GALATHEANTHEMUM PROFUNDALE (ANTHOZOA: ACTINIARIA) IN THE WESTERN ATLANTIC

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ABSTRACT

Galatheanthemum profundale Carlgren, 1956, is one of two known species of tube-forming sea anemones from abyssal-hadal depths. It was described from the trenches of the western Pacific Ocean, and has been reported from many trenches in the Pacific and at abyssal depths of Antarctica. Here we extend its range to the Atlantic Ocean, based on specimens collected in the Puerto Rico Trench and Virgin Islands Trough. In light of our research, it is likely that previous reports of Galatheanthemum sp. from the Atlantic Ocean refer to this species.

We identify to species for the first time a member of the sea anemone family Galatheanthemidae in the Atlantic Ocean. We studied some of the 330 specimens of *Galatheanthemum profundale* Carlgren, 1956, collected by vessels of the Rosenstiel School of Marine and Atmospheric Science, University of Miami (RSMAS) between 1969 and 1975, from 10 stations in the Puerto Rico Trench (5749–8026 m depth), two in the Virgin Islands Trough (4028–4408 m depth), and four on the abyssal plain about 100 km north of the Puerto Rico Trench (5541–5563 m depth).

Carlgren established the family and its single genus in 1956 for two species of tube-forming actiniarians collected by the Danish ship Galathea in the Philippine and Kermadec Trenches. *Galatheanthemum hadale* Carlgren, 1956 was the first organism seen when the trawl from the deepest depths thus far sampled was pulled aboard (Bruun et al., 1956: 178; T. Wolff, pers. comm. to D.G.F.). Since the description of these species, organisms identified as belonging to them, to the genus *Galatheanthemum*, or to the family Galatheanthemidae have been reported in from abyssal depths in much of the world; many of these records are summarized by Belyaev (1989) and Fautin (2006).

Belyaev and Sokolova (1960: 125) reported "типа Galatheanthemum profundale" (which can be translated as *G.* aff. *profundale*, according to T. Molodtsova, P. P. Shirshov Institute of Oceanology, Moscow) from the Marianas Trench at a depth of 10,630–10,710 m. In a review of hadal benthos, Belyaev (1966) retrospectively identified the "Ceriantharia" reported by Zenkevich et al. (1955) and by Wolff (1960) as members of this genus. "The family Galatheanthemidae, a highly characteristic element of the fauna of ultra-abyssal actinians, has also been found in most of the trenches examined of the Pacific," Belyaev (1966: 43) stated, commenting that specimens of it had been collected from at least 26 trench stations, none shallower than 5850 m, but he did not specify localities. Belyaev and Mironov (1977) reported eight more records of *Galatheanthemum* from five trenches in the western Pacific at depths of 6770–9750 m, only 1 km from the type locality of *G. hadale*. Dunn (1983) recorded *G. profundale* at 3947–5124 m from around much of Antarctica.

The first report of *Galatheanthemum* in the Atlantic Ocean was by Keller et al. (1975) from one station each in the Cayman Trough and the Puerto Rico Trench (5800–6500 m, and 7950–8100 m, respectively), but a remarkable in situ photograph published in Heezen and Hollister (1971) shows six specimens of *Galatheanthemum* attached to a rock in the Puerto Rico Trench (19°54′N, 65°57′W, 8143 m). George

and Higgins (1979: 56) included a photo of two of 64 specimens identified as "Tubedwelling actiniarian anthozoans (*Galatheanthemum*)" taken at 7600 m in the Puerto Rico Trench. It is likely that these reports were of *Galatheanthemum profundale*, the range of which we hereby extend to the Atlantic Ocean.

Materials and Methods

We studied in detail 19 specimens of *Galatheanthemum profundale* collected from the Puerto Rico Trench and Virgin Islands Trough collected by RSMAS—see Table 1 for specifics. We sectioned five of the specimens. Data on cnida sizes was obtained from squash preparations of five specimens; not all tissues were examined in all specimens.

INSTITUTIONAL ABBREVIATIONS: KUNHM—University of Kansas Natural History Museum, Lawrence, Kansas; UMML—University of Miami Marine Laboratory, Miami, Florida; USNM—United States National Museum of Natural History (Smithsonian Institution), Washington, DC; ZMUC—University of Copenhagen Zoological Museum, Copenhagen, Denmark.

