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Three new species of pennatulacean octocorals with the ability to attach to rocky substrata (Cnidaria: Anthozoa: Pennatulacea)

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Abstract

All sea pens have been thought to anchor in soft sediment using a basal, sausage-shaped, muscular peduncle. Based on underwater images and examination of specimens, we report an adaptation of the proximal portion of the peduncle for attachment to solid surfaces. We document four species with this adaptation, three new, *Anthoptilum lithophilum* sp. nov. (California, 669–700 m), *A. gowlettholmesae* sp. nov. (Tasmania, 729–1803 m), and *Calibelemnnon francesi* sp. nov. (the Bahamas, 1969 m), and one known, *A. decipiens* Thomson & Henderson, 1906 (Sri Lanka, 925 m). The peduncle of a colony with this adaptation is greatly expanded by an outgrowth of the coenenchyme that forms a sucker-like structure, beneath which a conical mass of tough tissue surrounds the proximal end of the internal axis. We infer this structure affects suction, increasing or decreasing the strength of adhesion to the substratum, and discuss the systematics and functional morphology of this new ecological phenomenon—pennatulaceans fastened to hard substrata. We alter the definition of the genus *Anthoptilum* to accommodate this morphology, reporting on specimens of the type species, *A. grandiflorum*; compare the two sea pen families—Anthoptilidae and Scleroptilidae—and the two genera; and present a key to the known rock-inhabiting species.

Key words: Octocorallia, Anthoptilidae, Scleroptilidae, new taxa, sea pens, benthic adaptation, rocky substrata

Introduction

Recent advances in deep-sea exploration technology have allowed for discoveries and observations not previously possible. In deep ocean research, the use of remotely operated vehicles (ROVs) has led to the ability to select individual deep sea organisms for collection and photography (both video and still images) (Williams and Lundsten, 2009), and permitted organisms on hard substrata (such as deep reefs and rocky outcrops) to be carefully collected in contrast to the severe limitations of bottom trawls, dredges, and bottom grabs in such habitats. Until now, sea pens (Pennatulacea) have been characterized by a basal muscular peduncle that has evolved to anchor them only in soft sediments (Williams, 1999), but in the past decade ROVs have enabled observations and collections to be made of pennatulacean octocorals attached to rocks or stones, sometimes covered in a thin layer of sediment (seen in images from the ROV *Jason*), from a depth range of 670–2060 m. These sea pens, which have been found in Australia, New Zealand, Hawai'i, central California in the Pacific, and the Bahamas in the western Atlantic (Chave & Malahoff 1998; below in this paper) are able to attach to rocky substrata by a remarkable morphological modification of the proximal portion of the peduncle.

The discovery and recognition of this structure is significant regarding evolutionary biology and ecology, in that sea pens are now known to have developed an adaptation and capability to live on rocky substrata permitting them to colonise habitats other than the soft sediments to which they were considered to be restricted.

Several octocoral genera are known to occupy both hard and soft substrata:

1. Some species of *Dendronephthya* can attach to hard reef material while others have short basal stolons to attach to small grains and gravel in sediments (e.g. hard substrate, *D. koellikeri* and *D. habereri* Kükenthal,

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- 1905, soft substrate, *D. quadrata* Henderson, 1909, and *D. puchella* Utinomi, 1952, see Vereseveldt, 1966; and see images in Fabricius & Alderslade 2001);
2. Species of *Solenocaulon* are described as having a spatulate basal extension to anchor them in soft substrate, while others have been photographed attached to reef material (Fabricius & Alderslade 2001).
 3. Some species of *Acanella* have developed calcareous, lobate holdfasts for holding in soft sediment in contrast to those attached with a disk-like holdfast to hard bottom (Bayer, 1990).

However, the sucker-like form of the adaptation in sea pens is without precedent.

As a result of the use of ROVs, three new species in two genera (*Anthoptilum* and *Calibelemnion*) are described here. In addition, a known species of *Anthoptilum* described from the collection of the RIMS Investigator obtained about the turn of the 19th century is assessed as also being able to attach to hard substrate. To define the genus *Anthoptilum* as accepted up till now, and to illustrate the form of the peduncle in sea pens that inhabit soft substrate, two specimens of *A. grandiflorum* (the type species of the genus) were also examined.

Abbreviations:

CAS	California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, California 94118-4503, U.S.A.
TMAG	Tasmanian Museum and Art Gallery, Winkleigh Place, Rosny, Hobart, Tasmania, Australia, 7018.
CSIRO	Commonwealth Scientific Industrial Research Organization, Australia.
HURL	Hawai'i Undersea Research Laboratory, Honolulu, Hawai'i, U.S.A.
MBARI	Monterey Bay Aquarium Research Institute, Moss Landing, California, U.S.A.
NIWA	National Institute of Water and Atmospheric Research, New Zealand.
NOAA	National Oceanic and Atmospheric Administration, U.S.A.

Material and methods

Besides specimens recently sent to first author because of their unusual peduncular form and then accessioned by CAS, and those collected by the ROV *Jason*, other material came from older CAS holdings.

The specimens collected from California and the Bahamas were placed straight into 75–95% ethanol. The specimens from Tasmania were frozen before being placed into 70% ethanol.

The sea pen specimens from off the southern coast of Tasmania, Australia, were collected by the deep-diving ROV *Jason*, operated from the U.S. RV *Thomas T. Thompson*, during December 2008–January 2009. The principal object of the cruise, led by chief scientists Jess Adkins (California Institute of Technology) and Ron Thresher (CSIRO Climate Adaptation and Wealth from Oceans Flagships), was to collect recent and sub-fossil deep-water corals as continuation of an oceanographic and climate reconstruction project.

During the expedition the ROV made ten dives to a maximum of 4011 m, amassed thousands of underwater photographs, hundreds of hours of video and collected over a thousand lots of invertebrates. For an extensive report on the RV *Thomas T. Thompson* expedition and associated research see Thresher *et al.* (2009).

Prior to the RV *Thomas T. Thompson* expedition, Karen Gowlett-Holmes, from CSIRO Marine and Atmospheric Research in Hobart, had noticed specimens of the unusual sea pens that are included in this paper whilst reviewing the still images and video taken on the CSIRO research expedition SS200611 using the CSIRO Deep Video System. The specimens were solitary and rare, and commonly on high relief, usually sloping, rocky terrain, which is difficult to sample using sleds and grabs, and despite attempts, no specimens were collected during the subsequent expedition, SS200702, to several of the specifically logged sites. Therefore, as the state of the art *Jason* is an ideal platform for such endeavours, the sea pen became one of the targeted species for that vehicle. Coincidentally, Karen Gowlett-Holmes was on duty on each occasion that one of the sea pens was seen on the monitor linked to the *Jason* and was able to alert the pilot who photographed the specimens and retrieved them in good condition.

Systematic account

Family Anthoptilidae Kölliker, 1880

Anthoptilum Kölliker, 1880

Anthoptilum grandiflorum (Verrill, 1879)

Figs. 1, 7A

Virgularia grandiflora Verrill, 1879: 239.

Anthoptilum thomsoni Kölliker, 1880: 13.

Anthoptilum simplex Kölliker, 1880: 15.

Anthoptilum grandiflorum Jungersen 1904: 66; Hickson 1904: 233; Küenthal & Broch 1911: 233; Thomson 1915: 17; Küenthal 1915: 32; Tixier-Durivault 1954: 629; Grasshoff 1982: 954; Williams 1990: 69.

Benthoptilum seratum Verrill, 1885: 510

Anthoptilum malayense Hickson, 1916: 143.

Thesioides inermis Thomson & Henderson, 1906: 91.

Material examined. CAS 122323, U.S.A., Oregon off shore, 44.00° $28.30'$ N, 125.00° $13.40'$ W, 1335–1372 m depth, 20 October 1961, J.E. McCauley aboard RV *Acona*, Oregon State University.

