

DANIÈLE CARRÉ*, CLAUDE CARRÉ* and CLAUDIA E. MILLST†

NOVEL CNIDOCYSTS OF NARCOMEDUSAE AND A MEDUSIVOROUS CTENOPHORE, AND CONFIRMATION OF KLEPTOCNIDISM

Keywords: Cnidocyst, nematocyst, apotrichous isorhiza, hydrozoa, ctenophora, jellyfish

ABSTRACT. Cnidocysts have been examined from the tentacles of the ctenophore *Haeckelia rubra* (*Euchlora rubra*) and five species of hydrozoan narcomedusae (*Solmundella bitentaculata*, *Aegina citrea*, *Solmissus marshalli*, *Solmissus albescens*, and *Cunina* sp.) using TEM, both in sections and by firing whole cnidocysts onto EM grids. The study revealed that these apotrichous isorhiza cnidocysts have a novel morphology in which the intracapsular inverted tubule has five circumferential pleats when viewed in transverse section, rather than the usual three pleats. Accordingly, the definition of helicoptychoneme cnidocysts has been broadened to include both the usual three-pleated cnidocysts and these new five-pleated cnidocysts. In general, apotrichous isorhizas have subspherical capsules with a thick, bilayered wall, whose interior is nearly filled with the regularly coiled, helically folded, five-pleated inverted tubule. Upon discharge, the everted tubule is several mm long and the five circumferential pleats become manifested as five helical rows of spines running up the tubule, which has three morphologically different segments. The very short basal segment is devoid of ornamentation; the remaining proximal portion is characterized by five spirals of uniform, closely packed short spines; the long distal portion is characterized by a single spiral of regularly spaced large spines that derive from all five spirals—the five spirals are otherwise demarcated in the distal portion by 'scales' that are visible only with the electron microscope.

Introduction

During a recent ultrastructural study of the ctenophore *Haeckelia* (*Euchlora*) *rubra* (Kölliker, 1853), which has cnidocysts rather than the typical ctenophoran colloblasts on its tentacles for the capture of prey, we discovered that these ctenophore cnidocysts have a novel morphology in that the intracapsular (inverted) tubule has five circumferential pleats when viewed in transverse section (Carré and Carré, 1980a, Fig. 8). All previously described cnidocysts (from cnidarian tissue) have only three circumferential pleats, with the exception of the unusual multi-folded ptychocysts used in tube build-

ing by cerianthid anemones (Mariscal *et al.*, 1977).

It was subsequently determined that the cnidocysts of *Haeckelia rubra* are of exogenous origin (Carré and Carré, 1980a,b) and that they are acquired when the ctenophore preys on the cnidocyst-laden tentacles of hydrozoan narcomedusae (Mills and Miller, 1984). After ingestion by the ctenophore, the medusan cnidocysts are incorporated into the ctenophore's own tentacles for use in further prey capture.

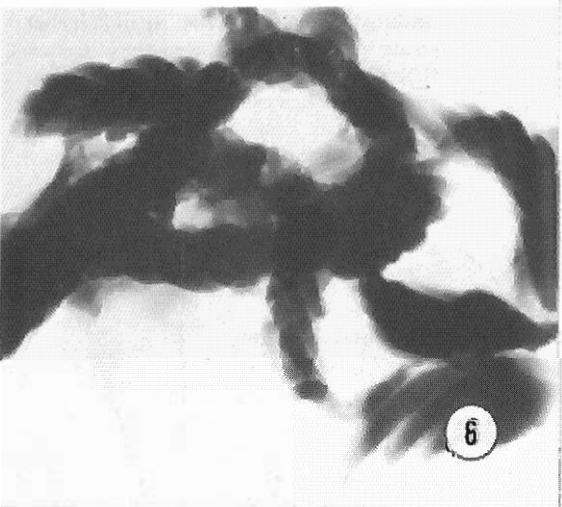
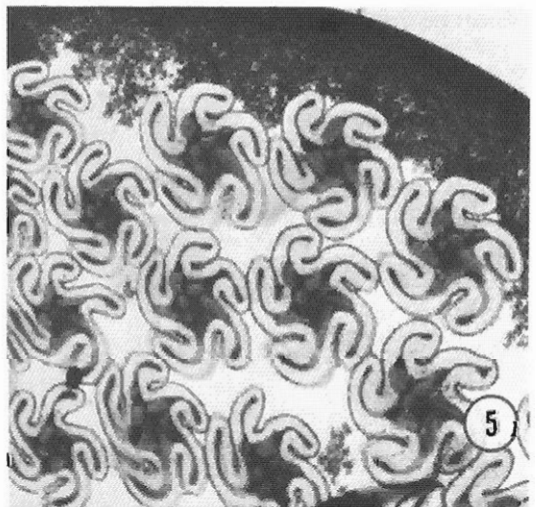
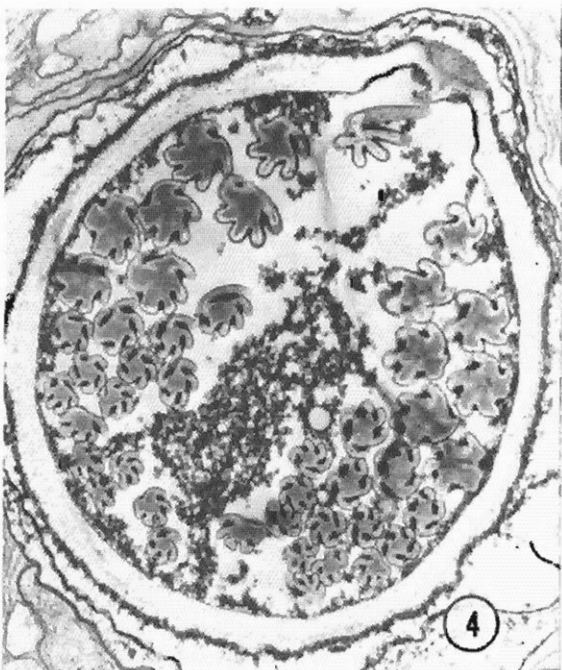
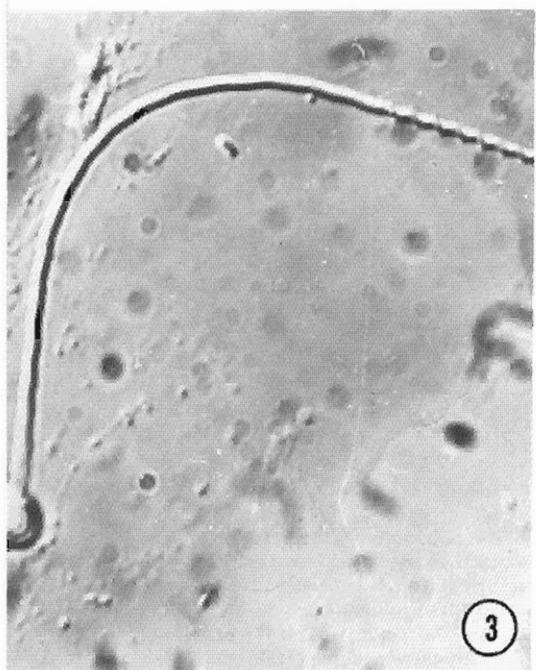
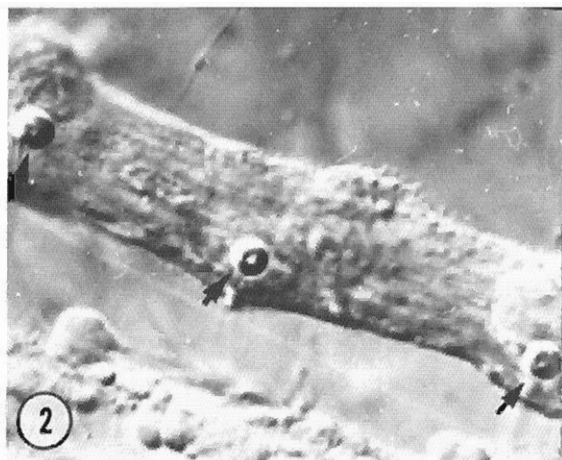
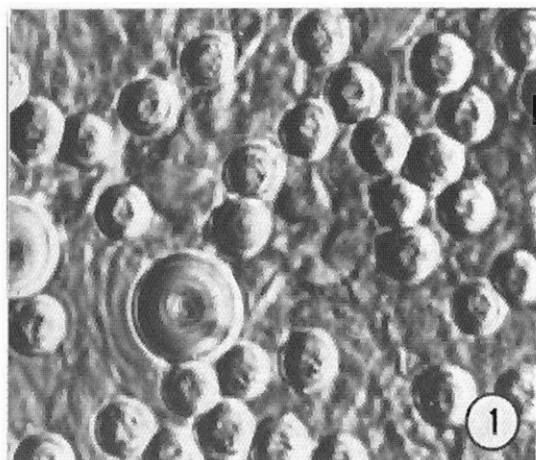
Having established the predatory link between the medusivorous ctenophore *Haeckelia rubra* and its narcomedusan prey, and having seen an indication of an unusual new morphology during the earlier study of ctenophore cnidocysts, we have now undertaken a more complete, comparative ultrastructural study of the tentacle cnidocysts of several species of narcomedusae and the cnidocysts of *H. rubra*.

