

Morphological study and taxonomical notes on Eudendriidae (Cnidaria: Hydrozoa: Athecatae/Anthomedusae)

A.C. Marques, H. Mergner, R. Höinghaus, C.M.D. Santos & W. Vervoort

Marques, A.C., H. Mergner, R. Höinghaus, C.M.D. Santos & W. Vervoort. Morphological study and taxonomical notes on Eudendriidae (Cnidaria: Hydrozoa: Athecatae/Anthomedusae).

Zool. Med. Leiden 74 (5), 15.ix.2000: 75-118, figs 1-99.— ISSN 0024-0672.

A.C. Marques & C.M.D. dos Santos, Departamento de Biologia - Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto - Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901, Ribeirão Preto, SP, Brazil (e-mail: marques@ffclrp.usp.br).

H. Mergner & R. Höinghaus, Abteilung für Biologie, Lehrstuhl für Spezielle Zoologie der Ruhr-Universität Bochum, Germany.

W. Vervoort, National Museum of Natural History (Nationaal Natuurhistorisch Museum), P.O. Box 9517, 2300 RA Leiden, The Netherlands (e-mail: vervoort@naturalis.nnm.nl).

(Correspondence should be addressed to A.C. Marques or W. Vervoort).

Key words: Hydrozoa; Eudendriidae; *Eudendrium*; *Myrionema*; systematics; morphology; SEM; optical microscopy.

The morphology of 25 species of the family Eudendriidae was studied, with special regard to their reproductive organs, using techniques of SEM and optical microscopy. Whenever possible a re-analysis of the diagnostic characters of these species was carried out. Furthermore, several synonymies were confirmed or discussed and remarks on taxonomical details are presented. A developmental (ontogenetical) series is proposed for the reproductive differentiation, and its usefulness for phylogenetic analysis is considered.

Contents

Introduction	76
Material and identification	77
SEM and optical study	77
Morphological and taxonomical remarks	77
<i>Eudendrium album</i> Nutting, 1896	77
<i>Eudendrium antarcticum</i> Stechow, 1921a	80
<i>Eudendrium arbuscula</i> Wright, 1859	81
<i>Eudendrium armatum</i> Tichomirow, 1887	82
<i>Eudendrium armstrongi</i> Stechow, 1909	83
<i>Eudendrium balei</i> Watson, 1985	84
<i>Eudendrium californicum</i> Torrey, 1902	85
<i>Eudendrium capillare</i> Alder, 1856	88
<i>Eudendrium carneum</i> Clarke, 1882	90
<i>Eudendrium cyathiferum</i> Jäderholm, 1904	92
<i>Eudendrium deciduum</i> Millard, 1957	92
<i>Eudendrium elsaeoswaldae</i> Stechow, 1921b	94
<i>Eudendrium generale</i> von Lendenfeld, 1885	94
<i>Eudendrium glomeratum</i> Picard, 1951	96
<i>Eudendrium infundibuliforme</i> Kirkpatrick, 1890	98
<i>Eudendrium kirkpatricki</i> Watson, 1985	98
<i>Eudendrium merulum</i> Watson, 1985	100

<i>Eudendrium racemosum</i> (Gmelin, 1791)	100
<i>Eudendrium rameum</i> (Pallas, 1766)	102
<i>Eudendrium ramosum</i> (Linnaeus, 1758)	104
<i>Eudendrium ritchiei</i> Millard, 1975	104
<i>Eudendrium terranova</i> Watson, 1985	106
<i>Eudendrium tottoni</i> Stechow, 1932	107
<i>Eudendrium vaginatum</i> Allman, 1863	107
<i>Myrionema amboinense</i> Pictet, 1893	111
General discussion	111
Acknowledgements	114
References	115

Introduction

The taxonomy of the family Eudendriidae L. Agassiz, 1862, concerns c. 110 scientific names that were attributed to different taxa in the course of its long taxonomical history. The family is composed of two genera, the apparently warm-water, monotypic genus *Myrionema* Pictet, 1893 (cf. Calder, 1988), and the genus *Eudendrium* Ehrenberg, 1834, distributed worldwide and rich in species (cf. Millard, 1975; Watson, 1985; Marques, 1996). Two previous phylogenetic studies deal with the family; Marinopoulos (1992) in a study on the Mediterranean representatives of the group, and Marques (1996), who commented on that study, suggesting characters to support the monophyletic origin of the family and of both its genera.

A revision including all species of Eudendriidae is lacking. However, there are several comprehensive studies on regional faunas (e.g., Millard, 1975, for South Africa; Watson, 1985, 1987, and Schuchert, 1996, for the Australian - New Zealand region; Hirohito, 1988, for Japan; Marques, 1993, for the Brazilian coast). Some additional recent studies of more local scope also helped to improve understanding the taxonomy of the family; among these we highlight Calder (1988), Bavestrello & Piraino (1991), Marques (1995), Marques & Migotto (1998), Marques & Calder (2000).

The collection studied here includes types and other materials of several species of Eudendriidae. It was brought together by one of the authors (H. Mergner) during almost four decades. At about the middle of the 1970s the material was studied by R. Rösler (now R. Höinghaus) as part of his undergraduate thesis, finished in 1978, but this thesis was never published. In 1996, after H. Mergner's retirement, the whole collection was donated to the National Museum of Natural History (Nationaal Natuurhistorisch Museum), Leiden, The Netherlands. Finally, in 1997/1998 the collection was re-studied by A.C. Marques in collaboration with the other authors. Part of this study is presented here.

It is now generally acknowledged that the cnidome is of crucial importance in the systematics of Eudendriidae (cf. Picard, 1951; Watson, 1985; Calder, 1988; Marinopoulos, 1992; Marques, 1993, 1995, 1996), but general morphology still plays an important role in the recognition of the species. Sometimes a certain species can be distinguished chiefly on external morphological features. We here present a morphological survey of several species of Eudendriidae, detailing their structures and commenting on their importance for the taxonomy of the family, using both microphotographs taken with an optical stereomicroscope and SEM photographs.

Material and identification

In addition to the Mergner collection, specimens were studied from the collection of the National Museum of Natural History, Leiden (RMNH) and The Natural History Museum, London, UK (BMNH). Additional material also came from the Bayerische Staatssammlung München (Munich), Germany (BSM); the South African Museum, Cape Town, South Africa (SAM); the Zoological Museum of the University of Copenhagen, Denmark (ZMC); the Swedish Museum of Natural History (Naturhistoriska Riksmuseet Stockholm, Sweden) (NRS), and the Musée Royale Afrique Centrale, Tervueren, Belgium (MRAC). Collection and registration numbers are given in the text. Besides morphological features, including general measurements, characters of the cnidome have been used, the terminology for nematocysts follows Weill (1934) and Mariscal (1974). A complete taxonomical study of all material available will be published elsewhere.

SEM and optical study

Specimens selected for electron microscopy were dried at critical point, sputter-coated with gold and studied with a Jeol-SMU 3 electron microscope. For conventional light microscopy stained sections and total mounts were used; the technique is more fully described in Marques et al. (2000). All photographs were made by R. Höinghaus and computer edited by C.M.D. dos Santos.

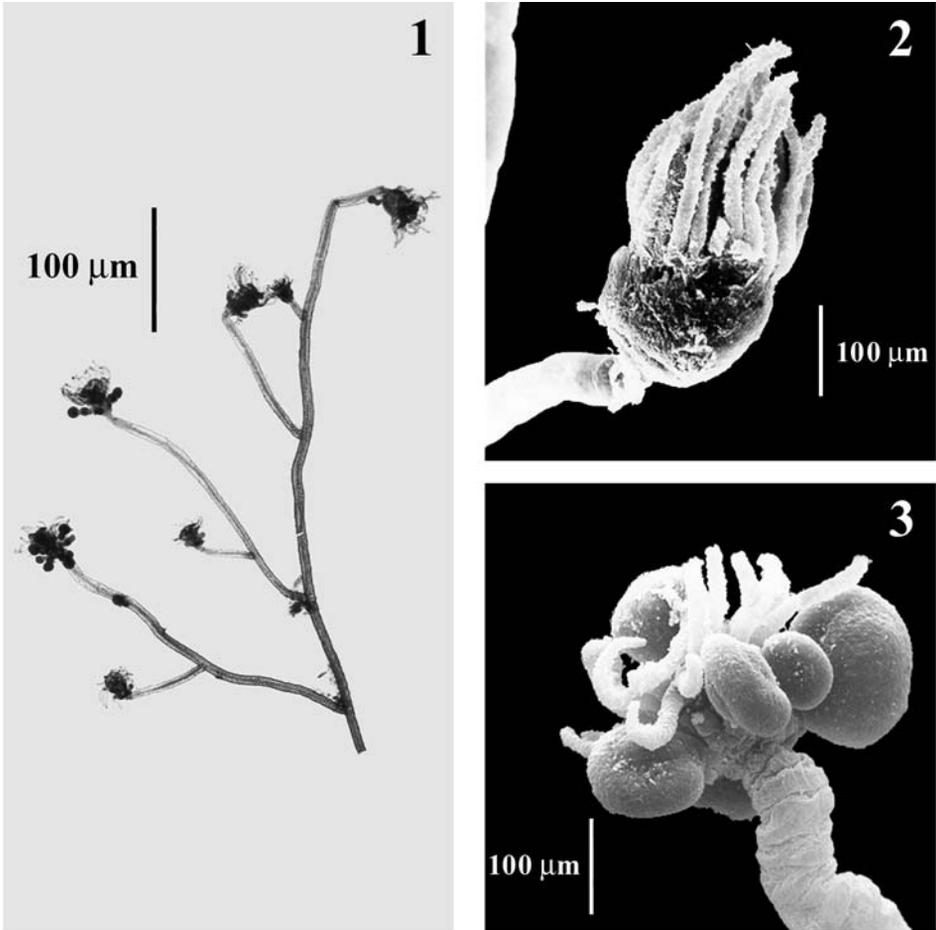
Morphological and taxonomical remarks

Eudendrium album Nutting, 1896
(figs 1-7)

Eudendrium album Nutting, 1896: 146; 1898: 362, pl. 14 fig. 1.

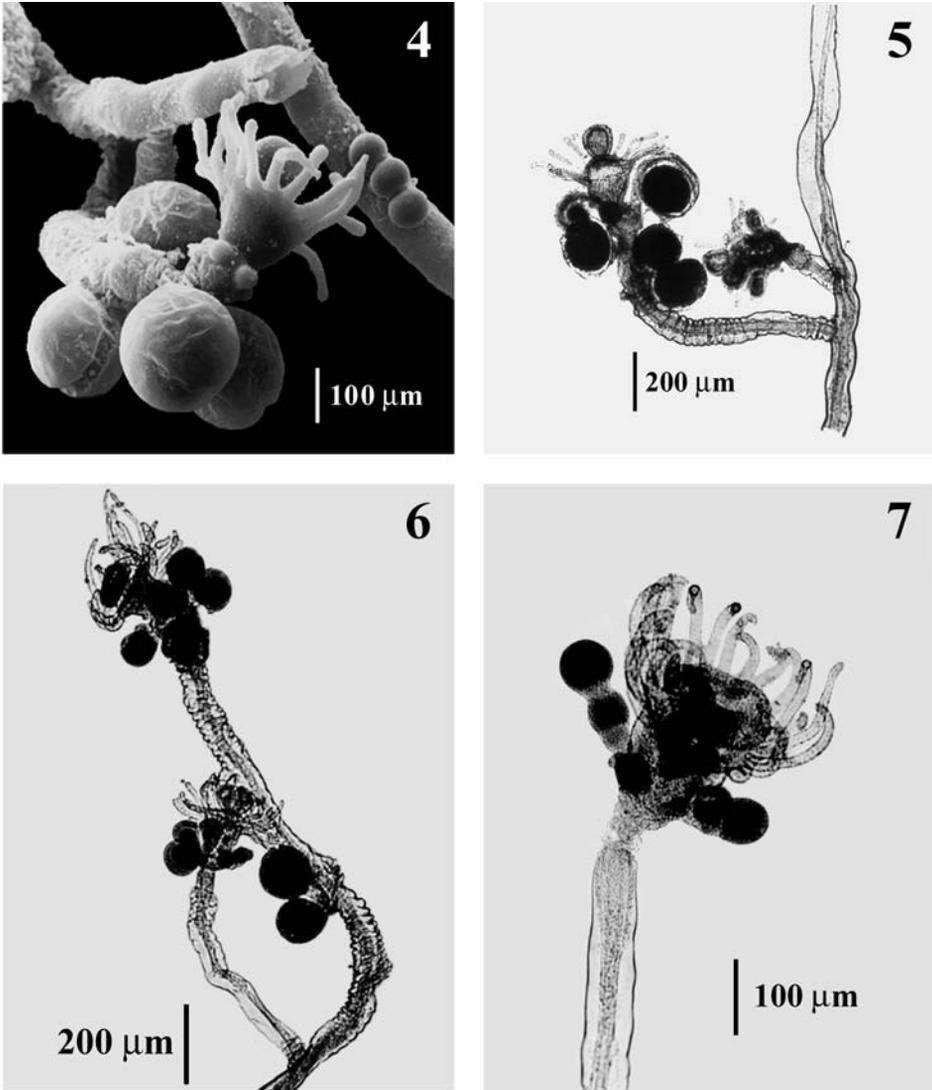
Material.— **England:** female colony, Plymouth, 50°22'N 04°09'W, alcohol preserved, 2 histological preparations and 2 total mounts, 11.vi.1898, leg. E.T. Browne, det. A.C. Marques (RMNH-Coel. 28439, BMNH 1948.9.8.83); female colony, Weymouth, Weymouth Bay, 50°36'N 02°29'W, 3 histological preparations and 3 total mounts, 18 m, no collection date, leg. R. Kirkpatrick, det. A.C. Marques (RMNH-Coel. 28450, BMNH 1897.8.9.7); female colony, Plymouth, 50°22'N 04°09'W, alcohol preserved, 8 histological preparations and 5 total mounts, 14.ix.1892, leg. E.T. Browne, det. A.C. Marques (RMNH-Coel. 28465, BMNH 1960.3.1.2). **Scotland:** male colony, Mill Bay Channel, alcohol preserved, 14 histological preparations and 2 total mounts, v.1900, leg. E.T. Browne, det. A.C. Marques (RMNH-Coel. 28449, BMNH 1948.10.1.122).

Remarks.— *Eudendrium album* (figs 1, 2) was originally described from Plymouth material. The species is characterized by whitish hydranths and a tiny trophosoma (stems, branches, and pedicels) (Nutting, 1896). The morphology of the colonies resembles that of other species of *Eudendrium* with small colonies, indicated by Watson (1985) as the “*E. capillare*-group”. In this group are included *Eudendrium antarcticum* Stechow, 1921a (cf. original description, and Millard, 1975); *E. capillare* Alder, 1856 (cf. Watson, 1985; pers. obs.), *E. fragile* Motz-Kossowska, 1905 (cf. original description), *E. generale* von Lendenfeld, 1885 (cf. Watson, 1985; pers. obs.), *E. motzkos-*



Figs 1-3. *Eudendrium album* Nutting, 1896. Fig. 1, general aspect of a colony with male blastostyles (RMNH-Coel. 28449); 2, hydranth (RMNH-Coel. 28439); 3, female blastostyle with developing eggs (RMNH-Coel. 28465).

sowskae Picard, 1951 (cf. Motz-Kossowska, 1905, as *Eudendrium simplex*; pers. obs.), *E. nambuccense* Watson, 1985 (cf. original description); *E. tottoni* Stechow, 1932 (= *Eudendrium antarcticum* Totton, 1930, cf. Stechow, 1932; pers. obs.) and *E. vervoorti* Marques & Migotto, 1998 (cf. original description). The cnidome is of paramount importance to distinguish between *E. album* and most of the other species of the *E. capillare*-group. *Eudendrium album* has large macrobasic euryteles, a type of nematocyst only shared with *E. fragile* and *E. motzkossowskae*; but the three species differ in the morphology of the female blastostyle. The female gonophores of *E. album* arise in a whorl around the body of a normally developed blastostyle (fig. 3), each egg supported by a simple (i.e. unbranched) encircling spadix. During development of the eggs, the hydranth continues to grow distally, and the spadices are shed. The mature eggs are enclosed by a layer of perisarc (fig. 4) and are located along the pedicel of the blastostyle (figs 4, 5),



Figs 4-7. *Eudendrium album* Nutting, 1896. Fig. 4, female blastostyle with mature eggs without spadix ; 5 , female blastostyle with developing and mature eggs (both RMNH-Coel. 28450); 6, female blastostyle with developing and mature eggs (RMNH-Coel. 28439); 7, male blastostyle (RMNH-Coel. 28449).

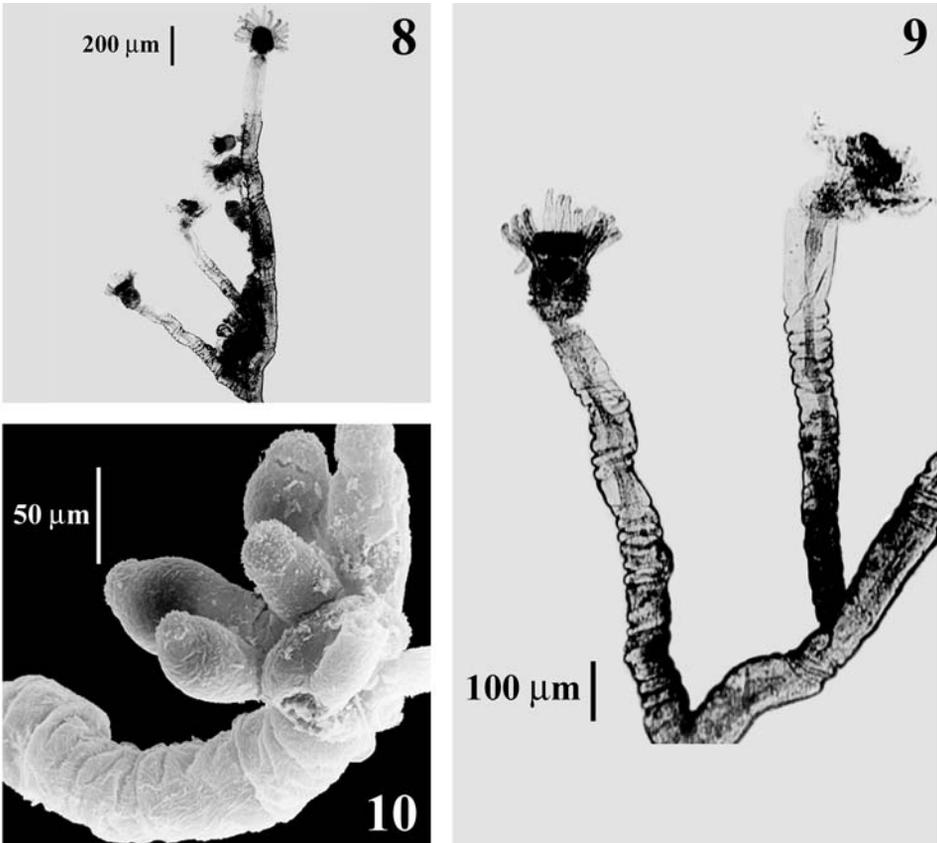
sometimes even far from the growing blastostyle, that can still have immature eggs or start another period of “breeding” (e.g., fig. 6). The male gonophores develop on non-reduced hydranths (i.e., those in which the hypostome is fully developed and number and size of tentacles are the same as in a non-reproductive hydranth), the sporosacs are generally two-chambered when mature (fig. 7).

Eudendrium antarcticum Stechow, 1921
(figs 8-10)

Eudendrium antarcticum Stechow, 1921a: 225; 1925: 415-416, fig. 5.
Eudendrium ?antarcticum; Millard, 1957: 183; 1975: 80-82, fig. 27C-D.

Material.— **South Africa:** male colony, False Bay, c. 34°07'S 18°29'E, alcohol preserved, 5 histological preparations and 3 total mounts, no collection date, leg. N.A.H. Millard, det. A.C. Marques (RMNH-Coel. 28441, BMNH 1957.4.26.12).

Remarks.— As stated above, *Eudendrium antarcticum* (figs 8, 9) is considered one of the species of the *E. capillare*-group because of its tiny size. Material and records of this species are rare. The only material deposited in the collection of the RMNH is part of the same material quoted by Millard (1957; 1975) as "*E. ?antarcticum*". The male gonophore of this species is different from that of all other species in the *E. capillare* group, being a reduced blastostyle with one-chambered sporosacs that have a peculiar, pointed extremity (fig. 10; cf. also Millard, 1975). This terminal tubercle



Figs 8-10. *Eudendrium antarcticum* Stechow, 1921. Fig. 8, distal part of colony; 9, hydranths; 10, male blastostyle with its characteristic, pointed tips (RMNH-Coel. 28441).

bears microbasic euryteles of small size. In some of the sporosacs, the only chamber is linked to the basal part of the blastostyle by a stalk, similar to the condition described for *E. nambuccense* (Watson, 1985). Nevertheless, the female reproductive structures of both species (that we could not observe) differ: those of *E. antarcticum* arise on a non-reduced blastostyle (Stechow, 1925) whereas those of *E. nambuccense* occur on a reduced blastostyle (Watson, 1985).

