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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 4

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 4. - This study reviews all European hydroids belonging to the filiferan family Eudendriidae. Two new species occurring in the northeastern Atlantic are described: *Eudendrium capillaroides* new spec. and *Eudendrium unispirum* new spec. *Eudendrium vaginatum* Allman, 1863, is redescribed. It is characterized by a special type of nematocysts and traits of the perisarc. It is distinct from *Eudendrium annulatum* Norman, 1864, which is a separate, valid species. *Eudendrium fragile* Motz-Kossowska, 1905 and *Eudendrium islandicum* Schuchert, 2000 are both recognized as synonyms of *E. album* Nutting, 1898. *Eudendrium stratum* Bonnevie, 1898 and *E. planum* Bonnevie, 1898 are both recognized as synonyms of *E. rameum* (Pallas, 1766). *Eudendrium insigne* Hincks, 1861 is indistinguishable from *E. ramosum* and newly collected material from the type locality confirmed this. *Eudendrium insigne* must thus be regarded as a synonym of *E. ramosum* (Linnaeus, 1758). A re-examination of the type material of *Eudendrium elsaeoswaldae* Stechow, 1921 revealed that it is conspecific with *E. ramosum* (Linnaeus, 1758), becoming thus a new synonym of the latter.

Perigonimus multicornis Allman, 1876 is indistinguishable from *Myrionema hargitti* (Congdon, 1906) and must be regarded as a senior synonym of the latter. Because it seems likely that the original type locality designation "Kattegat" was incorrect, it should not replace *M. hargitti* or *M. amboinense*.

Keywords: Cnidaria - marine - Hydrozoa – Eudendriidae - revision - taxonomy - north-eastern Atlantic - Mediterranean.

INTRODUCTION

This study is the fifth 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), Schuchert (2007; Bougainvilliidae, Cytaeididae, Rathkeidae, and Pandeidae), Schuchert (2008; Hydractiniidae, Rhysiidae, Stylasteridae). The current paper treats one family only, namely the Eudendriidae. Many of the European Eudendriidae have recently been studied by Marques *et al.*

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(2000a, 2000b), but an update and more complete species descriptions, including also all species of the northeastern Atlantic, was needed. Although the members of the genus *Eudendrium* are rather unique and it is easy to identify a hydroid as belonging to this genus (Fig. 1), the identification at the species level is sometimes rather difficult. As outlined by Marques *et al*. (2000b), the state of the *Eudendrium* species was confused until the middle of the last century, with many species being unrecognizable. The application of nematocyst data improved the situation considerably and nowadays species identification relies predominantly on the cnidome. This change in taxonomic practice made most previous species records untrustworthy. Other morphological characters are still important, though, especially in those species that have the same type of capsules (e. g. *E. ramosum*, *E. rameum*, *E. merulum* etc.). It seems, however, that the species diversity has been underestimated.

Concomitantly with this study, also a comparison of the 16S gene DNA sequence was begun, using besides the species and populations mentioned here many more from various places all over the world. Preliminary results of this study, which will be published elsewhere, indicate that several morphospecies of *Eudendrium* are actually composed of more than one lineage and thus likely belong to different species. Moura *et al*. (2008) arrived at a similar conclusion.

MATERIAL AND METHODS

See also Schuchert (2008). Where possible, it was attempted to supplement the species descriptions by sequence information of part of the 16S mitochondrial rRNA gene. The methods to obtain DNA sequences are described in Schuchert (2005, 2007). All sequences have been submitted to the EMBL database (accession numbers **AM991292-AM991307**). The origin and identity of the material used to obtain the 16S sequence data as well as the accession numbers are given for each species in the section "Material examined". 16S sequences of some non-European Eudendriidae were also determined, namely *Myrionema amboinense* (MHNG INVE60162, aquarium culture of unknown origin, **AM991292**), *Eudendrium maorianus* (MHNG INVE29972, New Zealand, **AM991303**), *E. ritchiei* (MHNG INVE29971, New Zealand, **AM991304**). All available sequences, including also those published by Moura *et al*. (2008), were used to visualize the relatedness by a Maximum Likelihood analysis of HKY distances using the program PHYML described by Guindon & Gascuel (2003). A bootstrap analysis using 100 pseudoreplicates was made.

ABBREVIATIONS

BELUM	Ulster Museum, Belfast, Northern Ireland
BMNH	The Natural History Museum, London, England
ERMS	European Register of Marine Species (Costello *et al*., 2001)
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
ICZN	International Code of Zoological Nomenclature
IRSN	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
SMNH	Swedish Museum of Natural History, Stockholm, Sweden
ZMO	Zological Museum of Oslo, Norway
ZMUC	Zoological Museum Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, Munich, Germany
r	ratio of nematocyst capsule length and width
s	ratio of shaft and capsule length in discharged capsules

GENERAL MORPHOLOGY AND IMPORTANT FEATURES

Eudendrium colonies are anchored to the substratum by tubular stolons. The stem of the colony may be branched or unbranched (=stolonal), either monosiphonic or polysiphonic (=fascicled, composed of several tubes). The stems and pedicels are always covered with firm perisarc which becomes abruptly very thin and filmy below the hydranths. The perisarc of the thicker tubules is usually smooth or wrinkled with characteristic groups of annulations at the origin of branches and sometimes also elsewhere.

The hydranths are relatively large for colonial marine hydroids and distinguished from all other families of the athecate hydroids by a wide, trumpet-shaped or spherical hypostome. The tentacles are filiform, their nematocysts often in transverse linear arrays, the density decreasing towards proximal. The nematocysts can be either oriented parallel to the tentacle resulting in rather smooth tentacles, or they can be inserted obliquely giving a spiny appearance (Puce *et al*., 2005). On the hydranth body, there can be a band or buttons of nematocysts (Figs 1A; 3B). Rarely, there is also a tentacle-like protrusion near the base of the body, a nematophore (Fig. 1A). Near the base of the hydranth column, sometimes also in the middle, there is always a ring of specialized cells that secrete the perisarc in a fold of the epidermis. This basal groove is always present, but in some species or under some circumstances it can become rather inconspicuous or almost invisible.

Male and female gonophores are normally produced in separate colonies, but a few species are hermaphrodites (e. g. *E. simplex*). Reproduction is by fixed sporosacs which in many cases develop in a whorl round the base of the hydranth. The hydranth bearing the gonophores can be fully formed or reduced to various extents and is then called a blastostyle. The development of the gonophores starts concomitantly with the development of the budding of the new hydranth (blastostyle), even before the tentacles develop (Fig. 16C-E). In some species the hydranth grows to the same size as of a non-reproductive polyp, in others the hydranth development stops and often it gets atrophied again (e. g. Fig. 34E-G). There is considerable variation of this process between the species and to some extent it could also depend on the environment. In some species the gonophores/sporosacs form without a trace of a hydranth, the gonophores issuing in a tuft from the end of a pedicel. It is thus important to bear in mind that the blastostyles can change form and size during development, which makes it sometimes difficult in preserved material to decide whether they are actually reduced or only in an early stage of development, this in particular also for female gonophores after their fertilization.

The female gonophores consist normally of a spadix (Fig. 1B) arching over a single, large egg (exception *E. vervoorti*). The spadix may be simple or branched, which is an important taxonomic character. As the egg matures and then is fertilized in-situ, the spadix is resorbed, the fertilized egg develops a perisarc capsule and is attached to the pedicel below (Fig. 9E). The embryonic development to the planula larva takes thus typically place within the capsule and while still attached to the mother colony (comp. Mergner, 1957 and Fig. 9E). The dispersal capacity of the planula larva is rather modest (Sommer, 1992).

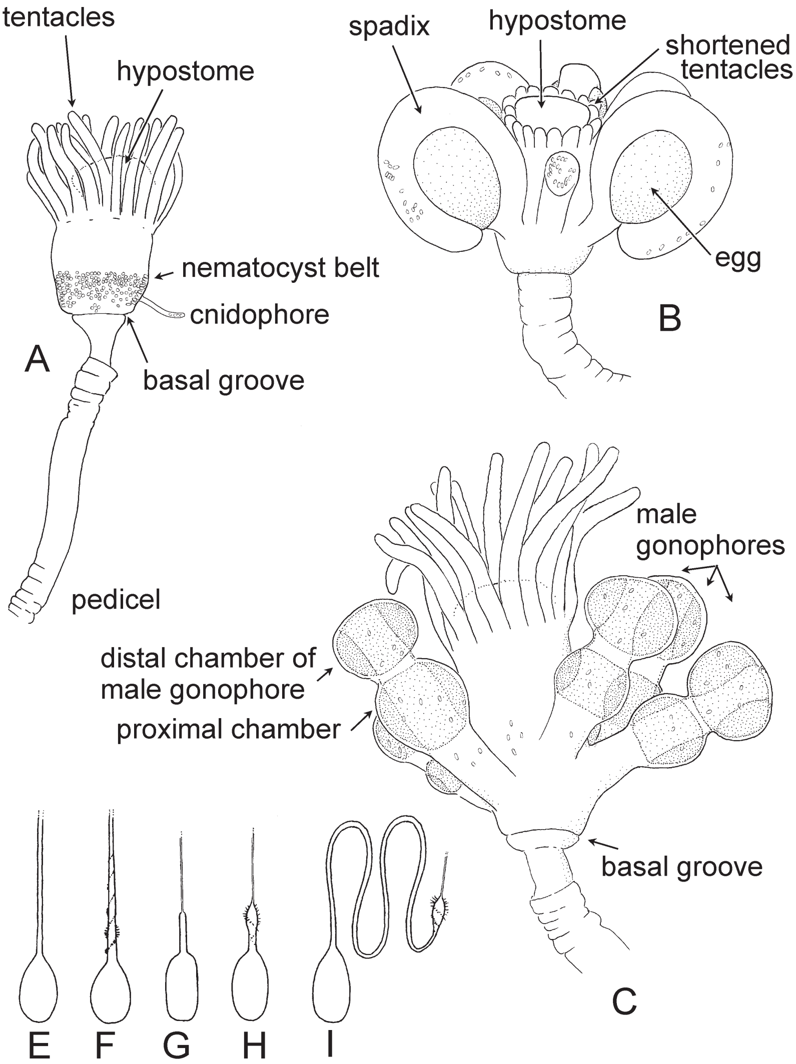

FIG. 1. Features and important terms of the Eudendriidae hydranths and gonozooids. (A) Hydranth and its pedicel. (B) Partially atrophies hydranth (blastostyle) bearing female gonophores. The gonophores are very simple, a large egg and a spadix that arches over it. In later stages after fertilization, the spadix is lost and the encapsulated embryos attach to the pedicels of the former blastostyle (Fig. 9D). (C) Hydranth with a whorl of male gonophores, each composed of two bulbous chambers. (E-H) Important nematocyst types found in the Eudendriidae, shown are discharged capsules. (E-F) Haplonemes, the everted tube has no thickened proximal part. (E) Isorhiza, the everted tubular part has a constant diameter. (E) Anisorhiza, the everted tubular part tapers constantly. (G-I) Heteroneme capsules, the everted tube is differentiated in to a thicker basal part, the shaft, which tapers abruptly into a thinner thread. (G) Microbasic mastigophores, the shaft is isodiametric and shorter than 2.5 capsule lengths. (H) Microbasic eurytele, the end of the shaft is swollen, the total length of the shaft is shorter than 2.5 capsule lengths. (I) Macrobasic eurytele, the shaft is more than 2.5 times as long as the capsule (=macrobasic), its end is swollen (=eurytele).

Male gonophores (Fig. 1C) typically consist of several bulbous chambers containing the spermatogenetic cells and arranged in linear series. In the earliest stages – in some species permanently – there is only one chamber, but as development proceeds additional chambers are added from below. Thus the number of chambers cannot be used as a diagnostic character although the maximal number may be characteristic for a species.

Crucial taxonomic characters are the types and sizes of the nematocysts (Fig. 1E-I). Also the absence of desmonemes from all species is notable. The Eudendriidae always possess small euryteles, present in large numbers on the tentacles and also in fewer numbers in the rest of the hydranth and coenosarc epidermis. This ubiquitous small type, also called the tentacular type, is taxonomically not important because it does not offer much interspecific variation. However, in most species there are one or more additional capsule types present which show considerable interspecific variation. These complementary nematocysts are less frequent but nevertheless abundant enough to be easily found. They never occur on the tentacles, but are confined to the hydranth body, hypostome, the coenosarc, and sometimes the gonophores. The complementary nematocysts are often – but not always – considerably larger than the tentacular type. The highest concentration is found on the hydranth body, sometimes in a broad horizontal band or in wart-like protrusions. The types of nematocysts relevant for the Eudendriidae are shown and explained in Fig. 1E-F. In order to observe discharged capsules, it is necessary to examine living material with a good compound microscope. One or two hydranths are placed in small drop of seawater on a microslide and then gently squeezed by covering them with a cover-glass. Occasionally, there are also some discharged capsules present in preserved material, which can be cleared by immersing in 50% lactic acid. Examination and measurement of nematocysts requires an oil-immersion objective that gives a final magnification of about 1000 times.

TAXONOMIC PART

FAMILY EUDENDRIIDAE L. AGASSIZ, 1862

SYNONYMS: *Eudendroidae* L. Agassiz, 1862: 342 [emended to Eudendriidae by Hincks, 1868]. – *Myrionemidae* Pictet, 1893.

DIAGNOSIS: Hydroid colony sometimes stolonal, but mostly with erect branched stem, arising from a creeping hydrorhiza; stem, branches and hydranth pedicels covered by perisarc, sometimes enveloping also lower half of hydranth in a cup-like process; hydranth large, urn-shaped with undercut hypostome, one or more whorls of solid filiform tentacles immediately below it, hydranth body sometimes with basal tentacle-like protrusion (nematophore); near base of hydranth an epidermal groove from which periderm is secreted, sometimes with a ring of nematocysts immediately above groove. Reproduction by fixed sporosacs borne on the hydranth body below the tentacles; reproductive hydranth can be partially reduced to a blastostyle or entirely reduced. Male gonophores usually with several bulbous chambers, successive chambers in linear series. Female gonophores sporosacs, initially with curved spadix supporting one large egg.

REMARKS: For a taxonomic history see Calder (1988) and Marques *et al.* (2000a). The family comprises only two genera, namely *Eudendrium* Ehrenberg, 1834

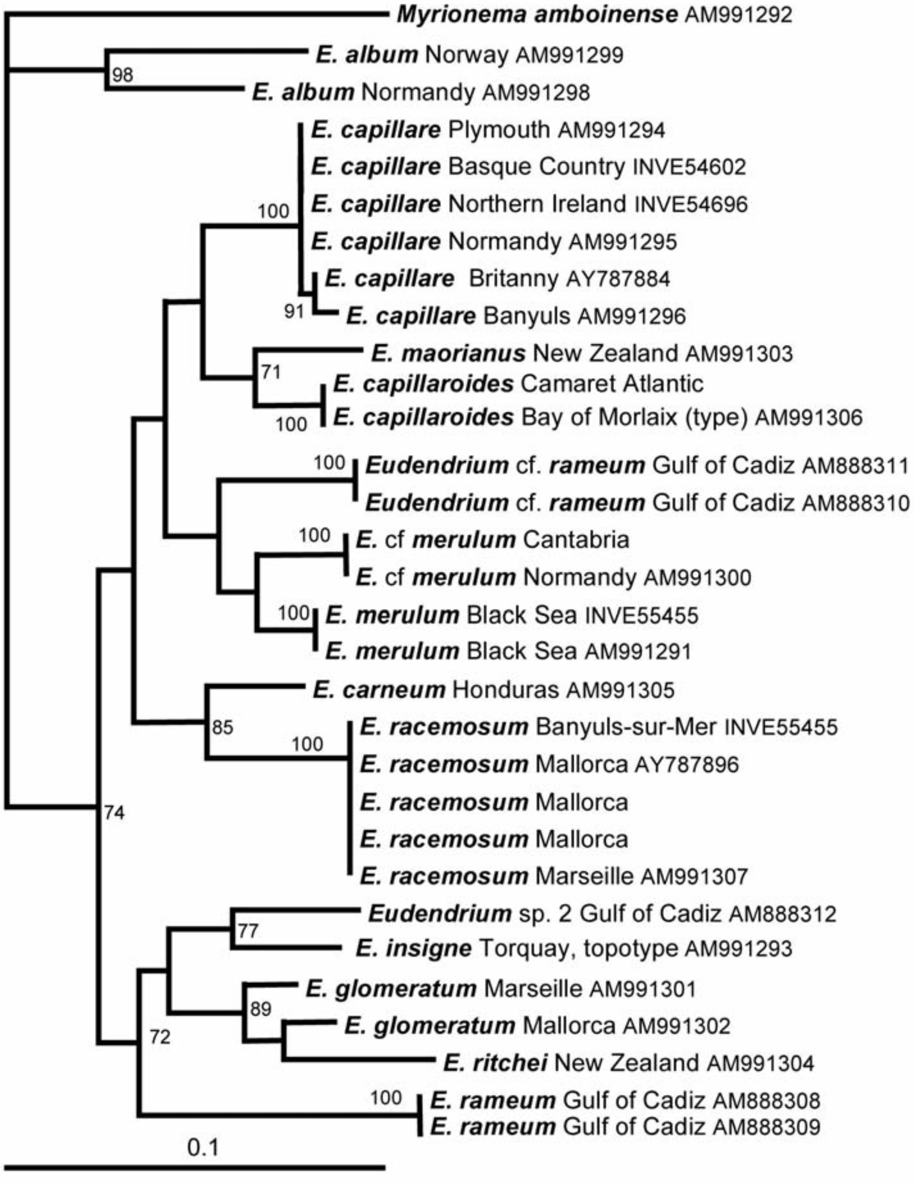

FIG. 2

Maximum Likelihood analysis of the partial 16S sequence differences of Eudendriidae samples discussed in this publication (HKY substitution model, indels ignored). Small numbers next to nodes indicate percent bootstrap support (only shown if >70%). The length of the sum of the horizontal lines is a measure of the sequence difference. The taxon labels are composed of the species name, the sampling region, followed by the EMBL/GenBank accession number or the voucher number if the sample has the same sequence as other known sequences (if available, see list of exmined material for each species).

and *Myrionema* Pictet 1893. The latter genus is characterized by a large (>35) number of tentacles arranged in more than one whorl. In the ERMS region (European Register of Marine Species; Costello *et al.*, 2001), only the genus *Eudendrium* is present. Some earlier Mediterranean records of *Myrionema* species are likely due to confusions with *E. moulouyensis* (comp. Marques *et al.*, 2000b). Another problematic species is *Myrionema multicornis* discussed at the end of this treatise.

Genus ***Eudendrium*** Ehrenberg, 1834

TYPE SPECIES: *Tubularia ramosa* Linnaeus, 1758 [designation by Allman, 1872].

SYNONYMS (after Calder, 1988): *Calamella* Oken, 1815: 55 [invalid name, ICZN Opinion 417]. – *Corymbogonium* Allman, 1861: 171. – *Edendrium* Allman, 1872 [incorrect spelling]. – *Erudendrium* Thompson, 1899 [incorrect spelling].

DIAGNOSIS: Eudendriidae with tentacles in one whorl, of varied number but usually fewer than 35.

REMARKS: For the taxonomic history see Calder (1988). Although Ehrenberg (1834) translates the genus name as "Pracht-Polyp" [splendour polyp], the name is likely derived from the Greek words "eu" (pleasing, good) and "dendron" (tree). The grammatical gender is neuter.

The species are here grouped and discussed according to their complimentary nematocyst types (instance 1 in the following key) and apparent similarity in order to allow an easier comparison. However, this does not imply a phylogenetic order.

KEY TO *EUDENDRIUM* SPECIES IN THE ERMS ZONE (PROBLEMATIC SPECIES EXCLUDED):

1a complementary nematocysts are large macrobasic euryteles (shaft length $s>2.5$) 2
1b complementary nematocysts are small or large haplonemes (iso- or anizorhizas) 5
1c complementary nematocysts are microbasic euryteles (shaft length $s<2.5$), either distinctly larger than tentacular euryteles or only slightly larger (1.3 times) 7
1d without complementary nematocysts or these haplonemes of same size as tentacular euryteles 16

2a macrobasic euryteles in buttons on hydranth body 3
2b macrobasic euryteles scattered on hydranth body, not in buttons 4

3a colonies large, usually polysiphonic, shaft of intact macrobasic eurytele in 2.5 loose coils . . . . *E. glomeratum*
3b colonies monosiphonic, female blastostyles after fertilization reduced to nematocyst knobs, shaft of intact macrobasic eurytele in more than 2.5 coils along capsule wall . . . . *E. cnidoferum*

4a macrobasic euryteles with 3-5 coils oblique to long axis, gonochoristic . . . . *E. album*
4b macrobasic euryteles with coils along long axis, female sporosac often with sperm chamber, usually on the Mediterranean sea grass *Posidonia oceanica* . . . . *E. simplex*

5a	haplonemes small (< 10 μm), colonies monosiphonic or stem base composed of a few tubes only	6
5b	strongly polysiphonic, no cnidophores, haplonemes large (> 20 μm)	*E. carneum*
6a	spadix of female sporosac bifid, some hydranths with cnidophores, large colonies	*E. racemosum*
6b	spadix of female sporosac simple, complimentary nematocysts are small haplonemes of same size as tentacular euryteles, presence variable, often absent, colonies small and delicate	*E. capillare*
7a	shaft in intact complimentary microbasic euryteles straight	8
7b	shaft in intact complimentary microbasic euryteles with a coil	15
8a	colonies large, trunk or base polysiphonic	9
8b	colonies monosiphonic or stem-base made up of a few tubes only	11
9a	complementary euryteles scattered on body, colony tree-like	*E. rameum*
9b	complementary euryteles forming a contiguous belt on body	10
10a	colony more tree-like, stems usually with bark-like covering, hydranths large (>0.4 mm diameter), blastostyles aggregated on upper side of branches, pedicels relatively short	*E. annulatum*
10b	colonies more bush-like, stem without bark-like covering, hydranths small (<0.3 mm diameter), blastostyles dispersed	*E. arbuscula*
11a	with zooxanthellae in gastrodermis	*E. moulouyensis*
11b	without zooxanthellae	12
12a	complimentary eurytele large, more than two times as large as tentacular euryteles	13
12b	complimentary eurytele small, only 1.3 times as large as tentacular capsules	*E. capillaroides* n. sp.
13a	gonophores develop on normal or slightly reduced hydranths	14
13b	gonophores develop on blastostyles without vestiges of a hydranth, shaft of discharged large euryteles with thick spines	*E.* cf. *merulum*
14a	colonies much branched, monosiphonic or exceptionally with few tubes near base, large euryteles scattered on body, spadix without swelling	*E. ramosum*
14b	colonies sparingly branched, large euryteles concentrated in belt on body, spadix of female sporosac with distal triangular swelling (axe-like shape)	*E. calceolatum*
15a	colonies usually polysiphonic, perisarc annulated throughout, thick, brown, lower half of hydranth in perisarc collar, coil size of shaft in large eurytele rather small	*E. vaginatum*
15b	colonies monosiphonic, perisarc thin, with smooth and annulated stretches, hydranth without perisarc collar, coil size of shaft in large eurytele about 1/4 or more of capsule length	*E. unispirum*
16a	female gonophores with spadix	17

16b female gonophores without spadix, eggs attached via long pedicels to normal hydranths . . . . *E. vervoorti*

17a colonies polysiphonic, some hydranths modified into long nematophores, without complimentary nematocysts . . . . *E. armatum*

17b colonies monophonic, no nematophores, without complimentary nematocysts or sometimes with small haplonemes of the same size as tentacular capsules . . . . *E. capillare*

Eudendrium glomeratum Picard, 1952 Figs 3-4

Eudendrium ramosum. – Browne, 1897: 243. – Motz-Kossowska, 1905: 54, pl. 3 fig. 16. [not *Eudendrium ramosum* (Linnaeus, 1758)]

Eudendrium arbuscula. – Schneider, 1898: 477. [not *Eudendrium arbuscula* Wright, 1859]

Eudendrium pusillum. – Jäderholm, 1916: 3. – Watson, 1985: 213. [not *Eudendrium pusillum* Lendenfeld, 1885: 352, = *E. lendenfeldi* Briggs, 1922]

? *Eudendrium indopacificum* Stechow, 1924: 59. [new name for *E. pusillum* in Thornely, 1904]

Eudendrium glomeratum Picard, 1951b: 260. [*nomem nudum*]

Eudendrium glomeratum Picard, 1952: 338, new name. – Castric & Michel, 1982: 82, fig. – Watson, 1985: 213, figs 89-94. – Boero *et al*., 1986: 81-85, fig. 1. – Boero & Cornelius, 1987: 244. – Marinopoulos, 1992: 59, fig. 1.9. – Watson, 1999: 7, fig. 5A-D. – Marques *et al*., 2000a: 96, figs 53-56. – Marques *et al*., 2000b: 205. – Peña Cantero & García Carrascosa, 2002: 29, fig. 4c-f. – Puce *et al*., 2005: 202, figs 1d, 2i.

MATERIAL EXAMINED: MHNG INVE29456; Mediterranean, France, Banyuls-sur-Mer, depth 2m, 14 Sept. 1995; fertile female. – MHNG INVE29457; Mediterranean, France, Banyuls-sur-Mer, 8 March 1993; 10 cm high, polysiphonic, infertile. – MHNG INVE32159; Mediterranean, Spain, Mallorca, Cala Murada; depth 2m; 27 July 2001; small polysiphonic colony on red algae, fertile female, hydranths intensively orange; 16S sequence accession number **AM991302**. – MHNG INVE39462; Mediterranean, France; 26 Nov. 1953, depth 40m. – MHNG INVE39473; Mediterranean, France, Marseille, Riou-Impériaux de Terre; depth 20m; 20 March 1966, two large infertile colonies. – MHNG INVE39717; Mediterranean, France, Marseille; depth 40m; 28 Sept. 2004; 15 cm colony, hydranths reddish; 16S sequence accession number **AM991301**. – Italy, Sardinia, depth 25m; October 2005; fertile female, 5 cm colony; in private collection of Dr S. Puce.

DIAGNOSIS: Colonies usually tall, polysiphonic when fully grown, with large macrobasic euryteles arranged in buttons or belt around hydranth body. Male and female blastostyles atrophied; spadix unbranched when immature, shed when mature. Hydranths red.

DESCRIPTION: Colonies large, bushy or tree-like, irregularly branching, when reproductive usually stems and some branches polysiphonic, monosiphonic stems can occur. Perisarc thick, smooth, occasionally some annulated stretches, usually at bases of branches. Hydranths with 15-27 tentacles (mostly 20-22), on hydranth body a ring composed of several nematocyst buttons (4-10), these buttons can coalesce into an irregular band, buttons can also be scattered on hydranth body. Tentacles with nematocysts along entire length but density decreasing towards proximal, in bands with arrays of 3-4 capsules, capsules oriented parallel to surface and tentacle surface thus smooth. Colours: older perisarc brown; hydranth characteristically red.

Male gonophores two-chambered and borne on blastostyles lacking tentacles at all stages; with or without terminal buttons; clusters of macrobasic euryteles can be present at base of blastostyle and at end of gonophores, not always in the terminal buttons.

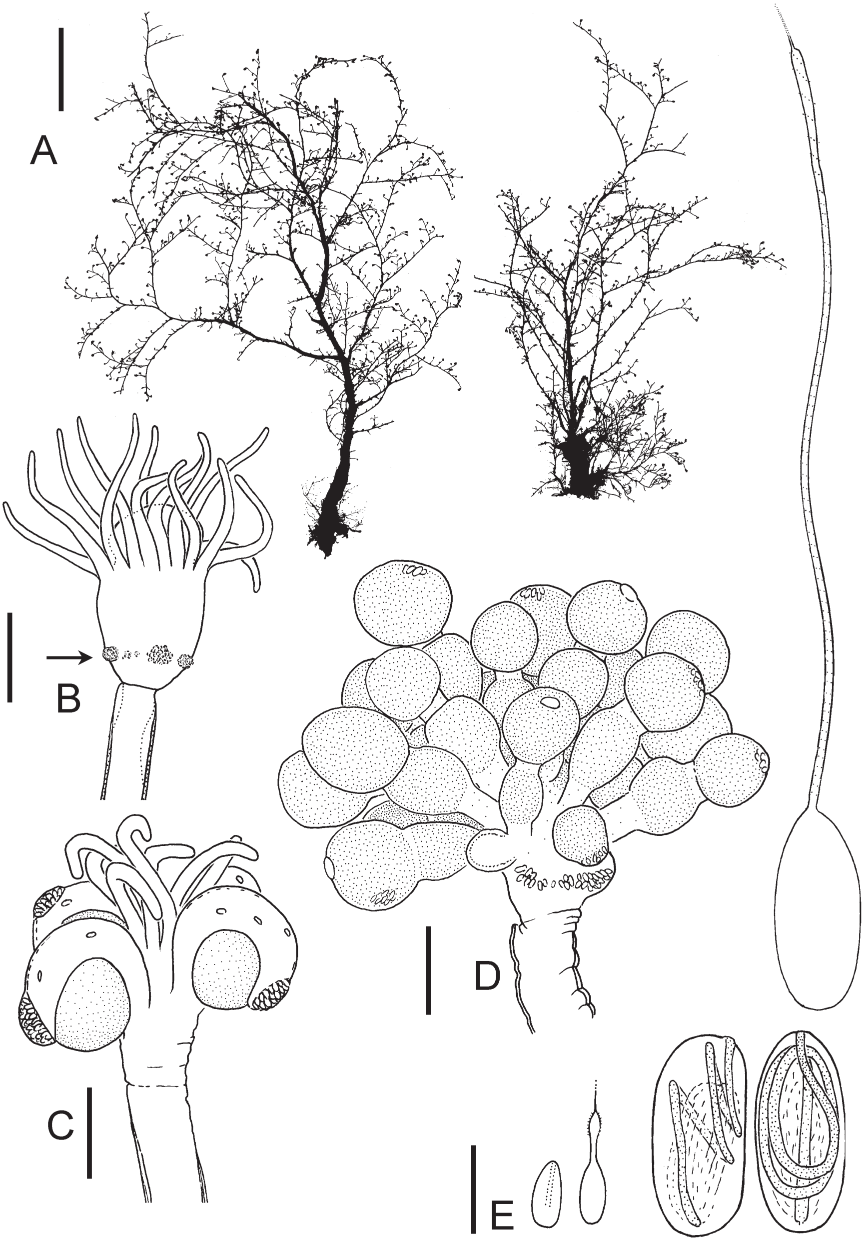

FIG. 3. *Eudendrium glomeratum* Picard, 1952, after preserved Mediterranean material, except E (native capsules). (A) Silhouettes of typical colonies (MHNG INVE39473), scale bar 2 cm. (B) Hydranth with characteristic nematocyst buttons (arrow), scale bar 0.5 mm. (C) Young female blastostyle (MHNG INVE32159), scale bar 0.2 mm. (D) Male blastostyle, note nematocysts at base of blastostyle, material from Sardinia, scale bar 0.2 mm. (E) Nematocysts (MHNG INVE39717): intact and discharged microbasic eurytele, two intact macrobasic euryteles in side and frontal view, above discharged macrobasic eurytele, scale bar 10 μm.