The present study began as a comparison

*Station Zoologique, CEROV, 06230 Villefranche-sur-Mer, France.

†Friday Harbor Laboratories, University of Washington, 620 University Road, Friday Harbor, Washington 98250, USA.

Received 17 January 1989.



of the tubule morphologies within undischarged cnidocyst capsules, and then expanded to include the microanatomy of the ornamentation of the tubules of discharged cnidocysts.

Both *Haeckelia rubra* and all of the species of narcomedusae that we examined have two sizes of subspherical cnidocysts on their tentacles. Similar cnidocysts are also found on the exumbrellas of most narcomedusae. Based on light microscopy, narcomedusan cnidocysts have previously been described as 'atrichs' (without spines) in the narcomedusae *Polypodium hydriforme* (Lipin, 1911 as interpreted by Weill, 1934), *Cunina lativentris* (Weill, 1934), in the pelagic larva of *Solmundella bitentaculata* (Weill, 1934, species identified by C. Carré), and on the exumbrellas of *Aegina citrea* and *Solmissus marshalli* (Mackie and Mackie, 1963), or as 'apotrighous isorhizas' (having an isodiametric tubule with spines only on the distal portion) in *Aegina citrea*, *Solmissus marshalli* and *Solmissus albescens* (Mackie and Mackie, 1963; Bouillon, 1985; Purcell and Mills, 1988). In the present study we have examined the two sizes of subspherical cnidocysts found in the tentacles of several species of narcomedusae, all of which can be classified as apotrighous isorhizas in the sense of Mackie and Mackie (1963) and Mariscal (1974).

Materials and Methods

The terminology for cnidocysts used in this paper is that agreed upon at the 1986 Sym-

posium on the Biology of Nematocysts in Irvine, California (Hessinger and Lenhoff, 1988).

Animals were collected from the Bay of Villefranche, Villefranche-sur-Mer, Mediterranean Sea [*Solmundella bitentaculata* (Quoy and Gaimard, 1833); *Solmissus albescens* (Gegenbaur, 1856); and *Haeckelia rubra*] and from Friday Harbor, Washington, NE Pacific [*Aegina citrea* (Eschscholtz, 1829); *Solmissus marshalli* (Agassiz and Mayer, 1902); and *Cunina* sp.].

Cnidocysts were examined both with the light microscope and transmission electron microscope (TEM). Material to be viewed in thin section was fixed using the low osmium-glutaraldehyde pre-fixative technique of Eisenman and Alferf (1982) and embedded in Spurr's epoxy resin. Thin sections were observed on a Hitachi HU600 TEM.

Whole discharged cnidocysts were examined by TEM using Robson's (1953) technique of discharging cnidocysts directly onto coated EM grids. Tentacles were snipped off living medusae and were then gently dragged across a parlodion-carbon or collodion-coated TEM grid. Each grid was then rinsed in distilled water, air-dried, and subsequently examined in a Hitachi HU600 or Philips EM300 TEM without further preparation.

Results

Cnidocysts of *Haeckelia rubra* (Ctenophora, Family Haekeliidae) (Figs 1-6)

Plate 1. *Haekelia rubra* (Figs 1-6).

Fig. 1. Stock of apotrighous macroisorhizas and microisorhizas at the tentacle base. $\times 2000$.

Fig. 2. Stretched tentacle, showing three microisorhizas (arrows). $\times 1400$.

Fig. 3. Discharged apotrighous microisorhiza. The tubule extends many times the width of the photograph. $\times 2000$.

