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First record of the genus *Candelabrum* (Cnidaria, Hydrozoa, Athecata) from the Mid-Atlantic Ridge: a description of a new species and a review of the genus

by Michel SEGONZAC and Willem VERVOORT

Abstract. — Two species of *Candelabrum* (Cnidaria, Hydrozoa, Athecata) have been discovered and collected at two hydrothermal areas of the Mid-Atlantic Ridge with French and American submersibles during five cruises in 1988, 1993 and 1994. The first, *Candelabrum serpentarii* nov. sp., has been found at the Snake Pit site (23°N, 3500 m depth) and represents an undescribed species. The second, *Candelabrum phrygium* (Fabricius, 1780), collected at the Lucky Strike site (37°N, 1700 m depth), is known to have a circumarctic distribution. In spite of great differences in depth of occurrence, considerable morphological similarities exist between the new species and the intertidal species *C. cocksii* (Vigurs, 1849). This discovery has given rise to a review of the genus *Candelabrum*. In addition, ecological remarks on these three species are presented.

Keywords. — Hydrothermal vents, Mid-Atlantic Ridge, Hydrozoa, *Candelabrum*, biogeography, plate tectonics.

Premières observations du genre *Candelabrum* (Cnidaria, Hydrozoa, Athecata) sur des zones hydrothermales de la dorsale médio-atlantique : description d'une nouvelle espèce et revue du genre

Résumé. — Deux espèces de *Candelabrum* (Cnidaria, Hydrozoa, Athecata) ont été découvertes et récoltées sur deux aires hydrothermales de la dorsale médio-atlantique grâce aux sous-marins français et américains au cours de cinq missions en 1988, 1993 et 1994. La première, *Candelabrum serpentarii* nov. sp., récoltée sur le site du Snake Pit (23° N, 3 500 m), est une espèce non décrite. La seconde, *Candelabrum phrygium* (Fabricius, 1780), récoltée sur le site Lucky Strike (37° N, 1 700 m), est connue pour sa répartition circumarctique. En dépit des différences de profondeur des habitats, on remarque de fortes ressemblances morphologiques entre l'espèce non décrite et l'espèce littorale connue *C. cocksii*. Ces découvertes donnent lieu à une revue des espèces du genre *Candelabrum*. Quelques remarques écologiques sur ces trois espèces sont présentées.

Mots-clés. — Sources hydrothermales, dorsale médio-atlantique, Hydrozoaire, *Candelabrum*, biogéographie, tectonique des plaques.

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INTRODUCTION

The first Atlantic hydrothermal communities found in the axial valley of the Mid-Atlantic Ridge: the TAG (Trans-Atlantic Geotraverse) area at 26°N (Fig. 1) and 3700 m depth, and the Snake Pit area at 23°N and 3500 m depth, have been described respectively by GALKIN *et al.* (1990) and SEGONZAC (1992). At the Snake Pit area, an undescribed species of *Candelabrum*

was collected by the submersible *Nautile* during the French cruise Hydrosnake in June 1988 and several other specimens were seen next to the active edifices. In June 1993, another specimen was collected at the same site with the submersible *Alvin* during the American-French cruise MAR 93. *In situ*, this organism, belonging to the class Hydrozoa, appeared as a whitish gelatinous pen, undulating according to the water movements. Fixed on pillow lava or sulfide rock, it is about 10 cm long and presents, on its base, pure white, clustered granulations (gonophores). It was the first time that such organism, known from shallower waters, had been observed among the hydrothermal communities.

Sampling of the hydrothermal fauna of the newly found Lucky Strike area (SW Azores Islands, 37°N, 1700 m depth), realized in May 1993 with the submersible *Alvin* (LANGMUIR *et al.*, 1993), allowed the collection of another species of hydroid, known as *Candelabrum phrygium* (FABRICIUS, 1780), among a sample of the mussel *Bathymodiolus* sp. During the French cruise Diva 2 (June 1994), several other specimens were observed and collected at the same location with the submersible *Nautile*.

In the Hydroida (hydropolyps-hydromedusae) of the Hydrozoa, the subclass Athecatae (Anthomedusae) is principally characterized by the absence of a distinct hydrotheca around the polyp. It comprises c. 50 families that are mostly marine. Among these families, the Candelabridae has only two genera: *Candelabrum* de Blainville, 1830, and *Monocoryne* Broch, 1910; *Candelabrum* has 14 species. The species of *Candelabrum* discovered at the Snake Pit is described here. It presents surprising morphological resemblances with the species *Candelabrum cocksii* (VIGURS,

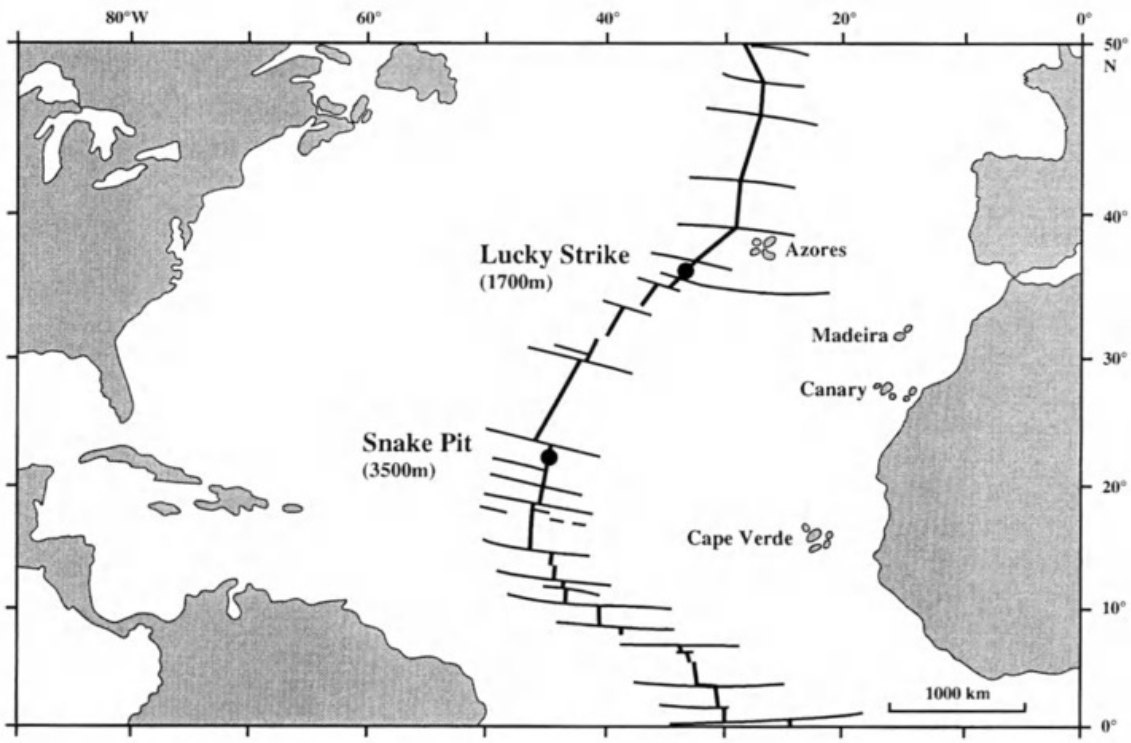


FIG. 1. — Map of the northern Atlantic showing the position of the Mid-Atlantic Ridge and hydrothermal sites Snake Pit (locality for *Candelabrum serpentarii* nov. sp.) and Lucky Strike [locality for *Candelabrum phrygium* (FABRICIUS, 1780)].

Carte de l'Atlantique Nord indiquant la position de la dorsale médio-atlantique et des sites hydrothermaux du Snake Pit (localité de Candelabrum serpentarii *nov. sp.) et de Lucky Strike [(localité de* Candelabrum phrygium *(FABRICIUS, 1780)].*

1849), well known from intertidal areas. The species *Candelabrum phrygium* (FABRICIUS, 1780), collected at Lucky Strike, is known to have a circumarctic distribution. These new data prompted us to review the genus, while in the course of our investigation it became imperative to compare the specimens from the Mid-Atlantic Ridge with the intertidal species. Ecological observations were added where appropriate.

Discussion of the trophic behaviour and hypothesis about the distribution of these two hydrothermal species on active sites are presented.

MATERIAL

Specimens of *Candelabrum serpentarii* nov. sp. were obtained from the Snake Pit hydrothermal vents area (Mid-Atlantic Ridge, 23°23'N-47°56'W, 3500 m depth), first during the French cruise Hydrosnake, submersible *Nautile*/N. O. *Nadir*, June 12-July 14, 1988, chief scientist: Catherine MÉVEL (Université Paris-VI); second by American cruise MAR 93, submersible *Alvin*/R. V. *Atlantis II* and J. *Charcot*, June 5-30, 1993, chief scientists: Cindy VAN DOVER (WHOI) and Aline FIALA (Université Paris-VI). The photograph of that species (Fig. 3A) originates from the same locality and was provided by the French cruise Gravinaut, *Nautile*/N.O. *Nadir*, September 7-October 4, 1993, chief scientist: Jacques DUBOIS (Institut de Physique du Globe, Paris).

The specimens of *Candelabrum phrygium* were obtained from the Lucky Strike hydrothermal vents area (Mid-Atlantic Ridge, 37°17'N-32°16'W, 1626-1700 m depth), first by the American cruise Lucky Strike, *Alvin*/R. V. *Atlantis II*, May 27-June 4, 1993, chief scientist: Charlie LANGMUIR (Lamont-Doherty Earth Observatory); second by the French cruise Diva 2, *Nautile*/N.O. *Nadir*, June 2-July 4, 1994, chief scientists: Daniel DESBRUYÈRES and Anne-Marie ALAYSE (IFREMER).

In addition, both species and their environment were observed *in situ*, on videotape and on photographs taken by the submersible *Nautile*.

Some specimens of *Candelabrum cocksii* were placed at our disposal by Dr A. CASTRIC-FEY (Collège de France, Concarneau) and came from her private collection. Specimens of *Candelabrum phrygium* and some of the other species of *Candelabrum* were studied by one of us (W. V.) in the collections of The Natural History Museum, London.

REVIEW OF THE GENUS

CANDELABRUM de Blainville, 1830

Candelabrum de Blainville, 1830: 284; type, by monotypy: *Lucernaria phrygia* Fabricius, 1780 (= *Arum* Vigurs, 1849: 90, type, by monotypy: *Arum Cocksii* Vigurs, 1849; *Myriothela* M. Sars, 1851: 126, type, by monotypy: *Myriothela arctica* M. Sars, 1851; *Spadix* Gosse, 1853b: 125, type, by monotypy: *Spadix purpurea* Gosse, 1853b; *Acandela* Stechow, 1920: 45, type, by monotypy and original designation: *Myriothela mitra* Bonnevie, 1898).

DESCRIPTION

Solitary hydroids of worm-like appearance; length varied, between 10 and 300 mm total body length. Body divisible into three regions: a basal region (foot, hydrorhiza) serving attachment of the specimen, a blastostyle bearing region and a distal body portion, usually tapering, having a small, circular mouth at its extreme end. Shape and development of foot differing in the various species and with age: flattened and lobed to a varied extent or root-shaped, being in that case a conical, pointed part of the body. Attaching filaments occur on both lobed and root-shaped types of foot, usually with chitinous discs for attachment to solid substrates. Whole or part of foot in some species with chitinous sheath, also including the attaching discs and occasionally of considerable thickness. Blastostyle region only distinguishable in sexually mature individuals, usually swollen compared to distal part of body; blastostyles are tubular to conical prolongation of the body wall bearing male and/or female cryptomedusoid gonophores; body cavity may continue in blastostyle; these arranged in one or several whorls or irregularly distributed. Dioecious, but in *C. cocksii* and *C. serpentarii* nov. sp. monoecious with hermaphroditic blastostyles. Development of larva to actinula in female gonophore, one or more may be present. Feeding tentacles (claspers) attaching to gonophore with developing egg described for one species (*C. cocksii*), may also be present on others. Distal part of body (trunk) as long as or much longer than blastostyle bearing region, usually set with numerous small, capitate tentacles. Occasionally tentacles continue downwards into the blastostyle bearing region and/or occur on the blastostyles. Some species have modified tentacles on blastostyle or foot. Enteron with folds of endoderm. Cnidome composed of (usually two types of) desmonemes, haplonemes (probably atrichous), heteronemes and stenoteles.

REMARKS

The type species was considered by FABRICIUS (1780) to be a species of stalked jellyfishes (Stauromedusae) and described as *Lucernaria phrygia*. DE BLAINVILLE (1830, 1834) placed it near the genus *Sipunculus*, now in the phylum Sipunculida, instituting for its reception the genus *Candelabrum*. M. SARS (1851) redescribed the species as *Myriothela arctica;* in 1857, M. SARS reported on the rediscovery of some of FABRICIUS's material in Copenhagen and referred FABRICIUS's species to *Myriothela*, this generic name being preferred by M. SARS (1871) and ALLMAN (1874). L. AGASSIZ (1860-1862) regarded *Candelabrum* de Blainville, 1830 and *Myriothela* M. Sars, 1851, as being congeneric, and also recognized *Candelabrum* as the oldest available name. The genus name *Arum* was used by VIGURS (1849) for his species *Arum Cocksii*, later on redescribed by GOSSE (1853b) as *Spadix purpurea. Spadix* Gosse, 1853(b) thus is a junior subjective synonym of *Arum* Vigurs, 1849. There are only two main characteristics separating *Arum* from the species of *Candelabrum (cf.* STECHOW, 1922: 144; 1923: 38): the development of the foot and the presence of claspers. The morphology of the foot in several species of *Myriothela* (= *Candelabrum*) has been studied by MANTON (1940). It seems clear that a foot surrounded by a continuous and conspicuous sheath of chitinous periderm begins with the development of such perisarc surrounding the place of contact between modified tentacles and the substrate, the tentacles being in many instances lobed extrusions of the foot (our observations). The chitinous perisarc, at least in *C. cocksii*, may ultimately fuse to form a continuous sheath

covering the foot, thinning out distally and merging with the thin cuticle covering the ectoderm. It thus appears that the morphology of the foot is dependent upon the age of the specimen and most likely also on the substrate and considering the limited number of species that has adequately been studied, in this respect it is, in our opinion, unsuitable for generic distinction. The use of the generic name *Candelabrum* has recently been reintroduced by HAND & GUILLIAM (1951), PREVOT (1959) and CORNELIUS (1977).

C. cocksii so far is the only species in which the presence of claspers has been established; they definitely seem to be absent from *Candelabrum phrygium*, the only remaining species in *Candelabrum* of which the life history has to some extent been studied. All other species (with the exception of course of *C. cocksii*) have been studied from preserved material. The presence of claspers, considered by MANTON (1940) to represent modified tentacles (for attachment) cannot altogether be excluded in such insufficiently known species of *Candelabrum*. It seems illogical to separate *Arum* from *Candelabrum* on the morphology of the foot, which is dependent upon development and substrate, and the presence or absence of claspers, a character which cannot be properly evaluated in all species of *Arum* and *Candelabrum*. We have therefore sunk *Arum* Vigurs, 1849, into the synonymy of *Candelabrum* de Blainville, 1830, the latter having priority. We thus follow CORNELIUS (1977) in referring *Arum*, *Myriothela* and *Spadix* to *Candelabrum*.

The genus *Acandela* Stechow, 1920, was instituted by STECHOW for *Myriothela mitra* Bonnevie, 1898, the only diagnostic character being the absence of (clavate) tentacles on the distal portion of the body. BONNEVIE's *Myriothela mitra* may be based on a single specimen (the number is not stated in the description), moreover it was obtained from deep water (2220 m), so it probably had a rough assent in a trawl net. The possibility that the specimen consequently was damaged, resulting in the loss of tentacles, cannot be excluded and has in fact been described in other species of *Candelabrum* (*e.g. C. austrogeorgiae*). We have relegated *Acandela* to the synonymy of *Candelabrum*.

REVIEW OF THE SPECIES AND DESCRIPTIONS

Candelabrum arcticum (M. Sars, 1851)

Myriothela arctica M. Sars, 1851: 126, 131, 134 [= *Candelabrum phrygium*[1] (Fabricius, 1780)].

Candelabrum australe (Briggs, 1928)

Myriothela australis Briggs, 1928: 307-312, Pl. 32, Pl. 33 Fig. 3, Pl. 34 Figs 1-4: BRIGGS, 1929: 244-264, Figs 1-4, Pls 42-44; BRIGGS, 1939: 10; MANTON, 1940: 280 et seq., Fig. 8a; DAKIN, BENNETT & POPE, 1948: 208; RALPH, 1966: 158, 162.

Candelabrum australe — HAND & GWILLIAM, 1951: 208.

LOCALITY. — Found "on the lobes of the thallus of a seaweed thrown up on the sandy beach of Maroubra Bay near Sydney, N. S. W." (BRIGGS, 1928).

