An unusual sea anemone from slope depths of the tropical west Pacific: range extension and redescription of *Isactinernus quadrilobatus* Carlgren, 1918 (Cnidaria: Actiniaria: Actinernidae)

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Abstract: The sea anemone species *Isactinernus quadrilobatus* Carlgren, 1918, and *Synactinernus flavus* Carlgren, 1918, which were described in new monotypic genera from few specimens collected in southern Japan, are synonymized, based on many more specimens from the South Pacific. As well as the geographic range, the depth range of this species has been extended to 110-700 m. The species had been distinguished primarily on whether the oral disc had four lobes (*I. quadrilobatus*) or eight (*Synactinernus flavus)* – we conclude their number is largely related to size of the animal. Other features that Carlgren had used to differentiate the genera (and species) are inconsistently present and do not correlate with lobe number.

Introduction

Acting as First Revisers (International Code of Zoological Nomenclature [ICZN] Article 24.2: International Commission on Zoological Nomenclature, 1999), we synonymize the sea anemone species *Isactinernus quadrilobatus* Carlgren, 1918, and *Synactinernus flavus* Carlgren, 1918. Under the Principle of Priority (ICZN Article 23: International Commission on Zoological Nomenclature, 1999), the valid name of the species is *Isactinernus quadrilobatus* Carlgren, 1918.

Carlgren (1918) described these species from Japan, each in a new genus. The type locality of *Isactinernus 4-lobatus* (correctly rendered as *I. quadrilobatus*) is listed as "Gote Inseln Kagoshima, 32°17'N 128°O 110 Faden [200 m]" (Carlgren, 1918: 29). The type locality of *Synactinernus flavus* is listed as "Japan. Kin Shin, Gote Inseln. 75 Faden [137 m]" (Carlgren, 1918: 31). The former was reportedly collected by Bock and Mortensen, the latter by Bock alone. Our interpretation is that current rendering of the collection locality is the Gotō Islands off Kyushu (Kiu Shiu in old orthography, incorrectly rendered as "Kin Shin" by Carlgren), southern Japan.

Because both genera are monospecific, the genus *Synactinernus* becomes a junior synonym of *Isactinernus*. Carlgren (1918) did not explicitly explain his decision to create separate genera for the animals rather than to assign them to different species of a single genus. According to his catalog (Carlgren, 1949: 20), the genera differ in three important particulars: the column surface, which is papillose in *Isactinernus* and smooth in *Synactinernus*; tentacle thickenings, which are present at the base of the

inner tentacles of *Isactinernus* but absent in *Synctinernus;* and the oral disc, which has four lobes in *Isactinernus* but eight in *Synactinernus*. We studied 81 specimens collected under the auspices of the Museum National d'Histoire Naturelle, Paris, that span the ostensible differences between the two: none of the features except lobe number distinguishes the two putative species - all other features supposedly confined to one or the other apply to both.

An animal of this species is distinctive externally (fig. 1), having a cylindrical column and abruptly flared oral disc; the oral disc is scalloped, with four or eight triangular flaps edged by many short tentacles (fig. 2). In contraction, the flaps neatly meet at their edges to form a dome over the oral disc. Preserved animals are firm in texture; most are hyaline or milky-white in colour. The internal anatomy of *I. quadrilobatus* is as unusual as its external anatomy: from the third cycle onward, mesenteries are added in endocoels rather than in exocoels, as is typical of sea anemones (*sensu stricto* - members of order Actiniaria).

The subject of Carlgren's 1918 publication was this distinctive anatomy; he created family Halcuriidae (which he also referred to as "Die Endocoelactiden") for the new genera plus three previously known ones that share this mesenterial arrangement. In 1922, Stephenson created family Actinernidae for all the genera Carlgren had placed in Halcuriidae except *Halcurias;* he added to Halcuriidae the genus *Carlgrenia* that he had created in 1918. Carlgren (1949) followed Stephenson's schema in his catalog, placing the two poorly-known families Actinernidae (by then containing eight nominal species in its four genera) and Halcuriidae Carlgren, 1918 (with six nominal species in its two genera) in their own suborder, Endocoelantheae, which Carlgren had created in 1924. Carlgren (1918), Grebelny (1982), and Riemann-Zürneck (1983) dealt with some of the phylogenetic implications of this mesenterial arrangement.

Materials and methods

We studied external and internal features of 81 recently-collected specimens (table 1), as well as the type specimens (below), the only material of these species previously known. Histological sections were made from four specimens; paraffin sections 8 μm thick were stained with hematoxylin and eosin (Humason, 1967). We measured cnidae from several animals; not all categories of cnidae were studied in every individual.

