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A new species of the sea anemone *Megalactis* (Cnidaria: Anthozoa: Actiniaria: Actinodendridae) from Taiwan and designation of a neotype for the type species of the genus

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Abstract.—*Megalactis comatus,* new species, from Taiwan is the third species in this genus of sea anemones with highly branched tentacles. The others are *M. hemprichii* Ehrenberg, 1834, from the Red Sea, and *M. griffithsi* Saville-Kent, 1893, from the Great Barrier Reef. Size of nematocysts from acrospheres and column clearly separate *M. comatus* from the other species of *Megalactis.* One of us (A.A.) observed asexual blastulae in *M. comatus.* This is the first record of asexual reproduction in the genus. Because type specimens of *M. hemprichii* have not been found and the original description cannot be used to distinguish this species from other species of *Megalactis,* we designate a neotype for the type species of the genus, *M. hemprichii* Ehrenberg, 1834. All the specimens of actinodendrids examined lacked basilar muscles; this calls into question the placement of family Actinodendridae among thenarian sea anemones.

The family Actinodendridae is a group of three genera of exclusively tropical Indo-Pacific sea anemones: *Actinodendron* Blainville, 1830, *Megalactis* Ehrenberg, 1834, and *Actinostephanus* Kwietniewski, 1897. An actinodendrid has the oral disc drawn out into a number of branched tentacles that make it resemble a tree (Blainville 1830, 1834; Quoy & Gaimard 1833; Haddon 1898; Carlgren 1949). The last branches of tentacles terminate in acrospheres that appear as white swellings of tissue; they are packed with nematocysts and spirocysts. Because the actinodendrids have been documented to sting humans badly (Saville-Kent 1893, Halstead 1970), knowledge of these animals is significant not only for taxonomy and phylogeny, but also for medicine and toxicology.

Actinodendridae was considered by Carlgren (1900, 1949) to belong to the suprafamilial group Thenaria. Basilar muscles, which are structures "running along both sides of the base of the mesentery, close to the pedal disc" (Carlgren 1949, p. 8), were used by Carlgren (1899, 1900, 1942, 1949) to define two major groups in sea anemones, Athenaria "Nyantheae without basilar muscles" (Carlgren 1949, p. 21) and Thenaria "Nyantheae with basilar muscles" (Carlgren 1949, p. 41). We did not find basilar muscles in specimens of actinodendrids studied, which makes placement of Actinodendridae among Thenaria questionable.

The morphology of the tentacles of these sea anemones varies with environment, behavior, and conditions of preservation. Although the number of species described in Actinodendridae is small, the lack of terminology for describing branched structures and the enormous variety that can be found makes identification of species difficult. In this paper we describe one species and redescribe two others of *Megalactis,* and standardize terminology for the branched tentacles of Actinodendridae.

Actinodendrids are found in shallow water in sheltered places with sandy or muddy bottoms. Members of the genus *Megalactis* reportedly attach the pedal disc to hard substrata in sand or mud into which the anemones burrow (Saville-Kent 1893, Fishelson 1970). The new species of *Megalactis* described here lives in thickets of the scleractinian coral *Acropora* in Taiwan; this might be the same species as that reported by den Hartog (1997) as an unidentified actinodendrid living attached to coral branches in Indonesia.

The description of *Megalactis hemprichii* Ehrenberg, 1834, the type species of the genus, was diagnostic in the early 19th century. Mentioning only that a sea anemone had bipinnately branched tentacles was sufficient to distinguish *M. hemprichii* from all sea anemones known at that time. With the current state of knowledge, the original description of *M. hemprichii* does not distinguish it from other species of *Megalactis*: bipinnate disposition of the branches is generic rather than specific. Type specimens of *M. hemprichii* Ehrenberg, 1834 have not been found (Klunzinger 1877, Fautin 2004 Hexacorallians of the World: http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm). We designate a neotype for *M. hemprichii* in accordance with Article 75.3 of the International Code of Zoological Nomenclature (International Commission of Zoological Nomenclature 1999); no new species can be described within *Megalactis* without having a basis of comparison with the type species of the genus.

In the course of this research, one of us (A.A.) found unusual gametogenic structures in male specimens: nodes filled with spermatic packets that have a three-dimensional structure more voluminous than the thickened band typical for gametogenic tissue in members of Actiniaria. Male and small individuals of *M. comatus* had blastulae inferred to be of asexual origin among the mesenteries. This is the first record of asexual reproduction in a member of Actinodendridae. The only female found contained no gametogenic nodes or blastulae among its mesenteries.

Materials and Methods

Specimens of the new species of *Megalactis* were investigated alive by diving and as preserved material; museum specimens of other species of *Megalactis* and *Actinodendron* were investigated for internal morphology and histology (Table 1); results from this study are based on examination of more than 400 museum lots and photographic documents of actinodendrids.

Animals were recorded in situ on Hi8 videotape using a CanonES6000A video camera in an Amphibico underwater housing. Live material was collected underwater by hand using gloves for protection against stinging. Geographic coordinates were read with an Eagle 12-channel GPS receiver at the point of collection. The animals were kept in aquaria with running seawater for two days; no food was given. Photographs were made in the aquarium using a Nikon Coolpix 950 digital camera. Archived videotapes and photographs are in the collection of the Division of Invertebrate Zoology, University of Kansas Natural History Museum (KUNHM). Specimens were relaxed with magnesium sulfate in seawater, then preserved in 10% seawater formalin. After at least two months, they were transferred to 10% freshwater formalin.