Eudendrium arbuscula Wright, 1859
(figs 11-15)

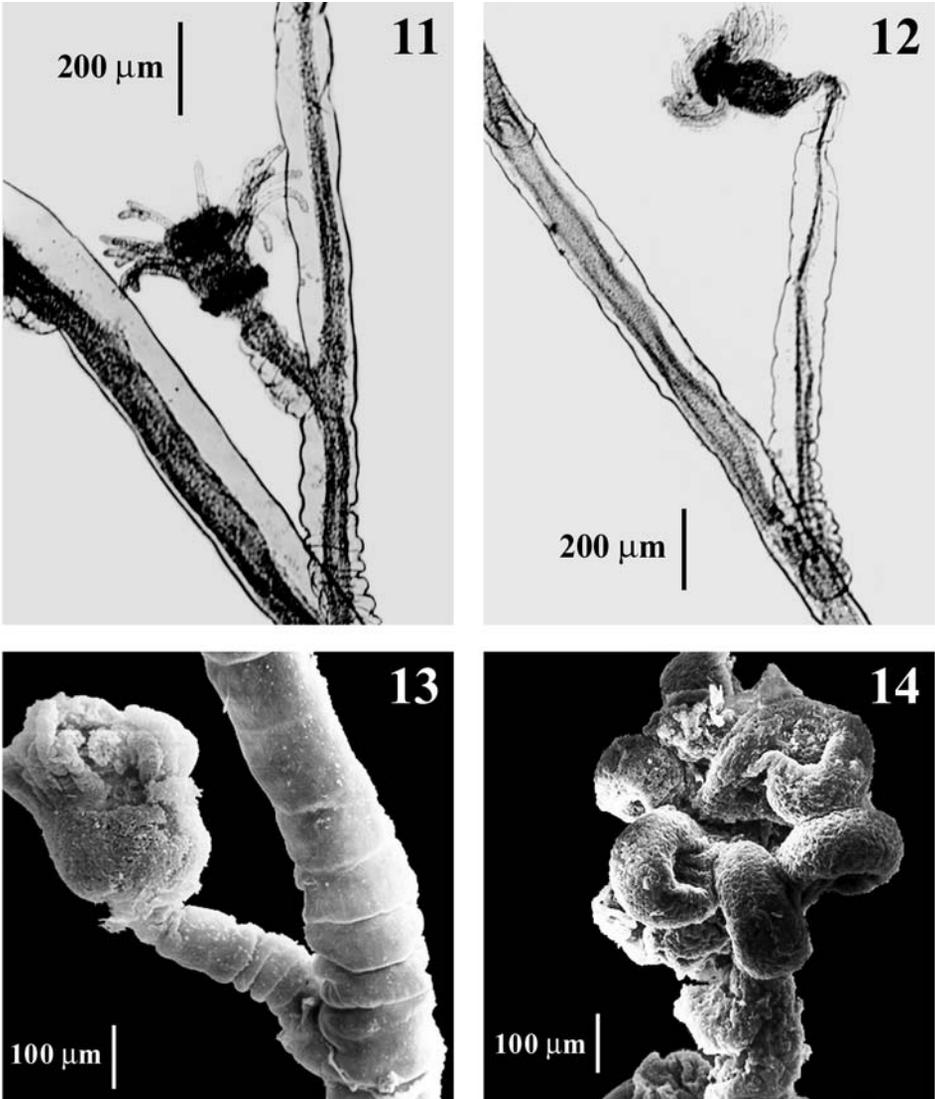
Eudendrium arbuscula Wright, 1859: 113, pl. 9 figs 5-6.

Eudendrium rigidum Allman, 1876: 253-254, pl. 9 figs 3-4.

Material.— **Denmark:** colony without gonophores, Middelfart, Little Belt Strait, 55°30'N 09°44'E, alcohol preserved, no collection date, leg. A.M. Norman, det. A.C. Marques (RMNH-Coel. 28458, BMNH 1912.12.21.98 and ZMC; all parts of the type series of *E. rigidum* Allman, 1876). **North Sea:** colony without gonophores, North Sea, Dogger Bank, SW Patch, c. 54°N 03°E, alcohol preserved, 5 histological preparations and 3 total mounts, no collection date, leg. Min. Agr. Fisheries, det. A.C. Marques (RMNH-Coel. 28488, BMNH 1922.6.20.2). **Norway:** colony without gonophores, Rong, Hjeltefjord, Rong Sund, ("z.N. IV, 51" on label), 60°27'N 04°55'E, alcohol preserved, 2 histological preparations and 2 total mounts, 17.viii.1937, leg. W.J. Rees, det. A.C. Marques (RMNH-Coel. 28473, BMNH without number). **Spain:** female colony, Bay of Biscay, Allen's Stat. Nr. XIII, 48°07'N 08°13' W, alcohol preserved, 2 histological preparations and 2 total mounts, 753 m, viii.1906, leg. E.T. Browne, det. A.C. Marques (RMNH-Coel. 28464, BMNH 1941.3.20.416). **Sweden:** male colony, Bohuslän, no coordinates, 4 histological preparations and 2 total mounts, 1898, leg. Östergren, det. A.C. Marques (RMNH-Coel. 28396, BSM).

Remarks.— We follow the recent proposal to preserve the name *Eudendrium arbuscula* for the species described by Wright (1859), in favour of the older name *Tubularia arbuscula* used by D'Orbigny (1846), for an athecate hydroid of doubtful identity (cf. Marques & Vervoort, 1999; cf. also Bedot, 1925). Hence, we have rejected the name *E. wrightii* proposed by Hartlaub (1905) to substitute Wright's *E. arbuscula*.

Eudendrium arbuscula as it stands now is a well known North Atlantic species, characterized by the presence of a ring of microbasic euryteles on the basal part of the body of the hydranth (fig. 11). However, as observed by Hincks (1868), this feature is variable even among the hydranths of a given colony (fig. 12). Kramp (1926) considered *E. rigidum* Allman, 1876 (fig. 13), based on material from Denmark, a junior synonym of *E. arbuscula*. We studied two fragments of the holotype of *E. rigidum* (BMNH 1912.12.21.98 and RMNH Coel. 28458) that appear to corroborate his proposal. The female gonophores of *E. arbuscula* arise on partially reduced blastostyles, with atrophied hypostome and degenerated tentacles; the immature eggs are supported by simple spadices (fig. 14). During development the blastostyle reduces completely, and becomes linked to the eggs by small peduncles (cf. Calder, 1972; pers. obs.). Hamond (1957) described partially atrophied blastostyles in early phases of development, reducing almost completely when the eggs reach maturity. Then a new polyp may arise and continue the distal growth of the branch, also including the production of a new series of eggs. The male blastostyle of *E. arbuscula* is completely reduced, the



Figs 11-14. *Eudendrium arbuscula* Wright, 1859. Fig. 11, hydranth with characteristic basal nematocyst ring (RMNH-Coel. 28488); 12, hydranth apparently lacking nematocyst ring (RMNH-Coel. 28473); 13, hydranth of *E. rigidum*; RMNH-Coel. 28458; part of type series); 14, female blastostyle with developing eggs (RMNH-Coel. 28464).

sporosacs are two-chambered and have an accumulation of large microbasic euryteles at the apex (fig. 15; Calder, 1972; pers. obs.).

Eudendrium armatum Tichomiroff, 1887
(figs 16-18)

Eudendrium armatum Tichomiroff, 1887: 31-39, pls. 1-2; 1890: 276, 277, 298-300.

Material.— **Italy:** male and female colonies, Tyrrhenian Sea, Sorrento, Punta di Sorrento, passage from open sea to V. di Pollio Felice, 40°38'N 14°22'E, alcohol-Susa preserved, 3 histological preparations and 4 total mounts, 1-3 m, 19.ix.1965, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28228).

Remarks.— *Eudendrium armatum* Tichomiroff, 1887 (not *E. armatum* Jäderholm, 1908 = *E. cnidiferum* Stechow, 1919, cf. Jäderholm, 1908: 372; Stechow, 1919: 154) is a common and well known Mediterranean species. Its colonies are much fascicled up to the distal branches; its best diagnostic feature is the presence of nematophores (fig. 16), arising everywhere in the colony, but in particular close to the fascicled main stem. As far as we know, nothing is known about the ontogeny of these nematophores. The male blastostyles are non-reduced, bearing sporosacs that are generally two-chambered (fig. 17). The female gonophores, supported by simple spadices, go through a complex process of reduction. During ontogeny, there is an alternate reduction in the size of the tentacles up to their complete disappearance (cf. example in *E. spec.*, fig. 99). After this first phase of reduction, the second phase starts with the reduction of the remaining tentacles. Finally, a third phase follows with reduction of the hypostome (fig. 18). Therefore, later phases of the female blastostyle have no tentacles at all or occasionally only a few club-shaped nematocyst-provided tentacle remnants and the hypostome is reduced to a stump. The mature eggs have their spadices shed, and are located along the axis of the blastostyle.

Eudendrium armstrongi Stechow, 1909
(figs 19-21)

Eudendrium ramosum Armstrong, 1879: 103, pl. 12.
Eudendrium armstrongi Stechow, 1909: 28-29.

Material.— **Japan:** male colony, Sagami Bay Stn 12, 35°06'30"N 139°40'40"E, alcohol-formol preserved, 2 histological preparations and 1 total mount, 800 m, 13.xi.1904, col. Doflein, det. E. Stechow (RMNH-Coel. 28397, BSM).

Remarks.— Armstrong (1879) described a new species as *Eudendrium ramosum* based on material from India, but the binomen was pre-occupied by *E. ramosum* (Lin-

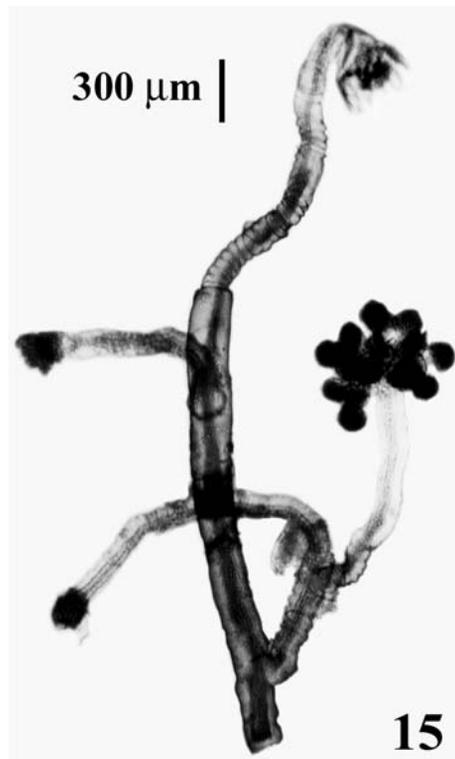


Fig. 15. *Eudendrium arbuscula* Wright, 1859, branch with mature male blastostyle (RMNH-Coel. 28396).

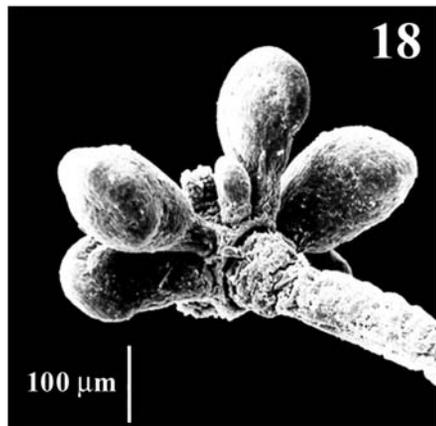
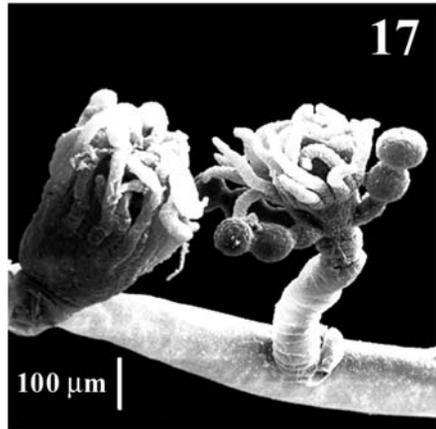
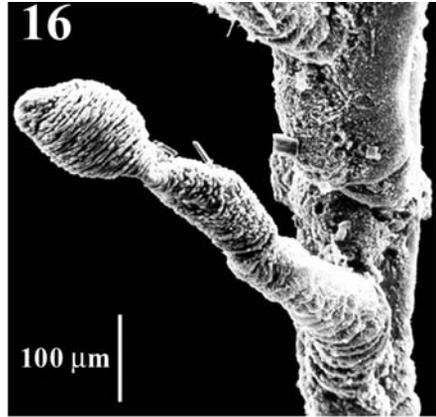
naeus, 1758). The nomenclatural problem was solved by Stechow (1909), who applied the name *E. armstrongi* Stechow, 1909, to the species. Stechow studied material collected in Sagami Bay (Japan) for a complementary description (fig. 19). It is remarkable that the bathymetrical distribution of both sets of specimens is quite different (18-126 m for the Indian material and 800 m for the Japanese material). We do not know where Armstrong's material has been deposited and it is not clear whether or not this material was studied by Stechow. His Sagami Bay material is in BSM; a fragment is now in the RMNH collection. Stechow (1909) considered the species recognizable by the completely reduced, one-chambered, male blastostyles (fig. 20). According to Stechow (1909) this type of gonophore resembles that of *Eudendrium planum* Bonnevie, 1898; however, the blastostyles described by Bonnevie (1898) were female (cf. also Calder & Vervoort, 1998, who described one and two chambered male gonophores on non-reduced hydranths). Another distinct character of the species is the small size of the hydranths, especially when compared to the supporting pedicels (fig. 21); the width of the hydranth barely surpasses that of the pedicel.

Eudendrium balei Watson, 1985
(figs 22-24)

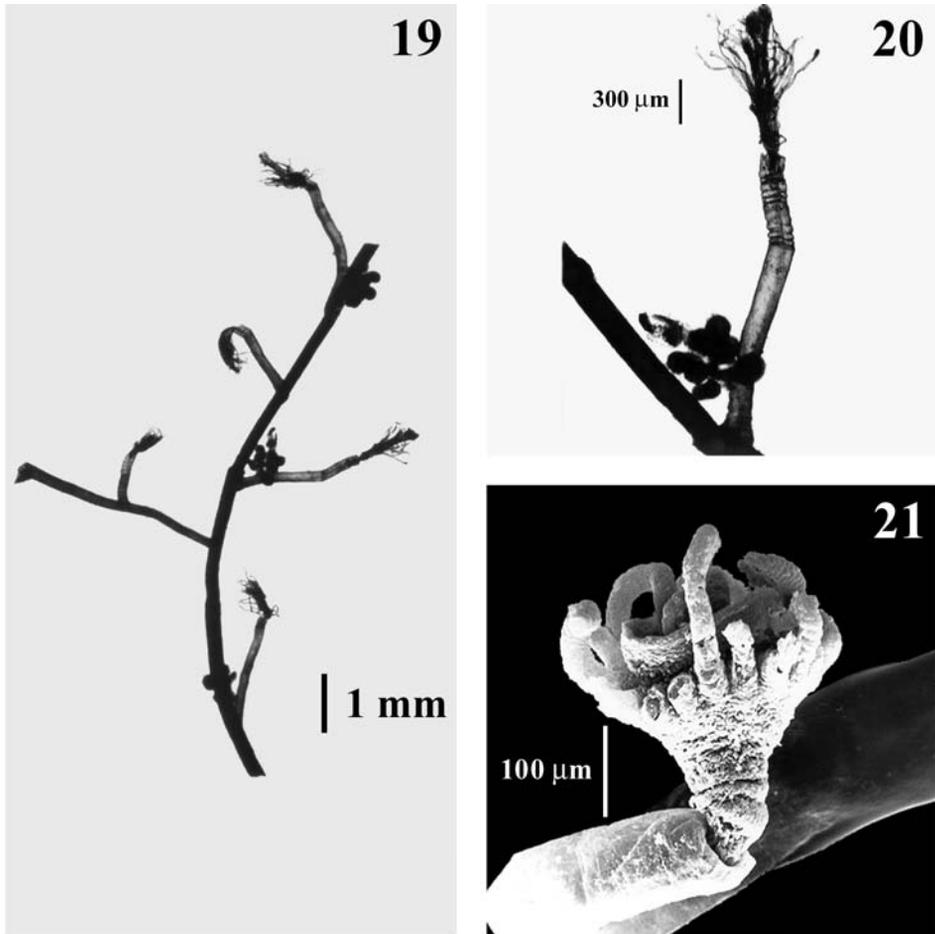
Eudendrium balei Watson, 1985: 205-207, figs 68-74.

Material.— **Australia:** male and female colonies, Melbourne, Port Phillip, Pope's Eye, 38°08'S 144°40'E, alcohol preserved, 14 histological preparations and 3 total mounts, 6-12 m, no collection date, det. A.C. Marques [RMNH-Coel. 28390 (together with *E. glomeratum*), National Museum of Victoria]; female colony, Port Phillip, 38°16'S 144°40'E, alcohol preserved, 4 histological preparations and 1 total mount, no collection date, leg. W.M. Bale, det. A.C. Marques (RMNH-Coel. 28453, BMNH 1911.12.3.1).

Remarks.— During development the



Figs 16-18. *Eudendrium armatum* Tichomirowf, 1887. Fig. 16, nematophore; 17, male blastostyle and hydranth; 18, female blastostyle in later and advanced stage of reduction (all figs RMNH-Coel. 28228).

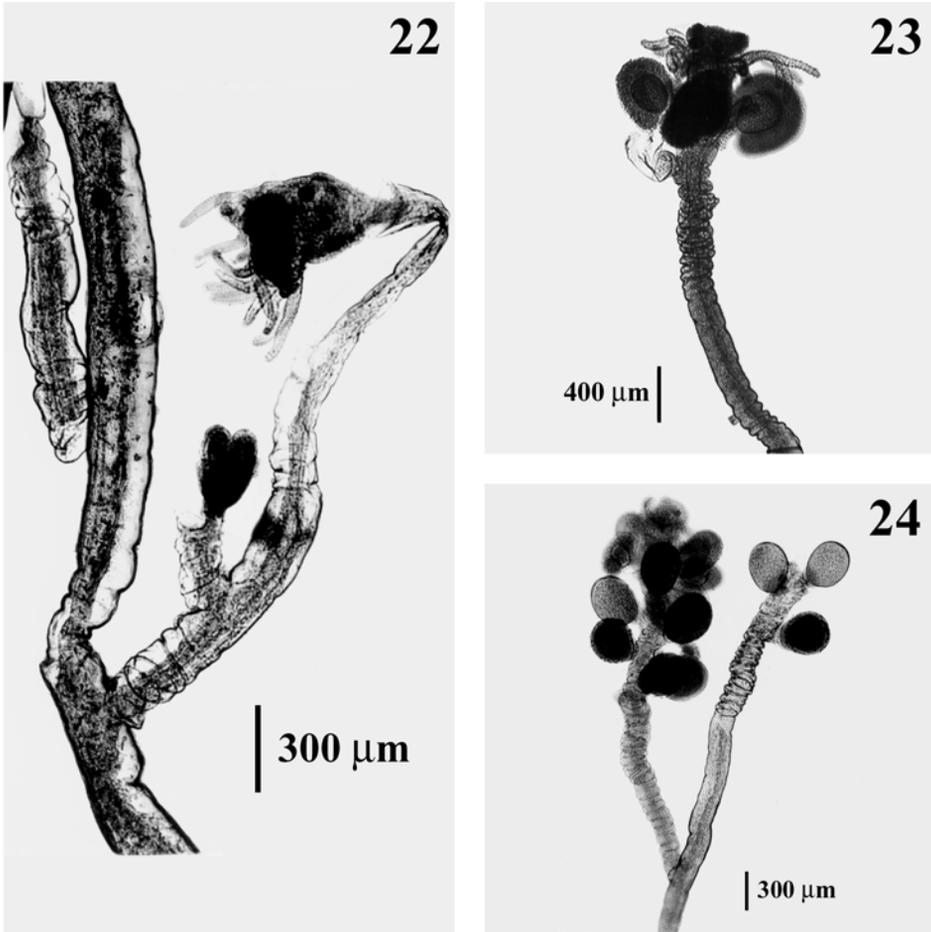


Figs 19-21. *Eudendrium armstrongi* Stechow, 1909. Fig. 19, fragment of branch; 20, hydranth and mature male blastostyle; 21, hydranth (all figs RMNH-Coel. 28397).

female blastostyle of *E. balei* bears the same number of tentacles as the non-reproductive hydranth (fig. 22), but only half of these are fully developed, the other half being reduced to club-shaped tentacles (Watson, 1985; cf. fig. 23). This pattern corresponds with the first phase of the development of *E. armatum* described above (cf. also fig. 99 for *E. spec.*). However, in *E. balei* blastostyle reduction is interrupted at this stage. The mature eggs lose their spadices and are enclosed by a thin, transparent pellicle, become scattered over the pedicel of the blastostyle and are connected to it by short peduncles (fig. 24).

