

Redescription and range extension of the sea anemone *Exocoelactis actinostoloides* (Wassilieff, 1908), with revision of genus *Exocoelactis* (Cnidaria, Anthozoa, Actiniaria)

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ABSTRACT

Among specimens of sea anemones collected from the tropical western Pacific on cruises under the auspices of the Institut de Recherche pour le Développement (IRD) and the Muséum national d'Histoire naturelle, Paris, are some we identify as *Exocoelactis actinostoloides* (Wassilieff, 1908). We synonymize under this name the species described as *Cymbactis maxima* Wassilieff, 1908, and *Exocoelactis valdiviae* Carlgren, 1928. The first two were described from one specimen each, collected at unspecified depths of Sagami Bay, Japan; the latter was based on five specimens reportedly collected off the coast of East Africa at depths of 741 to 823 m. We examined 23 specimens collected in New Caledonia, the Philippines, and Palau from depths of 175 to 480 m. Thus, we extend the geographical and bathymetric range of this species. These specimens allowed us to resolve discrepancies in the definition of the genus *Exocoelactis* concerning completeness and sterility of the mesenteries: the stronger partner of the mesenterial pairs *may* be complete and *may* be sterile.

KEY WORDS

Cnidaria,
Anthozoa,
Actiniaria,
Exocoelactiidae,
New Caledonia,
Philippines,
East Africa,
deep-sea,
redescription.

RÉSUMÉ

Redescription et augmentation de l'aire de l'actinie Exocoelactis actinostoloides (Wassilieff, 1908), avec révision du genre Exocoelactis (Cnidaria, Anthozoa, Actiniaria).

Parmi les Anémones de mer récoltées dans le Pacifique ouest tropical au cours de missions réalisées par l'Institut de Recherche pour le Développement (IRD) et le Muséum national d'Histoire naturelle, se trouvent des spécimens que nous identifions comme *Exocoelactis actinostoloides* (Wassilieff, 1908). Nous considérons que *Cymbactis maxima* Wassilieff, 1908 et *Exocoelactis valdiviae* Carlgren, 1928 sont des synonymes plus récents. Les deux premières espèces ont été chacune décrites à partir d'un seul spécimen, collectés à des profondeurs non spécifiées dans la Baie de Sagami au Japon ; la dernière est basée sur cinq spécimens récoltés au large des côtes d'Afrique de l'Est à des profondeurs de 741 à 823 m. Nous avons examiné 23 spécimens récoltés en Nouvelle-Calédonie, aux Philippines et à Palau à des profondeurs de 175 à 480 m. Nous étendons donc l'aire géographique et bathymétrique de cette espèce. Ces spécimens nous ont permis de résoudre des contradictions dans la définition du genre *Exocoelactis* concernant le caractère complet et la stérilité des mésentères : le partenaire le plus important de la paire de mésentères *peut* être complet et *peut* être stérile.

MOTS CLÉS

Cnidaria,
Anthozoa,
Actiniaria,
Exocoelactiidae,
Nouvelle-Calédonie,
Philippines,
Afrique de l'Est,
mer profonde,
redescription.

INTRODUCTION

We examined 23 specimens of a distinctive species of bathyal sea anemone (Fig. 1) collected since 1985 from depths of 175 to 480 m (Table 1). We redescribe this species as *Exocoelactis actinostoloides*, synonymizing under that name three species, *Cymbactis actinostoloides* Wassilieff, 1908, *C. maxima* Wassilieff, 1908, and *Exocoelactis valdiviae* Carlgren, 1928. We also extend its known geographical and bathymetric ranges.

The definition of the genus *Exocoelactis* in Carlgren's (1928) description differs from that in his catalog to sea anemones of the world (Carlgren 1949): the two disagree on whether both members of unequally developed pairs of mesenteries are fertile. We revise the definition of the genus *Exocoelactis* to resolve that issue – they may but need not be. Typically, the mesentery of a sea anemone is perforated by a marginal and an oral stoma (Stephenson 1928). The center of some complete mesenteries of *E. actinostoloides* is perforated by a stoma; this “central stoma” appears to be an oral stoma that is in an atypical position.

ABBREVIATIONS

- CAS California Academy of Sciences, San Francisco, California;
- KUNHM Kansas University Natural History Museum, Lawrence, Kansas;
- MNHN Muséum national d'Histoire naturelle, Paris;
- MNK Museum für Naturkunde der Humboldt Universität, Berlin;
- NHM Natural History Museum, London;
- SBNHM Santa Barbara Natural History Museum, Santa Barbara, California;
- SMNH Swedish Museum of Natural History, Stockholm;
- USNM United States National Museum of Natural History, Washington D.C.;
- ZMUC Zoological Museum, University of Copenhagen;
- ZSM Zoologische Staatssammlung, München.

MATERIAL AND METHODS

Of 23 recently-collected specimens of *Exocoelactis actinostoloides* we examined, 22 were collected under the auspices of IRD and MNHN between May 1985 and March 1990; one from the Coral Reef Research Foundation (CRRF) was collected

TABLE 1. — Specimens of *Exocoelactis actinostoloides* (Wassilieff, 1908) examined.