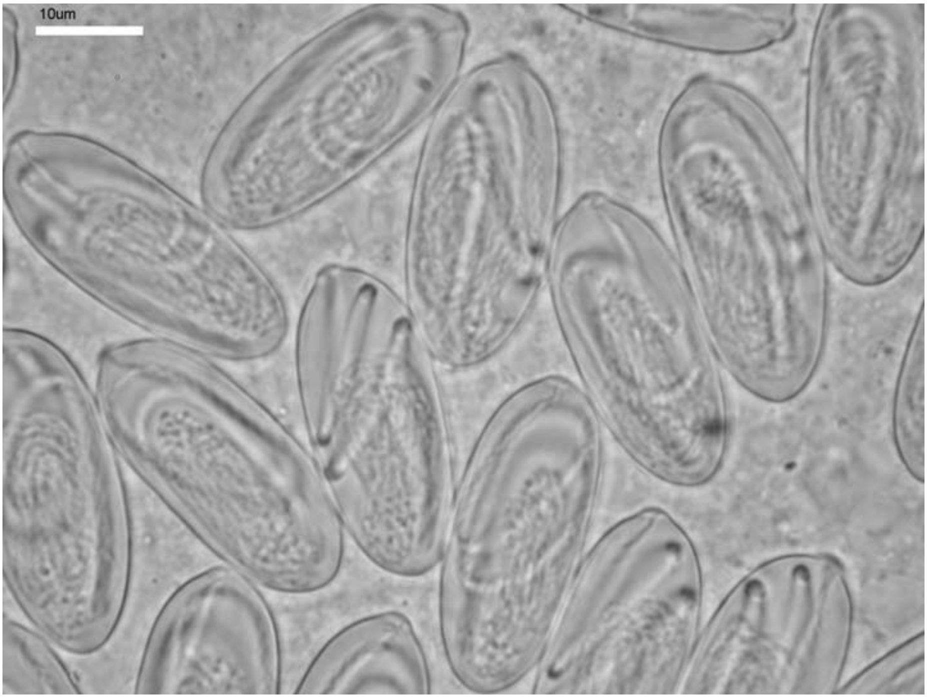

FIG. 4
Eudendrium glomeratum Picard, 1952, native macrobasic euryteles; MHNG INVE39717.

Female gonophores develop on reduced hydranth with few tentacles (up to 8), hydranth body small, hypostome absent, 4-6 gonophores per blastostyle, spadix simple, with one or more nematocyst buttons near tip, spadix later atrophied, also tentacles are lost during later development, eggs ultimately attached to blastostyle pedicels. Incipient oogonia visible in coenosarc of branches.

Nematocysts: microbasic euryteles, on tentacles; macrobasic euryteles in nematocyst buttons, shaft in intact capsule in about 2-3 loops following long axis of capsule, discharged about four times the length of the capsule, barbed.

DIMENSIONS: Height of reproductive colonies from a few cm to about 15 cm; hydranth diameter about 0.5 mm, variable even within the same colony; diameter of basal stem tubes 0.4-0.5 mm. Macrobasic euryteles in Mediterranean animals (22-33)x(9.5-13.5)μm, r= 2.2-2.4 (Marinopoulos, 1992; Marques *et al.*, 2000b; Peña Cantero & García Carrascosa, 2002; own data). Australian values show more variation (Watson, 1985; 1999). Microbasic euryteles (6-10)x(3-5)μm, r= 2.1-2.3 (Peña Cantero & García Carrascosa, 2002; Watson, 1985; own data).

BIOLOGY: Occurs on various solid substrata in depths of 0-200 m (Peña Cantero & García Carrascosa, 2002), more commonly in depths of 10-40 m (Fey, 1970; Boero *et al.*, 1986). In the Mediterranean, fertile colonies can be found all year round (Peña Cantero & García Carrascosa, 2002; own data), but the peak of reproduction seems to be during autumn and winter (Boero, 1984; Boero *et al.*, 1986). In the Atlantic, reproductive colonies have been found from June to October (Fey, 1970; Peña Cantero & García Carrascosa, 2002). More ecological data are given in Boero (1981), Boero & Fresi (1986), Boero *et al.* (1986), Arillo *et al.* (1988), and Bavestrello *et al.* (1994). Some colonies can be aggregates of colonies (Bavestrello & Cerrano, 1992).

DISTRIBUTION: Rather common and widespread in the western and eastern Mediterranean, including the African and Israeli coasts (see e. g. Marques *et al.*, 2000b and 2000b; Peña Cantero & García Carrascosa, 2002). In the western Atlantic known from the British Isles (Boero & Cornelius, 1987) (not in North Sea), Brittany (Teissier, 1965; Fey, 1970; Castric *et al.*, 1987), Northern Spain (Medel & López-González, 1996). Further records are known from Australia (Watson, 1985; 1999) and Brazil (Marques, 1993; cited in Peña Cantero & García Carrascosa, 2002). Type locality: Mediterranean, France, Banyuls-sur-Mer (Boero & Cornelius, 1987).

REMARKS: With its large colonies and the macrobasic euryteles in warts on the hydranth, *Eudendrium glomeratum* is relatively easily identifiable. Despite this and its relative abundance in the Mediterranean, it was described and recognized rather late. Many older records of *E. rameum* and even *E. ramosum* were therefore actually based on *E. glomeratum* (Marques *et al.*, 2000a).

Eudendrium cnidoferum Stechow, 1919 Fig. 5

Eudendrium armatum Jäderholm, 1907: 372. – Jäderholm, 1909: 52, pl. 4 figs 7-9.
[not *Eudendrium armatum* Tichomiroff, 1887]
Eudendrium cnidoferum Stechow, 1919: 154, new name.

TYPE MATERIAL EXAMINED: SNHM type 4274, Syntype colonies of *Eudendrium armatum* Jäderholm, 1907; loc. Bohuslän.

DIAGNOSIS: Monosiphonic colonies, hydranths with nematocyst buttons containing large macrobasic euryteles, female blastostyles after fertilization reduced to nematocyst knobs.

DESCRIPTION: Colonies on algae, monosiphonic, much branched, branching irregular, branches long. Perisarc mostly smooth, some annulation present, annulation usually present at origin of new branches and hydranth pedicels. Hydranths typical for genus but relatively small, 22-24 tentacles, near base wart-like nematocyst clusters with macrobasic euryteles.

Only advanced, presumably fertilized, egg stages present, these encapsulated and attached in whorls around pedicels of former blastostyles (Fig. 5B-C). Former blastostyle reduced to nematocyst knobs at end of pedicels.

Nematocysts: tentacular microbasic euryteles and large macrobasic euryteles in nematocyst buttons, shaft discharged more than four times as long as capsule, in undischarged capsule shaft coiled several times, coils along capsule wall and apparently filling capsule.

DIMENSIONS: Stems about 6 cm high, basal stem diameter 0.25 mm, hydranth pedicel diameters 0.14-0.17 mm. Preserved microbasic euryteles from tentacles (7-7.5)x(3-3.5)μm, r= 2-2.5; macrobasic euryteles (20.5-24)x(7.5-8.5)μm, r=2.6-3.0.

DISTRIBUTION: Only known from the type locality, Bohuslän, Sweden.

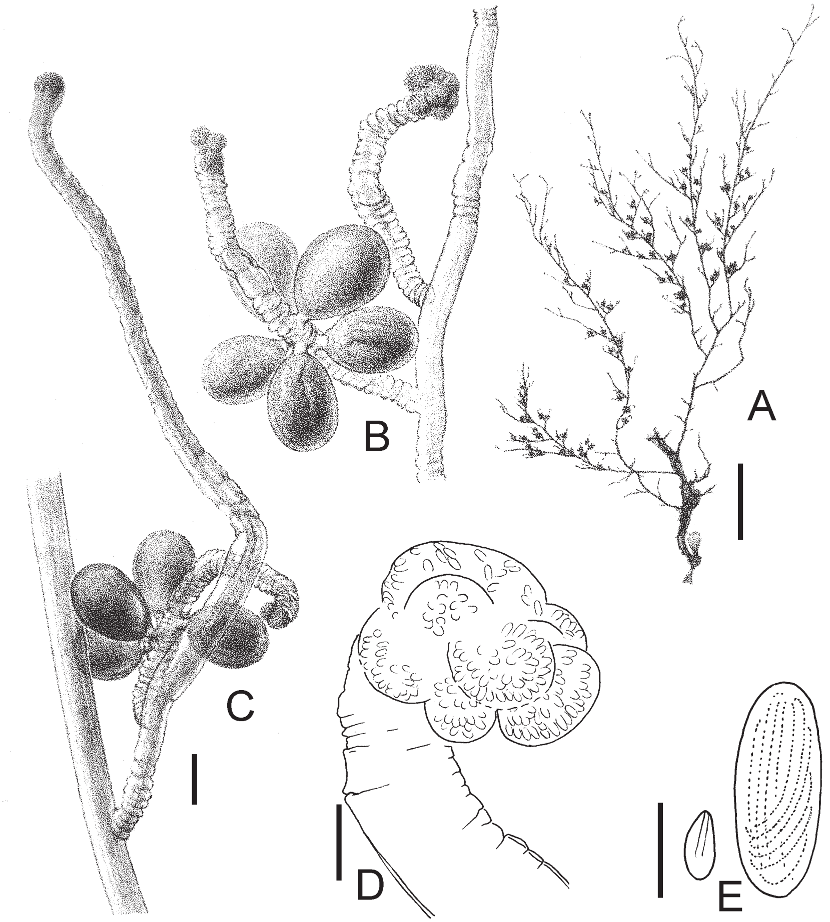

FIG. 5

Eudendrium cnidoferum Stechow, 1919, after syntype material, A-C modified from Jäderholm (1909). (A) Several stems, scale bar 1 cm. (B-C) Branches with encapsulated eggs/embryos. (D) Terminal portion of a blastostyle pedicel with nematocyst buttons. (E) Small microbasic eurytele and large macrobasic eurytele, the internal structure was only indistinctly visible, bar 10 μm.

REMARKS: When Jäderholm (1907) described *Eudendrium armatum* as new species, he was likely unaware that this name was already in use as *Eudendrium armatum* Tichomiroff, 1887. Stechow (1919) therefore proposed the replacement name *E. cnidoferum*, thus becoming also the author of the taxon. The species is only known from its type specimen and it was characterized by Jäderholm (1909) by what he considered the blastostyles. The eggs are attached in a whorl around a perisarc covered pedicel, the latter ending in several buttons full of large nematocysts (Fig. 5B, D), resembling the ends of tentaculozooids of *Hydractinia echinata*. Jäderholm considered them to be specialized nematophores. A re-examination of the type specimen confirmed Jäderholm's observation, but the blastostyles must be re-interpreted.

Additionally, although only very few hydranths are left, these have nematocyst buttons near the base of hydranth, just like in *E. glomeratum* (Fig. 3B). The gonophores are actually encapsulated – likely fertilized – eggs or embryos attached to the former pedicel of the blastostyle, as usually found in the final stages of the sequence of the development of the female sporosac (see General Morphology section). As in other *Eudendrium* species, the blastostyles became reduced once the eggs had been fertilized and what we see are likely only the vestiges of the former blastostyles. As also the blastostyles can have nematocyst buttons (e. g. *E. glomeratum*, Fig. 3C-D), these buttons might be the sole remainder of the former blastostyle. Nevertheless, they could be a constant feature of the species and perhaps allow a distinction from the otherwise almost identical *E. glomeratum*. There are only a few traits that would allow distinction of *E. glomeratum* from *E. cnidoferum*. The latter forms a monosiphonic colony, while the former species forms normally polysiphonic colonies, although Marques *et al.* (2000b) also report monosiphonic colonies. Perhaps also the undischarged large euryteles of the two species differ slightly. While in *E. glomeratum* the shaft makes only a few loose coils (Fig. 4), it seems to fill the capsule in *E. cnidoferum* (Fig. 5E). However, this observation is to be taken with some caution as the old material of *E. cnidoferum* did not permit a detailed, reliable observation of this trait.

Eudendrium cnidoferum remains an insufficiently known species and a conclusive evaluation of the status of can only be made once new material from Bohuslän becomes available. It seems nevertheless advisable to retain it as a valid species for the time being.

Eudendrium album Nutting, 1896 Figs 6-7

Eudendrium album Nutting, 1896: 146. – Nutting, 1898: 362, pl. 14, fig. 1. – Nutting, 1901: 334, fig. 11. – Kingsley, 1910: 20, pl. 2 fig. 11. – Fraser, 1912: 348, fig. 5 A-B. – Billard, 1927: 327. – Fraser, 1944: 61, pl. 7 fig. 32. – Leloup, 1947: 107: 18, fig. 9. – Leloup, 1952: 124, fig. 61. – Calder, 1971: 45, pl. 3 fig. B. – Watson, 1985: 185. – Marques *et al.*, 2000a: 77, figs 1-7. – Faasse & Vervoort, 2005: 58, figs 1-2.
not *Eudendrium album*. – Pennycuik, 1959: 167.
Eudendrium fragile Motz-Kossowska, 1905: 58, fig. 1, pl. 3 fig. 17. **new synonym**
Eudendrium fragile. – Marinopoulos 1992: 59, fig. 1. 11. – Boero & Freesi, 1986: 141. – Marques *et al.*, 2000a: 206. – Puce *et al.* 2005: 202, figs 1c, 2d, 2h.
Eudendrium islandicum Schuchert, 2000: 417, fig. 4. **new synonym**
Eudendrium islandicum Schuchert, 2001a: 29, fig. 17.

MATERIAL EXAMINED: BMNH 1912.12.21.85; as *Eudendrium album*; marked with red ink as "? type specimen"; A. M. Norman Collection; England, Plymouth; infertile, nematocysts not identifiable. – BMNH 1948.9.8.83; as *Eudendrium album*; England, Plymouth; 11 May 1898; female; E.T. Browne collection; has typical macrobasic euryteles. – BMNH 1948.9.8.81; as *Eudendrium album*; England, Plymouth; 11 May 1898; *Nemertesia antennina*; infertile; coll. E.T. Browne; nematocysts not preserved. – MHNG INVE37297; as *Eudendrium album*; France, Normandy, Cotentin, Herquemoulin, Treize Vents; 22 Aug. 2005; on *Halopitys incurvus*; male and female colonies; male sporosacs on fully formed hydranth, female likewise, 16 S sequence **AM991298**. – Norway, near Bergen, Flesland beacon, depth 20-100m; 20 June 2006; infertile colony on rock; has typical macrobasic euryteles; not preserved, **AM991299**. – BELUM Md617; Northern Ireland, Strangford Lough Narrows, W of Rue Point; 54.365°N 05.542°W; depth 7m; 02 Aug. 1983; female. – BELUM Md623; Northern Ireland, Strangford Lough Narrows, W of Rue Point; 54.365°N 05.542°W; depth 25m; 03 Aug. 1983; infertile. – BELUM Md618; Northern Ireland, Strangford Lough Narrows, W of Rue Point; 54.365°N 05.542°W; 25m; 03 Aug. 1983; female. – BELUM Md107; Northern Ireland, Mulroy Bay, Cranford, Broad Water,

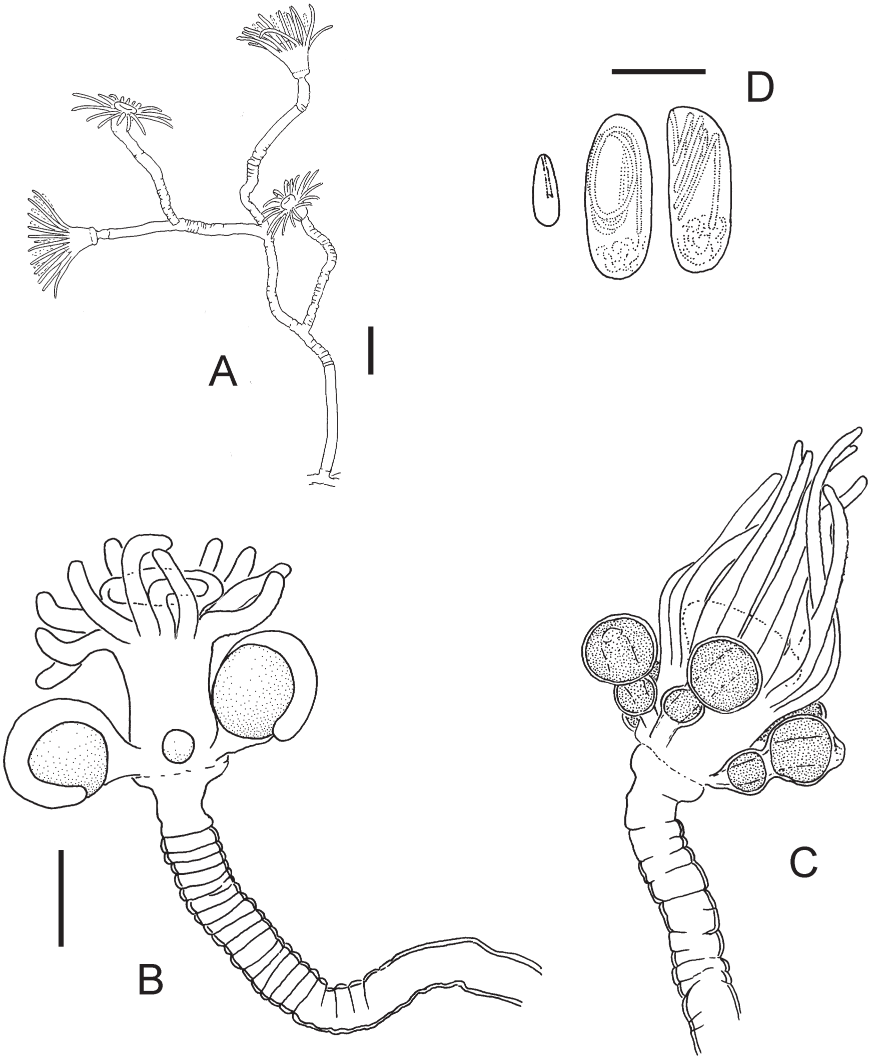

FIG. 6

Eudendrium album Nutting, 1896; after preserved material from the English Channel. (A) Colony from intertidal region, scale bar 0.5 mm. (B) Hydranth with female sporosacs, scale bar 0.2 mm. (C) Hydranth with male sporosacs, same scale as B. (D) Nematocysts: microbasic eurytele; two macrobasic euryteles, left frontal view, right lateral view. Scale bar 10 μm.

Deegagh Point; 55152°N 07.690°W; depth 10m; 25 March 1978; infertile. – BELUM Md106, as *Eudendrium ramosum*; Northern Ireland, Strangford Lough, E of Strangford; 54.373°N 05.554°W; depth 3m; 07 June 1976; female.

DIAGNOSIS: Colonies monosiphonic, small, gonochoristic; male and female sporosacs on normal hydranths; spadix simple; complementary nematocyst macrobasic eurytele; shaft inside capsule coiled obliquely in relation to long capsule axis, coil diameter max. 2/3 of capsule.

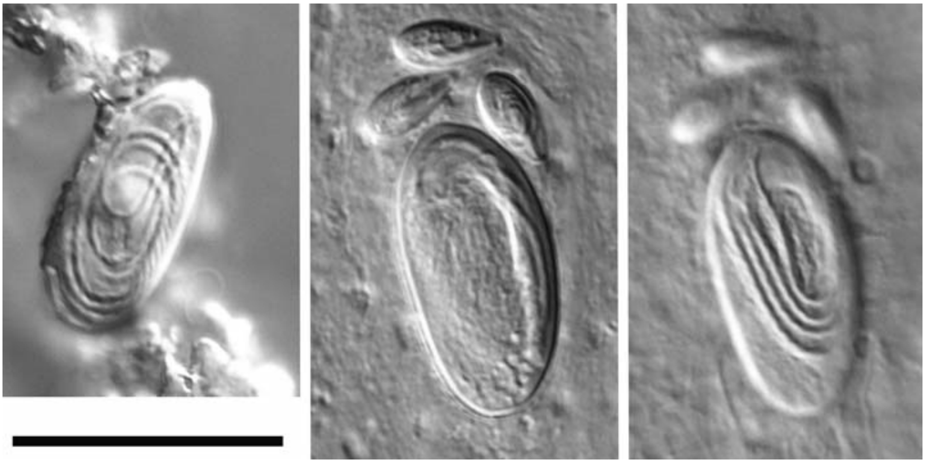

FIG. 7

Eudendrium album Nutting, 1896; nematocysts, living material from Norway. The two images at right depict the same capsules, but in different focusing planes.

DESCRIPTION: Colonies arising from creeping, branching stolons; stems monosiphonic, irregularly branched, 1-20 hydranths per shoot (up to 50 possible), shallow-water colonies small, Mediterranean colonies sometimes stolonal, cold-water colonies larger. Perisarc smooth with some corrugated or annulated stretches, perisarc of stem brown to yellowish, branches yellowish-brown fading to colourless. Hydranths cup-shaped as somewhat tapering towards base, hypostome rounded, large, around 17-22 tentacles; basal third of tentacles nearly free of nematocysts, in more distal region nematocysts in rings, capsule almost perpendicular to tentacles thus rendering it spiny. Colonies gonochoristic. Living hydranths of English Channel white to cream coloured, perisarc of preserved material yellowish.

Female gonophores develop in one whorl on body of a normally developed hydranth, about six sporosacs, initially with a simple curved spadix; hydranths can be somewhat reduced with ongoing gonophore maturation.

In older stages spadices shed and the embryos in their transparent capsules attached irregularly along the pedicel of the former blastostyle.

Male gonophores 2-3 (mostly 2) chambered, arising as single whorl from lower part of the body of either normally developed or only very slightly reduced hydranths, 6-8 gonophores, with or without distal button on last chamber, button if present without concentration of nematocysts. Nematocysts: small microbasic eurytele on tentacles, almond-shaped; larger macrobasic eurytele, shaft in intact capsule in 4-5 coils that are oblique in relation long axis of capsule (in side view), confined to upper 2/3 of capsule (Figs 6D, 7).

DIMENSIONS: Colony height is from a few mm in the intertidal region to 7 cm in deep waters. Hydranths 0.4-0.7 mm. Diameter of stems at base 0.12-0.20 mm, branches thinner. Nematocysts (preserved material): microbasic eurytele (7-8)x(2.5-4)μm, r = 2.0-2.8; macrobasic eurytele, size (18.5-27)x(7.5-14)μm, r = 2.0-2.7, s > 5.

BIOLOGY: Occurs from the intertidal to about 1000 m depth (deep-water records as *E. islandicum*). In the English Channel, gonophores are present from at least January to August (Russell, 1957, own observations). It occurs on stones, algae and other hydroids. More data on the biology of the American population are given in Calder (1971, 1976, 1990).

DISTRIBUTION: Mediterranean to North Atlantic. Only a minority of the known records are based on identifications that include nematocyst information. Without this information, identifications should be considered as tentative only. In the eastern Atlantic ranging from Galicia (Spain) to Norway (e. g. Nutting, 1898; Billard, 1927; Leloup, 1947, 1952; Russell, 1957; Teissier, 1965; Altuna Prados, 1994; Medel & López-González, 1996; Marques *et al.*, 2000b; Faasse & Vervoort 2005; this study). Has also been recorded in the Black Sea (Manea, 1977). In the western Mediterranean, it is known under the name *E. fragile* (Motz-Kossowska, 1905; Boero & Freesi, 1986; Marinopoulos, 1992; Marques *et al.* 2000b; Puce *et al.*, 2005). As *E. islandicum* it has been recorded from Iceland (Schuchert, 2000) and southern- to southwestern Greenland (Schuchert, 2001). Along the American continent it is known from the Gulf of St. Lawrence to Florida (Fraser, 1944; Calder, 1971, 2003). The following records must be confirmed again: California (Fraser, 1948) and Gulf of Mexico (Deevey, 1954). Type locality: Shallow waters near Millbay Channel, Plymouth, Great Britain.

REMARKS: Nutting (1898) regarded the small colony size and the white hydranths as diagnostic for this species. Colour is often not a reliable trait to distinguish species and the identity of *E. album* from Plymouth is not entirely clear as no unambiguous type material exists. The BMNH has a specimen from Plymouth marked with red ink as "? type". The specimen is from the Norman collection and there is no indication that it was obtained from Nutting. Furthermore, the material is infertile and does thus not correspond to Nutting's first description where he mentions fertile material. It is thus unlikely that it is the type specimen. The nematocysts of this specimen are too poorly preserved to be identified. Other potential type material could not be found and it must be assumed that no type material has survived (a potential type specimen formerly present in the Smithsonian Institution is likely lost; Dr A. Collins, pers. comm.). The BMNH has other, non-type samples of *E. album* from Plymouth, two of which still have identifiable nematocysts. The colony morphology of both match Nutting's description. Based on the nematocysts, one of them has macrobasic euryteles, while the other has apparently different nematocysts (see *Eudendrium unispirum*).

A search for *Eudendrium* species at and near the type locality (Millbay Channel, Plymouth) in June 2007 produced only *E. capillare*.

The scope and identity of *Eudendrium album* is thus not entirely clear, but Watson (1985) and Marques *et al.* (2000a) have re-defined this species by stating that its identification depends on the presence of macrobasic euryteles. As this form is apparently not uncommon in the English-Channel (see material examined) and thus might correspond to the Nutting's original species, it is advisable to maintain this usage. In order to stabilize the nomenclature, it might be necessary to designate a neotype based on fertile material of which the 16S and COI sequences are known.

Eudendrium fragile Motz-Kossowska, 1905 as re-defined in Marinopoulous (1992), Boero & Fresi (1986), and Marques *et al.* (2000b), appears indistinguishable from *E. album* and both are here regarded as conspecific.

Eudendrium islandicum Schuchert, 2000 is not objectively separable from *E. album*. *Eudendrium islandicum* has somewhat larger colonies than *E. album*, a feature likely attributable to the deeper and colder waters it was taken from. Apart from the colony size and the biogeographic zone (cold boreal to Arctic waters), there is thus nothing that would allow distinguishing them and they must therefore be regarded as conspecific.

The 16S sequences of two colonies of *E. album*, one originating from the intertidal of English Channel, the other from deeper waters in Norway, could be compared (Fig. 2). Although both colonies and their nematocysts appeared indistinguishable, the sequences were rather divergent, suggesting a possible cryptic speciation (or *E. islandicum* could nevertheless be valid, separable on biogeographic grounds).

Eudendrium simplex Pieper, 1884 Fig. 8

Eudendrium simplex Pieper, 1884: 150. – Motz-Kossowska, 1905: 56, pl. 3 figs 18-19. – Stechow, 1919: 30. – Marques *et al.*, 2000b: 205. – Bouillon *et al.*, 2004: 61, figs 36M-P.

Eudendrium motzkossowskae Picard, 1952: 339. – Marques *et al.*, 2000b: 206, synonym. – Boero, 1981: 188, fig. 4. – Marinopoulos, 1992: 59, fig. 1.10. – Boero & Freesi, 1986: 141.

? *Eudendrium motzkossowskae*. – Millard & Bouillon, 1974: 17, fig. 3J-K. – Millard, 1975: 84, fig. 29G-H.

MATERIAL EXAMINED: MHNG INVE27128, as *Eudendrium motzkossowskae*; Mediterranean, Mallorca, Cala Murada, depth 4m, on *Posidonia oceanica*; 26 Aug. 1999; male and female colonies. – Ionian Sea, Italy, S. Caterina; 27 Nov. 2001 and 11 Oct. 2006; fertile colonies; preserved material in pers. collection Doris De Vito.

DIAGNOSIS: Usually on *Posidonia oceanica*, stolonal or sparingly branched colonies, large macrobasic eurytele with several coils along long axis, blastostyles normal hydranths, spadix of female sporosacs often with a chamber containing male gametes.

DESCRIPTION: Colonies stolonal or sparingly branched with up to four hydranths per stem. Stolons creeping, ramified. Perisarc of stems smooth with some annulated or corrugated stretches, variable. Hydranths typical for genus, around 20 tentacles, basal grove visible, above basal grove large nematocysts, but not dense, few more large capsules scattered on other parts of hydranth. Male and female colonies separate, gonophores develop on normal hydranths that are not or only minimally reduced.

Male blastostyles with 1-4 sporosacs, two-chambered, no terminal nematocyst button (Fig. 8D).

Female blastostyles with 2-5 sporosacs, spadix simple, curved, bearing few scattered nematocysts, spadix in advanced stage often with one or rarely more bump-like swelling due to a chamber containing spermatogenic cells (Fig. 8C). Fertilized eggs form membranous perisarc capsule and get attached to pedicels of blastostyles (Fig. 8B).

Nematocysts: small microbasic euryteles on tentacles; large macrobasic euryteles, discharged shaft very long (r>4), densely barbed (holotrichous), shaft in

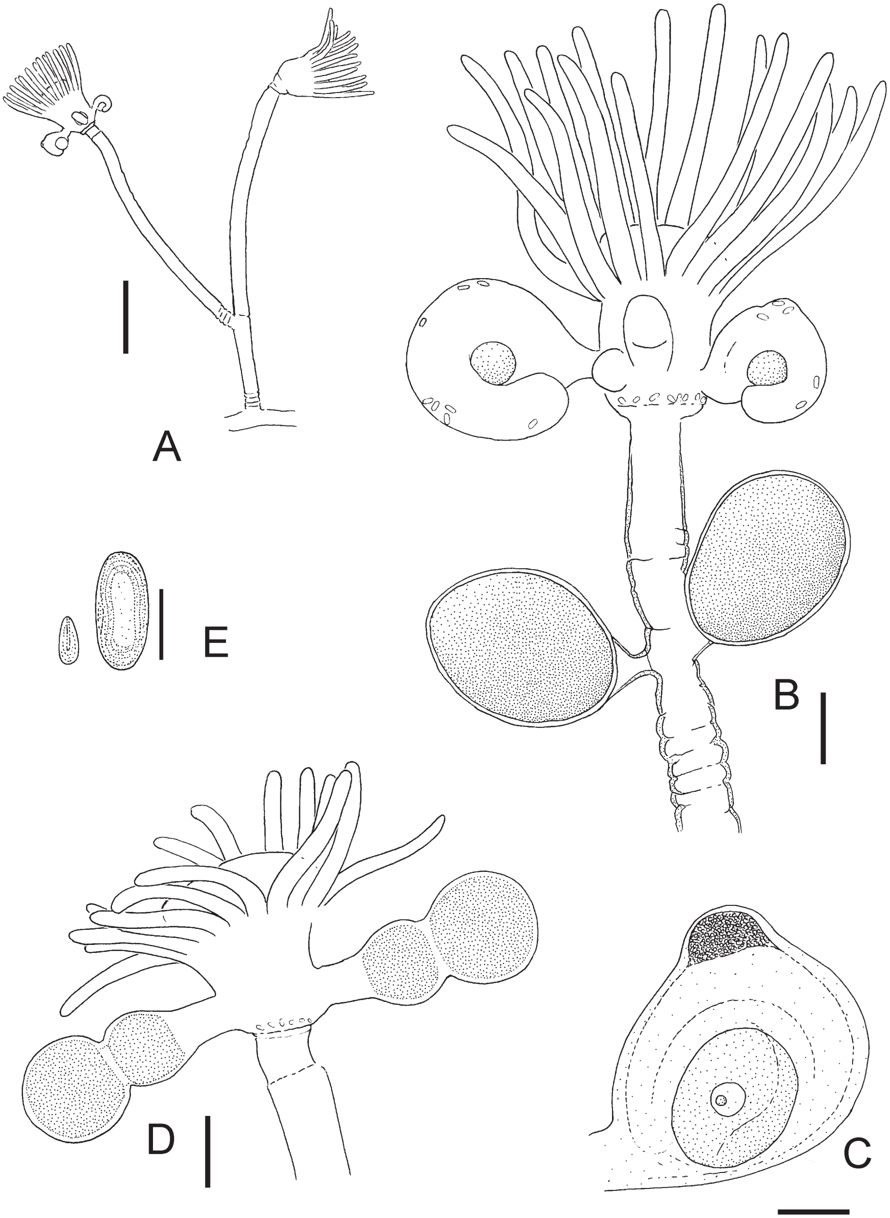

FIG. 8

Eudendrium simplex Pieper, 1884; after preserved Mediterranean material. (A) Stem with two hydranths, scale bar 0.5 mm. (B) Blastosyle (gonozooid) with developing female sporosacs and two encapsulated embryos attached to pedicel, scale bar 0.1 mm. (C) Optical section of female sporosac with mass of spermatogenic cells on spadix, scale bar 50 μm. (D) Blastostyle with male sporosacs, same scale as B. (E) Undischarged nematocysts: microbasic and macrobasic euryteles, scale bar 10 μm.

undischarged capsule in more than four coils along the capsule wall and oriented parallel to long axis.