Specimens and images were taken around New Caledonia by French scientists. Most of this material was deposited in the Museum National d'Histoire Naturelle, Paris (MNHN), but some specimens are now part of the collections of the Nationaal Natuurhistorisch Museum, formerly the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, and the University of Kansas Natural History Museum (KUNHM). We also examined specimens taken by the Coral Reef Research Foundation in the South Pacific.

All type specimens were examined; they are housed in the Evolutionsmuseet, Uppsala University, Uppsala, Sweden (UU), the Zoological Museum, Lund University, Lund, Sweden (LO), and the Museum of Natural History, University of Copenhagen, Copenhagen, Denmark (ZMUC). A syntype of *Synactinernus flavus* is UU232; syntypes of *Isactinernus quadrilobatus* are UU102a (x1), UU102b (x1), LO L14/3033 (x1), and one unnumbered lot (x3) in ZMUC (see Fautin, 2003).

Table 1. Non-type material examined - provenance and repository.

Locality	Depth (m)	Cruise, Station	# spex	Cat. #	# lobes
24°46.2-45.5'S, 168°08.7-08'E	240-260	SMIB 4, DW 40	3	RMNH 31158	8
same			5	KUNHM 1811	8
24°44.01-44.3'S, 168°08.6-08.7'E	230-235	SMIB 4, DW 41	2	RMNH 31159	8
same			4	MNHN 2374	8
24°47'S, 168°09'E	235-245	SMIB 4, DW 43	1	MNHN1547	8
24°46.2-45.5'S, 168°08.7-08.4'E	240-245	SMIB 4, DW 48	2	RMNH 31160	8
22°20.0'S, 168°42.9'E	240-260	SMIB 5, DW 85	1	RMNH 31161	8
same			4	MNHN 2375	8
22°19.6'S, 168°41.3'E	265-280	SMIB 5, DW 92	3	MNHN 2376	8
22°20.0'S, 168°42.3'E	240-255	SMIB 5, DW 93	3	MNHN 2377	8
19°55'S, 158°38'E	350	MUSORSTOM 5, DC 371	1	KUNHM 1812	8
20°41.80'S, 167°00.20'E	282	MUSORSTOM 6, DW 399	1	MNHN 1470	8
20°42.15'S, 167°00.35'E	270	MUSORSTOM 6, CP 401	2	KUNHM 1813	8
22°20'S, 168°42.3'E	240-255	MUSORSTOM 6, DW 418	1	RMNH 31163	8
20°41.65'S, 167°03.70'E	285	MUSORSTOM 6, DW 419	1	RMNH 31164	8
20°53.27'S, 167°17.46'E	250	MUSORSTOM 6, DW 443	1	MNHN 2378	8
21°00.30'S, 167°25.50'E	300	MUSORSTOM 6, DW 452	3	MNHN 2379	8
same			1	MNHN 2380	8
21°00.30'S, 167°55.30'E	236	MUSORSTOM 6, DW 473	2	RMNH 31165	8
21°08.80'S, 167°55.70'E	237	MUSORSTOM 6, DW 474	2	RMNH 17922	8
21°23.48'S, 167°59.33'E	350	MUSORSTOM 6, DW 485	1	MNHN 2381	8
20°48.35'S, 167°05.80'E	700	MUSORSTOM 6, DW 493	1	MNHN 2382	8
15°51.91'S, 167°'19.42'E	397-439	MUSORSTOM8, CP1083	1	MNHN 2569	8
16°12.03'S, 167°'20.80'E	319	MUSORSTOM8, DW1058	1	MNHN 2570	8
19°06'S, 174°'18'E	371-437	BORDAU2.2000, CH1596	1	MNHN 2568	8
24°43'S, 168°09'E	227-232	NORFOLK 1, CP 1676	2	MNHN 2571	8
24°48'S, 168°09'E	257	CHALCAL2, CH03	3	MNHN 1455	8
24°48'S, 168°09'E	250	BIOCAL, DW 64	1	MNHN 2411	8
22°23'S, 171°41'E	260-300	VOLSMAR, DW 17	1	MNHN 2485	8
22°17'S, 171°18'E	450-500	VOLSMAR, DW 30	15	MNHN 2487	4
22°26'S, 171°46'E	620-700	VOLSMAR, DW 5	5	KUNHM 1814	4
20°59.2'S, 170°01.9'E	710	VOLSMAR, DW 55	3	MNHN 2486	4
same			3	MNHN 2383	4

This manuscript is based on a partially-written manuscript that J.C. den Hartog left upon his death. Daphne Fautin added data, incorporated some notes and images from JCdH, and finalized the writing.