Fig. 4. Microisorhiza in its endocytotic vesicle, seen in longitudinal section. Note the five longitudinal pleats exhibited by each profile of the cnidocyst tubule, the coiled organization of the tubule around the axis of the capsule, and the reduction of the tubule diameter from its base (near the operculum, upper right) towards its distal end (at the opposite pole). $\times 22,000$.

Fig. 5. Profiles of a cnidocyst tubule in an undischarged macroisorhiza seen in section. Spines fill the lumen of the inverted tubule. $\times 60,000$.

Fig. 6. Inverted (undischarged) cnidocyst tubule showing the helically folded tubule supercoiled around its own axis. $\times 40,000$.

Specimens of *Haeckelia rubra* possessed both a small number of macroisorhizas (mean diameter in life of $8\ \mu\text{m}$) and many more microisorhizas ($4\ \mu\text{m}$) (Figs 1–3). These cnidocysts were regularly arranged in a row along the length of each of the two tentacles (Fig. 2) and in a cluster at the tentacle base (Fig. 1).

In sections, these two categories of cnidocysts could be differentiated by the diameters of the capsules as well as by the diameter and length of the tubule contained within—in other respects their morphologies are similar. The capsules were devoid of the cnidocil and all other accompanying structures of the cnidocyte (see Fig. 14 for a cnidocyte of *Aegina citrea*), as expected since only the naked cnidocyst capsules are incorporated within endocytotic vesicles (Fig. 4) into the tissues of the ctenophores (Carré and Carré, 1980a). The thick capsule wall is mostly electron-lucent, with a thin electron-dense outer layer (Fig. 4). The inside of the capsule is nearly filled by the inverted tubule, which is regularly coiled around the axis of the capsule. A uniform reduction in the diameter of the tubule along its length is indicated by the tubule profiles which are thicker proximally (i.e. near the operculum) and are narrower terminally (near the opposite pole of the capsule) (Fig. 4). Every transverse sec-

tional profile of the intracapsular inverted tubule shows the presence of five longitudinal pleats (Figs 4 and 5). It is also clear that the inverted tubule within the capsule is helically folded along its axis (Fig. 6).

Haeckelia rubra is a rare species in all known locations. Because of its scarcity, we have not had a chance to study the micro-anatomy of the everted tubules of its cnidocysts on grids in the electron microscope. By light microscopy, its cnidocysts correspond well to those we have seen in the five species of narcomedusae described below.

Cnidocysts from the tentacles of narcomedusae (Cnidaria, Class Hydrozoa)

We studied a total of five species of narcomedusae all of which co-occur with the ctenophore *Haeckelia rubra* (Carré and Carré, 1980a,b; Mills and Miller, 1984). The macroisorhizas and microisorhizas from all of the narcomedusae were ultrastructurally similar. The basic structure will be described in detail below for *Solmundella bitentaculata* and differences will then be reported under the other species names.

Solmundella bitentaculata (Narcomedusae, Family Aeginidae) (Figs 7–13)

Plate II. *Solmundella bitentaculata* (Figs 7–13).

Fig. 7. Undischarged macroisorhiza seen in longitudinal section, with its operculum at upper left. Note the regular packing of the inverted tubule, making more than 100 coils around the capsule axis. $\times 10,000$.

Fig. 8. Profiles of an inverted cnidocyst tubule seen in transverse section. Note the spines in the lumen of the inverted tubule. $\times 40,000$.

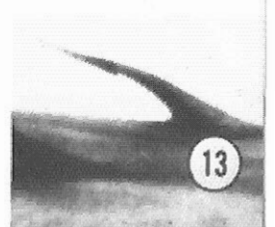
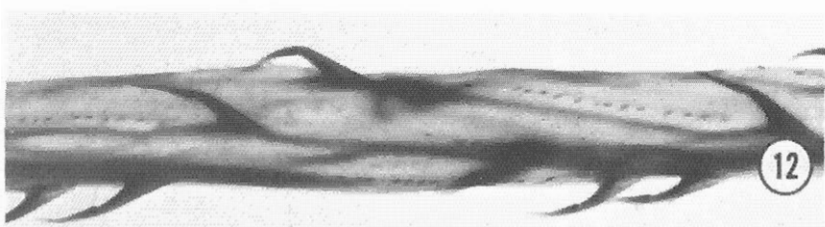
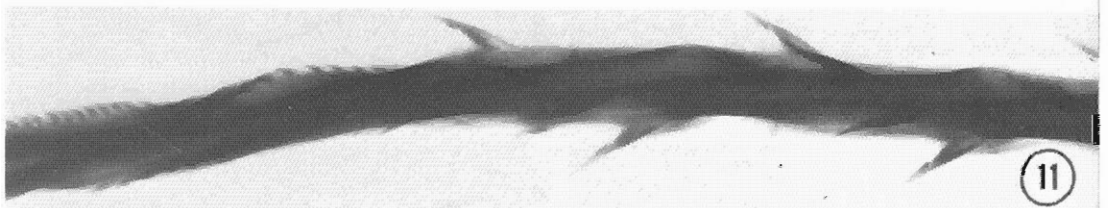
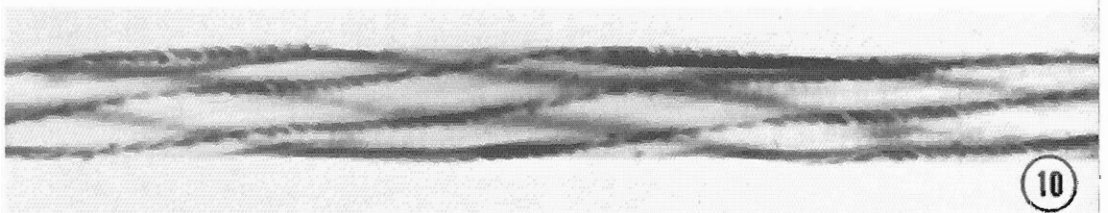
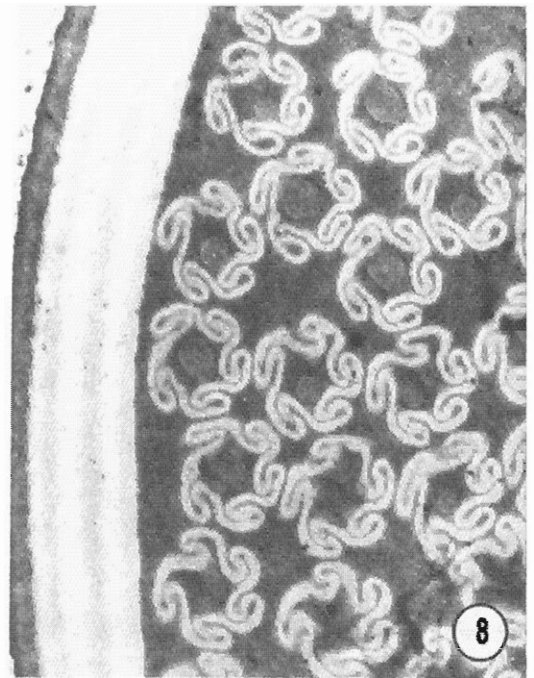
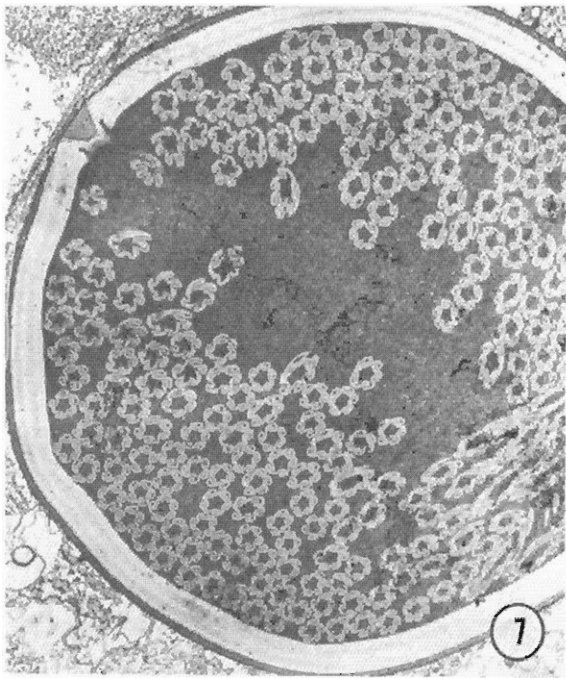
Fig. 9. Whole-mount of discharged apotrichous microisorhiza. Note the short spine-free basal segment of the tubule followed by the five spiral rows of small uniform spines that characterize the rest of the proximal portion of the tubule. $\times 9500$.

