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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3. - This study reviews all European hydroids belonging to the filiferan families Hydractiniidae, Rhysiidae, and Stylasteridae. Stylasterids are treated only summarily because a recent, exhaustive monograph is available.
Stylactaria claviformis Bouillon, 1965 and *Hydractinia calderi* Bouillon, Medel, & Peña Cantero, 1997 are both regarded as junior synonyms of *Hydractinia proboscidea* (Hincks, 1868). *Podocoryna corii* Stechow, 1929 is regarded as a new junior synonym of *H. borealis*. *Cytaeandrea polystyla* Haeckel, 1879 is perhaps a synonym of *Turritopsis polycirrha* (Keferstein, 1862). *Hydractinia areolata* Alder, 1862 is selected as type species for the genus *Cytaeandra* Haeckel, 1879. *Clavopsis adriatica* Graeffe, 1883a is an indeterminate species, perhaps belonging to *Turritopsis dohrnii* (Weismann, 1883).

Keywords: Cnidaria - marine - Hydrozoa - Hydractiniidae - Rhysiidae - Stylasteridae - revision - taxonomy - northeastern Atlantic - Mediterranean.

INTRODUCTION

This study is the fourth in a series of taxonomic revisions and reviews of the European Anthoathecata (=Anthomedusae, Athecata). The previous ones are: Schuchert (2004; Oceaniidae and Pachycordylidae), Schuchert (2006; Acaulidae, Boreohydridae, Candelabridae, Cladocorynidae, Cladonematidae, Margelopsidae, Pennariidae, Protohydridae, Tricyclusidae), and Schuchert (2007; Bougainvilliidae, Cytaeididae, Rathkeidae, and Pandeidae).

MATERIAL AND METHODS

For morphological methods see Schuchert (1996; 2004) or Bouillon *et al.* (2004). For technical terms see below and also in Boschma (1956), Millard (1975), Cornelius (1995a, b), and Bouillon *et al.* (2006).

Where possible, it was attempted to supplement the species descriptions by sequence information of the 16S mitochondrial rRNA gene. The methods to obtain DNA sequences are described in Schuchert (2005). All sequences have been submitted

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to the EMBL database. The origin and identity of the material used to obtain 16S sequence data as well as the accession numbers are given for each species in the section "Material examined". Some sequences have been determined by other laboratories using material described here.

DEFINITION OF SOME TERMS

ampulla: bubble-like cavity in the coenosteum of stylasterids containing the gonozooid, either at the surface or deeply buried in coenosteum, with efferent canals or pores. Female ampullae are generally larger than male ones.

blastostyle: structure carrying gonophores, often strongly reduced hydranths, but not all blastostyles are homologous.

coenosarc: living tissue of a colony.

coenosteum: calcified skeleton of stylasterids, hydrocorals, or corals.

cyclosystem: in stylasterids, concentric arrangement of dactylopores around a gastropore.

dactylopore: in stylasterids, tubular opening in the skeleton into which the dactylozooids can retract, usually smaller than the gastropore, in some genera encircling the gastropore, some dactylopores have a spine, a collar-like elevation of the rim.

dactylozooids: modified polyps with a defensive function, comprises tentaculozooids and spiral zooids.

diastema: in stylasterids, occlusion of dactylopore; some dactylopores in cyclosystems may be secondarily filled by coenosteum.

flabelliform: fan-shaped.

gastropore: tubular opening in the skeleton of stylasterids into which the gastrozooid can retract, usually larger than the dactylopore.

gastrostyle: in stylasterids, coaxial spine at base of gastropore, always ornamented with prickles.

gastrozooids: normal feeding polyps with mouth and normally with tentacles, without reproductive organs.

gonophore: reproductive structures formed during polyp stage, may develop into free medusa or remain fixed, phylogenetically derived from one medusa bud only.

gonozooids: reproductive polyps bearing gonophores, either modified gastrozooids that show various stages of reduction and loss of tentacles, or polyps that are distinct from gastrozooids from the beginning, later developing gonophores.

hydrorhiza: all structures by which polyps are attached to the substratum, usually stolons.

medusoid: reduced medusa, with umbrella, but without functional mouth and either no or only rudimentary tentacles.

nematopore: in stylasterids, small pore harbouring nematozooids.

nematozooid: similar to tentaculozooid, zooid with defensive function.

palisade, ring palisade: in stylasterids, columnar processes of lateral wall of gastropore, pointing towards the centre.

pedicel: stalk of polyp.

pseudoseptae: in cyclosystems of stylasterids the wall separating the gastropore and the surrounding dactylopores is often obliterated. With the radially arranged edges of the dactylopores, the cyclosystems thus resemble the calyces of scleractinian corals.

spine in stylasterids: elevatation of rim of dactylopore into mound- or collar-like structure.

stolonal: in stolonal colonies, polyps arise only from stolons, they may have a caulus, here used in the sense of colonies without branching stems.

sporosacs: gonophores that mostly remain fixed to the hydranth and release gametes from there; there is no further implication on its structure, but usually kept separate from attached medusoids that differ in having pulsating umbrella.

sympodial: stem axis forming a zigzag pattern through superposed lateral branches.

tentaculozooid: polyp similar to tentacle in structure, mostly with a solid core of gastrodermis and no mouth or gastric cavity. More delicate and slender than spiral zooids.

texture of coenosteum: microscopic surface texture of skeleton of stylasterids, e. g. linear-imbricate scales or reticular-granular.

unifacial: one-sided.

ABBREVIATIONS

BMNH	The Natural History Museum, London, England
ERMS	European Register of Marine Species (Costello *et al.,* 2001)
FNHM	The Faroes Natural History Museum
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
ICZN	International Code of Zoological Nomenclature
IRSN	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
ZMO	Zoological Museum Oslo, Norway
ZMUC	Zoological Museum Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, Munich, Germany

TAXONOMIC PART

FAMILY HYDRACTINIIDAE L. AGASSIZ, 1862

TYPE GENUS: *Hydractinia* van Beneden, 1841.

SYNONYMS: Podocorynidae Allman, 1864c: 353. – Stylactidae Haeckel, 1889: 79. – Hydrodendridae Nutting, 1906. – Janariidae Stechow, 1921a: 29.

DIAGNOSIS: Polyps colonial, lacking pedicels and thus sessile, polymorphic or not; hydrorhiza either perisarc-covered stolonal tubes, or an encrusting mat resulting from the coalescence of the stolonal system, either covered by a common layer of perisarc or with naked coenosarc; in some genera the hydrorhizal mat is reinforced by a calcareous skeleton; frequently with chitinous or calcareous spines sometimes forming pillars and branches, sometimes with protective tubes overarching the hydranths. Polyps either with one or several whorls of filiform tentacles beneath hypostome, or with scattered tentacles on the upper half of the body, exceptionally with one or two tentacles only; dactylozooids, when present, with no tentacles. Gonophores typically borne on gonozooids, these with one or more whorls of filiform tentacles or without tentacles and mouth (= blastostyles), giving rise to fixed sporosacs, eumedusoids, or free medusae.

Medusa umbrella more or less bell-shaped, with or without slight apical process; manubrium tubular to sac-shaped, not extending beyond bell margin; with or without gastric peduncle; mouth with four simple or branched oral lips drawn out to form arms with terminal nematocyst clusters; four, eight, or more, solid, marginal tentacles, tentacles not in groups; with or without ocelli; four radial canals and circular canal. Gonads on manubrium, interradial, sometimes extending along basal, perradial protrusions of the manubrium.

REFERENCES: Motz-Kossowska (1905), Goette (1916), Kramp (1927, 1932a), Calder (1988), Namikawa (1991), Bouillon *et al.* (1997).

REMARKS: The taxonomic history and the problems of this family have been outlined by Calder (1988). The generic subdivision of the Hydractiniidae is provisional and will certainly be changed in future again. Here, the classification of Bouillon *et al.* (1997, 2006) was adopted, though with some modifications. As discussed in Schuchert (2001a), the genus *Clava* Gmelin, 1791 is also regarded as a member of the Hydractiniidae. This leads to the awkward situation that the name Hydractiniidae L. Agassiz, 1862 formally becomes a junior synonym of Clavidae McCrady, 1859 [see also Schuchert (2001a) for further details]. Even without this, the scope of the family

Hydractiniidae remains contentious [see e.g. Schuchert (2007) for *Kinetocodium* and others]. Bouillon *et al.* (2006) provide a key and diagnoses for all genera.

Dysmorphosa minuta Mayer, 1900b and *Cytaeis minima* Trinci, 1903 have both been included in the Hydractiniidae, either in the genus *Podocoryne* or *Hydractinia* (e. g. Kramp, 1961; Bouillon *et al.*, 2006). In my previous study (Schuchert, 2007), I argued that both belong to the family Rathkeidae. Furthermore, *Dysmorphosa minuta* Mayer, 1900b is a subjective synonym of *Lizzia blondina* Forbes, 1848, and *Cytaeis minima* was transferred to a new genus as *Podocorynoides minima* (Trinci, 1903).

As with many other hydrozoans, non-reproductive hydroids in this family are not reliably identifiable. In order to identify hydroids producing a free medusa phase, information on the mature medusa stage is usually essential. This means that only living, cultivated material is reliably identifiable. This also holds true for some species producing medusoids, as some traits – like the rudimentary tentacles – will develop only rather late.

The nematocyst types of the Hydractiniidae examined here are rather uniform and do not offer much help in reliably discriminating the species. In future, barcoding approaches (e. g. Moura *et al.*, 2008) will certainly play a decisive role to resolving some of the problems.

KEY TO THE HYDRACTINIID GENERA OF THE ERMS ZONE:

1a Polyp tentacles in 1-3 whorls confined to a narrow region . . . . *Hydractinia*
1b Polyp tentacles scattered in broad region below hypostome, no polymorphism, with sporosacs . . . . *Clava*

Genus ***Hydractinia*** van Beneden, 1841

TYPE SPECIES: *Hydractinia lactea* van Beneden, 1844, a synonym of *H. echinata.*

SYNONYMS:

Echinochorium Hassal, 1841; type species *Echinochorium clavigerum* Hassall, 1841, a synonym of *H. echinata.*
Dysmorphosa Philippi, 1842*;* type species *Dysmorphosa conchicola* Philippi, 1842.
Podocoryna M. Sars, 1846; type species *Podocoryna carnea* M. Sars, 1846, by monotypy.
Podocoryne Lütken, 1850, introduction of incorrect spelling that became prevalent.
Synhydra Quatrefages, 1843; type species *Synhydra parasites* Quatrefages, 1843, a synonym of *H. echinata.*
Cionistes Wright, 1861; type species: *Cionistes reticulata* Wright, 1861, an indeterminate hydractiniid species.
Stylactis Allman, 1864c; type species *Podocoryna fucicola* Sars, 1857, designated by Mayer (1910).
Rhizocline Allman, 1864c; type specis *Hydractinia areolata* Alder, 1862.
Cytaeandra Haeckel, 1879; type species *Hydractinia areolata* Alder, 1862.
Hydrodendrium Nutting, 1906; type species *Hydrodendrium gorgonoides* Nutting, 1906 by monotypy.
Nuttingia Stechow, 1909; type species *Hydrodendrium gorgonoides* Nutting, 1906; invalid new name for *Hydrodendrium* Nutting, 1906 as junior synonym.
Euhydractinia Broch, 1910; introduced as subgenus of *Hydractinia*, no type species specified.
Hydronema Stechow, 1921b; type species *Hydractinia dendritica* Hickson & Gravely, 1907, name preoccupied by *Hydronema* Martynow (Trichoptera).
Stylactaria Stechow, 1921b; type species *Stylactis inermis* Allman, 1872 after original designation by Stechow (1921b).

Hydractomma Stechow, 1921b; type species: *Hydractinia pruvoti* Motz-Kossowska, 1905.
Hydrissa Stechow, 1922; type species *Hydractinia sodalis* Stimpson, 1859.
Podocorella Stechow, 1921c; type species *Stylactis minoi* Alcock, 1892.
Halorhiza Stechow, 1962; type species *Hydractinia dendritica* Hickson & Gravely, 1907.
? *Cnidostoma* Vanhöffen, 1911; type species of *Cnidostoma fallax* Vanhöffen, 1911.
? *Archaeoceania* Picard & Rahm, 1954; type species *Archaeoceania tournieri* Picard & Rahm, 1954, synonym of *Cnidostoma fallax* Vanhoeffen, 1911.
? not *Clavopsis* Graeffe, 1883; type species *Clavopsis adriatica* Graeffe, 1883.
not *Stylactella* Haeckel, 1889, belongs to Cytaeididae.
not *Oorhiza* Mereschowsky, 1877, belongs to Cytaeididae.
not *Halerella* Stechow, 1922, belongs to Rhysiidae.

DIAGNOSIS: Hydroid arising either from a reticular hydrorhiza formed by perisarc-covered stolonal tubes, or from an encrusting mat issued through the coalescence of stolonal system, covered by a common layer of perisarc or by naked coenosarc; hydrorhizal crust can secrete a calcareous skeleton in some genera; frequently with chitinous or calcareous spines, sometimes forming erect structures. Polyps sessile, naked, usually polymorphic; gastrozooids with one or more whorls of oral filiform tentacles confined to a small region below hypostome; dactylozooids, when present, with no tentacles; gonophores borne on gonozooids; gonozooids with or without tentacles, with or without mouth, giving rise to fixed sporosacs, fixed or free medusoids, or free medusae.

Medusa umbrella more or less bell-shaped; with or without slight apical process; manubrium tubular to sac-shaped, not extending beyond bell margin; with or without gastric peduncle; perradial corners of mouth with four nematocyst clusters or drawn out into simple or branched oral lips, sometimes elongated to form arms, ending in terminal nematocyst clusters; 4, 8, or more, solitary, solid, marginal tentacles; four radial canals and circular canal; gonads on manubrium, interradial, sometimes also on basal perradial pouches of the manubrium. With or without ocelli. Medusae budding from manubrium occasionally present.

REMARKS: Following Bouillon *et al.* (1997, 2006), the genera *Stylactaria* Stechow, 1921c and *Podocoryna* M. Sars, 1846 are here regarded as synonyms of *Hydractinia* van Beneden, 1841 as they cannot be separated unambiguously. As can be seen from the list above, there are many more synonyms that can be subsumed under *Hydractinia*.

The genus *Cytaeandra* Haeckel, 1879 was established for *Hydractinia areolata* Alder, 1862 and *H. polystyla* Haeckel, 1879. Haeckel (1879) did not select a type species. *Hydractinia areolata* Alder, 1862 is herewith selected as type species for the genus *Cytaeandra*, rendering it thus a synonym of *Hydractinia* as defined here. Kramp (1959, as *Podocoryne polystyla*) regarded the medusa *Cytaeandrea polystyla* Haeckel, 1879 as a doubtful species. It is characterised by 32 simple tentacles, bulbs with an ocellus, 16 nematocyst clusters on the mouth-rim, and crescent shaped gonads with their concave side facing towards the mouth. I think Haeckel's medusa was a young *Turritopsis polycirrha* (Keferstein, 1862) (see Schuchert, 2004 for a description).

Some nominal species of *Hydractinia* in the ERMS region have long been recognized as indeterminate (Bedot, 1910) and will not be discussed here. These are: *H. littoralis* Gosse, 1855; *H. incerta* van Beneden, 1867; *H. solitaria* van Beneden, 1867; and *H. tenuissima* van Beneden, 1867. This list is perhaps not complete.

The species are discussed in the same sequence in which they appear in the following key.

Key to *Hydractinia* species in the ERMS zone (problematic species excluded):

1a Gonophores released as free medusae having tentacles longer than bell when expanded 2
1b Gonophores sporosacs or medusoids with rudimentary tentacles 5
2a Manubrium of mature medusa with basal pouches bearing gonads, bell-margin with more than 40 tentacles of very unequal length . . . . . . *H. areolata*
2b Medusa without basal manubrium pouches, mature with 4-30 tentacles 3
3a Mature medusa with branched oral nematocyst clusters, 16-30 tentacles . . . . . . *H. borealis*
3b Oral nematocyst clusters simple, not branched 4
4a Mature medusa with 8-10 tentacles, newly liberated medusae 5-8 tentacles, British Isles to Norway . . . . . . *H. carnea*
4b Mature medusa with 4 tentacles, Mediterranean and Atlantic coast from Gibraltar to France . . . . . . *H. exigua*
5a Gonophores sporosacs or medusoids, in both cases with four radial canals . . . 6
5b Mature gonophores sporosacs without radial canals 10
6a Arctic species on gastropods, encrusting hydrorhiza, medusoid with 8 rudimentary tentacles, up to 100 eggs per medusoid . . . . . . *H. allmani*
6b Boreal or Mediterranean distribution, hydrorhiza stolonal 7
7a Gonozooids with much reduced number of tentacles (1-2, rarely 3); medusoids released, with gastric peduncle . . . . . . *H. pruvoti*
7b Gonozooids like smaller gastrozooids, more than 3 tentacles, produces sporosacs or medusoids without gastric peduncle 8
8b Gastrozooid tentacles in 2-3 close-set whorls, medusoids or sporosacs without distinct bulbs 9
8a Gastrozooid tentacles in one whorl, female medusoids with four small bulbs and 0-4 tentacle rudiments . . . . . . *H. aculeata*
9b Gastrozooid hypostome slightly necked, with or without spines, gonophores medusoid, with 4-10 tentacle rudiments, released or not . *H. proboscidea*
9b Gastrozooid hypostome not necked, no spines, gonophores sporosacs without tentacle rudiments, not released . . . . . . *H. inermis*
10a Gonozooids with tentacles, these fully formed or only somewhat shortened 11
10b Gonozooids without tentacles or these reduced to stumps or warts 12
11a On fixed substrata, Mediterranean to Brittany . . . . . . *H. fucicola*
11b On gastropod shells and other living, mobile substrates, distribution Norway to Arctic . . . . . . *H. sarsii*
12a Boreal shallow water occurrence, distal end of gonozooids with nematocyst buttons, spines with spiny ridges . . . . . . *H. echinata*
12b Predominantly arctic or deep-sea species 13
13a Growing on deep-sea ophiurid *Homalophiura tesselata,* hydrorhiza stolonal . . . . . . *H. ingolfi*

13b Arctic species growing on gastropod shells 14
14a Hydrorhiza stolonal, deep sea species, gonozooids with rudimentary tentacles, 10 eggs per sporosac .... *H. arctica*
14b Hydrorhiza encrusting 15
15a Spines high, slender 16
15b Spines low, conical, gonozooids 0-4 very short tentacles, 3-7 sporosacs, 5-6 eggs per female sporosac .... *H. carica*
16a 1-4 sporosacs at base of gonozooids, female sporosacs one egg, spines with four serrated ridges .... *H. serrata*
16b 1 sporosac in middle of gonozooid, female sporosacs with up to 50 eggs, spines without serrated ridges .... *H. monocarpa*

Hydractinia areolata Alder, 1862 Fig. 1

Hydractinia areolata Alder, 1862a: 144. – Alder, 1862b: 311, pl. 13 figs 1-4. – Alder, 1863: 314, pl. 14 figs 1-4. – Cornelius & Garfath, 1980: 277.
Rhizocline areolata. – Allman, 1864c: 11.
Podocoryne areolata. – Hincks, 1868: 32, pl. 6 figs 1 & 1a. – Allman, 1872: 353.
Cytaeandrea areolata. – Haeckel, 1879: 79.
in part *Podocoryne areolata*. – Hartlaub, 1911: 219, figs 191. [others *H. borealis*]
Podocoryne hartlaubi Neppi & Stiasny, 1911: 395. – Neppi & Stiasny, 1913: 25, pl. 2 fig. 14. – Russell, 1953: 130, figs 60A-D, 61A-B, pl. 6 figs 1, 4. – Kramp, 1961: 69. – Yamada, 1961: 134, figs 1-5. – Kramp, 1959: 101, fig. 66. – Brinckmann-Voss, 1970: pl. 7 fig. 2. – Edwards, 1972: 104, synonym.
not *Podocoryne areolata*. – Kramp & Damas, 1925: 268, figs 15-17.[= *H. borealis*]
Podocoryne areolata. – Edwards, 1972: 98, figs 1-2.
Hydractinia areolata. – Bouillon *et al.,* 2004: 63, figs 37B-I.

Material examined: FNHM, BIOFAR station 473; 62.603°N 05.717°W; The Faroes; 198 m; 6 June 1989; with medusa buds. – France, Brittany, Roscoff; 1 April 1998; 10 m depth; one mature medusa from plankton; material not preserved. – Norway, Raunefjord; 0-20 m; plankton net 190 μm; 19 June 2006; one mature medusa; material photographed but not preserved; 16S DNA sequence identical to **AM939651**. – MHNG INVE48749; Norway, Fanafjord, close to southern coast; fine mud; 60-80 m; 16 June 2006; triangular dredge; polyp on gastropod shell with hermit crab; liberated medusae have 16 tentacles, spines not distinctly grouped, but medusa and DNA sequences confirmed identification; 16S DNA sequence **AM939651**.

Diagnosis: Polyps relatively small (2 mm), gonozooids smaller than gastrozooids, spines when present often grouped, newly released medusa with 14-16 tentacles, mature medusa with perradial, basal pouches on manubrium bearing gonads, more than 40 tentacles of very unequal length.

Description: Hydroid growing on shells of hermit-crabs and crab carapaces. Hydrorhiza a small-meshed network of adhering stolons enclosed in perisarc, in more marginal region it can be less densely developed, in some regions network may become confluent and mat-like, layer of naked coenosarc rare or lacking. Spines present or not, presence depending on substrate and environment the host is living in. Spines rather high, slender, pointed, perisarc smooth. The spines can be arranged in a characteristic grouped pattern, either in linear arrays or small rows or groups of closely set spines, alternating with spine-free patches.

Polyps polymorphic, relatively small, differentiated into gastrozooids, gonozooids, tentaculozooids, and spiral zooids; the latter two types may be absent, their presence depending on host and environment.

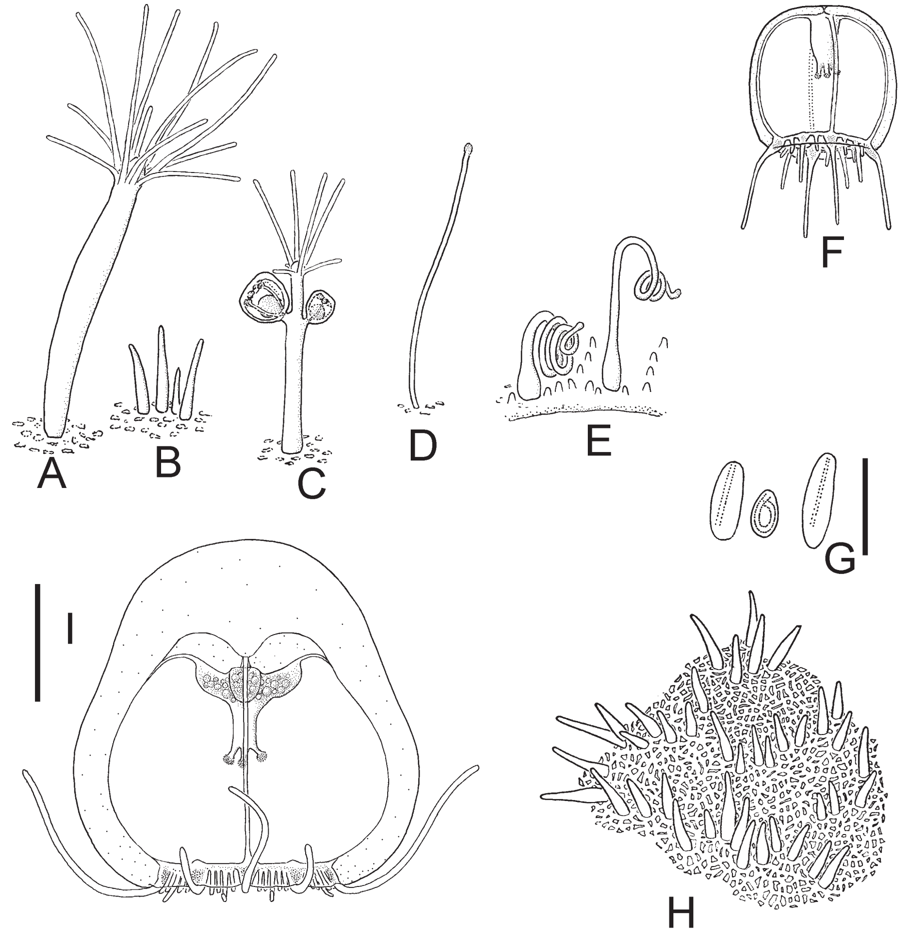

FIG. 1

Hydractinia areolata Alder, 1862; A-F, H modified after Edwards, 1972; G after preserved material; I after life. (A) Gastrozooid, ca 2 mm high. (B) Group of spines, same scale as A. (C) Gonozooid, same scale as A. (D) Tentaculozooid, same scale as A. This zooid-type is not always present. (E) Two spiral zooids at the margin of the colony. This zooid-type is not always present. (F) Newly released medusa. (G) Nematocysts: microbasic eurytele, desmoneme, elongate microbasic eurytele of oral lips of the medusa; scale bar 10 μm. (H) Perisarc skeleton showing mesh of stolons and the characteristically grouped spines. Note that the spines are not present in all colonies and they are sometimes evenly distributed, not grouped. (I) Lateral view of mature medusa from plankton, bell rim slightly contracted, scale bar 1 mm.

Gastrozooids with fusiform body, dome-shaped hypostome, one or two very closely set whorls of tentacles, 9-12 in number (range 4-14), unequal in length, alternately pointing upward and horizontal, base of hydranth without perisarc collar. Hypostome with scattered euryteles, but these not forming a contiguous layer.

Gonozooids smaller and more slender than feeding zooids (ca. 1/3 to 2/3 the size of the gastrozooids), 4-7 tentacles, medusa buds arising below tentacles, one to rarely five in number but usually two, when two buds occur, these opposed. Larger gonozooids are able to ingest prey. With progressing medusa-bud development, gonozooids becoming reduced to mere stumps (reproductive exhaustion), feigning development of the gonophores from stolons.

Tentaculozooids of about the size of gastrozooids, rare, very slender (1/10 of diameter of gastrozooids of similar height), not spirally coiled, uniform thickness, slightly swollen tip.

Spiral zooids sometimes present at the rim of the colony at the outer lip of the supporting gastropod shell, length comparable to large gastrozooids, base swollen, above this swelling tapering to a blunt tip armed with nematocysts, when active coiling and uncoiling frequently.

Nematocysts of polyps: oval microbasic euryteles, desmonemes. Colours: spine perisarc brown; hydranths white to pinkish.

Medusa at liberation usually with 16 tentacles or tentacle rudiments (range 14-16), four perradial tentacles well developed and each with a well developed basal bulb with red gastrodermal tissue, four interradial tentacle bulbs less developed than perradial ones, eight adradial tentacles short, without bulbs. Apical canal present, umbrella spherical, exumbrella sprinkled with numerous nematocysts, manubrium simple, about 1/2 the height of the subumbrellar cavity, square in cross-section, without any trace of gonads or basal pouches, four relatively long, unbranched oral lips.

Adult medusa bell-shaped, slightly wider than high, jelly thicker at apex, often with shallow gastric peduncle. Four radial canals and a circular canal. 40-56 tentacles (max. 66 in Mediterranean), eight tentacles (per- and interradial ones) long, others markedly shorter. Bulbs of variable size, correlated with tentacle length, without ocelli. Manubrium spans about 1/2 to entire height of subumbrella, cross-section cruciform to square, with four characteristic perradial basal pouches of variable size, pouches may reach a size of about 1/3 of radial canal length; four oral lips relatively long and tentacle-like, terminating in single, rounded mass of nematocysts. Gonads adradial on basal pouches and interradial regions between the pouches, separated perradially. Nematocysts: in tentacles shorter microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles. Medusa gastrodermis vermillion-red, yellow, or dark brown, colour probably depending on diet.

