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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)

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Abstract

Clavularia amboinensis Burchardt, a species described as possessing simple, pinnule-less tentacles (a fact refuted by later authors) is confirmed to be as described and is transferred as a new combination to *Acrossota* Bourne — a genus dismissed until now by a number of authors. The species is compared to recently collected material with live photographs. A second new genus and species, *Knopia octocontacanalis*, is also described. This taxon resembles *Acrossota* in general form, but has tentacles where the pinnules appear as though they are fused side to side along the tentacles' lateral margins. Preliminary phylogenetic analyses of two mitochondrial genes support placement of *Knopia* in Clavulariidae and retention of genus *Acrossota* in Bourne's unrecognised family Acrossotidae.

Key words: Cnidaria, Octocorallia, Clavulariidae, Acrossotidae, *Clavularia amboinensis*, *Knopia*, new genus, new species, Indonesia

Introduction

There are three instances in the literature where authors have claimed that the new octocoral taxa they were describing had polyps with tentacles that lacked pinnules. The first, proposed by Burchardt (1902: 657), was the stoloniferous *Clavularia amboinensis*. Not long after, Kuekenthal (1906: 11), and later Molander (1921: 3-5) and Thomson and Dean (1931: 20) listed the taxon as a species of the genus *Anthelia*. All three authors were clearly not interpreting *Anthelia* as it is known today, especially considering *C. amboinensis* was reported to have retractile polyps (although Molander seemed to have missed this character), (*Anthelia* has non-retractile polyps arising from a basal membrane and has rod-like sclerites with a crystalline surface structure [Alderslade, 2001: 60-61]). Surprisingly, Utinomi (1951: 195) also agreed with these latter authors' classification, even though he clearly knew more about the true characters of *Anthelia*, having described *A. formosana* the previous year.

The second species, described by Bourne (1914), was *Acrossota liposclera*. Apparently unaware of Burchardt's paper, Bourne stated that this was the first taxon to be discovered in which the tentacles lacked pinnules, and proposed the new family Acrossotidae to incorporate the new genus and species. Thomson and Dean (1931: 11) stated that they thought Bourne's species was identical to that of Burchardt, and Gohar (1940: 5) commented that the establishment of *Acrossota* and the Acrossotidae involved "much risk". Gohar based this on his opinion that Bourne's single specimen was contracted and badly preserved, and that pinnules were "an unstable character". He cited several xeniid species that he had shown were "capable of contraction

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until they completely disappear". Utinomi (1951: 195) cited Thomson's and Dean's opinion and stated that a number of authors, himself included, had examined specimens of various genera having some polyps with apparently pinnule-less tentacles and that this was probably just the result of contraction and bad preservation. These latter statements were made in a paper that described a new genus from Taiwan named *Asterospicularia*, which was reported to have simple, pinnule-less tentacles. Unfortunately, Utinomi failed to interpret correctly the histological sections of the tentacles as owing to the state of contraction. He noted zooxanthellae-filled cavities that united with one another and were confluent with the coelenteric cavity of the polyp, but because the tentacle surface was not deformed by them he did not think they could be contracted pinnules. We have fortunately been able to examine numerous specimens of *Asterospicularia* from diverse Indo-Pacific and tropical West Pacific locations, including Taiwan, and can confirm that it is not uncommon to find both polyps with pinnules and polyps so contracted as to appear, at first glance, to be without pinnules, on the same colony. Even the most tightly contracted tentacles, however, show some amount of contouring (although miniscule) where the pinnules are sited.

Two of the taxa referred to above, *Acrossota liposclera* and *Clavularia amboinensis*, were originally reported to have tentacles that were smooth and more or less cylindrical and colonies that had retractile polyps — clearly resembling the general polyp shape of small species of Indo-Pacific *Clavularia.* When material of this nature, along with underwater photographs, was sent to us by Julian Sprung, Daniel Knop and, later, Francis Dipper, we began a search for the holotypes of the two described species. After our failure to locate the whereabouts of the holotype of *Acrossota liposclera*, we asked Professor Elaine Robson, Redding University, for assistance. Unfortunately, despite conducting vigorous enquiries of marine laboratories, museums and universities in the United Kingdom, Professor Robson could unearth no evidence of its existence. The holotype of *Clavularia amboinensis*, however, was less trouble. Leen van Ofwegen (Naturalis, Leiden) noticed that it was still on the substratum supporting one of the type series of *Nephthea amboinensis* (Burchardt, 1902) held by the Musée Zoologique, Strasbourg. The holotype of *C. amboinensis* is redescribed in this paper, compared with the recently collected material, and transferred to the genus *Acrossota*. Although the holotype of *A. liposclera* is missing, the original description fits the material on hand extremely well, and confirms *Acrossota* as a valid genus. DNA analysis of the recently collected material shows that this genus does not belong in the family Clavulariidae, nor does it resolve with any other of the recognised families, and it is therefore retained in the neglected family Acrossotidae proposed by Bourne.

The latter simple form of tentacle construction is in sharp contrast to that of the new genus described below. In this new taxon, each tentacle is tongue-like, shaped rather like a short-handled canoe paddle, and each side of the blade of the paddle is formed as if from a single series of pinnules fused side by side like a rank of parallel pipes. Also, whereas *Acrossota liposclera* and *Clavularia amboinensis* are sclerite-free, in the new taxon the polyp head has a dense layer of minute sclerites of the kind found in several xeniid genera.

The abbreviation NTM indicates material held at the Museum and Art Gallery of the Northern Territory, Darwin, Australia.

Family Acrossotidae Bourne, 1914

Acrossota Bourne, 1914

Diagnosis. Colonies of upright polyps arising from stolons that may coalesce into small or extensive basal membranes. Polyp bodies, basal membranes and stolons are covered by a cuticle. Polyp tentacles snake-like, without pinnules, able to be withdrawn by a process of invagination. Sclerites absent. Zooxanthellate.

Type species. Clavularia amboinensis Burchardt, 1902, here designated = *Acrossota amboinensis* **n. comb.**

Acrossota amboinensis (Burchardt, 1902) n. comb. (Figs 1–4, 8)

Clavularia amboinensis Burchardt, 1902: 657–658, pl. 56, fig. 1; Kuekenthal 1906: 11 (in a list of species proposed to be transferred to *Anthelia*); Molander 1921: 3–5 (included in a list of, and key to, species of *Anthelia*); Thomson & Dean 1931: 20 (comments that it is a species of *Anthelia*); Utinomi 1951: 195 (comments that it is a species of *Anthelia*).

?*Acrossota liposclera* Bourne, 1914: 261–272, pl. 22; Thomson & Dean 1931: 20 (comments that it is the same as *Clavularia amboinensis*); Utinomi 1951: 195 (agreeing with Thomson & Dean).

Unidentified Stoloniferan Number Two: Sprung & Delbeek 1997: 173–174; Sprung 1999: 150.

Material examined: *Holotype:* Musée Zoologique, Strasbourg, #158, Ambon, Indonesia.

Other material: NTM C13618, Indonesia, May 1997, purchased from a dealer by Julian Sprung; NTM C13626, same data except October, 1999; NTM C15379, Indonesia, September 2002, purchased from a dealer by Daniel Knop; NTM C15380, same data except November 2002; NTM C15381, Kapikan, Semporna Islands, 04°38.843' N, 118°49.813' E, depth 10–20 m, F. Dipper, 28 March 2000; NTM C15506, Indonesia, August 2003, purchased from a dealer by Daniel Knop.

Description: *Holotype*. The colony described by Burchardt is shown in Figures 1–2. Virtually all of the polyps are on one valve of an oyster, situated on one side of the base of a syntype colony of *Nephthea amboinensis*. There is also much sponge and some bryozoan material on the shell. The two clusters of polyps that Burchardt thought were two colonies are joined by a few flat stolons that pass under a clump of sponge and the folded edge of the *Nephthea* colony. Very little of the network of stolons is visible without prising away the overgrowing sponge. The few main strands that are visible are about 0.8 mm wide, and these may be cross-linked by short, much narrower, strands. Wider portions, where the stolons are expanded into wider mats, can be uncovered, but their extent is unknown. Burchardt said that "Eine Hornscheide" was missing, but the stolons and the polyps are covered with a thin cuticle. It is not easy to detect on the polyps, but on some broken ones it can be seen to be peeling off as a very thin transparent sheet.