RESULTS

The specimens we studied were unusually well preserved in our experience. The poor preservation of most specimens of *Galatheanthemum* is probably due to a combination of the tube and the depth of the habitat: the former impedes fixative and preservative from penetrating the living tissue, and the latter means that in the considerable interval between collection and preservation, the animal has changed environment (in particular, it has been subjected to increased temperature).

Table 1. Previously unreported material of *Galatheanthemum profundale* examined. Unstarred localities are in the Puerto Rico Trench, and those indicated by * are from the Virgin Islands Trough.

Catalog number	Ship, station	Locality	Depth	Date	# specimens
UMML	GILLIS 63	17°50′N, 65°25′W*	4,028–4,172 m	22 Jan 1973	11
UMML	Gillis 64	17°54′N, 65°10′W*	4,408 m	23 Jan 1973	1
USNM 59997	PILLSBURY 1382	19°16′N, 65°50′W	7,626–7,712 m	5 Jul 1971	3
USNM 59998	Gillis 59	19°23′N, 65°50′W	7,820-7,861 m	18 Jan 1973	3
USNM 59994	Pillsbury 993	19°24′N, 66°11′W	7,667–7,905 m	25 Jul 1969	14
USNM 59990	Pillsbury 811	19°26′N, 66°24′W	7,725–7,937 m	25 Jan 1969	54
KUNHM 002153	Pillsbury 811	19°26′N, 66°24′W	7,725–7,937 m	25 Jan 1969	4
USNM 59995	PILLSBURY 1164	19°28′N, 66°21′W	7,686–7,725 m	19 Jan 1970	2
USNM 59991	Pillsbury 812	19°37′N, 66°50′W	7,910–8,026 m	26 Jan 1969	1
USNM 59996	PILLSBURY 1380	19°38′N, 65°04′W	7,732–7,606 m	4 Jul 1971	10
USNM 60120	Gillis 109	19°41′N, 67°20′W	8,595 m	12 Jul 1975	1
USNM 60121	Gillis 111	19°16′N, 67°26′W	6,755–7,406 m	13 Jul 1975	2
USNM 60122	Gillis 113	19°26′N, 66°25′W	8,015–8,026 m	14 Jul 1975	33
USNM 60123	Gillis 114	19°51′N, 65°31′W	7,972–8,130 m	15 Jul 1975	40
USNM 59992	Gillis 62	19°44′N, 64°51′W	7,283-7,810 m	21 Jan 1973	1
USNM 59993	Gillis 62	19°44′N, 64°51′W	7,283–7,810 m	21 Jan 1973	135
KUNHM 002154	Gillis 62	19°44′N, 64°51′W	7,283-7,810 m	21 Jan 1973	3
USNM 59999	Gillis 61	20°06′N, 65°26′W	6,869–7,312 m	20 Jan 1973	7
UMML	Pillsbury 1374	22°02′N, 65°10′W	5,749–5,773 m	2 Jul 1971	2

The specimens clearly belong to family Galatheanthemidae Carlgren, 1956, in being abasilar, having a mesogleal sphincter and one tentacle per endocoelic and exocoelic space, and forming a tube. The definition of the genus *Galatheanthemum*, being the only genus in the family, currently is that of the family (see Carlgren, 1956).

Galatheanthemum profundale Carlgren, 1956

Galatheanthemum profundale Carlgren, 1956: 10–12, figs. 2, 3 (original description); Dunn, 1983: 1, 44–48, figs. 51–54; Belyaev, 1989: 60–61, fig. 26b; Dawson, 1992: 40.

Actinian: Bruun et al., 1956: 193, fig. 5.

Cerianthids: Heezen and Hollister, 1971: 56, upper left figure.

Galatheanthemum sp.: Keller et al., 1975: 155; George and Higgins, 1979: 55-56, fig. 7C.

Material Examined.—See Table 1 for data on specimens not previously reported. We compared those we studied with material from the type locality of *G. profundale* (Galathea station 658—35°51′S, 178°31′W, 6660–6720 m): two topotypes (incorrectly referred to as paratypes by Dunn, 1983) in UMML, and the holotype in ZMUC (see Fautin, 2006, for further information on this one). Neither of these museums assigns catalog numbers.