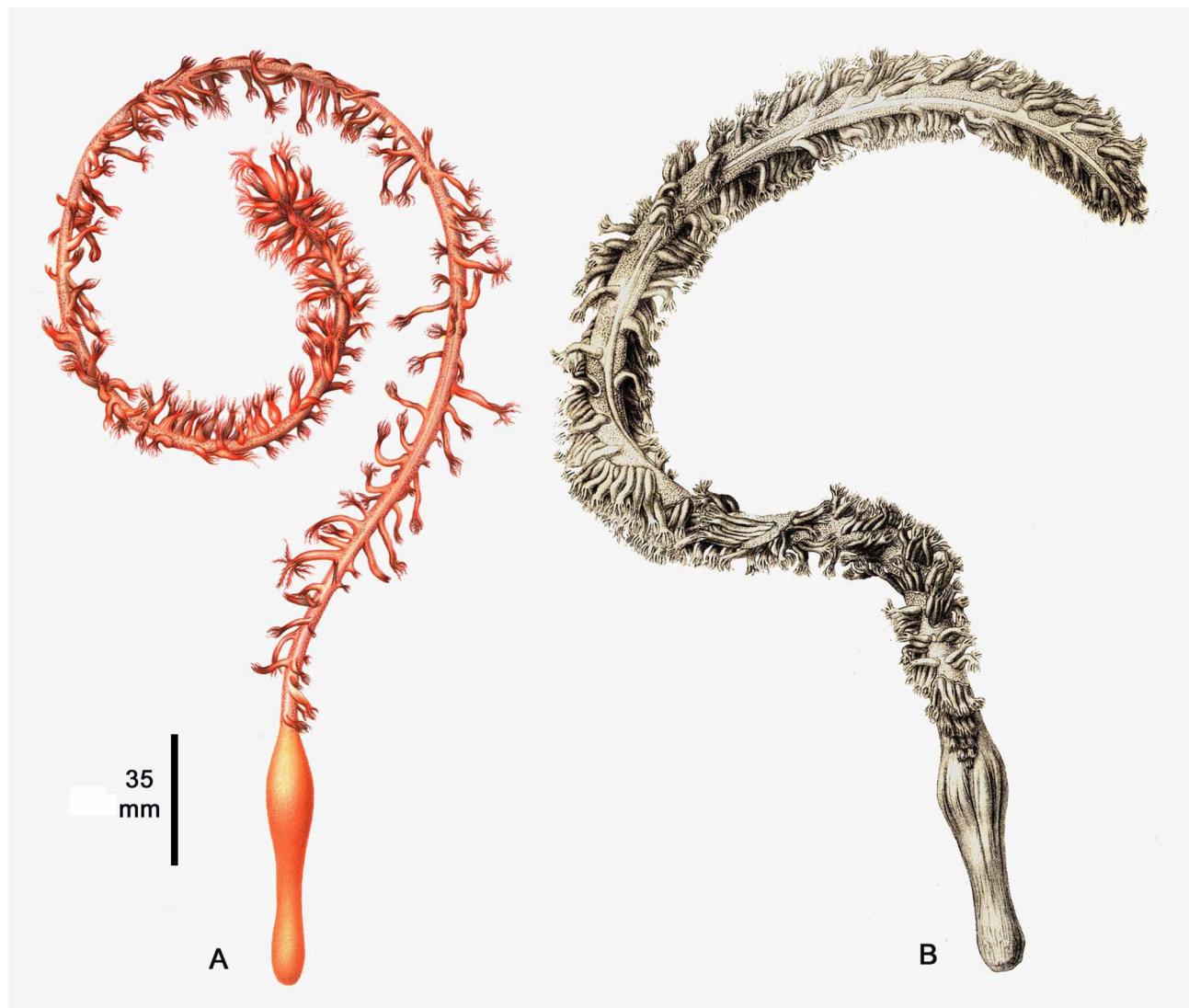


FIGURE 1. Illustrations of *Anthoptilum grandiflorum*: A, from Küenthal & Broch 1911, Pl. 14, Fig. 6; B. *Anthoptilum thomsoni* (considered a synonym of *A. grandiflorum* by Küenthal 1915) from Kölliker 1880, Pl. 4, Fig. 16.

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Description of CAS 122323. The wet-preserved colony is elongate, narrow, strongly curved and 460 mm long; the rachis is 378 mm long and 7–8 mm wide; and the peduncle is 82 mm long and 8–16 mm wide. The autozooids are up to 10 mm long and 2.5 mm wide, numerous and crowded around much of the circumference of the rachis, leaving only one side free of polyps. Siphonozooids are numerous (>20 per linear 10 mm), crowded between the autozooids, circular to slightly oval in shape, and mostly 0.25 mm in diameter. Sclerites of the peduncle interior are sparsely distributed, minute oval bodies up to 0.03 mm in length. Color of colony in alcohol is light tan.

Distribution. *Anthoptilum grandiflorum* occurs in all oceans, to 3150 m depth.

Remarks. We have been unable to examine the holotype of *Anthoptilum grandiflorum* (Verrill, 1879). The specimen was apparently deposited at the Peabody Museum of Natural History of Yale University and is recorded as being dry. A search and inventory of all dry type specimens at the Museum is currently under way (pers. comm. E.A. Lazo-Wasem, Senior Collection Manager), with an undetermined time of completion.

This relatively well known species was considered by Kükenthal (1915: 32–33) as possibly the only known valid species in the genus *Anthoptilum*, since *A. simplex*, *A. thomsoni*, and *A. murrayi* of Kölliker, 1880, and *A. decipiens* and *Thesioides inermis* of Thomson & Henderson, 1906 were listed by him as junior synonyms. In addition, in the same paper Kükenthal recorded *Anthoptilum sertum* (Verrill, 1885) as a dubious or uncertain species after having previously transferred *Benthoptilum sertum* (Verrill, 1885) (and Stephens 1909) to *Anthoptilum* as a valid species (Kükenthal & Broch 1911). Grasshoff (1982), however, regarded *A. sertum* as a synonym of *A. grandiflorum* and recognized *A. murrayi* as an additional valid species. We agree with Grasshoff's assessment, and we also believe *Anthoptilum malayense* Hickson, 1916, to be a junior synonym of *A. grandiflorum*.

Anthoptilum grandiflorum is a soft-sediment inhabiting species, with a sausage-shaped peduncle similar in structure to that of the vast majority of other pennatulaceans (Figs. 1, 7A), and does not exhibit modifications of the proximal apex for attachment to hard substrata (Figs. 7B, 8A–E). Colonies are whip-like or vermiform, some over 1,000 mm in total length with a rachis (minus polyps) commonly 10 mm in maximum width, giving a ratio of total colony length to rachis diameter of up to 100:1

***Anthoptilum decipiens* Thomson & Henderson, 1906**

(Fig. 10)

Anthoptilum decipiens Thomson & Henderson, 1906: 109.

Remarks. Part of Thomson and Henderson's (1906: 109) inadequately illustrated description of this species, follows. "The stalk is short and conical; it expands gradually from its junction with the rachis downwards, and has a large knob in the centre of the base. The base thus resembles a "tam o' shanter"; or, to put it another way, the stalk ends in a large knob, but before reaching the knob it expands into a large collar-like fold The most noteworthy features of this species are: 3. The shape of the basal expansion with its knob-like termination into which the end of the axis extends. Locality: 7° 55' N., 81° 47' E: 506 fathoms."

As a result of this detailed account of the proximal end of the peduncle, we regard *A. decipiens* as a rock-inhabiting sea pen. Other aspects of the description (elongate colony 720 mm in length, ratio of colony length to rachis diameter 180:1, siphonozooid distribution, minute rod-like sclerites in the peduncle that may form star-shaped groups) indicate that this is a fourth species of this type of sea pen, despite Kükenthal (1915) listing it as a synonym of *A. grandiflorum*. We are, however, unable to confirm this, as the specimen is probably in the Indian Museum in Kolkata (where the bulk of the samples from the *Investigator* expedition are stored), and we have never been able to obtain information or loans from this institution. Thomson and Henderson (1906) did not designate type specimens, but some of their specimens labeled as holotypes, or as parts of holotypes, are in the Natural History Museum, London—unfortunately *A. decipiens* is not among them.