The polyps in the small cluster (Fig. 2B) are mostly 2.5–5.0 mm tall, wider at the oral end, and mostly c. 0.9–1.6 mm in diameter. Those in the larger cluster (Fig. 2A) that are not surrounded by sponge are longer, at least up to 9 mm. Polyps that are growing through the sponge can be even longer; one measured 14.25 mm long and 1.37 mm diameter at the oral end. The protective cuticle on the lower part of these polyps where they pass though the sponge is much thicker than elsewhere and easily seen. It is yellowish brown against the yellowish white of the upper part of the polyps.

The polyps are moderately translucent and the mesenterial insertions can be seen through the walls of many of them. Quite a number of polyps have the distal ends missing, perhaps as a consequence of Burchardt's research. Of those that remain, all but a few have no tentacles visible. Burchardt's account indicates that some polyps had the tentacles fully unfolded when he examined the specimen, but in the material now, where tentacles are visible, they protrude only by very small amounts (Fig. 1B); there are no signs of pinnules. Through the body wall of many polyps, the withdrawn tentacles appear as an opaque cylinder or a cluster of opaque fingers in the distal part of the body (Fig. 1B). Dissection confirmed Burchardt's observation that the tentacles withdraw by invagination. They protrude into the gastric cavity of the polyp between the pharynx and the body wall.

There are no sclerites in any part of the colony.

NTM C13618. The specimen is shown in Figure 3. It consists of a dense cluster of polyps attached to a piece of coral rock. Narrow colonial stolons can be seen at the margins of the polyp cluster. They are flattened, c. 0.3–0.9 mm wide, and anastomose with, or cross, other stolons. The stolons disappear beneath the dense mass of polyps, where they may join to form broad membranous expansions. The fact that some stolons cross other stolons without anastomosing may indicate that there is more than one colony here. Stolons and polyp bodies are covered by a thin cuticle.

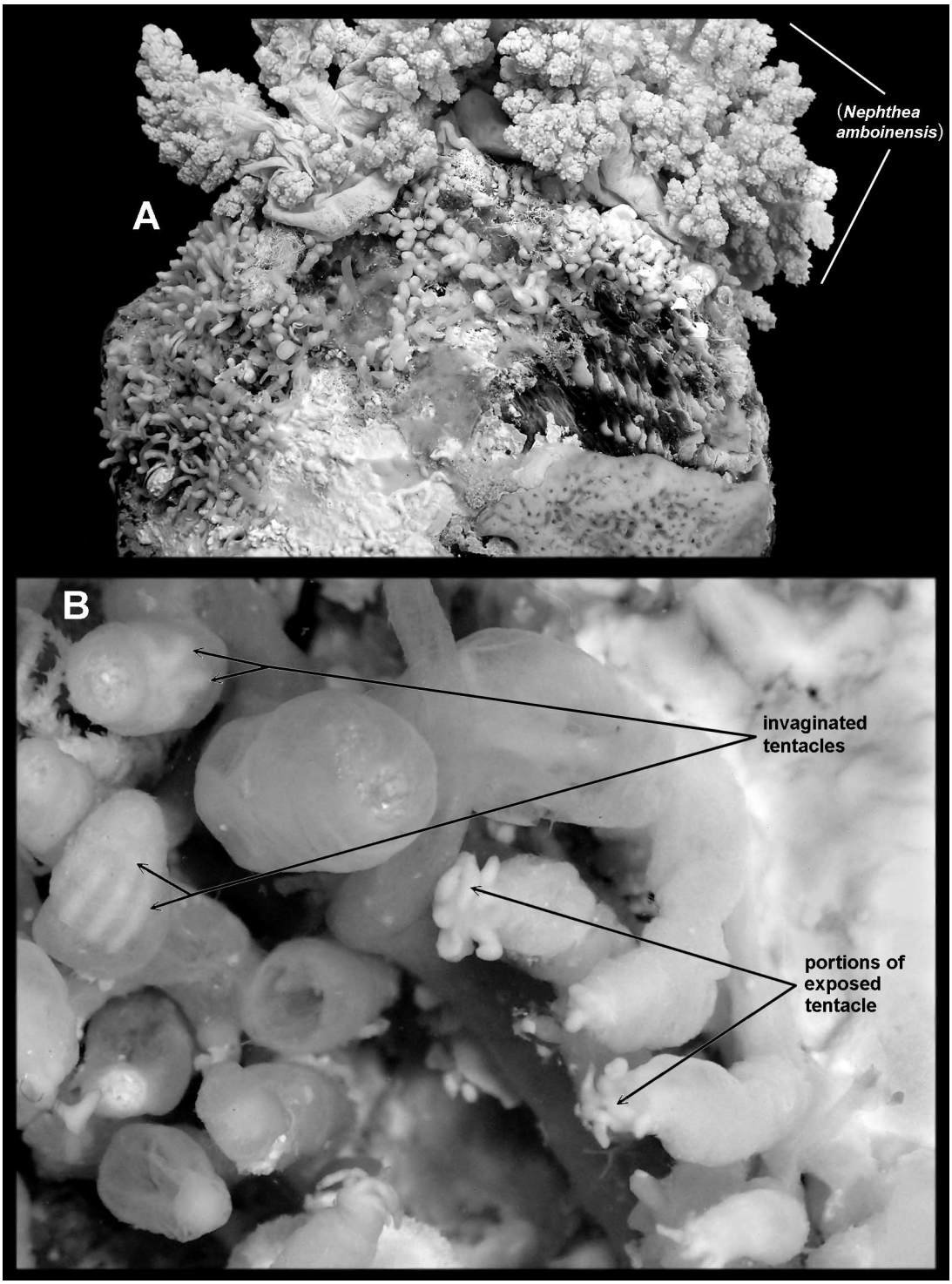

FIGURE 1. *Acrossota amboinensis,* **n. comb.**, holotype: A, with syntype of *Nephthea amboinensis*, life size; B, some polyps magnified.

The polyps are greyish yellow; a couple with the tips of the tentacles exposed are mostly opaque. Some are more inflated and the mesenterial insertions and withdrawn tentacles can be seen within. These tentacles lie outside the pharynx and are invaginated. Polyp sizes vary from juveniles, 0.9 mm tall and 1.4 mm in diameter, to the largest c. 7.5 mm tall and 2.4 mm in diameter.

There are a number of tubular, sinuous, stolonic outgrowths that rise free from the substratum, and have a very wrinkled cuticle. The outgrowths appear to be the vegetative parts of the colony that were involved in

increasing colony size. They are up to 9 mm in length and they end in a polyp of reduced dimensions. Several similar-looking structures occur on the type specimen of *Clavularia amboinensis* — up to c. 7 mm long — but they stand erect and may not be analogous.

Several polyps had had the head and tentacles removed while the colony was still alive and expanded. They are up to 4.4 mm long and 0.2–0.3 mm broad. A polyp head and close-up of the tentacles are shown in Figure 3B–C. A living colony is shown in Figure 8B.