Undischarged cnidae from preserved animals were examined at 1000× in squash preparations using a light microscope equipped with differential interference optics. Squash preparations were made from acrospheres, the oral face of the main branches of the tentacles, the proximal, middle, and distal column, the actinopharynx, and the mesenterial filaments. Sigma Scan Pro version 4.01.003 measurement software was used to measure the length and the width of undischarged capsules projected onto a Summa Sketch digitizing tablet (Summagraphics). Sampling nematocysts was done following the recommendations of Williams (1996).

For histology, tissue was embedded in Paraplast, sectioned at 9 μm, and stained with Heidenhain's Azan or hematoxylin and eosin (Presnell & Schreibman 1997). Serial sections for three-dimensional reconstruction were obtained from mesenterial structures, column, and two entire juvenile individuals. Images were obtained using a Nikon Coolpix 995 digital camera connected to an Olympus microscope through an Optem eyepiece digital coupler. Serial images were aligned manually using layers in Adobe Photoshop. Three-dimensional reconstruction was done using the software Vaytek VoxBlast Version 3.0 Light (http://www.vaytek.com/).

In the following discussion, as is conventional in sea anemones, the proximal direction is toward the pedal disc and distal is the opposite. Tentacles are arranged in four cycles. Branches of the tentacles are ordered by how close they are to the oral disc: a branch arising from the oral disc is considered to be of the first order; a branch that ramifies from a branch of the first order is of the second order, etc. (Fig. 1).

Abbreviations: CAS, California Academy of Sciences, San Francisco, CA, USA; KUNHM, University of Kansas Natural History Museum, Lawrence, KS, USA; NNM, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; NMNS, National Museum of Natural Sciences, Taichung, Taiwan; TAUI, Zoological Museum, Tel-Aviv University, Tel-Aviv, Israel.

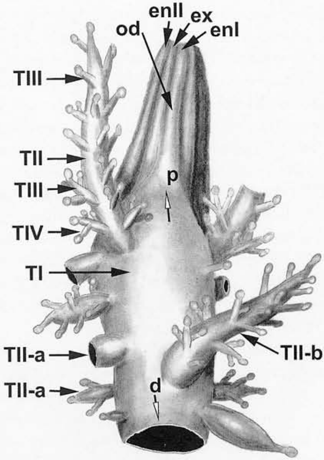

Fig. 1. Ramifications in a tentacle of the first cycle; view looking down a tentacle, i.e., proximally, to the oral disc. The arrow labeled "d" indicates the distal direction, that labeled "p" indicates the proximal direction. Abbreviations: enI, endocoel of the first cycle; enII, endocoel of the second cycle; ex, exocoel; od, oral disc; TI, first order branch; TII-a, lateral secondary order branch; TII-b, oral face secondary order branch; TIII, third order branch; TIV, fourth order branch.

Taxonomic Account

Order Actiniaria

Family Actinodendridae Haddon, 1898

Diagnosis (modified from Carlgren 1949; see remarks below).—Limbus not well defined. No marginal sphincter muscle. Fosse absent. Up to 48 branched tentacles cyclically arranged. Terminal branches of tentacles with acrospheres. Two or more well developed siphonoglyphs. Twenty-four pairs of mesenteries, all or almost all perfect and, apart from the directives, fertile. Retractor muscles diffuse, broad, band-like. Cnidom: spirocysts, basitrichs.

Remarks.—Carlgren (1949, p. 67) indicated a "well developed disc" and "pairs of mesenteries up to 48" for Actinodendridae. Pedal disc size varies greatly: that of some specimens is wide, but that of others is narrow with a limbus that is hard to recognize. None of the specimens studied had more than 24 pairs of mesenteries. Carlgren (1949) asserted that parietobasilar and basilar muscles are distinct in actinodendrids, but we found them to be absent in all genera of the family.

Genera.—Actinodendron Blainville,

1830, type genus; *Megalactis* Ehrenberg, 1834; *Actinostephanus* Kwietniewski, 1897.

Genus *Megalactis* Ehrenberg, 1834

Diagnosis (modified from Carlgren, 1949; see remarks below).—Actinodendridae with ramified tentacles having second-order branches arranged bipinnately. Last order branches with capitate acrospheres.

Remarks.—Carlgren (1949, p. 68) stated that *Megalactis* has "the oral face of the arms [branches of the first order] free from tentacles." All specimens of *Megalactis* we studied had two to three second-order branches on the oral face of branches of the first order. Carlgren (1949, p. 68) stated in his diagnosis for *Megalactis* that "the ultimate branches of the tentacles are simple and pointed." One of us (A.A.) found specimens of *Megalactis* that have capitate terminal tentacles.

Species.—*Megalactis hemprichii* Ehrenberg, 1834, type species by monotypy, Ras Kafil, Red Sea; *Megalactis griffithsi* Saville-Kent, 1893, Warrior Reef, Torres Strait, Great Barrier Reef, 9°30′S, 143°06′E. Coordinates from Gazetteer of Australia, 2001 (http://www.ga.gov.au/).

Megalactis hemprichii Ehrenberg, 1834

Megalactis Hemprichii Ehrenberg, 1834: 263 (original description).
Megalactis Hemprichii Ehrenberg: Milne Edwards & Haime, 1851:11.
Actineria Hemprichii Ehrb.: Klunzinger, 1877:90–91.
Megalactis Hemprichii Ehr.: Andres, 1883: 308–309.
Megalactis Hemprichii E.: Carlgren, 1899: 14.
Megalactis Hemprichii Klunzinger: Delage & Hérouard, 1901:539.
Megalactis hemprichii Ehrenberg, 1834: Carlgren, 1949:68.
Megalactis hemprichi Ehrenberg: Fishelson, 1970:109.
non *Megalactis hemprichii* Ehrenberg, 1834: Cutress & Arneson, 1987:53–62.

