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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 5

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 5. - This study reviews all European hydroids belonging to the filiferan families Bythotiaridae, Proboscidactylidae, Magapiidae, Ptilocodiidae, Eucodoniidae, Russelliidae, Niobiidae, Protiaridae, and Trichydridae. *Protiara tetranema* (Péron & Lesueur, 1810) is considered as an unrecognizable species. The gonozooids of *Halitiara formosa* and *Trichydra pudica* are described, both have reduced blastostyles in a gonotheca-like casing.

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

INTRODUCTION

This study is the sixth in a series of taxonomic revisions and reviews of the European athecate hydroids and their medusae (Order Anthoathecata = Anthomedusae = Athecata). The previous ones are: Schuchert (2004; Oceaniidae and Pachycordylidae), Schuchert (2006; Acaulidae, Boreohydridae, Candelabridae, Cladocorynidae, Cladonematidae, Margelopsidae, Pennariidae, Protohydridae, Tricyclusidae), Schuchert (2007; Bougainvilliidae, Cytaeididae, Rathkeidae, and Pandeidae), Schuchert (2008a; Hydractiniidae, Rhysiidae, Stylasteridae), Schuchert (2008b: Eudendriidae). This publication concludes the Filifera with the families Bythotiaridae, Proboscidactylidae, Magapiidae, Ptilocodiidae, Eucodoniidae, Russelliidae, Niobiidae, Protiaridae, and Trichydridae.

MATERIAL AND METHODS

See also Schuchert (2008a), for a general introduction to the Hydrozoa see Bouillon *et al.* (2004, 2006).

Where possible, it was attempted to supplement the species descriptions by sequence information from part of the 16S mitochondrial rRNA gene. The methods to obtain DNA sequences are described in Schuchert (2005, 2007). All sequences have been submitted to the EMBL database (accession numbers FN422378-FN422379). DNA of some specimens was also given to other researches who determined 16S or other gene sequences. The origin and identity of the material used to obtain the 16S sequence data as well as the accession numbers are given for each species in the section "Material examined".

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Abbreviations

BMNH	The Natural History Museum, London, England
ERMS	European Register of Marine Species (Costello *et al.*, 2001)
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
ICZN	International Code of Zoological Nomenclature
IRSN	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
ZMUC	Zoological Museum Copenhagen, Denmark
ZMA	Zoological Museum Amsterdam, The Netherlands
ZMB	Zoological Museum Berlin, Germany

TAXONOMIC PART

Family Bythotiaridae Maas, 1905b

Synonyms: Calycopsidae Mayer, 1910: 104. – Bythotiaridi Mayer, 1910: 183.

Diagnosis: Medusa without apical projection, marginal bulbs very indistinct or absent; four, eight or more hollow marginal tentacles, each terminating in large swelling covered by nematocysts, basal portion of tentacles usually adnate to exumbrella; with or without rudimentary or dwarf solid tentacles; four or eight radial canals, simple or branching, with or without centripetal canals growing from circular canal towards centre; without gastric peduncle, mouth with four simple or crenulated lips; gonads on manubrial wall, simple or horizontally folded, adradial or interradial. Rarely abaxial ocelli on tentacle bases.

Hydroid stage only known for *Bythotiara*, living in prebranchial cavities of tunicates, colonial or solitary, monomorphic; without perisarc; hydrorhiza root- or plate-like, hydranths unbranched, hydranth composed of a body and a sometimes indistinctly demarcated naked pedicel; with up to five irregular whorls of filiform tentacles concentrated in a narrow band below hypostome; medusa buds arising from polyps at junction of pedicel and hydranth body. Cnidome includes microbasic euryteles and large desmonemes.

Remarks: See Bouillon *et al.* (2006) for more details and a key to all genera. The subdivision of the family in genera is not well resolved and progress is hampered by the fact that many polyp stages of this family remain unknown. The genera sometimes intergrade and it is sometimes difficult to draw a clear line separating them.