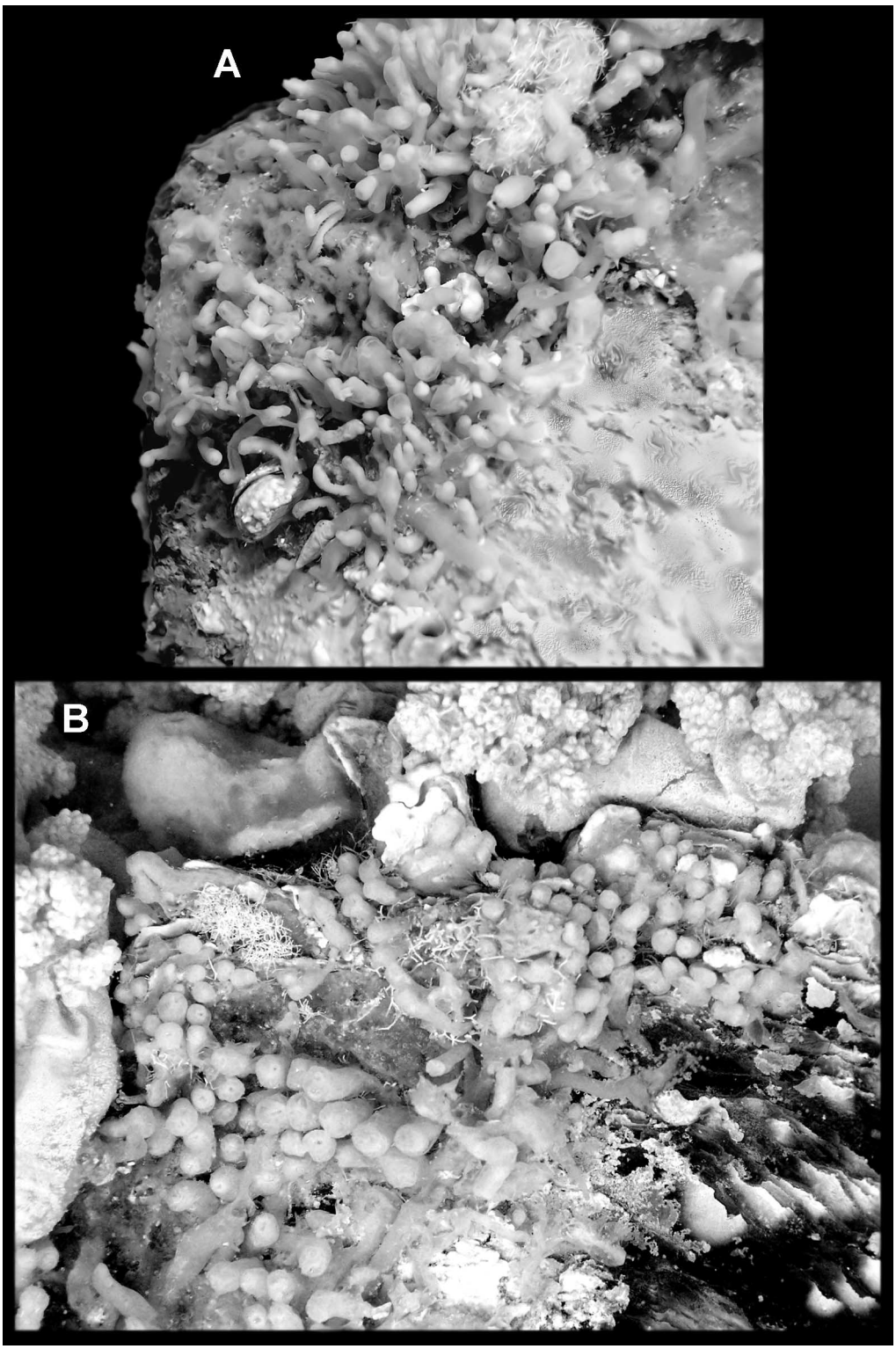

FIGURE 2. *Acrossota amboinensis*, **n. comb.**, holotype: A,B, close-ups of main portions of colony.

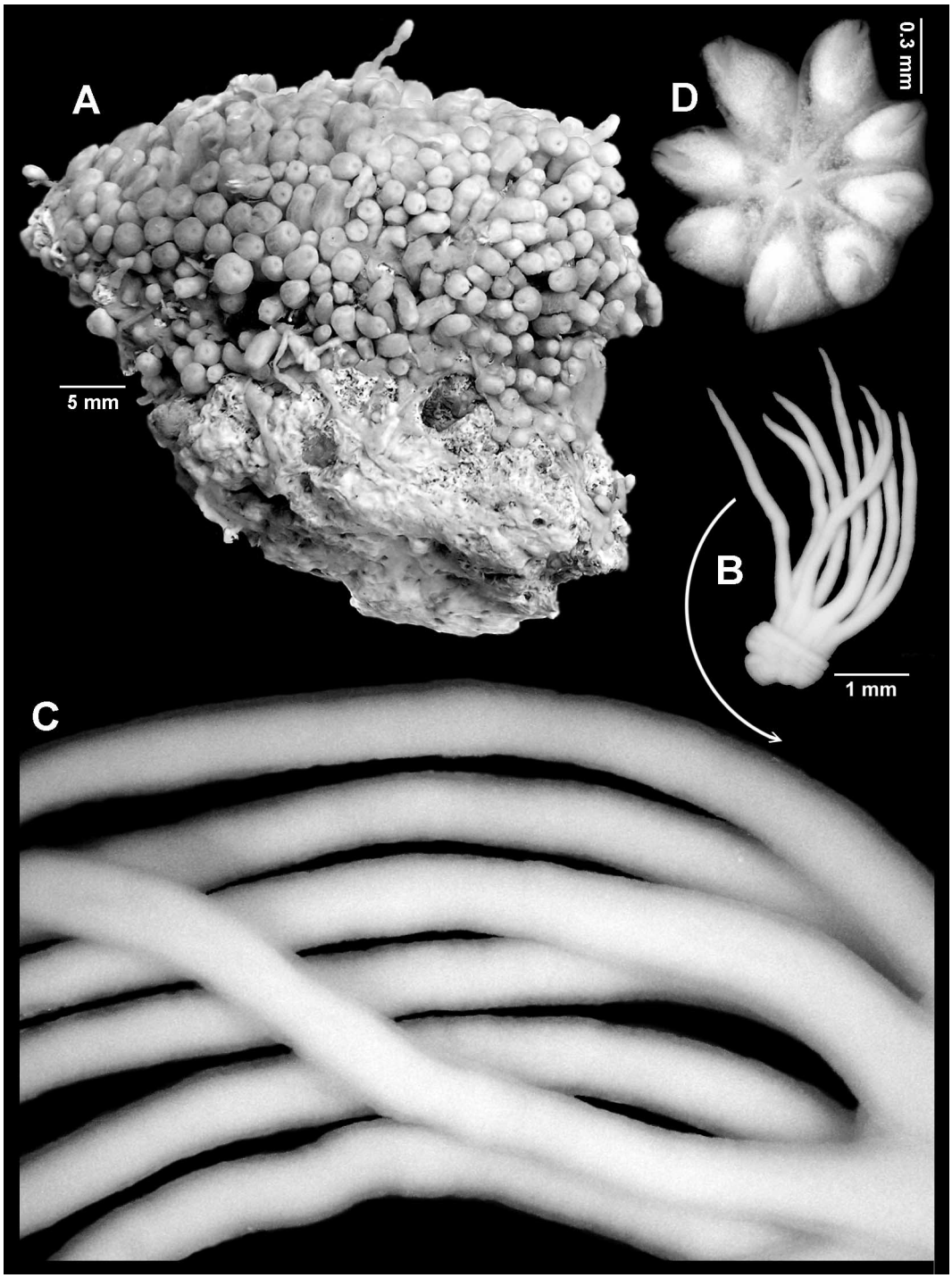

FIGURE 3. *Acrossota* cf. *amboinensis* **n. comb.**, NTM C13618: A, colony; B, tentacular region of a polyp; C, close-up of B; D, oral region of a polyp with partly invaginated tentacles.

NTM C13626. The lot consists of three parts — a cluster of polyps on a small fragment of coral rock, a large number of polyps on a larger piece of coral rock (Fig. 4A), and an unattached section of stolons and polyps (Fig. 4B).

Many of the polyps in the unattached specimen have the smooth, highly contracted tentacles everted and there are several vegetative stolonal outgrowths (Fig. 4B, arrowed), some of which have small swellings where autozooid polyps were developing. Stolons and polyp bodies have a thin covering of cuticle.