1. See discussion of synonymy of this species.

REMARKS

Description and studies on gonophore development based on forty specimens from the locality given above; no accurate depth record of the living specimens is given. Length ranging from 4 to 30 mm, body elongated, basally cylindrical; blastostyle bearing region narrowed, "marked by a series of well defined longitudinal furrows with finer transverse striations". Distal portion of body, above blastostyle region, covered by capitate tentacles. Blastostyles close together, abundant, unbranched, elongate, cylindrical and clavate at distal extremity, there bearing a bundle of tentacles differing from those on body by trumpet-shaped head and larger size, having a long, slender, cylindrical stem. Male and female blastostyles on separate individuals (dioecious). Female blastostyle with 3-4 mature and 6-8 immature gonophores on proximal portion; apex with 8-10 tentacles. Male blastostyles smaller and more numerous, some 15 being present; apex with 6-9 tentacles. "Male and female gonophores have an apical opening representing the velar aperture. The proximal end of the hydranth is truncated and is attached to the substrate by a number of tentacle-like filaments which constitute the hydrorhiza. At the truncated end of each of these short rooting processes is a small, circular, chitinous disc of dark brown colour" (BRIGGS, 1928). There are no claspers. Additional specimens from Port Phillip Bay, near Melbourne, Australia, are mentioned by RALPH (1966); length of preserved specimens 20-35 mm.

Candelabrum austrogeorgiae (Jäderholm, 1904)

Myriothela austro-georgiae Jäderholm, 1904: ii; JÄDERHOLM, 1905: 4, 6-9, 38, Pls 1-2, Pl. 3 Figs 1-3; BILLARD, 1906: 2, 4-9, Figs 1-3; HICKSON & GRAVELY, 1907: 19; RITCHIE, 1909: 67, 69-70; STECHOW, 1909: 37, 66; VANHÖFFEN, 1910: 272, 277, 339; BRIGGS, 1928: 315, 1939: 10; MANTON, 1940: 281, 282; REES & THURSFIELD, 1965: 45; STEPAN'YANTS, 1972: 63-64, Fig. 9, 1979: 27, Pl. 5 Fig. 5, Pl. 25 Fig. 2.

Candelabrum austrogeorgiae — STECHOW, 1922: 144; STECHOW, 1923: 45; HAND & GWILLIAM, 1951: 208.

Gonostyle of Siphonophore, THOMPSON, 1904: 19, Pl. 1.

LOCALITIES. — "Vor Cumberland, Sth Georgia, 252-310 m, 5. vi. 1902; Stn 81, Bransfield Strait, 849 m, 25. xi. 1902; Stn 90, Bransfield Strait, 719-726 m, 05. xii. 1902" (JÄDERHOLM, 1905).

Flanders Bay, Graham Land, 15. ii. 1904; Booth-Wandell Island, 26/30. ix and 28. x. 1904, low tide (BILLARD, 1906).

"Scotia Bay in the South Orkneys, 10 fms, iv. 1903; 9-10 fms, v. 1903; among mud and pebbles, 18. xii. 1903". "On surface of the water, in a hole which had been cut in the ice. The depth of the water at that place was 20-30 fathoms, the temperature was 29° F" (RITCHIE, 1909).

"Observatory Bay, Kerguelen, 05. i. 1902, 10 × 4 mm" (VANHÖFFEN, 1910).

Davis Sea, Antarctica, near station Mir, 15-18 m; panantarctic species (STEPAN'YANTS, 1979).

REMARKS

Original description, by JÄDERHOLM (1904, 1905), based on unknown number of specimens from South Georgia. Body worm-like, up to 300 mm long, composed of foot, blastostyle bearing region and distal part exclusively bearing tentacles. Foot up to 20 mm long, basally with 3-4 mm long projections bearing filaments for attachment, flattened at the tip. There is no perisarc. Blastostyle bearing region c. half length of distal region, with blastostyles and capitate tentacles.

Blastostyles slender, tubular, with a single terminal tentacle or a number of smaller tentacles, bearing male or female gonophores; species is dioecious. Female gonophores usually 1-3, occasionally up to 6; male gonophores up to 10, of smaller diameter. Blastostyle bearing region not wider than remaining, distal part of body, which tapers gradually and is covered by numerous small capitate tentacles without noticeable arrangement.

The nematocysts are described to some extent by BILLARD (1906), who distinguishes two types, viz. stenoteles and desmonemes; no measurements are given. Some additional morphological details are given in the description of RITCHIE (1909) of specimens from the South Orkneys; on these specimens THOMPSON's (1904) description of the gonostyle of an unknown giant Siphonophore is based, placed by RITCHIE in the synonymy of the present species. The species is also redescribed by STEPAN'YANTS (1972, 1979).

Candelabrum capensis (Manton, 1940)

Myriothela capensis Manton, 1940: 276-287, Figs 7, 8b, 9, Pl. 1 Figs 12, 13, Pl. 3 Fig. 27; MILLARD, 1957: 186, 1966: 437; DAY, FIELD & PENRITH, 1970: 12; BOUILLON, 1974: 143; MILLARD, 1975: 45, Figs 7D, 18A, F, G, 1978: 195 et seq., 1980: 130.

Candelabrum capensis — PREVOT, 1959: 98.

LOCALITIES. — "Aquarium Rocks, East London, Sth Africa, 17 & 19. vii. 1937, 8-17 m" (MANTON, 1940). False Bay, 34° 08.5' S-18° 34.5' E, 27 m, female specimen, 6.5 mm (MILLARD, 1957).

West coast Cape Peninsula, Kommetje, 34° 08.5' S-18° 19.4' E, almost mature male attached to weed. Ludertitz Bay, South-West Africa, 26° 38' S-15° 09.3' E, two mature male specimens and two young specimens attached to crustacean appendage, largest 16 mm. Lamberts Bay, West coast Cape Peninsula, 32° 04.7' S-18° 18.2' E, 17 m, mature female specimen attached to weed (MILLARD, 1966). According to MILLARD (1975) maximum body length c. 25 mm.

REMARKS

Body c. 25 mm long, cylindrical, slowly tapering from base onward; basal portion (foot) c. one tenth of body length, attached, usually to algae, by means of 20-30 adhesive processes capped by chitinoid discs (MILLARD, 1975: 45). Blastostyles up to 4 mm long in single whorl of c. 20 above foot; unbranched, up to nine gonophores in proximal region and 4-7 capitate tentacles in distal region; species dioecious. Female gonophores releasing up to three actinulae. Distal part of body bearing many (400-600) densely packed, capitate tentacles. Cnidome adequately described by MILLARD (1966, 1975), composed of desmonemes (7.8-16.8 × 5.5-12.6 μm), stenoteles (9.9-11.4 × 7.2-8.1 μm), heteronemes (11.7-19.2 × 3.6-6.0 μm), haplonemes (10.8 × 9.9 μm) and probably also atrichous isorhizas (18.0 × 6.0 μm).

Candelabrum cocksii (Vigurs, 1849)
(Fig. 2c-d, Table 1)

Arum Cocksii Vigurs, 1849: 90.

Arum Cocksi(i) — COCKS, 1849: 90, 1852: 22, 1853a: 34, Pl. 3 Figs 7-12; M. SARS, 1857: 195; STECHOW, 1922: 144; REES, 1956: 116; Marine Biological Association of the United Kingdom, 1957: 39; REES, 1957: 487, Fig. 39A, B; PREVOT, 1959: 97, Pl. 1 Fig. 1; BRUCE, COLMAN

& JONES, 1963: 48; TEISSIER, 1965: 11; VAN DE VYVER, 1968: 349, Figs 16, IV, V; FEY, 1970: 390; CASTRIC-FEY, 1970: 20; CORNELIUS, 1977: 521 et seq; VAN DE VYVER, 1980: 110, 112; CASTRIC & MICHEL, 1982: 79, Fig.

Spadix purpurea Gosse, 1853b: 126-127; COCKS, 1853b: 365.

Spadix purpurea p.p. FORBES, 1854: 31 (excl. synonyms).

Spadix cocksii — GOSSE, 1853b: 386: M. SARS, 1857: 195; G. O. SARS, 1877: 28, note.

Myriothela cocksi(i) — G. O. SARS, 1874: 96, 130, 135; HINCKS, 1874: 136, 137; STORM, 1882: 7, 28, 30, at least part of specimens belong to *Monocoryne gigantea* (BONNEVIE, 1898, fide SWENANDER, 1904); PENNINGTON, 1885: 58, Pl. 3 Fig. 4; BONNEVIE, 1899: 9, 31-34, 37; SWENANDER, 1904: 4, 6; JÄDERHOLM, 1905: 8; BILLARD, 1906: 5, 9; BROCH, 1910: 194, 233, 238; BEDOT, 1911: 212; BILLARD, 1912: 460, 1921: 12-17, Fig. 1; BENOÎT, 1923a: 1836-1838, 1923c: 507-510, Figs 1-4; PRENANT & TEISSIER, 1924: 26; BENOÎT, 1925: 89 et seq., 113-193, Figs 1-35; CHADWICK, 1926: 51; WEILL, 1926: 1244 et seq.; BILLARD, 1927: 513-514; Marine biological Association of the United Kingdom, 1931: 69; WEILL, 1934a, b: 44, 106, 124, 125, 355, 373-375, 444, Figs 114-116; MOORE, 1937: 40; BRUCE, 1939: 12; EALES, 1939: 38, Pl. 3 Fig. 8; PÉRÈS, 1939: 539, Pl. 25 Fig. 1; BASSINDALE, 1941: 147; MANTON, 1941: 143 et seq., Figs 1-2; BRUCE, 1948: 45; TEISSIER, 1950: 11; BARRETT & YONGE, 1958: 47, Pl. 1; EALES, 1961: 34, Pl. 3 Fig. 8, 1967: 34, Pl. 3 Fig. 8; HARVEY, 1969: 14; ROBINS, 1969: 329; NICHOLS, COOKE & WHITELEY, 1971: 9, Fig.; BOUILLON, 1974: 143; HISCOCk, 1974: 23; BEIGEL, 1976: 121, Fig. 1, Pls 1-4; BEIGEL-HEUWINKEL, 1982a: 225 et seq., 1982b: 199-210, Figs 1-22, 1984: 273, 1988: 57-66, Figs 1-12.

Candelabrum cocksi — KRAMP, 1938: 66; HAND & GWILLIAM, 1951: 208; CORNELIUS, 1977; CORNELIUS & RYLAND, 1990: 116, Fig. 4.6.

Myriothela arctica — WRIGHT, 1858: 433; WRIGHT, 1859: 108; HINCKS, 1861: 157-158; ALLMAN, 1864a: 411, 1864c: 63.

Myriothela arctica p.p. FORBES, 1854: 31 (excl. synonyms).

Candelabrum arcticum p.p. L. AGASSIZ, 1862: 341 (excl. synonyms).

Myriothela phrygia — HINCKS, 1868: 77, Pl. 12 Fig. 3 (excl. synonyms in part). [Not *Myriothela phrygia* (Fabricius, 1780)].

Myriothela phrygia — ALLMAN, 1874: 317-321, 1875a: 135; BOURNE, 1889: 5, 1890: 392; HARDY, 1891: 505 et seq., Pls 36-37; GARSTANG, 1894: 223; CRAWFORD, 1895: 259 (*Myriothela phrygia*); GAMBLE, 1896: 132; BROWNE, 1897: 243; PRUVOT, 1897: 584, Tab. 22; BLACKBURN, 1899: 58 et seq., Pl. 8; LABBÉ, 1899: 4 et seq., Pl. 1 Figs 1, 4-9, Pl. 2 Figs 13, 17, 21; BEAUMONT, 1900: 756, 766; BROWNE, 1904: 162, 188; HAECKEL, 1904: Pl. 6 Fig. 12; HARTLAUB, 1904: 100; BOULENGER, 1908: 360; MÜLLER, 1908: 73; BOULENGER, 1910: 775. [All not *Myriothela phrygia* (Fabricius, 1780)].

Myriothela phrygia p.p. ALLMAN, 1872: 168, 382 (excl. synonyms in part). [Not *Myriothela phrygia* (Fabricius, 1780)].

Myriothela — ALLMAN, 1875b: 250 et seq.; (De) KOROTNEFF, 1878: 363-365, 1879: 187-190.

Myriothela p.p. (De) KOROTNEV, 1880: 5-37, Figs 1-29, Pls 1-4.

Myriothèle — (De) KOROTNEFF, 1888: 21 et seq., Pls 1-2.

MATERIAL EXAMINED. — Three complete specimens and two damaged individuals from Glénan Islands, off the Atlantic coast of France, collected in 1964 and 1965, in the tidal zone and upper subtidal zone; depth up to 17 m.

DIAGNOSIS

Body composed of foot, blastostyle region and trunk. Foot large, only slightly shorter than blastostyle region, with a number of slender prolongations that attach body to substrate, basis of each prolongation with chitinous perisarcal disk; chitinous perisarc gradually extending upwards and covering whole foot, externally more or less spinous. Monoecious, blastostyles slender, with male and female gonophores and occasionally with some developing eggs attached by claspers; dispersed capitate tentacles also occur. There is no terminal circle of tentacles. Trunk in our specimens 15-20 mm long, collapsible, covered by small, capitate tentacles with ovoid to globular capitulum; nematocysts dispersed.

DESCRIPTION

The more noticeable difference with both *C. serpentarii* and *C. phrygium* is in the development of the foot, which in the present species represents a conspicuous part of the body, attached to the substrate by means of finger-shaped to lobed prolongations, that terminally have a distinct chitinous disk, by means of which the specimens are attached to the front of algae, to calcareous algae or to fragments of rock. The chitinous perisarc surrounding the attaching disks reaches upwards to cover the whole of the foot with a layer of yellowish-brown perisarc, externally rough to spinous. Development of this chitinous sheath is different in the various specimens. The region bearing the blastostyles is c. 8 mm long; the blastostyles number 5 to 8 and are long and thin, carrying male and female gonophores in various stages of development, the males vary in diameter between 0.30 and 0.42 mm; the ripe female gonophore (with ovum) measures 0.60 mm in diameter. In addition some of the blastostyles have a developing egg attached by means of one or several claspers, resembling tentacles with a disc-shaped apical portion attached to the hyaline egg membrane. Inside is a developing larva (actinula); diameter of whole structure c. 1 mm. The state of preservation of the material does not permit further, more detailed observation. The trunk portion of the body, in the present specimens, is 15-20 mm long, tube-shaped and quite weak, which may be largely the result of inadequate fixation followed by transportation of the specimens. No mouth could be found; the exterior of the trunk is covered with small, capitate tentacles, pedicel 200-250 µm long, capitulum (often elongated ovoid) 130-200 µm diameter. The nematocysts are dispersed over the exterior of the capitulum and have been studied in squash preparations. There are two size classes of desmonemes, as well as haplonemes and stenoteles. Large and small desmonemes are about equally abundant, ovoid and slightly asymmetrical because of the development of a slight elevation just besides the top of the capsule. Large desmonemes 13.8-14.0 × 8.8-9.1 µm; small desmonemes 6.5-8.5 × 4.5-4.9 µm. They contain a thick thread irregularly coiled inside capsule. Haplonemes present in small number, slenderer than in the other two species and more asymmetrical, occasionally slightly banana-shaped, 18.8-20.5 × 6.2-6.6 µm. The longitudinal portion of the thread is clearly visible but the obliquely transverse coils are difficult to see. Stenoteles found in considerable numbers, ovoid with flattened top, perfectly symmetrical, 9.8-10.7 × 8.2-8.6 µm; shaft visible with folded barbs inside.

REMARKS

The principal area of distribution of this species is in the intertidal zone of the English Channel coasts of Great Britain and France. It is definitely known to occur also at the Glénan

TABLE 1. — Synoptic table differentiating between three described species of *Candelabrum*

	C. cocksii	*C. phrygium*	*C. serpentarii*
Size	1-2 cm	4-40 cm	8-15 cm
Locality	Intertidal zone of NE Atlantic.	Circumarctic and at active hydrothermal vents in the NE Atlantic in water of c. 11° C loaded with sulfureous compounds.	Restricted to an area around hydrothermal vents in water of 2.4° C.
Food	Probably small Crustacea (Copepoda and Amphipoda).	Shrimps and small Crustacea (Amphipoda, Copepoda)	Probably Crustacea
Reproduction	Monoecious; claspers present; young polyp developing into actinula; dispersal consequently restricted.	Dioecious; no claspers observed; development of young polyp unknown.	Monoecious; no claspers observed; development of young polyp unknown.
Nematocysts*			
Desmonemes (in µm)	13.8-14.0 × 8.8-9.1 (large) 6.5-8.5 × 4.5-4.9 (small)	12.5-13.0 × 9.0-9.8 (large) 8.2-9.0 × 6.4 × 6.6 (small)	13.0-14.5 × 9.8-10.5 (large) small type not observed
Haplonemes (in µm)	18.8-20.5 × 6.2-6.6	19.7-20.5 × 8.2-9.9	16.5-18.0 × 7.8-8.2
Stenoteles (in µm)	9.8-10.7 × 8.2-8.6	10.6-11.5 × 8.2-9.8	9.8-11.5 × 9.5-10.5

* It should be borne in mind that all observations in the present material are based on observations of unexploded nematocysts; the identifications of the various types, particularly the haplonemes, are tentative.

