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Merotrichous isorhiza, a nematocyst new to the Campanulariidae (Cnidaria: Hydrozoa), and its relevance for the classification of Cnidae

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Abstract.—Merotrichous isorhizae, a nematocyst class found in only a few species of Cnidaria, are present in the hydroid *Clytia noliformis*. This nematocyst type is present in the hypostome, gonangium, and hydranth body, near the base of the tentacles but is absent in the tentacles themselves. The undischarged capsules are similar to the B-type microbasic b-mastigophores found in other species of *Clytia*. The presence of a prominent rod in undischarged capsules indicates that changes may be needed in the classification of heteronemes and haplonemes, categories that embrace the great majority of nematocysts.

Within the hydroid family Campanulariidae (Hydrozoa: Leptomedusae), knowledge on the cnidome has been shown to be valuable for the identification of more than 20 species (see Table 1 for references). Information on nematocysts has been crucial in solving taxonomic debates, such as the ones on the validity of *Clytia gracilis* (M. Sars, 1850) and *Obelia longissima* (Pallas, 1766) (Östman 1979a, 1979b, 1982; Cornelius & Östman 1986). Two classes of nematocysts have thus far been reported for the Campanulariidae, i.e., microbasic b-mastigophore and holotrichous isorhiza (sensu Östman 2000). These classes were subdivided into seven and four different types, respectively (Table 1), using intra- and interspecific size differences, as well as the morphology of the capsules and spines (Östman 1979a, 1979b, 1982, 1988, 1999). However, with a few exceptions (e.g., Migotto 1996), most cnidome studies within the Campanulariidae were based on species from temperate waters (e.g., Russell 1938; Kubota 1976, 1978a, 1978b; Östman 1979a, 1979b, 1982, 1988, 1999). By studying the tropical species *Clytia noliformis* auct., we found a nematocyst class not yet reported for the Campanulariidae and present only in a few species of the Phylum Cnidaria: the merotrichous isorhiza.

Materials and Methods

Clytia noliformis was identified according to Calder (1991). Discharged and undischarged capsules of nematocysts of *C. noliformis* were observed by squash preparations (Silveira & Migotto 1984) of living colonies collected along the shallow subtidal coasts of São Sebastião (23°49.72′S, 45°25.52′W) and Ilhabela (23°51.18′S, 45°25.07′W), southeast Brazil, between 1996–1998. Undischarged capsules of the proposed neotype of *C. noliformis* (see Lindner & Calder 2000), fixed in ETOH 70%, from Castle Harbour, Bermuda, were also observed. Nematocysts were measured and photographed by light microscopy. The nomenclature adopted is that of Mariscal (1974) and Östman (2000).

Table 1.—Cnidomes of campanulariid species. Nematocyst classes are in accordance with the classification of Östman (2000). The terminology adopted for the types is in accordance with the revision of Östman (1999). (−) absent; (N) not observed or reported; (MA) free medusa absent.