Eudendrium californicum Torrey, 1902
(figs 25-27)

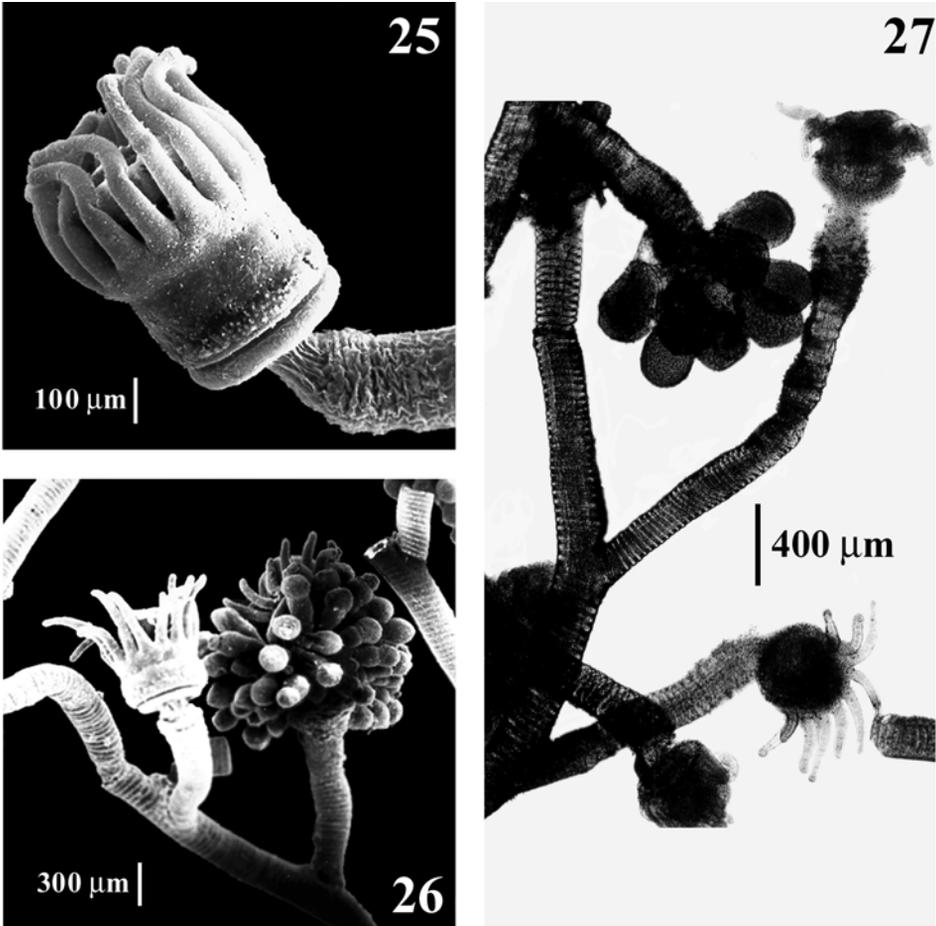
Eudendrium californicum Torrey, 1902: 32-33, pl. 2 figs 13-14.



Figs 22-24. *Eudendrium balei* Watson, 1985. Fig. 22, fragment of branch with hydranth (RMNH-Coel. 28453); 23, female blastostyle with partly reduced tentacles; 24, two mature female blastostyles, of which one (on right side) lacks the terminal hydranth (both RMNH-Coel. 28390).

Material.— USA: male and female colonies, Monterey, Cypress Point, Monterey Peninsula, 36°37'N 121°55'W, alcohol preserved, 12 histological preparations and 3 total mounts, i.1921, leg. W. Wallace, det. A.C. Marques (RMNH-Coel. 28442, BMNH 1921.5.30.6).

Remarks.— *Eudendrium californicum* is one of the largest and most conspicuous species of Eudendriidae, as for instance *Myrionema amboinense* Pictet, 1893, *Eudendrium carneum* Clarke, 1882, *E. racemosum* (Cavolini, 1785), *E. rameum* (Pallas, 1766) and *E. vaginatum* Allman, 1863. The huge hydranth of *E. californicum* is generally squarish, with a deep circular groove in its basal part (fig. 25), and a ring of large nematocysts just above. Weill (1934) identified these nematocysts as atrichous isorhizas. In all material that we studied the large nematocysts indeed have the appearance of atrichous isorhizas, though we never saw one discharged. The pedicels, branches and



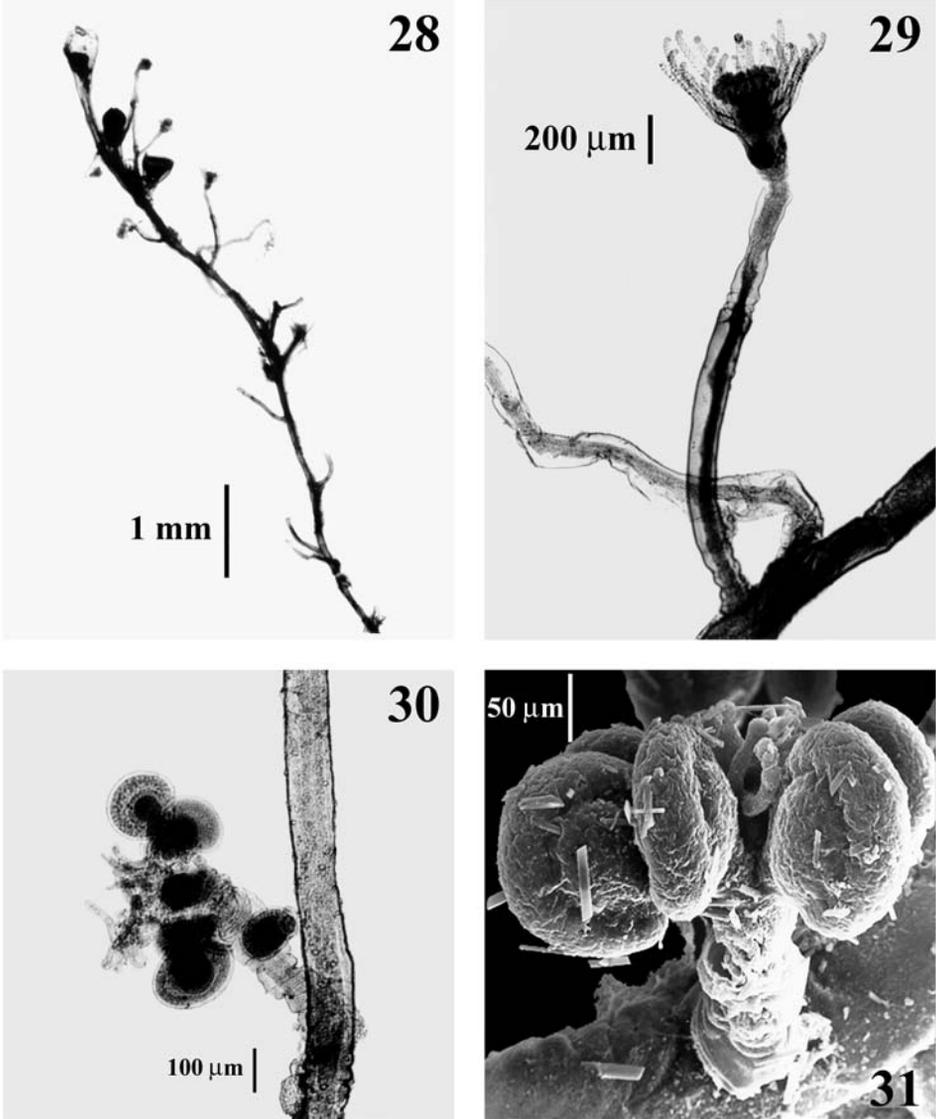
Figs 25-27. *Eudendrium californicum* Torrey, 1902. Fig. 25, typical squarish hydranth; 26, hydranth and male blastostyle with tentacles hidden by sporosacs; 27, fragment of branch with hydranths and mature female blastostyle (all RMNH-Coel. 28442).

stems of the colonies are tightly annulated throughout (fig. 26). The female gonophore arises on a partially reduced polyp, while the spadix is unbranched; during its development the blastostyle reduces, the spadices are shed and the eggs, encircled by perisarc, are scattered along the pedicel of the blastostyle (fig. 27). The male blastostyles have so numerous sporosacs that it is difficult to see the non-reduced tentacles (fig. 26). The species is similar to *E. vaginatum* in morphology, especially as regards general shape, dimensions, strong annulation of the trophosoma, and the female blastostyles. The cnidome and the absence of a pseudo-hydrotheca, however, are quite conspicuous features to distinguish both species (cf. also the notes on *E. vaginatum* below).

Eudendrium capillare Alder, 1856
(figs 28-34)

Eudendrium capillare Alder, 1856: 355, pl. 12 figs 9-12.

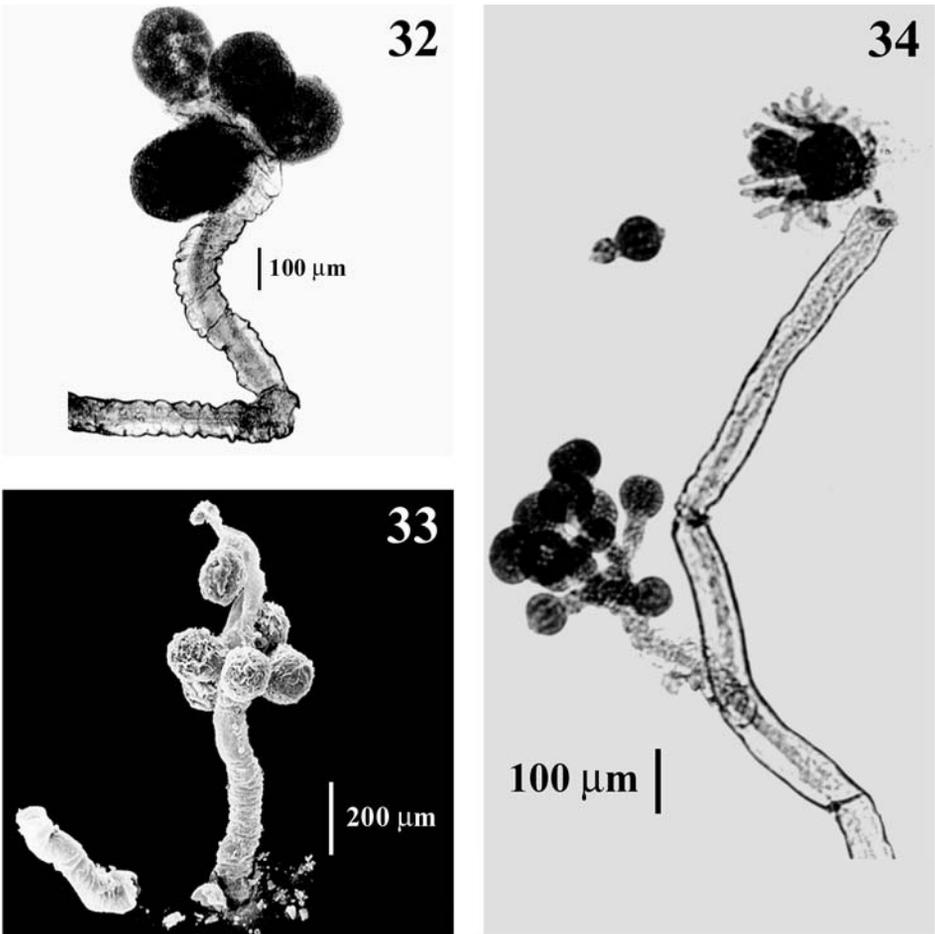
Material.— **Italy:** female colony, Naples, 40°49'N 14°12'E, 4 histological preparations and 1 total mount, 1898, det. A.C. Marques (RMNH-Coel. 28401, BSM). **England:** male colony, Plymouth, 50°22'N 04°09'W, alcohol preserved, 3 histological preparations and 4 total mounts, 15.ix.1897, leg.



Figs 28-31. *Eudendrium capillare* Alder, 1856. Fig. 28, colony; 29, hydranth (both RMNH-Coel. 28426); 30, immature female blastostyle (RMNH-Coel. 28456); 31, immature female blastostyle (RMNH-Coel. 28401).

E.T. Browne, det. A.C. Marques (RMNH-Coel. 28448, BMNH 1948.9.8.95). **South Africa:** female colony, Knysna, Durban, 34°03'S 23°03'E, alcohol preserved, 4 histological preparations and 5 total mounts, leg. E. Warren, det. A.C. Marques (RMNH-Coel. 28456, BMNH 1922.2.2.10). **Mozambique:** colony without gonophores, Inhaca Island, Barreira Vermelha, 26°02'S 32°54'E, alcohol preserved, 4 histological preparations and 1 total mount, 1969, leg. N.A.H. Millard, det. A.C. Marques (RMNH-Coel. 28426, MRAC 3066).

Remarks.— As stated above the *E. capillare* group (Watson, 1985) contains small, unfascicled species of Eudendriidae, their cnidome comprising only small microbasic euryteles. The distinction among the species of the group is dictated by the morphology of the reproductive structures. *Eudendrium capillare* (figs 28, 29) has immature female blastostyles with partially reduced tentacles and completely reduced hyposome (figs 30 and 31). The blastostyle becomes completely reduced (figs 32, 33) during its development, the spadix is shed and the encapsulated sessile eggs stay more or



Figs 32-34. *Eudendrium capillare* Alder, 1856. Fig. 32, mature female blastostyle (RMNH-Coel. 28456); 33, mature female blastostyle (RMNH-Coel. 28556); 34, fragment of colony with hydranth and male blastostyle (RMNH-Coel. 28448).

less in their original position on the pedicel. The male blastostyle suffers a reduction of its tentacles during development; the mature male blastostyle is completely reduced, having several two-chambered sporosacs (fig. 34).

Eudendrium carneum Clarke, 1882
(figs 35-41)

Eudendrium carneum Clarke, 1882: 137, pl. 7 figs 10-17.

Material.— **Bermuda**: female colony, Hamilton Sound and Gibbons Bay, 32°19'N 64°44'W, alcohol preserved, 13 histological preparations and 2 total mounts, 1 m, 24.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28368). **St Helena**: female colony, 15°59'S 05°41'W, 1 total mount, 55 m, no

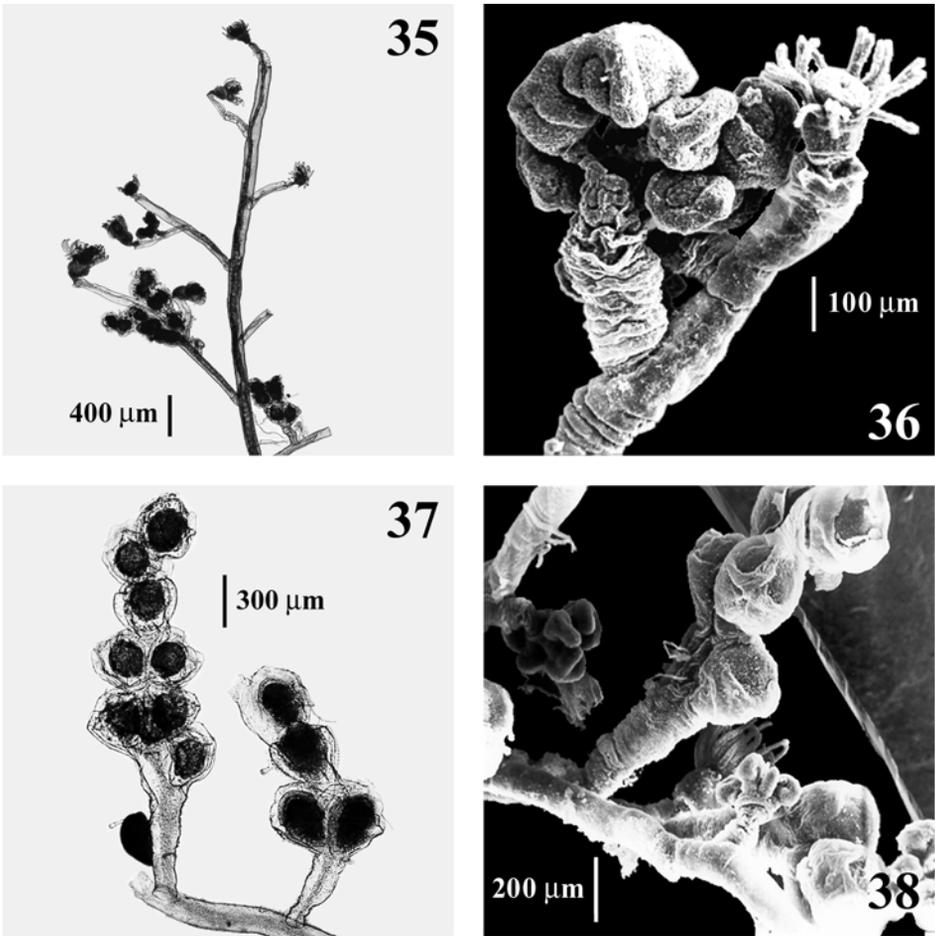


Fig. 35-38. *Eudendrium carneum* Clarke, 1882. Fig. 35, fragment of colony with female blastostyles (RMNH-Coel. 28368); 36, female blastostyle with immature eggs with branched spadix; 37, female blastostyle with mature eggs; 38, female blastostyle with mature eggs surrounded by basket-shaped perisarc capsule (all RMNH-Coel. 28379)

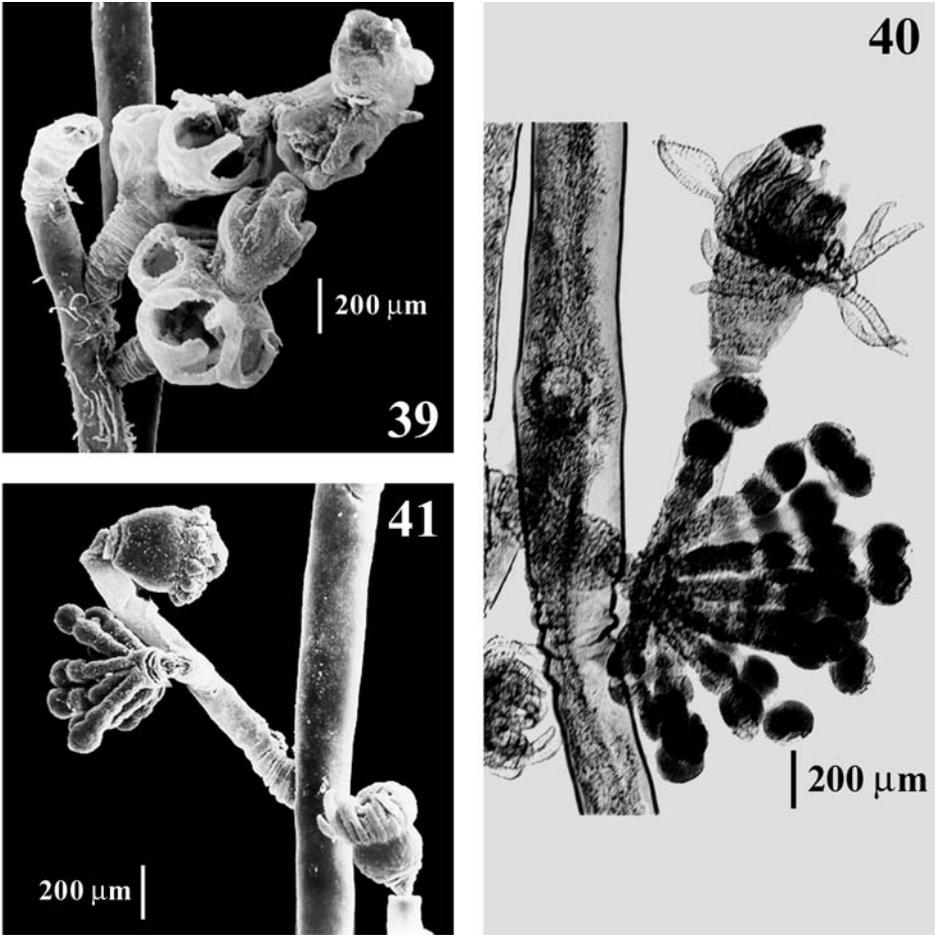


Fig. 39-41. *Eudendrium carneum* Clarke, 1882. Fig. 39 - female blastostyle with mature eggs surrounded by basket-shaped perisarc capsule (RMNH-Coel. 28480); 40, mature male blastostyle bearing long sporosacs, and hydranth; 41, male blastostyle and hydranth with tentacles arranged in two very close whorls (both RMNH-Coel. 28380).

collection date, leg. F.J. Cunningham, det. A.C. Marques, no polyps (RMNH-Coel. 28480, BMNH 1910.10.24.1, both part of the type series of *Eudendrium cunninghami* Kirkpatrick, 1910). USA: female colony, Miami, Ragged Keys, 25°47'N 80°11'W, alcohol-formol preserved, 13 histological preparations and 1 total mount, 1-2.5 m, 16.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28379); male colony, Miami, Guard Bridge, 25°47'N 80°11'W, alcohol-formol preserved, 16 histological preparations and 2 total mounts, 1 m, 19.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28380).