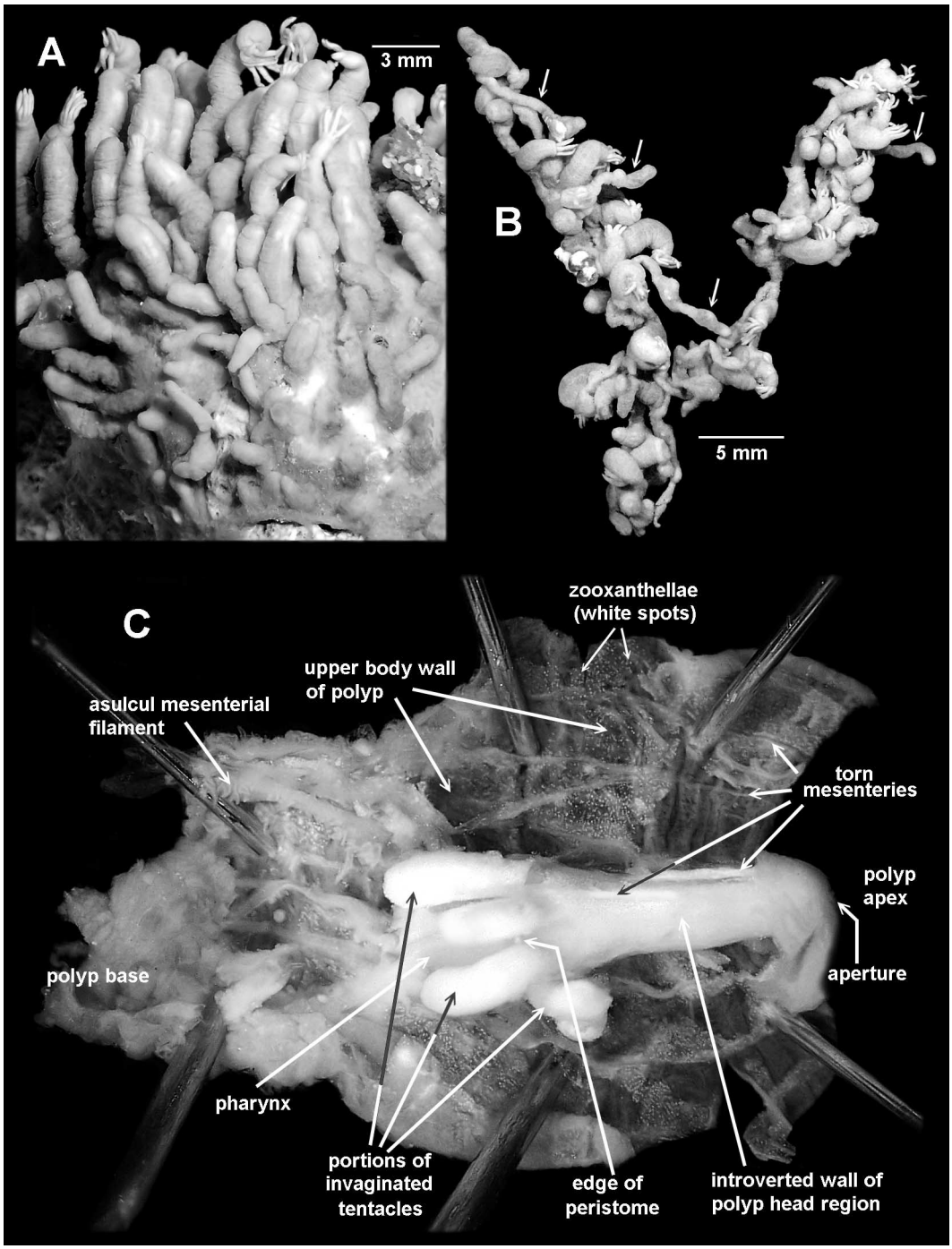

FIGURE 4. *Acrossota* cf. *amboinensis* **n. comb.**, NTM C13626: A, main portion of attached colony; B, unattached colony fragment; C, dissected polyp.

There are no stolons on the larger piece of coral rock, and all of the polyps arise from a broad basal membrane. The polyps are quite long, up to c. 10 mm long and 1.1–1.8 mm in diameter, and many have c. 1.5 mm of everted tentacles exposed. There is a cuticle covering the membrane and the polyp bodies, particularly noticeable on the transversely wrinkled proximal third of each polyp.

The third rock fragment has slightly more than 20 polyps on it that arise from a spreading membranous base. Many of the polyps have smooth tentacles protruding from the oral end.

The dissected polyp shown in Figure 4C, taken from the large rock, reveals the contortions involved in the process of retraction. Whole, or portions of, invaginated tentacles are free in the gastric cavity. They lie mostly

alongside the pharynx, which has been pulled down by the muscles in those parts of the mesenteries proximal to it. The cylindrical region distal to the pharynx and the invaginated tentacles is that part of the body wall, now turned inside out, that was previously outside of and adjacent to the pharynx in the expanded polyp. This region is attached to the pharynx by mesenteries that must undergo considerable stretching during the invagination process. Some of these mesenteries, torn during the dissection, are labelled at the right of the figure. Those parts of the mesenteries remaining attached to the invaginated body wall pass down between the invaginated tentacles, along the length of the pharynx and down to the base of the colony. When the invaginated, upper body wall cylinder was opened, portions of three tentacles that had not completely invaginated were lying longitudinally within. At the proximal end of the cylinder, the peristome lay like a domed membrane across the top of the pharynx. If the invaginated parts of the tentacles are magnified they can be seen to be covered in a thick layer of zooxanthellae — presumably that which was previously inside the expanded tentacle prior to polyp retraction. The oral aspect of a polyp with the tentacles preserved in the process of invagination or evagination is shown in Figure 3D. Clefts can be seen in the tip of each tentacle stub.

NTM C15379. This lot consists of two small clumps of fine gravel held together by a gelatinous substance. These support few polyps but many vegetative stolonic outgrowths with very little internal structure visible. The samples are portions of a colony initially obtained from a dealer in aquarium animals. The colony had been kept in an aquarium for some time, and its morphology is likely to have been affected by this.

NTM C15380. This lot consists of two small fragments of coral and coralline algae. There are 13 polyps on the largest fragment, and only one on the smallest piece. The largest piece has a number of anastomosed, narrow, flattened stolons supporting the polyps. Smooth tentacles protrude from a number of the polyps and can be seen within the gastric cavities of others. Polyps and stolons are of the same size range as the specimens described above. The live parent colony is shown in Figure 8A. The tentacles are clearly of a simple, pinnule-less construction. This material was also from a colony obtained from a marine animal dealer, but it had spent very little time in captivity.

NTM C15381. This specimen consists of a piece of thin coral rock, about 47 x 43 mm in size, supporting a large number of polyps almost all of which have the tentacles withdrawn. Unusually, this specimen has polyps typical of both *Acrossota amboinensis* and the new taxon described below. The retracted polyps of the two different species look more or less identical, but those polyps with portions of the tentacles visible reveal that there are two forms present. Upon cursory examination it can appear that the two different forms are actually united on the same basal stolons, but careful tracing of the intermixed stolons proves this is not the case.

NTM C15506. There are over 40 polyps making up this specimen, all closely arising from a more or less complete basal membrane encrusting a near-triangular coralline tile about 2 cm^2 in area. Most polyps are about 4 mm tall and 2.3 in diameter, one has the tentacles extended, and one is inflated to a height of 7 mm and a width of 3 mm. The cuticle covering the polyps and membrane is quite conspicuous in many places owing to its dark greenish-brown colouring, which result from a fine covering of marine turf.

Remarks: The main morphological characteristics used to distinguish between species within similar stolonate genera are sclerite position, arrangement, and architecture, and the number of pinnules on the tentacles. The fact there are no sclerites or pinnules in *Acrossota* presents an interesting challenge to the taxonomist. The material described above, extra to the holotype, serves to confirm the validity of the existence of a pinnule-less genus of soft coral, but we are unable to establish with certainty whether they are conspecific with each other or whether they represent the same species as *A. amboinensis*.

An identical situation pertains to *Acrossota liposclera*. The polyps of Bourne's specimen are described as being about 5 mm tall and 1.75–2.00 mm in diameter, connected by flat stolons, and all covered in a thin cuticle. The tentacles are invaginable and without pinnules, and there are no sclerites (*liposclera*). "From place to place a branch of the main stolon or a stolonar outgrowth of one of the zooids projects for some distance from the support as a long, free, thin-walled tube, near the end of which a zooid is developed ..." (Bourne 1914: 263). "(2) The portion of the body of the zooid immediately below the tentacles. This portion is invaginated in

retracted specimens ...” (ibid.: 267). Bourne’s specimen from the D’Entrecasteaux Islands of the eastern end of Papua New Guinea, could possibly be the same species as all or any of the above specimens.