Species	Nematocyst Class				Source[c]
	Microbasic b-mastigophore		Holotrichous isorhiza		
	Polyp	Medusa	Polyp	Medusa	
Clytia delicatula (Thornely, 1899)[a]	N	A-, C-, D-types	N	I_c-type	1
Clytia edwardsi (Nutting, 1901)[a]	A-type, B-type	A-, C-, D-types	−	I_c-type	2, 3
Clytia gracilis (M. Sars, 1850)	A-type, B-type	A-, C-, D-types	−	I_c-type	4–7
Clytia hemisphaerica (Linnaeus, 1767)	A-type, B-type	A-, C-, D-types	−	I_c-type	4–10
Clytia linearis (Thornely, 1899)	A-type, B-type	A-, C-, D-types	−	I_c-type	6, 7, 8, 11
Obelia bidentata Clark, 1875 (from England)	A-type, sB-type	N	−	N	6, 7
Obelia cf. bidentata (from Brazil)	A-type	N	?I_D-, I_d-types	N	7, 8
Obelia dichotoma (Linnaeus, 1758)	A-type	A-type	I_D-, I_d-types	I_D-, I_d-types	6, 7, 8, 12
Obelia geniculata (Linnaeus, 1758)	A-type	A-type	I_g-type	−	6, 7, 9, 12
Obelia longissima (Pallas, 1766)	A-type, F_1-type	A-type, F_1-type	−	−	6, 7, 12
Obelia plana (M. Sars, 1835)[a]	A-type, ?F_1-type	A-type, ?F_1-type	−	−	2
Orthopyxis asymmetrica Stechow, 1919	A-type, B-type	N	−	N	6, 7, 11
Orthopyxis integra (Macgillivray, 1842)	A-type, B-type	N	−	N	6, 7, 11
Orthopyxis sargassicola (Nutting, 1915)	A-type, sB-type	sB-type	−	−	7, 8
Campanularia hincksii Alder, 1856	A-type, B-type	MA	−	MA	6, 7, 13
Gonothyraea hyalina Hincks, 1866	A-type, sB-type	MA	−	MA	6, 7, 13
Gonothyraea loveni (Allman, 1859)	A-type	MA	−	MA	13
Hartlaubella gelatinosa (Pallas, 1766)	A-type, sB-type	MA	[b]	MA	6, 7
Laemedea angulata Hincks, 1861	N	MA	[b]	MA	6
Laomedea exigua M. Sars, 1857	A-type, sB-type	MA	−	MA	6, 7, 14
Laomedea flexuosa Alder, 1857	A-type, E_f-type	MA	−	MA	6, 7, 9, 12
Rhizocaulus verticillatus (Linnaeus, 1758)	A-type, B-type	MA	−	MA	7, 13

Sources: 1. Kubota 1978a; 2. Kubota 1976; 3. Kubota 1978b; 4. Östman 1979a; 5. Östman 1979b; 6. Östman 1987; 7. Östman 1999; 8. Migotto 1996; 9. Weill 1934; 10. Russell 1938; 11. Östman et al. 1987; 12. Östman 1982; 13. Östman 1988; 14. Cornelius & Östman 1987.

[a] Types inferred from descriptions (Kubota 1976, 1978a, 1978b).

[b] According to Östman (1987:77), isorhizae of *H. gelatinosa* and *L. angulata* "... have been identified, but only provisionally."

[c] Besides articles published before Östman's (1979a, 1979b, 1982) descriptions of the types, some publications adopted a slightly different terminology (e.g., Östman 1987). Not all publications dealing with nematocysts of the Campanulariidae are included in the table.

Table 2.—Measurements of undischarged merotrichous isorhiza capsules of *Clytia noliformis*.

Locality	Length (μm) [mean ± *SD* (range) (*n*)]	Width (μm) [mean ± *SD* (range) (*n*)]	Number of colonies observed
Brazil, São Sebastião	21.1 ± 1.6 (18.0–24.0) (37)	5.3 ± 0.6 (4.0–7.0) (37)	2
Brazil, Ilhabela	20.4 ± 1.1 (17.0–23.0) (26)	5.1 ± 0.3 (4.5–6.0) (26)	2
Bermuda	19.8 ± 0.6 (19.0–21.0) (10)	4.4 ± 0.3 (4.0–5.0) (10)	1