Description.—Dimensions: column diameter 14–26 mm distally and 14–15 mm in the middle; pedal disc diameter 5–9 mm; column length 23–41 mm; oral disc diameter 21–23 mm; tentacles of the first cycle 45–51 mm long; tentacles of the fourth cycle 10–11 mm long.

Color: Of live specimens unknown. Preserved specimens beige to pale yellow.

Column: Pyramidal to elongate with narrow pedal disc; limbus hardly recognizable (Fig. 2A). Column smooth and mesenterial insertions clearly visible through column in relaxed specimens. In contracted specimens, column with circumferential folds (Fig. 2A).

Oral disc and tentacles: Oral disc narrow. In preserved specimens, mesenterial insertions on oral disc visible as dark lines; radial bumps near mouth mainly on exocoelic intervals (Fig. 2D). Forty-eight tentacles arrayed in four cycles (6 + 6 + 12 + 24). Tentacles of first, second, and third cycles ramified in branches of up to three orders. Proximal secondary branches of first, second, and third tentacle cycles short (Fig. 2B).

Branches regularly oriented. Secondary branches pinnately disposed in one row on each side of a branch of the first order (Fig. 2E). Up to two long and broad secondary branches on aboral side of primary branches of tentacles belonging to first, second, and third cycles (Fig. 2E). Up to 45 secondary branches on tentacles of first and second cycle; up to 25 secondary branches on tentacles of third cycles; up to 11 secondary branches on tentacles of fourth cycle. Branches of last order relatively long. Large, round acrospheres.

Internal structure: Actinopharynx short with two deep siphonoglyphs. Twenty-four pairs of mesenteries in three cycles (6 + 6 + 12); first two cycles usually perfect. Oral stomata large; marginal stomata very small. Retractor muscles diffuse and strong. Fila-

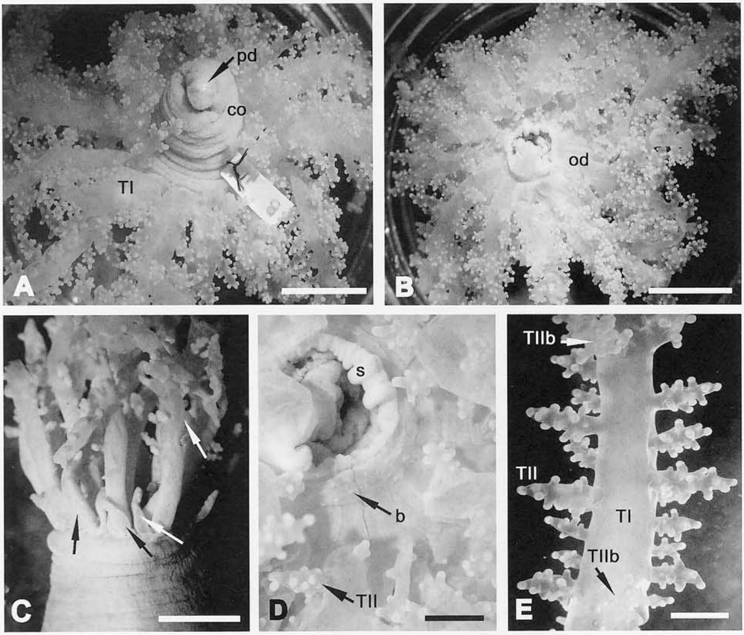

Fig. 2. *Megalactis hemprichii,* external morphology (TAUI 21560). A, Aboral view of entire animal. B, Crown of tentacles, oral view of entire animal. C, Regenerated tentacles (TAUI 7812). Arrows indicate tentacles with missing secondary branches. D, Detail of oral disc and mouth. E. First order branch. Abbreviations: b, radial bumps on exocoelic intervals; co, column; od, oral disc; pd, pedal disc; s, siphonoglyph; TI, branch of the first order; TII, short proximal secondary branch; TII-a, lateral secondary order branch; TII-b, oral face secondary order branch. Scale bars: A, B = 15 mm; C = 10 mm; D, E = 5 mm.

ments absent on mesenteries proximally. Parietobasilar and basilar muscles not seen. Gonochoric. The only specimen sectioned was female (Fig. 3).

Cnidae: Basitrichs densest in acrospheres. Cnidom: spirocysts and basitrichs (Fig. 4). Measurements in Table 2.

Type specimen and locality.—Neotype TAUI 31623, Red Sea, Gulf of Aqaba, Eilat, 29°30′N, 34°55′E. Coordinates from GEOnet Names Server of National Imagery and Mapping Agency (http://www.nima.mil).

Voucher specimens.—Table 1.

Megalactis comatus, new species
Figs. 4–10

Description.—Dimensions: Diameter of column 2–38 mm distally and 5–21 mm in the middle, of pedal disc 2–8 mm; column length 8–26 mm; tentacles of the first cycle 9–11 mm long; tentacles of the fourth cycle 2–3 mm long; oral disc diameter 13–25 mm; tentacle crown diameter 50–100 mm.

Color: In live specimens, oral disc and tentacle color ranges from dark brown to pale orange or pink. Tentacles translucent, without pattern (Fig. 5). Oral disc with ra-

Fig. 3. *Megalactis hemprichii,* histology (KUNHM 001948). Abbreviations: f, filament; m, mesoglea; 0, ova; r, retractor. Scale bar = 1 mm.

dial rows of white spots aligned along exocoelic spaces; radial spots may spread laterally onto adjacent endocoelic spaces (Fig. 5F). Insertions of mesenteries on oral disc visible as lighter lines (Fig. 5F). Column beige to white; distal column translucent tinged with brown or pale orange. Female gametogenic tissue purple and male gametogenic tissue white (Oscar Chen, currently at Institute of Oceanography, National Taiwan University, pers. comm.). Preserved specimens beige, column paler than oral disc or crown.