Catalog #	Cruise	Station	Location	Coordinates	Depth (in m)	Specimens
CAS 146035	AZTEQUE	CH 04	Southeast New Caledonia	23°42'S, 168°01'E	235-400	1
MNHN 1454	CHALCAL 2	CH 03	South New Caledonia	24°48'S, 168°09'E	257	1
MNHN 2346	MUSORSTOM 4	CP 213	"	22°51'S, 167°12'E	405-430	1
MNHN 2348	"	CP 214	"	22°54'S, 167°14'E	425-440	1
KUNHM 01266	SMIB 6	DW 113	"	19°03'S, 163°30'E	250	1
KUNHM 01267	"	"	"	"	"	1
MNHN 2317	MUSORSTOM 4	DW 185	North New Caledonia	19°06'S, 163°29'E	235	1
MNHN 2306	"	CC 173	"	19°02'S, 163°19'E	250-290	2
MNHN 2311	"	CP 179	"	18°57'S, 163°14'E	480	1
MNHN 2299	"	CP 171	"	18°58'S, 163°14'E	435	2
MNHN 2304	"	CP 172	"	19°01'S, 163°16'E	275-330	1
MNHN 2305	"	"	"	"	"	1
MNHN 2316	"	DW 184	"	19°04'S, 163°27'E	260	1
SBNHM 345504	"	DW 184	"	"	"	1
None	BATHUS 2	CP 737	New Caledonia	23°03'S, 167°00'E	350-400	1
USNM 100866	CALSUB	PL 121	Loyalty Islands Basin	22°45'S, 167°09'E	330-344	1
MNHN 1481	MUSORSTOM 5	CP 332	Chesterfield Islands	20°17'S, 158°49'E	400	1
None	CRRF	MUTR	Koror, Palau	7°16.269'S, 134°31.370'E	239	1
USNM 100867	MUSORSTOM 3	CP 98	Philippines	14°00'S, 120°18'E	194-205	1
MNHN 2249	"	CP 100	"	14°00'S, 120°17.6'E	175-184	1
MNHN 2238	"	CP 87	"	14°01'S, 120°20'E	191-197	1

in March 2001 (Table 1). Those from MNHN were preserved in 70% ethanol; that from CRRF was preserved in formalin. Portions of six specimens were embedded in Paraplast (melting point 56°C); 8 µm longitudinal and transverse histological sections were stained with hematoxylin and eosin. We studied gross anatomy of all the specimens. DGF also examined the holotypes (the only known specimens) of *Cymbactis actinostoloides* and *C. maxima* in ZSM, and two of the five syntypes of *Exocoelactis valdiviae* (MNK 7173 and SMNH 3976).

Cnidae measured in squash preparations at 1000X were from 10 specimens of *Exocoelactis actinostoloides* and the holotypes of *Cymbactis actinostoloides* and *C. maxima*. Measurements of cnidae from the acrospheres and stalks of inner and outer tentacles were recorded separately, but, because there were no differences among them, the data were combined.

SYSTEMATICS

Family EXOCOELACTIIDAE Carlgren, 1928

DEFINITION. — "Thenaria (Mesomyaria) with irregular arrangement of tentacles in connection with the bilateral development of the younger mesenteries. After the stage with 12 pairs of mesenteries the later mesenteries arise bilaterally in each sector of the animal, so that the youngest mesenteries appear in the middle of the secondary exocoels. In each pair of the younger mesenteries one mesentery is larger than its partner" (Carlgren 1949: 85).

The only genus currently placed in the family is *Exocoelactis* (Carlgren 1949).

Genus *Exocoelactis* Carlgren, 1925

TYPE SPECIES. — *Polysiphonia tuberosa* Hertwig, 1882, which was collected on the *Challenger* Expedition; 19 syntypes are in NHM (catalog #1889.11.25.15) and one is in SMNH (catalog #1181) (Fautin 2001).



FIG. 1. — *Exocoelactis actinostoloides* (Wassilieff, 1908), in life, photograph courtesy of CRRF.

Hertwig published his findings from the *Challenger* twice; the German-language version (Hertwig 1882b) has priority over the English-language version (Hertwig 1882a) (Fautin 2001). The other species included by Carlgren (1949) in the genus was described as *Exocoelactis valdiviae* by Carlgren (1928). Carlgren (1925) renamed *Exocoelactis* because a sponge preoccupied the name *Polysiphonia*.

DEFINITION. — Exocoelactiidae with well-developed base. Column smooth or somewhat nodular, thick-walled, and vase-shaped. Sphincter mesogleal, weak, so upper part of column cannot cover the tentacles. Margin tentaculate. Tentacles short to moderately long, in some species some thickened on outer side at the base. At least the 12 first tentacles, and sometimes at least some of those of third cycle, typically arranged; the other tentacles set in two rows, forming triangular groups continuous with one another. Inner tentacles the largest; tentacles decrease in size toward margin. Outermost tentacles communicate with exocoels, inner ones with endocoels. Longitudinal muscles of tentacles and radial muscles of oral disc mesogleal. Two broad siphonoglyphs and two pairs of directive mesenteries. Mesenteries of the two first cycles normally positioned, complete, and sterile. Later mesenteries arranged bilaterally, the youngest ones in the middle of the secondary exocoels. Each later pair consists of a larger and a smaller mesentery: the larger member of each pair may be complete and may be

sterile; nearly all incomplete mesenteries fertile. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

REMARKS

In the definition of *Exocoelactis* in his catalog to sea anemones of the world, referring to mesenterial arrangement, Carlgren (1949: 86) stated “the stronger partner in each of these [unequal] pairs is perfect and may be sterile, all the other mesenteries are fertile”. However, his original definition did not specify that the stronger partner is perfect (Carlgren 1928). Having found that in many unequally developed pairs, both partners are incomplete (imperfect), we revise the sentence of the definition referring to that structure. We make two other revisions to bring the definition into conformity with our experience of the animals. The tentaculate margin is not necessarily either “undulating or drawn out in 12 or more lobes”, as Carlgren (1949: 85) stated; this feature is probably due to contraction of the specimen. And the tentacle musculature is not necessarily near the endoderm. We also change the word “perfect” to “complete” (and “imperfect” to “incomplete”) to conform to current usage, make consistent the rendering of numbers, and phrase the entire definition telegraphically. We make no change to the description of tentacles in triangular fields, an arrangement that reflects the mesenterial arrangement, but this feature may not be clear in well-expanded individuals.

