

The life cycle of *Clytia linearis* and *Clytia noliformis*: metagenic campanulariids (Cnidaria: Hydrozoa) with contrasting polyp and medusa stages

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The life cycles of *Clytia linearis* and *Clytia noliformis*, two common campanulariids previously known solely from their polyp and young medusa stages, were investigated. Adult medusae of *C. linearis* have a bell diameter of 2.5–3.6 mm, and up to 29 tentacles. The bell is almost flat when relaxed and C-type microbasic mastigophore nematocysts form a cluster at the tip of the tentacles. Mature medusae of *C. noliformis* have a more hemispherical, saucer-shaped bell (3.5–4.5 mm in diameter), up to 16 tentacles, and no diagnostic nematocysts. Polyps of both species also differ in morphology, colour, and cnidome, and a possible resting structure is described for *C. linearis*. The relevance of characters from the perisarc and hydranths for taxonomy within the Campanulariidae is also evaluated, and whether the size of nematocysts is variable or not, and therefore appropriate for species identification.

INTRODUCTION

The family Campanulariidae includes some of the most common and familiar species of hydrozoans, especially those assigned to *Clytia* and *Obelia*. An important and abundant component of the plankton and benthos, the family is circumglobally distributed, with species occurring from the intertidal zone to depths that exceed 1000 m (e.g. Calder, 1991, 1997; Cornelius, 1995). Yet, despite being one of the most well known hydrozoan families and one of the first cnidarian taxa in which a metagenic life cycle was discovered (Cornelius, 1977), little is known about the life cycles of most campanulariids. For most metagenic species in the family, currently assigned to either *Clytia* or *Obelia*, a link between the polyp and medusa stages is still lacking. As a result, a dual classification (one for polyps and one for medusae) continues to impair the systematics of the family, as in many other hydrozoan taxa.

In addition to the lack of life cycle information, most species of Campanulariidae were described on the basis of a limited number of characters. To our knowledge, not a single original description of a species assigned to the family presents information, for example, on the nematocysts, which may be essential to identify species and solve taxonomic issues at the species level (e.g. Östman, 1979a, 1982; Cornelius & Östman, 1986). Not surprisingly, specific identification within the Campanulariidae remains a difficult task, and in many non-taxonomic studies, particularly those based solely on the medusa stage, species are not identified beyond the generic level (e.g. Matzakis, 1992).

We investigated the life cycle of *Clytia linearis* (Thornely, 1899) and *Clytia noliformis* (McCrary, 1859), two common campanulariids known only from the polyp and immature medusa stages. Whereas the former species is common in tropical regions and has been considered among the most widely distributed of marine invertebrates (Cornelius,

1987), *C. noliformis* is a major epizoic on holopelagic *Sargassum* in the North Atlantic (e.g. Picard, 1949; Calder, 1995) and has also been reported for the warm regions of the Mediterranean (e.g. Picard, 1949), and the Indian and Pacific oceans (Calder, 1991). Possible links between species previously described from the plankton and the adult medusae of *C. linearis* and *C. noliformis* reared in the laboratory are discussed. We also describe a possible resting structure in *C. linearis*, and discuss the relevance of characters from the perisarc, hydranths and cnidome (in particular the size of nematocysts) for identification.

MATERIALS AND METHODS

Colonies of *Clytia linearis* and *C. noliformis* were collected on a number of substrates from low intertidal and shallow subtidal environments on the coasts of São Sebastião and Ilhabela, São Paulo State, Brazil, between 1996 and 1999 (Figure 1; see Migotto, 1996 for a brief description of the study area). Colonies with gonangia were kept in a constant temperature chamber at 23°C with a 12:12 h L:D photoperiod in glass (210 cm³) or in polystyrene (85, 193 or 707 cm³) vessels filled with filtered seawater. Some vessels were also kept on a shaker at room temperature (22–24°C). Medusae of *C. linearis* reared through maturity were liberated from a colony collected at TEBAR, São Sebastião, in October 1999; those of *C. noliformis* were liberated in January and in July 1997 from polyps possibly belonging to the same colony growing on the red alga *Laurencia* sp. at Parcel da Praia Grande, Ilhabela (Figure 1). One to 25 medusae of both species were cultured in polystyrene vessels under a shaker at room temperature (22–24°C), and fed once a day with *Artemia* nauplii. The water was changed usually after feeding. Medusae of *C. noliformis* were also cultured in 600-ml glass beakers, as described by Migotto & Andrade (2000).

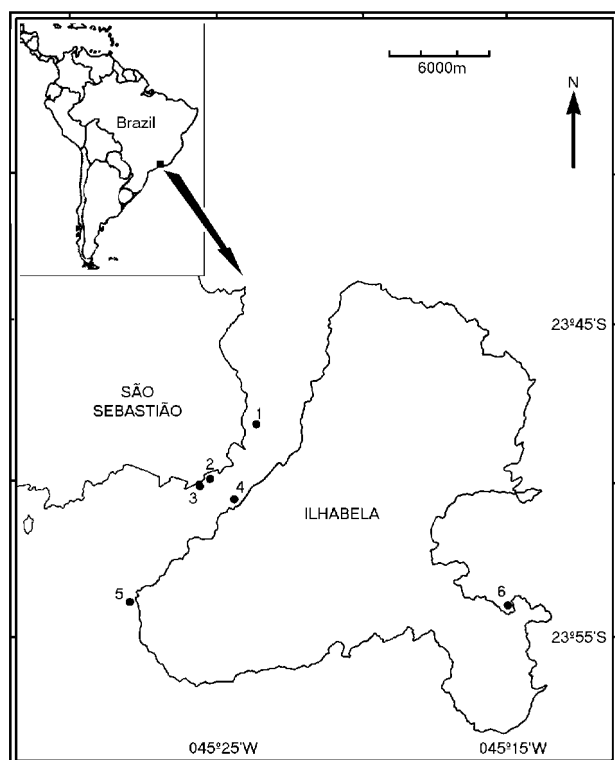


Figure 1. Collecting sites. (1) TEBAR; (2) Ponta do Jarobá; (3) Saco Grande; (4) Parcel da Praia Grande; (5) Ponta do Taubaté; (6) Saco do Sombrio. Collecting sites for *Clytia linearis*: 1–6; collecting sites for *C. noliformis*: 3 & 4.

Hydroids were cultured on glass slides and fed with *Artemia* nauplii. Hydranths and medusae were measured alive after relaxation in a 1:1 solution of 7.5% $MgCl_2$ solution and seawater. Measurements of the perisarc were made with colonies preserved in 4% formaldehyde solution in seawater. Polyps of the neotype of *C. noliformis* (see Lindner & Calder, 2000; Opinion 1986), preserved in 70% ethanol, were also measured. Specimens for scanning electron microscopy were preserved and prepared for analysis as described by Migotto & Andrade (2000).

Nematocyst types and distribution were determined using a light microscope equipped with interference-contrast optics. Nematocyst nomenclature follows that of Weill (1934), Mariscal (1974) and Östman (1979a,b). Unless otherwise mentioned, nematocyst measurements here presented were done *in vivo*.

The abbreviations used are: ROMIZ (Royal Ontario Museum, Canada); MZUSP (Museu de Zoologia da Universidade de São Paulo, Brazil); TEBAR (Terminal Marítimo Almirante Barroso—PETROBRAS).

RESULTS

Family CAMPANULARIIDAE Johnston, 1837

Genus *Clytia* Lamouroux, 1812

Clytia linearis (Thornely, 1899)

(Figures 2 & 3)

Material examined

(1) Colonies with gonangia on posts of a pier, growing on sponges, barnacles, bryozoans and *Corydendrium parasiticum* (Linnaeus, 1767) (Hydrozoa, Clavidae) (TEBAR, São Sebastião, SP, Brazil; coordinates: 23°47.97'S 045°22.98'W;

water depth: 5–10 m) [MZUSP 13.968, ROMIZ B3380]; collected by A. Lindner and A.E. Migotto, 22 October 1999. (2) Two 26-day-old medusae liberated from colony collected on 22 October 1999 [MZUSP 13.969]. (3) Idem [ROMIZ B3381]. Six additional colonies (see Figure 1 for collecting sites) and 41 additional medusae in A.E. Migotto collection.