Remarks.— *Eudendrium carneum* (fig. 35) is another cosmopolitan species belonging to the group of large species of the family. The colonies are generally fascicled (unfascicled colonies are presumed to be young). One of the distinctive features of the species is the female blastostyle. The eggs, supported by a bifid spadix, arise in a whorl around the body of the hydranth (sometimes still with a few remnants of

degenerated tentacles) (fig. 36). During development, the eggs scatter over the length of the axis of the blastostyle (fig. 37). At the same time, a thickening of perisarc occurs in the region of the spadix, enclosing the egg in a basket-shaped, bi-fenestrated capsule (figs 38, 39). These two fenestrae allow the release of the planula (cf. Vannucci, 1954). The male blastostyle is completely reduced; the bead-shaped sporosacs have up to 5 chambers (fig. 40). In some of the non-reproductive hydranths of *E. carneum* with tentacular reduction it is not unusual to observe the atrophied tentacles distributed in two close whorls (fig. 41).

Eudendrium cyathiferum Jäderholm, 1904
(fig. 42)

Eudendrium cyathiferum Jäderholm, 1904: 2; 1905: 4, 10, 38, pl. 4 figs 1-3.

Material.— **South Georgia:** female colony, Sandwich Islands, off Cumberland, 54°15'S 36°25'W, 1 total mount, 252-310 m, 05.vi.1902, leg. Swedish South Polar Expedition 1901-1903, det. E. Jäderholm (RMNH-Coel. 28479, BMNH 1960.8.29.4 and NRS; all part of the type series).

Remarks.— *Eudendrium cyathiferum* is a badly known species (cf. Marques & Migotto, 1998). The fragments of type material in RMNH and BMNH consist of female blastostyles only, without hydranths being present. These female blastostyles bear the presumed diagnostic feature of the species: eggs linked to the pedicel of the blastostyle by short, concave supporting structures formed by the perisarc (fig. 42); the concave base presumably remains attached to the pedicel after the eclosion of the planula from the egg (cf. Jäderholm, 1904, 1905; Stepan'yants, 1979). Nevertheless, the concave perisarc support is not an exclusive character of *E. cyathiferum*. It was, for instance, also observed in hatched eggs of *E. glomeratum* Picard, 1951 (see below). A comparable structure occurs in *E. vervoorti*, but in that species the concave bases of the eggs are not strengthened by perisarc, and are linked to the body of blastostyle or pedicel by long peduncles (cf. Marques & Migotto, 1998). The relationships between these three species are still dubious and must await further information on *E. cyathiferum*, specially on its cnidome.

Eudendrium deciduum Millard, 1957
(figs 43-46)

Eudendrium deciduum Millard, 1957: 184-185, fig. 2.

Material.— **South Africa:** colony without gono-

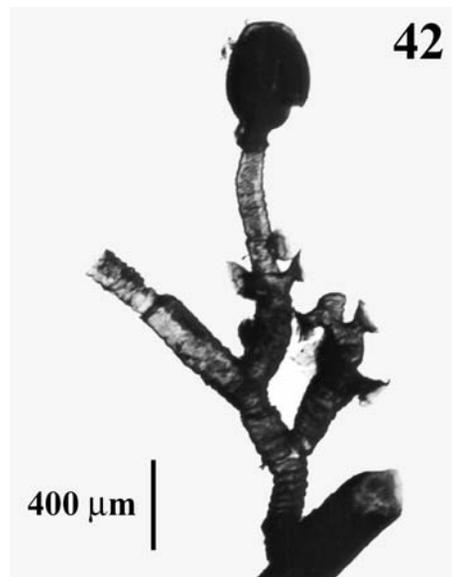
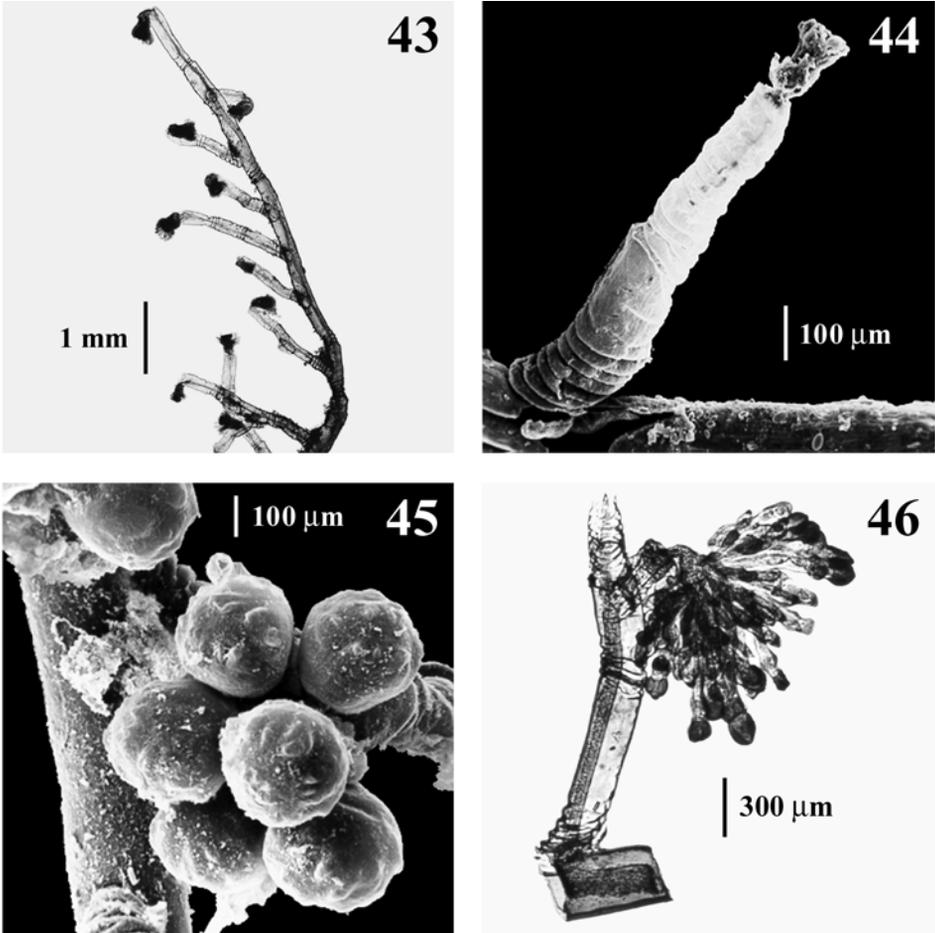


Fig. 42. *Eudendrium cyathiferum* Jäderholm, 1904, female blastostyle with concave egg bases and one mature egg (RMNH-Coel. 28479, part of type series).

phores, East London, Bat's Cave Rock, 33°02'N 25°55'E, alcohol preserved, 1 total mount, 10.vii.1937, leg. T.A. Stephenson, det. A.C. Marques (RMNH-Coel. 28440, BMNH 1937.12.13.17); male and female colonies, near Gordon's Bay, False Bay (bearing the label "UCT FAL 52V"), c. 34°09'S 18°50'E, alcohol preserved, 9 histological preparations and 4 total mounts, 18 m, 25.vi.1952, leg. & det. N.A.H. Millard (RMNH-Coel. 28477, RMNH-Coel. 28407, BMNH 1957.4.26.13, and SAM H098; all part of the type series).

Remarks.— The arborescent colonies of *E. deciduum* can reach a considerable size, their fasciculation even extending to the branches. The ultimate pedicels of branches show a tendency towards a unilateral arrangement (fig. 43; Millard, 1975, fig. 29E). The hydranths are not much wider than the supporting pedicels (fig. 44), with more or less the same characteristics also found in *Eudendrium armstrongi* Stechow, 1909,



Figs 43-46. *Eudendrium deciduum* Millard, 1957. Fig. 43, fragment of colony with pedicels showing tendency towards unilateral arrangement; 44, hydranth (narrower than supporting pedicel; both RMNH-Coel. 28440); 45, female blastostyle with mature eggs covered by perisarc (RMNH-Coel. 28447, part of type series); 46, mature male blastostyle with numerous sporosacs (RMNH-Coel. 28407, part of type series).

described from Japan (cf. Stechow, 1909). The immature female spadices of *E. deciduum* are branched, a unique feature of this species (Millard, 1975). These branched spadices are shed during development. The eggs are surrounded by perisarc, staying more or less in their original position on the blastostyle. The only other species of *Eudendrium* with a complex spadix (i.e., not simple or bifid) is *E. maorianus* Schuchert, 1996, in which the spadices are shed and the mature eggs are also covered by a thin layer of perisarc (cf. Schuchert, 1996: 84, fig. 50f). The fragments of *E. deciduum* that we have studied only have mature eggs, in which there is no trace of a spadix (fig. 45). The male blastostyles of *E. deciduum* are completely reduced, the sporosacs are numerous and long, 2-3 chambered with the distal chamber elongated; a terminal tubercle is sometimes present on the sporosacs (fig. 46).

Eudendrium deciduum was originally described from South Africa and was subsequently recorded from the Red Sea (Mergner & Wedler, 1977). After re-examination of Mergner & Wedler's material, we conclude that this material represents female colonies of *E. glomeratum* and *E. kirkpatricki* Watson, 1985. The female blastostyles with mature eggs of all three species are reduced, and the eggs more or less retain the original position on the blastostyle. So far *E. deciduum* has only been recorded from South Africa and is probably endemic to that area.

Eudendrium elsaeoswaldae Stechow, 1921
(figs 47-49)

Eudendrium elsae-oswaldae Stechow, 1921b: 252; 1923: 81-83, fig. G.

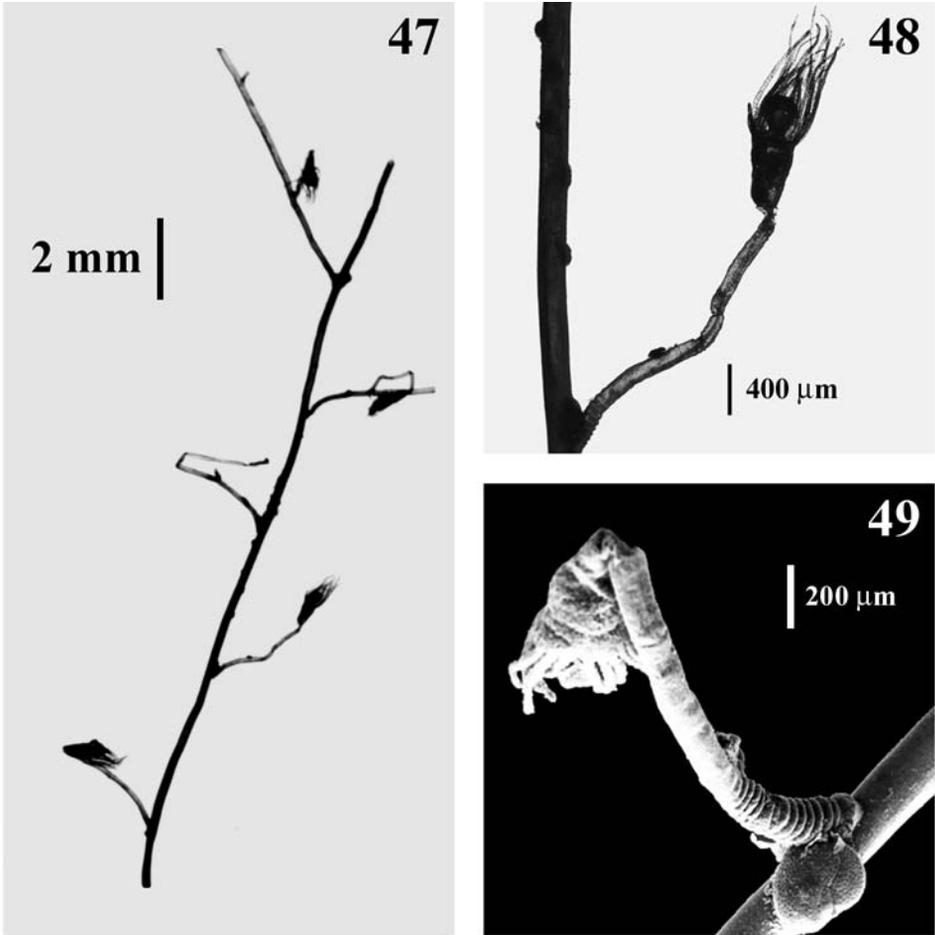
Material.— **Italy**: colony without gonophores, Naples, Posillipo, 40°49'N 14°12'E, alcohol-formol preserved, 3 histological preparations and 2 total mounts, 20 m, no collection date, leg. & det. E. Stechow (RMNH-Coel. 28402, BSM and Stazione Zoologica di Napoli Nr.7, all part of the type series).

Remarks.— *Eudendrium elsaeoswaldae* (fig. 47) was described from the Mediterranean Sea in general by Stechow (1921b) and was subsequently recorded from Naples (Stechow, 1923; Riedl, 1959). All these records are apparently based on the same material. The distinctive features of this species are the elongated hydranths and the long tentacles, and a thin pedicel (figs 48, 49). The gonophores are unknown. Picard (1958) excluded the species from his list of Mediterranean hydroids, probably because of poor knowledge of the species. Marinopoulos (1992) and Boero & Bouillon (1993) apparently followed Picard and did not mention the species in their studies of Mediterranean species of *Eudendrium*. We provisionally recognize this species on account of the hydranth characters referred to above.

Eudendrium generale von Lendenfeld, 1885
(figs 50-52)

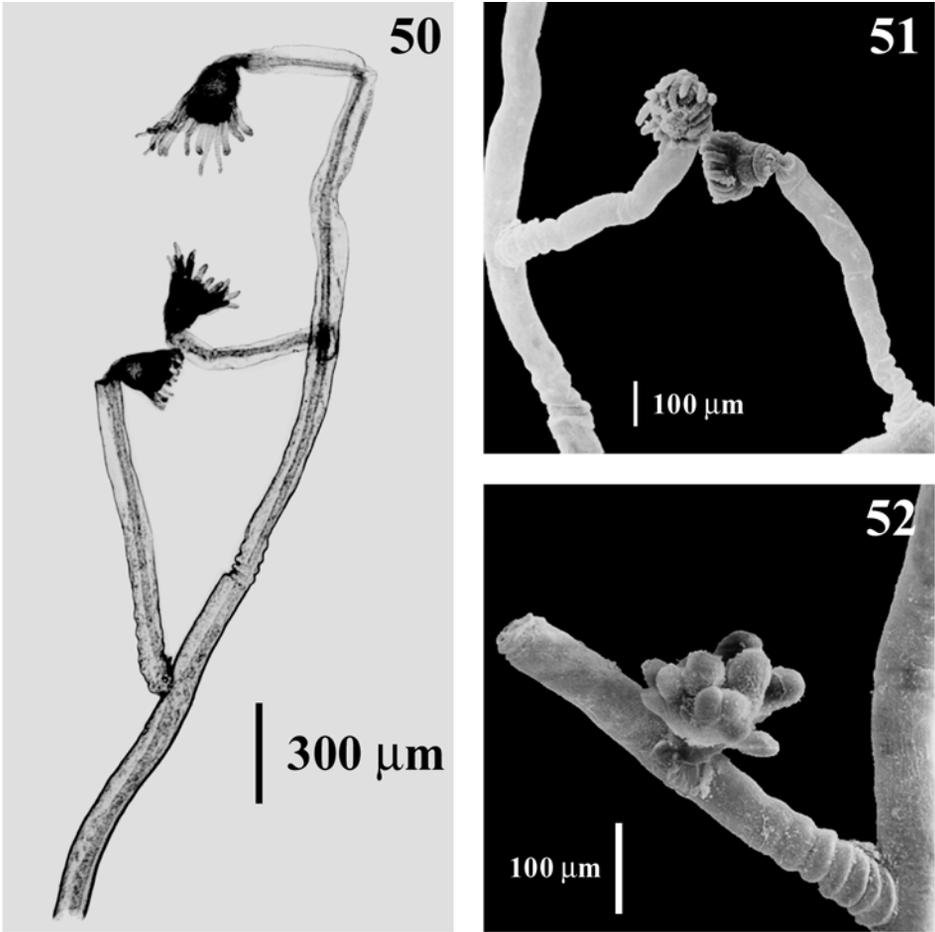
Eudendrium generale von Lendenfeld, 1885: 351, pl. 6.

Material.— **Australia**: colony without gonophores, Port Jackson, 33°52'S 151°25'E, alcohol preserved, 4 histological preparations and 1 total mount, no collection date, det. A.C. Marques (RMNH-Coel. 28457, BMNH 1886.6.8.36; both part of the paralectotype of *Eudendrium pusillum* von Lendenfeld, 1885).



Figs 47-49. *Eudendrium elsaeoswaldae* Stechow, 1921. Fig. 47, fragment of branch with hydranths; 48 and 49, hydranths (RMNH-Coel. 28402, part of type series).

Remarks.— Two species of the genus *Eudendrium* were described by von Lendenfeld (1885) from southeastern Australia: *E. generale* and *E. pusillum* (fig. 50); however, the author did not designate types. Lectotypes and paralectotypes for the two species were subsequently designated by Watson (1985), who pointed out that these species do not differ significantly and should be considered conspecific. As noticed by Watson (1985), the type series of *E. pusillum* is rather poor. The hydranths (fig. 51) have a basal groove (sometimes absent), but no other particular feature. The male blastostyle is already completely reduced in the beginning of its development, almost sessile (actually supported by a short pedicel), and there are numerous incipient sporosacs (fig. 52). These details agree with the initial phases of gonophore development in *E. generale*, supporting the synonymy proposed by Watson (1985).



Figs 50-52. *Eudendrium generale* von Lendenfeld, 1885. Fig. 50, branch with hydranths; 51, hydranths; 52, male blastostyle (all RMNH-Coel. 28457, paralectotype of *Eudendrium pusillum* von Lendenfeld, 1885).

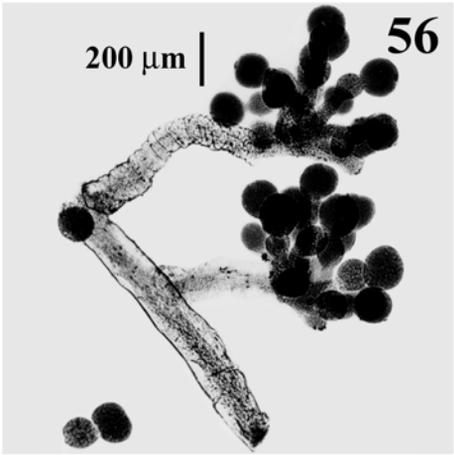
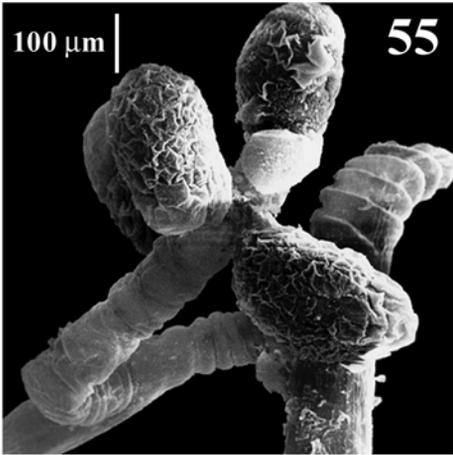
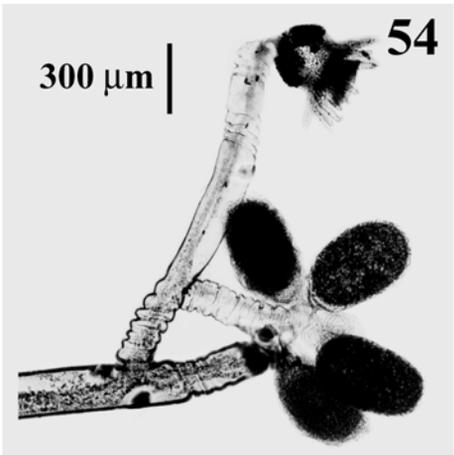
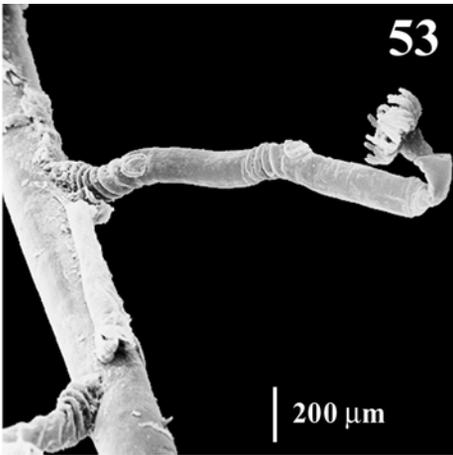
Eudendrium glomeratum Picard, 1951
(figs 53-56)

Eudendrium ramosum; Motz-Kossowska, 1905: 52-54, 59, pl. 3 fig. 16 [not *Eudendrium ramosum* (Linnaeus, 1758)].

Eudendrium glomeratum Picard, 1951: 260.

