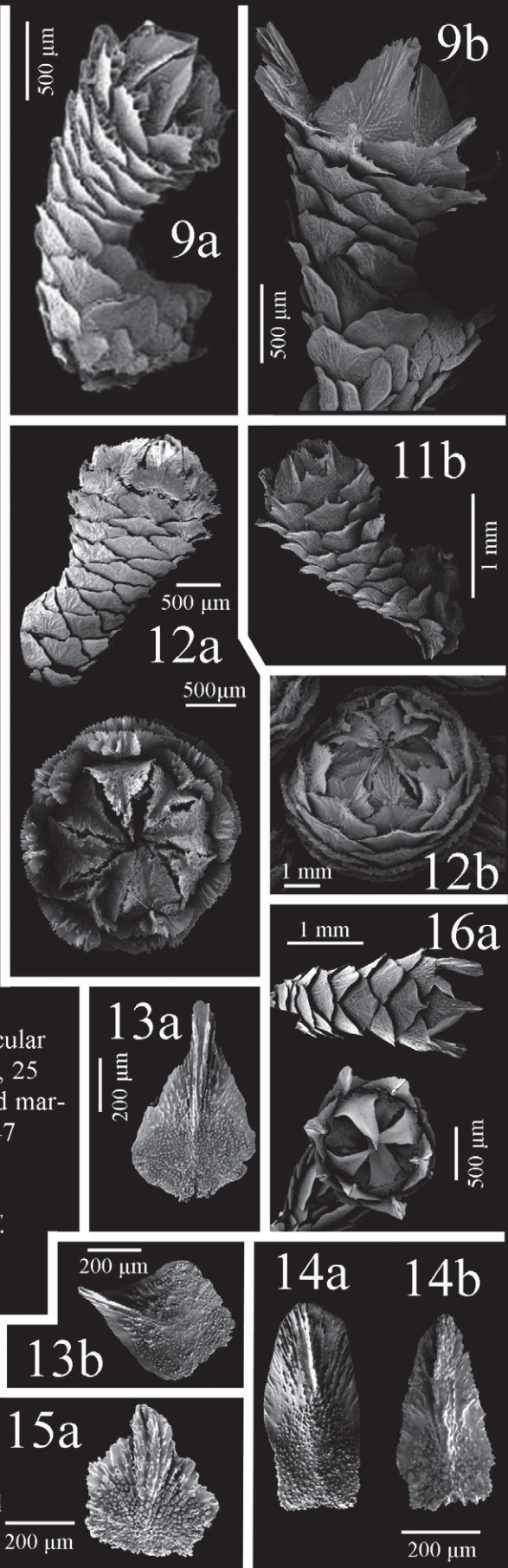
14b. Lanceolate/arrowhead operculars, heavily ridged: 15

15a. Thick, heavily ridged marginals and opercular scales, 7–9 abaxial scales. *T. chilensis*, figs. 24, 25

15b. Relatively smooth, delicate operculars and marginals with wide lateral projections off keel, 5–7 abaxial scales. *T. antarctica*, figs. 4, 5

16a. Polyps < 2mm long, 5–6 abaxial scales. *T. clavata*, figs. 20, 21

16b. Polyps > 2mm long, 6–8 abaxial scales. *T. brevispinosa* (also see 9b), figs. 8, 9



Group 2 – polyps in pairs or whorls

1a. Branchlets depart branch in two directions, uniplanar (*T. coronata*, colony 13 cm): 2

1b. Branchlets depart in at least three directions (*T. hilgendorfi*, branchlets 7 cm long): 6

2a. Branching dichotomous/sympodial: 3

2b. Branching pinnate: 5

3a. Operculum tall or polyps clavate, polyps depart branchlet at 45° (see 4a): 4

3b. Polyps distally flared, depart branchlet at 90° . *T. coronata* (also see 1a and figs. 34, 35)

4a. Small ridged keel on marginals, polyp with tall conical operculum. *T. parva*, figs. 40a,b

4b. Multi-keel on inner surface of marginals, rounded polyps. *T. biserialis*

5a. Branchlets alternately pinnate, paired distally flared polyps (rarely whorls of three), departing at $70\text{--}80^\circ$, elongated marginals. *T. tydemani*

5b. Branching opposite pinnate, paired clavate polyps depart at 90° , modestly pointed marginals. *T. moseleyi*, figs. 30, 31

6a. Long flexible branchlets depart in 3 directions (see i), although can appear pinnate, paired polyps depart at 90° (see below). *T. laxa*, figs. 32, 33

6b. Branchlets depart in all directions, true bottlebrush, polyps in pairs/ whorls of 3, depart branchlet at $45\text{--}60^\circ$: 7

7a. Polyps clavate. *T. grasshoffi*

7b. Polyps distally flared. *T. hilgendorfi*

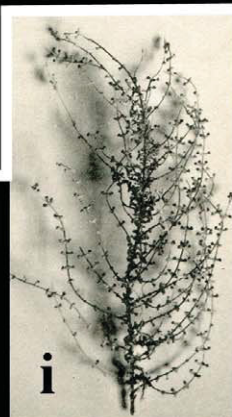
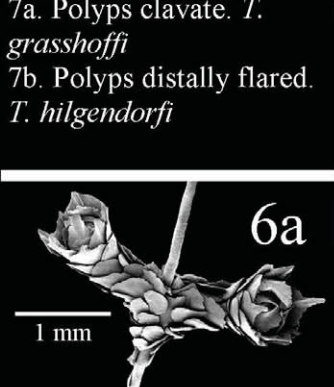
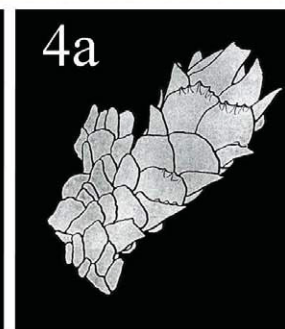
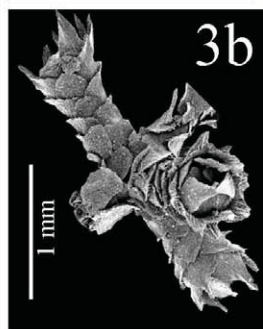


TABLE 3. Tabular key for the species of *Thouarella*.

GROUP 1 Isolated polyps		Branching pattern	Polyp arrangement & distribution (polyps/cm)	Polyp angle from branchlet	Polyp shape	Polyp height (mm)	No. of scales in LAB	Opercular keeled?	Opercular shape	Marginal keel	Marginal shape	Unique characters/ Comments
<i>T. bipinnata</i>		Uniplanar, pinnate to bipinnate	Isolated, roughly alternate 10–13	80–90°	Modestly clavate	2.4	3–5	Yes, simple with multiple striations	Lanceolate to arrowhead	Complex with lateral extensions	Rounded base, pointed distally	Clavate, large polyps, with tall oper.
<i>T. clavata</i>		bb./bilateral appearance	Isolated	45–60°	Distally flared	1.7–2	6–7	Yes, simple, large	Lanceolate to tri.	Simple, flat faced	tri., angular proximal edge	Very similar to <i>T. brucei</i> , require more specimens
<i>T. koelikeri</i>		Bushy, bb./bilateral appearance	Isolated, 12–15	45–60°	Clavate, tall, coned oper.	1.6–2.5	7–10	Yes, single, large	Arrow-headed/isosceles tri.	Large with small lateral projections	Short tri., rounded laterally	Rounded submarg. with small keel
<i>T. affinis</i>		bb./bilateral appearance	Isolated, 7–9	45–60°	Clavate, rarely modestly flared	1.1–2.1	6–7	Yes, low multi-keel	Tongue/ tri.	Ab. scale with keel; ad. no keel or striations	Widely tri. to diamond	Clavate/rare modest distally flared polyp, diamond marg., tongue-shape operculars
<i>T. viridis</i>		Bushy, bb./bilateral appearance	Isolated, 14–15	45–60°	Clavate, tall cone	1.5–2.5	6–7	Yes, single, large	Lanceolate/arrowhead	Multi-channel, adjacent striations	Wide tri./pentagonal	Often green when alive
<i>T. brucei</i>		Bushy, bb./bilateral	Isolated, 9–12	40–45°	Distally flared	1.5–2.3	4–5	Yes, single, large	tri./arrowhead	Complex, multi-keel, smooth laterally to keel	Diamond	4–5 ab. scales, operculars keeled & tri.
<i>T. andeep</i>		Bushy, bb./alternately pinnate appearance	Isolated, 10–11	80–90°	Distally flared, tall conical oper.	1.9–3.4	4–5	No	Tongue-shaped	Multi-keel, channelled	Wide tri.	Large polyp, tall oper.
<i>T. brevispinosa</i>		bb.	Isolated, 7–11	60°	Distally flared, oper. lower than marginals	2.5–3	6–7	Yes, simple, large	Isosceles tri./lanceolate	Channelled keel	Tall tri.	Similar to <i>T. brucei</i> , but more scales in LAB
<i>T. striata</i>		bb., colony flabellate	Isolated, 14–20	45–80°	Distally flared	1.5–2.2	4–6	Yes, multiple longitudinal striations	Lanceolate	Wide, flat, channelled	tri. distally, square proximally	Striated outer scale surface
<i>*T. antarctica</i>		bb.	Isolated, 25–30 at tip, 11–23 on branchlets	60–80°	Modest distal flare	1.6–2.3	5–7	Yes, simple, large	Arrowhead	Multi-keel, wide lateral projections	Tall tri.	Tight polyp placement, true bb., lateral projections to marg. keel
<i>T. chilensis</i>		bb.	Isolated, 11–23	45–80°	Modest distal flare, stout	2.5–2.75	6–8	Yes, multi-keel	tri. to arrowhead	Lateral projections	tri.	Clustered polyps, ornate scale distal edges
<i>T. crenelata</i>		bb., uniplanar appearance	Isolated, 5–11, 8–19 at tip	60–90°	Clavate	2.3–3	6–10	Yes, single, large	Lanceolate to arrow-headed	Multi-ridged, lateral ridges	Fan with curved or pointed distal edge	Large serrate distal edges on sclerites
<i>T. parachilensis</i>		bb., colony flabellate	Isolated, 18–48 at tip	45–90°	Clavate, bulbous	2.5–2.8	8–15	Yes, simple, multi-keel	Arrowhead/lanceolate	Simple with adjacent ridges	Elliptical with pointed distal edge	Bulbous polyps in 'barrel' clusters at tip
<i>T. variabilis</i>		bb.	Isolated, 5–10	60°	Distally flared	1.5–1.85	4–5	Yes, simple, flat faced	Isosceles triangles	Channelled	Tall tri., spinose	Spinose keeled marg.
<i>T. hicksoni</i>		bb.	Isolated, 16–22	30° to appressed	Modestly flared, oper. pointed	1–1.25	4–5	Yes, striations or simple keel	Tongue-shaped	Channelled	Tear-shaped	Small, clustered polyps, tongue operculars
<i>T. pendulina</i>		bb.	Isolated, 27–41	Appressed	Modestly clavate, pointed operculum	0.9–1.2	4–5	Yes, simple	tri./lanceolate	Modest simple keel	Short tri. to diamond	Small, clustered polyps, pointed operculars
<i>T. minuta</i>		bb.	Isolated, 11–18	Appressed	Tapered distally	0.7–1	3–4	Yes, simple	Isosceles tri./spoon-shaped	Simple to single channelled	Round to diamond-shaped	Very small polyps
GROUP 2 Paired / whorled polyps		Colony shape	Polyp arrangement & distribution	Polyp angle from branchlet	Polyp shape	Polyp height	No scales in LAB	Opercular keeled?	Opercular shape	Marginal keel		Unique characters/ Comments
<i>T. hilgendorfi</i>		Uniplanar flabellate colony, irregular dichot. branching, bb. branches	Pairs/ whorls of 3	45°	Distally flared	1–1.4	6–7	No	Tri.	Channelled	Tall triangle, spinose	Branches bb., short, sturdy branchlets
<i>T. grasshoffi</i>		Colony taller than wide, true bb.	Paired/ rare whorls of 3, 7–8	45–60°	Modest distal flare	max. 1.3	5	Yes, ridges/ striations	Isosceles tri.	Simple, sometimes with lateral projections	Broad base, tear-shaped	True bb.
<i>T. laxa</i>		bb., appears uniplanar pinnate	Paired/ whorls of 3, 5–7	45–60°	Distally flared	1.2–1.5	5–6	No, rare striations	tri., appear tongue-shaped	Simple, single channelled	Tall tri., circular to diamond base	Branches bb., flexible, long branchlets
<i>T. moseleyi</i>		Uniplanar pinnate	Paired	90°	Clavate with tall conical oper.	1.5	4–5	Yes, simple	Thin to wide lanceolate	Keeled abaxial marginal, remainder with ridges	Diamond	Polyps clavate, 90° from branchlets
<i>T. tydemani</i>		Uniplanar, alternately pinnate	Paired/ rare whorls of 3, 6/cm	80–90°	Distally flared	~1.5	~5	?	?	? simple, channelled	Tall tri., spinose	Ridged distal edge of body-wall scales
<i>T. parva</i>		Uniplanar, dichot.	Paired, 6/cm	45°	Tapered distally, conical	~1	5–6	Yes?	Lanceolate	?	Irregularly triangular?	Polyps tapered distally, inclined 45°
<i>T. coronata</i>		Uniplanar, dichot./sympodial branching	Paired/ rare whorls of 3, 5–7	90°	Distally flared	1.9–2.1	5–6	No	tri./lanceolate	Small, multi-keel	Equilateral tri.	Polyps distally flared, inclined 90°
<i>T. biserialis</i>		Uniplanar, dichot.?	Paired/ rare whorls of 3	45°	Clavate	1.2–1.5	6–7	No	Lanceolate to wide tri.	Multi-keel	tri.	Polyps clavate, 45° to branchlet

*type species of genus

LAB – longitudinal abaxial row

Abbreviations: sm. – small, oper. – operculum, marg. – marginal, submarg. – submarginal, ab. – abaxial, bb. – bottlebrush colony morphology (3 or more directions of branching), dichot. – dichotomous branching, tri. – triangular. 'Tip' refers to branchlet tip.

Species descriptions

All species descriptions are based on the holotype unless otherwise stated. Species are ordered first by group and then according to chronological precedence. All images of sclerites are of the holotype, paratypes, or syntypes, unless otherwise noted.

Systematic Account

Subclass Octocorallia

Order Alcyonacea

Suborder Calcaxonia Grasshoff, 1999¹

Family Primnoidae Milne-Edwards, 1857

Thouarella Gray, 1870

Primnoa Valenciennes, 1846: pl. 12, figs 2, 2a (only images); Milne-Edwards 1857: 140; Gray 1857: 286; 1859: 483; Kölliker 1865: 135

Thouarella Gray, 1870: 45; 1872: 746; Studer 1878: 649; 1887: 50; (in part), Wright & Studer 1889: 59–61 pl. 11, 14; Versluys 1906: 22–24; Thomson & Henderson 1906: 38–41 (comparison table); Kükenthal 1907: 202–208; 1908: 10–11; 1912: 292; (in part) Bayer 1961: 294 (key to genus); 1981: 936 (key to genus); Broch 1965: 24; Stibane 1987: 17–26, pl. 1(4), 2(4); Williams 1992: 277

Rhopalonella Roule, 1908: 2–3, pl. 1, figs 5–8

?*Hookerella* Gray, 1870: 45

Thouarella (*Diplocalyptra*) Kinoshita 1908b: 454, 457 (key to subgenus), pl. 17, fig. 2 (in Japanese, English translation at USNM); 1908c: 517–519 (in Japanese, English translation at USNM); 1908d: 52 (key to subgenus, in German)

Not *Primnodendron* Nutting 1912: 71–72, pl. 9, fig. 2, 2a; pl. 19, fig. 4

Thouarella (*Epithouarella*) Kükenthal 1915: 150–151 (key to subgenus and species); 1919: 435 (key to subgenus and species); 1924: 299 (key to subgenus and species); Bayer 1956: F220

Thouarella (*Euthouarella*) Kükenthal 1915: 149–150 (key to subgenus and species); 1919: 414–415 (key to subgenus and species); 1924: 292 (key to species); Bayer 1956: F220; Bayer & Stefani 1989: 455 (key to subgenus); Cairns 2006: 176, 187–188

Thouarella (*Parathouarella*) Kükenthal 1915: 150 (key to species); 1919: 425–426 (key to species); 1924: 296–297 (key to subgenus and species)

Thouarella (*Thouarella*): Bayer 1956: F220; Bayer & Stefani 1989: 455 (key to subgenus); Cairns 2006: 176

Definition

The colony consists of a main stem, generally simple with rare divisions. Branching is either pinnate, dichotomous, or in a bottlebrush manner (where it is branched in at least 3 directions). Polyps are isolated, paired, or in whorls, generally upwardly inclined at 45–90° from the branchlet. Polyp heads are wider than the base and completely protected by 5–8 rows of longitudinally arranged scales each of 5–15 (generally 5–8) scales. Adaxial body-wall scales are often reduced in size and number.

A well-developed, conical operculum consists of 8 operculars; on rare occasions accessory operculars are found beneath the operculum. Opercular scales are lanceolate, arrowhead-shaped, or tongue-shaped, often with a keel. The operculum is surrounded by 8 marginals, often in 2 alternating rings of 4 because the operculum circumference is not large enough to accommodate 8 adjacent marginals. Marginals are keeled on their inner surface; keels are simple, channelled, or a complex multi-keel. Marginals often fold over the operculum, with the keel fitting into the concave outer opercular surface. Opercular scales are lanceolate, arrowhead-shaped, or tongue-shaped, often with a keel.

Distribution

A wide global distribution: South Africa, Chile, western Atlantic from Burdwood Bank to northern Florida, Japan, Aleutian Islands, Australia, Tasman Sea, New Zealand, especially common around Antarctica/sub-Antarctic. Found from 60–2100 m depth.

1. Calcaxonia are not monophyletic in recent phylogenetic studies (McFadden *et al.* 2006; Taylor *et al.*, in prep), however a taxonomic revision has not been completed.

Comparisons

Thouarella was placed close to three genera within the most recent phylogenetic morphological analysis of Primnoidae (Cairns & Bayer 2009): *Pyrogorgia* Cairns and Bayer, 2009; *Amphilaphis* Studer and Wright, in Studer, 1887; and *Convexella* Bayer, 1996. The bottlebrush form of *Thouarella* can also be easily mistaken for several other genera with similar branching morphologies.

Species of *Convexella* have marginal scales with a smooth inner surface whereas those of *Thouarella* have a keel.

The only species of *Thouarella* that may be described as having the distinctive “radiating spinose ridges” (Cairns & Bayer 2009) found on the outer surface of body-wall scales of *Pyrogorgia*, is *T. striata*. However, the polyps of the latter are isolated and the colonies bushy, which is very unlike the uniplanar, dichotomous colony shape and polyp whorls of *Pyrogorgia* species, making *Thouarella* and *Pyrogorgia* clearly distinct.

According to Cairns and Bayer (2009) *Amphilaphis* differs from *Thouarella* in having polyps with eight ‘complete’ rows of body-wall scales, whereas the two adaxial rows of body-wall scales in *Thouarella* are relatively reduced in size. This scale size reduction is a particularly difficult character to quantify. *Amphilaphis* species are not considered within this revision as it was written prior to the recent revision of the genus *Amphilaphis* (Zapata-Guardiola & López-González, 2012).

Thouarella is most closely related, in terms of polyp morphology, to *Plumarella* and *Amphilaphis*. Species of *Plumarella* are uniplanar, often plumose, whereas only six species of *Thouarella* are truly uniplanar, although some bottlebrush arrangements are compressed giving a uniplanar appearance (e.g. *T. brucei*). The polyps of *Plumarella* species are usually placed in an alternately biserial manner (there are a few species with isolated polyps), whereas within *Thouarella* only *T. bipinnata* Cairns, 2006, *T. minuta*, and *T. koellikeri* have polyps that are approximately biserial. Marginal scales of *Plumarella* species are fixed, i.e. do not fold over the operculars (although this is a difficult character to judge, especially in species with long marginals, e.g. *T. variabilis*). Species of *Plumarella* have eight rows of body-wall scales; the number of scales in a row can be reduced adaxially, which is very similar to *Thouarella*. Polyps of *Plumarella* often stand at 90° to the branchlet, whereas those of *Thouarella* are mostly at 45–80°. All of these characters are not exclusive to either *Thouarella* or *Plumarella*. The only diagnostic character to separate the two genera is the presence or absence of keeled marginals; a keeled marginal is considered a character of *Thouarella*, unkeeled is *Plumarella* (Cairns 2010).

As already mentioned, there are a number of genera with bottlebrush colonies that are often mistaken for *Thouarella*. The similarities and differences between these genera and *Thouarella* are listed below:

Colonies of *Dasystenella* Versluys, 1906 have a bottlebrush formation and are often misidentified as *Thouarella*. *Dasystenella* primarily differs from *Thouarella* in having polyps with just five marginal scales, compared to eight in the latter. Only one species of *Dasystenella* has been described (*D. acanthina*) yet much variation was observed amongst specimens seen throughout this study. *Dasystenella* requires further investigation as there is likely more than one species (Cairns 2006).

Although it has a bottlebrush colony shape, the newly described genus *Tauroprimnoa* Zapata-Guardiola & López-González, 2010 differs from *Thouarella* in having polyps with only four marginals.

The recently described bottlebrush genus *Digitogorgia* Zapata-Guardiola & López-González, 2010 has marginals with a smooth inner surface and numerous irregular longitudinal rows of body-wall sclerites and is thus distinct from *Thouarella*.

Fannyella (*Scyphogorgia*) Cairns and Bayer, 2009 also has a bottlebrush form and is separated from *Fannyella* (*Cyathogorgia*) Cairns and Bayer, 2009 only by branching morphology (the latter being dichotomously branched, verging on pinnate). *Fannyella* Gray, 1872 has ascus-type body-wall scales, which have a distinct boundary separating their exposed distal area from the covered proximal area, whereas *Thouarella* has even, unsectioned, non-ascus body-wall scales.

Colonies of *Parastenella* Versluys, 1906 are mostly uniplanar, however, they can be bushy with isolated, paired, or whorled polyps and could be easily mistaken for *Thouarella*. The most distinctive difference between these two genera is the morphology of the distal border of the marginal scales of the polyps; marginal scales of *Parastenella* polyps have a fluted hollow structure whereas those of *Thouarella* are unfluted.

Species Group 1—isolated polyps

1. *Thouarella antarctica* (Valenciennes, 1846)

Figs 4, 5.

Primnoa antarctica Valenciennes, 1846: pl. 12, figs 2, 2a (only images); Milne-Edwards 1857: 140; Gray 1857: 286; 1859: 483; Kölliker 1865: 135; Bayer 1956: F220 (list).

Thouarella antarctica Gray 1870: 69; Wright & Studer 1889: 65–66, pl. 21 fig. 1; Thomson & Henderson 1906: 38 (list); Gravier 1914: 48–56, pl. 7 figs 31–34, pl. 10 figs 52–55 (samples not seen); Molander 1929: 75 (samples not seen)

Not *Thouarella antarctica* Hickson 1907: 9–10, pl. 2, figs 19, 24 (= unknown)

Thouarella (*Parathouarella*) *antarctica* Kükenthal 1915: 150 (key); 1919: 433–435; 1924: 299

Not *Thouarella* (*Euthouarella*) *antarctica* Broch 1965: 24–26, pl. 2, figs 5–7 (= *T. pendulina*)

Not *Thouarella* (*Thouarella*) *antarctica* Cairns & Bayer 2009: 27 (listed), 33–34, fig. 6g–l (= *T. chilensis*)

Material examined: **Holotype**, MNHN, Oct.0000–208, 1836–1839 *Venus* expedition, Malouine Islands, Falkland Islands, depth unknown.

Other material: ZMH, R/V *W. Herwig*, sta. 270, south of Falkland Islands, SW Atlantic, 53°00'S, 60°00'W, 375 m, 9 Feb 1971; ZMH, R/V *W. Herwig*, sta. 256, Burdwood Bank, SW Atlantic, 53°56'S, 63°40'W, 400 m, 6 Feb 1971; ZMH, R/V *W. Herwig*, sta. 311, off Patagonia, SW Atlantic, 46°54'S, 60°28'W, 480 m, 18 Feb 1971; ZMH, R/V *W. Herwig*, sta. 361, west of Falkland Islands, SW Atlantic, 51°55'S, 61°50'W, 200 m, 12 Jul 1966; NHM89.5.27.43, H.M.S. *Challenger*, sta. 148A, off Crozet Island, 46°53'S, 51°52'E, 1005 m, 3 Jan 1874; USNM 97965, R/V *Hero*, cruise 715, sta. 870, 54°34'S, 64°W, 84 m, 24 Oct 1971.

Thouarella antarctica is the type species of *Thouarella*. Unfortunately, the holotype, held in MNHN, is in very poor condition. F.M. Bayer studied the holotype and identified one NMNH catalogued specimen as *T. antarctica* (USNM 97966). Having studied the holotype we disagree with Cairns and Bayer (2009) that USNM 97966 is *T. antarctica*; this is in fact *T. chilensis* as it has more scales in the abaxial row than is usual for *T. antarctica*, wider and thicker operculars, and marginal scales that are not smooth edged. Some additional specimens of *T. antarctica*, listed above, were found at SMF (belonging to ZMH). Description of sclerites and images herein are from three holotype polyps; no SEM images of whole polyps were taken as the specimen is too fragile and thus only an opercular view without a full complement of marginal scales was possible (Fig. 4e,f). Colony and polyp descriptions are from the specimens listed above.

Description

Colonies are sparsely branched. Branchlets depart the main stem in up to 5 directions from all sides of branches in a typical bottlebrush arrangement. The branchlets are generally simple, however some secondary branching occurs. The axis is yellow, tough, horny, and can be brittle towards the apex. The holdfast is calcareous.

Polyps are isolated, 1.6–2.3 mm high (average 2 mm), and modestly flared distally; they project from all sides of the branchlet at 60–80°, and are tightly placed at 11–23 polyps per cm (such that, in lateral view, most polyps overlap), and are more clustered at branchlet tip (25–30). Some polyps occur on the main stem. There are 5–7 scales in each abaxial row (Fig. 4c), 5–6 scales in lateral rows and 8 longitudinal rows reducing to 5 at the polyp base.

There are 2 circles of 4 operculars: one upper, one lower (Fig. 4e), and they can join to form a full cone, although sometimes there are gaps. Operculars are arrowhead-shaped (Fig. 5a–f), 415–820 µm high (average 650 µm), 200–480 µm wide (330 average µm), with a H:W of 1.7–2.1 (average 2) and have a longitudinally concave outer surface with granules radially arranged from a proximal centre, fading towards the distal edges. The inner opercular surface has a large, simple keel with several longitudinal striations, and the proximal half has densely arranged, small tubercles in the centre and serrated striations towards the distal edge. Lateral and distal edges are finely serrate; the proximal edge is coarsely lobate.

Marginal scales are triangular (Fig. 5g–i), broader than operculars, 645–870 µm high (average 760 µm), 390–750 µm wide (average of 600 µm), and with a lower average H:W than the operculars (1.3, ranging from 1–1.7). The inner surface of marginals bears a complex multi-keel with lateral extensions (Fig. 5j), which can project beyond the scale edges, and thus be visible from the outer surface; tubercles cover the inner surface proximally and are found across the keel base. The outer surface is covered with granules radially arranged from the central proximal area. The distal area of the keel and the lateral edge of marginals are finely serrated; proximal edges are coarsely lobate and covered with tubercles.

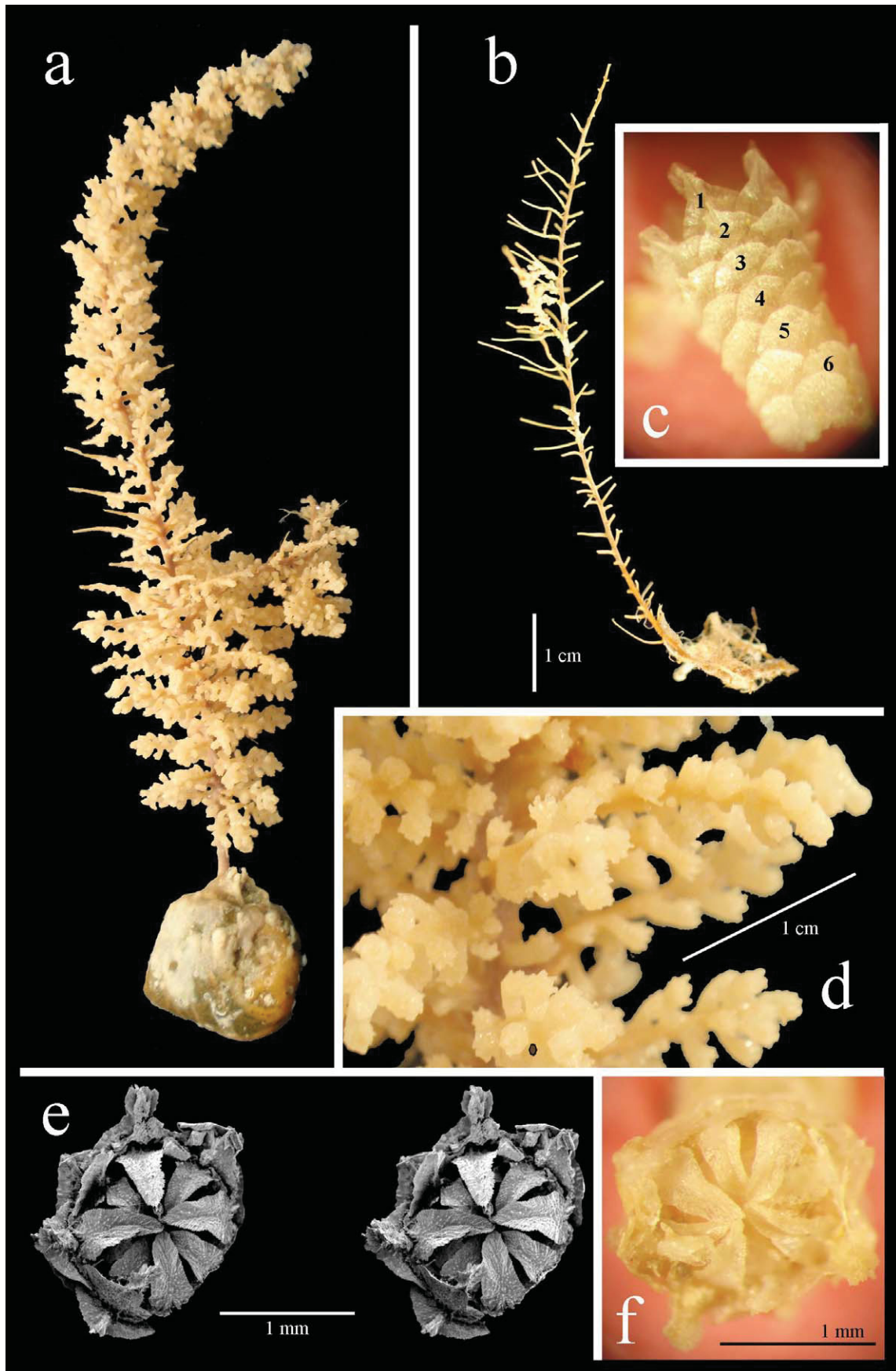


FIGURE 4. *Thouarella antarctica*. SMF, R/V *W. Hertwig* 1971, sta. 256: a) 21 cm colony; d) close up of branchlet. Holotype, MNHN, Oct.0000-208: b) holotype colony; c) abaxial polyp view; e) stereo opercular view of polyp, some marginals missing; f) opercular view of polyp with all marginals.

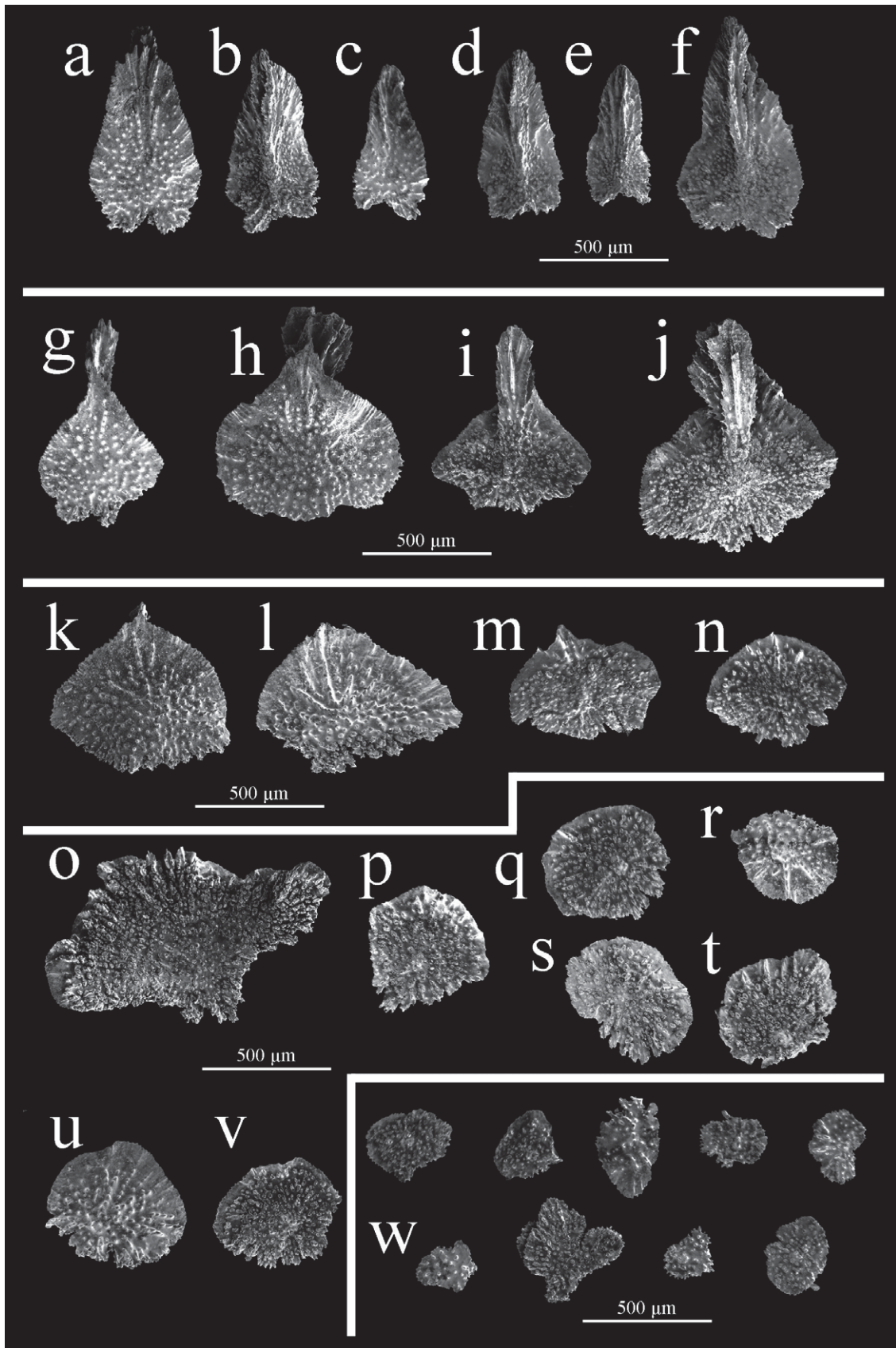


FIGURE 5. *Thouarella antarctica*, holotype, MNHN, Oct.0000-208: a,c) outer and b,d–f) inner surface of opercular scales; g,h) outer and i,j) inner surface of marginal scales; k,l) inner and m,n) outer surface of submarginal scales; o–q,s,t) inner and r,u,v) outer surface of body-wall scales; w) coenenchymal scales—inner surface top row first and second left, bottom row second left, remainder are of the outer surface.

Submarginals are circular to widely elliptical in shape (Fig. 5k–n), 430–650 µm high (average 760 µm), 370–750 µm wide (average 600 µm), with a H:W of 1–1.7 (average 1.3), and tend to have a pointed distal edge, and a small median distal keel (Fig. 5m) or teeth on the inner surface. The scales directly beneath the submarginals are also sometimes modified in the same manner.

Body-wall scales (Fig. 5o–v) form a variety of shapes from circular to elliptical. They are 380–460 µm high, 440–530 µm wide (average 420 and 500 µm respectively), usually wider than high, having an average H:W of 0.85 (range from 0.7–1), with small and sometimes strong ridges on the distal edge of the inner surface (Fig. 5o,t). Sometimes the abaxial body-wall scale at the polyp base is very wide (Fig. 5o). The inner body-wall scale surfaces are covered with dense tubercles and the outer surfaces sparsely covered with granules sometimes arranged radially from the central area.

The coenenchymal scales (Fig. 5w) are small, 160–330 µm high, 190–380 µm wide (average of 220 and 300 µm respectively), with a H:W of 0.4–1 (average 0.75), irregularly circular to oval in shape with a regular distribution of peaked granules on the outer surface, and a dense arrangement of tubercles on the inner surface. All polyp sclerites usually have an irregularly coarse, lobate proximal edge and a finely serrate distal edge.

Distribution

This species is known from 500 km north of the Falkland Islands to the southern tip of South America, from 200–480 m depth. An unseen sample has been described from Crozet Island (1005 m depth, Wright & Studer 1889), so the bathymetric range may extend deeper and the geographic range further east.

Remarks

The holotype is from the Falkland Islands and consists of one branch broken off mid-stem (Fig. 4b). The original description of *Thouarella antarctica* (as *Primnoa antarctica*) by Valenciennes has a beautiful illustration of the colony and polyps (see Fig. 1). Through a microscope, the operculars do appear elongated and the illustration reflects this, although it is exaggerated; the image is otherwise a good likeness. Descriptions thereafter rely heavily upon this drawing as well as Milne-Edwards' (1857) short description. Kölliker (1865) did give further details of body-wall scale dimensions (still under the name of *P. antarctica*), but Gray's (1870, p. 45) redescription as *T. antarctica* only gave a general description: "Coral simple, with long, simple filiform branches, spreading on all side of the stem. Bark formed in large imbricated scales. Polyp-cells smooth, bell-shaped, scattered on upperside of branches, covered with four or five series of imbricate scales."

Wright and Studer's (1889) description of *Thouarella*, alongside several new species, gives the first moderately detailed definition of the genus and more information about *T. antarctica*. Kükenthal (1915, 1919) correctly described *T. antarctica* as having marginal scales with lateral projections off the keel, and this remains one of the defining characteristics.

In 1924 Kükenthal listed *T. antarctica* as having nine or ten scales in the abaxial row but we believe this is a mistake, as he listed 4–6 abaxial scales in both his 1915 and 1919 keys.

A bottlebrush colony form, distally flared polyps, and complex multi-keeled marginal scales make *T. antarctica* just as representative of *Thouarella* as any species found within Group 1. Thus, *T. antarctica* is considered to be its type species.

Comparisons

As mentioned in the historical summary, the 'Köllikeri' (Kükenthal 1912) and 'Antarctica' groups (Versluys 1906; Kükenthal 1912) have very similar species. This includes *T. koellikeri* Wright & Studer, 1889, *T. variabilis*, *T. versluysi* Kükenthal, 1907, *T. striata* Kükenthal, 1907, *T. clavata* Kükenthal, 1908, *T. brucei* Thomson and Richie, 1906, and *T. hicksoni*, Thomson, 1911—the 'Köllikeri' group including species with isolated polyps and foliate, elongated marginals. In 1919, Kükenthal rearranged the entire genus, moving *T. antarctica* into the 'Köllikeri' group, as it has relatively tall marginals, leaving *T. crenelata*, *T. chilensis* and *T. affinis* in the 'Antarctica' group.

The polyps of *Thouarella crenelata* have marginal scales with distinctively serrate distal borders and a high number of scales in the longitudinal abaxial row and are thus quite different from the remaining 'Antarctica'/'Köllikeri' group species. *Thouarella koellikeri*, *T. viridis* Zapata-Guardiola and López-González, 2010, *T. antarctica*, and *T. chilensis* are all very similar, having isolated polyps larger than 1.5 mm and low triangular marginals. All of these species have very small differences in the number of body-wall scales in the abaxial row of the polyps and the complexity of the marginal keel. Although all species have a similar polyp size they vary in polyp density; the number of polyps per cm splits this group into two as *T. antarctica* and *T. chilensis* have very

clustered polyps, more than 15 per cm (up to double this in fact), whereas the remaining two species have lower polyp densities. *Thouarella antarctica* and *T. chilensis* are considered distinct from each other as the latter has polyps with operculars and marginals that have a heavily striated outer surface and a full opercular cone, all absent in *T. antarctica*. *Thouarella chilensis* also tends to have more scales in the abaxial row than *T. antarctica*. Both *T. koellikeri* and *T. viridis* have tall opercular cones and the latter has protruding toothed submarginals.

Thouarella koellikeri generally has longer polyps than *T. antarctica* due to the greater number of body-wall scales in the abaxial row (7–10 as against 5–7), and the operculars of the latter have simple keels whereas in the former there are several small striations adjacent to the keel. Also, the branchlets of the former leave the stem in mainly two directions, whereas *T. antarctica* has a true bottlebrush form.

The scales of the opercular cone of the polyps of *T. viridis* are more closely fitted than those of *T. antarctica*; and the former has shorter marginals that are less elongated, with wide lateral extensions of the keel that are rarely visible when viewed from the abaxial side of the polyp, something that is normal in *T. antarctica*. Also, the operculars of *T. viridis* have a larger, more pronounced keel than those of *T. antarctica*, the keel of the latter operculars being complex and spread laterally.

Several species have a similar number of longitudinal abaxial body-wall scales as *T. antarctica* and many were in the original ‘*Köllikeri*’ group and are thus compared here:

Thouarella variabilis differs from *T. antarctica* in having longer marginals, polyps that are more flared, and smaller, narrower, lanceolate operculars.

The polyps of *Thouarella brevispinosa* are generally longer than those of *T. antarctica*, and have more scales in the abaxial row. The marginals of polyps of *T. brevispinosa* are larger and have a longer, simple keel, lacking the lateral extensions common in *T. antarctica*.

The polyps of *Thouarella brucei* and *T. antarctica* are similarly shaped, but the marginal keels of the former are simpler with the inner and outer opercular scale surfaces tending to be smoother, the abaxial row with fewer scales, and colonies that can appear bilateral rather than bottlebrush, as in *T. antarctica*.

Thouarella striata has distinctive striations on the marginal scale inner surface that are absent in *T. antarctica*. In addition, the marginal scales of *T. striata* have a less complex keel (although not markedly), where the keel is not visible from an abaxial side view, and there are generally fewer scales in the abaxial row.

Thouarella clavata and *T. bipinnata* have polyps of a similar size as *T. antarctica* (the polyps of *T. bipinnata* are only slightly larger), however, polyps of *T. bipinnata* are clavate (*T. antarctica* has more splayed polyps) and its colony is uniplanar (whereas *T. antarctica* is bottlebrush). *Thouarella clavata* is bottlebrush (although branchlets sometimes bend creating a bilateral appearance) and has a similar number of abaxial scales as polyps of *T. antarctica*. However, the polyps of *T. bipinnata* are less densely arranged and branchlets are longer, narrower, and less rigid than those of *T. antarctica*.

Thouarella minuta polyps are under 1 mm tall making them considerably smaller than those of *T. antarctica*.

2. *Thouarella variabilis* Wright and Studer, 1889

Figs 6, 7

Thouarella variabilis var. a Wright & Studer, 1889: 68–69, pl. 21, fig. 1 (incorrectly listed as pl. 14, figs 1–2); Thomson & Henderson 1906: 40 (list)

Thouarella variabilis var. c *gracilis* Wright & Studer, 1889: 70; Thomson & Henderson 1906: 40 (list)

Thouarella variabilis Menneking 1905: 260–262, pl. 9, figs 9, 10, 21, 22 (samples not seen); Versluys 1906: 37–38; Gravier 1914: 56–61, pl. 1 fig. 6, pl. 3 fig. 13–14 (samples not seen); Kükenthal 1915: 150 (key); Molander 1929: 74–5 (samples not seen); Broch 1965: 30–31, pl. 6, figs 17–19; Brito, Tyler & Clarke 1997: 63–69

Not *Thouarella variabilis* Thomson 1927: 33, pl. 1, fig. 10 (=unknown)

Thouarella (*Parathouarella*) *variabilis* Kükenthal 1919: 428, fig. 202 (in text); 1924: 297 (key); Thomson & Rennet 1931: 27–30, pl. 7, fig. 3, pl. 9, figs 4–5 (samples not seen)

Thouarella aff. *variabilis* Kükenthal 1912: 305–306, figs 9–12 (in text), pl. 20, fig. 2

Thouarella (*Thouarella*) *variabilis typica* Cairns & Bayer 2009: 27 (listed)

Material examined: **Syntype** of *Thouarella variabilis* var. a, NHM 89.5.27.56, H.M.S. *Challenger*, sta. 145, SE of Prince Edward Island, 46°43’S, 38°4’30’’E, 256 m, 27 Dec 1873, 3.5 cm fragment seen; **Holotype**, *T. variabilis* var. *gracilis*, NHM 1889.5.27.55–56, sta. 145, SE of Prince Edward Island, 46°43’S, 38°4’30’’E, 256 m, 27 Dec 1873, 3.5 cm fragment seen.

Other material: USNM 76897, R/V *Eltanin*, Antipodes Island, New Zealand, 49°51'S, 178°35'E, 2010–2100 m, 26 Feb 1968, 1 colony; USNM 98226, R/V *Hero*, cruise 731, sta. 1842, west of Renaud Island, Biscoe Islands, Antarctic Peninsula, 65°30'S, 67°31'W, 180 m, 24 Feb 1973; USNM 1130283, R/V *Glacier*, cruise 1, sta. 5, 76°00'S, 55°00'W, 457 m, 9 Feb 1968, 2 colonies; SMF, EPOS 03, sta. 281, AGT21, 402 m, 18 Feb 1989; SMF, Am Twist, D. Sudpolar Expedition, 385 m, 1902.

Description of var. a typical

The main stem is simple. Wright and Studer (1889: pl. 21, fig. 1) recorded a specimen 300 mm long (which must have been damaged since as it now stands at 220 mm); its axis is brown-yellow and firm but brittle towards the base and more flexible distally. Branchlets leave the main stem in 3 to 4 directions; the fourth branch in a series is often in line with the first, in a spiral formation. Branchlets occur at intervals of 1.5–2.0 mm, at near right angles to the main stem; branchlets are 50–150 mm long, narrow, flexible, and frequently branched 2 or 3 times (usually dividing close to the stem in the proximal one third).

On the branchlets and stem there are wide, distally flared isolated polyps (Fig. 6b,d–f) which are upwardly inclined at 60° and arranged in irregular short spirals of 3 or 4 with 5–10 polyps per cm on the branchlets (sometimes more closely spaced at branchlet base). Polyps are 1.50–1.85 mm high (average 1.70 mm) including the long marginal point, with 4–5 scales in the abaxial row and 2–3 in adaxial rows; the number of longitudinal rows reduces quickly from 8 at the marginals to 4 or 5 at the base.

The polyps are sheathed in scales of 4 categories: 8 operculars, 8 marginals, 1 or 2 circlets of pointed submarginals and a variable number of body-wall scales.

The operculars do not form a perfect opercular cone and there are gaps into the opercular cavity (Fig. 6e). They are shaped like an isosceles triangle (Fig. 7a–c), range in size from 330–650 µm high (average 470 µm) and 150–370 µm wide (average 250 µm), with a H:W of 1.1–2.4 (average 1.9), which is just over half the size of marginals. The proximal half of the inner surface of the operculars are tuberculate; a flat-surfaced, relatively simple keel is present on the inner surface (Fig. 7c). The outer surfaces of the scales are covered with granules that extend radially from the central point in the proximal half.