External Appearance and Size.—Column long and narrow, broadening distally; completely surrounded by a corresponding dark-colored conical cuticular tube that may be straight, slightly curved, sharply curved, or bent (Fig. 1). Longest tube measured 240 mm. Tube composed of two layers: outer opaque brownish-black, with irregular and poorly defined circumferential ridges; inner much more delicate than outer, composed of 3–4 smooth, thin, translucent yellow laminae. Between tube and column may be a layer of mucous containing many spirocysts. In some specimens, tube appears to have another stacked inside it, with a tube of smaller diameter issuing from the slightly flared end of a more proximal portion.

Column smooth, divided into scapus and scapulus (Heezen and Hollister, 1971: 68). Longitudinal furrows extend entire length, each tracing a mesenterial insertion. Cinclides, each on a bump (Fig. 2), arrayed in longitudinal intermesenterial rows: 1–5 cinclides per row, distalmost 4–5 mm from oral end, maximum number per individual ~30.

Tentacles moderately long in life (Heezen and Hollister, 1971: 68) but short and stubby in preservation (most just over 1 mm long, about 0.5 mm diameter at tip, which is slightly bulbed); withdrawn in all specimens studied. Arrayed in marginal exocoelic and inner endocoelic circlets. Number equal to that of mesenteries; in specimens studied, range 32–48. Number of tentacles roughly proportional to column diameter.

Internal Anatomy and Histology.—Mesogleal sphincter muscle strong, reticulate (Fig. 3; see also fig. 54 in Dunn, 1983).

Maximum number of mesenteries in specimens studied 24 pairs (in three cycles) (Fig. 4 illustrates the relationship between scapus diameter and number of mesenteries). Primary mesenteries complete; two pairs of symmetrically-positioned directives, each attached to poorly differentiated siphonoglyph. Higher-order mesenteries incomplete. Mesenteries of first and second order typically arrayed; those of third order may be irregularly arrayed.



Figure 1. Specimens of *Galatheanthemum profundale* Carlgren, 1956. (A–B) Topotypic specimens from Galathea 658 deposited at RSMAS; (C–H), specimens from Gillis 62, showing various growth forms. The proximal end of the tube of some (G, H) is attached to the tube of other specimens, whereas that of others (D, E) is attached to an object that was presumably on the sea floor.

Mesenterial retractor muscles diffuse, weak (Figs. 5, 6). Parietal muscles more developed on endocoelic than exocoelic side (Fig. 5). Mesenterial filaments well developed on primary mesenteries; filaments absent on higher-order mesenteries in individuals examined with up to 21 pairs of mesenteries, but in one individual with 24 pairs of mesenteries, filaments on about half of secondary mesenteries.

Of five individuals sectioned, four were males; the smallest was sexually immature. Only primary mesenteries gametogenic in individuals with fewer than 24 pairs mesenteries, but that with 24 pairs had spermaries in secondary as well as primary mesenteries; thus, number of fertile mesenteries increases with mesentery number.

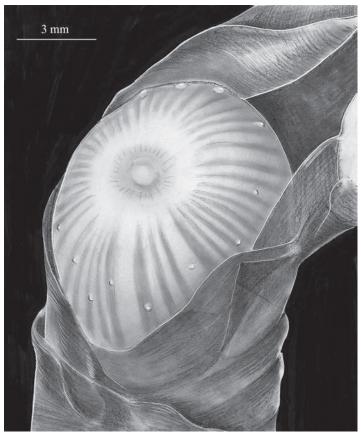


Figure 2. Distalmost end of a contracted specimen of *Galatheanthemum profundale* from GILLISS 62 (drawing by F. M. B.). Note cinclides on scapulus and layered nature of tube.

Gametogenic tissue extends proximally from proximal end of actinopharynx to basal end. Spermatozoan teardrop-shaped, $4\times5~\mu m$ diameter; tail 1–4 times body length so total length to 20 μm .

Cnidom: spirocysts, basitrichs, microbasic p-mastigophores, microbasic b-mastigophores. See Table 2 for data on size and distribution of cnidae.

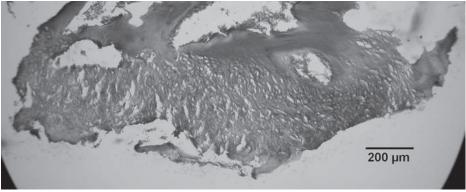


Figure 3. Reticulate mesogleal sphincter of Galatheanthemum profundale.