Column: Pyramidal to elongate with a narrow pedal disc; limbus hardly recognizable (Fig. 5C). Pedal disc and proximal column adhesive with strong ripples of ectodermal tissue in preserved specimens. Circumferential folds resulting from contraction of the column between pedal region and distal-most third of column (Fig. 5C). Distal-most third of column thinner and smoother than proximal column. Mesenterial insertions clearly visible through column.

Oral disc and tentacles: Oral disc narrow. Mesenterial insertions on oral disc visible as light lines in live specimens. Radial bumps close to mouth mainly on exocoelic intervals.

Appearance of tentacle crown shaggy because of numerous branches not regularly oriented (Fig. 5A, E). Forty-eight tentacles arrayed in four cycles (6 + 6 + 12 + 24). Tentacles of first, second, and third cycles ramified in branches of up to four orders. Proximal secondary branches of first, second, and third tentacle cycles long.

Secondary branches pinnately disposed in one row on each side of a primary branch (Fig. 5D). On contracted tentacles, pinnate arrangement unclear: secondary branches appear to be arranged in two or more lateral rows on each side of a primary branch. Some large secondary branches occur on aboral side of primary branches of tentacles belonging to first, second, and third cycles. Secondary branches variable in length. Up to 48 secondary branches on each tentacle of first and second cycle; up to 40 secondary branches on each tentacle of third cycle; up to 12 on each tentacle of fourth cycle. Branches of last order relatively long, terminate in small round to pointed acrospheres.

Internal structure and histology: Actinopharynx short, with two deep siphonoglyphs (two specimens had three: Fig. 6), each connected to a pair of directive mesenteries. Twenty-four pairs of mesenteries

Table 1.—Specimens of *Megalactis* and *Actinodendron* examined. ? = missing data.

Species	Locality	Depth (m)	Collection date	Catalog number	Collector	Lot size	Status
Megalactis comatus	Pacific Ocean, Taiwan, Henchun Peninsula, Nanwan, power plant water intake basin, 21°57.27′N 120°45.22′E	3	27 June 2000	KUNHM 001663	AA & Oscar Cheng	1	holotype
				KUNHM 001665		1	paratype
				NMNS 4158-001		1	paratype
				CASIZ 161680		1	paratype
				RMNH 32194		1	paratype
				KUNHM 001664		1	voucher
				KUNHM 001666		1	voucher
				KUNHM 001667		1	voucher
				KUNHM 001668		1	voucher
				KUNHM 001669		1	voucher
				KUNHM 001670		2	vouchers
				KUNHM 001251		15	vouchers
				KUNHM 001252		17	vouchers
		2–3	28 May 2002	KUNHM 001657	Fan Tung Yung and Tsai Wan Hsu	6	vouchers
	Pacific Ocean: Taiwan; Kenting: Houpihwu	?	1992	KUNHM 001611	Keryea Soong	1	voucher
		?	1992	KUNHM 001612		1	voucher
		?	1992	KUNHM 001613		1	voucher
Megalactis hemprichii	Red Sea, Gulf of Aqaba, Eilat	15	28 September 2002	TAUI CO 31623	Guy Ayalon	1	neotype
	Red Sea, Gulf of Aqaba	?	12 July 1969	TAUI CO 21560	?	1	voucher
				KUNHM 001948	?	1	voucher
	Red Sea, Gulf of Aqaba, Taba	?	August 1967	TAUI CO 7812	L. Fishelson?	1	voucher
Megalactis griffithsi	Pacific, Fiji, Great Astrolabe Reef			KUNHM 001159	Joan Koven	1	voucher
	Pacific, Papua New Guinea, Lion Isl., 9°31′60″S, 147°16′0″E	6	23 June 2000	KUNHM 001162	AA & DGF	1	voucher
Actinodendron plumosum	Pacific, New Caledonia, Baies des Citrones Station 109, HZ19	?	29 July 1980	MNHN 1562	P. Laboute	1	voucher
Actinodendron glomeratum	inferred Philippines	?	?	USNM 1025089	?	1	voucher

Table 2.—Size of nematocysts: average of measurements for a sample in which more than 40 nematocysts were measured are indicated in parentheses; n = number of nematocysts measured, N = ratio between number of individuals containing a type of nematocyst and number of individuals investigated. Basitrich 1 is illustrated in Fig. 4A; basitrich 2 in Fig. 4D, E; basitrich 3 in Fig. 4B, C; basitrich 4 in Fig. 4H.