Hydroid

Colony stolonial or usually with erect, monosiphonic, symphyllid flexuous stems; rarely branched (Figure 2B). Erect stems 3.9–21.5 mm high, with 2–26 hydranths and up to ten gonangia. Pedicels with 4–28 distal annuli. Internodes smooth, slightly curved and with 3–10 proximal annuli, more convex than pedicel annuli and with thicker perisarc. Distal end of pedicel bearing one hydrotheca. Internodes with a short, upward-curved apophysis supporting the next internode or the distal pedicel; apophyses alternating from side to side of stem, with a fold of perisarc projecting inward into the internode lumen (Figure 2B,C). Hydrotheca long, cylindrical, 557–1200 μm long and 271–596 μm wide at margin, with thin perisarc and walls almost parallel, sometimes with a subtle narrowing near margin (Figure 2C). Hydrothecal diaphragm thin, transverse, near base of hydrotheca; basal chamber 39–157 μm long and 110–220 μm wide at diaphragm. Hydrothecal margin with 10–14 sharp cusps (55–86 μm high); each cusp with a pleat projecting into cavity of hydrotheca and extending from apex of cusp towards middle of hydrotheca (Figure 2D). Hydrotheca breadth:length ratio: 0.37:0.55. Gonothecae smooth, cylindrical, 700–1254 μm long and 274–419 μm in maximum diameter, with a constriction (204–325 μm in diameter) under the truncated distal margin (212–345 μm in diameter) (Figure 2B & E). Gonothecae growing directly from hydrorhiza or from base of a hydrothecal pedicel, from short and annulated (2–4 annuli) pedicels. Each hydrothecal pedicel with up to two gonothecae; distal gonotheca usually smaller than proximal one (Figure 2B). Up to seven medusae in each gonangium. Just before release, distal medusa occupying almost entire terminal inner space of gonotheca (Figure 2E). Gonotheca breadth:length ratio: 0.26:0.42. Hydranth with elongated column, six to ten times as long as broad when extended; hypostome pedunculated, spherical in oral view and elongated in lateral view (Figure 2A); 20–26 filiform, amphicoronate tentacles (Appendix 1).

Newly released medusa

Umbrella hemispherical, with ring canal, four perradial canals; four perradial bulbs with tentacles; four interradial developing bulbs; 4–8 adradial statocysts, each with one statolith (Table 1). Gonads on median region of radial canals, 39–47 μm wide and 39–55 μm long in one-day-old medusae. Manubrium quadrate or laterally collapsed, ~0.5 height of bell (Figure 3A); lips smooth with A-type nematocysts. Velum broad. Tentacles hollow, with a terminal nematocyst cluster with only C-type nematocysts.

Adult medusa

Umbrella hemispherical during contraction (Figure 3C), saucer-shaped (~0.7–1.0 mm high) or almost flat when relaxed (Table 1; Figure 3D,E). Bell margin with up to 29

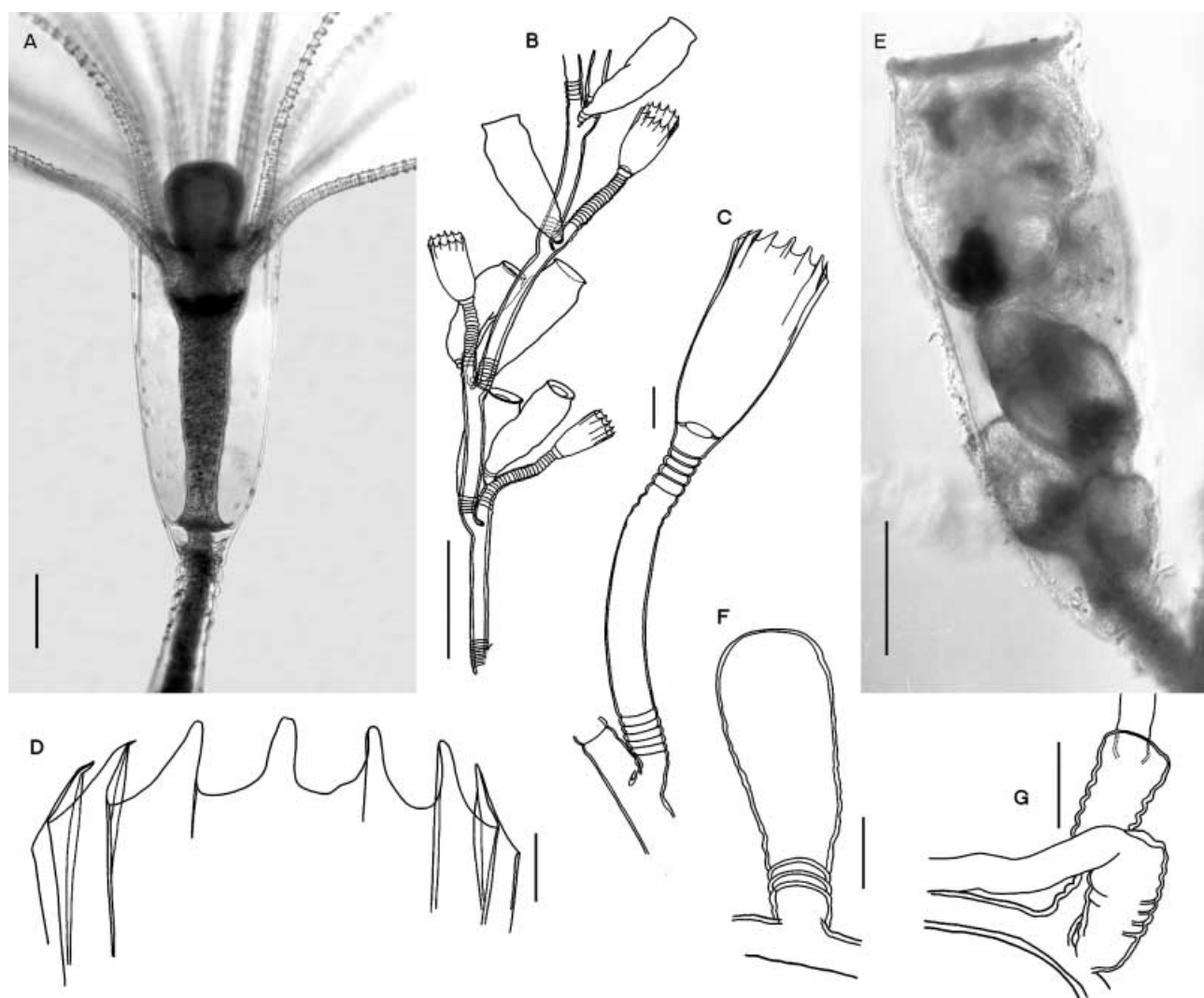


Figure 2. *Clytia linearis*. (A) Hydranth; (B) basal portion of a stem with hydrothecae and gonothecae; (C) distal portion of a stem with distal pedicel and hydrotheca; (D) hydrothecal margin with cusps; (E) gonangium with medusa buds; (F) possible resting structure and hydrorhiza; (G) possible resting structures with developing stolons. Scale bars: A, C, E–G, 200 μm ; B, 1 mm; D, 50 μm .

Table 1. Measurements {Mean \pm SD [range] (N)} and features of newly liberated and adult medusae of *Clytia linearis* and *C. noliformis*.