Archipelago (where some individuals were observed in May 1994) in the northern Bay of Biscay, at the Scilly Islands, at the Isle of Man and in the Bristol Channel. The records from Norway (*e.g.* KRAMP's, 1938, record from "Norway S. of Lofoten") are exclusively based on G. O. SARS's remarks on the occurrence of this species in deep water (100-200 m) off Aalesund, Norway; there are no recent records from the Norwegian coast. However, one of us (W. V.) has seen an undubitable specimen in an intertidal collection from the Bay of Cadiz, Atlantic coast of southern Spain, made by Dr M. D. MEDEL, Huelva, Spain.

It is quite a problem to state accurately the geographical distribution of this, apparently not quite rare, intertidal species because of its frequent confusion with *Candelabrum phrygium*. Since 1874, the differences between both species have been pointedly worded by G. O. SARS; his publication in Norwegian apparently escaping the notice of many later scientists. The confusion resulting from the tangled synonymy of the two species unfortunately has been aggravated by CORNELIUS' 1977 paper, in which both species are considered conspecific and the fact is overlooked that REES (1956) was fully aware of their specific differences.

(De) KOROTNEV's (1880) lengthy Russian description of *Myriothela* refers partly to *Candelabrum cocksii* which he studied at Roscoff; many details and some of the drawings have

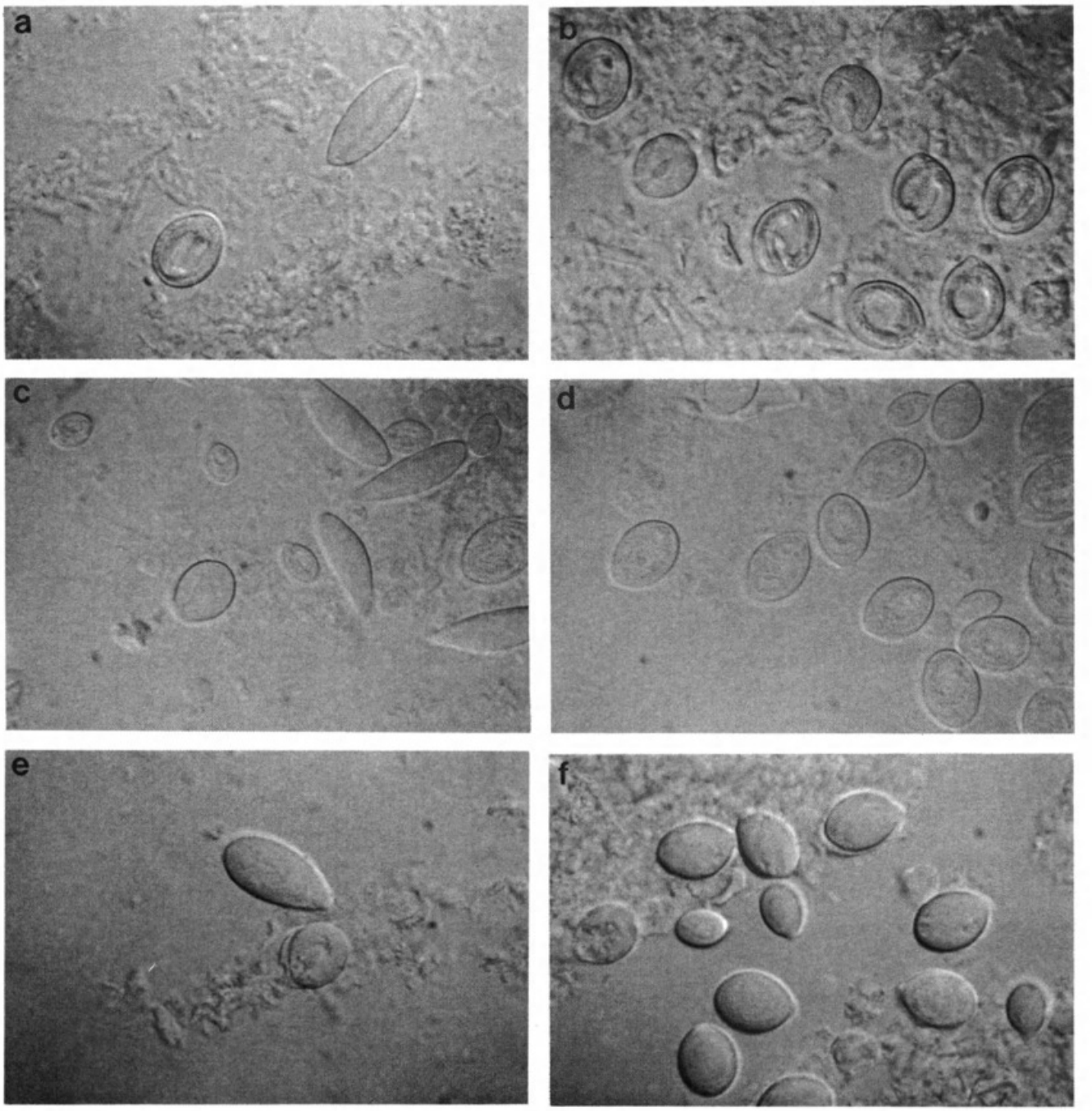


FIG. 2. — a, b, nematocysts of *Candelabrum serpentarii* nov. sp. (a, desmoneme and haploneme; b, six desmonenes, three stenoteles, one out of focus); c, d, nematocysts of *Candelabrum cocksii* (VIGURS, 1849) (c, four haplonemes, one large, five small desmonemes, and one stenotele; d, eleven large and two small desmonemes, two stenoteles, one partly); e, f, nematocysts of *Candelabrum phrygium* (Fabricius, 1780) (e, stenotele and haploneme; f, eight large and three small desmonemes, one stenotele). All nematocysts have been photographed with the aid of Nomarski interference contrast; × 750.

a, b, nématocystes de Candelabrum serpentarii *nov. sp. (a, desmonème et haplonème; b, six desmonèmes, trois sténotèles, un hors cadre); c, d, nématocystes de* Candelabrum cocksii *(VIGURS, 1849) (c, quatre haplonèmes, un grand et cinq petits desmonèmes, un sténotèle; d, onze grands et deux petits desmonèmes, deux sténostèles, un vu partiellement); e, f, nématocystes de* Candelabrum phrygium *(Fabricius, 1780) (e, sténostèle et haplonème; f, huit grands et trois petits desmonèmes, un sténostèle). Tous les nématocystes ont été photographiés à l'aide du microscope à contraste interférentiel Nomarski; × 750.*

been taken from ALLMAN's (1876) paper. It is not clear whether or not NAUMOV's (1960: 241-242, Figs 130, 131) notes on *Myriothela phrygia* refer to his own observations or those listed by (De) KOROTNEV. Certainly does NAUMOV's figure 130 refer to *Candelabrum cocksii*; it is taken from one of (De) KOROTNEV's plates and the claspers are distinctly visible. NAUMOV's figure 131, as he indicates, is taken from ALLMAN (1876) and refers to the actinula of *Candelabrum cocksii* [we have tacitly assumed that the major portion of detailed observations on *Myriothela phrygia* in NAUMOV's paper is based on solid observations (remarks on geographical distribution, bathymetrical record, life cycle, etc.)].

Candelabrum giganteum (Bonnevie, 1898)

Myriothela gigantea Bonnevie, 1898: 468, 490-491, Pl. 27 Figs 46-47; BONNEVIE, 1899: 9, 11, 37, 38, Pl. 4 Fig. 1; JÄDERHOLM, 1905: 7; BROCH, 1910: 194, 233, 236; MANTON, 1941: 143.

Candelabrum giganteum — STECHOW, 1922: 144, 1923: 45; HAND & GWILLIAM, 1951: 208.

LOCALITY. — Based on two more or less complete specimens and several fragments from deep water (2195 m) of the North Atlantic, 75°12'N-03°20'E.

REMARKS

Body elongated and thin, c. 300 mm long, basally thickest and slightly swollen, gradually tapering distally and terminating in fine filament. Below swollen or thickened basal portion a short, pointed foot with fine attaching filaments (no perisarc mentioned in original description). Blastostyles distributed over lower half of body; female blastostyles 10-20 mm long, with 1 or 2 big gonophores; male blastostyles shorter, 6-7 mm with many gonophores; both female and male gonophores have some terminal tentacles. Clavate tentacles on upper half of body, apparently also occurring in small numbers between blastostyles. Cnidome unknown. Curious filamentous appearance of distal part of body may be the result of inadequate fixation.

The species has not been rediscovered since the original description by BONNEVIE of specimens collected by the Norwegian North Atlantic Expedition 1876-1878.

Candelabrum harrisonii (Briggs, 1928)

Myriothela harrisonii Briggs, 1928: 312, Fig. 1, Pl. 33 Figs 1-2, Pl. 34 Fig. 5; BRIGGS, 1930: 5-14, Fig. 1, Pls 1-3, 1931: 270-278, Figs 1-3, 1939: 10.

Candelabrum harrisoni — HAND & GWILLIAM, 1951: 208.

LOCALITY. — Characterized as a "shallow water form, on underside of rocks below low-water mark at Bulli, 40 miles south of Sydney, N. S. W." (BRIGGS, 1928); number of individuals not stated.

REMARKS

Body cylindrical, elongated, divisible into foot, blastostyle bearing region and distal trunk. Foot set transversally towards length axis of body, with slender rooting processes, covered by translucent, chestnut-brown perisarc. Distal region of body cylindrical, slightly narrowing towards

blastostyle bearing region, with many capitate tentacles, diminishing in number towards blastostyle bearing zone. Blastostyles in single transverse row on swollen blastostyle region; that portion of body with fairly deep longitudinal furrows and fine transverse striae. Blastostyle with irregularly lobed base and a small number of gonophores (2-3 mature and 3-4 immature male gonophores; number in female unknown but less) with apical opening representing velar aperture. There is a single apical tentacle per blastostyle, often pushed aside by the developing gonophore. The size of the specimens is nowhere given in the description, nor can it be deduced from the figures. It probably had about the same size as *Candelabrum australe* with which it was simultaneously described.

Nematocysts described by BRIGGS (1930): desmonemes 10-12 × 8-9 µm; haplonemes 15-21 × 6-9 µm.

Candelabrum meridianum (Briggs, 1938)

Myriothela meridiana Briggs, 1938: 9-10, Pl. 15 Fig. 3; MILLARD, 1971: 399-401, Figs 1-2; STEPAN'YANTS, 1979: 26-27, Pl. 4 Fig. 4.

LOCALITIES. — "Six specimens 12-30 mm high attached to stones below low water, Macquarie Island" (BRIGGS, 1938). "Eight perfect or near-perfect individuals and about nine damaged specimens and fragments from below rock in the littoral region in Transvaal Cove, Marion Island", up to 27 mm long (MILLARD, 1971).

REMARKS

Original description by BRIGGS, 1939, supplemented by MILLARD, 1971. Species with tendency for subdivision of basal part of body, bi– or tripedal, fusion to single tubular distal region at c. one-third of height; body covered with small, capitate tentacles, continuing downward into blastostyle region at lower end of body. Base of body naked, occasionally ridged, "attached to substratum by a number of short adhesive tentacles each capped by a flat disc of brownish perisarc" (MILLARD, 1971). Blastostyles closely set, c. 2 mm long, occasionally branched once or twice, bearing 3-10 oval gonophores. Male gonophores sessile; female gonophores with short, thick stalk, larger than males, largest with 4-5 actinulae. Dioecious species. Cnidome described in detail by MILLARD (1971), composed of two size classes of oval desmonemes (11.3-14.9 × 8.7-11.3 and 6.2 × 5.2 µm), microbasic euryteles (14.9-16.5 × 5.7-6.1 µm), and other heteronemes (possibly stenoteles, 10.4-10.8 × 6.2-7.2 µm).

Candelabrum minutum (Bonnevie, 1898)

Myriothela minuta Bonnevie, 1898: 468, 489-490, Pl. 27 Fig. 44; BONNEVIE, 1890: 9, 35, 37, Pl. 3 Fig. 6a, b, Pl. 4 Fig. 4; JÄDERHOLM, 1905: 7; BROCH, 1910: 194, 233, 236; MANTON, 1941: 143.

Candelabrum minutum — STECHOW, 1922: 144, 1923: 45; HAND & GWILLIAM, 1951: 208.

LOCALITY. — Tromsö, northern Norway; no depth record.

REMARKS

Based on unknown number of specimens from Tromsö, where the species was found by M. SARS, apparently in the middle of the last century. Body small, cylindrical, thickest in middle (c. 2 mm), basally with pointed foot bearing attaching filaments; capitate tentacles only found in small number on extreme distal part of body and surrounding mouth. Blastostyles small, occurring on major part of body, bearing a single large (female) gonophore, the latter with a small, rudimentary tentacle. Cnidome unknown. The species has not been rediscovered since the original description.

Candelabrum mitra (Bonnevie, 1898)

Myriothela mitra Bonnevie, 1898: 468, 489, Pl. 27 Fig. 43; BONNEVIE, 1899: 9, 11, 33, 37, 38, 40, Pl. 3 Fig. 6c-e, Pl. 4 Fig. 3; JÄDERHOLM, 1905: 7; MANTON, 1941: 143.

Acandela mitra — STECHOW, 1920: 45, 1922: 144, 1923: 47.

Candelabrum mitrum — HAND & GWILLIAM, 1951: 208.

LOCALITY. — Based on a (male ?) specimen (or specimens) from deep water (2222 m) of the North Atlantic (63°22'N-05°29'W).

REMARKS

Body conical, basally widest, there 10 mm diameter, tapering distally, there 1-2 mm. Basal part of body with narrowly pointed, 10-20 mm long foot bearing rooting filaments; no perisarc described. Blastostyles on basal third to fourth of body, in many irregular whorls. Blastostyles conical, top with several capitate tentacles, curved; gonophores dispersed over blastostyle. There are no tentacles on rest of body.

The atentaculate condition of the body occasioned STECHOW (1920: 45) to institute a separate genus, *Acandela*, for its reception. This atentaculate condition may well result from damage sustained by the specimen studied by BONNEVIE. The number of specimens available to BONNEVIE is not unambiguously stated and may very well have been one single specimen, obtained in a haul from great depth. Moreover, in her 1898 paper BONNEVIE complains about the bad preservation of her specimen(s): "Das Ektoderm des Polypen hat eine eigenthümliche Struktur; und ich beklage, dass seine Konservirung nicht gut genug ist, um eine genauere Untersuchung zu gestatten, etc." (: 489). Loss of tentacles due to damage is also described by JÄDERHOLM (1905) for *Myriothela (= Candelabrum) austrogeorgiae*.

Candelabrum penola (Manton, 1940)

Myriothela penola Manton, 1940: 256-276, Figs 1-6, Pl. 1 Figs 10, 11, 14, Pl. 2 Figs 15-21, Pl. 3 Figs 22-26, 28, Pl. 4 Figs 29-34; BOUILLON, 1974: 143.

Candelabrum penola — BOUILLON, 1974: 143.

LOCALITY. — Based on two specimens, a mature female 850 mm long and an immature male of 55 mm body length, both found attached to the axis of a pennatulid and found floating alongside the research vessel *Penola* in a creek of the Argentine Islands, Graham Land, Antarctica.

REMARKS

MANTON describes the species as being dioecious. The following notes are based on the female specimen. Basal sixth of body, c. 100 mm long with a diameter of 12 mm, without tentacles and bearing numerous lobed blastostyles. Adhesive tentacles (rooting filaments) spring from basal part of body and some of proximal blastostyles and attach polyp to substrate; they are capped by a chitinoid disk; there is no perisarc. Female blastostyles 20-25 mm long, irregularly lobed or branched, with short, capitate tentacles (and on proximal blastostyles with some adhesive tentacles). Gonophores distributed over blastostyle, numbering up to 10; usually only one develops to maturity and is then quite large, 7.2 mm in diameter, considerably swollen by development of large actinula. Distal five-sixths of body, length c. 650 mm, diameter at oral end 7.5 mm, is covered by 0.5-2.5 mm long capitate tentacles; number estimated by MANTON at about 330,000.

The male specimen is quite young and will not be described here. The nematocysts are described by MANTON and consist of desmonemes of variable size (9-18 µm), haplonemes (13 × 9 µm) and heteronemes (10-18 × 7-13 µm).