		Megalactis comatus			*M. hemprichii*		
Species Tissue	Cnidae type	n	N	Range length × range width (μm)	n	N	Range length × range width (μm)
Acrospheres	Basitrich 1	2973	10/10	34.56–78.83 × 2.47–4.98 (58.0 × 3.8)	93	2/2	53.5–76.8 × 2.8–4.7 (67.8 × 3.5)
	Basitrich 3	36	6/6	42.44–70.69 × 3.93–10.41	2	2/2	76.3–81.7 × 4.8–5.4
	Spirocyst	60	6/6	18–31.22 × 2.28–3.80	20	2/2	18.8–25 × 2–2.8
Oral face tentacle	Basitrich 2	82	5/5	16.77–25.21 × 1.61–3.83	20	2/2	16.6–23.2 × 2.4–3.2
Actinopharynx	Basitrich 1	147	5/5	27.58–55.62 × 2.4–5.4	104	2/2	27.0–44.2 × 2.3–3.8
	Basitrich 2	0	0/5		54	2/2	17.6–26.3 × 2.2–3.5
	Basitrich 3	5	1/5	31.26–33.1 × 4.17–7.59	0	0/2	
Filaments	Basitrich 1	300	7/7	32.31–63.63 × 2.6–5.12	116	2/2	33.8–72.8 × 2.6–4.2
	Basitrich 2	63	5/7	17.91–31.97 × 2.24–4.35	54	2/2	18.8–26.1 × 2.2–3.2
	Basitrich 3	12	3/7	37.67–59.22 × 4.57–8.14	1	1/1	54.0 × 5.2
	Basitrich 4	0	0/7		1	1/1	over 150 × 15
	Spirocyst	41	4/7	23.24–39.54 × 2.63–4.05	10	1/1	18.4–27.0 × 1.9–3.8
Distal column	Basitrich 2	203	7/7	15.23–48.16 × 2.41–5.07	37	2/2	17.0–27.45 × 2.2–4.0
Middle column	Basitrich 2	435	10/10	23.07–42.96 × 2.63–5.54 (34.8 × 3.7)	103	2/2	21.9–30.0 × 2.5–4.51 (26.4 × 3.2)
	Basitrich 3	10	3/10	29.91–40.34 × 4.39–9.50	0	0/2	
Proximal column	Basitrich 2	127	5/5	15.96–40.24 × 2.6–4.52	23	2/2	22.2–30.3 × 2.6–4.4

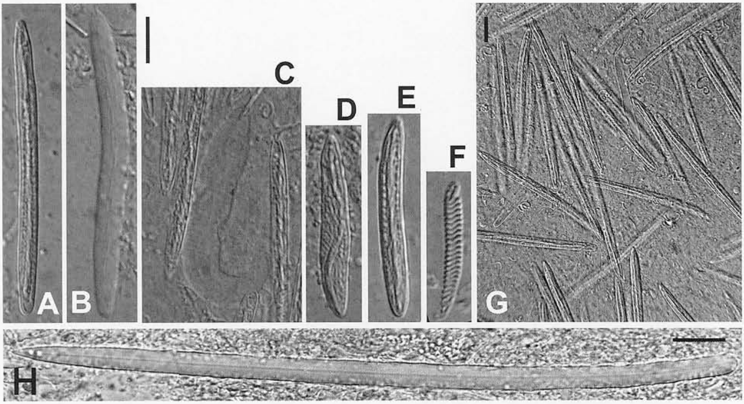

Fig. 4. Cnidae. Basitrichs of acrospheres (A, B), and middle column (C, D, E). Spirocyst (F). Image of a squash preparation from an acrosphere showing numerous basitrichs (G). Long basitrich (H) from filaments of *M. hemprichii* (TAUI 21560). Scale bars = 10 μm.

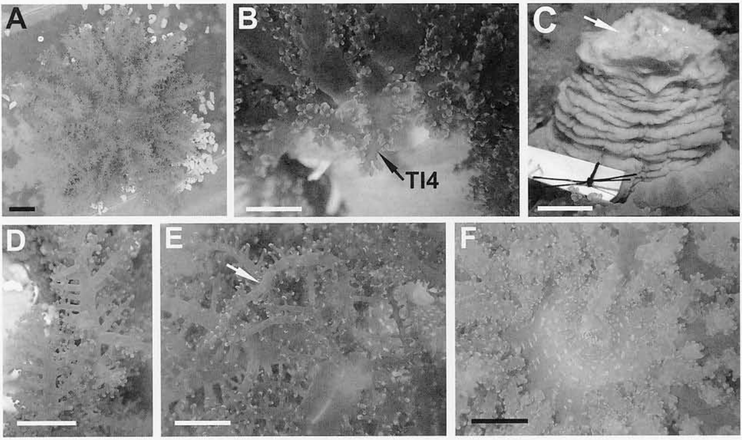

Fig. 5. *Megalactis comatus,* external morphology. A, Crown of tentacles, oral view of entire animal. B, Tentacles of the fourth cycle oriented toward substrate. C, Column in a preserved specimen. Arrow indicates deep ripples in the pedal disc region. D, Secondary branches in bipinnate arrangement. E, Long proximal secondary branches (arrow). F, Oral disc. Scale bars = 10 mm.

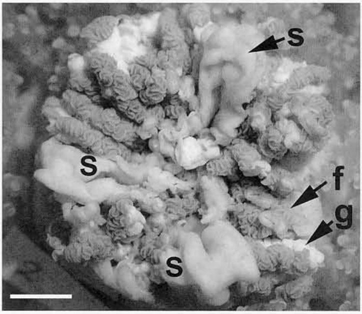

Fig. 6. *Megalactis comatus,* internal anatomy of a specimen with three siphonoglyphs (KUNHM 1664); transverse view. Abbreviations: f, filaments; g, gametogenic tissue; s, siphonoglyphs. Scale bar = 5 mm.

in three cycles (6 + 6 + 12); first two cycles usually perfect. Stomata not seen. Retractor muscles diffuse and strong (Fig. 7A–C). Filaments absent on mesenteries proximally. Parietobasilar and basilar muscles not seen.

Gonochoric: Mesenteries in male specimens have nodes filled with spermatic packets. Each spermatic node formed through plications of mesentery along oral-aboral axis; node digitiform, closed on one side of mesentery and open on the other (Fig. 8). The only female specimen found had ova in arrangement typical of Actiniaria.