Exocoelactis actinostoloides (Wassilieff, 1908)
n. comb.

Cymbactis actinostoloides Wassilieff, 1908: 25-27.

Cymbactis maxima Wassilieff, 1908: 25-27.

Exocoelactis valdiviae Carlgren, 1928: 187-190.

Parascyconis actinostoloides (Wassil.) – Carlgren 1921: 208.

Parascyconis maxima (Wassil.) – Carlgren 1921: 208.

Non *Parascyconis actinostoroides* (Wassilieff, 1908) – Uchida, Okamoto & Fukuda 1975: 31.

Non *Parascyconis maxima* (Wassilieff, 1908) – Uchida, Okamoto & Fukuda 1975: 32.

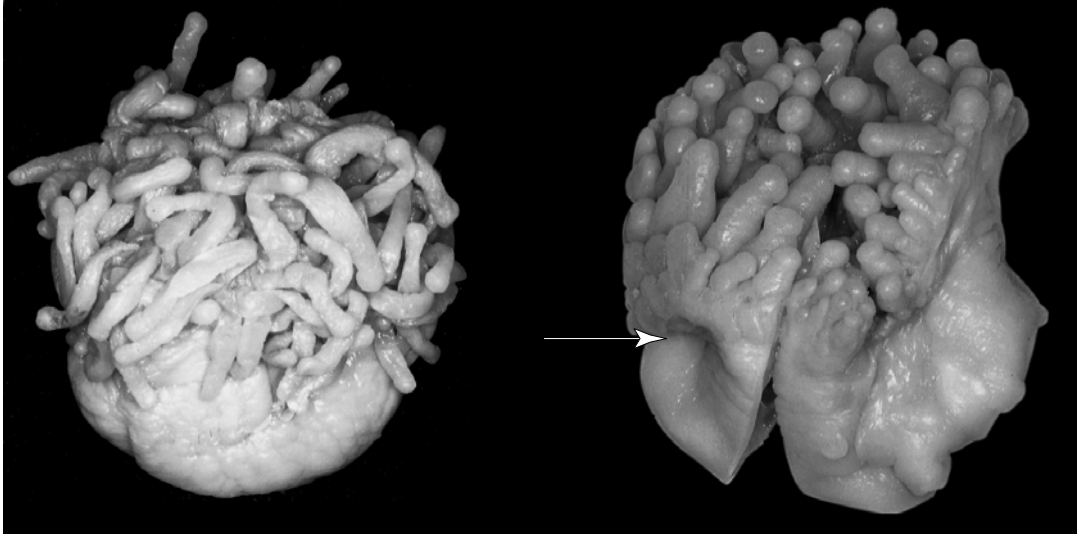


FIG. 2. — *Exocoelactis actinostoloides* (Wassilieff, 1908), the specimen at left (USNM 100867) has long tentacles, some of which are finger-like, and others that are only slightly capitate; the specimen at the right (MNHN 2304) has shorter, more robust capitate tentacles, and the characteristic circumferential crease about halfway down the vasiform column (arrow).

Non *Parascyonyx actinostoloides* (Wassilieff) – Moyer & Bell 1976: 24.

Non *Parascyonyx actinostroides* (Wassilieff) – Suzuki & Hayashi 1977: 198.

DISTRIBUTION. — *Cymbactis actinostoloides* and *C. maxima* were described by Wassilieff (1908) from one specimen each collected by Doflein “von den Ostküsten der japanischen Inseln” (Wassilieff 1908: 3); their provenance is given both in the publication and on the specimen labels (which are not original) as Sagami Bay, without indication of depth. The original description of *Exocoelactis valdiviae* Carlgren, 1928, was based on five specimens collected on the German Deep-Sea Expedition that were reported to have been collected from two stations off the coast of the Somali Peninsula, three from station 266 (741 m) and two from station 263 (823 m). Of the two specimens from station 263, one is now in MNK (catalog #7173). It is presumably the other specimen that is in SMNH (catalog #3976), but this jar contains two locality tags. One is for station 263 but the other is for station 208, located at 296 m near the Nicobar Islands in the Bay of Bengal. We infer that the label for station 208 was placed in the container in error. In addition to the description of the species not including that locality, the species is not among the sea anemones reported from station 208 (Carlgren 1928). Our extension of the species’ geographic range to New Caledonia, Palau, and Japan makes the provenance of that specimen moot – the Nicobar Islands are well within it. We also extend the bathymetric range upward to 175 m.

REDESCRIPTION

Color

Each preserved individual one color: most creamy white; others tan; few hyaline and greyish, with a purple-brown core visible through the outer layer of the tentacles. The single animal seen alive pinkish-beige with narrow radial stripes of deep mauve on oral disc (Fig. 1); rare preserved individuals with pinkish cast, especially of oral disc near margin.

Oral disc

Diameter 30 to 200 mm. Typically flat; in some individuals with many shallow, radial furrows (Wassilieff 1908: fig. 25). Tentacles densest at margin, primary tentacles about half-way between margin and mouth (Fig. 1). Some individuals have radially-aligned ovoid holes on oral disc where tentacles have been cast or plucked off. Mouth in most specimens slit-like to ovoid, in some raised on cone; maximum diameter typically 15 to 40 mm, commonly open, with actinopharynx partly everted.