DIMENSIONS: Gastrozooids up to 2 mm, 0.22 mm diameter. Largest spines 0.7-0.9 mm. Microbasic euryteles of polyp (7-8)x(2.5x3) μm, desmonemes 5x3 μm. Newly liberated medusa 0.7-0.8 mm in diameter and height, nematocysts like in polyp plus larger euryteles on oral lips ca. 10x3 μm (for more nematocyst measurements see Yamada, 1961). Gonads mature at a diameter of 1.84 mm (Edwards, 1972). Mature medusae from plankton 3-4 mm in diameter and height. Diameter of eggs 0.15-0.22 mm (Yamada, 1961). For more measurements see Edwards (1972), who also provides a table with the correlation of size, tentacle numbers, and gonad development.

BIOLOGY: The hydroid occurs in depths of 13-275 m, on muddy grounds or mixed mud, shell, and stone bottoms, usually on shells inhabited by various hermit crabs (in the Atlantic e. g. shells of *Natica montagui* and *Turritella communis*) or on crabs like *Inachus dorsettensis* (Pennant) (Mediterranean) or *Hyas coarctatus*

(Atlantic). The medusa can be found in surface waters. It takes about two months for the medusa to reach its full size (Yamada, 1961). In British waters and in the Mediterranean, the medusa has been reported from January to November (Edwards, 1972; Brinkmann-Voss, 1987).

Distribution: Southern Norway, British Isles, Atlantic coast of Spain, western Mediterranean (Yamada, 1961; Russell, 1957, 1970; Edwards, 1972; Medel & López-González, 1996; this study). Not in southern North Sea and Baltic Sea. Type locality: England, Northumberland, Cullercoats, on shell of the gastropod *Natica alderi*.

Remarks: The synonymy and taxonomic history was outlined in detail by Edwards, (1972). Edwards also synonymized the Mediterranean *Pododcoryna hartlaubi* Neppi & Stiasny, 1911 with *H. areolata*. However, some doubts on this synonymy remain and molecular investigations should re-address the question.

The smooth, rather thin and long spines that are aggregated into groups or lines are a characteristic feature of the polyp stage of this species (Fig. 1H). However, the spines are not always present and even when spines are present, not all colonies show this grouping (own observations on material from Norway, cultivation of the medusa and sequence data allowed a reliable identification of the colony). The polyps are conspicuously smaller than *H. borealis* (factor 2). For a reliable identification of the hydroid, the newly liberated medusa must be examined. It has more tentacles (14-16) than any other European *Hydractinia* species. The mature medusa is very distinctive through its perradial stomach pouches and the large number and unequal size of the tentacles (Fig. 1I).

Hydractinia borealis (Mayer, 1900a) Figs 2-3

? *Podocoryna tubulariae* M. Sars, 1857: 145.
Limnorea norvegica Broch, 1905: 5.
? *Podocoryne alderi* Hodge, 1863: 82, pl. 2 fig. 10. – Edwards, 1972: 135. – Calder, 1988: 27.
Lymnorea borealis Mayer, 1900a: 6, pl. 5 figs 16-18. – Mayer, 1910: 154, pl. 15 figs 1-3.
Podocoryna corii Stechow, 1929: 150. **new synonym**
Podocoryne areolata. – Kramp & Damas, 1925: 268, figs 15-17.
[not *Hydractinia areolata* Alder, 1862]
in part *Podocoryne areolata*. – Hartlaub, 1911: 219, figs 19192-194 [Fig. 191 is *H. areolata*].
Podocoryne borealis. – Rees, 1941: 307, fig. 1. – Russell, 1953: 125, figs 57B, 59A, C-F, pl. 6 fig. 5. – Russell, 1970: 235. – Edwards, 1972: 111, figs 4-6, synonymy.
Hydractinia borealis. – Schuchert, 2001a: 9, fig. 2A-B.

Material examined: MHNG INVE29474; Iceland, Sandgerdi; 11 May 2000; polyp colony on *Buccinum* inhabited by *Pagurus bernhardus*, medusa development followed to maturity; 16S sequence **AY787878**. – Scotland, Firth of Lorn, Dunstaffnage Bay; 0 m; 10 May 2004; 2 mature medusae from plankton; not preserved; 16S sequence of one specimen gave identical sequence as **AY787878**. – MHNG INVE48806; Norway, Raunefjord; 10 m; 15 June 2006; 2 mature medusae from plankton; 16S sequence of one specimen gave identical sequence as **AY787878**. – Norway, Raunefjord; 0-20 m; 19 June 2006; young medusa with beginning gonad maturation; not preserved.

Diagnosis: Polyps polymorphic, hydrorhiza encrusting, spines smooth, small, not grouped, may be absent. Newly liberated medusa with 6-8 tentacles. Mature medusa with 16 or more tentacles, oral lips divided, manubrium without basal pouches.

Description: Colonies usually growing on shells, crustaceans, *Tubularia*, and other substrates. Stolons in young colonies or at colony margin reticulate and

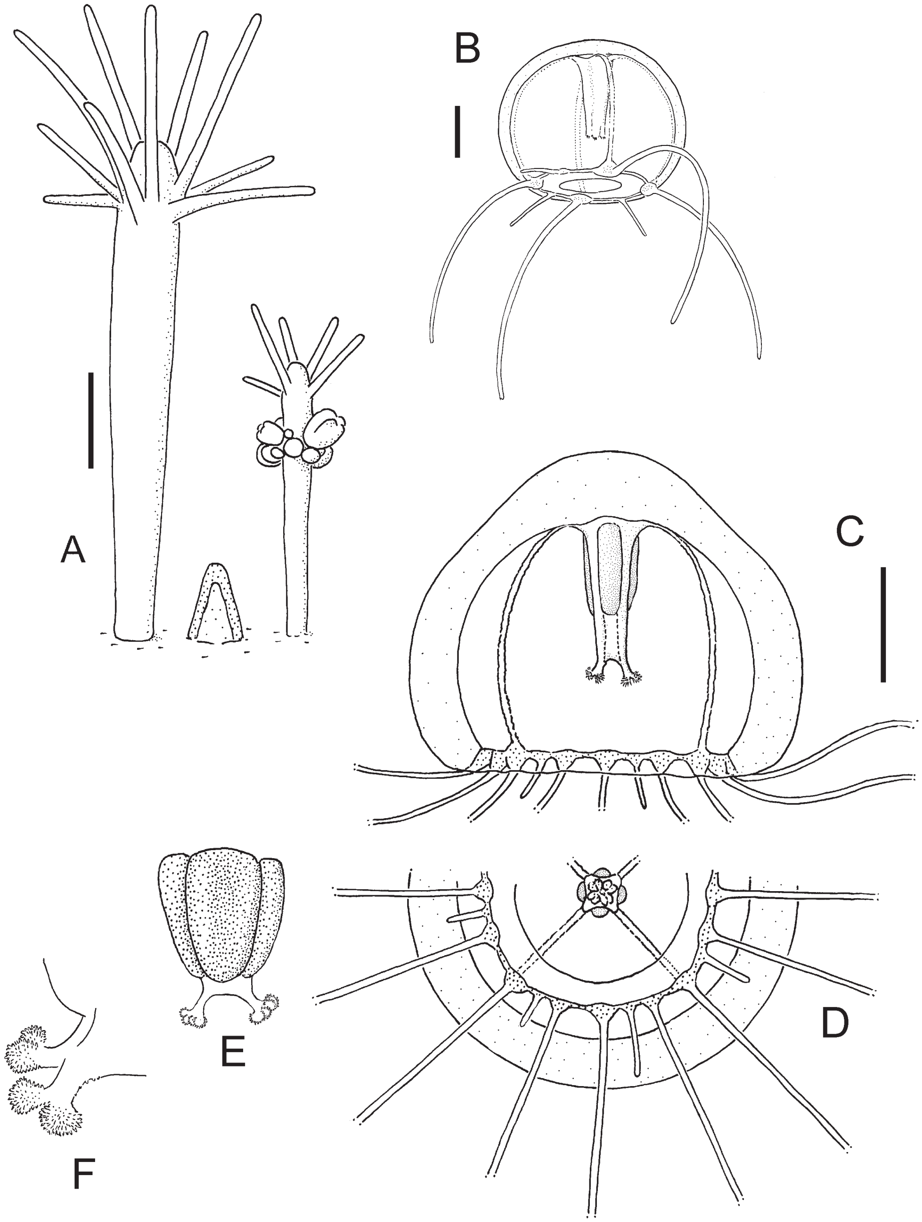

FIG. 2

Hydractinia borealis (Mayer, 1900a); after living material from Iceland and Scotland. (A) Polyp phase with gastrozooid, spine and gonozooid, scale bar 0.5 mm. (B) Newly liberated medusa, scale bar 0.2 mm (C) Subadult medusa in lateral and oral view, most tentacles are not shown in full length, scale bar 1 mm. (D) Same as C, oral view, same scale as C. (E) Manubrium of a fully mature animal. (F) Oral lips, note division of each perradial lip.

composed of perisarc covered tubules, later coalescing to a crust that can be covered by coenosarc tissue. Few shallow, conical spines present, not in groups. Polyps polymorphic, with gastrozooids, gonozooids and sometimes tentaculozooids.

Gastrozooids with fusiform body, large dome-shaped hypostome, hypostome with scattered euryteles, but these not forming a contiguous layer, two very closely set whorls of tentacles, 10-16 in number, unequal in length, alternately pointing upward or horizontal, base of hydranth sometimes sitting on shallow, calotte-shaped perisarc beaker, may be absent in some colonies.

Gonozooids smaller and more slender than feeding zooids (ca. 1/4 to 1/2 the size of the gastrozooids), 4-10 tentacles, below tentacles one whorl of up to 10 medusae buds; larger gonozooids able to ingest prey. Nematocysts of polyps: microbasic euryteles (of two similar size classes), desmonemes. Colours: spine perisarc brown; hydranths white to pinkish.

Medusa at liberation with 6-8 tentacles, four perradial and 2-4 short interradial ones, four perradial marginal bulbs, interradial bulbs absent or inconspicuous, manubrium simple, square in cross-section, without any trace of gonads.

Adult medusa slightly wider than high, jelly thicker at apex, no gastric peduncle. Four relatively broad radial canals and a circular canal, 16-30 tentacles of unequal length, perradial and interradial bulbs largest, without ocelli. Manubrium spans about 2/3 of subumbrella, cross-section distinctly cross-shaped to square, with four perradial, long, oral lips. Each oral lip branched at least once and ending in round clusters of cnidophores. Cnidophores are long cells bearing at distal end an elongated eurytele. Gonads oblong pads on manubrium in interradial positions. No medusae budding. Colours: marginal bulbs red-brown or reddish yellow; stomach yellowish brown. Nematocysts: in tentacles shorter microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles.

ADDITIONAL INFORMATION: Simple, rather thin tentaculozooids can be present in colonies growing on shells inhabited by hermit crabs (Edwards, 1972).

DIMENSIONS (Edwards, 1972; own data): Spines 0.2-0.6 mm high, diameter 0.12 mm. Stolon diameter 0.03-0.06 mm. Gastrozooids usually 4-5 mm high, fully extended reaching up to 15 mm, length of tentacles up to 3.2 mm. Medusa after liberation 0.8 mm, adult medusa up to 3-4 mm high (reportedly up to 5 mm in the western Atlantic), diameter up to 4 mm. Nematocysts of medusa: desmonemes (4.5-6)x(3-3.5) μm; microbasic euryteles of tentacles (8)x(3.5-4) μm; microbasic euryteles of oral lips (10-12.5)x(3) μm. More data, including the relationship of medusa size and tentacle numbers, are given in Russell (1953) and Edwards (1972).

OTHER DATA: The number of spines depends on the environment and the behaviour of the host organism. Colonies from soft muddy localities have few spines whereas those from mixed grounds are often more spiny. It appears that the presence of spines is governed by the roughness of the substratum and by the reaction of the colony to abrasive contact with hard bodies (Edwards, 1972).

BIOLOGY: *Hydractinia borealis* is not very substrate specific, it occurs most commonly on shells inhabited by a variety of hermit crabs, but also on *Tubularia indivisa,* carapaces of crustaceans, mollusc shells, and the polychaete *Aphrodite aculeata*

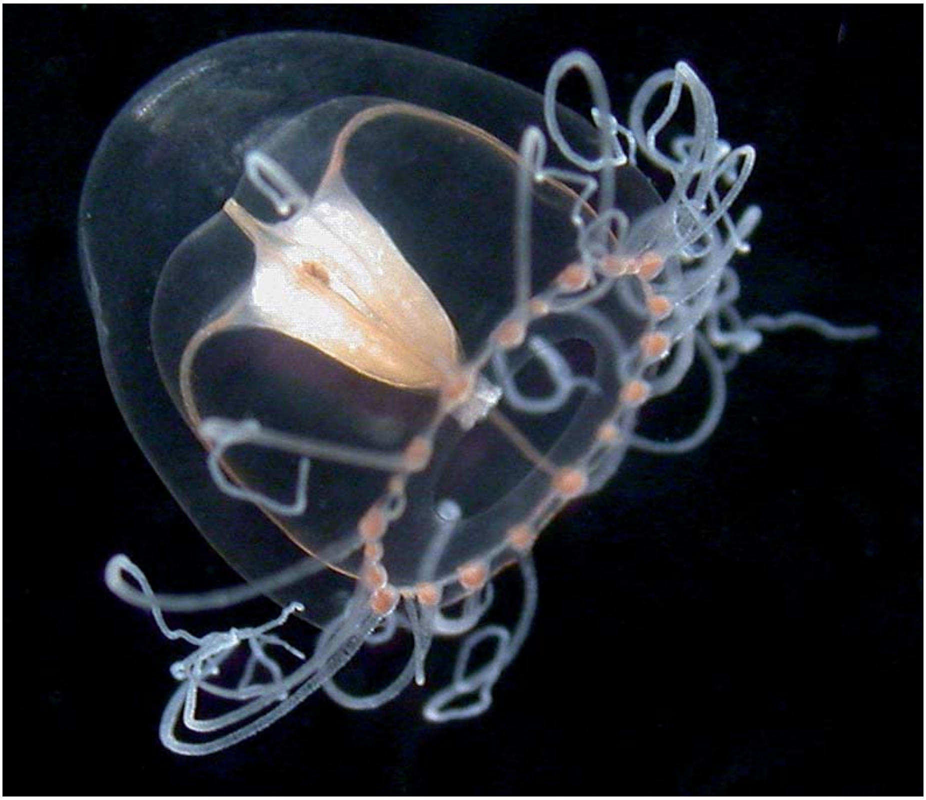

FIG. 3
Hydractinia borealis (Mayer, 1900a), mature medusa from Dunstaffnage, Scotland.

(Edwards, 1972). The hydroid can occur from the low-water mark down to depths of more than 100 m. The medusa is found in the surface waters. In the Clyde Sea Area (western Scotland) it can be found from February to November; more frequently in spring and early summer (Russell, 1953).

DISTRIBUTION (Edwards, 1972): Maine, USA; Iceland; British Isles from the Channel coast to Shetland; North Sea; southern and western Norway. The Mediterranean records are unreliable. Type locality: Eastport, Maine, USA.

REMARKS: This species was studied in detail by Edwards (1972), who provides an excellent, comprehensive report on its taxonomy, life-cycle, and biology. There is only one new synonym to add.

Stechow (1929) described *Podocoryne corii* based on an infertile colony he had obtained from off Oostende (Belgium). He did not publish a figure, but apparently left a drawing with the type material. This illustration will be shown in a forthcoming publication by Ruthensteiner *et al.* (2008). There is nothing in his description or figure that would make this species identifiable, except that it grew on the polychaete *Aphrodite aculeata* (Linnaeus). The only hydractiniid from the region that is known to occur on this substrate is *H. borealis* (see Edwards, 1972: 112). *Podocoryne corii* is therefore here regarded as a questionable synonym of *H. borealis*.

Hydractinia carnea (M. Sars, 1846) Fig. 4

Podocoryna carnea M. Sars, 1846: 4, pl. 1 figs 7-18, not pl. 2 figs 5-11. [=*H. sarsii*]
Podocoryna albida M. Sars, 1846: 7. – Allman, 1872: 349, synonym.
Sarsia nodosa Busch, 1851: 17, pl. 2, figs 6-8. – Edwards, 1972: 133, synonym.
Hydractinia echinata. – Lovèn, 1857: 305, pl. 4. [not *Hydractinia echinata* (Fleming, 1828)]
Podocoryne inermis Allman, 1876: 255, pl. 10, figs 4-5.
Podocoryne carnea. – Hincks, 1868: 29, pl. 5. – Browne, 1896: 463. – Bonnevie, 1898: 486. – Jäderholm, 1909: 50, pl. 3 figs 1-3. – Broch, 1911: 19, fig. 15. – Kramp, 1927: 72, fig. 1. – Rees, 1941: 310, fig. 1b. – Vervoort, 1946: 126, fig 49. – Kramp, 1961: 68. – Russell, 1953: 121, Figs 57A, 58A, 59A, pl. 6 figs 2-3. – Kramp, 1959: 101, fig. 65. – Avset, 1961: 49, figs 1-4. – Edwards, 1972: 122, figs 7-9, synonymy, bibliography.
in part *Podocoryne carnea.* – Allman, 1872: 349, pl. 16 figs 1-9. – Mayer, 1910: 136, fig. 75, pl. 14.
? *Podocoryne carnea* var. *chilensis* Kramp, 1952: 4, figs 1-2.
Hydractinia carnea. – Naumov, 1969: 219, figs 51c & 87.

MATERIAL EXAMINED: BMHNH 1877.4.12.12, syntype material of *Podocoryne inermis* Allman 1876; 6 colonies on gastropod shells, loc. Denmark. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Frederikshavn; 31 Jul.-11 Aug. 1933; several 100 medusae released from polyp, leg. P. Kramp. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Middelfart Sund; 16 Jul. 909; 2 medusae from plankton, leg. Kramp. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Hirshomene; 14 Jul. 1956; several medusae from plankton, leg. K.W. Petersen. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Randers Fjord; 6-9 m depth; 28 Aug. 1915; polyp colony on *Nassarius reticulatus* (L.). – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Frederikshavn; 28 June 1909; polyp colony on *Nassarius reticulatus* (L.).

DIAGNOSIS: Polyps polymorphic, hydrorhiza stolonal or encrusting, spines smooth, not grouped, may be absent. Newly liberated medusa with 5-8 tentacles, with or without immature gonads. Mature medusa with 8 tentacles, oral lips undivided, without basal extensions of manubrium.

DESCRIPTION (after Edwards, 1972 and examined material): Colonies usually growing on gastropods of the genus *Nassarius* and on shells inhabited by hermit crabs. Hydrorhiza either reticulate stolons or forming an encrusting plate covered by coenosarc tissue. Spines rather shallow, not grouped, blunt, density variable, often absent, presence depends on host and exposure to abrasive contact. No perisarc collar at base of hydranths except rarely for some polyps near the colony margin. Polyps polymorphic with gastrozooids, gonozooids and sometimes tentaculozooids and spiral zooids.

Gastrozooids with fusiform to cylindrical body when relaxed, dome-shaped hypostome, hypostome with scattered euryteles not forming a contiguous layer, one whorl of 12-19 tentacles of different length, alternately pointing upward or horizontal, longest ones shorter than hydranth body height.

Gonozooids usually smaller and more slender than feeding zooids (ca. 1/4 to nearly same size as gastrozooids), 4-10 tentacles, shorter than those of gastrozooids, below tentacles one whorl of 1-10 medusa buds. With continued medusa-budding the gastrozooids may become reduced to mere stumps (reproductive exhaustion).

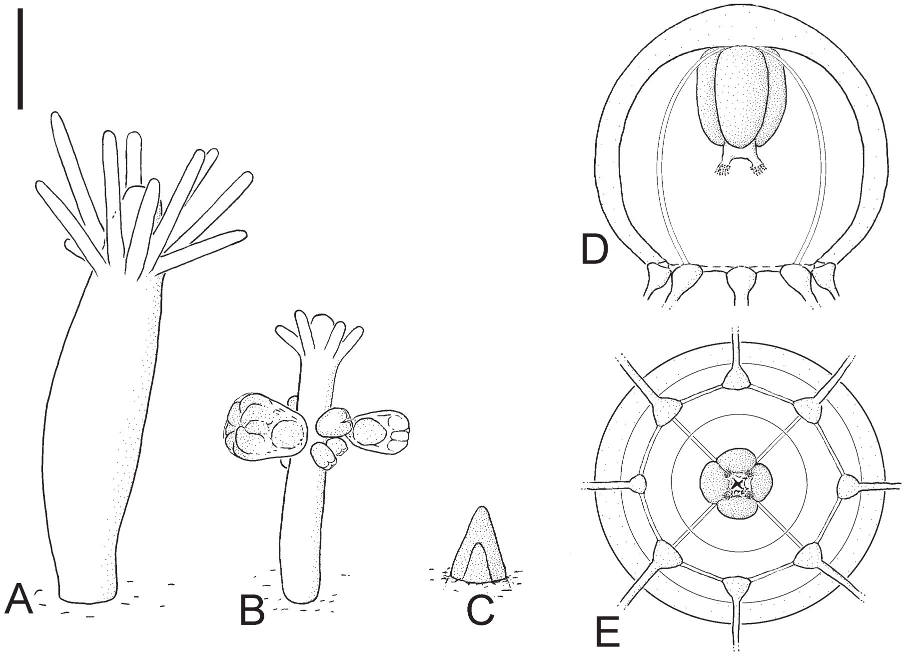

FIG. 4

Hydractinia carnea (M. Sars, 1846), schematic after several preserved samples, scale bar 0.5 mm. (A) Gastrozooid. (B) Gonozooid with medusa buds. (C) Spine. (D) Mature medusa from plankton in side view. (E) Oral view of medusa.

Spiral- and tentaculozooids only in colonies on hermit crabs. Spiral zooids on lip of shell opening, coiled a few times when contracted, distal end slightly swollen. Tentaculozooids very slender, within colony.

Nematocysts of polyps: microbasic euryteles of two size classes, desmonemes. Colours: spine perisarc brown; hydranths white to pinkish, variable.

Medusa at liberation with 5-8 tentacles, four perradial and 2-4 short interradial ones, four perradial marginal bulbs, interradial bulbs sometimes smaller or inconspicuous; manubrium simple, square in cross-section, with or without visible gonads (esp. oogonia are easy to see); numerous nematocysts scattered over the exumbrella.

Adult medusa slightly wider than high, jelly thicker at apex, without gastric peduncle (a slight gastric peduncle may be formed transiently in juvenile specimens). Four radial canals and a circular canal. Eight tentacles of approximately equal length, eight bulbs all of similar size, without ocelli. Exumbrella with no or few nematocysts. Manubrium spans about 1/2 of subumbrella, cross-section distinctly cross-shaped to square, mouth with four perradial unbranched tufts of long cnidophores. Cnidophores long cells bearing at distal end an elongated eurytele. Gonads oblong, vertical pads on manubrium in interradial positions. No medusae budding.

Nematocysts: in tentacles microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles.

DIMENSIONS (after Edwards, 1972 and examined material): Gastrozooids up to 5.5 mm, more commonly 2-3 mm. Spines 0.2-0.3 mm. Nematocysts of polyps (preserved): microbasic euryteles (9-10)x(2.5-3) μm, (6.5-7)x(2-2.5) μm; desmonemes (4.5-5.5)x(2.5-3) μm. Newly released medusae 0.7-0.8 mm. Medusae from plankton 1.6-1.8 mm in diameter, largest specimens 2.4 mm in diameter and 2.1 mm high. More data are provided by Edwards (1972).

OTHER DATA: Rarely some medusae may have 9 or 10 tentacles. The degree of spininess shows great variation and depends on the host species. The hydrorhizal base is also variable, either a stolonal mesh or encrusting. It is mostly encrusting on shells inhabited by hermit crabs. For additional details see Edwards (1972). Rasmussen (1973) examined and depicted the distribution of the polyps on the host shell. Some authors found that the newly liberated medusae had no gonads yet (M. Sars, 1846), while others observed medusae with incipient gonads (Lovèn, 1857, as *H. echinata*; Avset, 1961; Edwards, 1972). Avset (1961) describes the histology of the medusa-bud development and the gametogenesis.

BIOLOGY (after Edwards, 1972): Occurs on shells with living gastropods or inhabited by hermit crabs. When living on gastropods, then *Nassarius reticulatus* (L.) is the preferred host, sometimes also *N. incrassatus* (Ström). The species shows less specificity for hermit crabs (shells of *Buccinum, Nassarius, Natica, Littorina, Turritella,* hermit crabs like *Pagurus prideauxi, P. bernhardus, Anapagurus laevis*). Occurs from the low water mark (on *N. reticulatus*) to 180 m (Christiansen, 1972). Christiansen (1972, Oslofjord, Norway) found polyps with medusae buds from gonophores April to October, with a maximum June-July. Rasmussen (1973, Denmark, in Isefjord) observed medusae buds from June to October, with maximum from July to August. Edwards (1972) found the medusa in the plankton of the Clyde Sea (Scotland) from March to October. Under laboratory conditions the medusae had a life span of up to 24 days.

DISTRIBUTION: British Isles including the Channel coast, Denmark, Sweden, and Norway. In the Baltic Sea, it seems to occur only along the Danish peninsula (Stechow, 1927). Absent from Helgoland (Hartlaub, 1911); Leloup (1947) qualifies it as rare along the Belgian coast. Many records, especially those outside the region outlined above, are doubtful as information on the medusa stages was not taken into consideration (see below). Type locality: The material of Sars was collected near Florö and Manger, Norway.

REMARKS: A full description, synonymy, and revision of this species are provided by Edwards (1972). Edwards also separated the North American form of *H. carnea* (see also Mayer, 1910) as a separate species *H. americana* (Edwards, 1972). There are other very similar species like *H. selena* (Mills, 1976) in the Gulf of Mexico and *H. australis* (Schuchert, 1996) in New Zealand. These species can be distinguished only in the medusa phase and the differences are rather minute. This underlines again the opinion of Edwards (1972: 124): "...it is in general unsafe to give an identification without details of the stages of growth and maturity of the medusa." In view of the subtle differences of these species, and in contradistinction of Edwards (1972), *Hydractinia exigua* is here regarded as distinct from *H. carnea* (see Remarks for *H. exigua*).

The mature medusa is not commonly found in the plankton, although he hydroid may be rather common (Kramp, 1937; Russell, 1953; Edwards, 1972).

Hydractinia exigua (Haeckel, 1880) Figs 5-6

?*Dysmorphosa conchicola* Philippi, 1842: 37.
Podocoryna carnea. – Krohn, 1851: 263. – M. Sars, 1857: 144. – Grobben, 1876: 455-486, pls 1-2. – Weisman, 1883: 65, pl. 19. – Goette, 1916: 455, pl. 13 figs 4-10, pl. 14 fig. 24. – Brinckmann-Voss, 1970: pl. 7 fig 3. [not *Hydractinia carnea* (M. Sars, 1846)]
Cytaeis exigua Haeckel, 1880: 634. – Neppi & Stiasny, 1913: 22, pl. 1 fig. 11; pl. 4 figs 1-2.
Podocoryne conchicola. – Hargitt, 1904: 581, pl. 22 fig. 26
Hydractinia carnea. – Motz-Kossowska, 1905: 85.
Hydractinia carnea var. *inermis*. – Motz-Kossowska, 1905: 85. [not *Podocoryne inermis* Allman, 1876]
Hydractinia carnea var. *mediterranea* Neppi, 1917: 39.
Podocoryne exigua. – Picard, 1958: 190. – Cerrano *et al*., 1998: 1101, fig. 5.
Podocoryne exigua. – Edwards, 1972: 131.

Material examined: MHNG INVE54615, MHNG INVE54616, MHNG INVE54625; Italy, Naples. – MHNG INVE54617; France, Roscoff; coll. 20 May-6 Jun. 1910, leg. M. Bedot. – Atlantic, France, Brittany, Roscoff; several colonies cultivated in aquariums, 1991-92, medusae mature at release; 16S sequence accession number **AM939652**. – Mediterranean, Italy, Naples; several colonies cultivated in aquariums, 1991-92, medusae reared to maturity; 16S sequence identical to **AM939652**. – Mediterranean, France, Banyuls-sur-Mer; 9 May 2002; several colonies on shells of *Nassarius* spec. (with gastropod and hermit crabs), medusa reared to maturity; not preserved; 16S sequence accession number **AM939653**. – Mediterranean, France, Banyuls-sur-Mer; 6 May 2002; several colonies on *Bolinus brandaris* (L.); not preserved. – Mediterranean, France, Roussillon, Ste Marie-la-Mer, depth 2 m; 15 July 1998, several colonies with medusa buds, on shells inhabited by hermit crabs. – Atlantic, France, Brittany, Roscoff, l'Estacade, low water level of spring tide; 14 Sept. 2004; on *Nassarius reticulatus* (L.) (gastropod); not preserved. – Atlantic, Spain, San Sebastián (Guipúzcoa), depth 6 m; collected August 2006 by Dr. A. Altuna, with medusa buds, material used to make DNA; 16S sequence **AM939654**.