Candelabrum phrygium (Fabricius, 1780)
(Figs 2e-f, 3E-F, Table 1)

Lucernaria phrygia Fabricius, 1780: 343; GMELIN, 1791: 3151.

Candelabrum [phrygium] — DE BLAINVILLE, 1830: 284, 1834: 318.

Candelabrum phrygium — L. AGASSIZ, 1862: 341; ALLMAN, 1864b: 358 (*Candelabrum Phrygia*); A. AGASSIZ, 1865: 186, 225, 226; STECHOW, 1922: 144; 1923: 45; KRAMP, 1932a: 5, 26, 1932b: 68, Tab. 1; 1943: 42; HAND & GWILLIAM, 1951: 208; CORNELIUS, 1977: 521 et seq.; STEPAN'YANTS, 1985: 85; ANTSULEVICH, 1987: 27; STEPAN'YANTS, 1989: 412 et seq.; CORNELIUS & RYLAND, 1990 116; ANTSULEVICH, 1991: 40; CAIRNS *et al.*, 1991: 16.

Myriothela phrygia — G. O. SARS, 1873: 86, 119; HINCKS, 1874: 136; G. O. SARS, 1874: 130, 140-142; LÜTKEN, 1875: 188; G. O. SARS, 1877: 26, note; M. SARS, 1877: 23, Pl. 2 Figs 29-36; STORM, 1879: 27; D'URBAN, 1880: 255, 257, 258; HINCKS, 1880a: 257; STORM, 1880: 122; WINTHER, 1880: 270; STORM, 1882: 8, 28, 30; ALLMAN, 1888: xxi, xliv; DRIESCH, 1890: 154; HARDY, 1891: 505-537, Figs 36-37; LEVINSEN, 1893: 150; VANHÖFFEN, 1897: 245; BONNEVIE, 1898: 491, 1899: 9, 11, 31, 33, 35, 37, 38, Pl. 4 Figs 5-6; BLACKBURN, 1899: 58-63, Pl. 8; WHITEAVES, 1901: 20; BROCH, 1903: Tab.; SWENANDER, 1904: 4-6; STEPHENS, 1905: 40; BILLARD, 1906: 5; JÄDERHOLM, 1908: 192, 233, 237; BROCH, 1910; 192, 233, 237; DERYUGIN, 1915: 304; BROCH, 1916: 19-21, Pl. 1 Figs 3, 8; HARTLAUB, 1916: 110, Figs 38-39; FRASER, 1918: 332, 341, 1921: 148, Fig. 18; SVARCHEVSKII, 1923: 99; CHADWICK, 1926: 51; MANTON, 1941: 143; FRASER, 1944: 88-89 [not Pl. 15 Fig. 63 = *Candelabrum cocksii* (Vigurs, 1849)]; BEREZINA, 1948: 50, Pl. 14 Fig. 1; REES, 1956: 116; NAUMOV, 1960: 241-243, Figs 130-131; CALDER, 1972: 222, Pl. 1 Fig. 5; CAMPBELL, 1974: 151, Fig. 9D; PETERSEN, 1990: 203.

Myriothela phrygia p.p. ALLMAN, 1872: 382 (excl. synonyms).

Corymorpha phrygia — MÖRCH, 1857: 24.

Myriothela arctica M. Sars, 1851: 126, 131, 134; ALDER, 1853: 35 (*Myristhela phrygia*); GOSSE, 1855: 20, Fig. 25; M. SARS, 1857: 192, 194; WRIGHT, 1858: 433, 1859: 108; M. SARS, 1860 (German translation): 342; HINCKS, 1861: 157; M. SARS, 1861: 693; ALLMAN, 1864a: 411, 1864c: 63; PARFITT, 1866: 5; VERRILL, 1879: 19; G. O. SARS, 1877: 26, note.

Myriothela arctica p.p. FORBES, 1854: 31 (excl. synonyms).

Candelabrum arcticum — ALLMAN, 1864b: 358.

Candelabrum arcticum p.p. L. AGASSIZ, 1862: 341 (excl. synonyms in part).

MATERIAL EXAMINED. — All specimens were obtained from the Lucky Strike hydrothermal vents area:

— two from the Lucky Strike cruise (site *Sintra*, marker 3, 37°17.50'N-32°16.47'W, 1622 m depth; dive 2606, June 1st, 1993; collected by Meg TIVEY); well preserved male specimens, both with developing male gonophores on blastostyles; one specimen attached to rock fragment (Fig. 3F), the other to a 20 mm long living specimen of mussel *Bathymodiolus* sp;

— seven from the Diva 2 cruise:

— two fixed and preserved in formalin (one female with large, mature eggs attached to blastostyles), obtained at dive PL 02, site *Sintra*, June 4, 1994; collected by Philippe CRASSOUS;

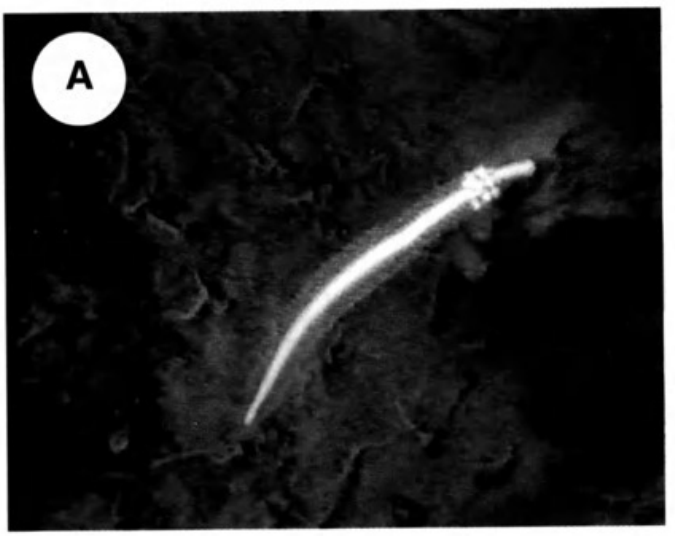
— two fixed in Bouin and tranferred to ethanol 70 %, from dive PL 09, site *Tour Eiffel* (37°17.31'N-32°16.51'W; 1690 m depth), June 11, 1994; collected by Luis SALDANHA. Also a basal part of a male specimen with many blastostyles with mature male gonophores, attached to a sulfide rock, and two parts of male specimen, the basal part with rock fragments and some developing gonophores, the second part a segment of the trunk with a complete, more or less digested shrimp[2] inside. The organic debris found in association with the three specimens of *Candelabrum phrygium* contains remnants of an amphipod, of a small shrimp, of a calanoid copepod, a complete healthy looking Ectinosomid (Copepoda Harpacticoida) and some unidentifiable animal remains;

— three (two females and a male: a 40 mm long female, eggs developing in gonophores; also a 65 mm long female with some large gonophores and rest of amphipod attached to tentacles; in addition, c. 50 mm long male, proximal part of trunk decomposed; blastostyle bearing region about as long as rest of trunk, with a great number of blastostyles bearing many developing and mature gonophores) preserved in formalin, from dive PL 10, site *Tour Eiffel*, June 12, 1994; collected by Marie-Claire FABRI.

2. This is probably a specimen of a newly described crustacean *Chorocaris fortunata* (MARTIN & CHRISTIANSEN, 1995, L. B. Holthuis, pers. comm.); TL c. 10 mm, diameter 2-3 mm.

FIG. 3. — A: *Candelabrum serpentarii* nov. sp. (length c. 10 cm), Snake Pit area, next to *Élan* site, 3515 m, on sulfide rock, surrounded by polychaete tubes; B: *Candelabrum serpentarii* nov. sp. (length c. 8 cm), Snake Pit area, next to *Les Ruches* site, 3505 m, on sulfide rock, surrounded with tubes of polychaeta Chaetopteridae and Zoantharia (Cnidaria); C: *Candelabrum serpentarii* nov. sp. (paratype, length c. 7.5 cm), Snake Pit area, next to *Les Ruches* site, 3523 m, on pillow lava; D: The same specimen, freshly collected, natural colours (however, one can notice the difference of colour with *in situ* organism of photo A); the black spots are sulfidic metal particles precipitated on the animal in the slurp gun box; E: *Candelabrum phrygium* (FABRICIUS, 1780), length 7-9 cm, Lucky Strike area, *La Pagode* site, 1626 m, on flange mineral formation covered with white silica; one mussel (*Bathymodiolus* sp.) is visible; F: *Candelabrum phrygium* (Fabricius, 1780), Lucky Strike area, *Sintra* site, 1622 m, on flange block.

A: Candelabrum serpentarii *nov. sp. (L = env. 10 cm), zone du Snake Pit, près du site* L'Élan, *3 515 m, sur un bloc de sulfure, entouré de tubes de polychètes; B:* Candelabrum serpentarii *nov. sp. (L = env. 8 cm), zone du Snake Pit, près du site des* Ruches, *3 505 m, sur un bloc de sulfure, entouré de tubes de polychètes Chaetopteridae et de zoanthaires (Cnidaires); C:* Candelabrum serpentarii *nov. sp. (paratype, L = env. 7,5 cm), zone du Snake Pit, près du site des* Ruches, *3 525 m, sur des laves en coussin; D: le même spécimen, fraîchement récolté, couleurs naturelles (on notera toutefois la différence de couleur avec l'organisme* in situ *de la photo A); les taches noires sont des particules de sulfures métalliques précipités sur l'organisme dans le collecteur du système d'aspiration; E:* Candelabrum phrygium *(FABRICIUS, 1780), L = 7-9 cm, zone de Lucky Strike, site de* La Pagode, *1 626 m, sur formation minérale "flange", couverte de silice blanche; une moule (*Bathymodiolus *sp.) est visible; F:* Candelabrum phrygium *(Fabricius, 1780), zone de Lucky Strike, site* Sintra, *1 622 m, sur un bloc de "flange".*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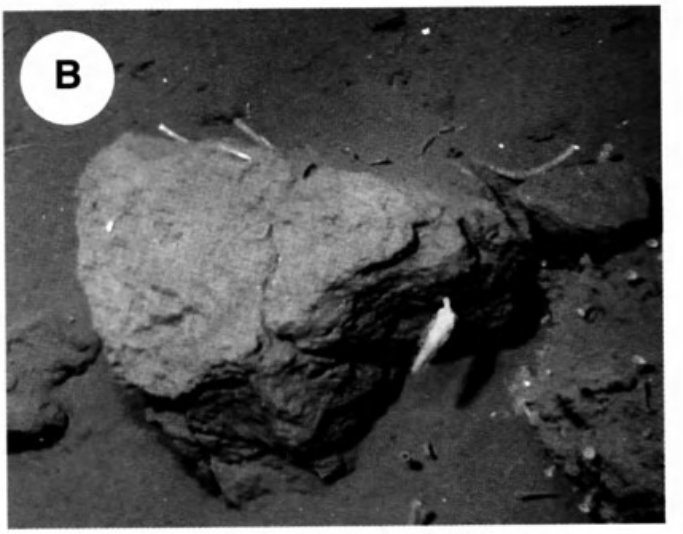
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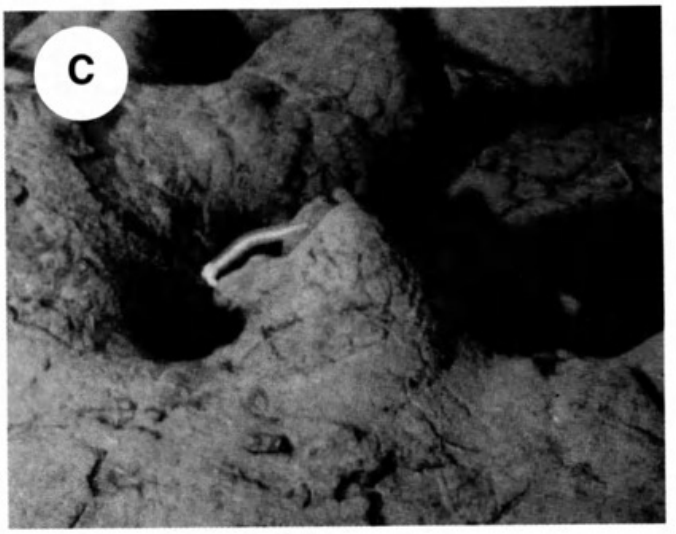
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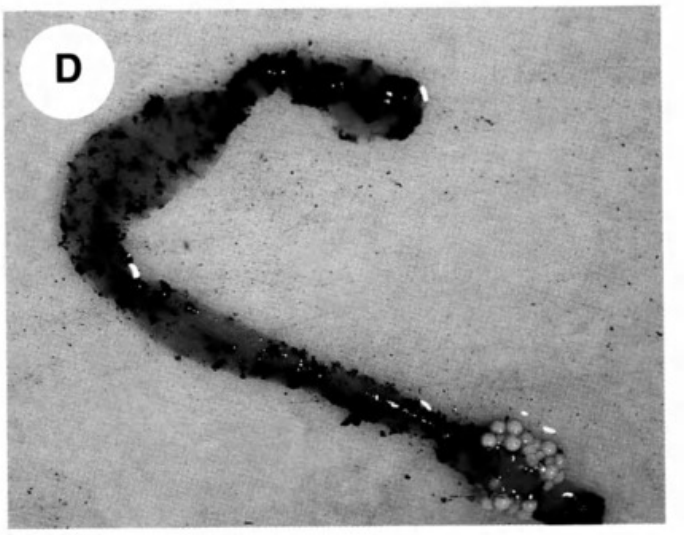
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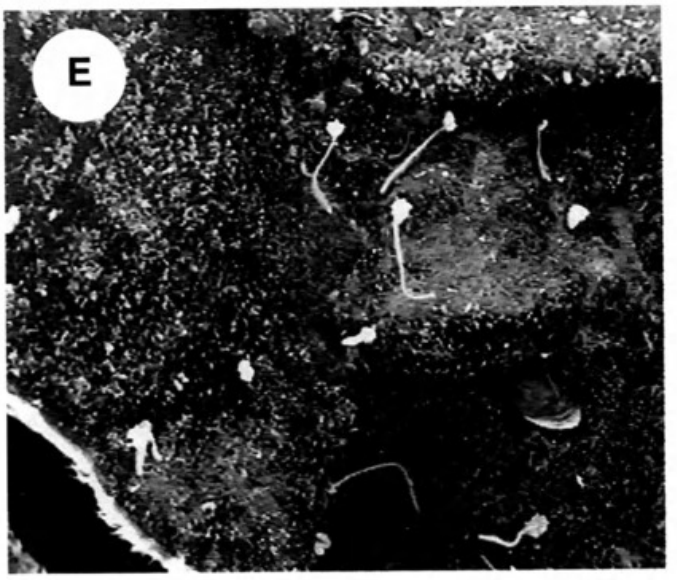
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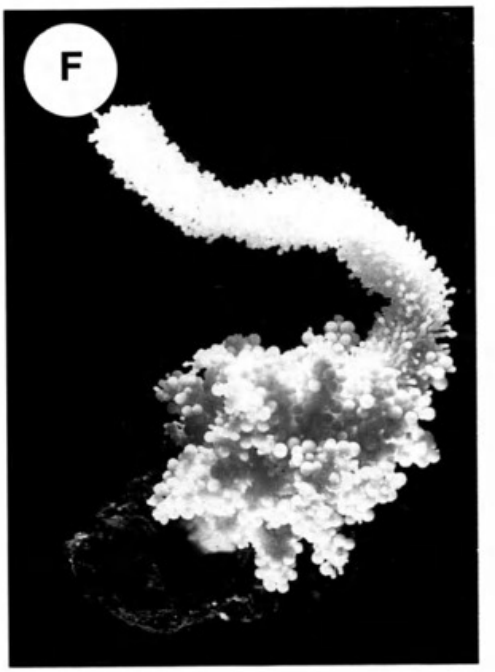
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DIAGNOSIS

Body composed of foot, blastostyle bearing region and trunk. Foot: a lobed, flattened part of body, attaching animal to rock or substrate (bivalve molluscs), without chitinous adhesive portion. Blastostyle bearing region forming lower third to fourth of body, with a large number (10 to 15) of big, tubular blastostyles, bearing male gonophores in various stages of development and dispersed, capitate tentacles; apex of each blastostyle with circle of 4 or 5 tentacles. Remainder of body forming elongated, tubular trunk, completely covered by capitate tentacles. Mouth distinct, at end of trunk.