Actinopharynx shallowly furrowed longitudinally; commonly white, rarely with cream, yellowish, or

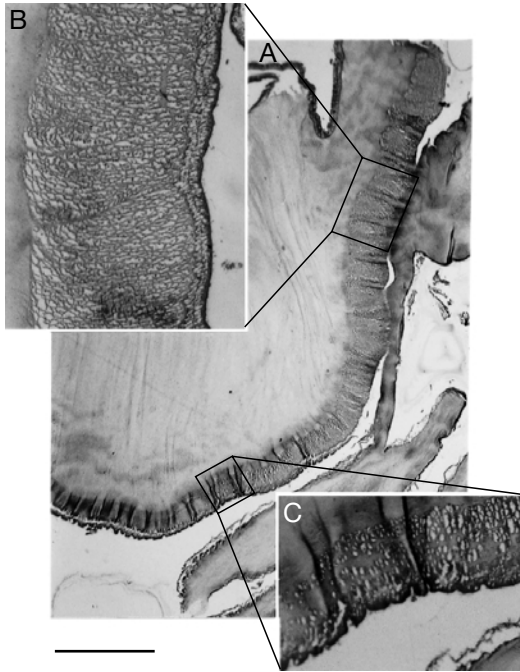


FIG. 3. — **A**, longitudinal section at margin of *Exocoelactis actinostoloides* (Wassilieff, 1908) (KUNHM 01267) illustrating the location and length of the sphincter muscle and texture of the mesoglea; note strands of mesoglea extending across sphincter muscle; **B**, close-up of sphincter muscle. Magnification is 3.9 times that of A (KUNHM 01266); **C**, proximal terminus of the sphincter. Magnification is 3.75 times that of A (KUNHM 01267). Scale bar: A, 1 mm.

mauve cast in preserved specimens. Two symmetrical, broad, white siphonoglyphs somewhat longer than rest of actinopharynx; one or two narrow brown lines run the length of some.

Tentacles

Number 85 to about 200; regularly arrayed except two individuals slightly asymmetrical, with patches of many small tentacles grouped together. Most capitate with broader base that narrows toward bulbous end (Figs 1; 2); shaft of tentacle may be shallowly wrinkled or longitudinally furrowed; some tentacles with terminal pore. In some individuals, diameter of bulb hardly or only slightly larger than diameter of tentacle immediately proximal to it; in a few, terminal bulb bifurcate (Fig. 1). Inner tentacles: diameter of base 9.0

to 20.0 mm, of distal end proximal to bulb 4.0 to 8.0 mm, of bulb 5.5 to 10.0 mm. Marginal tentacles: diameter of base 4.0 to 8.0 mm, of distal end proximal to bulb 2.0 to 6.4 mm, of bulb 2.4 to 7.0 mm. Tentacles nearest mouth longest (6 to 70 mm), 25 to 50% oral disc diameter; marginal tentacles shortest (2 to 15 mm), about 40% length of longest tentacles. Some tentacles blunt-ended, lacking prominent acrosphere; a few pointed.

Column

Vasiform; length 15 to 80 mm, as much as 50% oral disc diameter; margin indistinct. Retracted in most specimens, some with circumferential crease around part of column about halfway down (Fig. 2; Wassilieff 1908: fig. 24; Carlgren 1928: pl. XII [III], fig. 1). In most individuals, ectoderm mostly sloughed off. Mesoglea opaque; texture rubbery; that of both large and small specimens typically 2 mm thick, but twice that at proximal end of some strongly retracted specimens.

Pedal disc

Diameter 20 to 110 mm, approximately 70% oral disc diameter. Flat in some; more commonly, edges turned under as if had been wrapped around something. Many with adherent sponge spicules, but the one photographed *in situ* (Fig. 1) attached to rock. Uniform tan color, with shallow radial and concentric ridges.

Mesenteries

Very thin so difficult to count. Number about equal to that of tentacles; as many as 112 pairs in individuals studied, arranged in manner characteristic of genus, 12 pairs in each cycle from third onward. Sexes separate; yellow to orange eggs to 1 mm diameter without trophonemata. Nearly all incomplete mesenteries fertile; in a pair consisting of an incomplete and a complete member, both sterile, both fertile, or only incomplete one fertile. No marginal stomata; some with oral stomata. The center of some complete mesenteries perforated by a stoma; this “central stoma” apparently an atypically positioned oral stoma.