		<i>Clytia linearis</i>	<i>Clytia noliformis</i>
Newly liberated medusae	Height of bell (μm)	394.0 \pm 39.8 [336–480] (16)	376.4 \pm 52.3 [300–540] (30)
	Maximum diameter of bell (μm)	597.5 \pm 50.2 [480–660] (19)	489.2 \pm 45.5 [420–600] (30)
	Diameter of bell at base (μm)	418.7 \pm 43.1 [348–540] (19)	326.9 \pm 38.6 [264–420] (30)
	Diameter of subumbrellar aperture (μm)	166.9 \pm 41.4 [84–240] (11)	133.9 \pm 25.8 [84–180] (30)
	Height of the manubrium (μm)	197.3 \pm 20.0 [180–228] (9)	147.1 \pm 20.4 [120–180] (29)
	Number of tentacles	4	4
	Presence of nematocyst cluster on tentacles	+	+
	Presence of gonads	+	–
	Shape of bell	Hemispherical, slightly compressed	Hemispherical
Adult medusae	Maximum diameter of bell (mm)	2.5–3.6	3.5–4.5
	Maximum length/breadth of gonads (μm)	684/372	540/456
	Number of tentacles	20–29	12–16
	Presence of nematocyst clusters on tentacles	+	–
	Shape of the bell when relaxed	Saucer-shaped to flattened	Saucer-shaped
	Minimum time to first spawning (22–24°C)	14 days	14 days

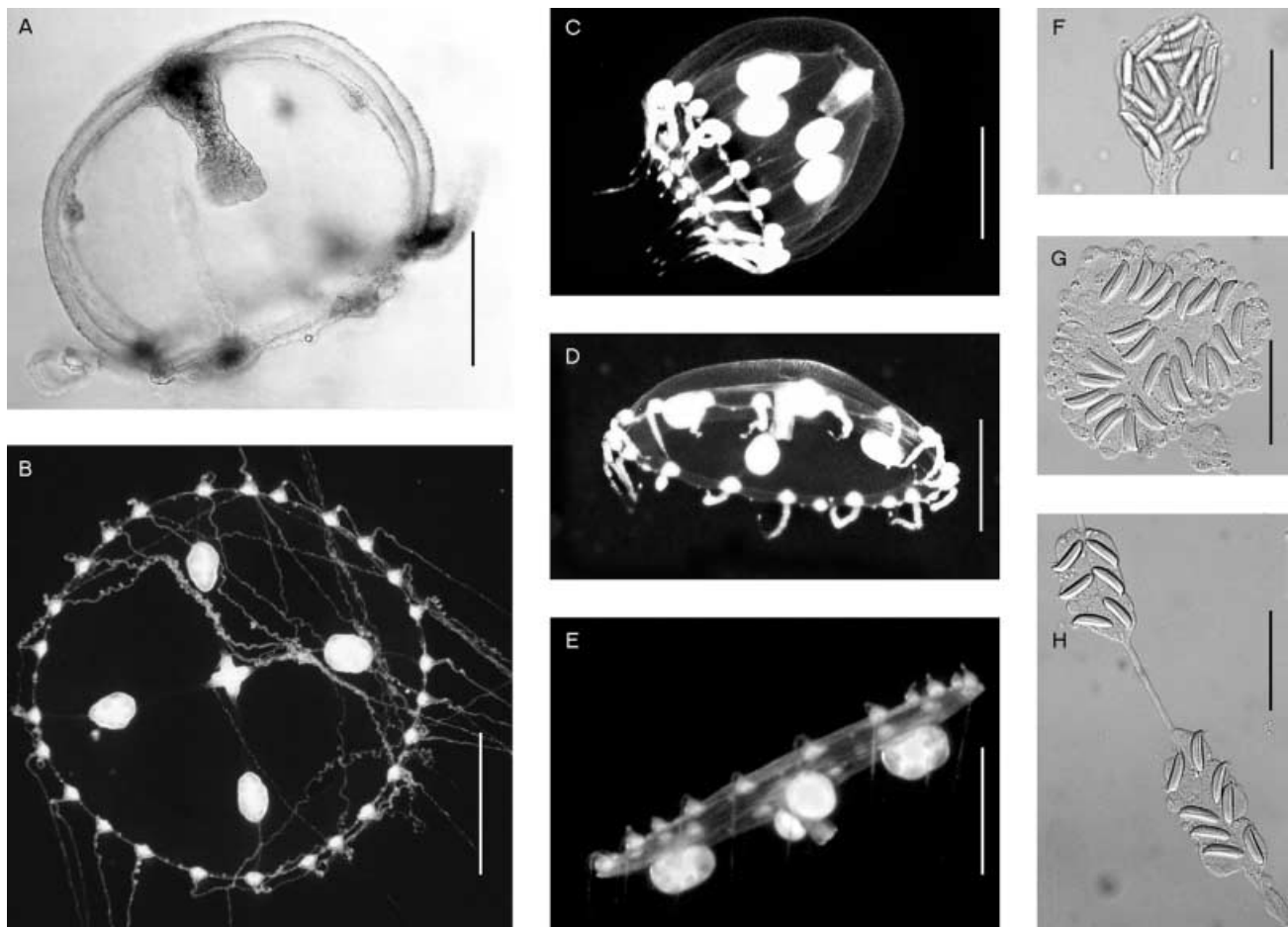


Figure 3. *Clytia linearis*. (A) Newly liberated medusa, lateral view; (B) mature medusa, 27 days old, oral-aboral view; (C-E) 22-day-old medusa in different contraction stages of the bell; (F) tip of a tentacle with cluster of C-type nematocysts, 12-day-old medusa; (G) tip of a tentacle with cluster of C-type nematocysts, 21-day-old medusa; (H) clusters of C-type nematocysts along the tentacles, 21-day-old medusa. Scale bars: A, 200 μm ; B-E, 1 mm; F-H, 35 μm .

bulbs with tentacles, and 28 statocysts, each with one statolith. Gonads oval (in oral and lateral views) on distal half of radial canals (252–372 μm wide; 284–684 μm long) (Figure 3B). Manubrium 480–600 μm long, cruciform, with four simple lips with A-type nematocysts. Marginal tentacles hollow, long, with a terminal cluster of nematocysts with only C-type nematocysts (up to 24) (Figure 3F,G); other clusters, with up to 11 C-type nematocysts also found along the tentacles (Figure 3H). Exumbrella without nematocysts. Bell transparent; gonads, manubrium, bulbs and tentacles assuming the colour of food. Male medusae not seen.

Nematocysts

A- and B-type microbasic mastigophores present in coenosarc of hydrorhiza, pedicels, hydranths and gonangia. Hydranth tentacles only with A-type nematocysts. Those of A-type 8.3 \pm 0.4 μm (7.5–9.0, N=20) long and 2.5 \pm 0.4 μm (2.0–3.0, N=20) wide *in vivo* and 7.8 \pm 0.3 μm (7.0–8.5, N=80) long and 2.1 \pm 0.2 μm (2.0–2.5, N=80) wide in formalin; length of B-type \sim 12 μm *in vivo* and 11 μm in formalin (Table 2). A- and C-type microbasic mastigophores and holotrichous isorhizae on tentacles and bulbs in both young and adult medusae; D-type microbasic mastigophores only in the exumbrella

Table 2. Length {Mean \pm SD [range] (N)} of B-type microbasic mastigophore nematocysts of *Clytia linearis*, in μm . (N=10 unless otherwise mentioned). Data from Ischia, Italy, obtained from Östman *et al.* (1987).

	Pedicel	Hydranth
Ischia, Italy	12.0 \pm 0.5 [10.5–13.0] (57)	12.0 \pm 0.7 [10.0–13.5] (61)
TEBAR, São Sebastião, Brazil (<i>in vivo</i>)	12.2 \pm 0.2 [12.0–12.5]	12.4 \pm 0.5 [12.0–13.0]
TEBAR, São Sebastião, Brazil (formalin)	11.2 \pm 0.3 [11.0–12.0]	11.0 \pm 0.0
Saco do Sombrio, Ilhabela, Brazil (formalin)	11.1 \pm 0.2 [11.0–11.5]	11.0 \pm 0.2 [10.5–11.5] (20)
Saco Grande, São Sebastião, Brazil (formalin)	10.8 \pm 0.4 [10.0–11.0]* ¹	10.6 \pm 0.5 [10.0–11.0]* ²

*¹, measurements of a pedicel and hydranth; *², measurements of a gonangium.

Table 3. Measurements {Mean \pm SD [range] (*N*)} of nematocysts of medusae of *Clytia linearis*, in μm . (*N*=10 unless otherwise mentioned).