DESCRIPTION

All specimens available are attached to rock fragments, one male is attached to the exterior of a living bivalve. In all specimens the foot attaches the body to the substrate; there are no chitinous adhesive disks or chitinous portions of the foot. In the specimen on the mollusc, the foot is more distinctly lobed than in the others. Directly above the foot is the blastostyle bearing part of the body, 12-15 mm high and bearing a considerable number (10 to ca. 50 in the male, usually less in the female) of tube-shaped blastostyles, the body cavity continuing into the blastostyles. Male and female blastostyles are found on separate polyps; the species consequently is dioecious. Each male blastostyle is 8-10 mm long and carries many developing male gonophores, with dispersed, capitate tentacles in between. The apex of each blastostyle carries a circle of 4 or 5 capitate tentacles. Male gonophores 0.40-0.80 mm in diameter, attached by means of thin tissue strand and easily detached in the preserved specimens, apparently filled with developing spermatocytes. The female blastostyles are shorter and thinner than the males and have less gonophores. In the specimens inspected each blastostyle has gonophores in various stages of development, the youngest in the basal part, the mature gonophores at the top; there are only few tentacles. The smallest gonophores measured are 0.40 mm, the largest, apparently mature gonophores are 1.40 mm. The gonophores that have been supposed to be mature contain a single, large egg; it is attached to the blastostyle by means of a thin strand of tissue, being the continuation of a thin layer of tissue covering the egg. Trunk vermiform, diameter c. 2.5 mm, in the preserved specimens 25-30 mm long, completely covered by short, capitate tentacles. Each tentacle has a 0.35-0.50 mm long pedicel and a capitulum of 0.17-0.25 mm diameter; nematocysts dispersed over capitulum.

Nematocysts studied in squash preparations of capitulum of trunk tentacles, composed of two size classes of desmonemes, haplonemes and stenoteles.

Haplonemes slightly longer than those of *C. serpentarii*, but of the same general shape: elongated ovoid and slightly narrowed apically, as a result more or less pyriform, 19.7-20.5 × 8.2-9.9 µm, found more frequently than in capitulum of *C. serpentarii*. Internal structure fairly obscure, but a longitudinally descending shaft and oblique coils of the thread could be observed.

Desmonemes of two size classes occur in profusion, the larger being almost identical with those of *C. serpentarii*, broadly ovoid, slightly asymmetrical apically and there with a slight elevation just outside middle of top, 12.5-13.0 × 9.0-9.8 µm. The smaller type is slightly more elongated, 8.2-9.0 × 6.4-6.6 µm. Both types with a thick thread in irregular coils; in desmonemes in perfect lateral view part of thread parallel to internal wall of basal portion. Both types were found to occur in almost equal numbers.

Stenoteles scarce and apparently badly preserved, as internal structure was quite obscure; they could best be recognized by the flattened top (when in good position), 10.6-11.5 × 8.2. × 9.8 µm. Details of shaft and thread could not be discerned. It was difficult to estimate the occurrence of stenoteles because of bad preservation: they could only with certainty be distinguished from desmonemes when in good position to see apical flattening.

REMARKS

The various locality records are not specified here. The species is circumarctic, occurring in both Atlantic (BONNEVIE, 1898-99: Norwegian North Atlantic Expedition, Stn 303, 75°12′N-03°02′E, 2195 m) and Pacific (NAUMOV, 1960) parts of the Arctic seas. In the Atlantic at least it also penetrates boreal waters, though there usually at greater depths. It is now also known to occur in deep water of the NE Atlantic.

The Lucky Strike specimens were generally found at the base of the active edifices, attached to organic support (shell of living bivalve) or, more frequently, to mineral formations called "flanges" and composed of a mixture of pyrite, marcasite and baritine, with sometimes some white silica at the surface. The specimens are frequently observed at the site *Sintra*, but they occur also at the site *Tour Eiffel*. At the *Pagode* site 7 or 8 individuals were observed together on 0,5 m^2 (Fig. 3E). At that locality, a few animals (mussels, crabs and shrimps) are present, but generally the surrounding faunal community is largely composed of bivalved Mytilidae (*Bathymodiolus*) (VAN DOVER *et al.*, submitted), shrimps (Alvinocarididae), crabs (Bythograeidae) and several smaller Crustacea (Copepoda Siphonostomatoida, Amphipoda) living in a mixture of sea water and hydrothermal fluid (loaded with sulfurous compounds), mean temperature ca. 11° C. Other animals observed at the Lucky Strike hydrothermal vents area include sponges (*Cladorhiza* sp.) and hydroids (*Eudendrium* sp.), both found on the top of the inactive edifices. In many cases these animals carry white, filamentous bacteria.

Candelabrum serpentarii nov. sp.
(Figs 2a-b, 3A, B, C, D, 4, Table 1)

MATERIAL EXAMINED. — One complete specimen, total body length 75 mm, and a 40 mm long upper part of body of second specimen, both from the Hydrosnake cruise at the Snake Pit hydrothermal area (site *Les Ruches*, 23°23'N-47°57'W, 3489 m depth, dive HS 10, June 28, 1988; collected by M. S.). Specimen with large female and smaller male gonophores and presently slightly deteriorated because of frequent inspections; chitinous covering of foot lost; remains in National Museum of Natural History, Leiden (paratype, RMNH Coll. No 27111).

Well preserved specimen in three parts, total body length c. 80 mm, composed of basal body region with gonophores (in two parts) and trunk, from the MAR 93 cruise next to the site *Élan* in the Snake Pit area, about 30 m to the west of the site *Les Ruches* (dive 2619; 3525 m depth, June 20, 1993; collector: Jean-Paul Truchot). This specimen was fixed in Bouin and later on transferred to ethanol 70 %, now preserved in Muséum national d'Histoire naturelle, Paris (holotype, MNHN Hy No 1133).

ETYMOLOGY. — *serpentarii*, from the Latin *serpentarium*, snake pit.

DIAGNOSIS

Large *Candelabrum;* total body length 60-80 mm, attached to solid substrate by means of laterally flattened, basal foot covered by thick, curved, brownish-black perisarcal sheath. Rest

of body composed of proximal region bearing large blastostyles each bearing a number of male and female gonophores in various stages of development, and an elongated trunk completely covered with short, capitate tentacles. Capitulum of each tentacle with distal layer of nematocyst bearing ectoderm. Cnidome (of capitate tentacles) composed of desmonemes (predominant), large haplonemes and two size classes of stenoteles, of which the smaller class has only occasionally been observed.

DESCRIPTION

Since none of the specimens is fully intact, parts of the following description are the result of reconstruction.

The c. 60 mm long body can be divided into a foot, a blastostyle bearing region and the apical trunk. The foot has only been observed in the paratype (Fig. 2), where it is a laterally flattened, rounded portion of the body, attaching the polyp to the hard substrate (pillow lava) by a considerable portion of its surface. The foot was covered by a thick, brownish-black, c. 1 mm thick perisarcal shield, at first firmly attached to the foot, but later on spontaneously loosening itself. No perisarcal threads with or without apical button, attaching the foot to the rock have been observed.

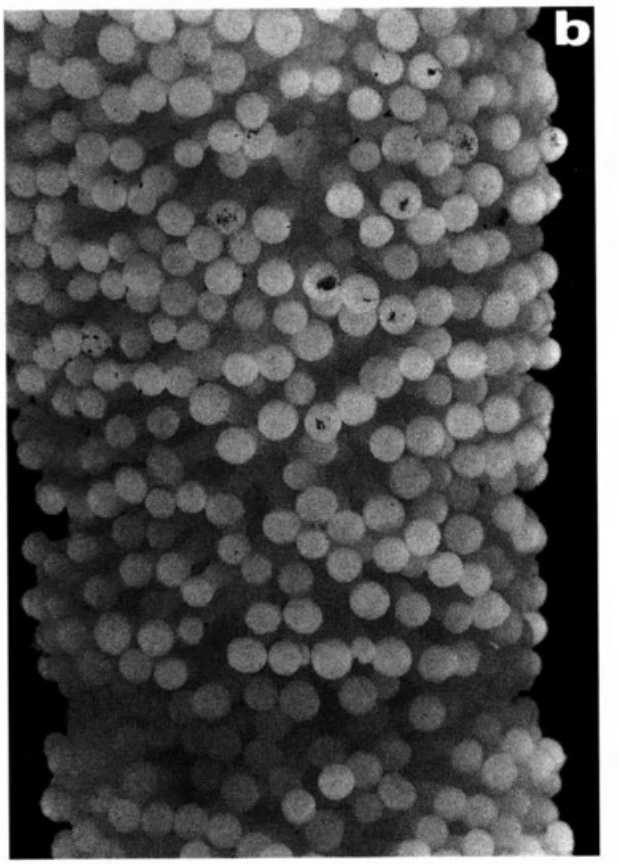
The blastostyle bearing zone of the body has about the same diameter as the trunk (c. 7 mm), the body cavity continues in that zone and in the blastostyles, that represent lateral, tentacle bearing elevations of the body wall. Blastostyles 3-5 mm long, with c. 10 male and 3-5 apparently fully mature female gonophores. The tentacles observed on the body between the blastostyles as well as those on the blastostyles (between the gonophores and at the apex) are indistinguishable from those on the trunk. Male gonophores c. 1-1.5 mm in diameter, apparently filled with developing spermatocytes. The female gonophores are large, 4-5 mm in diameter, attached to the blastostyle by means of a short, stubby neck and surrounded by an opaque layer of ectodermal cells; no nematocysts having been observed. The large egg can be dislodged by carefully cutting the ectodermal covering; the egg in the well preserved specimen from the Snake Pit appeared to be entirely filled with yolk with many fat goblets and was surrounded by a hyaline membrane. No structure could externally be observed and it is presumed that the eggs, at least in this specimen, are still unfertilized. No traces of claspers or aberrant tentacles could be found in the blastostyle bearing zone.

The trunk is a tube-like expansion of the body externally fully covered by capitate tentacles. The lumen of the gastral cavity is considerable; the mouth at the end of the trunk is closed. The tentacles consist of a short, 0.6-0.8 mm long stalk and a globular capitulum of 0.4-0.6 mm diameter; the apex of the capitulum is covered by a semiglobular layer of ectodermal cells with

FIG. 4 — *Candelabrum serpentarii* nov. sp., holotype, from Snake Pit area; a, distal part of body, completely covered with small, capitate tentacles; b, close up of the capitate tentacles; c, proximal part of body with capitate tentacles on distal zone and blastostyles, with male and female gonophores, as well as capitate tentacles, on the basal zone; d, close up of one of the gonophores.

Candelabrum serpentarii *nov. sp., holotype, provenant du Snake Pit; a, partie distale du corps, complètement recouvert de petits tentacules capités; b, détail des tentacules capités; c, partie proximale du corps avec des tentacules capités au niveau de la zone distale et des blastostyles, avec des gonophores mâles et femelles sur la partie basale; d, détail des gonophores.*


a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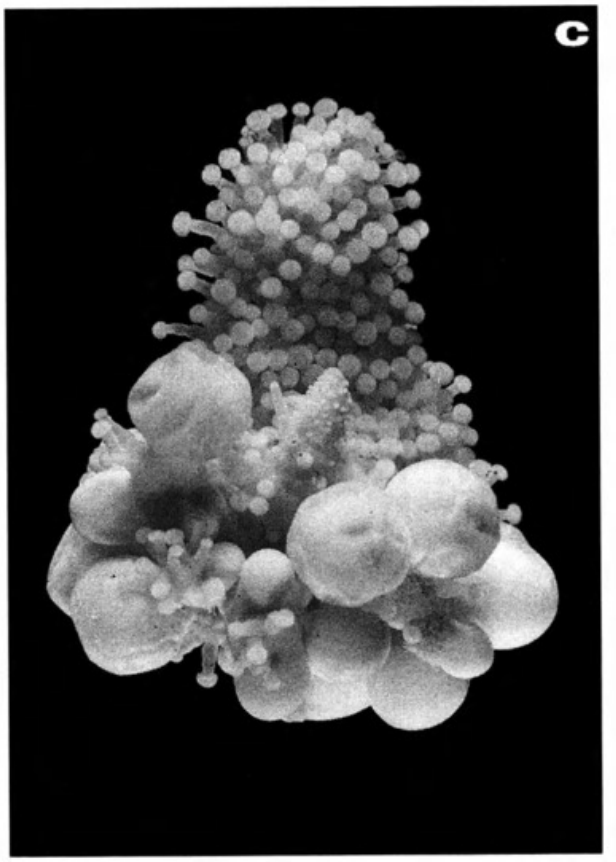
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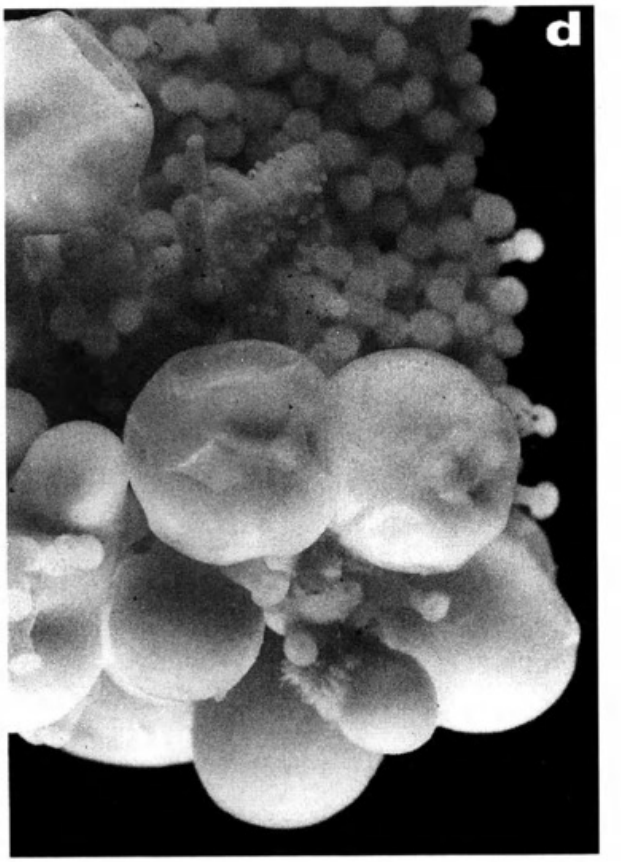
d

many nematocysts. The tentacular stalks, as can be seen from the photographs of living specimens, are hightly contracted in the preserved specimens, the capitulum standing off a distance of several mm from the body surface.

The nematocysts have been studied in squash preparations of the capitulum of tentacles of the trunk. There appear to be three types of nematocysts: haplonemes, stenoteles and desmonemes.

Haplonemes elongated ovoid, slightly narrowed distally and as a result also a bit pyriform and slightly asymmetrical, 16.5-18 × 7.8-8.2 µm, rather uniform of size and shape. They have not been found in exploded condition, consequently the characters of the thread could not be studied. In unexploded condition the thread is seen to descent from the apex down to the bottom in a straight line; the rest of the thread is coiled in obliquely transverse coils.

Stenoteles almost globular, in perfect position observed to be broadly ovoid, perfectly symmetrical, with indistinctly flattened top. Shaft and barbs forming a central column in the unexploded capsule and about three-fourth the height of the capsule; thread in indistinct transverse coils in the basal third of the capsule. Size 9.8-11.5 × 9.5-10.5 µm. A second type of stenotele has occasionally been observed, but only in exploded condition, the capsule measuring 5.4 × 7.4 µm. Details of barbs and thread could not be observed.

Desmonemes broadly ovoid, but for the apical protrusion almost perfectly symmetrical, 13-14.5 × 9.8-10.5 µm. Apical protrusion low, slightly besides middle of apex; thread thick, forming a small number of loose coils following the internal desmonemal wall.

In the tentacular capitulum the desmonemes predominate; haplonemes and (large) stenoteles forming c. 5 % of the capsular number. The smaller stenoteles have only occasionally been observed.

REMARKS

In the Snake Pit field the occurrence of this species is restricted to an area of several meters from an active structure and it is not observed outside a radius of some twenty or thirty meters. The species may thus be considered to indicate the proximity of hydrothermal activity, though one individual has been observed at inactive vents. Depending upon the proximity of the active sites the specimens are attached to pillow lava (Fig. 3C) or sulfide rocks (Fig. 3A-B). They are quite irregularly distributed, occasionally 2 or 3 individuals are found within one meter distance. At this level there are probably no thermal anomalies, the temperature at those abyssal depths being generally 2.4° C. Surrounding fauna is scarse (SEGONZAC, 1992), composed of some fishes (Pisces Synaphobranchidae), galatheides (Crustacea Galatheidae), and occasionally one or two isolated shrimps (*Rimicaris exoculata*), Williams & Rona, 1986 (Crustacea Alvinocarididae).

Candelabrum tentaculatum Millard, 1966

Myriothela tentaculata Millard, 1966: 437-440, Fig. 2; BOUILLON, 1974: 143; MILLARD, 1975: 46-48, Figs 17C, 18B-E; 1978: 195 et seq., 1979: 134.

LOCALITY. — Based on five specimens from off Slangkop on west coast of Cape Peninsula, 34°09.3'S-18° 17.5'E, 24 March 1959, 43 m depth.