The marginals are long, spinose (Fig. 7e–g), 650–960 µm in height (average 800 µm), 430–580 µm wide (average 520 µm), with an average H:W of 1.6, usually splayed out and too long to fold over the operculum neatly. Sometimes the abaxial 2 or 3 marginals are much longer than the adaxial ones (Fig. 6e). The outer marginal surface has 2 or 3 longitudinal furrows down the length of the elongated distal point and granules cover the remaining scale area (Fig. 7e,g). The keel is channelled and the base of the keel is tuberculate.

The submarginals have a pointed distal edge (Fig. 7h–k). They are wider than the marginals, with a width of 440–610 µm (average 525 µm), and a height of 520–600 µm (average 560 µm). They curve away from the polyp body (similar slant to marginals) and are thus visible from an anterior view (see Figs 6e, marked 1, and 6f).

The body-wall scales are round to elliptical in shape (Fig. 7l–n), larger and wider towards polyp head (average of 400 µm high, 485 µm wide, H:W 0.9), smaller and round towards polyp base (average of 325 µm high, 455 µm wide, H:W 1.2). The distal edge of the sclerites in all the above categories is finely serrate; proximal edge is irregularly lobate.

The outer layer of coenenchymal scales are elliptical (Fig. 7o,s,p), 190–320 µm high (average 240 µm), 590–750 µm wide (average 680 µm) with an average H:W of 0.35. The outer surface of these scales is covered in granules, the inner surface is tuberculate. The inner layer of scales are smaller, thin and roughly circular (Fig. 7q,r), with granules on the outer surface and a finely tuberculate inner surface. Coenenchymal scales generally have finely serrated proximal and distal edges.

Distribution

Circum-Antarctic, from 115 to 2100 m depth.

Remarks

Thouarella variabilis var. *a* (hereafter called *T. variabilis typica*) and *T. variabilis* var. *gracilis* Wright & Studer, 1889 have identical polyp shape and structure, and sclerite sizes and shapes. *Thouarella variabilis* var. *gracilis* is described as, what we interpret from Wright and Studer (1889), having more secondary and tertiary ramification than *T. variabilis typica*. However, there are varying degrees of ramification within a single colony and given the similar nature of all sclerites these two varieties are thus proposed to be synonymous with *T. variabilis*.

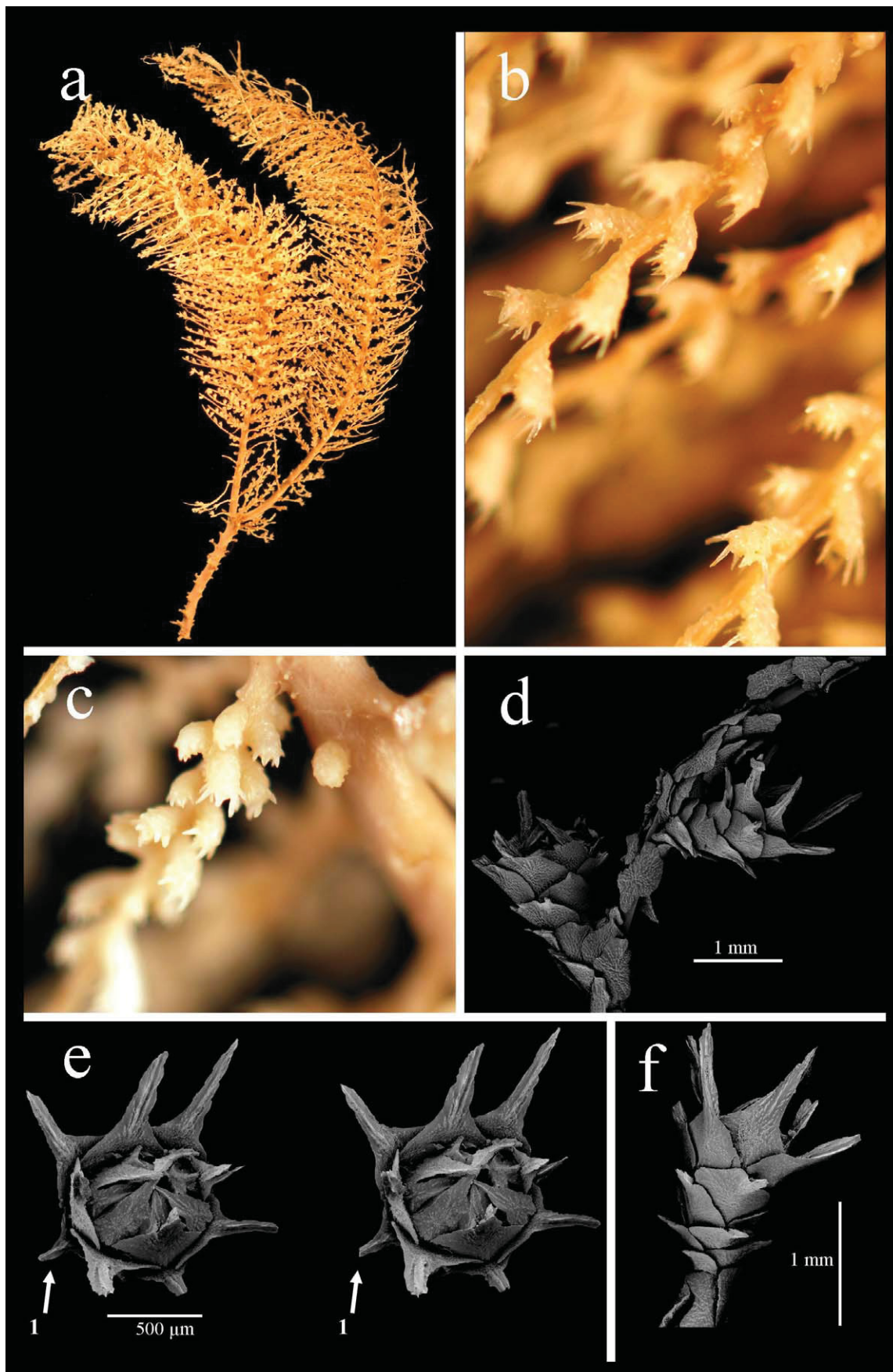


FIGURE 6. *Thouarella variabilis* var. a typical, syntype, NHM 89.5.27.56: a) syntype, 22 cm long; b) close up of several polyps; c) close up of brooding polyps; d) lateral view of two polyps; e) stereo opercular view, NB—1 indicates submarginal scale; f) abaxial polyp view.

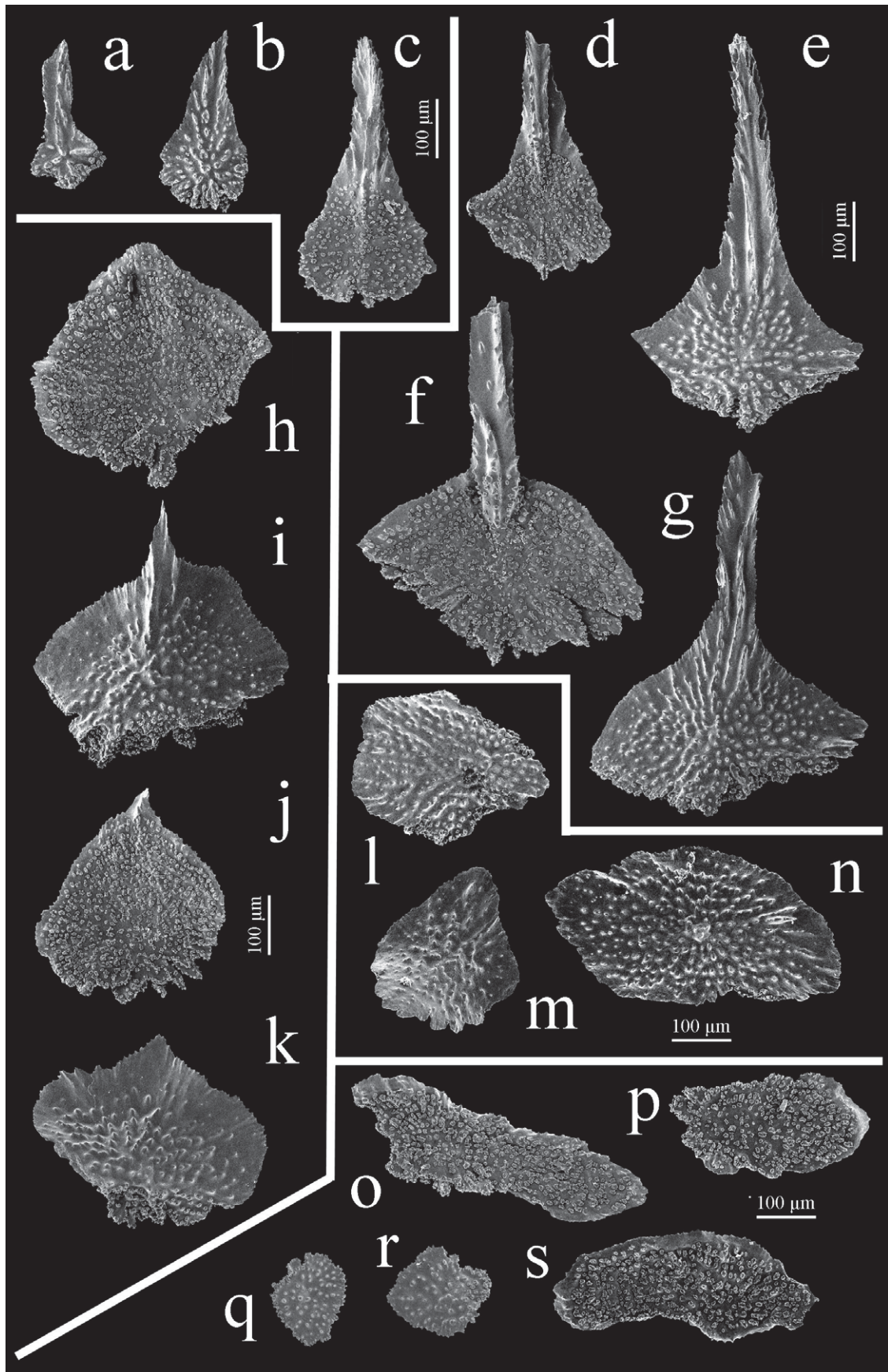


FIGURE 7. *Thouarella variabilis*, syntype, NHM 89.5.27.56: a,b) outer and c) inner surface of operculars; d,f) inner and e,g) outer surface of marginals; h,j) inner and i,k) outer surface of submarginals; l–n) outer surface of body-wall scales; o,p,s) inner and q,r) outer surface of coenenchymal scales.

Within the material examined, we found the branching of *T. variabilis* to occur in up to four directions (rather than three directions as noted in Wright & Studer 1889). Some juvenile colonies can appear almost pinnate (e.g. SMF, EPOS 03, sta. 281), although on closer inspection branchlets depart in three directions. Also, although there is some regularity with spiral branchlet placement, it is not consistent.

USNM 1130283 and SMF 'Am Twist' samples have smaller polyps than the holotype, their maximum length being 1.5 mm rather than 1.5–1.85 mm, but are otherwise identical.

The complex bushy bottlebrush shape of *T. variabilis* specimens make them ideal habitat for associates and worms, brittlestars, and ascidians were found within their branches.

True to its name, *T. variabilis* can have polyps that look dissimilar (Brito 1993); polyps with elongated claw-like marginals are shown in Fig. 6c (some of these polyps were brooding) and open, flared polyps (Fig. 6b) with elongated submarginals (Fig. 6b1) are also common.

Comparisons

Thouarella variabilis is unusual within the genus *Thouarella* in having elongated marginals that do not fold over the operculum neatly, and it is this character that makes this species distinct from all others. The species has a similar number of scales in the abaxial row as *T. pendulina*, *T. hicksoni*, *T. brucei*, and *T. striata* and comparisons to these species are made here:

Polyps of *T. pendulina* are much smaller and more clustered (up to 70 per cm) than those of *T. variabilis*.

Polyps of *T. hicksoni* are a similar size and have a comparable number of abaxial scales to those of *T. variabilis*, however, the isosceles triangle-shaped operculars in the latter differ from the operculars of the former which have a blunt, rounded distal edge (and operculars of *T. variabilis* which consequently form a tighter opercular cone). Also, *T. hicksoni* lacks elongated submarginals, although they can have a pointed distal edge.

Polyps of *T. brucei* are a similar size to *T. variabilis* but have wider triangular operculars.

Opercular, marginal, and submarginal sclerites of *T. striata* have densely arranged granules on their outer surface that could be confused with those on sclerites of *T. variabilis*. However, the inner surface of *T. striata* marginals have sharp striations running perpendicular to the distal edges; these are absent in *T. variabilis*.

Although now transferred to *Plumarella*, the species originally described as *Thouarella diadema* has polyps with 3–5 body-wall scales in the abaxial row and polyps of a similar-size and shape to those of *T. variabilis*. The major difference between these two species is that marginals of the former species lack a keel (the defining difference between *Plumarella* and *Thouarella*).

3. *Thouarella brevispinosa* Wright and Studer, 1889, new rank

Figs 8, 9

Thouarella variabilis var. *brevispinosa* Wright & Studer, 1889: 69; Thomson & Henderson 1906: 38 (list); Molander 1929: vol. 2, 74–5

Thouarella (Thouarella) var. *brevispinosa* Cairns & Bayer 2009: 27 (listed)

Material examined: **Holotype**, NHM89.5.27.54, 12 cm, H.M.S. *Challenger*, sta. 145A, 46°41'S, 38°10'E, off Prince Edward Island, 566 m, 27 Dec 1873.

Other material: ZMH, R/V *W. Herwig*, sta. 245, SW Atlantic, 36°49'S, 54°02'W, 550 m, 14 Jun 1966.

Description

The holotype consists of a single branch (Fig. 8a). The branchlets are mostly simple (some secondary, and even tertiary branching), the longest being 25 mm, arranged around the main stem in at least 4 directions, in a bottlebrush formation.

The polyps are large, 2.5–3 mm high, and isolated on branches and branchlets at wide intervals of 7–11 per cm. They are inclined at 60° and distally flared with splayed marginals (Fig. 8b–d). Each polyp has 6–7 scales in the abaxial row (Fig. 8c) and 7 longitudinal rows reducing to 4 at the polyp base. Scales of 4 categories cover each polyp: 8 operculars, 8 marginals, pointed submarginals and a variable number of body-wall scales.

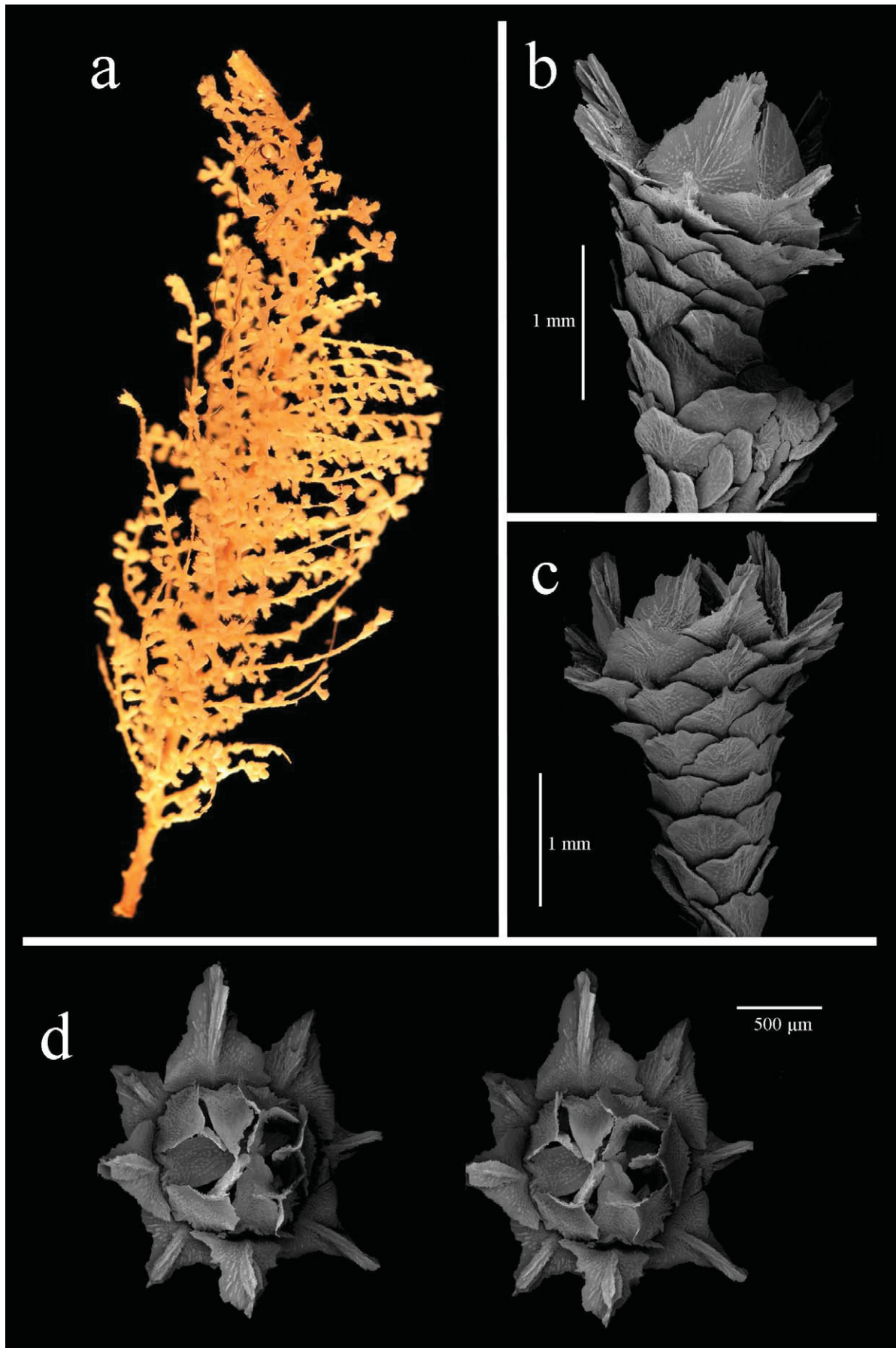


FIGURE 8. *Thouarella brevispinosa*, holotype, NHM89.5.27.54: a) 12 cm colony; b) lateral polyp view; c) abaxial polyp view; d) stereo opercular view.

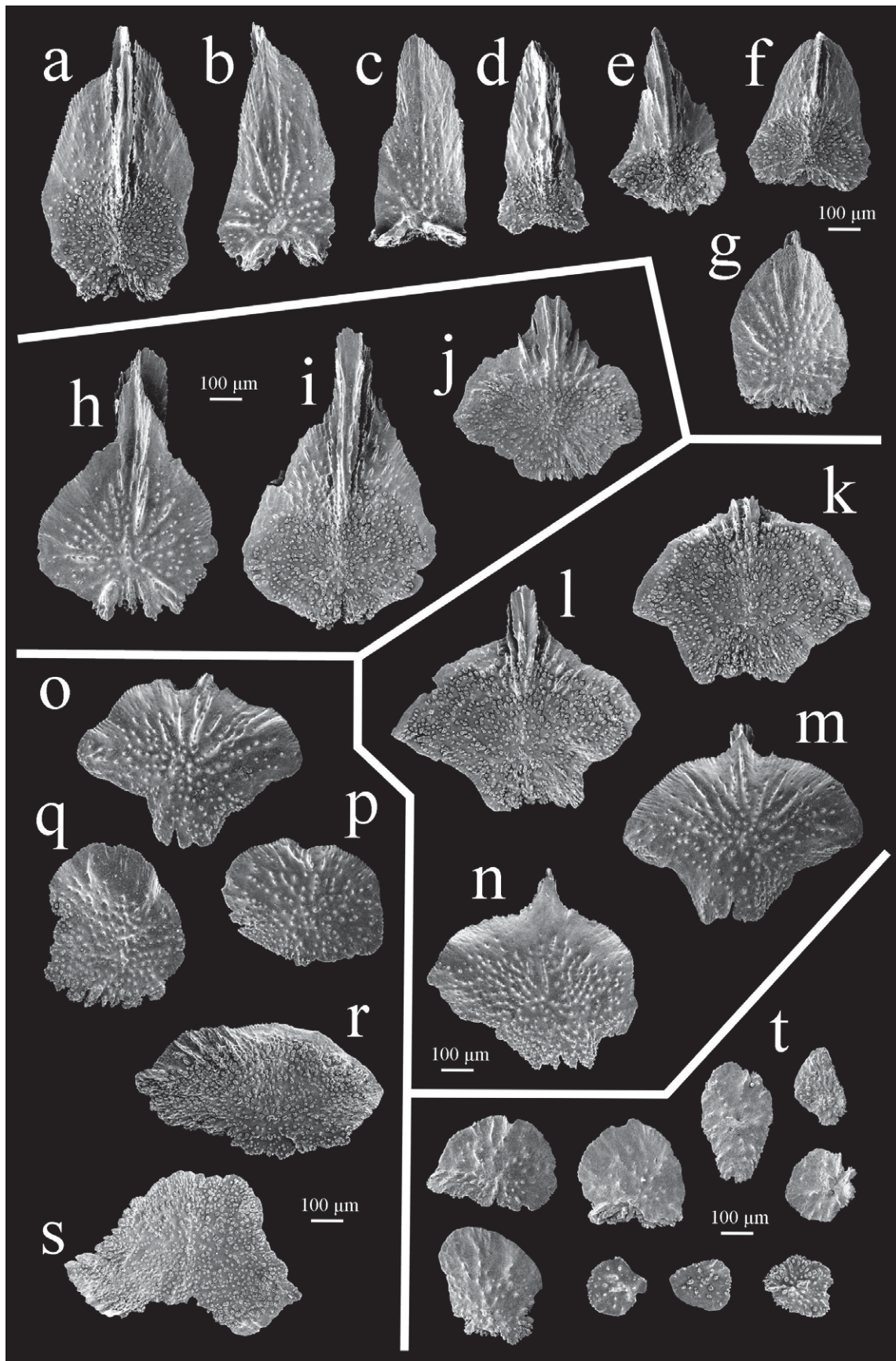


FIGURE 9. *Thouarella brevispinosa*, holotype, NHM89.5.27.54: a,d–f) inner and b,c,g) outer surface of opercular scales; h) inner and i,j) outer surface of marginal scales—the lateral and distal edges of j are eroded; k,l) inner and m,n) outer surface of submarginal scales; o–q) outer and r,s) inner surface of body-wall scales; t) coenenchymal scales—inner surface on top right and bottom three right scales, remainder show the outer surface.

The tips of the operculars meet in an apex to form a cone. The operculars are lanceolate, or isosceles triangle-shape with a squared proximal edge (Fig. 9f,g), to arrowhead shape (Fig. 9a–e; although sometimes they have a rounded distal edge, Fig. 9f,g). They are 270–770 µm high (average 540 µm) and 200–410 µm wide (average 310 µm), with a H:W of 1.2–2.1 (average 1.7). They have a single, large simple keel on the inner surface that is sometimes channelled with small lateral striations running parallel (Fig. 9a). The proximal half to third of the inner surface is tuberculate; the outer surface is longitudinally concave towards the distal edge and there are sparse granules and occasional fine striations in a radial pattern from the proximal area.

Marginals are 510–830 µm high (average 730 µm), 490–600 µm wide (average 530 µm), with a H:W of 1.0–1.6 (average 1.4). They have a broad angular base (Fig. 9i,j) and a central triangular distal projection (Fig. 9h). The inner scale surface is keeled, the keel having a single channel running longitudinally from the scale centre. There are 2–3 ridges parallel to the keel (more developed than in operculars) and tubercles cover the proximal area with a smooth band distally that has infrequent small ridges perpendicular to distal edge. The outer marginal surface has rows of granules radiating from the centre of the scale.

Generally there are 2 circlets of abaxial and lateral submarginals; the submarginals have a pointed distal edge (Fig. 9l–n) and a reduced keel on the inner surface (Fig. 9k, l). The adaxial submarginals have a more rounded distal edge, more typical of body-wall scales (Fig. 9k). Submarginals are wider than marginals, 550–690 µm (average 610 µm), 450–620 µm high (average 540 µm), with a H:W of 0.8–1.0 (average 0.9). The inner surface is tuberculate and the outer surface has sparse granules sometimes spread radially towards distal edges (Fig. 9m).

Body-wall scales are elliptical to circular (Fig. 9o–s) and similar in size to submarginal scales; their distal edge curves gently away from the polyp body. The inner surface is covered in tubercles and the outer surface with sparse granules; the proximal edge can also be covered in tubercles. The distal edges of all sclerites of this species are finely serrate; the proximal edges are irregularly lobate.

Coenenchymal scales are oval to round or angular in shape (Fig. 9t), 100–200 µm long or wide, with very sparse, irregular, granules on the outer surface; the inner surface is tuberculate.

Distribution

Known only from two locations: the type location off Prince Edward Island, and east of Buenos Aires, Argentina, approximately 7300 km away. Depth range is 550–566 m.

Comparisons

Colonies of *T. variabilis* var. *brevispinosa* have larger polyps with more scales in the abaxial row than those of *T. variabilis*. The former also has sparser branching and taller operculars with a more complete opercular cone than the latter. We thus propose this variety to be elevated to species rank, namely *Thouarella brevispinosa*.

The polyps of *T. brevispinosa* are distally flared and a similar size to the polyps of *T. antarctica* (comparison is made previously), *T. striata*, and *T. affinis* which are thus compared below.

The polyps of *T. affinis* have a similar number of scales in the abaxial row as those of *T. brevispinosa*, however, the majority of polyps in the latter have taller marginals that are more acutely elongate than the former, whose marginals are modestly pointed.

The size and shape of the marginals of polyps of *T. brevispinosa* and *T. striata* are very similar, however the inner surface of the marginals of the latter have robust striations flanking the keel whereas the former have fine striations. Sclerites of *T. striata* are thick; those of *T. brevispinosa* are more delicate. Also, tubercles on the scales of *T. striata* are more densely arranged and the polyps tend to be smaller.

The polyps of *T. brevispinosa* have fewer scales in the abaxial row than those of *T. koellikeri* and the abaxial marginals are taller and wider, creating a more flared polyp shape whereas the polyps of the latter are smaller and clavate.

4. *Thouarella affinis* Wright and Studer, 1889

Figs 10, 11

Thouarella affinis Wright & Studer, 1889: 66–68, pl.11, fig. 3; Thomson & Henderson 1906: 38 (list); Kükenthal 1912: 302 (listed)

Thouarella (Epithouarella) affinis Kükenthal 1915: 151 (key); 1919: 435–436; 1924: 300 (key)

Thouarella (Thouarella) affinis Cairns & Bayer 2009: 27 (listed)

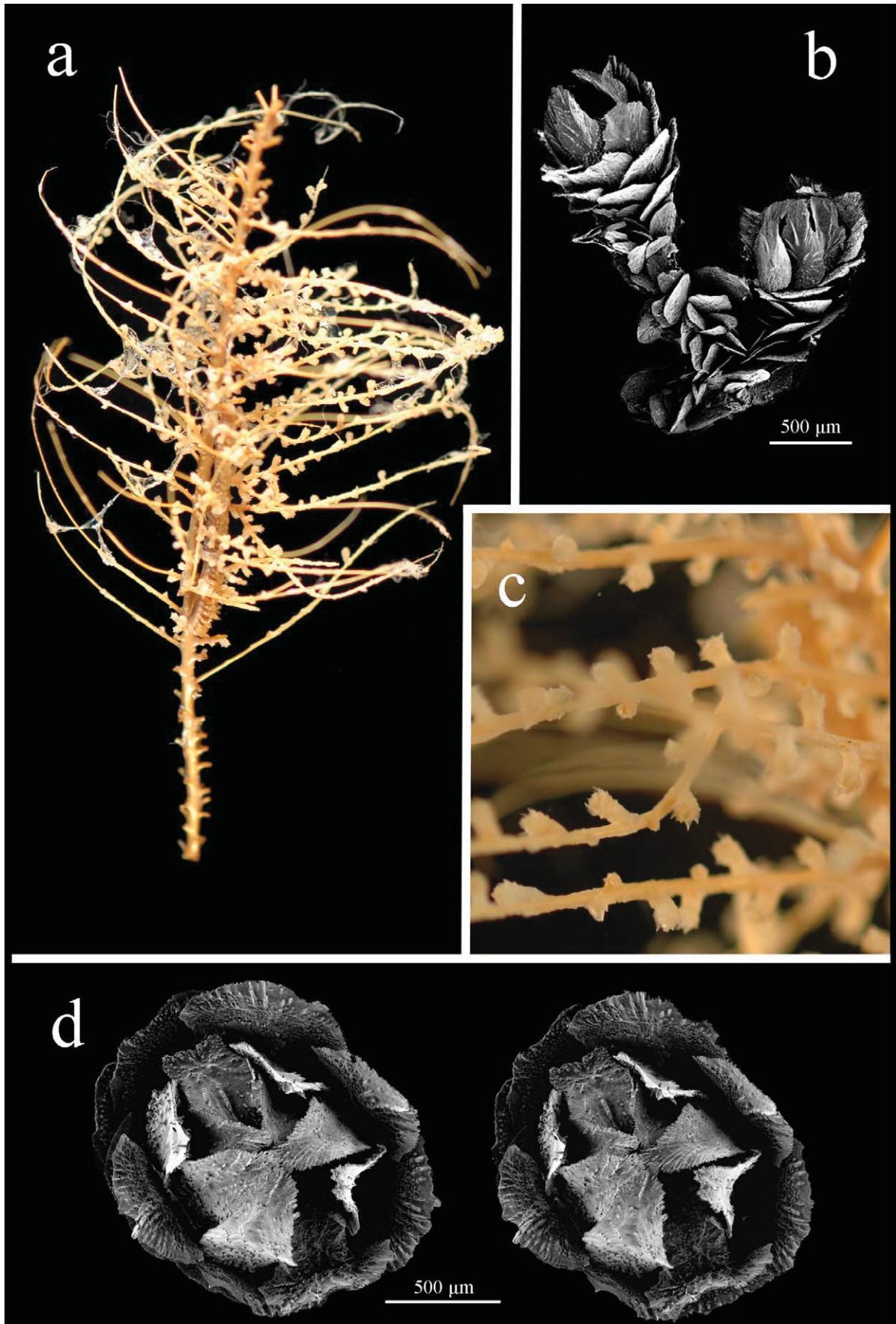


FIGURE 10. *Thouarella affinis*, holotype, NHM 1889.5.27.44: a) 13 cm long colony, with polychaete along stem; b) lateral polyp view; c) close up of polyps; d) stereo opercular view.

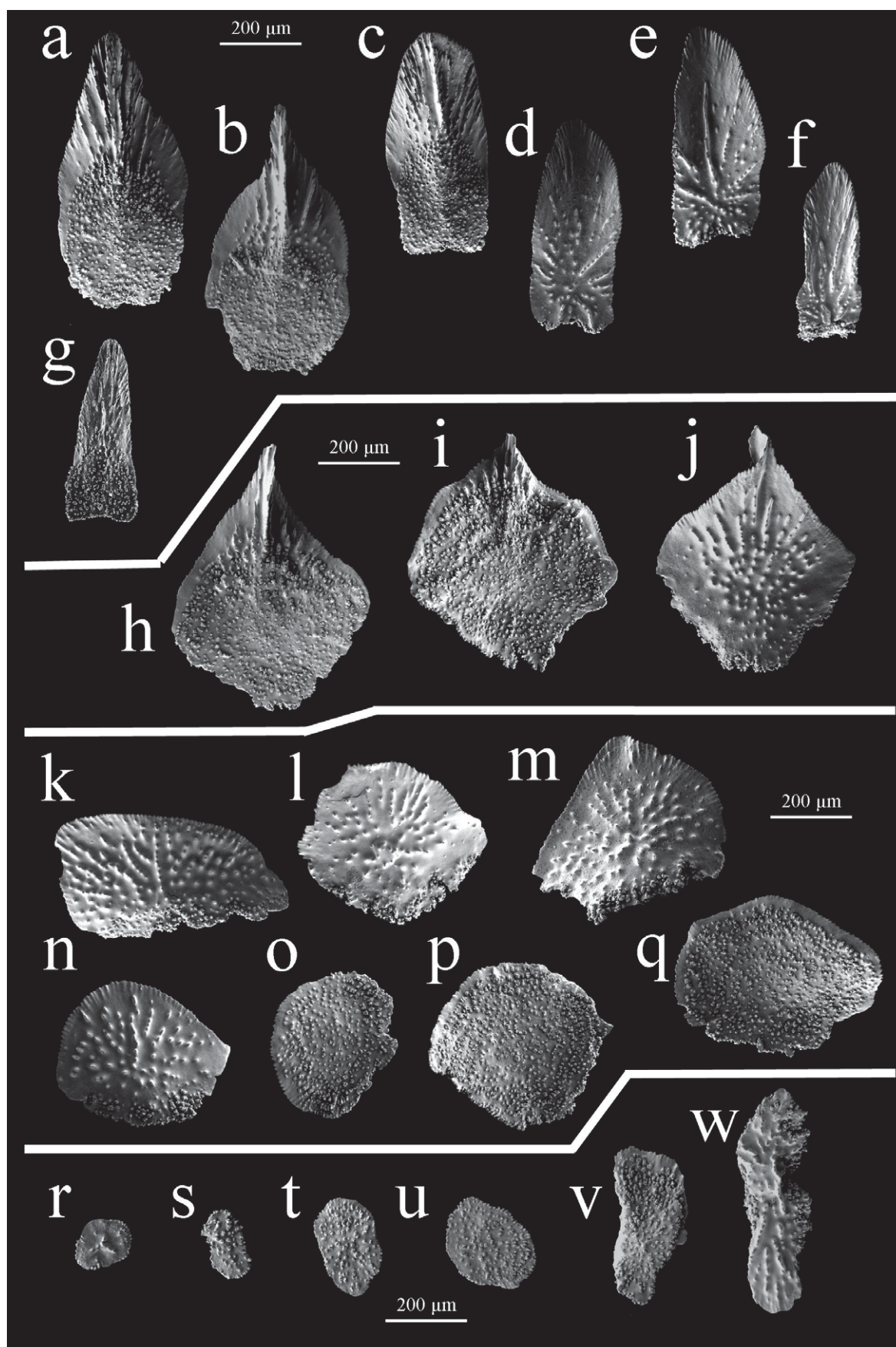


FIGURE 11. *Thouarella affinis*, holotype, NHM 1889.5.27.44: a–c,g) inner and d–f) outer surface of opercular scales; h,i) inner and j) outer surface of marginal scales; k–n) outer and o–q) inner surface of body-wall scales; r,w) outer and s–v) inner surface of coenenchymal scales. Some SEM images by ZGR.

Material examined: **Holotype**, NHM1889.5.27.44, 65 mm fragment, H.M.S. *Challenger*, sta. 135D, off Inaccessible Island, Tristan de Cunha, 37°25'S, 12°22'30"W, 91–128 m, 15 Jul 1874.

Other material: ZMH, R/V *W. Herwig*, sta. 232, east of Isla de los Estados, Tierra del Fuego, Argentina, SW Atlantic, 54°46'S, 62°30'W, 800 m, 1971.

Description

As only a small fragment was available, descriptions of axis and colony morphology were taken from the type description.

The colony is bottlebrush, (Fig. 10a) but can appear bilateral. The axis is yellow, stiff, and brittle, although the branch apex is more flexible. The stem twists in a spiral from base to a quarter-length from the apex whereupon the next twist commences.

The branching of this species is dense, with only 1.5–2 mm between branchlets; becoming denser towards the apex. The branchlets are mostly simple, with some forking (dividing usually in basal region of branchlet), upwardly inclined 60–90°, and up to 50 mm long. The branchlets are arranged in spirals from 3 sides of the main stem with 4 branchlets occurring within one spiral, but as the stem twists the spiral is difficult to follow.

The polyps are isolated, 1.1–2.1 mm high, at a density of 7–9 per cm (with denser placement at branchlet apex, which generally has a polyp at the tip). The polyps can be modestly flared but generally have a wide, rounded head extending from a slender polyp body making them clavate (Fig. 10b,c; H:W of 1.3–2.1, average 1.7). The polyps are arranged in short spirals of 3–4 and angled distally at 45–60°. Each polyp has 8 longitudinal rows with 6–7 scales in each abaxial row and 5 adaxially.

The tall rounded operculum rises above the marginal scales. The operculars are isosceles-triangle shaped (Fig. 11a,b), tongue-shaped (Fig. 11c–f), or lanceolate (Fig. 11g), 540–780 µm high (average 610 µm) and 220–350 µm wide (average 280 µm), with an average H:W of 2.2 (range from 1.8–2.5). The outer scale surface is longitudinally concave with granules across the proximal area and occasional low striations spreading radially from centre towards distal edge (Fig. 11d–f). The inner surface has a low, complex multi-keel (Fig. 11a,b), or a dense area of low striations (Fig. 11c); the proximal half of the scale is tuberculate.

The marginals are somewhat diamond-shaped (Fig. 11h–j), 460–610 µm high (average 525 µm) and 460–640 µm wide, with an average H:W of 1 (ranges from 0.8–1.3). The inner surface has a smooth band along the distal edge which is broken by a small, simple keel (Fig. 11h) with 2 or 3 adjacent striations whilst the remainder is tuberculate. The adaxial marginals frequently have no defined keel with just 4 or 5 short, sharp striations perpendicular to the distal edge (Fig. 11i). The outer surface is mostly smooth with some granules that often form radial striations (Fig. 11j).

The body-wall scales occur in a range of shapes from circular and irregular to elliptical (Fig. 11k–q). They are generally broader than high, 350–490 µm high (average 430 µm), 380–780 µm wide (average 540 µm), with an average H:W of 0.8 (ranges from 0.6–1.1), and curved slightly away from the polyp body. Tubercles cover the inner scale surface. Granules occur sparsely on the outer surface and sometimes tubercles occur along the proximal edge. The distal edge of all sclerites of this species is finely serrate whilst the proximal edge is irregularly lobate.

There is a single layer of roughly circular (Fig. 11r–u) or sometimes elongated coenenchymal scales (Fig. 11v, w) that are 190–280 µm high (average 225 µm), 230–430 µm wide (average 300 µm), with an average H:W of 0.8 (range from 0.4–1.1). There are large prominent granules on the outer surface of the scales and fine tubercles on the inner surface.

Distribution

This species is known only from the type location Tristan de Cunha, and also Inaccessible Island, mid-South Atlantic. The depth of observed occurrence is 91–800 m.

Remarks

The holotype material examined is damaged so the number of polyps per cm may be an underestimate.

Comparisons

Wright and Studer (1889) considered *T. affinis* to be very similar to *T. antarctica* and the polyps of these species do have a similar number of scales in the abaxial rows (6–7 *T. affinis*, 5–7 *T. antarctica*). However, the latter has a

more complexly structured marginal keel with large lateral projections compared to the modest keel found on marginals of the former.

The polyps of *T. viridis* are a similar shape and size to *T. affinis* and they also have similar shaped marginals, although those of *T. viridis* are slightly taller. However, the operculars of the polyps of *T. viridis* are pointed, while those of *T. affinis* are mostly tongue-shaped (with some triangular-shaped operculars with squared proximal edges). In addition, the body-wall scales of the former have more pronounced striations perpendicular to the distal edge (that are visible in lateral polyp view) than the latter.

The polyps of *T. affinis* are more rounded than those of *T. brucei*. The polyps of the latter also have fewer scales in the abaxial row and marginals that are narrower with a higher H:W ratio.

Polyps of *T. koellikeri* tend to be longer than those of *T. affinis*, with more scales in the abaxial row. Also, the former has pointed triangular operculars whereas those of the latter are mostly tongue-shaped.

5. *Thouarella koellikeri* Wright and Studer, 1889

Figs 12, 13

Thouarella Köllikeri Wright & Studer, 1889: 64–65, pl. 11 fig. 5; Thomson & Henderson 1906: 38 (list); Versluys 1906: 35
Thouarella (Parathouarella) köllikeri Kükenthal 1915: 150 (key); 1919: 435; 1924: 299
Thouarella (Thouarella) koellikeri Cairns & Bayer 2009: 27 (list)

Material examined: **Holotype**, NHM 1889.5.27.41 and USNM 1002247, which is a fragment of the holotype, H.M.S. *Challenger*, sta. 308, 50°08'30"S, 74°41'W, 320 m, 5 Jan 1876, 1 colony.

Other material: USNM 1112997, sample 5, Puyuhapi, Chile, South Pacific Ocean, 30 m, 10 Jan 2000, 2 colonies, no location information; USNM 1002247, sample 174, Chile, South Pacific Ocean, no location information, 25 m, 12 Mar 2006, 2 colonies; NHM (no catalogue number), H.M.S. *Challenger*, 51°27'30"S, 74°3'W, 730 m, 10 Jan 1856, fragment; SMF, R/V *W. Herwig*, sta. 245, SW Atlantic, 36°49'S, 54°02'W, 550 m, 14 Jun 1966; SMF, R/V *W. Herwig*, sta. 376, SW Atlantic, 43°23'S, 60°19'W, 100 m, 16 Jul 1966; SMF, R/V *W. Herwig*, sta. 311, Patagonian Shelf, SW Atlantic, 46°54'S, 60°28'W, 480 m, 18 Feb 1971; SMF, R/V *W. Herwig*, sta. 293, North Falkland Islands, 49°36'S, 59°25'W, 350 m, 13 Feb 1971; USNM 97997, R/V *Eltanin*, cruise 7, sta. 499, south of Coronation Island, South Orkney Islands, sub-Antarctic, 62°06'S 45°08'W to 62°06'S 45°10'W, 485 m, 20 Feb 1963, 7 colonies; USNM 98169, R/V *Eltanin*, cruise 6, sta. 339, west of Beauchene Island, Falkland Islands, sub-Antarctic, 53°06'S, 59°27'W, 512–586 m, 3 Dec 1962; USNM 98019, R/V *Eltanin*, cruise 12, sta. 1089, NE of Clarence Island, South Shetland Islands, Antarctic Ocean, 60°47'S, 53°30'W, 641 m, 14 Apr 1964; USNM 79475, R/V *Eltanin*, cruise 9, sta. 740, east of Cape Horn, Drake Passage, South Atlantic Ocean, 56°06'S, 66°19'W, 384–494 m, 18 Sep 1963; USNM 1130298, R/V *Hero*, cruise 721, sta. 1075, 64°47'24"S, 64°07'36"W, south of Anverse Island, Palmer Basin, Antarctica, 91–110 m, 23 Feb 1972.

Description

The holotype has one main branch off the stem (Fig. 12a). The branchlets are mostly undivided, leaving the main stem primarily in 4 directions. Two of the 4 directions are consistently around 120° apart, roughly alternately pinnate, and between these 2 rows of branchlets there is often another row of branchlets. These 3 planes/rows of branchlets depart on one side and there are occasional branchlets directly opposite, which tend to be short or broken, especially towards the colony base (possibly because of the reduced protection these branchlets receive). The arrangement of branching can appear pinnate, however, the branchlets are on all sides of the main stem in 4 directions, and thus the colony is bottlebrush.

The polyps are isolated and clavate with a rounded opercular cone (Fig. 12c,e). They emanate from branches and branchlets in a roughly alternating arrangement (Fig. 12b), 12–15 per cm (more clustered towards branchlet tip), upwardly inclined at 45–60° and are 1.6–2.5 mm high (average 2.2). The sclerites are in 8 longitudinal rows with 7–10 scales in abaxial rows (Fig. 12d) but reduced in number adaxially to only 5–7.

The scales on each polyp fit into 4 categories: 8 operculars, 8 marginals, 8 submarginals and many body-wall scales.

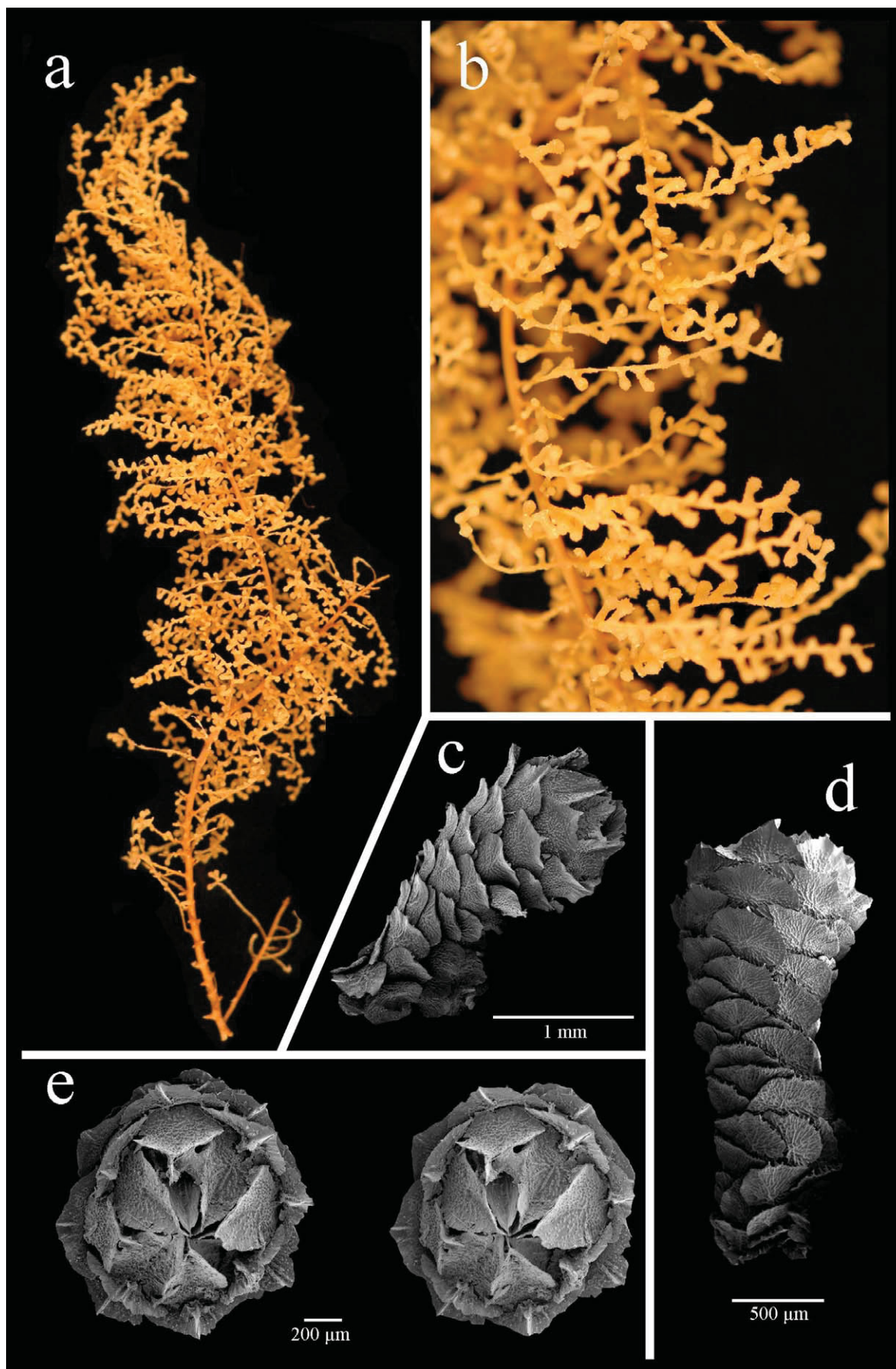


FIGURE 12. *Thouarella koellikeri*, holotype, NHM 1889.5.27.41: a) 19 cm long colony; b) close up of branchlet; c) lateral polyp view; d) abaxial polyp view; e) stereo opercular view.