***Anthoptilum lithophilum* sp. nov.**

Figs. 2–3, 6C, 8D, 10

Material examined. HOLOTYPE: CAS 179453, sample number T666-R10, California, Northeast Bank, Outer California Borderlands, 32.2716305° N, 119.6724745° W, 669 m depth, 3 May 2004, MBARI, on basaltic lava.

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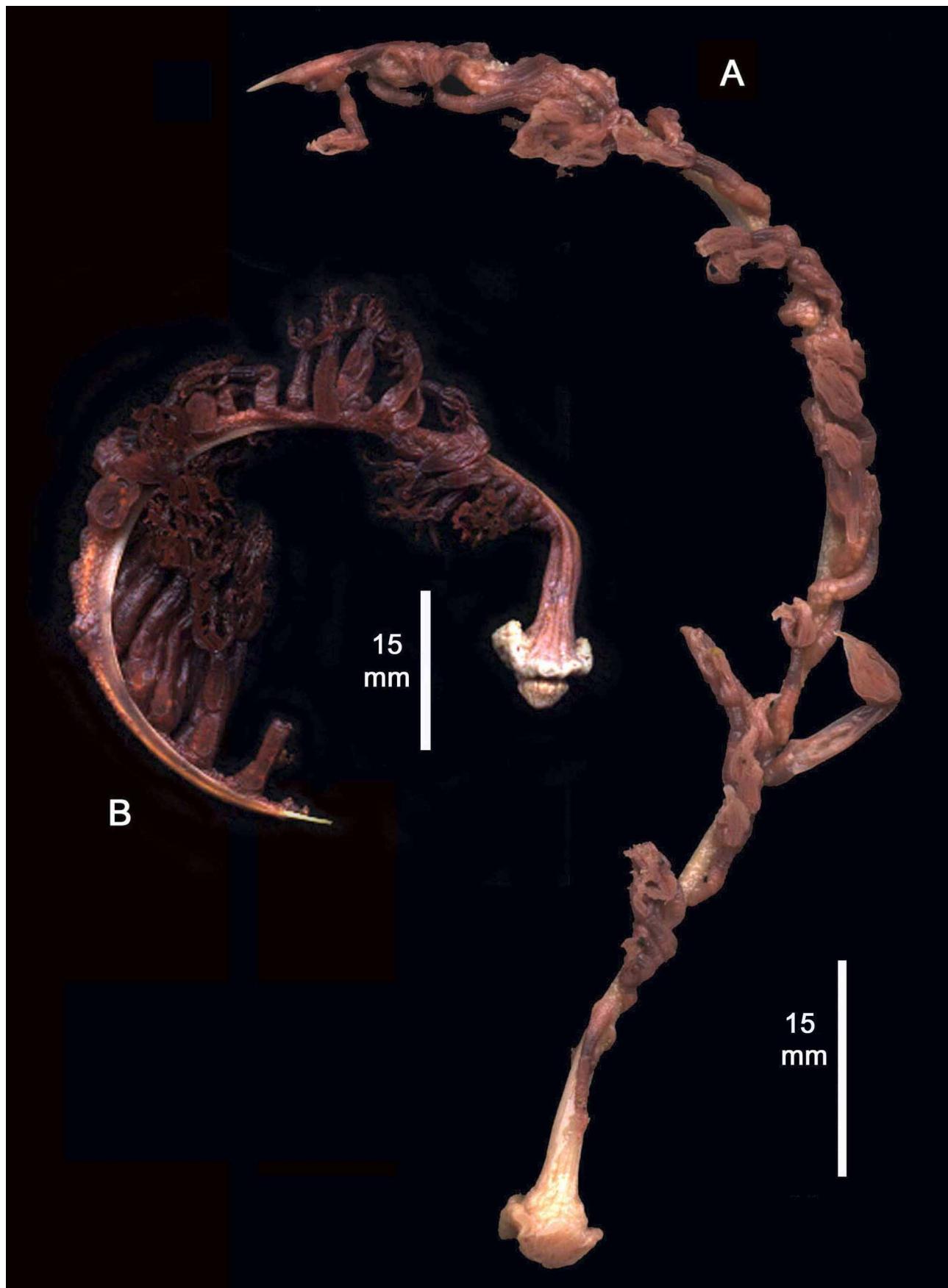


FIGURE 2. *Anthoptilum lithophilum* sp. nov.: A, holotype CAS 179453; B, paratype CAS 179454.

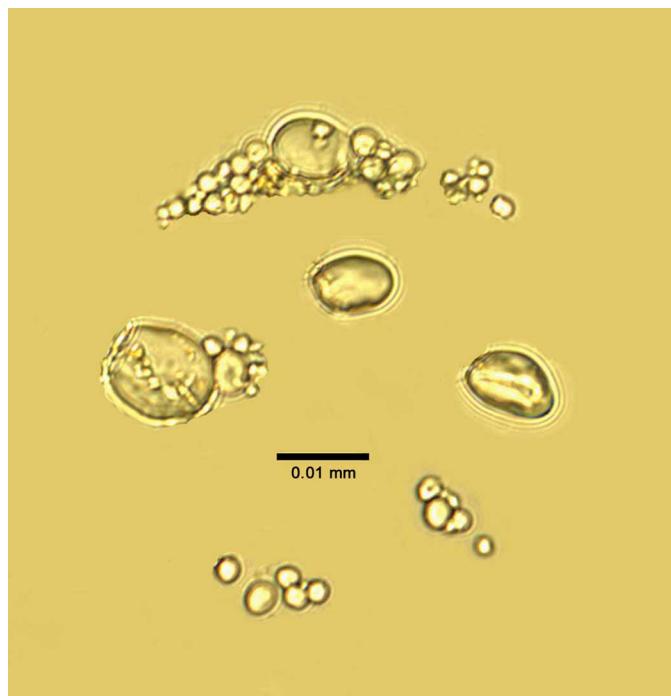


FIGURE 3. *Anthoptilum lithophilum* sp. nov.: Polyp wall sclerites from paratype.

PARATYPE: CAS 179454, sample number T628-A4, California, Rodriguez Seamount, 34.057368° N, 121.052983° W, 700 m depth, 14 October 2003, MBARI, on volcaniclastic pavement. **OTHER:** CAS 179456, *Anthoptilum* sp. indet., Hawai'i, Niihau, 21° 59.250'N, 160° 12.631' W, Site: NW-1c, 368 m depth, 3 May 2010, HURL, one damaged specimen.

Diagnosis. Ratio of total colony length to rachis diameter approximately 50:1. Autozooids 10–15 mm long, 2–4 mm wide. Adjacent autozooids closely placed in indistinct, slightly oblique rows. Autozooid walls with minute oval sclerites, each usually less than 0.01 mm in length. Proximal terminus of peduncle modified into a markedly widened structure with a protruding, conical, terminal knob covering the end of the axis.

Description. The holotype (Fig. 2A) is 118 mm long with the polyp-bearing rachis occupying 98 mm (or 83%) of the entire length. Approximately 45 autozooids are arranged along the length of the rachis, which are 9–16 mm long and not readily discernible as biserial, opposite, sub-opposite or alternate, being more randomly placed. In one 10 mm long autozooid, the polyp wall is 7 mm long, while tentacle length is 3 mm. Siphonozooids are conspicuous, approximately 0.3–0.4 mm in diameter, and appear as white hemispherical protuberances arranged in several longitudinal rows on both sides of each longitudinal row of autozooids. Sclerites are scattered, minute oval bodies, less than or equal to 0.01 mm long, present only in the body walls of the autozooids (Fig. 3). The rachis of the preserved specimen is grayish-white and the autozooids are tan.

Variability. The paratype is 95 mm long with a mauve rachis/peduncle and dark purplish-brown autozooids.

Etymology. The specific epithet *lithophilum* is derived from the Greek (*lithos*—stone) and (*philos*—loving, fond of, having affinity for), alluding to this species inhabiting rocky substrata.

Distribution. Presently known only from off the coast of California, U.S.A.; 669–700 m in depth (Fig. 10).