Taxonomy

We provide the definitions of suborder Endocoelantheae, family Actinernidae, and genus *Isactinernus* from Carlgren's catalog (1949: 18, 19, and 20, respectively) because they are such good statements of the general features of these animals. The definitions of suborder and family are verbatim from Carlgren (1949); changes in the generic definition we introduce to accommodate our findings are indicated in italics. In the species definition, we do not repeat attributes that characterize these higher taxa.

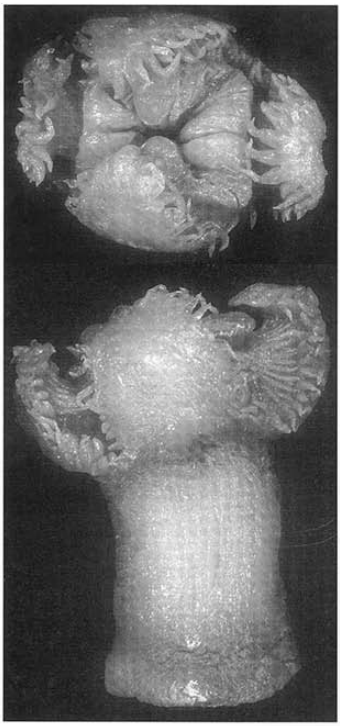

Fig. 1. *Isactinernus quadrilobatus*: syntype LO L14/3033. Upper image is oral view, lower image is entire specimen. Its length is about 50 mm. (From Fautin, 2003).

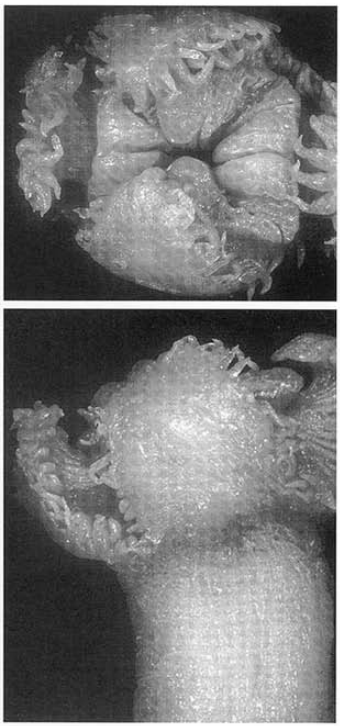

Fig. 2. Oral end of *Isactinernus quadrilobatus*: upper image KUNHM 001814, lower image RMNH 31158. The latter specimen is slightly larger than the former.

Suborder Endocoelantheae Carlgren, 1924 [not 1925 as stated by Carlgren, 1949]

Actiniaria with well-developed pedal disc but without basilar muscles. Column without vesicles and verrucae, nearly always with spirocysts. Margin tentaculate. No sphincter. Tentacles in variable number, often with their aboral side thickened, either in two alternating cycles or, owing to the curious development of the mesenteries, arranged in a way very different from the normal type, but usually in cycles. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal, with a slight

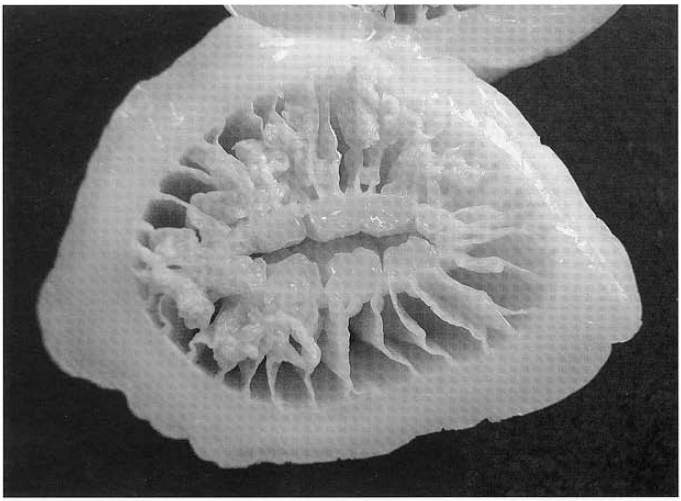

Fig. 3. Cross section through mid-column of *Isactinernus quadrilobatus*: KUNHM 001811. Greatest diameter = 50 mm.

mesogloeal tendency. Oral disc sometimes lobed. One siphonoglyph or two. Usually more mesenteries than the directives attached to the siphonoglyph. Arrangement of the mesenteries curious. After the first 12 mesenteries (six couples) are developed, all subsequent pairs appear in the lateral endocoels and have their longitudinal muscles oriented as in the directives. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Actinernidae Stephenson, 1922

Endocoelantheae with the thick body usually expanded above and then drawn out into lobes which are typically 4 or 8 in number. Sometimes there are small nematocyst batteries in the ectoderm of the column. Tentacles numerous, simple, or thickened on their aboral sides, 2 siphonoglyphs. Mesenteries numerous, not divisible into macro- and microcnemes, many are perfect. The later ones are arranged either cyclically or bilaterally, and the partners of a pair may be equal or unequal. Retractors weak. All stronger mesenteries fertile.