Diagnosis: Polyps polymorphic, hydrorhiza stolonal or encrusting, spines smooth, not grouped, may be absent. Newly liberated medusa with 4 tentacles, gonads mature or in development. Mature medusa with 4 tentacles, oral lips undivided, without basal extensions of manubrium.

Description: Colonies usually growing on gastropods of the genus *Nassarius* (=*Hinia*) or on shells inhabited by hermit crabs. Hydrorhiza either reticulate stolons or forming an encrusting plate covered by coenosarc tissue. Spines present or not, rather shallow, not grouped, blunt, density variable within colony. No perisarc collar at base of hydranths. Polyps polymorphic with gastrozooids, gonozooids and sometimes tentaculozooids and spiral zooids.

Gastrozooids with fusiform to cylindrical body when relaxed, dome-shaped hypostome, hypostome with scattered euryteles, but these not forming a contiguous layer, one whorl of 10-13 tentacles of different length, alternately pointing upward or horizontal, longest ones shorter than hydranth body height.

Gonozooids usually somewhat smaller and more slender than feeding zooids (ca. 1/2 to nearly same size as gastrozooids), 4-8 tentacles, shorter than those of gastrozooids, below tentacles one whorl of up to 10 medusa buds. With continued medusa budding, the gastrozooids can sometimes become reduced to mere stumps (reproductive exhaustion).

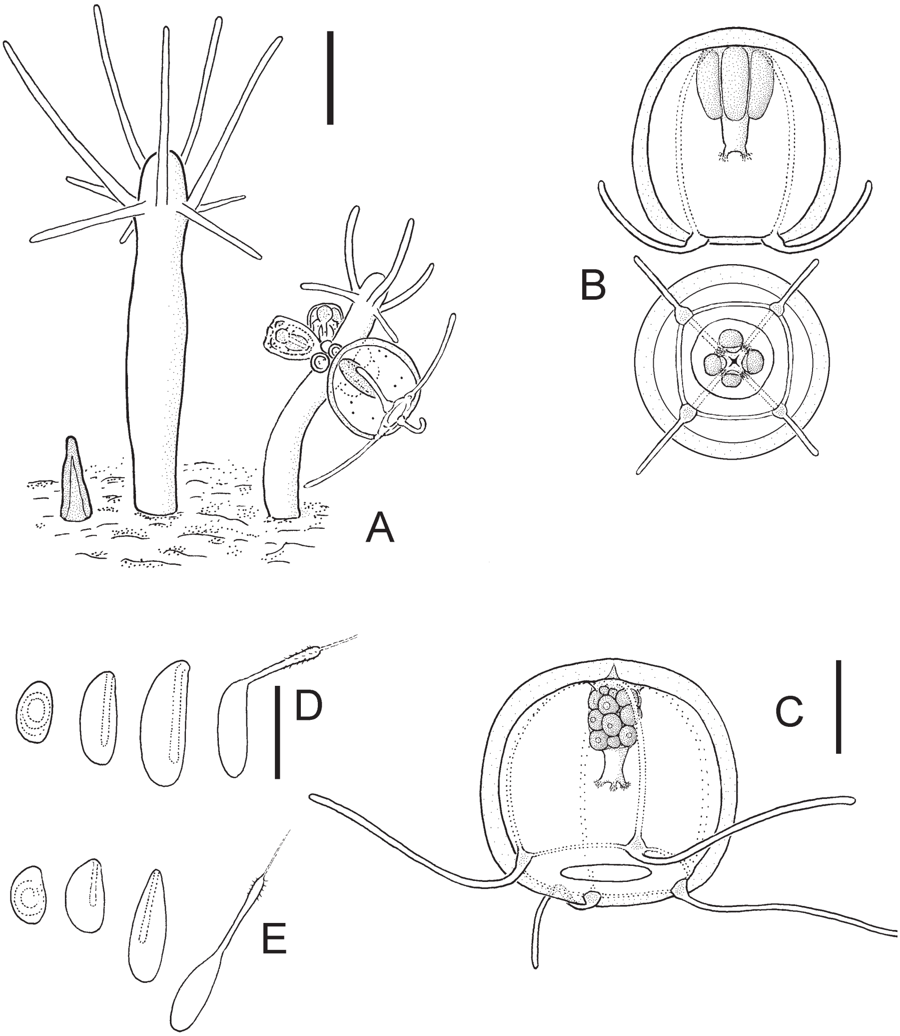

FIG. 5

Hydractinia exigua (Haeckel, 1880); all after life, A-B, after colony from Banyuls; C, from Roscoff; D-E, from Naples. (A) Part of colony with spine, gastrozooid, and gonozooid releasing a medusa; scale bar 0.5 mm. (B) Mature male medusa six days after release, side and oral view, same scale as A. (C) Newly liberated female medusa, note mature gonads, scale bar 0.5 mm. (D) Nematocysts of polyps: desmoneme, small microbasic eurytele, large microbasic eurytele, same discharged, scale bar 10 μm. (E) Nematocysts of newly liberated medusa: desmoneme, small microbasic eurytele from tentacles and exumbrella, elongated microbasic eurytele from mouth clusters, same discharged, magnification as in D.

Spiral- and tentaculozooids only in colonies on hermit crabs. Spiral zooids on lip of shell opening, coiled a few times when contracted, distal end slightly swollen. Tentaculozooids very slender, within colony.

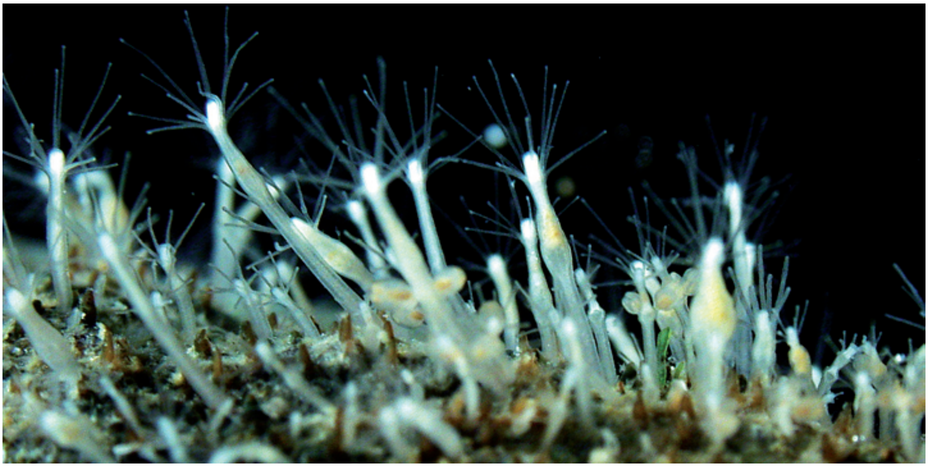

FIG. 6

Hydractinia exigua (Haeckel, 1880), living colony from Roscoff, showing spines, gastro-, and gonozooids.

Nematocysts of polyps: microbasic euryteles of two size classes, desmonemes. Colours: spine perisarc brown; hydranths cream to pinkish, variable.

Medusa at liberation similar to mature medusa, either with mature gonads or with immature gonads (better observable in females); numerous nematocysts scattered over the exumbrella, umbilical canal.

Fully grown medusa approximately spherical, jelly even or apex thickened, without gastric peduncle. Four radial canals and a circular canal. Four perradial tentacles of approximately equal length, four bulbs all of similar size, without ocelli. Exumbrella with no or few nematocysts. Manubrium spans about 1/2 of subumbrella, cross-section distinctly cruciform to square, mouth with four perradial tufts of cnidophores, lips unbranched. Cnidophores are long cells bearing at distal end an elongated eurytele. Gonads vertical, interradial, oblong pads on manubrium in interradial positions, perradial interruption visible in males only. No medusa-budding.

Nematocysts in tentacles microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles.

DIMENSIONS: Colonies from a few mm^2 up to a few cm^2 in size. Polyps 2-6 mm (in life), spines 0.4 mm. Newly liberated medusa 0.4-1.2 mm (correlating with gonad development); fully grown medusa 1-1.2 mm high and wide. Nematocysts (native) of polyp: small microbasic euryteles (7.5-10.5)x(3-3.5) μm, large microbasic euryteles (10.5-13)x(4-5) μm, desmonemes (6-7)x(3.5-4) μm. Nematocysts (native) of medusa: small microbasic euryteles (11-12)x(4-5) μm, microbasic euryteles from lips (14-17.5)x(4-5) μm.

OTHER DATA: At liberation, the medusae of the population in Roscoff (Brittany) possess mature gonads that can spawn gametes (induced by a change from darkness to light). Mediterranean populations produce medusae with immature gonads that take a few days (6-7) to mature (own observations based on animals taken from nature).

Rarely (one in several hundreds), the medusa has 5 or 6 tentacles, sometimes accompanied by other abnormalities (Neppi & Stiasny, 1913). Some or most populations never produce medusae with more than four tentacles (Cerrano *et al.*, 1998; own observations).

Cerrano *et al.* (1998) demonstrated that spines replace regressing polyps. Goette (1916, as *P. carnea*) examined the formation of the stolonal plate. The development of the medusa bud was investigated by e. g. Weismann (1883), Frey (1968), Schmid & Tardent (1969), and Boelsterli (1977). For the embryonic development see Bénard-Boirard, (1962) or Bodo & Bouillon (1968). This species, although under the name *Podocoryne carnea*, was also used for numerous studies in molecular- and cell-biology (e. g. by Prof. V. Schmid and his students).

BIOLOGY: Occurs from the tidal level to about 50 m (Peña Cantero & García Carrascosa, 2002), living on gastropods (mainly *Nassarius* spec., *Bolinus brandaris*, and *Aporrhais*) and on shells inhabited by hermit crabs, rarely also on other substrata (not all records are reliable). In the Atlantic, it seems to occur almost exclusively on *Nassarius reticulatus* (L.). The number of hosts bearing polyps declines from spring to summer for a factor of 10 (Cerrano *et al.*, 1998). Medusa budding can occur all year round (Cerrano *et al.*, 1998; Ligurian Sea). Teissier (1965; English Channel, as *P. carnea*) reported a budding period from May to September. Brinkmann-Voss (1987) observed the medusa in the plankton of the Gulf of Naples from January to April. Cerrano *et al.* (1998) found that medusa-budding zooids are able to detach from the colony, continue to live individually, and re-colonize new hosts.

DISTRIBUTION (some records as *P. carnea*): Western Mediterranean and Adriatic Sea (e. g. Krohn, 1851; Grobben, 1876; Motz-Kossowska, 1905; Hargitt, 1904; Neppi & Stiasny, 1913; Brinkmann-Voss, 1987; this study), Black Sea (Stantschew, 1940), perhaps also Morocco (Patriti, 1970), ? Portugal (Da Cunha, 1944), Atlantic coast of Spain (A. Altuna, pers. comm.), Brittany (Bénard-Boirard, 1962; Teissier, 1965; this study). The northernmost records are from Roscoff (southern coast of the English Channel). Surprisingly, it seems to be absent from the nearby English coast. Type locality: Naples, Italy.

REMARKS: The specific status of *H. exigua* (Haeckel, 1880) is not entirely clear. Some recent authors (Peña Cantero & García Carrascosa, 2002; Bouillon *et al.,* 2004) considered it conspecific with *H. carnea*, others regarded it as clearly distinct from this species (e. g. Hargitt, 1904; Neppi & Stiasny, 1913; Picard, 1958; Cerrano *et al.,* 1998). Edwards (1972) elegantly evaded the problem by regarding it as a subspecies. As the *carnea*- and *exigua*-form occur in disjunct areas, this is a perfectly valid hypothesis. Edwards view gains some further support by the observations of Rees (1941d), who observed intermediate forms with six tentacles in the region of Plymouth, a region where the distribution areas of both forms comes close together. The species *exigua* was here nevertheless upheld, mainly for the reason that subspecies can usually be regarded as equivalent to a full species as well. Population genetic methods must be applied to clarify the status of both forms. Another argument can be constructed using *H. selena* (Mills, 1976) and *H. australis* (Schuchert, 1996), nominal species which are distinguished based on similarly minute details from *H. carnea* as is *H. exigua*.

As outlined by Edwards (1972), *Dysmorphosa conchicola* Philippi, 1842 is likely a senior synonym of *H. exigua*, but it is was so inadequately described that is must be regarded as an indeterminate species.

Hydractinia allmanii Bonnevie, 1898 Fig. 7

Hydractinia allmanii Bonnevie, 1898: 485, pl. 26 figs 36-37. – Bonnevie, 1899: 47, pl. 1 fig. 1. – Jäderholm, 1902: 8. – Jäderholm, 1908: 7, pl. 1 fig. 5, pl. 2 figs 2-5. – Jäderholm, 1909: 49. – Rees, 1956b: 109. – Rees, 1956a: 352, pl. 2 figs 1-7. – Naumov, 1969: 220, fig. 88. – Schuchert, 2001a: 13, fig. 3.

Hydractinia ornata Bonnevie, 1898: 485, pl. 26 fig. 4. – Rees, 1956b: 112, synonym.

MATERIAL EXAMINED: FNHM BIOFAR station 169; The Faroes, 62.625°N 03.546°W, 808 m, one fertile colony. – MHNG INVE27332; Eastern Greenland, 74.21°N 19.72°W, 43-53 m, 19 July 1930. More in Schuchert (2001a).

DIAGNOSIS: Arctic species, on gastropod shells, hydrorhiza encrusting, gonozooids with few tentacles and two gonophores, gonophores medusoid, large, with eight rudimentary tentacles and bulbs, up to 100 eggs.

DESCRIPTION: Colonies growing in dense and large colonies on gastropod shells, preferably *Colus* spec. Hydrorhiza coalesced into a crust with a top layer of naked coenosarc, spines either small or smooth, needle-like tubes, basal plate without prickles. Polyps dimorphic with gastrozooids and gonozooids; tentaculozooids and spiral zooids not known.

Gastrozooids very large, with a thin, shallow basal perisarc collar, body below tentacles often slightly thinner, hypostome large and dome-shaped, one whorl of 10-16 tentacles, hypostome with a broad band of contiguous euryteles.

Gonozooids only about half the height of the gastrozooids, with 4 (range 0-6) short tentacles, region above gonophores often thinner, hypostome densely studded with nematocysts. Gonozooids also have a shallow perisarc collar at base. Gonophores arise in upper third of gonozooid, normally two in opposite position, one small and one advanced. Mature gonophores spherical or slightly oblong.

Gonophores are medusoids, presumably remaining fixed. Medusoids with thin jelly, swollen manubrium with a length of 2/3 of the bell, velum present, four distinct radial canals and eight rudimentary marginal bulbs or tentacles. Fully mature gonophores have eight rudimentary tentacles, four perradial larger and four smaller interradial ones. Gonads cover manubrium and nearly entirely fill the subumbrella. Mature females with up to 100 eggs in one layer. Nematocysts: larger capsules on hypostome of both zooid types; heteronemes on tentacles of both zooid types; desmonemes, on tentacles of gastrozooids only.

DIMENSIONS: Colonies can cover several cm^2, gastrozooids 5-10 mm (max. 15 mm, Jäderholm, 1902), spines up to 1 mm, but usually much smaller. Mature gonophores about 1.0-1.2 mm in length. Nematocysts: large capsules on hypostome (14-16)x(4-5) μm; heteronemes in tentacles (9-11)x(3-4) μm; desmonemes (6-7)x (3-4) μm.

DISTRIBUTION: An arctic species, occurring in deep waters off northern Norway, eastern Greenland, Spitsbergen, Iceland, Arctic seas north of Russia, Sea of Okhotsk, Kuriles (Rees, 1956a; Naumov, 1969). Along the European coasts, it occurs as far

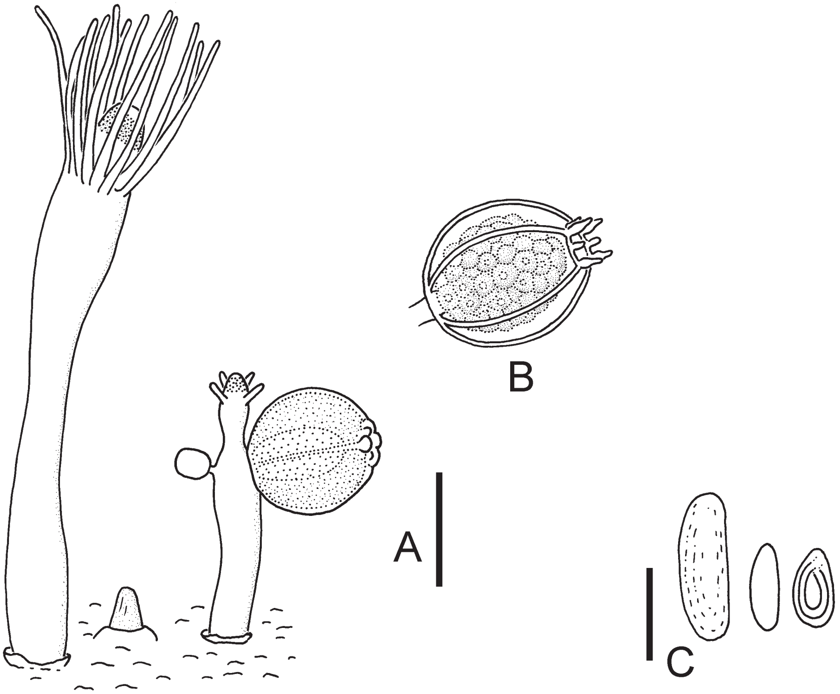

FIG. 7

Hydractinia allmanii Bonnevie, 1898; from Schuchert (2001a). (A) Part of colony with gastrozooid (left), spine (middle), and male gonozooid (right), scale bar 1 mm. (B) Female medusoid, same scale as A. (C) Nematocysts (preserved material): large capsule from hypostome, small capsule from tentacles, desmonemes, scale bar 10 μm.

south as in deep waters near the Faroe Islands (this study). Type locality: off Norway, 67.40°N 8.97°E, 827 m.

BIOLOGY: Epizooic on gastropod shells inhabited by molluscs, preferably of the genus *Colus* (syn. *Sipho*) (Family Buccinidae), in depths of 3-1500 m, mainly between 40 and 250 m. Water temperatures -1.2 to 2.7 °C (Rees, 1956a).

REMARKS: A distinct and unproblematic species, the synonymy and history of which has been outlined by Rees (1956a, 1956b). The morphology is rather variable, the gonozooids are very prone to reproductive exhaustion. Male and female medusoids can occur in the same colony (Rees, 1956a).

It is not known whether the medusoids are released.

The species resembles *Hydractinia hooperi* Sigerfoos, 1899, but which does not form an encrusting hydrorhiza.

Hydractinia pruvoti Motz-Kossowska, 1905 Fig. 8

Hydractinia pruvoti Motz-Kossowska, 1905: 89, figs 12-13. – Neppi, 1917: 40, figs 5-6, pl. 4 figs 12-13. – Iwasa, 1934: 260, figs 13-14. – Bouillon *et al.,* 1997: 480. – Bavestrello *et al.*, 2000: 361, fig. 1. – Bouillon *et al.,* 2004: 66, fig. 39H-I.

Stylactis pruvoti. – Behner, 1914: 407, fig. 13-18, pl. 7 fig. 7-8. – Kramp, 1959: 103, fig. 74. – Kramp, 1961: 71.

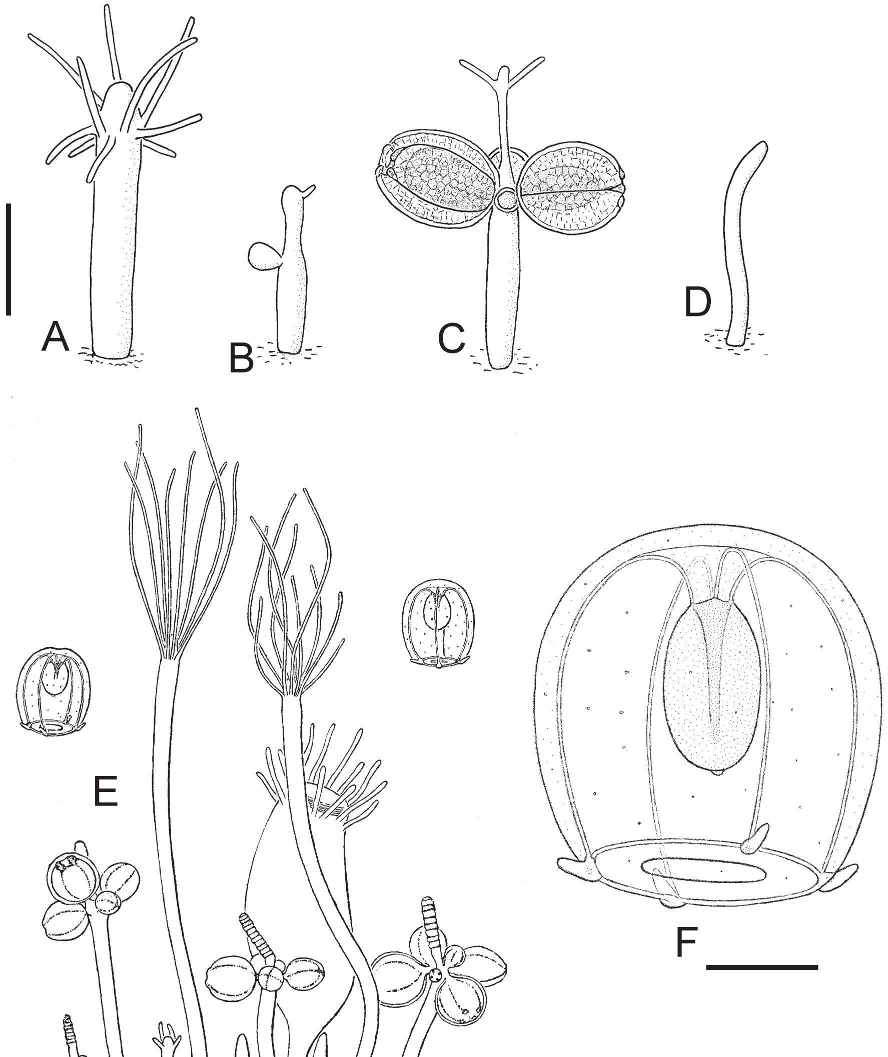

FIG. 8

Hydractinia pruvoti Motz-Kossowska, 1905; A-D after living material from Banyuls-sur-Mer, E-F modified from Behner (1914). (A) Gastrozooid, scale bar 0.5 mm (valid also for B-D). (B) Developing gonozooid with one tentacle. (C) Gonozooid with two tentacles and four medusa buds. (D) Tentaculozooid or other, modified zooid. (E) part of colony, showing gonozooids of various developmental stages, gastrozooids, spines, two free medusoids. (F) Liberated male medusoid, scale bar 0.5 mm.

MATERIAL EXAMINED: MHNG INVE32973; Mediterranean, France, off Banyuls-sur-Mer, depth 62 m, bottom type sand-mud-gravel; 42.506°N 03.167°E; 15 May 2002, on *Nassarius pigmaeus* (Lamarck) (Gastropoda), examined alive, some polyps used to extract DNA, 16S sequence will be published elsewhere by Dr M. P. Miglietta.

DIAGNOSIS: Encrusting or stolonal hydrorhiza, gastrozooids 10-12 tentacles in one whorl, gonozooids smaller and only 1-2 tentacles, no functional mouth, short-lived medusoids with mature gonads, with gastric peduncle, released or not, > 100 eggs, four tentacles stumps.

DESCRIPTION (after literature and examined material): Colonies growing on various gastropod shells inhabited by molluscs or hermit crabs. Hydrorhiza variable, either reticulate stolons or encrusting with top-layer of coenosarc (covered by filmy perisarc), small spines present or not, smooth. Polyps polymorphic, gastrozooids, gonozooids, and tentaculozooids.

Gastrozooids with dome-shaped hypostome, without band of contiguous nematocysts; 8-14 tentacles in one whorl, unequal in length, alternately pointing upward and horizontal.

Gonozooids smaller and more slender than feeding zooids (ca. 1/3 to same size as gastrozooids), upper part above medusa buds narrow, without mouth, only with one or two thin tentacles, rarely three tentacles, tentacles very contractile, can be contracted to short stumps; in upper third one whorl of 3-5 (max. 8) medusa buds, mature buds large, globular to oblong, filled with gametes, radial canals and bulbs well visible.

Nematocysts: desmonemes and two (?) heteronemes of different size, the larger ones in groups of 20-30 on hydranth body.

Gonophores short-lived medusoids that can be released or which remain attached to the gonozooid. Liberated medusoid spherical to slightly higher than wide, jelly thin and even, covered by nematocysts, with gastric peduncle (ca. 1/5 of subumbrella height), wide circular canal and velum present. Four radial canals, four small perradial tentacle bulbs, four short tentacle stumps. Manubrium spanning about half the subumbrellar height, thin, without mouth, surrounded by a very thick gonad without perradial interruptions, females with numerous (>100) eggs. Colonies unisexual.

DIMENSIONS: Gastrozooids in observed material 1-2 mm high (also Bavestrello *et al.*, 2000), others observed larger polyps. Motz-Kossowska (1905) gives a maximum of 15 mm but in her figures they are 2.7 mm high; Behner (1914) 4-5 mm; Neppi (1917) up to 6 mm. Gonozooids with mature medusae half to same size as gastrozooids. Spines 0.2-0.3 mm (Bavestrello *et al.*, 2000) or 0.5-0.6 mm (Behner, 1917). Mature gonophores 0.5 mm long (examined material), Neppi (1917) gives 0.84 mm. Released medusoid 1 mm and 0.6-0.7 mm wide (Behner, 1917).

OTHER DATA: Bavestrello *et al.* (2000) found that water currents induce all polyp types to pinch off fragments of their body. These propagules can settle on other substrates – also inorganic ones – and produce new colonies. The medusoids can swim and spawn for several days (Bavestrello *et al.*, 2000).

BIOLOGY: Grows on gastropod shells of various species and sizes, either inhabited by a hermit crab or mollusc Motz-Kossowska (1905) found it on *Galeodea rugosa* (L.) inhabited by *Dardanus arrosor* (Herbst) [as *Pagurus striatus*]. Behner (1914) found his colony on a *Cerithium* shell, Bavestrello *et al.* (2000) on *Monodonta turbinata* [now *Osilinus turbinatus* (Von Born)] inhabited by *Clibanarius erythropus*. The present material was on the gastropod *Nassarius pigmaeus* (Lamarck). Depth range 10-62 m. Gonophores were observed from May to September.

DISTRIBUTION: Endemic to the western Mediterranean. It is quite a rare species, mostly reported as single findings only. Type locality: Balearic Islands, Mediterranean.

REMARKS: This species is usually portrayed as having gonozooids with a single tentacle only, although already Motz-Kossowska (1905) mentioned that some might have up to three tentacles. The gonozooids of colony examined for this study had mostly two tentacles, a few had one only (see Fig. 8B-C). Behner (1914), Neppi (1917), and Bavestrello *et al.* (2000) observed that the medusoids are released and are able to swim for some days. The colony observed by me developed pulsating medusoids with four tentacle rudiments, just as observed by the other authors, but they remained attached to the polyp while they spawned. These differences can certainly be attributed to intraspecific variation. Allowing some more tentacles on the gonozooids brings *H. pruvoti* rather close to *H. aculeata*, especially as it was described by Wagner (1833)(see Fig. 9A-D). The differences of the gonozooids are clearly gradual and might in other species fall within the range of intraspecific variation. *Hydractinia pruvoti* appears nevertheless to differ in the development of the gonozooids. These develop as reduced polyps with one tentacle only and they produce medusae buds at a very early stage (Fig. 8E). They differ from the gastrozooids at all stages. In *Hydractinia aculeata,* the gonozooids appear to be derived from gastrozooids that develop medusa buds and may then reduce the tentacle number.