Cnidae: Largest and densest basitrichs in acrospheres (Fig. 4G). Cnidom: spirocysts and basitrichs (Fig. 4). Measurements in Table 2.

Type specimens and locality.—Holotype KUNHM 1663, Pacific Ocean, Taiwan, Henchun Peninsula, Nanwan, power plant water intake basin, 21°57.27′N 120°45.22′E. See Table 1 for paratype and voucher specimens.

Etymology.—The epithet *comatus,* which means "with long hair, shaggy" in Latin (Brown 1978), refers to the hairy and irregular aspect of the tentacle crown in this species.

Natural history.—Animals live in symbiosis with zooxanthellae. We found specimens of *M. comatus* in water a few centimeters to 4 m deep. Each specimen of *M. comatus* attaches to a coral skeleton with its pedal disc and proximal part of the column. The color, similar to that of brown and red algae, and shaggy aspect of the tentacle crown make specimens difficult to find even when abundant.

The water intake basin of the nuclear power plant from which the type specimens were collected was 18 years old at the time. It was inhabited by a large number of specimens of *M. comatus* and other species of sea anemones tentatively identified as *Boloceroides mcmurrichi* (Kwietniewski, 1898), *Thalassianthus* sp., and a species of family Actiniidae. The initially large population of *M. comatus* had decreased in the previous decade (Dr. Keryea Soong, National Sun Yat-sen University, Kaohsiung, Taiwan, and Oscar Chen, pers. comm.), and has been replaced by the actiniid.

One of us (A.A.) found in nature specimens of *M. comatus* that appeared to be undergoing transverse fission; several specimens had their columns strongly constricted. One specimen, KUNHM 1667, lacks a pedal disc, having a circular opening into the gastrovascular cavity (Fig. 9A, B); specimens KUNHM 1670 and KUNHM 1251 are sacciform, lack tentacles, and have a small opening rather than an oral disc (Fig. 9C), or have small undeveloped tentacles (Fig. 9D). Specimens of *M. comatus* are easy to collect, so it is not likely that the pedal or oral disc of a specimen was torn off during collection as can happen in other sea anemones that attach or are deeply buried in the substrate. Further observations in aquaria should be made to confirm transverse fission.

Some sectioned individuals of *M. comatus,* including males and infertile individuals, had blastulae among their mesenteries (Fig. 10). These larvae contained syncitial blastoderm (solid blastula or stereoblastula in Fautin et al. 1992) and were similar to

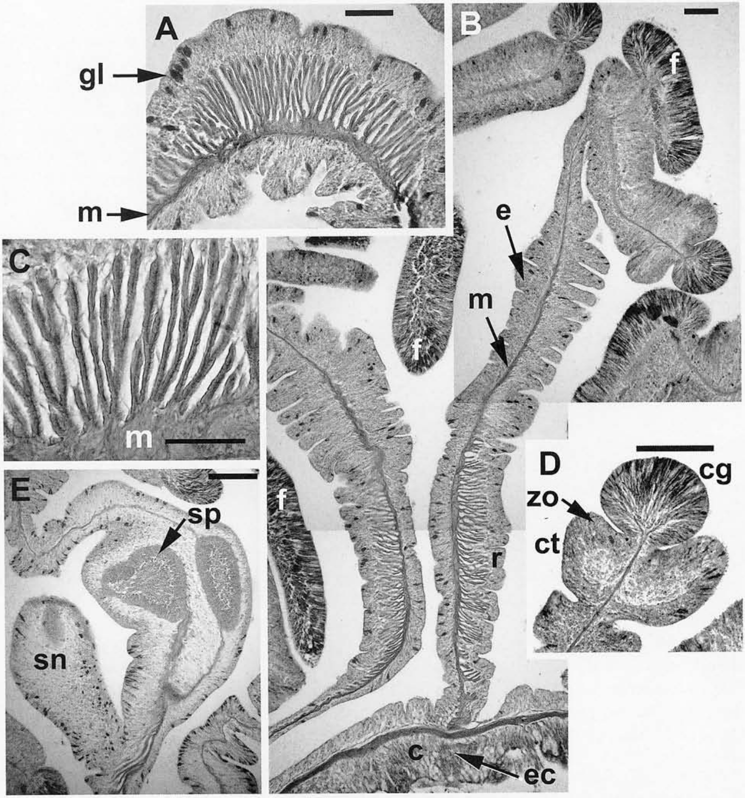

Fig. 7. *Megalactis comatus,* histology. A, Retractor muscle. B, Mesenteries. C, Detail of retractor muscle. D, Detail of mesenterial filament. E, Male gonads with the beginning of spermatic node. Abbreviations: c, column; cg, cnido-glandular tract; ct, ciliated tract; e, endoderm; ec, ectoderm; f, filament; gl, glandular cells; m, mesoglea; sn, spermatic node; sp, spermatic packet; zo, zooxanthellae. Scale bars: A, B, D, E = 100 μm; C = 50 μm.

those depicted in Yanagi et al. (1999). A.A. also found larvae in an individual lacking tentacles presumably because of transverse fission. Some larvae showed incipient blastopores, indicating an early gastrula stage (Fig. 10B, C). In some larvae, the outer layer contained nematocysts at regular intervals (Fig. 10D, E). Juvenile stages were not found in histological sections.