Key to the genera of Bythotiaridae medusae of the ERMS zone:

1a	centripetal radial canals present, blindly ending or joining base of stomach . . . . . *Calycopsis*
1b	without centripetal radial canals 2
2a	radial canals not bifurcated or more usually bifurcated once (some few additional branches may occur as abnormalities) . . . . . *Bythotiara*
2b	radial canals branching repeatedly at various levels . . . . . *Sibogita*

Genus ***Bythotiara*** Guenther, 1903

Synonyms: *Ascidioclava* Kirk, 1915, type species *Ascidioclava parasitica* Kirk, 1915. – *Crypta* Fraser, 1911 [name preoccupied]. – *Endocrypta* Fraser, 1912, type species *Crypta huntsmani* Fraser, 1911.

Type species: *Bythotiara murrayi* Guenther, 1903 by monotypy.

DIAGNOSIS: Bythotiaridae medusae with four simple or bifurcated radial canals, without centripetal canals; with or without secondary (rudimentary) tentacles, these entirely covered with nematocysts; gonads interradial, with transverse furrows; no ocelli. Polyp stage as given in family diagnosis.

REMARKS: Pagès *et al.* (1992) provided a table with the characteristics of all known *Bythotiara* medusae. Recently, Raskoff & Robison (2005) described a new *Bythotiara* polyp from pelagic tunicates, making it necessary to modify slightly the diagnosis of the polyp stage. Only one *Bythotiara* species occurs in the ERMS zone.

Bythotiara murrayi Guenther, 1903 Fig. 1

Bythotiara murrayi Guenther, 1903: 424, pl. 10 figs 4-5. – Mayer, 1910: 185, figs 97-98. – Vanhöffen, 1911: 213, figs 9a-c. – Kramp & Damas, 1925: 281. – Hartlaub, 1914: 355, figs 304-306. – Kramp, 1924: 12, figs 8-12. – Kramp, 1926: 97, figs 38-40. – Ranson, 1936: 98, pl. 1 fig. 12. – Russell, 1940: 515, figs 8-10. – Russell, 1953: 215, figs 113a-b, 114a-b, 115-116, pl. 13 fig. 1. – Kramp, 1959: 125, figs 1, 132. – Kramp, 1961: 118. – Kramp, 1968: 54, fig. 142. – Van der Spoel & Bleeker, 1988: 167, fig. 17. – Pagès *et al.*, 1992: 7, fig. 7. – Schuchert, 1996: 22, fig. 8.

TYPE MATERIAL: Not located (not found in BMNH).

MATERIAL EXAMINED: BMNH 1985.10.21.1-4; North Atlantic; depth 821 m; 3 medusae collected 20.07.1955 to 20.06.1957.

DIAGNOSIS: Medusa about 20 mm high and wide, thick walls; stomach small; four interradial gonads with transverse furrows, no vertical subdivision. Four primary radial canals each bifurcating once (but additional branching may occur); eight or more tentacles (as many tentacles as radial canals); with small secondary and minute tertiary tentacles.

DESCRIPTION (after Russell (1953) and own observations): Umbrella hemispherical or somewhat bell-shaped, about as high as or slightly higher than wide, with rounded apex, jelly thick, no gastric peduncle.

Stomach small, somewhat rhomboid in shape; mouth with four short simple lips. Four gonads, one covering each interradial wall of stomach, with few transverse folds subdividing them into several masses, top mass triangular and with central depression (Fig. 1B).

Four primary radial canals, each bifurcating near point of origin from stomach to form eight straight, narrow, smooth canals joining narrow ring canal; each primary canal leaves stomach as short narrow funnel (= mesentery); additional branchings and irregularities of radials canals frequent (Fig. 1C-F). No ocelli.

Eight or more primary marginal tentacles (as many tentacles as radial canals), large, smooth, hollow, without bulbs or basal swellings, tentacles at base flattened oral-aborally and adnate to umbrella margin, each tentacle terminating in large hemispherical nematocyst cluster composed of desmonemes; one to five small hollow secondary marginal tentacles between every two primary marginal tentacles, secondary tentacles contain ?euryteles and desmonemes, otherwise similar to primary tentacles; additional tertiary dwarf tentacles may be present.