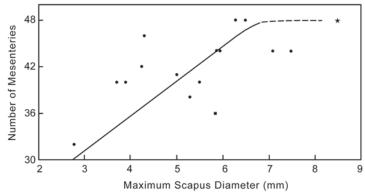


Figure 4. Relationship between maximum scapus diameter and number of mesenteries in *Galatheanthemum profundale*.

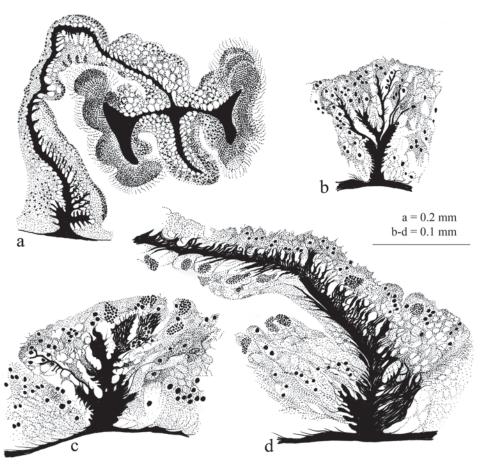


Figure 5. Cross-sections of mesenteries of *Galatheanthenum profundale* from Pillsbury 811, showing retractor and parietal muscles (drawings by F.M.B.). (A) first cycle mesentery and filament; (B) third cycle mesentery; (C) second cycle mesentery; and (D) first cycle mesentery at level of actinopharynx.

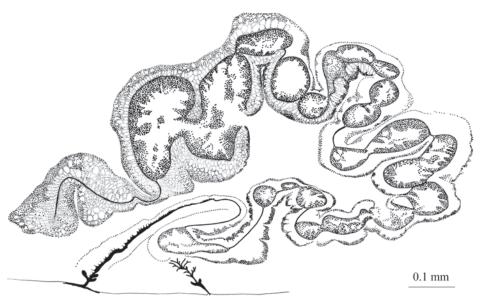


Figure 6. Cross section of fertile male mesentery of *Galatheanthemum profundale* from PILLS-BURY 811 (drawing by F.M.B.).

Discussion

The differences between the specimens examined by us from the Caribbean, by D.G.F. from the Southern Seas (as Dunn, 1983), and by Carlgren (1956) from the Philippine Trench are minor. Discrepancies with Carlgren (1956) are likely to be attributable mostly to the fact that his description was published posthumously from incomplete notes. Carlgren (1956: 11) reported a maximum of "about 36" mesenteries (one he examined had 38), which is a number that includes some tertiary mesenteries, so a maximum is likely to be 48. This is particularly so since, as Carlgren (1956: 11) reported and we observed, third cycle mesenteries are "as a rule developed on only one side of the mesenteries of the second cycle." Some of the secondary mesenteries of specimens Carlgren examined had filaments and gametes, whereas that condition was present only in the individual with 48 mesenteries we examined. Data on size and distribution of cnidae agree closely with published data (Table 2); data for the actinopharynx are more complete than those previously published. Despite excellent preservation of the specimens, tissue suitable for measuring nematocysts-coherent tissue free of contamination-was difficult to obtain. The small basitrichs Carlgren (1956) reported from the actinopharynx are similar in size to those of the tentacles; having experienced the difficulties of obtaining clean actinopharynx tissue, we infer that Carlgren's figures are from contaminants. We are not concerned about apparent difference in size of cnidae from the column for two reasons. (1) Tissue is difficult to obtain because debris tends to accumulate in the tube and peeling the tube away tends to disrupt the ectoderm. (2) Carlgren reported that he obtained cnidae from the scapus, which is difficult to credit because it is the part entirely enclosed by the tube. We sampled the scapulus, the distal part that emerges from the tube; attempts to obtain cnidae from the lower column (the scapus) were unsuccessful. D.G.F. (as

Table 2. Distribution and size of cuidae of Galatheanthemum profundale. Dimensions are range of length x width in µm; figures in parentheses are of single