Fig. 10. Detail of the five spirals of small spines on the proximal portion of an everted apotrichous microisorhiza tubule. $\times 22,500$.

Fig. 11. Junction between the small-spined proximal portion and large-spined distal portion of an everted apotrichous isorhiza tubule. $\times 18,000$.

Fig. 12. Large-spined distal portion of an everted tubule, showing alternation of isolated long spines with series of scales, forming each of the five spirals. $\times 20,000$.

Fig. 13. Detail of a large spine in the distal portion of an everted tubule of a discharged apotrichous isorhiza. Note that the large spines in this species are barbed near the distal end. $\times 30,000$.



Two types of subspherical cnidocysts occur along the entire length of the tentacles: macroisorhizas (mean diameter in life of 10 μm) and microisorhizas (5 μm), which are more numerous. As has been described above for *Haeckelia rubra*, these two kinds of cnidocysts can be distinguished in EM sections both by capsule diameter and by the diameter and length of the intracapsular tubule.

The capsule is always delimited by a wall composed of a thin electron-dense outer layer and a thicker electron-lucent inner layer containing three or four concentric striae (Figs 7 and 8) and the inverted cnidocyst tubule is coiled within the capsule in large regular coils arranged neatly around the axis of the capsule and nearly filling it (Fig. 7). The diameter of the tubule decreases progressively from the base (near the operculum) to the distal end. In transverse section, all of the tubule profiles (Figs 7 and 8) have five pleats which run the entire length of the tubule. Longitudinal sections of the tubule show that it is helically folded along its axis as it lies coiled in the capsule.

After discharge, one can identify three segments along the length of the everted tubule: a very short basal segment, shorter than the diameter of the capsule, that is devoid of ornamentation (Fig. 9); the remainder of the

proximal portion of the tubule, which is covered by five spiralling rows of tightly packed, uniform, small spines (Figs 9–11); and a long distal portion of the tubule on which the five spirals are marked by tiny 'scales' (visible only by electron microscopy) that are spaced similarly to the short spines of the proximal portion, and interrupted by large spines that are regularly inserted at intervals along the five spirals (Figs 11 and 12). These large spines, whose free tips point basally, can be seen to form a secondary spiral that turns in the opposite sense to the primary five spirals of the tubule (Fig. 12). The large spines measure 0.6 μm in length and are visible before discharge in the lumen of the inverted intracapsular tubule (Fig. 8). The large spines of *Solmundella bitentaculata* are characteristically barbed near the distal end of each spine (Figs 12 and 13), whereas the large spines of other species described below are barbed near their bases or not at all.

Aegina citrea (Narcomedusae, Family Aeginidae) (Figs 14–19)

The tentacles have a bicnidome of macroisorhizas (mean diameter in life of 18 μm) and microisorhizas (7 μm) (diameters after

Plate III. *Aegina citrea* (Figs 14–19).

Fig. 14. Undischarged apotrichous microisorhiza seen in longitudinal section, showing the regularly coiled arrangement of the tubule with respect to the capsule axis and the progressive reduction of tubule diameter towards the base of the capsule. Note the cnidocil (C) and nucleus (N) of the cnidocyte. $\times 12,000$.