Isactinernus Carlgren, 1918

Actinernidae with well-developed pedal disc. Column *may have* very small mesogloeal papillae, the ectoderm of which forms small nematocyst batteries; cylin-

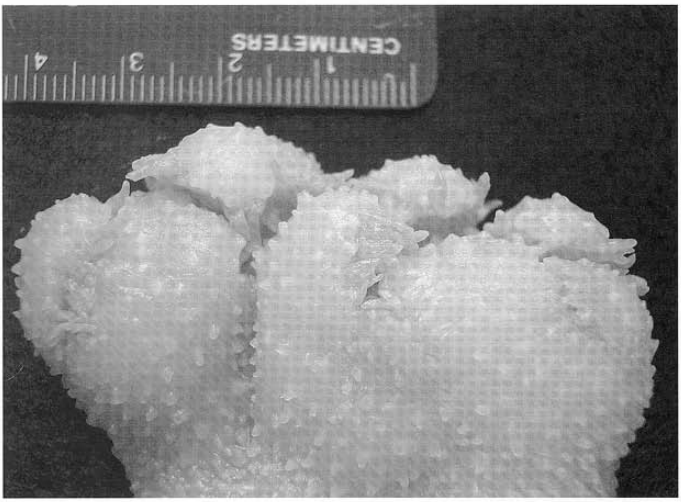

Fig. 4. Distal part of papillose specimen of *Isactinernus quadrilobatus* (KUNHM 001812).

drical, in the distal part drawn out into 4 *or 8* triangular lobes which are able to cover the oral disc and the mouth. No sphincter. Tentacles very short, conical, numerous in at least 2 cycles, largest at the apices of the lobes, the inner *may have* narrow aboral mesogloel thickeneings at the base, the outer with slighter or no thickenings. Longitudinal muscles of tentacles ectodermal, radial muscles of oral disc very strong, chiefly ectodermal. 2 siphonoglyphs. Mesogloea of actinopharynx very thick. Numerous perfect mesenteries arranged in cycles, the partners equally developed. Weak retractors in lower parts of older mesenteries, parietobasilar muscles weak. *May be hermaphroditic.*

Type species by monotypy and only known member *Isactinernus quadrilobatus* Carlgren, 1918.

Isactinernus quadrilobatus Carlgren, 1918

Isactinernus 4-lobatus Carlgren, 1918: 29-30; 1940: 22; 1949: 20.
Synactinernus flavus Carlgren, 1918: 31; 1949: 20; 1949: 20; Stephenson, 1922: 259.
Isactinernus quadrilobatus Stephenson, 1922: 260; Grebelny, 1982: 109, 110, 116.

Body form and size.— Cylindrical column abruptly flared at oral end (fig. 1), edges of oral disc form 4 or 8 lobes; in specimens examined, lobes domed over oral disc; in most, edges of adjacent lobes appressed, tips of all 4 or 8 lobes meeting centrally conceal oral disc (fig. 2). Texture of column, including distalmost portion form-

Fig. 5. Histological cross section of KUNHM 001814 showing very weak retractor muscles, oocytes, and sperm packets. For scale, body wall is 3 mm thick.

ing underside of lobes, stiff due to thick body wall (fig. 3) with plastic mesoglea to 6 mm thick in large specimens, reminescent of the texture of squid flesh. Surface of some specimens wrinkled or pleated; some with macroscopically visible papillae (e.g. KUNHM 001812 [fig. 4, with 8 lobes] has papillae 1-2 mm in diameter), others with papillae a fraction of a millimetre in diameter visible only under magnification (e.g. MNHN 2485 [with 8 lobes] and MNHN 2487 [with 4 lobes]), but some appear genuinely smooth (e.g. MNHN 2486 with 4 lobes; RMNH 31158 with 8 lobes); column of most specimens examined largely devoid of ectoderm. Oral and pedal disc also firm, thinner than column. Pedal disc slightly to markedly concave, in some specimens with adherent debris such as foraminiferans; limbus generally slightly curved inward. Column diameter 15-50 mm, folded oral disc diameter 15-70 mm, total length 10-80 mm.