Material.— **Italy**: female colony, Gulf of Genoa, Portofino, San Fruttuoso, Stat. IXC, 44°18'N 09°12'E, alcohol preserved, 8 histological preparations and 3 total mounts, 20-40 m, no collection date, leg. L. Rossi, det. A.C. Marques (RMNH-Coel. 28451, BMNH 1961.10.9.1); female and male colonies, Bay of Naples, c. 40°50'N 14°17'E, alcohol preserved, 11 histological preparations and 4 total mounts, 10-15 m, x.1957, leg. W.J. Rees, det. A.C. Marques (RMNH-Coel. 28503, BMNH 1957.10.21.3).

Remarks.— As many other species of the genus, *Eudendrium glomeratum* (fig. 53) must have a wider distribution than that currently known as it has probably been overlooked because of misidentification in former papers (cf. Boero & Cornelius, 1987). In our experience many records of *E. rameum* (Pallas, 1766) and *E. ramosum* (Linnaeus, 1758), actually refer to *E. glomeratum*. Nevertheless, *E. glomeratum* is easily distinguishable by its large macrobasal euryteles, forming pads in some hydranths (fig. 54) and in spadices of immature female gonophores (Boero et al., 1986; Watson, 1985). During development, the simple spadix is shed and the egg is enclosed by a cover of perisarc (fig. 55). Mature eggs are scattered along the pedicel of completely reduced blastostyles, supported by a concave base covered by perisarc. After eclosion of the egg and release of the planula, this concave base can persist and remain attached to the pedicel (pers. obs.). When this happens, the appearance of the



Figs 53-56. *Eudendrium glomeratum* Picard, 1951. fig. 53, hydranth with detached perisarc at its base, resembling a pseudo-hydrotheca (nematocyst pads not visible); 54, mature female blastostyle and hydranth with nematocyst pads; 55, female blastostyle showing mature eggs with shed spadix (all RMNH-Coel. 28451); 56, mature male blastostyle (RMNH-Coel. 28503).

gonophore resembles that of *E. cyathiferum* (cf. fig. 42 and remarks on *E. cyathiferum*). This suggests that both species might be conspecific, but additional information concerning the cnidome of *E. cyathiferum* is necessary to verify this suggestion. The male blastostyles are completely reduced, sometimes bearing numerous 2-3 chambered sporosacs (fig. 56).

Eudendrium infundibuliforme Kirkpatrick, 1890
(fig. 57)

Eudendrium infundibuliforme Kirkpatrick, 1890: 606-607, pl. 14 fig. 3.

Material.— **Australia:** colony without gonophores, Torres Strait, 32 km NNW Warrior Island, Station 2, 09°30'S 142°54'E, alcohol preserved, 5 histological preparations and 1 total mount, 10 m, no collection date, leg. & det. R. Kirkpatrick (RMNH-Coel. 28478, BMNH 1890.7.23.3; both part of the type series).

Remarks: *Eudendrium infundibuliforme* is the most unusual species of Eudendriidae morphologically. It was first described by Kirkpatrick (1890); that description was supplemented by Watson (1985). The species is currently considered endemic to the Australian waters. The reproductive structures have only been described from material from Carter Reef, in which the male blastostyles are fully developed, bearing one or two 2-3 chambered sporosacs (Watson, 1985). The species is also peculiar with regard to its cnidome, as it has three types of nematocyst: small microbasic euryteles, and small and large macrobasic euryteles (Watson, 1985; pers. obs). Besides, the pedicels widen distally and a striking, extensive glandular region occurs in the basal part of the elongated hydranth (fig. 57), unique among Eudendriidae. These hydranths in general aspect resemble those of certain Haleciidae, a family of thecate hydroids also characterized by the presence of a primary hydrotheca, a feature never observed in Eudendriidae (present observations).

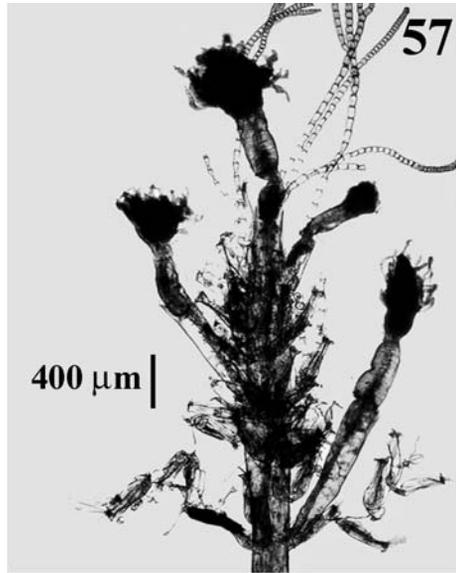
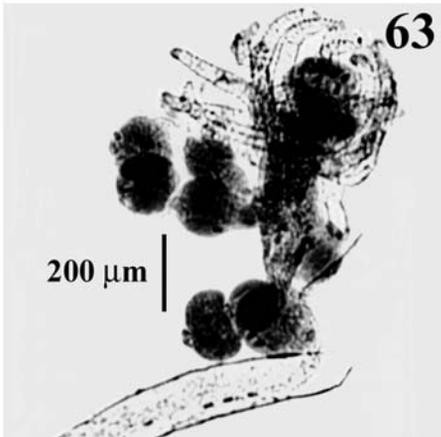
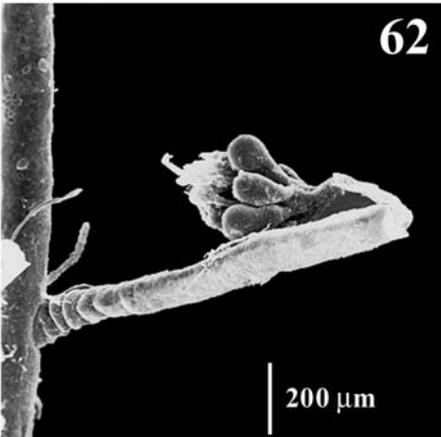
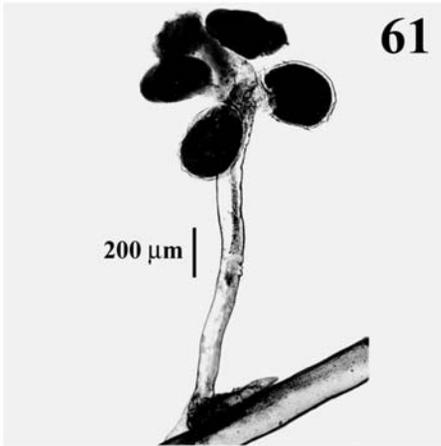
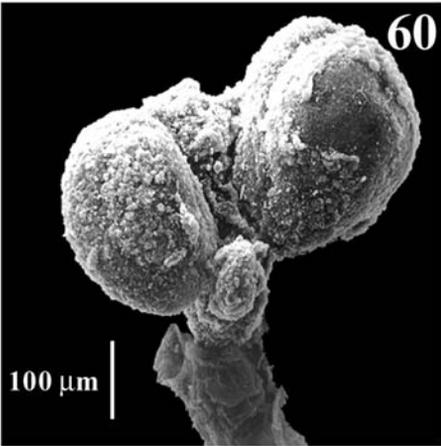
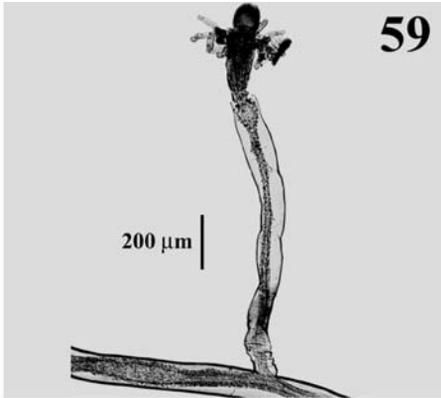
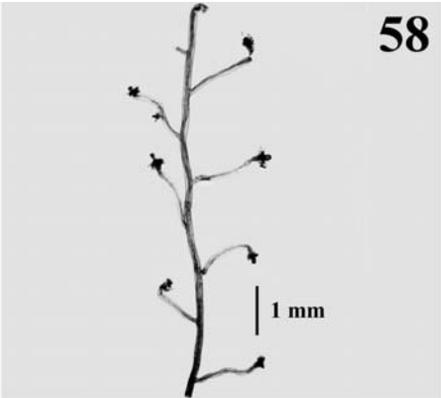


Fig. 57. *Eudendrium infundibuliforme* Kirkpatrick, 1890, fragment of colony with elongated hydranths and distally widening pedicels (RMNH-Coel. 28478, part of type series).

Eudendrium kirkpatricki Watson, 1985
(figs 58-63)

Eudendrium kirkpatricki Watson, 1985: 194-196, figs 35-39.

Material.— **Australia:** female colony, Murray Is., Torres Straits, 09°55'S 144°08'W, alcohol preserved, 5 histological preparations and 2 total mounts, 27-37 m, no collection date, leg. A.C. Haddon, det. J. Watson (RMNH-Coel. 28452, BMNH 1890.3.24.113-120 [part]; both part of the type series); male colony, Torres Strait, Warrior Is, Stn 2, 09°30'S 142°54'E, alcohol preserved, 5 histological preparations



Figs 58-63. *Eudendrium kirkpatricki* Watson, 1985. 58, distal portion of branch; 59, hydranth (both RMNH-Coel. 28343); 60, female blastostyle with eggs in various stages of development, one with spadix and the other with remnant of spadix only; 61, mature female blastostyle (both RMNH-Coel. 28452); 62, male blastostyle in early stage of development; 63, mature male blastostyle (both RMNH-Coel. 28454).

and 3 total mounts, no collection date, leg. A.C. Haddon, det. A.C. Marques (RMNH-Coel. 28454, BMNH 1890.11.22.33). **Yemen:** female colony, Red Sea, Meteor Stn M063, 26 Km NNW Perim Island, 12°53'N 43°17'E, alcohol-formol-cocainechloride preserved, 18 histological preparations and 1 total mount, 174 m, on sponge, 05.xii.1964, det. A.C. Marques (RMNH-Coel. 28343).

Remarks.— Together with the cnidome, the reproductive structures give important complementary information for the identification of *Eudendrium kirkpatricki* (Watson, 1985; cf. figs 58, 59). The female gonophores of the species develop on reduced blastostyles (fig. 60), the eggs are supported by a simple spadix. During development the spadix is shed, and the mature egg remains more or less in its original position on the blastostyle (fig. 61). The male sporosacs arise on non-reduced blastostyles (fig. 62) that are still fully developed even when the two-chambered sporosacs are mature (fig. 63).

Eudendrium merulum Watson, 1985
(figs 64-66)

Eudendrium merulum Watson, 1985: 200-202, figs 53-58.

Material.— **Yemen:** colony without gonophores, 26 km NNW Perim Is, Meteor Stn M063, 12°53'N 43°17'E, alcohol-formol-cocainechloride preserved, 10 histological preparations and 3 total mounts, 174 m, 5.xii.1964, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28346). **Australia:** Palm Isles, 18°40'S 146°30'E, alcohol preserved, 6 histological preparations and 2 total mounts, 5-10 m, 28.vi.1973, leg. J. E. Watson, det. A.C. Marques (RMNH-Coel. 28391, Museum of Victoria, Melbourne, F50518).

Remarks.— *Eudendrium merulum* (figs 64, 65) resembles *E. ramosum* in several respects: general dimensions, cnidome, unfascicled habitus of the colonies, and annulation. However, the two species are clearly distinguishable by the reproductive structures. *Eudendrium merulum* has completely reduced female blastostyles (fig. 66); when mature the eggs are scattered along the wrinkled blastostyle (cf. Watson, 1985). The male gonophore, not represented here, is also borne on a completely reduced blastostyle, and the two to three chambers of the sporosacs are connected by a distinct "neck" (Watson, 1985).

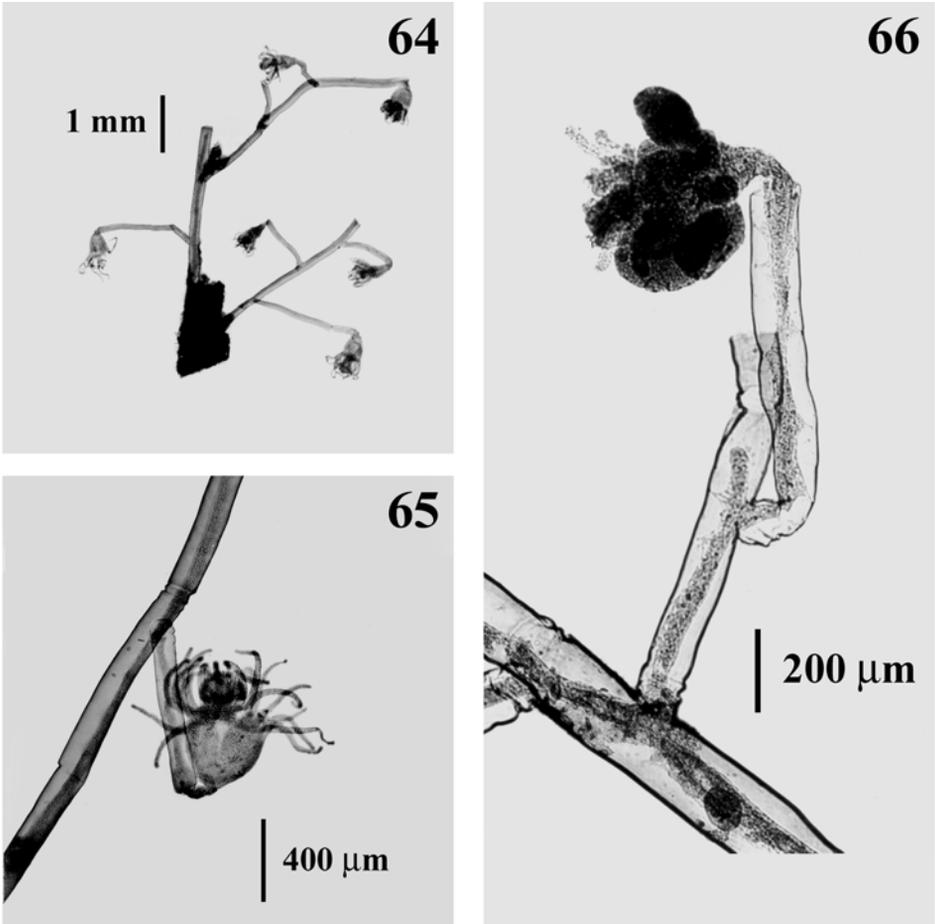
Eudendrium racemosum (Cavolini, 1785)
(figs 67-70)

Sertolara racemosa Cavolini, 1785: 160, pl. 6 figs 1-7, 14-15.

Sertularia racemosa Gmelin, 1791: 3854.

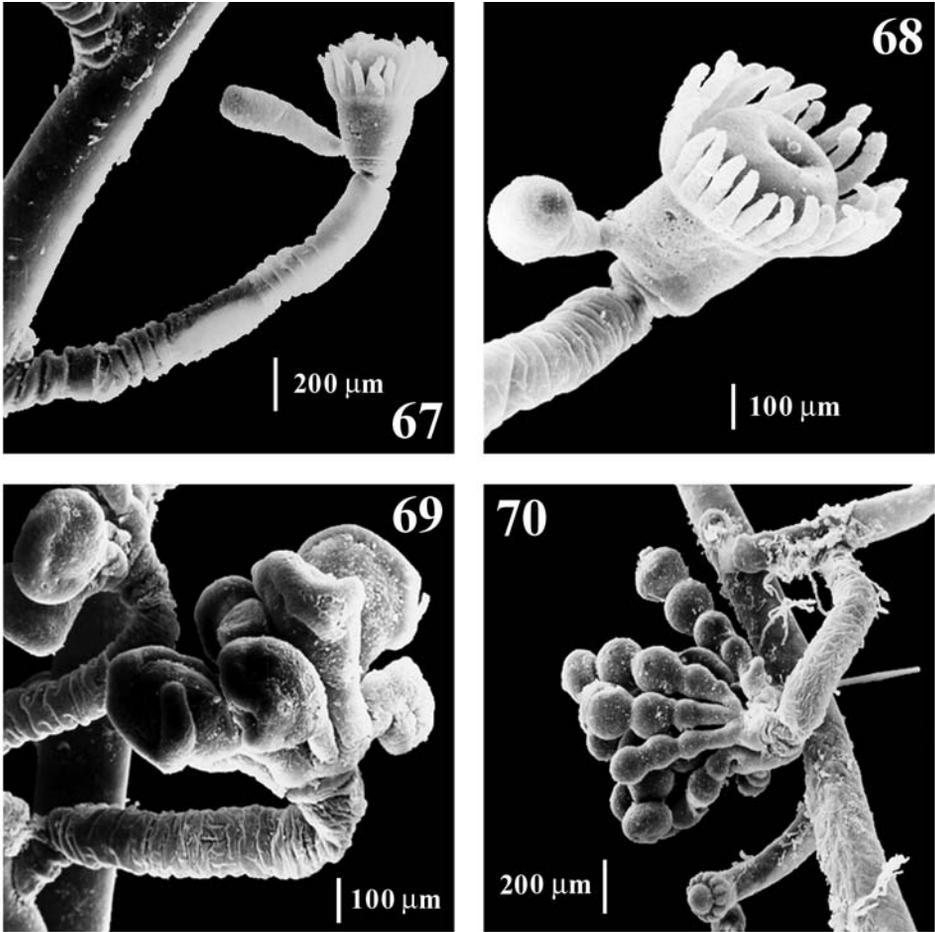
Material.— **Italy:** female and male colonies, Tyrrhenian Sea, no coordinates, alcohol preserved and stained with Heidenhain haematoxylin, 20 histological preparations, 11.viii.1951, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28006).

Remarks.— *Eudendrium racemosum* is a well known species with a wide distribution (cf. Watson, 1985). Its complementary nematocysts are atrichous isorhizas, a distinctive feature among Eudendriidae. Besides, its characteristic morphology makes the species easy to recognize. Some of the hydranths of the colony, a minority (about



Figs 64-66. *Eudendrium merulum* Watson, 1985. Fig. 64, fragment of colony; 65, hydranth (both RMNH-Coel. 28391); 66, female blastostyle (RMNH-Coel. 28346).

20% after Watson, 1985; frequently less, pers. obs.) have a cnidophore arising at the base of the hydranth (figs 67, 68); these cnidophores are different from the pseudocnidophores described in *E. ramosum*, the latter being hollow structures with a proximal aggregation of nematocysts (Watson, 1985: 194). The reproductive structures of *E. racemosum* are also quite peculiar. The female gonophores are borne on reduced hydranths with few degenerated tentacles, and with a simple spadix. Early in development the hydranth becomes completely reduced and the spadix bifid (fig. 69). Mature eggs lose their spadices, and are surrounded by a sheath of perisarc, becoming scattered along the axis of the blastostyle and its pedicel. The mature eggs of the female blastostyle of *E. racemosum* differ from those of *E. carneum* by not having fenestrate capsules. The male blastostyle (fig. 70) resembles that of *E. carneum*, being completely reduced and bearing long sporosacs with up to 5 chambers.



Figs 67-70. *Eudendrium racemosum* (Cavolini, 1785). Figs 67, 68, hydranths with cnidophore; 69, female blastostyle with immature eggs; 70, male blastostyle (all RMNH-Coel. 28006).

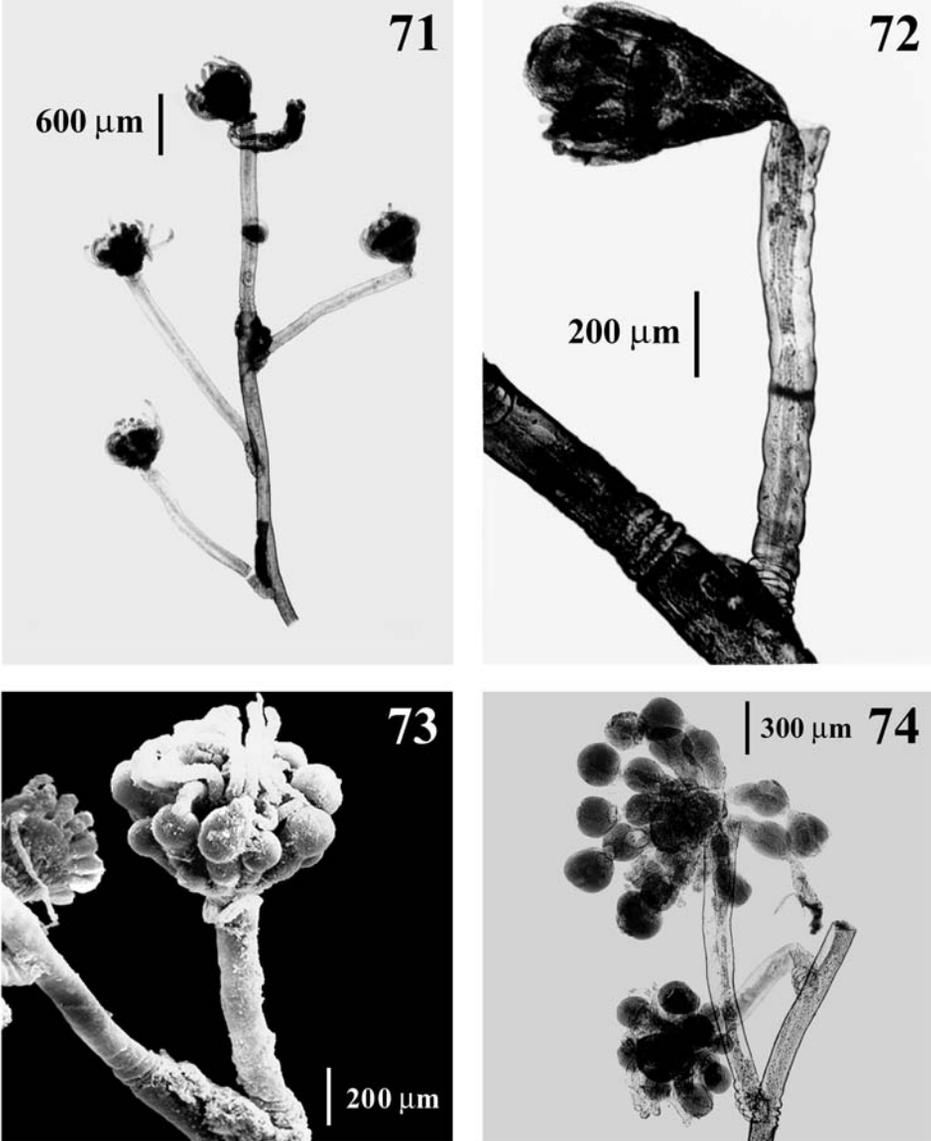
Eudendrium rameum (Pallas, 1766)
(figs 71-74)

Tubularia ramea Pallas, 1766: 83.