Differential diagnosis. *Anthoptilum lithophilum* sp. nov. has sclerites in the polyp walls but these are lacking in all other species of the genus. The ratio of colony length to rachis diameter is 50:1, but the ratio in the other species is as follows: *A. grandiflorum*, up to 100:1; *A. murrayi* (Kölliker, 1880), 93:1; *A. decipiens* sp. nov., 180:1; *A. gowlettholmesae* sp. nov., up to 30:1.

Remarks. One damaged, additional specimen collected from Niihau, Hawai'i (CAS 179456), is considerably laterally compressed and significantly flattened. Although it does show a superficial resemblance to *Anthoptilum lithophilum* sp. nov., its identification remains uncertain.

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***Anthoptilum gowlettholmesae* sp. nov.**

Figs. 4–5, 7B, 8A,B,E, 9, 10

Material examined. HOLOTYPE: TMAG K3876, Cruise TN 228, Dive J2-387, sample 012-005, ROV *Jason*, RV *Thomas T. Thompson*, 26 December 2008, Australia, Tasmanian Seamounts Marine Reserve (Location: Hill Z40), 44° 38.2'S, 147° 26.3'E, 1776 m depth, one whole specimen collected by slurp gun, 370 mm in length.

PARATYPES: TMAG K3877, Cruise TN 228, Dive J2-382, sample 005-001, ROV *Jason*, RV *Thomas T. Thompson*, 17 December 2008, Australia, outside Huon Commonwealth Marine Reserve (Location: A1), 44°33.4'S, 147° 28.1'E, 1441 m depth, one whole specimen collected by coral grab, 410 mm in length; TMAG K3878, Cruise TN 228, Dive J2-393, sample 008-001, ROV *Jason*, RV *Thomas T. Thompson*, 12 January 2009, Australia, Tasman Fracture Zone (Location: The Knob), 45° 14.3'S, 145° 98.5'E, 1613 m depth, one whole specimen collected by bio grab, 350 mm in length; CAS 179452, Cruise TN 228, Dive J2-386, sample 001-001, ROV *Jason*, RV *Thomas T. Thompson*, 24 December 2008, Australia, Tasmanian Sea Mounts Marine Reserve (Location: Mongrel), 44° 25.04'S, 147° 26.33'E, 1109 m depth, one whole specimen collected by coral grab, 430 mm in length.



FIGURE 4. *Anthoptilum gowlettholmesae* sp. nov.: A, paratype TMAG K3878 live; B, wet-preserved paratype TMAG K3877; C, wet-preserved holotype TMAG K3876.

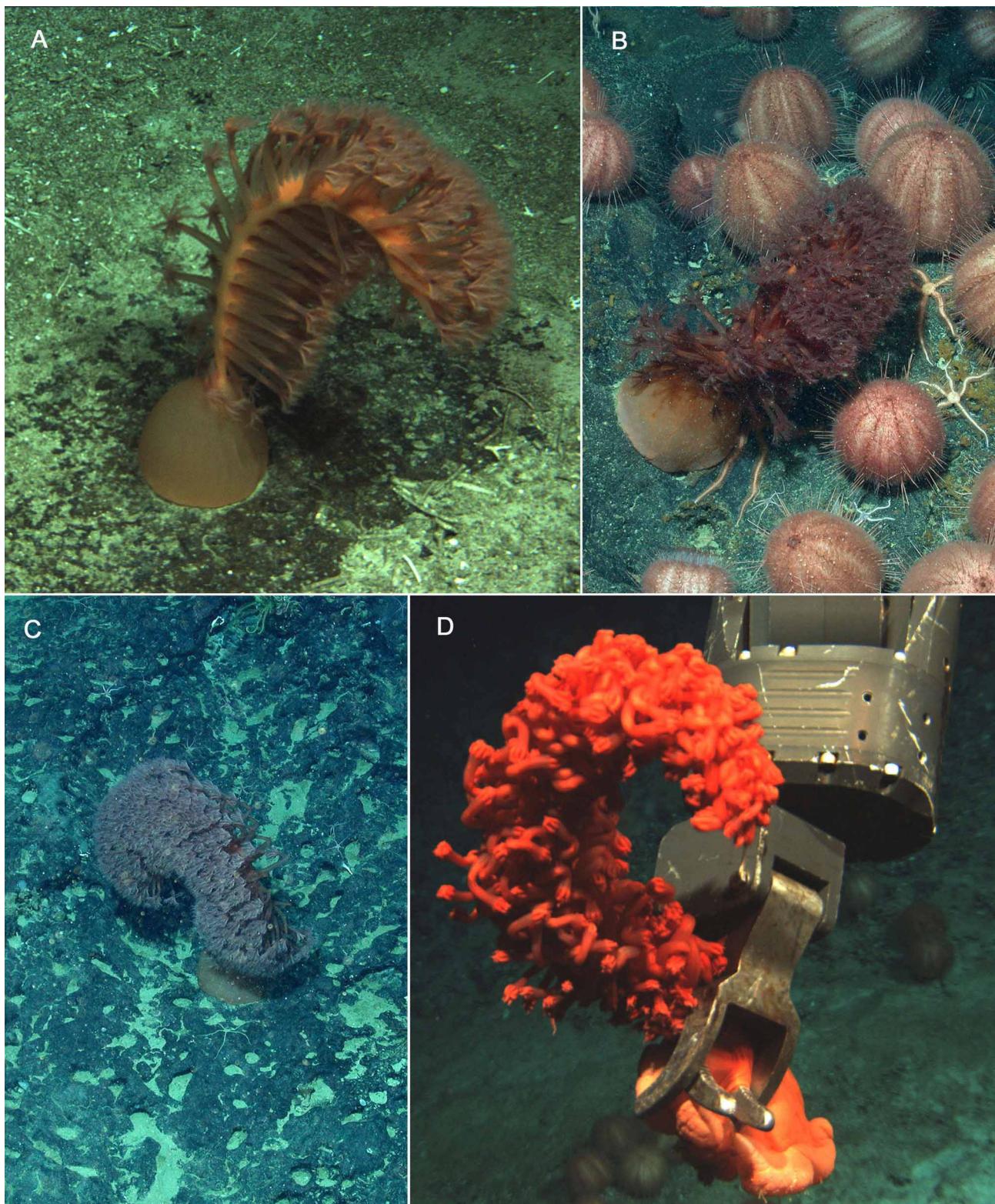


FIGURE 5. *Anthoptilum gowlettholmesae* sp. nov., *in situ*; scales not given: A, entire colony attached to a bare rock surface; B, single colony with numerous individuals of the echinoid *Dermechinus horridus*; C, single colony attached to an extensive area of bare rock; D, colony grasped by the collecting arm of the ROV *Jason*. Image copyright, Advanced Imaging and Visualisation Laboratory WHOI.

Diagnosis. Ratio of total colony length to rachis diameter circa 30:1. Autozooids up to 50 mm in length, crowded along rachis in oblique rows, 4–9 per row. Proximal terminus of peduncle sucker-shaped, hemispherical in life, with a proximally protruding, conical, terminal knob covering the end of the axis.

Description. The holotype is 370 mm long (Fig. 4C), with the 300 mm rachis occupying 81% of the total length. The autozooids originate directly from surface of the rachis and measure 3–8 mm wide and up to 50 mm long, and are disposed in two series of oblique rows along the lateral sides, 6–10 per row. Polyp bodies are tubular, narrow elongate, up 35 mm long, with tentacles up to 15 mm long bearing numerous, narrow, elongate pinnules, 1.5–2.0 mm long. Siphonozooids are abundant and crowded, approximately 0.25 mm in diameter, forming round to slightly oval hemispheres on two sides of the rachis between the autozooid bases. The peduncle is 70 mm long, occupying 19% of the colony, and the proximal portion is significantly enlarged with an expanded coenenchymal sheath immediately above a conical terminal bulb (Fig. 4C, 8E). No sclerites were found in numerous samples taken throughout the colony. The rachis and peduncle in the wet-preserved holotype are tan, while the autozooids are dark purplish brown (Fig. 4C).