Family Clavulariidae Hickson, 1894

***Knopia* n. gen.**

Diagnosis. Colonies of upright polyps arising from stolons that may coalesce but do not form extensive basal membranes. Polyp bodies and stolons covered with thin cuticle. Polyps retractile. Tentacles lacking free pinnules; instead, the margins of the tentacle are very broad and divided into a series of finger-like caeca as if a single row of closely appressed pinnules had become fused side-to-side along the length of the tentacle. Sclerites, present only on the introvert and tentacles, are minute platelets and small scales that are constructed from sinuous, dendritic, calcite rods that are more or less radially arranged. Zooxanthellate.

Type species. *Knopia octocontacanalis* **n. sp.**, by original designation and monotypy.

Etymology. The genus is named for Daniel Knop who collected most of the material and supplied colour images of live colonies. Gender feminine, as is traditional.

Remarks. The specimens of this genus available for examination have not formed extensive basal mats as seen in one specimen of *Acrossota* described above. But, it is quite possible that specimens may be found in the future with a similar growth form, as it is not rare for taxa that are mainly stolonate to be found with broad, coalescing, basal ribbons, especially if luxuriant (e.g. *Clavularia australiensis* in Hickson, 1894: 338; *Clavularia viridis, C. inflata* in Roxas, 1933: 57–58; *Sansibia* in Alderslade, 2000: 243; *Orangaslia* in Alderslade 2001: 42-49; and *Acrossota* above.) At present, specimens of *Acrossota* and *Knopia* that have only stolons cannot easily be distinguished unless the tentacles are extended. Both of these genera can also be confused with an as-yet-undescribed taxon figured by Fabricius and Alderslade (2001: 68) that has pinnulated tentacles and no sclerites. Dissection to establish tentacle form is necessary in such instances.

***Knopia octocontacanalis* n. sp. (Figs 5–7, 9, 10)**

“*Acrossota* sp.?” Sprung & Delbeek 1997: 172.
Acrossota: Sprung 1999: 149.
Clavularia sp. Erhardt & Knop 2005: 68 (bottom figure).

***Material examined*:** *Holotype:* NTM C13568, Kapikan, Semporna Islands, Sabah, Malaysia, 04º38.843'N, 118º49.813' E, depth 10–20 m, F. Dipper, 28 March 2000.

Paratypes: NTM C13563, Kapikan, Semporna Islands, 04º37.794’ N, 118º50.085' E, depth 12 m, F. Dipper, 6 October 1999; NTM C13566, Pelu Beach, Boheydulang, Semporna Islands, 04º36.230' N, 118º47.610' E, depth 28 m, F. Dipper, 8 April 2000; NTM C13567, Kapikan, Semporna Islands, depth 5–10 m, F. Dipper, 30 April 1999; NTM C15381, Kapikan, Semporna Islands, 04°38.843' N, 118°49.813' E, depth 10–20 m, F. Dipper, 28 March 2000; NTM C15382, Biaro, Indonesia, 02º08.48' N, 125º21.15' E, depth 3 m, Coral Reef Research Foundation (CRRF), 23 May 1993; NTM C15383–15387, NTM C15392–15394, Kotok, Island, Thousand Islands, Kotok Is., Indonesia, 5°42.77' S, 106°33.675' E, depth 15–22 m, Daniel Knop, 16 July 2002; NTM C15388–15391, NTM C15395, same data but 24 September 2002; NTM C15396, same data but December 2004; NTM C15398, probably Indonesia, purchased from a dealer by Daniel Knop, December 2004.

Description: The holotype is fragmented owing to the process of removal of the colony from the reef. It consists of several groups of polyps attached by stolons to pieces of hard, coral reef-derived substratum and a

portion of sponge (Fig 5A).

The sclerite-free polyp bodies are inflated to various degrees and most are transparent and acorn-shaped, e.g. 7.2 mm long and 4.8 mm in diameter. Taller polyps are narrower, e.g. 8.7 mm x 3.8 mm and 9.5 mm x 3.3 mm and can be up to c. 11 mm long. The polyp bodies are covered by a thin cuticle that is continuous with that covering the basal colonial stolons. In general, the greater the extent of inflation the more transparent is the polyp body wall. Small, contracted polyps are opaque.

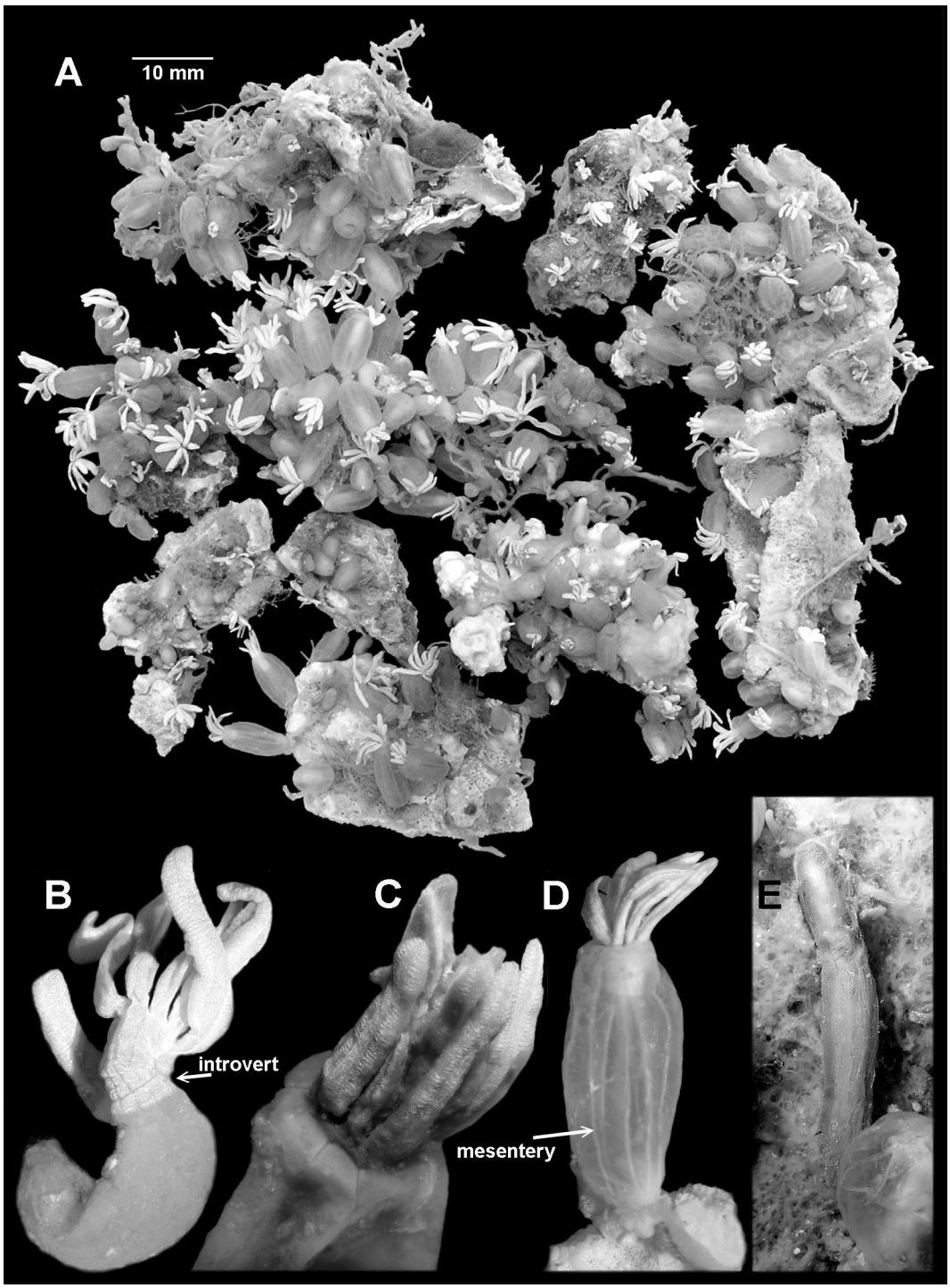

FIGURE 5. *Knopia octocontacanalis* **n. gen.**, **n. sp.**, holotype: A, fragmented colony; B–D, whole or partial polyps; E, stolonic outgrowth laying over sponge.