Hydractinia aculeata (Wagner, 1833) Fig. 9

Hydra ovipara s. *aculeata* Wagner, 1833: 256, pl. 11 figs 1-10.
Coryne aculeata. – Ehrenberg, 1834: 294.
Hydra aculeata. – M. Sars, 1846: 8.
Hydractinia aculeata. – Allman, 1872: 352. – Motz-Kossowska, 1905: 86, fig. 10. – Herberts, 1964: 161. – Herberts, 1969: 351. – Bouillon *et al*., 2004: 63, fig. 37A.
Stylactis aculeata. – Bavestrello, 1985: 351, fig. 2.

MATERIAL EXAMINED: Mediterranean, Banyuls-sur-Mer, one colony collected January 1992, on small *Nassarius* spec. (*incrassata* or *pygmaeus*), examined alive, no material preserved. – MHNG INVE39471; Mediterranean, Corsica, Coti-Chiavari, 18 Jul. 1946, few polyps without substrate, identification somewhat uncertain.

DIAGNOSIS: Encrusting or stolonal hydrorhiza, gastrozooids up to 5 mm, with 8-12 tentacles in one whorl, gonozooids smaller, 3-7 tentacles, with mouth. Short-lived medusoid with mature gonads, released or not, > 40 eggs, four tentacle bulbs, with or without four tentacles stumps.

DESCRIPTION (after literature and examined material): Colonies growing on various gastropod shells inhabited by molluscs or hermit crabs. Hydrorhiza variable, either reticulate stolons or encrusting, small spines present or not, smooth. Polyps polymorphic, with gastrozooids, gonozooids, and tentaculozooids.

Gastrozooids with dome-shaped hypostome, with band of contiguous nematocysts; 8-12 tentacles in one whorl (range 5-18).

Gonozooids resembling gastrozooids and derived from them, size smaller (ca. 1/2 to same size as gastrozooids), with mouth, 4-7 tentacles; in upper third of body one whorl of 1-6 medusa buds, globular to oblong, filled with gametes, radial canals and bulbs well visible.

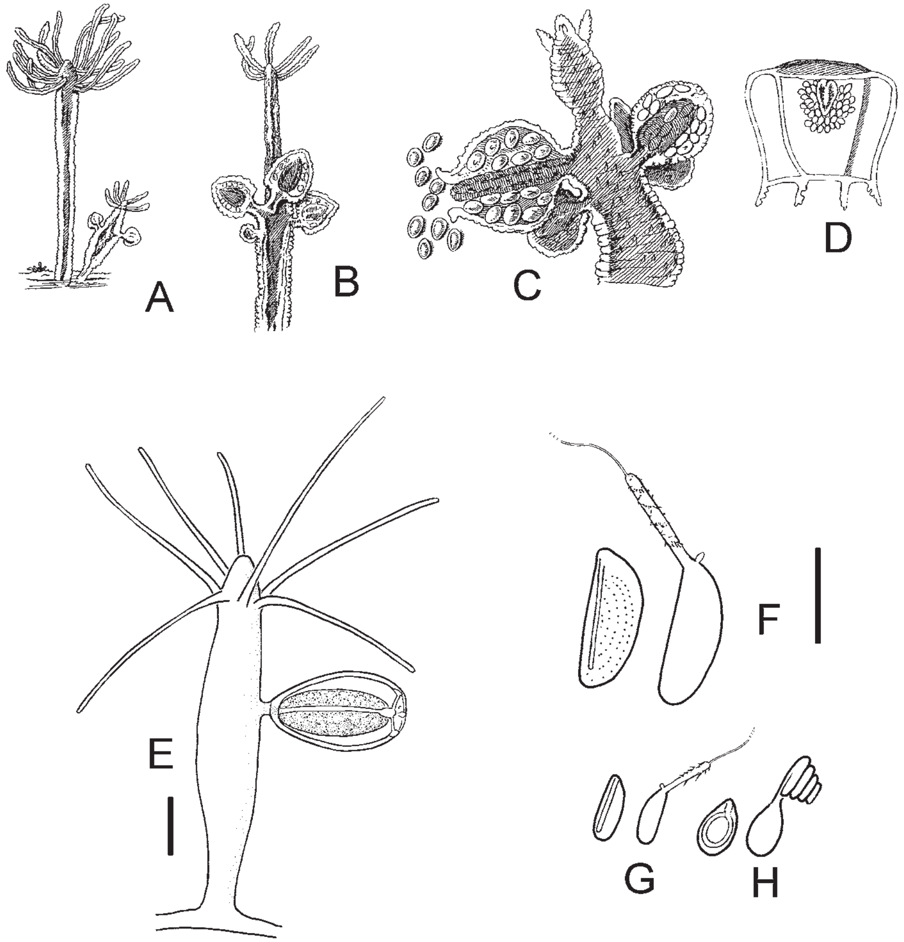

FIG. 9

Hydractinia aculeata (Wagner, 1833); A-D from Wagner (1833), E-F after living material from Banyuls-sur-Mer. (A) Part of colony with nutritive- and reproductive zooid. (B) Gonozooid with young medusa buds. (C) Gonozooid with spawning medusoid still attached to polyp. (D) Freely swimming medusoid. (E) Gonozooid with an advanced medusa bud, scale bar 0.2 mm. (F) Intact and discharged large heteronemes, scale bar 10 µm. (G) Smaller microbasic euryteles, same scale as F. (G) Desmonemes, same scale as F.

Nematocysts, large microbasic heteronemes (mastigophores or euryteles with faint swelling of shaft) on hypostome and body; smaller microbasic euryteles and desmonemes on body.

Gonophores short-lived medusoids that can be released or that remain attached. Liberated medusoid rather inactive, spherical, jelly thin and even, exumbrella without nematocysts, with velum, four small perradial bulbs, with or without tentacle stumps. Manubrium spanning about half the subumbrellar height, without mouth, surrounded by a very thick gonad without perradial interruptions, females with numerous (>40) eggs. Colonies unisexual.

DIMENSIONS: Gastrozooids about 2 mm (this study), Wagner (1833) gives 5 mm, Motz-Kossowska (1905) depicts them in figure as 1.2 mm high; gonozooids smaller. Free medusoid 0.6-0.8 mm in diameter (Herberts, 1964). Nematocysts (native): larger heteronemes (14-17)x(3.5-4) μm, microbasic euryteles (6.5-8)x(2.5-3) μm, desmonemes (5-7.5)x(3.5-4) μm.

BIOLOGY: Grows on various gastropod shells, inhabited either by molluscs or hermit crabs. Wagner (1833) found it on gastropods of the genera *Cerithium, Trochus,* and *Buccinum*; Motz-Kossowska (1905) on *Bolinus* (=*Murex*); Herberts (1964) on *Nassarius pygmaeus* (Lamarck); Bavestrello (1985) on shells of *Nassarius incrassatus* inhabited by the hermit crab *Catapaguroides timidus* (Rows). Depth range 0.5-20 m (Herberts, 1964; Boero & Fresi, 1986). Fertile specimens have been reported from January to November (this study; Herberts, 1964; Boero & Fresi, 1986). Wagner (1833) found his specimens in May. Herberts (1964, 1969) found that the population from Marseilles reproduced from April to August, more than 55% of the collected *N. pygmeus* were colonized by the hydroid during any month of the year. This contrasts with the observations of Bavestrello (1985) made in the adjacent Ligurian Sea. He found reproductive animals in winter only, but he examined a different host. Herberts (1964) noted that the planulae are able to settle on glass, indicating that they have no strict substrate preference (confirming the observations of Wagner (1833), but see Morri *et al.* (1991) for a different view).

DISTRIBUTION: Mediterranean. Type locality: Adriatic Sea, Trieste.

REMARKS: The description of Wagner (1833) is surprisingly precise and complete for its time (see also Fig. 9A-D). Although he noted the resemblance of the gonophores to planktonic medusae, he stopped just short of concluding that medusae and polyps are just life stages of the same animal. This was shortly afterwards recognized by M. Sars (1835). Wagner did not introduce the name as a strict binomen, he used *Hydra* ovipara s. *aculeata*. The s. likely stands for "species" and his intention, however, to name his animals *H. aculeata* is obvious. The first author to use the correct binomial nomenclature was Ehrenberg (1834) as *Coryne aculeata*.

Motz-Kossowska (1905) observed medusoids that lacked tentacle rudiments. This, and also its different host, led Herberts (1964) suspect that she had in fact a different species. The tentacle rudiments were also absent in the material examined here. This difference likely represents intraspecific variation. Also other hydroids with fixed medusoids show this variation, e. g. *Sarsia lovenii* (M. Sars, 1846) (see Schuchert, 2001b). The medusoids of this species remain always attached to the hydroid, but the tentacles are reduced to a variable degree. Some populations of *S. lovenii* produce medusoids without any tentacles, while others develop medusoids with short tentacle rudiments.

Some important details remain unknown. It is unclear whether the medusoid has a gastric peduncle and also the number of eggs per medusoid is not precisely known. Wagner (1833) depicts an animal with more than 40 eggs, likewise also Bavestrello (1985). The animals examined here had clearly more than 100 eggs, but the gonophores were perhaps not fully ripe yet (the egg number decreases during maturation in many hydrozoans). It also not known whether there is always a contiguous band of nematocysts on the hypostome.

Spineless *H. aculeata* with not fully developed medusoids are perhaps not readily distinguishable from *H. inermis*, but both forms differ in their substrate preference and the number of tentacle whorls.

As discussed under *H. pruvoti*, the morphology of this species and *H. aculeata* appear to intergrade somewhat, but both are distinct species.

Hydractinia proboscidea (Hincks, 1868) Figs 10-11

Podocoryne proboscidea Hincks, 1868: 317, pl. 23 fig. 4. – Allman, 1872: 351.
? *Hydractinia michaelseni* Broch, 1914b: 21, fig. 1a-b.
Stylactis claviformis Bouillon, 1965: 54. **new synonym**
Stylactis claviformis. – Bouillon, 1971: 347, figs 8-9, pls 5-6.
Stylactaria claviformis. – Ramil *et al.*, 1994: 104, figs 2-3.
Hydractinia calderi Bouillon, Medel & Peña Cantero, 1997: 477, figs 1-2, 3A-B. **new synonym**
Hydractinia calderi. – Peña Cantero & Garcia Carrascosa, 2002: 39.
? *Hydractinia calderi.* – Vervoort, 2006: 201.
? *Hydractinia hooperii.* – Bouillon *et al.*, 1997: 478. – Peña Cantero & García Carrascosa, 2002: 41, fig. 8c-e.
Not *Stylactis hooperii* Sigerfoos, 1899: 806, figs 1-5.

MATERIAL EXAMINED: BMNH 1899.5.1.132, Syntype colony of *Podocoryne proboscidea* Hincks, 1868; Ilfracombe, England. – BMNH 1982.9.21.2, as *Stylactis claviformis* topotype material; approx. 7 km north of Roscoff, 16 Aug. 1982, det. L. Cabioch and P. F. S. Cornelius, on pebble, fertile female. – Syntype specimen of *H. calderi*, obtained through Dr. A. L. Peña (University of Valencia, Spain); loc. Chafarinas Islands, Arrastre Baños de la Reina; fertile female colony on *Bolma rugosa* (Linnaeus) [Gastropoda], some polyps as permanent slide preparations deposited as MHNG INVE60720. – *Hydractinia hooperii* material of Peña Cantero & García Carrascosa (2002), obtained as loan from Dr A. L. Peña Cantero; loc. Mediterranean, Chafarinas Islands, Baños de la Reina, no collection date, fertile female, on *Cerithium* species (45 mm high).

DIAGNOSIS: Hydrorhiza stolonal, polyps large, gastrozooids with 10-32 tentacles in 2-3 whorls, hypostome usually slightly necked; gonozooids smaller, fewer tentacles; gonophores medusoids, liberated or not, with 4-10 tentacle stumps when fully mature, females with 20-70 eggs.

DESCRIPTION (after examined material; Hincks, 1868; and Bouillon, 1971): Colonies growing on various substrates like pebbles, laminarian holdfasts, and large gastropod shells. Hydrorhiza a network of perisarc covered stolons, smooth spines present or not. Polyps polymorphic, gastrozooids, gonozooids, and tentaculozooids.

Gastrozooids distinctly club-shaped, with very prominent, hypostome large (1/6 to 1/4 of total height, variable), usually somewhat necked, upper part ellipsoid to barrel-shaped, covered by a band of contiguous nematocysts; 2-3 close set whorls of 10-32 tentacles (usually 14-22); base of hydranth can be surrounded by a shallow, filmy perisarc collar.

Gonozooids similar like gastrozooids but smaller (1/2 to 3/4 their height), 6-12 tentacles in one whorl, hypostome elongated, with band of contiguous nematocysts. 2-10 gonophores in one whorl in upper third of polyp, hydranth body above tentacles thinner.

Tentaculozooids rare, smaller than gastrozooids, solid gastrodermis, smooth, end may be slightly swollen.

Gonophores are ovoid medusoids with rudimentary tentacles issued from a thin ring-canal with a narrow diameter, no distinct bulbs, four radial canals, large manu-

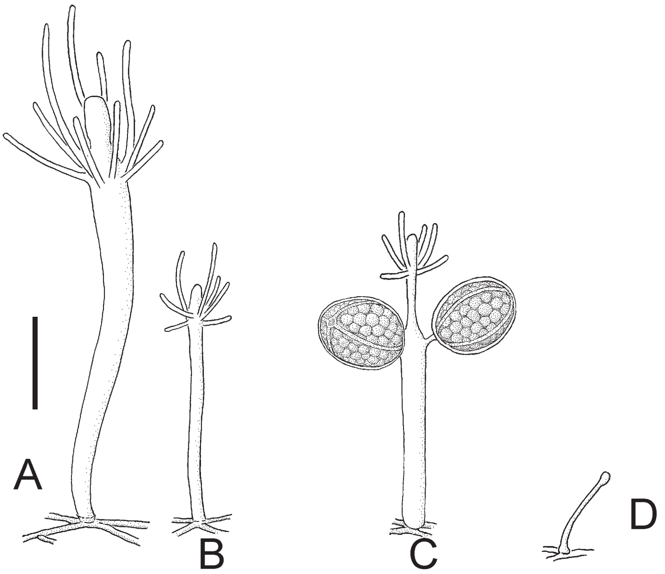

FIG. 10
Hydractinia proboscidea (Hincks, 1869); A-D after preserved material from the English Channel («topotype» material) identified as *H. claviformis*, scale bar 1 mm. (A) Gastrozooid. (B) Smaller, perhaps younger polyp. (C) Gonozooid with two female medusoids, their umbrella not yet inflated. (D) Tentaculozooid.

brium without mouth spanning the whole subumbrella, with narrow velum when fully mature, gametes fill subumbrella. Female gonophores are only rarely liberated, 4-8 tentacle stumps, egg number 16-70, larviparous. Male gonophores may be liberated into plankton or may remain attached, 8-10 thin tentacle stumps of unequal length, gonads large and filling subumbrella, encircling manubrium without perradial separation.

Nematocysts: microbasic euryteles and desmonemes. Colour: orange-brown or pink-salmon.

DIMENSIONS: Gastrozooids 1-5 mm (preserved material), Bouillon (1971) observed that the polyps can extend to 16 mm, but those in his figures are a few mm in height. Gonozooids somewhat smaller. Gonophores ca 0.7 mm long. Medusoids from plankton 1.5 mm high and 1 mm wide (Bouillon, 1971). Nematocysts (Bouillon, 1871; for *H. claviformis*): microbasic euryteles (12)x(3-4) μm, desmonemes (8-9)x(4) μm. The type specimens of *H. proboscidea* and *H. calderi* have capsules that fall within this range.

BIOLOGY: Grows on pebbles (Hincks, 1868; Bouillon, 1971), laminarian holdfasts (Hincks, 1868; Ramil *et al.,* 1994), gastropods. Depth range 0-70 m. Mature colonies were observed in the months of April, August, and September. Polyps have been observed from February to November.

DISTRIBUTION: Bristol Channel (Hincks, 1868), English Channel (Bouillon, 1971; *as S. claviformis*), Galicia in Spain (Ramil *et al.,* 1994; *as S. claviformis*), and

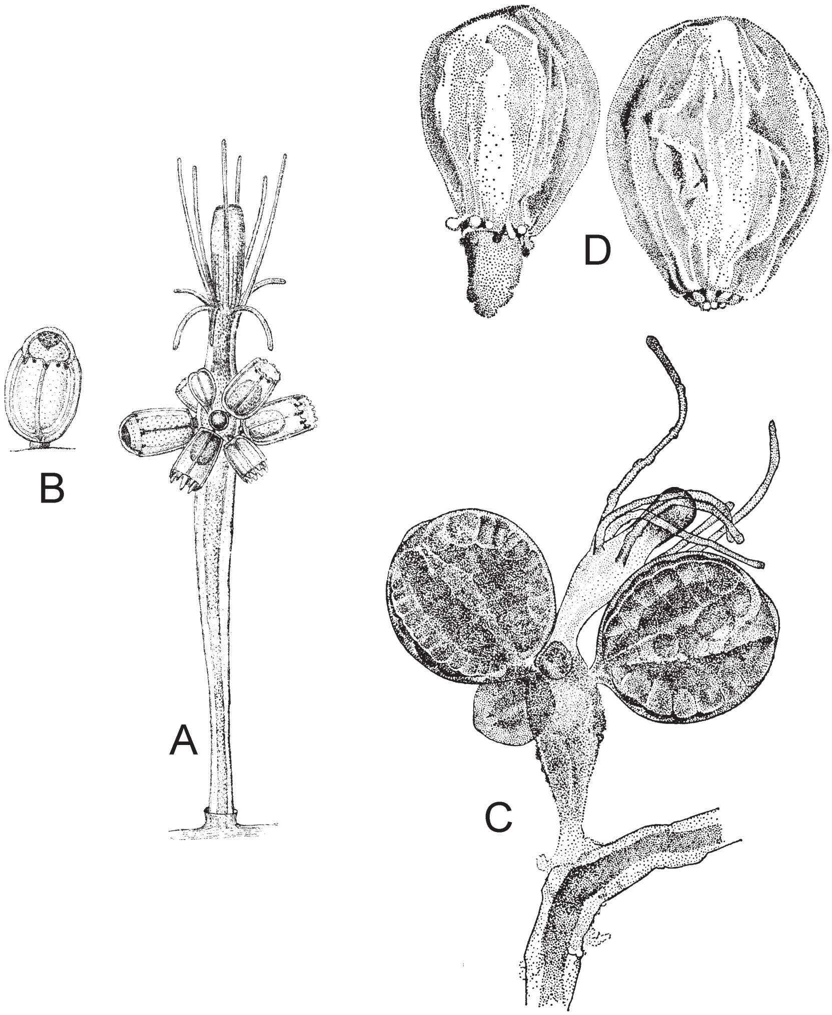

Fig. 11

Hydractinia proboscidea (Hincks, 1869); A-B from Hincks (1868); C-D from Bouillon (1971, as *S. claviformis*). (A) Gonozooid with male medusoids. (B) Male medusoid with bulging sperm mass (C) Gonozooid with female medusoids. (D) Two free, male medusoids.

Alborean Sea (Bouillon *et al*., 1997; as *Hydractinia calderi*).Type locality: Bristol Channel, Devon, Ilfracombe, Capstone.

Remarks: When describing *S. claviformis*, Bouillon (1971) did not discuss its relationship to *H. proboscidea* (Hincks, 1868). The latter species was described in an appendix of Hincks's book and placed in the genus *Podocoryne*. It has thus perhaps escaped the attention of Bouillon. Comparing Hincks's figures (Fig. 11A-B) of *H. proboscidea* – in particular the male medusoids – with *H. claviformis* (Fig. 11C-D), it is rather evident that they are indistinguishable and both species are here regarded as conspecific.

The type material of *H. proboscidea* is not well preserved, but its examination confirmed the accuracy of the original description. The polyp-tentacles are lost, but their remaining bases are clearly in two close-set whorls, the hydrorhiza is stolonal, the gastrozooids are of a similar size as the gonozooids. This material could be compared with a female colony of *H. claviformis* originating from the type locality ("topotype"). The gastrozooids are indistinguishable from *H. proboscidea*, the only apparent difference being the higher number of medusa buds of the gonozooids of *H. proboscidea* (up to 10 versus 4). The difference is considered as insignificant and both nominal species are regarded as conspecific.

The figures and description of *H. calderi* Bouillon, Medel & Peña Cantero, 1997 appear also hardly distinguishable from the concept of *H. proboscidea* (=*H. claviformis*) given above. The only differences according to the literature are: it was observed on gastropod shells, it has some rare spines, and the female medusoid has also small interradial marginal bulbs. A re-examination of the type material of *H. calderi* showed that the bulbs are in fact small, rudimentary tentacles. I regard the remaining differences as insignificant and both species are likely conspecific. The presence of spines is usually related to the substrate, which might also be that case for *H. calderi*. Bouillon *et al.* (1997) list the following differences allowing a distinction of *H. claviformis* and *H. calderi*: the dimorphism of its gonophores by having free male medusoids with ten tentacles instead of eight and the cnidome of the gonozooids. These arguments are not so convincing and there are no apparent differences of the cnidomes.

Hydractinia hooperii was recorded for the Mediterranean by Bouillon *et al.* (1997). The same specimen was then described and depicted in Peña Cantero & García Carrascosa (2002) and it was also kindly made available for this study. The material is very similar to *H. proboscidea*, differing principally only in the number of tentacle whorls. The gastrozooids have the same necked hypostome as *H. proboscidea*, but in contracted polyps the tentacles are in two close set whorls, while in expanded ones they appear to be arranged in one whorl only. The tentacle number is somewhat lower (12-20). The gonophores are medusoids with eight very short tentacle rudiments. I think that these differences are due to environmental influences or that they reflect intraspecific variation. This material is therefore also assigned to *H. proboscidea*, although with some doubts.

Hydractinia proboscidea is not easily separable from *H. inermis,* but differs by the presence of spines, the tentacle rudiments of the medusoids, the necked hypostome, and a higher egg number per gonophore.

Hydractinia michaelseni Broch, 1914b from Nigeria, western Africa, was originally found on a shell inhabited by a hermit crab, but it remains insufficiently known. Its gonophores are apparently medusoids with four bulbs, but they might not have been fully developed. Perhaps the record of *H. calderi* from the Cape Verde Islands by Vervoort (2006) is better referred to this species.

There are actually a number of nominal *Hydractinia* species resembling *Hydractinia proboscidea* and their relationships and validity are not resolved satisfactorily. In the examined region or adjacent to it, there are also *Hydractinia aculeata, H. hooperii, H. inermis,* and *H. michaelseni* that resemble *Hydractinia proboscidea*. Considering also more remote regions, more similar species have to be added to this list (comp. e. g. Millard, 1975; Calder, 1988; Hirohito, 1988). *Hydractinia* species offer far too few diagnostic characters and it seems almost impossible to disentangle the complicated situation, only molecular data and detailed investigations on their biology have the potential to do so.

Hydractinia inermis (Allman, 1872) Fig. 12

Stylactis inermis Allman, 1872: 305, fig. 79. – Du Plessis, 1888: 541.
? *Clava nana* Motz-Kossowska, 1905: 62, fig 3. – Stechow, 1919: 10, synonym.
not *Stylactis inermis*. – Goette, 1916: 451, fig. A, pl. 13 fig. 3, pl 14 figs 25-37. [= *H. fucicola*]
Stylactis inermis. – Stechow, 1919: 23. – Iwasa, 1934: 251. – Boero, 1981: 188, fig. 3. – Gili & Castello, 1985: 11, fig. 2E. – Namikawa, 1991: 810.
Stylactaria inermis. – Stechow, 1921c: 250.
Stylactella inermis. – Stechow, 1923: 63.
? *Hydractinia inermis*. – Bouillon, Medel & Peña Cantero, 1997: 478. – Peña Cantero & García Carrascosa, 2002: 41, fig. 8f. – Bouillon *et al.*, 2004: 65, fig. 39C.

MATERIAL EXAMINED: ZSM 20040316, 20000684, 20000685, as *Stylactis inermis*, alcohol and slide preparations; Italy, Naples; collected end of April 1911; on *Sargassum vulgare*; fertile males; part of material described by Stechow (1919). – MHNG INVE 32950; Adriatic Sea, Italy, Brindisi; 23 March 1997; fertile female on *Cystoseira* spec. – Mediterranean, Banyuls-sur-Mer; 8 May 2002; small male colony on sponge growing on coralligenous concretions, depth likely more than 10 m, not preserved, used to make DNA (tissues turned intensely blue in concentrated alcohol), 16S sequence **AM940002**.

DIAGNOSIS: On algae and other fixed substrates, hydrorhiza stolonal network, without spines, gastrozooids with 12-20 tentacles in two close-set whorls, broad and dense band of nematocysts on hypostome, gonozooids smaller and with 8-16 tentacles, several gonophores, gonophores fixed sporosacs with four radial canals, no bulbs or tentacle rudiments, 10-20 eggs.

DESCRIPTION: Colonies usually growing on algae, barnacles and other fixed substrates, but not on shells and crabs. Stolons tightly reticulate and composed of tubules covered by perisarc, spines absent.

Polyps only slightly polymorphic, gastrozooids and gonozooids similar.

Gastrozooids relatively large, extensile, club-shaped to fusiform body; hypostome large, dome- to barrel-shaped, with a broad band of contiguous nematocysts; 12-22 tentacles (usually 16-18) in two close set whorls, unequal in length, alternately pointing upward or horizontal; base of hydranth often with filmy perisarc collar (needs examination with compound microscope).

Gonozooids smaller and more slender than feeding zooids (ca. 1/3 to 1/4 the size of the gastrozooids), 6-16 tentacles, hypostome with a broad band of contiguous nematocysts, in middle of body or below one whorl of four to eight gonophores.

Gonophores fixed sporosacs, initially spherical, fully mature with slight distal thickening, with radial canals and a narrow ring canal, no tentacle bulbs, no tentacle rudiments, no velum. Sporosacs not medusoid (no umbrella) and gametes appear to be released from the attached sporosacs. Colonies unisexual. Female sporosacs with 10-20 eggs. Nematocysts: microbasic euryteles of two size classes, desmonemes. Colours: hydranths pale pink to brownish.

DIMENSIONS: Colonies size is variable from a few hydranths to many cm^2 (Boero, 1981), gastrozooids 1.5-6 mm (usually 2-3 mm); sporosacs 0.4 mm. Nema-

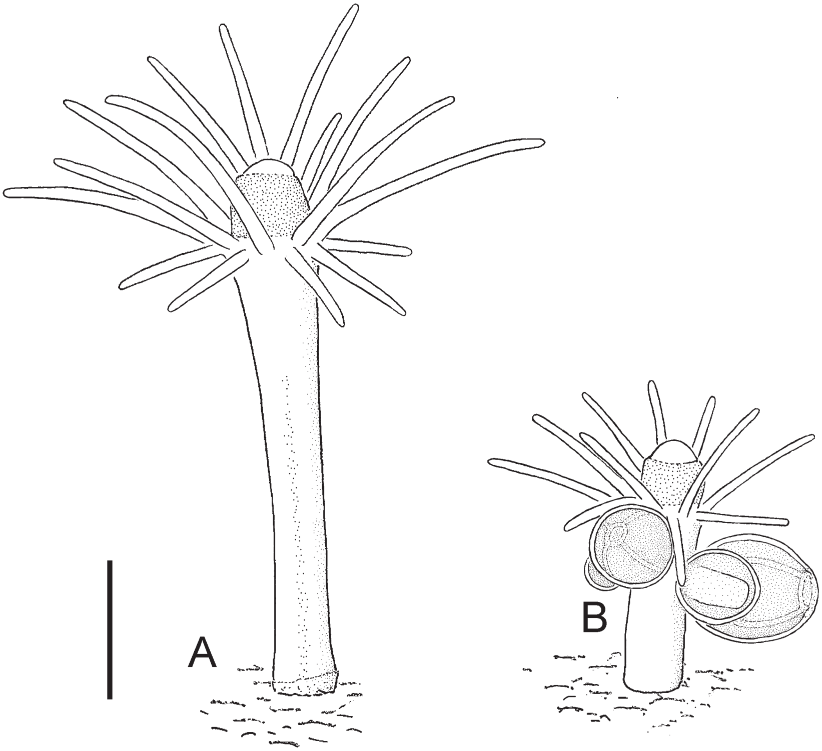

FIG. 12
Hydractinia inermis (Allman, 1872), after preserved material from Naples, tentacles partially contracted, scale bar 0.5 mm. (A) Gastrozooid. (B) Gonozooid with male gonophores.

tocysts (preserved material): euryteles on hypostome (9)x(3) μm, euryteles on tentacles (7.5-8)x(2.5) μm, desmonemes (4.5-5)x(2.5) μm.