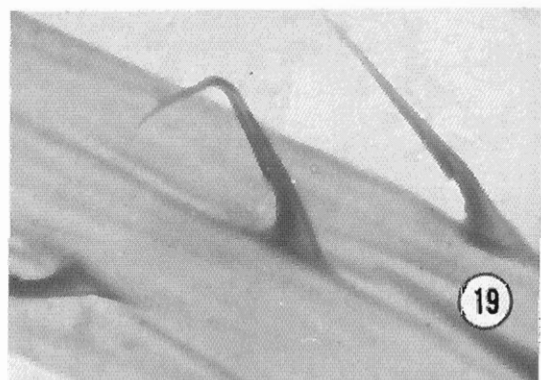
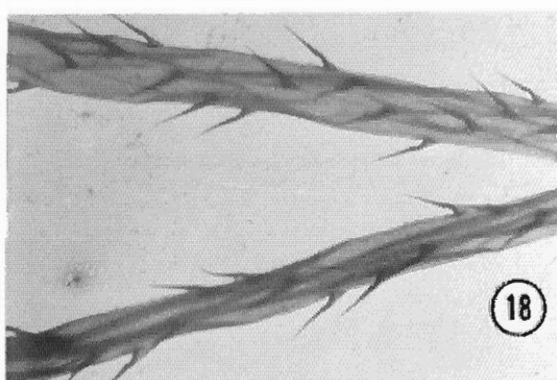
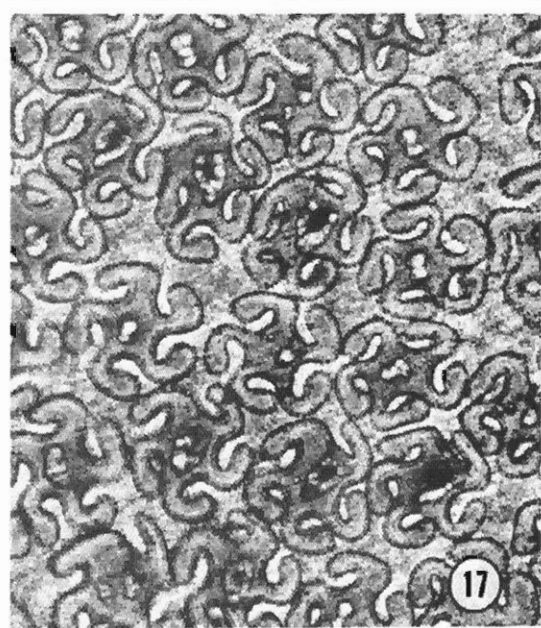
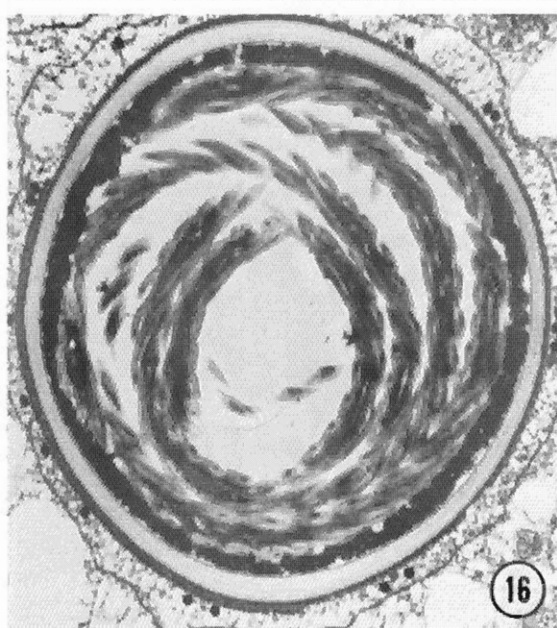
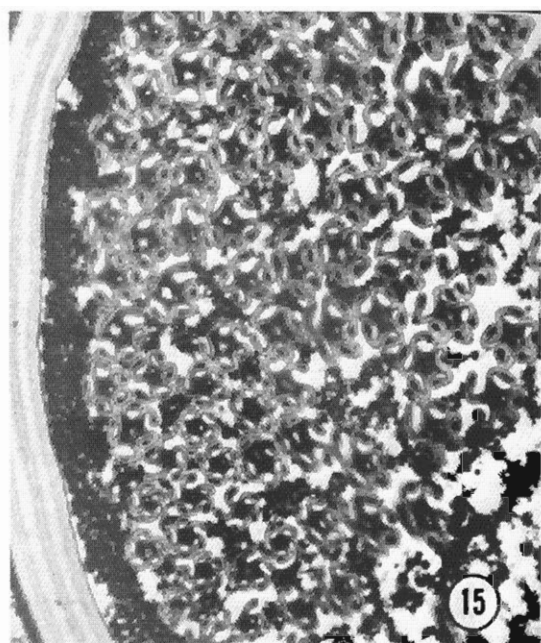
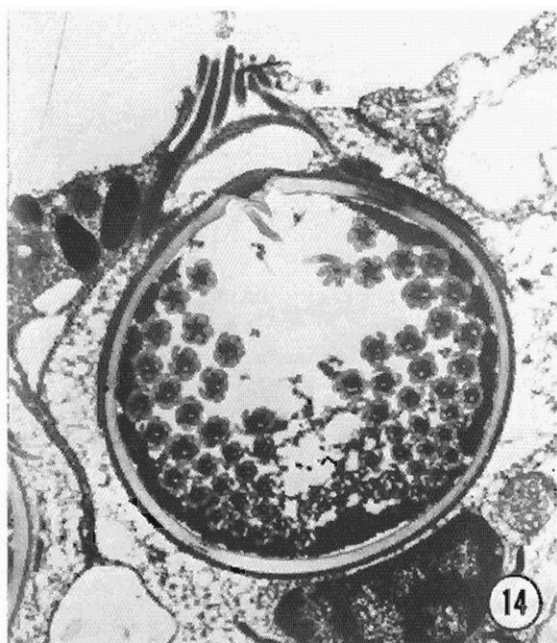
Fig. 15. Intracapsular tubule of an undischarged macroisorhiza seen in transverse section. $\times 22,000$.

Fig. 16. Undischarged apotrichous isorhiza seen in transverse section, showing both the primary coiling of the inverted tubule around the axis of the capsule and the secondary helical folding of the tubule along its axis. $\times 15,000$.

Fig. 17. Detail of the closely packed cnidocyst tubule seen in transverse section, showing the lumen of the inverted tubule obstructed by spines. $\times 40,000$.

Fig. 18. Distal portions of the everted tubules of two discharged apotrichous isorhizas, showing large spines. $\times 5000$.

Fig. 19. Detail of large barbed spines from the distal portion of an everted tubule. Note that the overall morphology of these spines is different than is seen in *Solmundella bitentaculata* (Fig. 13). Scales that run between the large isolated spines and demarcate the five spirals of spines do not show; the large spines form a single secondary spiral turning in the opposite sense. $\times 25,000$.



fixation 13 and 4.5 μm , respectively). The capsule wall morphology (Fig. 15), intracapsular coiling of the tubule (Figs 14 and 15), and helical folding (Fig. 16) of the inverted tubule are as described for *Solmundella*. Up to 200 coils of the intracapsular tubule have been counted in some macroisorhizas. The tubule has the characteristic five pleats in transverse section (Fig. 17).