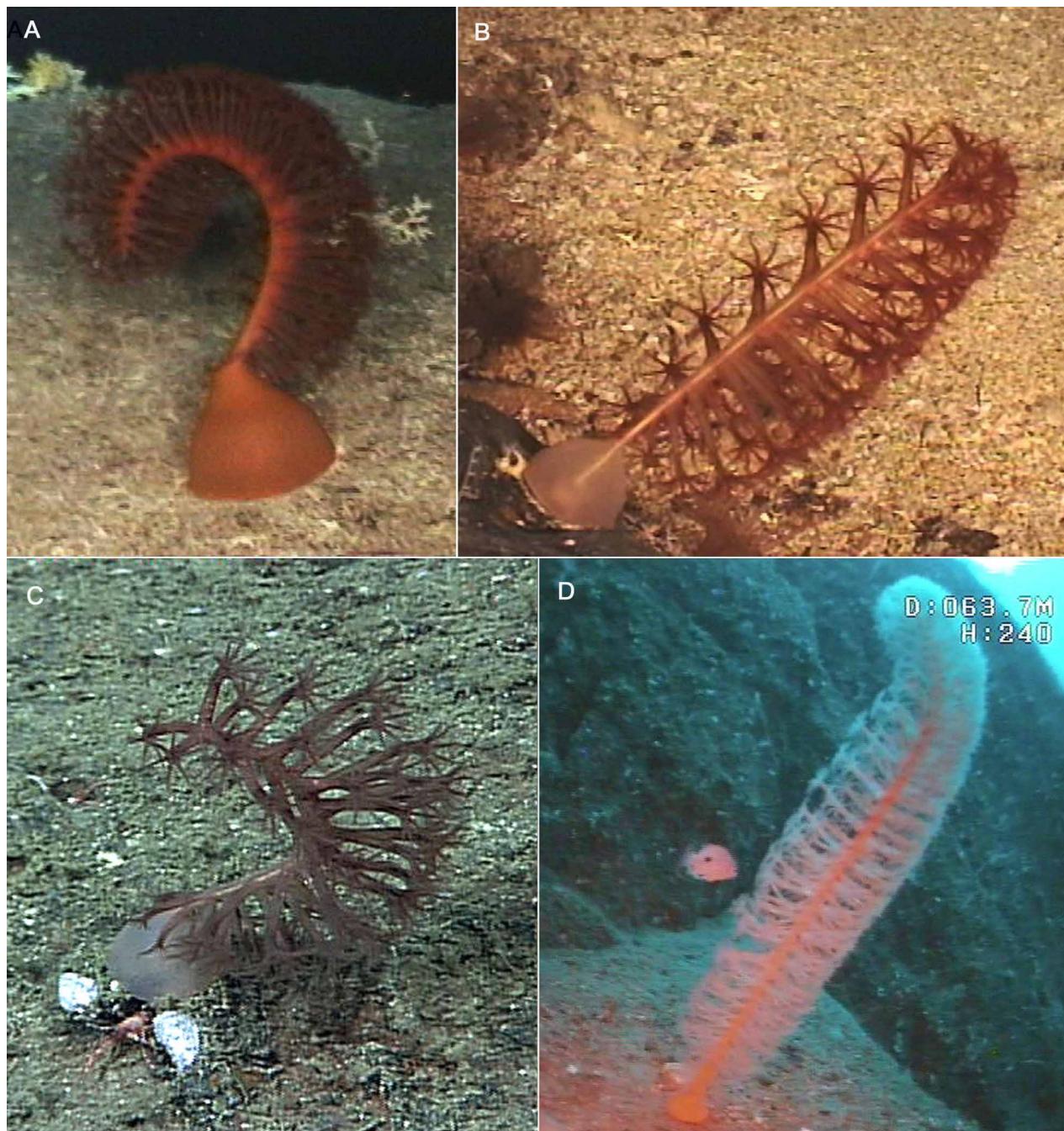


FIGURE 6. Rock-inhabiting sea pens, *in situ*, scales not given: A–B, indeterminate taxon, Hawai'i, note the axis in the translucent sucker in image B (images courtesy of HURL); C, *Anthoptilum lithophilum* sp. nov., central California (photo courtesy of MBARI); D, indeterminate taxon, New Zealand (photo courtesy of NIWA). [Colonies in A,B,C only photographed and assumed to be on hard substrate]

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Variability. The four wet-preserved specimens examined vary from 370 to 430 mm in length. The autozooids vary from 20 to 50 mm in length and are often up to 5 mm in diameter proximally. The oblique rows are relatively easy to distinguish, and contain 4–9 autozooids each. In life, paratype TMAG K3878 was deep yellow to orange with bright red-orange autozooids (Fig. 4A). The wet-preserved paratype TMAG K3877 is tan to light maroon with deep purplish brown autozooids (Fig. 4B), and paratype CAS 179452 is pale tan throughout (not figured).

Etymology. This species is named for Karen Gowlett-Holmes, who had been endeavouring to collect specimens of it for several years.

Distribution. South Tasman Rise (southwest of Tasmania, Australia); 729–1803 m in depth (Figs. 9, 10).

Differential diagnosis. The only other species in the genus that has a similar gross morphology (i.e. robust with a thick rachis densely covered with large autozooids) is *A. grandiflorum*. In that species the wet-preserved autozooids are usually circa 8–25 mm long and 2–3 mm wide and there are 5–10 in each oblique row. However, the oblique rows of some specimens are often not distinguishable or are difficult to distinguish since the autozooids are often extremely crowded, appearing more-or-less longitudinally disposed along the length of the rachis. On the other hand, in *Anthoptilum gowlettholmesae* sp. nov., the wet-preserved autozooids can be 20–50 mm long and 3–5 mm wide, and there are 4–9 in each well defined oblique row. The new species is also more robust, up to 440 mm long, with a rachis 15 mm in diameter, giving a ratio of colony length to rachis diameter of up to 30:1 compared to 100:1 for *A. grandiflorum*. Additionally, the interior of the peduncle of *A. grandiflorum* contains sparsely distributed sclerites, which are minute ovals <0.03 mm long, but no sclerites have been found in *A. gowlettholmesae* sp. nov.

Remarks. Numerous individuals of an echinoid identified by K. Gowlett-Holmes as *Dermechinus horridus* (Agassiz, 1879) (family Echinidae) were photographed beside a colony of *Anthoptilum gowlettholmesae* sp. nov. on a rocky outcrop in the Tasmanian Sea Mounts Marine Reserve (Fig. 5B).

Family Scleroptilidae Jungersen, 1904

Calibelemnon Nutting, 1908

Calibelemnon francei sp. nov.

Figs. 7C, 8C, 10

Material examined. HOLOTYPE: CAS 179455, Sta. No. ELE210-1, Bahamas—Bahama Escarpment, Eleuthera Island West, 25°40.1191' N, 76° 46.2572' W, 1969 m depth, 28 March 2009, coll. S.C. France; Bahamas Deep-Sea Coral Expedition, RV *F.G. Walton Smith*, ROV *Global Explorer*.

Diagnosis. Axis straight, autozooids arranged more-or-less in sub-alternate to opposite pairs along length of rachis with each pair separated by areas of bare rachis. Basal terminus of peduncle enlarged to form a plunger-shaped structure with a conical proximally protruding knob covering the end of the axis. No sclerites found in tissues sampled from several areas.

Description. The damaged holotype (Fig. 7C) is slender, straight, and 122 mm long. The approximately 0.5 mm diameter rachis occupies 90% of the colony and the axis is clearly observable beneath the thin coenenchyme. There are 25 autozooids, mostly 4–6 mm long, which are arranged biserially, opposite to alternately along the rachis in pairs. Areas of bare rachis between adjacent autozooids or pairs of autozooids vary from 4 to 12 mm long. The swollen and oblong basal regions of some autozooids contain several spherical ova, each approximately 0.25 mm in diameter. The siphonozooids are ovoid, approximately 0.2 mm long, and are arranged in two longitudinal rows along the bare areas of rachis. The peduncle represents approximately 10% of the total colony length and the proximal terminus, 5 mm long by 3–4 mm wide (Figs. 7C, 8C), is structurally similar to that of the other known species of rock-inhabiting pennatulaceans. No sclerites were found in numerous samples taken throughout the colony. The opaque autozooids of the wet-preserved colony are deep chocolate brown; the rachis is dark red, the peduncle tan, and the siphonozooids brown.