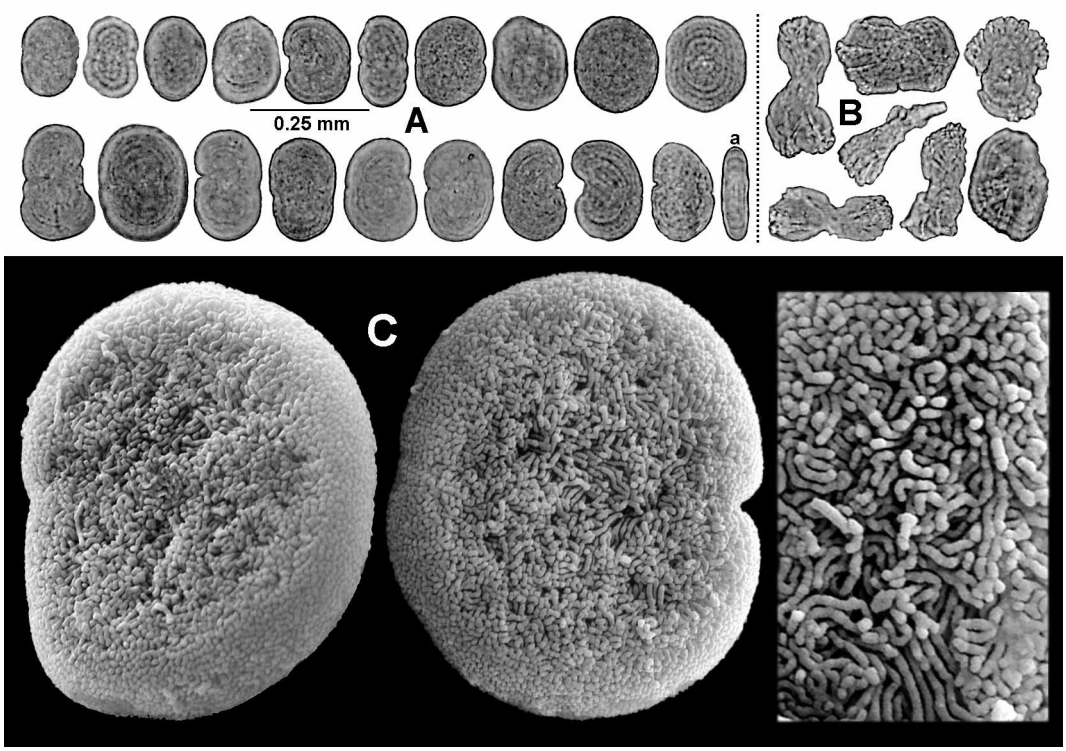

FIGURE 6. *Knopia octocontacanalis* **n. gen.**, **n. sp.**, sclerites of the holotype : A-B, light micrographs; C, electronmicrographs.

Many of the polyps have the tentacles partially exposed (Fig. 5C, D), and in a few they are completely exposed (Fig. 5B). Some of the latter are sufficiently expanded to reveal that the polyps have an introvertible neck zone, which, although only 1–2 mm long in the preserved material (Fig. 5B), can be quite extensive in life (Fig. 10A). The mesenterial insertions into the wall of the introvert can be seen as distinct longitudinal lines (Fig. 5B). When the neck region is invaginated, it is visible through the body wall as a pale cylinder that may hold part or all the tentacles packed longitudinally in a bundle (Fig 5D). The mesenteries are also clearly visible through the body wall of most polyps (Fig. 5D).

The polyps arise from reticulate stolons adherent to fragments of reef substratum, but the polyp density obscures much of the network. Most of the stolons are flattened and the narrowest are about 0.8 mm broad. Other portions of the network are 2–3 time as wide, especially where several branches of the network anastomose, but no large membranous expansions are present. Figure 7A shows a similar stolonal network in a paratype. Not all of the holotype stolons are fully attached to the substratum. Some arch across the rock and they also cross or lie upon other stolons without anastomosing. The terminal shoots of the stolonal network are cylindrical. They are about 0.8 mm in diameter and commonly project free of the surface. Their cuticle seems to be thicker than the stolons of the established network, and all but the smooth rounded tip is noticeably wrinkled (Fig. 5E).

The preserved tentacles are each shaped like a long, narrow, tongue (Figs 7B,C). The lateral edges are often more or less parallel, and the tip is usually rounded although the distal part of the tentacle may taper. In life, the tentacles are narrowly elliptical (Fig. 9A). The margins of the tentacle are very broad and are divided into a series of finger-like caeca, as if a single row of closely appressed pinnules had become fused side-to-side along the length of the tentacle. This is easily seen in the decalcified tentacle shown in Figure 7C (the gaps along the left-hand margin of this tentacle are tears). In the preserved specimens, the end of a pseudopinnule may bulge very slightly, but in most cases this is not obvious. As shown in Figures 9B,C, it is not even obvious in live colonies where the hydrostatic pressure within the tentacle would be expected to distend the

tissue. In this figure it is also possible to see that the margins of pseudopinnules do not extend over the total length of the tentacle, but the proximal portion, just before the tentacle meets the oral region, remains free. The inflated rachis of the tentacle can also be seen to be narrower in this region — a feature that is quite marked in the preserved material.