REMARKS

Body up to 31 mm long, attached to encrusting Bryozoa by means of nine short, adhesive processes capped by chitinoid discs springing from irregularly shaped basal portion. Blastostyles in single whorl of 17, reaching 20 mm length, with c. 25 rather poorly developed capitate tentacles on distal region and scattered amongst 4-6 gonophores on proximal 5 mm. Only male gonophores known, species apparently dioecious. Rest of body densely covered with capitate tentacles. Cnidome adequately described by MILLARD (1975) and composed of heteronemes (up to 45 µm long!), two size classes of desmonemes, stenoteles and atrichous isorhizas.

Candelabrum verrucosum (Bonnevie, 1898)

Myriothela verrucosa Bonnevie, 1898: 468, 490, Pl. 27 Fig. 45; BONNEVIE, 1899: 9, 37, Pl. 4 Fig. 2.

Candelabrum verrucosum — STECHOW, 1922: 144, 1923: 45; HAND & GWILLIAM, 1951: 208.

LOCALITY. — No locality mentioned in original description (BONNEVIE, 1898), but in BONNEVIE's 1899 paper the species is mentioned in a table and Hammerfest (Norway) is given as the locality; there is no (definite) depth record.

REMARKS

Small species, total body length c. 40 mm, diameter 1-2 mm, thickest just under mouth. Attached by means of attaching filaments springing from basal part of body. Lower fifth of body bearing blastostyles, rest of body covered with capitate tentacles. Blastostyles short, with one or two gonophores and with tentacles distally. Gonophores with dispersed clusters of nematocysts over their surface. The species may be based on a single specimen (number of specimens or variability not stated); it should be recognizable by the clusters of nematocysts on the gonophores, though according to Bonnevie these are difficult to perceive!

Candelabrum sp. 1

Myriothela (?) HICKSON & GRAVELY, 1907: 18-19, Pl. 3 Fig. 18.

LOCALITY. — Based on single specimen from Winter Quarters of Discovery expedition, Hut Point, McMurdo Sound, Ross Sea, 13 October1902 (Hickson & Gravely, 1907).

REMARKS

Composed of c. 8 mm long hydrocaulus, 2 mm in diameter, basally with numerous filaments attaching specimen to debris of sponge spicules. Body of hydranth c. 6 mm long, spindle shaped, thickening from hydrocaulus and tapering apically to form conical hypostome. Distal half of hydranth covered with short, thick capitate tentacles. No blastostyles or gonophores developed on proximal part of body. Might turn out to be a juvenile specimen of one of the antarctic species.

Candelabrum sp. 2

Candelabrum spec. HAND & GWILLIAM, 1951: 207, 208.
Candelabra sp. AUSTIN, 1985: 46 (sic).

LOCALITY. — Three specimens were found in a pholad hole on the undersurface of a rock at mean lower water at Pigeon Point, San Mateo County, California, USA, 6 May 1950.

REMARKS

Based on three not fully mature specimens. The description by HAND & GWILLIAM (1951) is repeated here verbatim: "Hydranth: Not branched, solitary, naked, and arising from a creeping hydrorhiza or possibly a disc. Hydrorhizae invested with perisarc. Exclusive of hydrorhizae, polyp divisible into two zones; a distal tentacle-bearing zone and a proximal tentacle-free blastostylar zone. The tentacle-bearing zone composes five-sixths or more of the polyp length and bears approximately 500 tentacles in the adult; cylindrical, approximately the same diameter throughout. Tentacles densely packed, short, capitate and not arranged in any discernible pattern. Mouth terminal. Blastostylar zone swollen, of a slightly greater diameter than the tentacle bearing zone. Sometimes separated from tentacle-bearing zone by a constriction; at the proximal end tapering sharply to hydrorhiza. Structures referred to by ALLMAN (1875) as claspers not present on specimens examined. Blastostyles giving rise to more than one gonophore. Largest specimen (preserved) 2.5 cm long by 0.15 cm in diameter (including the tentacle)".

Compared by HAND & GWILLIAM with *Candelabrum harrisoni* Briggs, which it resembles closely.

Candelabrum sp. 3

Dr Chad HEWITT and Dr GODDARD (University of Tennessee, USA) recently informed us that they will describe a species of *Candelabrum* from intertidal waters of the Pacific coast of Oregon.

ECOLOGICAL REMARKS

1 — *Trophic behaviour.*

As stated above, a fairly large (c. 10 mm TL), partly decomposed shrimp (*Chorocaris fortunata* Martin & Christiansen, 1995) was found in the enteron of a specimen of *Candelabrum phrygium*, demonstrating their ability to capture large preys, as also indicated by their considerable armament. This, and the presence of other small Crustacea (Amphipoda and Copepoda Siphonostomatoida) in their immediate vicinity, makes it likely that they can be considered to prey upon the Lucky Strike faunal community.

Candelabrum serpentarii, on the contrary, does not actually live in a hydrothermal habitat. It was found outside but close to the active sites, in an area deprived of visible fauna and

consequently less rich in prey. The absence (noticed during the submersible explorations) of *C. serpentarii* outside an area of 20 or 30 m radius of the active sites leads to the consideration that the species, directly or indirectly, benefits from the active sites communities. It has been observed that an important bacterial production (both free and associated with invertebrates) gives rise to a community largely dominated by the shrimp *Rimicaris exoculata* (SEGONZAC *et al.*, 1993). Though the type of food consumed by *C. serpentarii* so far has not been observed directly, it seems reasonable to suggest that, as in *C. phrygium*, it consists mainly of shrimps and other small Crustacea. The metabolism, in this animal, might be adapted to the occasional capture of (large) preys, as is the case in many abyssal predators.

It should be remembered that in *Candelabrum* the number of tentacles is considerable, the nematocysts being concentrated in the tentacular capitulum. As indicated above the considerable amount of nematocysts allows the capture of large preys, for which action the haplonemes, stenosteles and heteronemes, if present, are responsible. The numerous desmonemes may serve for the attachment of preys, that can either be transported to the mouth or swallowed after curvature of the trunk towards the place of attachment. Many athecate hydroids have an extensible mouth capable of devouring a prey of considerable size. The *Candelabrum* species probably are no exception in this respect.

2 — *Biogeography.*

Most *Candelabrum* species live in intertidal waters. Geographical distribution in the members of this genus is usually restricted by the absence of a planktonic stage and by the necessity to be attached to hard substrates. The circumarctic distribution of *C. phrygium,* which has a non-planktonic actinula larva, is not in agreement with the ecological status observed on the Lucky Strike site. Indeed, its distribution there is restricted to areas of active venting (living in a mixture of sea water and hydrothermal fluid loaded with sulfurous compounds, mean temperature: 11° C). Moreover, direct observations and video analysis indicate the absence of individuals outside the sites. It is thus difficult to understand why this species, is strongly linked to such peculiar and very confined physical and chemical conditions.

The status of *C. serpentarii* is likewise difficult to explain, but it is different. As stated above, this species has affinities with *C. cocksii*, a species only known from the NE Atlantic intertidal zone. Both species have low dispersal abilities (the fertilized eggs develop into the actinulae before they separate from blastostyles); they were never observed or collected on the abyssal plains.

Considering those facts, and bearing in mind the difficulties in understanding the colonization processes without fossil records, the isolation of the various *Candelabrum* populations could be explained in terms of plate tectonics viz. the movement of oceanic plates. For example, it could be hypothesized that *Candelabrum serpentarii* results from allopatric speciation (with the preservation of several morphologic features and the mode of reproduction) from an ancient intertidal stock of *C. cocksii* (or, more likely, a common ancestral form) that became isolated as a result of the successive events that led to the rifting and further spreading of the Atlantic Ocean floor. One of the populations may progressively have adapted to the deep hydrothermal environment where the hard substrate and the trophic conditions represented favourable living conditions.

In order to answer questions concerning the present distribution of these species of *Candelabrum*, several kinds of studies should be carried out:

1) a profound study leading towards a better understanding about their life-cycle;

2) a study of the deep water circulation pattern in this part of Atlantic Ocean;

3) the exploration of other ridge segments to gain additional records of species of *Candelabrum*.

Technical aid

All *C. cocksii*, *C. phrygium* and *C. serpentarii* nematocysts (Fig. 2) have been photographed by Dr J. C. DEN HARTOG (Nationaal Natuurhistorisch Museum, Leiden). Fig. 3D-F and Fig. 4 were made from photographs taken by Patrick BRIAND (IFREMER). The map shown in Fig. 1 was realized by Violaine MARTIN (IFREMER). The pictures Fig. 3A, B, C and E, partly resulting from videotape enlargements, were placed at our disposal by Gérard VINCENT and Valérie BATY (Picture library, IFREMER).

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The specimens of *C. serpentarii* and *C. phrygium* originate from cruises Hydrosnake, Lucky Strike, MAR 93, Gravinaut and Diva 2 organized by INSU, IFREMER and WHOI institutions within the framework of the FARA program (French American Ridge Atlantic).

REFERENCES

AGASSIZ, A., 1865. — North American Acalephae. *Illustrated Catalogue of the Museum of Comparative Zoölogie*, at Harvard College, No 2: 1-234. Cambridge, Mass., USA.

AGASSIZ, L., 1862. — *Contributions to the natural history of the United States of America.* Second monograph. Vol. **4**: i-viii, 1-380 + (10), Pls 20-35. Little, Brown & Co., Boston.

ALDER, J., 1853. — *In*: W. P. COCKS, 1853a: 35.

ALLMAN, G. J., 1864a. — Report on the present state of our knowledge of the reproductive system in the Hydroida. *Rep. Br. Assoc. Advmt Sci.*, **33** (Newcastle-Upon-Tyne, 1863) (1): 351-426.

— 1864b. — On the construction and limitation of genera among the Hydroida. *Ann. Mag. nat. Hist.*, (3) **13**: 345-380.

— 1864c. — Notes on the Hydroida. *Ann. Mag. nat. Hist.*, (3) **14**: 57-64, Pl. 2.

— 1871, 1872. — *A monograph of the gymnoblastic or tubularian hydroids. I. The Hydroida in general: i-xxii, 1-154, text-Figs, Pls 1-12 (1871). II. Conclusion of part I, and part II, containing descriptions of the genera and species of the Gymnoblastea*: xiii-xxiv, 155-450, text-Figs, Pls 13-23 (1872). London, Ray Society.

— 1874. — Notes on the structure and development of *Myriothela phrygia*. *Ann. Mag. nat. Hist.*, (4) **14**: 317-321.

— 1875a. — On some points in the histology of *Myriothela phrygia*. *Rep. 44th Meet. Brit. Assoc. Adv. Sci.*, (Belfast, 11874) (2): 135-136.

— 1875b. — On the structure and development of *Myriothela*. *Proc. R. Soc. London*, **23**: 250-254. — Also *in*: *Ann. Mag. nat. Hist.*, (4) **15**: 297-300.

— 1876. — On the structure and development of *Myriothela*. *Phil. Trans. R. Soc. Lond.*, **165**: 549-575, Pls 55-58.

— 1888. — Report on the Hydroida dredged by H. M. S. "Challenger" during the years 1873-76. Part II. The Tubularinae, Corymorphinae, Campanularinae, Sertularinae and Thalamophora. *Rep. scient. Results Voy. Challenger, Zool.* **23** (70): i-lxix, 1-90, Pls 1-39, 1 map.

ANTSULEVICH, A. E., 1987. — Gidroidy shel'fa Kuril'skykh ostrovov (Hydroids from the shelf waters of Kurile Islands): 1-165, Figs 1-51. *Zoologicheski Institut, Akad. Nauk SSSR, Leningrad* (Russian with English summary).

— 1991. — Ob endemizme Belomorsko fauny gidroidov i svyazi mezhdu faunami Belogo i Barentseva more. On the White Sea hydrozoan fauna endimismus: White and Barentz Seas faunas connection (*sic*). *In*: Bentos Belogo Morya. Populyatsii, biotsenozy, fauna. *Trudy Zool. Inst. Leningr.*, **233**: 35-43, Fig. [Russian with English summary].

AUSTIN, W. C., 1985. — *An annotated checklist of marine invertebrates in the cold temperate northeast Pacific*: 1-682 (*in* 3 volumes, Mimeogr.). Khoyatan Marine Laboratory, Cowichan Bay, British Columbia.

BARRETT, J. H., & C. M. YONGE, 1958. — *Collins pocket guide to the sea shore*. Collins, London: 1-272, Pls 1-40 and col. plates 1-40, Figs 1-170 (Hydrozoa: 45-53, Figs 2-15, Pl. 1, colour Pl. 2 No 3f-j).

BASSINDALE, R., 1941. — Studies on the biology of the Bristol Channel. IV. The invertebrate fauna of the southern shores of the Bristol Channel and Severn Estuary. *Proc. Bristol Nat. Soc.*, (4) **9** (2): 143-201.

BEAUMONT, W. J., 1900. — Report on the results of dredging and shore collecting. *In*: The fauna and flora of Valencia Harbour on the west coast of Ireland. *Proc. R. Ir. Acad.*, (3) **5**: 754-798.

BEDOT, M., 1911. — Notes sur les hydroïdes de Roscoff. *Archs Zool. exp. gén.*, (5) **6** (6): 201-228, Pl. 1.

BEIGEL, U., 1976. — Gonophorenentwicklung der Hydroide *Myriothela*. *Cah. Biol. mar.*, **17** (2): 119-129, Fig. 1, Pls 1-4.

BEIGEL-HEUWINKEL, U., 1982a. — Helical fibrils in the mesogloa of a hydropolyp. *Tissue Cell*, **14** (2): 225-230, Figs 1-7.

— 1982b. — Experiments and observations on regeneration in *Myriothela cocksi*. *Acta zool., Stockh.*, **63** (4): 199-210, Figs 1-18.

— 1984. — Aspects of egg development in *Myriothela cocksi* (Hydrozoa, Athecata). Zur Eientwicklung bei *Myriothela cocksi* (Hydrozoa, Athecata). *Verh. dt. Zool. Ges.*, **77**: 273.

— 1988. — Brutpflege bei den marinen Hydroidpolypen *Myriothela cocksi* (Vigurs) mit Hilfe spezieller Tentakel. *Acta Biol. Benrodis*, **1** (1): 56-67, Figs 1-13, Tab. 1.

BENOÎT, P., 1923a. — L'ovogénèse et la segmentation de *Myriothela Cocksi* (Vigurs). *C. r. hebd. Séanc. Acad. Sci., Paris*, **176** (25): 1836-1838.

— 1923b. — Le gonophore hermaphrodite de *Myriothela Cocksi* (Vigurs). *C. r. Séanc. Soc. Biol.*, **89** (25): 507-510, Figs 1-4.

— 1925. — L'ovogénèse et les premiers stades du développement chez la Myriothèle et chez la Tubularie. *Archs Zool. exp. gén.*, **64** (2): 85-326, Figs 1-45, Pls 3-12.

BEREZINA, N. A., 1948. — Podtip Cnidaria — Strekayushchie. Klass Hydrozoa Gidroidy. Podklass Hydroidea Gidroidnye. Otryad Leptolina. *In*: N. S. Gaevskaya, ed., *Opredelitel' fauny i flory severnykh morei SSSR*; Moscow: 47-65, Figs 16-17, Pls 14-17 [Russian].

BILLARD, A., 1906. — Hydroïdes. *In*: Expédition antarctique française (1903-1905) commandée par le Dr Jean CHARCOT: 1-20, Figs.

— 1912. — Hydroïdes de Roscoff. *Archs Zool. exp. gén.*, **51** (2): 459-478, Figs 1-8.

— 1921. — Note sur la biologie et la régénération de la Myriothèle. *Bull. Soc. zool. Fr.*, **46**: 12-17, Fig. 1.

— 1927. — Note relative à certains nématocystes d'hydroïdes. *Bull. Soc. zool. Fr.*, **51**: 513-514.

BLACKBURN, W., 1899. — *Myriothela phrygia*, a Tubularian Hydroid. *Trans. Manchester microsc. Soc.*, 1898: 58-63, Pl. 8.

BLAINVILLE, H. M. D., DE, 1830. — Zoophytes. *In*: Dictionnaire des sciences naturelles, **60**: 1-548. Paris, F. G. Levrault.

— 1834. — Manuel d'actinologie ou de zoophytologie, 2 vols: 1-695, Pls 1-99. Paris, F. G. Levrault.

BONNEVIE, K., 1898. — Zur Systematik der Hydroiden. *Z. wiss. Zool.*, **63**: 465-495, Pls 25-27.

— 1899. — Hydroida. *Norske Nordhavs-Exped., Zool.* **26**: 1-104, Figs 1-3, Pls 1-8, 1 map.