Etymology. We name this species for Scott C. France, University of Louisiana at Lafayette, for his discovery and collection of the holotype.

Distribution. This new species is presently known only from the type locality, Bahama Escarpment in the western Atlantic, 1969 m depth (Fig. 10).

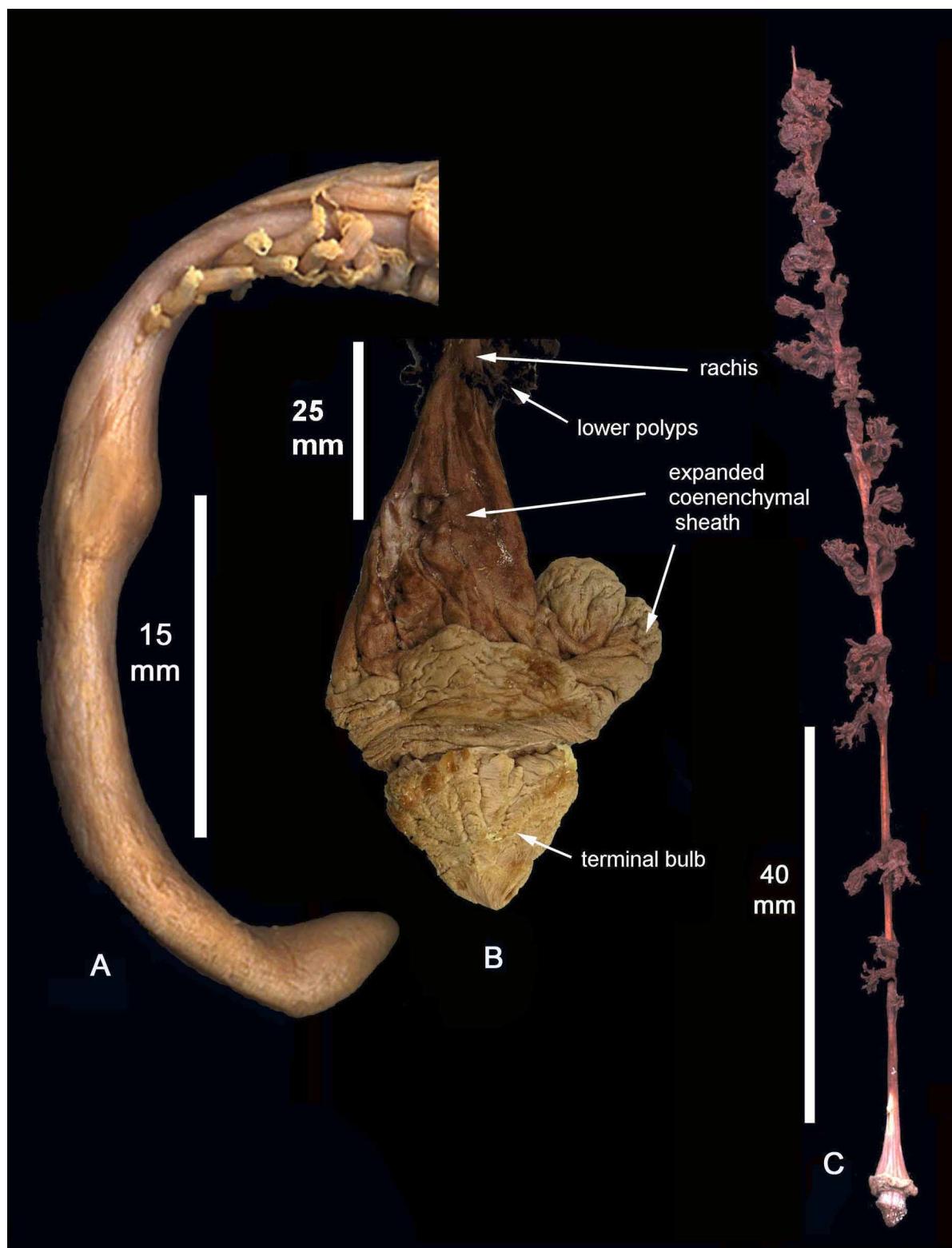


FIGURE 7. A, peduncle of *Anthoptilum grandiflorum* CAS 122323; B, *Anthoptilum gowlettholmesae* sp. nov. proximal portion of peduncle of paratype TMAG K3878; C, *Calibelemnnon francei* sp. nov. holotype.

Differential diagnosis. There are three nominal species of *Calibelemnnon*, *C. symmetricum* Nutting, 1908 (the type species), *C. indicum* (Thomson & Henderson, 1906), and *C. hertwigi* (Balss, 1909), of which the last is considered invalid (Williams 1995: 117). *Calibelemnnon francei* sp. nov. can be distinguished from the former two of these by its remarkably small peduncle, which occupies only 10% of the total colony length compared to 30%–46% for *C. indicum* and 47% for *C. symmetricum*. It also differs from *C. symmetricum* by having the siphonozooids

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arranged in two longitudinal rows compared to them being distributed all over the rachis in that species, except for a longitudinal band along the ventral and dorsal tracks.