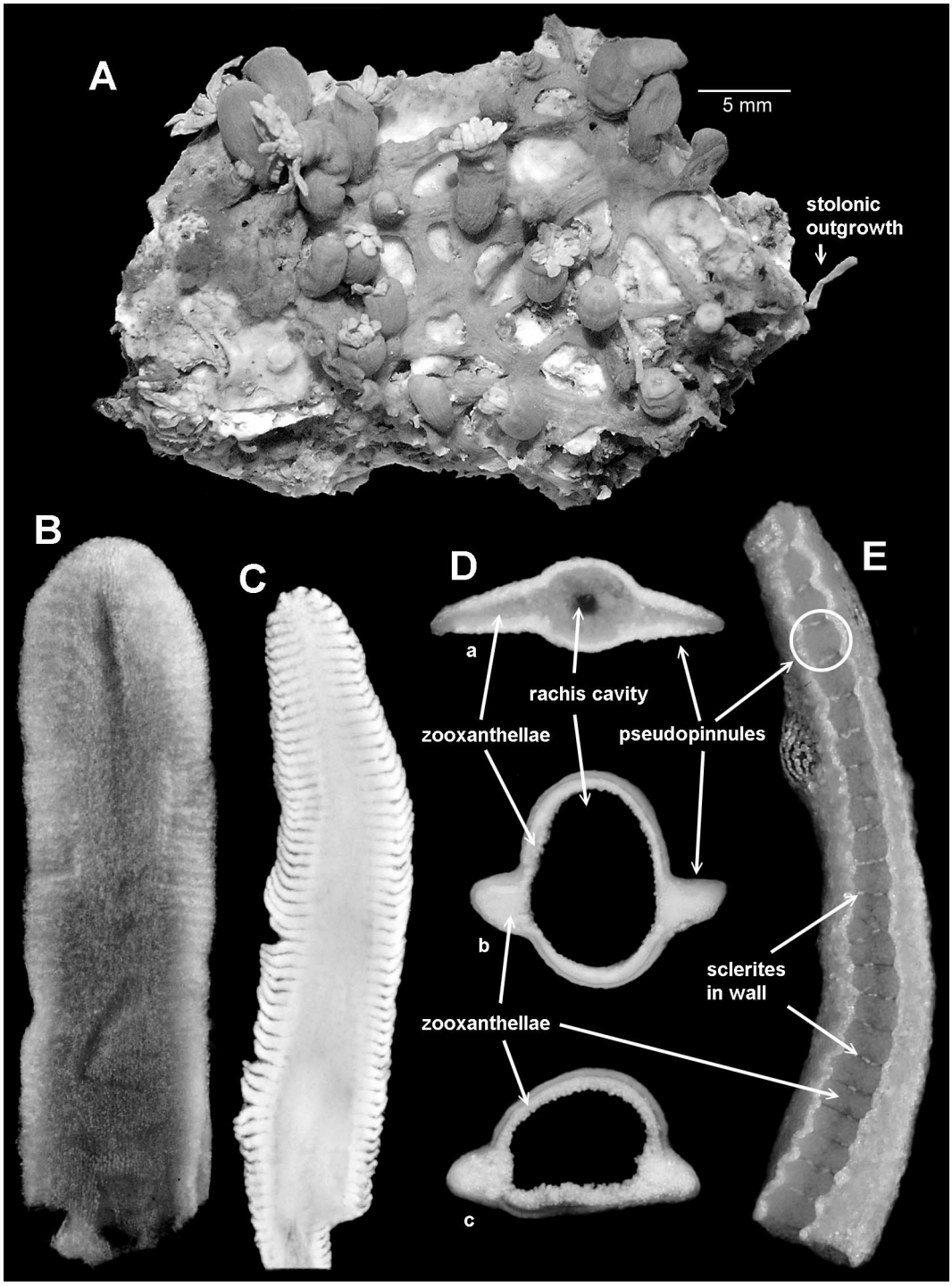

FIGURE 7. *Knopia octocontacanalis* **n. gen.**, **n. sp.** A, paratype NTM C15391. B–E, holotype: B, preserved tentacle; C, decalcified tentacle; D, transverse cross-sections of tentacles; E, longitudinal cross-section of tentacle through pseudopinnules.

The pseudopinnule caeca are confluent with the longitudinal lumen of the tentacle rachis and are full of zooxanthellae. The rachis is also packed with zooxanthellae, but in preserved material there is a free space in the centre running the length of the tentacle, as can be seen in the transverse cross section in Figure 7Da . The

other two transverse sections in this figure (Fig. 7Db,c) are from a paratype that was fixed in formalin prior to being preserved in ethanol, and clearly show that tentacle shrinkage in the ethanol-fixed holotype has condensed the zooxanthellae into a smaller area and reduced the amount of free space within the tentacle. A longitudinal section through the blade of a tentacle from this paratype shows that the interior of the pseudopinnules is packed with zooxanthellae (Fig. 7E).

In the holotype, the tentacles are up to c. 5.4 mm in length. There are about 70–80 pseudopinnules in each tentacle margin. Most of these are 0.30–0.34 mm long but they can be as long as 0.40 mm. The polyp mouth is slit-like and sits at the apex of a dome-shaped hypostome.

FIGURE 8. *Acrossota* cf. *amboinensis* **n. comb.**: A, NTM C15379 in life; B, NTM C13626 in life.

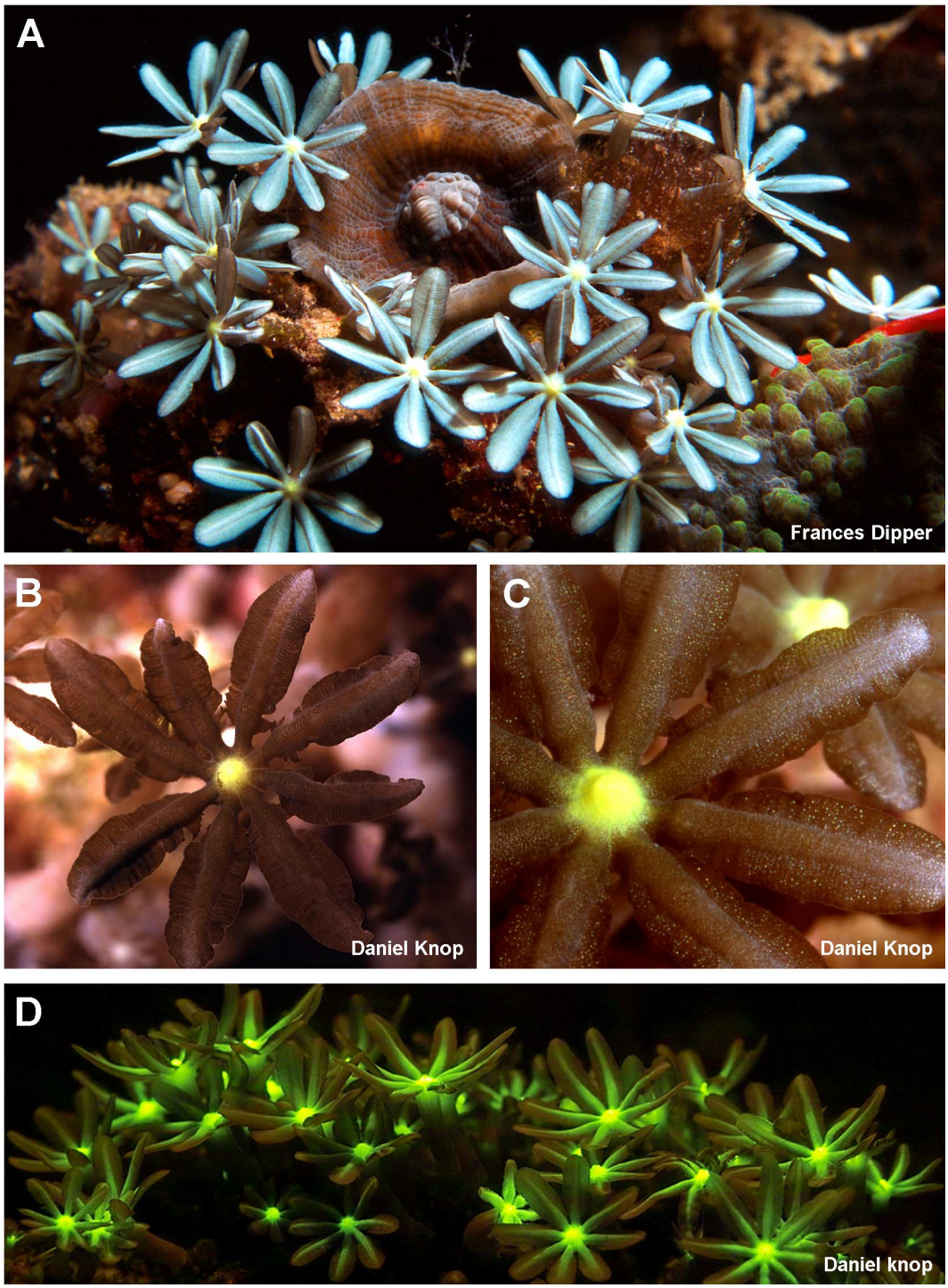

FIGURE 9. *Knopia octocontacanalis* **n. gen.**, **n. sp.**: A, holotype in life; B-C, live polyps co-collected with paratypes from Kotok Is.; D, same material as B-C under UV light.

The upper part of the introvert (sometimes all of it), the tentacles, and all but the summit of the oral hypostome are densely covered in minute sclerites which give a pale, pinkish-white sheen. Highly magnified under a dissecting microscope, the sclerites appear opalescent with flecks of red, blue, and green. The sclerites on the tentacles are arranged in rows; longitudinally on the rachis (Fig. 10C) and at right angles to these on the surface of the pseudopinnules. There are also sclerites in the dividing walls between the pseudopinnules (Fig. 7C). The majority of the sclerites are very small corpuscle-like platelets with a circular, oval, peanut-, or kidney-shaped outline (Fig. 6A); those shaped like Fig 6Aa are actually platelets seen edge-on. Scattered

amongst the platelets are a few small scale-like sclerites (Fig 6B). Polyp sclerites mostly measure 0.011–0.025 mm along the greatest diameter, and the platelets are constructed from sinuous, dendritic, calcite rods that are more or less radially arranged (Fig. 6C).