Discussion

Systematics.—Type specimens of *Megalactis hemprichii* have not been found

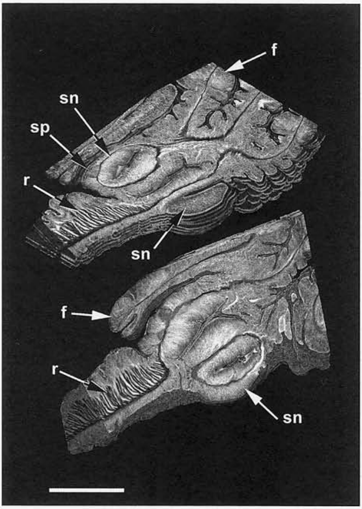

Fig. 8. Three-dimensional reconstruction of spermatic nodes in mesenteries of *M. comatus* from 20 serial slices each 9 μm thick. Abbreviations: f, filament; r, retractor muscle; sp, spermatic packet; sn, spermatic node. Scale bar = 0.5 mm.

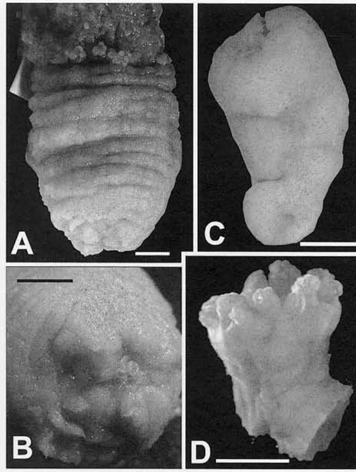

Fig. 9. *Megalactis comatus,* transverse fission. A, B, Column without pedal disc KUNHM 1667. C, Specimen without oral disc (KUNHM 1670). D, Specimen with short tentacles (KUNHM 1668). Scale bars = 5 mm.

(Klunzinger 1877, Fautin 2004 Hexacorallians of the World: http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm). To typify the genus, we designate a neotype for *M. hemprichii.* Specimens of *M. hemprichii* from the type locality of Ras Kafil in the Red Sea bordering Sinai (now part of Egypt) were unavailable and collection in this region is not feasible. We designate as neotype specimen TAUI 31623 from the Gulf of Aqaba in the Red Sea, a locality "as near as practicable from the original type locality" (Art. 75.3.6, International Commission of Zoological Nomenclature 1999).

Because of poor descriptions and complex morphology of the tentacles, species of *Megalactis* are difficult to distinguish from each other. Ehrenberg's (1834) description of *M. hemprichii* includes a very brief Latin description and no illustration. The only illustration for *M. hemprichii* in Klunzinger (1877) is based on drawings left by Ehrenberg. Subsequent references to *M. hemprichii* are translations of the original description (Milne-Edwards 1857, Andres 1883, Delage & Hérouard 1901) and a distribution record (Fishelson 1970). The specimen identified as *M. hemprichii* depicted in figure 2A of Cutress & Arneson (1987) has secondary branches not bipinnately disposed, and therefore is probably a specimen of *Actinodendron.*

Differences and similarities between the species of *Megalactis* are presented in Table 3. Type specimens of all the species described by Saville-Kent (1893), if they existed, have not been located (Fautin 2004 Hexacorallians of the World: http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm). The photograph and description of the color pattern of the oral disc in *M. griffithsi*

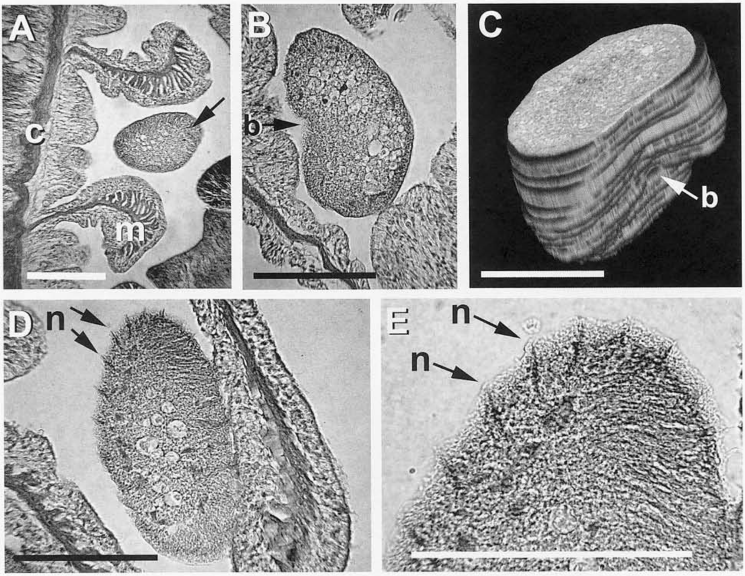

Fig. 10. *Megalactis comatus,* asexual larvae. A. Larva (arrow) among mesenteries. B. Late blastula (arrow). C. Three-dimensional reconstruction of a larva from 17 serial slides each 9 μm thick. D, E. Larva with nematocysts. Abbreviations: b, blastopore; c, column wall; m, mesentery; n, nematocyst. Scale bars = 0.25 mm.

Saville-Kent, 1893, can be used to identify specimens and distinguish this species from *M. comatus.*

Haddon (1898) used the shape of acrospheres to distinguish *M. griffithsi* from *M. hemprichii*: clubbed for *M. hemprichii* and pointed for *M. griffithsi.* The shape of acrospheres cannot be used as a diagnostic character in either living or preserved specimens of *Megalactis* because it is influenced by behavior and preservation. It is common to find a museum specimen that has acrospheres of both shapes.