Colour.— Preserved specimens milky white to hyaline dirty white, some with orangish or pinkish scattered ectoderm; tentacles grey to pinkish to orange; oral disc may be yellowish. In photographs by Helmut Zibrowius, two freshly-collected specimens that lacked column ectoderm white with faintly opalescent lilac discal lobes (except for white median ridges); in two other specimens, column partly covered by a dirty ochre ectoderm, lobes (lacking ectoderm) lilac, with paler, opaque median ridges; column of a fifth specimen and aboral surface of its discal lobes hazel to reddish brown, with oral surface of lobes brownish or ochreous; tentacles of all five speci-

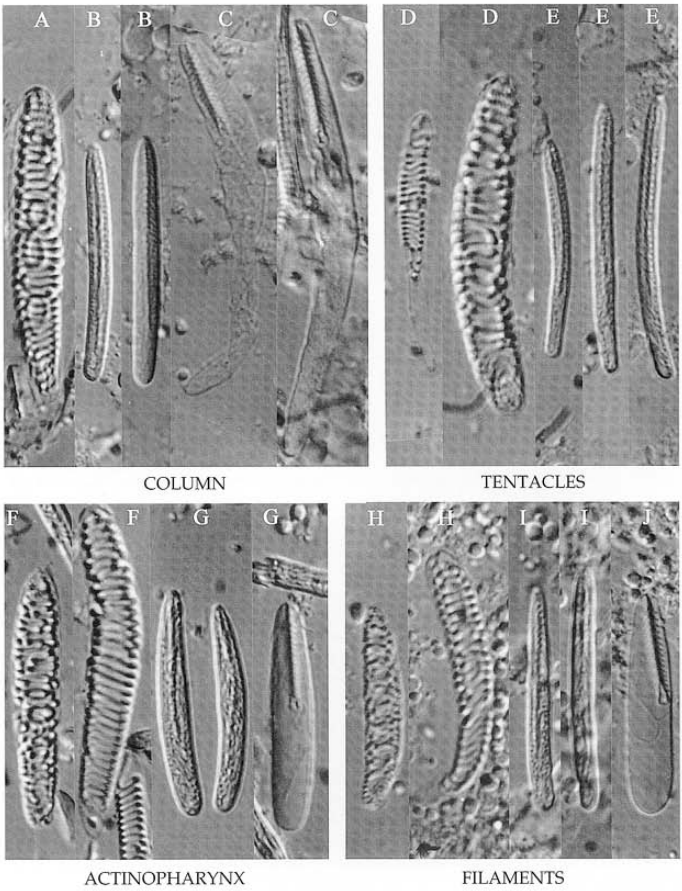

Fig. 6. Cnidae of *Isactinernus quadrilobatus*. Sizes are given in Table 2.

mens whitish. In photographs by Patrick and Lori Colin, column pink or orangish beige to tan, some streaked with darker brown.

Oral disc and tentacles.— Oral disc not circular but with scalloped edge: drawn out into conspicuous, fleshy, more-or-less triangular, inwardly curved lobes; most

smaller individuals (to about 35-40 mm long) with 4 lobes of equal size, all larger individuals with 8 lobes, of equal size or alternating larger and smaller. Diameter of oral disc from apex of lobe to apex of lobe about twice that from base of lobe to base of lobe; the latter diameter slightly greater than that of the column. Typical lobe 10-15 mm across its base and in length. Oral surface of lobes same thickness and structure as rest of oral disc. Distalmost column forming aboral surface of each lobe no firmer than rest of column in most specimens; rare specimens with a relatively smooth thickened median band with two faint lateral bands, rounded and raised at lobe tip, fading at lobe base. Edges of each lobe fringed by short pointed tentacles; tentacles only along margin, so oral disc naked. Fine radial grooves on disc along mesenterial insertions, areas between slightly raised; these marks especially prominent centrally. Fine transverse striae concentric around mouth are contracted fibers of ectodermal circular muscle layer. Large, central, protuberant mouth; actinopharynx ridges (see anatomy; fig. 1 upper image) may be visible through it.

Tentacles pointed (figs 1, 2, 4), of equal diameter most of length (1 mm maximum at base), in two alternating rows along margin; shallowly longitudinally sulcate in some individuals. Largest tentacle at tip of each lobe: to 12-15 mm long in largest anemones examined. Typically tentacles gradually smaller from tip to base of lobe; smallest 1-2 mm long. In some individuals, the single tentacle between each two lobes nearly as large at those at lobe tip. Large anemones have to 50 tentacles per lobe (i.e. 25 on each side). Thus, a large individual with 8 lobes could have a total of about 400 but actual number in specimens examined 336 to 384; the smallest specimen with 8 lobes (20 mm long and 12 mm wide) had 190 tentacles (20-24 per lobe).