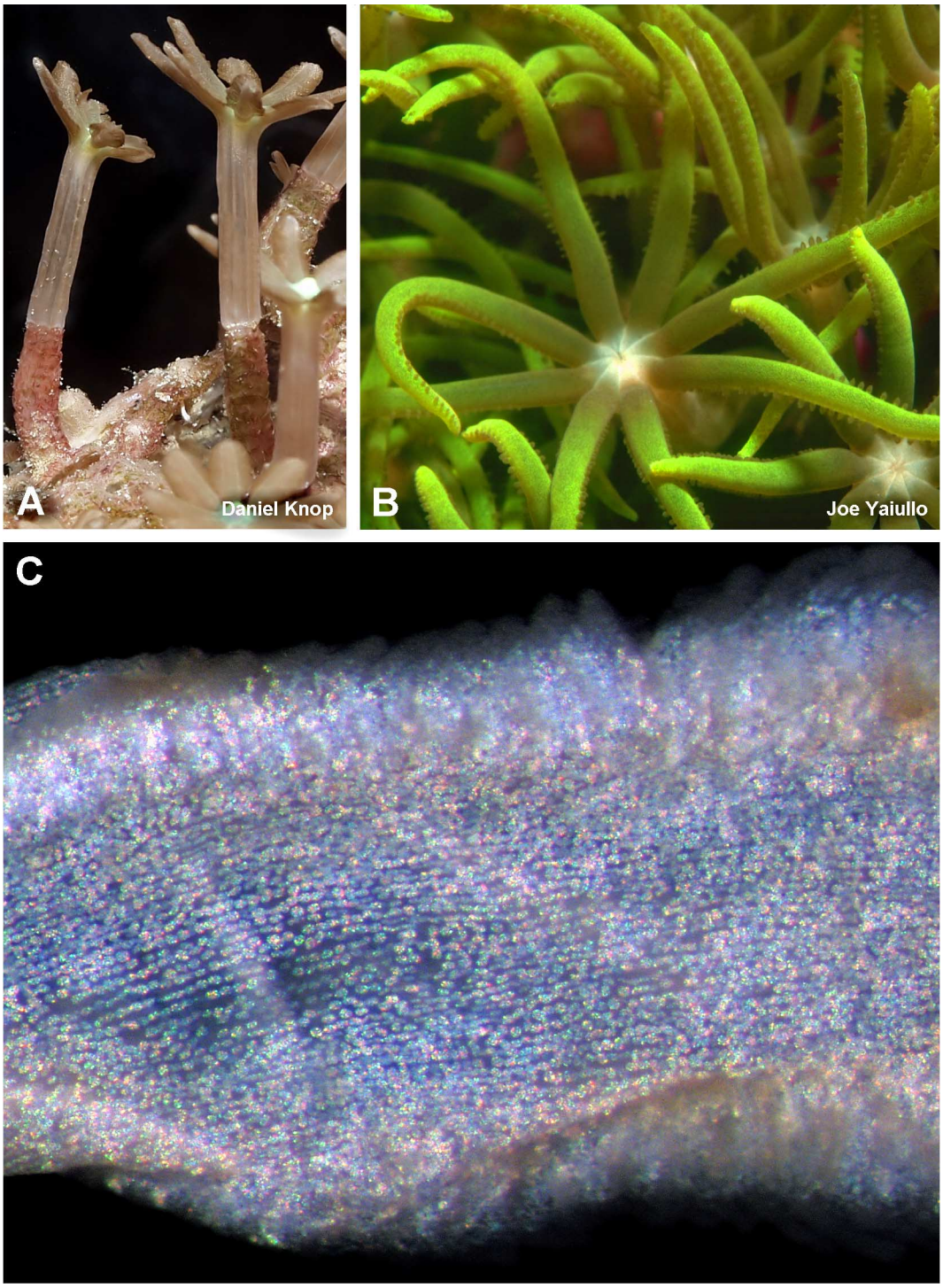

FIGURE 10. *Knopia octocontacanalis* **n. gen.**, **n. sp.**: A, live polyps co-collected with paratypes from Kotok Is.; B, polyps of *Briareum* cf. *stechei*, note very small pinnules; C, holotype tentacular sclerites *in situ*.

Variability: Polyp density is variable, as are the density and broadness of the stolons, as can be seen in Figure 7A of sample NTM C15391.

The number of pseudopinnules in the largest polyps in a colony does not vary greatly, with counts of about 65–75 being common.

The distribution of the sclerites is quite variable as is the colour. In several specimens, all or most polyps have very few sclerites. In those with few sclerites, they are predominantly present in the tentacle rachis; the pseudopinnules in some specimens can be almost sclerite-free. Besides the colours described above, sclerites can also appear to refract mainly green or gold, commonly with some red. In a number of specimens the sclerite-free hypostome retains its live yellow colour.

Because polyp size can be influenced by so many factors, measurements of polyps in taxa like this are not a reliable species character unless the differences are dramatic. Expanded polyps and tightly contracted ones are generally of similar size in all colonies to hand. The longest expanded polyp has a body length of 12.5 mm and tentacle length of 5 mm (NTM C15398).

Etymology: "Eighty-piped". There are up to 80 pseudopinnules along each margin of a tentacle; *octoconta* (Greek transliteration for 80) and *canalis* (Latin for a water pipe).

Remarks: Daniel Knop has documented the pattern of fluorescence of the polyps of *Knopia octocontacanalis* under ultraviolet light (Fig. 9D). He claims (pers. com.) that this pattern is the same for species of Tubiporidae with the same tentacle structure.

Discussion

Molecular systematics: We compared preliminary unpublished DNA sequence data for *K. octocontacanalis* NTM C15392 and *A. amboinensis* NTM C15380 with data for 103 genera included in a recently published mitochondrial gene phylogeny of subclass Octocorallia (McFadden et al. 2006b). Combined analysis of NADH-dehydrogenase subunit 2 (*ND2*) and octocoral-specific mutS homolog (*msh1*) sequences (GenBank accession numbers DQ985953, DQ985954) support the placement of *Knopia* in the Clavulariidae (Bayesian posterior probability = 100%). It differed from species in that family by a genetic distance of 0.025 (uncorrected p), comparable to the average distances among genera in most other octocoral families (McFadden et al. 2006a). *ND2* and *msh1* sequences obtained for *A. amboinensis* (DQ985955, DQ985956), on the other hand, were highly divergent from those of other octocoral taxa, supporting its placement in a separate family. Phylogenetically, this species fell among a heterogeneous mix of scleraxonians (*Briareum*, *Erythropodium*) and a stoloniferan (*Telestula*) whose relationships to one another and to other octocoral taxa remain poorly resolved (McFadden et al. 2006b). Unfortunately, lack of resolution at the presumed base of the octocoral phylogeny coupled with our inability to root the tree with confidence (McFadden et al. 2006b) prevent us from determining at this time whether the pinnule-less polyps of *Acrossota* represent the ancestral character state in Octocorallia or simply a secondary loss of pinnules in that genus. We are hopeful that our ongoing studies of several nuclear genes will shed further light on the evolution of this trait.

Final remarks: A number of other species of soft corals that appear to lack free pinnules in the polyps have been illustrated in recent popular literature, but have yet to make it to the scientific literature (e.g. Veron 1986, p. 613; Allen & Steene 1994, p. 118; Sprung & Delbeek 1997, p. 182; Fosså & Nilsen 1998, p. 114; Sprung 1999, pp. 152–153; Fabricius & Alderslade 2001, p. 77; Erhardt & Knop 2005, pp. 69, 72). By far the majority of these are species of Tubiporidae. There are also a number of illustrations of soft-coral polyps with very minute pinnules (e.g. Sprung & Delbeek 1997, pp. 183–187; Fosså & Nilsen 1998, pp. 115, 121; Sprung 1999, pp. 154–156; Fabricius & Alderslade 2001, p. 157). The majority of these are species of *Briareum*. Our personal observations on live colonies of *B. violaceum* (Roule, 1908) and an undescribed species from Darwin, plus those made by Gohar on *B. hamra* (Gohar, 1948) revealed that the pinnules are small enough to allow the tentacles to be withdrawn by invagination. In our experience, some species of *Briareum* can seem on first appearance to lack pinnules on the tentacles, but closer inspection reveals them (see Fig. 10B). There is a continuum among the stoloniferous octocoral genera, from polyp tentacles with long pinnules to those with no pinnules at all. At present, the tongue-like form of tentacle found in *Knopia* and some Tubiporidae seems to be

discrete.

The data presented in this paper confirm the existence of taxa with polyp tentacles lacking free pinnules. This discovery has important implications for the definition of the subclass Octocorallia because the possession of pinnated tentacles has been one of the major diagnostic features of the group.

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