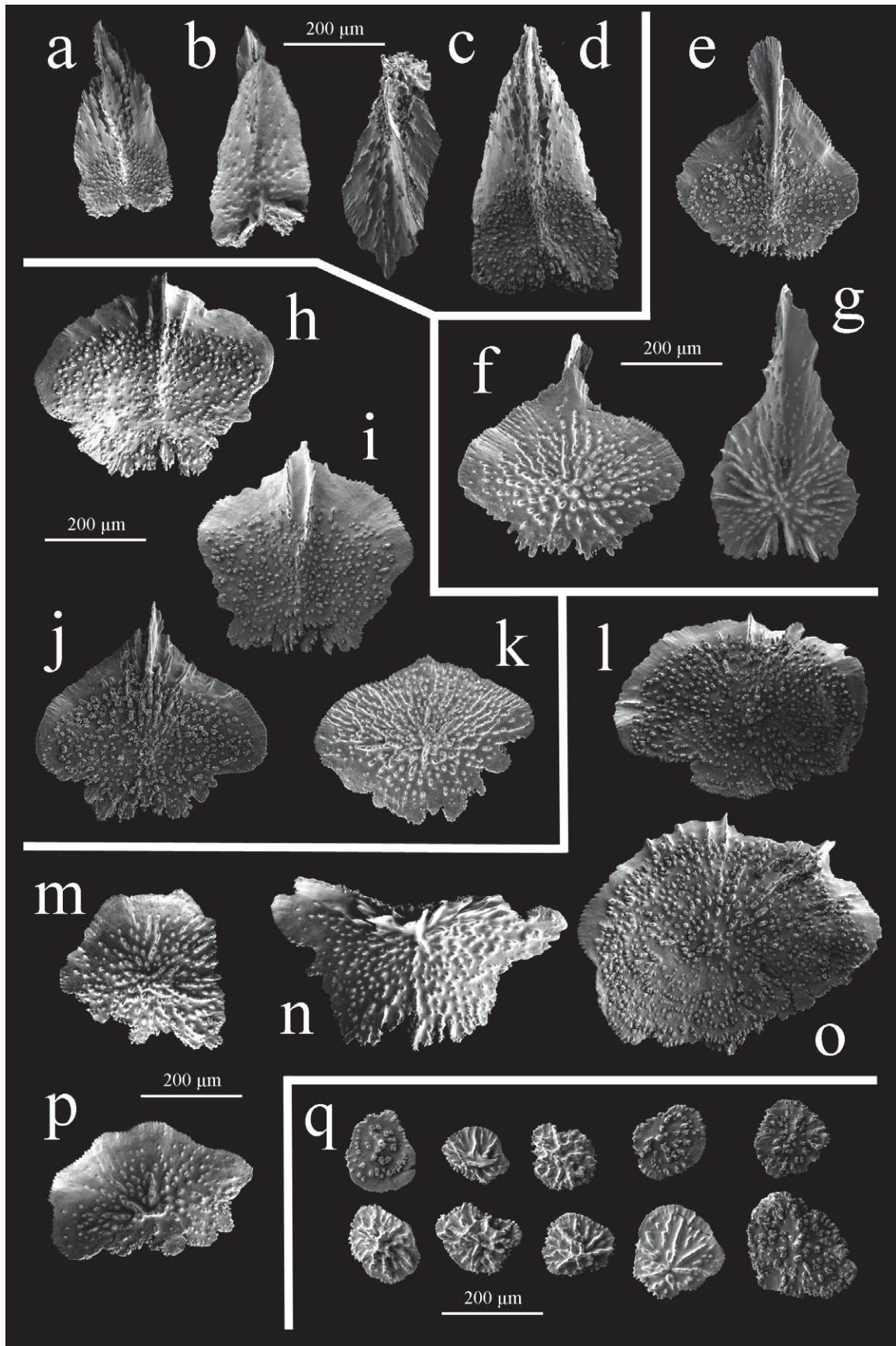


FIGURE 13. *Thouarella koellikeri*, holotype, NHM 1889.5.27.41: a,d) inner and b) outer surface of opercular scales; c) side view of opercular keel; e) inner and f,g) outer surface of marginal scales; h–j) inner and k) outer surface of submarginal scales; l,o) inner, and m,n,p) outer surface of body-wall scales; q) top left, fourth and fifth from left on top row and fifth on bottom row are of the inner surface of coenenchymal scales, the remainder are outer surface images. Some SEM by ZGR.

The operculars are isosceles triangle- (Fig. 13a,d) to arrowhead-shaped (Fig. 13b), 360–560 μm high (average 480), 180–350 μm wide (average 250), with an average H:W of 1.95. They have a large, single keel on their inner surface (side view of keel, Fig. 13c), with a corresponding deeply concave longitudinal outer surface (Fig. 13b). The proximal half of the inner surface is covered with small densely placed tubercles. The outer surface has granules that are often aligned to form striations arranged radially from the proximal third.

As the distal circumference of a polyp is not wide enough to accommodate 8 marginal scales they are arranged in 2 alternating circles of 4 with their lateral edges overlapping (Fig. 12e). The marginals fold over the operculars, fitting into their concave outer surface. The marginals are mostly triangular distally (Fig. 13e–g), and rounded laterally with a flat proximal edge. They are 420–580 μm high (average 480 μm), wider than operculars (340–520 μm , average 430), with an average H:W of 1.1. Abaxial marginals are more pointed than the adaxial. The inner surface bears a large keel usually with a single channel running its length and lateral projections (Fig. 13e). Tubercles are more widely spaced than on operculars but still cover the basal portion of the inner surface. The outer surface has granules in radial rows from the central proximal area that fade towards scale edges (Fig. 13g).

The submarginals are shorter than the marginals (Fig. 13h–k), 320–590 μm high (average 430 μm), 230–490 μm wide (average 430 μm), with an average H:W of 1. Generally the submarginals have a more rounded distal edge than the marginals. The submarginals are more pointed on the abaxial side of the polyp (Fig. 13h,j) than the adaxial (Fig. 13k). The scales proximal to the submarginals also sometimes have a modest distal point and a small keel on their inner surface. The submarginals differ from the marginals as tubercles cover a larger proportion of inner surface.

The body-wall scales arch slightly away from the polyp body and are of various shapes. They are often pentagonal with a rounded distal edge, or circular to elliptical (Fig. 13l–p), 280–520 μm high (average 390 μm), 220–600 μm wide (average 380 μm), with an average H:W of 1. The inner surface is tuberculate with a narrow smooth band distally that can bear a few small ridges (Fig. 13l,o) whilst the outer surface is covered in granules.

The coenenchymal scales are small, circular (Fig. 13q), 120–180 μm diameter (average 150 μm), with an average H:W of 1. The outer surface has radial striations from centre to the scale edge whilst the inner surface is tuberculate. The distal edge of all sclerites are finely serrate and the proximal edge irregularly lobate.

Distribution

This species has been found along the southern coast of Chile, Argentina, and off the Antarctic Peninsula from 91–1920 m.

Remarks

Contrary to Wright and Studer (1889), who described dorsal branchlets as simple and short (10–25 mm), some colonies have dorsal branchlets up to 51 mm long with similar polyp orientation and stem flexibility as the ventral and lateral branchlets.

Comparisons

Thouarella koellikeri most closely resembles *T. viridis*, as both have clavate polyps and a bushy, bottlebrush to bilateral appearance. However, the marginal scales of the polyps of *T. koellikeri* are high with a single-channelled keel, whereas those of *T. viridis* are shorter and have 2–4, and sometimes five, longitudinal ridges instead of a keel. Distal inner surface ridges are found on submarginal scales of the polyps of *T. viridis* whereas the polyps of *T. koellikeri* specimens tend to have a small, single keel on the submarginals of the first row. The polyps of *T. koellikeri* also have more scales in the abaxial row than those of *T. viridis*.

Versluys (1906) described the ramification of *T. koellikeri* as similar to that of *T. moseleyi* and the two species do have long, fine, flexible branchlets that could appear similar. However, the latter has pinnate, uniplanar colonies and the former has colonies that are bottlebrush to bilateral. Also, the polyps of *T. koellikeri* specimens are isolated while those of *T. moseleyi* occur in pairs.

Although most are modestly flared, some polyps of *T. antarctica* have a similar clavate shape to those of *T. koellikeri*, but the polyps of the latter tend to have more scales in the abaxial row (7–10, rather than 5–7). Also the marginals of *T. antarctica* are larger and bear a more complex keel than those found on the polyps of *T. koellikeri*. Lastly, *T. antarctica* has a true bottlebrush colony form whereas the branchlets of *T. koellikeri* colonies leave the main stem in two or three directions giving it a bushy to bilateral appearance.

The bushy appearance of colonies of *T. koellikeri* is similar to that of *T. bipinnata* however the former has polyps with a wider head and, when dried, the body-wall scales reflect away from the polyp body, something that is not seen in polyps of *T. bipinnata*. The polyps of *T. koellikeri* are also longer and narrower, with taller operculars, and marginals with a higher H:W ratio than those of *T. bipinnata*.

Thouarella koellikeri has similar sclerite shapes to both *T. brevispinosa* and *T. brucei*, however, colonies of *T. brucei* have distally flared polyps, fewer scales in the abaxial row, longer marginals bearing a more acute distal point, and flatter keels than *T. koellikeri*. *Thouarella brevispinosa*, although having a similar number of abaxial scales as *T. koellikeri*, has taller marginals and more flared, open polyps (see Table 3).

6. *Thouarella brucei* Thomson and Ritchie, 1906

Figs 14, 15

Thouarella brucei Thomson & Ritchie, 1906: 852–854, pl. 1 fig. 1, pl. 2 fig. 1; Kükenthal 1919: 439; 1924: 301

Thouarella versluysi Kükenthal, 1907: 202–203

Thouarella (Thouarella) brucei Cairns & Bayer 2009: 27 (listed)

Not *Thouarella brucei* Broch 1965: 27–28, pl. 4 (= *Digitogorgia* sp.)

Material examined: **Holotype**, NHM 1933.3.13.130, *Scotia* (Scottish National Antarctic expedition of 1902–04), Burdwood Bank or Gough Island, 102–182 m, 1 Dec 1903 or 22 April 1904; fragment of holotype, ZMA COEL03574; **Syntype** of *Thouarella versluysi*, MNHWU, D.T.E. sta. 103, South Africa, 35°10'S, 23°2'W, 500 m, two 2.5 cm fragments.

Other material: USNM 1130164, R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia, sub-Antarctic, 54°30'S, 39°20'W, 659–686 m, 8 Feb 1966, 6 colonies; USNM 98029, R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia, Antarctica, 54°29'S, 39°22'W, 659–686 m, 8 Feb 1966, 2 colonies (30 cm, 12 cm); USNM 98337, R/V *Eltanin*, cruise 21, sta. 290, west mouth of Strait of Magellan, Antarctica, 52°41'S 74°35'W to 52°45'S 74°28'W, 188–247 m, 6 Jan 1966, 3 colonies; USNM 98195, R/V *Islas Orcadas*, cruise 575, sta. 93, South Georgia Island, Antarctic Ocean, 54°38'48"S, 38°51'18"W, 261–270 m, 9 Jun 1975, 1 colony.

Description

The holotype is a rigid and sparsely branched colony (not shown). The main stem is robust and stiff although the smaller branchlets are more flexible. The axis is circular in cross-section and light yellow, with side branchlets an even lighter shade.

Branching occurs in up to 4 directions all around the main stem at irregular intervals. The branchlets emanate at 60°, and are upwardly inclined. Overall colony structure appears more bilateral than bottlebrush as the close-set branchlets curve into one plane. Secondary and tertiary branching of the branchlets is common.

The polyps are isolated, 1.5–2.3 mm high, with some occurring on the main stem, and arising in all directions on branchlets. There are 9–12 polyps per cm, modestly flared distally (Fig. 14a,c) and upwardly inclined at 40–45°. Each polyp has 7 longitudinal rows, with 4–5 scales in the abaxial row and 2–3 in the adaxial.

Two rings, the lower consisting of 4 smaller operculars, the upper of 4 larger operculars, form the operculum. Upper operculars align with the outer ring of marginals whilst the lower operculars align with the inner ring of marginals. The operculars range in size from 390–680 µm high (average of 510 µm), 170–330 µm wide (average of 250 µm), with a H:W of 1.5–2 (average 2). The operculars are arrowhead shaped with a rounded apex (Fig. 15a–e). The outer surface of operculars is longitudinally concave with sparse granules (Fig. 15a,b). Every opercular has a simple keel on its inner surface and is tuberculate proximally.

The marginals also occur in 2 rings, upper and lower. They are diamond-shaped (Fig. 15f–h), 490–760 µm high (average of 635 µm), 350–570 µm wide (average of 470 µm), with a H:W of 1.1–1.7 (average 1.4) in the holotype (smaller sizes in voucher specimens). The inner surface of the marginal scales has a complex multi-keel (Fig. 15f) sometimes with a flat central area. The inner marginal surface is tuberculate below the keel base whilst the outer surface has granules at the centre and is smooth towards scale edge.

The submarginals are diamond to oval-shaped, with an arched distal edge (Fig. 15j,i), 230–670 µm high (average 440 µm), 230–615 µm wide (average 380 µm) with a smaller H:W than the marginal scales (average of 1.14). The inner surface is tuberculate with a narrow smooth band along the distal edge whilst the outer surface has sparsely placed granules.

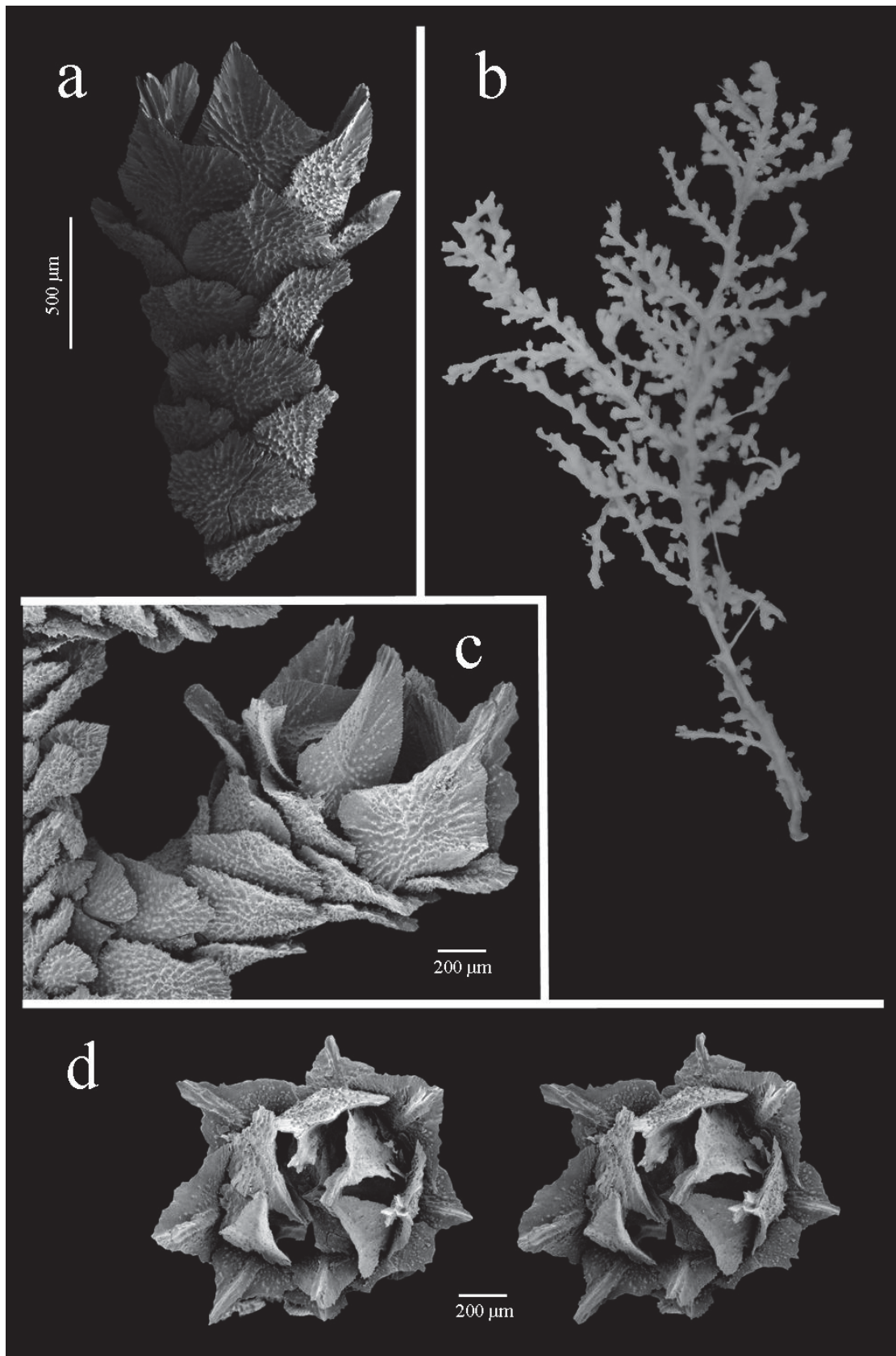


FIGURE 14. *Thouarella brucei*, holotype, ZMA. COEL03574: a) abaxial view of polyp; b) 6.5 cm long fragment of holotype; c) lateral view of polyp; d) stereo opercular view

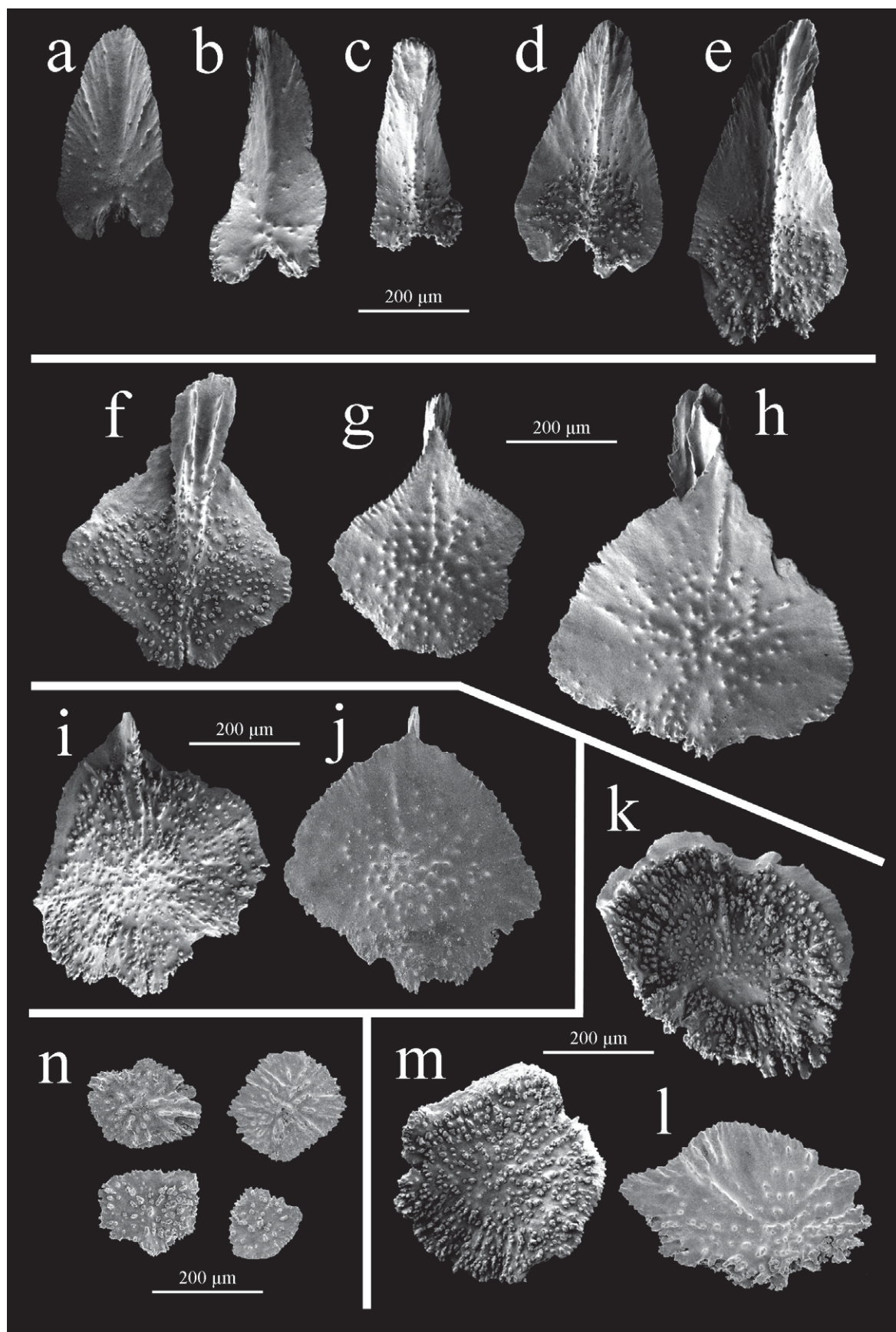


FIGURE 15. *Thouarella brucei*, holotype, ZMA. COEL03574: a,b) outer surface and c–e) inner surface of opercular scales; f) inner and g,h) outer surface of marginal scales; i) inner and j) outer surface of submarginal scales; k,m) inner and l) outer surface of body-wall scales; n) coenenchymal scales, top row outer surface, bottom row inner surface. Photo and some SEM by ZGR.

The body-wall scales are large (Fig. 15k–l), 160–560 µm high (average 320 µm), 160–590 µm wide (average 350 µm), and generally circular to elliptical in shape (average H:W 0.9). The outer surface has granules and small striations at the distal edge and the inner surface is tuberculate. The proximal edge of all the scales above is coarsely lobate; the distal edge is finely serrate.

The coenenchymal scales are circular (Fig. 15n) with a diameter of 50–150 µm. The outer surface is covered with sharp-peaked granules and small radial striations and the inner surface is tuberculate.

Distribution

Mid- to southwest Atlantic, off the southern coast of Chile and the Antarctic Peninsula, at depths from 100–686 m.

Remarks

Thouarella versluysi was described by Kükenthal (1907) one year after *T. brucei*. Kükenthal mentioned that *T. versluysi* was very similar to *T. brucei* but offered no explanation. Kükenthal also went as far as listing *T. brucei* as *species dubiae atque incertae sedis* in his 1924 key. *Thouarella versluysi* and *T. brucei* both have a bottlebrush colony morphology (although *T. brucei* can appear bilateral it is technically bottlebrush). There was not enough material to determine the colony shape of the *T. versluysi* syntype, however the original description and colony picture depict a bottlebrush colony (Kükenthal 1907). Both species have isolated polyps that are upwardly inclined at between 40–60° and 4–6 scales in the abaxial row of polyps. *Thouarella versluysi* has slightly smaller polyps than *T. brucei*, a slightly lower opercular scale H:W (average of 1.8 versus 2), a higher marginal scale H:W ratio (average of 1.7 versus 1.4), and the abaxial surface of sclerites of *T. brucei* have more peaked granules. These are very minor differences and not enough, in our opinion, to separate these specimens as individual species; *Thouarella versluysi* is thus synonymised with *T. brucei*.

Specimens examined in this study have slightly smaller polyp lengths and, as a consequence, smaller sclerite sizes than the holotype.

Comparisons

The polyps of *Thouarella brucei* and *T. brevispinosa* have marginal and opercular scales of an almost identical shape. *Thouarella brevispinosa* has larger polyps with more scales in the abaxial row than *T. brucei* (6–8 rather than 4–5) and the branchlets of the former are more tightly placed. More material is required of both species to confirm the differences and similarities listed here.

Thouarella brucei shares a similar bilateral–bottlebrush branching morphology with *T. koellikeri*, *T. bipinnata* and *T. andeep*. However, the polyps of *T. brucei* are distally flared, similar to those of *T. andeep*, whereas polyps of *T. koellikeri* and *T. bipinnata* are clavate and arranged in an irregular alternate manner. The operculars of the polyps of *T. andeep* have a smooth inner surface whereas those of *T. brucei*, whose polyps are also smaller, have a simple keel (see Table 3). Lastly, the polyps of *T. brucei* have fewer scales in the abaxial row than the polyps of *T. koellikeri*.

The polyps of *T. brucei* examined in this study have a similar size and number of abaxial scales as *T. hicksoni*, although those of *T. brucei* are larger. *Thouarella brucei*, however, has polyps with operculars that form a full cone, whereas the operculars of the polyps of *T. hicksoni* are narrower and do not form an opercular cone. The polyps of the *T. hicksoni* are also far more clustered.

7. *Thouarella striata* Kükenthal, 1907

Figs 16, 17

Thouarella striata Kükenthal, 1907: 204–205; 1915: 150 (key); 1919: 426–428, text figs 197–201; Broch 1965: 31–32, pl. 7, figs 20–21 (sample not seen)

Not *Thouarella striata* Nutting, 1912: 69, pl. 10 figs 2, 2a (sample not seen)

Thouarella stricta Molander 1929: 75 (incorrect subsequent spelling)

Thouarella (Parathouarella) striata Thomson & Rennet 1931: 27

Thouarella (Thouarella) striata Cairns & Bayer 2009: 27 (listed)

Material examined: **Holotype**, MNHWU, Nr. 57, Bouvet Island, 54°26'S, 3°24'E, 457 m.

Other material: ZMH, R/V *W. Herwig*, sta. 285, Patagonian Shelf, SW Atlantic, 42°19'S, 58°01'W, 825 m, 21 Jun 1966, 2.5 cm fragment; ZMH, R/V *W. Herwig*, sta. 244, SW Atlantic, 36°51'S, 54°01'W, 800 m, 14 Jun 1966.

Description

As only a 2.5 cm fragment of the holotype was examined, the general morphology is taken from the original description (Kükenthal 1907) and the new specimens listed above. The colonies are branched once or twice and flabellate, with branchlets in a bottlebrush arrangement. The branchlets are mostly simple (rare secondary branching), 25 mm in length, emerging from the main stem at almost 90°; some branchlets are arranged in one plane.

The polyps are isolated, weakly inclined towards the branchlets at 45–80° (Fig. 16b) and closely spaced, 14–20 per cm (more densely arranged at branchlet base). They are variable in shape, some clavate, some modestly flared distally (the holotype has distally flared polyps, Fig. 16c,d), 1.5–2.2 mm high (average 1.85 mm). There are 4–6 scales in abaxial rows (Fig. 16d) and 3–4 in the adaxial row.

The operculars are triangle to lanceolate-shaped and acutely pointed (Fig. 17 a–c), 520–780 µm high (average 660 µm), 230–350 µm wide (average 295 µm), with an average H:W of 2.3. The inner opercular surface is keeled with the keel often having multiple longitudinal striations (Fig. 17b,c) that spread radially from proximal keel area towards lateral edges of the scale. The proximal third of the inner surface is tuberculate. The outer surface is concave longitudinally with low striations radiating from a proximal centre (Fig. 17a).

The marginals are arranged in 2 alternate circles of 4, one inner and one outer (Fig. 16e), (although this is not consistent), and they are wider than the operculars, 530–680 µm (average 600 µm), and slightly shorter, 520–680 µm (average of 600 µm), with an average H:W of 1. They have a triangular distal area and are more squared proximally than the operculars (Fig. 17d–f) and they have a strong, multi-channelled keel with striations perpendicular to the distal edge. The proximal half of the inner surface is heavily tuberculate whilst the outer surface is densely covered with granules, with some scales having shallow radial striations towards the distal edge of the scale (Fig. 17f).

The submarginals are shorter than the marginals, 530–540 µm high, 520–700 µm (average 610 µm) wide, with an average H:W of 0.88, and have a modest distal point (Fig. 17g,h). The inner surface is tuberculate across the basal four-fifths of the scale, with a band of striations running perpendicular to the distal edge. The outer surface is covered with densely placed granules.

The body-wall scales are generally rounded (average H:W 1; Fig. 17 j–m) with a pointed arch-shaped distal edge (Fig. 17k,m). Some abaxial body-wall scales have a sculpted distal edge (Fig. 17i). Body-wall scales are 270–580 µm high (average 428 µm), 240–650 µm wide (average 448 µm), progressively reducing in size from the polyp head to base. The body-wall scales have a heavily tuberculate inner surface, with a smooth band bearing a few ridges perpendicular to the distal edge and the outer surface is covered in granules (Fig. 17k). Some scales have deep radial striations running from the central proximal area (Fig. 17i).

All the sclerites have an irregular distal edge and the proximal edge is coarsely lobate.

The coenenchymal scales are elliptical to circular-shaped (Fig. 17n–q) with serrated edges and are 100–500 µm long. The outer surface is covered in granules or is heavily sculpted (Fig. 17q) whilst the inner surface is densely tuberculate.

Distribution

This species has been recorded from the South Atlantic, including Bouvet Island to Burdwood Bank (Broch 1965) and the Patagonian Shelf at depths from 457–800 m. Broch's unconfirmed identification (1965) was from 110 m depth.

Remarks

Thouarella striata has a variable polyp form. The surfaces of scales of the polyps from the holotype, both inner and outer, are deeply striated. Other specimens have finer striations on the outer surface but similar deep striations on the inner.

The specimen from station 244 from ZMH (June 1966) was brooding.

Comparisons

With the number of abaxial scales on the polyps ranging from 4–6, *T. striata* is comparable to several species, namely *T. variabilis*, *T. brucei*, *T. pendulina*, *T. hicksoni*, *T. bipinnata* and *T. andeep* (see Table 3).

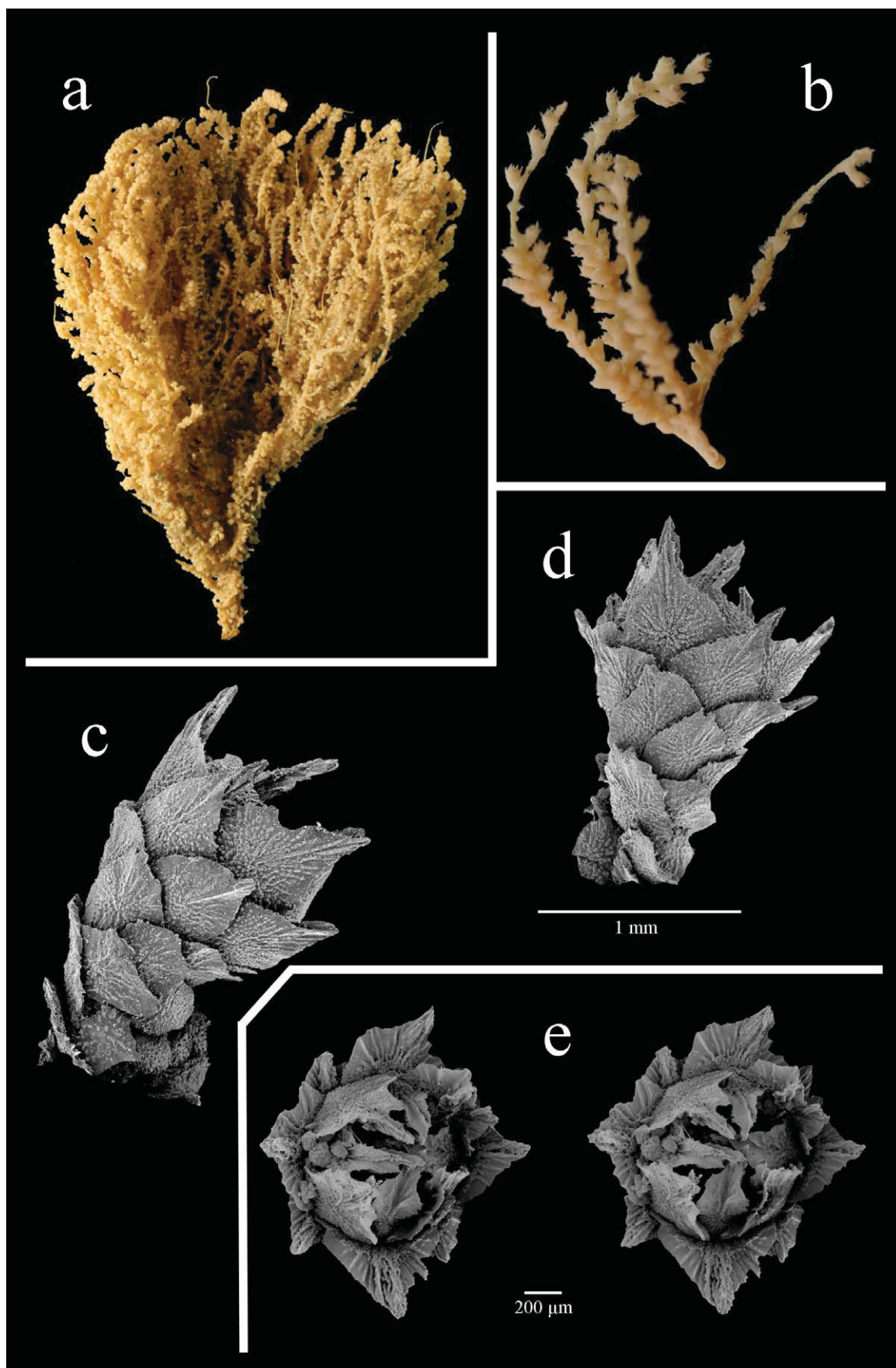


FIGURE 16. *Thouarella striata*, SMF 1966, sta. 285: a) 14 cm long colony. Holotype, MNHWU: b) 2.5 cm long fragment; c) lateral polyp view; d) abaxial polyp view; e) stereo opercular view. Photo b) by ZGR.

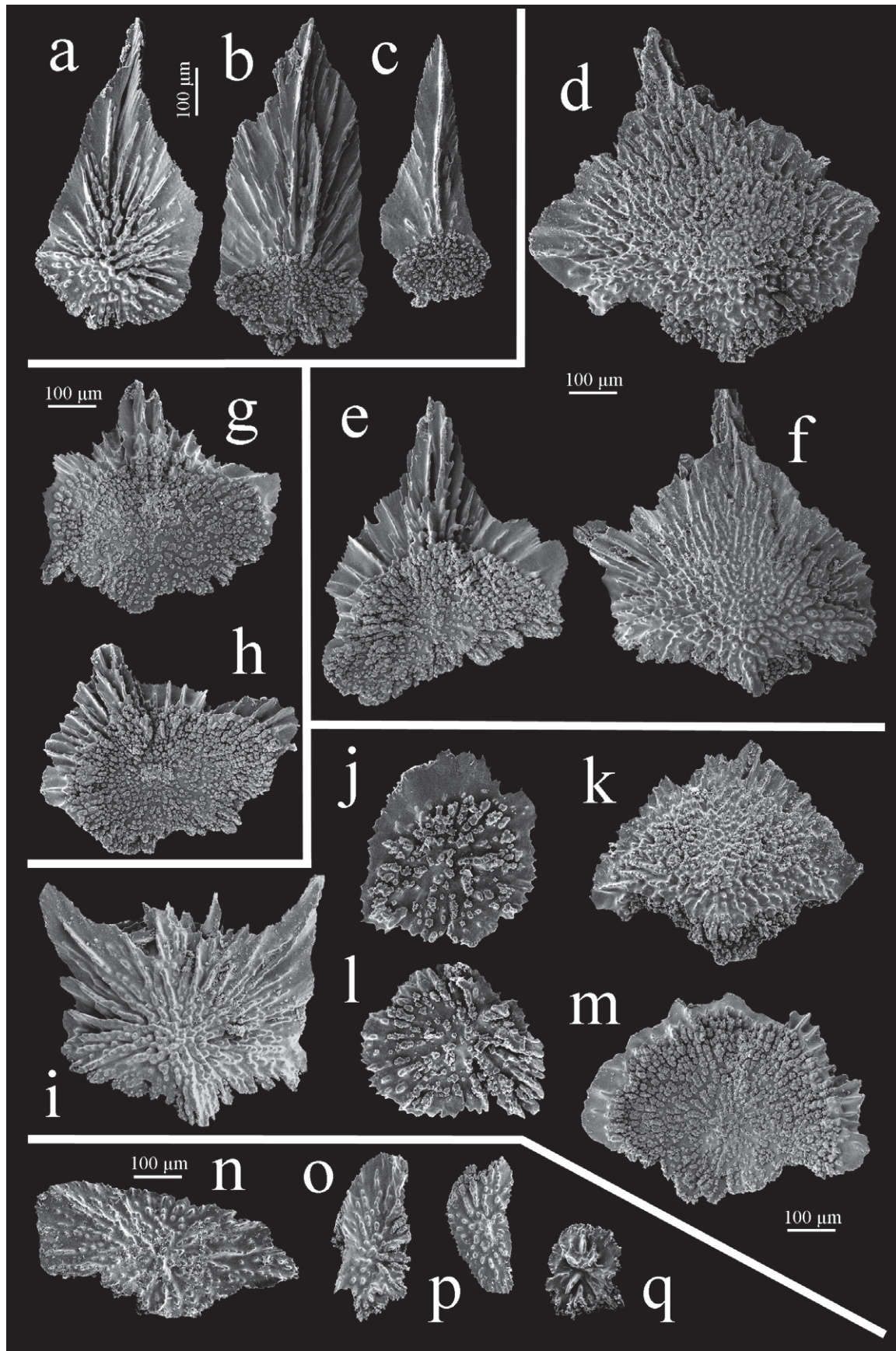


FIGURE 17. *Thouarella striata*, holotype, MNHWU: a) outer and b,c) inner surface of operculars; d,f) outer and e) inner surface of marginal scales; g,h) inner surface of submarginal scales; i) abaxial body-wall scale with sculpted distal edge, j,l) inner surface of circular body-wall scales, k) inner and m) outer surface of body-wall scales; n–p) outer and q) inner surface of coenenchymal scales.

Thouarella variabilis generally has fewer scales in the abaxial row than *T. striata* and lacks wide triangular marginals and striations on the distal edge of the inner surface of marginal and opercular scales. This lack of striations is the primary difference between *T. striata* and the other species listed above. In addition, the operculars of the polyps of *T. andeep* have a smooth inner surface and a rounded distal edge whereas operculars of the polyps of *T. striata* are triangular with a strong keel. The polyps of *T. andeep* also have fewer scales in the abaxial row and have accessory operculars, which have so far not been found in specimens of *T. striata*.

When compared to the polyps of *T. striata*, those of *T. pendulina* are smaller and more tightly placed, and the outer surface of the sclerites lack striations. In addition, the colonies of *T. pendulina* have a true bottlebrush colony shape.

The polyps of *T. hicksoni* are smaller and more densely arranged than those of *T. striata*.

Colonies of *T. bipinnata* are uniplanar whereas those of *T. striata* have a bushy, bottlebrush shape. The polyps of the former are also clavate.

8. *Thouarella crenelata* Kükenthal, 1907

Figs 18, 19

Thouarella crenelata Kükenthal, 1907: 205; 1912: 302

Thouarella (Epithouarella) crenelata Kükenthal 1915: 151 (key); 1919: 436–438, text figs 216–219, pl. 43, fig. 70; 1924: 300–301; Cairns & Bayer 2009: 28 (listed), fig. 7i–m

Material unavailable: The **holotype** is held in ZMB however material was too fragile to send from ZMB or MNHWU (where fragments are held). The type locality is eastern Bouvet Island, southern Atlantic Ocean, 457 m depth.

Material examined: USNM 98086 (SEM stubs T53 & T68, stored at NMNH), R/V *Hero*, cruise 824, sta. 26–1, Lecoite Island, Brabant Island, Palmer Archipelago, Antarctic Peninsula, 64°14'03"S, 61°57'57"W, 238–285 m, 24 Mar 1982; USNM 99148, R/V *Marion Dufresne*, cruise 42, sta. 22, Mac Robertson Land, Lars Christensen Coast, north of Cape Darnley, Antarctica, 66°58'S, 72°52'E, 525 m, 26 Jan 1958; USNM 98160, R/V *Hero*, cruise 731, sta. 1947, Flandres Bay, Danco Coast, Antarctic Peninsula, 65°00'31"S, 63°28'06"W, 204–250 m, 11 Mar 1973; USNM 1128900, R/V *Hero*, cruise 731, sta. 1939, Wednesday Island, Butler Passage, Palmer Archipelago, Antarctic Peninsula, 64°58'39"S, 63°45'46"W, 75–120 m, 9 Mar 1973; USNM 1071563, R/V *Hero*, cruise 731, sta. 1812, Bismarck Strait, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°51'54"S, 63°39'45"W, 280–300 m, 19 Feb 1973; USNM 80154, R/V *Professor Siedlecki*, cruise 601, sta. 29, South Georgia Island, sub-Antarctic, 54°32'S, 39°05'W, 201–210 m, 3 Dec 1986; USNM 98028, R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia Island, sub-Antarctic, 54°29'S, 39°22'W, 659–686 m, 8 Feb 1966; USNM 97996, R/V *Eltanin*, cruise 7, sta. 499, south of Coronation Island, South Orkney Islands, sub-Antarctic, 62°06'S 45°08'W to 62°06'S 45°10'W, 485 m, 20 Feb 1963; USNM 58162, R/V *Eastwind*, sta. 006C, west of Brabant Island, South Shetland Islands, Antarctic Peninsula, 64°50'S, 63°12'W, 283.5 m, 29 Jan 1966; USNM 76900, R/V *Edisto*, Deep Freeze IV, sta. 31, Nansen Island, Biscoe Islands, Antarctic Peninsula, 66°20'S, 67°47'W, 25 Mar 1959; USNM 98030, R/V *Eltanin*, cruise 22, sta. 1536, 54°30'S, 39°20'W, west tip of South Georgia Island, sub-Antarctic, 659–686 m, 8 Feb 1966; USNM 84342, R/V *Eltanin*, cruise 9, sta. 732, South Georgia Island, sub-Antarctic, 53°36'S, 36°51'W, 220–265 m, 12 Sep 1963; USNM 84343, R/V *Professor Siedlecki*, cruise 86–01, sta. 2, Shag Rocks, South Georgia Island, sub-Antarctic, 53°20'S, 42°42'W, 417–514 m, 29 Nov 1986; USNM 98102, R/V *Professor Siedlecki*, cruise 86–01, sta. 3, Shag Rocks, South Georgia Island, sub-Antarctic Ocean, 53°26'S, 42°29'W, 294–329 m, 29 Nov 1986; USNM 98099, R/V *Hero*, cruise 702, sta. 510, Antarctic, 64°48'S, 63°31'18"W, 219 m, 18 Mar 1970; USNM 1129152, R/V *Hero*, cruise 721, sta. 1143, Wauwermans Island, Bismarck Strait, Palmer Archipelago, Antarctic Peninsula, 64°57'11"S, 63°43'W, 230–260 m, 14 Mar 1972; USNM 1129153, R/V *Eastwind*, cruise 66, sta. 006C, haul 3, 64°50'24"S, 63°12'54"W, 283 m, 29 Jan 1966; USNM 1129151, R/V *Hero*, cruise 731, sta. 1945, Paradise Harbor, Gerlache Strait, Palmer Archipelago, Antarctic Peninsula, 64°48'27"S, 63°05'24"W, 260 m, 11 Mar 1973; SMF, EPO5, 3, sta. 291, GSN 14, 19 Feb 1989.

Although no material was located in the Smithsonian collection, or elsewhere from the type locality, many specimens that match descriptions of *T. crenelata* and a photograph of the holotype (Fig. 18d) were located, all from the sub-Antarctic.

Description

The colonies are sparsely branched with the longest specimen (USNM 98086) measuring 35 cm (Fig. 18a). The branchlets are in a bottlebrush arrangement on branches although some colonies appear uniplanar where the branchlets curve in 2 directions. The branchlets are mostly simple with some secondary branching and branchlets are up to 30 mm long, arising in all directions (although most are only in 3–4 directions) at an angle of between 60–90°. Colonies tend to be dark to light yellow.

The polyps are isolated, clavate (Fig. 18b–d), 2.3–3.0 mm high (average 2.1 mm), upwardly inclined at 60–90°, at a density of 5–11 per cm at the branchlet base, reaching 8–19 at tip. Each polyp has 8 longitudinal rows of scales, 6–10 (average 8) in the abaxial row (Fig. 18c) reducing to 6–7 per row adaxially. Sclerites get shorter and wider from polyp tip to base.

The operculars are lanceolate (Fig. 19c) to arrow-head shaped (Fig. 19a,b,d), 530–710 µm high (average 610 µm), 270–380 µm wide (average 325 µm), with a H:W of 1.7–2.4 (average 1.9). The inner surface has a single large keel (keel side view Fig. 19e) and there are many lateral projections adjacent to the keel. These multiple sharp lateral ridges lead to an irregular distal edge. Lateral areas above the tuberculate base on the inner surface are relatively smooth with a finely serrate edge. The outer surface has many sharp radial ridges or striations from the central proximal area extending towards the distal edge. However, the centre of the scale is smooth with a deep longitudinal valley (Fig. 19d), and there are granules proximally and some tubercles showing at the proximal edge.

The marginals are fan-shaped with a curved to pointed, dentate distal edge (Fig. 19f,g). They are 380–510 µm high (average 438 µm), 340–480 µm wide (average 420 µm), with a H:W of 1 (average 0.9–1.2). They bear a large keel on the inner surface with multiple dentate projections (Fig. 19f) whilst there are smooth areas adjacent to the keel and sparse tubercles across the proximal half. The outer surface has sparse, large granules, some stretching into radial ridges from the central proximal area and tubercles are also visible at the proximal edge (Fig. 19g). The marginals have a serrate lateral edge. The adaxial marginals have a reduced keel with tubercles covering the majority of the inner surface of the scales.

The submarginals are elliptical in shape (Fig. 19h–l), 410–450 µm high (average 430 µm), 600–610 µm wide (average 600 µm), with a H:W of 0.7–0.75 (average 0.7). The proximal two-thirds of the inner surface is tuberculate with a smooth band across the distal third. There are 3 or 4 small keels and ridges perpendicular to the distal edge (Fig. 19j–l). From a side view the keel and ridges have large serrations. The outer surface is smooth with sparse granules centrally (Fig. 19h,i) and rare radial ridges and tubercles proximally. The distal edge has wide serrations and the proximal edge is coarsely lobate.

The body-wall scales are relatively wide, short and elliptical (Fig. 19m–o), 600–620 µm (average 610 µm) wide, 290–400 µm high (average 345 µm), with a H:W of 0.5–0.7 (average 0.6). The inner surface is tuberculate with a smooth band along the distal edge (Fig. 19m). Radial striations along the distal edge of the outer surface result in a serrated distal edge whilst the lateral areas are relatively smooth. There are granules across the proximal area with some tubercles visible at the proximal edge (Fig. 19n,o).

The coenenchymal scales are smaller than the body-wall scales, with a circular to irregular shape (Fig. 19p), 150 µm diameter, with an irregularly serrate distal edge. The outer surface has granules and radial striations whilst the inner surface is tuberculate.

Distribution

This species has a circum sub-Antarctic distribution, found from depths of 75–686 m.

Remarks

Some branches appear uniplanar, as in the holotype (Kükenthal, 1907), as the branchlets curve in 2 directions. Kükenthal (1912) referred to this structure as ‘biradial’. It is likely that this is the result of a commensal annelid inducing the branchlets to form around its body.