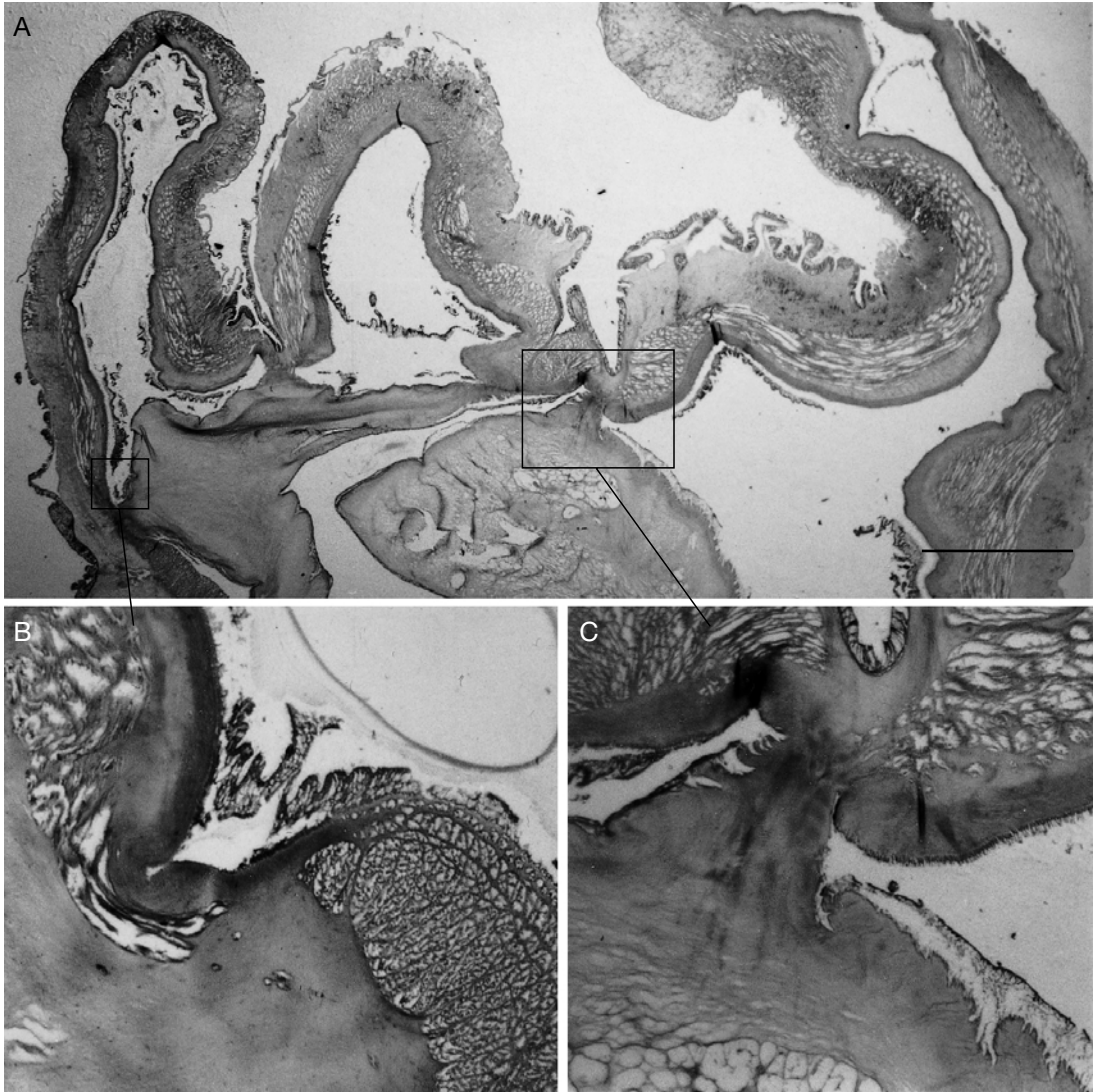


FIG. 4. — **A**, longitudinal muscles of tentacles and radial muscles of oral disc of *Exocoelactis actinostoloides* (Wassilieff, 1908), (KUNHM 01266), musculature is located in about the middle of the mesoglea; **B**, interruption between the longitudinal muscles of tentacles and the distal end of the sphincter muscle, magnification is 6.3 times that of A (KUNHM 01267); **C**, mesenterial insertion on oral disc, magnification is four times that of A (KUNHM 01266). Scale bar: A, 2 mm.

Histology

Mesogleal texture smooth with some radial striations (Fig. 3A).

Sphincter muscle mesogleal, weak; lies along endoderm; length to 20% that of column; width as much as 25% that of mesoglea (Fig. 3; Wassilieff 1908: fig. 10; Carlgren

1928: text fig. 32). Musculature mesh-like with small alveoli of uniform size and shape (Fig. 3; Wassilieff 1908: pl. VII, fig. 77); at intervals, tapering strands of mesoglea extend about 25% the distance across sphincter from ectodermal side. Proximal half tapers slightly toward proximal end, which abruptly terminates

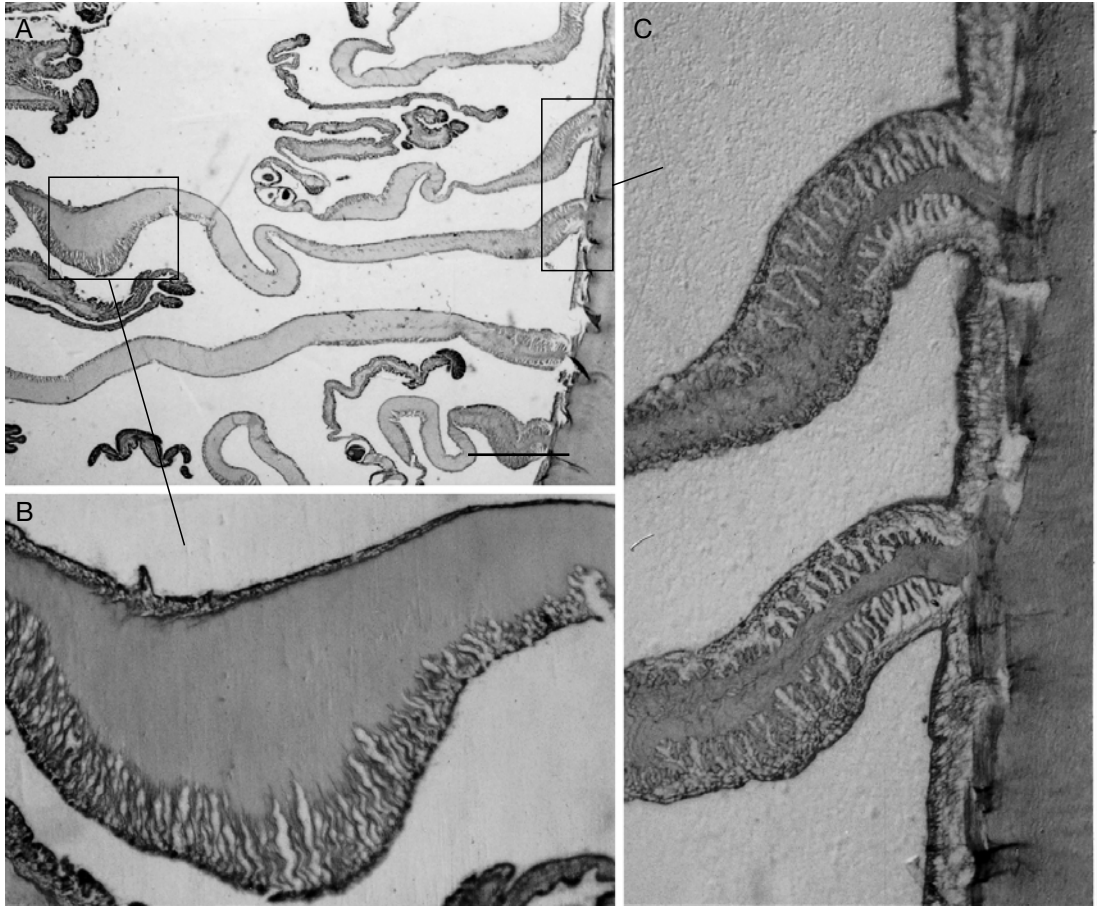


Fig. 5. — Transverse section of *Exocoelactis actinostoloides* (Wassilieff, 1908), (USNM 100866), boxed areas in A are enlarged in B and C; **B**, retractor muscle, magnification is 4.5 times that of A; **C**, parietobasilar muscles, magnification is 4.5 times that of A. Scale bar: A, 1 mm.