DIMENSIONS: Stems up to 12 mm, hydranth pedicel diameter 0.08-0.090 mm, stem diameter at base ca. 0.1 mm, hydranth height 0.25-0.3 mm, encapsulated embryos 0.2-0.25 mm. Microbasic euryteles (6-6.5)x(2.5-3.5)μm, r=2.0-2.6. Macrobasic euryteles (16-19)x(6.5-8.5)μm, r=1.7-2.5. For more nematocyst measurements see Marinopoulos (1992) and Marques *et al*. (2000b).

BIOLOGY: Occurs in shallow water (down to 15 m), predominantly or perhaps exclusively on *Posidonia oceanica*. Mature from April to November (Gili & Garcia Rubies, 1985; Bouillon *et al*., 2004; own data).

DISTRIBUTION: Mediterranean (Marques *et al*., 2000b). The records from southern Africa (Millard & Bouillon, 1974; Millard, 1975; as *E. motzkossowskae*) are uncertain as no hermaphroditic sporosacs were observed. Type locality: Dalmatian coast, Adriatic Sea.

REMARKS: The synonymy of this species was outlined by Marques *et al*. (2000b). If present, the unique hermaphroditic sporosacs allow a reliable identification of this species. Its occurrence on *Posidonia oceanica* also helps to identify it. *Eudendrium fragile*, a subjective synonym of *E. album*, is otherwise quite similar, but the macrobasic euryteles differ slightly (comp. Figs 7 and 8E).

Eudendrium racemosum (Cavolini, 1785) Figs 9-10

Sertolara racemosa Cavolini, 1785: 160, pl. 6 figs 1-7, 14-15.
Sertularia racemosa Gmelin, 1788: 3854.
Eudendrium racemosum. – Ehrenberg, 1834: 296. – Allman, 1872: 341. – Morri, 1981: 59, fig. 18, pl. 1 fig. – Gili, 1982: 42, fig. 10. – Gili & Castello, 1985: 11, fig. 2. – Watson, 1985: 204, figs 63-67. – Marinopoulos, 1992: 60, figs 1.1, 2, 5. – Marques *et al*., 2000a: 100, figs 67-70. – Marques *et al*., 2000b: 207. – Peña Cantero & García Carrascosa, 2002: 33, fig. 6. – Puce *at al*., 2005: 302, figs. 1f, 2m. – Puce *at al*., 2006: 622, fig. 4a-c.
? *Eudendrium racemosum*. – Stechow, 1913: 63. – Yamada, 1954: 5, fig. 4. – Hirohito, 1988: 84, fig. 29.
not *Eudendrium racemosum mucronatum* Billard, 1926: 88, fig. 8.

MATERIAL EXAMINED: BELUM Md1005; Atlantic, France, Brittany, Anse de Camaret; 4 Aug. 1986. – MHNG INVE25854; France, Corsica, Calvi; depth 2m; 6 Jul. 1992; fertile female and male colonies. – MHNG INVE26505; Mediterranean, France, Banyuls-sur-Mer; depth 4m; male colony; 12 Jul. 1999. – MHNG INVE27671; Spain, Canary Islands, Lanzarote; 23 Sep 1999; depth 25-30m; male. – MHNG INVE27672; Canary Islands, Tenerife, Radazul; 4 Oct. 1999; depth 20-30m; fertile. – MHNG INVE29810; Mediterranean, Spain, Mallorca, Cala Murada; 14 Aug. 2000; depth 2m; 16S sequence **AY787896**. – MHNG INVE32164; Mediterranean, Spain, Mallorca, Cala Murada; 30 Jul. 2001, depth 1 m. – MHNG INVE39448; Mediterranean, port of Monaco, artificial cave; 6 Jul. 2001; depth 9m. – MHNG INVE49719; Mediterranean, France, Marseille, Impériaux de Terre; 14 Jun. 2004; on rock; male; 16S sequence **AM991307**. – MHNG INVE49718; Mediterranean, France, Marseille, Grand Conglu; depth 3m; 16 Jun. 2004; on rock; female. – MHNG INVE49884; Italy, Naples; 23.12.1891; male and female stems. – MHNG INVE49885; Italy, Naples, Nisida; coll. ca. 1900, male. – MHNG INVE25958; Italy, Naples, coll. 1892. – Mediterranean, France, Banyuls-sur-Mer; 4m; male colony; 7 Nov. 1997; material not deposited; 16S sequence **AM991297**. – Mediterranean, Spain, Mallorca, Cala Murada; under rock overhang, depth 1-2m; 13 Jul. 2006, female; not deposited; 16S sequence identical to AY787896 – Mediterranean, Spain, Mallorca, Cala Murada; under rock overhang, depth 1-2m; 13 Jul. 2006, female; not deposited; 16S sequence identical to AY787896.

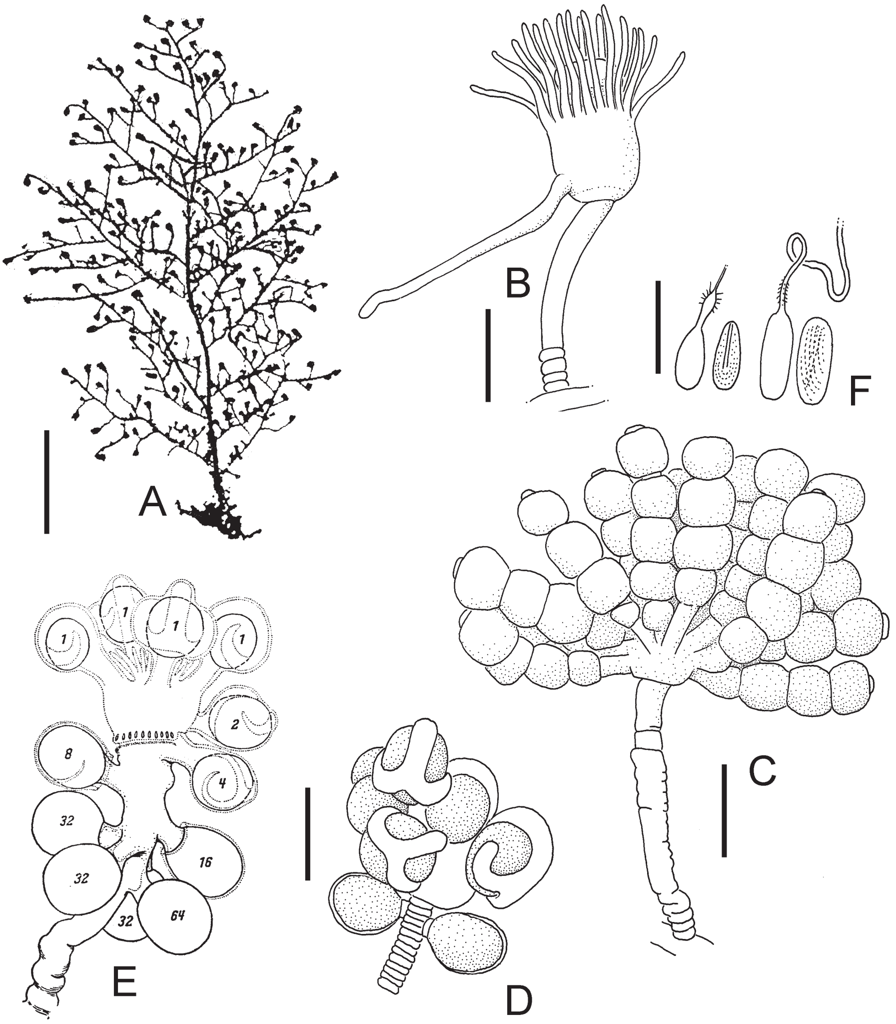

FIG. 9

Eudendrium racemosum (Cavolini, 1785), after preserved Mediterranean material. (A) Colony silhouette, scale bar 10 mm. (B) Hydranth with basal nematophore, scale bar 0.5 mm. (C) Male blastostyle, scale bar 0.5 mm. (D) Gonozooid with female sporosacs, note bifid spadix, scale bar 0.5 mm. (E) Schema of developmental stages on female blastostyle, the numbers indicate the number of nuclei during the embryonic development; figure modified after Mergner (1957). At the top, the eggs are held by the spadices, they are not yet fertilized. Fertilization has taken place in the eggs below, starting with the two nuclei stage to the 64 nuclei stage. Through the consecutive growth of the blastostyle the embryos come to lie more proximally and are ultimately attached to the pedicel. They are enveloped by a periderm membrane. (F) Nematocysts as pairs of discharged and native capsule: microbasic euryteles and basitrichous isorhizas.

DIAGNOSIS: Large colonies, mostly monosiphonic, some hydranths with cnidophores; blastostyles reduced; spadix of female gonophore branched; complementary nematocysts are isorhizas.

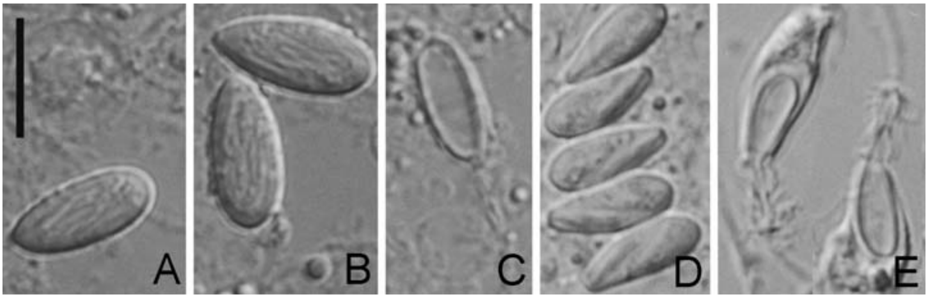

FIG. 10
Eudendrium racemosum (Cavolini, 1785), native nematocysts, scale bar 10 μm. (A-B) Undischarged isorhizas. (C) Discharged isorhiza. (D) Microbasic euryteles. (E) Discharged euryteles.

DESCRIPTION: Colonies much branched, often quite regular, bushy to tree-like. Stems usually monosiphonic, large colonies can be somewhat polysiphonic. Perisarc annulation of variable extent, intermittent with smooth regions. Hydranths typical for genus, 25-34 tentacles, frequently with tentacle-like process from lower part of hydranth body (cnidophore), length of cnidophore 1-3 times the size of hydranth, thicker than tentacles. Nematocysts on tentacles present in rings along entire length but density decreasing towards proximal, capsules erect and tentacle surface thus spiny. At lower fifth of hydranth body basal groove with origin of perisarc, perisarc here filmy and very thin (only visible at high magnifications). Above groove usually a concentration of mastigophores. Colonies dioecious.

Male gonophores develop on reduced hydranths, may have initially small tentacles, later atrophied; mature male sporosacs in a dense tuft at ending of a branch, each gonophore with 3-4 chambers, sometime terminal button, without dense nematocyst cluster.

Female gonophores develop on reduced (1/3 size) hydranths that are later completely atrophied. Gonophores typical for genus but spadix of younger gonophores bifid, may be lost in mature gonophores. Fertilized eggs encapsulated and attached to perisarc of blastostyle pedicels.

Nematocysts: microbasic euryteles on tentacles and atrichous or basitrichous isorhizas concentrated above basal groove.

Polyps whitish to light orange-pink, eggs in gonophores dark orange-red, perisarc brown.

DIMENSIONS: Stems 2-12 cm high, colonies from deeper waters up to 25 cm (Motz-Kossowska, 1905). Hydranths 0.5-1 mm, nematophore length 0.4-0.6 mm, hydranth pedicel diameter about 0.15 mm, diameter of stem at base 0.33-0.50 mm. Nematocysts: isorhizas (8-9)x(3.5)μm; microbasic euryteles (7-8)x(2.5-3.5)μm.

BIOLOGY: In the Mediterranean, *E. racemosum* occurs rather abundantly in the first few metres, but it may be found in deeper waters up to 125 m depth (Motz-Kossowska, 1905; Boero & Fresi, 1986; Marques *et al.*, 2000b; Peña Cantero & García

Carrascosa, 2002). It grows on rocks, concretions, barnacles, mussels, gorgonians, and algae. It is present throughout the year but is rare from December to February when it likely overwinters as a stolonal system. Fertile animals can be found from March to December, the main reproductive season seems to be during the summer.

More ecological data are given in Palombi (1940), Gili & Ros (1985), Barange *et al.* (1987), Sommer (1992), Azzini *et al.* (2003). Aspects of its feeding behaviour and ecology are described in Barange (1988), Barange, & Gili (1988), and Puce *et al.* (2002).

OTHER DATA: Details of the histology, gametogenesis, and development are given in Weismann (1883), Ishikawa (1887), Neppi (1917), Mergner (1957), Hanisch (1970), Sommer (1990). The egg maturation is also shown in Fig. 9E. Regeneration was studied by Billard (1904). Predation and the use of its nematocysts by nudibranch gastropods are described by Martin (2003), Martin & Walther (2002, 2003).

DISTRIBUTION: In the Mediterranean, this is a very common and easily obtainable hydroid. It occurs in the entire Mediterranean, this along the European, Asian and African shores (see references in Marques *et al.*, 2000b; Peña Cantero & García Carrascosa, 2002). It also occurs in Mediterranean lagoons (Morri, 1981). In the Atlantic, it is quite rare. Its northernmost records are from Brittany (Castric-Fey *et al.*, 2001; this study). It is present along the Iberian Peninsula (Medel & Lopez Gonzalez, 1996), the Canaries (this study), and western Africa (Leloup, 1940; Picard, 1951a; Buchanan, 1957; Bouillon *et al.*, 1995). In the Indian- and Pacific Ocean it has been found in the Seychelles, (Millard & Bouillon, 1973), tropical Australia (Watson, 1985), Vietnam (Leloup, 1937), Indonesia (Puce *et al.*, 2006), and Japan (Yamada 1954, Hirohito, 1988). The Japanese samples had strongly polysiphonic colonies, lacked nematophores and its nematocysts were not examined. As suspected by Hirohoto (1988), I think that the Japanese *E. racemeosum* belongs to a separate, unnamed species. Type locality: Mediterranean, Gulf of Naples, Cave of Gajola, Nisita Island (now Nisida) and Vico Equano (now Vico Equense) (Cavolini, 1785).

REMARKS: The name *Eudendrium racemosum* is here attributed to Cavolini (1785), but one might argue that Cavolini did not use a correct binomial nomenclature. Although he used indeed the Italian name for the genus (Sertulara), it was clearly used in a binomial context in the sense of Linnaeus. He treats several recognizable hydroids which he either assigned to *Sertolara* or to *Tubulara*, thus adopting clearly the system of Linnaeus.

Eudendrium racemosum mucronatum Billard, 1926, a species originally described from the Suez Canal, does not belong to *E. racemosum*. Marques *et al.* (2000b) re-examined the type specimen and also the other material of Billard. They found that part of the original material probably belongs to *E. carneum*, but the holotype represents likely a valid species neither referable to *E. racemosum* nor *E. carneum*. It should thus be used as *Eudendrium mucronatum* Billard, 1926.

Eudendrium racemosum is one of most common and conspicuous hydroids of the Mediterranean. It is also relatively easy and reliable to identify due to its isorhiza capsule, the nematophores, and the branched spadix.

Eudendrium carneum Clarke, 1882 Fig. 11

Eudendrium carneum Clarke, 1882: 137, pl. 7 figs 10-17. – Fraser, 1944: 64, pl. 8 fig. 36. – Vervoort, 1968: 8. – Millard, 1975: 82, fig. 28. – Watson, 1985: 202, figs. 59-62. – Wedler & Larson, 1986: 84, fig. 6Ba-b. – Calder, 1988: 43, figs 33-35. – Bavestrello & Piraino, 1991: 197, figs 1a-c. – Marinopoulos, 1992: 57, fig. 2.3. – Marques *et al.*, 2000a: 90, figs 35-41. – Marques *et al.*, 2000b: 206.

Eudendrium cunninghami Kirkpatrick, 1910: 127, pl. 7 figs 1-3. – Vannucci, 1954: 101, synonym. – Marques *et al.*, 2000b: 207, synonym.

Eudendrium ramosum. – Weill, 1934b: 388, figs 237. [not *Eudendrium ramosum* (Linnaeus, 1758)]

Material examined: MHNG INVE35472; Honduras, Utila, 16.0687°N 86.9555°W, depth 20 m; 11 Feb. 2004; fertile female; DNA extracted, 16S DNA sequence accession number **AM991305**. – MHNG INVE39470; France, Corsica, Ajaccio; 4 July 1950; male colony. – ZMUC, without number, as *E. ramosum*; USA, Cape Cod, Lagoon Pond Bridge; 17 July 1964; fertile male. – Lebanon; depth 12m; July 2003; male colony; personal collection of Dr S. Puce. – Lebanon, Beirut Harbour; depth 3m; Sept. 2002; female colony; personal collection of Dr S. Puce.

Diagnosis: Large, polysiphonic colonies, complementary nematocyst a large haploneme (anisorhiza); male blastostyles completely atrophied; female blastostyle completely atrophied or with some few and small tentacle rudiments; female sporosacs with bifid spadix, during later development reduced but forming a periderm membrane holding encapsulated embryos.

Description (Calder, 1988; Bavestrello & Piraino, 1991; own data): Colony extensively branched and irregularly bushy, arising from a creeping mass of stolons. Basal part and sometimes also major branches polysiphonic. Perisarc thick, brown in older parts of colony, thinner and paler towards extremities, annulated or wrinkled at bases of branches and hydranth pedicels, with occasional annulations elsewhere but mostly smooth, terminating almost imperceptibly at groove around hydranth base. Hydranths with large hypostome, up to 32 tentacles.

Male gonophores (>10) in a tuft at end of pedicel, without vestiges of hydranth, gonophores with 3-4 chambers each, distal end of gonophore with scattered nematocysts.

Female gonophores (4-10) on almost entirely atrophied hydranths, sometimes transiently with a few reduced tentacles; spadix bifid, curving over egg. After fertilization the spadix is reduced, but before this the spadix secretes a covering of periderm which then holds the encapsulated embryos in a dense clusters on the blastostyle pedicels; perisarc membranes often moulded into shape of enlarged spadix, with two openings, but often also irregular (Fig. 11E).

Nematocysts: microbasic euryteles on tentacles and in other tissues; anisorhizas with shaft tapering only towards its distal end, thus appearing as isorhiza, scattered on hydranth base, hypostome, tips of male gonophores.

Colours (Clarke, 1882): hydranths and gonophores red.

Dimensions: Colonies of variable height reaching up to 24 cm (Bavestrello & Piraino, 1991), more commonly around 10 cm. Hydranths 0.4-0.8 mm total height and 0.5-0.6 mm wide (Bavestrello & Piraino, 1991). Male gonophores 0.5-0.6 mm long, maximal diameter 0.2 mm; embryo capsules (0.25-0.3)x(0.4)mm. Haploneme (21-26)x(9-11)μm, r=2.1-2.6; microbasic eurytele (7.5-9)x(3.5-4)μm r=2.3-2.5. Non-

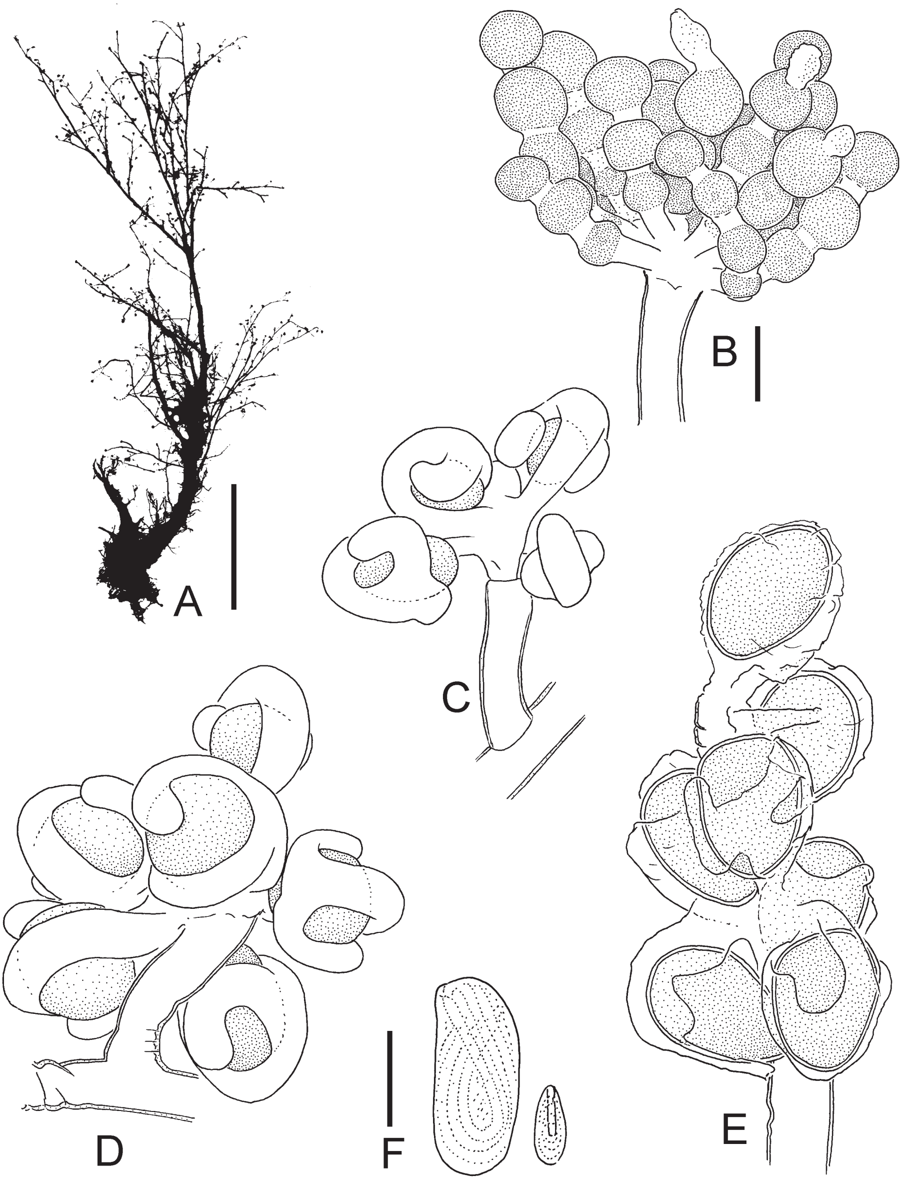

FIG. 11

Eudendrium carneum Clarke, 1882; after preserved Mediterranean material. (A) Colony silhouette, scale bar 2 cm. (B) Male blastostyle, some terminal chambers have spent their gametes, scale bar 0.2 mm. (C) Young female blastostyle, same scale as B. (D) More advanced female blastostyle, note branched spadices, same scale as B. (E) Encapsulated embryos attached to pedicel of former blastostyle, note fenestrated periderm membranes that hold capsules, same scale as B. (F) Nematocysts: haploneme and microbasic eurytele. Scale bar 10 μm.

European populations have quite similar values (Millard, 1975; Watson, 1985; Calder, 1988).

Biology: This species often occurs on ship hulls and is thus potentially easily introduced to other regions (Millard, 1975). In the Mediterranean, this is not a frequent species, but along the American coast it can occur in dense stands (Clarke, 1882; Calder, 1988). It is usually found in depths from 0-20 m (Marques *et al.*, 2000b), but prefers shady environments (Bavestrello & Piraino, 1991). Fertile colonies have been found in the Mediterranean from July to December (Marques *et al.*, 2000b; this study). Detailed ecological studies are provided by McDougall (1943), Wedler (1975), Calder (1976, 1990). Summers (1972, as *E. ramosum*) examined the ultrastructure of the spermatids.

Distribution: Mediterranean, perhaps introduced by human activity (Picard, 1958; Bavestrello & Piraino, 1991; Marques *et al.*, 2000b), western Atlantic from New England to Florida (Fraser, 1944; Marques *et al.*, 2000b), tropical eastern Atlantic (Vervoort, 1968, Wedler, 1975; Wedler & Larson, 1986), Brazil (Vannucci, 1954), French Guyana (Bouillon *et al.*, 1995), Island of St Helena (Kirkpatrick, 1910), southern Africa (Millard, 1959; 1975); western Australia (Watson, 1985), California to tropical eastern Pacific (Fraser, 1939; 1948), perhaps also Korea (Park, 1991). Type locality: USA, Virginia, Fort Wool, in the entrance to Hampton Roads (Clarke, 1882).

Remarks: Although *E. carneum* has some similarities with *E. racemosum* (large colonies, bifid spadix, reduced blastostyles), it can be distinguished rather reliably: its haplonemes are much larger, mature colonies are always polysiphonic, and the embryos are held by periderm membranes.

The halplonemes have been variably identified as isorhizas or anisorhizas. Watson (1985) showed that these capsules have a very long thread (1 mm) which tapers only in the very terminal region. It is thus easily mistaken for an isorhiza. The differences between anisorhiza and isorhiza are anyway gradual and often not so clear. Using the more inclusive term haploneme is thus preferable.

Infertile or male colonies can be mistaken for *E. glomeratum* if no discharged nematocysts can be examined. However, *E. carneum* lacks the characteristic nematocyst buttons of *E. glomeratum*.

Eudendrium racemosum mucronatum Billard, 1926, a species originally described from the Suez Canal, does not belong to *E. racemosum*. Marques *et al.* (2000b) re-examined the type specimen and also the other material of Billard. They found that part of the original material probably belongs to *E. carneum*, but the holotype likely represents a valid species neither referable to *E. racemosum* nor *E. carneum*. It should thus be used as *Eudendrium mucronatum* Billard, 1926.

Eudendrium ramosum (Linnaeus, 1758) Figs 12-14

Tubularia cylindris ramosis Ellis, 1755: 31, pl. 16a, pl. 17A, a.
Tubularia ramosa Linnaeus, 1758: 804.
Tubularia trichoides Pallas, 1766: 84. – Hincks, 1868: 82, synonym.
Eudendrium insigne Hincks, 1861: 160. **new synonym**
Eudendrium insigne. – Hincks, 1868: 86, pl. 14 fig. 3. – Allman, 1872: 337, pl. 14 figs 4-6.
Eudendrium ramosum. – Hincks, 1868: 82, pl. 13. – Allman, 1872: 332, pl. 13. – Fraser, 1937: 42, pl. 7 fig. 32. – Fraser, 1944: 72, pl. 12 fig. 48. – Yamada, 1954: 27. – Hamond, 1957:

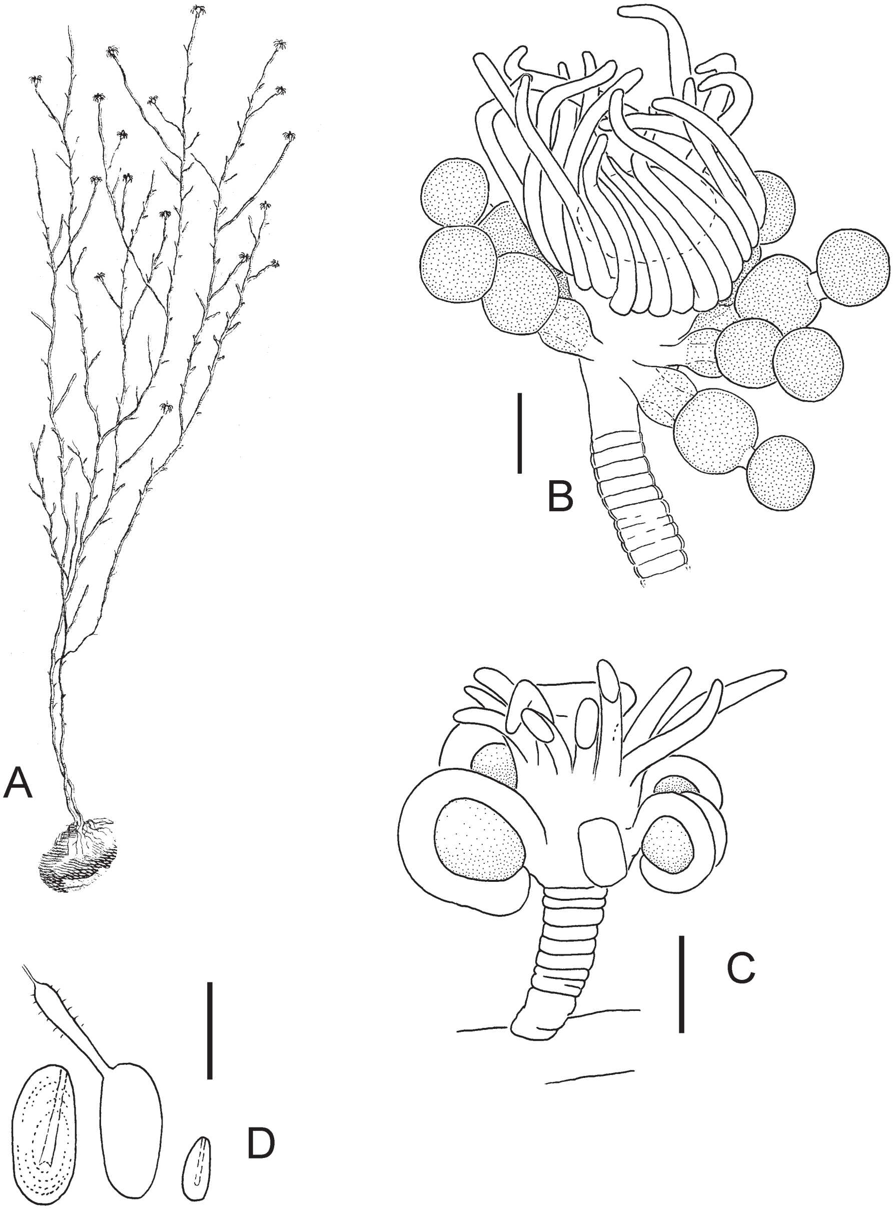

FIG. 12

Eudendrium ramosum (Linnaeus, 1758). (A) Colony, from Ellis (1755). (B) Male gonozooid, scale bar 0.2 mm, after preserved material from the Mediterranean. (C) Female gonozooid, scale bar 0.2 mm, after preserved material from the Mediterranean. (D) Nematocysts of Atlantic material: large microbasic eurytele, same discharged, small tentacular microbasic eurytele.