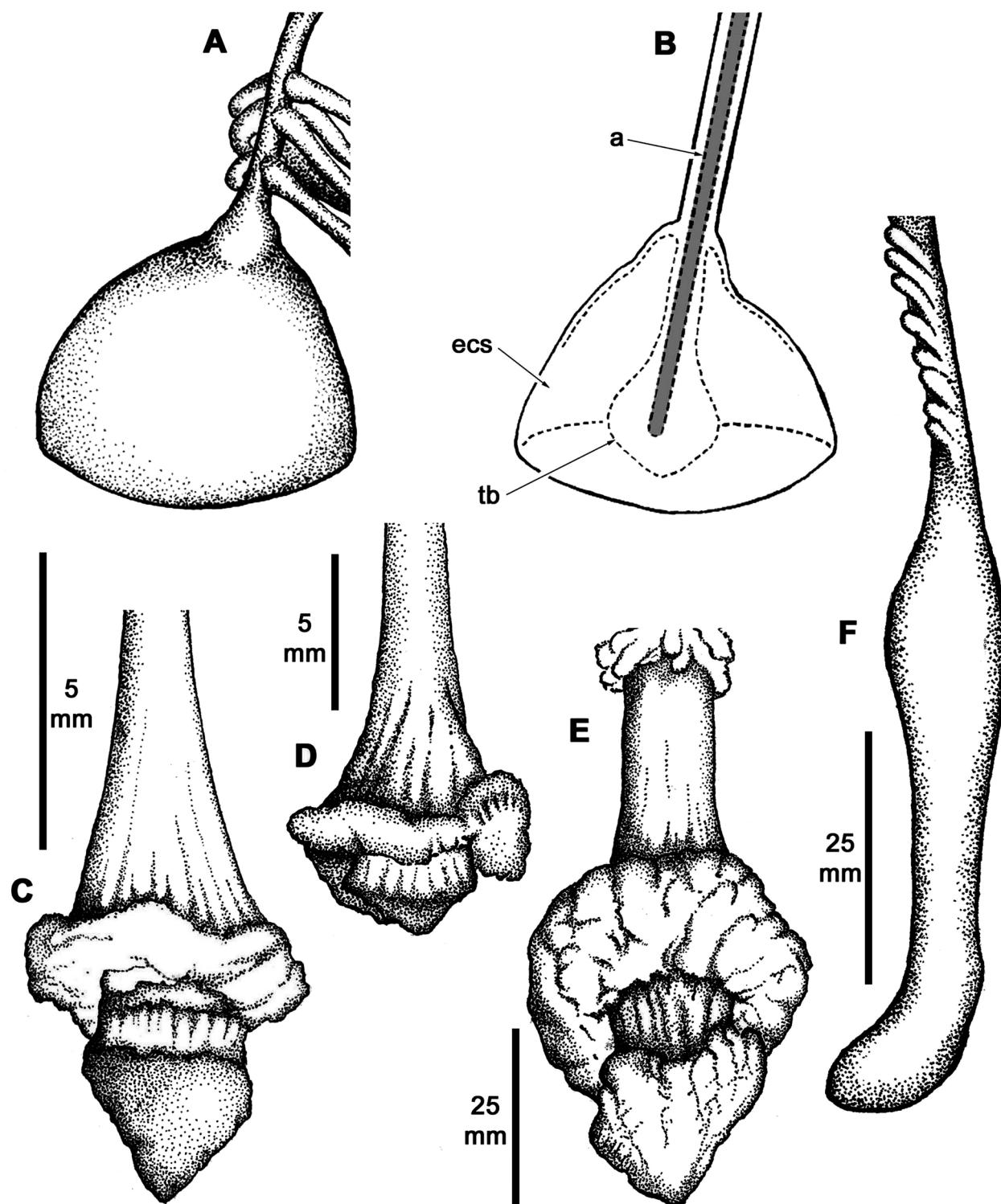


FIGURE 8. Comparative morphology of pennatulacean peduncles: A–B, Illustrations adapted from photographs of live colonies *in situ* (scale bars not given); A, *Anthoptilum gowlettholmesae* sp. nov. adapted from image number CSIRO-11208802-SS1106-019-20330 (courtesy CSIRO); B, indeterminate taxon, Hawai'i, with a translucent sucker — representational diagram of the proximal portion of a peduncle attached to rocky substratum — dotted lines represent conjectural internal structure, a = axis, ecs = expanded coenenchymal sheath, tb = terminal bulb, adapted from image number R-119-d1-03331 (courtesy NOAA, HURL archives). C–F, Illustrations from wet-preserved material: C, *Calibelemnion francei* sp. nov. (CAS 179453); D, *Anthoptilum lithophilum* sp. nov. (CAS 179453); E, *Anthoptilum gowlettholmesae* sp. nov. (TMAG K3876).

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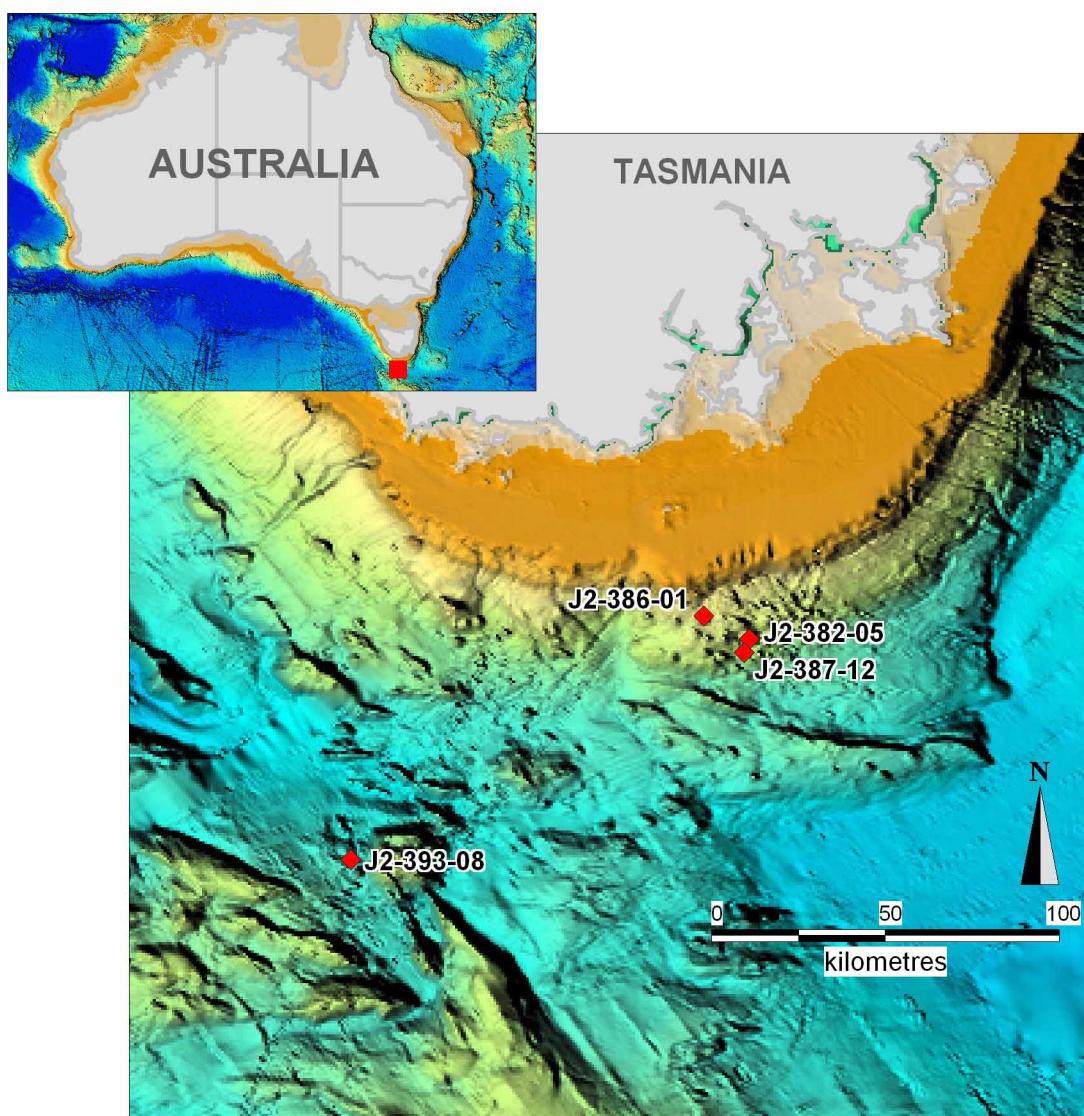


FIGURE 9. Bathymetric map of the southern Tasmanian region showing collection stations for *Anthoptilum gowletholmesae* sp. nov. (Adapted from Commonwealth of Australia, 2005).

Remarks. The holotype is the only known specimen of this species and does seem to have two characteristics that agree with the definition of the genus—more-or-less biserial polyps and bare regions of rachis between polyp pairs. However, since there are no other specimens for comparison at this point, it is possible these features may be at least partially due to specimen damage and/or poor preservation. If undamaged material is found that conforms to the description of *Calibelemnon francei* sp. nov., specialists may eventually agree that all known rock-inhabiting sea pens should be allocated to *Anthoptilum*. But without further evidence we assign the new species to *Calibelemnon*.

Discussion

A comparison of the known families and genera of rock-inhabiting sea pens follows.

Family Anthoptilidae—Colonies elongate; rachis curved; polyp leaves absent; autozooids elongate and tubular, often arranged in oblique rows along length of rachis; calyces absent; sclerites minute ovals or absent; axis present throughout entire colony; peduncle sausage-shaped throughout or proximal end modified as a sucker-like holdfast. Monogeneric; circum-global distribution.