Everted tubules show the same three segments along their lengths as described above: a very short non-ornamented basal area, the remainder of the proximal portion with five rows of uniform small spines, and the long distal portion with intermittent large spines. These large spines measure 1.4 μm in length; they are barbed near the base of each spine (Figs 18 and 19), making them morphologically distinct from the long spines of *Solmundella bitentaculata*.

Solmissus marshalli (Narcomedusae, Family Cuninidae) (Figs 20–24)

The tentacles have a bicnidome of macroisorhizas (mean diameter in life of 22 μm) and microisorhizas (8 μm). Sections of undischarged cnidocysts (Figs 20 and 21) show them to be basically as described above. The everted tubules (Figs 22–24) again show the

three familiar segments, but the large spines (0.8 μm) on the distal portion are simple and unbarbed (Fig. 24).

Solmissus albescens (Narcomedusae, Family Cuninidae) (Figs 25–26)

Cnidocysts of this narcomedusan were examined with the light microscope and as whole-mounts on grids by TEM, but not in sections. The tentacles have a bicnidome of macroisorhizas (mean diameter in life of 24 μm) and microisorhizas (9 μm). The proximal segments (Fig. 25) of the everted tubule are as in the other narcomedusae, but the distal portion is characterized by large spines that are stouter and shorter (0.45 μm in length) (Fig. 26) than in the other narcomedusae studied. The large spines of *Solmissus albescens* are unbarbed like those of its congener, *S. marshalli*.

Cunina sp. (Narcomedusae, Family Cuninidae)

We looked at the cnidocysts of this species only as whole-mounts on TEM grids. Like the two species of *Solmissus* above, the large spines on the distal portion of the tubule were simple and unbarbed.

Plate IV. *Solmissus marshalli* (Figs 20–24) and *Solmissus albescens* (Figs 25–26).

Fig. 20. Undischarged microisorhiza seen in section. $\times 12,000$.

Fig. 21. Intracapsular tubule of an undischarged apotrichous isorhiza seen in longitudinal section, showing helical folding of the coiled inverted tubule along its axis. $\times 30,000$.

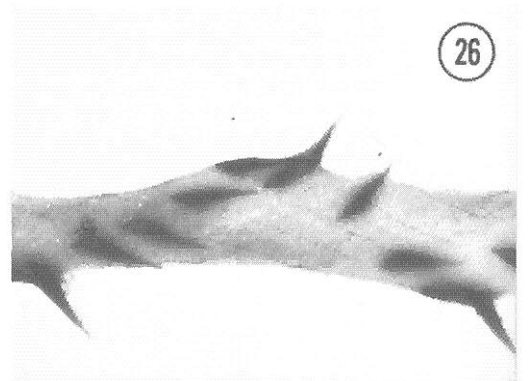
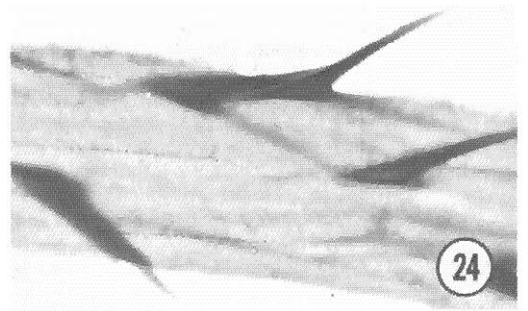
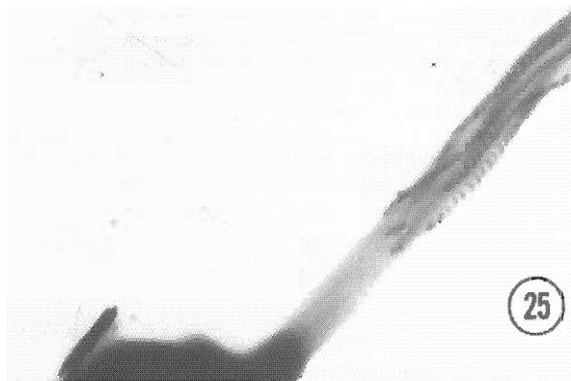
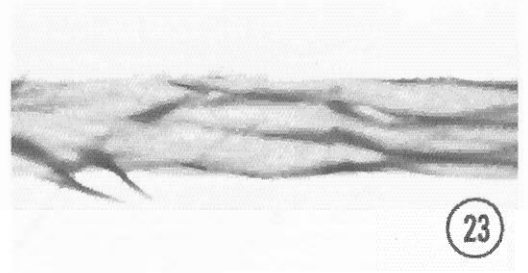
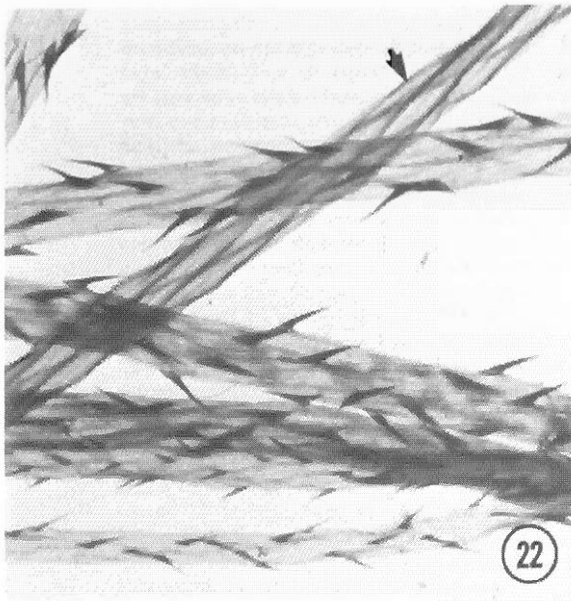
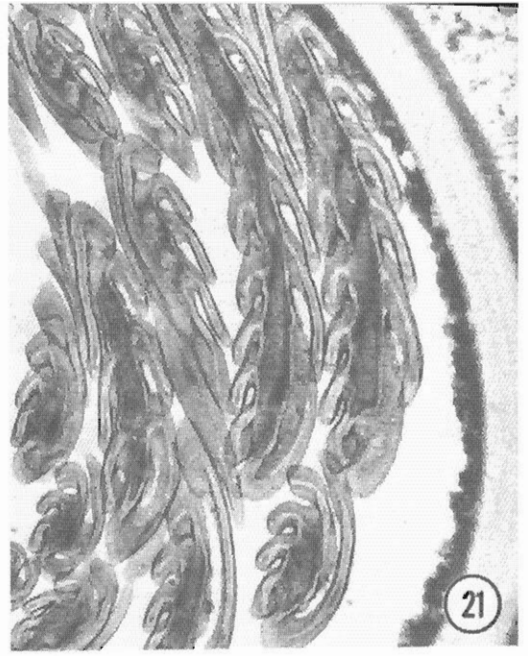
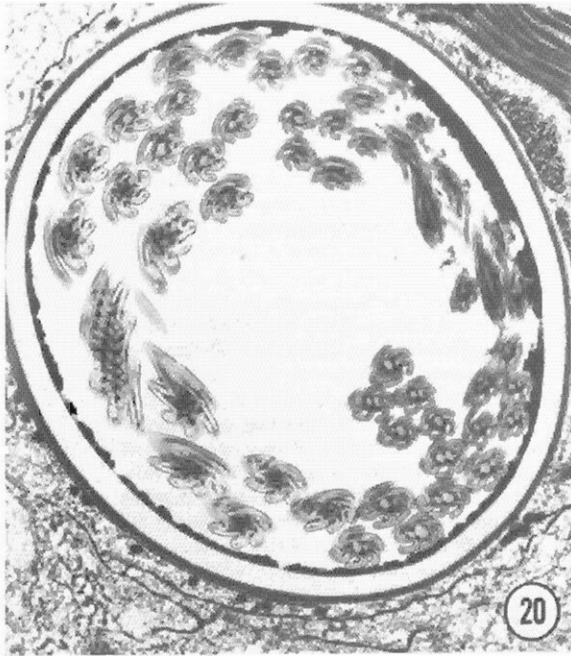
Fig. 22. Everted tubules of several discharged apotrichous isorhizas. Uniform small spines characterize the proximal portion of one tubule (arrow), whereas the other tubules are distal portions characterized by widely-spaced large spines. $\times 5000$.