Comparisons

For a number of characters, *Thouarella crenelata*, *T. chilensis*, and *T. parachilensis* are morphologically similar and are probably closely related (see Table 3). The polyp shapes of these species are similar, although those of *T. parachilensis* are more bulbous distally than the more modestly clavate polyps of *T. crenelata* and the polyps of *T. chilensis* are more flared. Although there are differences in the number of abaxial scales the range of abaxial scale counts in all 3 species overlap making this a poor defining character: *T. crenelata* 6–11,

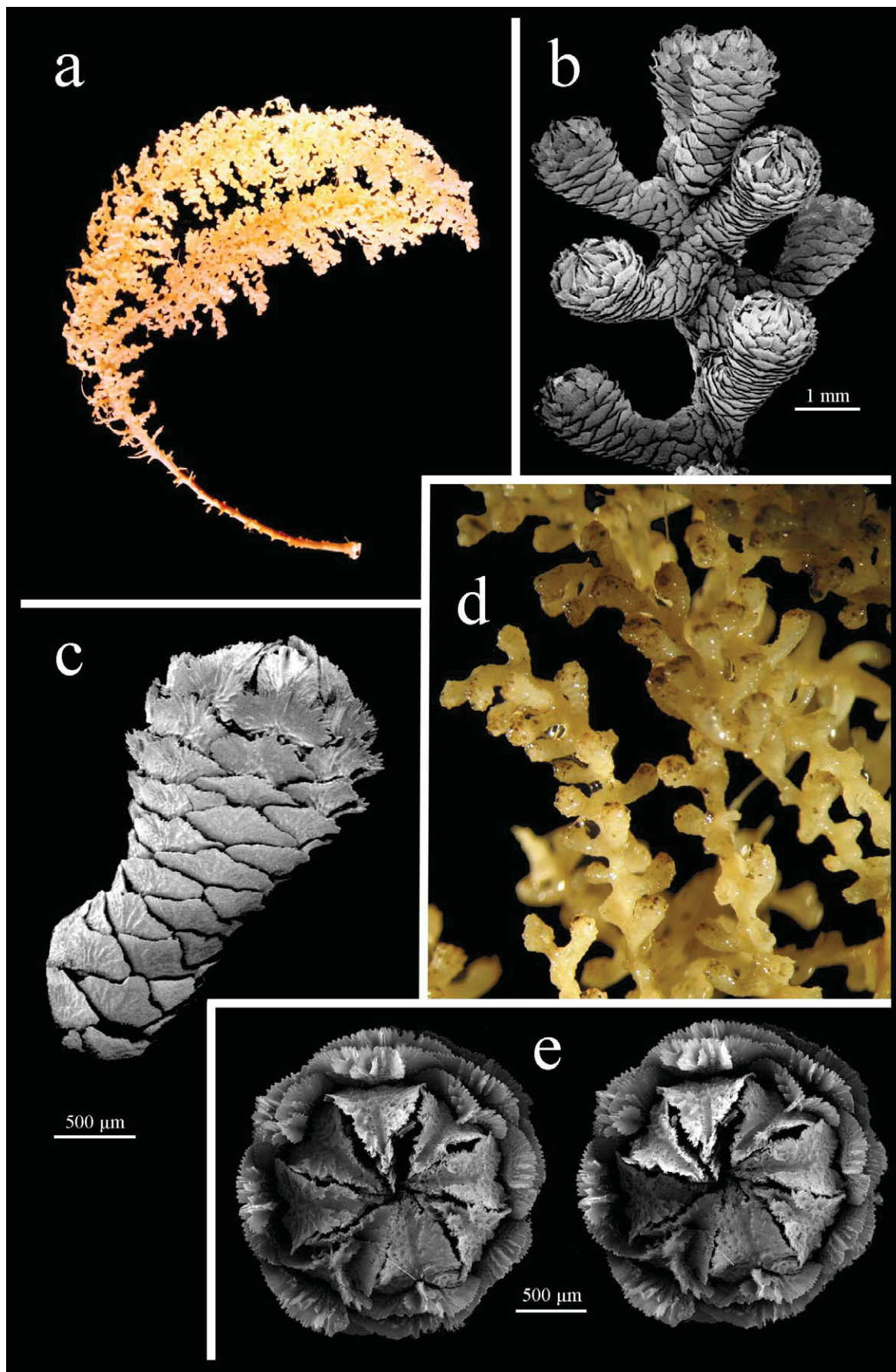


FIGURE 18. *Thouarella crenelata*. USNM 98086: a) colony, 35 cm; b) polyps; c) abaxial polyp view, e) stereo opercular view of polyp. Holotype, ZMB; d) close up of polyps. Photo d) by Carsten Lueter, ZMB.

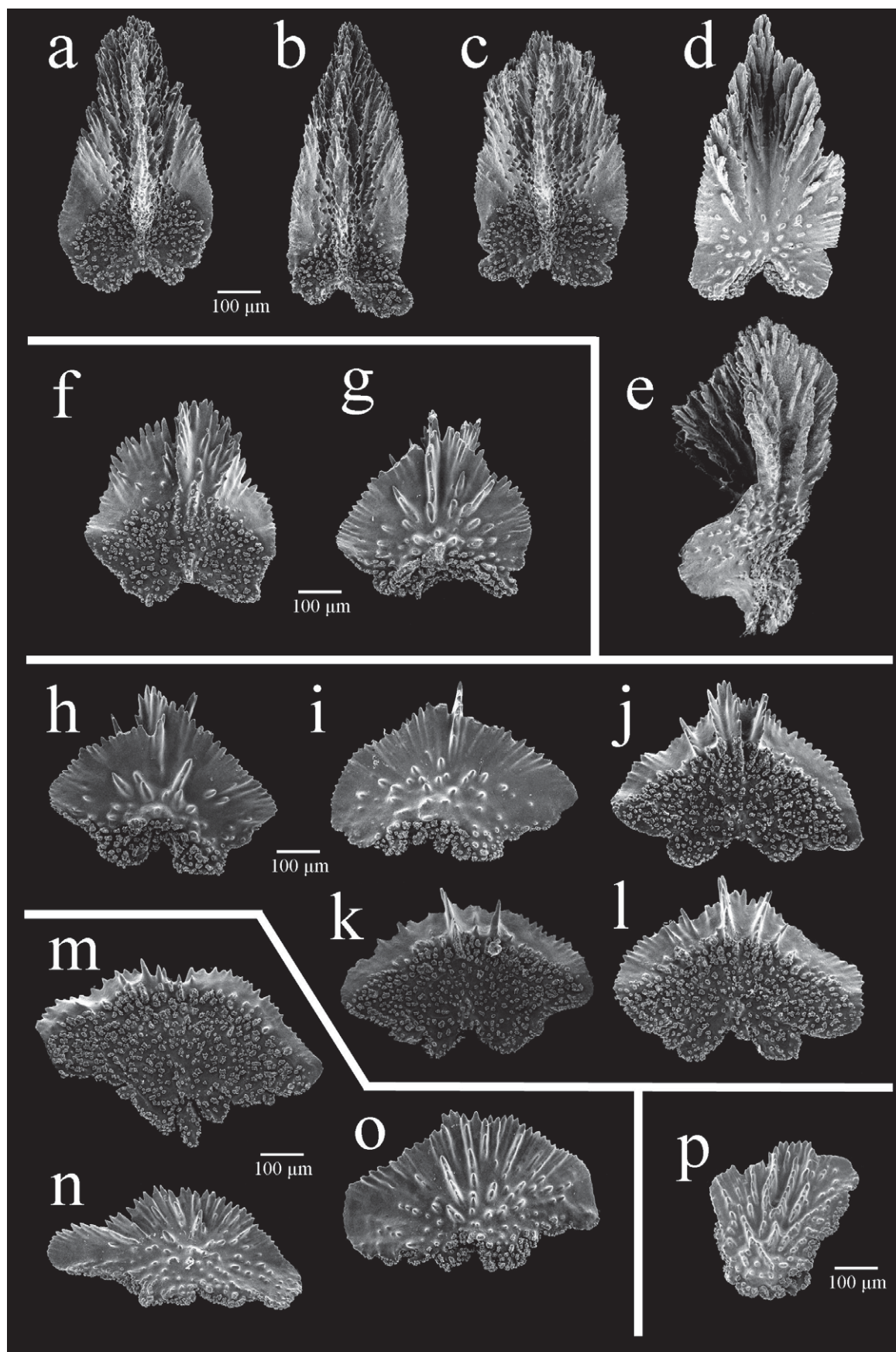


FIGURE 19. *Thouarella crenelata*, USNM 98086: a–c) inner, d) outer and e) lateral view of operculars; f) inner and g) outer surface of marginal scales; h,i) outer and j–l) inner surface of submarginal scales; m) inner and n,o) outer surface of body-wall scales; p) outer surface of coenenchymal scale.

T. parachilensis 8–15 and *T. chilensis* 6–8. As well as the varying sclerite shapes and sizes, the most prominent difference among these species is the density of polyp placement at the tip of a branchlet: *Thouarella crenelata* has 9–19 polyps per cm (average 11), *T. parachilensis* 18–48 (average 32) and *T. chilensis* 21–28 (average 22). Although there is moderate overlap in these ranges the branchlet tip of *T. parachilensis* specimens are ‘barrel-shaped’ with tight polyp placement and thus is distinguishable from *T. crenelata*. The marginal scales of *T. crenelata* also have a more pronounced dentate distal edge and the opercular scale surface is much more deeply and distinctly ridged than that found on the polyps of *T. chilensis* or *T. parachilensis*.

Thouarella crenelata and *T. viridis* are very similar species. They were described as different species based on the number of scales in the abaxial row and the surface ornamentation of the marginal scales (Zapata-Guardiola & López-González 2010a). Our study reports an expansion in the range of the number of scales in the abaxial row of the polyps of *T. crenelata* from the 9–10 of Kükenthal (1915; 1924) to 6–11 (average of 8), which overlaps that of *T. viridis* (6–7). The scales of polyps of *T. crenelata* have a dentate distal edge whereas those of polyps of *T. viridis* lack this character.

The colony form of *Thouarella crenelata* was originally described as similar to that of *T. koellikeri* (Kükenthal 1907), which has nearly pinnate branching, leaving one side of the stem without branchlets (described as “biradial” by Kükenthal 1919). Specimens identified here as *T. crenelata* are bottlebrush but can have a bilateral appearance when the branchlets curve in two directions. There are a similar number of scales in the abaxial row of the polyps of both *T. crenelata* and *T. koellikeri* and both have polyps that are clavate, however those of the latter have operculars with a simpler keel.

Polyps of *T. crenelata* have a comparable number of scales in the abaxial row, and a similar number of polyps per cm as colonies of *T. clavata*. But the former has more densely placed polyps at the tip of the branchlets, longer polyps, and polyps with marginals with larger serrations on the distal edge in comparison to the smooth to finely serrate edge of the latter.

9. *Thouarella clavata* Kükenthal, 1908

Figs 20, 21

Thouarella aff. *antarctica* Kükenthal 1907: 203–4

Thouarella clavata Kükenthal, 1908: 11

Thouarella (*Parathouarella*) *clavata* Kükenthal 1919: 430–433, text figs 209–212, pl.43, fig. 69

Thouarella (*Thouarella*) *clavata* Cairns & Bayer 2009: 27 (listed)

Material examined: **Holotype**, ZMB Cni 6080, D.T.E Agulhasstrom, sta. 103, SW of Port Elizabeth, South Africa, 35°10.5'S, 23°2.0'E, 500 m; **Syntype**, MNHWU, 2 cm dried fragment; USNM 1140264, University of Cape Town Ecological Surveys, LBT 75 G, 32°03.3' S 16°02' E, 680–800 m, 25 Sep 1971.

As so little material was available for study the colony description is based on Kükenthal's 1908 study and his more detailed 1919 record of this species. There is some confusion surrounding this species as the specimen from ZMB has clavate polyps, very unlike those seen in Kükenthal (1919) and they in fact look similar to *T. crenelata*. As the MNHWU syntype more closely resembles images within Kükenthal (1919) we have based descriptions on this specimen. Unfortunately, it was not possible to take adequate SEM images of sclerites and polyps of the syntype as the specimen is in a very poor condition and disintegrated in SEM preparations. Using microscopy it was possible to identify a second *T. clavata* specimen: USNM 1140264. We thus illustrate specimen USNM 1140264, whose polyps and sclerites are identical to the few poor SEM images obtained from the syntype.

Description

The holotype stem base is slightly curved, the main stem is straighter (no holdfast), and branching is dense and in all directions (Fig. 20a), although the branchlets curve to create ventral and dorsal colony planes. The branchlets are mostly 30 mm long (some 35 mm), often forked at the branchlet base, and orientated at almost 90° to the main stem or branch. The dorsal plane branchlets of USNM 1140264 are greatly shortened and the proximal branchlets are also reduced in length (Fig. 20d).

We believe that USNM 1140264 is conspecific to the MNHWU syntype. The following descriptions are of USNM 1140264 (unless stated) as this is the only known whole colony of *T. clavata* from which it was possible to take clear SEM images. Isolated polyps are sparsely placed on branchlets (Fig. 20d), 7–8 per cm. They are distally

flared (Fig. 20e, 21c) with a low conical operculum, 1.4–1.7 mm high (average 1.5), and mostly in a single plane. Each polyp has 6–7 scales in one abaxial row (Fig. 21a) and 4 scales in each adaxial row.

The operculars are arranged in 2 rings, an inner ring made up of smaller operculars and an outer ring of large operculars. The inner operculars are a tall-triangular shape (Fig. 21d,h), 350–390 µm high (average 370 µm), 150–230 µm wide (average 180 µm), with a H:W of 1.6–2.5 (average 2.1). Most of the outer operculars are larger with a wider lanceolate shape (Fig. 21e–g), 590–770 µm high (average 680), 340–420 µm wide (average 390), with a H:W of 1.5–1.9 (average 1.7). The operculars have a simple keel on the inner surface (Fig. 21e), are tuberculate proximally, and the outer surface is deeply concave and smooth (Fig. 21g). The proximal edge is coarsely lobate whilst the distal edge is serrate.

The distal edge of the marginals are triangular with an angular proximal edge and are tuberculate across most of the inner surface, 790–900 µm high (average 860 µm), 480–650 µm wide (average 600 µm), with a H:W of 1.4–1.6 (average 1.5). The keel is simple and flat faced (Fig. 21j) and the outer surface is covered in granules with a smooth distal border (Fig. 21i).

The submarginals are diamond-shaped, 690–750 µm high (average 720 µm), 650–730 µm wide (690 average µm), with a H:W of 1. There is a small keel on the inner surface corresponding to the peak on the distal edge (Fig. 21k). The remainder of the inner surface is tuberculate whilst the outer surface is covered in granules (Fig. 21l).

The body-wall scales have a circular distal edge, are often irregular in shape (Fig. 21m, n), 220–340 µm high (average 260 µm), 250–490 µm wide (average 330 µm), with a H:W of 0.4–1.5 (average 0.9). The proximal edge is coarsely lobate. The inner surface is tuberculate, with a narrow smooth band along the distal margin whilst the outer surface is relatively smooth but has sparsely distributed granules.

The coenenchymal scales are smaller than the body-wall scales, 120–220 µm high (average 160 µm), 140–250 µm wide (average 190 µm), with a H:W of 0.5–1.2 (average 0.9). They are circular to widely elliptical in shape (Fig. 21o–s) with a very smooth outer surface that bears a few small granules and a tuberculate inner surface.

Distribution

This species is only known from the type locality, southwest of Port Elizabeth, South Africa, at 500 m depth.

Remarks

The hand-drawn images in Kükenthal's 1919 publication (text figs 209, 210) show modestly flared polyps like those on his plate XLIII. However, he described these polyps as clavate. We use the word 'clavate' to describe a polyp with a rounded distal head region, and Kükenthal appears to use the word to describe any polyp with a wider head than base. The syntype from MHWU is in bad condition, the sclerites are brittle and they partially disintegrated when they were cleaned in an attempt to carry out SEM observations—however, the polyps are distally flared, as in Kükenthal's (1919) illustrations. The ZMB sample afforded clearer SEM images but the polyps are clavate and not like those illustrated by Kükenthal (1919), and also the opercular keel is strong, whereas it was described by Kükenthal (1907) as weak. The illustration of *T. clavata* (Kükenthal 1919: text figs 209, 210) shows a distally flared polyp with pointed marginals and the holotype description mentions clustered polyps. The MHWU sample most closely resembles this description and we are thus inclined to believe this is the true *T. clavata*, although this makes the name *T. clavata* a contradiction to our current use of this descriptive term.

More samples of this species are required from the type locality to complete a full description and improve comparisons (below).

Two polyp morphs were illustrated by Kükenthal (1919, Fig. 210), one of which may have been brooding.

Comparisons

The number of polyps per cm, number of pairs of abaxial scales (5–6), and flared polyp shape makes this species comparable to *T. antarctica*, *T. brucei*, and *T. andeep* (Table 3). *Thouarella antarctica* has a bottlebrush colony shape and shorter, more rigid branchlets than colonies of *T. clavata*. The remaining species have a bottlebrush to bilateral appearance similar to *T. clavata*, although colonies of *T. andeep* have shorter more rigid branchlets and marginals that are more acutely pointed than those of *T. clavata*. The polyps of *T. clavata* and *T. brucei* look almost identical, but branchlets of colonies of *T. brucei* are more sparsely placed than those of *T. clavata* (Fig. 20a). However, these differences in growth form are very minor. *Thouarella brucei* was originally described from Burdwood Bank and is found around Antarctica whereas *T. clavata* has been found only off the south coast of South Africa so there could be a separation in geographical distribution. More material of *T. clavata* is required to confirm that these two species are distinct.

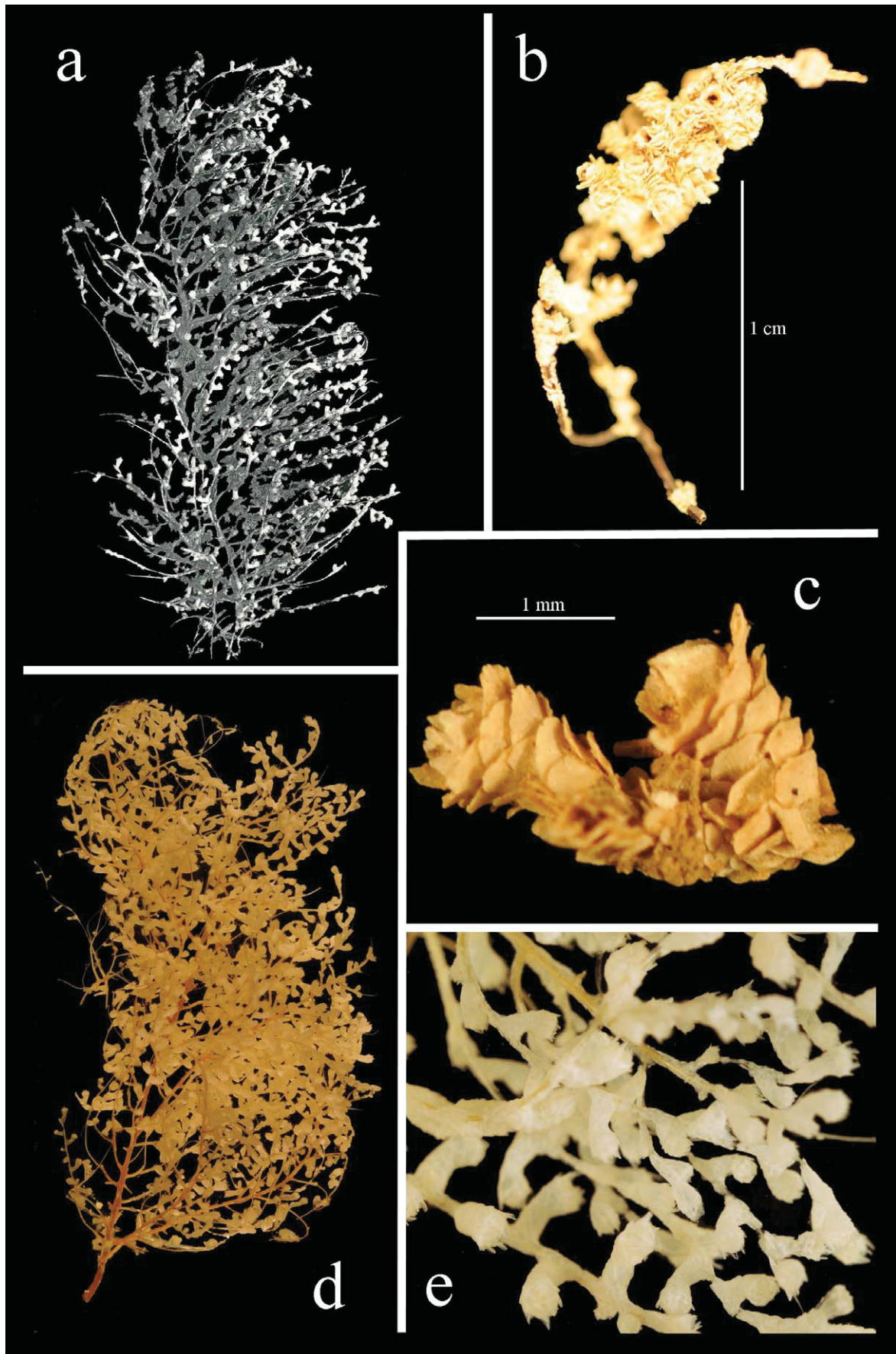


FIGURE 20. *Thouarella clavata*, holotype ZMB Cni 6080: a) image of 11 cm colony, fig. 69 from Kükenthal 1919. Syntype, MNHWU: b) fragment of branchlet; c) close up of two polyps. USNM 1140264: d) colony; e) close up of polyps. Photos by SJ.

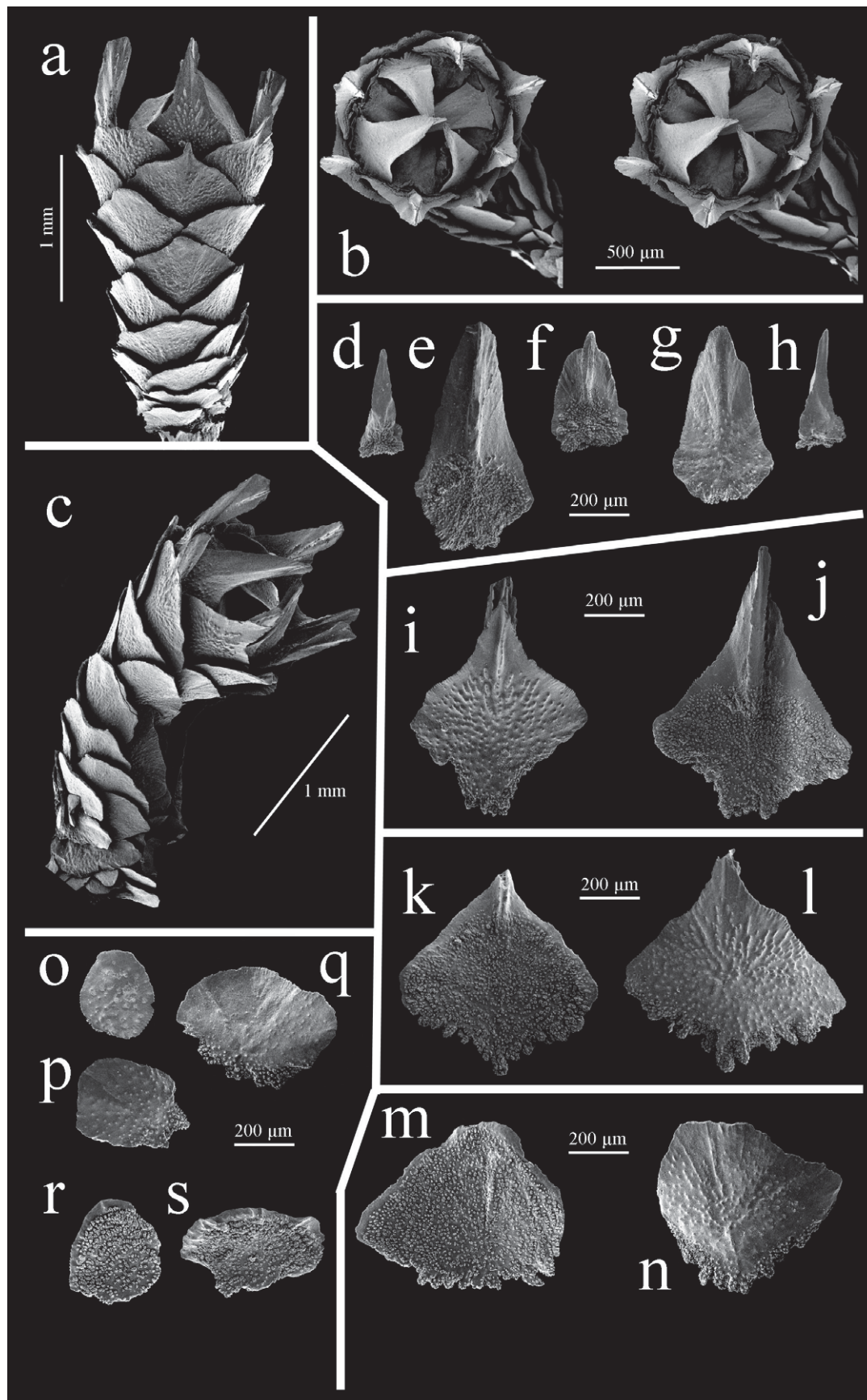


FIGURE 21. *Thouarella clavata*, USNM 1140264: a) abaxial view of polyp; b) stereo opercular view of polyp; c) lateral polyp view; d,e,f) inner and g,h) outer surface of operculars; i) outer and j) inner surface of marginals; k) inner and l) outer surface of submarginals; m) inner and n) outer surface of body-wall scales; o,p,q) outer and r,s) inner surface of coenenchymal scales.

10. *Thouarella pendulina* (Roule, 1908)

Figs 22, 23

Rhopalonella pendulina Roule, 1908: 4, pl.1, fig. 5–8; Gravier 1914: 70–77, text figs 86–98, pl. 5, figs 21–15; Kükenthal 1912: 290

Thouarella pendulina Kükenthal 1915: 151; 1919: 440; 1924: 302

Thouarella (Thouarella) pendulina Cairns & Bayer 2009: 27 (listed); Zapata-Guardiola & López-González 2010a: 179

Thouarella antarctica Broch 1965: 24–26, pl. 2, figs 5–7

Material examined: **Holotype**, MNHN–Octo.0000–0232 and **paratype**, MNHN–Octo.0000–0211, Expedition *Antarctique Française* (1903–1905), no. 640 collected, Booth (Wandel) Island.

Other material: USNM 98341, R/V *Islas Orcadas*, cruise 876, sta. 111, Coronation Island, South Orkney Islands, sub-Antarctic, 60°25'36"S, 46°25'18"W, 97–128 m, 16 Feb 1976, 2 colonies; USNM 98359, R/V *Hero*, cruise 721, sta. 1075, Arthur Harbour, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'24"S, 64°7'36"W, 91–104 m, 23 Feb 1972, 3 colonies; USNM 1130339, R/V *Eltanin*, cruise 27, sta. 1896, Franklin Island, Victoria Land, Antarctica, 76°10'S, 168°17'E, 70–81 m, 18 Jan 1967; USNM 1130348, south end of Balleny Islands, Buckle Island, Antarctica, 66°53'S, 163°19'E, 55–164 m, 10 Feb 1974, 15 colonies; USNM 1130344, R/V *Hero*, cruise 731, sta. 1756, Arthur Harbour, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'14"S, 64°06'43"W, 91 m, 17 Feb 1973; USNM 85314, R/V *Hero*, cruise 721, sta. 1073, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'30"S, 64°07'36"W, 64–100 m, 23 Feb 1972; USNM 98149, R/V *Hero*, cruise 691, sta. 33, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 63°46'30"S, 61°47'51"W, 73–91 m, 13 Feb 1969; USNM 98150, R/V *Hero*, cruise 702, sta. 507, Port Lockroy, Wiencke Island, Palmer Archipelago, Antarctic Peninsula, 64°49'18"S, 63°31'21"W, 64–128 m, 17 Mar 1970; USNM 98158, R/V *Hero*, cruise 731, sta. 1944, Neumayer Channel, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°46'40"S, 63°25'33"W, 100–150 m, 11 Mar 1973; USNM 98170, R/V *Eltanin*, cruise 6, sta. 435, Astrolabe Island, Bransfield Strait, Antarctic Peninsula, 63°14'S, 58°42'W, 73 m, 8 Jan 1963; USNM 98171, R/V *Eltanin*, cruise 6, sta. 436, Astrolabe Island, Bransfield Strait, Antarctic Peninsula, 63°13'S, 58°47'W, 73 m, 8 Jan 1963; USNM 98228, R/V *Islas Orcadas*, cruise 876, sta. 107, Coronation Island, South Orkney Islands, sub-Antarctic, 60°26'30"S, 46°22'48"W, 102–108 m, 16 Feb 1976; USNM 98335, off south end of Buckle Island, Balleny Islands, Antarctic, 66°53'S, 163°19'E, 55–164 m, 10 Feb 1974; USNM 98343, USAP, SOSC–L46, Antarctic, 63°17'S, 62°09'W, 12 Jan 1973; USNM 98360, R/V *Hero*, cruise 721, sta. 5438, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'27"S, 64°07'W, 32–90 m, 27 Mar 1972; USNM 98363 and 98390 (same location), R/V *Islas Orcadas*, cruise 876, sta. 112, Coronation Island, South Orkney Islands, sub-Antarctic, 60°27'48"S, 46°23'06"W, 93–102 m, 16 Feb 1976; USNM 1120943, R/V *Hero*, cruise 691, sta. 28, south of Low Island, South Shetland Islands, sub-Antarctic, 63°25'30"S, 62°09'30"W, 91 m, 10 Feb 1969; USNM 1129159, R/V *Eltanin*, cruise 32, sta. 2059, south of Pennall Bank, Ross Sea, Antarctica, 77°58'30"S, 178°4'58"E, 655 m, 25 Jan 1968; USNM 1130330, R/V *Hero*, cruise 691, sta. 33, Hoseason Island, Bransfield Strait, Antarctic Peninsula, 63°36'30"S, 61°47'51"W, 73–91 m, 13 Feb 1969; USNM 1130342, R/V *Eltanin*, cruise 27, sta. 1896, Victoria Land, Franklin Island, Ross Sea, Antarctic, 76°10'01"S, 168°16'58"E, 70–81 m, 18 Jan 1967; USNM 1130344, R/V *Hero*, cruise 731, sta. 1756, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'13"S, 64°6'42"W, 91 m, 17 Feb 1973; USNM 1130345, R/V *Eltanin*, cruise 51, sta. 5762, Moubay Pennell Bank, Victoria Land, Ross Sea, Antarctic, 76°2'6"S, 179°57'W, 347–358 m, 9 Feb 1972; USNM 1130347, R/V *Hero*, cruise 731, sta. 1915, west of Bonaparte Point, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'S, 64°4'32"W, 35–60 m, 6 Mar 1973; USNM 1130349, R/V *Hero*, cruise 731, sta. 1823, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47'20"S, 64°6'58"W, 90–110 m, 20 Feb 1973; SMF, EPOS 03, sta. 212, GSN 2, Weddell Sea, 60°50'S, 55°38.9'W, 414 m, 15 Jan 1989; SMF, Terre Adélie, Antarctica, D114, Patrick Arnaud leg, no precise location or depth information; SMF, R/V *Hero*, sta. 90, South Janus Island, Palmer Archipelago, Antarctica, 73–100 m, 23 Mar 1972, no precise location information; SMF, R/V *Hero*, sta. 90, South Janus Island, Palmer Archipelago, Antarctica, 62–90 m, 23 Mar 1972, no precise location information.

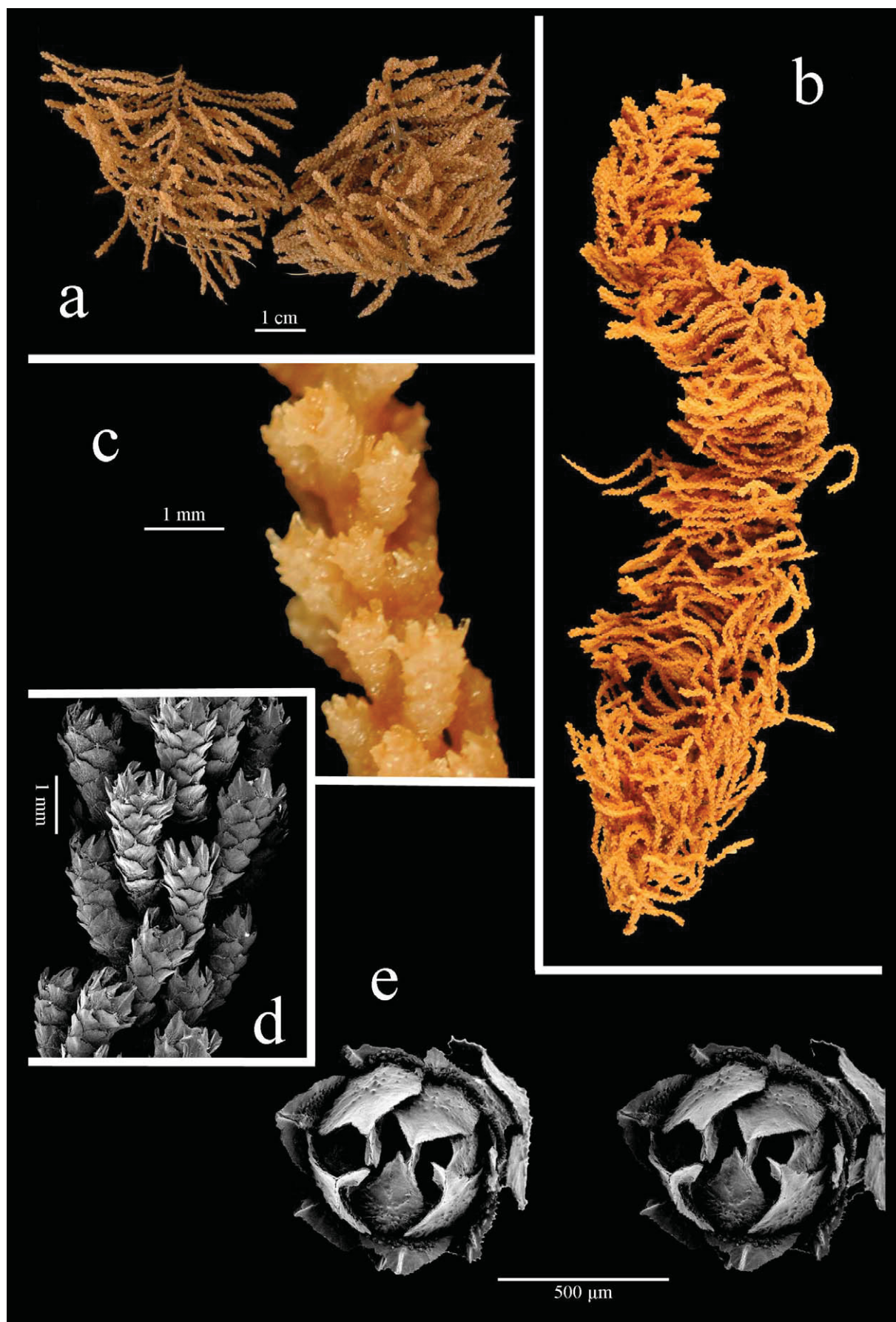


FIGURE 22. *Thouarella pendulina*: a,d,e) Paratype, MNHN, Oct.0000-0211: a) broken colony; d) abaxial and lateral view of polyps on branchlet; e) stereo opercular view of polyps. USNM 98359: b) colony, 22 cm; c) close up of polyps.

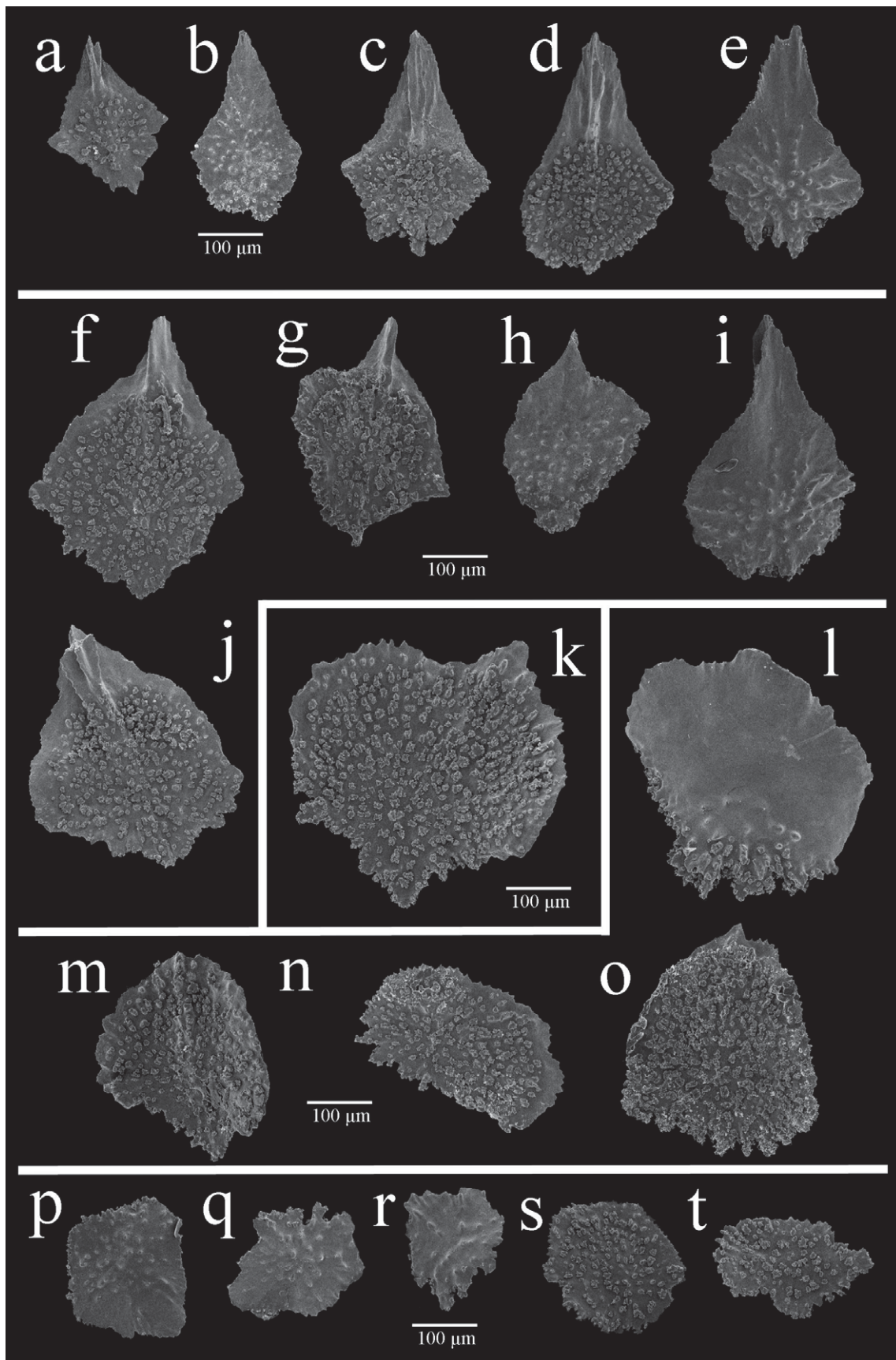


FIGURE 23. *Thouarella pendulina*, paratype, MNHN, Oct.0000-0211: a,c,d) inner and b,e) outer surface of opercular scales; f,g,h) inner and h,i) outer surface of marginal scales; k) inner surface of submarginal; l) outer and m–o) inner surface of body-wall scales; p–r) outer and s,t) inner surface of coenenchymal scales.

Description

The description of the holotype is of a 34.5 cm long colony, 60 mm at its widest point. Colonies of this species are generally of an unbranched bottlebrush arrangement (Fig. 22a,b), although a few have been seen to have limited branching with 2 or more stems. The branchlets leave the main stem in at least 4 directions, extend horizontally, then droop, most having secondary and tertiary branching which can appear simple as divisions are very close to the stem. The branchlets are 1–3 mm apart, and up to 40–42 mm long. The axis is woody with fine longitudinal striations, flexible (except at colony base which is thickened into a calcified holdfast) and is 5–6 mm diameter base.

The polyps are crowded (Fig. 22c,d), with a density of 27–41 per cm (average 34). They are 0.9–1.2 mm high (average of 1 mm), appressed against the branchlets, 2–3 times longer than their diameter, and irregularly arranged. There are fewer polyps at the branchlet base, and they are more clustered at the centre and tip of the branchlets whilst there are no polyps on the main stem. The polyps are cylindrical at their base, thicker towards the operculum, with a slightly rounded shape and pointed summit. There are 4–5 scales in the abaxial row (Fig. 22d) but fewer in the adaxial row.

Eight operculars create a tall cone rising above the marginals with the 2 adaxial operculars being reduced in size. The operculars are in 2 alternate circles, one inner, one outer, however this is not strict as the adaxial operculars are often inside the inner opercular circle. There are 6–7 isosceles triangle to lanceolate-shaped operculars, each having an acutely pointed distal edge (Fig. 23b–e). Opercular scale sizes range from 260–490 μm high (average 357 μm), 150–320 μm wide (average 240 μm), with an average H:W of 1.5. There are 1 or 2 adaxially placed, smaller, diamond-shaped operculars (Fig. 23a). The outer opercular surface is moderately concave longitudinally and there are granules sparsely covering the proximal area, sometimes these are aligned radially. The inner surface has a simple keel, which may be half the opercular length (Fig. 23c,d), and is sometimes channelled and flat-faced whilst the proximal half of the inner surface is tuberculate.

The marginals are in inner and outer alternate circles of 4, although the adaxial marginals are reduced and do not conform to this pattern (Fig. 22e). Six of the 8 marginals are diamond to triangular shaped (Fig. 23f–j), higher, wider, and rounder than the operculars, 330–650 μm high (average 460 μm), 250–430 μm wide (average 330 μm), with an average H:W of 1.4. Generally the inner lateral marginals have a pointed distal edge that is angled to the right or left (Fig. 23g,h). The remaining 2 adaxial marginals are reduced in size and more circular. This reduction can be extreme such that these scales are sometimes not visible from an anterior view. The outer surface of marginals has granules sparsely covering the proximal area and some tubercles at the proximal margin. The inner surface has a modest simple keel and is tuberculate proximally with a narrow smooth band along the distal edge. Some abaxial submarginals have a pointed distal edge (Fig. 23k).

Large angular, circular and elliptical body-wall scales (Fig. 23l–o) of variable number cover the polyp in rows. These scales are 210–600 μm high (average 350 μm), 230–510 μm wide (average 340 μm), with an average H:W of 1, and are larger towards the polyp anterior. The outer surface is smooth with a few granules at the base whilst the inner surface is tuberculate. All the sclerites of this species have a finely serrate distal edge and roughly lobate proximal edge.

The coenenchymal scales are small, 150–280 μm high (average 220 μm), 120–200 μm wide (average 165 μm), and irregularly circular (Fig. 23p–t), with an average H:W of 1.34. The inner surface is tuberculate and granules sparsely placed across the outer surface.

Distribution

This species has a circum-Antarctic distribution and is found from 32–655 m depth.

Remarks

Thouarella pendulina was originally described within *Rhopalonella* Roule, 1908, a genus purportedly differentiated from *Thouarella* in having densely arranged polyps (Roule 1908). This tight clustering remains one of the distinguishing characteristics of this species although it is now considered to be within the range of variation of *Thouarella*.

The polyps of this species have two alternating rings of marginals, however the adaxial marginals are usually not synchronised with the alternating pattern and are reduced and thus not visible from the anterior (Fig. 22e). The polyps of *Thouarella pendulina* can in fact be compressed against the stem, reducing the number of adaxial body-

wall scales per row to one or two. This is an oddity within *Thouarella* whose polyps generally depart the branchlets at 45–60° and have at least 3–4 adaxial body-wall scales per row.

Thouarella pendulina has a variable gross morphology. Some colonies have tightly packed simple branchlets, which are densely covered in polyps. Other colonies have sparser branching (1–2 per cm) with fewer polyps per cm on branchlets. Some colonies have branching between these extremes.

Comparisons

There are several species that have a similar number of abaxial scales (4–5) as *T. pendulina* and should thus be compared (Table 3).

Thouarella pendulina could most easily be mistaken for *T. hicksoni*, whose colony form is bottlebrush and polyps similar in size (with 4–5 scales in the abaxial row), shape, and are also clustered (although in *T. pendulina* they are more clustered). However, the operculars of the polyps of *T. hicksoni* are tongue-shaped, whereas those of *T. pendulina* are lanceolate with a pointed distal edge. Also, the inner surfaces of the operculars of *T. hicksoni* do not have a well-defined keel, instead tending to have an area of longitudinal striations.

Although the polyps of *T. brucei* have a similar number of abaxial body-wall scales as those of *T. pendulina*, the latter has an almost bilateral colony appearance (although it is technically bottlebrush), polyps that are larger and more flared, and larger operculars than the former.

Thouarella andeep also has 4–5 scales in the abaxial rows, however its polyps are flared and larger, making the operculars and marginals larger than those in the polyps of *T. pendulina*. The polyps of *T. andeep* are also less clustered, and more splayed than those of *T. pendulina*.

The gross morphology of some ramified colonies of *T. pendulina* is very similar to that of *T. variabilis*. However, colonies of *T. variabilis* have longer polyps that are less clustered and elongated marginals that are absent in the former.

Thouarella striata has larger polyps than those found on *T. pendulina* and distinctive striations on the inner surface of sclerites (lateral to the keel on the marginals and perpendicular to the distal edge on other sclerites) that are absent in *T. pendulina*.

Thouarella pendulina has a similar shaped polyp to *T. longispinosa* (= *Dasystenella acanthina*). However, the former has eight marginals (not five as in *Dasystenella*) and polyps of *T. pendulina* do not occur in whorls.

11. *Thouarella chilensis* Kükenthal, 1908

Figs 24, 25

Thouarella chilensis Kükenthal, 1908: 11; 1912: 302–304 (incorrectly described as new), text figs 4–8, pl.11, fig. 5; 1915: 150 (key)

Thouarella (*Epithouarella*) *chilensis* Kükenthal 1919: 436, text fig. 215; 1924: 300; Cairns & Bayer 2009: 28 (listed)

Material examined: **Holotype**, C1780, ZMH, Iquique, Chile, no depth, 14 cm colony.