OTHER DATA: Boero (1981) also found very small anisorhiza-type nematocysts. This type could not be found in the preserved material examined here.

BIOLOGY: Locally common on rocky coasts, occurs from a few meters to 30 m depth (Boero, 1981; Boero & Fresi, 1986; Gili & Castello, 1985) from October to May, very abundant from March to May; on algae, sponges, hydroids, barnacles; reproduction from April to May. In the three months of its maximum occurrence, it can cover almost everything forming a temporary facies (Boero & Freesi, 1986). Dormant in hydrorhiza in summer and autumn.

DISTRIBUTION: Mediterranean (western Mediterranean and Adriatic Sea). Type locality: Nice, Ligurian Sea.

REMARKS: Allman (1872) described *Stylactis inermis* based on material sent to him by G. Du Plessis (professor of Zoology, Lausanne, Switzerland). The specimens available to Allman were colonies – certainly preserved – that had developed on aquarium cultivated seaweeds collected near Nice. Du Plessis (1888), who must have seen the living type material, qualifies the species as "planulipare" (as opposed to producing medusae). Allman (1872) gives no precise details on the nature of the gonophores, but qualifies them as sporosacs (p. 306) and he does not mention radial canals. These radial canals can be very difficult to see in preserved material and he may have overlooked them. Unfortunately, the type material seems to be lost. Allman's description nevertheless contains some distinct features that allow *H. inermis* to be distinguished from the similar *H. fucicola*, a species that also occurs on the same substrates: about 20 tentacles in two close set whorls, polyps up to 5 mm high, hydrorhiza stolonal, without spines, base of polyp with perisarc collar, female sporosacs with more than 10 eggs (taken from figure).

Bouillon *et al.* (1997: 478) characterized the gonophores as eumedusoids with eight tentacular bulbs. In the material examined here, there were no marginal bulbs. As bulbs are normally quite obvious in mature gonophores, they would most likely not have escaped the attention of Allman.

The material identified by Goette (1916) as *Stylactis inermis* was more likely *H. fucicola*. His polyps had 12 or less tentacles and the mature sporosacs had no radial canals.

The nematocyst band on the hypostome has also not been reported so far. It is somewhat less refringent and thus less obvious than the one in *H. fucicola*. Preserved material must be examined at high magnifications by transmitted light microscopy.

Allman (1876) also described *Podocoryne inermis* as a new species based on material from Denmark, distinct from *Stylactis inermis* Allman, 1872. This species produces medusae and is evidently conspecific with *H. carnea* (see discussion there).

Spineless, immature stages of *H. aculeata* with not fully developed medusoids are perhaps not distinguishable from *H. inermis*, but both forms apparently differ in their substrate preference. More details on the development of the gonophores and the reproductive biology of *H. inermis* are nevertheless needed to allow a better separation.

Hydractinia fucicola (M. Sars, 1857) Figs 13-14

Podocoryna fucicola Sars, 1857: 145, pl. 2 figs 6-13.
? *Podocoryne Haeckelii* Hamann, 1882: 519, pl. 5 figs 15-16.
Stylactis fucicola. – Allman, 1872: 304.
Hydractinia fucicola. – Bonnevie, 1898: 486. – Motz-Kossowska, 1905: 87, fig. 11, pl. 3 fig. 20.
Stylactis inermis. – Goette, 1916: 451, fig. A, pl. 13 fig. 3, pl 14 figs 25-37. [not *Hydractinia inermis* (Allman, 1872)]
Hydractinia fucicola. – Stechow, 1919: 13. – Castric-Fey, 1970: 2, figs 1-9. – Bouillon, Medel & Peña Cantero, 1997: 479. – Bouillon *et al.,* 2004: 65, fig. 39A.
Stylactis fucicola. – Iwasa, 1934: 249, fig. 1. – Boero & Freesi, 1986: 140.

MATERIAL EXAMINED: Syntype, ZMO B1348; as *Hydractinia fucicola*; leg. & det. M. Sars, loc. Messina; several excellently preserved, fertile colonies on *Cystoseira compressa*. – MHNG INVE36838; Mediterranean, France, Port of Villefranche-sur-Mer France, 0 m depth, 5 May 2005, fertile male colony on *Cystoseira* spec. (Fig. 14). – Mediterranean, France, Cassis, Presque île, Plage Bleue, 0-1 m depth, 23 April 2003, fertile female colony on barnacles, examined alive, not preserved.

DIAGNOSIS: On algae and other fixed substrates, hydrorhiza encrusting, with smooth spines, gastrozooids up to 12 tentacles in one whorl, broad band of nema-

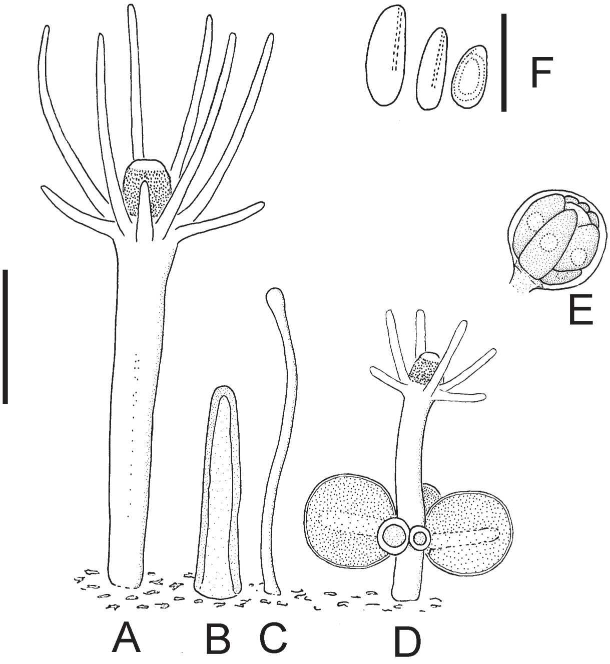

FIG. 13

Hydractinia fucicola (M. Sars, 1857), after living material from the Mediterranean, scale bar 0.5 mm for A-E, 10 μm for F. (A) Gastrozooid. (B) Spine. (C) Tentaculozooid (not always present). (D) Gonozooid with male sporosacs. (E) Female gonophore with mature eggs. (F) Nematocysts: two microbasic euryteles, desmoneme.

tocysts on hypostome, gonozooids smaller and only up to 8 tentacles, several gonophores, gonophores fixed sporosacs without radial canals or bulbs, 6-12 eggs.

DESCRIPTION: Dense colonies usually growing on algae, barnacles and many other fixed substrates, but not on shells or crabs. Stolons in young colonies or at colony periphery tightly reticulate and composed of tubules covered by thin perisarc, in older colonies and in centre usually coalescing into a thick crust covered by coenosarc tissue. Spines rare to frequent, slender, pointed, perisarc smooth or undulated.

Polyps polymorphic, composed of gastrozooids, gonozooids, and sometimes tentaculozooids.

Gastrozooids with fusiform to cylindrical body; hypostome dome-, barrel-, or ball-shaped, with a broad, refringent band of contiguous nematocysts; one whorl of 6-12 tentacles, distinctly unequal in length, alternately pointing upward or horizontal, terminal region of tentacles can be transiently swollen, base of hydranth without perisarc collar.

Gonozooids usually smaller and more slender than feeding zooids (ca. 1/2 the size of the gastrozooids, but in some population sizes equal), up to eight tentacles, hypostome with a broad, refringent band of contiguous nematocysts, in middle of body or below one whorl of four to eight gonophores.

FIG. 14
Hydractinia fucicola (M. Sars, 1857); photograph of living male colony from Villefranche-sur-Mer, Mediterranean.

Gonophores fixed sporosacs, covered by numerous nematocysts, spherical, without radial canals or tentacle rudiments (heteromedusoid), spadix present. Colonies unisexual. Female sporosacs with 6-12 eggs, frequently arranged in a circle around spadix.

Nematocysts: microbasic euryteles of two size classes, desmonemes. Colours: spine perisarc brown; hydranths orange or pink.

DIMENSIONS: Colonies can spread several cm^2, gastrozooids 1-2 mm (max. 3 mm in Atlantic), spines up to 0.7 mm, diameter of sporosacs 0.3-0.4 mm.

OTHER DATA: The very young sporosacs develop anlagen of the radial canals which are rapidly lost in later development (Motz-Kossowska, 1905; Castric-Fey, 1970). The presence of spines depends on the substrate. Motz-Kossowska (1905) observed a colony that was spreading from barnacles onto a stem of *Sertularella* spec. While the part on the barnacle had no spines, these were abundant on the *Sertularella* substrate.

BIOLOGY: In the Mediterranean, *H. fucicola* occurs only in very shallow waters (0-4 m), between 5 and 20 m in the Atlantic (Castric-Fey, 1970; Boero & Fresi, 1986). It can occur on a variety of substrata, most commonly on algae, barnacles, and hydroids. It seems not to occur on mobile substrata like gastropods or hermit crabs. In the Mediterranean it is fertile from April to August (Boero & Fresi, 1986), in the Atlantic from July to September (Castric-Fey, 1970).

DISTRIBUTION: Western Mediterranean, Southern Brittany (Castric-Fey, 1970). Type locality: Messina, Italy.

REMARKS: Contrary to the data given in Iwasa (1934), the gonophores of this species are cryptomedusoid sporosacs and not eumedusoids (see Motz-Kossowska, 1905; Castric-Fey, 1970).

The type material of Sars was re-examined for this study. It is composed of several, perfectly preserved colonies. The hypostomes of the polyps have a band of contiguous nematocysts as found in other samples and the type material was indistinguishable from the other samples from the Mediterranean examined for this study.

The hypostome of *H. fucicola* is densely studded with euryteles. These were only described relatively late by Castric-Fey (1970). This band of nematocysts is very refringent and well visible in living material, but in preserved and contracted material it can get almost invisible and requires an examination by transmitted light microscopy. Such a nematocyst band is found in several species and it is not diagnostic for *H. fucicola*.

Stylactis inermis Allman, 1872 was regarded as a junior synonym of *Hydractinia fucicola* by Picard (1958b: 190). However, I believe they are distinct, even though they can be difficult to distinguish in being similar morphologically and in occurring on the same substrates. *Hydractinia inermis* differs in the following aspects from *H. fuciola*: spines are absent, hydrorhiza mostly stolonal and not forming crust covered by coenosarc, gastrozooids about two times larger and more extensile, more tentacles (up to 22, mostly more than 12) and these in two whorls, basal perisarc collar frequent, gonozooids also with about twice as many tentacles, mature sporosacs with four radial canals, females with more eggs.

Hydractinia fucicola also closely resembles *Hydractinia sarsii*, the latter differing only by its preference for mobile substrata, like crustaceans and gastropod shells, and the higher tentacle numbers. Tentacle numbers are admittedly usually only a poor taxonomic character for hydractiniids, but *H. fucicola* gastrozooids seem to have a tentacle number (8-12) that shows relatively little variation.

The material identified by Goette (1916) as *Stylactis inermis* was more likely *H. fucicola.* His polyps had 12 or less tentacles and the mature sporosacs had no radial canals.

Clava nana Motz-Kossowska, 1905 is an indeterminable species based on a juvenile hydractiniid. Stechow (1919) regarded it as conspecific with *H. inermis*, while Picard (1958) treated it as a synonym of *H. fucicola*. As *H. fucicola* has only one whorl of tentacles, Stechow's assumption is more likely correct.

Hydractinia sarsii (Steenstrup, 1850) Fig. 15

in part *Podocoryna carnea* M. Sars, 1846: 7, pl. 2 figs 5-11, not pl. 1 figs 7-18.
Podocoryna Sarsii Steenstrup, 1850: 33, new name.
Stylactis Sarsii. – Allman, 1864c: 66. – Allman, 1872: 303. – Iwasa, 1934: 230.
Hydractinia sarsii. – Bonnevie, 1898: 486, pl. 26 fig. 42. – Bonnevie, 1899: 45. – Broch, 1916: 45, fig. M, pl. 1 fig. 12. – Schuchert, 2001a: 18, fig. 8.

MATERIAL EXAMINED: ZMO, no. B1347, as *Hydractinia sarsii* Steenstrup, identified by M. Sars, locality and collection date unknown; sample comprises three shells of *Littorina* spec. (up to 18 mm size), one inhabited by a juvenile *Pagurus pubescens* Krøyer, shells covered by encrusting hydrorhiza, most coenosarc lost, a few gastrozooids remain, some also detached. Although this material is not explicitly marked as type material, the fact that it was identified

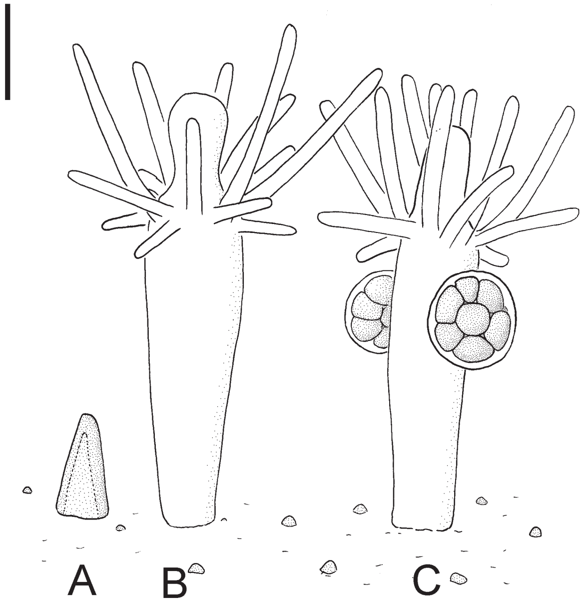

FIG. 15
Hydractinia sarsii Steenstrup, 1850; after preserved material from Greenland growing on a crab leg; scale bar 0.5 mm. (A) Spine. (B) Gastrozooid. (C) Gonozooid with female sporosacs.

(labelled) by M. Sars and that it was part of the collection that includes also the other type specimens of species described by M. Sars, this material must be regarded as the type material. (conf. also Bonnevie, 1898). – Another colony was examined for the study of Schuchert (2001a).

DIAGNOSIS: On gastropod shells and other mobile substrates, hydrorhiza encrusting, with smooth spines, gastrozooids and gonozooids identical, up to 30 tentacles in two close-set whorls, usually with broad band of nematocysts on hypostome, several gonophores, gonophores fixed sporosacs without radial canals or bulbs, up to 10 eggs.

DESCRIPTION: Colonies on crustaceans or on gastropod shells inhabited by hermit crabs. Hydrorhiza an encrusting plate, covered by coenosarc tissue; spines present, conical rounded tip, perisarc smooth or undulated; numerous small prickles penetrating coenosarc layer. Gastrozooids and gonozooids not much different, the latter ones may be somewhat smaller, hypostome high, usually with a broad, refringent band of contiguous nematocysts; up to 30 tentacles in two close-set whorls, distinctly unequal in length. Gonozooids with one whorl of 2-6 gonophores in upper third of hydranth. Gonophores spherical, fixed sporosacs without ring- or radial canals, spadix present, females with 2-10 eggs, larviparous. Nematocysts: heteronemes and desmonemes.

DIMENSIONS: Polyps 1-3 mm; spines 0.5-1 mm high. Nematocysts: desmonemes, (5-6)x(3-3.5) μm; heteronemes (8-11)x(3-4.5) μm.

BIOLOGY: Christiansen (1972) found several colonies of this species in the Oslo Fjord, growing on the crab *Geryon trispinosus* collected in depths of 80-100 m on mud bottom [reported as *Gerion tridens*, a junior synonym of *Geryon trispinosus* (Herbst)]. The colony described by M. Sars was growing on gastropod shells used by hermit crabs.

DISTRIBUTION: A northern boreal to arctic species, known from Norway, the Faroes, Iceland, and Greenland (Broch, 1916; Kramp, 1942; Christiansen, 1972; Schuchert, 2001a). Type locality: south-western Norway.

REMARKS: This species has been recorded only a few times and its biology remains inadequately known. A re-examination of the type material provided few new data besides an observation that the hypostome has a belt of contiguous nematocysts. No such belt was found in the material from Greenland growing on a crab, in addition to the somewhat lower tentacle numbers (up to 20). Perhaps this indicates that we are dealing with a species complex. The morphology of *H. sarsii* is very similar to *H. fucicola*, the latter differing mainly only in the lower tentacle number and the smaller gonozooids. Both species differ in their substrate preference: while *H. fucicola* grows on fixed substrata like algae, *H. sarsii* occurs on mobile substrata like crustaceans. Their disjunct distributions also help to separate the two.

See also remarks under *H. carica*.

Hydractinia echinata (Fleming, 1828) Fig. 16

Alcyonium echinatum Fleming, 1828: 517.
Coryne squamosa var. Johnston, 1938: pl. 2 figs 4-5. – Allman, 1872: 345, synonym.
Hydractinia rosea van Beneden, 1844: 41, 63, pl. 6 figs 1-6. – van Beneden, 1867: 134, synonym.
Hydractinia lactea van Beneden, 1844: 41, 64, pl. 6 figs 7-14. – van Beneden, 1867: 134, synonym.
Echinochorium clavigerum Hassall, 1841: 371, pl. 10 fig. 5. – Hincks, 1868: 23 synonym.
Coryne Hassalli Forbes, 1843: 189. – Bedot, 1905, synonym.
Synhydra parasites Quatrefages, 1843: 230, pls 8-9. – Hincks, 1868: 23, synonym.
Clava capitata Thompson, 1844: 283.
Hydractinia grisea Leuckart, 1847: 138.
not *Hydractinia polyclina* Agassiz, 1862: 227. – Buss & Yund, 1989: 869, figs 1-2.
Hydractinia echinata – Hincks, 1868: 23, pl. 4 figs 1-6. – Allman, 1871: 220. – Allman, 1872: 345, pls 15 and 16 figs 10-12. – Weismann, 1883: 73, pl. 23. – Jäderholm, 1909: 48, pl. 2 figs 6-9. – Broch, 1911: 18, fig. 14, pl. 2 fig 3. – Goette, 1916: 464, text fig. C, pl. 13 figs 1-2, 11-19, pl. 14 figs 20-22, pl. 15 figs 56-59. – Vervoort, 1946: 130, fig 51. – Naumov, 1969: 223, fig. 91. – Buss *et al.*, 1989: 862. – Schuchert, 2001a: 15, fig. 6A-G.

MATERIAL EXAMINED: MHNG INVE29281; France, Roscoff; intertidal pool; 2 June 2000; on shells of hermit crabs; several fertile colonies, examine alive. – MHNG INVE49491; France, Roscoff; 18 Sept. 2006; on hermit crab shells; several fertile colonies. – MHNG INVE60166; France, Brittany, Baie de Morlaix, Ile Callot, 25 Oct. 2007; part of fertile colony; 16S sequence accession number **AM939655**.

DIAGNOSIS: Polyps strongly polymorphic, distal end of gonozooids with nematocyst buttons, without tentacles, gonophores sessile sporosacs without radial canals or tentacles, 6-8 eggs, hydrorhiza encrusting, covered by naked tissue, spines with spiny ridges.

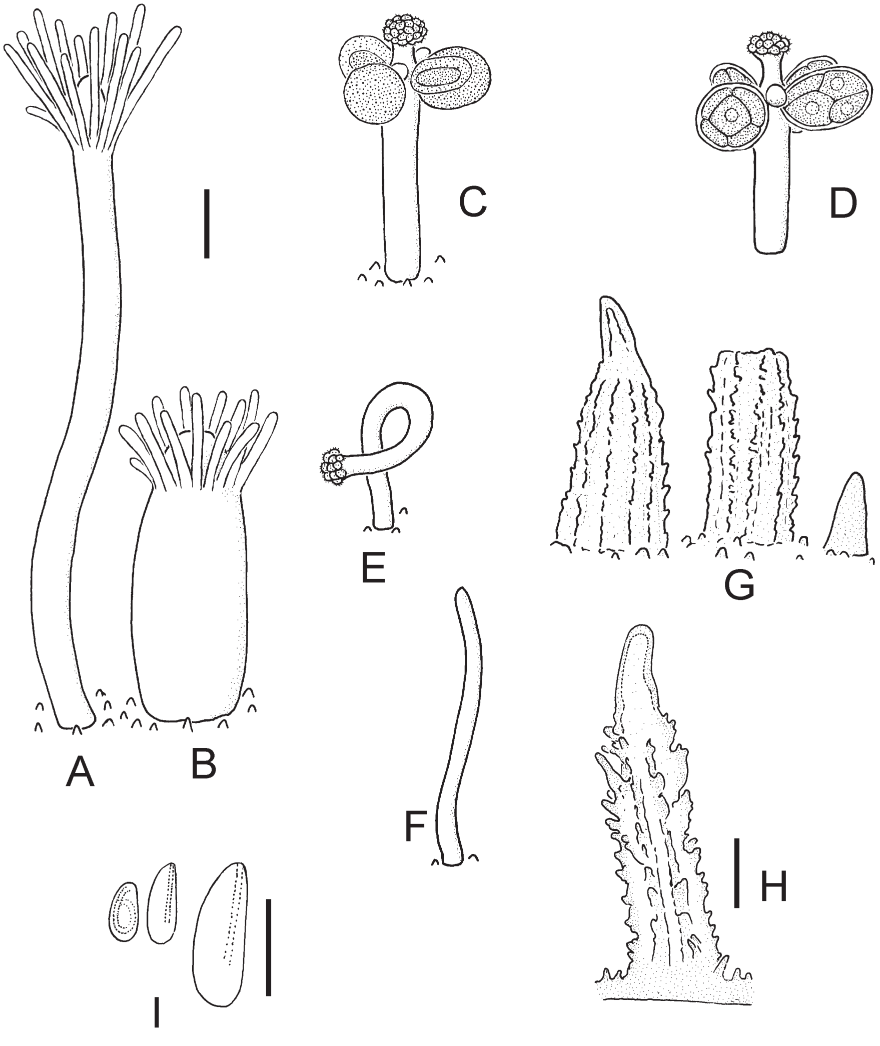

FIG. 16

Hydractinia echinata Fleming, 1820; A-G, I after life, H after preserved material (A) Extended gastrozooid, scale bar 0.5 mm. (B) Contracted gastrozooid, same scale as A. (C) Male gonozooid, same scale as A. (D) Female gonozooid, same scale as A. (E) Spiral zooid, same scale as A. (F) Tentaculozooid, same scale as A. (G) Different spine forms, same scale as A. (H) Typical spine, coenosarc removed, scale bar 0.1 mm. (I) Undischarged nematocysts: desmoneme, small microbasic eurytele from gastrozooids, large eurytele from gonozooids, scale bar 10 μm.

DESCRIPTION: Hydroid normally growing on gastropod shells inhabited by hermit crabs. Hydrorhiza initially a network of adhering stolons enclosed in perisarc, later forming a thick, crust-like layer, covered by coenosarc from which spines, prickles and polyps emerge. Perisarc spines frequent but not always present, dispersed, some regions of colony lacking spines (depends on contact with substratum), size and shape variable but usually rather large, filled with coenosarc, usually with several irregularly spiny ridges running from base to upper regions, top of spines pointed or blunt, smooth or rough; smaller spines smooth. Numerous small prickles rise through the coenosarc of the stolonal plate. Larger spines partly covered by naked coenosarc, mostly in the longitudinal grooves, sometimes even bearing polyps.

Polyps dense, polymorphic, composed of gastrozooids, gonozooids, tentaculozooids, and spiral zooids; the latter two types may be absent, their presence depending on host and environment.

Gastrozooids with cylindrical to fusiform body, large dome-shaped hypostome, two very closely set whorls of tentacles, 15-20 in number (max. 30), unequal in length, alternately pointing upward and horizontal, lower ones shorter, base of hydranth without perisarc collar. Hypostome with scattered euryteles, but these not forming a contiguous layer. Colour pinkish to white.

Gonozooids much smaller and more slender than feeding zooids (ca. 1/5 to 1/3 the size of the gastrozooids), without tentacles, these reduced to wart-like nematocyst buttons tightly clustered into a calotte or band at top of gonozooid. Polyp body somewhat narrowing in diameter below nematocyst buttons and above gonophores, up to 12 gonophores in one whorl in upper region of gonozooid. Gonozooids do not feed. With progressing gonophore development, the gonozooids may become reduced to mere stumps (reproductive exhaustion).

Tentaculozooids may occur or not at margin of colony, smaller then gastrozooids, slender, not spirally coiled, uniform thickness, no tentacles.

Spiral zooids sometimes present at the rim of the colony at the outer lip of the supporting gastropod shell, shorter than gastrozooids, roughly isodiametric, distal end swollen and with nematocyst buttons like in gonozooids.

Gonophores are fixed sporosacs without any canal system or tentacle rudiments, spherical to oblong, male ones white, female ones orange, mature with 4-8 eggs. Colonies unisexual.

Nematocysts: two types of microbasic euryteles, and desmonemes, larger euryteles found on gonozooids.

DIMENSIONS: Colonies can cover several cm^2, living gastrozooids up to 5-12 mm when extended, size depends to some degree on environment, spines up to 2 mm, gonophores about 0.4 mm, the stolonal mat can reach 3 mm of thickness. Desmonemes (5-6)x(3)μm; microbasic euryteles (7-9)x(2.5-3)μm; larger microbasic euryteles of gonozooids, (14-16)x(5-6)μm.

OTHER DATA: Sometimes a few sporosacs can also arise from the hydrorhiza (Goette, 1916). For details on the hydrorhiza and spines see Goette (1916), for gonophores see Weismann (1883), Goette (1916), Avset (1959, 1960) and Hertwig & Hündgen (1984). There exist many more publications on the development, ultrastructure, cell biology, and experimental biology of *Hydractinia echinata*, too many to give a comprehensive overview in this more taxonomically oriented review.

BIOLOGY: Quite common in shallow waters around the British Isles, most frequently found on various gastropod shells inhabited by the hermit crab *Eupagurus bernhardus*, but also other hermit crabs possible. Apparently it can also grow rarely on other substrates (e. g. pieces of wood, Hamond, 1963). The depth range is from intertidal pools to more than 100 m, but it is scarce below 100 m (Jäderholm, 1909; Vervoort, 1946; Rees & Rowe, 1969; Christiansen, 1972). Fertile colonies can be found all year round, but more frequently in spring and early summer (Robson, 1914; Teissier, 1965; Hamond, 1957; Christiansen, 1972). Aspects of its feeding biology were investigated by Christensen (1967).

DISTRIBUTION: Northeastern Atlantic from the Arctic Seas south to NW Africa (Patriti, 1970). Includes also the North Sea (Hartlaub, 1894; Rasmussen, 1973) and parts of the Baltic Sea (Schönborn *et al.,* 1993). Its distribution is treated in e. g. Hincks (1868), Allman (1872), Jäderholm (1909), Broch (1911), Da Cunha (1944, 1950), Vervoort, 1946; Leloup (1947), Hamond (1957), Teissier (1965), Naumov (1969), Rees & Rowe (1969), Fey (1970), Christiansen (1972). It also occurs at Iceland (Schuchert, 2001a).

Hydractinia echinata has also been recorded in the Mediterranean a few times (e. g. Du Plessis, 1888; Lo Bianco, 1909; Rossi, 1950; Gili, 1986 cited in Medel & López-González, 1996). However, these records give no figures and no voucher material is known. Goette (1916) thinks that Lo Bianco's *H. echinata* from Naples were in fact *H. inermis* [more likely *H. fucicola,* as Goette misidentified his *H. fucicola* as *H. inermis*]. Therefore, there remain some doubts on the correct identification and the presence of *H. echinata* in the Mediterranean needs confirmation.