Fig. 23. Junction between the small-spined proximal portion and large-spined distal portion of an everted apotrichous isorhiza tubule. $\times 8500$.

Fig. 24. Detail of distal large-spined portion of an everted tubule, showing alternation of isolated long spines with series of small scales, forming each of the five spirals. Note that the long spines in this species are not barbed. $\times 25,000$.

Fig. 25. Whole-mount of a discharged capsule and its everted tubule, showing the short spine-free basal segment preceding the rest of the proximal portion of the tubule with its five spirals of uniform small spines. $\times 8000$.

Fig. 26. Detail of distal large-spined portion of an everted tubule, showing alternation of isolated long spines with series of small scales, forming each of the five spirals. Note that the large unbarbed spines in this species are morphologically distinct from those of *Solmissus marshalli* (Fig. 24). $\times 15,000$.



Discussion

Mariscal *et al.* (1974, 1977) divided all cnidarian cnidocysts into two primary groups, based on the morphologies of their tubules: helicoptychonemes (which constitute nearly all cnidocysts), in which the undischarged inverted tubule is helically folded to form multiple pleats in length and three pleats in circumference, and heteroptychonemes (of which ptychocysts from the cerianthid anemones are the sole example), in which the undischarged inverted thread is not helically folded, with a variable number of pleats in circumference, but none in length.

From narcomedusan cnidarians and from the medusivorous ctenophore *Haeckelia rubra*, we have now described the ultrastructure of a new kind of cnidocyst, which has a helically folded tubule, as seen in longitudinal section, with five circumferential pleats, as seen in transverse section. Upon discharge, the five circumferential pleats are manifested as five longitudinal spirals of spines. Based on this morphology, it is now necessary to modify the Mariscal *et al.* (1977) classification of cnidocysts, or, as we prefer, to broaden the definition for helicoptychonemes to 'cnidocysts in which the undischarged tubule is helically folded to form multiple pleats in length and three or five pleats in circumference'.

All of the narcomedusan (and ctenophore) cnidocysts that we examined have similar morphologies. They have subspherical capsules with a thick wall composed of both an electron-dense outer layer and an electron-lucent inner layer, and whose interior is nearly filled by the regularly coiled, helically folded, five-pleated inverted tubule. It can be seen both in longitudinal sections of the undischarged cnidocysts (*see* Figs 4 and 14), and by following the very long everted tubules across EM grids, that the tubules are very gradually anisodiametric, progressively tapering distally to about half of their basal diameter. The everted tubule has three segments, based on ornamentation: a basal segment of a few micrometers that is always shorter than the capsule diameter and is devoid of ornamentation; the remaining proximal portion, which is several tens of micrometers in length and is characterized by five spirals of uniform, closely packed short spines; and the long distal portion,

which measures several thousand micrometers in length and is characterized by widely-spaced large spines inserted along the five spirals that are otherwise demarcated by scales that are visible only with the electron microscope. The large spines are secondarily aligned to form a single spiral that turns in the opposite sense to the five primary spirals from which they derive.

Even though these cnidocysts have gradually tapering anisodiametric tubules, we feel that they should still be categorized as 'isorhizas' (isometric tubule). This is consistent with Mariscal's (1974) recommendation that electron microscopical details not be grounds for altering the well-known classification of cnidocysts of Weill (1934) and subsequent authors. In a similar vein, it should be noted that our electron microscopical observations have shown that apotrichous isorhizas, in fact, have two sizes of spines along their tubules—very small spines along the proximal portion that are not visible in the light microscope, as well as the large easily seen spines on the distal portion of the tubule.

The only previous ultrastructural work on narcomedusan cnidocysts are the incidental observations of Raikova (1978). She published a single electron micrograph of an oblique section through an undischarged cnidocyst from *Polypodium hydriforme* in which the bilayered capsule wall was evident, as was the helical folding of the inverted tubule. Raikova was also able to see spines within the lumen of the inverted tubule and stated that the tubule could no longer be considered to be unarmed (atrichous), as previously suggested by light microscopic studies on the cnidocysts of this species (Lipin, 1911; Weill, 1934). The five circumferential pleats that are uniquely characteristic of narcomedusan cnidocysts were not evident in Raikova's published TEM section.

It is interesting that all five of the species of narcomedusae that we have investigated can be distinguished from one another by the morphologies of the long spines on the distal portion of their discharged cnidocyst tubules. This difference also holds at the Family level, in that the two investigated members of the Aeginidae (*Solmundella bitentaculata* and *Aegina citrea*) have long barbed spines and the three investigated members of the Cuniidae (*Solmissus marshalli*, *S. albescens*, and

Cunina sp.) have simple unbarbed tubules. Many more species will have to be examined before it can be determined whether spine morphology is a taxonomically useful character.