Anatomy.— Number of mesenteries greater distally than proximally, mesenteries of highest orders present only in discal lobes. Curvature and tapering of the lobes makes number and arrangement of highest-order mesenteries difficult to determine; they appear to lack filaments and gametogenic tissue. In column, all mesenteries perfect: typically about 18 to 40 pairs, including two pairs of directives, symmetrically arrayed (figs 3, 5); with well-developed mesenterial filaments and gametogenic tissue. Filaments fine proximally, coarse distally. Judging by size in preserved specimens, oocytes probably reach 1 mm diameter in life; a strand between germinal vesicle and edge of mesentery in large oocytes may be a trophonema or analogous structure (e.g. Dunn, 1975; Larkman, 1983). Spermatozoa blunt-headed (head ca 3-3.5 μm long and 2-2.5 μm wide). Retractor muscles very weak and diffuse. Due to weak retractor muscles and equal development of all mesenteries, pattern of addition cannot be inferred.

Actinopharynx supported by very thick longitudinal mesogleal ridges, triangular to more or less square in cross section (fig. 3), typically alternating larger and smaller; positions do not correspond with those of lobes, and mesenterial attachment to them in no particular pattern.

Cnidae.— Cnidom spirocysts, basitrichs, microbasic p-mastigophores.

Distribution and size of cnidae variable; table 2 presents data from published sources and our own measurements of the types present consistently and in large numbers. Some rare, probably autochthonous cnidae difficult to quantify and of limited practical value because of their rarity: among them are long microbasic *p*-mastigophores with relatively short shaft that occur sporadically in the column, and long

fiber-like structures possibly representing very slender basitrichs. As illustrated in figure 6, spirocysts of two sorts: the larger robust form has a thick, loosel coiled tubule filling the entire blunt-ended capsule, and the smaller gracile form has a capsule that tapers at one end and a neatly-coiled tubule that is confined to the opposite end of the capsule. The two forms are most distinct in the tentacles, but intermediates in size and morphology occur in all tissues; because they had not been distinguished in published figures, we lump our measurements of them. Other rare cnidae, such as anisorhizas, presumably contaminants from prey, as remarked on by den Hartog et al. (1993: 49).

Table 2. Cnidae measurements for specimens identified as *Isactinernus quadrilobatus* and *Synactinernus flavus* in publication, plus measurements we made on specimens with 4 and 8 oral lobes (# indicates the latter; lines lacking a symbol refer to the former). The data indicated as from UU102 were collected by JCdH but whether from one or both syntypes of *I. quadrilobatus* is uncertain; possibly one or both of the specimens were the source of data for the species in Carlgren, 1918 and 1940. Likewise, UU 232 was probably the source of data for *S. flavus* in Carlgren, 1918. Dimensions = range of length x range of width; data on rare capsules that fell outside the usual range are given in parentheses. N = number of capsules measured; n = ratio of the number of animals in which that type of cnida was found to the number of animals examined. Letters refer to illustrations in figure 6.

Structure	Cnida	Specimens	Dimensions (μm)	N	n
Column	Spirocysts	#UU 232	26 - 40 x 4.5 - 8.0	unstated	1/1
	A	#Carlgren, 1918	26 - 38 x 3 - 5	unstated	1/1
		#Other	22.5 - 53.0 x 4.0 - 8.0	unstated	3/3
		UU102	30 - 50 x 5.5 - 8.0	unstated	?
		Carlgren, 1918	29 - 38 (48) x 4 - 5 (6)	unstated	?
		Carlgren, 1940	present	unstated	?
		Other	25.2 – 63.3 x 2.8 - 9.0	25+	3/3
		SUMMARY	**22.5 – 63.3 x 4.0 – 9.0**		
	Basitrichs	#UU 232	25.2 - 34.2 x 2.5 - 2.9	50	1/1
	B	#Carlgren, 1918	26 - 31 x 2 - 2.5	unstated	1/1
		#Other	27.0 - 41.4 x 2.7 - 3.6	95	3/3
		UU 102	39.6 - 47.7 x 3.2 - 3.4	20	?
		Carlgren, 1918	36 - 48 x 2.5 - 3	unstated	?
		Carlgren, 1940	36 - 48 x 2.5 - 3	unstated	?
		Other	34.4 - 63.1 x 2.5 - 4.3	43	3/3
		SUMMARY	**25.2 – 63.1 x 2.5 – 4.3**		
	Microbasic	#UU 232	ca. 50 x 5.4	1	1/1
	p-mastigophores	#Other	38.3 - 68.5 x 4.5 - 6.2	21	3/3
	C	UU 102	54.0 - 68.4 x 5.4 - 6.8	16	?
		Carlgren, 1918	65 - 70 x 6	unstated	?
		Carlgren, 1940	65 - 70 x 4 – 6	unstated	?
		Other	47.4 - 56.1 x 7.2 - 7.6	6	1/3
		SUMMARY	**38.3 – 68.5 x 4.5 – 7.6**		
Tentacles	Spirocysts	#UU 232	22.5 - 45 x 3.2 - 8.6	unstated	1/1
	D	#Carlgren, 1918	to 35 x 5	unstated	1/1
		#Other	22.5 - 50 x 3.6 - 8.0	unstated	3/3
		UU 102	27.0 - 58.5 x 4.1 - 10.8	unstated	?
		Carlgren, 1918	to 50 x 7	unstated	?
		Carlgren, 1940	present	unstated	?
		Other	24.8 - 60.0 x 3.1 - 9.5	16+	3/3
		SUMMARY	**22.5 – 60.0 x 3.2 – 10.8**		