Results

Two classes of nematocysts, i.e., microbasic b-mastigophore (sensu Östman 2000) and merotrichous isorhiza (sensu Mariscal 1974), are present in the hydroid *C. noliformis*. The microbasic b-mastigophores are 7.1 ± 0.6 μm (mean ± *SD*, $n = 59$) in length and 2.5 ± 0.5 μm (mean ± *SD*, $n = 59$) in width. These nematocysts are abundant in the entire colony and correspond to the A-type described by Östman (1979a). Merotrichous isorhizae are abundant in the hypostome, gonangium, and hydranth body, near the base of the tentacles but are absent in the tentacles. The undischarged capsule is elongated (ca. 20 μm in length; see Table 2), with rounded ends. In a lateral view, one side is slightly convex and the other approximately straight; a distinct axial rod, corresponding to the region of the armature, is visible inside the undischarged capsule, running longitudinally from its tip to the posterior end (Fig. 1A). The aperture is turned towards the straighter side. The everted tubule forms a 20–80° angle with the straighter side of the capsule (Fig. 1B). The region with prominent spines (armature) is slightly shorter than one capsule-length (17.95 ± 1.58 μm; $n = 19$); the distance between its distal end and the tip of the capsule is about 4 capsule-lengths (80.68 ± 8.37 μm; $n = 70$). The diameter of the tubule shortly before and after the armature is identical. Medusae of *C. noliformis* have the same types of nematocysts so far reported for the genus *Clytia* (Table 1)—microbasic b-mastigophores (A-, C- and D-types) and holotrichous isorhizae (I_c-type).

Discussion

The A-type microbasic b-mastigophore is the most common nematocyst in the Campanulariidae, showing almost no variation in shape and size in all species studied so far (Östman 1999). In contrast, the B-type microbasic b-mastigophore—another common nematocyst present in all species of *Clytia,* except *C. noliformis*—differs in shape and size among species and is used for species identification (Östman 1979a, 1987, 1988, 1999; Östman et al. 1987). Undischarged capsules of the latter type are morphologically similar to the merotrichous isorhiza of *C. noliformis*. With light microscopy, both nematocysts can only be distinguished by the position of the prominent armature in the everted tubule. These nematocysts also have a similar distribution in the colony—absent from the tentacles and abundant in the hypostome, gonangium, and near the base of the tentacles (Östman 1979a, 1988; Lindner 2000). This suggests that, within the Campanulariidae, the merotrichous isorhiza may have evolved from microbasic b-mastigophores (or vice-versa), i.e., the prominent armature possibly "migrated" either from the proximal part of the tubule to a more distal part (microbasic → merotrichous) or from a distal to a proximal position (merotrichous → microbasic).

Instead of merotrichous isorhizae, B-type microbasic b-mastigophores were reported for colonies identified as *C. noliformis* from Italy (Östman et al. 1987, redefined as sB-type by Östman 1987, 1999). Since these capsules also measured only approximately one-third of the length of the capsules found in colonies of *C. noliformis* from