The species has also been recorded from the western Atlantic, but these records refer to other species as has been shown by Buss & Yund (1989). Type locality: British Isles.

REMARKS: In the NE Atlantic this is a characteristic and easily identifiable species. In contradistinction, Buss and Yund (1989) demonstrated that in the western Atlantic the *H. echinata*-like hydroids belong to a complex of sibling species. Traditional morphometric characters are largely inadequate to distinguish between species. Each of the three *Hydractinia* species is predominantly, but not exclusively, associated with a single host hermit crab species. The species are best distinguished using molecular methods.

Hydractinia ingolfi Kramp, 1932 Fig. 17

Hydractinia (*Stylactis*) *ingolfi* Kramp, 1932: 13, figs 5-6.
Stylactis ingolfi.– Iwasa, 1934: 266, figs 20-21.
Hydractinia ingolfi. – Svoboda *et al*., 1995: figs 1b, 2d. – Svoboda *et al*., 1997: figs 3.1b, 3.2d, 3.4. – Schuchert, 2001a: 16.

DIAGNOSIS: Growing on the deep-sea ophiurid *Homalophiura tesselata*, hydrorhiza a stolonal network; gastrozooids with large hypostome, 15-17 tentacles; gonozooids reduced, without tentacles. Gonophores cryptomedusoids, females with > 50 eggs.

DESCRIPTION (Kramp, 1932): Colonies growing on the deep-sea ophiurid *Homalophiura tesselata*. Hydrorhiza a stolonal network, not coalescing into plate, perisarc very thin, no spines, perisarc collar at base of hydranths. Polyps polymorphic with gastrozooids and gonozooids.

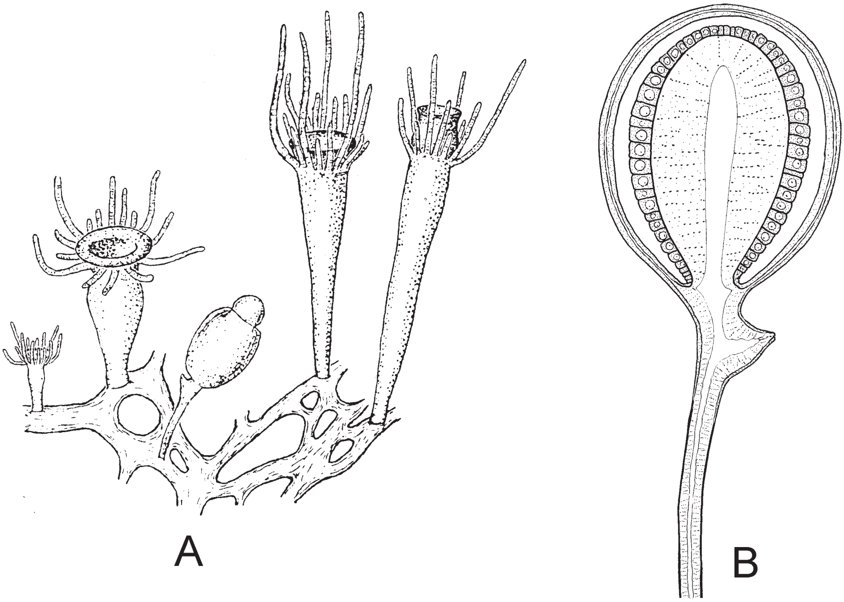

FIG. 17

Hydractinia ingolfi Kramp, 1932; modified after Kramp (1932a), for sizes see text. (A) Part of colony with four gastrozooids and a gonozooid. (B) Schematic, longitudinal, optical section of a gonozooid bearing one female sporosac; note the high number of eggs and also the alignment of the sporosac axis as a continuation of the polyp axis; the hypostome is a conical protrusion pointing towards the right side.

Gastrozooids club-shaped, base narrow, hypostome large and trumpet-shaped, surrounded by a whorl of 15-17 tentacles, some tentacles very long and reaching length of hydranth height, others short, short and long ones not alternating regularly.

Gonozooids small and slender, without tentacles, bearing one or rarely two sporosacs, sporosac axis and body of gastrozooid in one line, hypostome a small protuberance below the sporosac, directed sideways.

Gonophores are sessile sporosacs, ovoid, without radial or ring canal, with large spadix covered by single layer of much more than 50 small eggs.

DIMENSIONS: Gastrozooids up to 2.5 mm; sporosacs about 0.5 mm.

DISTRIBUTION AND BIOLOGY: A deep-sea arctic to northern boreal species, species living on the ophiurid *Homalophiura tesselata* (Verrill). Only known from its original descriptions based on several samples from south of Greenland and Iceland (Kramp, 1932). Depth range ca. 2100-3200 m. Type locality: North Atlantic, 58°20'N 40°48'W, 3192 m depth, on *Homalophiura tesselata* (Verrill) (Echinodermata, Ophiuridae).

REMARKS: Contrary to the opinion of Bouillon *et al.* (1997), *H. ingolfi* is most likely not conspecific with *H. arctica* (see Schuchert, 2001a). Judging from its rather unusual, specific, association with a deep-sea ophiurid it appears as a distinct species.

The large, trumpet shaped hypostome seems to be a characteristic trait of the species. The significance of such an enlarged hypostome and the epizoism on ophiurids was outlined by Svoboda *et al.* (1995, 1997).

Hydractinia arctica (Jäderholm, 1902) Fig. 18

Stylactis arctica Jäderholm, 1902: 5, pl. 1 figs 1-2. – Iwasa, 1934: 258, fig. 10.
Hydractinia arctica. – Bouillon *et al*., 1997: 467, table 1. – Schuchert, 2001a: 14, fig. 4.

MATERIAL EXAMINED: SMNH, Syntypes, 72°42'N 14°49'W, 3 colonies on gastropod shells, some with gonozooids (see also Schuchert, 2001a).

DIAGNOSIS: Arctic, deep-sea species, usually on buccinid gastropods, hydrorhiza stolonal, gastrozooids with basal perisarc collar, hypostome cylindrical, with nematocysts, tentacles in 2-3 whorls, gonozooids smaller, tentacles rudimentary, 2 sporosacs, with ring canal, about 10 eggs per sporosac.

DESCRIPTION: Colonies usually growing on gastropod shells, stolons forming a loose mesh, not coalescing or encrusting, covered by perisarc, without spines. Polyps polymorphic with gastrozooids and gonozooids.

Gastrozooids with shallow basal perisarc collar, club-shaped, broadest in region of tentacles, hypostome high, thick, cylindrical to trumpet-shaped, with a broad band of contiguous euryteles, below hypostome 18-22 filiform tentacles in 2-3 whorls.

Gonozooids much smaller than gastrozooids (1/4), tentacles reduced to a few stumps, with 2 spherical gonophores. Gonophores with ring canal and perhaps also radial canals. Female gonophores with about 10 eggs.

Nematocysts: desmonemes, on tentacles; microbasic euryteles, on tentacles; microbasic mastigophores or euryteles with faint swelling, on hypostome.

DIMENSIONS: Gastrozooids about 2 mm high. Desmonemes 6x4 μm, smaller microbasic euryteles, on tentacles (8.5-9.5)x(2.5-3.0) μm, discharged shaft ~0.9 of capsule length; microbasic mastigophores on hypostome, (12-14)x(4-5) μm, discharged shaft ~0.9 of capsule length.

BIOLOGY: Deep-sea species. The type material grew on gastropod shells. Kramp (1932a) attributed a sterile colony growing on a *Eudendrium* species to *H. arctica*, but this identification should be regarded with much caution.

DISTRIBUTION: An arctic species, reliable records are confined to type locality east of Greenland. Type locality: 72.70°N 14.82°W, depth 2000 m, on shell of the buccinid gastropod *Mohnia mohni* Friele.

REMARKS: See Schuchert (2001a) for a discussion of the species. The high cylindrical hypostome is likely a characteristic trait of this species (Kramp, 1932), but similar hypostomes can also be found in e. g. *H. ingolfi* and *H. fucicola*.

Hydractinia carica Bergh, 1887 Fig. 19

Hydractinia carica Bergh, 1887: 331, pl. 28, fig. 1. – Jäderholm, 1908: 8. – Jäderholm, 1909: 48, pl. 2 figs 10-11. – Broch, 1916: 48, pl. 1 fig. 11. – Fraser, 1944: 77, pl. 13 fig. 53. – Rees, 1956a: 355, figs 1-2, synonymy, bibliography. – Naumov, 1969: 221, fig. 89. – Calder, 1972: 223, pl. 2 fig. 2. – Schuchert, 2001a: 15, fig. 5.
Hydractinia minuta Bonnevie, 1898; 487, pl. 26 fig. 38. – Rees, 1956a: 355.

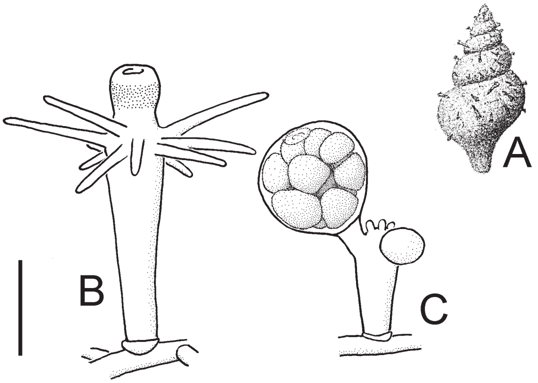

FIG. 18
Hydractinia arctica (Jäderholm, 1902); A, after Jäderholm (1902), B-C after type material. (A) Colony on *Mohnia mohni* Friele, shell height 22 mm. (B) Gastrozooid, scale bar 0.5 mm. (C) Female gonozooid, same scale as B.

MATERIAL EXAMINED: Syntypes, ZMUC, no registration number, leg. Dijmpha, loc. Petuchoffskoi Schar, Kara Sea, on *Buccinum groenlandicum*.

DIAGNOSIS: Usually on gastropods of the genus *Buccinum,* encrusting hydrorhiza, smooth spines, no prickles, gastrozooids with one whorl of 12-16 tentacles, gonozooids much reduced, no tentacles or 2-4 very short ones, 3-7 sporosacs without radial canals, 5-6 eggs per sporosac.

DESCRIPTION: Colonies preferentially on gastropods of the genus *Buccinum*, forming encrusting hydrorhiza covered by coenosarc layer, few conical spines, smooth, tip rounded, stolonal plate without prickles. Gastrozooids with a single whorl of 12 to 16 (max. up 22) tentacles; hypostome without belt of nematocysts, high, nipple-shaped. Spiral zooids and tentaculozooids unknown.

Gonozooids thinner than gastrozooids, size variable but usually much smaller than gastrozooids, sometimes initially of same height as gastrozooids and with up to eight tentacles, gonozooids usually becoming gradually reduced to short stumps lacking tentacles or with few (2-4) short tentacles, degree of reduction of mature gonozooids quite variable; hypostome tightly beset with nematocysts; 3-7 gonophores in one whorl in upper 2/3 of gonozooid.

Gonophores cryptomedusoids, spherical, relatively small, without ring- and radial canals, with spadix, distal calotte sometimes thickened and containing nematocysts, females with 5-6 eggs.

Nematocysts: desmonemes and two other types, probably heteronemes.

DIMENSIONS: Spines 0.3-0.7 mm; extended gastrozooids up to 2.5 mm; diameter of sporosacs 0.25-0.4 mm. For additional measurements see Rees (1956a).

DISTRIBUTION: A predominantly arctic species, recorded from Norway, Arctic Sea north of Russia, Spitsbergen, western Greenland, and NE Canada (Jäderholm, 1909; Fraser, 1944; Rees, 1956a; Naumov, 1969; Calder, 1972). Naumov (1969) recorded it also from the Bering Sea, Sea of Okhotsk, and Japan Sea. Along the

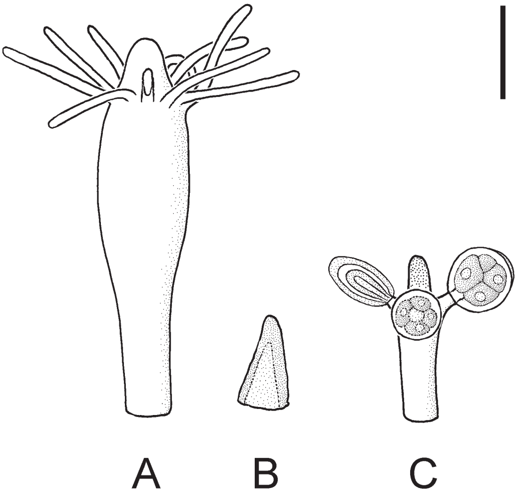

Fig. 19
Hydractinia carica Bergh, 1887; after type material, scale bar 0.5 mm. (A) Gastrozooid. (B) Spine. (C) Female gonozooid with three sporosacs of different developmental stages.

European costs, it can rarely be found as far south as Bergen in Norway (Bonnevie, 1901; as *H. minuta*). Most records are from Spitsbergen. Type locality: Petuchoffskoi Schar, Kara Sea, 15 m.

BIOLOGY: The species favours as substratum the shells of the various northern species of *Buccinum* (like *B. undatum, B. scalariforme, B. glaciale, B. ovum, B. groenlandicum, B. ciliatum*; all still used by the gastropod and not by hermit crabs) (Jäderholm, 1909; Rees, 1956a). Jäderholm (1909) also found it also on *Boreotrophon clathratus* (family Muricidae). The bathymetric range is 0 to 120 m.

REMARKS: Broch (1916) and Rees (1956a) re-examined type material of *Hydractinia carica* Bergh, 1887 and *H. minuta* Bonnevie, 1898. Both authors concluded that the two species must be conspecific. Rees (1956a) re-described *H. carica*, but unfortunately made contradictory statements. In his diagnosis (p. 356) he describes the gonophores as "... with 4 radial canals and rudiments of tentacles...", while later (pp. 358 and 359) he describes the female gonophores of the type material as having no radial canals. Bonnevie (1899: 48) and Jäderholm (1908) describe the gonophores as devoid of radial canals. I was also unable to see any indication of radial canals in the type material and it appears that Rees's (1956a) diagnosis contains a typographic error. The male sporosacs have apparently not yet been described.

Hydractinia carica can be distinguished from *H. echinata* by its smaller polyps (about half the size), the smooth spines, and the absence of wart-like nematocyst clusters on the gonozooids, the absence of small perisarc prickles on the hydrorhiza, and its host preference.

It even more resembles *H. sarsii*, the most obvious difference being the more reduced gonozooids. However, this can sometimes be a character of limited value for discriminating *Hydractinia* species (Bouillon *et al.*, 1997). Other differences are the absence of small perisarc prickles on the hydrorhiza, gastrozooids with somewhat fewer tentacles, and – likely the most significant difference – its host preference: shells of the genus *Buccinum* still inhabited by the gastropod and not by hermit crabs.

Hydractinia monocarpa can easily be confounded with *H. carica*, but it has significantly more eggs per sporosac (50 versus 5-6), fewer gonophores (1-2 versus 3-7), and has more pointed and longer spines.

Hydractinia serrata Kramp, 1943 Fig. 20

Hydractinia monocarpa. – Kramp, 1932: 16. [not *Hydractinia monocarpa* Allman, 1867]
Hydractinia serrata Kramp, 1943: 9, figs 1-3. – Naumov, 1969: 223, fig. 92. – Schuchert, 2001a: 18, fig. 9.

MATERIAL EXAMINED: ZMUC, Godthaab station 107, near Cape Aholl, 76.41°N 69.63°W, 165 m, 15 Aug. 1928, on living *Buccinum* shell; labelled *Hydractinia monocarpa,* described by Kramp (1932a). – ZMUC, Just & Vibe station 35, as *Hydractinia serrata* Kramp, 1943; 76.447°N 69.705°W, western Greenland, Bylot Sound, 260 m, 14 Aug. 1968, fertile colony on gastropod shell.

DIAGNOSIS: Arctic species, encrusting hydrorhiza, spines slender and with four serrated ridges, gonozooids small with few short tentacles, sporosacs pyriform originating from base of gonozooids, female sporosacs with one egg.

DESCRIPTION (in part after Kramp, 1943b): Dense colonies growing on arctic gastropods of the genus *Buccinum,* forming encrusting hydrorhiza covered by coenosarc. Spines numerous, not grouped, high and slender, usually with four longitudinal ridges, their edges irregularly serrated, overgrown by living tissue except for the tip. Polyps polymorphic, differentiated into gastrozooids and gonozooids.

Gastrozooid fusiform to cylindrical, hypostome short and dome-shaped, 8-12 tentacles in one whorl.

Gonozooids small, tentacles in one whorl, reduced to 0-8 short stumps. Gonophores develop near base of gonozooid or even from stolonal plate close to gonozooid, 1-4 per gonozooid, pear-shaped, colonies unisexual. Gonophores develop into sessile sporosacs without canal system (cryptomedusoid), spadix present, females with one egg only. Nematocysts: desmonemes, microbasic euryteles with discharged shaft longer than capsule.

DIMENSIONS: Colonies several cm^2, gastrozooids up to 3 mm, gonozooids up to 0.5 mm, sporosacs up to 0.5 mm, spines 0.45-1.2 mm. Preserved microbasic euryteles ca. (10.5-12)x(3.5-4) μm.

BIOLOGY: Grows on arctic gastropods of the genus *Buccinum* (e. g. *Buccinum belcheri* Reeve, *Buccinum hydrophanum* Hancock, and *Buccinum glaciale* [syn *B. groenlandicum*]), depth range 15-300 m (Naumov, 1969).

DISTRIBUTION: Strictly Arctic; reported from eastern- and western Greenland, Barents Sea (Kramp, 1943; Naumov, 1969; Schuchert, 2001a). Type locality: eastern Greenland, Lindenows Fjord, 20-35 m, on *Buccinum glaciale* Linnaeus (by designation of Kramp, 1943).

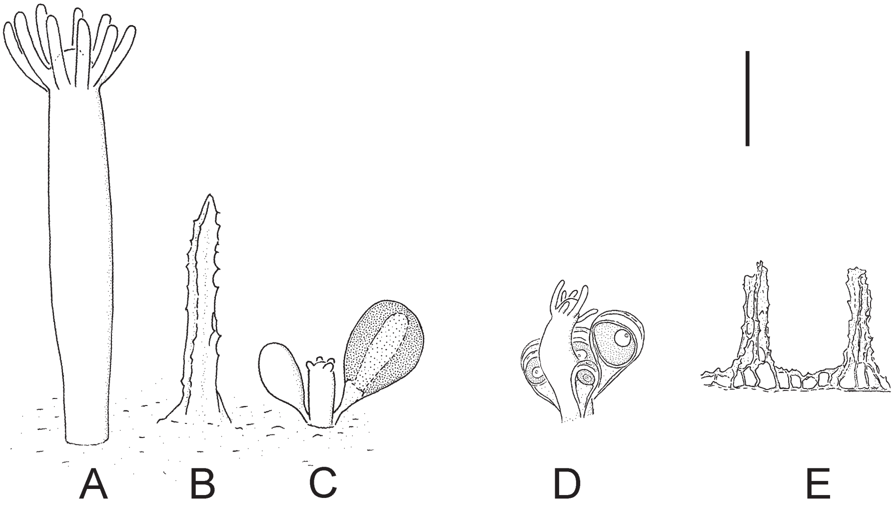

FIG. 20

Hydractinia serrata Kramp, 1943; A-C after preserved material, D-E redrawn from Kramp (1943b), scale bar 0.5 mm. (A) Gastrozooid. (B) Spine, note serrated ridges. (C) Male gonozooid, note origin of sporosacs near base of hydranth or from basal plate. (D) Female gonozooid. (E) Section of perisarc skeleton with two spines and basal plate.

Hydractinia monocarpa Allman, 1876 Fig. 21

Hydractinia monocarpa Allman, 1876: 254, pl. 10 figs 1-3. – Jäderholm, 1909: 49, pl. 2 figs 12-13. – Schuchert, 2001a: 17, fig. 7.
? *Hydractinia monocarpa*. – Calder, 1972: 225, pl. 2 fig. 3.
not *Hydractinia monocarpa*. – Jäderholm, 1908: 8, pl. 1 fig. 6, pl. 2 figs 6-9. – Kramp, 1932: 16 [= *H. serrata*]. – Rees, 1956a: 359, pl. 12 figs 8-11. – Naumov, 1969: 222, fig. 90.

MATERIAL EXAMINED: Syntype, ZMUC, without registration number; loc. Spitsbergen, on 2 cm shell. – Syntype, BMNH 1877.4.12.28; Spitzbergen; on shell of gastropod *Boreotrophon* inhabited by mollusc; female colony.

DIAGNOSIS: Arctic species, usually on *Boreotrophon* gastropods, hydrorhiza encrusting with coenosarc on top, spines tall and pointed, overgrown by coenosarc, gonozooids with no or very reduced tentacles, only one sporosac fully developed, female sporosacs with up to 50 eggs.

DESCRIPTION: Colonies usually growing on gastropod shells of the genus *Boreotrophon*, forming encrusting hydrorhiza covered by coenosarc. Spines numerous, not grouped, high and slender, often needle-like, hollow, straight or curved, very few branched, either smooth or some with undulated or warty ridges, spines overgrown by living tissue except for the tip.

Polyps polymorphic, differentiated into gastrozooids and gonozooids. Gastrozooid fusiform to cylindrical, hypostome short and dome-shaped, about 12 tentacles in one whorl.

Gonozooids much smaller than gastrozooids, rod-shaped, without tentacles or with a few stumps only, usually only one large gonophore, sometimes two opposite but

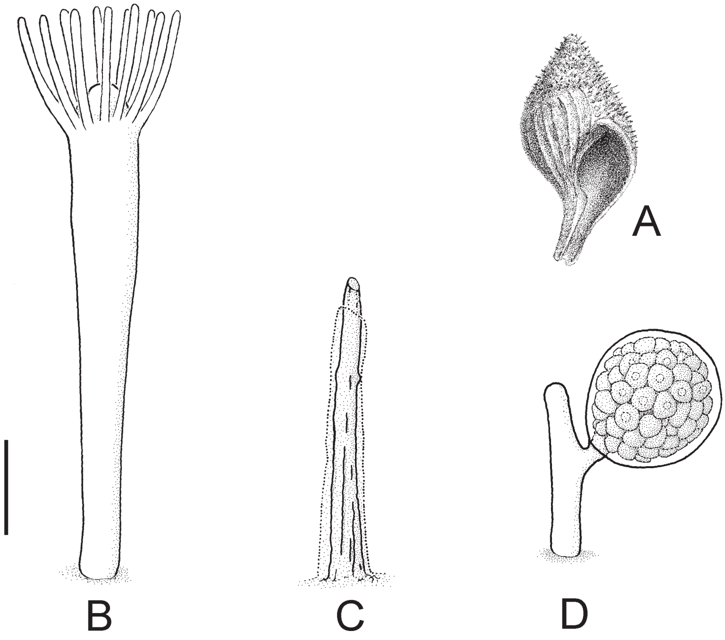

FIG. 21
Hydractinia monocarpa Allman, 1876; A, from Allman (1876), B-D, after type material, scale bar 0.5 mm. (A) Colony on *Boreotrophon* shell, size about 2 cm. (B) Gastrozooid. (C) Spine, overgrown by coenosarc. (D) Gonozooid with female sporosac.

one very small, developing near middle of gonozooid. Gonophores spherical, sessile sporosacs without canal system, spadix present, females with about 50 eggs.

DIMENSIONS: Colonies several cm^2, limited by shell surface, gastrozooids up 3 mm, gonozooids up to 1 mm, spines up to 1.5 mm, gonophore diameter up to 0.6 mm.

BIOLOGY: The type colony grew on gastropod shells of the species *Boreotrophon clathratus* (L.)[identification by Allman, 1876], Jäderholm (1909) reported it also on a *Bela* spec. (Gastropoda). Calder (1972) recorded it on a sertularian hydroid, which is perhaps an unusual substrate for this species.

DISTRIBUTION: High Arctic species, known from Spitsbergen and Canada (Calder, 1972), perhaps more widespread. Type locality: Spitsbergen.

REMARKS: This is a rarely reported species that has been misidentified several times. An examination of the type specimens showed that some gonozooids have stumps of tentacles and sometimes two opposite sporosacs of very different size.

The species very much resembles *H. carica*, but has significantly more eggs per sporosac (50 versus 5-6), fewer gonophores (1-2 versus 3-7), and has more pointed and longer spines.

The non-type material examined by Jäderholm (1908), Rees (1956), and Naumov (1969) had sporosacs with radial canals. However, I was unable to find any radial canals in the female gonophores of the type material. Also Allman (1876) and Calder (1972) do not mention radial canals. Jäderholm (1908) identified material from the Russian Arctic Seas as *H. monocarpa,* although he initially thought that it could be a new species. His material differed from typical *H. monocarpa* by sporosacs arising from the base of the gonozooids (comparable to *H. serrata*), the presence of four radial canals, and the branched, stout spines. I therefore think that Jäderholm's specimens cannot be referred to *H. monocarpa*. They also do not belong to *H. serrata* due to the sporosacs with radial canals and the high number of eggs. It is rather probable that the material of Jäderholm, Rees, and Naumov belonged to different, probably new species. New investigations on Arctic hydractiniids using living material must be made to clarify the situation.

Genus ***Clava*** Gmelin, 1788

TYPE SPECIES: *Clava parasitica* Gmelin, 1788 = *Clava multicornis* (Forsskål, 1775).

DIAGNOSIS: Hydroids sessile, not polymorphic, rising directly from hydrorhiza, naked, with or without a low perisarcal collar round base, with conical to dome-shaped hypostome, filiform tentacles scattered or in indistinct whorls, confined to upper third or less of the hydranth; gonophores fixed sporosacs, on hydranth body below tentacles.

REMARKS: This is currently a monotypic genus.

Clava multicornis (Forsskål, 1775) Figs 22-23

Hydra multicornis Forsskål, 1775: 131. – Forsskål, 1776: pl. 26, fig. B b.
Hydra squamata Müller, 1776. 230.
Clava parasitica Gmelin, 1788: 3131.
Tubularia affinis Gmelin, 1788: 3834.
Clava repens Wright, 1857: 227, pl. 11 fig. 1.
Clava membranacea Wright, 1857: 228, pl. 11 figs 2-3.
Clava cornea Wright, 1857: 228. – Hincks, 1868: 5, pl. 1 figs 3, 3a.
Clava discreta Allman, 1859: 369.
Clava leptostyla L. Agassiz, 1862: 218, pl. 20 figs 11-16, pl. 21. – Hincks, 1868: 6, pl. 2 fig. 1. – Nutting, 1901: 327, fig 1.
Clava diffusa Allman, 1863: 8. – Allman, 1872: 247, pl. 2 figs 3-4. – Hincks, 1868: 9.
Clava nodosa Wright, 1863: 378. – Hincks, 1868: 9.
Clava glomerata Lönneberg, 1899: 45, fig. – Jäderholm, 1909: 44, synonym.
Clava multicornis. – Hincks, 1868: 2, pl. 1 fig. 1. – Allman, 1872: 246, pl. 2 figs 1-2. – Broch, 1916: 38, fig. K, pl. 1 fig. 5. – Weill, 1934: 382. – Vervoort, 1946: 116, figs 24a & 46. – Naumov, 1969: 195, fig. 65. – Edwards & Harvey, 1975: 879, synonymy. – Barnes, 1994: 62, fig . – Broch, 1916: 38, fig. K, pl. 1 fig. 5. – Schuchert, 2001a: 9, fig. 1.
not *Clava multicornis.* – Bedot, 1911: 202. [= *Rhizogeton* spec.]
Clava squamata. – Hincks, 1868: 4, pl. 1 fig. 2. – Allman, 1872: 243, pl. 1. – Lönneberg, 1899: 17. – Bedot, 1911: 202. – Broch, 1911: 12, fig. 8. – Kramp, 1914: 976. – Weill, 1934: 381.
? not *Clava multicornis*? – Wedler & Larson, 1986: 82, fig. 5A.
? not *Clava multicornis.* – Peña Cantero & García Carrascosa, 2002: 25, fig. 3d. [?= *Rhizogeton* spec.]