with few scattered alveoli (Fig. 3C; Carlgren 1928: text fig. 32). Distal half of uniform width throughout or somewhat wider at distal end, which typically terminates without tapering (Figs 3A; 4B; Carlgren 1928: text fig. 32).

Longitudinal muscle of tentacles and radial muscles of oral disc mesogleal, in approximate center of mesogleal layer but slightly nearer endodermal than ectodermal side, to 33% width of mesoglea (Fig. 4; Wassilieff 1908: fig. 11; Carlgren 1928: text fig. 33). Longitudinal musculature of tentacles discontinuous with that of sphincter (Fig. 4B); musculature an

open mesh with large alveoli (Fig. 4; Wassilieff 1908: pl. VII, figs 79, 80; Carlgren 1928: text fig. 33). Oral disc musculature interrupted at mesenterial insertions (Fig. 4C; Wassilieff 1908: pl. VII, fig. 74).

Mesenterial retractor muscles diffuse, weak (Fig. 5A, B; Wassilieff 1908: pl. VII, figs 75, 76). Parietobasilar muscles undeveloped, diffuse; without free pennon (Fig. 5A; Wassilieff 1908: pl. VII, figs 75, 76).

Cnidom

Spirocysts, basitrichs, microbasic *p*-mastigophores (Table 2; Fig. 6).

DIAGNOSIS

Exocoelactis actinostoloides is a large anemone, typically entirely tan to white in preservation. The mildly to strongly capitate tentacles are more robust than those of a corallimorpharian. Characteristically, the tentacle base and acrosphere are similar in diameter; the shaft tapers slightly to strongly; some tentacles, however, are digitiform. By contrast, each tentacle of *E. tuberosa* has a basal swelling on the aboral side; moreover, tentacles of *E. actinostoloides* are fewer, longer, and more robust. In many preserved specimens, the column, which is about as long as the radius of the oral disc, has a circumferential crease about halfway down it. The mesogleal sphincter muscle is extraordinarily long. Mesenteries of the tertiary pairs and higher order are unequally developed; some consist of a complete and an incomplete member, but they do not follow the *Actinostola* rule. Rather, the younger mesenteries are added bilaterally in the secondary exocoels, in the manner typical of the family Exocoelactiidae. Thus, in each of the 12 coelenteric spaces between a primary and a secondary pair of mesenteries, the youngest mesenteries are at the center, with pairs of successively older mesenteries flanking them.

DISCUSSION

Our synonymization of *Cymbactis actinostoloides* Wassilieff, 1908, *C. maxima* Wassilieff, 1908, and *Exocoelactis valdiviae* Carlgren, 1928 is based on morphology, histology, and size and distribution of cnidae. We used information and images from Wassilieff (1908) as well as data DGF gathered in examining the holotypes (the only known specimens) of *Cymbactis actinostoloides* and *C. maxima* (both in ZSM; they bear no catalog numbers), and data from Carlgren (1928) for *Exocoelactis valdiviae*. Having examined more specimens than did either Wassilieff or Carlgren, we are able to distinguish features that are peculiar to a specimen from those that are typical of the species. Acting as

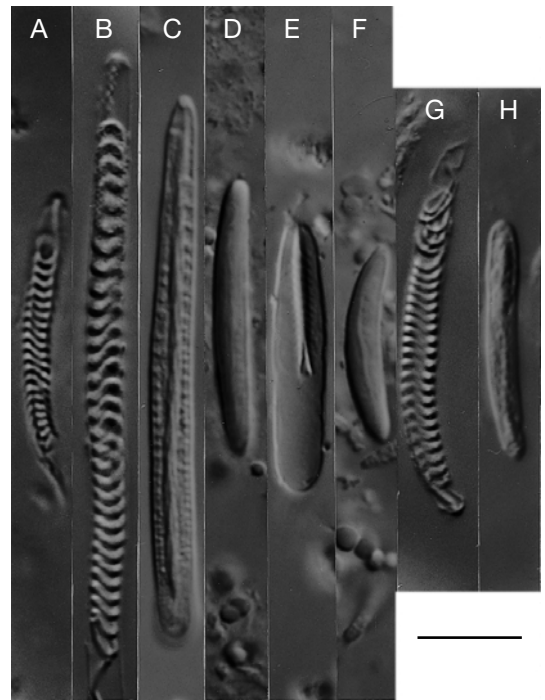


FIG. 6. — Types of cnidae; see Table 2 for explanation. Scale bar: 10 μ m.

First Revisers (Code Art. 24.2), we here give the name *Cymbactis actinostoloides* precedence over the name *C. maxima*.