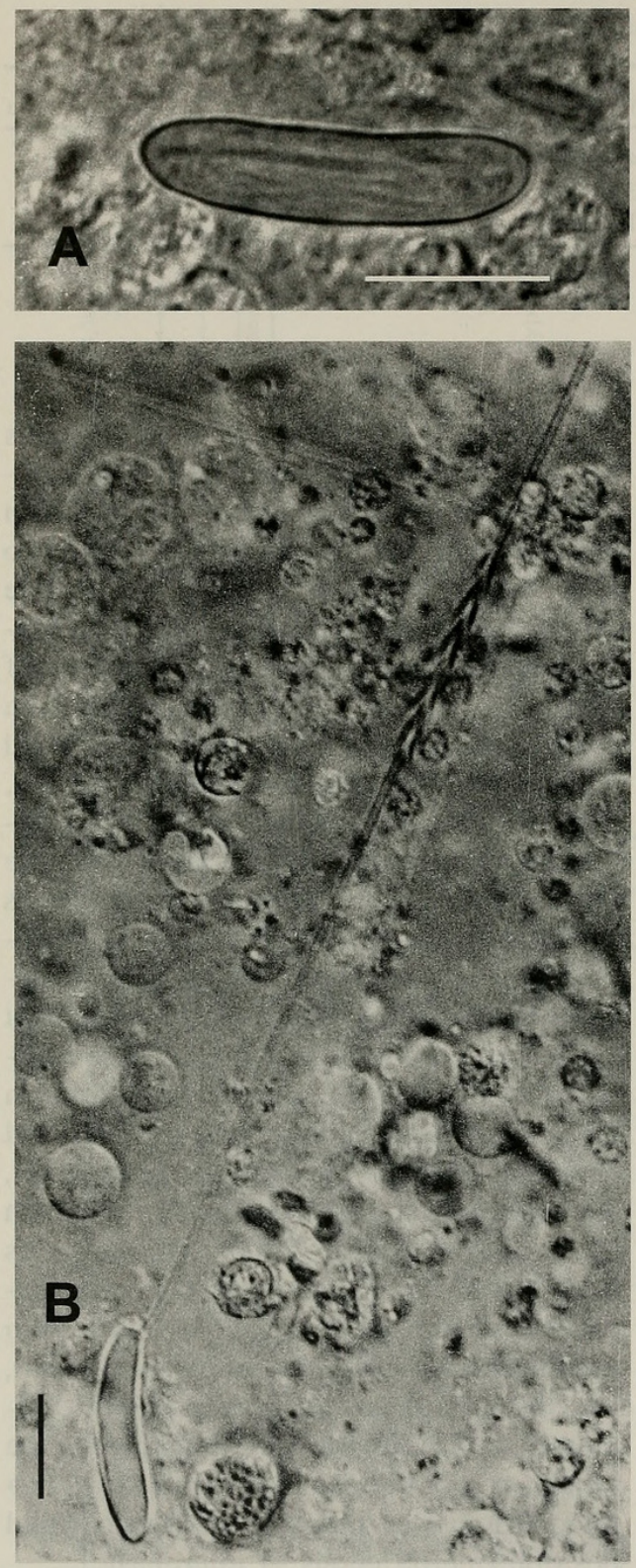

Fig. 1. Merotrichous isorhiza of *Clytia noliformis*. A, undischarged capsule; B, discharged capsule with everted tubule. Scale bars: 10 μm.

Brazil and Bermuda [ca. 7 μm (see Östman et al. 1987:302) and 20 μm (Table 2), respectively], it is possible that the authors based their observations on another species. Although differences in cnidome may be indicative of different species (see Östman 1982, 1988), the taxonomic relevance of the size differences of nematocysts has not yet been evaluated. However, the mean size of the merotrichous isorhiza among different colonies of *C. noliformis* shows little variation (Table 2). The large size may, therefore, help to identify the species, and it is particularly important for the identification of fixed samples having only undischarged capsules. The slightly smaller size of capsules of nematocysts from Bermuda in comparison to those from Brazil (particularly width, ca. 16% smaller in the colony from Bermuda; see Table 2) is probably due to fixation, a procedure that causes a 15–20% decrease in the width of B-type microbasic b-mastigophores in other species of *Clytia* (Lindner 2000).

Until recently, the merotrichous isorhiza was a nematocyst category reported only for the class Hydrozoa, where it was found in a few species of five families of Leptomedusae (Eirenidae, Eucheilotidae, Lovenellidae, Haleciidae and Tiaropsidae), and in *Halitiara,* a genus of Anthomedusae with features paralleling somewhat features found in the Leptomedusae (Bouillon et al. 1988). According to Bouillon et al. (1988), the presence of merotrichous isorhizae suggests affinities between the families Eirenidae and Eucheilotidae, as well as between the latter family and the Lovenellidae.