Age (days)	A-type microbasic mastigophore Tentacles		D-type microbasic mastigophore Exumbrella		Holotrichous isorhiza Tentacles	
	Length	Width	Length	Width	Length	Width
1	8.0 \pm 0.2 [7.5–8.0]	2.2 \pm 0.2 [2.0–2.5]	8.2 \pm 0.3 [8.0–9.0]	2.3 \pm 0.3 [2.0–2.5]	5.8 \pm 0.3 [5.0–6.0]	2.0 \pm 0.0
5	8.3 \pm 0.4 [8.0–9.0]	2.1 \pm 0.2 [2.0–2.5]	8.4 \pm 0.2 [8.0–8.5]	2.4 \pm 0.2 [2.0–2.5]	6.4 \pm 0.4 [6.0–7.0]	2.1 \pm 0.2 [2.0–2.5]
11	9.0 \pm 0.6 [8.0–10.0]	2.4 \pm 0.2 [2.0–2.5]	absent	absent	7.2 \pm 0.3 [7.0–8.0]	2.5 \pm 0.2 [2.0–2.5]
21	10.0 \pm 0.2 [9.5–10.0]	2.9 \pm 0.2 [2.5–3.0]	absent	absent	8.4 \pm 0.5 [8.0–9.0]	2.5 \pm 0.0
C-type microbasic mastigophore						
Age (days)	Cluster at the tip of tentacles		Bulbs and along the tentacles			
	Length	Width	Length		Width	
1	9.4 \pm 0.5 [9.0–10.5]	3.4 \pm 0.3 [3.0–4.0]	9.7 \pm 0.7 [8.0–10.0]		3.7 \pm 0.3 [3.0–4.0]	
5	10.6 \pm 0.5 [10.0–11.0]	3.5 \pm 0.2 [3.0–4.0]	10.5 \pm 0.5 [10.0–11.0]		3.5 \pm 0.2 [3.0–3.5]	
11	14.9 \pm 0.2 [14.5–15.0]	4.4 \pm 0.3 [4.0–5.0]	15.3 \pm 0.6 [14.5–16.0]		4.6 \pm 0.3 [4.0–5.0]	
21	18.3 \pm 0.6 [17.0–19.0]	4.9 \pm 0.2 [4.5–5.0]	18.4 \pm 0.7 [17.0–19.0]		4.9 \pm 0.2 [4.5–5.0]	

of the former, in an equatorial band and along radial canals (Table 3).

Biological notes

One colony, collected on Saco Grande, São Sebastião (Figure 1), had six structures (276–840 μm long and 156–348 μm in maximum diameter), with slightly waved perisarc and with short, wide and usually annulated pedicels, growing directly from hydrorhiza, resembling gonangia and containing no medusae but a mass of tissue (Figure 2F,G). The hydranths and coenosarc of this colony regressed almost completely after its transfer to the laboratory, and new stolons were observed growing from the gonangium-like structures (Figure 2G). These structures may thus function as resting stages, and possibly explain the periodical absence of *C. linearis* in some regions (Boero & Bouillon, 1994).

During medusa development, the umbrella became gradually wider than higher and the velum became proportionally narrower, leaving the subumbrellar aperture nearly as wide as the bell margin. Seven-day-old medusae had up to eight tentacles. D-type nematocysts gradually disappeared from the exumbrella, being completely absent in 11-day-old medusae. The terminal nematocyst cluster of the tentacles enlarged during growth, holding gradually more nematocysts, which were also about twice as long in 21-day-old than in one-day-old medusae (Table 3). C-type nematocysts were observed migrating to the terminal cluster along the tentacular lumen, but no size differences were observed between the nematocysts at the tip of the tentacles and those in the bulbs and along the tentacles (Table 3).

Although there was no perceivable growth of the umbrella from the 11th day after liberation on (maximum diameter of 2.5–3.6 mm at the 11th day; 2.8–3.4 mm at the 27th), there was an increase in the number of tentacles and

statocysts (18–23 tentacles and 19–24 statocysts at the 12th day, up to 29 tentacles and 28 statocysts in 27-day-old medusae). The gonads elongated in the direction of the circular canal, becoming undulated due to the eggs inside. The germinal vesicle breakdown was observed in eggs still inside the gonads. About three hours before spawning the medusae swam vigorously and started to alternate short and fast lateral movements. Spawning occurred during this kind of dance, when the eggs protruded (usually singly) from the gonadal epithelium and were subsequently expelled from the subumbrellar cavity. About six eggs (165–212 μm in diameter) were liberated from each gonad in a spawning event, taking about ten min between the first and the last liberation. The same individuals spawned at regular intervals of approximately 48 h, usually at dusk, after 2–3 h in darkness. One pentameric medusa (with five radial canals and five manubrial lips) reached maturity, forming five normal gonads and releasing eggs.

Diagnosis

Clytia linearis is distinguished from its congeners and other campanulariids by the combination of the following characters:

polyp: stems monosiphonic, stolonial or sympodial and flexuose. Hydrothecal cusps with a pleat projecting into hydrotheca and extending from apex of cusp towards middle of hydrotheca. B-type microbasic mastigophores \sim 12 μm long *in vivo* and 11 μm long in formalin;

adult medusa: bell \sim 3 mm in marginal diameter, up to 29 tentacles and 28 statocysts. Manubrium with four simple marginal lips. C-type microbasic mastigophores \sim 16–19 μm long, forming a cluster at tip of tentacles (no character or combination of characters so far observed is diagnostic for young medusae).

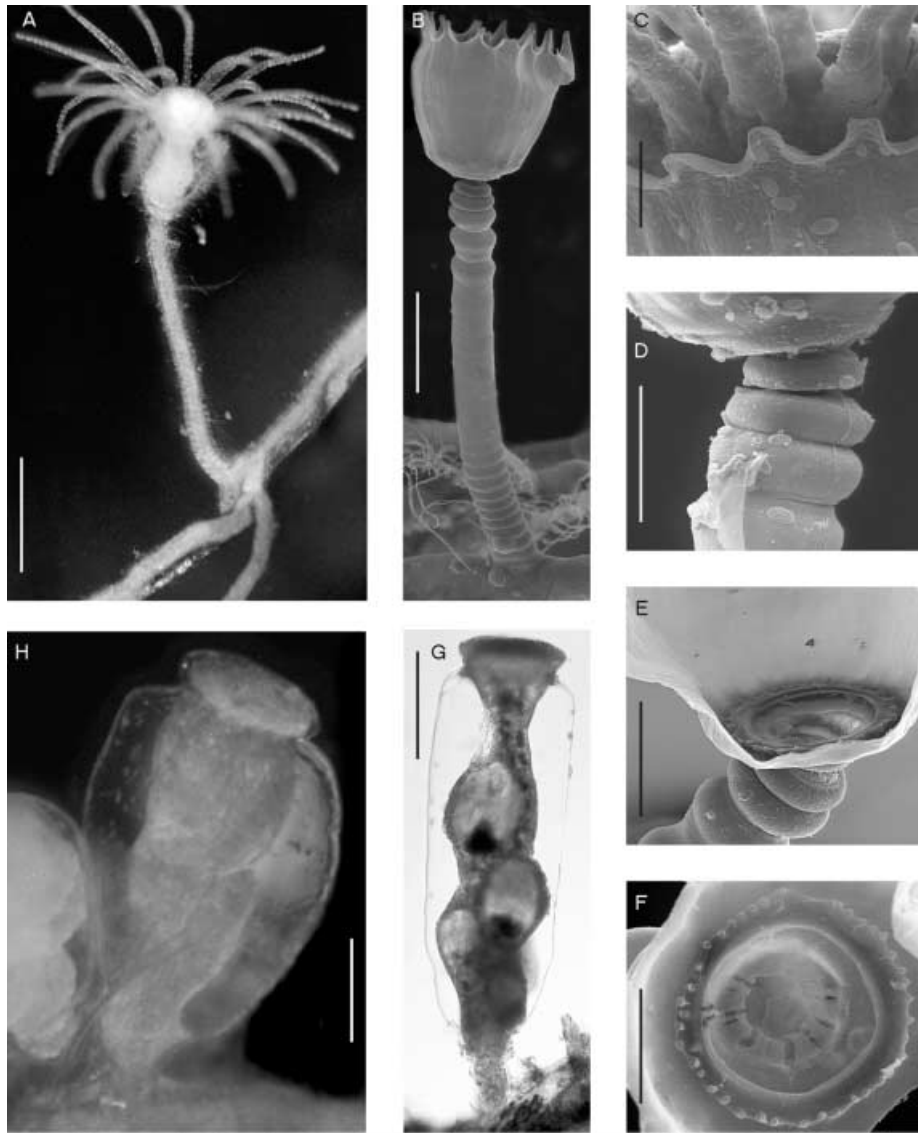


Figure 4. *Clytia noliformis*. (A) Hydranth, pedicel, and hydrorhiza, on the rhodophyte *Hypnea* sp.; (B) hydrotheca and pedicel; (C) hydrothecal margin with hydrothecal cusps and tentacles; (D) distal portion of pedicel with subhydrothecal spherule; (E) diaphragm and basal portion of hydrotheca (part of the hydrothecal wall removed); (F) internal view of hydrothecae, with diaphragm, foramen and desmocytes; (G) lateral view of a laboratory-cultured gonangium, with medusa buds; (H) lateral view of a field-collected gonangium with medusa buds. Scale bars: A, 500 μm ; B, 400 μm ; C–F, 100 μm ; G&H, 200 μm .