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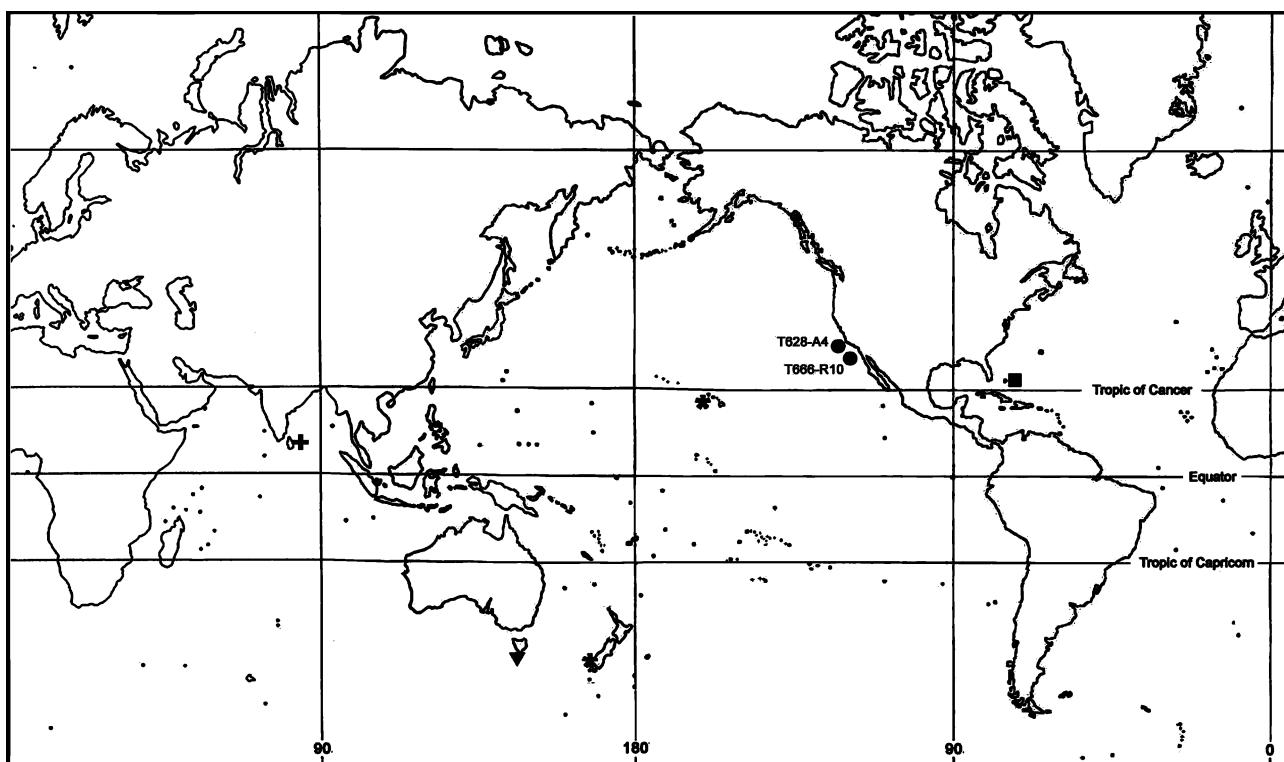


FIGURE 10. World map showing known geographic locations of rock-inhabiting sea pens: ▼ = *Anthoptilum gowlethholmesae* sp. nov.; ● = *Anthoptilum lithophilum* sp. nov.; ■ = *Calibelemnon francei* sp. nov.; + = *Anthoptilum decipiens*; * = taxa indeterminate; from specimen CAS 179456 (Hawai'i) and/or underwater images (Hawai'i and New Zealand).

Genus *Anthoptilum*—Colonies relatively robust; rachis curved; symmetry bilateral; axis present throughout entire colony; autozooids numerous and elongate emanating directly from surface of rachis, either arranged separately along sides of rachis or in oblique rows situated in two longitudinal series; siphonozooids minute and numerous on bare areas of rachis between autozooids; sclerites minute oval bodies that may occur in the surface or interior coenenchyme or walls of the autozooids, or be absent; peduncle sausage-shaped for anchoring in soft sediment, or proximally modified, sucker-like, for attachment to hard substrata; colonies red-orange in life, tan to brown to deep maroon wet-preserved. A genus of five valid species, three of which are rock-inhabiting sea pens; Pacific, Indian, Atlantic, and Arctic Oceans; 155–3150 m depth.

Family Scleroptilidae—Colonies straight, slender, delicate; rachis bilateral with numerous autozooids arranged in pairs, separated by bare regions of rachis of more-or-less equal length; axis present throughout entire colony; peduncle sausage-like or modified as a sucker-like holdfast; terminal polyp present; siphonozooids sparsely distributed on rachis; sclerites present in one genus and absent or highly reduced in the other. Two genera; widespread distribution.

Genus *Calibelemnon*—Colonies slender; rachis straight throughout; autozooids relatively short, mostly biserial and in pairs, distributed evenly and longitudinally along entire length of rachis; axis present throughout entire colony; peduncle sausage-like or proximally modified, sucker-like, for attachment to hard substrata; sclerites minute ovoid bodies or absent; wet-preserved color white, or wine red to chocolate brown. Three valid species, one of which is a rock-inhabiting sea pen.

Kükenthal (1915: 43) considered two genera—*Scleroptilum* Kölliker, 1880 (with sclerites) and *Calibelemnon* (without sclerites)—to comprise the family Scleroptilidae. Due to the relative paucity of adequate morphological characters and lack of molecular analysis, the phylogenetic status and validity of monophyly of the family is not possible to ascertain at present. Williams (1995) included the genus *Calibelemnon* in the Chunellidae based on the absence of conspicuous sclerites. However, we here regard the genus as part of the Scleroptilidae on the basis of evenly distributed polyps along the rachis (as in *Scleroptilum*), which do not form conspicuously clustered groups as in genera of the Chunellidae.

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Key to the species of rock-inhabiting sea pens

1. Polyps arranged along length of rachis more-or-less in pairs, separated by bare areas *Calibelemonn franciei* sp. nov.
- 1'. Polyps closely placed along length of rachis sometimes in oblique rows 2
2. Minute rod-like sclerites in base of stalk, which may form star-shaped groups *Anthoptilum decipiens*
- 2'. Sclerites absent, or if present, not forming star-shaped groups 3
3. Ratio of total colony length to rachis diameter circa 30:1, autozooids 20–50 mm long, 3–5 mm wide, sclerites apparently absent *Anthoptilum gowlettholmesae* sp. nov.
- 3'. Ratio of total colony length to rachis diameter approximately 50:1, autozooids 10–15 mm long, 2–4 mm wide, with minute oval sclerites in the walls *Anthoptilum lithophilum* sp. nov.

Adaptations of the peduncle in rock-inhabiting sea pens

Adaptations of the basal portion of the peduncle as a holdfast for attachment to rocky substrata are remarkable and unlike that of all other known pennatulaceans. The following presumptive functional morphology is based on examination of wet-preserved material and *in situ* ROV photographs.

The proximal terminal portion of the peduncle is greatly expanded due to an outgrowth of the peduncular coenenchyme that forms a plunger-like structure (Fig. 7B, 8A). The central axis ends inside a conical mass of tough tissue below the expanded coenenchyme and can presumably be used to change the degree of suction inside the plunger (Figs. 6B, 8B), thus increasing or decreasing the strength of adhesion to the substratum. [Note, the sea pens in Fig. 6A,B,D were not manipulated, but are assumed to be on hard substrate].

Acknowledgements

We are grateful to the following colleagues for providing specimens and images from five widespread worldwide locations: Karen Gowlett-Holmes (CSIRO, Division of Marine and Atmospheric Research, Hobart, Australia); Scott France (University of Louisiana at Lafayette, Louisiana); Deetsie Chave and Christopher Kelley (Hawai'i Undersea Research Laboratory, Oahu, Hawai'i); Trevor Willis (National Institute of Water and Atmospheric Research, Nelson, New Zealand); Linda Kuhnz and Lonny Lundsten (Monterey Bay Aquarium Research Institute, Monterey, California). We thank Fransiz Althaus (CSIRO, Division of Marine and Atmospheric Research, Hobart, Australia) for constructing the locality map for *Anthoptilum gowlettholmesae* sp. nov.

We thank J. Adkins, E. Anagnostou, A. Beck, W. Cho, A. Gagnon, K. Gowlett-Holmes, S. John, N. Meckler, D. Staples, A. Subhas and N. Thiagarajan, and the crews of the ROV *Jason* and RV *Thomas T. Thompson* for their invaluable and professional assistance in the field. Components of this work were supported by the National Science Foundation, the Australian Department of Environment, Water, Heritage, and the Arts, the Australian Commonwealth Environmental Research Fund, and the CSIRO Climate Adaptation Flagship.

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