Other material: NHM 89.5.27.43, H.M.S. *Challenger*, sta. 148A, off Crozet Island, sub-Antarctic, 46°5'S, 51°52'E, 1005 m, 3 Jan 1874, 1 fragment; USNM 1129149, R/V *Islas Orcadas*, cruise 575, sta. 65, Candlemas Island, South Sandwich Islands, Scotia Sea, 56°44'17"S, 26°58'36"W, 302–375 m, 31 May 1975; USNM 97967, R/V *Hero*, cruise 715, sta. 873, Thetis Bay, Tierra del Fuego, Argentina, 54°34'S, 65°50'W, 118 m, 26 Oct 1971; USNM 97966, R/V *Hero*, cruise 715, sta. 873, Thetis Bay, Tierra del Fuego, Argentina, 54°34'S, 65°50'W, 119 m, 26 Oct 1971, 2 colonies (8.5 cm, 9 cm); USNM 1099387, R/V *Lawrence M. Gould*, cruise LMG06–05, sta. 2, off Isla Grande de Tierra del Fuego, Argentina, South Atlantic Ocean, 53°47'S, 64°53'W, 120 m, 15 May 2006, 3 small fragments; USNM 98283, R/V *Eltanin*, cruise 11, sta. 974, north of Cape San Diego, Tierra del Fuego, Argentina, South Atlantic Ocean, 53°33'S, 64°56'W, 119–124 m, 12 Feb 1964, 7 colonies; USNM 97965, R/V *Hero*, cruise 715, sta. 870, north of Islas de los Estados, Argentina, 54°34'S, 64°00'W, 84 m, 24 Oct 1971; MNHN, MD 42, sta. 5, CP 30, Williams Bank, SE Indian Ocean, 53°18'S, 73°19'E, 250 m, 15 Jan 1983; SMF, EPOS 3, sta. 290, AT 24, Cape Norvegia, Weddell Sea, Antarctica, 71°05.9'S, 12°34'W, 522–531 m, 19 Feb 1985; ZMH, R/V *W. Herwig*, sta. 278, Patagonian Shelf, SW Atlantic, 40°57'S, 56°52'W, 200 m, 21 Jun 1966; ZMH, R/V *W. Herwig*, sta. 142, Patagonian Shelf, SW Atlantic, 42°06'S, 57°55'W, 788–765 m, 04 Jan 1971; ZMH, R/V *W. Herwig*, sta. 590, Burdwood Bank, SW Atlantic, 54°39.1'S, 61°44.6'W, 940–960 m, 1978; MNHN, MD 24, sta. 42, CM 59, L?na Bank, sub-Antarctic, 52°59'S, 44°22.7'E, 295–325 m, 4 Sep 1980; SMF, R/V *W. Herwig* 1971, sta. 277, 52°S, 55°20'W, 1200 m; SMF, MD 42, sta. 22, 1968, no location information.

Description

The holotype is a single bottlebrush branch (Fig. 24a), with short, 15 mm long, rigid branchlets that depart the main stem in at least 4 directions.

The polyps are isolated, upwardly inclined at 45–80°, 2.5–2.75 mm high, with a density of 11–23 per cm on branchlets, and densely placed at the branchlet tip, at 21–28 per cm (Fig. 24b). The polyps are modestly distally flared, stout, and have 8 longitudinal rows of body-wall scales and 6–8 scales in each abaxial row (Fig. 24c).

The operculars are triangular to arrow-head shaped (Fig. 25e–g), 415–510 µm high (average 460 µm), 200–300 µm wide (average 250 µm), with a H:W of 1.65–2.00 (average 1.8). The outer surface has granules arranged radially from the proximal central area (Fig. 25e,f) that develop into striations towards the distal edge whilst the inner surface bears a complex, multi-keel (Fig. 25g). Accessory operculars are occasionally present (Fig. 25a–d), approximately 225–150 µm high, 100–115 µm wide, with an average H:W of 1.7 (1.5–1.95).

The marginals are a wide triangle to lanceolate shape (Fig. 25h–l), 520–565 µm high (average 535 µm), 460–560 µm wide (average 510 µm), with a H:W of 0.9–1.2 (average 1). The outer surface, similar to the operculars, has granules arranged radially from the proximal central area that develop into striations towards the distal edge (Fig. 25h,i,l). The inner surface has a channelled multi-keel with rough edges (Fig. 25j,k). Sometimes the keel has lateral extensions that are visible from the outer surface. The proximal inner surface is covered with tubercles and areas lateral to the keel are often ridged/striated.

Submarginals are wider (with rounded lateral edges), and shorter than the marginals, having a modest distal point (Fig. 25m–o), a height around 350 µm, width around 400 µm and a H:W of 0.8. The inner surface is tuberculate, with occasional ridges perpendicular to the distal edge. The outer surface has granules in a radial pattern that develop into striations towards the distal edge, which is similar to the marginals and the operculars.

The body-wall scales are roughly elliptical (Fig. 25p–t), 290–400 µm high (average 350 µm), 445–700 µm wide (average 560 µm), with a H:W of 0.4–0.8 (average 0.6). Generally, the outer surface bears peaked granules towards the central proximal area, while the rest is covered in pronounced striations that extend radially to the distal edge (Fig. 25p,t). Tubercles are visible at the proximal edge. The inner surface is tuberculate, with a relatively smooth band along the distal edge that often has small ridges. The proximal edge of all the above sclerites is coarsely lobate with a distal edge that is irregular to serrate (unless otherwise stated).

The coenenchymal scales are similarly shaped to body-wall scales except more circular and slightly smaller, down to 250 µm diameter (Fig. 25u–w).

Distribution

This species is found on the Patagonian Shelf, southern Atlantic Ocean, around the Antarctic Peninsula, and in the southern Indian Ocean, at depths between 84–960 m.

Remarks

The holotype of *T. chilensis* was located in the ZMH, however, it was not marked as the holotype. The location and date of the inscription by Kükenthal (1908) match the data in the original type description as does the morphology and we therefore believe C1780 to be the holotype. This specimen was originally listed by the collector Schnehagen (possibly Capt. J. Schnehagen, although his collections were primarily from the South China Seas) as *T. antarctica* and was described by Kükenthal as *T. chilensis* in 1908.

Some colonies are sparsely branched, similar to *T. parachilensis* (Fig. 28a). The colonies are generally a light yellow to white shade of colour.

The dense cylindrical clusters of polyps of *T. chilensis* were used by Kükenthal to distinguish this species from *T. affinis* and *T. crenelata* (Kükenthal 1915; 1924). As the original diagrams and descriptions did not quantify the density of clustering there have been several specimens identified as *T. chilensis* in museums that have denser clusters of polyps at the branchlet tip than the holotype of *T. chilensis*. These are in fact a new species, *T. parachilensis* (described below). A sample of *T. chilensis* (USNM 97966) was also incorrectly considered to be a voucher of *T. antarctica* by Cairns & Bayer (2009, Fig. 6g–l).

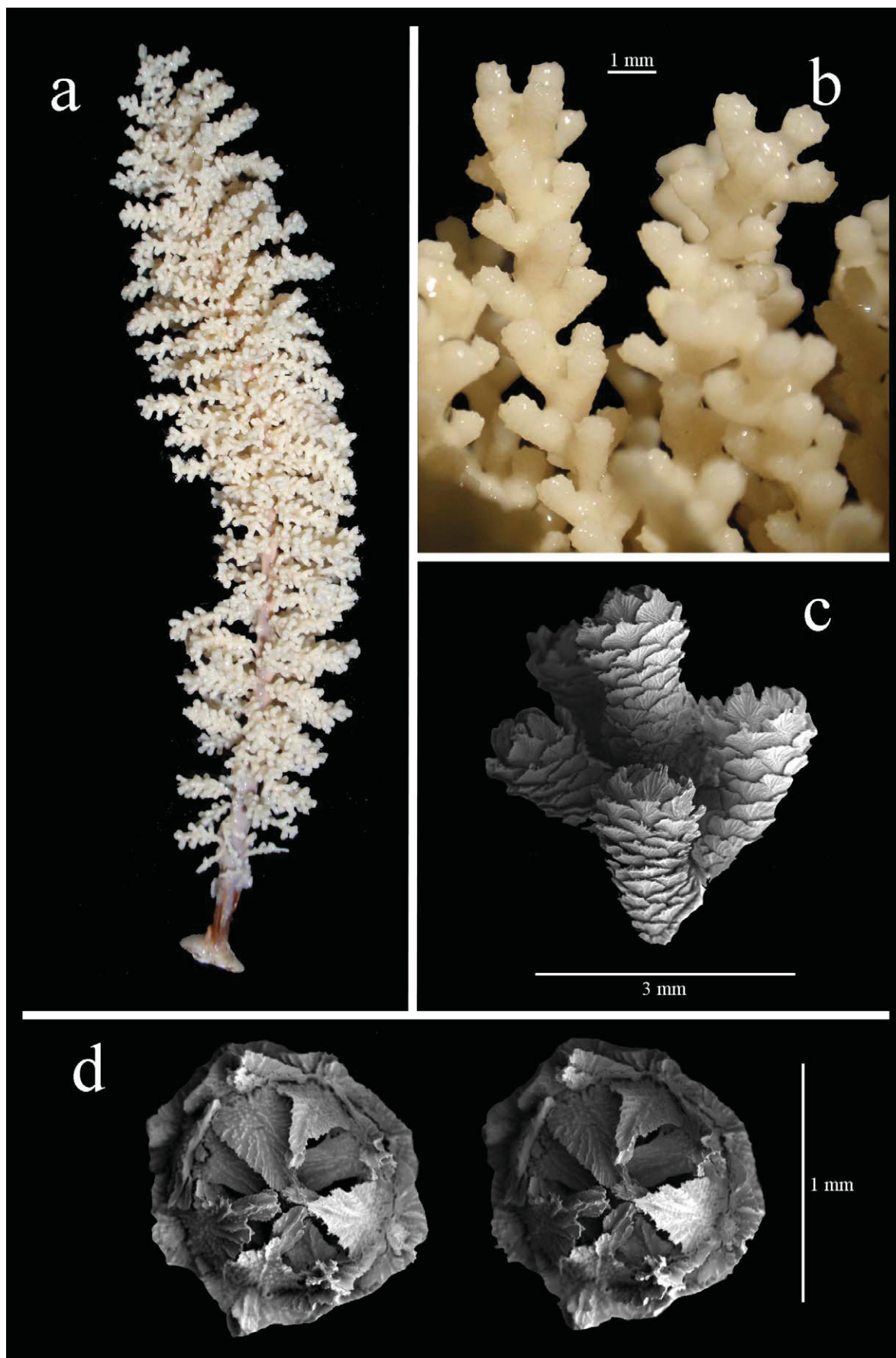


FIGURE 24. *Thouarella chilensis*, holotype, ZMH C1780: a) colony, 14 cm; b) close up of polyps; c) abaxial and lateral views of polyps; d) stereo opercular view of polyp.

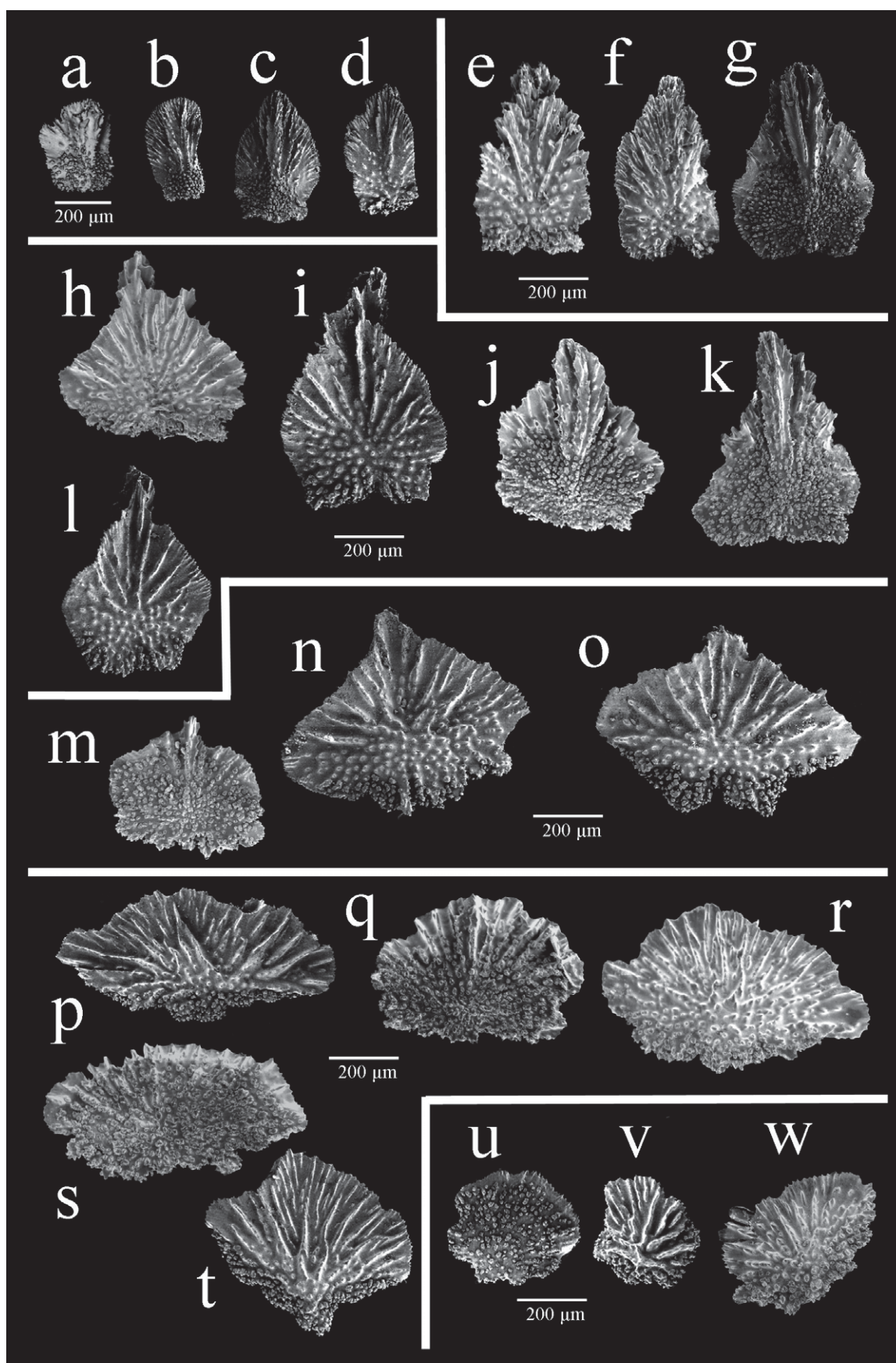


FIGURE 25. *Thouarella chilensis*, holotype, ZMH C1780: a–c) inner and d) outer surface of accessory operculars; e,f) outer and g) inner surface of opercular scales; h,i,l) outer and j,k) inner surface of marginal scales; m) inner and n,o) outer surface of submarginal scales; p,r,t) outer and q,s) inner surface of body-wall scales; u) inner and v,w) outer surface of coenenchymal scales.

Comparisons

The dense polyp arrangement of *T. chilensis* makes it easily mistaken for both *T. antarctica* and *T. parachilensis*. Marginals, submarginals and body-wall scales of *T. chilensis* have an ornamented distal edge with several ridges/striations adjacent to the keel. The marginals of *T. antarctica* have a smoother edge that is more acutely pointed than on the marginals of *T. chilensis*. The polyps of the latter species also have, on average, more scales in the abaxial rows than the former. The operculars of the polyps of *T. antarctica* also tend to be thinner and more delicate than those of *T. chilensis*. The polyps of *T. parachilensis* are rounded and bulbous with 8–15 scales in the abaxial row whilst in contrast, polyps of *T. chilensis* are more squat and stout with just 6–8 abaxial scales.

The polyps of *T. chilensis* are very similar to those of *T. crenelata*, both species having similar polyp and sclerite sizes and shapes. The polyps of *T. chilensis* are, however, more clustered on the branchlets than those of *T. crenelata*, whose polyps are more evenly spaced. The polyps of *T. chilensis* generally have fewer scales in the abaxial row than *T. crenelata* and the outer surfaces of sclerites of the latter are smoother than the striated surfaces found on the scales of *T. chilensis*. The specimens identified in museums and the literature seen within this study suggest that polyps of *T. crenelata* are more rounded than those of *T. chilensis*, however, without having viewed the holotype of *T. crenelata* it is difficult to be certain.

Polyps of *Thouarella chilensis* have a similar number of abaxial body-wall scales (6–8) to those of *T. viridis* (6–7) and *T. affinis* (6–7). Both of the latter have a sparser polyp placement, and taller body-wall scales with a higher H:W than *T. chilensis*. *Thouarella affinis* also has flared rather than clavate polyps.

Polyps of *Thouarella koellikeri* have a similar number of scales in the abaxial row as those of *T. chilensis*. The sclerites of the former are more delicate, the polyps having thinner body-wall scales, marginals that curve away from the polyp body and have a simple keel, whereas sclerites of the latter are thicker with more ornamented marginals that have a wide, complex keel (the lateral extensions of which can sometimes be seen from an abaxial view).

12. *Thouarella hicksoni* Thomson, 1911

Figs 26, 27

Thouarella hicksoni Thomson, 1911: 886–887, pl. 44, figs 3, 3a, pl. 45, fig. 1; Kükenthal 1919: 439–40; 1924: 301–2; Stiansy 1940: 32, text fig. G, pl. 4, fig. 21; Williams 1992: 277–280, fig. 1H, 66–68; Cairns & Bayer 2009: 27 (listed)
Thouarella Hicksoni Tixier-Durivault 1954: 625

Material examined: **Holotype**, NHM 1962.7.20.36, off Cape St. Francis, South Africa, 135 m, rocky substratum, 19 Feb 1902, 8.5 cm and 4.5 cm fragments seen.

Other material: USNM 53911, south of Port Elizabeth, South Africa, 34°15'S, 25°05'E, 11 m, SCD 8–J, collected by J. Day, 1958, 2 colonies; USNM 53912 + USNM 53813 (same location), SCD 3–D, South Africa, 34°30'S, 24°40'E, collected by J. Day, 102 m, 18 Apr 1958.

Description

The holotype is bottlebrush in shape, tapering at the tip (Fig. 26a). The branchlets emanate in 4 directions approximately perpendicular to the main stem, and are tightly placed at 1 mm intervals (Fig. 26b,e). Secondary and tertiary ramification is common and occurs close to the branchlet base. The axis is yellow, iridescent, and has fine longitudinal striations.

The polyps rarely occur on the stem but are usually isolated on branchlets and can be placed in a spiral in 3 directions, but this is inconsistent. The polyps are modestly flared (Fig. 26c,d), angled at 30° to being appressed against the branchlet, and are 1–1.25 mm high, with a H:W of 1.79–1.95, with a clustered arrangement (Fig. 26e) of 16–22 per cm, less towards the branchlet base. Each polyp has 7 longitudinal rows of body-wall scales reducing to 4 rows at the base. There are 4–5 scales in the abaxial rows (Fig. 26c), 3–4 in the outer and inner lateral rows, and 2–3 scales in the adaxial rows.

There are 8 operculars, measuring 300–360 µm high (average 330 µm), 170–210 µm wide (average 190 µm), with an average H:W of 1.7. Two to three of the largest operculars are lanceolate with a pointed distal edge (Fig. 27e) whilst the remainder are tongue-shaped (Fig. 27d). The operculars have a longitudinally concave outer surface, which is smooth, with tubercles sparsely arranged across the proximal area. The inner surface of the operculars have longitudinal median striations or a small simple keel, and the proximal third is tuberculate.

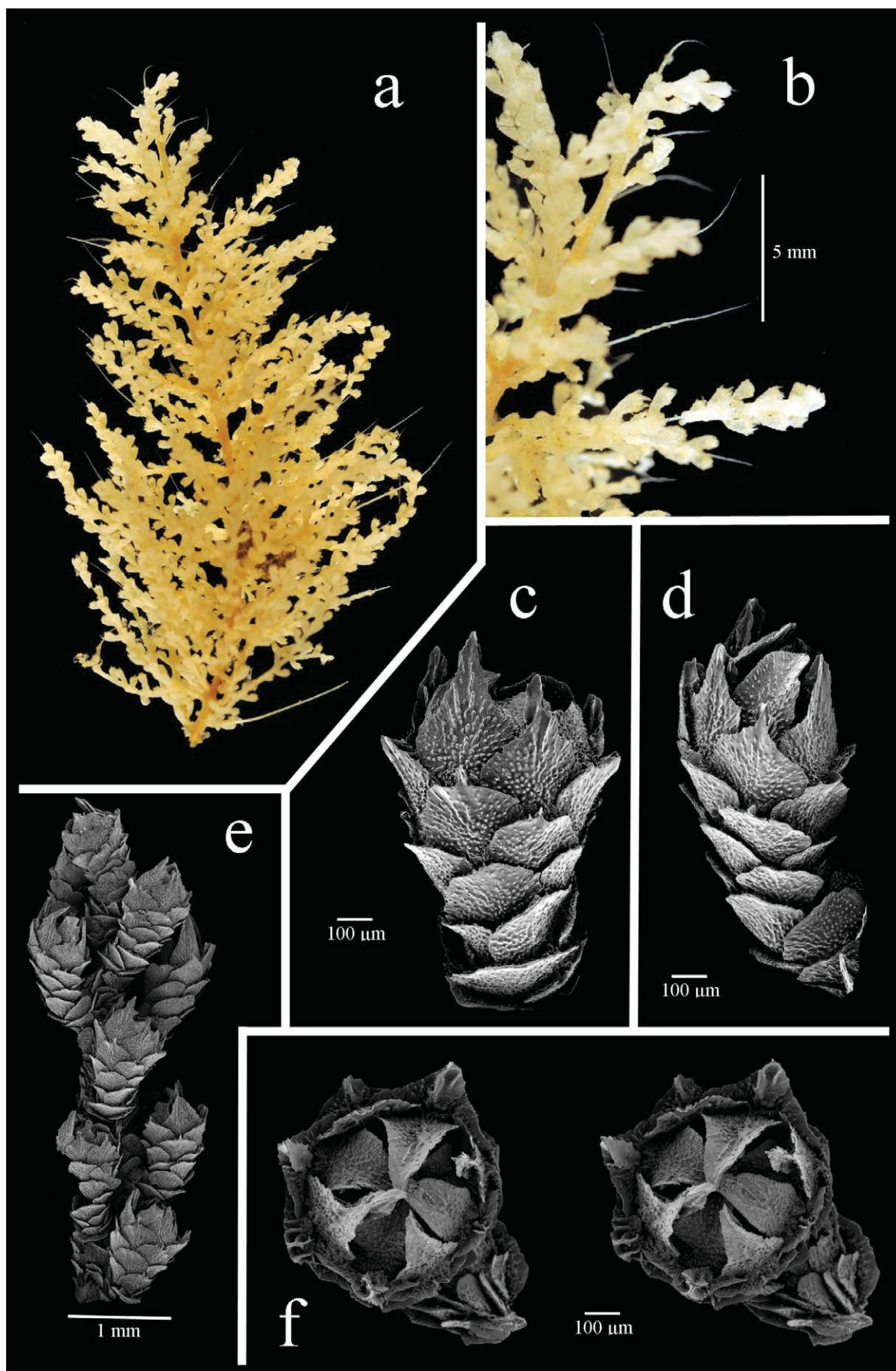


FIGURE 26. *Thouarella hicksoni*, holotype, NHM 1962.7.20.36: a) 4.5 cm colony; b) close up of branchlet; c) abaxial polyp view; d) lateral polyp view; e) branchlet; f) stereo opercular view of polyp.

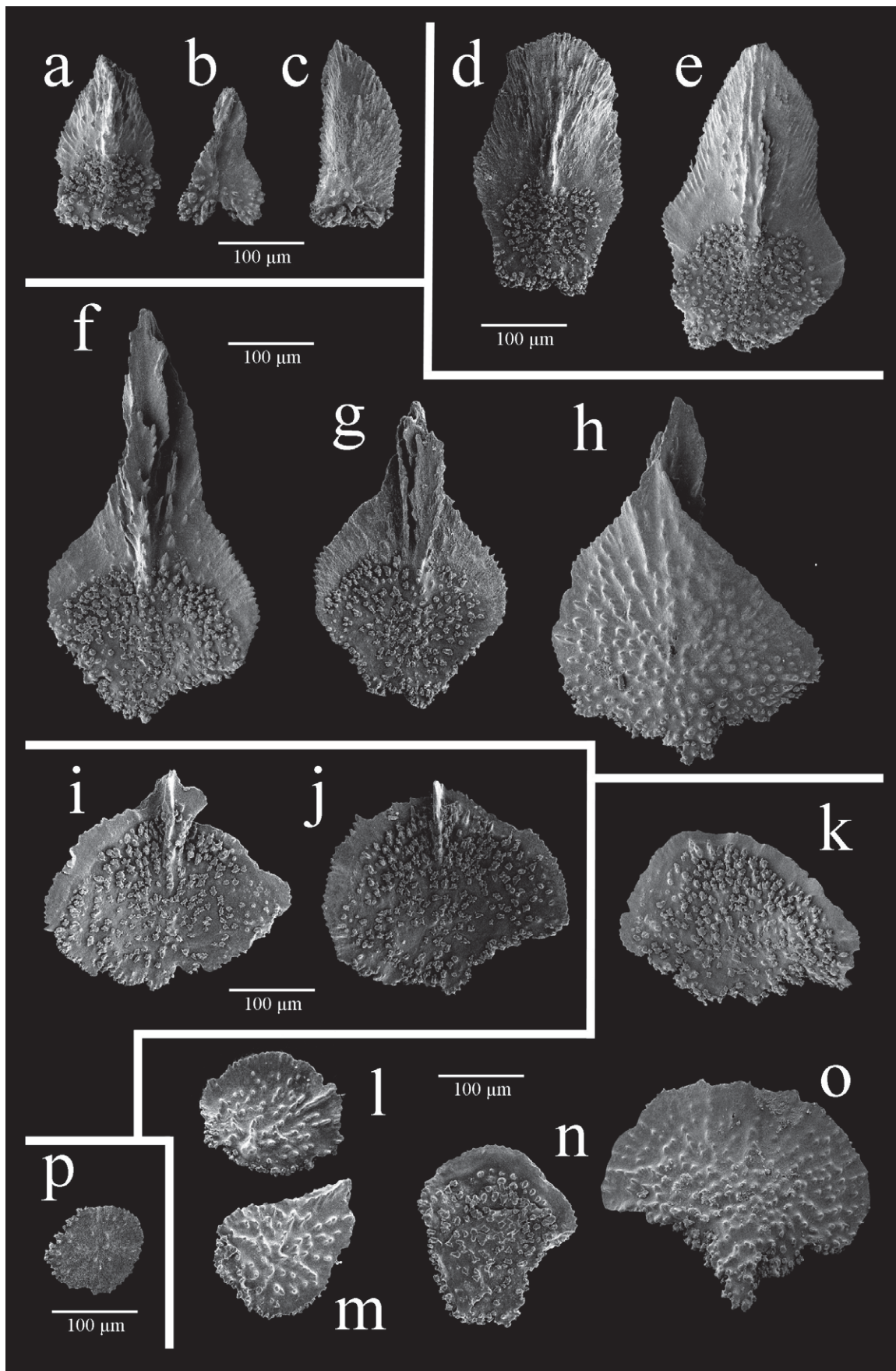


FIGURE 27. *Thouarella hicksoni*, holotype, NHM 1962.7.20.36: a) inner and (c) outer surface of accessory opercular scales; d,e) inner surface of opercular scales; f,g) inner and h) outer surface of marginal scales; i,j) inner surface of submarginal scales; k,n) inner and l,m,o) outer surface of body-wall scales; p) outer surface of a coenenchymal scales. Photos by SJ.

Beneath the 8 operculars are 2–4 (perhaps more in other colonies) accessory operculars (Fig. 27a–c) that are 200–210 μm high (average 200 μm), 110 μm wide, a fraction the size of regular operculars, with a H:W of 1.75–1.9 (average 1.8). They have a relatively smooth outer surface with tubercles visible at the proximal edge and small median longitudinal striations or a small keel (Fig. 27a) on the inner surface, as is present on the larger operculars.

The marginals form 2 alternate circles of 4 inner and 4 outer scales, although the pattern is not strict. They have a wide circular to oval body and are pointed distally (Fig. 27f–h) with a channelled keel on the inner surface (lateral keel projections can sometimes be visible from an abaxial view). Their dimensions are 350–480 μm high (average 400 μm), 220–320 μm wide (average 280 μm), with an average H:W of 1.4 (range of 1.1–2). The adaxial marginals are often shorter with a reduced or absent distal point (probably because these sclerites are compressed against the polyp and thus reduced in size). The inner surface of all marginals is tuberculate with smooth lateral areas adjacent to the keel. The outer surface is covered with granules which are placed more densely in the proximal central area, gradually diminishing in number towards the distal edge.

The submarginals are elliptical with those of the abaxial side often having a moderately pointed distal edge (Fig. 27i,j). They are 250–270 μm high (average 260 μm), 260–280 μm wide (average 270 μm), with an average H:W of 0.9. The inner surface has small, simple single or double (and rarely treble) keels. The central area is tuberculate with a smooth band along the distal edge lateral to the keels. The outer surface is identical to that of the body-wall scales, as described below.

Body-wall scales are semi-circular (Fig. 27k), fan-shaped (Fig. 27o), circular (Fig. 27l) or irregular in shape (Fig. 27n,m), often with an irregularly lobate proximal edge. Body-wall scales are 190–270 μm high (average 220 μm), 140–310 μm wide (average 240 μm), average H:W of 0.9 (range of 0.7–1.4). The outer surface is covered with granules proximally, with some tubercles at the proximal edge; the inner surface is tuberculate with a smooth band along the distal edge.

The coenenchymal scales are circular (Fig. 27p), 110–150 μm high (average 130 μm), 100–180 μm wide (average 140 μm), with an average H:W of 1, with a smooth outer surface and tuberculate inner surface.

Distribution

This species is only known from the Port Elizabeth region, South Africa, at depths of 11–135 m.

Remarks

Contrary to Thomson's description (1911), the branchlets at the colony base tend to be shorter; likely as a result of damage when collected.

A small, circular, pebble-encrusted casing (perhaps an egg case) was found within the branchlets of the holotype.

Comparisons

Thouarella hicksoni and *T. pendulina* are very similar, sharing a similar number of abaxial body-wall scales, polyp length, and a clustered polyp arrangement (see Table 3). However, *T. hicksoni* has fewer polyps per cm and some operculars that have a tongue-shaped distal edge (Table 3).

The polyps of *T. striata*, *T. variabilis*, and *T. andeep* have a similar number of scales in the abaxial row as the polyps of *T. hicksoni*, however, these three species have large, distally flared polyps that are arranged less densely on the branchlets than is found on specimens of *T. hicksoni*.

The polyps of *T. hicksoni* have a similar number of scales in the abaxial rows, and similar marginal shapes as found in the polyps of *T. brucei*, however, the former species generally has smaller (noting that some additional specimens of *T. brucei* have smaller polyps than the holotype), more pointed polyps, and more clustered, finer, flexible branchlets.

13. *Thouarella bipinnata* Cairns, 2006

Thouarella bipinnata Cairns, 2006: 176–181, figs 8, 9; Cairns & Bayer 2009: 28 (listed)

Material examined: **Holotype**, USNM 53015, *Gerda* 177, Straits of Florida, off northwest corner of Little Bahamas Bank, 27°17'N, 79°34'W, 686 m depth, 30 Jun 1963.

Other material: all other specimens are from the original description (Cairns 2006).

Description

Description modified from the original (Cairns 2006).

Colonies are uniplanar, delicate, and irregularly pinnate to bipinnate (occasionally 2 branchlets occur contiguously on the same side of the stem). The largest specimen (the holotype) is 9 cm long and 10 cm wide with a basal axis diameter of 1.6 mm. The holotype has 4 larger diameter branchlets near the colony base, each with a series of smaller branchlets, up to 30 mm long, that are placed roughly alternately at intervals of 5–15 mm. The axis is golden-yellow colour with a white calcareous discoidal holdfast.

The polyps occur on the main stem and branchlets in a roughly alternating arrangement. Occasionally 2 polyps are arranged opposite to each other but there is no consistent tendency towards pairing or whorls. The polyps of the holotype are orientated toward one face of the colony, with a density of 11–14 per cm, they stand perpendicular to the branchlet, are modestly clavate, and up to 2.4 mm high with a H:W of 1.8–2.2. Each polyp has 6–8 longitudinal rows of scales with 3–5 in the abaxial row. The scales increase in size proximally as the polyp diameter decreases such that at the polyp base there are no adaxial scales and the inner-laterals are either reduced or absent.

The operculars are lanceolate to arrowhead-shaped, up to 900 μm high, with a H:W of 2.1–2.9, and form a well-defined operculum. The outer surface has radial striations from the proximal centre and a deep depression, corresponding to a large simple keel on the inner surface, the keel having many adjacent striations. Tubercles cover the proximal third of the inner surface of the opercular scales.

The marginals are arranged in inner and outer rings of 4 scales each with their distal edges overlapping. The marginal scales are the same size as the operculars but more rounded proximally and have a pointed distal edge and a lower H:W of 1.3–2.1. The inner surface bears a complex keel with wide lateral projections whilst the remaining inner surface area is tuberculate with a narrow smooth distal band along the lateral edges. The outer surface has low radial striations from the proximal centre and some granular markings.

The submarginals are elliptical, with a short, pointed distal edge, and are 500–600 μm high with a H:W of 0.9–0.95. The inner surface is tuberculate with a wide smooth edge distally and some ridges perpendicular to the edge whilst the outer surface is mostly smooth with rare granules arranged radially from the proximal centre.

The body-wall scales are roughly rectangular, sometimes rounded, usually broader than wide (H:W of 0.85–0.9), and can be 800 μm wide towards the polyp base. The proximal outer surface is covered in granules and sometimes striations. The inner surface is tuberculate, often with ridges perpendicular to the distal edge. As with all polyp sclerites of this species, the distal edge is finely serrate and the proximal edge coarsely lobate.

The coenenchymal scales are irregular shaped, up to 600 μm in diameter, and have a highly concave outer surface.

For images see Cairns (2006).

Distribution

Blake Plateau, off northern Florida, and Straits of Florida, off Little Bahamas Bank, to Guyana, from depths of 507–1000 m.

Comparisons

Thouarella bipinnata is the only species within Group 1 that is truly uniplanar with bipinnate to pinnate branching. There are several species that can appear bilateral e.g. *T. koellikeri*, the colonies of which also have roughly alternating polyps of a similar size to *T. bipinnata*. However, the polyps of *T. koellikeri* are more rounded, there are double the number of scales in the abaxial rows (7–10, rather than 3–5 in *T. bipinnata*), and polyps of *T. koellikeri* have a lower opercular cone than those of *T. bipinnata*. *Thouarella affinis* and *T. viridis* have colonies that can both appear bilateral, however, the polyps of both have more scales in the abaxial rows (6–7) than *T. bipinnata*. *Thouarella brucei* and *T. andeep* can have a bilateral colony shape and both have 4–5 scales in the abaxial rows of polyps, comparable to *T. bipinnata*. However, *T. bipinnata* has modestly clavate polyps, very different from the distally flared polyps of *T. andeep* and *T. brucei*.

14. *Thouarella viridis* Zapata-Guardiola and López-González, 2010a

Thouarella viridis Zapata-Guardiola & López-González, 2010a: 169–180, figs 7–10.

Holotype (not examined): ZMH C11744, ANT XIX/5, sta. PS61/164–01, west of South Georgia, Antarctica, 53°23.8'S, 42°42.03'W, 312.5–321.6 m, 9 Apr 2002.

Material examined: **Paratype**, USNM 1128949, Antarktis XIX/5, R/V *Polarstern*, sta. PS61/167–01, west of South Georgia Island, sub-Antarctic, 53°23.68'S, 42°42.23'W, 306–342.7 m, 9 Apr 2002, 1 colony, 1 fragment.

Other material: USNM 1130303 and USNM 98027 (same location), R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia Island, sub-Antarctic, 54°30'S, 39°20'W, 659–686 m, 8 Feb 1966; USNM 78401, R/V *Eltanin*, cruise 5, sta. 217, Le Maire Strait, Tierra del Fuego, Argentina, 54°22'S, 64°42'W, 106–110 m, 23 Sep 1962; ZMH, R/V *W. Herwig*, sta. 328, Patagonian Shelf, SW Atlantic, 42°52'S, 58°38'W, 1200 m, 22 Feb 1971; ZMH, R/V *W. Herwig*, sta. 285, Patagonian Shelf, SW Atlantic, 42°19'S, 58°01'W, 825 m, 21 Jun 1966; ZMH, R/V *W. Herwig*, sta. 311, Patagonian Shelf, SW Atlantic, 46°54'S, 60°28'W, 480 m, 18 Feb 1971; ZMH, R/V *W. Herwig*, sta. 243, Burdwood Bank, SW Atlantic, 54°57'S, 56°54'W, 500 m, 04 Feb 1971; ZMH, R/V *W. Herwig*, sta. 271, south Falkland Islands, sub-Antarctic, 52°40'S, 60°39'W, 405 m, 09 Feb 1971.

Description

Description modified from Zapata-Guardiola and López-González (2010a).

The holotype consists of a fragment of one colony. Branching is in at least 3 directions, and thus bottlebrush, however branches can be curved, giving the colony a bilateral appearance. The branchlets are up to 30 mm long, at a density of 7–8 per cm, and usually simple with occasional secondary branching. Fresh specimens are a shade of green, fading to white after preservation. The axis is ochre coloured, stiff and thick, with a basal axis diameter of 4 mm.

The polyps are clavate with a conical operculum, 1.5–2.5 mm high, isolated (occasionally opposite) but emanating from branchlets in irregular spirals. The polyps are more clustered towards the branchlet tip and sparser at the base, with an average density of 14–15 per cm. The polyps have 8 longitudinal rows of body-wall scales, 6–7 scales in each abaxial row.

The operculars are lanceolate to arrow-head shaped, some with a wide bilobate base, and are 620–780 µm high and 470–640 µm wide. The inner surface bears a prominent simple keel that often has lateral projections and adjacent longitudinal ridges; tubercles densely cover the proximal third of the scale. The outer surface is deeply longitudinally concave, corresponding to the keel on the inner surface whilst the proximal region has radial striations extending from a proximal centre, and granules distally.

The marginal scales are pentagonal to widely triangular in shape, 450–630 µm high and 470–640 µm wide. The inner surface has a wide, multiple keel with ridges adjacent and tubercles cover the proximal two-thirds to three-quarters of the inner surface. The outer marginal surface is covered with low relief granules that are more concentrated proximally.

The body-wall scales and submarginals cannot be differentiated. Both are fan-shaped with a rounded distal edge, wider than they are high, 270–510 µm high, 340–740 µm wide, decreasing in size towards the polyp base. The inner surface is tuberculate, with a smooth distal band broken by several ridges perpendicular to the distal scale edge with the occurrence of ridging decreasing from polyp tip to its base. The outer scale surface is similar to that of the marginals. All polyp sclerites of this species have a coarsely lobate proximal edge.

The coenenchymal scales are round to elliptical in shape and up to 130–360 µm high. The inner surface is tuberculate and the outer surface has closely spaced granules that stretch into striations. The scale edges are irregular with warts proximally whilst the distal edge is finely serrate.

For images see the original description (Zapata-Guardiola and López-González 2010a).

Distribution

Our specimens extend the range of this species from the Falkland Islands and South Georgia Island, west to the Patagonian Shelf at depths from 106–825 m.

Remarks

The green shading makes this species easily recognisable.

Comparisons

The opercular scales of the polyps of *Thouarella viridis* have a deep longitudinal groove on the outer surface, and a complex keel, with many longitudinal adjacent ridges, on the inner surface. Conversely, those of *T. antarctica* has a relatively shallow groove on the outer surface and the keel is more simple, with multiple projections extending from a central point. The polyps of *T. antarctica* are also more flared than those of *T. viridis*, the latter having clavate polyps.

The polyps of *Thouarella koellikeri* have more scales in the abaxial rows than *T. viridis* (7–10 in the former, 6–7 the latter), so although the polyps are of a comparable size, the scales of *T. koellikeri* are generally smaller. The keels on the marginal scales of the former are simple whereas those of the latter have adjacent ridges. The abaxial body-wall scales of the polyps of *T. koellikeri* also lack the distinctive teeth/ridges found on those of *T. viridis*.

The polyps of *Thouarella parachilensis* are densely clustered at a branchlet tip. This clustering is absent on the branchlets of *T. viridis*, and the flat operculum of the former differs markedly from the tall, rounded operculum of the latter.

The polyps of *Thouarella affinis* have a similar number of scales in the abaxial rows as the polyps of *T. viridis* however the marginals of the former have simpler keels. The submarginal scales of *T. viridis* also have multiple ridges on their inner distal edge and on some of the body-wall scales, which are absent in the former.

The polyps of *Thouarella crenelata* are clavate, similar to those of *T. viridis* however, the latter has a tall operculum whereas the former has an operculum not visible in lateral view. The polyps of *T. crenelata* also tend to have more scales in the abaxial rows than is found on the polyps of *T. viridis*.

15. *Thouarella minuta* Zapata-Guardiola and López-González, 2010a

Thouarella minuta Zapata-Guardiola & López-González, 2010a: 169–180, figs 11–13.

Material unavailable: **Holotype**, ZIZMH C11742, ANT XXI–2, sta. PS65–166–01, Austasen, Antarctica, 70°56.83'S, 10°32.61'W, 253.2–338 m, 15 Dec 2003.

Material examined: **Paratype**, USNM 1128948, ANT XXI/2, sta. PS65/166–01, Austanen, Cape Norvegia, Antarctica, 70°56.83'S, 10°32.61'W, 253.2–338 m, 15 Dec 2003.

Other material: USNM 82873, Deep Freeze II, sta. 17, Staten Island, Tierra del Fuego, Argentina, 71°18'S, 13°32'W, 238 m, 27 Dec 1956; SMF, EPOS 3, sta. 257, AT19, Weddell Sea, Cape Norvegia, Antarctica, 71°39.5'S, 12°34.7'W, 301–330 m, 15 Feb 1989.

Description

Description modified from the original (Zapata-Guardiola and López-González 2010a):

The holotype is a single branch which is 66 cm long, 5.5 cm wide, with branchlets emerging from all sides in a bottlebrush arrangement although the basal 9 cm of the main branch lacks branchlets. The branchlets are up to 45 mm long, simple at the base, then dividing into 2, sometimes 3, branchlets with the terminal branchlets being up to 35 mm long. The axis is woody, light brown in colour, with a diameter of 3 mm. The holotype is fixed to a rock by a greyish discoidal holdfast, which is 13 mm in diameter.

The polyps are isolated, arranged alternately or in loose spirals, 11–18 per cm, and are very small, 0.71–0.96 mm high, 0.3–0.44 mm wide, cone-shaped, and appressed against both the branchlets and the main stem. There is a quick reduction from 8 marginals at the polyp tip as the polyp scales are arranged in 5 longitudinal rows. The polyps have 3–4 scales in the abaxial rows.

The tall, conical operculum gives the polyp a tapered distal shape. The operculum is composed of isosceles triangle or spoon-shaped operculars 250–450 µm high, 70–160 µm wide, which are reduced in size on the adaxial side of the polyp. The inner opercular surface has a simple, sometimes flat surfaced keel, with tubercles across the keel base and a smooth band along the lateral edges of the scale. The outer opercular surface is smooth with a few, small granules towards the proximal edge.

The marginals are round to diamond-shaped, 210–280 µm high, 160–230 µm wide, and reduced in size on the adaxial side of the polyp. The proximal two-thirds of the inner surface is tuberculate with a smooth band along the distal edge broken by a small, simple keel whilst the outer surface is smooth.

The submarginals are indistinguishable from body-wall scales; both are roughly circular, 220–280 µm diameter, with adaxial scales being reduced in size. The inner scale surface is tuberculate and the outer surface is smooth. All polyp sclerites have a finely serrate distal edge and coarsely lobate proximal edge.

The coenenchymal scales are round to elliptical, 120–220 µm maximum diameter/width. The inner surface is sparsely tuberculate whilst the outer surface is smooth to slightly sculpted with sparse ridges and granules sometimes arranged radially.

The images of the colony and sclerites are in the original description by Zapata-Guardiola and López-González (2010a).

Distribution

Our specimens extend the range of *T. minuta* from Austasen, eastern Weddell Sea, Antarctica, to circum-Antarctic, at depths of 226–610 m.

Remarks

Thouarella minuta has the smallest polyps of any described *Thouarella* species.

Comparisons

With only three or four scales in the longitudinal abaxial rows, *Thouarella minuta* is comparable to *T. variabilis*, *T. striata*, *T. pendulina*, *T. hicksoni* and *T. andeep* (Table 3). However, all these species generally have polyps of 1 mm or greater length. The smallest polyps are found on colonies of *T. pendulina* and *T. hicksoni*, which sometimes have polyps of 1 mm (polyps of *T. minuta* are 0.71–0.96 mm high). The operculars of the polyps of *T. hicksoni* are blunt-tipped and those of *T. pendulina* are more triangular than the spoon-shaped operculars of *T. minuta*.

16. *Thouarella andeep* Zapata-Guardiola and López-González, 2010b

Fig. 40c,d

Thouarella andeep Zapata-Guardiola & López-González, 2010b: 142–145, fig. 8c,d, 11–13

Material unavailable: **Holotype**, ZMH C11744, R/V *Polarstern*, Antarktis XXIV/2, sample no. PS7/048–01, off Atka Bay, Antarctica, 70°24'S, 8°19'43"W, 601.8 m, 17 Jan 2008, 2 fragments.

Material examined: **Paratype**, USNM 1123418, details same as holotype.

Other material: USNM 98298, R/V *Eltanin*, sta. 1089, Clarence Island, NE of South Shetland Islands, sub-Antarctic, 60°47'S, 53°30'W, 641 m, 17 Apr 1964; USNM 1130294, R/V *Hero*, cruise 721, sta. 1144, Bismarck Strait, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°52'09"S, 63°50'09"W, 440–480 m, 14 Mar 1972; USNM 1130291, R/V *Hero*, cruise 824, sta. 35–B, 64°50'33"S, 63°51'00"W, 312–330 m, 26 Mar 1982, 1 fragment; USNM 1130289, R/V *Eltanin*, cruise 12, sta. 1081, east of South Orkney Islands, Scotia Ridge, Antarctica, 60°34'S, 40°44'W, 345–350 m, 13 Apr 1964; USNM 98276, R/V *Eltanin*, cruise 27, sta. 1870, Cape Adare, Victoria Land, Ross Sea, Antarctica, 71°16'S, 171°31'E, 659–714 m, 14 Jan 1967; USNM 85296, R/V *Eltanin*, cruise 11, sta. 970, SW coast of Staten Island, Tierra del Fuego, Argentina, 54°59'S, 64°53'W, 586–641 m, 11 Feb 1964, 1 fragment; USNM 1130287, R/V *Eltanin*, cruise 12, sta. 1089, NE of Clarence Island, South Shetland Islands, Antarctic Ocean, 60°47'S, 53°30'W, 641 m, 14 Apr 1964; SMF, EPOS 3, sta. 293, GSN 15, 20 Feb 1989, 1 colony, no location information.

Description

Description modified from Zapata-Guardiola and López-González (2010b):

The colonies appear alternately pinnate although branching is in 3 directions with 2 pinnate rows creating a plane and one row of branching between these 2 rows. The colonies are light pink or white with a bronze axis. The largest colony is 8 cm long (USNM 98276) with a very rigid stem and branchlets, the latter being 21–22 mm long.

The polyps of the paratype are isolated, with a density of 10–11 per cm (more clustered at branchlet tip) and upwardly inclined 80–90° from branchlets and main stem. They are 1.9–3.4 mm high, very wide at 0.7–0.95 mm

and distally flared in shape, with a tall conical operculum. The polyps have 7 longitudinal rows of body-wall scales, quickly reducing to 4 at the base with 4–5 scales in each abaxial row.

There are 5 to 6 tongue-shaped accessory operculars, 240–420 µm high, 70–300 µm wide, which lie underneath the operculars. The inner surface is tuberculate across the proximal half, smooth distally, and has no keel whilst the outer surface is smooth sometimes with low striations proximally.

The operculars are arranged in 2 alternate circles of 4, they are tongue-shaped, sometimes constricted distally, 510–1100 µm high, 340–520 µm wide. The outer circle of operculars is larger than the inner circle. The inner surface of the larger scales have striations perpendicular to the distal edge, no distinct keel, and densely arranged tubercles proximally. Smaller operculars have a smooth inner surface and no striations. The outer surface has striations radiating from a central proximal area.