Distribution

Clytia linearis has been reported for shallow warm waters of the Atlantic, Pacific, and Indian oceans (Calder, 1991), including the Red Sea (e.g. Hirohito, 1977). The species has also been reported from subtropical regions, such as Sagami Bay, Japan (e.g. Yamada, 1959), the Spanish Catalanian (Llobet et al., 1986) and Basque (e.g. Altuna-Prados, 1994) coasts, and Italy (e.g. Boero & Bouillon, 1994). In Brazil the species has been reported for São Sebastião, SP (Migotto, 1996), Ubatuba, SP (Rosso & Marques, 1997), Angra dos Reis, RJ (Nogueira et al., 1997) and Vitória, ES (Grohmann et al., 1997).

Clytia noliformis (McCraday, 1859)
(Figures 4 & 5)

Material examined

Neotype: colony with gonangia, on dead octocoral, and 35 one-day-old medusae. (Castle Harbour, Bermuda;

water depth: 1 m) [ROMIZ B365]. Colony collected by D.R. Calder, 01 October 1986.

Other materials: (1) colony with gonangia, on *Sertularia marginata* Kirchenpauer, 1864 (Hydrozoa, Sertulariidae). (Parcel da Praia Grande, Ilhabela, Brazil; coordinates: 23°51.18'S 045°25.07'W; water depth: 1 m) [MZUSP 13.970]. Collected by A.E. Migotto, 26 July 1996. (2) Idem [MZUSP 13.971]. Collected by A.E. Migotto, 19 September 1996. (3) Colony with gonangia, on *Laurencia* sp. (Rhodophyta) (Parcel da Praia Grande, Ilhabela, Brazil; water depth: 2–2.5 m) [ROMIZ B3382]. Collected by A. Lindner and L.P. de Andrade, 16 January 1997. (4) Idem [ROMIZ B3383]. Collected by A. Lindner, 7 July 1997. (5) 31 one-day-old medusae liberated on 16 January 1997 from material ROMIZ B3382 [MZUSP 13.972]. (6) Ten newly liberated medusae, idem [ROMIZ B3384]. (7) Twenty newly liberated and one-day-old medusa, idem [ROMIZ B3385]. (8) Three 18-day-old medusae, idem [ROMIZ B3386]. (9) Three 18-day-old medusae, idem

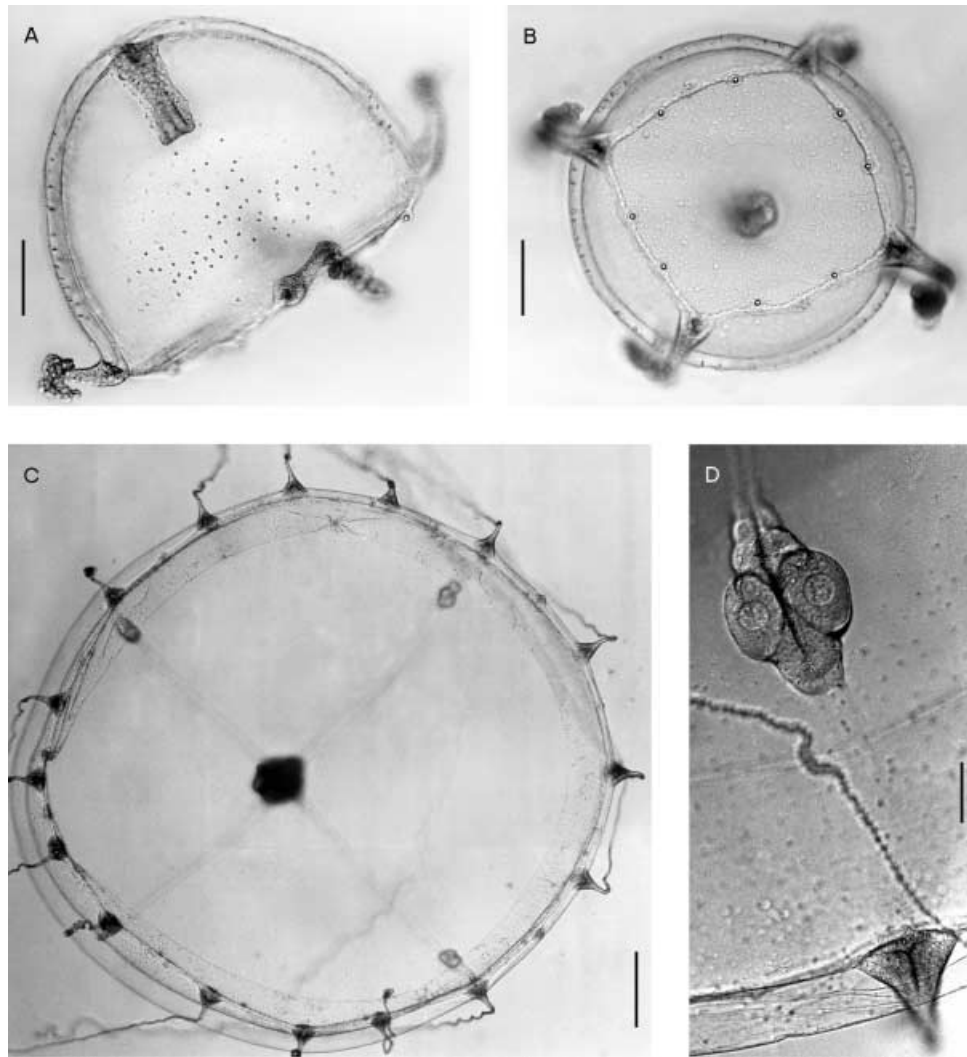


Figure 5. *Clytia noliformis*. (A) Newly liberated medusa with nematocysts on the exumbrella, lateral view; (B) newly liberated medusa, oral view, showing circular canal, statocysts, bulbs and subumbrellar aperture. (C) fully-grown medusa, 19 days old, with immature gonads; (D) maturing gonad, with two eggs with distinct germinal vesicles. Scale bars: A, B&D, 100 μm ; C, 500 μm .

[MZUSP 13.973]. Seven additional colonies (see Figure 1 for collecting sites) and 117 additional medusae on A.E. Migotto collection.

Hyroid

Colony stolonial, pedicel smooth, 0.9–5.0 mm long, with 5–28 and 2–18 annuli at basal and distal portions, respectively (Figure 4B). Some pedicels with a few annuli in median regions or, particularly short ones, entirely annulated (Figure 4A). Distal annulus differentiated in a subhydrothecal spherule (Figure 4D), smaller than adjacent annuli (Appendix 2). Distal end of pedicel bearing one hydrotheca. Hydrotheca shallow. Hydrothecal diaphragm thin, transverse, near base of hydrotheca (Figure 4E,F); basal chamber shallow; hydrothecal margin sometimes nearly smooth but usually with 9–14 triangular, rounded cusps, up to 70 μm high (Figure 4C). Gonothecae smooth, somewhat cylindrical or laterally compressed, with a constriction just under the truncated distal margin (Appendix 2). Gonothecal walls undulated in field collected colonies, straighter in laboratory-reared specimens (Figure 4G,H). Gonothecae arising from hydrorhiza on short annulated pedicels. Up to seven

medusae in each gonangium. Just before release, distal medusa occupying almost entire terminal inner space of gonotheca (Figure 4H). Hydranth and coenosarc yellowish. Hydranth with short column, 1–3 times as long as broad when extended; hypostome pedunculated, spherical in oral and lateral view; 24–34 filiform, amphiconate tentacles (Appendix 1).