Material.— **Ireland**: colony without gonophores, SW Ireland, c. 51°N 10°W, alcohol preserved, 5 histological preparations and 1 total mount, 100 m, no collection date, leg. W.S. Green, det. A.C. Marques (RMNH-Coel. 28460, BMNH 1899.9.1.1-3). **Norway**: male colony, East Finmark, Long Fjord, c. 70°N 23°E. alcohol preserved, 14 histological preparations and 4 total mounts, 1890, leg. A.M. Norman, det. A.C. Marques (RMNH-Coel. 28463, BMNH 1898.5.7.43). **Scotland**: colony without gonophores, Aberdeen, Valdivia Stn St3, 57°26'N 01°28'W, alcohol-formol preserved, 2 histological preparations and 1 total mount, 79 m, 05.viii.1898, det. A.C. Marques (RMNH-Coel. 28406, BSM).

Remarks.— *Eudendrium rameum* (figs 71, 72) is a species with large and fascicled

colonies, apparently with worldwide distribution. However, it may have been confused with some of the larger species of the genus (especially *E. ramosum*; though the latter has unfascicled colonies). The male blastostyle of *E. rameum* has tentacles and a non-reduced hypostome (figs 73, 74). This is an important feature to distinguish the species from *E. arbuscula*, in which the male blastostyle is completely reduced (cf. remarks in *E. arbuscula* above). Besides, the two species are sympatric in the North



Figs 71-74. *Eudendrium rameum* (Pallas, 1766). Fig. 71, distal part of branch (RMNH-Coel. 28460); 72, hydranth (RMNH-Coel. 28406); 73, male blastostyle, not reduced; 74, two male blastostyles (both RMNH-Coel. 28463).

Sea, have a similar trophosoma (fascicled colonies, fasciculation running up to the distal branches) and cnidome (complementary nematocysts are microbasic euryteles, slightly larger in *E. rameum*). We believe that this may have caused *E. arbuscula* to be overlooked to a considerable extent in the collections.

Eudendrium ramosum (Linnaeus, 1758)
(figs 75-78)

Tubularia ramosa Linnaeus, 1758: 804.

Material.— **USA:** female colony, Miami, SW side of Key Biscayne, 25°41'N 80°11'W, alcohol preserved, 5 histological preparations, on rope, 2 m, 15.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28357). **Bermuda:** colony without gonophores, St. George, Castle Harbor, Long Bird Bridge, 32°22'N 64°43'W, alcohol-formol preserved, 7 histological preparations and 3 total mounts, 1-12 m, 22.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28384).

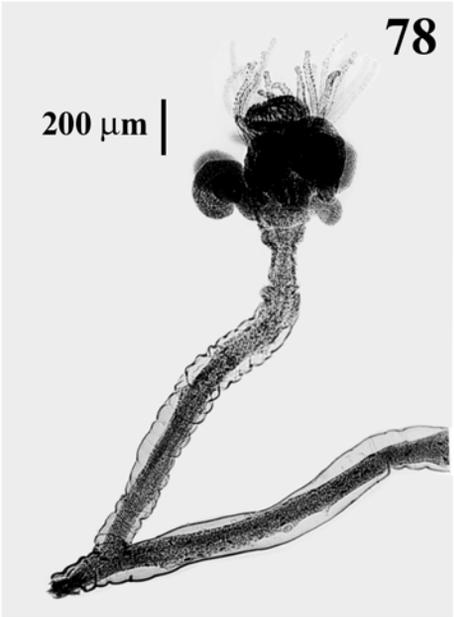
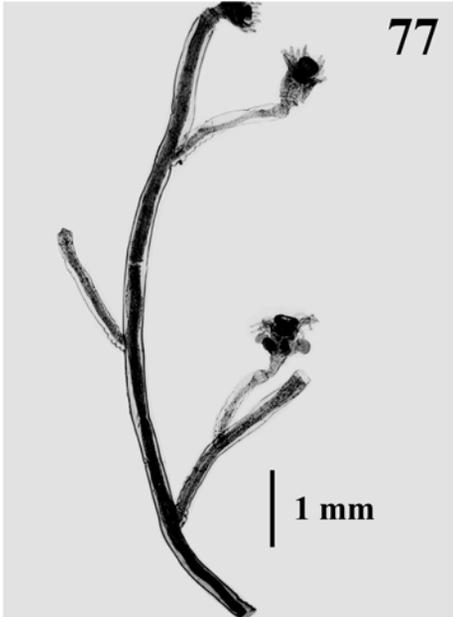
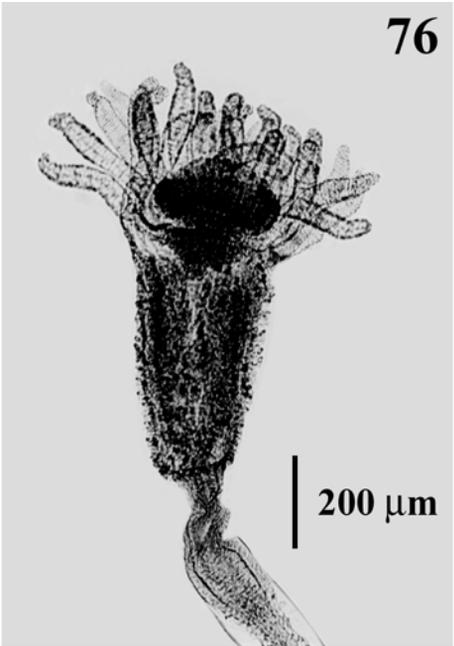
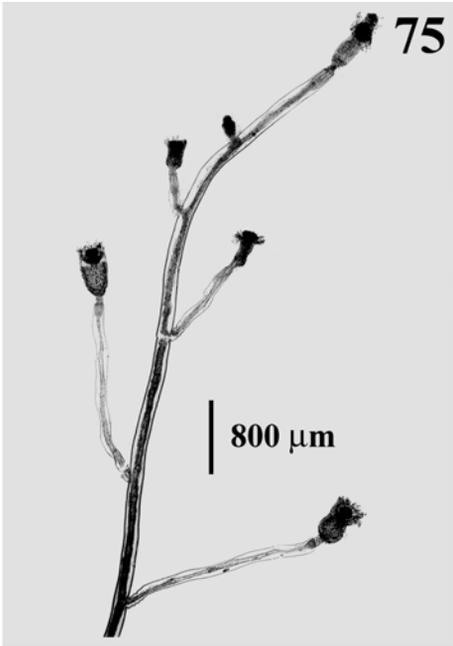
Remarks.— Boero & Cornelius (1987) pointed out that the holotype of *E. ramosum* apparently has become lost. As a consequence there are many varying definitions of the species in the literature, especially concerning fasciculation, dimensions of nematocysts, or the degree of blastostyle reduction (cf. Millard & Bouillon, 1973, 1974; Millard, 1975; Watson, 1985; Hirohito, 1988). Consequently, the geographical range of the species is badly defined. The scattered distribution of the large microbasic euryteles over the hypostome is generally considered a distinctive character of *E. ramosum*; however, as Marques (1995) pointed out, this character is widespread in Eudendriidae; moreover it is plesiomorphic. Marques (1995) attempted to characterize the various "morphotypes" assembled under the name "*E. ramosum*" and described a new species, *E. pocaruquarum* Marques, 1995, based on size differences of the larger microbasic euryteles. However, the problem concerning *E. ramosum* persists. What we describe here as *E. ramosum* (figs 75, 76) in morphology closely resembles the Brazilian specimens described by Marques (1993). The eggs develop around the body of the female blastostyle. During development the tentacles become atrophied in size but not in number, the spadices are shed, and the enclosed eggs maintain their position around the hydranth or are scattered over the blastostyle pedicel (figs 77, 78). The male blastostyle, not represented here, is unreduced, bearing three-chambered sporosacs.

Eudendrium ritchiei Millard, 1975
(figs 79-80)

Eudendrium ritchiei Millard, 1975: 87-88, fig. 30.

Material.— **South Africa:** female colony, Scottish National Antarctic Expedition 1902-1904, entrance of Saldanha Bay, 33°03'S 16°56'E, alcohol preserved, 7 histological preparations and 2 total mounts, 46 m, 21.v.1904, leg. W. S. Bruce, det. A.C. Marques (RMNH-Coel. 28504, BMNH 1921.143.1323).

Remarks.— *Eudendrium ritchiei* is a species so far only recorded from South Africa and New Zealand. Its bifid spadix supporting the egg is a character shared with *E. carneum*, *E. racemosum* and *E. japonicum* Yamada, 1954, but it is differentiated from all



Figs 75-78. *Eudendrium ramosum* (Linnaeus, 1758). Fig. 75, fragment of colony; 76, hydranth (both RMNH-Coel. 28384); 77, colony with hydranth and female gonophore; 78, immature female gonophore (both RMNH-Coel. 28357).

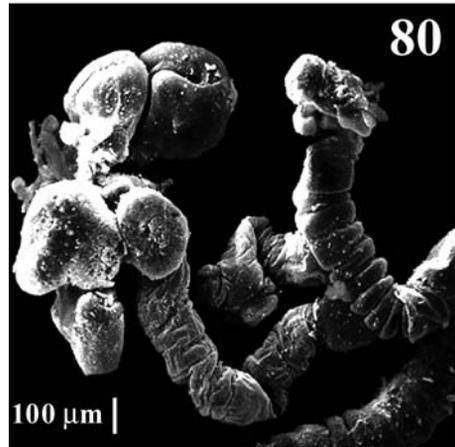
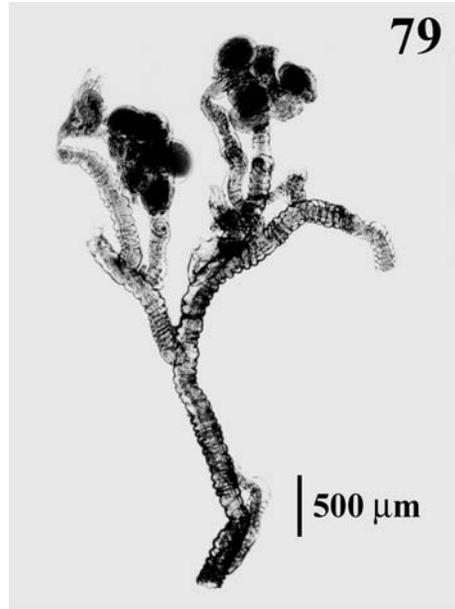
these species by the cnidome. Millard (1975) claimed the cnidome of the species to include macrobasic euryteles, but Watson (1985) correctly identified these nematocysts as microbasic euryteles. Even so, *E. carneum* and *E. racemosum* (Watson, 1985; pers. obs.) do not possess the larger class of euryteles in their cnidome, while in *E. japonicum* a larger type of nematocyst is altogether absent (Hirohito, 1988). The hydrocauli of *E. ritchiei* are completely annulated (fig. 79), a character shared with some other species of *Eudendrium* (e.g., *E. vaginatum* Allman, 1863; *E. californicum*; and *E. pocaruquarum*). The female gonophores occur on fairly reduced blastostyles with only some tentacles remaining, while the blastostyle becomes completely reduced during its development and the mature eggs are enclosed by a thick layer of perisarc and are placed scattered along the blastostyle (Millard, 1975; Watson, 1987; pers. obs.; figs 79, 80). The male blastostyles, not represented here, are completely reduced, with one- to two-chambered sporosacs (Millard, 1975; Watson, 1987).

Eudendrium terranova Watson, 1985
(figs 81-82)

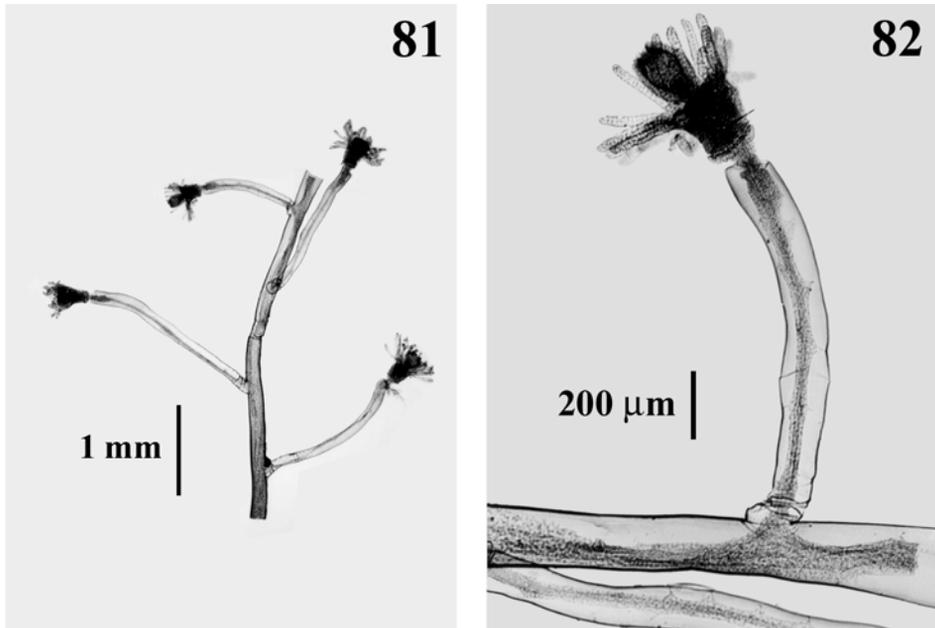
Eudendrium terranova Watson, 1985: 189-191, figs 20-23.

Material.— **New Zealand:** colony without gonophores, North Cape, British Antarctic Terra Nova Expedition Stn 134, 34°18'S 172°20'E, alcohol preserved, 1 histological preparation and 1 total mount, 20-37 m, 1910-1913, det. J. E. Watson (RMNH-Coel. 28486, BMNH 1929.10.28.11).

Remarks.— *Eudendrium terranova* (figs 81, 82) is known from southern Australia and New Zealand (Watson, 1985; Schuchert, 1996; pers. obs.). We only dealt with sterile colonies of this species. The female gonophores are borne on a blastostyle with atrophied tentacles that are completely resorbed during development; male blastostyles are completely reduced with numerous two-chambered sporosacs (Watson, 1985; Schuchert, 1996).



Figs 79-80. *Eudendrium ritchiei* Millard, 1975. Fig. 79, fragment with hydranths and female gonophores; 80, female blastostyle in later stage of development (both RMNH-Coel. 28504).



Figs 81-82. *Eudendrium terranova* Watson, 1985. Fig. 81, fragment of colony; 82, hydranth (both RMNH-Coel. 28486).

Eudendrium tottoni Stechow, 1932
(figs 83, 84)

Eudendrium insigne; Hickson & Gravely, 1907: 7-8, pl. 1 fig. 4 (not *E. insigne* Hincks, 1861)

Eudendrium antarcticum Totton, 1930: 140-141.

Eudendrium tottoni Stechow, 1932: 84.

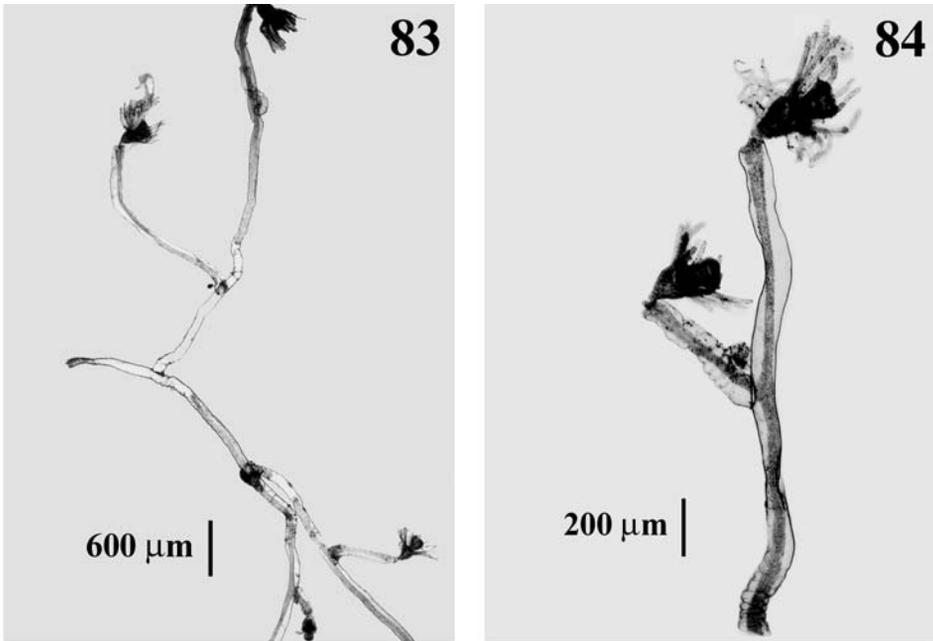
Material examined: **Antarctica**: colony without gonophores, Ross Sea, Mc Murdo Sound, c. 73°37'S 168°56'E, alcohol preserved, 2 histological preparations, 2 total mounts, 1901-1904, leg. Discovery Expedition, det. A. K. Totton (RMNH Coel. 28476, additional material BMNH 1907.8.20.3, both part of type series).

Remarks.— *Eudendrium tottoni* (figs 83, 84) is a new name given by Stechow (1932) to *Eudendrium antarcticum* Totton, 1930, a pre-occupied name. Totton (1930) considered several earlier records from the Antarctic region as belonging to this species. It is restricted to the Antarctic and subantarctic regions. However, the species is still dubious as it is ill-defined and its cnidome is unknown.

Eudendrium vaginatum Allman, 1863
(figs 85-92)

Eudendrium vaginatum Allman, 1863: 10.