Similarly, Boero & Sarà (1987) considered the presence of merotrichous isorhizae in polyps of *Campalecium medusiferum* (Torrey, 1902) and *Hydranthea margarica* (Hincks, 1862) (Haleciidae), and in medusae of *Eucheilota maculata* Hartlaub, 1894 (Eucheilotidae), as a further evidence that the families Haleciidae and Campanulinidae s.l. are phylogenetically related. Werner (1965), who first described this nematocyst class (for *Eucheilota maculata*), and included it in the category haploneme in the system of Weill (1934), also attributed taxonomic value to the presence of merotrichous isorhizae (as "merotriche Haplone-

me") in the cirri of medusae of *Eucheilota* and *Eutima.* However, the presence of merotrichous isorhizae in the scyphomedusa *Cyanea nozakii* Kishinouye, 1891 (see Wang & Xu 1990) and possible misidentifications of this nematocyst class as microbasic or macrobasic mastigophores (as, for example, in *Campalecium medusiferum,* see Boero et al. 1987) indicate that merotrichous isorhizae may be actually more common among the Medusozoa. Moreover, this kind of nematocyst may have evolved more than once, and some phylogenetic inferences based on the presence of merotrichous isorhizae may be misleading if not corresponding to appropriate generality levels. Phylogenetic relationships within the class Hydrozoa are poorly understood, and the relevance of merotrichous isorhizae for the systematics of the Leptomedusae (e.g., if they represent or not a synapomorphy of some taxa) can only be assessed after a comprehensive phylogenetic analysis. It is also important to emphasize that the name merotrichous isorhiza refers solely to features of the tubule of the nematocyst; other characters, such as a visible rod in the undischarged capsule and the shape of the capsule, for example, should also be considered when comparing nematocysts of this and other categories.

The presence and absence of an internal axial rod in the undischarged capsule is a key character for the definition of the categories heteronemes and haplonemes in the new classification of Östman (2000). Heteronemes and haplonemes were originally defined by Weill (1934) by the presence and absence, respectively, of a basally enlarged region of the everted tubule, the so-called shaft, seen in discharged capsules. In contrast, Östman (2000), in an attempt to improve the classification of Weill (1934) by incorporating information not available at his time—but without changing the nomenclature—redefined heteronemes and haplonemes by the presence and absence, respectively, of a prominent rod-shaped shaft, corresponding to the region of the prominent armature, visible inside the undischarged capsule (regardless of the presence of an enlargement of the everted tubule). Since an internal rod is visible inside the undischarged capsule of the merotrichous isorhiza of *C. noliformis,* this nematocyst—a haploneme sensu Mariscal (1974)—must be classified as a heteroneme in the system of Östman (2000).

The presence of an internal rod (inferred by drawings) is also observed in the merotrichous isorhiza of, for example, *Hydranthea margarica* (Boero & Sarà 1987:133), *Lovenella assimilis* (Browne, 1905) (Hirano & Yamada 1985:133) and *Tiaropsidium roseum* (Maas, 1905) (Boero et al. 1987:296). However, in contrast to the classification of Mariscal (1974), the class merotrichous is not applicable in the classification of Östman (2000). Moreover, in adopting the latter classification, the merotrichous isorhiza of *C. noliformis* may be assigned to two distinct classes of heteronemes, since the length of the proximal tubule with prominent armature is variable. Those nematocysts with the proximal tubule with prominent armature slightly shorter than 4 capsule-lengths would be classified as mesobasic, whereas those with the proximal tubule with prominent armature slightly longer than 4 capsule-lengths would be classified, according to Östman (2000), as macrobasic.

Even if the merotrichous isorhiza of *C. noliformis* could be objectively classified as a mesobasic or macrobasic b-mastigophore, we believe that this would represent a hindrance, since nematocysts with distinct armatures (i.e., those with a long region with prominent spines starting at the base of the tubule and those with prominent spines only at a more distal position) would be grouped in the same categories. Since the merotrichous isorhiza is a nematocyst easy to identify and important for species identification, such as *C. noliformis,* it seems more appropriate to maintain it as a category in the classification of cnidae.

Furthermore, we believe that the visibil-

ity of an internal rod may not be a suitable trait to distinguish all heteronemes and haplonemes—two categories that include the great majority of nematocysts. This opinion, however, does not deny that further improvements in the definitions of the nematocysts categories may be needed in the future.

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