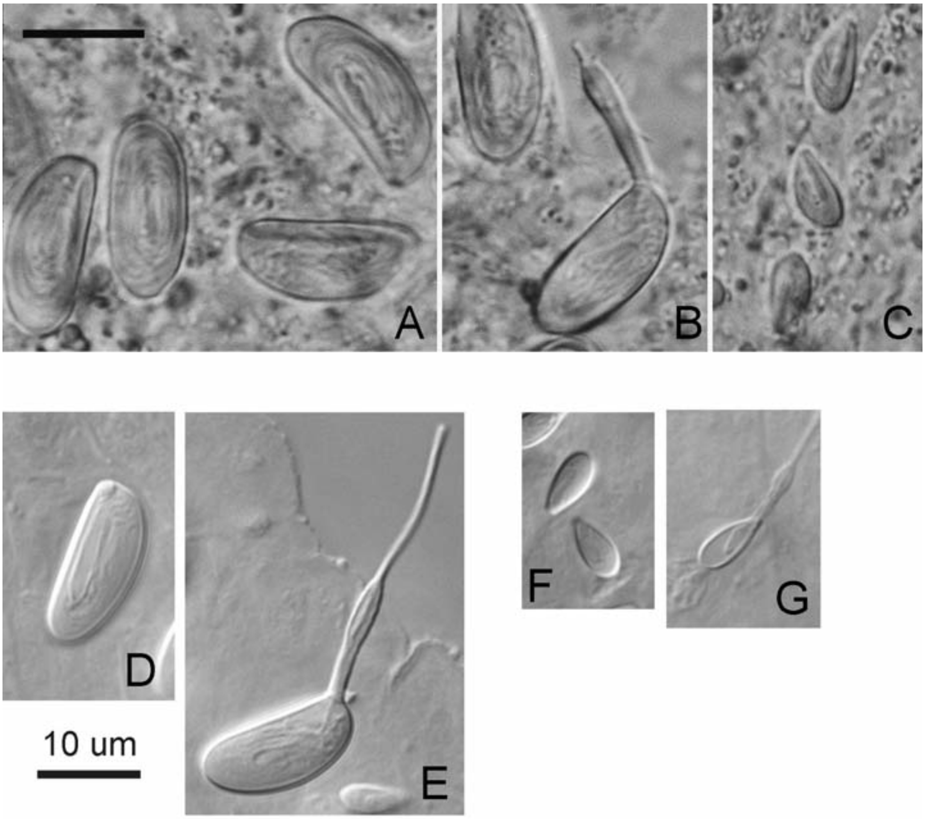

FIG. 13

(A-C) *Eudendrium ramosum* (Linnaeus, 1758); native nematocysts of Mediterranean material, scale bar 10 μm. (A) Large microbasic eurytele. (B) Same discharged. (C) Small microbasic eurytele.

(D-G) Topotype material of *Eudendrium insigne*; nematocysts of alcohol preserved material, scale bar 10 μm. (A) Intact large microbasic eurytele. (B) Same discharged. (C) Small microbasic euryteles. (D) Same discharged.

300. – Naumov, 1969: 266, fig. 135. – Millard & Bouillon, 1973: 32, fig. 31A-D. – Millard & Bouillon, 1974: 19, fig. 3A-D. – Millard, 1975: 85, fig. 31A-D. – Hirohito, 1988: 87, figs 30d-e, 31a-c, pl. 2 fig. C. – Ramil & Vervoort, 1992: 20. – Marinopoulos, 1992: 59, fig. 5. – Marques *et al.*, 2000a: 104, figs 75-78. – Marques *et al.*, 2000b: 204. – Schuchert, 2001: 32, fig. 20. – Peña Cantero & García Carrascosa, 2002: 37, fig. 7a-c.

Eudendrium elsae-oswaldae Stechow, 1921: 252. – Stechow, 1923: 81, fig. G. **new synonym**

Eudendrium elsaeoswaldae. – Marques *et al.*, 2000a: 94, figs 47-49. – in part Marques *et al.*, 2000b: 209.

? *Eudendrium ramosum*. – Watson, 1985: 191, figs 29-34.

not *Eudendrium ramosum*. – van Beneden, 1844. [= *Bougainvillia muscus* (Allman, 1863)]

not *Eudendrium ramosum*. – Motz-Kossowska, 1905: 54, pl. 3 fig. 16. [= *Eudendrium glomeratum* Picard, 1952]

not *Eudendrium ramosum*. – Weill, 1934b: 388, figs 237. [=*Eudendrium carneum* Clarke, 1882]

not *Eudendrium ramosum*. – Kramp, 1926: 241. [= *Myrionema multicornis* (Allman, 1876)]

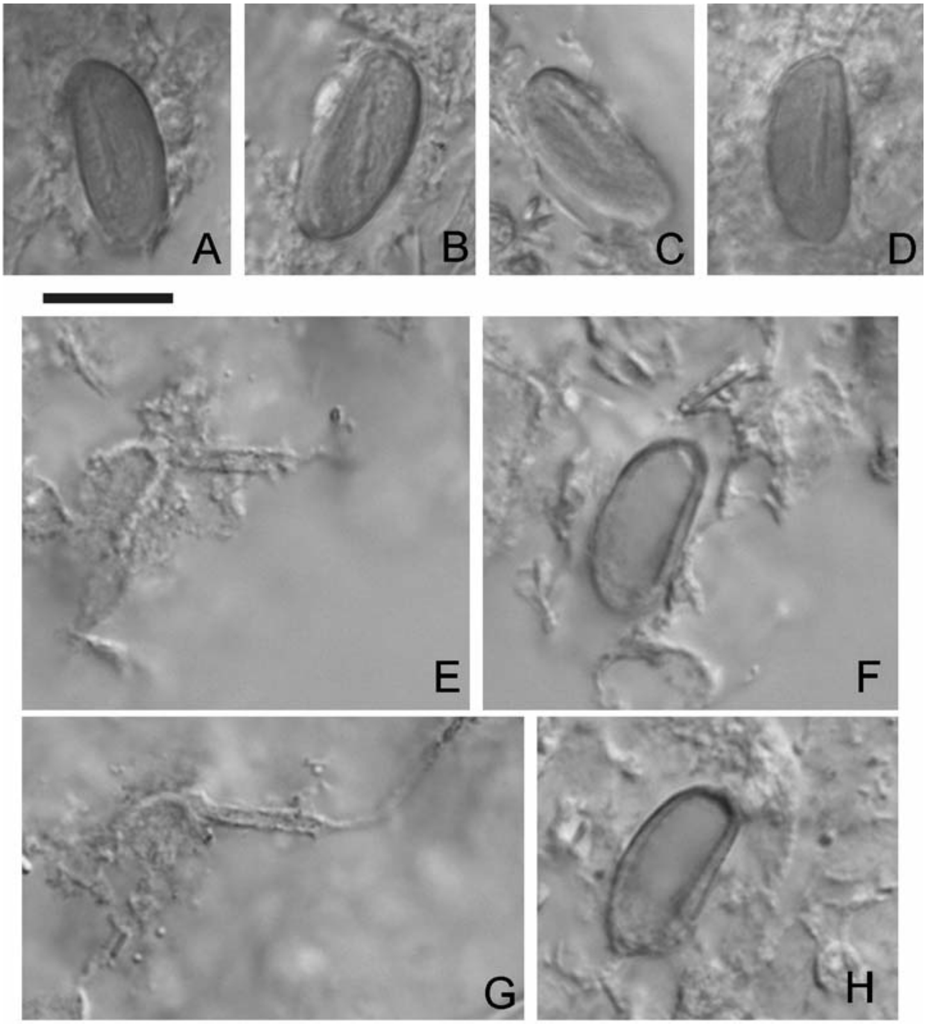

FIG. 14
Compementary nematocysts of the syntype material of *Eudendrium elsaeoswaldae*, ZSM no 20040383, scale bar 10 μm. (A-D) Intact large microbasic euryteles. (E-H) Two discharged large microbasic euryteles. The image-pairs E+F and G+H depict each the same capsule, but in different focusing planes, this in order to better visualize the shaft (E, G) or the capsule (F, H).

E. RAMOSUM MATERIAL EXAMINED: MHNG INVE25956; Italy, Naples, 23 Dec. 1891; female. – MHNG INVE25957; Italy, Naples, coll. 1892, infertile. – MHNG INVE3945; France, Banyuls-sur-Mer, Cap Abeille; 30 Oct. 1947. – BELUM Md354; Northern Ireland, Strangford Lough, NW Limestone Rock; 54.421° N 5.611°W; depth 28m; 20 May 1982; female. – BELUM Md105; Northern Ireland, Strangford Lough, Bay to N of Audley's Point; 54.386°N 5568°W; depth 12m; 25 April 1976; male. – BELUM, without registration number, field number 900620/01; loc. Ireland; 20 June 1990; male and female colonies. – BELUM, without registration number, field number 910328/01; Scotland, Sound of Mull, Hispania wreck, depth 18m, 28 march 1991, male. – ZSM, CT356; Plymouth Zoological Station, coll. 1909; 12cm colony. – Italy, Portofino, Sept. 2004, depth 15-20m; males; in pers. collection of S. Puce (as *E. moulouensis*). – Italy, Sardinia, Oct. 2005, depth 24m; females; in pers. collection. S. Puce (as *E. moulouensis*).

E. INSIGNE MATERIAL EXAMINED: MHNG INVE54560, topotype material for *Eudendrium insigne*; England, Torquay, Hope's Nose, rock pool at low water level; 16 June 2007; fertile female; part used to extract DNA, **AM991293**. – IRSNB, Ig 11365, as *Eudendrium insigne*; Germany, Helgoland, leg. Leloup; female colony of 16 mm. – BELUM Md615; as *E. insigne*; Northern Ireland, Strangford Lough Narrows, Rue Point; 54.365°N 5.541°W; depth 25m; 11 Aug. 1983; male. – BELUM Md614; as *E. insigne*; Northern Ireland; Strangford Lough Narrows, W of Rue Point; 54.365°N 5542°W; depth 7m; 2 Aug. 1980; female.

E. ELSAEOSWALDAE MATERIAL EXAMINED: Syntype material *Eudendrium elsaeoswaldae*, ZSM no 20040383, alcohol and slide preparations, Naples, Posilippo, 20 m.

DIAGNOSIS: Colonies monosiphonic or exceptionally with few complementary tubes near base; complementary nematocysts large microbasic euryteles with rather small spines, dispersed on hydranth body. Female and male sporosacs developing on unreduced hydranths, in later development sometimes partially reduced.

DESCRIPTION: Colonies usually much branched, intertidal colonies can be small, colony shape slender, elongate with a tendency to pinnate growth (Atlantic populations); stem usually monosiphonic or occasionally only slightly polysiphonic (2-5 tubes) very close to base. Hydranths with 20-30 tentacles, large euryteles dispersed on hydranth body, not clustered along basal groove.

Male sporosacs on non-reduced hydranths, up to five per hydranth, two-chambered; in advanced stages tentacles sometimes atrophied.

Female gonophores develop on normal or slightly smaller hydranths with normal number of tentacles, up to seven gonophores per gonozooid, spadix simple, long; gonozooid during later development not or only tentacles atrophied. Encapsulated embryos attached along pedicel.

Nematocysts: small tentacular microbasic euryteles; large complementary microbasic euryteles, shaft in intact capsule spanning 2/3 to 4/5 of capsule length, spines on discharged shaft small.

Colours (Allman, 1872): Hydranths reddish; male sporosacs with red spadix; female gonophores orange-red.

DIMENSIONS: Shoots up to 15 cm high, width usually much less (2-5 cm); hydranth 0.7-0.8 mm high, diameter 0.4-0.5 mm, pedicel 0.17-0.22 mm. Large microbasic euryteles: (13-19.5)x(6.5-9)μm, r=1.9-2.3; small microbasic euryteles (6.5-8.3)x(2.5-4.3)μm r=2.0-2.5.

VARIATION: The colonies are stout in shallow water and more slender in deeper waters (Boero & Fresi, 1986). Some Mediterranean colonies had hydranths with distinct bright bodies (about 30 μm) in their gastrodermis, resembling large cells densely filled with spherical bodies. They did not stain with iodine and are thus unlikely to be zoxanthellae. The bodies were seen in the hydranth body, pedicels, and rarely in the tentacles. It remained unclear whether they are formation of the hydroid or exogenous, e. g. parasitic protists.

BIOLOGY: The colonies grow on a large variety of solid substrata. Along the European coasts occurring usually in depths of few metres to about 80 m (Russell, 1957; Teissier, 1965; Rees & Rowe, 1969; Christiansen, 1972; Peña Cantero & García Carrascosa, 2002). The fertility period in the Atlantic is at least from March to November (Allman, 1872; Philbert, 1935; Billard, 1927; Russell, 1957; Teissier, 1965; Christiansen, 1972). In the Mediterranean, it is present all year round except June, it is more abundant from October to March; the reproductive period is July to February (Boero & Fresi, 1986).

DISTRIBUTION: Reportedly circumglobal in warm or temperate waters, also in the Arctic, but most of the records are doubtful (Marques *et al.*, 2000b). The known distribution includes the Mediterranean and, all European coasts from the Arctic to Africa; absent from the Baltic Sea? (Billard, 1927; Leloup, 1947; Rees, 1952; Picard, 1955; Buchanan, 1956; Hamond, 1957; Russell, 1957; Christiansen, 1972; Morri *et al.*, 1991; Marques *et al.*, 2000a, 2000b; Schuchert, 2001; Peña Cantero & García Carrascosa, 2002; Vervoort, 2006). Type locality: North Sea, Whitstable, Kent, England (Boero & Cornelius, 1987).

REMARKS: *Eudendrium ramosum* is difficult to separate from a number of other species, notably also *E. merulum*, *E. arbusculum*, and *E. rameum* (Marques *et al.*, 2000b). When identifying *E. ramosum*, emphasis must be laid on the monosiphonic or only lightly fascicled stem base, the dispersed large euryteles on the hydranth body, and the non reduced gonozooids. The typical colony form was already well depicted and described by Ellis (1755) (see Fig. 12). These figures served Linnaeus to give it its present name (hence the figures can be considered as depicting the type specimen).

The diagnosis of *Eudendrium insigne* Hincks, 1861 is (after Hincks, 1868): "Colonies 10-20 mm with few branches, monosiphonic, perisarc annulated throughout, hydranths yellowish-red, male and female gonophores on intact hydranths."

Eudendrium insigne is thus also not readily separable from other *Eudendrium* species, particularly *E. ramosum*, primarily because so far no information on the nematocysts is available. Searches for type material of *E. insigne* in several museums yielded nothing. I therefore tried to collect the species again at its type locality, given by Hincks as “intertidal, on sponge, Hope's Nose”. Hope's Nose is a rocky promontory east of Torquay (Devon, England). When visited in 2007, there were only few suitable places in the intertidal zone where sponges and hydroids could grow, except for a set of three small but deep rock pools at low-water level on a quite flat rock platform. At least two of them harboured dense populations of hydroids, mainly an *Aglaophenia* species, but also *Coryne muscoides* and Campanulariidae. In one of the pools, underneath an overhang, several stems of a *Eudendrium* associated with a sponge were found. Although we have no idea on how long intertidal rock pools exist over time, their depth (40 cm) suggests that they could have been present even in Hincks's time and it is very likely that he collected *E. insigne* from these three rock pools. The recently collected *Eudendrium* stems (MHNG INVE54560) are rather small (up to 10 mm), are branched a few times, have pale orange-red hydranths, the perisarc is extensively annulated but some smooth stretches are present, and the female sporosacs are on intact or almost intact hydranths. This material thus matches Hincks's description almost perfectly and it can be assigned to *E. insigne* without hesitation. The nematocysts proved to be identical to those seen in *E. ramosum* (Fig. 13). Except for the stem heights, there is thus nothing that distinguishes *E. insigne* from *E. ramosum*. The stem size and the more pronounced annulation, however, can easily be attributed to its origin in the intertidal, wave-exposed region. *Eudendrium insigne* Hincks, 1861 must therefore be regarded as conspecific with *Eudendrium ramosum* (Linnaeus, 1758) as defined here.

Eudendrium elseoswaldae Stechow, 1921 from the region of Naples was characterized by Stechow (1923) by its long, monosiphonic stems (up to 23 cm) and the elongated hydranths without perisarc groove. Stechow (1923), who did not have fertile material, admitted that his material closely resembled *Eudendrium ramosum* depicted in Hincks (1868: pl. 13). Later authors (e. g. Picard, 1958; Marinopoulos, 1992; Boero & Bouillon, 1993) implicitly considered the species either a synonym or doubtful as they did not include it in their lists of the Mediterranean *Eudendrium* species. Marques *et al.* (2000a, 2000b) redescribed the species based on type and non-material and considered it as a distinct species characterized by the presence of large atrichous isorhizas. The type material of *Eudendrium elsaeoswaldae* (ZSM number 20040383) was also re-examined for this study. Although the colonies are rather large (up to 15 cm), there is nothing that distinguishes this material from *Eudendrium ramosum* sensu Hincks. The polyps are not all particularly elongated and those that are so appear artificially stretched. A perisarc groove is present very low on the hydranth body. An examination of the nematocysts (slide material and alcohol preserved material) gave deviant results from those reported by Marques *et al.* (2000b). The complementary capsules are clearly microbasic euryteles (Fig. 14A-H) that are indistinguishable from those of *E. ramosum*. There is thus nothing that distinguishes the type material of *Eudendrium elsaeoswaldae* from *Eudendrium ramosum* auct. *Eudendrium elsaeoswaldae* Stechow, 1921 is therefore here synonymized with *Eudendrium ramosum* (Linnaeus, 1758). As Marques *et al.* (2000b) had also other material they considered to belong to *E. elseoswaldae*, they have perhaps based their nematocyst observations on this non-type material.

Perigonimus multicornis Allman, 1876 was attributed to *Eudendrium ramosum* by Kramp (1926), but a re-examination of the type material showed that it has macrobasic euryteles and belongs to the genus *Myrionema*.

Watson (1985) found cnidophores in her Australian material identified as *E. ramosum*. Nematophores have never been found in European *E. ramosum* and Watson's material belongs perhaps to a new species.

Eudendrium rameum (Pallas, 1766) Fig. 15

Tubularia ramea Pallas, 1766: 83.

Eudendrium rameum. – Hincks, 1868: 80, frontispiece. – Allman, 1872: 334. – Fraser, 1937: 42, pl. 7 fig. 31. – Fraser, 1944: 71, pl. 11 fig. 47. – Yamada, 1954: 7, fig. 6. – Naumov, 1969: 264, fig. 133. – Millard, 1977: 3. – Marinopoulos, 1992: 58 fig. 1.6. – Marques *et al.*, 2000a: 102, figs 71-74. – Marques *et al.*, 2000b: 204. – Schuchert, 2001: 31, fig. 19A-B – Peña Cantero & García Carrascosa 2002: 35, fig. 7d-e.

Eudendrium planum Bonnevie, 1898a: 483, pl. 26 figs 28-30. **news synonym**

not *Eudendrium planum*. – Kramp, 1939: 516. – Calder & Vervoort, 1998: 9, fig. 2a-b. – Kramp, 1932a: 20, figs 9-11, 31. – Schuchert, 2001: 30, fig. 18A-B.

Eudendrium stratum Bonnevie, 1898a: 483, pl. 26 figs 22-24. **news synonym**

not *Eudendrium rameum*. – Hirohito, 1988: 84, fig. 30a-c.

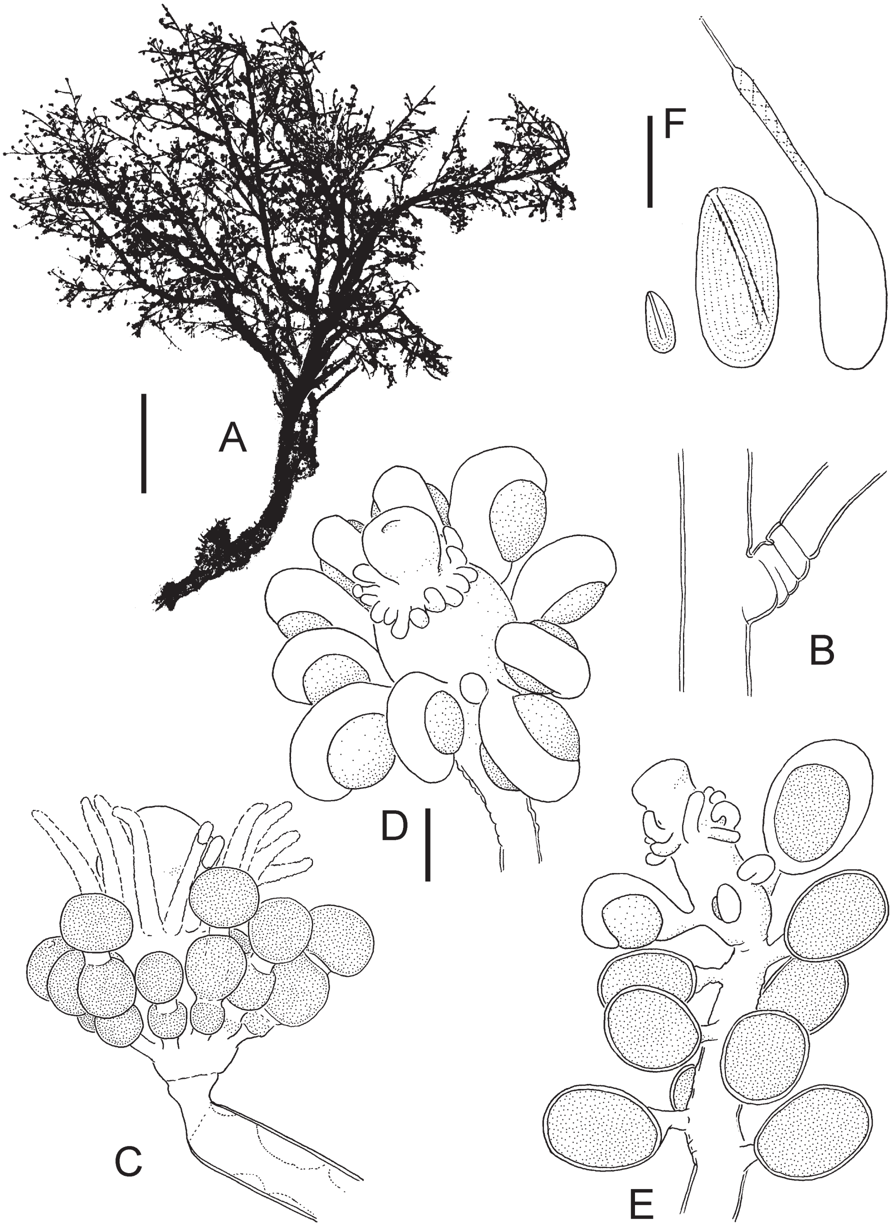

FIG. 15

Eudendrium rameum (Pallas, 1766), after preserved material from Norway (Trondheim Fjord). (A) Colony silhouette, scale bar 2 cm. (B) Base of side branch with annulation, same scale as D. (C) Hydranth with male gonophores, same scale as D. (D) Female gonophores on slightly reduced hydranth (tentacles shortened), scale bar 0.2 mm. (E) Blastostyle with eggs on partially reduced hydranth and encapsulated embryos attached to pedicel, same scale as D. (F) Nematocysts: small microbasic eurytele, large microbasic eurytele, same discharged, scale bar 10 μm.

TYPE MATERIAL EXAMINED: ZMO B1238, syntype colonies of *Eudendrium planum*, Zoological museum of Oslo; no locality or date; on label note that also *Lafoea serpens* and *Campanulina fastigata* Alder present. – ZMO B1239, type colony of *Eudendrium stratum*; no locality; fragments of polysiphonic colony, with male gonophores.

Other MATERIAL EXAMINED: MHNG INVE33539, BIOFAR station 726; The Faroes, 60.66°N 06.91°W, depth 400m; 29 Sept. 1990, infertile. – MHNG INVE33588, BIOFAR station 554; The Faroes, 61.93°N 6.49°W, depth 62m; 22 Sept. 1989, 2 infertile colonies. – MHNG INVE38221; Mediterranean, France, Marseille, Grotte de Figuier; 24 April 1970; leg. H. Zibrowius; fertile female. – MHNG INVE49888; Italy, Naples; 21 Jan. 1892; infertile. – SMNH89692; Norway, SE to S off Bergen, 182-291m; collected ca. 1874; material mentioned in Jäderholm (1909); no hydranths or gonophores left. – ZSM, Stechow collection, Valdivia station 3, Aberdeen, Scotland, depth 79m, 57°26'N 1°28'W, det. E. Stechow, without gonophores. – ZSM, CT349, Material Bedot Nr. 69, det. E. Stechow, Cap Misano near Naples, 23 Jan. 1892, several colonies, max. 5cm, fertile male. – ZSM, slide 20000794, Naples, fragments of male and female colony. – ZMUC, without number; Norway, Trondheim Fjord, Vennes; depth 6.5m; 18 Sept. 1934; female and male colonies.

DIAGNOSIS: Colonies large, polysiphonic, usually tree-like with a distinct trunk, female on hydranth with hypostome, with variably developed tentacles, spadix simple; male gonophores on normal hydranth which can get somewhat reduced during maturation. Complementary nematocysts a microbasic eurytele, dispersed on hydranth body, shaft thin, in undischarged capsule spanning 4/5 or more of capsule.

DESCRIPTION: Colonies much branched, stem and branches polysiphonic, terminal branches simple. Colony form usually tree-like with a thick trunk. Hydrorhiza root-like, creeping. Perisarc thick, short stretches of annulation frequent, especially at bases of branches. Hydranths typical for genus, without nematocyst buttons or ring, 16-24 tentacles.

Male gonophores on normal, tentacle bearing hydranth which is not or only slightly reduced after maturation of the gonads, up to 12 gonophores per hydranth, in dense whorl around body of hydranth, with one to three chambers, without terminal nematocyst clusters.

Female gonophores (up to 16 per hydranth) develop on hydranths with a hypostome and with shortened tentacles, spadices simple, tentacles get variably reduced: Fertilized eggs loose spadix and get encapsulated in perisarc membrane and attached to pedicels of former blastostyle, the latter can resume growth.

Nematocysts: small microbasic euryteles predominantly on tentacles; large microbasic euryteles, shaft with fine spines, only slightly swollen and sometimes indistinguishable from mastigophores type, shaft in undischarged capsule long, spanning 4/5 to 1/1 of capsule length, discharged shaft about as long or slightly longer than capsule.

Colours: perisarc brown, hydranths pale.

DIMENSIONS: Colonies 4-20 cm, mostly below 12 cm; hydranths 0.5 mm diameter and total height 0.7-0.8 mm; diameter of hydranth pedicels 0.15-0.2 mm, diameter of basal stem tubes 0.23-0.26 mm. Small microbasic eurytele (7-9)x(3-5)μm, r= 1.8-2.5. Large microbasic eurytele (20-26)x(8-11)μm, r= 2.4-2.8.

BIOLOGY: Mostly recorded in depths from a few metres to about 100 m on hard bottoms (Christiansen, 1972). There are not enough data on the fertility periods available. Fertile colonies from the Mediterranean have been found in the months

January, April, and September (Marques *et al.*, 2000b; this study). For the North Sea, Hamond (1957) give a fertile period of November to March. In Norway, Christiansen (1972) observed sporosacs between June and October.

DISTRIBUTION: The species has been recorded in almost all oceans, but only identifications also using nematocyst morphology can be considered reliable. It is thus certainly present in the Mediterranean, along the European Atlantic coast, Greenland, Iceland (Marques *et al.*, 2000a and 2000b; Schuchert, 2001; Peña Cantero & García Carrascosa, 2002), and southern Indian Ocean (Millard, 1977). Type locality: Mediterranean (Pallas, 1766).

REMARKS: Pallas (1766) described *Eudendrium rameum* as a polysiphonic, tree-like colony which he qualified as common in the Mediterranean ("Locus: *Mare Mediterraneum, præcipue ubi Filigrana Planci abundat*"). The species as conceived today is not common in the Mediterranean and Pallas's diagnosis could either refer to *E. rameum*, *E. glomeratum*, or even *E. racemosum*. While earlier authors diagnosed this species mostly through its tree-like colony form, our current scope of the species relies additionally on the presence of dispersed large microbasic euryteles and on the unreduced or only moderately reduced blastostyles. However, Marques *et al.* (2000a) are right by qualifying this species and *E. ramosum* as confusing. Preliminary molecular data (Moura *et al.*, 2008 and Fig. 2) indicate that our current concept of *E. rameum* comprises several lineages and perhaps also several species.

The type specimens (2 colonies plus some fragments) of *Eudendrium planum* Bonnevie, 1898a were examined for this study. The stems are up to 6 cm high, strongly polysiphonic. The colonies are female, only encapsulated embryos attached to blastostyle pedicels are present. There are no gonophore stages with spadices. The arrangement is in no way particular. As nematocysts there are two types of microbasic euryteles, small almond-shaped (7-8)x(3)μm (tentacular type) and large elongate oval ones sized (16-19)x(6-7)μm, r=2.5-3.2. The shaft in the intact larger eurytele spans almost the whole length of the capsule. All these data match perfectly our current concept of *Eudendrium rameum*. *Eudendrium planum* should therefore be regarded as a synonym of the former species. Calder, & Vervoort (1998) and Schuchert (2001) also described nematocysts of tentatively identified *E. planum*. Both studies found macrobasic euryteles, meaning that these specimens are neither *E. planum* nor *E. rameum*. The specimen of *E. planum* described by Kramp (1939; Kara Sea; kept by ZMUC) has differently shaped complementary capsules (with pointed ends) without a visible shaft inside. Also this record is thus not *E. planum*, more likely it is an undescribed species.

Together with *E. planum*, Bonnevie (1898a) also described *Eudendrium stratum*. She characterized this species by the peculiar covering of the stem. The type specimen was re-examined for this study. It consists of several polysiphonic stem fragments. Male gonophores with 3 chambers are present on unreduced hydranths. The stem is covered by a soft tissue with a spongy, cellular structure containing no nematocysts. It is unclear what this covering is, but is very unlikely that it was produced by the hydroid and it must be foreign. The nematocysts of the hydroid appear identical to *E. planum*, though somewhat larger. The complementary capsules are likely heteronemes (none seen discharged) with a size of (20-22)x(9-10)μm. The apparent shaft is often not well visible, but when visible, it spans the entire length of the capsule, sometimes it is even somewhat curved. There are no traits visible in this material that would preclude its identification as *E. rameum* as defined here. *Eudendrium stratum* is therefore regarded as a synonym of *E. rameum*.

Eudendrium moulouyensis Marques, Peña Cantero & Vervoort, 2000 Figs 16-19

? *Eudendrium hargitti*. – Castric & Michel, 1982: 82, fig. [not *Myrionema hargitti* (Congdon, 1906)]

Eudendrium moulouyensis Marques, Peña Cantero & Vervoort, 2000: 200, fig. 1. – Peña Cantero & García Carrascosa 2002: 31. – Puce *et al*., 2005: 202, fig. 1e, 2l-m. – De Vito *et al*., 2008: in press.