The marginals have a wide triangle-shape with a pointed distal edge, which can be acutely elongated. The scales are 950–1320 µm high and 740–990 µm wide. The inner surface can have a complex multi-keel (Fig. 40c,d) or an area of striations. The area adjacent to the keel is smooth, and there are tubercles densely arranged below this. The outer surface is densely covered in granules.

The submarginals are not differentiated from body-wall scales and both are irregularly fan-shaped, elliptical, and oval, with a maximum height of 540–840 µm. The inner surface has a dense covering of tubercles, sometimes with a very narrow smooth band along the distal edge whilst the outer surface has densely arranged granules. As with all body-wall sclerites, the distal edge is finely serrate and the proximal edge coarsely lobate.

The coenenchymal scales have a diverse range of shapes from circular to oval to lobate. These scales have a densely tuberculate inner surface and an outer surface with densely arranged granules, that is also often heavily striated. The scale has a maximum length of 60–93 µm.

The images of this species are found in the original description by Zapata-Guardiola and López-González (2010b).

Distribution

The specimens described here extend the range of *T. andeep* to include the southwest Atlantic Ocean, off the tip of South America, and circum-Antarctic areas, at depths from 312–714 m.

Remarks

Thouarella andeep was originally described as having a bottlebrush colony. This is true in the strictest sense of the word, however, as in many *Thouarella* species, branching is not in all directions (usually just in 3), the overall appearance of which can look alternately pinnate. We also add that the marginals do have a keel (see Fig. 40c,d, from paratype).

Comparisons

With four to five scales in each longitudinal abaxial row, a bottlebrush branching arrangement, and distally flared polyps, *Thouarella andeep* is comparable to: *T. minuta*, *T. pendulina*, *T. hicksoni*, *T. variabilis*, *T. striata*, and *T. brucei* (Table 3). *Thouarella minuta*, *T. pendulina*, *T. hicksoni*, and *T. variabilis* all have polyps smaller than those of *T. andeep*. Of the remainder, *T. striata* often has distinct striations on the outer surface of the body-wall sclerites, whereas *T. andeep* has fine granules, and the latter also lacks the striations common on the inner surface of *T. striata* sclerites. Furthermore, *T. brucei* has a keel on the operculars that is lacking in *T. andeep*. *Thouarella brucei* also usually has smaller polyps than *T. andeep*.

17. *Thouarella parachilensis* sp. nov.

Figs 28, 29

Material examined: **Holotype**, USNM 98338, R/V *Islas Orcadas*, cruise 575, sta. 90, South Georgia Island, sub-Antarctic, 54°50'36"S, 37°23'48"W, 223–227 m, 7 Jun 1975, 1 colony; **Paratype**: USNM 98190 (SEM images), R/V *Professor Siedlecki*, cruise 86–01, sta. 121, 53°57'S, 38°10'W, South Georgia Island, sub-Antarctic, 90–100 m, 6 Dec 1986, 1 colony; **Paratype**, ZSL SG09, Ev. 35, 53°44.07'S, 37°14.58'W, NW of South Georgia Island, sub-Antarctic, 125 m, 18 Jan 2009.

Other material: USNM 84341, R/V *Professor Siedlecki*, cruise 86–01, sta. 122, 53°55'S, 38°03'W, South Georgia Island, sub-Antarctic, 119–130 m, 16 Dec 1986; USNM 97951, R/V *Islas Orcadas*, cruise 575, sta. 12, 53°38'12"S, 37°54'42"W, South Georgia Island, sub-Antarctic, 130–137 m, 13 May 1975; USNM 98087, R/V *Professor Siedlecki*, cruise 86–01, sta. 19, 54°02'S, 39°06'W, South Georgia Island, sub-Antarctic, 212–224 m, 2 Dec 1986; USNM 98387, R/V *Hero*, cruise 721, sta. 1144, Bismarck Strait, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°52'09"S, 63°50'09"W, 440–480 m, 14 Mar 1972; USNM 98361, R/V *Hero*, cruise 731, sta. 1884, Quintana Island, Wilhelm Archipelago, Antarctic Peninsula, 65°06'12"S, 64°59'51"W, 100–180 m, 3 Mar 1973; USNM 98104, R/V *Professor Siedlecki*, cruise 86–01, sta. 9 and 10, Shag Rocks, South Georgia Island, sub-Antarctic, 53°3'S, 41°57'W, 133–165 m, 30 Nov 1986; USNM 98173, R/V *Eltanin*, cruise 22, sta. 1536, west tip South Georgia Island, sub-Antarctic, 54°30'S, 39°20'W, 659–686 m, 8 Feb 1966; USNM 98085, R/V *Eltanin*, cruise 12, sta. 993, west of Aspland Island, South Shetland Islands, Antarctic Ocean, 61°25'01"S, 56°31'01"W, 300 m, 13 March 1963; USNM 98159, R/V *Hero*, cruise 731, sta. 1944, Neumayer Channel, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°46'40"S, 63°25'33"W, 100–150 m, 11 Mar 1973.

Etymology

The name refers to *Thouarella chilensis*, for which this species was often mistaken.

Description

The colonies are flabellate (Fig. 28a), sparsely branched, and usually brown-red in coloration. The largest specimen (the holotype) is 290 mm long and 200 mm wide. The branches are feather-shaped with shorter branchlets at the apex and towards the base. The branchlets are sturdy, departing perpendicular to the branch on all sides, in a bottlebrush arrangement. There are 3–5 branchlets per cm, they are usually a maximum of 30 mm long, shorter towards colony base, mostly simple with some secondary branching, and ramification usually occurs close to the branchlet base.

The polyps of the holotype are clavate and bulbous (Fig. 28b,c), sometimes with a flat adaxial surface (being compressed against neighbouring inner polyps; Fig. 28e). The polyps are 2.5–2.8 mm high, placed at an almost right-angle to the branchlets at the branchlet base but upwardly inclined towards the branchlet tip (up to 45°). They are spaced at 9–30 per cm at branchlet base and in a dense cluster at branchlet tip, where they form an almost solid cylinder of polyps ('barrel-shaped', Fig. 28c) with 18–48 per cm. Each polyp has 8 longitudinal rows of scales, 8–15 scales in the abaxial rows (average 11, Fig. 28d), and a reduced number adaxially. The scales are progressively wider and shorter from polyp head to base.

The operculum is flat. The operculars are arrowhead or lanceolate in shape (Fig. 29a–f) but can be wider and pentagonal, up to 420–510 µm high (average 460 µm), 230–410 µm wide (average 340 µm), with an average H:W of 1.4 (1.2–1.8). The inner opercular surface has a large, multi-keel (Fig. 29a,f) and many adjacent ridges resulting in a serrate distal edge whilst the proximal half is tuberculate. The outer scale surface has a deep longitudinal indentation (Fig. 29b–e), large granules extend into ridges that run perpendicular to the distal edge, and there can be tubercles along the proximal edge.

The marginals are wider than the operculars, 340–510 µm (average 440 µm), 380–470 µm high (average 430 µm), with an average H:W of 1 (range from 0.7–1.2). The marginals are elliptical in shape with a pointed distal edge (Fig. 29g,h). The inner surface has a small, simple keel with smaller adjacent keels leading to a serrated distal edge. The proximal two-thirds is tuberculate and distal third smooth lateral to the keel and ridges. The outer surface has a longitudinal groove with sparse, large granules occurring towards the proximal edge, where tubercles are also visible.

The submarginals are clearly visible from an anterior polyp view (Fig. 28e) as the distal edges curve slightly away from the polyp body. They are elliptical (Fig. 29i–k), wider than the marginals, 540–890 µm (average 700 µm), and about the same height, 350–550 µm (average 430 µm), with an average H:W of 0.6 (range from 0.4–0.9). The ridges are infrequent on the inner surface perpendicular to distal edge, the edge being serrate whilst the remainder of the inner surface is tuberculate. The outer surface has sparse granules proximally.

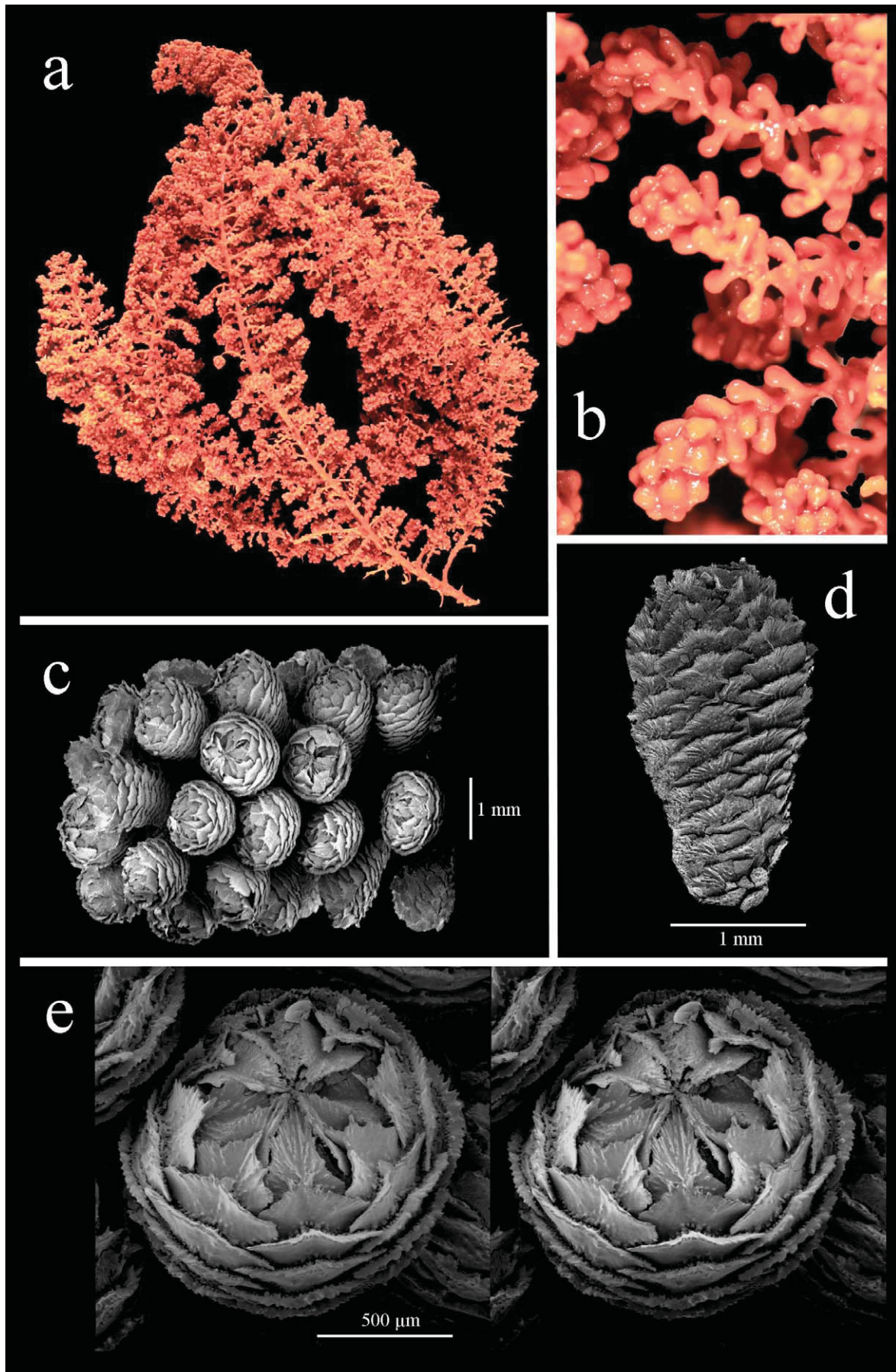


FIGURE 28. *Thouarella parachilensis* sp. nov, holotype, USNM 98338: a) colony, 29 cm long, 20 cm wide; b,c) close up of ‘barrel-shaped’ clusters of polyps; d) abaxial polyp view; e) stereo opercular view. Photo by SJ.

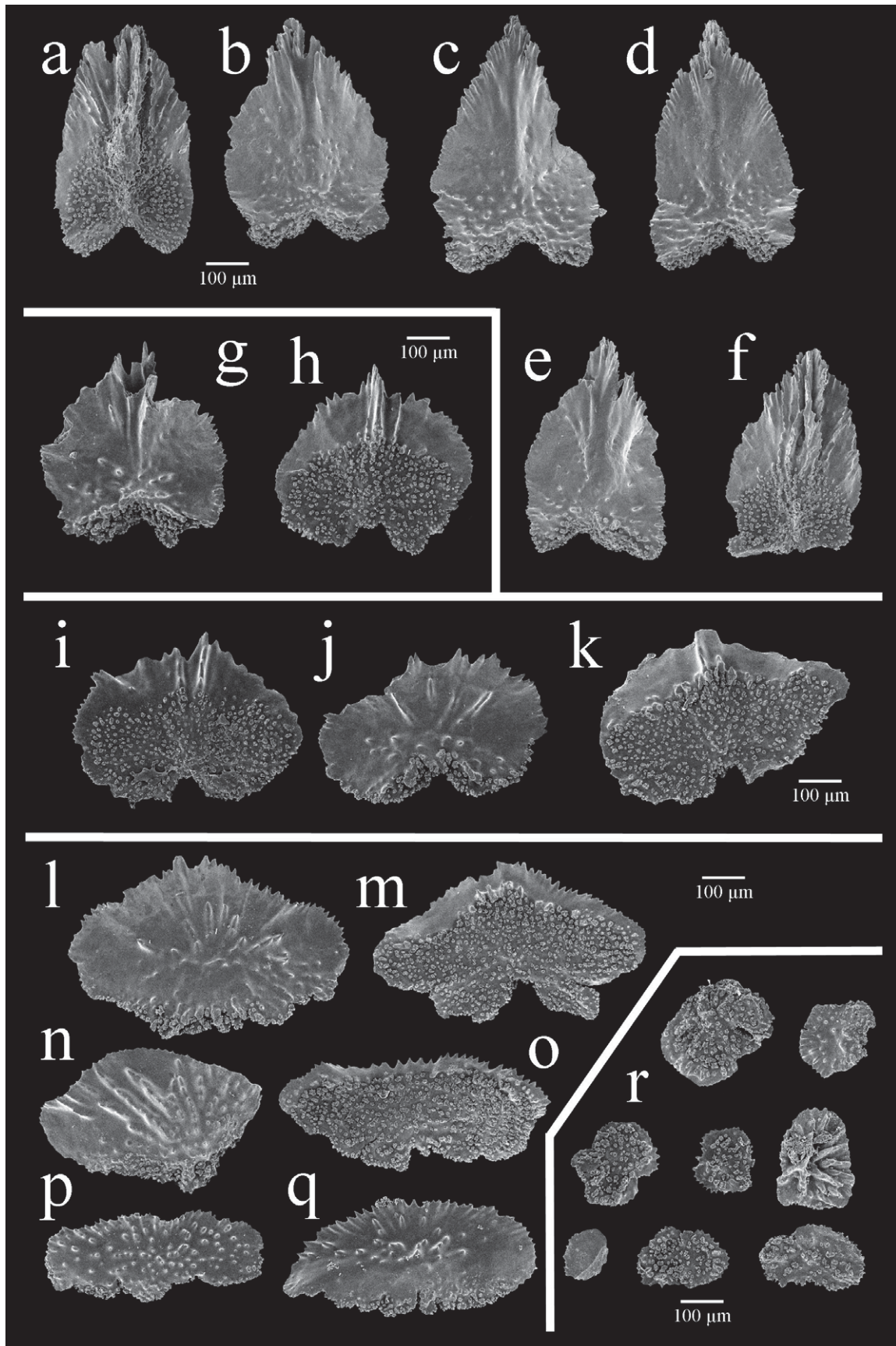


FIGURE 29. *Thouarella parachilensis* sp. nov, holotype, USNM 98338: a,f) inner and b–e) outer surface of opercular sclerites; g) outer and h) inner surface of marginal scales; i,k) outer and j) inner surface of submarginal scales; l,n,p,q) outer and m,o) inner surface of body-wall scales; r) coenenchymal scales—top row right, middle row right, bottom row left show the outer surface, remainder inner surface.

The body-wall scales are elliptical, very broad (Fig. 29l–q), curved around the polyp circumference, average height 380 µm (270–520 µm), width 790 µm (620–1000 µm), with an average H:W of 0.5 (range from 0.4–0.6). The inner surface is tuberculate with a narrow smooth band along the distal edge. The outer surface has large, sparse, peaked granules concentrated in the centre of the scale and sporadic tubercles proximally with the remainder being smooth whilst the distal edge has large serrations. All of the above sclerites of this species have a coarsely lobate proximal edge.

The coenenchymal scales are circular to elliptical (Fig. 29r), 240–320 µm diameter, with similar dimensions to the small body-wall scales, but flatter, with less curvature, and a strongly jagged distal edge.

Distribution

Thouarella parachilensis has been found 1000 km west of, and around, the waters of South Georgia Island and south to the Antarctic Peninsula, 90–480 m.

Remarks

The specimens of this species have long been incorrectly identified as *Thouarella chilensis* because of the densely clustered polyps at the branchlet tip that were mistaken for the densely arranged polyps found on that species, as described by Kükenthal (1908; 1915; 1924).

Comparisons

It is the cylindrical arrangement of the clustered, bulbous polyps at the branchlet tip that make *T. parachilensis* noticeably different from other *Thouarella* species, except for *T. chilensis*. *Thouarella parachilensis* has 8–15 abaxial body-wall scales per row (average of 11), a comparable number to *T. koellikeri*, *T. chilensis*, *T. crenelata* and *T. brevispinosa*.

The polyps of *T. koellikeri* have 7–10 scales in the abaxial rows and a tall operculum of large operculars with a simple keel. This is distinct from *T. parachilensis*, which has a flat operculum with much smaller operculars bearing a complex keel. *Thouarella brevispinosa* has 6–8 scales in the abaxial rows, which are distally flared, and colonies have more evenly spaced polyps than the clavate, clustered polyps of *T. parachilensis* (Table 3).

The polyps of *T. parachilensis* are bulbous and more rounded, usually with a higher number of scales in the abaxial rows than those of *T. crenelata* or *T. chilensis*. The polyps of *T. crenelata* have a more open operculum in anterior view than those of *T. parachilensis* and polyps of *T. chilensis* are more stout and stocky in shape.

Species Group 2—polyps in pairs or whorls

18. *Thouarella hilgendorfi* (Studer, 1878)

Plumarella hilgendorfi Studer, 1878: 648–649, pl. 2, figs 15a–e

Thouarella hilgendorfi Wright & Studer 1889: 62, figs 18–25; Versluys 1906: 24–29, pl. 2, fig. 7, text figs; Thomson & Henderson 1906:38 (list); Roule 1908: 1; Kinoshita 1908a: 21–22, pl. 5, fig. 42; Nutting 1912: 66–67; Aurivillius 1931: 248–252, pl. 5, fig. 8, text fig. 48; Chave & Malahoff 1998: Table 1 (listed)

Not *Thouarella hilgendorfi* Thomson 1927: 33–34, pl. 1, fig. 23, pl. 4, fig. 4, 5; Carpine & Grasshoff 1985: 32 (= *T. grasshoffi*)

Thouarella typica Kinoshita, 1907: 230; 1908a: 23–24, pl. 2, fig. 9, pl. 5, fig. 43; Nutting 1912: 68

Thouarella hilgendorfi forma *plumatilis* Aurivillius, 1931: 252–256, pl. 5, fig. 9

Thouarella (Euthouarella) hilgendorfi Kükenthal 1915: 150; 1919: 415–416; Cairns 2006: 188 (discussion); Cairns & Bayer 2009: 28, figs 6m–s (listed); Cairns 2010: 415–422

Thouarella sp. cf. *T. typica* Grigg & Bayer 1976: 171 (listed); Parrish & Baco 2007: 192 (listed)

Material examined: **Holotype**, ZMB Cni 2070 (see Versluys, 1906). “Jeddobay” (=Tokyo Bay), Japan, 548 m, 60 mm fragment.

Other material: USNM 56812, *Star II* (station unknown), Kaiwi Channel between Oahu and Molokai, 21°18'N, 157°32'W, 366 m, 1977, 1 large dried colony, SEM C1393-1397.

Description

Modified from description in Cairns (2010):

The colonies are flabellate, consisting of several main branches that are irregularly dichotomous. Each main branch is covered by numerous closely spaced, undivided, 20–25 mm length branchlets originating from all sides of the main branches in a bottlebrush arrangement. The largest specimen (USNM 56812) is 48 cm tall, 34 cm wide, with a broken basal stem, the diameter of which is 9.5 mm. The axis of the holotype is pale yellow to bronze in colour, and covered by white coenenchyme and polyps.

The polyps of the holotype are 1–1.4 mm high, flared distally, slightly inclined upward, in whorls of 3 on branchlets and placed randomly on larger-diameter branches, with 6–7 whorls per cm. Approximately 1 in 20 polyps are highly modified by a pair of parasitic copepods, with each modified polyp being much larger, up to 1.6 mm high and 1.2 mm in diameter and thus 2–3 times the volume of a typical polyp. The parasite-modified polyps lack operculars, and their body-wall scales flare outward, having a ridged inner face, and a coarsely serrate distal margin. Generally the polyps have 8 longitudinal rows of body-wall scales, usually 6 or 7 abaxial pairs, 5 or 6 outer-lateral pairs, 3 or 4 inner-lateral pairs, and only 1 or 2 adaxial pairs.

The operculars are triangular, often arranged in 2 quartets, alternating in size, with the larger operculars reaching 350–450 µm high (H:W of 1.4–2.1) but the smaller operculars only reaching 180–230 µm high (H:W of 1.6–2.2) and are highly curved. The opercular outer surface is smooth with a serrate distal edge. The longitudinally concave outer surface corresponds to the smooth, convex (not ridged or keeled) inner surface.

The marginals also occur in 2 quartets, as do submarginals, the innermost 4 aligned with inner marginals, and outer 4 submarginals with outer marginals. The marginal scales have a broad elliptical base, a prominently spinose distal projection, and are up to 500–600 µm high and 300–400 µm wide (H:W of 1.2–1.8). The distal 60–65% of the scale is occupied by a projecting spine. The outer distal surface is smooth and the proximal area is covered with granules. The inner surface bears 3–4 prominent spines, and finely serrate ridges that form a complex keel that fits into the longitudinal furrow on the corresponding opercular outer surface.

The submarginal scales are similar to the marginals but with a much shorter distal spine (35% length of scale) and a correspondingly lower H:W of 1.2 with a small simple keel on their inner surface. The body-wall scales are crescent-shaped with a finely serrate distal edge, a smooth outer surface, and are usually wider than high (H:W of 0.6–0.8). The adaxial side of the polyps are covered with particularly wide adaxial and inner lateral body-wall scales.

The coenenchymal scales are similar to body-wall scales, mostly elliptical in shape with a smooth, flat outer surface, approximately 250 µm wide and 150 µm high, and a finely serrate distal edge.

For images see Cairns (2010).

Distribution

Hawaii, Japan, Indonesia, and Indian Ocean at depths from 164–750 m.

Remarks

Thouarella typica is identical to *T. hilgendorfi* and were synonymised in Cairns (2010).

Comparisons

Within Group 2 only three species have a bottlebrush branching arrangement: *T. grasshoffi* Cairns, 2006, *T. hilgendorfi*, and *T. laxa*. *Thouarella grasshoffi* and *T. hilgendorfi* have true bottlebrush branching arrangements whereas branchlets of *T. laxa* are found mostly in one plane, although the length and flexibility of branchlets means the latter can appear bottlebrush. The colonies of *T. grasshoffi* tend to be taller than they are wide, with rare branching, whereas colonies of *T. hilgendorfi* are wider than tall, and flabellate. The polyps of *T. grasshoffi* and *T. hilgendorfi* have a very similar size, those of the former being pointed and conical, with slightly shorter marginals, compared with the distally flared polyps of the latter.

19. *Thouarella moseleyi* Wright and Studer, 1889

Figs 30, 31

Thouarella moseleyi Wright & Studer, 1889: 61–62, pl. 14, fig. 1, 1a, pl. 21, fig. 2; Versluys 1906: 29–30, figs 26, 27 (in text)
Thouarella (Euthouarella) moseleyi Kükenthal 1915: 150; 1919: 417–418; 1924: 292, 294; Cairns & Bayer 2009: 28 (listed)
Thouarella moseleyi var. *spicata* Thomson & Henderson, 1906: 38, 42–43, pl. 3, figs 2, 4 (sample not seen)

Material examined: **Holotype**, NHM 1889.5.27.39, H.M.S. *Challenger*, sta. 171, Kermadec Islands, NE of New Zealand, 28°33'S, 177°50'E, 1097 m, 15 Jul 1874, 6 cm colony.

Description

The holotype was originally approximately 160 mm long (from Wright & Studer 1889: pl. 14, fig. 1) but only a 60 mm fragment now remains. The branchlets are pinnate, possibly alternately pinnate (Fig. 30a,b), although the colony can appear bottlebrush as branchlets are flexible and curve in all directions. The branchlets are mostly simple, some with secondary branching and they are 15–20 mm long. The axis is thin, calcareous, flexible, and “somewhat flattened” (Wright & Studer 1889).

The polyps are clavate with a tall, conical operculum (Fig. 30c), 1.5 mm high, paired, standing perpendicular to the branchlet, with some on the main stem. Each polyp has 6 longitudinal rows of body-wall scales and that number reduces rapidly adaxially from the marginal. There are 4–5 scales in the longitudinal abaxial row, and 3–4 in the adaxial rows.

The thin, lanceolate operculars (can be wider with rounded distal edge, Fig. 31b) measure 450–640 μm high (average 510 μm), 140–270 μm wide (average 200 μm), with a H:W of 2.2–3.1 (average 2.6). The inner surface is smooth with a simple keel running longitudinally from the tip for three-quarters of the scale length (Fig. 31c) whilst the proximal quarter is tuberculate. Wider operculars have a wider, ridged area on the inner surface rather than a distinct keel (Fig. 31b). The outer scale surface is longitudinally concave and smooth, with granules arranged radially from the proximal centre and tubercles are visible at the proximal edge. The opercular edge appears smooth, but may be worn and thus not representative.

The marginals are twice as wide as the operculars, 400–410 μm (average 406 μm), 455–510 μm high (average 480 μm), with a H:W of 1.1–1.3 (average 1.2), and are diamond-shaped (Fig. 31d–f). The inner surface has 4 or 5 tall, thin keels (Fig. 31d,f) with smooth areas lateral to the keels whilst the remainder is tuberculate. The outer surface is longitudinally concave and smooth, with granules distributed radially from the proximal centre with some tubercles being visible at the proximal edge (Fig. 31e). The distal edge is irregular, possibly worn, and the proximal edge is coarsely lobate.

The submarginals are fan-shaped to elliptical (Fig. 31g,h), 320–420 μm high (average 383 μm), 470–480 μm wide (average 475 μm), with a H:W of 0.7–0.9 (average 0.8). The inner surface is tuberculate, the distal edge having a wide area of perpendicular ridges rather than a keel. The outer surface and scale edges are as the body-wall scales, below.

The body-wall scales are circular to fan-shaped (Fig. 31i–l), 300–400 μm high (average 340 μm), 300–475 μm wide (average 370 μm), with a H:W of 0.7–1.2 (average 0.9). The inner surface is tuberculate with a narrow smooth band along the distal edge, and occasionally, small teeth perpendicular to the distal edge. The outer scale surface is smooth with sparse granules across the proximal area whilst the distal edge is smooth and the proximal edge is coarsely lobate.

There are 2 layers of coenenchymal scales (Fig. 31m): sclerites from the inner layer are circular in shape and sclerites from the outside layer are elliptical. The inner surface of the coenenchymal scales is tuberculate with a smooth band running along the distal edge whilst the outer surface is smooth, sometimes with sparsely placed granules. The distal edge is smooth and the proximal edge is coarsely lobate.

Distribution

This species is known from 2 locations (excluding var. *spicata*), northwest of the Kermadec Islands in the South Pacific and north of Sumbawa Island in Indonesia, 6600 km away. It has been recorded from depths of 794–1097 m.

Remarks

The number of polyps per cm was impossible to tell from the small holotype fragment that remains. More material of this species from the type locality is required to confirm the differences between it and *T. laxa*, which has a very similar polyp morphology and pinnate branching.

A variety of *T. moseleyi* (var. *spicata*) was described in Thomson and Henderson (1906). The differences between the polyps of the holotype and those of the variant are mainly that the latter has a taller conical operculum and marginal scales with a more elongated, pointed spine (which may be bifid). The tall conical operculum is similar to that of the polyps of *T. grasshoffi*. However, colonies of *T. grasshoffi* have a true bottlebrush branching arrangement.

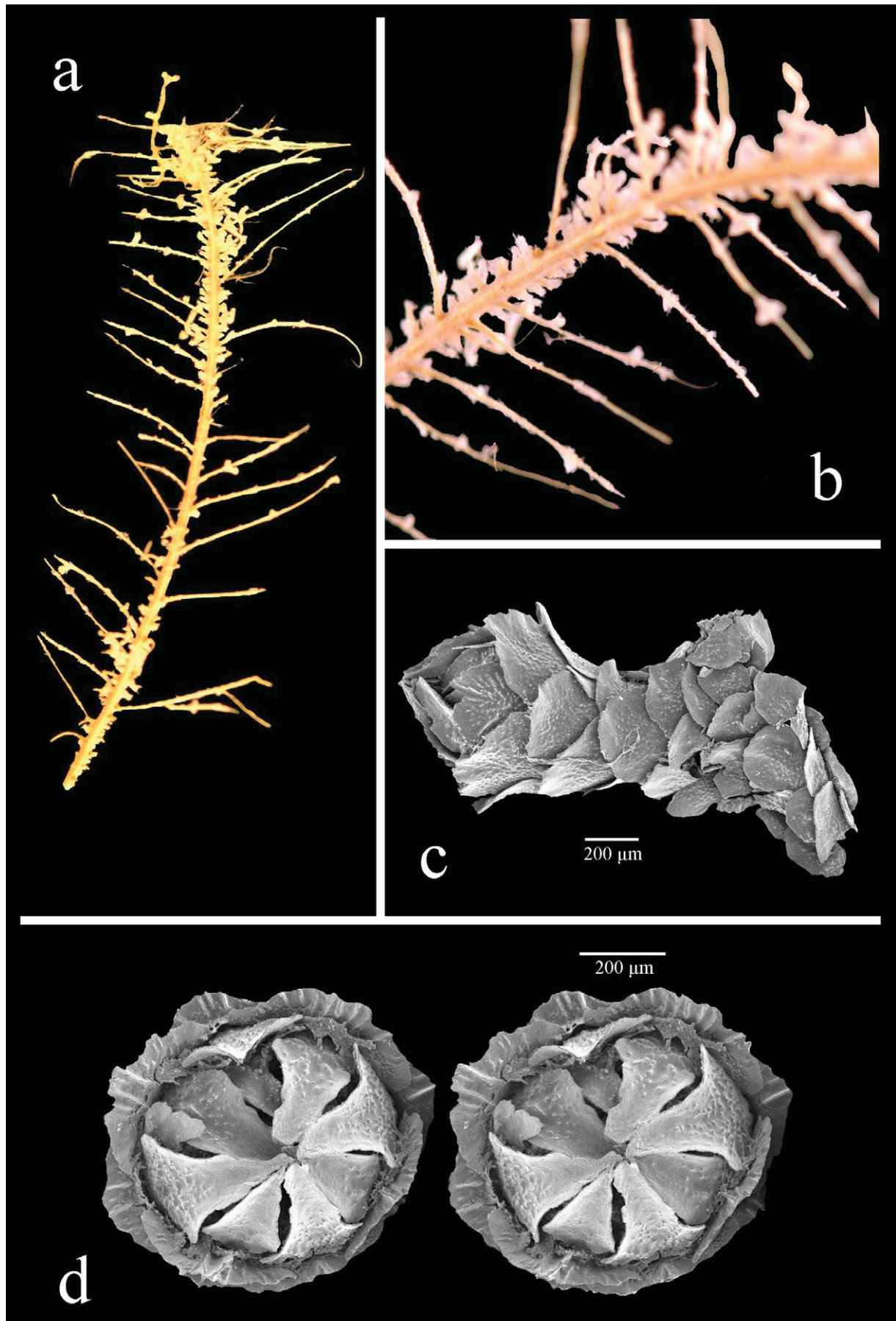


FIGURE 30. *Thouarella moseleyi*, holotype, NHM 1889.5.27.39: a) 6 cm colony; b) close up of the few remaining polyps; c) lateral view of polyp; d) stereo opercular view.

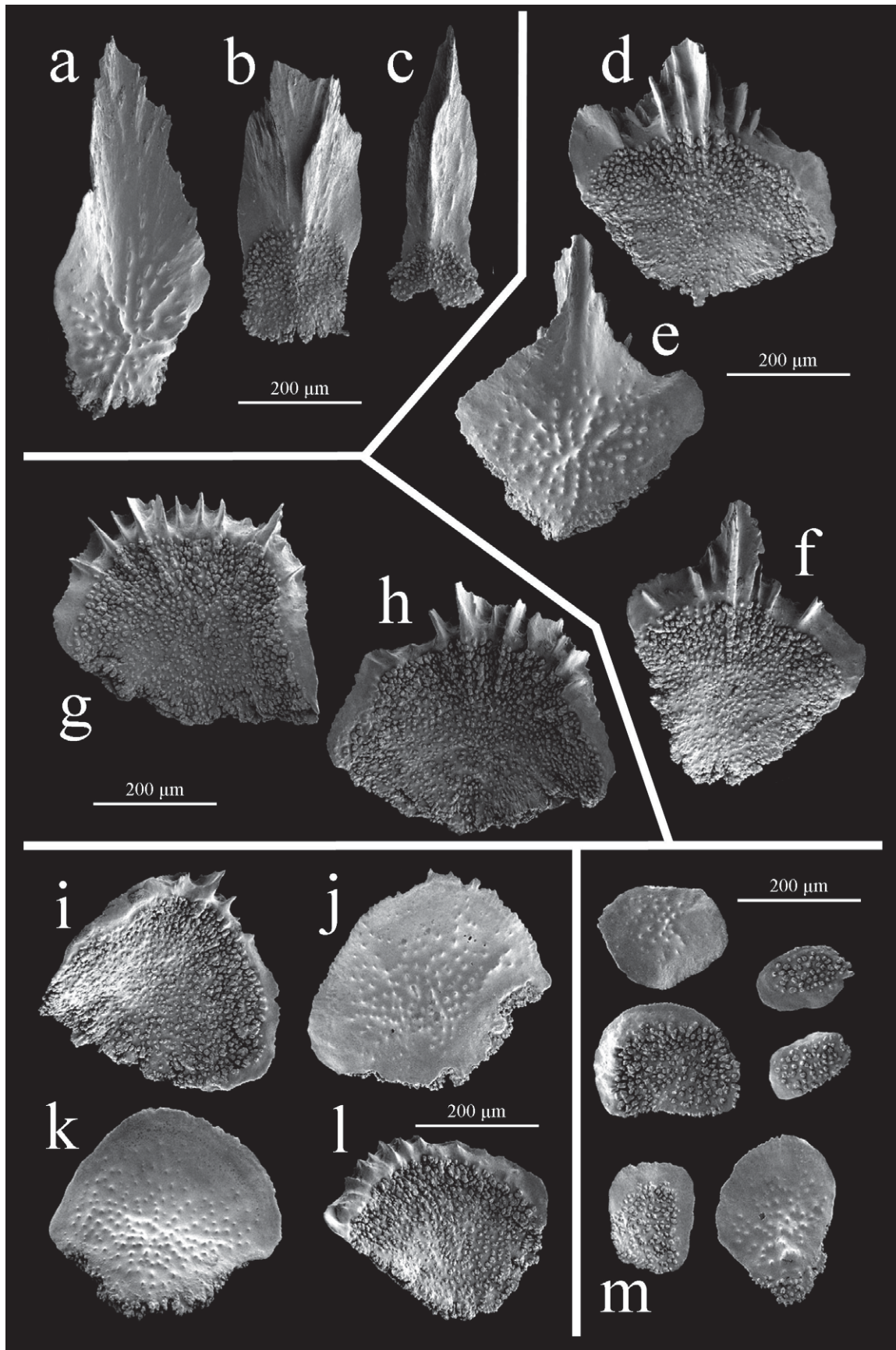


FIGURE 31. *Thouarella moseleyi*, holotype, NHM 1889.5.27.39: a) outer and b,c) inner surface of opercular scales; d,f) inner and e) outer surface of marginal scales; g,h) inner surface of submarginal scales; i,l) inner and j,k) outer surface of body-wall scales; m) coenenchymal scales—outer surface shown on top left and bottom right scales, remainder show the inner surface. Some SEM by ZGR.

Comparisons

Within Group 2 only two other species, *T. laxa* and *T. tydemani*, have pinnate colonies or colonies that appear pinnate. The ridges running perpendicular to the distal edge of the body-wall scales on the polyps of *T. moseleyi* are similar to those reported on the body-wall scales in a recent description of *T. tydemani* (Zapata-Guardiola and López-González 2010a). The polyps of *T. tydemani*, however, have long spinose marginals and are distally flared, whereas polyps of *T. moseleyi* are clavate with shorter marginals.

The polyps of *T. moseleyi* are more robust than those of *T. laxa*, with wider marginals that are not as spinose, and a fitted opercular cone. There are also several ridges running perpendicular to the distal edge of the submarginals, which are absent in the polyps of *T. laxa*.

20. *Thouarella laxa* Versluys, 1906

Figs 32, 33

Thouarella laxa Versluys, 1906: 30–32, pl. 1, fig. 5; pl. 3, fig. 8; text figs 28–33; Aurivillius 1931: 255–256

Not *Thouarella laxa* Kükenthal & Grozawsky 1908: 36–37, pl. 2, fig. 13

Thouarella (Euthouarella) laxa Kükenthal 1915: 150; 1919: 417; 1924: 293–294, text fig. 164; Cairns & Bayer 2009: 28 (in list) 4; Zapata-Guardiola and López-González 2010a: 72–78

Thouarella flabellata Kükenthal, 1907: 207

Thouarella (Euthouarella) flabellata Kükenthal 1915: 150 (key); 1919: 408 (key), 418–420, pl. 42, fig. 64, figs 182–186 in text; 1924: 294–295; Cairns & Bayer 2009: 28 (listed)

Thouarella regularis Kükenthal, 1907: 206–207

Thouarella tenuisquamis Kükenthal, 1908: 11; 1915: 150 (key), 151

Thouarella (Euthouarella) tenuisquamis Kükenthal 1919: 408 (key), 421, pl. 42, fig. 65, figs 187–190 (in text); 1924: 295; Cairns & Bayer 2009: 28 (listed)

Thouarella carinata Kükenthal, 1908: 11–12; 1915: 150 (key)

Thouarella (Euthouarella) carinata Kükenthal 1915: 150 (key); 1919: 408 (key), 423–425, pl. 42, fig. 66; 1924: 296; Cairns & Bayer 2009: 28 (listed)

Material examined: **Holotype** of *T. laxa*, ZMA, COEL03576, *Siboga* expedition, sta. 88, Strait of Makassar, Sulawesi, Indonesia, 0°34'06"N, 119°08'05"E, 1301 m, 20 June 1899, 2 branchlets (80 mm, 90 mm); **Holotype** of *Thouarella flabellata*, sta. 257, east coast of Somalia, 1°48'02"N, 45°42'05"E, 1644 m, 3 fragments of 75 mm, 45 mm and 40 mm; **Syntype** of *Thouarella tenuisquamis*, MNHWU, northwest of Sumatra, Malaysia, south of Nicobar, 4°53'01"N, 93°33'05"E, 752 m; **Syntype** of *Thouarella carinata*, USNM 50127, *Golden Hind*, sta. 38, Okinawa and “Urugakanal”, Japan, 731 m, 85 mm fragment.

Description

The colonies are sparsely branched (Fig. 32a). The branches generally have alternate pinnate branchlets with infrequent branching between these 2 planes and sometimes on the dorsal face. This forms a rudimentary bottlebrush arrangement (Fig. 32b) that can form a feather-shape. Branchlets are flexible, upwardly inclined at 45°, generally simple, with the longest being approximately 40 mm.

Polyps of the holotype are rarely on the main stem, usually in pairs or whorls of 3 on branchlets, with a density of 5–7 pairs per cm, distally flared (Fig. 32c,d), upwardly inclined at 45–60°, and 1.2–1.5 mm high. Each polyp has 7 longitudinal rows, 5–6 scales in each abaxial row.

The operculars are arranged in roughly 2 alternate rings of 4 (Fig. 32e). In the inner ring the scales are smaller (Fig. 33a–c), 280–300 µm high (average 292 µm), 140–210 µm wide (average 166 µm), with a H:W of 1.8 (range from 1.4–2.1). In the outer ring the scales are larger 370–630 µm high (average 500 µm), 120–370 µm wide (average 292 µm), with a H:W of 1.9 (ranges from 1.3–3.1). The larger operculars are triangular (Fig. 33e) although, if broken, they have a rounded, blunt apex, usually tapering slightly to a narrow distal edge (Fig. 33f), making them tongue-shaped. The outer opercular surface is smooth and concave longitudinally, having small granules proximally and tubercles at the base. The inner surface has fine tubercles covering the proximal third to half of the scale, the remainder is smooth with longitudinal central ridges (no distinct keel). The smaller operculars are lanceolate with a smooth outer surface that has a small number of granules at the base and is slightly concave; the inner surface is smooth with fine tubercles over the proximal quarter to third.

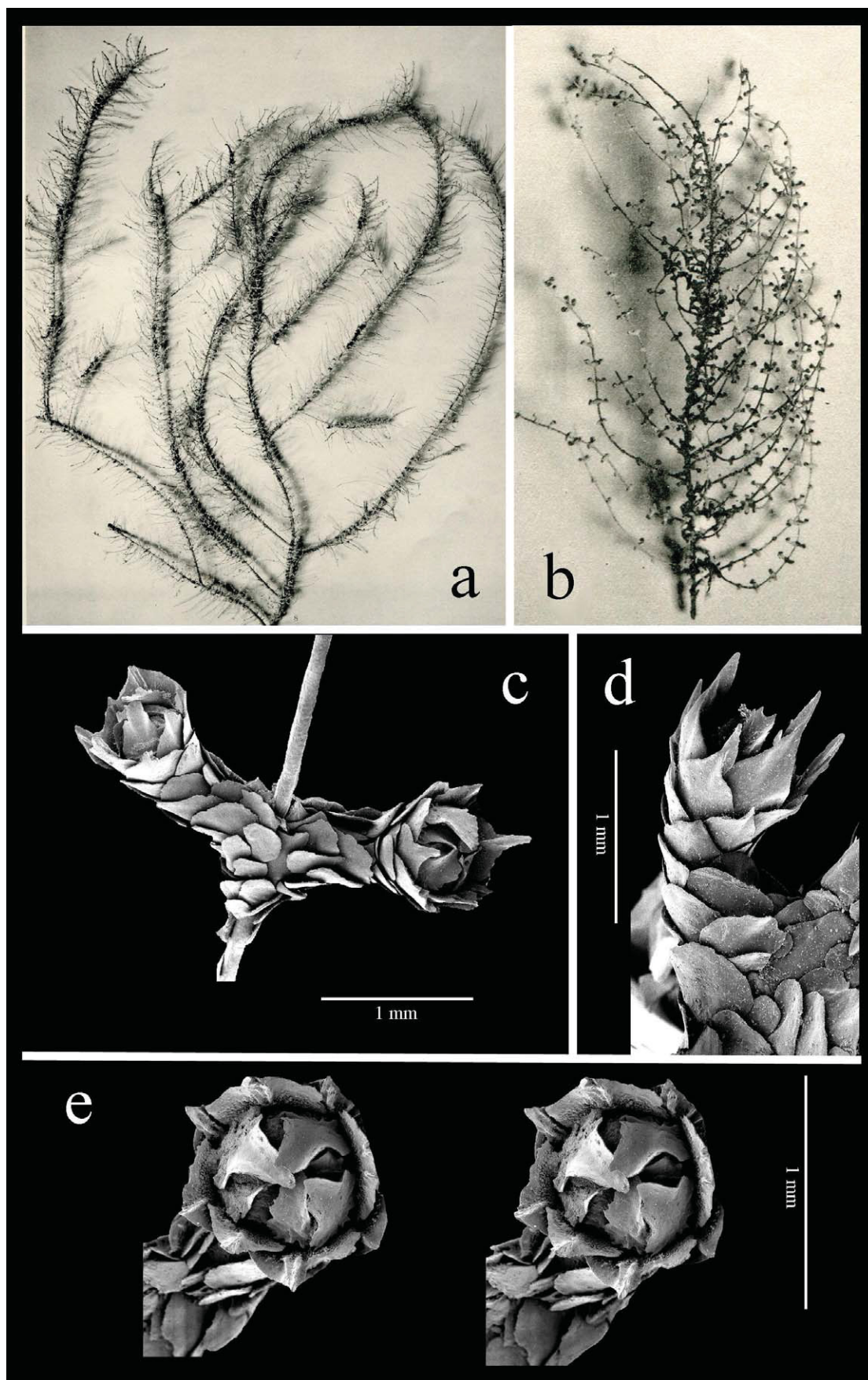


FIGURE 32. *Thouarella laxa*, holotype, ZMA COEL03576: a–c,e) original images of holotype from Versluys, 1906, a) 20 cm colony; b) close up of small branch; c) pair of polyps; e) stereo opercular view of polyps. *Thouarella carinata* (now synonymised with *T. laxa*), syntype, USNM 50127: d) polyp.

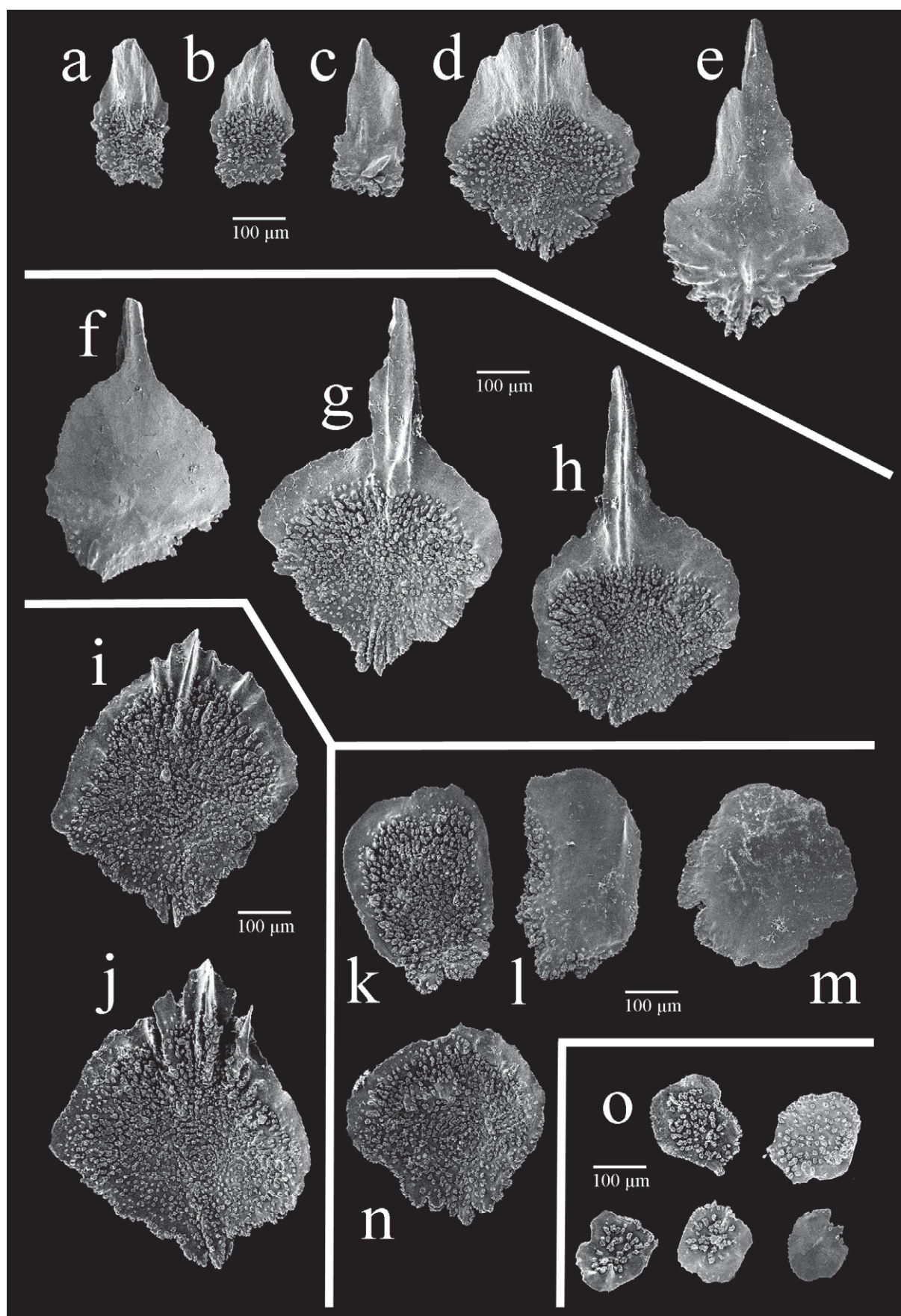


FIGURE 33. *Thouarella laxa*, holotype, ZMA COEL03576: a,b,d) inner and c,e) outer surface of opercular scales; f) outer and g,h) inner surface of marginal scales; i,j) inner surface of submarginal scales; k,n) inner and l,m) outer surface of body-wall scales; o) coenenchymal scales—outer surface bottom right, remainder are the inner surface.