	Basitrichs	#UU 232	23.4 - 27.0 x 2.5 - 2.7	20	1/1
	E	#Carlgren, 1918	26 - 31 x 2 - 2.5	?	1/1
		#Other	26.7 - 42.3 x 2.5 - 3.6	85	3/3
		UU 102	33.3 - 43.2 x 2.9 - 3.4	30	1/1
		Carlgren, 1918	31 - 38 x 2.5 (3.5)	unstated	?
		Carlgren, 1940	31 – 38 x 2.5 (3.5)	unstated	?
		Other	33.3 - 45.3 x 2.3 – 5.4	62	4/4
		SUMMARY	**23.4 – 45.3 x 2.5 – 5.4**		
Actinopharynx	Spirocysts	#UU 232	29.5 - ? x 5.0 - 8.0	unstated	1/1
	F	#Carlgren, 1918	to 36 x 5	unstated	1/1
		#Other	25.0 – 50.0 x 4.0 - 8.0	unstated	3/3
		UU 102	36.0 - 50.0 x 6.3 - 9.9	unstated	?
		Carlgren, 1918	36 - 46 x 4 – 5	unstated	?
		Carlgren, 1940	present	unstated	?
		Other	35.0 - 55.0 x 4.2 - 8.4	9+	3/3
		SUMMARY	**25.0 - 55.0 x 4.0 - 9.9**		
	Basitrichs	#UU 232	26.1 - 31.5 x 2.7 - 2.9	20	1/1
	like B	#Carlgren, 1918	26 - 31 x 2 - 2.5	unstated	1/1
		#Other	24.3 - 36.9 x 2.9 - 4.5	80	3/3
		UU 102	35.1 - 43.2 x 2.9 - 3.4	30	?
		Carlgren, 1940	35 - 41 x 2.5 - 3 (3.5)	unstated	?
		Other	35.1 - 52.1 x 2.6 - 7.7	51	3/3
		SUMMARY	**24.3 - 52.1 x 2.7 - 7.7**		
	Microbasic	#UU 232	17.8 - 24.9 x 3.8 - 4.7	20	1/1
	p-mastigophores	#Other	25.2 - 37.8 x 5.3 - 6.3	52	3/3
	G	UU 102	32.4 - 37.8 x 5.4 - 6.3	20	?
		Carlgren, 1940	36 - 40 x 5	very rare	?
		Other	30.8 - 40.2 (44.3) x 5.2 - 7.9	43	3/3
		SUMMARY	**17.8 - 40 x 3.8 - 7.7**		
Mesenterial filaments	Spirocysts	#UU 232	20 - 30 x 4.0 - 6.2	unstated	1/1
	H	#Other	22.5 - 50 x 3.6 - 9.0	unstated	3/3
		UU 102	33.0 - 40.0 x 6.3 - 6.8	unstated	?
		Carlgren, 1940	present	unstated	?
		Other	35.0 – 49.1 x 4.5 - 8.1	5+	3/3
		SUMMARY	**20 - 50 x 3.6 - 9.0**		
	Basitrichs	#UU 232	28.8 - 34.2 x 2.7 - 3.2	30	1/1
	I	#Other	23.0 - 35.1 x 2.7 - 4.1	55	3/3
		UU 102	36.5 - 43.2 x 2.9 - 3.4	20	?
		Carlgren, 1940	35 - 42 x 3	unstated	?
		Other	(27.3) 34.2 - 50.2 x 2.8 - 3.8	46	3/3
		SUMMARY	**23.0 – 43.2 x 2.7 – 4.1**		
	Microbasic	#UU 232	17.8 - 24.0 x 4.0 - 4.7	30	1/1
	p-mastigophores	#Other	24.9 - 36.0 x 5.3 - 6.7	100	3/3
	J	UU 102	32.4 - 44.1 x 5.4 - 6.3	25	?
		Carlgren, 1940	31 - 41 x 5	unstated	?
		Other	29.7 - 41.2 (46.2) x 4.8 - 7.3	48	3/3
		SUMMARY	**17.8 – 44.1 (46.2) x 4.0 – 7.3**		
Pedal disc	Basitrichs	#UU232	18.0 - 27.0 x 2.5 - 2.7	20	1/1
	like B	#Carlgren, 1918	23 - 25 x 2	?	1/1
		#Other	20.7 - 32.0 x 2.7 - 3.6	55	3/3
		UU 102	31.5 - 45.0 x 2.7 - 3.4	20	?
		Carlgren, 1918	31 - 39 x 2.5	unstated	?
		Carlgren, 1940	31 – 39 x 2.5	?	?
		Other	32.0 - 43.6 x 2.7 - 3.6	10	1/1
		SUMMARY	**18.0 – 45.0 x 2 – 3.6**		