MATERIAL EXAMINED: MHNG INVE49716; Mediterranean, Spain, Mallorca, Cala Murada, depth 4m, 20 Aug. 1999; female and male colonies on roots and old leaves of *Posidonia oceanica*. – Italy, Calabria, Punta Palascìa, depth 10-15m, 19 Aug. 2004, infertile colonies; private collection of D. De Vito. – Italy, Calabria, Punta Palascìa, depth 10-15m, 8 Nov. 2006, infertile colonies; private collection of D. De Vito. – Italy, Calabria, Punta Facì, depth 5-10 m, 14 Dec. 2004, female and male colonies; private collection of D. De Vito.

DIAGNOSIS: Colonies branched, gastrodermis with numerous zooxanthellae, complementary nematocysts large microbasic euryteles, male blastostyle normal hydranth, female gonophores on hydranth with shortened tentacles.

DESCRIPTION: Colonies erect, branched, mostly monosiphonic, sometimes stem base moderately polysiphonic (2-4 tubes), perisarc smooth, occasional annulated stretches especially near origin of branches. Gastrodermis of coenosarc and hydranths contains zooxanthellae (Fig. 17), density variable, some hydranths may have only few zooxanthellae. Hydranths with one whorl of 25-30 tentacles, scattered large euryteles on hydranth body. Epidermis of hydranths often, but not always, with spumous inclusion bodies (Fig. 18D), especially between tentacle bases.

Male blastostyles develop as normal hydranths, not reduced when mature, with up to 10 sporosacs per hydranth, sporosacs two-chambered, with scattered euryteles, without terminal nematocyst button.

Female sporosacs develop concomitantly with hydranth bearing them, the latter remains usually somewhat reduced, the size small and the tentacles short; spadix simple, with scattered large euryteles; fertilized eggs encapsulated and attached to perisarc of blastostyle pedicels. Nematocysts: small and large microbasic euryteles. Colour: gastrodermis brownish due to zooxanthellae.

DIMENSIONS: Colonies up to 4 cm high; hydranths 0.5-0.75 mm high and 0.35 mm wide; pedicel diameters 0.1-0.16 mm. Small microbasic euryteles (7-8.5)x(3-3.5)μm, r=2.1-2.8. Large microbasic euryteles (13-17)x(6-8.5), r= 1.9-2.6. Diameter of zooxanthellae 8.5-13 μm.

BIOLOGY: Occurs in shallow waters from about 1 to 15 m.

DISTRIBUTION: Mediterranean, perhaps also southern Brittany (Castric *et al*., 1987, as *Eudendrium hargitti*). Type locality: Mediterranean Sea, Morocco, Chafarinas Islands.

REMARKS: Except for the zooxanthellae, this species resembles closely – or is indistinguishable – from *Eudendrium ramosum*. Some colonies from Calabria even

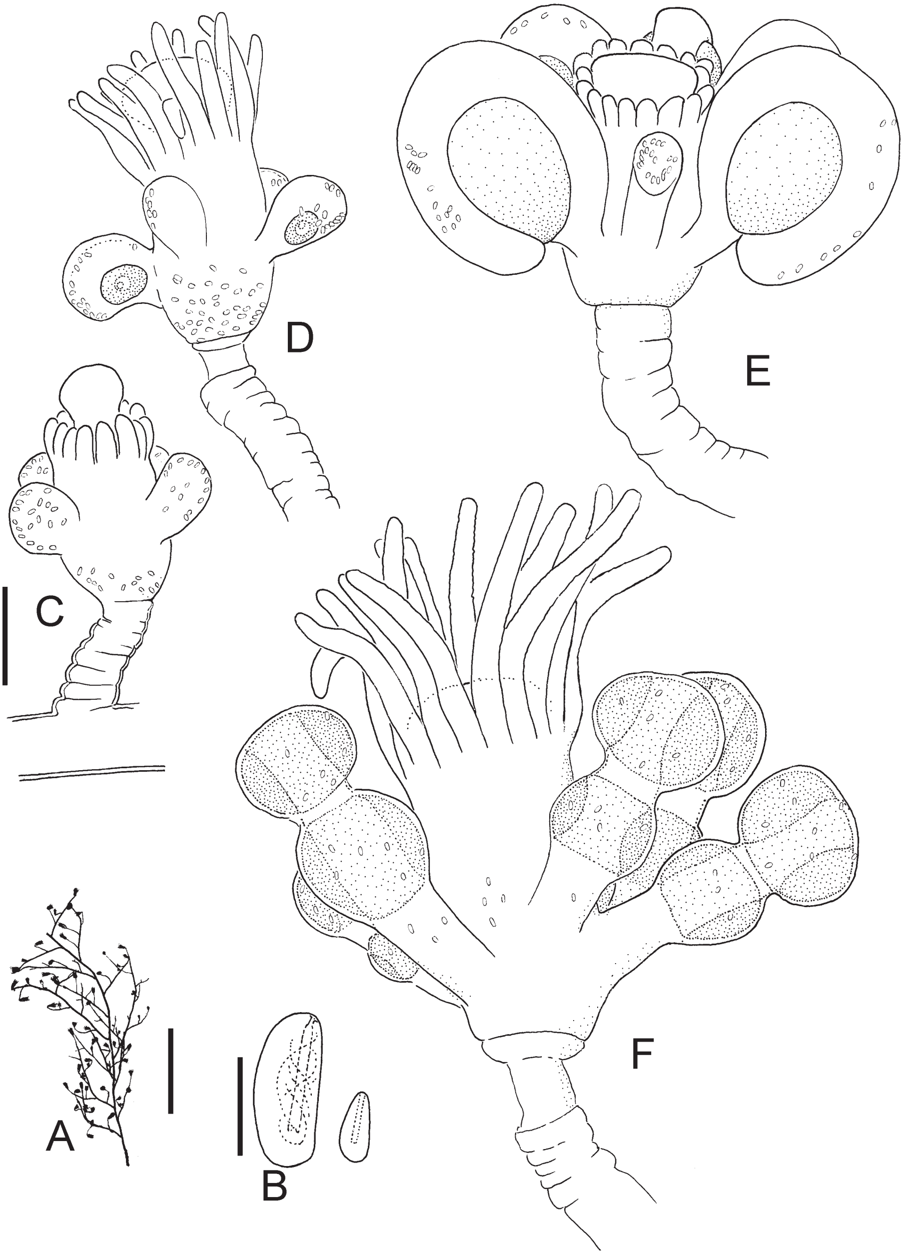

FIG. 16

Eudendrium moulouyensis Marques, Peña Cantero & Vervoort, 2000, after preserved material. (A) Colony silhouette, scale bar 1 cm. (B) Nematocysts: undischarged large and small microbasic euryteles, scale bar 10 μm. (C) Developing female blastostyle, scale bar 0.2 mm. (D) More advanced female blastostyle, same scale as C. (E) Mature female blastostyle, same scale as C. (F) Mature male gonozooid, same scale as C.

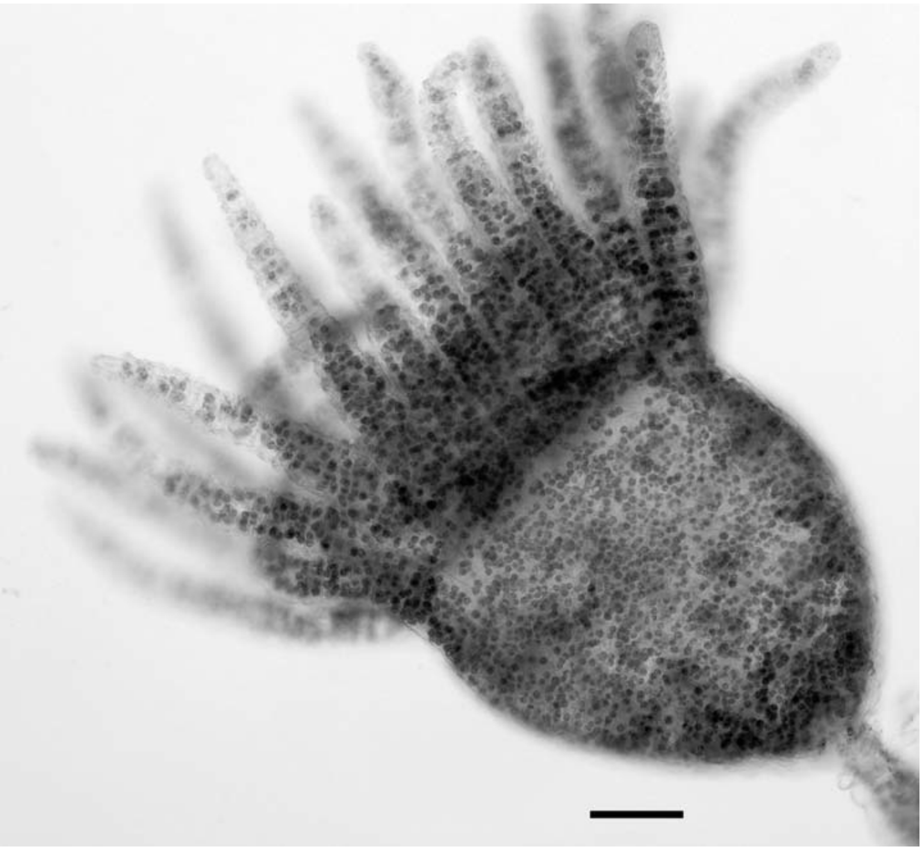

FIG. 17

Eudendrium moulouyensis Marques, Peña Cantero & Vervoort, 2000; hydranth with stained zooxanthellae (iodine reaction); scale bar 0.1 mm.

had a moderately polysiphonic stem base, thus reinforcing the similarity. The density of the zooxanthellae is variable, while some hydranths have only few, others of the same colony may have many. The density is also variable between colonies.

Several samples had conspicuous white inclusion bodies in the epidermis, especially between the tentacle bases. They are easily visible in living and preserved material as white spots. Under the microscope, these bodies look like spumous cells (Fig. 18D). The content does not react with iodine, thus it contains no starch, nor is it calcareous as it does not react with lactic acid. Not all colonies have them. Identical spumous bodies were also found in some *E. ramosum*. It is not clear what these inclusions are; perhaps they are parasitic protists.

Castric *et al*. (1987) depict a zooxanthellae containing *Eudendrium* they identified as *Eudendrium hargitti*. Although they give not enough details, the depicted microbasic eurytele matches *E. moulouyensis* rather than *Myrionema hargitti* (=*M. amboinense*) which has macrobasic euryteles. *Eudendrium moulouyensis* thus likely also occurs along the southern coasts of Brittany.

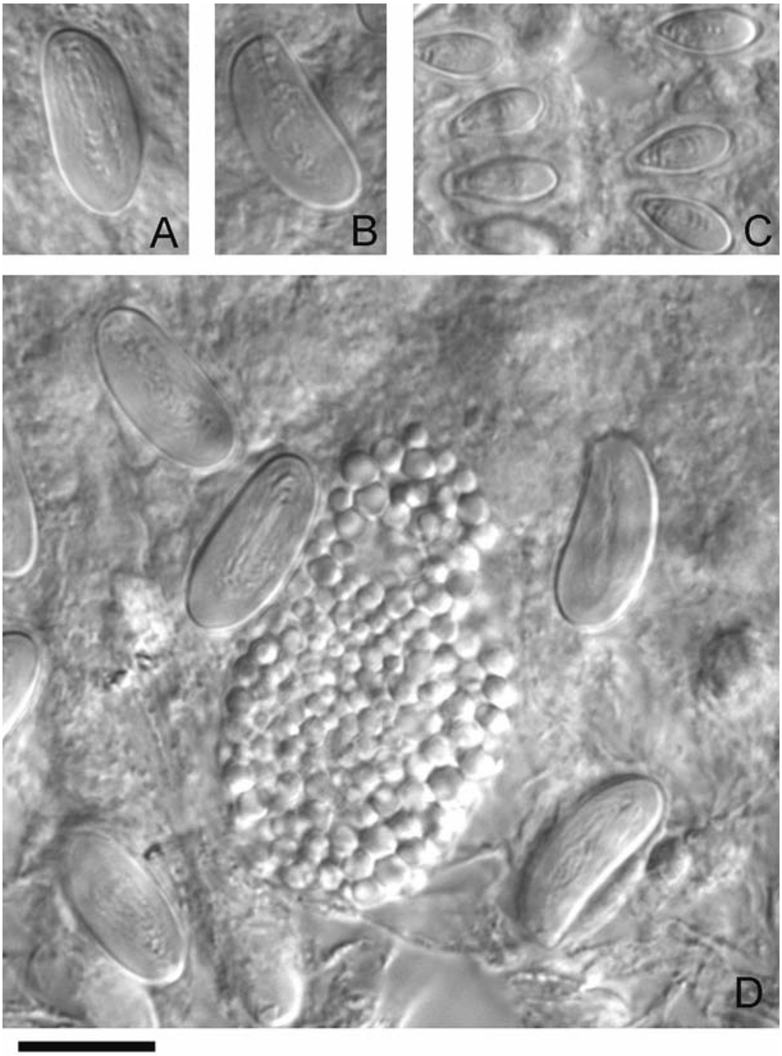

FIG. 18

Eudendrium moulouyensis Marques, Peña Cantero & Vervoort, 2000, microscopic preparations of preserved material from Otranto, scale bar 10 μm valid for all sections. (A-B) Undischarged large euryteles. (C) Small microbasic euryteles. (D) Undischarged large euryteles and a spumous inclusion body (centre).

***Eudendrium* cf. *merulum* Watson, 1985 Figs 19-20**

Eudendrium merulum Watson, 1985: 200, figs 53-58. – Bavestrello & Piraino, 1991: 200, figs 2-4. – Marques *et al*., 2000a: 100, figs 64-66. – Marques *et al*., 2000b: 203. – Peña Cantero & García Carrascosa, 2002: 30, fig. 5a-b. – Bouillon *et al*., 2004: 59, fig. 35A-G.

MATERIAL EXAMINED: MHNG INVE49879; Black Sea, Bulgaria, Varna, St. Constantine and Helena yacht port; 1 m; 17 Aug. 2003; female colonies. – MHNG INVE49880; Bulgaria, Varna, St. Constantine and Helena yacht port; 1 m; 14 July 2003; female and male colonies. –

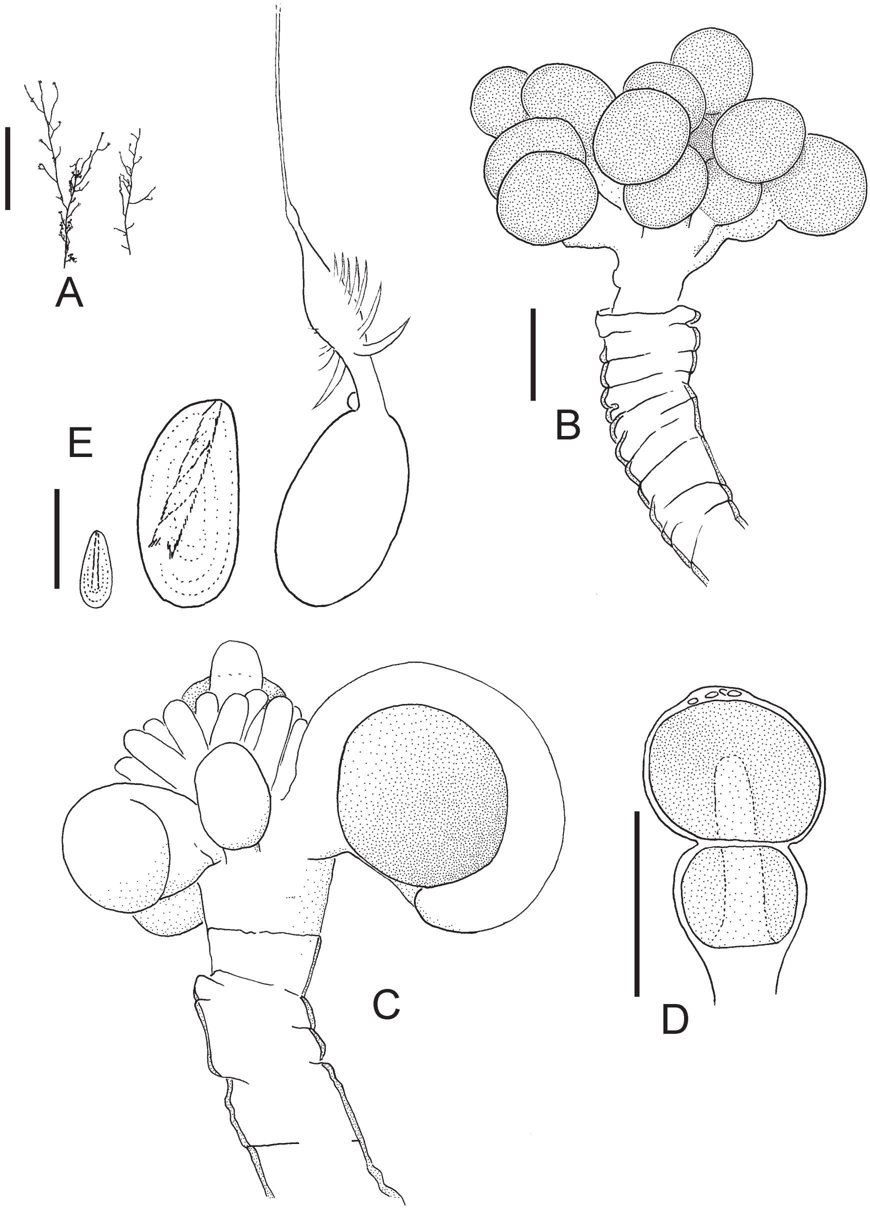

FIG. 19

Eudendrium cf. *merulum* Watson, 1985; A-C after preserved material from the Black Sea, D after Mediterranean material. (A) Colony silhouettes, scale bar 1 cm. (B) A small male blastostyle, note that they can be larger and comprise twice as many sporosacs; scale bar 0.2 mm. (C) Female blastostyle, some gonophores at early stages of development, short tentacles are present; same scale as B. (D) Male sporosac in semitransparent view, note terminal button with a few nematocysts; scale bar 0.1 mm, (E) Nematocysts: small microbasic euryteles, undischarged and discharged large microbasic eurytele, note the prominent spines; scale bar 10 μm.

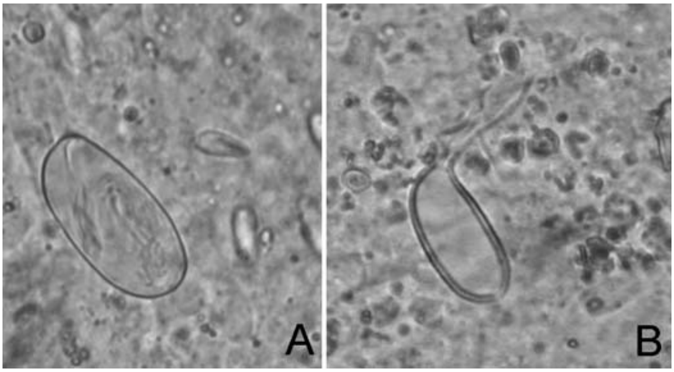

FIG. 20
Eudendrium cf. *merulum* Watson, 1985; complementary microbasic eurytele of colony from the English Channel. Length of undischarged capsule 21-23 μm, magnifications of A and B are not identical. (A) Undischarged capsule. (B) Same discharged.

MHNG INVE55454; Black Sea, Bulgaria, Varna, St. Constantine and Helena yacht port; 1 m; 30 July 2007; female and male colonies; 16S DNA sequence accession number of one male stem **AM991291**. – MHNG INVE55455; Bulgaria, Varna, St. Constantine and Helena yacht port; 1 m; 25 July 2007; female and male colonies; 16S DNA sequence of one male colony identical to **AM991291**. – Italy, Otranto, Punta Facì; 5-10 m; 25 July 2005; infertile; pers. collection D. De Vito. – Italy, Otranto, Punta Facì; 1-5 m; 23 July 2004; infertile; pers. collection D. De Vito. – English Channel, France, Normandy, Cotentin Penisula, Agon; depth 0 m; 20 Aug. 2005; small infertile monosiphonic colonies on sponge; material not preserved, all used for nematocyst examination and DNA extraction; 16S DNA sequence accession number **AM991300**. – Atlantic, Spain, Cantabria, Noja, Playa de Ris, depth 0-2 m; 19 Jul. 2003; small stolonal colony on sponge, male blastostyles completely reduced, large (24μm) supplementary microbasic euryteles with thick shaft; material not preserved, all used to make DNA, 16S DNA sequence identical to AM991300. – MHNG INVE27670, as *Eudendrium* cf. *merulum*; Canary Islands, Tenerife, Radazul, 20-30 m; 2 Oct. 1999; male and female colonies.

DIAGNOSIS: Colonies branched, monosiphonic, cnidome comprises large microbasic eurytele having a thick shaft and large spines; male blastostyle completely reduced, gonophores without terminal button; female blastostyles reduced hydranth with rudimentary tentacles and without hypostome.

DESCRIPTION: Colonies erect, branched, monosiphonic, arising from creeping stolons. Stems with up to 15 hydranths, rarely more; perisarc with smooth, corrugated, or annulated stretches. Hydranths as typical for genus, 16-24 tentacles; basal grove near proximal end, large nematocysts scattered on hydranth body, sometimes concentrated in indistinct band above basal grove.

Male blastostyles completely reduced, sporosacs as tuft at end of pedicels, 1-2 chambered, rarely a third smaller proximal chamber present, connection between chambers thick, without distinct neck, terminal nematocyst button with some large euryteles can be present in mature sporosacs.

Female blastostyle small, reduced hydranth without hypostome, with few tentacle rudiments, about 4-6 sporosacs per blastostyle; sporosacs with simple, curved spadix. Fertilized eggs encapsulated in thin perisarc membrane and attached to blastostyle pedicels.

Nematocysts: small microbasic euryteles occurring predominantly on tentacles; large microbasic euryteles, shaft of undischarged capsule spanning 3/5 of capsule and rather thick, discharged shaft also thick and with strong swelling, with numerous and strong barbs, thread relatively thick and also barbed.

Colours (Bavestrello & Piraino, 1991); hydranths are whitish.

DIMENSIONS: Stems usually up to 2 cm, diameter of hydranth pedicels 0.18-0.2 mm, hydranths 0.45-0.6 mm from groove to mouth, stem diameter at base 0.15 mm. Small microbasic euryteles (6-8)x(2.5-4)μm, r= 2-2.8; large microbasic euryteles (18-26)x(9-13.5)μm, r= 1.8-2.4 (nematocyst measured in preserved material).

BIOLOGY: Occurs in depths of 1-15 m. In the Mediterranean and Black Sea it grows on rocks, barnacles and other solid substrata, gonophores were observed from January to August. The Atlantic colonies grew on sponges and other substrates.

DISTRIBUTION: Australia (Watson, 1985); Yemen (Marques *et al.*, 2000a); western and eastern Mediterranean (Bavestrello & Piraino, 1991; Marques *et al.*, 2000b; Peña Cantero & García Carrascosa, 2002); Black Sea (new record); Canary islands, Gulf of Biscaya and English Channel (new records, but see below). Type locality: Bass Strait, Victoria, Australia.

REMARKS: *Eudendrium merulum* as conceived by Marques *et al.* (2000b) and also the present paper resembles *E. ramosum*, but has completely or strongly reduced blastostyles. The shaft of the large microbasic euryteles of *E. merulum* also differs in being much thicker and in having large spines (comp. Figs 13 and 19E). Marques *et al.* (2000b) state that the male sporosacs have a narrow connection between the successive chambers. This was not found in the material examined in this study.

Some available 16S sequence data (publication in preparation, see also Fig. 2) indicate that the Atlantic, Mediterranean, and Black Sea populations here attributed to *E. merulum* belong to at least three unrelated lineages, likely representing three different biological species. As it is likely that they are also distinct from the Australian *E. merulum*, the species as currently perceived is certainly a species complex and it was here therefore listed as *Eudendrium* cf. *merulum* only.

Eudendrium merulum was originally described based on material from southern Australia, where it is a rather rare species (J. Watson, pers. com.). Bavestrello & Piraino (1991) then found several Mediterranean colonies that matched the diagnosis of *E. merulum*. Later also Marques *et al.* (2000b) described additional Mediterranean material. The referral to the European material to the Australian *E. merulum* is somewhat arbitrary, it could as well have been attributed to *E. kirkpatriki* Watson, 1985. This is especially true for the material seen in this study which had female blastostyles with some tentacle rudiments. In the previously described specimens, the female blastostyles were completely atrophied. However, the presence of rudimentary tentacles on the blastostyles is often only transitory and their presence/absence falls within the intraspecific variation observed in other species. Other observed slight differences to the description of Watson (1985) and Bavestrello & Piraino (1991) concern the male gonophore: they have 1-2 chambers instead of 2-3, lack the thin neck between them, and have an occasional terminal button with some euryteles. All these small differences are thought to be insignificant, or in current taxonomic practice they are considered at least insufficient to separate different species. The material from the Canaries was particularly difficult to evaluate and differed from the other samples, but without showing acceptable diagnostic traits that would have allowed diagnosing it as a distinct species. The colonies were much larger (10 cm, mostly monosiphonic, shape resembling *E. ramosum*), the stem diameter was much thicker than in the other *E. merulum* (0.34 mm), the hydranths were larger (0.7 mm), the spadix longer with a tendance to form a spiral, and the large euryteles were larger (25-30 μm long) and they were concentrated in an indistinct band near the basal groove. The colonies appeared thus intermediate between *E. ramosum* and *E. arbuscula*.

Eudendrium merulum is part of the *E. ramosum* group, which comprises several *Eudendrium* species with a large complimentary eurytele and which are often not reliably identifiable (see also Marques, 1995). It is unlikely that detailed morphological analyses of allopatric populations can provide us with reliable species diagnoses. Useful diagnostic features might become more evident only after a DNA analysis will have provided us with a robust phylogenetic tree of the species.

Eudendrium annulatum Norman, 1864 Figs 21-24

Eudendrium annulatum Norman, 1864: 83, pl. 9 figs 1-2. – Hincks, 1868: 83, pl. 15 fig. 1. – Allman, 1872: 339. – Bétencourt, 1899: 4, pl. 1 figs. 1-4. – Bonnevie, 1898a: 482, pl. 26 figs 31-33. – Broch, 1910: 201. – Broch, 1916: 62, fig. T. – Fraser, 1944: 62, pl. 7 fig. 33. – Christiansen, 1972: 289.

in part *Eudendrium annulatum*. – Jäderholm 1909: 51, pl. 4, figs 3-4. – Naumov, 1969: 265, fig. 134.

not *Eudendrium annulatum*. – Leloup, 1940: 5, 29. –Yamada, 1954: 2, text-fig. 1.

not *Eudendrium annulatum*. – Schuchert 2001: 26, fig. 15A-C. [=*E. vaginatum* Allman, 1863]

Eudendrium cf. *arbuscula*. – Schuchert, 2001: 33, fig. 21. [not *Eudendrium arbuscula* Wright, 1859]

TYPE MATERIAL EXAMINED: BMNH 1898.5.7.40; syntypes of *Eudendrium annulatum* Norman, 1864; Shetland Isles, Burrafirth Caves, "Burness Hall"; coll. 1863; 2 infertile colonies, one colony likely depicted in Norman (1864). – RMNH Coel28436, syntype (slide preparation); Great Britain, Shetland, Burrafirth Caves, "Burness Hall".

OTHER MATERIAL EXAMINED: BELUM Md363; Scotland, Outer Hebrides, Scarba, NE Rubh A Chuil; 56°11.96'N 05°41.30'W; 27 m; 12 July 1982; infertile. – BELUM Md628; Scotland, Outer Hebrides, St. Kilda, NE of Stac Lee; 57°52.01'N 08°30.45'W; 25 m; 9 July 1984; infertile. – BELUM Md421; Scotland, Outer Hebrides, Scarba, Bealach a Choin Glais (Grey Dogs Race); 56°12.50'N 05°41.70'W; 17 July 1982; infertile. – BELUM Md108, as *E. ramosum*; Northern Ireland, Donegal, south side of Rathlin O'Birne; 54°22.38'N 05°33.15'W; 30m; 21 Nov. 1976; fertile females and males. – BELUM Md109; Northern Ireland, Donegal, Torneady Point; 55°01.51'N 08°32.43'W; 36 m; 8 April 1978; infertile. – BELUM Md629; Northern Ireland, Antrim, Rathlin Island, NE of Farganlack Point; 55°18.74'N 06°15.06'W; 24m; 7 July 1984; infertile. – BELUM Md630; Northern Ireland, Antrim, Maidens, W Side of The Bushes; 54°55.38'N 05°43.84'W; 25m; 25 July 1983; infertile.

DIAGNOSIS: Large polysiphonic colonies, stems with bark-like covering, hydranths large (>0.4 mm diameter), usually with basal ring of large microbasic euryteles, blastostyles aggregated on upper side of branches, their pedicels relatively short, gonophores with distal nematocyst buttons.