The holotypes of *Cymbactis actinostoloides* and *C. maxima* are strikingly similar in size and appearance to one another and to recently-collected specimens we studied, given that the former had been compressed (Wassilieff 1908; DGF personal observation). The oral disc of the holotype of *C. maxima* is 10 mm wider than in any other specimen we examined, and the tentacles are correspondingly longer; some tentacles are missing, leaving characteristic holes. The holotype of *C. actinostoloides* has a typical constriction at mid-column (Wassilieff 1908: fig. 24), but lacks the dark stripes on the actinopharynx remarked on by Wassilieff (1908: 25) and that we observed in the siphonoglyphs of some specimens. The resemblance in cnidae is obvious from Table 2: the major difference is that small basitrichs were recorded in the tentacles of

TABLE 2. — Size and distribution of cnidae in *Exocoelactis actinostoloides*, the holotype of *Cymbactis maxima*, and the holotype of *Cymbactis actinostoloides*. Column cnidae were not measured in type specimens. “#” is the number of capsules measured; measurements in parentheses are of single capsules that fell outside the typical range; length and width are in μm . “Proportion” is the ratio of individuals in which a particular type of cnida was found relative to all those in which that tissue type was examined, a parameter irrelevant for data from holotypes. The letter following each type refers to the illustration of it in Fig. 6.

Tissue Type of cnida	<i>Exocoelactis actinostoloides</i> Range of length × width	#	Proportion	<i>Cymbactis maxima</i> Range of length × width	#	<i>Cymbactis actinostoloides</i> Range of length × width	#
Tentacles							
Gracile spirocysts (A)	24.0-45.0 × 2.0-3.0	26	4/6	31.2-53.0 × 2.3-3.1	38	28.1-40.6 × 2.3-3.1	20
Robust spirocysts (B)	(38.0) 45.0-76.0 × 2.2-4.0	49	5/6	51.5-78.0 × 2.9-3.9	46	(40.6) 43.7-60.8 × 3.1-4.7	33
Basitrichs (C)	34.0-60.0 × 2.5-4.0 (generally larger in larger individuals)	82	6/6	21.8-56.2 × 2.3-3.1	75	25.0-39.0 × 2.3-3.1 14.8-20.3 × 2.3	35 3
Actinopharynx Basitrichs (D)	(19.0) 25.4-43.8 × 2.5-5.0	100	8/8	(25.0) 29.6-49.9 (56.2) × 2.3-3.3	25	(21.8) 25.0-34.3 × 2.9-3.1	16
Microbasic <i>p</i> -mastigophores (E)	25.0-41.5 × 4.0-5.2	34	6/8	23.4-28.1 × 3.9-6.2	13	26.5-29.6 × 3.9-4.7	10
Mesenterial filaments							
Small basitrichs (F)	(12.2) 16.9-27.0 × (1.9) 2.2-3.8	62	6/7	21.1-25.0 × 2.3-3.1	13	14.8-19.5 × 1.8-2.9	10
Large basitrichs (C)	26.0-55.0 (59.0) × 2.0-4.0	30	5/7	34.3-46.8 × 2.9-3.1	3	None	
Microbasic <i>p</i> -mastigophores (E)	19.1-39.3 × 3.1-7.3	143	7/7	25.0-27.3 × 4.5-4.7	3	25.0-31.2 × 4.5-4.9	11
Column							
Spirocysts (G)	17.9-101.9 (113.2) × (2.0) 2.5-5.7	25	5/5				
Small basitrichs (H)	20.1-29.5 × 2.3-4.8 (6.1) (larger in larger individuals)	51	5/5				
Large basitrichs (C)	(43.6) 48.3-75.9 (89.2) × (2.6) 3.7-6.7 (7.1) (only in large individuals)	32	2/5				

C. actinostoloides, but only three could be found in a search that produced 35 of the larger ones. We infer from this that the small basitrichs were contaminants, or so rare that their occurrence is not taxonomically significant (Fautin 1988). Wassilieff (1908) provided data for aspects of *C. actinostoloides* that he did not for *C. maxima* and *vice versa*, so it is difficult to understand why he considered them not to belong to the same species. He did remark on the size difference (which is also reflected in his choice of names) and that the tentacle tips of *C. actinostoloides* were perforated but those of *C. maxima* were not (this

feature varies even within an individual), but the only explicit comparison was the position of the tentacle musculature, a feature that can appear to vary with angle of section or state of contraction. Wassilieff (1908) was doubtful about the generic assignment of the species he described as *C. actinostoloides* and *C. maxima*, but was unwilling to describe a new genus on the basis of two poorly-preserved specimens. He thought they strongly resembled members of Actinostolidae except the mesentery pairs did not consist of partners of unequal size, which at the time, or at least according to the understanding of Wassilieff, was

requisite for members of the family. Wassilieff's ambivalence is reflected in his choice of name for the smaller specimen: "Wegen der grossen Ähnlichkeit mit den Actinostoliden benenne ich das Tier *Cymbactis actinostoloides*" (1908: 27), *Cymbactis* at that time being placed in Paractidae. Wassilieff expressed the sentiment that later the definition of Actinostolidae might be broadened to include animals in which all mesentery pairs consist of partners of equal size. That is now the case (Carlgren 1949), and the genus *Cymbactis* was moved to it. Ironically, though, contrary to Wassilieff's assertion, the partners of a pair of higher-order mesenteries in the animals he studied are unequally developed, but the pattern of mesentery insertion precludes placing them in Actinostolidae.

In his analysis of mesentery development, Grebelny'i (1982) recognized a fundamental difference in ontogeny of actinostolids and members of the genus *Exocoelactis*. In the former, as in typical sea anemones, the number of mesenteries doubles incrementally through ontogeny because each "meristematic zone" – that region in which mesenteries are added – splits into two with the development of each cycle of mesenteries so that there is such a zone between the members of each pair of new mesenteries and the members of the pair on either side. In *Exocoelactis*, "meristematic zones" are confined to the regions between primary and secondary mesenteries, so their number never increases beyond 12, and therefore 12 pairs of new mesenteries are added in each cycle from the third onward.