Newly released medusa

Umbrella hemispherical, with ring canal, four perradial canals; four perradial bulbs with tentacles; two or four interradial nascent bulbs usually present; eight adradial statocysts, each with one statolith (Table 1). Gonads absent. Manubrium ~ 0.4 height of bell (Figure 5A), quadrate, lips smooth with A-type nematocysts. Velum broad (Figure 5B). Tentacles hollow, with a terminal nematocyst cluster (also observed in one-day-old medusae from Bermuda) having only C-type nematocysts.

Adult medusa

Umbrella saucer-shaped, 3.5–4.5 mm in diameter. Bell margin with up to 16 bulbs with tentacles (Table 1; Figure 5C). Gonads oval when fully developed (in oral

and lateral views) on distal 1/3 of radial canals (Figure 5D). Manubrium short, cruciform, with four simple lips with A-type nematocysts. Marginal tentacles hollow, long. C-type and D-type nematocysts absent. Bell transparent; gonads, manubrium, bulbs and tentacles assuming the colour of food. Male medusae not seen.

Nematocysts

A-type microbasic mastigophores ($\sim 7 \mu\text{m}$ long) and merotrichous isorhizae (17–24 μm long) present in coenosarc of hydrorhiza, pedicels, hydranths and gonangia (Lindner & Migotto, 2001). Hydranth tentacles only with A-type, $5.8 \pm 0.6 \mu\text{m}$ (5.0–7.0, N=56) long. A-, C- and D-type microbasic mastigophores and holotrichous isorhizae present in young medusae; length of A-type: $6.9 \pm 0.4 \mu\text{m}$ (6.0–8.0; N=55); length of D-type: $9.1 \pm 0.7 \mu\text{m}$ (7.5–11.0; N=50); length of holotrichous isorhiza: $5.4 \pm 0.6 \mu\text{m}$ (4.5–6.5; N=35). C-type not measured. Only A-type, $7.1 \pm 0.2 \mu\text{m}$ (6.5–7.5; N=20) long (measurements in formalin), were observed on tentacles of adult specimens. However, solely undischarged capsules of a preserved specimen were observed, and it is possible that holotrichous isorhizae, a nematocyst type similar in capsule shape to the A-type microbasic mastigophores, are also present in adult medusae of *C. noliformis*.

Biological notes

The colonies from the low intertidal zone of Saco Grande, São Sebastião, differed in size and shape from the colonies collected in the subtidal zone of Parcel da Praia Grande, Ilhabela and Castle Harbour, Bermuda. The hydrotheca of the former colonies are narrower (breadth:length ratio mean=0.75) when compared with the latter (breadth:length ratio mean ~ 0.90) (Appendix 2). Merotrichous isorhizae of colonies from the three sites were nearly of the same size (mean length of $\sim 20 \mu\text{m}$; see Lindner & Migotto, 2001).

Further morphological variations were observed between colonies from the field and those reared in the laboratory. For example, a cultivated colony had small hydranths, with only 15 tentacles and elongated gonothecae (840 μm long; breadth:length ratio ~ 0.33 , Figure 4G) with straight walls, contrasting with those from the wild, usually shorter and with more undulated walls (Appendix 2; Figure 4H). The size of merotrichous isorhizae found in the laboratory-cultured colonies [length of $21.0 \pm 1.0 \mu\text{m}$ (20.0–23.0, N=12)] did not differ from those collected in the field.

As in *C. linearis*, during medusa growth the umbrella became gradually wider than higher and the velum became proportionally narrower. D-type nematocysts disappeared from the exumbrella, as well as the C-type cluster in the tentacles. Seven-day-old medusae had up to 12 tentacles, and the maximum diameter of the umbrella (3.5–4.5 mm) was reached at 14 days after liberation, when the medusae also started to release eggs. No additional increase in bell size was observed until the culture ended 23 days after liberation [maximum diameter of the umbrella, on average: 4.0 mm (N=5) at the 14th day, 3.6 mm (N=5) at the 18th and 4.0 mm (N=3) at the 23rd]. The gonads became visible from the third day on, at the middle region of the radial canals; they elongated in the direction of the circular canal, becoming undulated

due to the eggs inside. The germinal vesicle was visible in eggs inside the gonads (Figure 5D). As in *C. linearis*, before end of spawning the medusae swam vigorously and started to alternate short and fast lateral movements, and spawning also occurred during this kind of dance. About six eggs (180–240 μm in diameter) were liberated in a spawning event from each gonad. Two medusae were liberated with three radial canals; one of those reached maturity, forming three normal gonads and releasing eggs.

Diagnosis

polyp: the presence of merotrichous isorhizae distinguishes the species from all other campanulariids so far studied. Regarding the macromorphology, *C. noliformis* can also be distinguished from its congeners by the combination of the following characters: colonies monosiphonic, stolonal; hydrotheca about as high as broad (at margin), with triangular cusps and shallow basal chamber; subhydrothecal spherule present; hydranths and coenosarc yellowish.

medusa: no character or combination of characters so far observed is diagnostic for young and adult medusae.

Distribution

Clytia noliformis is abundant on holopelagic *Sargassum* in the north-west Atlantic and has also been reported for many localities of the Indian and Pacific oceans, and in the Mediterranean (Picard, 1949; Calder, 1991). In Brazil, *C. noliformis* has been reported for São Sebastião, SP (Lindner & Migotto, 2001) and Santos, SP (Vannucci, 1946; as *C. folleata*).

DISCUSSION

A major incongruence in the systematics of *Clytia* is that the number of species described based on the medusa stage is larger than the number of species currently considered valid based on the polyp stage (Cornelius, 1987). Difficulties in accurately estimating the diversity within the genus result from at least three major phenomena: (1) morphological similarity among species, what has led to the synonymization of species based on polypoid characters [e.g. *Clytia gracilis* (M. Sars, 1850) and *Clytia hemisphaerica* (Linnaeus, 1767), see Cornelius & Östman, 1986]; (2) high phenotypic plasticity, with the possibility that individual species may have been described as new more than once (Cornelius, 1982); and (3) lack of the life cycle information needed to link species described based on polyps with those described based on medusae.

The difficulty in determining species boundaries within the Campanulariidae applies on either polyp or medusa stages, but the first group has been more extensively studied (e.g. Cornelius, 1982; Östman, 1979a; 1982, 1988; reviewed in Cornelius, 1999). The similarity among medusae of species of *Clytia*, in particular immature medusae, is even higher than among polyps, making it difficult to link the medusae of *C. linearis* and *C. noliformis* described here unequivocally to species described based on medusae collected in the plankton. For example, *C. gracilis* and *Clytia folleata* (McCrary, 1859) (see Cornelius, 1995, and Mayer, 1910, respectively) are very similar to *C. noliformis*: also with 16 tentacles when mature, four oral lips and gonads round and close to the circular canal.

Clytia folleata has even been considered conspecific with *C. noliformis* by Brooks (1883), but there is no compelling evidence supporting this conclusion. Brooks (1883) does not mention any character currently considered diagnostic of *C. noliformis*, and his observations may have been based on *C. gracilis* or *C. hemisphaerica* (Calder, 1991; Lindner & Calder, 2000).