DESCRIPTION: Colonies large, stiff, rather stout and coarse, stems and branches polysiphonic, typically with rather elongate stem or primary branches provided with shorter side-branches resembling somewhat a bottle-brush (Fig. 21A). Stem and

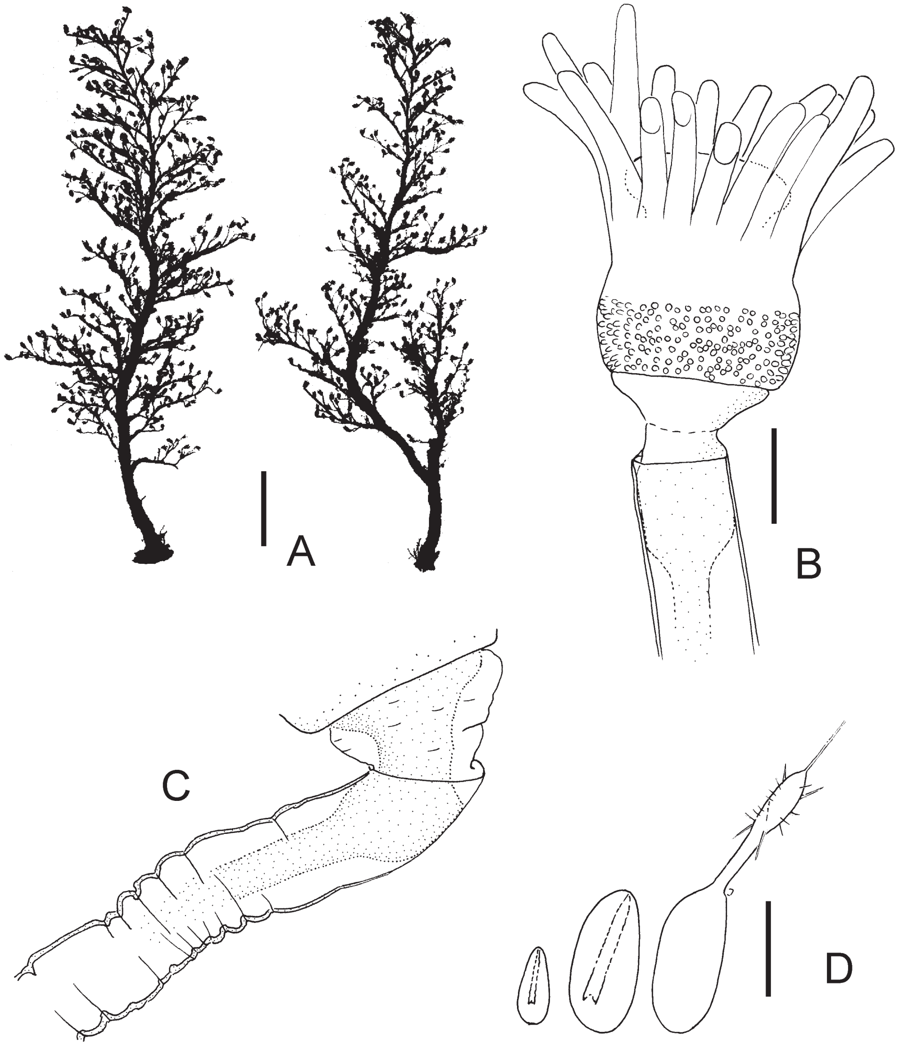

FIG. 21

Eudendrium annulatum, after preserved material from Northern Ireland. (A) Colony silhouettes showing typical colony form, scale bar 1 cm. (B) Typical hydranth, note broad band of nematocysts on body, no perisarc collar present, scale bar 0.2 mm. (C) Terminal branchlet and hydranth base with short, filmy perisarc collar, same scale as B. (D) Nematocysts: small microbasic euryteles, large microbasic eurytele, large eurytele discharged.

thicker branches often covered by a smooth layer of coalesced stolonal tubes forming a dense-meshed, bark-like covering (Fig. 23). Perisarc of branches brown, thick, with smooth stretches and some annulated or corrugated stretches. Hydranths large, 16-22 tentacles, on body a broad band densely beset with large euryteles, these may be missing or inconspicuous in some colonies; basal groove marked, near base of body, filmy perisarc originating in basal groove sometimes loose and forming a short perisarc

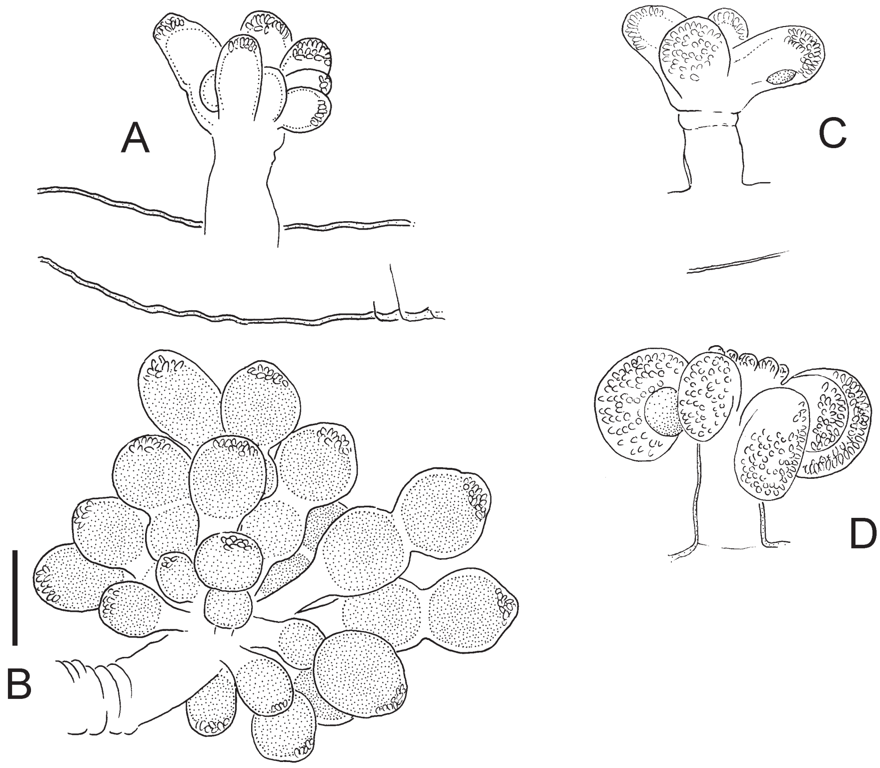

FIG. 22

Eudendrium annulatum, after preserved material from Northern Ireland. (A) Developing male blastostyle, note presence of large euryteles at the tips of the developing gonophores, same scale as B. (B) Mature male blastostyle, scale bar 0.2 mm. (C) Developing female blastostyle, in the gonophore at right an immature egg is visible, same scale as B. (D) Slightly more advanced female blastostyle than shown in C, the spadices with euryteles curve over immature eggs, some tentacle rudiments with large euryteles are visible at the top, same scale as B.

collar (Fig. 21C). Colonies dioecious, blastostyles on short pedicels, often in dense aggregates on upper side of distal, monosiphonic hydrocladia (Fig. 24).

Male gonophores are formed in tufts at the end of short branchlets (Fig. 22A), hydranths absent at all stages of development, distal ends of sporosacs with numerous large eurytele capsules, mature gonophores 1-2 chambered, when two-chambered both chambers equivalent, terminal nematocyst button nearly always present (Fig. 22B).

Female gonophores develop like male ones at end of branchlets, eggs present at early stage, curved spadix beset with euryteles, during later development some transient, very short tentacle rudiments may form (Fig. 22C-D) that are later lost.

Nematocysts: small microbasic euryteles in tentacles; larger microbasic eurytele, relatively rounded capsule, shaft in intact capsule ca. 3/4 of capsule length, discharged slightly longer than capsule, directed obliquely, distinctly swollen and with coarse spines, unambiguously identifiable as eurytele. Colours: perisarc brownish, hydranths white.

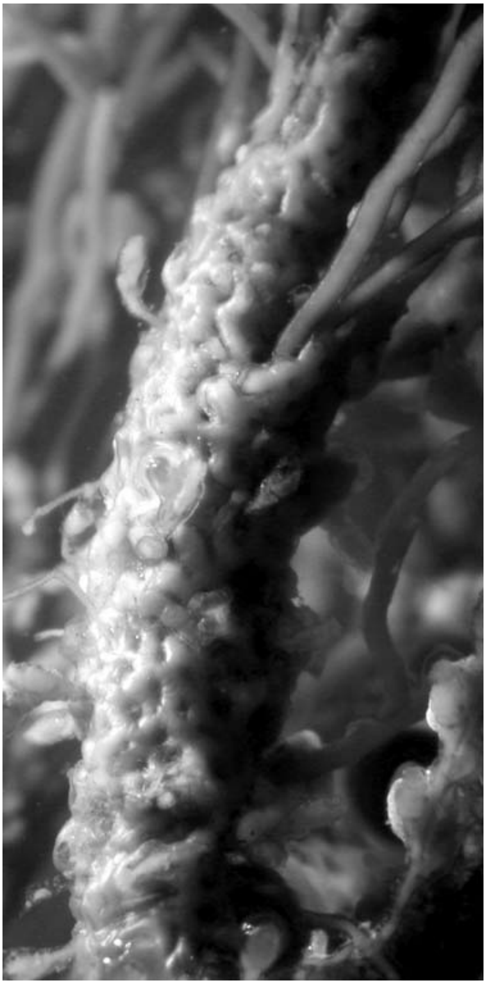

FIG. 23
Eudendrium annulatum, type colony, bark-like overgrowth on stem.

DIMENSIONS: Colony height 4-10 cm. Hydranth diameter below tentacles 0.35-0.57 mm, height from basal groove to mouth 0.5-0.6 mm. Diameter of hydranth pedicels 0.18-0.24 mm. Small eurytele (8-9.5)x(3.5-4.5)μm, r= 2-2.7. Large eurytele (15-17)x(6.5-7.5)μm, r= 2.1-2.5.

BIOLOGY: Insufficient data on fertility periods are available, perhaps fertile during autumn and winter (comp. examined material; Bétencourt, 1899).

DISTRIBUTION: North Atlantic, boreal to Arctic regions (Norman, 1864; Levinsen, 1893; Bonnevie, 1898a; Broch, 1910, 1916; Fraser, 1944; Naumov, 1969; Christiansen, 1972). The southernmost trustworthy record is by Bétencourt (1899) for

FIG. 24

Eudendrium annulatum, preserved material from Northern Ireland showing male blastostyles in dense stands on upper side of hydrocladium.

the English Channel, although he had beached material only. There are also several unreliable records. Type locality: Shetland Isles, Burrafirth, Bunness Hall cave, depth 0.3 m below ELWS.

REMARKS: The epithet of *E. annulatum* is misleading. Neither the type material nor the other samples from Scotland and Ireland are extensively annulated. There are annulated stretches at the origin of branches and some hydranth pedicels are entirely annulated, but most of the perisarc is smooth. The suggestive name has occasionally led other authors to use it for species with a complete annulation like *E. ritchiei* (see e.g. Millard, 1975).

Eudendrium annulatum has been synonymized with *E. vaginatum* Allman, 1863 by Marques *et al.* (2000a), but this is incorrect (see discussion under *E. vaginatum*).

It has so far been ignored that *E. annulatum* has usually a belt of nematocysts on the hydranth body and that it has male gonophores with terminal nematocyst buttons (Figs 21B, 22A-B). It resembles thus closely *E. arbuscula* Wright, 1859 with which it also shares the same nematocysts and the characteristics of the blastostyles. However, both species appear to be distinct and their differences are given under *E. arbuscula* and in the key to the species. The belt of nematocysts can apparently be absent in some specimens. In the syntype material, only one colony of the two had such a belt.

The material from Spitsbergen identified by Leloup (1940) as *E. annulatum* was re-examined for this study (IRSNB IG12981). It is a small *Eudendrium*, originally growing on *Halecium muricatum*, and it does unlikely belong to *E. annulatum*. The state of the material does not allow a reliable identification, but it resembles *E. capillare*.

Eudendrium arbuscula Wright, 1859 Figs 25-27

not *Tubularia arbuscula* D'Orbigny, 1846.
Eudendrium arbuscula Wright, 1859: 113, pl. 9 figs 5-6.
Eudendrium arbusculum. – Hincks, 1868: 84, pl. 14 fig. 1. – Calder, 1972: 225, pl. 2 fig. 5.
Eudendrium arbuscula. – Allman, 1872: 336. – Bonnevie, 1899: 50. – Broch, 1928: 113. – Weill, 1934a: 77, fig 70a-b. – Weill, 1934b: 386, fig. 236. – Castric & Michel, 1982: 82, fig. – Marques & Vervoort, 1999: 16. – Marques *et al.*, 2000b: 81, figs 11-15. – ICZN, 2000: 180-181. – Faasse & Vervoort, 2005: 61, fig. 4, photos 4, 7, 8.
Eudendrium rigidum Allman, 1876: 253, pl. 9 figs 3-4. – Kramp 1926: 242, synonym.
Eudendrium wrightii Hartlaub, 1905: 547, new name.
? *Eudendrium caricum* Jäderholm, 1908: 5, pl. 1 fig. 4, pl. 2 fig. 1. – Calder, 1972: 225, synonym.
Eudendrium wrighti. – Broch, 1916: 60, map. T.
not *Eudendrium arbusculum*. – Hamond, 1957: 300, figs. 7, 8.
not *Eudendrium arbuscula*. – Marinopoulos, 1992: 58, fig. 1.8.
not *Eudendrium* cf. *arbuscula*. – Schuchert, 2001: 33, fig. 21. [= *E. annulatum*]

TYPE MATERIAL EXAMINED: ZMUC; syntype material of *Eudendrium rigidum* Allman, 1876; Denmark, Middelfart Sund; infertile; leg. Lütken, compare Kramp (1926: 242). – BMNH 1912.12.21.98; ?syntype of *Eudendrium rigidum* Allman, 1876; Denmark; infertile.

OTHER MATERIAL EXAMINED: ZMUC, as *Eudendrium wrighti*; Denmark, off Treindelens Lightship; 27 Jul. 1904; infertile. – ZMUC, as *Eudendrium wrighti*; Denmark, Little Belt; depth 16-20m; 26 March 1915; infertile. – BELUM Md424; 55° 13.51'N 06° 38.97'W; Northern Ireland, Antrim, NW of Little Skerry Potrush; depth 36m; 03 Aug. 1982; infertile. – BELUM Md492; 54°23.39'N 05°34.64'W; Northern Ireland, Down, Strangford Lough, Ballyhenry Island; depth 25m; 30 June 1982; infertile. – BELUM Md624; 54°41.66'N 05°47.15'W; Northern Ireland, Antrim, Belfast Lough, SE of Carrickfergus; depth 7.5m; 15 May 1984; infertile. – BELUM Md627; 55°08.82'N 07°04.95'W; Northern Ireland, Londonderry, Lough Foyle, East Channel; depth 7.5m; 22 June 1983; infertile. – BELUM Md626; 51°30.04'N 09°17.70'W; Ireland, Cork, Lough Hyne, E Whirlpool Cliff; 31 Aug. 1974; infertile. – BELUM Md625; 51°26.90'N 09°49.45'W; Ireland, Cork, SW of Mizen Head; 16 July 1983; infertile. – BELUM

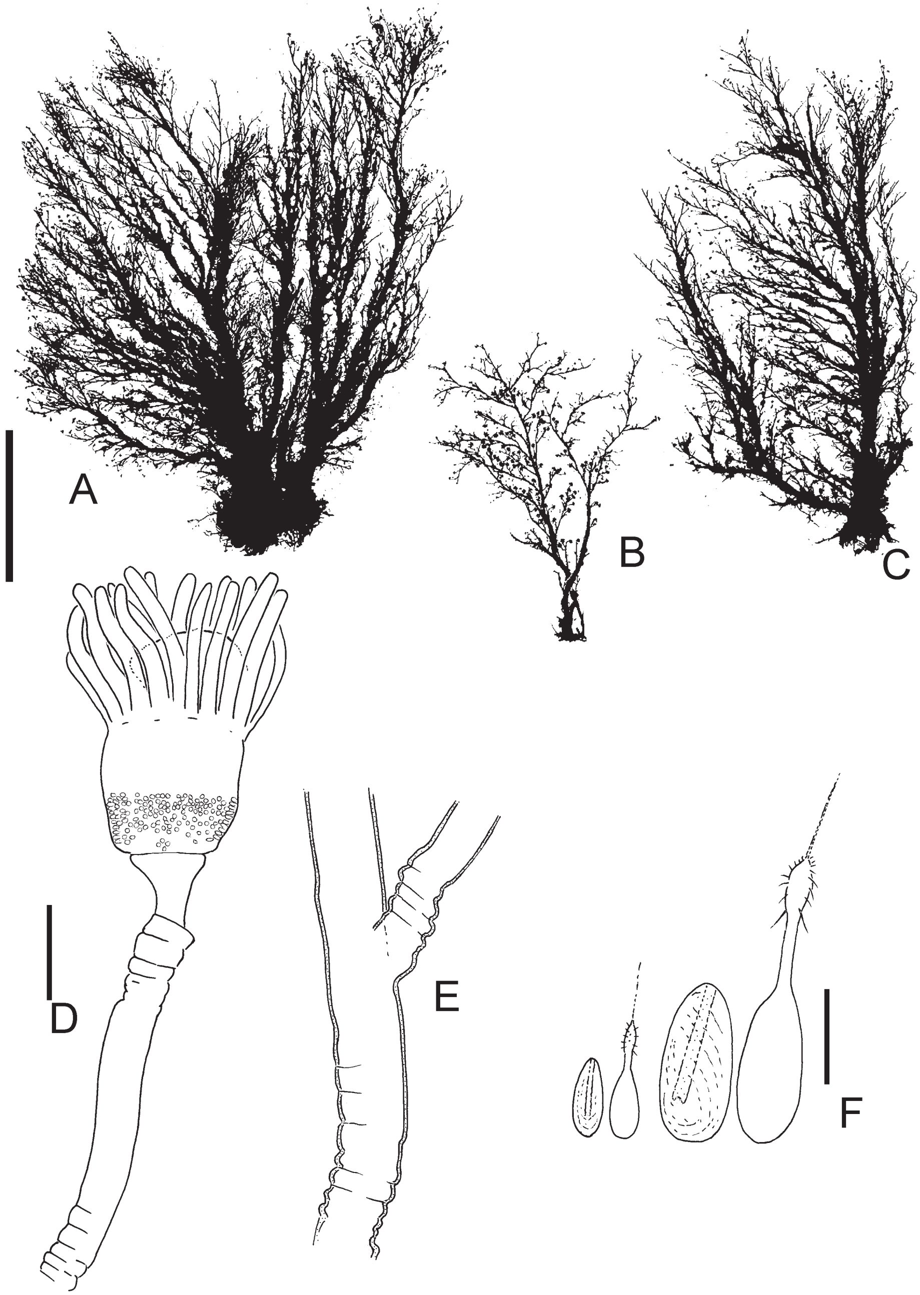

FIG. 25

Eudendrium arbuscula Wright, 1859, after preserved material from Northern Ireland. (A-C) Colony silhouettes, scale bar 2 cm. (D) Hydranth with nematocyst belt, scale bar 0.2 mm. (E) Perisarc of branch, same scale as B. (F) Nematocysts: undischarged and discharged small and large euryteles, scale bar 10 μm.

Md535; 57°57.79'N 05°31.30'W; Scotland, Outer Hebrides, Summer Isles, W Priest Island; 7 Sept. 1981; fertile male. – RMNH-Coel 30986; The Netherlands, Zeeland, Goesse Sars; 15 Nov. 2003; female colonies. – RMNH-Coel 30985; The Netherlands, Zeeland, Zeelandbrug-Noord; 9 Oct. 2004; male colonies. – RMNH-Coel 30983; The Netherlands, Zeeland, Zeelandbrug-Noord; 8 Oct. 1998; male colonies. – RMNH-Coel 30992; The Netherlands, Zeeland, Zeelandbrug-Noord; 9 Oct. 2004; female colonies.

DIAGNOSIS: Colonies polysiphonic, much branched, up to 6 cm, stems without bark-like covering, hydranths small (<0.3 mm diameter), with basal belt of microbasic euryteles, blastostyles dispersed, without hydranths, gonophores with distal nematocyst buttons.

DESCRIPTION: Colonies bushy, irregular, much branched, usually with numerous terminal branches and rather dense, either with a rather short basal trunk or no clear trunk but several main branches issuing from hydrorhiza, polysiphonic, thinning out to monosiphonic terminal branches, in polysiphonic parts tubes usually rather loosely and irregularly aggregated and not neatly parallel; perisarc with smooth, corrugated and annulated stretches, never annulated throughout. Stem not covered by bark-like covering of coalesced stolonal tubes.

Hydranths relatively small, 16-25 tentacles, on body a broad, dense belt of large euryteles, basal groove faint, near base of body (Fig. 25D). Colonies dioecious, blastostyles dispersed over colony.

Male gonophores develop in tufts at the end of branchlets (Fig. 26A), hydranths absent at all stages of development, distal end of sporosacs with numerous large euryteles, mature gonophores one-chambered, sometimes a second proximal swelling, rarely a second chamber, terminal nematocyst button nearly always present.

Female gonophores develop at the end of branchlets (Fig. 26B), concomitantly with gonophores a small hydranth develops, it has only a small body, short tentacles stumps, and no hypostome; at later stages it may be reduced entirely; curved spadix with nematocyst buttons containing large euryteles; after fertilization spadix reduced, embryos encased in thin membrane and several ones attached along pedicels of former blastostyles.

Nematocysts: small microbasic euryteles in tentacles; large microbasic euryteles, shaft in intact capsule ca. 3/4 of capsule length, discharged slightly longer than capsule, directed upwards, distinctly swollen and with coarse spines, unambiguously identifiable as eurytele.

Colours: perisarc light brownish, hydranths white or rose-orange.

DIMENSIONS: Colonies 2-6 cm. Hydranth diameter below tentacles 0.17-0.3 mm; height from basal groove to mouth 0.28-0.5 mm; hydranth pedicel diameter 0.10-0.12 mm. Small euryteles (7-8.5)x(2.5-3.5)μm, r= 2.3-2.5. Large euryteles (14-17)x(6-7.5)μm r=2.1-2.7.

BIOLOGY: Occurs in rather shallow depths down to about 40 metres. Faasse & Vervoort (2005) found fertile colonies only during wintertime.

DISTRIBUTION: From Brittany to Norway, also North Sea (Jäderholm, 1909; Broch, 1916; Kramp, 1942; Rees & Rowe, 1969; Christiansen, 1972; Castric *et al.*, 1987; Marques *et al.*, 2000a; Faasse & Vervoort, 2005); more frequent along the

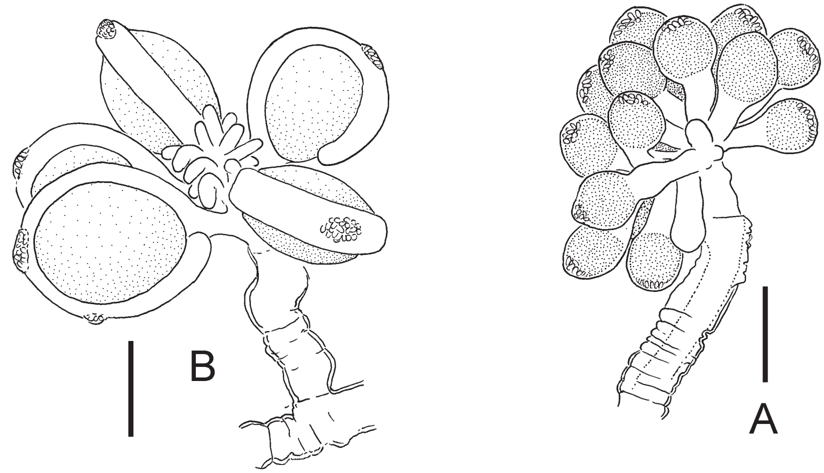

FIG. 26
Eudendrium arbuscula Wright, 1859, blastostyles after preserved material from Holland, scale bars 0.2 mm. (A) Male sporosacs, note terminal button with nematocysts. (B) Female sporosacs

Danish and Irish coast; perhaps also Portugal (Da Cunha, 1944) and NW Atlantic (Calder, 1972). Due to the unclear synonymy the distribution patter is not well known. The Mediterranean records (e. g. Marinopoulos, 1992) are likely misidentifications. Type locality: Queensferry (close to Edinburgh), Firth of Forth, Scotland.

REMARKS: Because *Tubularia arbuscula* D'Orbigny, 1846, an indeterminate species, is perhaps referable to the genus *Eudendrium*, Hartlaub (1905) proposed the new name *Eudendrium wrightii* for *E. arbuscula* Wright, 1859. Following the proposal of Marques & Vervoort (1999), the International Commission of Zoological Nomenclature (2000) decided that the name *Eudendrium arbuscula* Wright, 1859 (Cnidaria, Hydrozoa) is to be conserved and placed it on the list of the official names. The spelling of the specific epithet is *arbuscula* as it is a noun in apposition (Marques & Vervoort, 1999).

Unfortunately, no type material of *Eudendrium arbuscula* could be located, it must be considered as lost. *Eudendrium arbuscula* Wright, 1859 was initially characterized (Wright, 1859b) by the broad band of nematocysts on the hydranth body and the terminal nematocyst button of male sporosacs. Wright's description does not permit to distinguish it with absolute certainty from *E. annulatum* as conceived here. However, as Wright describes the branches as very slender and depicts male sporosacs with one chamber, it can be excluded with reasonable probability that his material belonged to *E. annulatum* Norman, 1864. The present scope of *Eudendrium arbuscula* is thus almost certainly correct.

Eudendrium arbuscula nonetheless resembles *E. annulatum*, notably they share the same nematocysts, the polysiphonic colonies, the belt of euryteles on the hydranth, the terminal nematocyst buttons of the gonophores, and the type of blastostyles. They differ in characters that are usually regarded as taxonomically quite unreliableand and both could arguably be regarded as only two different forms of the same species.

FIG. 27
Eudendrium arbuscula Wright, 1859, male blastostyles in preserved material from Northern Ireland.

However, material of both species from the same region (Northern Ireland) was strikingly distinct when compared side by side. The colony forms differ (comp. Fig. 21A and 25A), *Eudendrium annulatum* forms more open, coarse, and rather stiff colonies. The main branches are often covered by a bark-like overgrowth, which is diagnostic for *E. annulatum* when present. The hydranths of *E. annulatum* are distinctly larger, the diameters are nearly twice as large as those of *E. arbuscula*. Another difference is the distribution of the blastostyles, which occur in dense stands on the upper side of distal branches in *E. annulatum*, while they are not so regularly grouped in *E. arbuscula* (based on rather few observations, difference may be due to limited number of observations). The pedicels of the blastostyles of *E. annulatum* are relatively short.

Eudendrium rigidum Allman, 1876, based on infertile material from Denmark, was synonymized with *E. arbuscula* by Kramp (1926). The type material of *E. rigidum* was also examined for this study and the results confirmed Kramp's findings.

The Greenlandic material identified by Schuchert (2001) as *Eudendrium* cf. *arbuscula* had stems with a bark-like covering, which is found only in *E. annulatum* and *E. vaginatum*. Colony size and form matched *E. annulatum* and the material is therefore here re-assigned to the latter species.

Calder (1972) proposed that also *Eudendrium caricum* Jäderholm, 1908 could be a synonym of *E. arbuscula*. Due to the similarity of *E. annulatum*, the type material of *Eudendrium caricum* should be re-examined to prove this possibility.

Hamond's (1957) material identified as *E. arbuscula* unlikely belongs to this species. The colonies were rather small and both female and male gonophores developed on normal hydranths and not reduced blastostyles. Hamond's material most probably belongs to an unnamed species. It could not be named here as Hamond's description is not complete enough and no material could be located. Note that also the fertility period given by Hamond (summer) does not agree with the observations of Faasse & Vervoort (2005) made for *E. arbuscula* of the neighbouring Dutch coast.

Eudendrium calceolatum Motz-Kossowska, 1905 Fig. 28

Eudendrium calceolatum Motz-Kossowska, 1905: 59, fig. 2. – Picard, 1955: 182. – Marinopoulos, 1992: 58, figs 1.7, 2.1. – Marques *et al.*, 2000b: 203.

DIAGNOSIS: Sparingly branched colonies, hydranth with belt of large nematocysts, some capsules also dispersed. Gonophores on normal hydranth, male one two-chambered, female ones with spadix that has a distal triangular swelling (axe-like shape). Complementary capsules are large microbasic euryteles (Marinopoulos, 1992), (20-30)x(8-13)μm, on hypostome, body, and hydrocaulus; shaft in undischarged capsule thick, with two swellings, spanning 2/3 of capsule.

DESCRIPTION: See Motz-Kossowska (1905).

DISTRIBUTION: Endemic to the Mediterranean, recorded from Banyuls (Motz-Kossowska, 1905), Algeria (Picard, 1955), and Marseille (Marinopoulos, 1992). Type locality: Banyuls-sur-Mer, close to marine laboratory, on *Cystoseira* algae of rocky littoral.

REMARKS: This is an insufficiently known species and Marques *et al.* (2000b) considered it dubious. Marinopoulos (1992; via pers. com. by J. Picard) mentions that is now very rare, although it was once common in the vicinity of Marseille. The species is characterized by the axe-shaped spadix of the female gonophore.

***Eudendrium capillaroides* new spec.** Figs 29-30

? *Eudendrium teissieri*. – Fey, 1970: 392. [nomen nudum]
? *Eudendrium tessieri*. – Castric *et al.*, 1987: 97, fig. [note variant spelling]

TYPE MATERIAL: Syntype colonies MHNG INVE36293; Atlantic Ocean, France, Britanny, Bay of Morlaix, more than 20m depth, 13 Sept. 2004, female colonies on ascidians (including also *Styela clava*), accession number of partial 16S gene sequence **AM991306**.

OTHER MATERIAL: France, Camaret near Brest, depth 20-30m, 18 Sept. 2006, infertile colony on *Nemertesia antennina*, not preserved, used to make DNA, 16S sequence identical to AM991306.

DIAGNOSIS: Colonies small, monosiphonic, female gonophores borne on incompletely developed hydranths, these later reduced entirely or nearly so, spadix simple; males unknown; cnidome comprises two euryteles of slightly different size (length ratio 1.3).

DESCRIPTION: Colonies small, monosiphonic, sparsely and irregularly branched, up to 10 hydranths per stem. Perisarc smooth with occasional short annulated or irregularly corrugated stretches, usually at origin of branches and hydranth pedicels. Hydranths with up to 25 tentacles, hypostome relatively large, tentacular nematocyst confined to proximal 2/3 of tentacles, arranged in regular rings, nematocyst oblique to tentacle axis giving it thus a spiny appearance. Perisarc groove on hydranth body well marked, relatively distal (basal third of body, Fig. 29B).

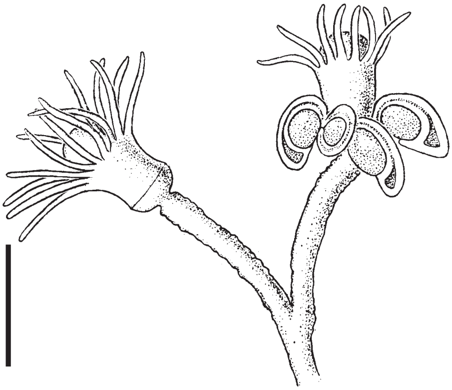

FIG. 28

Eudendrium calceolatum Motz-Kossowska, 1905, infertile and fertile hydranth, note particular shape of spadices, scale bar 0.5 mm, modified from Motz-Kossowska (1905).

Female gonophores (up to 6) formed on blastostyles that concomitantly develop about 12-18 tentacles of reduced size, tentacles later atrophied, no hypostome formed, spadix simple, long and thin (Fig. 29D). In older stages tentacles strongly atrophied or lost, spadices shed and the embryos in their transparent capsules attached irregularly along the pedicel of the former blastostyle (Fig. 29E-F).

Male gonophores not known.

Nematocysts: microbasic euryteles of two different size classes (Fig. 30), size ratio of length of larger and smaller eurytele 1.3, ratio of width of larger and smaller eurytele 1.4, larger capsule thus somewhat thicker. Smaller capsule abundant on tentacles, also on hydranth body and coenosarc. Larger capsules (complementary nematocysts) scattered in a band above the perisarc grove and also in coenosarc of stem and pedicels.

DIMENSIONS: Stems 5-12 mm high; hydranth height about 0.3-0.4 mm, width 0.2-0.35 mm; hydranth pedicels diameter 0.12 mm, stem diameter at base 0.12-0.13 mm; encapsulated eggs about 0.2 mm. Nematocyst dimensions in preserved material see table 1.