The generic name *Cymbactis* was created by McMurrich (1893) for the species *C. faeculenta*, which Carlgren (1949) questionably placed in genus *Paractinostola*; the genus *Paractinostola* was created by Carlgren (1928) for a new species, *Paractinostola bulbosa*. If the species originally named *C. faeculenta* truly belongs to the same genus as *Paractinostola bulbosa*, the correct generic name is *Cymbactis*. Despite some superficial similarities to *C. faeculenta*, the nominal species *C. actinostoloides* and *C. maxima* clearly belong in a different genus on the basis of mesenterial arrangement: *Cymbactis* and

Paractinostola belong to family Actinostolidae (Carlgren 1949).

In 1921, Carlgren created the genus *Parasicyonis* for the new species *Parasicyonis sarsii*; he also assigned to that genus *C. actinostoloides* and *C. maxima*, remarking "the whole of their exterior namely recalls that of *P. sarsii*, and the imperfect description, given by Wassilieff [sic], in no way contradicts that we have to do with specimens of the genus *Parasicyonis*" (p. 208). The specimen of *P. sarsii* that is the subject of pl. III, fig. 12 of Carlgren (1921) superficially resembles *Exocoelactis actinostoloides*, especially in being drawn in around mid-column. The nematocysts of *P. sarsii* can be slightly smaller than what we found, based on figures in Carlgren (1921); otherwise, his data did not allow us to be certain we were dealing with a different species. We therefore examined the two syntypes of *Parasicyonis sarsii* in ZMUC (which bear no catalog numbers) and one from SMNH (catalog #5268) (Fautin 2001). They differed both externally and internally from *E. actinostoloides*: the tentacles are very short and wrinkled circumferentially; the mesenteries, which are of typical thickness for an actinostolid, are arrayed according to the *Actinostola* rule. Therefore, the genus *Parasicyonis* does belong to family Actinostolidae, and is not synonymous with *Exocoelactis*, contrary to Carlgren (1921). Moreover, the sphincter muscle of *P. sarsii*, although aligned along the endodermal side of the mesoglea, is not unusually long, and the texture of the body is not rubbery, like that of *E. actinostoloides*, but is typical of an actinostolid.

The names *Parasicyonis actinostoloides* (Wassilieff, 1908) and *P. maxima* (Wassilieff, 1908) have been used erroneously to refer to *Entacmaea quadricolor* Rppell & Leuckart, 1828, a species of sea anemone that is symbiotic with clownfishes and some crustaceans (Dunn 1981). The first published misapplication of these names seems to have been by Uchida, Okamoto & Fukuda (1975), and the error has been perpetuated in the Japanese literature (e.g., Moyer & Bell 1976), in some cases *P. actinostoloides* being misspelled *P. actinostoroides* and *P. actinostroides*. The latter

usages have no nomenclatural standing (ICZN 1999: art. 33.3).

Clownfish anemones are shallow-water animals belonging to families in which the sphincter muscle is endodermal (Dunn 1981), whereas *Exocoelactis actinostoloides* occurs at depth and has a mesogleal sphincter. Like *Exocoelactis*, *Entacmaea quadricolor* has tentacles that may bulge at or, more commonly, below the tip (Fautin & Allen 1992). Two morphs of *Entacmaea quadricolor* differ in habitat, anemonefish symbionts, size, and (in some cases) degree of tentacle bulging, but are indistinguishable by the criteria used to define anemone species (Dunn 1981). Wassilieff (1908) separated the two species of *Cymbactis* by size and bulging of tentacles, *C. maxima* being larger and lacking acrospheres. Although the holotype of *C. maxima* is larger than any other specimen we examined, the difference is slight, and its tentacle form is well within the variability we found. Thus, of sea anemones that had been reported from Japan by 1975, *Parasicyonis actinostoloides* and *P. maxima* seemed to be two that resembled one another but differed in the very features that Uchida, Okamoto & Fukuda (1975) noted in what appeared to be two species of anemonefish hosts. Their report contains no information on how their identifications were made.

The report of *Parasicyonis actinostoloides* (Wassilieff, 1908) from Korea by Cha & Song (2001) also appears to be a misapplication of the name to individuals of *E. quadricolor*. Depth of occurrence, possession of zooxanthellae, whole-animal morphology, and size, morphology, and arrangement of mesenteries as described or illustrated by Cha & Song (2001) are all characteristic of *E. quadricolor* but not of *P. actinostoloides*. A feature characteristic of *P. actinostoloides* is the reportedly mesogleal sphincter muscle; Cha & Song (2001), however, provided no illustration of it, and Dunn (1981: 21) stated “[i]n rare cases lamellae [of the sphincter muscle] invade [the] mesoglea” of *E. quadricolor*. The size ranges of nematocysts reported by Cha & Song (2001) more or less agree with those of either species

except for those of the filaments, which are larger than reported for either species.

An anemone in a photograph taken at 2000 m near the 11°N hydrothermal vent field in the East Pacific, and identified as “Hexactinaire (Corallimorpharia?)” by Doumenc & Van-Praët (1988: fig. 1), resembles *E. actinostoloides*. If it is *E. actinostoloides*, the geographical and bathymetric range of the species would be extended even more. *Exocoelactis actinostoloides* superficially resembles a corallimorpharian because of its capitate tentacles, but the column of a corallimorpharian is typically shorter than that of the depicted animal. Moreover, the tentacles of *E. actinostoloides* are more robust than those of a corallimorpharian, each having a relatively larger acrosphere and base, like those of the animal in the photograph. Capitate tentacles are uncommon among actiniarians, occurring mainly in some small anemones (e.g., *Anemonactis mazeli*; see Fautin 1998) and the genus *Telmatactis*, some species of which can grow to large size. *Telmatactis* (family Isophelliidae) has acontia, which are absent in *Exocoelactis*; being internal, acontia typically cannot be detected in a photograph.

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