In addition to *C. folleata*, *C. gracilis* and *C. noliformis*, other medusae of *Clytia* with 16 tentacles are those of *Clytia delicatula* Thornely, 1899 and *Clytia cylindrica* (L. Agassiz, 1862) (= *C. gracilis sensu* Calder, 1991), whose life cycles were investigated by Kubota (1978a) and Vannucci & Ribeiro (1955), respectively. Whereas the adult medusae of *C. delicatula* are 8.25–10.0 mm in diameter, those of *C. cylindrica* are similar in diameter to *C. noliformis* (~4 mm), but have larger gonads, with 20–35 eggs (Vannucci & Ribeiro, 1955). Notwithstanding the relevant information provided by Kubota (1978a) and Vannucci & Ribeiro (1955), these authors reared medusae already liberated (found in an aquarium and collected in the plankton, respectively), without certainty of the polyps from which they were released. Consequently, the links between polyps and medusae are not unequivocal. Another species with 16 tentacles is *Clytia maccradyi* (Brooks, 1888), the only known species of *Clytia* whose gonangia (i.e. the polyp stage) develop on the gonads of the medusa (see Mayer, 1910; Carré et al., 1995). Medusae of *Clytia viridicans* (Leuckart, 1856), from the Mediterranean, also have up to 16 tentacles, and the manubrium, gonads and tentacular bulbs are bright green (Pagliara et al., 2000). The green colour has also been reported by Mayer (1910) for *C. folleata* from the west Atlantic and for some specimens identified as *C. hemisphaerica* from the English coast.

Except for the life cycle of *C. hemisphaerica*, first investigated probably by Agassiz (1865, as *Clytia bicophora* L. Agassiz, 1862; published in Agassiz, 1862 as *C. cylindrica*), the life cycles of only three more species of *Clytia* (all from the North Pacific) have thus far been studied. Medusae of *Clytia edwardsi* (Nutting, 1901), from Japan, may attain 12 mm in diameter and 36 tentacles (Kubota, 1978b), whereas those of *Clytia attenuata* (Calkins, 1899) (see West & Renshaw, 1970) and *Clytia gregaria* (L. Agassiz, 1865) (see Roosen-Runge, 1970), both from the USA Pacific coast, are similar in size (6–10 mm in diameter) and number of tentacles: 20–28 for the former and average of 23 for the latter.

In addition to the similarities in shape, size and colour among many medusae of *Clytia*, specific identification is also hindered by the fact that the description of species from the plankton may have been based on developmental stages of other species. For example, six different species are considered as developmental stages of *C. hemisphaerica* (Mayer, 1910). Other nominal species may have been described after anomalous specimens, as *Pseudoclytia pentata* Mayer, 1900, based on a medusa with five radial canals that reached maturity, like the pentameric *C. linearis* and the trimeric *C. noliformis* we observed here. Similar medusae have been obtained by Mayer (1910) in the plankton, and considered as variations of *C. folleata*. Other abnormal medusae have even been assigned to different genera (e.g. *Gastroblastia*, see Russell, 1953), and variations in symmetry have also been reported for the class Scyphozoa (Gershwin, 1999).

For *Clytia* and probably also for *Obelia*, whose medusae are virtually indistinguishable (Vervoort, 1987), it is clear that the most commonly adopted medusa characters (e.g. the size of the umbrella, the shape of the gonads and the number of statocysts and tentacles) are not sufficient to distinguish many, and maybe most, species. Therefore, other characters must also be observed. Information on the cnidome of both young and mature medusae, such as here reported for *C. linearis* and *C. noliformis*, was previously provided solely for *C. delicatula* and *C. edwardsi* (Kubota, 1978a,b). For young medusae of *C. edwardsi*, Kubota (1978b) observed the same types of nematocysts here reported for *C. linearis* and *C. noliformis*, and by Östman (1979b) for *C. gracilis* and *C. hemisphaerica*: (i) a larger microbasic mastigophore in the exumbrella (the D-type *sensu* Östman, 1979b), which disappears during medusa growth; (ii) two kinds of microbasic mastigophores in the tentacles (the A-type and a stumper one, found in a cluster at the tip of the tentacles: the C-type *sensu* Östman, 1979b); and (iii) an atrichous isorhiza, which should be classified as holotrichous, since minute spines, seen under scanning electronic microscopy, are present in the tubule (Östman, 1979b). In addition to the interspecific similarity in the cnidomes of young medusae, some intra-specific differences in the number of nematocysts may occur (e.g. Mediterranean medusae of *C. linearis* observed by Östman et al. (1987) lacked D-types), and it seems likely that most species of *Clytia* cannot be distinguished based on the cnidome of young medusae.

The cnidome of adult medusae, however, differs among species and may be essential for species identification. The C-type, found in *C. linearis*, is lacking in *C. noliformis* and *C. edwardsi*, and a larger microbasic mastigophore (similar to the B-type of polyps) is solely present in the tentacles of the latter (Kubota, 1978b). The C-type of *C. linearis* is also larger in size (Table 3) and number in the cluster at the tip of tentacles in adult than in young medusae. Östman (1979b) also reported an increase in the number of C-type nematocysts for *C. gracilis* and *C. hemisphaerica*, but those medusae have not been cultivated to maturity. If no other adult medusa of *Clytia* has C-type nematocysts, this character may be diagnostic for *C. linearis*. A species described from the plankton and possibly conspecific to *C. linearis* is *Clytia macrogonia* Bouillon, 1984 (J. Bouillon & F. Boero, personal communication), but its cnidome has not yet been determined to reveal its identity.

Fortunately, cnidome studies of hydroids are becoming routine, even in faunistic surveys (e.g. Calder, 1988; Migotto, 1996). The Campanulariidae is one of the families most studied in terms of cnidome, which provided essential information for its systematics (Östman, 1979a,b, 1982, 1988, 1999; Cornelius & Östman, 1986; Cornelius, 1999). However, the relevance of the size of nematocysts—a systematic character considered important for many anthozoan taxa (e.g. Pires & Pitombo, 1992)—had not yet been evaluated within the Hydrozoa. For *C. linearis*, no considerable size differences were observed among B-type nematocysts of different parts of the same colonies and among colonies in a regional scale (Table 2). The size of B-type of *C. linearis* and of merotrichous isorhizae of *C. noliformis* is also very similar among colonies from distant locations (Table 2; Lindner & Migotto, 2001) as well as among wild colonies and those cultivated in the

laboratory. Since the mean length of nematocysts is almost invariable intraspecifically (in contrast to the highly plastic perisarc and hydranth characters, see below), it is an important character for the correct identification of *C. linearis* and *C. noliformis*, and eventually for other hydrozoan species. Moreover, the size of the large nematocyst of campanulariid hydroids (i.e. the B-, Ef-, Fl- and sB-types and the merotrichous isorhiza of *C. noliformis*) differs considerably among species (see Östman, 1999) and may be important in distinguishing some species similar in perisarc and hydranth morphologies.

Characters of the hydranths have only recently been used in the taxonomy of the Campanulariidae, but plasticity may limit their utilization for species identification. Even for *C. linearis* and *C. noliformis*, two remarkably different species, there is overlap in the size ranges of many hydranth parts (Appendix 1). Intraspecifically, the length ratios of hydranth parts are somewhat constant for *C. linearis* (Cornelius, 1987; Appendix 1), but were more variable for the colonies of *C. noliformis* studied here. For example, the tentacles, which were uniform in length in *C. gracilis*, *C. hemisphaerica* and *C. linearis* observed by Cornelius (1987), were about twice as long, on average, in hydranths of *C. noliformis* from Parcel da Praia Grande than in those from Saco Grande, Brazil (Appendix 1).

Besides characters of nematocysts and hydranths, perisarc features have been used in the taxonomy of the family at the species, genus, and subfamily levels for over a century (e.g. Cornelius, 1982). However, these characters are also variable (e.g. Ralph, 1957; Cornelius, 1982). For example, the number of annuli in the pedicels of colonies of *Obelia* may vary depending on hydrodynamism (Hughes, 1980), whereas some other morphological variations in species of *Clytia* and *Obelia* (e.g. the shape of gonothecae, one of the most relevant characters for species identification) are believed to be correlated with latitude (Ralph, 1957). Gonothecae of *C. noliformis* from colonies growing on different substrates indeed vary considerably in size (Appendix 2). Moreover, gonothecal shape in *C. noliformis* was different in specimens from the field (short and with undulated walls) than in those from laboratory cultures (longer and with straighter walls, see Figure 4H and 4G, respectively). A similar observation has been made by Kubota (1978b) for *C. edwardsi*, indicating that this kind of plasticity may be common.