TABLE 1. *Eudendrium capillaroides* new. spec., dimensions in [μm] and proportions of nematocysts, values from two preserved colonies

	length of tentacular capsules	width of tentacular capsules	length of larger capsules	width of larger capsules
mean	6.5	2.7	8.5	3.9
s. error of men	0.30	0.34	0.27	0.18
range	6-7.5	2.5-3.5	7-9	3.5-4.5
number of values	25	25	24	24
ratio length/width	2.4		2.2	

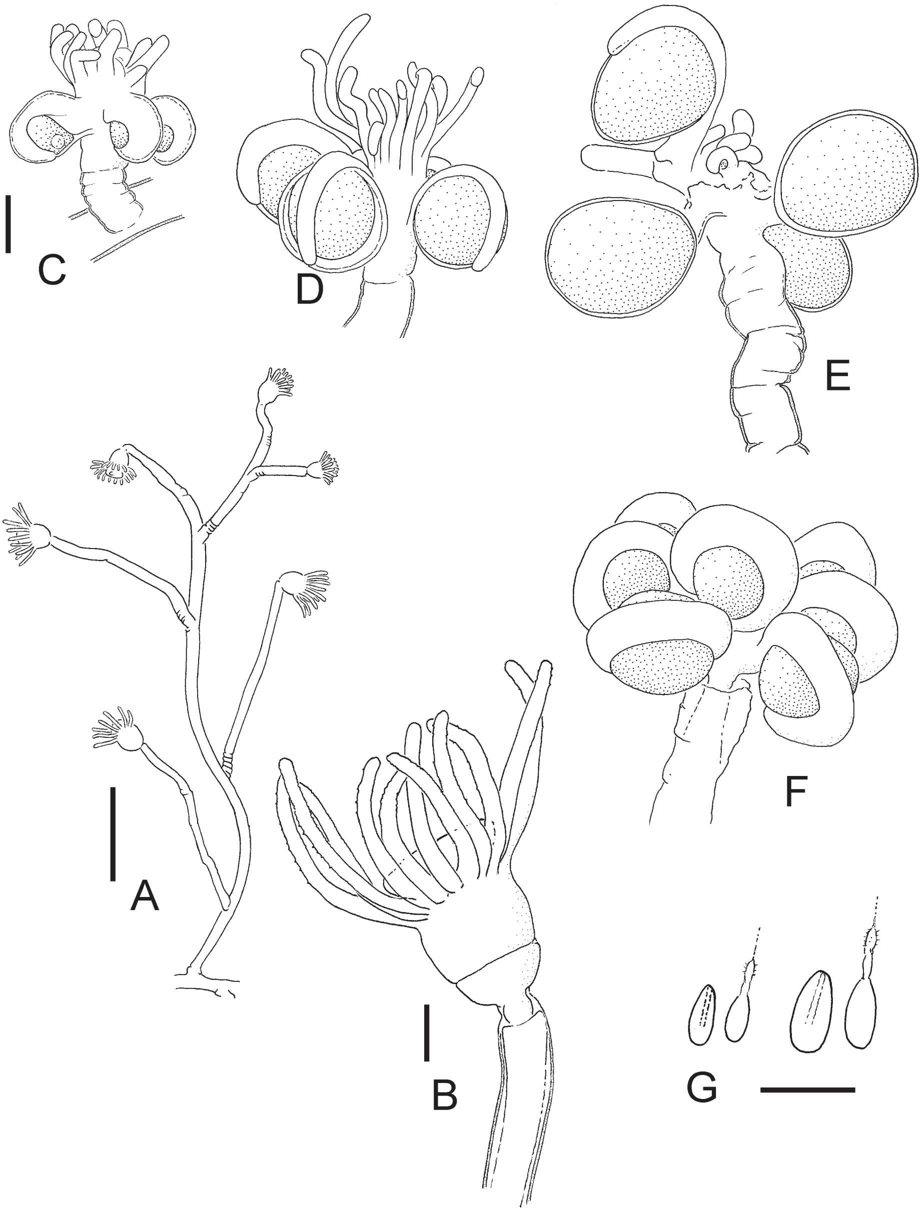

FIG. 29

Eudendrium capillaroides new spec., after preserved type material. (A) One stem of colony, scale bar 1 mm. (B) Hydranth, scale bar 0.1 mm. (C) Early developmental stage of female blastostyle, scale bar 0.1 mm. (D-F) Later stages of female blastostyle, note atrophy of hydranth and tentacles, same scale as C. (G) Cnidome: two microbasic euryteles of different size classes, pairs of intact and discharged capsules, scale bar 10 μm,

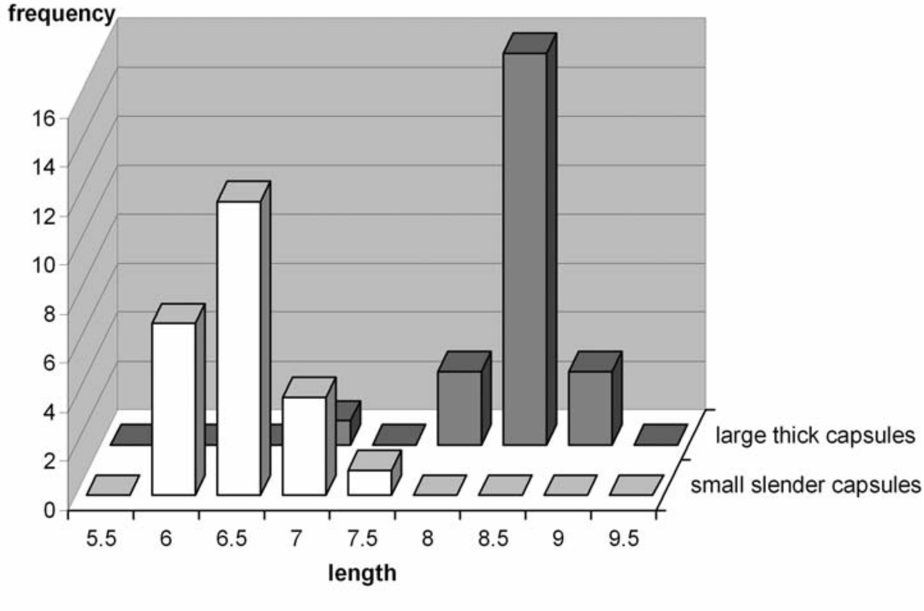

FIG. 30
Eudendrium capillaroides new spec., frequency distribution of the lengths of the two nematocyst capsules, length in μm.

BIOLOGY: Occurs in depths of 20-30 m.

DISTRIBUTION: Brittany. Type locality: France, English Channel, Bay of Morlaix, about 20 m depth.

ETYMOLOGY: The specific epithet refers to the similarity to *E. capillare*, a species with which it was initially confused.

REMARKS: This species resembles very closely *E. capillare*, the only difference being their cnidomes. The cnidome of *E. capillaroides* comprises heteronemes of two slightly different size classes, the ratio of their lengths being 1.3. The larger capsule is somewhat thicker, the width ratio of the two types being 1.4. Although the dimensions intergrade somewhat (table 1, Fig. 30), it is rather easy to see in a microscopic squash preparation that there are actually two different populations of capsules. The cnidome makes it immediately distinguishable from the otherwise similar *E. merulum* which has much larger complimentary euryteles (see key to species). 16S sequence data confirmed that *E. capillare*, *E. capillaroides*, and the European *E. merulum* are clearly distinct lineages (Fig. 2). A species with a similar cnidome is *E. maorianus* Schuchert, 1996 from New Zealand, whose morphology, except for the bifid spadix, is almost identical. Also *E. maorianus* has two types of euryteles that differ only minimally, the ratio being also about 1.3. Interestingly, its 16S sequence is also rather similar to *E. capillaroides* (Fig. 2).

It is likely that *E. capillaroides* corresponds to the invalid nominal species *Eudendrium teissieri*. Fey (1970), in a study dealing with the hydroids of the Glenan Islands in southern Brittany, listed also *Eudendrium* sp. 3, with a remark that this species would be described as *E. teissieri* by Cabioch in a forthcoming publication. However, this apparently never happened and the name *Eudendrium teissieri* is not valid (ICZN art. 13.1). It was not possible to locate any original material. Castric & Michel (1982) and Castric *et al*. (1987) later included the name in a key to a faunistic guide under the name *Eudendrium tessieri* [note different spelling], solely providing a sketch of the hydranth and the complementary nematocysts. Also this publication cannot be seen as a valid introduction of the name. There is no accompanying text, but the sketch indicates that the complementary nematocysts are relatively small and concentrated in a band on the hydranth body.

Eudendrium vaginatum Allman, 1863 Figs 31-32

Eudendrium vaginatum Allman, 1863: 10. – Allman, 1872: 339, pl. 14 figs 7-8. – Jäderholm, 1909: 53, pl. 3 figs 10-11. – Nutting, 1901: 167, pl. 15 figs. 3-6. – Fraser, 1944: 76, pl. 13 fig. 52.

not *Eudendrium vaginatum*. – Bonnevie, 1898a: 484, pl. 26 figs 24-26. – Weill, 1934a: 77, text-fig. 70a-b. – Weill, 1934b: 389, text-fig. 239.

? *Eudendrium vaginatum*– Berrill, 1952: 22, figs 7-8.

Eudendrium annulatum. – Levinsen, 1893: 154. – Schuchert, 2001: 26, fig. 15A-C. [not *Eudendrium annulatum* Norman, 1864]

in part *Eudendrium vaginatum*. – Marques *et al*. 2000a: 107, fig. 85. [others = *E. annulatum*]

MATERIAL EXAMINED: BMNH 1912.12.21.99; Scotland, Shetland Islands, Balta Sound; depth 90m, non-type specimen; coll. A. M. Norman (material of Norman, 1869), all soft tissues gone, colony typical. – ZSM 20040386, as *Eudendrium insigne*; Norway, Bergen; no collection date; infertile colonies on laminarian algae, with numerous well preserved hydranths, undischarged larger microbasic euryteles with shaft coiled near origin. – RMNH Coel28403; as *Eudendrium insigne*; Norway, Bergen; slide made of ZSM 20040386. – RMNH Coel28437; 65.42°N 52.93°W; Greenland, Sukkertoppen; slide preparation; female, but tissues damaged, depicted in Marques et al. 2000a, has large microbasic euryteles, undischarged shaft curved near origin. – IRSNB IG11365; Canada, Newfoundland, Trinity Bay, whaling station; material mentioned of Leloup (1939b); well preserved male colony, has typical large eurytele with coiled shaft. – Norway, Korsfjord, Great Skorpa Island; depth 80-160m; triangular dredge; 16 June 2006; on rock; infertile, material not preserved. – Icelandic Museum of natural History, sample BIOICE2000; 65.354°N 13.794°W; Iceland; 26m; 18 July 1987; infertile; figure published in Schuchert (2001) as *E. annulatum*; re-examined material & changed id. 4 Apr. 2007.

DIAGNOSIS: Branched colonies, mostly polysiphonic when mature, straggling growth, perisarc often dark-brown, rigid, sharply and regularly annulated throughout, with bark (stolonal overgrowth of stem), irregular, convoluted; perisarc originates in groove in upper half of hydranth body and not at base, in preserved material giving impression of pseudohydrotheca; complementary capsule a microbasic eurytele with one small coil in undischarged capsule, discharged shaft longer than capsule.

DESCRIPTION: Colonies much branched, shrubby, straggling in appearance, rather stiff and bristly, stem thick, monosiphonic or more usually polysiphonic, branches mostly monosiphonic and short, branching irregular, branches often curved and of uneven length. Hydrorhiza creeping stolons, anastomosed to tight-meshed net on even surfaces, smooth perisarc. Tubes of stem and branches comparatively thick,

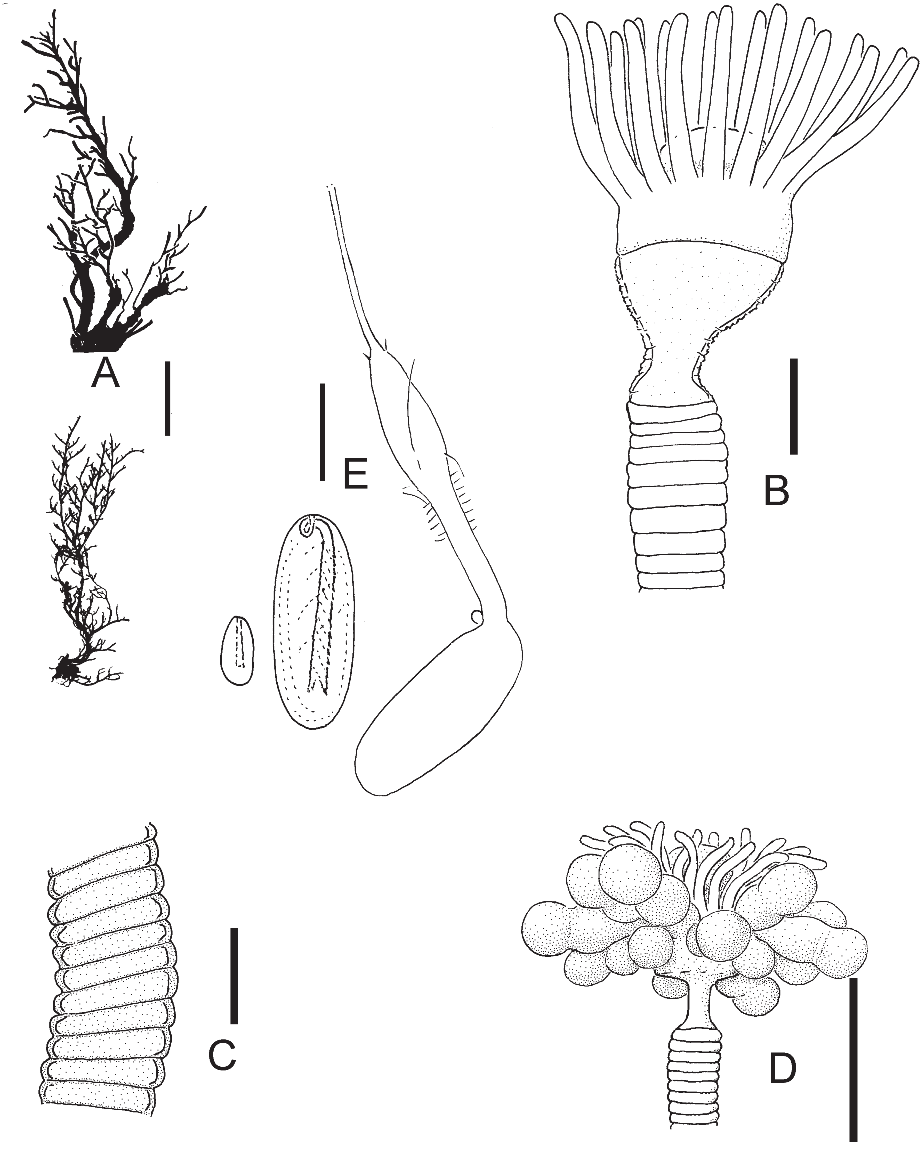

FIG. 31

Eudendrium vaginatum, all except of E after preserved material, D redrawn from Jäderholm (1909). (A) Colony silhouettes, top colony from Iceland, below one from the Shetland Islands, scale bar 5 mm. (B) Hydranth with the characteristic pseudohydrotheca, scale bar 0.2 mm. (C) Part of branch showing the annulation of the perisarc that is present throughout the colony, scale bar 0.2 mm. (D) Young male gonozooid, in more advanced stages the hydranth is reduced variably, scale bar 0.5 mm. (E) Nematocysts: small undischarged microbasic eurytele, large undischarged and discharged microbasic euryteles; scale bar 10 μm.

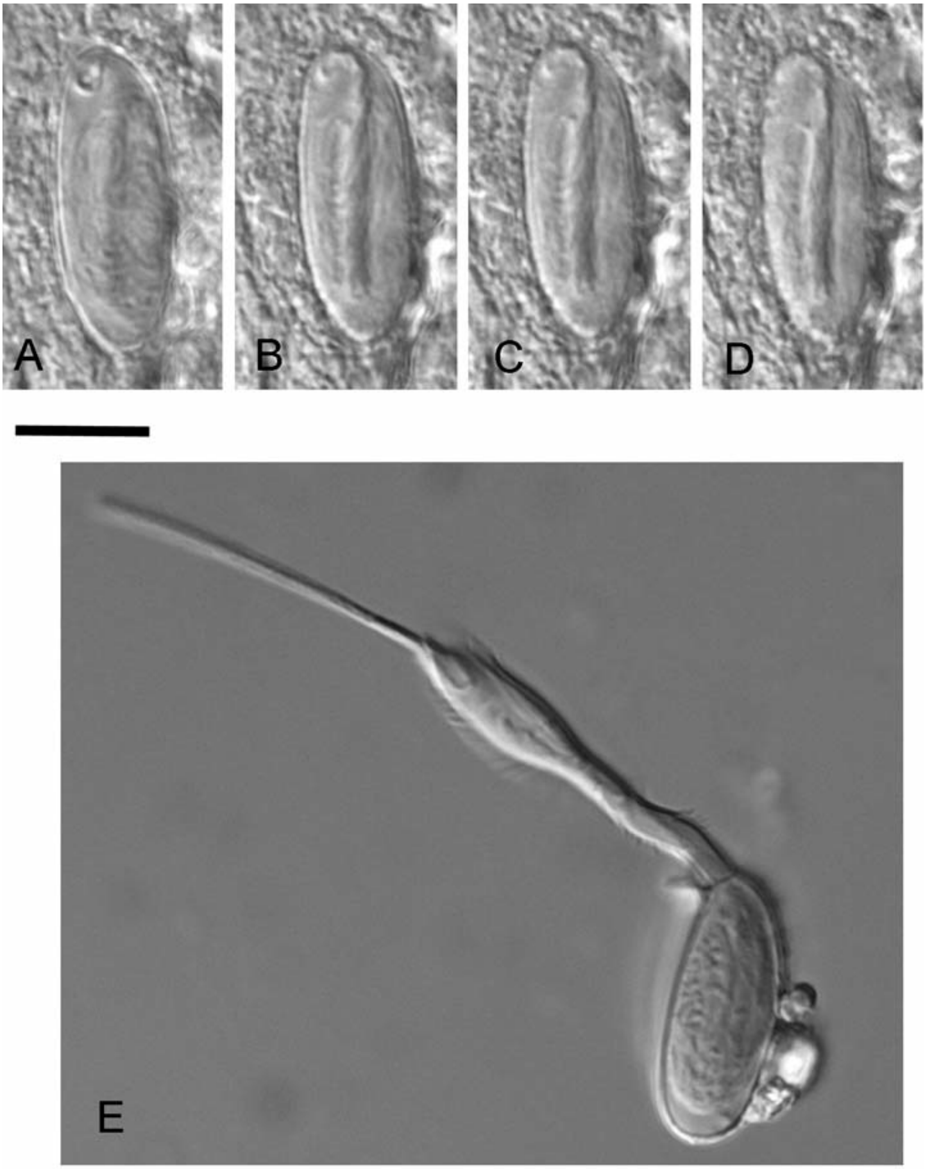

FIG. 32
Eudendrium vaginatum Allman, 1863, native capsules from Norwegian material, scale bar 10 μm. (A-D) Undischarged capsule, the four sections depict the same capsule, but in different focusing planes, note the small coil of the shaft near its origin. (E) Discharged capsule, note the length of shaft which surpasses the capsule length.

annulated throughout, annulation distinct and very regular (Fig. 31C). Base of colony often overgrown by smooth, contorted, stolon-like tubules forming a bark-like covering.

Hydranths with 18-20 tentacles, perisarc originates as thin film in well defined groove in upper half of fully grown hydranth body, perisarc thus forming a characteristic closely adhering cup-like pseudohydrotheca (or loose and collar-like in preserved material that has undergone some tissue shrinking).

Gonophores on normal or somewhat atrophied hydranths. Male gonophores initially on normal hydranths, in more advanced stages reduced (hypostome disappears, tentacles shorten, body gets smaller), gonophores two chambered, more than 10 per hydranth. Female gonophores with unbranched spadix on normal polyps or polyps with shortened tentacles, hypostome present (at least in younger stages), six or more gonophores per hydranth.

Colours: perisarc light to dark brown, sometimes almost black; soft tissues characteristically red.

Nematocysts: small tentacular microbasic euryteles and large microbasic euryteles, in dense ring on hydranth body primarily along groove and on hypostome, shaft in undischarged capsule thick, forming a small, complete coil near junction to capsule wall (Figs 31E, 32A-D), coil diameter about 1/10 of capsule length; discharged shaft distinctly longer than capsule (s>1.5, Fig. 32E), thick, distal half much swollen, barbed even along narrow part, tread thick.

Dimensions: Colonies up to about 3 cm high. Hydranth height from base to mouth about 0.5 mm. Hydranth pedicel diameters 0.2-0.4 mm. Annulation of perisarc 50-70 μm high. Small microbasic euryteles (7-8)x(3-4), r=2-2.8; large microbasic eurytele (20-23)x(9-9.5) μm, r= 2.2-2.6.

Biology: Depth range 0-180 m, known substrates are rock and laminarians.

Distribution: An Arctic to northern boreal species, with reliable records from the Shetland Islands (Allman, 1864; this study), Norway (this study), Jan Mayen (Jäderholm, 1909), Iceland (Schuchert, 2001 as *E. annulatum*; this study), Western Greenland (this study), Newfoundland (Leloup, 1939; this study). Pacific records (e. g. Nutting, 1901; Stechow, 1913; Fraser, 1937) need confirmation by examining their nematocysts. Type locality: Shetland Isles, in rockpools at ELS level and below.

Remarks: *Eudendrium vaginatum* Allman, 1863 is a characteristic species that can also be identified in the absence of gonophores. The hydranth produces the perisarc from a circular groove located in the upper half of the hydranth body, this in contrast to most other *Eudendrium* species where it is located in the basal region. The newly formed filmy perisarc thus adheres to the lower part of the hydranth like a pseudohydrotheca (easier to observe in preserved material that has undergone some tissue shrinking). Further characteristic traits of the species are the completely and regularly annulated perisarc, the dark-brown colour of the perisarc, and the red colour of the living tissues. Although the high position of the groove is very typical for this species, the location could be variable to some degree, but in the examined hydranths (>30), the vast majority had the groove in the upper half of the hydranth.

Although the type material could not be examined – it could not be found in the museums of London, Edinburgh nor Dublin – the characteristics listed above allow to identify the samples listed above quite unambiguously as belonging to Allman's *Eudendrium vaginatum*. Several of these samples permitted the examination of the nematocysts. Besides the normal tentacular microbasic euryteles, there is also a large microbasic eurytele with a relatively long and thick shaft. The discharged shaft is distinctly longer than the capsule, but the ratio is smaller than 2.5, which qualifies it as a microbasic eurytele. In the undischarged capsule, the shaft forms a characteristic tiny coil near the junction with the capsule wall (Figs 31E, 32). This type of capsule is rather uncommon, but another *Eudendrium* in the NE Atlantic has a similar, but distinguishable capsule (see *Eudendrium unispirum*; coil in capsule ca. 1/3 of capsule length).

With these results at hand, it is thus evident that *E. vaginatum* Allman, 1863 and *E. annulatum* Norman, 1864 are distinct species. Both species have occasionally been synonymized (e. g. Marques *et al.*, 2000a). When Normann (1864) described *E. annulatum*, he stated: "the tubes [hydranth pedicels] are not expanded at their extremities to receive the polypites, as is the case in some allied species". This remark certainly concerns *E. vaginatum*, which at the time of Norman's writing (December 1863) had already been published (January issue of the same journal). This is also reflected in his Latin diagnosis: "*... polypis calices non expansos obsidentibus,...*" Thus Norman likely wanted to keep his species distinct from Allman's one. Although I found some *Eudendrium annulatum* hydranths with a filmy perisarc collar (Fig. 21C), these were rare and rather small, unlike in typical *E. vaginatum* where they extend up to the middle of the body of fully grown hydranths (Fig. 31B). The perisarc of *Eudendrium annulatum*, despite its name, is not annulated throughout. Both *E. annulatum* and *E. vaginatum* form a bark-like covering of the stem base. In the former species (Fig. 23) it is rather regular and sheet-like, while in the latter it is more irregular and convoluted. Moreover, Norman has also found *Eudendrium vaginatum* at Shetland and he kept it distinct from his *E. annulatum* (see Norman, 1869). Norman's specimen (BMNH 1912.12.21.99) was re-examined for this study and it is evidently *E. vaginatum* (the nematocysts could not be examined, though).

Although Jäderholm's (1909) material could not be re-examined, his figures of the hydranth and the perisarc leave no doubt that his identification as *E. vaginatum* must be correct.

The material from Iceland described in Schuchert (2001) as *E. annulatum* was re-examined for this study. It is clearly referable to *E. vaginatum* and not *E. annulatum*.

Nutting (1901) attributed some samples from Alaska to *Eudendrium vaginatum*. Although his material was also completely annulated and possessed pseudohydrothecae, I think it could belong to a separate species as the female gonophores were borne on reduced hydranths. An examination of the nematocysts is necessary to establish the identity of the Alaskan population.

A number of other authors thought to have found *Eudendrium vaginatum*. However, as it has been confounded regularly with *E. annulatum* or *E. insigne*, most records are likely incorrect.

***Eudendrium unispirum* new spec.** Fig. 33

TYPE MATERIAL: Syntypes, BMNH 1948.9.8.82; several stems of one colony, originally identified as *Eudendrium album*; England, Plymouth; collected 1898 by E. T. Browne; growing on *Tubularia indivisa*; male colony.

Other Material: BELUM Md621; Northern Ireland, Down, Strangford Lough, W of Colin Rock, 54°25.54' N 005°36.33' W, depth 24m, 7 June 1989; infertile colony. – BELUM Md622; Northern Ireland, Down, Strangford Lough, SE of Abbey Rock, 54°25.51'N 05°35.12'W, 15m depth, 1 June 1983: infertile colony on stem of *T. indivisa*. – Spitzbergen, Svalbard, Hornsund, 2 small infertile colonies, coll. 12. July 2000 and 18 July 2006, depth about 16m, in private collection of Marta Ronowicz.

Diagnosis: Small branched monosiphonic colonies, complementary nematocysts microbasic eurytele with shaft 2-2.4 times as long as capsule, in intact capsule coiled 1-1.5 times, coil large (> 1/3 capsule length). Male sporosacs on intact hydranths.

Description: Colonies delicate, bushy, monosiphonic, larger colonies much branched with up to 40 hydranths per colony, branching irregular, branches long. Perisarc mostly smooth, some annulation present, annulation usually present at origin of new branches and hydranth pedicels. Hydranths typical for genus but relatively small, 20-30 tentacles (mostly 24), on body a few scattered large nematocysts, more in circle around mouth, perisarc groove near base of body, usually difficult to see. Developing hydranth buds with layer of contiguous large euryteles.

Male sporosacs develop on intact hydranths, 2-4 per hydranth, 1-2 chambered, younger ones with distal tubercle with large nematocysts. Females unknown.

Nematocysts: small (tentacular) microbasic euryteles, shaft in intact capsule thick; large microbasic euryteles, discharged shaft 2-2.4 times as long as capsule, with spines along whole length but getting shorter towards capsule, in intact capsule shaft coiled with one to 1.5 turns, usually in upper half of capsule, size and form of coil somewhat variable from capsule to capsule but size > 1/3 capsule length, coiled part of shaft thin.

Dimensions: Colonies from a few mm to 20 mm high. Hydranth diameter 0.1-0.18 mm, height from base to mouth 0.25-0.35 mm, hydranth pedicel diameter 0.06-0.10 mm, diameter of stem near base 0.13-0.17 mm. Nematocysts (from 4 preserved colonies): small microbasic eurytele (tentacular) (6.5-7.5)x(2.5-3.5)μm; large eurytele (19-22)x(8-9.5)μm.

Etymology: The specific epithet is derived from the Latin words *uni* (single) and *spirum* (coil), an allusion to the conspicuous, single coil of the shaft in the complementary eurytele capsule.

Biology: The known depth range is 15-24 m. Two colonies were found growing on stems of *Tubularia indivisa*.

Distribution: Plymouth (U. K.), Northern Ireland, Spitzbergen. Type locality: Plymouth, on stems of *Tubularia indivisa*.

Remarks: This species resembles closely *E. album*. In fact, except for the complementary capsules, both species are identical. The undischarged complementary capsules of *E. unispirum* present a shaft that has only 1-1.5 coils, this in contrast to *E. album* which has four or five coils (Figs 6 and 33C). Also the lengths of the discharged shafts are significantly different. In *E. unispirum* the ratio of shaft/capsule length (=s) is 2-2.4, in *E. album* it is larger than 5. As these characters shows rather little variation in *E. album*, the capsule of *E. unispirum* is quite reliably distinguishable. Applying

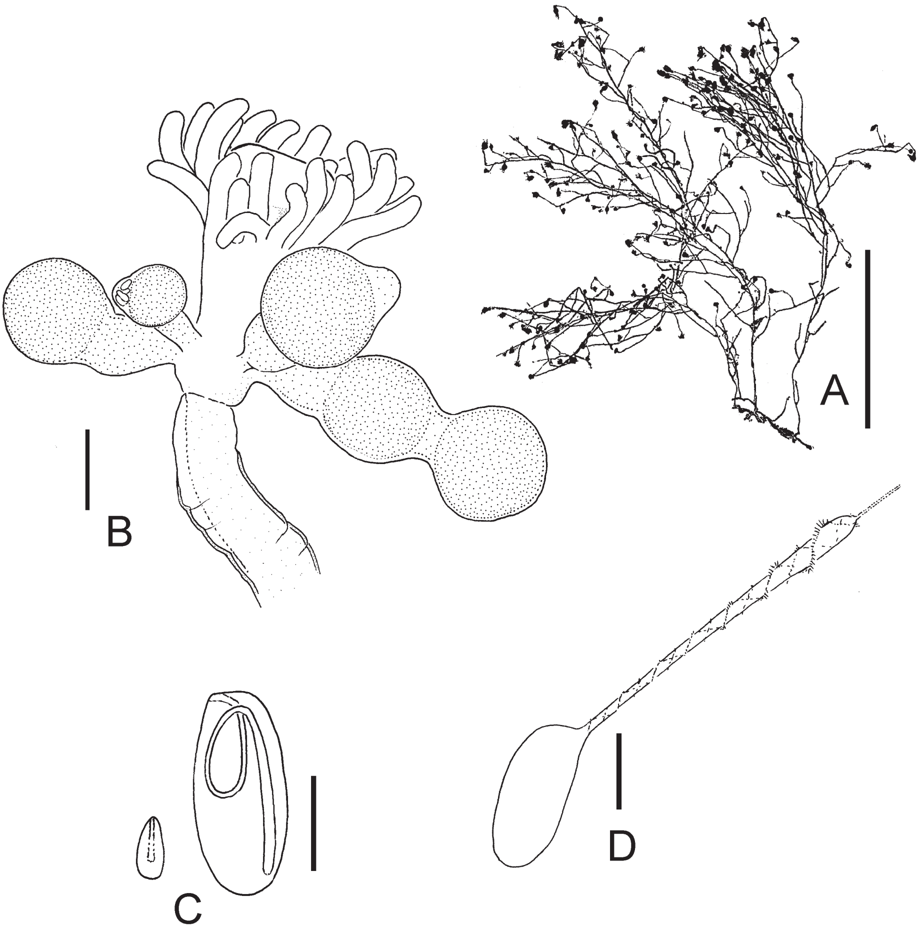

FIG. 33

Eudendrium unispirum new spec., after preserved material, A and D from Northern Ireland, B-C type material (A) Colony silhouette, scale bar 1 cm. (B) Hydranth with male sporosacs, scale bar 0.1 mm. (C) Undischarged nematocysts: small and large microbasic eurytele, scale bar 10 μm. (D) Schema of discharged large microbasic eurytele, scale bar 10 μm.

currently used diagnoses (e. g. Bouillon *et al.*, 2006), the shaft/capsule length ratio of <2.5 qualifies the complimentary capsules of *E. unispirum* as microbasic, while the one of *E. album* is macrobasic. A similar eurytele with one coil in the undischarged capsule is found in *E.vaginatum* (Fig. 32). However here the coil is very small and the species is otherwise rather easily separable from *E. unispirum* (see key on page 684).