BOUILLON, J., 1974. — Description de *Teissiera milleporoides*, nouveau genre et nouvelle espèce de Zancleidae des Seychelles (Hydrozoaires, Athécates, Anthoméduses), avec une révision des hydroïdes Pteronematoidea. *Cah. Biol. mar.*, **15**: 113-154, Figs 1-14, Pls 1-6, Tabs 1-5.

BOULENGER, C. L., 1908. — On *Moerisia lyonsi*, a new Hydromedusan from Lake Qurun. *Q. Jl micr. Sci.*, n. ser, **52**: 357-378, Pls 22-23.

— 1910. — On the origin and migration of the stinging-cells in Craspedote Medusae. *Q. Jl microsc. Sci.*, n. ser. **55**: 763-783, Pls 42-43.

BOURNE, G. C., 1889. — The director's report. N° 1. *J. mar. biol. Ass. U. K.*, n. ser. **1** (1): 1-9.

— 1890. — Notes on the hydroids of Plymouth. *J. mar. biol. Ass. U.K.*, n. ser. **1** (4): 391-398, Pl. 26.

BRIGGS, E. A., 1928. — Studies in Australian athecate hydroids. N° 1. Two new species of the genus *Myriothela*. *Rec. Aust. Mus.*, **16** (7): 305-315, Fig. 1, Pls 32-34.

— 1929. — Studies in Australian athecate hydroids. N° 2. Development of the gonophores and formation of the egg in *Myriothela australis*, Briggs. *Rec. Aust. Mus.*, **17** (5): 244-264, Figs 1-4, Pls 42-44.

— 1930. — Studies in Australian athecate hydroids. N° 3. The histology of *Myriothela harrisoni*, Briggs. *Rec. Aust. Mus.*, **18** (1): 5-14, Fig. 1, Pls 1-3.

— 1931. — Studies in Australian athecate hydroids. N° 4. Development of the gonophores and formation of the egg in *Myriothela harrisoni*, Briggs. *Rec. Aust. Mus.*, **18**: 270-278, Figs 1-3.

— 1938. — Hydroida. *Scient. Rep. Australasian Antarct. exped.*, (C) **9** (4): 1-46, Figs 1-3, Pls 15-16.

BROCH, H., 1903. — Die von dem norwegischen Fischereidampfer "Michael Sars" in den Jahren 1900-1902 in dem Nordmeer gesammelten Hydroiden. *Bergens Mus. Aarb.*, 1903 (9): 1-14, Pls 1-4, Tab. 1.

— 1910. — Die Hydroiden der Arktischen Meere. *In*: F. RÖMER & F. SCHAUDINN, *Fauna arctica*, **5** (1): 127-248, Figs 1-46, Pls 2-4.

— 1916. — Hydroida (Part I). *Danish Ingolf Exped.*, **5** (6): 1-66, Figs A-U, Pls 1-2.

BROWNE, E. T., 1897. — The hydroids of Valencia Harbour, Ireland. *Ir. Nat.*, **6**: 241-246.

BROWNE, E. T., 1904a. — Hydrozoa. Ex: Plymouth marine Invertebrate fauna being notes of the local distribution of species occurring in the neigbourhood. Compiled from the records of the Laboratory of the Marine Biological Association. *Journ. mar. biol. Ass.*, n. ser. **7** (2): 153-298, Pl. 1.

BRUCE, J. R., 1939. — Faunistic notes and records. *Rep. mar. biol. Stn Port Erin*, **52**: 11-17.

— 1948. — Additions to faunal records, 1941-46. *Rep. mar. biol. Stn Port Erin*, **58-60**: 39-58. (Coelenterata: 44-46).

BRUCE, J. R., J. S. COLMAN & N. S. JONES, 1963. — Marine Fauna of the Isle of Man and its surrounding seas: i-ix, 1-307. Liverpool University Press (Coelenterata: 47-66).

CAIRNS, S. D., D. R. CALDER, A. BRINCKMANN-VOSS, C. B. CASTRO, P. R. PUGH, C. E. CUTRESS, W. C. JAAP, D. G. FAUTIN, R. J. LARSON, G. R. HARBISON, M. N. ARAI & D. M. OPRESKO, 1991. — Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. *Spec. Publ. Am. Fish. Soc.*, **22**: 1-75, Figs 1-20 (in colour).

CALDER, D. R., 1972. — Some athecate hydroids from the shelf waters of northern Canada. *J. Fish. Res. Bd Can.*, **29** (3): 217-228, Fig. 1, Pls 1-2, Tab. 1.

CAMPBELL, R. D., 1974b. — Cnidaria. *In*: A. C. GIESE & J. S. PEARSE, eds., Reproduction of marine invertebrates, 1. Acoelomate and pseudocoelomate invertebrates: 133-199, Figs 1-22, Pls 1-5, Tab. Academic Press, New York & London: 1-546, Figs, Pls, Tabs.

CASTRIC, A., & C. MICHEL, 1982. — Flore et faune fixées sous-marines de Bretagne: 1-100, Figs. Laboratoire Maritime, Concarneau & Laboratoire d'Océanographie Biologique, U.B.O. Brest.

CASTRIC-FEY, A., 1970. — Sur quelques hydraires de l'archipel de Glénan (Sud-Finistère). *Vie et Milieu*, (A) **21** (1): 1-23, Figs 1-23.

CHADWICK, H. C., 1926. — Natural History notes. *In*: J. JOHNSTONE, The marine biological Station at Port Erin, being the fourthieth annual report, etc. *Proc. Trans. Lpool biol. Soc.*, **41**: 51-52.

COCKS, W. P., 1849. — Contributions to the fauna of Falmouth. *Rep. R. Cornwall Polytech. Soc.*, **17**: 38-103.

— 1850. — Contributions to the Fauna of Falmouth. *Rep. R. Cornwall Polytech. Soc.*, **18**: 10-12.

— 1852. — Contributions to the Falmouth Fauna. *Rep. R. Cornwall Polytech. Soc.*, **20**: 168.

— 1853a. — Contributions to the fauna of Falmouth. *Rep. R. Cornwall Polythec. Soc.*, **21**: 28-36.

— 1853b. — *Spadix purpurea*, Gosse. *Ann. Mag. nat. Hist.* (2) **12**: 365.

CORNELIUS, P. F. S., 1977. — On the nomenclature of the hydroid, *Candelabrum phrygium* (Fabricius, 1780) (= *Myriothela phrygia*, *Arum cocksi*). *J. mar. biol. Ass. U.K.*, **57** (2): 521-524.

CORNELIUS, P. F. S., & J. S. RYLAND, 1990. — Hydrozoa. *In* P. J. HAYWARD & J. S. RYLAND eds. The marine fauna of the British Isles and North-West Europe. Volume 1. Introduction and Protozoans to Arthropods: 107-159, Figs 4.3-4.25. Oxford University Press (volume 1: i-xvi, 1-627 plus 44 pp indices, Figs 1-11, 32).

CRAWFORD, J. H., 1895. — The Hydroids of St-Andrews Bay. *Ann. Mag. nat. Hist.*, (6) **16**: 256-262.

DAKIN, W. J., I. BENNETT & E. POPE, 1948. — A study of certain aspects of the ecology of the intertidal zone of the New South Wales coast. *Aust. J. scient. Res.*, (B) **1** (2): 176-230, Figs 1-3, Pls 1-9.

DAY, J. H., J. G. FIELD & M. J. PENRITH, 1970. — The benthic fauna and fishes of False Bay, South Africa. *Trans. R. Soc. S. Afr.*, **39** (1): 1-108, map 1.

(DE) KOROTNEFF, A., 1878. Histologische Notizen über die *Myriothela*. *Zool. Anz.*, **1**: 363-365.

— 1879. — Entwickelung der *Myriothela*. *Zool. Anz.*, **2**: 187-190.

(DE) KOROTNEV (= KOROTNEFF), A., 1880. — Opyt' sravitel'nago izucheniya Coelenterata. Chast vtoraya. *Myriothela*, eya stroenie, razvitie i mésto v' sistemé [A comparative study of Coelenterata. Part 2, *Myriothela*, its structure, development and systematic position]. *Izv. Obshch. Lyub. Estest., Antropol., Entogr. Mosk. Univ.*, **37** (2): 5-37, Figs 1-29, Pls 1-4.

— 1888. — Contribution à l'étude des Hydraires. *Archs Zool. exp. gen.*, (2) **6**: 21-31, Pls 1-2.

D'URBAN, W. S. M., 1880. — The Zoology of Barents Sea. *Ann. Mag. nat. Hist.*, (5) **6**: 253-277.

DERYUGIN, K. M., 1915. — Fauna Kol'skago zaliva i usloviya ee sushchestvovaniya. *Zap. imp. Akad. Nauk, Fiz.Mat. Otdel.*, (8) **34** (1): 1-929, Figs 1-55, Pls 1-13, Tab. 1, maps 1-2, 1-12.

DRIESCH, H., 1890. — Heliotropismus bei Hydroïdpolypen. *Zool. Jb., Syst.*, **5** (1): 147-156, Figs.

EALES, N. B., 1939. — *The littoral fauna of Great Britain. A handbook for collectors*. Cambridge: i-xviii, 1-301, Figs 1-110 on Pls 1-24 (Hydrozoa: 36-42).

— 1961. — *The littoral fauna of Great Britain. A handbook for collectors*, ed. 3. Cambridge: i-xvii, 1-306, Figs 1-111.

— 1967. — *The littoral fauna of Great Britain. A handbook for collectors*, ed. 4. Cambridge: i-xvii, 1-306, Figs 1-111, Pls A-H.

FABRICIUS, O., 1780. — *Fauna groenlandica*: i-xvi, 1-452, Pl. 1. I. G. Rothe, Hafniae & Lipsiae.

FEY, A., 1970. — Peuplements sessiles de l'archipel de Glénan. 1. Inventaire: hydraires. *Vie et Milieu*, (B) **20** (2): 387-413.

FORBES, E., 1854. — Note on *Spadix purpurea*, Gosse. *Ann. Mag. nat. Hist.*, (2) **13**: 31-32.

FRASER, C. MCLEAN, 1918. — Hydroids of eastern Canada. *Contr. Can. Biol. Fish.*, 1917-1918 (16): 329-367, Pls 1-2.

— 1921. — Hydroids. Key to the hydroids of eastern Canada. *In*: Canadian Atlantic Fauna, 3a. *Contr. Can. Biol. Fish.*, **17**: 137-180, Figs 1-107.

— 1944. — *Hydroids of the Atlantic coast of North America*: 1-451, Pls 1-94. The University of Toronto Press, Toronto.

GALKIN, S. V., & L. I. MOSKALEV, 1990. — Hydrothermal Fauna of the Mid-Atlantic Ridge. *Oceanology*, **30** (5): 624-627.

GAMBLE, F. W., 1896. — Notes on a zoological expedition to Valencia Island, Co Kerry. Shore-collecting and dredging. *Ir. Nat.*, **5** (5): 129-136.

GARSTANG, W., 1894. — Faunistic notes at Plymouth during 1893-1894. With observations on the breeding seasons of marine animals, and on the periodic changes of the floating fauna. *Jour. mar. biol. Assoc. U. K.*, n. ser. **3** (3): 210-235.

GMELIN, J. F., 1791. — *Linnaeus, C., Systema naturae*. Thirteenth edition, edited by J. F. GMELIN. Vol. 1, part 6 (Vermes): 3021-3910. Lipsiae, G. E. Beer [Dating of this part follows Woodward and Wilson, 1933].

GOSSE, P. H., 1853a. — *A naturalist's rambles on the Devonshire coast*: i-xvi, 1-451. Van Voorst, London.

— 1853b. — Notes on some new or little-known marine animals. *Ann. Mag. nat. Hist.*, (2) **12**: 124-128, 153-159, 384-386.

— 1855. — *A manual of marine Zoology for the British Isles*. 2 vols, Figs. London, 1855-56 (Zoophytes, vol. 1, 1855).

HAECKEL, E., 1904. — *Kunstformen der Natur. Hundert Illustrationstafeln mit beschreibendem Text, allgemeine Erläuterung und systematische Übersicht*. Verlag des Bibliographischen Institut, Leipzig & Wien.

HAND, C., & G. F. GWILLIAM, 1951. — New distributional records for two athecate hydroids, *Cordylophora lacustris* and *Candelabrum* sp., from the west coast of North America, with revisions of their nomenclature. *J. Wash. Acad. Sci.*, **41**: 206-209.

HARDY, W. B, 1891. — On some points in the histology and development of *Myriothela phrygia*. *Q. Jl microsc. Sci.*, n. ser. **32** (1): 505-537, Pls 36-37.

HARTLAUB, C., 1904. — Bericht über eine zoologische Studienreise nach Frankreich, Grossbritannien und Norwegen, ausgeführt im Frühjahre 1902. *Wiss. Meeresunters., Helgoland*, n. ser. **5**: 97-106, Figs.

— 1916. — Über das Altern einer Kolonie von *Syncoryne* und damit verbundene Knospungen am Hydrathenköpchen. *Wiss. Meeresunters., Helgoland*, n. ser. **11**: 91-125, Figs 1-46, Pls 19-20.

HARVEY, L. A., 1969. — The marine flora and fauna of the Isles of Scilly. The islands and their ecology. *J. nat. Hist.*, **3** (1): 3-18, Figs, Tabs.

HICKSON, S. J., & F. H. GRAVELEY, 1907. — Coelenterata. II. Hydroid zoophytes. *National Antarctic Expedition 1901-1904, Nat. Hist.*, **3**: 1-34, Pls 1-4.

HINCKS, Th., 1861. — A catalogue of the Zoophytes of South Devon and South Cornwall. *Ann. Mag. nat. Hist.*, (3) **8**: 152-161; 251-262; 290-297; Pls 6-8.

— 1862a. — A catalogue of the Zoophytes of South Devon and South Cornwall. *Ann. Mag. nat. Hist.*, (3) **9**: 22-30, Pl. 7.

— 1862b. — A catalogue of the Zoophytes of South Devon and South Cornwall. Appendix. *Ann. Mag. nat. Hist.*, (3) **10**: 360-363.

— 1868. — *A history of the British hydroid zoophytes*. Volume 1: i-lxviii + 1-338, frontispiece, Figs 1-45; volume 2: Pls 1-67. Van Voorst, London.

— 1874. — Notes on Norwegian Hydroida from deep water. *Ann. Mag. nat. Hist.*, (4) **13**: 125-137.

— 1880. — *In*: D'URBAN, 1880, p.257.

HISCOCK, K., 1974. — The marine fauna of Lundy. Coelenterata. *A. Rep. Lundy Fld Soc.*, **25**: 20-32.

JÄDERHOLM, E., 1904. — Mitteilungen über einige von der Schwedischen Antarktich-Expedition 1901-1903 eingesammelte Hydroiden. *Archs Zool. exp. gén.*, (4) **3**, notes et revue: i-xiv.

— 1905.— Hydroiden aus antarktischen und subantarktischen Meeres, gesammelt von der schwedischen Südpolar-Expedition. *Wiss. Ergeb. Schwed. Südpolar-Exped. 1901-1903*, **5** (8): 1-41, Pls 1-14.

— 1908. — Die Hydroiden des sibirischen Eismeeres, gesammelt von der russischen Polar-Expedition 1900-1903. *Mém. Acad. Sci. St-Pétersbourg*, (8) **18** (12): 1-28, Pls 1-3.

KRAMP, P. L., 1932a. — Hydroids collected in the West-Greenland fjords in 1911 and 1912. *Meddr Grönland*, **91** (3): 1-35, Figs 1-8.

— 1932b. — Hydroids. *In*: The Godthaab expedition 1928. *Meddr Grönland*, **79** (1): 1-86, Figs 1-34.

— 1938. — Marine Hydrozoa. Hydroida. *The Zoology of Iceland*, **2** (5a): 1-82, Figs 1-5, Tabs 1-3.

— 1943. — Hydroida. *In*: The Zoology of East Greenland. *Meddr Grönland*, **121** (11): 1-52, Figs 1-4, Tabs 1-3.

LABBÉ, A., 1899. — Recherches sur la formation de l'œuf chez les Hydraires. L'ovogénèse dans les genres *Myriothela* et *Tubularia*. *Archs Zool. expér. gén.*, (3) **7:** 1-32, Pls 1-2.

LANGMUIR, C. H., D. FORNARI, D. COLODNER, J.-L. CHARLOU, I. COSTA, D. DESBRUYÈRES, D. DESONIE, T. EMERSON, A. FIALA-MÉDIONI, Y. FOUQUET, S. HUMPHRIS, L. SALDANHA, R. SOURS-PAGE, M. THATCHER, M. TIVEY, C. VAN DOVER, K. VON DAMM, K. WIESE & C. WILSON, 1993. — Geological setting and characteristics of the Lucky Strike vent field at 17°17'N on the Mid-Atlantic Ridge. *Eos Trans.*, AGU Fall Meeting, **74:** 553.