The marginals are 570–800 μm high (average 705 μm), 370–550 μm broad (wider than largest opercular), with an average H:W of 1.5 (range from 1.3–1.7). They have a circular to diamond-shaped base and a triangular, acutely pointed distal edge (Fig. 33f–h). The outer surface is smooth with low relief granules proximally whilst the inner surface has 2 or 3 ridges longitudinally placed along the keel (which is sometimes flattened) and tubercles covering the proximal half in a semi-circle leaving smooth wings lateral to the keel and along the distal edge.

The submarginals are as described below for body-wall scales but slightly wider, 410–490 μm (average 470 μm), and taller, 500–610 μm (average 570 μm), with a H:W of 1.2. They have a pointed distal edge and a small keel on the inner surface (Fig. 33i,j), which has adjacent ridges perpendicular to the distal edge.

The body-wall scales are usually circular (Fig. 33k–n), 250–590 μm high (average 320 μm), 280–390 μm wide (average 310 μm), with an average H:W of 1 (range from 0.6–1.7). The outer surface is mostly smooth with some granules proximally whilst the inner surface is tuberculate with a smooth band along the distal edge.

The coenenchymal scales are circular to elliptical (Fig. 33o), 100–310 μm high (average 200 μm), 130–290 μm wide (average 200 μm), with a H:W of 0.4–1.5 (average 1). All the sclerites of this species have a finely serrate distal edge and roughly lobate proximal edge.

Distribution

This species occurs from the east coast of Africa (Somalia) to eastern Asia (Sumatra, Philippines, Japan) at depths of 400–1644 m.

Remarks

Thouarella laxa was recently redescribed by Zapata-Guardiola and López-González (2010a). However, the polyp illustrated was incongruent with the holotype in that it showed the polyp head turning at an angle rather than a regular distally flared shape (Fig. 32c,d).

Although *T. laxa*, *T. carinata*, *T. flabellata*, and *T. tenuisquamis* have been described from disparate locations such as Somalia and Japan, at a polyp and sclerite level these specimens are identical. *Thouarella flabellata* has fewer pairs/whorls of polyps per cm (5–6) than *T. tenuisquamis* (7–8), *T. laxa* (5–7), and *T. carinata* (7–8). *Thouarella carinata* is more likely to have 3 polyps in a whorl whereas the remaining species tend towards pairs. However, the number of polyps per whorl may increase with colony age and is variable in other *Thouarella* species (e.g. *T. grasshoffi*), so this small discrepancy should not be considered in defining species. The *T. carinata* and *T. tenuisquamis* holotypes are single branches and may even be one branch of a flabellate colony (see Fig. 32a,b of *T. laxa*). *Thouarella carinata* also has a more extended distal edge on its marginals, and the holotypes of the remaining species are in a relatively poor condition with few intact polyps, many having marginals reduced in length through wear. However, the marginals that were intact looked identical to those of *T. laxa*. In all these specimens the inner surface of the small operculars tended to be smooth and larger operculars had a longitudinally ridged area distally. The outer surface of all sclerites is smooth with sparsely placed granules. The differences described above are minor and despite the long distances between type localities, the minor differences in branching, polyp and sclerite shapes are not sufficient to delineate unique species. Therefore, *T. carinata*, *T. flabellata*, and *T. tenuisquamis* are thus proposed for synonymisation with *T. laxa*, this name having priority.

Comparisons

Polyps of *T. laxa* have a similar distal flare as those of *T. hilgendorfi* and *T. tydemani* and the sclerites of these species are all nearly identical in shape. Colonies of *T. laxa* however have long, flexible branchlets emanating from the stem in at least three directions whilst branching on *T. tydemani* is alternately pinnate. The branchlets of *T. hilgendorfi* are bottlebrush but branching is denser, with sturdier, less flexible branchlets, and there are more whorls and pairs per cm than found on *T. laxa*. These characters could be affected by environmental factors and, at a polyp level, these species are similar. Sampling of fresh material from type locations and perhaps genetic studies could shed light on the relationship between these two species and *T. grasshoffi*, which also has a similar polyp structure.

The polyps of *T. moseleyi* are more rounded than those of *T. laxa* and consequently the former have shorter, narrower marginals. Additionally, the operculars of the former make a better-formed cone than those in the polyps of the latter and there are several ridges running perpendicular to the distal edge of the submarginals, a character not present in the polyps of *T. laxa*. Only a minute piece of *T. moseleyi* was examined, so more material is required

to confirm the difference between these species as sclerite measurements, sclerite arrangement, and polyp arrangement are very similar.

21. *Thouarella tydemani* Versluys, 1906

Thouarella tydemani Versluys, 1906: 34–35, pl. 1, fig. 2, figs 34–37 (in text)

Thouarella tydemany Brito 1993: 220–221

?*Hookerella pulchella* Gray, 1870: 45

Thouarella (Euthouarella) tydemani Cairns & Bayer 2009: 28 (listed)

Material unavailable: **Holotype**, COEL09256, ZMA, *Siboga* expedition, sta. 297, Lesser Sunda Islands, Indonesia, 10°39'S, 123°40'E, 520 m, 27 Jan 1900, 200 mm colony. Only 3 mounted slides remain of this species, images of which were seen. They contain 2 branchlets, polyps and coenenchymal scales. The original colony is presumed lost as the holotype was not present at ZMA (Zapata-Guardiola & López-González 2010a) or any of the other museums contacted within this study. As no material was available the type description was used for species comparisons.

Description

The colony is flat with infrequent uniplanar branching. The branchlets are simple, 15–20 mm long, rarely 30 mm, alternately pinnate with a few ventral branchlets.

The polyps are distally flared, approximately 1.5 mm high, standing at 80–90° inclination from branchlets, paired, rarely in whorls, 3–6 per cm with some polyps on the main branch.

The operculars are in a modest cone of 4 larger, outer, longitudinally concave operculars and 4 smaller, inner, distally blunt operculars. The marginals are 450–500 µm high, almost spinose with a keel visible on the inner surface. Body-wall scales appear circular, some bearing ridges perpendicular to the distal edge.

Recently published additional description and images are in Zapata-Guardiola and López-González (2010a).

Distribution

Known only from the type location off the Lesser Sunda Islands, Indonesia, at 520 m depth.

Remarks

Versluys (1906) separated *Thouarella laxa* and *T. tydemani*, the latter having wider and larger polyps. Zapata-Guardiola and López-González (2010a) illustrated that the variation in nearly all characters (size of polyps, number of whorls per cm, number of polyps per whorl etc) in *T. laxa* was broad enough to encompass the dimensions seen in *T. tydemani*. The only difference found between *T. laxa* and *T. tydemani* was that the body-wall scales of the latter have short ridges perpendicular to the distal edge, which are absent in *T. laxa*.

Versluys (1906) also considered *Hookerella pulchella* Gray, 1870 very similar to *T. tydemani* in colony form but he did not mention the number of polyps per cm or the sclerite shape. Without a reliable illustration or accurate description from Gray (1870), Versluys described *T. tydemani*, ignoring *H. pulchella* (the holotype or a specimen of which cannot be located).

Comparisons

Thouarella tydemani was compared to *T. laxa* by Versluys (1906) and rightly so as the polyps of these species are nearly identical in every respect. Body-wall scales of *T. tydemani* may bend away from the polyp body, have ridges perpendicular to their distal edge, and have slightly shorter marginals than are found on *T. laxa* (this is in contrast to Zapata-Guardiola & López-González, 2010a, who found polyps of *T. laxa* had marginals that were on average 370 µm and thus shorter than those of *T. tydemani*). However it is the branching pattern that makes these species truly distinct. Colonies of *T. laxa* have long, flexible branchlets, departing the stem in at least 3 directions, whereas colonies of *T. tydemani* are mostly pinnate with more rigid branchlets. Additionally, the polyps of *T. laxa* have a flat operculum and branchlets inclined at a 45–60°, rather than 90° as in *T. tydemani*. More material of *T. tydemani* would help to assess further differences between these two species.

Polyps of *T. tydemani* are distally flared and look very similar to those of *T. hilgendorfi*. However, the pinnate branching structure of *T. tydemani* differentiates this species from the bottlebrush branches of *T. hilgendorfi*.

22. *Thouarella coronata* Kinoshita, 1908

Figs 34, 35

Thouarella (Diplocalyptra) coronata Kinoshita, 1908c: 519–520, fig. 2; 1908b: 56–59, figs 4–6 (in text); Cairns & Bayer 2009: 28 (list), 35, figs 7a–g

Thouarella coronata Aurivillius 1931: 255 (listed)

Thouarella (Euthouarella) coronata Kükenthal 1915: 150 (key); 1924: 296 (key)

Material examined: USNM 50118, fragment of **holotype**, UMUT, Uji Island, Kyushu Island, 146 m, May 1908, 13 cm colony of which we viewed 20 mm. A small fragment of the holotype was available for study, however, the colony shape and branchlet arrangement narrative below relies heavily on the original description.

Description

The colony is mostly sympodially branched with dichotomous branching in one upper portion of the colony (top left of Fig. 34a). Basal branchlets are up to 50 mm long, 5–12 mm apart, and on rare occasions 20 mm apart. The axis is brown with a yellowish metallic lustre.

The polyps are distally flared with a slender polyp body (Fig. 34d,e) 1.9–2.1 mm high, standing perpendicular to the branchlet in pairs and sometimes whorls of 3 (Fig. 34c), with 5–7 pairs or whorls per cm. There are 8 marginals, but only 7 longitudinal rows of body-wall scales with 5–6 scales in the abaxial rows.

The operculars are lanceolate to triangular in shape (Fig. 35d–h), 260–455 μm high (average 290 μm), 120–240 μm wide (average 180 μm), with an average H:W of 1.6 (range from 1.3–2). The outer surface is smooth whilst the inner surface has a small elliptical tuberculate area proximally and a smooth distal area.

Beneath the operculars are 3–4 (perhaps more in other samples) small accessory operculars (Fig. 35a–c) which are irregular or tear-shaped, 80–200 μm high (average 150 μm), 70–140 μm wide (average 100 μm), with an average H:W of 1.1. The outer surface is smooth, the inner surface is also smooth with a small patch of tubercles proximally. The scale edges are relatively smooth (not serrated).

The marginals are equilateral triangle-shaped with a rounded proximal edge (Fig. 35i–k), 430–560 μm high (average 490 μm), 270–330 μm wide (average 310 μm), with an average H:W of 1.6 (range from 1.3–2.1). The outer scale surface is smooth distally with granules proximally. The inner surface has a multi-channelled keel with smooth areas lateral to the keel and tubercles covering the proximal half below the keel base. A marginal scale's proximal edge is roughly lobate, and may be angular.

Some submarginals have small keels or ridges on the distal edge of the inner surface and are a wide tear-shape and pointed distally (Fig. 35l,m). They have a tuberculate inner surface with a narrow smooth band along the distal edge whilst the outer surface is smooth with some granules proximally.

Body-wall scales are circular (Fig. 35n–p), 190–340 μm high (average 250 μm), 200–310 μm wide (average 240 μm), with an average H:W of 1.1 (range from 0.9–1.2). The outer surface is smooth, sometimes with granules proximally whilst the inner surface is tuberculate with a smooth band along the distal edge and infrequent small ridges running perpendicular to the edge. The distal edge of all polyp sclerites of this species is finely serrate (unless otherwise stated) whilst the proximal edge is coarsely lobate.

The coenenchymal scales are circular (Fig. 35q), around 130 μm diameter and much smaller than the body-wall scales. The outer scale surface is smooth and slightly concave with edges raised from the axis whilst the inner surface is tuberculate.

Several hundred cylindrical rodlets were found in each tentacle.

Distribution

Known only from type locality, Kyushu Island, Japan, 146 m depth.

Remarks

This is the only *Thouarella* species known to contain tentacular rodlets, a form of sclerite often found in *Plumarella*. It is also the only *Thouarella* species known to have a sympodial branching pattern.

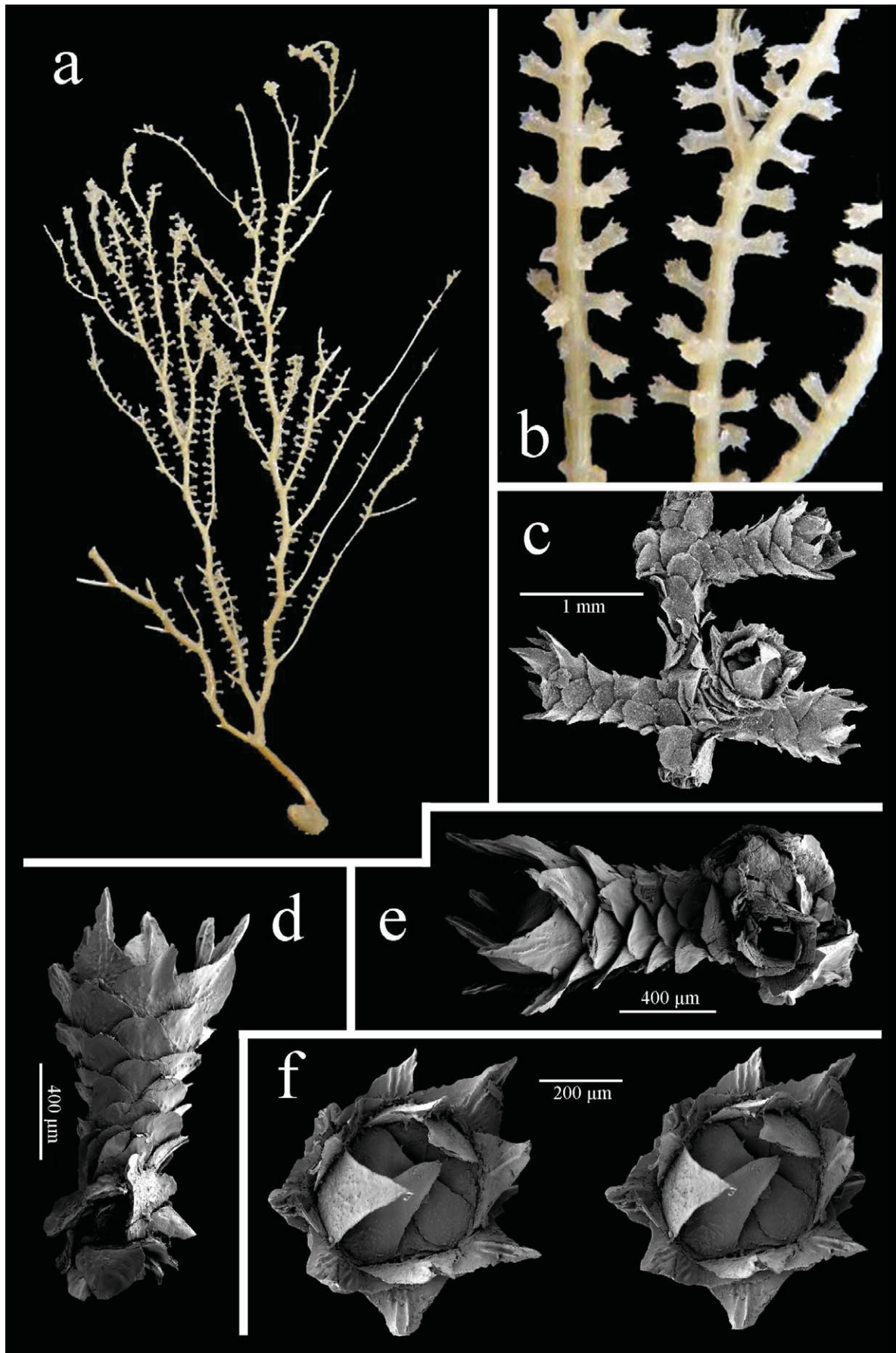


FIGURE 34. *Thouarella coronata*, holotype, UMUT: a) 13 cm colony; b) close up of polyps; c) whorl of three polyps; d) abaxial polyp view; e) lateral polyp view; f) stereo opercular view. SEM by RZG.

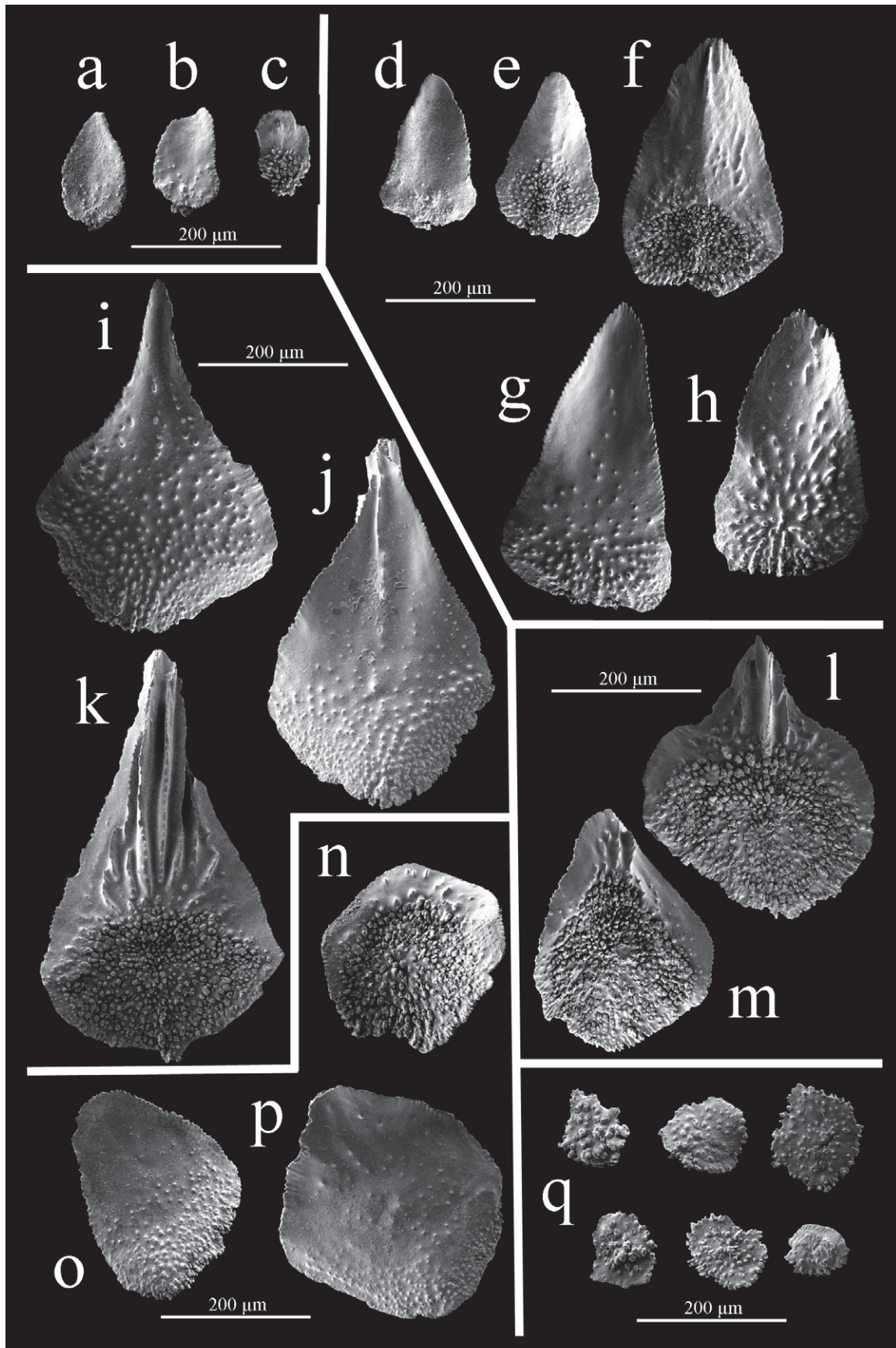


FIGURE 35. *Thouarella coronata*, holotype, UMUT: a,b) outer and c) inner surface of accessory operculars; d,g,h) outer and e,f) inner surface of opercular scales; i,j) outer and k) inner surface of marginal scales; l,m) inner surface of submarginal scales; n) inner and o,p) outer surface of body-wall scales; q) coenenchymal scales—inner surface top row left, bottom row right and middle; remainder are the outer surface. Some SEM by ZGR.

Comparisons

Although the majority of the *T. coronata* colony is sympodially branched a portion is dichotomously branched (more examples of this species are required to confirm the branching pattern). Apart from *T. coronata*, only two other species within Group 2 have dichotomous, uniplanar branching: *T. parva*, also from Japan, and *T. biserialis* (Nutting, 1908), from Hawai'i. Kinoshita's drawings (1908d, figs 1, 2) indicate that *T. parva* differs from *T. coronata* in having shorter, more rounded marginals and polyps diverging from branchlets at approximately 45° rather than 90°.

The sclerites of polyps of *T. biserialis* and *T. coronata* are very similar. The marginals of polyps of *T. biserialis* appear to curve over the operculum creating a cylindrical, rounded polyp, whereas those of *T. coronata* are flared outward. The polyps of the former are inclined at 45° and of the latter are perpendicular to branchlets. The importance of these characters remains unclear, so for now these species are considered to be distinct.

23. *Thouarella parva* Kinoshita, 1908

Fig. 40 a,b

Thouarella (Diplocalyptra) parva Kinoshita, 1908d: 53–56, figs 1–3; Cairns & Bayer 2009: 28 (list)

Thouarella (Amphilaphis) parva Kükenthal 1915: 149 (key); 1919: 410; 1924: 290 (key)

Material unavailable: **Holotype**, Kodzu Island, Japan, depth unknown. Unfortunately the holotype was not present within the University of Tokyo Museum collection (Dr Ueshima, pers. comm.), and so Kinoshita's original description of a 73 mm fragment (1908d) is summarised below.

Description

The colony is uniplanar with dichotomous branching. The branchlets diverge from the main stem at around 50°, 5–13 mm between branchlets. The colony colour is white to light yellow.

The polyps are 1 mm high and upwardly inclined to the branchlets at around 45°, the widest point being around the marginals. They are slender toward the base (Fig. 40a), arranged in pairs, with a density of about 6 per cm, and each has 8 longitudinal rows of body-wall scales. There are 5–6 scales in the abaxial rows, and 5 in the outer and inner lateral rows, reducing to 4 adaxially.

From a lateral view the operculars are completely concealed by the marginals. Very small accessory operculars are present (Fig. 40bI). The operculars are lanceolate (Fig. 40bII), 160–360 µm high and 90–160 µm wide. The distal half of the outer opercular surface is slightly concave and both the inner and outer surfaces have granules arranged radially in the proximal area. The inner surface is likely to be tuberculate proximally, as is typical for the genus.

The marginals are an irregular triangle-shape (Fig. 40bIII) and approximately the same size as the largest opercular (400 µm), although wider proximally.

The body-wall scales are not as tall as the marginals (350–380 µm) and are broader (Fig. 40bV, bVI). The outer surface of the body-wall scales has radially arranged granules from the central proximal area whilst the inner scale surface is tuberculate with a smooth band along the distal edge, occasionally with several ridges perpendicular to the distal edge.

The coenenchymal scales are smaller than body-wall scales, and circular to elliptical in shape. The outer surface is sculpted and folded with sparse tubercles on the inner surface. The distal and lateral edges of all sclerites are finely serrate with a coarsely lobate proximal edge.

Distribution

This species is only known from Kodzu Island and Sagami Bay, Japan. The depth from which the sample was taken is unknown.

Remarks

Kinoshita was the first to note accessory operculars in *Thouarella* (1908d, Fig. 2, shown here in Fig. 40b) and *T. parva* remains one of the few *Thouarella* species with this kind of sclerite.

The marginals of the polyps of *T. parva* (Fig. 40bIII) appear to have a small keel on their inner surface, and the specimen is thus considered to be *Thouarella*. However, this is far from clear and the rounded distal edge of what appear to be marginals in Fig. 40b, and lack of a clear keel could indicate that this is actually a species of

Plumarella. More material is required to confirm the placement of *T. parva* within *Thouarella*.

Comparisons

Dichotomous branching precludes this species from being *T. hilgendorfi*, *T. moseleyi*, *T. laxa*, *T. tydemani*, or *T. grasshoffi* from within Group 2. Additionally, these species all have tall, triangular marginals that are absent in *T. parva*.

Only two other *Thouarella* species have dichotomous branching: *T. coronata* and *T. biserialis*. The polyps of *T. coronata* diverge at 90° to the branch, whereas those of *T. parva* depart at 45°. This seems to be a very small difference, however, without more material of *T. parva* it is impossible to determine the extent of the character differences between these species. There are believed to be specimens of *T. parva* in Japan (Cairns, pers. comm.), but until this material is examined these species are considered to be distinct.

Polyps of both *T. parva* and *T. biserialis* depart from branchlets at approximately 45° and all their sclerites appear to be very similar shapes and sizes. The polyps of *T. biserialis* have marginals with a distinct keel, which may be present on *T. parva*, but the polyps of *T. biserialis* are clavate whereas those of *T. parva* are modestly flared with a relatively tall operculum.

24. *Thouarella biserialis* (Nutting, 1908)

Amphilaphis biserialis Nutting, 1908: 573, pl. 43, fig. 4, pl. 47, fig. 4; Cairns & Bayer 2009: 28 (listed)

Thouarella biserialis Kinoshita 1908c: 519–520, 2 text figs; Kükenthal 1915: 151 (listed); 1919: 438–9; 1924: 301; Parrish & Baco 2007: 192 (listed)

Thouarella (Diplocalyptra) biserialis Cairns, 2010: 417, figs 2–3

Material examined: **Holotype**, USNM 22583, USFWS *Albatross* 398210, Mawiliwili, Kaua'i Island, Hawaii, North Pacific Ocean, 21°56'25"N, 159°21'40"W, 73–426 m, June 1902, 2 short branches.

Description

Modified from description in Cairns (2010):

The holotype, now in 2 fragments of 4 cm and 3 cm length, appears to be from a dichotomously branched, uniplanar colony. The polyps are cylindrical to clavate, 1.2–1.5 mm high, curved upward at 45°, and arranged in pairs standing on opposite sides of the branchlets with the plane of the colony. The polyps are rarely in whorls of 3. There are 6–7 scales in 8 longitudinal rows, 5–6 in the outer lateral rows, 2–3 in the inner lateral rows and 1–2 adaxially. Adaxial rows are short, revealing a largely naked adaxial face.

The operculars are lanceolate to widely-triangular, small (up to 280 µm high), and bluntly tipped, with a H:W of 1.6–2.0. The outer opercular surface is flat and has granules proximally whilst the distal inner surface is smooth (unkeeled), bearing rounded longitudinal bulges.

The marginal scales are triangular, up to 400 µm high, with a H:W of 1.5–1.8, with a wide multi-keel area on the inner surface and granules sparsely covering the outer surface. The marginal scales fold over the smaller operculars, shielding them from view.

The body-wall scales are often wider than high, up to 290 µm high with a H:W of 0.67–1.1. Those in the upper part of the polyp have a series of longitudinal ridges on the distal inner surface, resulting in a serrated distal edge.

The coenenchymal scales are elliptical, up to 300 µm in diameter and their outer surface is concave and smooth with some granules.

For images see Cairns (2010).

Distribution

Known only from type locality southeast of Kaua'i, Hawaii, at depths of 73–426 m.

Comparisons

Being dichotomously branched with polyps in pairs, *T. biserialis* is comparable to *T. parva* and *T. coronata*. *Thouarella parva* is most similar to *T. biserialis* as both have polyps that depart branchlets at 45° and more rounded marginals than those found on polyps of *T. coronata*. However, the polyps of *T. biserialis* have a distinct keel on the inner surface of marginals, something not clearly illustrated for *T. parva*. Additionally, polyps of *T. biserialis* appear more clavate than those of *T. parva* and *T. coronata*. The polyps of *T. coronata* are a similar size to those of

T. biserialis, however, they diverge from branchlets at 90° rather than 45°. Additionally, the polyps of *T. biserialis* are clavate rather than being distally flared, as in *T. coronata*, which also has polyps with taller, more pointed marginals than found on *T. parva*.

25. *Thouarella grasshoffi* Cairns, 2006

Thouarella (*Euthouarella*) *grasshoffi* Cairns, 2006: 184–188, figs 1a, 12, 13; Cairns & Bayer 2009: 28 (listed)

Material examined: **Holotype**, USNM 1078188, Manning Seamount, North Atlantic Ocean, 38°08.74'N, 61°05.473'W, 1458 m, 16 May 2004.

Other material: all lots from Cairns (2006).

Description

Description modified from Cairns (2006):

The colonies consist of 1–3 main branches from which numerous closely spaced (usually less than 2 mm apart) branchlets originate on all sides of the main branch, in a bottlebrush arrangement. The branchlets are undivided, up to 4 cm long and flexible in tension. The holotype is a single main stem 35 cm long and 8–9 cm wide that has been broken from its base. The axis is 2.4 mm in diameter and is a brownish colour.

The polyps of the holotype occur randomly on the main stem and in regular pairs (10–20% of polyp projections are whorls of 3) every 1.5–1.9 mm on branchlets. They are modestly distally flared, curved upward toward branchlet tip, and are rarely greater than 1.3 mm in length and 0.7 mm in diameter. The sclerites are in 6–8 longitudinal rows with 5–7 scales in the longitudinal abaxial rows.

The operculars form a tall cone and are isosceles triangle-shaped with a pointed apex, 260–620 µm high but most are 450–550 µm, with a H:W of 2.1–3.2. The proximal quarter of the inner surface is tuberculate, the distal half bearing a multi-keel. The outer surface has granules radiating from the central proximal area.

The marginal scales are not arranged in 2 defined rings, as in most *Thouarella* species, but as 2 sets of 3 with both lateral edges overlapping those of the adjacent marginal and the 2 remaining marginals with one lateral edge above and the other below their adjacent marginal. The marginals have an acutely pointed tip with a broad base, with a H:W of 0.93–2.1 and are up to 540 µm long. The proximal half of the inner surface is tuberculate, the distal half bears 1–3 modest longitudinal keels, sometimes bearing lateral projections. The outer surface is covered in granules.

The submarginal scales are rounded, up to 340 µm high, almost elliptical, and broader than high (H:W of 0.65–0.89). The adaxial scales are rarely larger than 220 µm. Some of the submarginals have a small point at the distal edge and a corresponding small ridge perpendicular to the distal edge on the inner surface. The inner surface of both these and the body-wall scales has a smooth band along the distal edge and tubercles occur across the proximal three-quarters of the scales. The outer surface of the sclerites is smooth with a few granules proximally. The distal edge of all polyp sclerites of this species is finely serrate with a coarsely lobate proximal edge.

The coenenchymal scales are elliptical to elongate in shape, rarely more than 320 µm high with a H:W of 1.3–1.8. These scales have a tuberculate inner surface and a slightly concave, smooth outer surface, sometimes with rare granules.

For images see Cairns (2006).

Distribution

This species is found in the western Atlantic, on the New England Seamount Chain; at depths from 814–1458 m. It also occurs in the eastern Atlantic including off the Cape Verde Archipelago, the Great Meteor Seamount, the Azores Archipelago and the Celtic Sea, at depths from 720–1760 m.

Comparisons

Thouarella grasshoffi is unique within Group 2 in having a true bottlebrush colony shape (*T. hilgendorfi* does have bottlebrush branches but has a wider, flabellate colony shape, see Table 3). The placement of the branchlets of *T. laxa* is pinnate but can appear bottlebrush because its flexible branchlets can be curved. The polyps of *T. laxa* are a similar size with similar spacing as those of *T. grasshoffi*, however, the former has a low opercular cone and shorter

operculars with a blunt distal edge, whereas *T. grasshoffi* has a tall opercular cone, reflected in tall, triangular operculars. There is also a geographical separation between the two species with *T. grasshoffi* being found in the North Atlantic and *T. laxa* in the Indo-West Pacific.

Most species within Group 2 have polyps that are distally flared whilst *Thouarella grasshoffi* and *T. moseleyi* have more rounded, clavate polyps. The latter species differs from the former in having polyps with shorter marginals and a colony with a pinnate branching arrangement (so the colony can appear bilateral), whereas *T. grasshoffi* has a bottlebrush colony form.

Recent and new species combinations

Plumarella diadema (Cairns, 2006)

Fig. 36

Thouarella (Thouarella) diadema Cairns, 2006: 181–184, figs 10–11; Cairns & Bayer 2009: 28 (listed)

Thouarella sardana Zapata-Guardiola & López-González, 2010b: 136–139, figs 2c,d, 5, 7

Plumarella diadema Cairns 2011: 8

Material examined: **Holotype**, USNM 1078187, R/V *Calypso*, sta. 1776, 241 km SE of Sao Paulo, Brazil, 24°54'04"S, 44°26'00"W, 1000 m; **Paratype** of *Thouarella sardana* USNM 1123420, Antarktis XIX/5, R/V *Polarstern*, sample no. PS61/164–01, west of South Georgia Island, sub-Antarctic, 53°23'48"S, 42°42'02"W, 312–321 m, 9 Apr 2002; **Paratype** of *T. sardana*, USNM 1123420; USNM 1130273, USNM 1129185 and USNM 1130274 (from same location), R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia Island, sub-Antarctic, 54°30'S, 39°20'W, 659–686 m, 8 Feb 1966.

Other material: USNM 98090, R/V *Eltanin*, cruise 6, sta. 339, west of Beauchene Island, south of Falkland Islands, sub-Antarctic, 53°06'S, 59°27'W, 512–586 m, 3 Dec 1962, 2 colonies; USNM 98095 and USNM 98094 (same location), R/V *Eltanin*, cruise 9, sta. 740, east of Cape Horn, Drake Passage, Tierra del Fuego, Argentina, 56°06'S, 66°24'W, 384–494 m, 18 Sep 1963; USNM 98098 and USNM 77396 (from same location), R/V *Eltanin*, cruise 22, sta. 1592, Burdwood Bank, Scotia Sea, 54°44'S, 55°33'W, 1647–2044 m, 14 Mar 1966; USNM 98089, R/V *Eltanin*, cruise 5, sta. 283, west of Adelaide Island, Antarctic Peninsula, 66°26'S, 74°46'W, 3350–3693 m, 25 Oct 1962; USNM 77396, ZMH, R/V *W. Herwig*, sta. 226, SW Atlantic, 33°53'S, 51°52'W, 460 m, 11 Jun 1966; ZMH, R/V *W. Herwig*, sta. 191, SW Atlantic, 46°13'S, 59°49'W, 805 m, 17 Jan 1971; USNM 98101, R/V *Professor Siedlecki*, cruise 86–01, sta. 2, Shag Rocks, South Georgia Island, Sub-Antarctic, 53°20'S, 42°42'W, 417–514 m, 29 Nov 1986.

Description

See the holotypic publication for full taxonomic description (Cairns 2006). We add that that the specimens reported herein, including the holotype of *T. diadema* (now *Plumarella diadema*), usually reveal 2–8 small accessory operculars beneath the operculars.

The polyp arrangement was originally described as “roughly alternating” (Cairns 2006, p.181), however, with the wider body of material examined here, we conclude that this is not strictly true as usually the polyps originate from all sides of the branchlet. Also, *P. diadema* can have a pinnate colony structure (USNM 98089, Fig. 36b,c) and most colonies appear bilateral, although they have branching in 3 directions and are thus technically bottlebrush.

The marginals of some polyps of USNM 98030 have double spines and operculars that are bifurcate, likely a variation in a single colony (Fig. 36d,e).

Distribution

Additional specimens expand the range of *P. diadema* from São Paulo, Brazil, south to the tip of Argentina and east to South Georgia Island, sub-Antarctic. The depth of occurrence ranges from 278–3693 m.

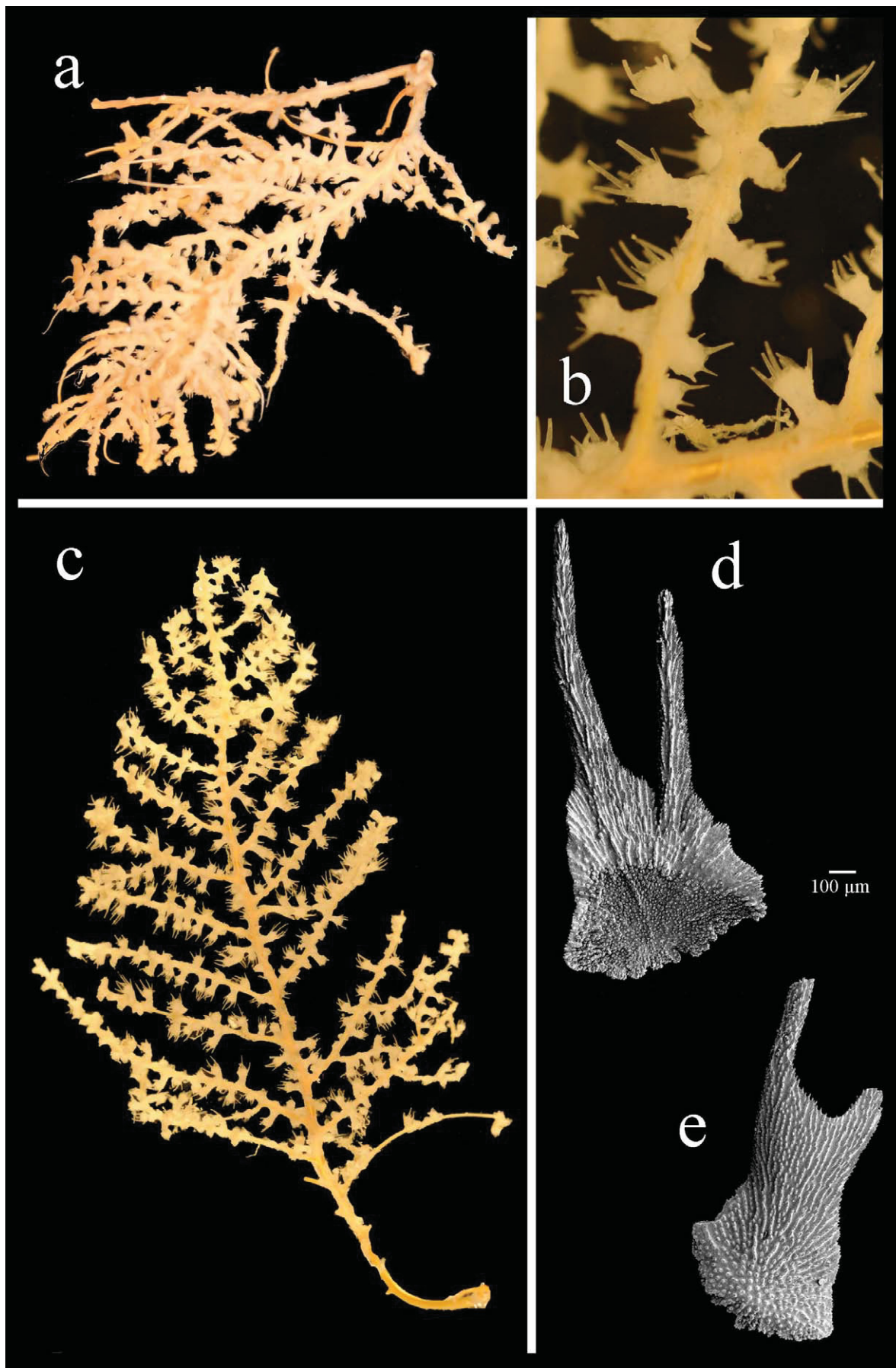


FIGURE 36. *Plumarella diadema*. Holotype, USNM 1078187: a) 6 cm colony; d) inner and e) outer surface of bifurcate marginal. USNM 98089: b) close up of polyps; c) pinnate colony form, 10 cm; c) 10 cm pinnate colony form. Photos by SJ.

Remarks

Thouarella sardana was differentiated from *T. diadema* because it has accessory operculars (Zapata-Guardiola & López-González 2010b). However, the holotype of *T. diadema* also has accessory operculars (although they do not occur in every polyp), which were not mentioned specifically in the original description (Cairns 2006), and thus these species are considered to be conspecific, as was suggested in Cairns (2011). *Thouarella diadema* has no keel on the inner surface of its marginals and it is thus considered to be a *Plumarella*, in agreement with Cairns (2011).

A deep-living specimen of *P. diadema* (USNM 98098, 1647–2044 m), did not have accessory operculars in any of the polyps studied but was identical in every other respect to this species. The deepest specimen, USNM 98089 (3350–3693 m), is pinnate but the polyps and sclerites are identical to those of *P. diadema*.

One specimen from SMF (WH 1971, sta. 191) has much smaller polyps, a maximum height of 2 mm (half the size of other specimens) and a very bushy, ramified branching structure. Some marginal scales of this specimen have a wider, winged base and a smoother inner surface. However, in all other respects, this specimen was identical to *P. diadema* and is thus included here; it may be a juvenile specimen.

Comparisons

Plumarella diadema differs from *Plumarella* (formerly *Thouarella*) *bayeri* Zapata-Guardiola & López-González 2010b in having more acutely triangular/arrowhead-shaped operculars, and colonies with bushy/bottlebrush rather than dichotomous branching.

Thouarella variabilis is very similar to *P. diadema* except polyps on colonies of *T. variabilis* are smaller and the spines of the marginals are keeled, rather than being channelled and circular in cross-section, as in *P. diadema*. The difference between these two forms of spines, one keeled, one not, differentiate *Thouarella* and *Plumarella*. Additionally, operculars on the polyps of *T. variabilis* tend to be narrower, leaving visible gaps into the sub-opercular region when viewed from the anterior, whereas the operculars of polyps of *P. diadema* are wider, and form a more complete covering.

The long spines of the marginals on polyps *P. diadema* can be mistaken for those of *Dasystenella acanthina*, but the polyps of the latter occur in whorls, and that genus is defined by having five, rather than eight, marginal scales.

Plumarella recta (Nutting, 1912)

Figs 37c,d, 38

Thouarella recta Nutting, 1912: 67–68, pl. 7, figs 1, 1a, pl. 19, fig. 2; Kükenthal 1919: 440–1; 1924: 302; Aurivillius 1931: 255–256

Thouarella (Thouarella) recta Cairns & Bayer 2009: 28 (listed)

Plumarella recta Cairns 2011:8

Material examined: **Holotype**, USNM 30040, R/V *Albatross*, sta. 5079, south of Omae Zaki, Honshu Island, Japan, 34°15'N, 138°E, 475–505 m, 19 Oct 1906, 5 cm fragment.

Description

The colony appears uniplanar, however, branchlets depart the main stem in 3 directions (2 rows at 160° creating an almost flat surface, with a third row placed sporadically along the dorsal spine at 260°), thus it is technically bottlebrush (Fig. 37c). The ventral branchlets (in 2 rows) depart alternately from the stem. The branchlets are usually simple, sometimes forked, upwardly inclined at 60°, and the longest branchlet is 24 mm.

The polyps stand at 90° to the branchlets (Fig. 37d), 1.2–1.4 mm high, generally isolated in one plane along the branchlet, with a density of 7–9 polyps per cm, and are modestly distally flared (Fig. 38m).

The operculum is a raised cone of 8 acute triangle-shaped operculars (Fig. 38n,c–e), 260–320 µm high (average 290 µm), 120–230 µm wide (average 165 µm), with a H:W of 1.4–2.3 (average 1.8). The distal and lateral scale edges are serrate although the lateral edges of some are pectinate whilst the proximal edges are roughly lobate. The inner surface is smooth (unkeeled) with a small patch of tubercles in the centre proximally. The outer surface is smooth with several small granules in the central proximal area.

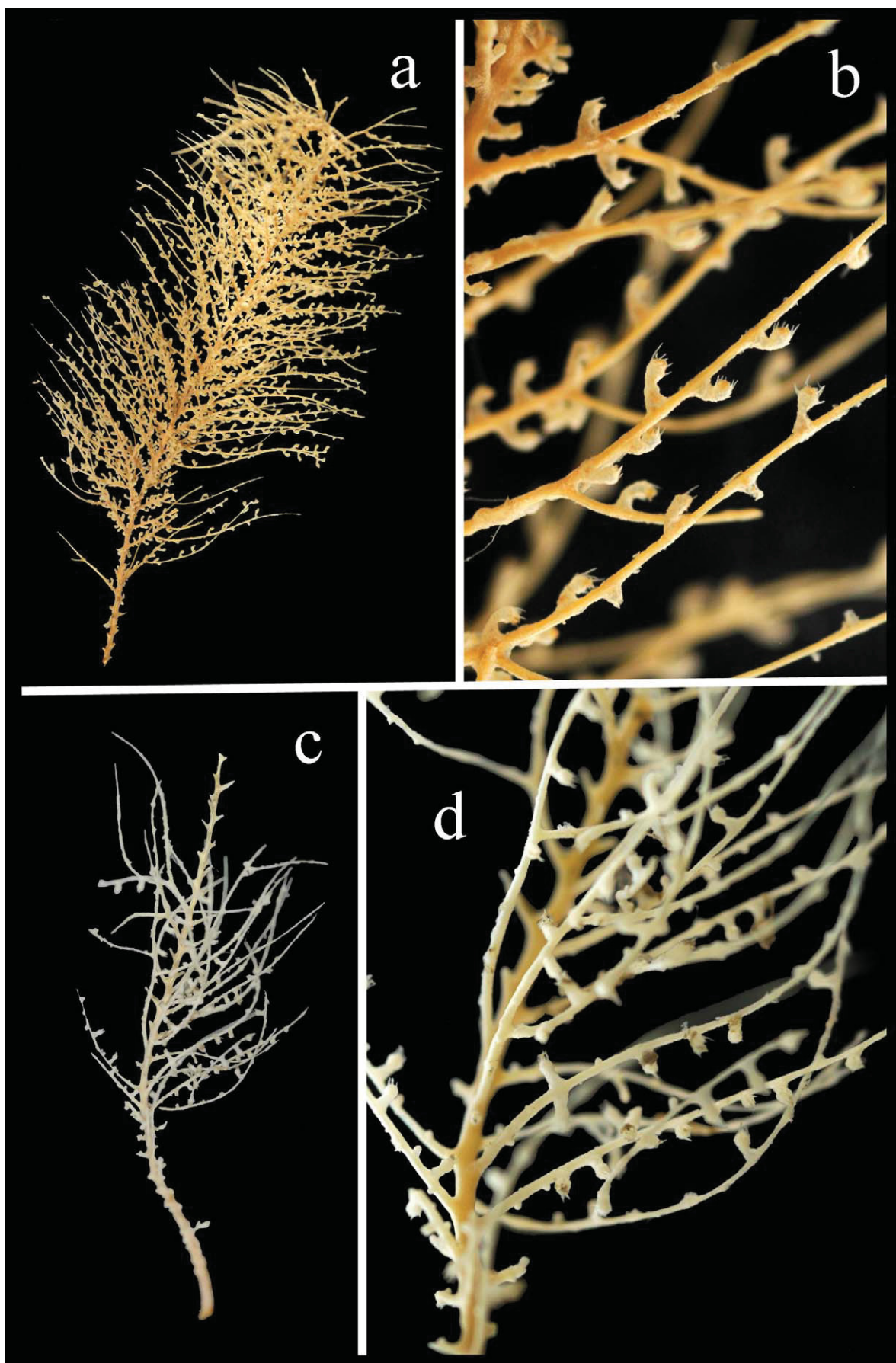


FIGURE 37. *Plumarella alternata*, holotype, USNM 30097: a) colony, approx. 16 cm long; b) close up of polyps. *Plumarella recta*, holotype, USNM 30040: c) colony 5.5 cm long; d) close up of polyps. Photos by RZG.