Colonies of *Eudendrium unispirum* and *E. album* were found to occur sympatrically (Plymouth and Strangford Lough), which can be regarded as another argument for them being distinct species.

No female sporosacs could be found, but as the male sporosacs develop on normal hydranths, the same can also be expected for the female ones.

Eudendrium capillare Alder, 1856 Fig. 34

Eudendrium capillare Alder, 1856: 355, pl. 12 figs 9-12. – Allman, 1864: 362. – Hincks, 1868: 84, pl. 14 fig. 2. – Allman, 1872: 335, pl. 14 figs 1-3. – Weismann, 1883: 109, pls 1-2. – Jäderholm, 1909: 53, pl. 3 figs. 8-9. – Bedot, 1914: 79. – Vervoort, 1946: 154, fig. 62. – Naumov, 1969: 263, fig. 132. – Calder, 1972: 226, pl. 2 fig. 6. – Millard & Bouillon, 1974: 17, fig. 3E-H. – Millard, 1975: 82, fig. 27E-J. – Kubota, 1976: 235, figs 3.7-8. – Cornelius & Garfath, 1980: 278, type material. – Calder, 1988: 41, fig. 30-32, synonymy. – Hirohito, 1988: 77, figs 24g-h, 25. – Marinopoulos, 1992: 60, fig. 3.1. – Marques *et al.*, 2000a: 88, figs 28-34. – Marques *et al.*, 2000b: 201. – Schuchert, 2001: 27, fig. 16A-F. – Peña Cantero & García Carrascosa, 2002: 27, fig. 4a-b. – Puce *et al.*, 2005: 202, figs 1b & 2c.

Corymbogonium capillare. – Allman, 1861: 171.

? *Eudendrium humile* var. *corymbifera* Allman, 1863: 10.

Eudendrium tenellum Allman, 1877: 8, pl. 4 figs 3-4. – Kramp, 1914: 99. – Fraser, 1937: 43, pl. 8 fig. 3. – Yamada, 1954: 17, fig. 15. – Calder, 1972: 226, pl. 2 fig. 8. – Hirohito, 1988: 88, fig. 31d-h. – Schuchert, 2001: 33.

Eudendrium hyalinum Bonnevie, 1898b: 7. – Bonnevie, 1899: 50. – Naumov, 1969: 263, synonym.

Eudendrium tenue A. Agassiz, 1865: 160, fig. 250. – Bedot, 1914: 79, synonym.

Eudendrium parvum Warren, 1908: 272, fig. 1, pl. 45 figs 1-4. – Millard, 1975: 82, synonym

? *Eudendrium capillare* var. *mediterranea* Neppi, 1917: 30, fig. 1, pl. 4 figs. 1, 1a.

Eudendrium sagaminum Yamada, 1954: 14, fig. 12. – Hirohito, 1988: 77, synonym.

not *Eudendrium capillare*. – Kramp, 1932a: 18. – Kramp 1932b: 7. [= *E. album*]

? not *Eudendrium capillare*. – Ramil & Vervoort, 1992: 18, fig. 1b-c.

TYPE MATERIAL EXAMINED: Syntype material of *E. hyalinum*, Bergen Museum no. 13628; Skjærgården St. 5-6, and no 10854, Bergens Skj. St. 3, 4, 5; 30-35 m. Both colonies infertile, originating from the vicinity of Bergen.

OTHER MATERIAL EXAMINED: MHNG INVE29390 Atlantic, France, Brittany, near St. Pol de Léon, 6 June 2000; depth 20m; on *Ciona intestinalis*; female colony; no haplonemes found; 16S sequence, **AY787884**. – Mediterranean, France, Banyuls-sur-Mer, October 1991, female colony on *Phallusia mammilata*, not preserved. – MHNG INVE32951; Mediterranean, France, port of Banyuls-sur-Mer; 9 May 2002; haplonemes present; depth 1m; male; 16S sequence **AM991296**. – MHNG INVE34231; Italy, Naples, Nisida; 14 April 1911; depth 1m, female. – MHNG INVE34234; Italy, Naples, Santa Lucia; 14 April 1911; depth 1m; male. – MHNG INVE36196; Mediterranean, France, Bay of Marseille; 24 April 1970, depth 5m; male and female colonies. – ZSM, Stechow collection; England, Plymouth, female. – BELUM Md616; Scotland, Outer Hebrides, St. Kilda, Levenish; 57.792°N 08.509°W; depth 30m; 18.07.1982; males and females. – BELUM Md619; Northern Ireland, Strangford Lough Narrows, Cloghy Rocks; 54.355°N 05.546°W; 7.5 m; 04.08.1983; males. – BELUM Md620; Northern Ireland, Strangford Lough Narrows, Rue Point; 54.365°N 05.541°W; depth 6m; 11.08.1983; females. – MHNG INVE37298; Atlantic, France, Normandy, Herquemoulin, Treize Vents; 22 Aug 2005; 0m; male; haplonemes rare; 16S sequence **AM991295**. – MHNG INVE54569; England; Plymouth, Firestone Bay; depth 12-18 m; 19 June 2007; on sponge and *Tubularia*; fertile female colony; haplonemes present; 16S DNA sequence **AM991294**. – MHNG INVE54592; England; Plymouth; depth 25m; 26 June 2007; on *Tubularia indivisa*; fertile female colony; haplonemes present. – England; Plymouth, Mew Stone; depth 25m; 23 June 2007; infertile colony; haplonemes present; material not preserved. – MHNG INVE54602; Spain; Basque Countrty, Guipúzcoa, Fuenterrabía; 0m depth; 12 July 2007; floating docks of harbour; fertile female colony; haplonemes present; 16S DNA sequence identical to AM991294. – MHNG INVE54696; Northern Ireland; Strangford Loch; 26 July 2007; fertile male colony; haplonemes present; 16S DNA sequence identical to AM991294.

DIAGNOSIS: Small monosiphonic colonies, cnidome comprises small microbasic euryteles and facultatively isorhizas of about the same size, both not concentrated in basal ring. Male blastostyle without tentacles, females with or without short tentacles, later atrophied, spadix simple.

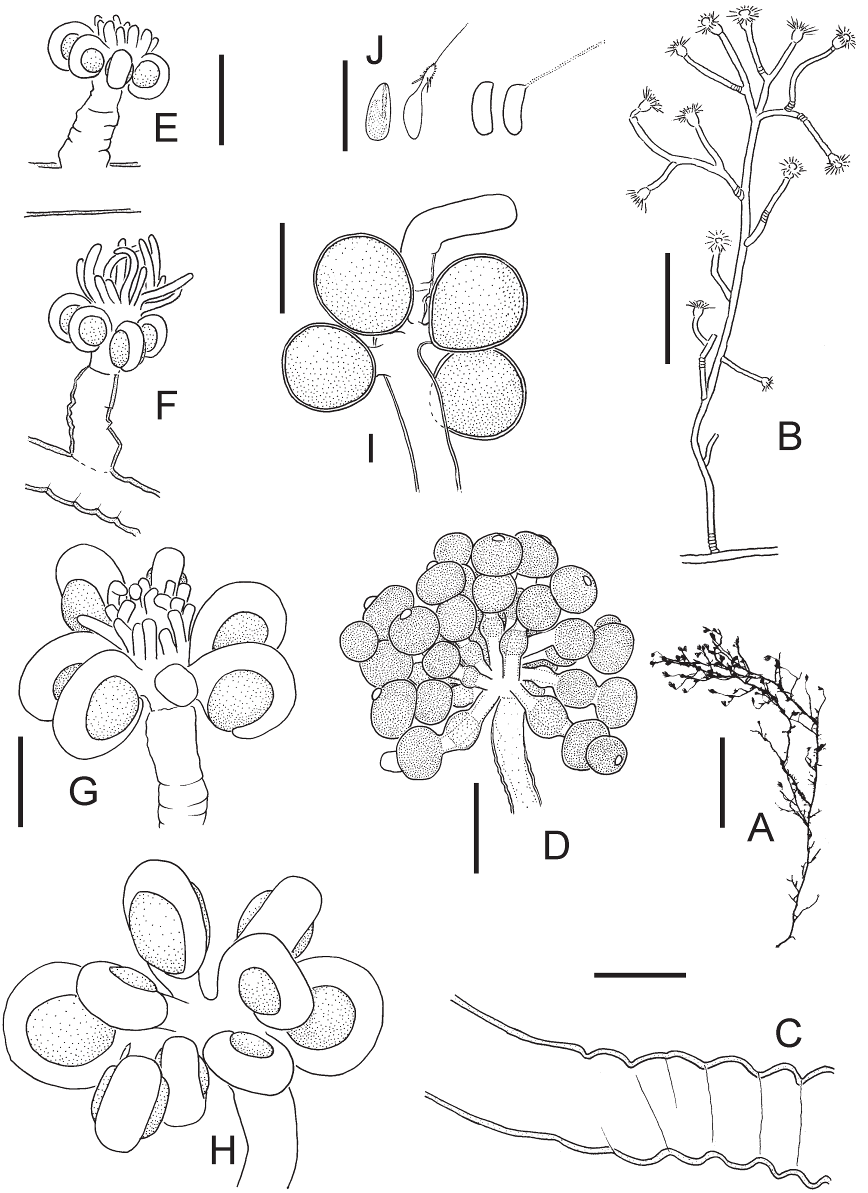

FIG. 34

Eudendrium capillare Alder, 1856; after preserved Mediterranean (B, D, H, I) and Atlantic (A, C, E-G, J) material. (A) Colony silhouette, scale bar 1 cm. (B) Single stem, scale bar 2 mm. (C) Higher magnification of branch with smooth and annulated perisarc, scale bar 0.1 mm. (D) Male blastostyle, scale bar 0.2 mm. (E-H) Sequence of development of female blastostyle, note the presence of short tentacles. In later stages (H) the blastostyle is completely reduced, scale bar 0.2 mm. (I) Encapsulated embryos attached to the former blastostyle pedicel, same scale as E. (J) Nematocysts: intact and discharged microbasic euryteles; intact and discharged haplonemes; scale bar 10 μm.

DESCRIPTION: Colonies small, delicate, monosiphonic, usually irregularly branched. Perisarc smooth with occasional short annulated or irregularly corrugated stretches, usually at origin of branches and hydranth pedicels. Hydranths with about 20 tentacles (15-24 range), hypostome relatively large, tentacular nematocyst confined to proximal 3/4 of tentacles, arranged in regular rings, nematocyst oriented obliquely to tentacle axis, giving it thus a spiny appearance.

Male gonophores borne like tuft on blastostyles without tentacles at all stages, 12-15 gonophores and more per blastostyle, one- to three chambered, sometimes with terminal tubercle without nematocysts.

Female gonophores borne on hydranths with much shortened tentacles and body much reduced, hypostome absent; 5-12 eggs per blastostyle, with curved and unbranched spadix; in older stages tentacles completely atrophied. After fertilization the spadices are shed and the embryos in their transparent capsules attached irregularly along the pedicel of the former blastostyle.

Nematocysts: microbasic euryteles, one end tapering, not concentrated in a basal ring; isorhiza capsules with two blunt ends, same size as euryteles, numbers present rather variable, may be missing.

Colours: variable, either not much coloured, cream to light rose-orange, or red.

DIMENSIONS: Colony heights when mature 5 mm to 4 cm; hydranths 0.3-0.43 mm high (incl. hypostome), diameter of body 0.2-0.34 mm; stem diameter at base 0.12 mm; length of male gonophores 0.3-0.35 mm; embryos in capsules 0.2 mm. Microbasic euryteles (preserved material): Atlantic (3 colonies) (6-8)x(2.5-3) μm, r= 2.3-2.8; Mediterranean (3 colonies) (5.5-9)x(2.5-4)mm, r=2.4-2.9. More measurements for other regions are given in Millard & Bouillon (1974), Millard (1975), Kubota (1976), Calder (1988), Marques *et al.* (2000b), and Peña Cantero & García Carrascosa (2002). All lie more or less within the limits given above. Haplonemes (preserved material): (5-6) x(2-2.5)μm.

OTHER DATA: Weismann (1883) described the oogenesis and the development of the female gonozooids. The oogonia become first visible in the gastrodermis of the coenosarc, although he could not localize their origin. The oogonia are present before the gonozooids develops. Fertilization takes place while the eggs were still clasped by the spadix. Later the spadix is shed and the embryos develop a chitinous envelope (similar to *E. racemosum*, see Fig. 9E). Neppi (1917) described the metamorphosis of the planula.

BIOLOGY: Occurs usually from zero to about 80 m depth, deeper records are known. Mature colonies have been observed May to September (NE Atlantic) or April to November (Mediterranean). The reproductive period is likely longer than indicated by these intervals. Grows on a variety of solid substrata and other animals and algae. Boero & Fresi (1986) found it regularly, sometimes abundantly, in a rocky zone of the Mediterranean. See also Boero (1981).

DISTRIBUTION: Reportedly nearly cosmopolitan, but only identifications using nematocyst information are reliable. Reliable records are from the northeastern Atlantic, Greenland, the Mediterranean, Bermudas, southern Africa, and Japan (Millard & Bouillon, 1974; Millard, 1975; Kubota, 1976; Calder, 1988; Schuchert, 2001). Along the European coasts certainly occurring from Norway to Gibraltar, including the North Sea but not the Baltic Sea (Jäderholm, 1909; Bouillon *et al.*, 1995; Peña Cantero & García Carrascosa, 2002; this study), also frequent in the Mediterranean (Marques *et al.*, 2000a, 2000b). Type locality: North Sea, Embleton Bay, Northumberland, Great Britain, on the hydroid *Nemertesia ramosa*.

REMARKS: Contrary to most other authors (Millard, 1975, South Africa; Watson, 1985, Australia; Calder, 1988, Bermuda; Marques *et al.*, 2000a Mediterranean), I occasionally found two types of nematocysts in this species. Besides the abundant, almond-shaped microbasic eurytele, there is a differently shaped haploneme (isorhiza, see Fig. 34J). It occurred in much lower and rather variable numbers. In some samples it was absent or very rare (Mediterranean), in others it was rare to quite frequent (NE Atlantic). Also Marinopoulos (1982) observed isorhizas in this species, although his schematic drawing (fig. 1.3) shows a different shape. The colonies which had them in higher numbers (Atlantic specimens) were indistinguishable from others in which these capsules were not noted. Because these capsules are usually much less frequent and have approximately the same size as the euryteles, they are very easily overlooked. Moreover, they discharge rarely in microscopic preparations. Preliminary 16S sequence data (Fig. 2) of colonies with haplonemes (see Material examined) and one colony in which it could not be found (MHNG INVE29390, AY787884) clustered all in one clade. I therefore assume that they all belong to one species and that *E. capillare* has variably also small haploneme capsules.

I have examined the type material of *E. hyalinum* Bonnevie, 1898b. The colonies are small, sparingly branched and infertile. I found only small capsules of one size class. *Eudendrium hyalinum* Bonnevie, 1898b is thus here regarded as a synonym of *E. capillare* as has been done before by Naumov (1969).

Allman (1877) described *E. tenellum* from infertile material without hydranths, he was even not sure whether it was a *Eudendrium*. This species – although it has been repeatedly identified by other authors – must certainly be considered unrecognizable. It was thought to be conspecific with *E. capillare* by Naumov (1969), but other authors like Calder (1972) kept it distinct from *E. capillare* on account of its non-reduced male gonozooids. I have seen type material of this species. There are only few fragments left containing only little soft tissue. There is apparently only one type of nematocyst present like in *E. capillare* and *E. tenellum* may be regarded as synonym of *E. capillare* (see also Bulletin of Zoological nomenclature Volume 64(3), opinion 2175; on type specimen).

Working with colonies from the Gulf of Naples, Weismann (1883) and Neppi (1917) observed that their colonies had female gonozooids with some tentacles, which were nevertheless reduced in later stages. The male sporosacs had terminal nematocyst tubercules (Neppi, 1921). This prompted to Neppi (1917) to propose a variant name for this population, namely *Eudendrium capillare* var. *mediterranea*. As such a tentacle formation of the female gonozooid has also been observed in other populations (e. g. Millard, 1975; Calder, 1988; Schuchert, 2001; this study), Neppi's variant is likely not distinct from the nominal form, although the absence of information on the nematocysts precludes any reliable conclusion. Marques *et al.* (2000b) think that Neppi's variant does not belong to *E. capillare*, but the lack of information precludes a reliable identification.

Material from Greenland described in Schuchert (2001) had much less reduced female and male blastostyles. The same morphotype, or sometimes with even less reduced blastostyles, was also found at Spitsbergen (M. Ronowicz, pers. com.; MHNG INVE60719). The slight morphological differences in observed in these Arctic populations could be either due to population or environmental differences, or more likely an indicator of two separate species being involved. Genetic data from these populations are needed for a further assessment.

Eudendrium armatum Tichomiroff, 1887 Fig. 35

Eudendrium armatum Tichomiroff, 1887: 31, fig. 25, pl. 1 figs 3-4, pl. 2, figs 3-4. – Wasserthal, 1973: 93, figs 1-40. – Laukötter, 1985: 67, figs 1-15. – Boero & Fresi, 1986: 141. – Marinopoulos, 1992: 60, fig. 1.4. – Marques *et al.*, 2000a: 82, figs 16-18. – Marques *et al.*, 2000b: 202. – Puce *et al.*, 2005:202, figs 1a, 2a, 2e.

not *Eudendrium armatum* Jäderholm, 1907: 372. – Jäderholm, 1909: 52, pl 4 figs 7-9. [= *Eudendrium cnidoferum* Stechow, 1919]

MATERIAL EXAMINED: MHNG INVE39474; France, Marseille, Riou-Impériaux de Terre; depth 37m; 9 July 1966; male and female colonies. – MHNG INVE29458; Greece, Island of Paros; depth 1-2m; 1 Sept. 1990; infertile colony. – MHNG INVE4987; Italy, Naples; 23 Feb. 1892, infertile. – MHNG INVE49886; Italy, Naples; collected 1896, female.

DIAGNOSIS: Colonies polysiphonic, with long nematophores replacing hydranths, male blastostyles fully developed hydranths, female blastostyles hydranths with short tentacles. Only microbasic euryteles of one size class.

DESCRIPTION: Colonies much branched, polysiphonic, tree- or bush-like. Hydranths typical for genus, basal groove near base, approximately 24 tentacles, proximal portion of tentacles devoid of nematocysts, density gradually increasing towards distal, in untidy bands, axis of capsules parallel to tentacle and thus tentacle surface not spiny. Some hydranths replaced by long, filiform, contractile nematophores, epidermis of nematophores studded densely with nematocysts, gastrodermis parenchymatic.

Male sporosacs 2-3 chambered, no terminal nematocyst button, up to 14 carried on fully developed hydranths, small minority with reduced tentacles.

Female gonophores with simple, curved spadix, up to 14 on hydranth with hypostome, somewhat smaller than usual hydranth body and short, stubby tentacles. Fertilized eggs get encapsulated and attached to pedicels of blastostyle.

Nematocysts: only one type and size of microbasic euryteles, discharged shaft shorter than capsule.

DIMENSIONS: Fertile colonies 2-8 cm high, hydranths 0.5-0.6 mm high, diameter of hydranth pedicels 0.11-0.13 mm, diameter of basal stem tubes ca. 0.18 mm. Microbasic euryteles (6-7)x(3-3.5)μm, r=2.0-2.3.

BIOLOGY: Abundant in certain regions of the Mediterranean, from 1 to 40 m, generally on rocks. Gonophores present February-March, July-October (Boero & Fresi, 1986; Marques *et al.*, 2000b).

Wasserthal (1973) described the egg, gonophore and blastostyle development in great detail. Laukötter (1985) provided the same information for males.

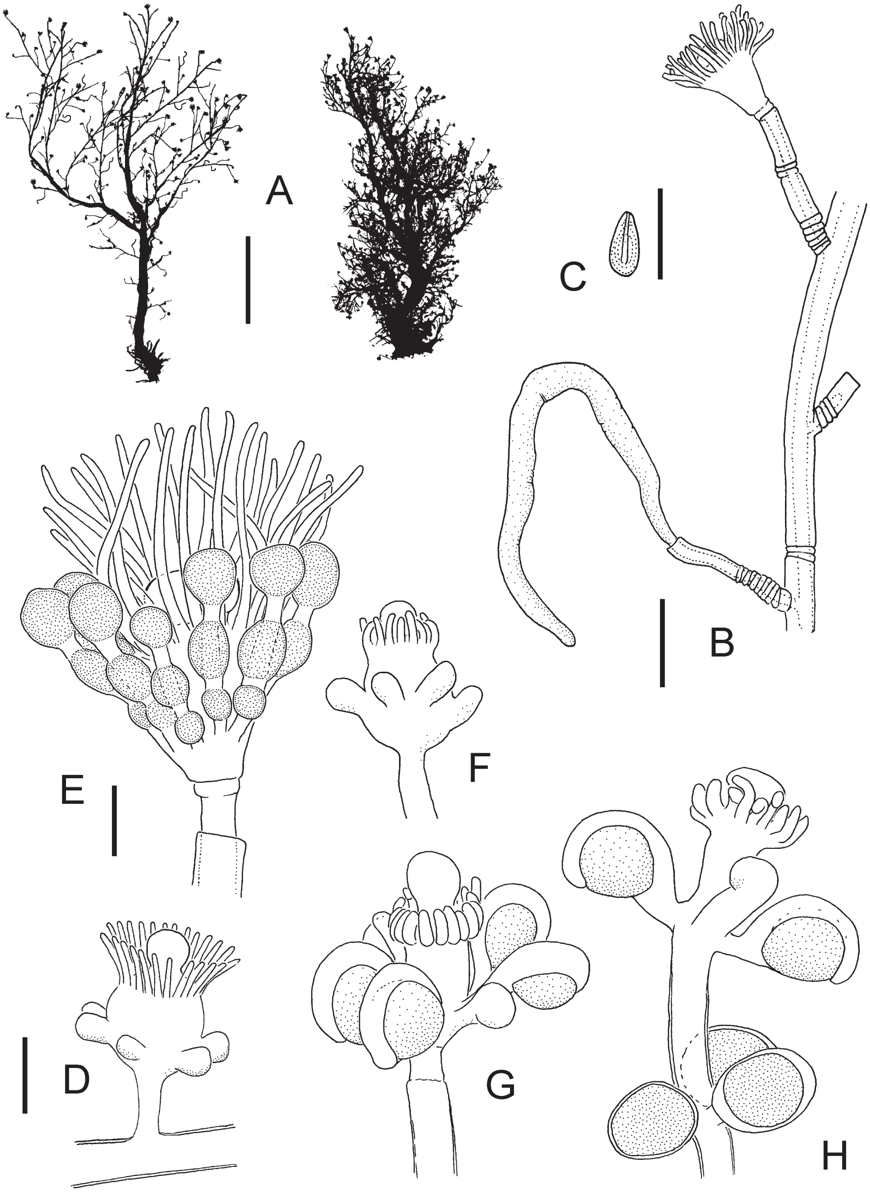

FIG. 35

Eudendrium armatum Tichomiroff, 1887, after preserved Mediterranean material. (A) Colony silhouettes illustrating variation of growth form and density, scale bar 1 cm. (B) Branch with hydranth and contracted nematophore, scale bar 0.5 mm. (C) Nematocysts: undischarged microbasic eurytele, scale bar 10 μm. (D) Young, developing male blastostyle, scale bar 0.2 mm. (E) Mature male blastostyle (intact hydranth), same scale as in D. (F) Young, developing female blastostyle, same scale as D. (G) Female blastostyle (slightly reduced hydranth) with mature eggs held by spadix; same scale as D. (H) Advanced mature female blastostyle and encapsulated embryos attached to pedicel, same scale as D.

DISTRIBUTION: Endemic to the Mediterranean, present in the western and eastern Mediterranean (Marques *et al.*, 2000b; this study). Type locality: Mediterranean.

REMARKS: Although its nematophores make it easily recognizable, *Eudendrium armatum* has likely been repeatedly confused with the similar *E. rameum*.

Eudendrium vervoorti Marques & Migotto, 1998 Fig. 36

Eudendrium vervoorti Marques & Migotto, 1998: 149, fig. 1. – Faasse & Vervoort, 2005: 60, figs 1-2.

DIAGNOSIS: Small monosiphonic colonies, female gonophores without spadix, attached via long pedicels to normal hydranths, only small microbasic euryteles of one size class.

DESCRIPTION: Colonies small, sparingly branched, monosiphonic. Perisarc mostly smooth, some indistinct rings, no clear annulation. Hydranths rather slender, no distinct basal groove, 15-20 tentacles. Female gonophores arising from body of normal hydranths, 2-6 per hydranth, without spadix, tentacles and hypostome of blastostyle not reduced during later development. Mature eggs (embryos?) encapsulated in thin perisarc, linked by long peduncles to basal part of hydranth or to hydranth-pedicel, distal part broadened. Male gonophores unknown. Nematocysts: microbasic euryteles of one size class (5.3-5.8)x(3.3-3.6)μm, r= 1.6.

DIMENSIONS: Colonies up to 7 mm, hydranth ca. 0.57 mm high and 0.15 wide, branches 0.13 mm in diameter, eggs 0.22-0.28 mm.

BIOLOGY: Found once in a shallow seawater pool separated from the sea.

DISTRIBUTION: Type locality only, 51.633°N 03.983°E, The Netherlands, Zeeland.

REMARKS: This species is based on a single colony collected in 1962 and no further records are known. The species is rather unique among the genus *Eudendrium* as its female gonophores do not develop a spadix. In other *Eudendrium* species, a spadix is always present, but often only during the initial stages of the gonophore development. It could also be that the type material is an aberrant *E. capillare* and the absence of a spadix due to some developmental abnormalities, e. g. caused by the particular environmental conditions it was growing in. New findings must be obtained to confirm the identity of the species.

PROBLEMATIC SPECIES

Myrionema multicornis (Allman, 1876) new comb.

Perigonimus multicornis Allman, 1876: 252, pl. 9 figs 1-2. – Kramp, 1926: 241.
Eudendrium ramosum. – Kramp, 1926: 241. [not *Eudendrium ramosum* (Linnaeus, 1758)]

TYPE MATERIAL EXAMINED – Syntype, BMNH 1877.4.12.21, as *Perigonimus multicornis*, type, loc. Kattegatt, leg. G. Allman.

REMARKS: Allman (1876) based his description of *Perigonimus multicornis* on samples sent to him by Christian Frederik Lütken of the Copenhagen Museum. The specimens itself was collected by the botanist A. S. Ørsted. The provenience of the

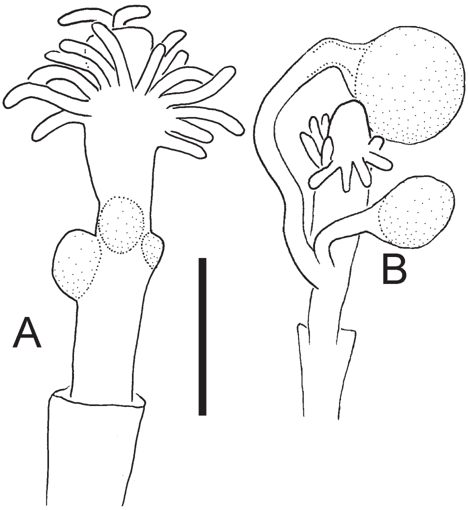

FIG. 36
Eudendrium vervoorti Marques & Migotto, 1998; modified after original publication, scale bar 0.5 mm. (A) Hydranth with putative developing eggs. (B) Hydranth with mature eggs.

sample was purportedly from the Kattegat (Denmark). Allman identified it as a new *Perigonimus* species characterized by the high number of tentacles (he gives 40 as number).

Kramp (1926) re-examined the type material in possession of the Copenhagen museum and recognized that it belonged to the Eudendriidae. He found that Allman must have mistaken hydranth-buds for incipient gonophores. True female gonophores were, however, present in the lower portion of the colony, arranged in a whorl on a normally developed hydranth. The colony was monosiphonic and Kramp thus referred it to *Eudendrium ramosum*. Kramp did not discuss the discrepancy of the tentacle number, which is much too high for *E. ramosum*.

While working at the Natural History Museum in London, I found another syntype specimen of *Perigonimus multicornis* (BMNH1877.4.12.21). It was given to the museum by Allman in 1877 and is certainly a part of the original material he had obtained from the museum in Copenhagen. An examination of these stems, growing on an unidentifiable substrate (soft tube of a polychaete?), confirmed the description of Allman, but more importantly also the observations of Kramp (1926). This specimen evidently belongs to the Eudendriidae and it even has some fertile female hydranths. The gonophores have a simple spadix and are arranged in a whorl at the base of a normally developed hydranth. The hydranths are not well preserved, likely due to prefixation damage by abrasion and compression, but it is evident that they are typical for the Eudendriidae. However, the large numbers of tentacle is immediately striking and they are arranged in two close-set whorls. I could find hydranths with up to 50 tentacles. An examination of the nematocysts showed that besides the usual small microbasic euryteles there are also large macrobasic euryteles. The most revealing feature, however, is the conspicuous presence of zooxanthellae in the gastrodermal layer. The zooxanthellae are especially well visible in the tentacles and some of them still give a purple staining reaction with an iodine solution. By all means, this sample is indistinguishable from *Myrionema hargitti* (Congdon, 1906) [e. g. MHNG INVE60793 material from Guadeloupe or an unregistered sample from Belize]. The other syntype colony is still in the museum of Copenhagen and it must also be attributed to the genus *Myrionema* (Dr O. Tendal, ZMUC, pers. comm.). This makes it sure that the syntype of the London museum was not confounded with another sample after Allaman had deposited it.

Allman's species is thus a senior synonym of *Myrionema hargitti*, a species that is regarded by some authors as a synonym of the Pacific *M. amboinense* Pictet, 1893 (e. g. Calder, 1988). Mainly for biogeographic reasons I think that the Caribbean *H. hargitti* should be kept distinct from the Pacific *M. amboinense*, but both species seem also to differ in the tentacle numbers. Whatsoever, hydroids of the genus *Myrionema* are confined to tropical regions and it is quite unlikely that the genus occurs along the Danish coast. It is much more probable that the origin of the type material of *M. multicornis* was given incorrectly. The collector – Anders Sandøe Ørsted (1816-1872) – was a well known Danish botanist who travelled and collected extensively in Central America and the Caribbean (e. g. Ørsted, 1863). Allman obtained the sample from Copenhagen certainly only after the death of Ørsted and it appears likely that some labels were incorrect or were confounded before he obtained it.

Until the historic presence of *Myrionema multicornis* (Allman, 1876) in the North Sea can be confirmed, it seems better to regard the type locality Kattegat of *Myrionema multicornis* as doubtful. Because the type locality is doubtful, the name *M. multicornis* should also not replace its junior synonym *Myrionema hargitti* (Congdon, 1906).

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