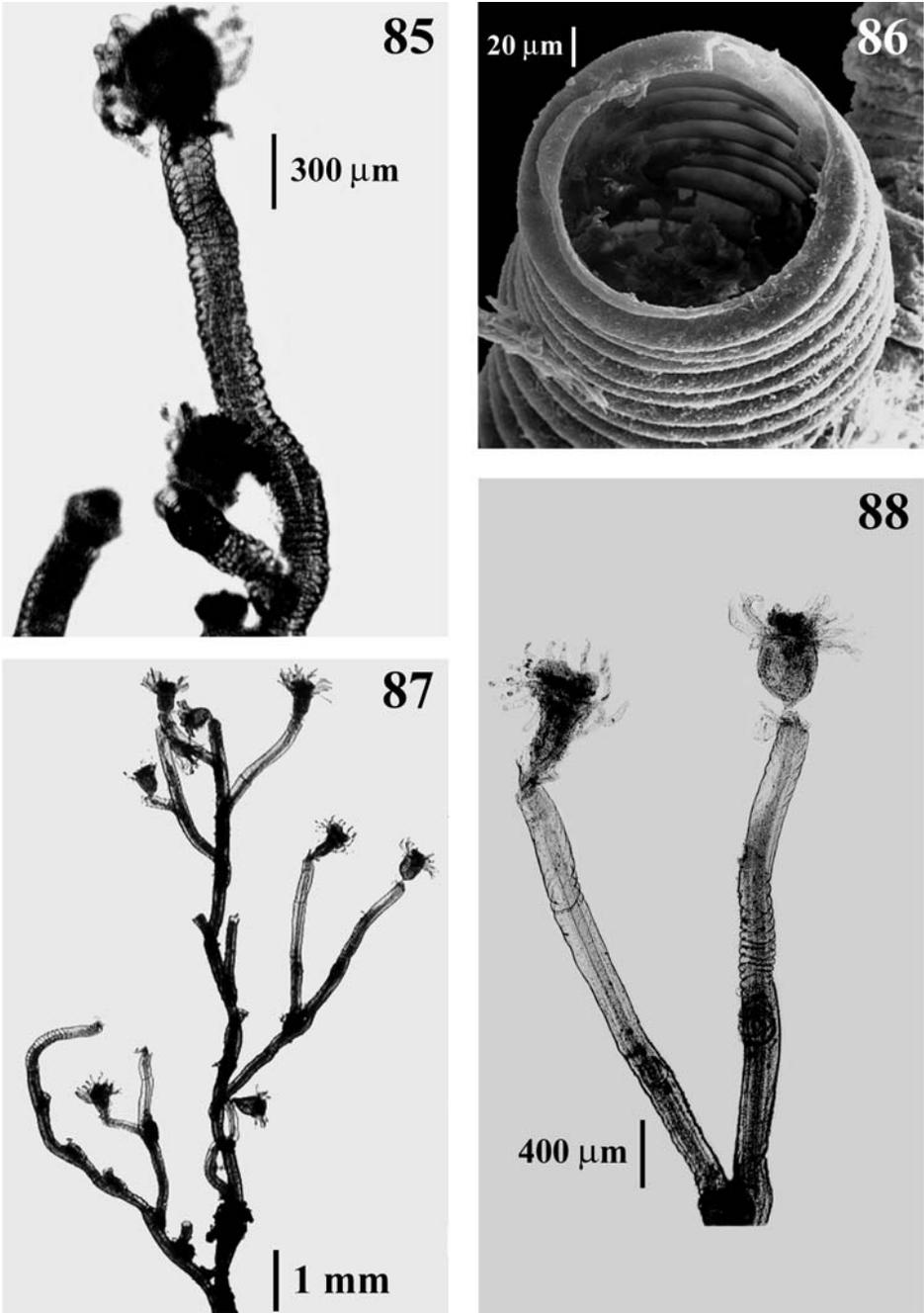
Eudendrium annulatum Norman, 1864: 83, pl. 9 figs 1-3.



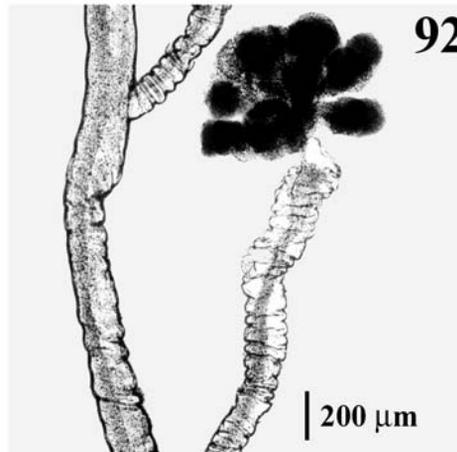
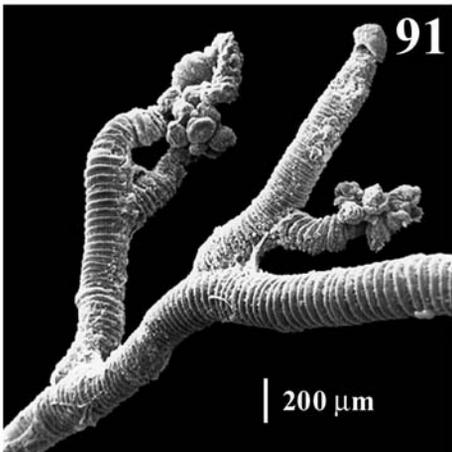
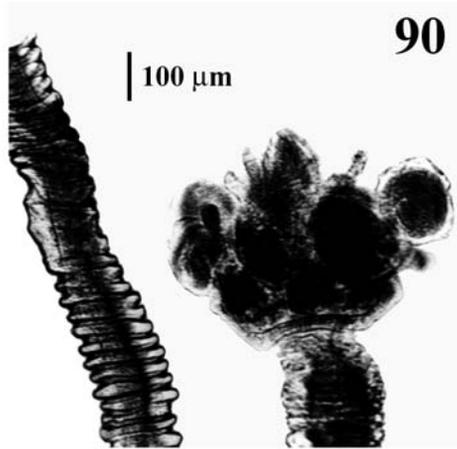
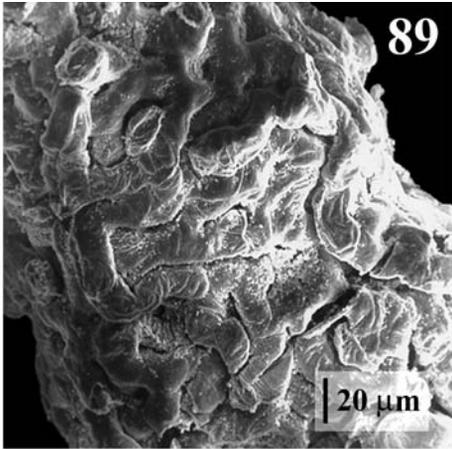
Figs 83-84. *Eudendrium tottoni* Stechow, 1932. Fig. 83, fragment of colony; 84, two hydranths (both RMNH-Coel. 28476).

Material.— **Ireland:** male colony, no location specified, alcohol preserved, 4 histological preparations and 2 total mounts, 03.v.1901, leg E.T. Browne, det. A.C. Marques (RMNH-Coel. 28467, BMNH 1941.3.20.415). **Norway:** colony without gonophores, Bergen, c. 60°24'N 05°19'E, alcohol-formol preserved, 3 histological preparations and 1 total mount, no collection date, det. A.C. Marques (RMNH-Coel. 28403, BSM). **Scotland:** colony without gonophores, Shetland Is., Cave Bunnes Hall, Eastern side of Burrafirth, c. 60°48'N 00°53'W, alcohol preserved, 63 histological preparations and 2 total mounts, 1 m, on rock, 1863, leg. A.M. Norman, det. A.C. Marques (RMNH-Coel. 28436, BMNH 1898.5.7.40; both part of the syntype series of *Eudendrium annulatum* Norman, 1864). **Greenland:** female colony, Sukkertoppen, 65°25'N 52°56'W, alcohol preserved, 9 histological preparations and 2 total mounts, no collection date, leg. A.M. Norman, det. A.C. Marques (RMNH-Coel. 28437, BMNH 1912.12.21.61, and Coll. Norman in ZMC).

Remarks.— *Eudendrium vaginatum* is characterized by the presence of a pseudo-hydrotheca (fig. 85), a continuation of the perisarc over the base of the hydranth (Allman, 1863). From the literature, it is not clear whether or not *E. vaginatum* is a senior synonym of *Eudendrium annulatum* Norman, 1864. Both species have a completely annulated trophosoma (cf. for instance fig. 86), and both were described from the same locality (Shetland Islands). The major difference between the two species is the presumed absence of a pseudo-hydrotheca in *E. annulatum*. The first allusion to the two species being conspecific was made by Nutting (1901). Recently this idea was expressed again by Cornelius (1995), but without argumentation. Later on, Sheiko & Stepan'jants (1997), in a study of hydroids from Commander Islands, argued that only c. 20% of the colonies in that region have pseudo-hydrothecae, which suggests



Figs 85-88. *Eudendrium vaginatum* Allman, 1863. Fig. 85, hydranth with typical pseudo-hydrotheca (RMNH-Coel. 284023); 86, detail of ringed perisarc, internal and external view (RMNH-Coel. 28437); 87, fragment of colony; 88, two hydranths of *E. annulatum* with pseudo-hydrothecae (both RMNH-Coel. 28436, syntype series of *E. annulatum* Norman, 1864).



Figs 89-92. *Eudendrium vaginatum* Allman, 1863. Fig. 89, detail of fascicled part of main stem surrounded by mucous sheath (RMNH-Coel. 28436, syntype series of *E. annulatum* Norman, 1864); 90, 91, female blastostyle in early stage of development (RMNH-Coel. 28437); 92, immature male blastostyle (RMNH-Coel. 28467).

that the character is polymorphic in *E. vaginatum*. We studied the syntype of *E. annulatum* (fig. 87), and indeed pseudo-hydrothecae were found in some of the polyps (fig. 88), a fact apparently overlooked by Norman (1864). This observation confirms the suggestion of Sheiko & Stepan'yants (1997). Norman (1864), in the original description of *E. annulatum*, described strongly fascicled colonies covered by a sheath of mucous (fig. 89). However, fasciculation is optional in *E. vaginatum*, since we saw both fascicled and unfascicled colonies. The female gonophores (figs 90, 91) develop on reduced hydranths, and their spadices are simple. During development the spadices are shed and the mature eggs become enclosed by perisarc and may become scattered along the axis of completely reduced blastostyles. The male, non reduced blastostyles bear numerous two-chambered sporosacs (fig. 92, still immature; cf. Berrill, 1952).

Myrionema amboinense Pictet, 1893
(figs 93-98)

Myrionema amboinense Pictet, 1893: 19-20, pl. 1 figs 12-13.

Material.— **Bermuda**: male colony, St. George, North tail of Hardington Sound, near Kirche, 32°22'N 64°40'W, alcohol-formol preserved, 13 histological preparations and 3 total mounts, 2.5 m, 23.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28370); male colony, Hamilton Parish, Walsingham Pond, 32°19'N 64°44'W, alcohol-formol preserved, 13 histological preparations and 1 total mount, 1-3 m, 26.vi.1967, leg. H. Mergner, det. A.C. Marques (RMNH-Coel. 28374).

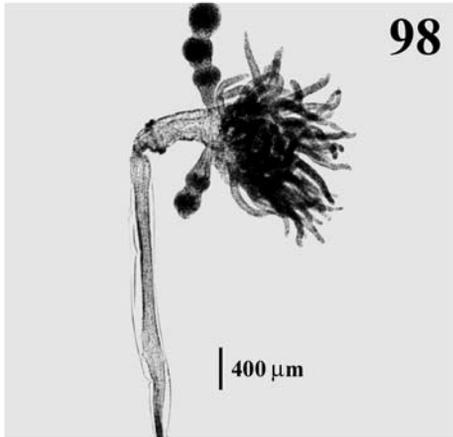
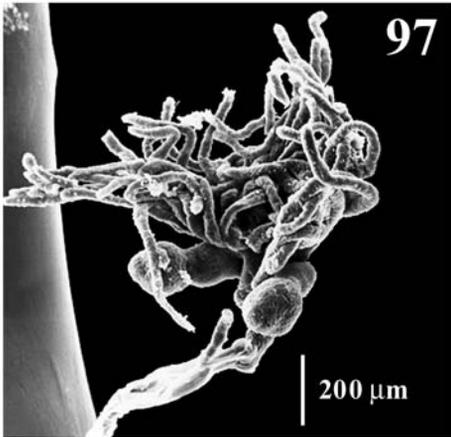
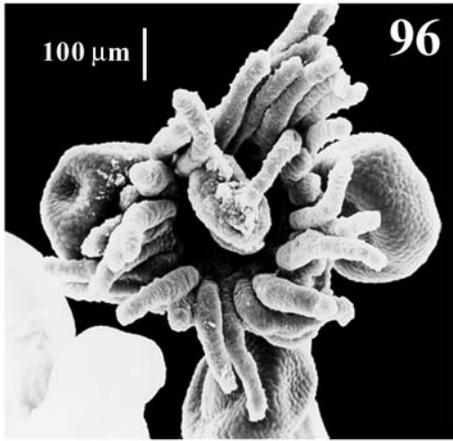
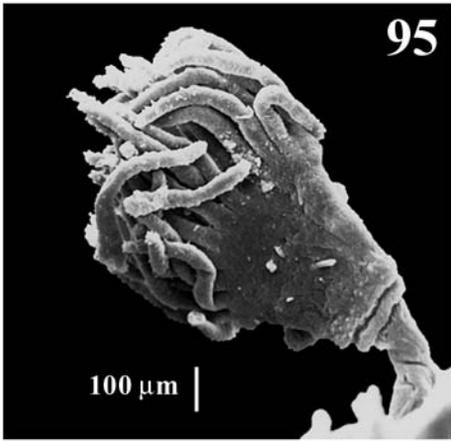
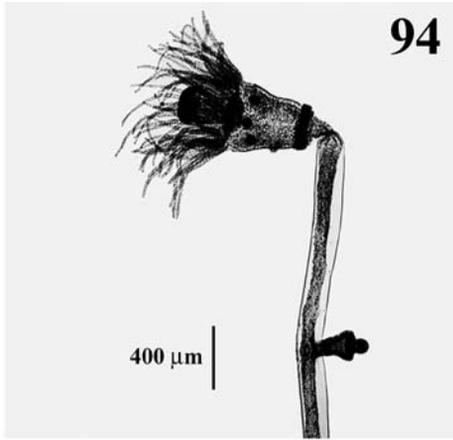
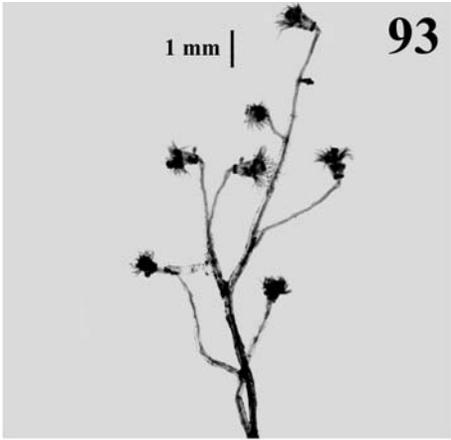
Remarks.— The genus *Myrionema* comprises three nominal species: *M. amboinense* Pictet, 1893, *M. hargitti* (Congdon, 1906), and *M. griffini* (Light, 1913). Calder (1988) considered them conspecific, the oldest available name being *M. amboinense* (fig. 93). The genus (and consequently its only species) is characterized by a high number of tentacles arranged in two close whorls (figs 94, 95) and by the presence of symbiotic zooxanthellae (Pictet, 1893; Millard, 1975; Calder, 1988). The female blastostyles are not reduced and are surrounded by immature eggs supported by simple spadices (fig. 96); when mature, the spadices are shed and the sessile eggs are distributed along the pedicel of the blastostyle. Also the male blastostyle is not reduced and supports a few (2-3) sporosacs, generally two-chambered when mature (figs 97, 98).

General discussion

It is beyond the scope of this study to present a phylogenetic analysis of the Eudendriidae; the information necessary to do that is still too incomplete. However, some of the developmental series are here commented upon from a cladistic point of view (cf. Hennig, 1950, 1966; Eldredge & Cracraft, 1980; Ferrarezzi & Marques, 1997; Kitching et al., 1998).

Ontogenetic data are an important source of information for the interpretation of transformation series of characters. Such series are supposed to allow a direct inference of the ancestral (plesiomorphic) state of a given character and sometimes also an inference of the ordination of the successive states of the character (if it concerns a multistate character). For this reason, the use of ontogenetical/developmental data for polarization/ordination is referred to as the "direct method" (Nelson, 1978; Forey et al., 1992). For the discussion of the characters this principle will be used.

The importance of developmental characters and their suitability to identify general patterns amongst hydrozoans, or even medusozoans, was hitherto overlooked. Moreover, in rare exceptions, it is possible to identify two different trends by using ontogenetical information. To the first category belong those studies that base a phylogenetic hypothesis on a single ontogenetical series, i.e., constructing a scenario of evolution for the developmental character in which the taxa are "hung" (Boero & Sarà, 1987). Studies of the second category use the ontogenetic information to infer transformation series (polarity) of the character-states to use these for analysis in a data matrix, together with character-states without ontogenetic information (Marques, 1993; Peña Cantero & Marques, 1999; for explanations of this procedure, cf. Nelson, 1978), or to root unrooted cladograms after a parsimony analysis of a given data matrix (Marques, 1997; Peña Cantero & Mar-



Figs 93-98. *Myrionema amboinense* Pictet, 1893. Fig. 93, fragment of colony; 94, hydranth (both RMNH-Coel. 28370); 95, hydranth; 96, female blastostyle, oral view showing tentacles arranged in two close whorls; 97, 98, male blastostyle (all RMNH-Coel. 28374).

ques, 1999; for explanations of this procedure, cf. Nixon & Carpenter, 1993; de Pinna, 1994; Ferrarezzi & Marques, 1997).

Even from a classical point of view, developmental characters can furnish useful information for a better understanding of the taxonomy of a given group. Specifically for the Eudendriidae, Watson (1985) presents one of the few studies that, besides the cnidome, also focus on the importance of reproductive morphology and development. Therein she noticed the existence of a differential reduction in male and female blastostyles, and depicted some general "sequences" of reduction in their development, adopting this information under an essentialistic viewpoint (Hull, 1988).

The blastostyle development series of some species of Eudendriidae is complex. For instance, Watson (1985) described a transformation series occurring in *E. balei*, in which an alternate reduction of the tentacles up to a club-shaped vestige occurs, the mature blastostyle having half of the number of tentacles of the non-reproductive hydranth. A complement for this series can be visualized in the notes on *E. armatum* presented above; reduction of tentacles is also described here for other species.

In fact, the alternate reduction of the tentacles suggests that even in the genus *Eudendrium* there is an indication of differentiation of the tentacles in two whorls. This could be a physiological differentiation, or an anatomical solution for lack of space of the remaining tentacles in the blastostyle and the developing gonophores (Watson, 1985: 207). Whether these hypotheses are valid or not is a matter of speculation: the real pattern is a phase with "half number of tentacles in the mature blastostyle".

However, the reduction of tentacles does not exclusively occur in reproductive development. In some of the non-reproductive hydranths of *E. carneum*, where a tentacular reduction is occurring, it is not unusual to observe the atrophied tentacles distributed in two close whorls (fig. 41). The same feature was already observed in some other species of "*Eudendrium*" (e.g. *E. album*, *E. glomeratum*; pers. obs.). Again, this fact corroborates the hypothesis of a determined differentiation among the tentacles. Besides, living specimens of *Eudendrium* (e.g., *E. carneum*, *E. glomeratum*, *E. pocaruarum*; pers. obs.) have amphicoronate arrangement of the tentacles (i.e. arrangement in two alternate whorls, one upwards, one downwards). This fact is also known for several other hydroids, for instance in some species of Campanulariidae, Campanulinidae, Lafoeidae, Thyroscyphidae (Leptomedusae) and several anthomedusans.

The point is that, at least in the Eudendriidae, this tentacular pattern appears to be more than behavioural and physiological, being developmentally controlled. The fact

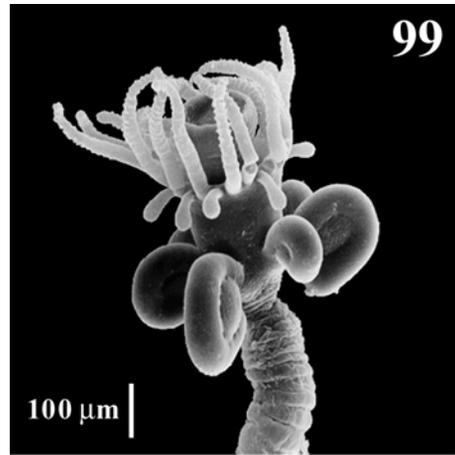


Fig. 99. *Eudendrium* spec., female blastostyle in early stage of alternate reduction of tentacles (RMNH-Coel 28472, female colony from Norway, Bergen, Mangeljord, z.N. IV, 34, 60°27'N 05°16'E, alcohol-Bouin preserved, 19 histological preparations + 5 total mounts, 10 m, 02.viii.1937, leg. W.J. Rees, det. A.C. Marques (material with same label in BMNH, without number).

that *Myrionema* has its tentacles arranged in two close whorls (cf. remarks in *M. amboinense*) suggests an ontogenetic link between the development as shown by certain species of *Eudendrium* and by *Myrionema*, which can be explored phylogenetically. The later stages of the development in *Eudendrium* (like regression of hydranths or beginning development of the blastostyles when compared to the "normal" hydranths) tend to have a characteristic two-whorl arrangement of tentacles. This new data and interpretation suggests that the condition "two whorls of tentacles" precedes the "one whorl of tentacles" condition. Hence, the apomorphic condition, at least in Eudendriidae, would be the presence of a two-whorl arrangement. In terms of phylogenetic inference, this character would be non-informative because it would be an autapomorphy in *M. amboinense*.

Nevertheless, the hypothesis above contradicts those of Petersen (1979, 1990), Millard (1975: 70), and Marques (1996), who considered the one-whorl state as the apomorphic condition in the family. This new point of view would have two direct phylogenetic consequences for the family: 1) the ancestral state of the monophyletic Eudendriidae (Marques, 1996) would be the arrangement of the tentacles in one-whorl and, consequently 2) there does not exist a synapomorphy to justify the genus *Eudendrium* any longer, since the only one proposed (Marques, 1996: tentacles arranged in one whorl) is a plesiomorphy that also includes the apomorphic condition of the species *M. amboinense*.

For taxonomical purposes, the Linnaean (traditional, essentialistic) taxonomy does not demand apomorphic characters to justify taxa, and under this point of view both genera can still be considered valid. On the other hand, strictly under the cladistic paradigm, the genus *Eudendrium* has no apomorphic character-states to support itself. This does not necessarily mean that the genus is paraphyletic but it is wise to consider the group a metataxon (Archibald, 1994). The systematic problem will hopefully be resolved with further (phylogenetic) evidence and an analysis including most of the species of the family.