MATERIAL EXAMINED: MHNG INVE54612; Atlantic, France, Roscoff; 15 June 1910, material *Clava multicornis* of Bedot (1911). – MHNG INVE27333; Scotland, Kames Bay; 3 June 1992, on *Ascophyllum* and *Fucus*. – MHNG INVE35753; Scotland, Argyll, Connel Bridge rapids; 4 May 2004, numerous living colonies growing mainly on *Ascophyllum nodosum*. – Atlantic, France, Roscoff; April-May 1998 and 2000, numerous living colonies growing on

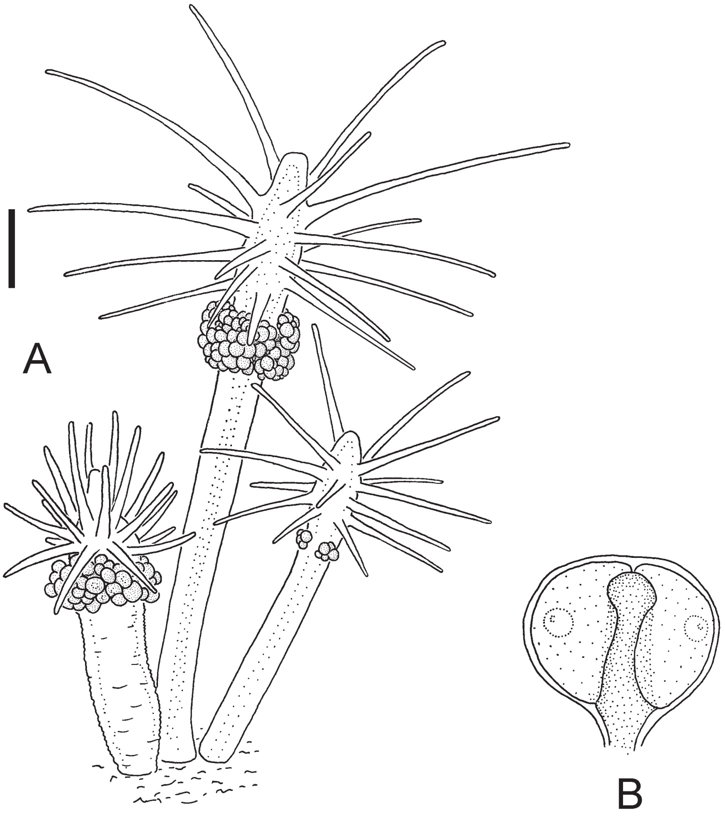

FIG. 22

Clava multicornis (Forsskål, 1775), after living material from Scotland. (A) Part of colony, scale bar 1mm. (B) Female sporosac, diameter ca. 0.2 mm.

Ascophyllum nodosum and other substrates; not preserved; several independent colonies gave the same 16S DNA sequence as EMBL/GenBank number **EU272552**. – MHNG INVE54079; Atlantic, Spain, Basque Country, San Sebastián (Guipúzcoa), Punta de Mompás; May 2006, one colony; leg. A. Altuna; 16S DNA sequence identical to **EU272552**. – Iceland, Sandgerdi, south of harbour, intertidal, 4 May 2000, numerous fertile colonies on *Fucus* spec. and other substrates, included *multicornis* and *squamata* form, examined alive and used for DNA extraction, not preserved, 16S DNA sequence identical to **EU272552**.

DIAGNOSIS: As for genus.

DESCRIPTION: Mainly growing on fucoid algae, but also on other substrata. Colony form variable, either densely clustered polyps borne on a compact hydrorhizal base of anastomosing stolons that give the impression of a crust (*squamata* form), or scattered polyps arising from an open hydrorhizal network of creeping stolons (*multicornis* form). Intermediate forms also frequent. Stolons always covered by perisarc, without spines. Polyps not polymorphic, in fertile colonies almost all polyps with gonophores, except for the smallest ones.

FIG. 23
Clava multicornis (Forsskål, 1775); Dunstaffnage, Scotland, contracted.

Hydranths very large for the family, club-shaped, thickest in region of tentacles and gonophores, very contractile, slender when expanded, base with or without collar of thin perisarc, base sometimes with a constriction (*leptostyla* form). Hypostome dome-shaped, without concentration of nematocysts; 20-40 tapering tentacles, confined to distal 1/3 to 1/6 of hydranth body, scattered or in four indistinct whorls, very contractile. Gonophores small, up to 50 per hydranth, initially separated into groups of several small gonophores, later contiguous in a dense collar below tentacles, sometimes also spreading and thinning out towards base (*diffusa* form).

Gonophores are simple, sessile sporosacs without canal system. Female sporosacs produce mostly 1 or 2 eggs, occasionally 3 eggs. Eggs develop into planula in sporosac, thus larviparous. Colonies unisexual, but some colonies have male and female polyps due to gregarious settlement of several larvae.

Nematocysts: microbasic euryteles and desmonemes. Colours: hydranth pink to cream, spadix dark orange, eggs white.

DIMENSIONS: Colonies from a few hydranths to several cm^2. Polyps up to 30 mm if fully expanded, usually shorter and about 10 mm, diameter when fully expanded 0.5 mm. Sporosacs about 0.2 mm. Nematocysts (preserved): microbasic euryteles (7-8)x(2.5-3) μm, desmonemes (4.5-5)x(3) μm.

OTHER DATA: The histology of the sporosacs and the gametogenesis were examined by Weismann (1883) and Brien (1942). The influence of environmental factors on the morphology of the polyp was examined in detail by Kinne & Paffenhöfer (1965, 1966), Thiel (1970), and Edwards & Harvey (1975). The colony form and hydranth size and shape are determined by a range of environmental factors such as substratum type, tidal exposure, food availability and water movement.

Biology: Usually a very common species in the boreal NE Atlantic, abundant at places with good tidal flow. Occurs preferentially on Phaeophyta (*Fucus*, *Ascophyllum*), but is also able to colonize a number of other solid substrata, like rock, timber, barnacles. Its main depth range lies between the mean tide level and the low-water mark of ordinary spring tides, and accordingly it is adapted to aerial exposure twice daily for several hours. Some deeper records are also known (e. g. Rasmussen, 1973: 20 m), but deeper findings should be regarded with suspicion. When exposed to the air during low water, the colonies form compact jelly-like masses, able to withstand desiccation (Edwards & Harvey, 1975). Under good conditions it is perennial (English Channel, Teissier, 1965; Scotland, Edwards & Harvey, 1975). Christiansen (1972) observed gonophores in the Oslofjord (Norway) from May to September. It can live in estuaries and in reduced salinities down to 6 ppt (Barnes, 1994; Schönborn *et al.*, 1993). Its diet appears not to be very selective. It has been observed to feed on small crustaceans, annelids, molluscs, small fish larvae (Kinne & Paffenhöfer, 1965). Additional aspects of its biology can be found e. g. in: Allman (1872), Harm (1902), Ephrussi (1923), Föyn (1927a, 1927b, 1929), Williams (1965), Aldrich *et al.* (1980), Orlov & Marfenin (1993), Orlov (1996), and Rossi *et al.* (2000).

Distribution: Mainly North-eastern Atlantic, ranging from the Arctic Sea south to Portugal, including also the North Sea and the Baltic Sea (Hincks, 1868; Allman, 1872; Hartlaub, 1894; Naumov, 1969; Bonnevie, 1901; Jäderholm, 1909; Bedot, 1911; Robson, 1914; Philbert, 1935; Kramp, 1942; Vervoort, 1946; Leloup, 1947; Rees, 1952; Hamond, 1957; Russell, 1957; Teissier, 1965; Castric-Fey, 1970; Christiansen, 1972; Rasmussen, 1973; Schönborn *et al.,* 1993; Medel & López-González, 1996). Also present along the Atlantic coast of North America (Fraser, 1944, as *Clava leptostyla*). Occurs also along the coasts of Iceland, but it is not known to occur in Greenland (Schuchert, 2001a). It has also repeatedly been reported from the Mediterranean (Peña Cantero & García Carrascosa, 2002; Bouillon *et al.,* 2004), but see remarks below. Wedler & Larson (1986) found it in the tropical Atlantic, but due to its occurrence in tropical waters they think that their find might belong to a separate species, an opinion I share with them. The figure given by them, however, looks like *C. multicornis*. Type locality: Øresund (Denmark or Sweden), on bottom between *Fucus.*

Remarks: In the northern Atlantic, *Clava multicornis* can locally be the most abundant and most conspicuous hydroid. Its morphology is modulated by environmental factors and it is therefore not surprising that it was given numerous different names. The synonymy has fortunately been worked out by the authoritative work of Edwards & Harvey (1975), on which also the synonymy of this study is based.

So far, I have seen no convincing evidence (e. g. museum samples, unambiguous figures) that this species also occurs in the Mediterranean. If it is present in the Mediterranean, it is a rather rare species there. It could be that many Mediterranean records refer actually to an undescribed *Rhizogeton* species. This species has been observed repeatedly in the western Mediterranean (Ligurian Sea, pers. com H. Galea; Banyuls-sur-Mer, own observations), but also along the northern coast of Spain (A. Altuna, pers. com.), and the English Channel (Brittany and Normandy, own observations). The sample identified by Bedot (1911) as *Clava multicornis* belongs also to this *Rhizogeton* species. The polyps resemble somewhat *Clava multicornis*, but they are much smaller (2 mm), are more delicate, they have their tentacles (20-30) more widely spaced and they spread over the distal half or more of the hydranth. The polyps are almost indistingishable from *Rhizogeton nudus* Broch, 1910 (see Schuchert, 2004), but 16S sequence data show that it is distinct from it (unpublished). The naming and description of this species has to wait until some fertile material becomes available.

Problematic Hydractinidae species

Hydractinia humilis Bonnevie, 1898

Hydractinia humilis Bonnevie, 1898: 486, pl. 26 figs 39-40. – Rees, 1956b: 109.
[Not *Podocoryne humilis* Hartlaub, 1905: 523, fig. E.]

DIAGNOSIS: Encrusting hydrorhiza, gastrozooids 1-2 mm, 20 tentacles in two close set whorls, gonozooids somewhat smaller and fewer tentacles; sporosacs hermaphroditic, few eggs.

DISTRIBUTION: Only known from the type locality at Manger in Norway.

REMARKS: This is a somewhat problematic species that has never been found again since its original description. It was based on a colony originally collected by M. Sars, but described only in 1898 by Bonnevie. She made histological sections and found spermatids and eggs in the same sporosacs. If not based on a misinterpretation, this is likely a distinct species. Rees (1956b) re-examined the type material, but was unable to investigate the hermaphroditic gonophores. He found the specimen much resembled *Hydractinia carica*. The validity of the species depends on the confirmation of C. Bonnevie's observations.

Hydractinia reticulata (Wright, 1861)

Cionistes reticulata Wright, 1861: 123, fig. 1. – Hincks, 1868: 135. – Allman, 1872: 309.
[not *Stylactis reticulata* Hirohito, 1988: 139, fig. 51d-f]
[not *Podocoryne reticulata* Fraser, 1938: 24, fig. 23]

REMARKS: This is an indeterminate species. Already Hincks (1868) and Allman (1872) considered its description as insufficient. Its origin and the fixed sporosacs indicate that it is perhaps referable to *H. echinata.* Note that when applying the concept of *Hydractinia* as used here, then *Stylactis reticulata* Hirohito, 1988 and *Podocoryne reticulata* Fraser, 1938 will become secondary homonyms of *H. reticulata* Wright, 1861a.

Clavopsis adriatica Graeffe, 1883) Fig. 24

Clavopsis adriatica Graeffe, 1883: 84, plate. – Stechow, 1913: 21. – Picard, 1958: 190.

DIAGNOSIS: Hydrorhiza perisarc covered stolons, continued as thin film over basal part of hydranth, hydranths club-shaped, up to 7 mm, 8-14 tentacles in 1-2 whorls, hypostome trumpet-shaped, gonophore producing polyps with fewer tentacles, 5-7 gonophores per polyp, developing well below tentacles, gonophores released as sac-shaped medusoids, gonads not yet formed, four radial canals, four tentacle rudiments, bulbs with pigment spot.

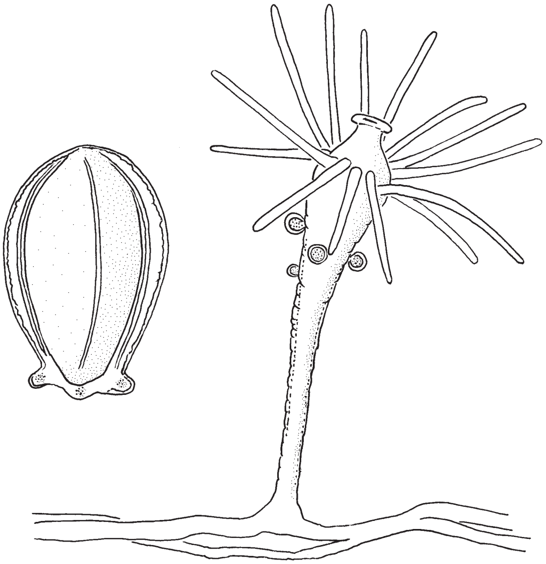

FIG. 24

Clavopsis adriatica Graeffe, modified after Graeffe (1883). At right a polyp with gonophores. Left, at higher magnification, a released medusoid.

BIOLOGY: Colonizes tubes of the polychaete *Spirographis spallanzani* and old *Eudendrium* stems.

DISTRIBUTION: Only known from type locality, Harbour of Trieste, Adriatic Sea.

REMARKS: *Clavopsis adriatica* Graeffe, 1883 is only known from its first description. No type material could be located, it is likely lost. Stechow (1923) included it in the Hydractiniidae, Picard (1958b) considered it even as conspecific with *Hydractinia areolata,* which is very unlikely.

Graeffe described the polyps as naked, although there was a thin, filmy perisarc covering at least part of the base and hydranth. This perisarc is also indistinctly indicated in Graeffe's figure and Calder's (1988) conclusion is therefore correct that this species is likely not a hydractiniid, but more likely a member of Pandeidae or Bougainvilliidae.

Some, so far neglected details, allow a re-assessment of this species. Graeffe made his observations on colonies he cultivated in an aquarium. He qualified the polyps as identical with *Clava* and placed it into a new genus solely for the gonophores that did not match this genus. Each bulb of the medusoid had a pigment spot, thus perhaps an ocellus. The gonads of the released medusoids were not yet developed as must be concluded from a passage in Graeffe on page 84: "...ist die medusoide Generation dadurch ausgezeichnet, dass ihr die Erzeugung von Geschlechtsprodukten abgeht..." [the medusoid generation of this species is distinguished by the absence of the production of gametes]. The sentence following this is even more revealing. Graeffe summarizes how the medusoids fell to the bottom of the jar and reverted into the polyp phase again. This unique feature of a life-cycle reversion has been observed for some *Turritopsis* medusae (Piraino *et al.*, 1996). Only the Mediterranean *Turritopsis dohrnii* (Weismann, 1883) is actually able to so (see Schuchert, 2004), a process that is initiated by adverse conditions. Taken also into account the perisarc covered pedicels of the polyps and the medusoids lacking gonads, this makes me suspect that *Clavopsis adriatica* was actually *Turritopsis dohrnii*. Graeffe's colonies were perhaps not kept under good conditions and produced medusae with shrivelled bells and reduced tentacles that then re-differentiated back to the polyp stage. If Graeffe had indeed *Turritopsis dohrnii*, then his illustration of the polyp-tentacles must be incorrect (comp. Fig. 24).

Family Rhysiidae Brinckmann, 1965

Type Genus: *Rhysia* Brinckmann, 1965.

Diagnosis: Hydroids polymorphic, with gastrozooids, with or without distinct gonozooids, with or without dactylozooids. Polyps issuing from creeping stolons, these covered with perisarc. Gastrozooids naked, sessile, columnar, one whorl of filiform tentacles, large nematocysts on hypostome. Tentaculozooids in perisarc sheath, with swollen naked end studded with nematocysts. Gonozooids naked, sessile, either derived by reduction from gastrozooids or developing as distinct type with fewer or no tentacles; with sexual dimorphism. Gonophores absent, gonad develops on one side of the polyp between the epidermis and gastrodermis, females producing a single large egg only that develops in situ. Cnidome of microbasic euryteles and desmonemes.

Remarks: Hirohito (1988) regarded the Rhysiidae as part of the Hydractiniidae. I agree with Brinckmann-Voss *et al.* (1993) that this family should be kept separate. The extreme reduction of the gonophore makes it impossible to find convincing synapomorphies. The Rhysiidae could be related to the Hydractiniidae as well as to the Cytaeididae. For the moment, they are thus best kept separate. There is only one genus in this family.

Genus ***Rhysia*** Brinckmann, 1965

Type species: *Rhysia autumnalis* Brinckmann, 1965, by original designation.

Diagnosis: As for the family.

Remarks: There is only one *Rhysia* species in the in the ERMS zone.

Rhysia autumnalis Brinckman, 1965 Fig. 25

Rhysia autumnalis Brinckmann, 1965: 942, figs 1-15. – Boero & Fresi, 1986: 139. – Bouillon *et al.*, 2004: 78, fig. 44I.
not *Stylactis halecii* Hickson & Gravely, 1907: 8 pl. 1 figs 5-6, pl. 4 fig. 33. – Iwasa, 1934: 262, figs 15-16.
not *Stylactaria halecii*. – Hirohito, 1988: 131, fig. 48a-b. – Namikawa. 1991: 810.

Material examined: Holotype, BMNH 1965.8.31.1; Italy, Vico Equense; 30 m; 18.11.1961; male colony on *Vermetus* and the algae *Flabellia petiolata* (syn. *Udotea petiolata*). – Paratype, BMNH 1965.8.31.2; Italy, Vico Equense; 30 m; 12.12.1961; colony on *Vermetus*.

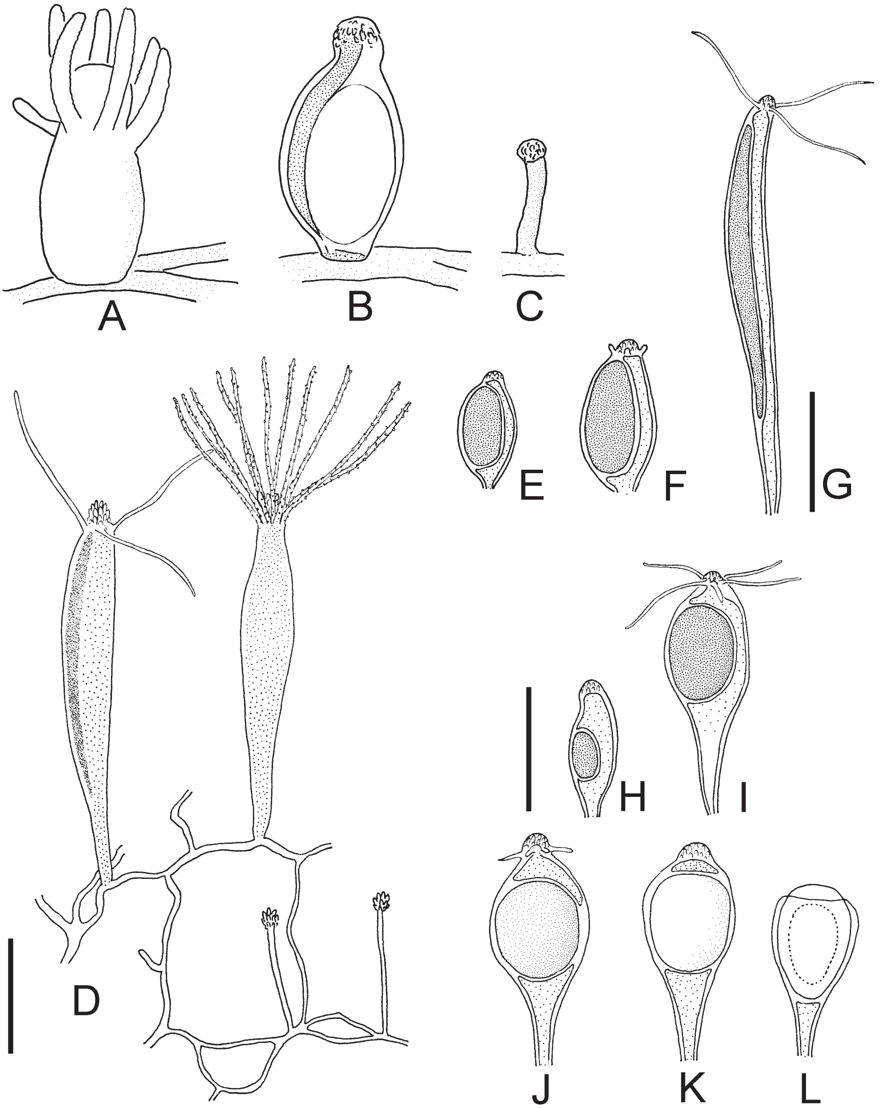

FIG. 25

Rhysia autumnalis Brinckman, 1965; A-C after preserved type material, D-L modified from Brinckmann (1965). (A) Contracted nutritive zooid, size about 0.5 mm. (B) Contracted male gonozooid lacking tentacles. (C) Tentaculozooid. (D) Part of colony with gonozooid, gastrozooid, two tentaculozooids, scale bar 0.5 mm. (E) Young gonozooid, same scale as G. (F) More advanced stage of male gonozooid, same scale as G. (G) Extended mature male gonozooid, scale bar 0.5 mm. (H) Young female gonozooid, scale bar 0.5 mm. (I) Mature female gonozooid, same scale as H. (J-L) Development of planula and concomitant reduction of polyp, same scale as H.

DIAGNOSIS: Polyps sessile, polymorphic, tentaculozooids with perisac sheath, gonozooids with few or no tentacles, without gonophores, gametes develop in body-wall.

DESCRIPTION (after Brinckmann, 1965, own observations): Colonies small, polyp issuing from an open hydrorhizal network of creeping stolons. Stolons covered by thin perisarc. Polyps polymorphic, with gastro-gonozooids and tentaculozooids.

Tentaculozooids composed of a thin stem and a terminal spherule beset with nematocysts. Stem enveloped in tube of thin perisarc.

Hydranths naked, sessile, spindle-shaped, with short, rounded or conical hypostome, hypostome covered by large nematocysts. Tentacles filiform, 8-12 in one whorl, nematocysts concentrated in irregular patches.

Gonozooids with bilateral symmetry, develop as small, tentacle-less polyps, the incipient gametes already visible at an early stage, hypostome with large nematocysts, some tentacles may form in later stages. Gonozooids not feeding, male and female polyps in separate colonies.

Male polyps produce a gonad on one side of the polyp between the epidermis and gastrodermis. The gonad is elongated, almost as long as the height of the polyp. The male polyps grow to about the same size as nutritive polyps, but have fewer (0-4), shorter, and thinner tentacles.

Female polyps produce a single, large egg on one side of the polyp between the epidermis and gastrodermis. Egg surrounded by a layer of cells. Mature polyps with 6-10 thin tentacles, nematocysts confined to tentacle tips. Fertilisation and embryonic development takes place in situ, the tentacles and gastrodermis of the gonozooid are concomitantly reduced. Planula becomes free by rupture of the polyp. Colours: male gonads white when young, whitish-blue when completely ripe.

Nematocysts: Microbasic euryteles of three size classes, desmonemes.

DIMENSIONS: Nutritive hydranths extended 1-1.7 mm high, 0.13 mm wide, contracted about 0.4 mm. Tentaculozooids 0.5 mm high. Largest type of euryteles (29-31)x(11) μm, medium sized eurytels on hypostome (16)x(5-6) μm, small euryteles on tentacles ca (8)x(4-5) μm, desmonemes ca (4-5)x(3) μm.

OTHER DATA: For more details on the histology of the polyps and their gonads see Brinckmann (1965).

BIOLOGY: Occurs on the tubes of the sedentary gastropods of the genus *Vermetus,* spreading also to neighbouring algae. Depth range 7-50 m (Brinckmann, 1965; Boero & Fresi, 1986). Fertile colonies have been found from October to January (Brinckmann, 1965; Boero & Fresi, 1986).

DISTRIBUTION: Western Mediterranean (Gulf of Naples and Ligurian Sea). Type locality: Mediterranean, Italy, Gulf of Naples, Vico Equense.

FAMILY STYLASTERIDAE GRAY, 1847

TYPE GENUS: *Stylaster* Gray, 1831.

DIAGNOSIS: Hydroid colony erect, branched, usually flabellate, more rarely encrusting, with a thick calcareous skeleton (coenosteum); polyps polymorphic and retractile; gastrozooids and dactylozooids retractable into special skeletal depressions: gastropores and dactylopores; bottom of gastropores and dactylopores with or without an upright pointed or rounded toothed spine (gastrostyle or dactylospine); gastro- and

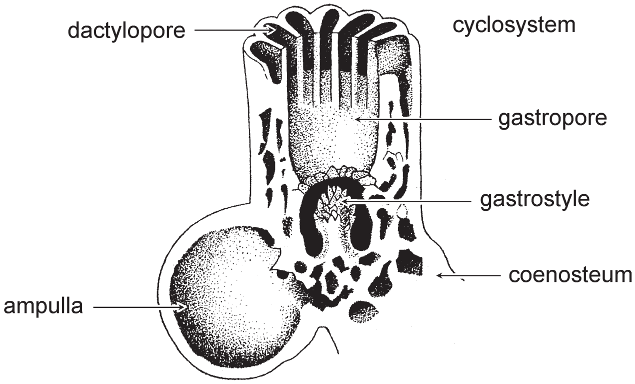

FIG. 26

Schematic longitudinal section of through the skeleton of a stylasterid cyclosystem and an ampulla, modified after Moseley (1879).

dactylozooids either irregularly distributed over colony, or limited to certain regions of colony, or arranged in circles (cyclosystems) where one gastrozooid is surrounded by several dactylozooids. Gastrozooids with one whorl of filiform tentacles, exceptionally without tentacles; dactylozooids filiform, without tentacles. Gonophores fixed sporosacs and developed inside vesicles (ampullae) covered by or buried in coenosteum.

REMARKS: The European species of this family have been revised and monographed in detail by Zibrowius & Cairns (1992). Therefore, only a summary of the species found in the ERMS region is given here and only a few species that also occur in more shallow waters are illustrated. Some important technical terms necessary for the usage of the keys are explained under Material and Methods and in Fig. 26. For introductions to the Stylasteridae see Moseley (1879), Boschma (1956b) and Cairns (1983b).

KEY TO THE GENERA FOUND IN THE ERMS ZONE (AFTER ZIBROWIUS & CAIRNS, 1992):

1a Gastro- and dactylopores independent, not arranged in cyclosystems 2
1b Gastro- and dactylopores arranged in cyclosystems 4
2a Gastropore without gastrostyle . . . . **Pliobothrus**
2b Gastropore with gastrostyle 3
3a Dactylopores are low, apically perforated cones (Fig. 27B) . . . . . . **Lepidopora**
3b Dactylopores surrounded by U-shaped collar (spine with slit, see Fig. 28C) . . . . **Errina**
4a Cyclosystem (partially) overarched by fixed lid; gastropore double chambered; gastro- and dactylostyles absent . . . . **Cryptothelia**
4b Cyclosystem without lid; gastropore tube cylindrical; gastro-and dactylostyles present 5
5a Cyclosystems on anterior branch face; gastropore tube long and curved; ampullae usually clustered near cyclosystems . . . . **Stenohelia**
5b Cyclosystems randomly or sympodially arranged; gastropore tube (usually) short and (nearly) straight; ampullae scattered randomly over coenosteum . . . . **Stylaster**

Genus ***Pliobothrus*** Pourtalès, 1868

TYPE SPECIES: *Pliobothrus symmetricus* Pourtales, 1868.

DIAGNOSIS: Gastro- and dactylopores randomly arranged. Coenosteal texture linear-imbricate; coenosteal pores large. Gastropore tube double-chambered; no gastrostyles. Dactylopore spines conical or tubular; dactylopore tubes quite long; no dactylostyles. Ampullae usually internal (females external *P. gracilis*).