Nematocysts from the acrospheres and middle column differ in size between specimens of *M. comatus* and *M. griffithsi.* The ratio between length and width of nematocysts shows a clear difference between the two species (Fig. 11). Three specimens of *M. hemprichii* from the Red Sea have a similar gross morphology to specimens of *M. griffithsi* but the nematocysts of the acrospheres have size values close to those of *M. comatus.* The nematocysts in the middle column of *M. comatus* are larger than those in *M. hemprichii.*

The number of tentacles for all species of *Megalactis* is given as 10+10 for *M. hemprichii* by Ehrenberg (1834), Milne-Edwards (1857), Andres (1883), Delage & Hérouard (1901), and Klunzinger (1877) and 6+6+12 for *M. griffithsi* by Saville-Kent (1893) and Haddon (1898). We agree with Haddon (1898) that the number of tentacles indicated by Ehrenberg (1834) for *M. hemprichii* might be an individual peculiarity. One of the three specimens of *M. hemprichii* studied (TAUI 7812) had only 41

Table 3.—Diagnostic characters of species of *Megalactis*. ? = missing data.

Species/character	*M. comatus*	*M. griffithsi*	*M. hemprichii* original description	*M. hemprichii* neotype
Tentacle crown aspect	Irregular, shaggy	Regular	Regular	Regular
Secondary branches	Elongated, usually constricted proximally	Relatively short, constricted proximally	?, may be constricted proximally	Relatively short, usually constricted proximally
Number secondary branches	Up to 48	Up to 35	?	Up to 45
Proximal secondary branches	Long to very long	Short	?	Short
Distal secondary branches	Present	Present	?	Present
Oral disc pattern of live specimens	Rows of white spots	Complex pattern of radiating lines and alternating dark and white regions	?	No pattern
Color of live specimens	Oral disc and tentacles pink to brown; column white, beige	Oral disc and tentacles brown or green; column beige	Oral disc brick red and gray; tentacles pale pink; column white	Light brown

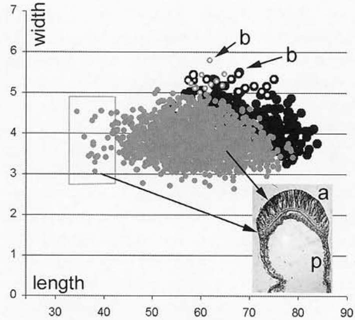

Fig. 11. Length in μm of basitrichs from acrospheres of *M. comatus* (gray dots) and *M. griffithsi* (black dots). In the region delimited by the rectangle are measurements of nematocysts from the region where acrosphere (a) meets peduncle (p); open circles represent basitrichs type 2 (see Fig. 4B).

tentacles, all of which showed signs of regeneration—lacking secondary branches, or having branches not bipinnately arranged (Fig. 2C). It is possible that *M. hemprichii* has predators that feed on its tentacles. We infer that in both previously described species of *Megalactis,* the fourth cycle of tentacles was overlooked, being probably considered secondary branches on the adjacent tentacles. In situ, members of Actinodendridae usually orient the tentacles of the fourth cycle towards the substrate. All specimens of actinodendrids studied, including those belonging to *Megalactis,* had a typical tentacle arrangement in multiples of six (6 + 6 + 12 + 24).

Because we did not find basilar muscles in specimens of *Actinodendron plumosum* Haddon, 1898, *A. glomeratum* Haddon, 1898, *Megalactis griffithsii* Saville-Kent, 1893, and *M. comatus,* the position of family Actinodendridae among Thenaria as defined by Carlgren (1899, 1900, 1942, 1949) is questionable. It is possible that basilar muscles are reduced in size or have been lost in the family Actinodendridae; basilar muscles are reduced or absent in many burrowing sea anemones (Carlgren 1949, Daly et al. 2002). Basilar muscles are absent in the thenarian family Aliciidae. Another explanation may be that the basilar muscles were not present in the ancestral lineage of Actinodendridae and this family does not belong to Thenaria.

Spermatic nodes.—We report for the first time spermatic nodes in Actiniaria. Hyman (1940, p. 583) stated that generally the gametogenic tissues in actiniarians "occur as thickened bands on the septa behind the septal filaments." Atypical organization of gametogenic tissue is reported in the hexacorallian groups Actiniaria (Excoffon & Zamponi 1999), Zoanthidea (Ryland 2000), and Scleractinia (Harrison & Wallace 1990). The most similar structure to spermatic nodes in *M. comatus* are the "gonadal nodes" reported by Ryland (2000) that are lens-shaped folds in the perfect mesenteries of females of the zoanthid *Parazoanthus anguicomus* and of a male of *P. axinellae.* Spermatophores were described by Excoffon & Zamponi (1999) in the sea anemone *Sagartia troglodytes.* The spermatic nodes in *M. comatus* are not stalked like the spermatophores in *S. troglodytes* but have a three-dimensional structure more developed than a simple fold of the mesentery like the "gonadal nodes" reported by Ryland (2000). Excoffon & Zamponi (1999) reported that spermatozoa in *S. troglodytes* were released from spermatophores through the stalk, the region by which the spermatophores are attached to the mesenteries, and the mesogleal wall of the spermatophores is continuous with that of adjacent mesentery. Thus, like spermatic nodes, spermatophores must develop from folds of mesenteries through evagination. We agree with Ryland (2000) that one function of the "gonadal nodes" is to increase the number of "gonadal packets" with no increase in length of body.

Asexual larvae.—The origin of larvae found in the coelenteron of some sea anemones is uncertain (Fautin 2002). Chia & Rostron (1970) assumed that the larvae inside *Actinia equina* (Linnaeus, 1758) were sexually produced, but Carter & Thorp (1979) found this to be unlikely because the phenotypes were identical between a brood and the adult host. In fungiid corals, any tissue fragment in the coelenteron is able to transform into a larva (Kramarsky-Winter & Loya 1996). Because one of us (A. A.) found blastulae in immature and male individuals of *M. comatus,* they are considered to be of asexual origin.

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