Distribution.— Specimens from New Caledonia, the Loyalty Islands, and Palau considerably extend the known geographical range of the species from southern Japan. Depth range 110-700 m; most samples collected between 230 and 300 m.

Discussion

Two of the three particulars used by Carlgren (1949) to differentiate the two genera do not uniquely characterize them. The one that does is the most obvious – the number of oral lobes, said to number 8 ("four larger and four smaller alternating") in *Synactinernus*, and 4 (by implication of equal size) in *Isactinernus*. Most of the smaller individuals we examined had 4 equal-sized lobes, and all those more than 35-40 mm long had 8 lobes; the 8 lobes were of equal size in most individuals but alternately large and small in some. We found no animals with intermediate features such as six lobes or four large and four tiny lobes. However, the other two putatively genus-specific features did not correlate with lobe number. The column surface, said to be papillose in *Isactinernus* and smooth in *Synactinernus*, is papillose in some individuals with 8 lobes (e.g. KUNHM 001812: fig. 4). Thickenings at the base of the inner tentacles were said to be characteristic of *Isactinernus* but absent in *Synctinernus*; there is no consistency in them that we could find; in fact, few individuals had such thickenings.

Carlgren (1949: 20) also described the parietobasilar muscles of *Isactinernus* as "weak" and those of *Synactinernus* as "rather well developed." Perception of degree of development of parietobasilar muscles can be affected by where along the length of the animal the muscles were studied, so these ostensible differences are not reliable as species characters. Because data on arrangement of mesenteries in Carlgren's (1918) descriptions of the two species are not comparable, the status not being specified in the proximal part of the body for *Synactinernus* and in the distal for *Isactinernus*, we infer that Carlgren studied the distal part of the former and the proximal part of the latter, which could account for the difference he found in parietobasilar muscles. Carlgren (1949: 20) reported *Isactinernus* to be "dioecious" and included nothing about sexuality of *Synactinernus*; we found oocytes and sperm in a single individual (fig. 5), although apparently an individual mesentery produces one or the other.

We did find that cnidae of some categories differ in size, although not distribution, between specimens with 4 and 8 lobes. These are basitrichs of pedal disc, column, and actinopharynx, in all cases the former being larger than the latter, but there is some overlap.

The smallest tentacles are situated between the oral lobes, which may imply growth zones at the base of the lobes. The inference that mesenteries are added in the regions between lobes is further supported by tentacle numbers and arrangement, which in *I. quadrilobatus* are not typical of sea anemones. It is also consistent with the lobes developing in two cycles, four first, then four more. The implications of this pattern for phylogeny were discussed by Carlgren (1918), Grebelny (1982), and Riemann-Zürneck (1983).

Because the specimens we studied had the oral lobes domed over the oral disc, it is possible that the lobes are formed by contraction. If this were so, and the oral disc of an expanded individual were circular rather than scalloped, expanded individuals might be identified as members of a different species. We regard this possibility as unlikely for several reasons. Even without the lobes, the form and texture of these ani-

mals is peculiar. Moreover, the distinctive internal anatomy of such specimens would identify them as members of family Actinernidae. The actinernid most similar to *Isactinernus quadrilobatus* is the type genus, *Actinernus*, which has transient or incipient lobes that do seem to be formed by contraction, since they are irregular in position, number, and shape, each consisting of bunched-together marginal tentacles (an actinernid tentacle is rather long, with a filamentous end and thickened base) (e.g. Dunn, 1983: 5-8). By contrast, the lobes of *I. quadrilobatus* are regular in number and shape. The way they fold over the oral disc calls to mind deep-sea anemones of several groups that assume a form like that of a Venus fly-trap (e.g. Riemann-Zürneck, 1978).

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