KEY TO THE *PLIOBOTHRUS* SPECIES OF THE ERMS REGION

1a Female ampullae internal, gastropores 0.30-0.45 mm in diameter . . . . *P. symmetricus*

1b Female ampullae superficial mounds, gastropores 0.18-0.25 mm in diameter . . . . *P. gracilis*

Pliobothrus symmetricus Pourtalès, 1868 Fig. 27

Pliobothrus symmetricus Pourtalès, 1868: 141. – Pourtalès, 1871: 57, pl 4 figs 7-8. – Cairns, 1983: 439, figs 3A-H, 24G, 25G, 27B. – Boschma, 1956b: F104, fig. 85.1a-b. – Boschma, 1967: 333, pl. 1 figs 5-6. – Zibrowius & Cairns, 1992: 38, figs 5A-G & 6A-G.
Hornera gravierei Calvet, 1911: 7, fig 5.

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies in eastern Atlantic around 6 cm, gastropores 0.30-0.45 mm in diameter (developing ones smaller, 0.2 mm), more data in Zibrowius & Cairns (1992).

DISTRIBUTION: In the western Atlantic from South Carolina through the Lesser Antilles, depths 150-400 m. In the eastern Atlantic southeast of Iceland, east of The Faroes, between Faroes and Hebrides, Norway, west of Ireland, Celtic Sea, Bay of Biscay, Galicia and Josephine Seamounts, ? Madeira, Azores, ranging from 80 to 1600 m, usually below 250 m. Type locality: Off Sand Key, Key West, Florida.

Pliobothrus gracilis Zibrowius & Cairns, 1992

Pliobothrus gracilis Zibrowius & Cairns, 1992: 44, Fig. 5H-N, 8A-G.

DIAGNOSIS: See keys to genus and species.

DESCRIPTION and Illustration: Zibrowius & Cairns (1992)

DISTRIBUTION: Known from type locality only, Hyères Seamount, west of Morocco, depth 620-700 m.

Genus ***Lepidopora*** Pourtalès, 1871

TYPE SPECIES: *Errina glabra* Pourtalès, 1867.

DIAGNOSIS: Coordination of gastro- and dactylopores usually random; however, in some species dactylopores serially arranged on branch edges, and gastropores serially arranged on anterior or antolateral branch faces. Coenosteal texture quite

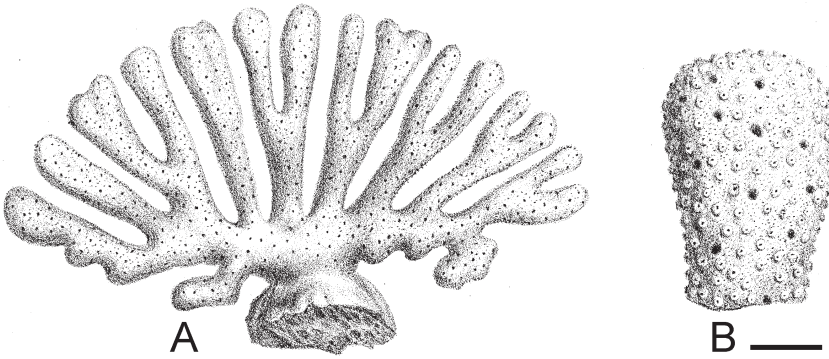

FIG. 27

Pliobothrus symmetricus Pourtalès, 1868; from Pourtalès (1871). (A) Colony. (B) Part of branch. The flush, larger holes are the gastropores, the smaller holes on round tubercules are the dactylopores, scale bar 2.5 mm

variable. Gastropores often bordered by proximal lip, gastro- and dactylore tubes long. Gastrostyles usually not ridged; height:width ratio high. Dactylopores apically perforate mounds; no dactylostyles.

REMARKS: Only *Lepidopora eburnea* is present in the ERMS zone.

Lepidopora eburnea (Calvet, 1903)

Horneara eburnea Calvet, 1903: 162, pl. 18 fig 5a-c.
Errina (*Lepidopora*) *hicksoni* Boschma, 1963: 339, fig. 1, pl. 1 figs 1-3.
Lepidopora eburna. – Zibrowius & Cairns, 1992: 27, figs 1A-F, 2A-J.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION AND ILLUSTRATIONS: See Zibrowius & Cairns (1992).

DISTRIBUTION: Azores, depth range 480-983 m. Type locality: 38°22'N 28°14.4'W, 736 m (Azores).

Genus ***Errina*** Gray, 1835

TYPE SPECIES: *Millepora aspera* Linnaeus, 1767.

DIAGNOSIS: Gastro- and dactylopores usually randomly arranged. Coenosteal texture reticulate-granular or linear-imbricate. Proximal gastropore often with lip-like process (hood); gastrostyles present, having a moderate height: width ratio. Dactylopore spines U-shaped, with groove directed proximally; walls of dactylopore spine thick; no dactylostyles. Ampullae superficial or internal.

KEY TO THE *ERRINA* SPECIES FOUND IN THE ERMS ZONE:

1a Colony branches with rather blunt ends; gastropore with lip . . *Errina dabneyi*
1b Branches taper gradually; gastropore without lip 2
2a Colony uniplanar to slightly bushy, dactylopore spines high (up to 0.65 mm), some dactylopores without spines . . . . *Errina aspera*
2b Colony bushy, sparsely branched, dactylopore spines shallow 0.14-0.16 mm . . . . *Errina atlantica*

For a more elaborate table of differences see Zibrowius & Cairns (1992).

Errina dabneyi (Pourtalès, 1871)

Lepidopora dabneyi Pourtalès, 1871: 41, pl. 7 figs 10-11.
Hornera verrucosa Calvet, 1903: 161, pl. 18 fig. 6a-c.
Errina amoena Boschma, 1956a: 281, figs 1-3, pls 1-2, pl. 3 figs 1-4.
Errina dabneyi. – Zibrowius & Cairns, 1992: 53, figs 11A-I, 12A-F, 13A-B.

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 30 cm, branches tapering to about 0.6 mm, gastropores 0.15-0.20 mm in diameter, dactylopore spines up to 0.15 mm high.

DISTRIBUTION: Azores, and Mid-Atlantic Ridge southwest of the Azores, 140-2200 m. Type locality: Azores, Faial.

Errina aspera (Linnaeus, 1767) Fig. 28

Millepora aspera Linnaeus, 1767: 1282.
Errina aspera – Fol, 1885: 668. – Boschma, 1954: 143, fig. 1a-c, pls 1-3. – Cairns, 1983: 459, fig. 11A-G. – Zibrowius & Cairns, 1992: 46, figs 9A-I & 10A-H, synonymy. – Bouillon *et al*., 2004: 79, fig. 45B-C.
Errina aspera mascarina Boschma, 1965: 3, figs 1-2, pl. 1-2.

MATERIAL EXAMINED: MHNG INVE55452 and INVE55453; Mediterranean, Italy, Messina; several colonies or fragments; no collection date, material mentioned in Fol (1885) and Zibrowius & Cairns (1992).

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 20 cm, branches tapering to about 0.7 mm, gastropores 0.18-0.25 mm in diameter, dactylopore spines up to 0.65 mm high.

DISTRIBUTION: Mediterranean Sea (mainly Strait of Messina), Strait of Gibraltar, off Morocco, ? off Cape Verde Islands, depth range 80-226 m. Type locality: Mediterranean.

Errina atlantica Hickson, 1912

Errina atlantica Hickson, 1912: 464. – Boschma, 1967: 331, fig. 3a-b, pl. 1 fig. 7-10. – Zibrowius & Cairns, 1992: 58, figs 14A-F, G-I?, 15 A-G.

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 12 cm, branches tapering to about 0.7 mm, gastropores 0.22-0.30 mm in diameter, dactylopore spines 0-0.16 mm high.

DISTRIBUTION: Azores, 610-938 m. Type locality: Azores, 38°07'N 27°11.75'W, 983 m.

Genus ***Stylaster*** Gray, 1831

TYPE SPECIES: *Madrepora rosea* Pallas, 1766: 312.

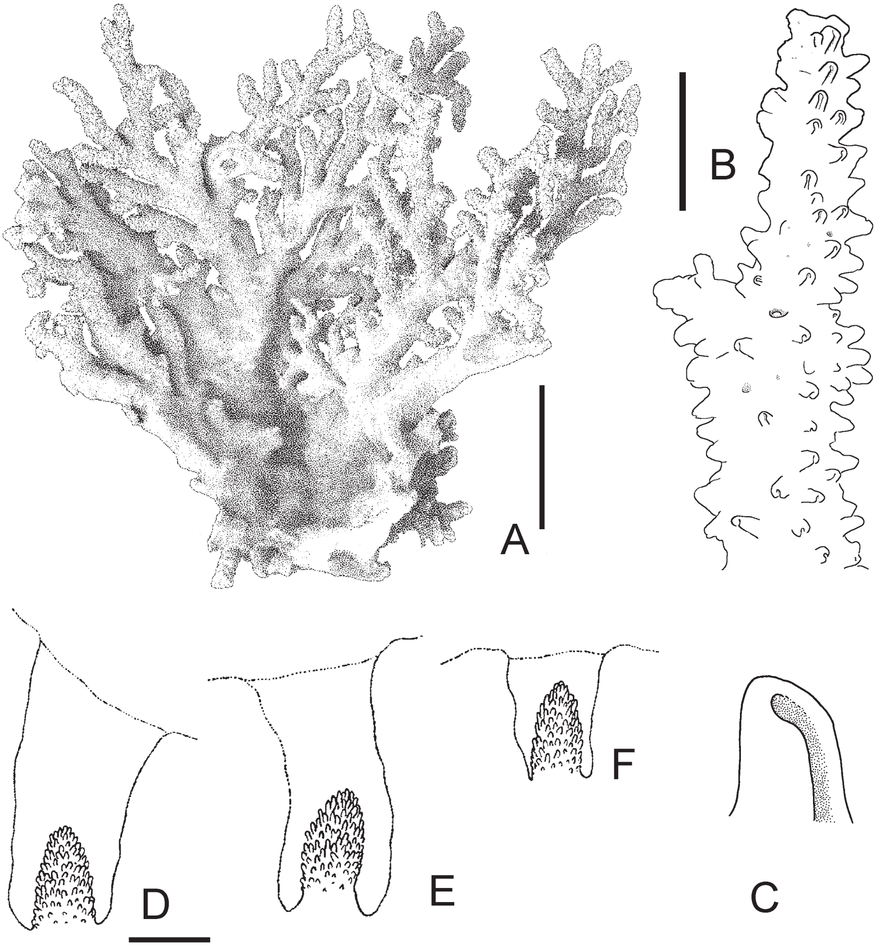

FIG. 28

Errina aspera (Linnaeus, 1767); A-C after MHNG INVE55452, D-F from Boschma (1954). (A) Colony, scale bar 2 cm. (B) Terminal branch, scale bar 5 mm. (C) Characteristic dactylopore spine, height about 0.6 mm. (D-F) Transversal sections of gastropore, showing gastrostyle and variability of gastropore depth, scale bar 0.2 mm.

DIAGNOSIS: Gastro- and dactylopores arranged in cyclosystems. Cyclosystems variable in location, ranging from uniform coverage of all branch surfaces (Group A) to a strictly sympodial arrangement (Group C), with many intermediate arrangements (Group B). Coenosteal colour and texture variable: most common textures reticulate-granular and linear imbricate. Gastro- and dactylostyles present, the latter robust in Group A, more moderate to rudimentary in Groups B and C. Gastrostyles usually ridged and bearing long, pointed spines. Ring palisade often present; gastropore inner shelf sometimes present in Group C. Ampullae usuallly superficial, usually with distinct efferent pores.

REMARKS: The differences of the *Stylaster* species and subspecies found in the ERMS zone do not easily lend themselves to construct a robust, reliable identification key. For identifications use preferably the detailed table in Zibrowius & Cairns (1992).

KEY TO THE *STYLASTER* SPECIES FOUND IN THE ERMS ZONE

1a	Cyclosystems dispersed, tips of branch diameter larger than cyclosystems, coenosteum smooth	*Stylaster norvegicus*
1b	Cyclosystems primarily on sides of branches, some on anterior and posterior sides, branch tips usually tapering to diameter of cyclosystems, coenosteum rough or smooth	2
2a	Cyclosystems flared (Fig. 30C), coenosteum rough	*Stylaster gemmascens*
2b	Cyclosystems not flaring, coenosteum rough or smooth	3
3a	Smooth, porcellanous coenosteum	*Stylaster ibericus*
3b	Coenosteum granulate, rough	4
4a	Cyclosystems sympodial and on anterior face, colonies small (1 cm), gastrostyle elongate cylindrical	*Stylaster maroccanus*
4b	Cyclosystems primarily on sides of branches, some on anterior and posterior sides, colonies 1-15 cm	*Stylaster erubescens*

Stylaster norvegicus (Gunnerus, 1768) Fig. 29

Millepora norvegica Gunnerus, 1768: 64, pl. 2 figs 20-22.
? *Allopora oculina* Ehrenberg, 1834: 147.
Stylaster (*Allopora*) *norvegicus* forma *atlantica* Broch, 1936: 49, fig. 14, pl. 7 figs 20-21.
Not *Stylaster* (*Allopora*) *norvegicus* forma *pacifica* Broch, 1936: 52, fig. 15, pl. 6 figs 18-19.
Stylaster norvegicus. – Zibrowius & Cairns, 1992: 62, figs 16A-G & 17A-I.

DIAGNOSIS: See key to the *Stylaster* species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 10 cm high and 15 cm wide, diameter of branches at tip 2-3 mm, cyclosystems 0.9-1.1 mm in diameter.

DISTRIBUTION: Known from a wide area of the North Atlantic: from Denmark Strait, the northwest, southwest, and southeast of Iceland, Faroes and Hebrides, Rockall, and along the coast of Norway. In Norway it is common in depths of 80-300 m, frequently found together with the bank-forming scleractinian *Lophelia pertusa*. Elsewhere the shallowest records are from 75 m in the Faroes. In the Iceland-Faroes area, this species has been obtained as deep as 1400 m. Type locality: Nordmør, Norway.

REMARKS: See under *Stylaster gemmascens.*

Stylaster gemmascens (Esper, 1794) Fig. 30

Madrepora gemmascens Esper, 1790: pl. 55 figs 1-2; corresponding text 1794: 60.
Stylaster gemmascens. – Broch, 1914a: 8, fig. C, pl. 1 figs 4-7, pl. 2 fig. 16, pl. 3 figs 21, 24-26, 30-31, pl. 4 fig. 32-33, pl. 5 figs 46, 49-50. – Zibrowius & Cairns, 1992: 79, figs 23A-H, 24A-F, synonymy.
not *Stylaster gemmascens alascanus* Fisher, 1938: 500, pls 47-48, pl. 54 fig. 1. – Naumov, 1969: 584, figs 430-431, pl. 27 fig. 1.
Stylaster gemmascens. – Boschma, 1955: 22, figs 1-3, pls 1-2.

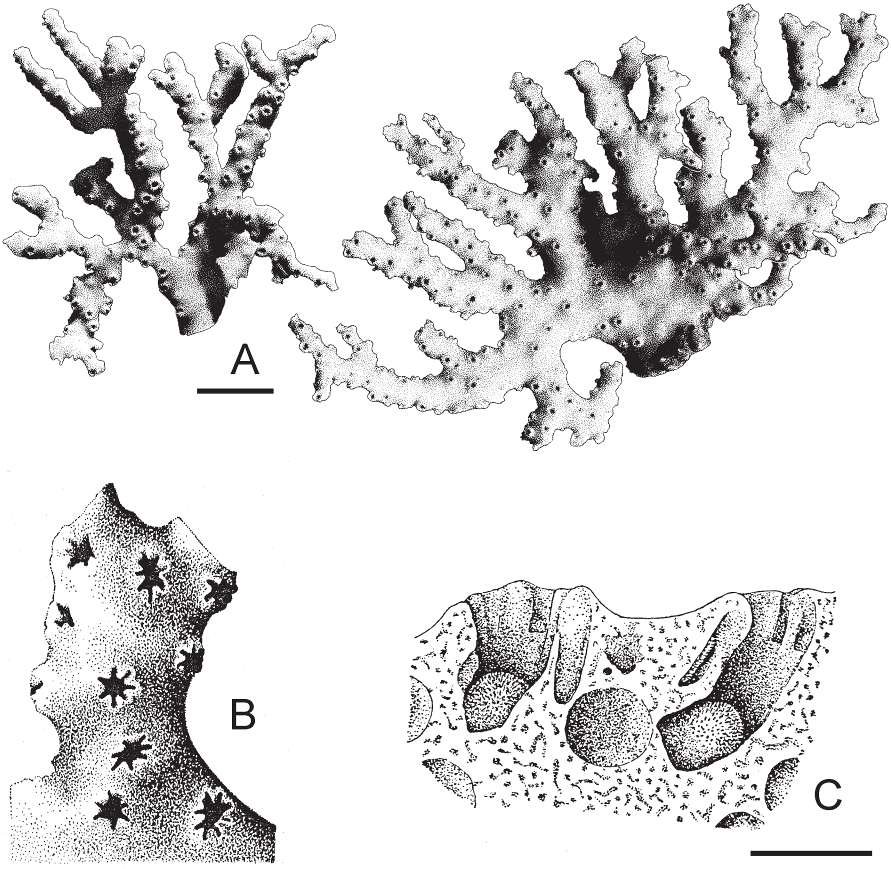

FIG. 29

Stylaster norvegicus (Gunnerus, 1768); A redrawn after photographs in Zibrowius & Cairns (1992), B from Boschma (1956b), C from Broch (1934). (A) Parts of two colonies, scale bar 1 cm. (B) Branch of colony in higher magnifications. (C) Longitudinal section through the coenosteum showing two gastropores and their gastrostyles, in-between them an ampulla; scale bar 1 mm.

DIAGNOSIS: See key to the *Stylaster* species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 11 cm high and wide, terminal branch width about as diameter of cyclosystems (1.3 mm, oval ones 1.6 x 0.7 mm).

DISTRIBUTION: North Atlantic from Denmark Strait, east of Greenland, northwest of Iceland through Faroes-Hebrides area to Norway and Rockall. Along the Norwegian coast the species is common in depths of about 40 to 400 m, frequently found together with the bankforming scleractininan *Lophelia pertusa*. Depth range elsewhere down to depths of 665 m. Type locality: Norway (see Zibrowius & Cairns, 1992 for details).

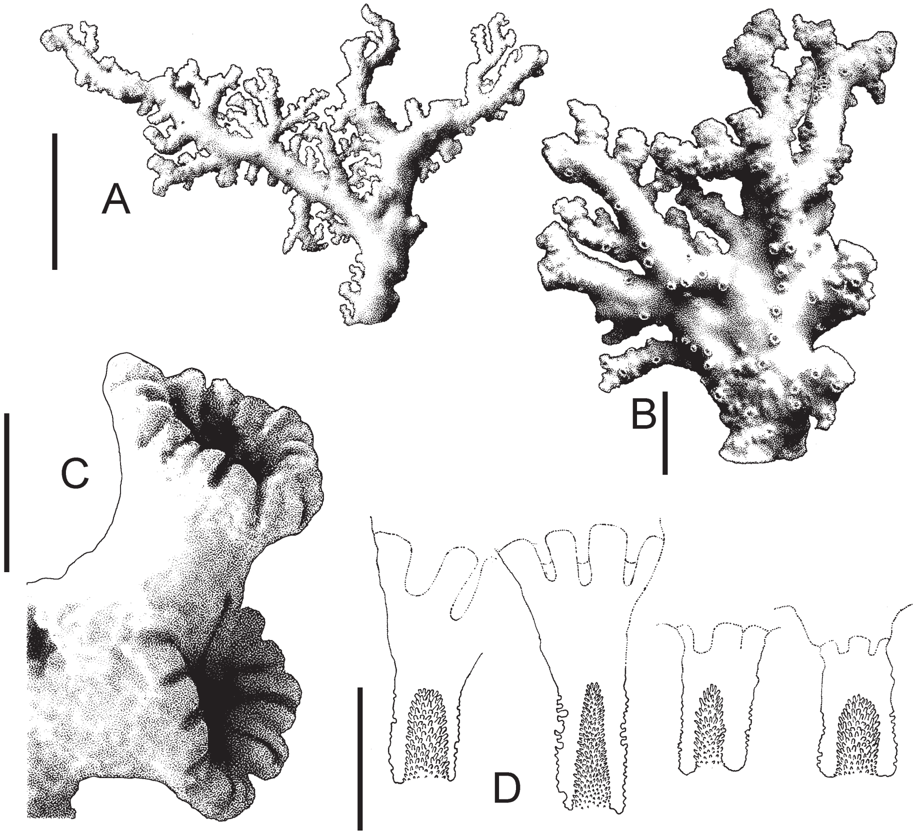

FIG. 30

Stylaster gemmascens (Esper, 1794) A-C modified and redrawn from Zibrowius & Cairns (1992), D from Boschma (1955). (A-B) Colonies, scale bar 1 cm. (C) Terminal region of branch with two cyclosystems, note flaring openings; scale bar 1 mm. (D) Longitudinal sections of gastropores, note variability of gastrostyle and pore length, scale bar 0.5 mm.

REMARKS: *Stylaster gemmascens* (Esper, 1794) and *Stylaster norvegicus* (Gunnerus, 1768) are the most common stylasterids in the north-eastern Atlantic, although both still occur in deeper waters (below 40 m depth, while most other NE Atlantic species occur below 200 m). The two species can occur together and have been confused repeatedly. *Stylaster gemmascens* can be distinguished by its flared cyclosystems (Fig. 30C), the rough surface, the narrow gastropore tubes (Fig 30D), and a male ampulla with a crest. In *S. norvegicus* the skeleton surface is smooth and the cyclosystems are scattered evenly over the colony (Fig. 29A), while in *S. gemmascens* they tend to be concentrated on the lateral branch edges (but some do also occur on posterior and anterior faces) (Fig. 30A-B)

Stylaster ibericus Zibrowius & Cairns, 1992

Stylaster ibericus Zibrowius & Cairns, 1992: 84, figs 25A-O, 26A-G.

Diagnosis: See key to the *Stylaster* species.

Description: See Zibrowius & Cairns (1992).

Distribution: Off north-western Spain, depth range 490-620 m. Type locality: 44°01.6N 08°40.6’W, 500 m.

Stylaster maroccanus Zibrowius & Cairns, 1992

Stylaster maroccanus Zibrowius & Cairns, 1992: 76, figs 21A-D & 22A-G.

Diagnosis: See key to the *Stylaster* species.

Description: See Zibrowius & Cairns (1992).

Distribution: Only known from type locality, off Atlantic coast of Morocco, 34°24.7’N 07°39.3W, 1378 m.

Stylaster erubescens britannicus Zibrowius & Cairns, 1992

Stylaster erubescens britannicus Zibrowius & Cairns, 1992: 92 figs 29A-G, 30A-G.

Diagnosis: *Stylaster erubescens* with coarse, granular surface of coenosteum, granules rounded.

Description: See Zibrowius & Cairns (1992).

Distribution: Southeast of Iceland through the Faroes-Hebrides area and the Rockall Trough to the Celtic Sea, depth range 350-1080 m. Type locality: Southeast of Iceland, 64°16’N 11°15’ W, 350 m.

Stylaster erubescens groenlandicus Zibrowius & Cairns, 1992

Stylaster roseus. – Broch, 1914a; 12, pl. 1 figs 8-9, pl. 2 figs 10-11, 17, pl. 3 fig. 22, pl. 4 fig. 36, 39, pl. 5 fig. 43, 47-48.
[not *Stylaster roseus* (Pallas, 1766)]
Stylaster erubescens groenlandicus Zibrowius & Cairns, 1992: 89, figs 27A-H, 28A-H.

Diagnosis: *Stylaster erubescens* of Greenland.

Description: See Zibrowius & Cairns (1992).

Distribution: East of Greenland to northwest of and southeast of Iceland, all north of 60°, depth range 263-1440 m. Type locality: Denmark Strait, northwest of Iceland, 66°18’N 25°59’W, 621 m.

Stylaster erubescens meteorensis Zibrowius & Cairns, 1992

Stylaster erubescens meteorensis Zibrowius & Cairns, 1992: 96, figs 31A-H, 32A-H.

Diagnosis: *Stylaster erubescens* with bushy colony, coenosteum texture reticulate-smooth, strips with numerous symmetrical lateral protuberances.

Description: See Zibrowius & Cairns (1992).

Distribution: Great Meteor Seamount, 29°59’N 28°33’W, 290 m (type locality).

Genus ***Stenohelia*** Saville Kent, 1870

Type species: *Allopora maderensis* Johnson, 1862.

DIAGNOSIS: Gastro- and dactylopores arranged in cyclosystems, which occur exclusively on the anterior branch face. Cyclosystems without lips or lids. Coenosteum white or light brown, either linear-imbricate or reticular-granular in texture. Gastropores long and usually curved; gastrostyles present, usually encircled by a robust ring palisade. Dactylostyles rudimentary. Ampullae superficial, often clustered around base of cyclosystem. Ampullar efferent pores of both sexes usually well distinguished.

REMARKS: There occurs only one named *Stenohelia* species in the ERMS zone, but a second, unnamed species is present (Zibrowius & Cairns, 1992).

Stenohelia maderensis (Johnson, 1862)

Allopra maderensis Johnson, 1862: 196, figs 1-3.
Stenohelia maderensis. – Cairns, 1983: 487, fig. 20A-B, D-G. – Zibrowius & Cairns, 1992: 99, figs 33A-L & 34A-J. – Alvarez, 1995: 263, fig 1.
Not *Stylaster maderensis* – Boschma, 1964b: 64, pl. 1 figs 13-14 [= *S. profunda*].

DIAGNOSIS: See key to the genera and genus diagnosis.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: The Faroes and Hebrides (665 m), north-western Spain and southern Bay of Biscay (490-910 m), Galicia Seamount, Madeira, Cape Verde Islands; depth range 110-1125 m. Type locality: Madeira.

Genus ***Crypthelia*** Milne Edwards & Haime, 1849

TYPE SPECIES: *Crypthelia pudica* Milne Edwards & Haime, 1849.

DIAGNOSIS: Gastro- and dactylopores arranged in cyclosystems, which usually occur exclusively on anterior branch face. Cyclosystems partially or entirely covered by one or more fixed lids. Coenosteum white or light brown, linear imbricate in texture, and often spinose as well. Nematopores usually present, especially on cyclosystem lids, pseudoseptae, and ampullae. Gastropores double-chambered; no gastro- or dactylostyles. Ampullae usually superficial and large, occurring in various position and with a variety of efferent pore location.

REMARKS: The lid over the cyclosystem makes this genus quite easily recognizable. See Zibrowius & Cairns (1992) for a table to distinguish the species of the ERMS zone.

Crypthelia affinis Moseley, 1879

Crypthelia affinis Moseley, 1879: legend on pl. 42. – Zibrowius & Cairns, 1992: 106, figs 36A-I, 37A-I.
Crypthelia moseleyi Hickson & England, 1905: 21.

DISTRIBUTION: Azores, depth range 712-1557 m, perhaps as deep as 2790 m. Type locality: uncertain, Southwest of the Canary Islands, 25°45'N 20°12'W, 2790 m.

Crypthelia medioatlantica Zibrowius & Cairns, 1992

Crypthelia medioatlantica Zibrowius & Cairns, 1992: 112, figs 36J-M, 38A-H.

Distribution: Azores, Azores and Mid-Atlantic Ridge, depth range 861-2644 m. Type locality: Mid-Atlantic Ridge, 36°50.9'N 32°57.9'W, 1400-2200 m.

Crypthelia tenuiseptata Cairns, 1986

in part *Crypthelia tenuiseptata* Cairns, 1986a: 115, figs 52A-G, 53K.
Crypthelia vascomarquesi.– Zibrowius & Cairns, 1992: 117, figs 41A-J, 42A-I.

Distribution: Virgin Islands, Lesser Antilles, and Azores; depth range 761-1557 m. Type locality: Grenada, 12°03.25'N 61°48.50E, 761 m.

Crypthelia vascomarquesi Zibrowius & Cairns, 1992

Crypthelia vascomarquesi Zibrowius & Cairns, 1992: 114, Figs 39A-J, 40A-J.

Distribution: Azores, Hyères Seamount, Madeira, depth range 390-1520 m. Type locality: 38°07'N 27°11.75'W, 983 m.

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