LEVINSEN, G. M. R., 1893. — Meduser, Ctenophorer og Hydroider fra Grönlands vestkyst, tilligemed Bemaerkninger om Hydroidernes Systematik. *Vidensk. Meddr dansk naturh. Foren.*, (5) **4**: 143-212, 215-220, Pls 5-8.

LÜTKEN, C., 1875. — A revised list of the Acalephae and Hydrozoa of Greenland. *In*: T. R. JONES, *Manual of the natural history, geology and physics of Greenland and the neigbouring regions: prepared for the use of the arctic Expedition of 1875*: 187-190.

MANTON, S., 1940. — On two new species of the hydroid *Myriothela*. *Scient. Rep. Br. Graham Land Exped.*, **1** (4): 255-293, Figs 1-9, Pls 1-4, Tabs 1-2.

— 1941. — On the hydrorhiza and claspers of the hydroid *Myriothela cocksi* (Vigurs). *J. mar. biol. Ass. U.K.*, n. ser., **25**: 143-150, Figs 1-2.

Marine Biological Association of the United Kingdom, 1931. — *Plymouth marine Fauna. Being notes of the local distribution of species occurring in the neighbourhood*, 2nd ed.: 1-371, map. Plymouth, U.K (Hydrozoa: 66-84).

— 1957. — *Plymouth marine Fauna*, ed. **3**: 1-457, maps 1-4. Plymouth, U.K.

MARTIN, J. W., & J. C. CHRISTIANSEN, 1995. — A new species of the shrimp genus *Chorocaris* Martin and Hessler, 1990 (Crustacea: Decapoda: Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge. *Proc. biol. Soc. Wash.*, **108** (2): 220-227.

MILLARD, N. A. H., 1957. — The Hydrozoa of False Bay, South Africa. *Ann. S. Afr. Mus.*, **43** (4) 7-487, Figs 1-15, Pl. 1.

— 1971. — Hydrozoa. *In*: E.M. VAN ZINDEREN BAKKER, Sr., J.M. WINTERBOTTOM, & R. A. DYER, eds., *Marion and Prince Edward Islands*: 396-408, Figs 1-7. Cape Town.

— 1975. — Monograph on the Hydroida of southern Africa. *Ann. S. Afr. Mus.*, **68**: 1-513, colour plate, Figs 1-143.

— 1978. — The geographical distribution of southern African hydroids. *Ann. S. Afr. Mus.*, **74** (6): 159-200, Figs 1-9, Tabs 1-2, appendices 1 & 2.

— 1979. — Type specimens of Hydroida (Coelenterata) in the South African Museum. *Ann. S. Afr. Mus.*, **77** (8): 133-150.

— 1980. — Hydroida. The South African Museum's Meiring Naude cruises. Part 11. *Ann. S. Afr. Mus.*, **82** (4): 129-153, Figs 1-7, Tabs 1-2.

MOORE, H. B., 1937. — The marine fauna of the Isle of Man. *Proc. Lpool biol. Soc.*, **50**: 1-293, charts 1-3 (Coelenterata: 38-57).

MÖRCH, O. A. L., 1857. — Fortegnelse over Grönlands Blöddyr. Prodromus faunae Moluscorum Grönlandiae. Kjöbenhavn. Reprint from: RINK, H., *Grönland Geographisk og Statistisk beskrevet*, 2 vols. Kjöbenhavn. German translation by VON ETZEL, Stuttgart, 1860.

MÜLLER, H., 1908. — Untersuchungen über Eibildung bei Cladonemiden und Codoniden. *Z. wiss. Zool.*, **89**: 28-80, Pls 3-5.

NAUMOV, D. V., 1960. — Gidroidi i gidromedusy morskikh, solonovatovodnykh i presnovodnykh basseinov SSSR. *Opred. Faune SSSR*, **70**: 1-626, Figs 1-463, Pls 1-30, Tab. 1 [Russian]. English translation by Israel Program for scientific translations, cat. no. 5108, as "Hydroids and Hydromedusae of the USSR", i-vi, 1-631, Figs 1-463, Pls 1-30, Tab. 1, 1 folding plate (1969).

NICHOLS, D., J. A. L. COOKE & D. WHITELEY, 1971. — The Oxford book of invertebrates. Protozoa, Sponges, Coelenterates, Worms, Molluscs, Echinoderms, and Arthropods (other than insects). *Oxford University Press*, i-viii, 1-218, colour Pls.

PARFITT, E., 1866. — *A catalogue of the fauna of Devon, with notes and observations. Zoophytes*: 1-40 pp. Exeter.

PENNINGTON, A. S., 1885. — *British Zoophytes: An introduction to the Hydroida, Actinozoa and Polyzoa found in Great Britain, Ireland, and the Channel Islands*: 1-363, Pls 1-24. London.

PÉRÈS, C., 1939. — Quelques anomalies observées chez les hydraires gymnoblastiques. *Trav. Stn zool. Wimereux*, **13**: 539-544, Figs 1-2, Pls 25-26.

PETERSEN, K. W., 1990. — Evolution and taxonomy in capitate hydroids and medusae. *Zool. Jl linn. Soc.*, **100**: 101-231, Figs 1-49.

PRENANT, M., & G. TEISSIER, 1924. — Notes éthologiques sur la faune marine sessile des environs de Roscoff. Cirripèdes, bryozoaires, hydraires. *Trav. Stn biol. Roscoff*, **2**: 1-49, Fig. 1.

PREVOT, E., 1959. — Morphologie et évolution des structures tentaculaires chez les hydraires Gymnoblastes Capitata. *Recl. Trav. Stn mar. Endoume*, **29** (Bull. 17): 91-126, Figs 1-3, Pls 1-6.

PRUVOT, G., 1897. — Essai sur les fonds et la faune de la Manche occidentale (côtes de Bretagne) comparés à ceux du Golfe du Lion. *Archs Zool. exp. gén.*, (3) **5**: 510-617, Tabs 1-22.

RALPH, P. M., 1966. — Hydroida. *In:* Port Phillip Survey 1957-1963. *Mem. natn. Mus. Vict.*, **27**: 157-166, Figs 1-4.

REES, W. J., 1956. — A revision of some northern gymnoblastic hydroids in the Zoological Museum, Oslo. *Nytt Mag. Zool.*, **4**: 109-120, Figs 1-2.

— 1957. — Evolutionary trends in the classification of capitate hydroids and medusae. *Bull. Br. Mus. nat. Hist., Zool.* **4** (9): 455-534, Figs 1-54, Pl. 12.

REES, W. J., & S. THURSFIELD, 1965. — The hydroid collections of James RITCHIE. *Proc. R. Soc. Edinb.*, (B) **69** (1-2) (2): 34-220.

RITCHIE, J. S., 1909. — Supplementary report on the Hydroida of the Scottish National Antarctic Expedition. *Trans. R. Soc. Edinb.*, **47** (I, 4): 65-101.

ROBINS, M. W., 1969. — The marine flora and fauna of the Isles of Scilly. *J. nat. Hist.*, **3**: 329-343 (18.vii.1969).

SARS, G. O., 1873. — Bidrag til Kundskaben om Dyrelivet paa vore Havbanker. *Forh. VidenskSelsk. Krist.*, 1872: 73-119.

— 1874. — Bidrag til Kundskaben om Norges Hydroider. *Forh. VidenskSelsk. Krist.*, 1873: 91-150, Pls 2-6.

— 1877. — *In*: M. SARS, 1877.

— 1851. — Beretning om en i Sommeren 1849 foretagen Zoologisk Reise i Lofoten og Finmarken. *Nyt Mag. Naturvid.*, **6**: 121-211.

— 1857. — Oplysninger om *Pennatula stellifera* Müll., *Corynactis mediterranea*, *Tubularia larynx*, *Podocoryne fuscicola* og *Myriothela arctica*. *Forh. skand. Naturf. Möte*, **7**: 192-202.

— 1860. — Udtog af en Afhandling, som med de tilhörende talrige Afbildninger er bestemt for naeste Hefte af Fauna littoralis Norvegiae, om Ammeslaegten *Corymorpha* og dens Arter samt de af disse opammede Meduser. *Forh. VidenskSelsk. Krist.*, 1859: 96-105. German translation in: *Arch. Naturgesch.*, **26**: 341-351. English translation in: *Ann. Mag. nat. Hist.*, (3) **8**: 363-360.

— 1861. — [Oplysninger om nogle Coelenterater fra Norges Kyster]. *Forh. skand. Naturf. Möte*, **8**: 690-698.

— 1877. — Nye og mindre bekjendte Coelenterater. New and little known Coelenterates. *In*: J. KOREN & D. C. DANIELSSEN, *Fauna littoralis Norvegiae*, **3**: 1-32, Pls 1-2.

SEGONZAC, M., 1992. — Les peuplements associés à l'hydrothermalisme océanique du Snake Pit (dorsale médio-atlantique; 23°N, 3 480 m): composition et distribution de la mégafaune. *C. R. Acad. Sci. Paris*, (3) **314**: 593-600.

SEGONZAC, M., M. DE SAINT LAURENT & B. CASANOVA, 1993. — L'énigme du comportement trophique des crevettes Alvinocarididae des sites hydrothermaux de la dorsale médio-atlantique. *Cah. Biol. Mar.*, **34**: 535-571. English transl. IFREMER, 1994: The enigma of the trophic behaviour of Alvinocaridid shrimps from hydrothermal vent sites on the Mid-Atlantic Ridge, pp. 1-20.

STECHOW, E., 1909. — Hydroidpolypen der japanischen Ostküste. I. Teil: Athecata und Plumularidae. *In*: F. Doflein, Beiträge zur Naturgeschichte Ostasiens. *Abh. math.-phys. Kl. Kön. bayer. Akad. Wiss.*, suppl. 1 (6): 1-111, Figs 1-3, Pls 1-7.

— 1920. — Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. *Sb. Ges. Morph. Phys., München*, **31**: 9-45, Figs 1-10.

— 1922. — Zur Systematik der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren. *Arch. Naturgesch.*, (A) **88** (3): 141-155.

— 1923. — Zur Kenntis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zool. Jb., Syst.* **47** (1-3): 29-270, Figs 1-35.

STEPAN'YANTS, S. D., 1972. — Gidroidy pribrezhnykh vod morya devisa (po materialam XI sovetsko antarkti-chesko ekspeditsii 1965/66 g.). Hydroidea of the coastal waters of the Davis Sea (collected by the XI Soviet Antarctic Expedition of 1965-66). *In*: Resultaty biologicheskikh isledovani sovetskikh antarkti-cheskikh ekspeditsi. *Issled. Fauny Morei*, **11** (19): 56-79, Figs 1-20 [Russian].

— 1979. — Gidroidy vod antarktiki i subantarktiki. *In*: Rezul'taty biologicheskikh issledovanii sovetskikh ant-arkticheskikh ekspeditsii, 6. *Issled. Fauny Morei*, **22** (30): 1-99, Figs 1-9, Pls 1-25, 3 coloured figures on 2 plates, Tabs 1-17 [Russian].

— 1985. — Tip Coelenterata Kishechnopolostnye, Klass Hydrozoa Gidrozoi. *In*: K.V. GALAKTIONOV, ed., Zhizn' i usloviya ee sushchestvovaniya v bentali Barentseva morya. Life and conditions for its existence in the benthic zone of the Barents Sea: 83-87. *Akad. Nauk SSSR*, Apatity: 1-220 [Russian].

— 1989. — Hydrozoa of the Eurasian arctic seas. *In* Y. HERMAN, ed., The Arctic Seas. Climatology, Oceanography, Geology, and Biology: 397-430, maps 16.1-16.3. New York, Van Ostrand Reihold Co.

STEPHENS, J., 1905. — A list of Irish Coelenterata, including the Ctenophora. *Proc. R. Ir. Acad.*, (B) **25**: 25-92.

STORM, V., 1879. — Bidrag til Kundskab om Throndhjemsfjordens Fauna. *K. norske Vidensk. Selsk. Skr.*, 1878: 9-36.

— 1880. — Bidrag til Kundskab om Throndhjemsfjordens Fauna. II. *K. norske Vidensk. Selsk. Skr.*, 1879: 109-125.

— 1882. — Bidrag til Kundskab om Throndhjemsfjordens Fauna. IV. *K. norske Vidensk. Selsk. Skr.*, 1881: 1-30.

SVARCHEVSKI, B. A., 1923. — Ocherki po Hydraria I. *Hydra baicalensis* n. sp.: II. K voprosu o filogenii *Hydra*. (Essays on Hydra's. I. *Hydra baicalensis* n. sp. II. On the question of Hydra's phylogeny). *Sb. Trud. Prof. Prepod. gos. Irkutsk. Univ.*, **4**: 90-102 [Russian].

SWENANDER, G., 1904. — Über die Athecaten Hydroiden des Drontheimsfjordes. *K. norske Vidensk. Selsk. Skr.*, 1903 (6): 1-18, Pl. 1.

TEISSIER, G., 1950b. — Inventaire de la faune marine de Roscoff. Cnidaires et Cténaires. *Trav. biol. Roscoff.*, n. ser., suppl. **1**: 1-43.

—1965. — Inventaire de la faune marine de Roscoff. Cnidaires-Cténaires. *Trav. Stn biol. Roscoff*, **16**: 1-53 [64].

THOMSON, J. A., 1904. — Scotia collections. Note on the gonostyle of two antarctic Siphonophora. *Proc. R. phys. Soc. Edinb.*, **16** (1): 19-22, Pl. 1.

VAN DE VYVER, G., 1968a. — Étude du développement embryonnaire des hydraires athécates (Gymnoblastiques) à gonophores. 2. Formes à actinulas. *Archs Biol., Paris*, **79**: 327-363, Figs 1-7, i-v.

VAN DE VYVER, G., 1968b. — Étude du développement embryonnaire des hydraires athécates (Gymnoblastiques) à gonophores. 3. Discussion et conclusions générales. *Archs Biol., Paris*, **79**: 365-379.

VAN DE VYVER, G., 1980. — A comparative study of the embryonic development of Hydrozoa Athecata. *In*: P. TARDENT & R. TARDENT, eds., Developmental and cellular biology of coelenterates. Proceedings IV. International Coelenterate Conference, Interlaken, 4-8 Sept., 1979: 109-120, Figs 1-6, Tab. Elsevier/N. Holland Biomed. Press, Amsterdam, etc.: i-xxvi, 1-499, Figs, Tabs.

VAN DOVER, C. L., D. DESBRUYÈRES, M. SEGONZAC, T. COMTET, L. SALDANHA, A. FIALA-MÉDIONI & C. LANGMUIR, submitted. — Biology of the Lucky Strike Hydrothermal Field. *Deep-sea Research.*

VANHÖFFEN, E., 1897. — *Die Fauna und Flora Grönlands. Grönland Expedition der Gesellschaft für Erdkunde zu Berlin*, 1891-1893, unter Leitung von E. VON DRYGALSKI, **2** (1): 1-383, Pls 1-8.

— 1910. — Die Hydroiden der Deutschen Südpolar-Expedition 1901-1903. *Deutsche Südpolar-Expedition*, **11** (= Zool. 3): 269-340, Figs 1-49.

VERRILL, A. E., 1879. — *Preliminary check-list of the marine Invertebrata of the Atlantic coast, from Cape Cod to the Gulf of St. Lawrence*: 1-32. New Haven, Connecticut.

VIGURS, 1849. — *In*: Cocks W. P., 1849: 90.

WEILL, R., 1926. — Une catégorie spéciale de nématocystes commune aux seuls Hydrides, Gymnoblastides et Siphonophores. *C. r. hebd. Séanc. Acad. Sci. Paris*, **182** (20): 1244-1247, Figs 1-4.

— 1934a.— Contribution à l'étude des Cnidaires et de leurs nématocystes. I. Recherches sur les nématocystes. Morphologie – Physiologie – Développement. *Trav. Stn zool. Wimereux*, **10**: 1-347, Figs 1-208.

— 1934b. — Contribution à l'étude des Cnidaires et de leurs nématocystes. II. Valeur taxonomique du cnidome. *Trav. Stn zool. Wimereux*, **11**: 349-701, Figs 209-432.

WHITEAVES, J. F., 1901. — Catalogue of the Invertebrata of Eastern Canada. *Geol. Survey Canada*, **722**: 1-272.

WINTHER, G., 1880. — Fortegnelse over de i Danmark og dets nordlige Bilande fundne Hydroide. *Naturh. Tidsskr.*, **12**: 223-278.

WRIGHT, T. S., 1858. — [A specimen of the *Hydra tuba* (Dalyell) throwing off Medusae; *Myriothela arctica* of Sars]. *Proc. R. phys. Soc. Edinb.*, **1**: 432-433.

WRIGHT, T. S., 1859. — Observations on British zoophytes. *Edinb. New philos. J.*, n. ser. **10**: 105-114, Pls 8-9.