The tubules of narcomedusan cnidocysts are exceptionally long, measuring up to 8.5 μm (Mackie and Mackie, 1963; Mills and Goy, 1988). The tubule length and unusual spination pattern may be adaptations for adhering to gelatinous prey. Narcomedusae are usually found in oceanic waters and although their biology is not well understood, they seem to feed mostly, if not exclusively, on gelatinous prey, including other species of medusae, pteropods, salps, and doliolids (Purcell and Mills, 1988; Mills and Goy, 1988; R. J. Larson, personal communication).

The ultrastructural evidence presented here for identical morphologies between the cnidocysts of narcomedusae and those of the medusivorous *Haeckelia rubra* constitutes supplementary proof that this ctenophore obtains its cnidocysts as kleptocnidae from prey narcomedusae. All *H. rubra* have similarly-shaped apotrichous cnidocysts and the sizes of these cnidocysts remain consistent, but different, within each of the three known

geographic locations for *H. rubra* (Mediterranean Sea, west coast of the United States, and Sea of Japan). The size difference between regions implies that different prey species may be eaten according to their availability in each region. It is likely that the prey species of *H. rubra* can be precisely identified in the future by examining spine morphology both on the everted tubules of *H. rubra* cnidocysts and on the everted tubules of those species of narcomedusae with which they coexist.

Acknowledgements

C.E.M. was partially supported by a fellowship from the International Exchange of Scientists Program between the National Science Foundation (USA) and the Centre National de la Recherche Scientifique of France. Facilities were provided by the Directors of the Station Zoologique of Villefranche-sur-Mer, France, the Station Biologique of Roscoff, France, and the Friday Harbor Laboratories, USA. Thanks to T. E. Schroeder for instructing C.E.M. on use of the transmission electron microscope and for suggestions that greatly improved the manuscript.

Glossary

- Bicnidome.** A cnidome consisting of two types of cnidocysts.
- Cnidocil.** Flagellum or flagellar derivative, usually accompanied by a complex of stereocilia and microvilli, on the apical portion of a cnidocyte, whose purpose appears to be mechanosensory.
- Cnidocyst** (also known as cnida or nematocyst). An intracellular secretory product produced by members of the phylum Cnidaria, consisting of a capsule containing a highly-folded eversible tubule.
- Cnidocyte.** The cell that synthesizes the cnidocyst, and from which the cnidocyst discharges.
- Cnidome.** An inventor 9 of the different types of cnidocysts present in an organism.
- Colloblast.** A type of adhesive cell produced by members of the phylum Ctenophora, consisting of a hemispherical head covered with adhesive granules and two filaments (one straight and the other spiral) that anchor the cell into the tentacular epidermis.
- Helicoptychoneme.** A cnidocyst in which the undischarged inverted tubule is helically folded to form multiple pleats in length and three to five pleats in circumference.
- Heteroptychoneme.** A cnidocyst in which the undischarged inverted tubule is not helically folded, with a variable number of pleats in circumference, but none in length.
- Kleptocnidae.** Cnidocysts (cnidae) that are not endogenously produced, but are obtained by feeding on organisms that produce cnidocysts.
- Ptychocyst.** A type of cnidocyst lacking any kind of spines, in which the inverted tubule is not helically folded, but is packed into the capsule as a folded flattened belt that expands in only two dimensions upon discharge; used in tube construction by cerianthid anemones.

References

- Bouillon, J. 1985. Essai de classification des hydropolypes-hydrôméduses (Hydrozoa-Cnidaria). *Indo-Malayan Zool.*, 1, 29-243.

- Carré, C. and Carré, D. 1980a. Les cnidocystes du cténoptère *Euchlora rubra* (Kölliker, 1853). *Cah. Biol. mar.*, **21**, 221–226.
- Carré, D. and Carré, C. 1980b. On triggering and control of cnidocyst discharge. *Mar. Behav. Physiol.*, **7**, 109–117.
- Eisenman, E. A. and Alfert, M. 1982. A new fixation procedure for preserving the ultrastructure of marine invertebrate tissues. *J. Microsc.*, **125**, 117–120.
- Hessinger, D. A. Lenhoff, H. F. (eds) 1988. *The Biology of Nematocysts*. Academic Press, San Diego, 600.
- Lipin, A. 1911. Die Morphologie und Biologie von *Polypodium hydriforme* Uss. *Zool. Jahrb. (Anat.)*, **31**, 317–426.
- Mackie, G. O. and Mackie, G. V. 1963. Systematic and biological notes on living hydromedusae from Puget Sound. *National Museum of Canada Bulletin No. 199, Contributions to Zoology*, 63–84.
- Mariscal, R. N. 1974. Nematocysts. In *Coelenterate Biology: Reviews and New Perspectives* (eds L. Muscatine and H. M. Lenhoff), pp. 129–178. Academic Press, New York.
- Mariscal, R. N., Conklin, E. J. and Bigger, C. H. 1977. The ptychocyst, a major new category of cnida used in tube construction by a cerianthid anemone. *Biol. Bull.*, **152**, 392–405.
- Mills, C. E. and Goy, J. 1988. *In situ* observations of the behavior of mesopelagic *Solmissus narcomedusae* (Cnidaria, Hydrozoa). *Bull. Mar. Sci.*, **43** (3): 739–751.
- Mills, C. E. and Miller, R. L. 1984. Ingestion of a medusa (*Aegina citrea*) by the nematocyst-containing ctenophore *Haeckelia rubra* (formerly *Euchlora rubra*): phylogenetic implications. *Mar. Biol.*, **78**, 215–221.
- Purcell, J. E. and Mills, C. E. 1988. The correlation between nematocyst types and diets in pelagic hydromedusae. In *The Biology of Nematocysts* (eds D. A. Hessinger and H. M. Lenhoff) pp. 463–485. Academic Press, San Diego.
- Raikova, E. V. 1978. Electron microscopical investigation of the nematocyst development in the parasitic stolon of *Polypodium hydriforme* Ussov (Coelenterata). *Tsitologiya S.S.S.R.*, **20**, 384–390. (In Russian, with English Abstract.)
- Robson, E. A. 1953. Nematocysts of *Corynactis*: the activity of the filament during discharge. *Quart. J. Microscop. Sci.*, **94**, 229–235.
- Weill, R. 1934. Contribution à l'étude des Cnidaires et de leurs nématocystes. *Trav. Stat. Zool. Wimereux*, 10–11, 1–701.