	Caribbean specimens	u	z	Carlgren, 1959	Dunn, 1983
Tentacles					
Spirocysts	$25.2-60.6 \times (3.1) \ 3.7-10.9$	29	4/4	to about 70×7	$22.1 - 41.0 \times 3.1 - 5.3 (5.7)$
(there are both gracile and	(there are both gracile and robust varieties; some capsules could not be assigned	e assigned			38.5–57.4 (77.1) x 4.7–7.0 (8.2)
unambiguously, so measur	unambiguously, so measurements are presented as a single category)				
Basitrichs	$13.4 - 31.9 \times 1.3 - 3.9 (4.7)$	36	4/4	$17-24 \times 3-4$	$(13.1) 15.6 - 23.8 (27.9) \times 2.5 - 3.7 (4.1)$
Actinopharynx					
Basitrichs	$(21.4) 22.7 - 33.1 (34.0) \times 2.5 - 4.0$	23	2/2	$22.5-29.6 \times 3.5-4.2$ $22.1-31.2 \times 2.9-4.5$	$22.1 - 31.2 \times 2.9 - 4.5$
				$13.4 - 19.7 \times 2.8 - 3.5$	
Microbasic <i>p</i> -mastigophores 20.1	$20.1-28.2 (30.7) \times 3.0-4.9$	28	2/2	$22.6-29.6 \times \sim 4.2$	$20.5-26.2 \times 3.3-4.1$
Mesenterial Filaments					
Basitrichs	$(11.3) 14.5 - 27.7 \times 1.3 - 3.1$	50	3/3	$12-17.6 \times 2.2-2.8$	$(13.1) 14.8-20.5 \times 1.6-2.3$
					$20.5-28.7 \times 2.5-4.1$
Microbasic <i>p</i> -mastigophores $17.5-29.8 (30.7) \times 2.6-4.9$	$17.5-29.8 (30.7) \times 2.6-4.9$	39	3/3	$22.6 - 26.8 \times 3.5 - 4.2$	$19.7-26.2 (30.3) \times 2.9-4.1 (4.5)$
Scapulus				Scapus	Column
Basitrichs	$7.6 - 13.1 \times 1.0 - 2.3$	16	3/4	$10-11.3 \times 2.2-2.8$	$(12.3) 16.4 - 26.2 \times (2.7) 3.1 - 4.3 (4.9)$
	$(22.4) 23.1 - 27.7 \times 2.6 - 5.0$	17	2/4	$22.6 - 28.2 \times 4.5 - 5$	
Microbacio n mastigophoras	Microbasic n-mastigonhores (16.3) 17.3–79.8 (31.2) \times 2.3–5.5 (6.2)	48	7/7		148_180 × 31_41

Dunn, 1983) did not specify (and cannot recall) the part of the column from which tissue was obtained, but it is likely to have been the scapulus.

Some small specimens are attached to the tube of a larger one (Fig. 1G,H). This is not budding: the former is clearly attached to the latter rather than arising from it, with tube material from both between the animals' tissues. A tube removed from a smaller specimen narrows basally but its most proximal part is expanded into a broad, flat disc with which it is anchored to the tube of the larger specimen. This form is exactly like that of a specimen attached to a rock—a narrow neck between the broad, flat disc by which the tube is attached to the substratum and the conical tube. Carlgren (1956) remarked on this phenomenon in his description of the species. No empty tubes were found among the material we examined. The somewhat flexible cuticular material of the tube was described by Dunn (1983: 44) as "chitinous"; the precise nature of the tube material should be ascertained, but secretion of chitin by a sea anemone was documented by Dunn and Liberman (1983).

The geographic range of *G. profundale* is remarkable. Of shallow-water sea anemones, only Diadumene lineata (Verrill, 1869) [also known as Haliplanella luciae (Verrill, 1898)] has a range to rival it (Fautin, 2006), having spread during the 20th century through human agency (Fautin and Hand, 2007). The ostensibly large geographical ranges of some species, such as that summarized by Fautin (2006) for Actinauge verrilli McMurrich, 1893, may be due to misapplication of names. However, what is certainly a single species of abyssal actiniarian, Bathyphellia australis Dunn, 1983, has been recorded from five specimens in the sub-Antarctic Pacific (Dunn, 1983) and hundreds in the North Pacific off California (Fautin, 1997) and Oregon (D.G.F., pers. obs.). Riemann-Zürneck (1986) remarked on some wide-ranging South Atlantic anemones that she associated with circum-Antarctic hydrographic conditions. Antarctic Bottom Water is the source of much of the water at depth in the Pacific basin and along the west side of the Atlantic (summarized by Gage and Tyler, 1991). We infer that propagules of the abyssal species G. profundale and B. australis are entrained in such water. Outside the Antarctic region, G. profundale appears to be confined to trenches, which would be filled with the densest water which presumably is generated in the Antarctic and that provides the biological connection among these geographically scattered habitats.

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