Acknowledgments

The authors are indebted to Dr A. Svoboda (University of Bochum, Germany) who helped in many ways to facilitate this study, in arranging meetings, in obtaining material, and in helping to locate material. We are thankful to Dr A. E. Migotto (Universidade de São Paulo, São Sebastião, Brazil) for the revision of our manuscript and for valuable suggestions. Dr Jeanette E. Watson, Essendon, Victoria, Australia, read the manuscript and suggested several improvements; we are most grateful for her suggestions. We thank the Centro de Biologia Marinha (Universidade de São Paulo, São Sebastião, Brazil) for support in the collection and study of living material of *Eudendrium*. Antonio C. Marques had financial support for this study from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 96/10544-0 and 97/04572-4), and from the Nationaal Natuurhistorisch Museum (NNM), Leiden, during 1997/1998 in connection with a program to enhance the scientific value of the museum's collections. Charles M.D. Santos had financial support from FAPESP (98/14822-0).

References

- Alder, J. 1856. A notice of some new genera and species of British hydroid zoophytes.— *Ann. Mag. nat. Hist.* (2) 18 (107): 353-362, pls 12-14.
- Allman, G.J., 1863. Notes on the hydroid zoophytes.— *Ann. Mag. nat. Hist.* (3) 11: 1-12.
- Allman, G.J., 1876. Diagnoses of new genera and species of hydroids.— *J. Linn. Soc. Zool.* 12: 251-284, pls 9-23.
- Archibald, J. D., 1994. Metataxon concepts and assessing possible ancestry using phylogenetic systematics.— *Syst. Biol.* 43: 27-40.
- Armstrong, S.J., 1879. A description of some new species of hydroid zoophytes from the Indian coast and seas.— *J. Asiat. Soc. Bengal* 48 (2): 1-9, pls 9-12.
- Bavestrello, G. & S. Piraino, 1991. On two *Eudendrium* (Cnidaria, Hydrozoa) species from the Mediterranean Sea.— *Oebalia*, n.s. 17: 197-207, figs 1-4.
- Bedot, M., 1925. Matériaux pour servir à l'histoire des hydroides. 7e période (1901 à 1910).— *Revue suisse Zool.* 32, suppl.: 1-657.
- Berrill, N.J., 1952. Growth and form in gymnoblastic hydroids. II. Sexual and seasonal reproduction in *Rathkea*. III. Hydranth and gonophore development in *Pennaria* and *Acaulis*. IV. Relative growth in *Eudendrium*.— *J. Morph.* 90(1): 1-32, figs 1-10.
- Boero, F. & J. Bouillon, 1993. Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria).— *Biol. J. Linn. Soc.* 48: 239-266.
- Boero, F., A. Balduzzi, G. Bavestrello, B. Caffa & R. Cattaneo Vietti, 1986. Population dynamics of *Eudendrium glomeratum* (Cnidaria: Anthomedusae) on the Portofino promontory (Ligurian Sea).— *Mar. Biol., Berl.* 92 (1): 81-85, figs 1-4.
- Boero, F. & P.F.S. Cornelius, 1987. First records of *Eudendrium glomeratum* (Cnidaria: Hydroida) in British and Irish waters, and taxonomic comments.— *Ir. Nat. J.* 22 (6): 244-246.
- Boero, F. & M. Sarà, 1987. Motile sexual stages and evolution of Leptomedusae (Cnidaria).— *Boll. Zool.* 54 (2): 131-139, figs 1-8.
- Bonnevie, K., 1898. Zur Systematik der Hydroiden.— *Z. wiss. Zool.* 63: 465-495.
- Calder, D.R., 1972. Some athecate hydroids from the shelf waters of northern Canada.— *J. Fish. Res. Bd Can.* 29 (3): 217-228, fig. 1, pls 1-2, tab. 1.
- Calder, D.R., 1988. Shallow water hydroids of Bermuda. The Athecatae.— *Life Sci. Contr. R. Ontario Mus.* 148: i-iv, 1-107, figs 1-59.
- Calder D.R. & W. Vervoort, 1998. Some hydroids (Cnidaria: Hydrozoa) from the Mid-Atlantic Ridge, in the North Atlantic Ocean.— *Zool. Verh., Leiden* 319: 1-65, figs 1-25.
- Cornelius, P.F.S., 1995. North-West European Thecate hydroids and their medusae. In: R.S.K. Barnes & J.H. Crothers (eds). *Synopses of the British Fauna (New Series)* 50 (1): i-vii +1-347; (2): i-vii +1-386. Linnean Society of London and The Estuarine and Coastal Sciences Association.
- Cavolini, Fil., 1785. Memorie per servire alla storia de' Polipi marini: 1-279, pls 1-8.
- Clarke, S.F., 1882. New and interesting hydroids from Chesapeake Bay.— *Mem. Boston Soc. nat. Hist.* 3 (4): 135-142, pls 7-9.
- Congdon, E.D., 1906. Notes on the morphology and development of two species of *Eudendrium*.— *Biol. Bull. mar. biol. Lab. Woods Hole* 11: 27-46, figs 1-11.
- D'Orbigny, A., 1846. Zoophytes: 17-28. In: *Voyage dans l'Amérique méridionale* 5 (4): 1-28.— Paris and Strasbourg.
- Eldredge, N. & J. Cracraft, 1980. Phylogenetic patterns and the evolutionary process: i-ix, 1-349.— New York.
- Ferrarezzi, H. & A.C. Marques, 1997. Análises cladísticas numéricas e ferramentas computacionais: 161-186. In: D.S. Amorim. *Elementos Básicos de Sistemática Filogenética*.— *Holos / Sociedade Brasileira de Entomologia, Ribeirão Preto*.
- Forey, P.L., C.J. Humphries, I.L. Kitching, R.W. Scotland, D.J. Siebert & D.M. Williams, 1992. *Cladistics, a practical course in systematics*.— The Systematics Association, Publication 10: i-x, 1-191.— Oxford.
- Gmelin, J.F., ed., 1791. C. Linnaeus, *Systema naturae per regna tria Naturae, etc.* Thirteenth edition 1 (6) (Vermes): 3021-3910.— Lipsiae.

- Hamond, R., 1957. Notes on the Hydrozoa of the Norfolk coast.— J. Linn. Soc., Zool. 43 (291): 294-324, figs 1-26, pl. 7.
- Hartlaub, C., 1905. Die Hydroiden der magelhaensischen Region und chilenischen Küste. Fauna Chilensis.— Zool. Jahrb., (Suppl. Bd.) 6(3): 497-702.
- Hennig, W., 1950. Grundzüge einer Theorie der phylogenetischen Systematik: 1-370.— Berlin.
- Hennig, W., 1966. Phylogenetic systematics: 1-263.— Urbana.
- Hickson, S.J. & F.H. Gravely, 1907. Hydroid zoophytes.— Nat. Antarct. Exped. 1901-1904, Nat. Hist. 3: 1-34, pls 1-4.
- Hincks, T., 1861. A catalogue of the zoophytes of South Devon and South Cornwall.— Ann. Mag. nat. Hist. (3) 8: 152-161, 251-262, 290-297, pls 6-8.
- Hincks, T., 1868. A history of the British hydroid zoophytes. 1: 1-328, text-figs 1-45; 2: pls 1-67.— London.
- Hirohito, 1988. The hydroids of Sagami Bay. (Part 1. Athecata).— Pubs Biol. Lab., Imp. Household, Tokyo 1988: i-x, 1-179 (English text), 1-110 (Japanese text), figs 1-54, pls 1-4, map.
- Hull, D.L., 1988. Science as a process: 1-586.— Chicago.
- Jäderholm, E., 1904. Mitteilungen über einige von der schwedischen Antarctic-Expedition 1901-1903 eingesammelte Hydroiden.— Archs Zool. Exp. Gén. 4 (3), notes et revue: 1-14.
- Jäderholm, E., 1905. Hydroiden aus antarktischen und subantarktischen Meeren.— Wiss. Ergebn. Schwed. Südpolar-Exped. 1901-1903 5(8): 1-41, pls 1-14.
- Jäderholm, E., 1908. Über einige nordische Hydroiden.— Zool. Anz. 32: 371-376.
- Kirkpatrick, R., 1890. Reports on the zoological collections made in Torres Straits by Professor A.C. Haddon, 1888-1889. Hydroida and Polyzoa.— Proc. Roy. Dublin Soc., n.s. 6: 603-626.
- Kirkpatrick, R., 1910. Hydrozoa and Porifera. In: J.T. Cunningham, On the marine fishes and invertebrates of St Helena.— Proc. zool. Soc. Lond. 1910: 86-131, pls 4-7.
- Kitching, I.J., P.L. Forey, C.J. Humphries & D.M. Williams, 1998. Cladistics, the theory and a practice of parsimony analysis. 2nd edition.— The Systematics Association Publication 11: 1-228.— Oxford.
- Kramp, P.L., 1926. Occasional notes on Coelenterata. 1.— Vidensk. Meddr dansk naturh. Foren. 82: 241-247, fig. 1.
- Light, S.F., 1913. Morphology of *Eudendrium griffini* sp. nov.— Philipp. J. Sci. (D) 8 (5): 333-356, figs 1-5, pls 1-2.
- Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata: 1-823.— Holmiae (Stockholm).
- Marinopoulos, J., 1992. Contribution à l'étude du genre *Eudendrium* (Hydrozoa : Hydroida) de la Méditerranée: taxonomie et phylogénie.— Bull. Inst. océanogr. Monaco, numéro spécial 9: 53-66.
- Mariscal, R.N., 1974. Nematocysts: 129-178, figs 1-17, tabs 1-3. In: L. Muscatine & H.M. Lenhoff (eds). Coelenterate Biology. Reviews and new perspectives: i-ix, 1-501, figs, tabs.— New York, San Francisco & London.
- Marques, A.C., 1993. Sistemática dos Eudendriidae L. Agassiz, 1862 (Cnidaria, Hydrozoa) do litoral paulista - Universidade de São Paulo, São Paulo. (Unpublished M.Sc. thesis).
- Marques, A.C., 1995. *Eudendrium pocaruquarum* n. sp. (Hydrozoa, Eudendriidae) from the southeastern coast of Brazil, with remarks on taxonomic approaches to the family Eudendriidae.— Contr. Zool. 65 (1): 35-40.
- Marques, A.C., 1996. A critical analysis of a cladistic study of the genus *Eudendrium* (Cnidaria: Hydrozoa), with some comments on the family Eudendriidae.— J. Comp. Biol. 1 (3/4): 153-162.
- Marques, A.C., 1997. Evolução basal nos Metazoa, com ênfase nas relações entre os Cnidaria.— Universidade de São Paulo, São Paulo. (Unpublished Ph.D. thesis).
- Marques, A.C. & D.R. Calder, 2000. *Eudendrium bathyale*, a new species of hydroid (Hydrozoa, Anthomedusae, Eudendriidae) from Bermuda.— Proc. Biol. Soc. Wash., 113 (1): 124-128, fig. 1.
- Marques, A.C., H. Mergner, R. Höinghaus & W. Vervoort. *Bimeria vestita* (Hydrozoa: Anthomedusae: Bougainvilliidae) senior synonym of *Eudendrium vestitum* (Hydrozoa: Anthomedusae: Eudendriidae). — Zool. Med. Leiden 73 (22): 321-325, figs 1-3.
- Marques, A.C. & A.E. Migotto, 1998. A new species of *Eudendrium* (Hydrozoa, Anthomedusae, Eudendriidae) from the Netherlands.— Zool. Verh., Leiden 323: 149-154, fig. 1.

- Marques, A.C. & W. Vervoort, 1999. (Case 3074). *Eudendrium arbusculum* Wright, 1859: proposed preservation under the plenary powers and removal of homonymy with *Eudendrium arbusculum* (D'Orbigny, 1846) (Cnidaria, Hydrozoa). Bull. Zool. Nom. 56 (1): 16-18.
- Mergner, H. & E. Wedler, 1977. Ueber die Hydroidpolypenfauna des Roten Meeres und seiner Ausgänge.— "Meteor" Forschungs-Ergebnisse, (D) 24: 1-32, text-figs 1-2, figs 1-81 on pls 1-12, tabs 1-3.
- Millard, N.A.H., 1957. The Hydrozoa of False Bay, South Africa.— Ann. S. Afr. Mus., 43 (4): 173-243, figs 1-15.
- Millard, N.A.H., 1975. Monograph on the Hydroida of southern Africa.— Ann. S. Afr. Mus. 68: 1-513, colour plate, figs 1-143.
- Millard, N.A.H. & J. Bojillon, 1973. Hydroids from the Seychelles (Coelenterata).— Annls Mus. r. Afr. Centrale, Série in 8, Sci. Zool. 206: 1-106, figs 1-11, pls 1-5, map.
- Millard, N.A.H. & J. Bouillon, 1974. A collection of hydroids from Moçambique, East Africa.— Ann. S. Afr. Mus., 65 (1): 1-40, figs 1-9.
- Motz-Kossowska, S., 1905. Contribution à la connaissance des hydraires de la Méditerranée Occidentale. I. Hydraire Gymnoblastiques.— Arch. Zool. exp. gén., (4) 3: 39-98.
- Nelson, G., 1978. Ontogeny, phylogeny, paleontology and the biogenetic law.— Syst. Zool. 27: 324-345.
- Nixon, K.C. & J.M. Carpenter, 1993. On outgroups.— Cladistics 9: 413-426.
- Norman, A.M., 1864. On undescribed British Hydrozoa, Actinozoa, and Polyzoa.— Ann. Mag. Nat. Hist. (3) 13: 82-90.
- Nutting, C.C., 1896. Notes on the Plymouth hydroids.— J. mar. Biol. Ass. U.K. 4 (2): 146-154.
- Nutting, C.C., 1898. On three new species of hydroids and one new to Britain.— Ann. Mag. nat. Hist. (7) 1: 362-366, pls 14-16.
- Nutting, C.C., 1901. Papers from the Harriman Alaska Expedition. XXI. The Hydroids.— Proc. Wash. Acad. Sci. 3: 157-216.
- Pallas, P.S., 1766. Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones, cum selectis auctorum synonymis: 1-28, 1-451.— Hagae Comitum.
- Peña Cantero, A.L. & A.C. Marques, 1999. Phylogenetic analysis of the Antarctic genus *Oswaldella* Stechow, 1919 (Hydrozoa, Leptomedusae, Kirchenpaueriidae).— Contr. Zool. 68 (2): 83-93, figs 1-2.
- Petersen, K.W., 1979. Development of coloniality in Hydrozoa: 105-139. In: G. Larwood & B. Rosen (eds). Biology and systematics of colonial organisms.— The Systematics Association special volume 11: i-xxxv, 1-589. — London, N.Y.
- Petersen, K.W., 1990. Evolution and taxonomy in capitate hydroids and medusae.— Zool. Jl linn. Soc. 100: 101-231, figs 1-49.
- Picard, J., 1951. Note sur les hydraires littoraux de Banyuls-sur-Mer.— Vie Milieu 2 (3): 338-349, figs 1-3.
- Picard, J., 1958. Origines et affinités de la faune d'hydropolypes (Gymnoblastes et Calyptoblastes) et d'hydroméduses (Anthoméduses et Leptoméduses) de la Méditerranée.— Rapp. P.-v. Réunion. Commn int. Explor. scient. Mer Méditerr. 14: 187-199, tabs 1-2.
- Pictet, C., 1893. Étude sur les hydraires de la Baie d'Amboine.— Revue suisse Zool. 1: 1-64.
- De Pinna, M.C.C., 1994. Ontogeny, rooting and polarity: 157-172. In: R.W. Scotland; D.J. Siebert. & D.M. Williams (eds). Models of phylogeny reconstruction.— The Systematics Association special volume 52: i-xi, 1-360.— Oxford.
- Riedl, R., 1959. Die Hydroiden des Golfes von Neapel und ihr Anteil an der Fauna unterseeischen Höhlen. In: Ergebnisse der österreichischen Tyrrhenia-Expedition 1952, Teil xvi.— Pubbl. Staz. zool. Napoli 30, suppl.: 591-755, figs 1-15, pls 9-11, tabs 1-7.
- Rösler, R., 1978. Zur Systematik der Hydroidengattung *Eudendrium* Ehrenberg. Hausarbeit der Fachprüfung für das Lehramt an Gymnasien.— Wissenschaftliches Prüfungsamt, Bochum: 1-188, pls 1-41. (Unpublished thesis).
- Schuchert, P., 1996. The marine fauna of New Zealand: Athecate hydroids and their medusae (Cnidaria: Hydrozoa).— Mem. New Zealand Oceanogr. Inst. 106: 1-159.
- Sheiko, O. & S. Stepan'jants, 1997. Medusozoa (Cnidaria: Anthozoa excepted) from Commander

- Islands, faunistic composition and biogeography.— Proc. 6th Int. Conf. Coel. Biol. 1995: 437-445, figs 1-6, tabs 1-2.
- Stechow, E., 1909. Beiträge zur Naturgeschichte Ostasiens: Hydroid-polypen der japanischen Ostküste.— Abh. Bayer. Akad. Wiss. (Math.-phys. Kl.), suppl. Bd. 1 (6): 1-111.
- Stechow, E., 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden.— Zool. Jb., Syst. 42 (1): 1-172, figs 1-56.
- Stechow, E., 1921a. Ueber Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen.— Zool. Anz. 53 (9-10): 223-236.
- Stechow, E., 1921b. Neue Genera und Species von Hydrozoen und anderen Evertebraten.— Arch. Naturgesch. (A) 87 (3): 248-265.
- Stechow, E., 1923. Die Hydroidenfauna der japanischen Region.— J. Coll. Sci. Imperial Univ. Tokyo, 44 (8): 1-23.
- Stechow, E., 1925. Hydroiden der Deutschen Tiefsee-Expedition.— Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia' 1898-1899 27: 383-546, figs 1-54.
- Stechow, E., 1932. Neue Hydroiden aus dem Mittelmeer und dem Pazifischen Ozean, nebst Bemerkungen über einige wenig bekannte Formen.— Zool. Anz. 100 (3-4): 81-92.
- Stepan'yants, S.D., 1979. Gidroidy vod antarktiki i subantarktiki. In: Rezul'taty biologicheskikh issledovaniy sovetskikh antarkticheskikh ekspeditsii, 6.— Issled. Fauny Morei 22(30): 1-99, figs 1-9, pls 1-25, 3 coloured figures on 2 plates, tabs 1-17.
- Tichomirowf, A.A., 1887. Zur Geschichte der Entwicklung der Hydroiden. Teil 2.— Sitzungsprotokolle Zool. Abt. Kaiserl. Ges. Naturwiss. Anthropol. Ethnogr. 1, Ausgabe 2, Anlage 1: 31-39, pls 1-2.
- Tichomirowf, A.A., 1890. In: J. Wagner, 1890, Recherches, etc.— Archs Biol. 10: 276, 277, 298-300.
- Torrey, H.B., 1902. The Hydroida of the Pacific coast of North America.— Univ. Calif. Publs Zool. 1 (1): 1-104, pls 1-11.
- Totton, A.K., 1930. Coelenterata. Part V.- Hydroida.— Nat. Hist. Rep. Br. Antarct. ('Terra Nova') Exped., 1910 Zool. 5 (5): 131-252, figs 1-70, pls 1-3.
- Vannucci, M., 1954. Hidrozoa e Scyphozoa existentes no Instituto Oceanográfico. II.— Bolm Inst. Oceanogr. São Paulo, 5 (1-2): 95-149, pls 1-6.
- Von Lendenfeld, R., 1885. The Australian Hydromedusae. II. Proc. Linn. Soc. N.S.W. 9: 345-353, pl. 6.
- Wagner, J., 1890. Recherches sur l'organisation de *Monobrachium parasiticum* Merejk.— Archs Biol. 10: 273-309, pls 8-9.
- Watson, J.E., 1985. The genus *Eudendrium* (Hydrozoa: Hydroida) from Australia.— Proc. R. Soc. Vict. 97 (4): 179-221, figs 1-95, tab. 1.
- Watson, J.E., 1987. Records of *Eudendrium* (Hydrozoa: Hydroida) from New Zealand.— Proc. Linn. Soc. N.S.W. 109 (4): 325-330, figs 1-8.
- Weill, R., 1934. Contribution à l'étude des Cnidaires et de leurs nématocystes. I. Recherches sur les nématocystes. Morphologie - Physiologie - Développement.— Trav. Stn zool. Wimereux 10: 1-347, figs. 1-208. II. Valeur taxonomique du cnidôme.— Trav. Stn zool. Wimereux 11: 349-701, figs 209-432.
- Wright, T.S., 1859. Observations on British Zoophytes.— The Edinburgh New Philosophical Journal, n.s.10: 105-114.
- Yamada, M., 1954. Species of the genus *Eudendrium* from Japan.— Publs Akkeshi mar. biol. Stn 2: 1-19, figs 1-15.

Received: 13.iv.1999

Accepted: 23.ii.2000

Edited: J.C. den Hartog