In contrast to polyps, the shape and size of young and adult medusae of *C. linearis* and *C. noliformis* did not vary considerably. Growth of medusae in both species seemed to be determined. Although variation was observed in number of tentacles and statocysts, little intraspecific variation was noted in the shape and size of the bell and gonads. However, as previously discussed, correct identification of many species is hindered by interspecific similarity. Although adult medusae of *C. linearis* may be identified by their small size (the smallest known among species of *Clytia*), almost flat umbrella, large number of tentacles, and presence of a nematocyst cluster at the tip of the tentacles, those of *C. noliformis* are virtually identical to medusae of many other species. Nevertheless, some characters, though not diagnostic, may be helpful in identification of at least newly liberated medusae. To our knowledge, the lack of gonads in newly liberated medusae, for example, has been reported only in

C. noliformis, *C. delicatula* (Kubota, 1978a) and *C. viridicans* (Pagliara et al., 2000) and the slightly compressed bell of *C. linearis* may eventually be unique.

Although little morphological plasticity was observed here in medusae of *C. linearis* and *C. noliformis*, life cycle plasticity has been reported for *C. linearis* and some other species of Campanulariidae (Cornelius, 1990). For *C. linearis*, Boero & Sarà (1987) and Boero & Bouillon (1994) reported that, instead of immature medusae, short-lived mature medusae are released in the autumn in the Mediterranean. Thus, a colony of *C. linearis* may either release medusae that need to feed in the plankton to reach maturity (as described in the present study), or mature medusae that may not need to feed at all. This resembles the case of facultative feeding planktonic stages reported for other marine invertebrates, perhaps an important evolutionary step towards the possibly irreversible loss of a feeding planktonic stage—usually the larva—in the life cycle (see Wray, 1996 for an example on echinoids). Within the Hydrozoa, the paedomorphic loss of either feeding medusae or even the whole medusa stage in the life cycle has happened independently at least 60 times (Cornelius, 1992). Further investigations of the abbreviated life cycle of *C. linearis* (not seen in specimens from Brazil) may help in better understanding the evolution of life cycles within the Campanulariidae, a family with many paedomorphic species, including those currently assigned to *Campanularia*, *Gonothyrea*, *Hartlaubella*, *Laomedea*, *Orthopyxis*, *Rhizocaulus*, *Silicularia* and *Tulpa*.

The comprehension of life cycles within the Campanulariidae is also important in taxonomy, since the degree of reduction of the medusa stage is a character used in defining genera (e.g. Boero et al., 1996). This approach has been shown to result in non-monophyletic groupings within other hydrozoan groups (Petersen, 1990; Cunningham & Buss, 1993; see Marques & Migotto, 2001 for a contradictory result on the family Tubulariidae), but the question has not yet been evaluated in the Campanulariidae. Although a number of authors have conjectured about the evolution of the family and proposed different classification schemes (see Calder, 1991; Cornelius, 1999) a comprehensive phylogenetic hypothesis for the Campanulariidae has not yet been proposed. We hope that further species-level studies are undertaken so that the phylogeny of the Campanulariidae can be investigated. Longstanding incongruences in classification of the family may be resolved once the evolution of polyps, medusae, and life cycles in the group are better understood.

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APPENDICES

Appendix 1. Measurements {Mean \pm SD [range]} of hydranths of *Clytia linearis* and *C. noliformis*, in μ m.

Locality		<i>Clytia linearis</i>		<i>Clytia noliformis</i>	
		TEBAR and Saco Grande, São Sebastião, Brazil (N=20)	Ischia, Italy (data from Cornelius, 1987) (N=5)	Saco Grande, São Sebastião, Brazil (N=17)	Parcel da Praia Grande, Ilhabela, Brazil (N=5)
<i>Column</i>	Length	628.2 \pm 89.5 [420–744]	600–700	278.8 \pm 46.6 [216–360]	324.0 \pm 68.4 [240–420]
	Diameter at a median position	78.6 \pm 12.0 [60–96]	70 (minimum diameter)	145.3 \pm 28.8 [120–216]	180.0 \pm 36.0 [144–240]
	Ratio length:diameter	8.05 \pm 0.94 [6.25–10.0]	—	2.01 \pm 0.58 [1.0–3.0]	1.81 \pm 0.26 [1.4–2.1]
<i>Hypostome</i>	Length	255.6 \pm 43.7 [180–360]	480	194.8 \pm 38.8 [120–252]	255.6 \pm 44.0 [198–300]
	Diameter	176.4 \pm 21.7 [120–216]	70	201.9 \pm 36.3 [144–264]	240.0 \pm 48.0 [180–300]
<i>Tentacles</i>	Length	980.7 \pm 232.7 [600–1440]	650–800	480.0 \pm 89.7 [312–624]	936.0 \pm 141.0 [720–1080]
	Number	20–26	24	24–30	27–29
<i>Ratios of lengths, as proposed by Cornelius (1987)</i>					
	Tentacle:column	1.15–2.4	0.9–1.3	1.0–2.6	2.0–3.7
	Tentacle:hypostome	2.8–5.9	1.3–1.6	1.5–4.0	3.0–4.5
	Column:hypostome	2.0–3.4	1.25–1.45	1.1–2.1	1.0–1.5

Appendix 2. Measurements {Mean \pm SD [range] (N)} of hydrothecal pedicels, hydrothecae and gonothecae of *Clytia noliformis*, in μm .

Locality and depth		Saco Grande, São Sebastião, Brazil (low intertidal)	Parcel da Praia Grande, Ilhabela, Brazil (subtidal, 1 m)	Castle Harbour, Bermuda (subtidal, 1 m)
<i>Hydrothecal pedicel</i>	Length	1690.0 \pm 583.8 [880–2600] (10)	2202.9 \pm 713.5 [1000–3520] (21)	2146.4 \pm 1067.0 [1019–5016] (15)
	Diameter of proximal annuli	91.1 \pm 6.1 [80–96] (7)	118.9 \pm 14.5 [92–146] (20)	99.8 \pm 12.1 [80–110] (5)
	Diameter of distal annuli	94.4 \pm 11.6 [82–112] (9)	110.3 \pm 15.8 [76–144] (21)	101.7 \pm 8.3 [89–114] (10)
	Diameter of subhydrothecal spherule	88.2 \pm 10.4 [74–104] (10)	95.2 \pm 12.8 [68–120] (19)	90.8 \pm 8.8 [82–109] (7)
<i>Hydrotheca</i>	Length	476.4 \pm 61.5 [360–528] (9)	493.3 \pm 55.6 [400–584] (21)	427.8 \pm 40.3 [361–501] (14)
	Breadth at margin	356.4 \pm 36.7 [288–400] (9)	441.1 \pm 66.5 [288–552] (21)	382.1 \pm 46.9 [305–458] (10)
	Breadth:length ratio	0.75 \pm 0.08 [0.65–0.92] (9)	0.90 \pm 0.12 [0.65–1.20] (21)	0.91 \pm 0.09 [0.75–1.05] (10)
	Number of cusps	9–11	10–13	12–14
Locality and substrate		Parcel da Praia Grande, Ilhabela, Brazil on <i>Laurencia</i> sp.	Parcel da Praia Grande, Ilhabela, Brazil on <i>Sertularia marginata</i>	Castle Harbour, Bermuda on dead octocoral
<i>Gonotheca</i>	Length	380.8 \pm 62.6 [320–480] (5)	780.3 \pm 107.1 [624–980] (12)	711.0 \pm 51.6 [611–763] (10)
	Breadth at distal margin	140.0 \pm 10.3 [128–152] (4)	262.0 \pm 30.7 [200–296] (12)	202.8 \pm 14.7 [174.5–218] (10)
	Maximum breadth	264.4 \pm 35.1 [208–272] (5)	376.7 \pm 66.6 [240–496] (12)	308.6 \pm 30.9 [251–349] (10)
	Maximum breadth:length ratio	0.66 \pm 0.16 [0.43–0.85] (5)	0.49 \pm 0.09 [0.32–0.60] (12)	0.44 \pm 0.05 [0.34–0.54] (10)