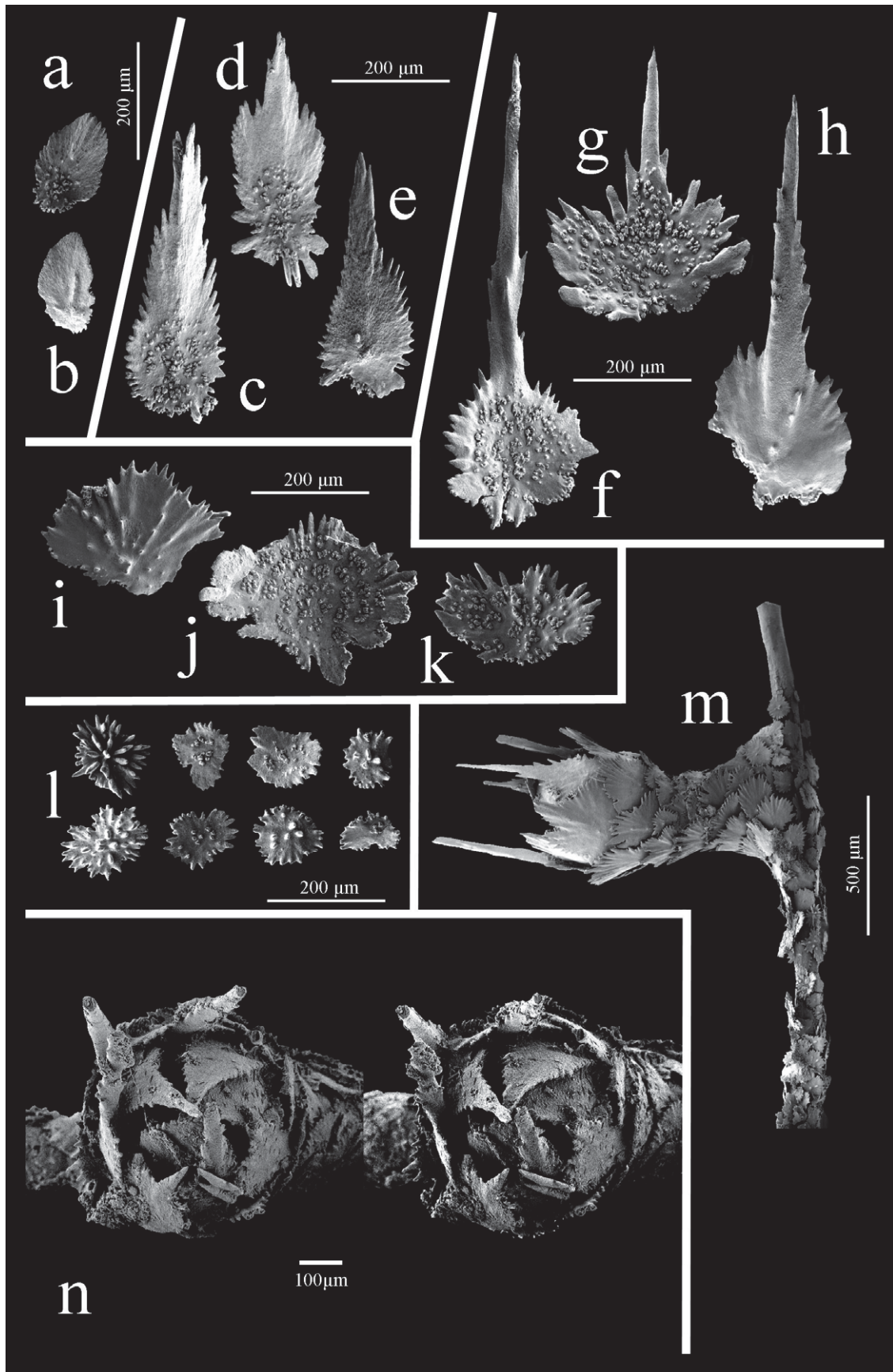


FIGURE 38. *Plumarella recta*, holotype, USNM 30040, identical sclerites to those of *P. alternata*: a) inner and b) outer surface of accessory operculars; c,d) inner and e) outer surface of opercular scales; f,g) inner and h) outer surface of marginal scales; i) outer and j,k) inner surface of body-wall scales; l) coenenchymal scales—first column of scales show the inner surface, remainder are the outer surface; m) lateral view of polyp; n) stereo opercular view of polyp. SEM taken by ZGR.

Between 2 and 4 accessory operculars are found underneath the operculars (Fig. 38a,b), which are identical to those of *P. alternata*. They are generally less than 200 µm high and 100 µm wide, round-tipped, tongue-shaped with a small patch of tubercles at the base of the inner surface and a smooth outer surface.

The marginal scales have a circular base with an elongated smooth distal spine. The circular base has a pectinate edge which can continue up the edges of the spine (Fig. 38f–h). These scales, 320–840 µm high (average 530 µm), 165–350 µm wide (average 220 µm), with a H:W of 1.4–3.3 (average 2.5), are too long to fold over the operculars. The adaxial marginals are smaller than those found abaxially. The inner surface is smooth with a sparsely tuberculate central circle at the base. The outer surface is smooth with few small granules towards the proximal area of the basal circle.

The body-wall scales are mostly elliptical to fan-shaped (Fig. 38i–k), although the shape is obscured by the large pectinate lateral and distal edges. Some are smaller and placed irregularly, disrupting row placement. The body-wall scales are 190–290 µm high (average 230 µm), 255–365 µm wide (average 290 µm) with a H:W of 0.7–1 (average 0.8). The outer surface is smooth with few granules whilst the inner surface has sparse tubercles and a tuberculate proximal edge.

The coenenchymal scales are numerous, small, and circular to elliptical in shape with finely serrate edges (Fig. 38l), 100–120 µm high (average 110 µm), 80–160 µm wide (average 125 µm), with a H:W of 0.7–1.4 (average 0.9). The inner surface has only several sparse tubercles whilst the outer surface is smooth with just a few granules.

Distribution

This species is only known from the south coast of Honshu Island, Japan, at depths of 475–505 m.

Remarks

All species of *Thouarella* have polyps with keeled marginals, however *T. recta* does not, and was thus transferred to *Plumarella* (Cairns 2011). The mostly smooth, unkeeled inner surface of the operculars and the marginals, the elongated marginals unable to fold over the operculum, and the smooth outer surface of the body-wall scales are characters found in *P. recta* and common to *Plumarella*. Unlike Cairns (2011), we keep *P. recta* and *P. alternata* as separate species.

The holotype is mostly denuded of polyps making the estimation of the density of polyps per cm tentative.

The longitudinal rows of scales along the polyp body are disrupted with smaller, circular body-wall scales (see Fig. 38m), which makes counting the number of scales in the two abaxial rows difficult. Nutting (1912) counted 8–9 scales in a longitudinal row. Within this study we count 4–6 large scales in the abaxial rows, discounting smaller proximal circular scales.

Comparisons

Plumarella recta is most similar to *P. alternata* (see below) except that its polyps stand at 90° to the branchlet whereas those of the latter are at 45°, and roughly alternating. Without being certain of the importance of this morphological feature, and despite the identical appearance of these polyps, these species are kept distinct.

***Plumarella alternata* (Nutting, 1912)**

Fig. 37 a,b

Thouarella alternata Nutting, 1912: 69–70, pl. 9, figs 1, 1a, pl. 19, fig. 3; Aurivillius 1931: 255–256

Thouarella attenuata Kükenthal 1919: 438 (spelled incorrectly); 1924: 301

Thouarella (Thouarella) alternata Cairns & Bayer 2009: 27 (listed)

Plumarella alternata Cairns 2011:8

Material examined: **Holotype**, USNM 30053, R/V *Albatross*, Northwestern Pacific Expedition, sta. 5080, west of Izu Islands, Honshu Island, Japan, 34°10'30"N, 138°40'E, 924 m, 19 Oct 1906; **Paratype**, USNM 30054, R/V *Albatross*, Northwestern Pacific Expedition, sta. 5079, south of Omae Zaki, Honshu Island, Japan, 34°15'N, 138°E, 869–924 m, 19 Oct 1906.

Diagnosis

Identical to *P. recta* (identical sclerites to Fig. 38), except the polyps are upwardly facing at 45° and roughly alternating in arrangement.

Distribution

This species is currently only known from Honshu Island, Japan, at depths of 869–924 m.

Remarks

The alternating polyps and a lack of keels on the marginal scales suggest that this species be placed within *Plumarella*, as suggested in Cairns (2011).

Comparisons

Without further material or knowing the importance of polyp orientation, we are hesitant to synonymise *P. alternata* and *P. recta* despite their identical sclerite and polyp sizes and shapes. This is in contrast to Cairns (2011), where these species are synonymised.

Plumarella superba (Nutting, 1912)

Primnodendron superbum Nutting, 1912: 71–72, pl. 9, fig. 2, 2a; pl. 19, fig. 4

Thouarella (Amphilaphis) superba Kükenthal 1919: 412; 1924: 291

Thouarella superba Dautova 2007: 299 (sample not seen)

Thouarella (Thouarella) superba Cairns & Bayer 2009: 28 (listed); Heifetz et al. 2005: 133 (listed)

Plumarella superba Cairns 2011: 13–14, figs 2C, 9a–l

Material examined: **Holotype**, USNM 50150, R/V *Albatross*, Northwestern Pacific Expedition, sta. 4778, Semisopochini Island, western Aleutian Islands, North Pacific, 78–133 m, 5 Jun 1906.

Description

See full description in Cairns (2011).

Distribution

This species occurs in the Aleutian Islands, possibly to the western boreal Pacific, Sakhalin Island (Dautova 2007) at depths from 29–133 m.

Remarks

The gross morphology of the colony is dichotomously uniplanar, with clear dorsal and ventral faces. The branches have branchlets on all sides in a bottlebrush arrangement, however, ventral and dorsal branchlets are much shorter than lateral branchlets.

The lack of a keel on the inner surface of the marginals suggests that this species is a *Plumarella*, as the genus description of *Plumarella* is now known to include bottlebrush colonies and specifically species with a smooth inner marginal surface, i.e. unkeeled (Cairns, 2010).

Plumarella bayeri (Zapata-Guardiola and López-González, 2010b), new combination

Thouarella bayeri Zapata-Guardiola & López-González, 2010b: 133–135, figs 2a,b, 3, 4.

Material examined: **Paratype**, USNM 1123419, details same as holotype, R/V *Polarstern*, ANT XIX/5, sta. PS61/164–01, west South Georgia Island, sub-Antarctic, 53°23.80'S, 42°42.03'W, 312.5–321.6 m, 9 Apr 2002.

Description

Fully described in Zapata-Guardiola and López-González (2010b).

Distribution

This species is currently known only from the west coast of South Georgia Island, at depths from 306–342 m.

Remarks

The marginals of the polyps of *Thouarella bayeri* are unkeeled (they have a long spine that is circular in cross section, and have longitudinal grooves on the inner surface), which suggests that the species should not be considered a *Thouarella* but a *Plumarella*. The diagnosis of *Plumarella* has expanded to include colonies with bottlebrush branches, such as *P. superba* (Cairns, 2011), making *T. bayeri* more suitably classified as *Plumarella*.

Apart from the colony shape, *P. bayeri* is identical to *P. diadema*, which is bottlebrush (although it can appear bilateral).

Plumarella undulata (Zapata-Guardiola and López-González, 2010b), new combination

Thouarella undulata Zapata-Guardiola & López-González, 2010b: 133–135, figs 2a,b, 3, 4

Material unavailable: **Holotype**, ZIZMH C11742, ANT XIX/5, sta. PS61/167–01, west of South Georgia, Antarctica, 53°23.68'S, 42°42.23'W, 306–342.7 m, 9 Apr 2002.

Material examined: **Paratype**, USNM 1123421, sample PS61/167–01, Antarktis XIX/5, R/V *Polarstern*, west of South Georgia Island, sub-Antarctic, 53°23'41"S, 42°42'14"W, 306–342.7 m, 9 Apr 2002.

Other material: USNM 98291, R/V *Eltanin*, sta. 305, west of Sars Bank, Drake Passage, Chile, Antarctic, 59°59'S/ 70°43'W to 59°58'S/ 70°32'W, 2782–2827 m, 1 Nov 1962, 2 colonies; USNM 99150, R/V *Polarstern*, EPOS3, sta. 295, AGT 26, Queen Maud Land, Coats Land, Off Cape Norvegia, Antarctic, 71°08'48"S, 13°48'06"W, 2037 m, 21 Feb 1989; USNM 1129186 and USNM 1130315 (same location), R/V *Eltanin*, cruise 22, sta. 1536, 54°30'S, 39°20'31"W, 659–686 m, 8 Feb 1966.

Description

Fully described in Zapata-Guardiola and López-González (2010b).

In addition to the original description, we would like to emphasize the radially arranged granules and striations on the outer surface of the operculars.

Distribution

Specimens from this study extend the known range of *P. undulata* across the southwest Atlantic Ocean and south to Cape Norvegia, Antarctica, 306–2827 m depth.

Remarks

Because the marginals of the polyps are long, spinose, and unkeeled, this species is considered to be a *Plumarella* (see Cairns, 2010).

The only character that differentiates *P. diadema* from *P. undulata* is the extreme longitudinal curving and outer surface striations of operculars on the polyps of the latter. The operculars of the polyps of *P. diadema* can be curved and the two largest tend to have some abaxial striations, however, less so than are found on *P. undulata*, and the majority of operculars are generally smooth.

Dasystenella acanthina (Wright and Studer, 1889)

Fig. 39

Stenella acanthina Wright & Studer, 1889: 59, pl. 14, fig. 3, pl. 20, fig. 10

Stenella (Dasystenella) acanthina Versluys 1906: 39, 48

Thouarella longispinosa Kükenthal, 1912: 299, figs 1–3

Thouarella (Euthouarella) longispinosa Kükenthal 1915: 151 (in part); 1919: 441 (in part); 1924: 302 (in part); Broch 1965: 26–27, pl. 3 figs 8–10

Thouarella longispinosa Gravier 1914: 61–63, pl. 7, figs 35–36, pl. 10, figs 52–55; Thomson & Rennet 1931: 24–26; Utinomi 1964: 11–12, fig. 6, pl. 2

Thouarella acanthina Brito 1993: 242–243

Dasystenella acanthina Bayer 1981: 934, 937, 946 (key to genus); Bayer & Stefani 1989: 454 (key to genus); Cairns 2006: 188–189; Cairns & Bayer 2009: 32 (listed), 47–49, fig. 18 i–p

Material examined: **Syntype** of *Stenella acanthina*, NHM 89.5.27.48a, *Deutsch Subpolar Expedition* 1901–1903, Gauss–Station, off Argentina, 385 m, 12 Jan 1903; **Syntype** of *Thouarella longispinosa*, MNHWU and SMF; USNM 84325, R/V *Eltanin*, cruise 12, sta. 1083, east of South Orkney Islands, Scotia Ridge, Antarctic, 60°51'S, 42°57'W, 284 m, 14 Apr 1964.

The MNHWU syntype of *T. longispinosa* is in poor condition with few intact polyps. The SMF sample is in a good condition. Examination of all the polyps confirmed the proposed synonymy. The colony description was taken from Kükenthal (1912).

Description of Thouarella longispinosa syntype (MNHWU)

The colony is bottlebrush in branching, with branchlets up to 22 mm long.

The polyps are 1.5–2.0 mm long, distally flared (Fig. 39c), and upwardly inclined, in whorls of 3 or 4, rarely in pairs, with 5 whorls per cm. The polyps are covered with a small number of scales in 5 longitudinal rows, reducing to 4 at the polyp base. Each polyp has 4 scales in an abaxial row (Fig. 39c), 2 lateral rows, each with 3 scales, and 2 reduced rows of 3 small scales adaxially.

The operculum is tall and conical, composed of 8 elongated isosceles triangle-shaped operculars. The operculars are not evenly spread around the circumference, the 2 reduced inner adaxial operculars being smaller (Fig. 39h) than the abaxial operculars (Fig. 39k), the latter of which have a proximally diagonal basal edge, depending on their opercular position. The inner surface of all operculars bears a simple, flattened keel. The operculars are 100–430 µm wide (average 260 µm), and 555–970 µm long (average 770 µm). Tubercles cover the proximal half of the inner surface and smaller operculars have fewer tubercles. The outer surface has a slightly concave median longitudinal groove and is usually smooth. Infrequent striations radiate from the central proximal area.

Each polyp has 5 marginals. Three are very long abaxial marginals (Fig. 39n, similar in shape to large operculars), 530–1340 µm high (average 840 µm), 300–570 µm wide (average 440 µm), with a H:W of 1.3–2.6 (average 1.9). Two of these 3 are outer laterals (Fig. 39m) with the remaining 2 small, square to circular-shaped marginals placed adaxially (Fig. 39b1) and of a similar size to smaller body-wall scales (Fig. 39f,g). Large marginals do not fold over the operculum but are upwardly inclined and lean slightly adaxially giving the 2 laterals a diagonal proximal edge (Fig. 39m, n). The proximal half of the inner surface is covered in tubercles to the base of the keel, which is channelled. The outer surface is smooth with sparse granules and a modest longitudinal groove.

The body-wall scales can be large (same size as largest operculars) and circular (Fig. 39e), 220–500 µm high (average 350 µm), 200–570 µm wide (average 420 µm), with a H:W of 0.8–1.1 (average 0.9). Tubercles cover the inner surface whilst the outer surface is smooth with some granules across the central proximal area of larger scales. Body-wall scales have a finely serrated distal edge.

The coenenchymal scales are small and circular to elliptical in shape (Fig. 39l), 150–200 µm wide and high. All sclerites of this species have a coarsely lobate proximal edge.

Distribution

This species is found off Tierra del Fuego, the South Shetland Islands and the South Scotia Ridge between the South Orkney and South Sandwich Islands, from 110–5087 m depth.

Remarks

When Kükenthal (1912) transferred *Stenella acanthina* to *Thouarella* he mentioned that it was very similar to *T. longispinosa* Kükenthal, 1915. Thomson and Rennet (1931) described *T. longispinosa* as having 4–5 marginals. *Thouarella longispinosa* does have five marginals and is thus *Dasystenella*. Brito (1993) does not explain clearly the inclusion of *D. acanthina* in *Thouarella* and we believe this is incorrect based on the lower number of marginals found in *D. acanthina*.

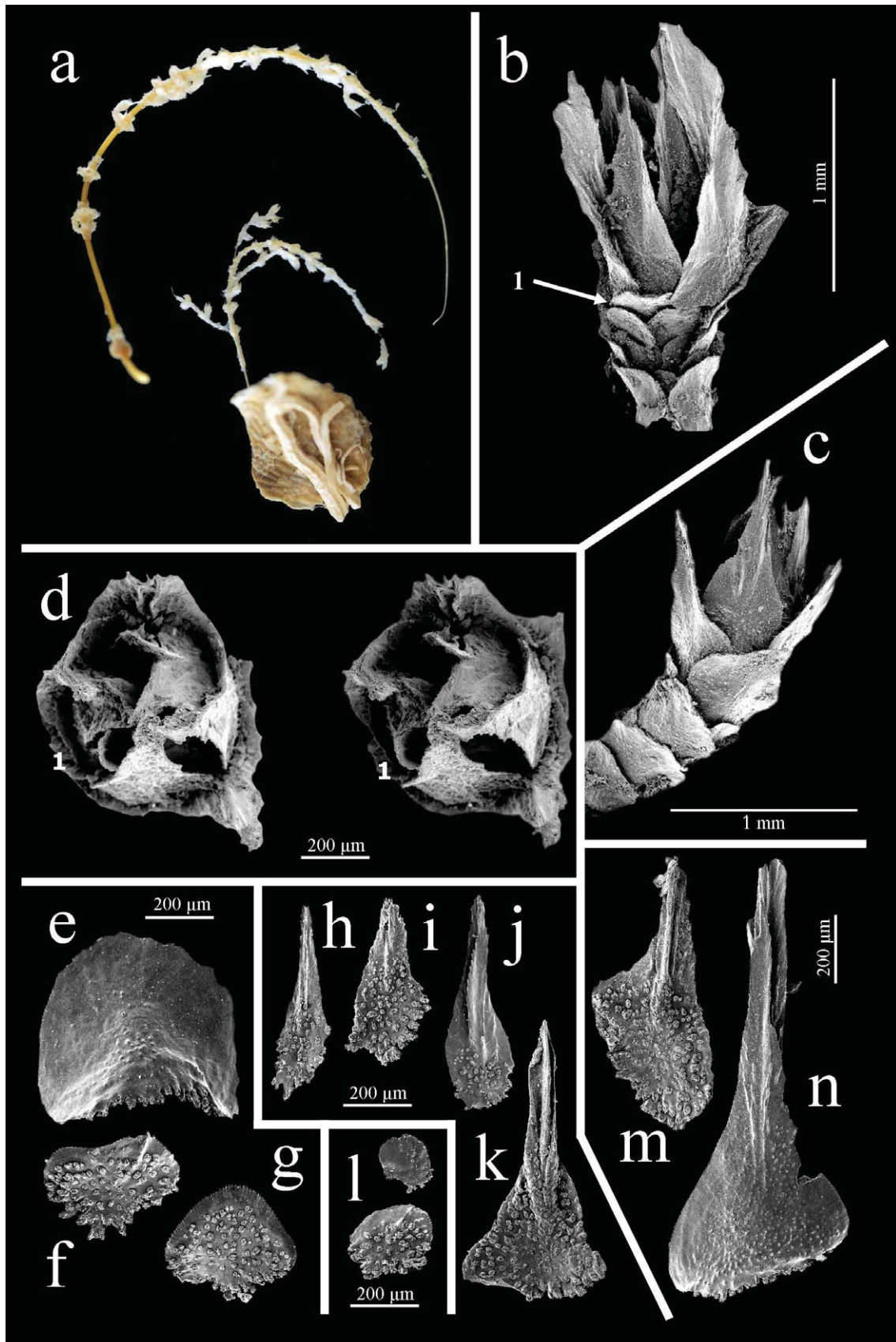


FIGURE 39. *Dasytenella acanthina*, images from syntype of *Thouarella longispinosa* (synonymised here with *D. acanthina*), MNHWU: a) 4.8 cm and 2 cm colony fragments; b) adaxial polyp view; c) abaxial polyp view; d) stereo opercular view; e) outer and f,g) inner body-wall scales; h–k) inner surface opercular scales; l) coenenchymal scales, upper scale outer surface, lower scale inner surface; m) inner and n) outer surface of marginal scales. NB—some operculars are missing. ‘1’ indicates small adaxial marginal scale. Image a) by ZGR.

The specimens of *Thouarella longispinosa* from MNHWU and SMF differ from the holotype of *D. acanthina* in having polyps with operculars and marginals more similar in size to each other, although, marginals of the specimens of *T. longispinosa* are generally longer and have a higher H:W of 2.7, compared to 2.1 in *D. acanthina* (Cairns 2006). However, Cairns (2006) lists some specimens of *D. acanthina* from southerly latitudes with polyps that are smaller and more upwardly inclined with marginals that have a much higher H:W of 3.5. Given this wide variation and the limited differences between specimens of *T. longispinosa* and the description of *D. acanthina*, we propose that *T. longispinosa* be synonymised with *D. acanthina*, noting that a revision of *Dasystenella* is required.

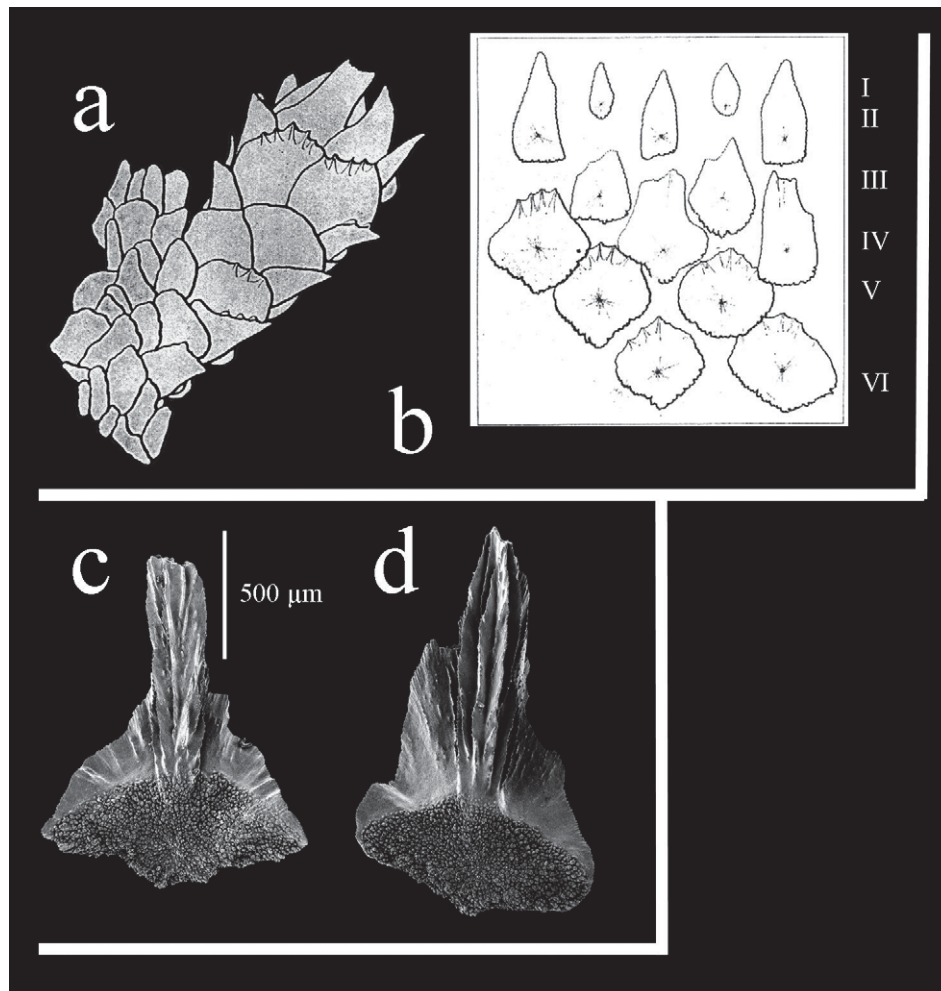


FIGURE 40. *Thouarella parva*, holotype: a) lateral polyp view, modified from Fig. 1 Kinoshita, 1908d; b) sclerites from Kinoshita, 1908d—I. accessory operculars, II. operculars, III. marginals, IV. submarginals, V, VI. body-wall scales. *Thouarella andeep*, USNM 1123418: c,d) inner surface of marginal scales.

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References

- Alderslade, P. (1998) Revisionary systematics in the gorgonian family Isididae, with descriptions of numerous new taxa (Coelenterata: Octocorallia). *Records of the Western Australian Museum*, Supplement 55, 1–359.
- Alderslade, P. & McFadden, C.S. (2007) Pinnule-less polyps: a new genus and new species of Indo-Pacific Clavulariidae and validation of the soft coral genus *Acrossota* and the family Acrossotidae (Coelenterata: Octocorallia). *Zootaxa*, 1400, 27–44.
- Aurivillius, M. (1931) The Gorgonarians from Dr. Sixten Bock's expedition to Japan and Bonin Islands 1914. *Kungliga Svenska Vetenskaps-Akademiens Handlinga*, Series 3, 9(4), 1–337.
- Bayer, F.M. (1956) Octocorallia. In: Moore, R.C. (Ed.) *Treatise on Invertebrate Palaeontology*, University of Kansas Press, Lawrence, Kansas, pp. F166–F189, F192–F231.
- Bayer, F.M. (1981) Key to genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnosis of new taxa. *Proceedings of the Biological Society of Washington*, 94, 902–947.
- Bayer, F.M. (1988) *Mirostenella articulata*, a remarkable new genus and species of primnoid octocoral (Gorgonacea) with uncalcified axial nodes. *Proceedings of the Biological Society of Washington*, 101(2), 251–256.
- Bayer, F.M. (1996) New primnoid gorgonians (Coelenterata: Octocorallia) from Antarctic waters. *Bulletin Marine Science*, 58(2), 511–530.
- Bayer, F.M., Grasshoff, M. & Verseveldt, J. (1983) *Illustrated Trilingual Glossary of Morphological and Anatomical Terms Applied to Octocorallia*. E.J. Brill, Leiden, 1–75 pp.
- Bayer, F.M. & Stefani, J. (1989) Primnoidae (Gorgonacea) de Nouvelle-Calédonie. *Bulletin de Muséum National d'Histoire Naturelle, Paris, Serie 4*, 10(3), 449–518.
- Brazeau, D.A. & Lasker, H.R. (1989) The reproductive cycle and spawning in a Caribbean gorgonian. *Biological Bulletin*, 176, 1–7. <http://dx.doi.org/10.2307/1541882>
- Briggs, J.C. (2003) Marine centres of origin as evolutionary engines. *Journal of Biogeography*, 30, 1–18. <http://dx.doi.org/10.1046/j.1365-2699.2003.00810.x>
- Brito, T.A.S. (1993) Taxonomic and ecological studies on Antarctic octocorals of the genus *Thouarella* (Octocorallia: Primnoidae). University of Southampton. PhD thesis.
- Brito, T.A.S., Tyler, P.A. & Clarke, A. (1997) Reproductive biology of the Antarctic octocoral *Thouarella variabilis* Wright and Studer, 1889. *Proceedings of the Sixth International Conference on Coelenterate Biology*, 1995, 63–69.
- Broch, H. (1965) Some octocorals from Antarctica waters. Scientific results of the “Bratigg” expedition, 1947–48. *Christensens Hvalfangstmuseum I Sandeford Publikasjon*, 26, 19–38.
- Cairns, S.D. (2006) Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 6: The genera *Primnoella* Gray, 1858; *Thouarella* Gray, 1870; *Dasystenella* Versluys, 1906. *Proceedings of the Biological Society of Washington*, 119(2), 161–194. [http://dx.doi.org/10.2988/0006-324X\(2006\)119\[161:SOWAOC\]2.0.CO;2](http://dx.doi.org/10.2988/0006-324X(2006)119[161:SOWAOC]2.0.CO;2)
- Cairns, S.D. (2010) Review of Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts. Part 3: Genera *Thouarella*, *Plumarella*, *Callogorgia*, *Fanellia*, and *Parastenella*. *Pacific Science*, 64(3), 413–440. <http://dx.doi.org/10.2984/64.3.413>
- Cairns, S.D. (2011) A revision of the Primnoidae (Octocorallia: Alcyonacea) from the Aleutian Islands and Bering Sea. *Smithsonian Contributions to Zoology*, 634, 1–55. <http://dx.doi.org/10.5479/si.00810282.634>
- Cairns, S.D. & Bayer, F.M. (2009) A generic revision and phylogenetic analysis of the Primnoidae (Cnidaria: Octocorallia). *Smithsonian Contributions to Zoology*, 629, 1–79. <http://dx.doi.org/10.5479/si.00810282.629>
- Carpine, C. & Grasshoff, M. (1985) Catalogue critique des Octocoralliaires des collections du Musée océanographique de Monaco I. Gorgonaires et Pennatulaires. *Bulletin de l'Institut Océanographique*, 73(1435), 1–72.
- Chave, E.H. & Malahoff, A. (1998) *In Deeper Waters: Photographic Studies of Hawaiian Deep-Sea Habitats and Life-Forms*, University of Hawai'i Press, Honolulu, 1–125 pp.
- Clarke, A. & Crame, J.A. (1989) The origin of the Southern Ocean marine fauna. In: Crame, J.A. (Ed.) *Origins and Evolution of the Antarctic Biota*, Geological Society, London, pp. 253–268.
- Clarke, A. & Crame, J.A. (2010) Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365(1558), 3655–3666. <http://dx.doi.org/10.1098/rstb.2010.0270>
- Cordes, E.E., Nybakken, J.W. & van Dykhuizen, G. (2001) Reproduction and growth of *Anthomastus ritteri* (Octocorallia: Alcyonacea) from Monterey Bay, California, USA. *Marine Biology*, 138(3), 491–501. <http://dx.doi.org/10.1007/s002270000470>
- Dautova, T. (2007) Gorgonians (Anthozoa: Octocorallia) of the northwestern Sea of Japan. *Russian Journal of Marine Biology*, 33(5), 297–304. <http://dx.doi.org/10.1134/S1063074007050045>
- Eckelbarger, K.J., Watling, L. & Fournier, H. (2005) Reproductive biology of the deep-sea polychaete *Gorgoniapolynoe caeciliae* (Polynoidae), a commensal species associated with octocorals. *Journal of the Marine Biological Association of the United Kingdom*, 85, 1425–1433. <http://dx.doi.org/10.1017/S0025315405012609>
- Gebruk, A.V. (1990) *Deep-sea Holothurians of the Family Elpidiidae*, Nauka, Moscow, 160 pp. (In Russian).

- Grasshoff, M. (1999) The shallow water gorgonians of New Caledonia and adjacent islands (Coelenterata: Octocorallia). *Senckenbergiana Biologica*, 78, 1–245.
- Gravier, C.H. (1914) Alcyonaires. Deuxieme Expedition antarctique Francaise (1908-1910). *Sciences Naturelles: Documents scientifiques*, 1–118.
- Gray, J.E. (1857) Synopsis of the families and genera of Axiferous zoophytes or barked corals. *Proceedings of the Zoological Society of London for 1857*, 278–294.
- Gray, J.E. (1859) Descriptions of some new genera of Lithophytes, or stony zoophytes. *Proceedings of the Zoological Society of London for 1859*, 479–486.
- Gray, J.E. (1870) *Catalogue of the Lithophytes or Stony Corals in the Collection of the British Museum*, British Museum, London, 51 pp.
- Gray, J.E. (1872) Notes on corals from South and Antarctic Seas. *Proceedings of the Zoological Society of London for 1872*, 744–747.
- Grigg, R.W. & Bayer, F.M. (1976) Present knowledge of the systematics and zoogeography of the order Gorgonacea in Hawaii. *Pacific Science*, 30(2), 167–175.
- Heifetz, J., Wing, B.L., Stone, R.P., Malecha, P.W. & Courtney, D.L. (2005) Corals of the Aleutian Islands. *Fisheries Oceanography*, 14, 131–138. <http://dx.doi.org/10.1111/j.1365-2419.2005.00371.x>
- Hickson, S.J. (1907) Coelenterata I. Alcyonaria. *National Antarctic (Discovery) Expedition, Natural History (British Museum)*, 3, 1–15.
- Kinoshita, K. (1907) Vorläufige Mitteilung über Einige Neue Japanische Primnoidkorallen. *Annotationes Zoologicae Japonensis*, 6(3), 229–237.
- Kinoshita, K. (1908a) Gorgonacea no ikka Primnoidae ni tsuite. *Dobutsugaku zasshi [Zoological Magazine]*, 20(240), 409–419. (In Japanese, translation at NMNH).
- Kinoshita, K. (1908b) Gorgonacea no ikka Primnoidae ni tsuite. *Dobutsugaku zasshi [Zoological Magazine]*, 20(241), 453–459. (In Japanese, translation at NMNH).
- Kinoshita, K. (1908c) Gorgonacea no ikka Primnoidae ni tsuite. *Dobutsugaku zasshi [Zoological Magazine]*, 20(242), 517–528. (In Japanese, translation at NMNH).
- Kinoshita, K. (1908d) *Diplocalyptra*, eine neue Untergattung von *Thouarella* (Primnoidae). *Annotationes Zoologicae Japonenses*, 7(1), 49–60.
- Kölliker, R.A. von (1865) *Icones Histologicae oder Atlas der vergleichenden Gewebelehre*. Die Bindesubstanz der Coelenteraten. Verlag von Wilhelm Engelmann, Leipzig, 87–181 pp.
- Kükenthal, W. (1907) Gorgoniden der Deutschen Tiefsee-Expedition. *Zoologischer Anzeiger*, 31, 202–212.
- Kükenthal, W. (1908) Diagnosen neuer Gorgoniden (4. Mitteilung). *Zoologischer Anzeiger*, 33(1), 9–20.
- Kükenthal, W. (1912) Die Alcyonaria der Deutschen Südpolar, Expedition 1901–1903. *Deutsche Südpolar Expedition 1901–1903, Zoologie*, 5(3), 289–349.
- Kükenthal, W. (1915) System und Stammesgeschichte der Primnoidae. *Zoologischer Anzeiger*, 46(5), 142–158.
- Kükenthal, W. (1919) Gorgonaria. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 13, 1–946 pp.
- Kükenthal, W. (1924) Coelenterata: Gorgonaria. *Das Tierreich*. Walter de Gruyter & Co., Berlin, 47, 1–478 pp.
- Kükenthal, W. & Gorzawsky, H. (1908) Diagnosen neuer japanischer Gorgoniden (Reise Doflein 1904–1905). *Zoologischer Anzeiger*, 32, 621–631.
- Lamouroux, J.V.F. (1812) Extrait d'un mémoire sur la classification des polypiers coralligènes non entierement pierreux. *Nouveau Bulletin des Sciences par la Société Philomatique de Paris*, 3(63), 181–188.
- Lewis, J.C. & Wallis, E.V. (1991) The function of surface sclerites in Gorgonians (Coelenterata, Octocorallia). *Biological Bulletin*, 181(2), 275–288. <http://dx.doi.org/10.2307/1542099>
- McFadden, C.S., France, S.C., Sanchez, J.A. & Alderslade, P. (2006) A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. *Molecular Phylogenetics and Evolution*, 41(3), 513–527. <http://dx.doi.org/10.1016/j.ympev.2006.06.010>
- Menneking, F. (1905) Über die Anordnung der Schuppen und das Kanalsystem bei *Stachyodes ambigua* (Stud.), *Caligorgia flabellum* (Ehrb.), *Calyptraphora agassizii* (Stud.), *Amphilaphis abietina* (Stud.) und *Thouarella variabilis* (Stud.). *Archiv fuer Naturgeschichte*, 71(3), 245–266.
- Milne-Edwards, H. (1857) *Histoire naturelle des coralliaires ou polypes proprement dits*. Vol. 2, Roret, Paris, 1–633 pp.
- Molander, A.R. (1929) Die Octactiniariien. *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903*, 2(2), 1–86.
- Nutting, C.C. (1908) Descriptions of the Alcyonaria collected by the U.S. Bureau of Fisheries steamer *Albatross* in the vicinity of the Hawaiian Islands in 1902. *Proceedings of the United States National Museum*, 34, 543–601. <http://dx.doi.org/10.5479/si.00963801.34-1624.543>
- Nutting, C.C. (1912) Descriptions of the Alcyonaria collected by the U.S. Fisheries steamer “*Albatross*”, mainly in Japanese waters, during 1906. *Proceedings of the United States National Museum, Smithsonian Institution*, 43, 1–104. <http://dx.doi.org/10.5479/si.00963801.43-1923.1>
- Orejas, C., Gili, J., López-González, P., Hasemann, C. & Arntz, W. (2007) Reproduction patterns of four Antarctic octocorals in the Weddell Sea: an inter-specific, shape, and latitudinal comparison. *Marine Biology*, 150(4), 551–563. <http://dx.doi.org/10.1007/s00227-006-0370-9>
- Orejas, C., López-González, P.J., Gili, J.M., Teixidó, N., Gutt, J. & Arntz, W.E. (2002) Patterns of density and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea. *Marine Ecology Progress Series*, 231, 101–114. <http://dx.doi.org/10.3354/meps231101>
- Parrish, F.A. & Baco, A.R. (2007) State of deep coral ecosystems in the U.S. Pacific Islands Region: Hawaii and the U.S. Pacific

- Territories. In: Lumsden, S. E., Hourigan, T. F., Bruckner, A. W. and Dorr, G (Eds.) *The State of Deep Coral Ecosystems of the United States*. Silver Spring, MD, USA, U.S. Dept. Com., NOAA Tech. Memo CRCP—3, 155–194 pp.
- Pearse, J.S., McClintock, J.B. & Bosch, I. (1991) Reproduction of Antarctic marine invertebrates: tempos, modes and timing. *American Zoologist*, 31, 65–80.
- Rogers, A.D. (2007) Evolution and biodiversity of Antarctic organisms: a molecular perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1488), 2191–2214. <http://dx.doi.org/10.1098/rstb.2006.1948>
- Rogers, A.D. (2012) Evolution and biodiversity of Antarctic organisms: a molecular perspective. In: Rogers, A.D., Johnston, N.M., Murphy, E.J. & Clarke, A. (Eds.) *Antarctic Ecosystems: An Extreme Environment in a Changing World*, Wiley Publishers, Oxford, UK, pp 417–467. <http://dx.doi.org/10.1002/9781444347241.ch14>
- Roule, L. (1908) Alcyonaires. *Expedition Antarctique Française (1903–1905), Sciences Naturelles: Documents Scientifiques*, 15, 1–6.
- Slattery, M. & McClintock, J. (1997) An overview of the population biology and chemical ecology of three species of Antarctic soft corals. In: Battaglia, B., Valencia, J. & Walton, D. W. (Eds.) *Antarctic Communities: Proceedings 6th International SCAR Symposia, Venice, Italy*. Cambridge University Press, pp. 309–315.
- Stiasny, G. (1940) Alcyonaria und Gorgonaria von Südafrika aus der Sammlung des South African Museum, Cape Town. *Verhandelingen der Nederlandsche akademie van wetenschappen, Afdeling Natuurkunde, Tweede Sectie*, 39(3), 1–37.
- Stibane, F.A. (1987) Primnoide Oktokorallen (Coelenterata: Anthozoa, Ordo Gorgonacea Lamouroux, 1816) aus dem Sudatlantik. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 84, 17–26.
- Strugnell, J.M., Rogers, A.D., Prodöhl, P.A., Collins, M.A. & Allcock, L.A. (2008) The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics*, 24(6), 853–60. <http://dx.doi.org/10.1111/j.1096-0031.2008.00234.x>
- Studer, T. (1878) Übersicht der Anthozoa Alcyonaria, welche während der Reise S.M.S. *Gazelle* um die Erde gesammelt wurden. *Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 632–688.
- Studer, T. (1887) Versuch eines Systemes der Alcyonaria. *Archiv für Naturgeschichte*, 53(1), 1–74.
- Thomson, J.A. (1911) Zoological studies chiefly on alcyonarians (fifth and sixth series). University of Aberdeen, 48, 177.
- Thomson, J.A. (1927) Alcyonaires provenant des campagnes scientifiques du Prince Albert 1er de Monaco. *Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert 1er, Monaco*, 73, 1–77.
- Thomson, J.A. & Henderson, W.D. (1906) *An Account of the Alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. Part 1. The Alcyonarians of the Deep Sea*. The Indian Museum, Calcutta, 1–132.
- Thomson, J.A. & Rennet, N.I. (1931) Alcyonaria, Madreporaria, and Antipatharia. *Scientific Reports, Australasian Antarctic Expedition 1911–1914, (C- Zoology and Botany)*, 9(3), 1–46.
- Thomson, J.A. & Richie, J. (1906) The Alcyonarians of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh*, 41(3), 851–860.
- Tixier-Durivault, A. (1954) Les octocoralliaires d'Afrique du sud. *Bulletin du Muséum National d'Histoire Naturelle*, 26(2), 261–268.
- Tripathi, A., Backman, J., Elderfield, H. & Ferretti, P. (2005) Eocene bipolar glaciation associated with global carbon cycle changes. *Nature*, 436(7049), 341–346. <http://dx.doi.org/10.1038/nature03874>
- Utinomi, H. (1964) Some octocorals from the Antarctic waters off Prince Harald Coast. *Japanese Antarctic Research Expedition Scientific Report, Series E*, 23, 1–14.
- Valenciennes, A. (1846) Atlas of Zoophytes In: Dupetit-Thouars (Ed.) *Voyage autour du monde sur la frégate la Vénus, pendant les années 1836–1839*, pl. XII, Fig. 2.
- Valenciennes, A. (1855a) Extrait d'une monographie de la famille des Gorgonidées de la classe des polypes. *Comptes Rendus Académie des Sciences de Paris*, 41, 7–15.
- Valenciennes, M. (1855b) XVI.—Abstract of a monograph of the family Gorgonidae. *The Annals and Magazine of Natural History including Zoology, Botany and Geology*. Translated by Selby, P.J., Babington, C.C., Balfour, J.H. & Taylor, R. London, Taylor and Francis, 177–183.
- Versluys, J. (1906) Die Gorgoniden der Siboga-Expedition. *Siboga-Expeditie*, 13a, 1–187.
- Williams, G.C. (1992) The Alcyonacea of Southern Africa. Gorgonian corals. *Annals of the South African Museum*, 101(8), 181–296.
- Wright, E.P. & Studer, T. (1889) Report on the Alcyonaria collected by H.M.S. *Challenger* during the years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76, Zoology*, 31(64), 1–314.
- Zapata-Guardiola, R. & López-González, P.J. (2010a) Two new species of Antarctic gorgonians (Octocorallia: Primnoidae) with a redescription of *Thouarella laxa* Versluys, 1906. *Helgoland Marine Research*, 64(3), 169–180. <http://dx.doi.org/10.1007/s10152-009-0176-5>
- Zapata-Guardiola, R. & López-González, P.J. (2010b) Four new species of *Thouarella* (Anthozoa: Octocorallia: Primnoidae) from Antarctic waters. *Scientia Marina*, 74(1), 131–146. <http://dx.doi.org/10.3989/scimar.2010.74n1131>
- Zapata-Guardiola, R. & López-González, P.J. (2010c) Two new gorgonian genera (Octocorallia: Primnoidae) from Southern Ocean waters. *Polar Biology*, 33(3), 313–320. <http://dx.doi.org/10.1007/s00300-009-0707-1>
- Zapata-Guardiola, R. & López-González, P.J. (2012) Revision and redescription of the species previously included in the genus *Amphilaphis* Studer and Wright in Studer, 1887 (Octocorallia: Primnoidae). *Scientia Marina*, 76(2). <http://dx.doi.org/10.3989/scimar.03278.18B>