Nematocysts: ? microbasic euryteles and desmonemes, discharged desmonemes with five coils.

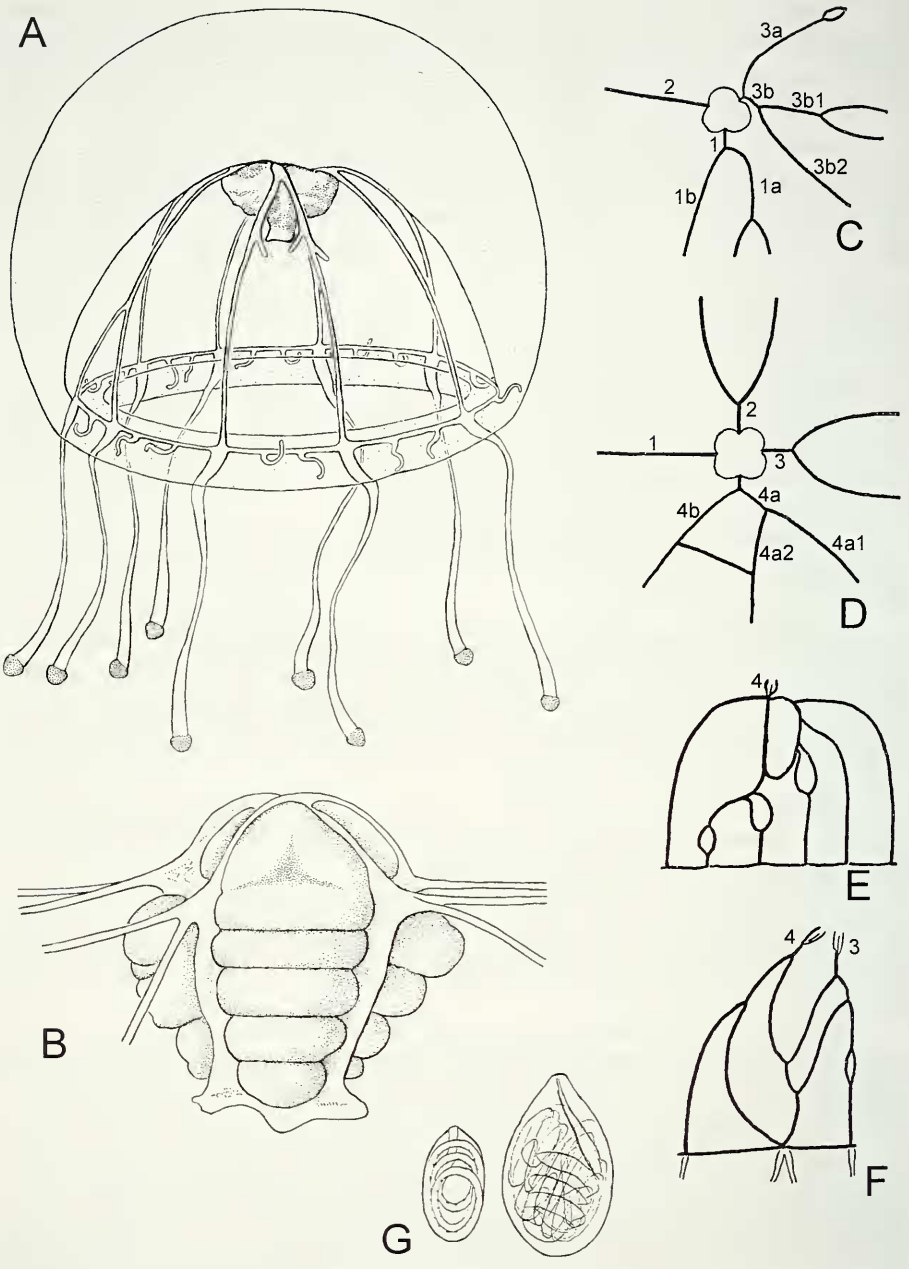

FIG. 1. *Bythotiara murrayi* Guenther, 1903. (A) Mature medusa, maximal diameter about 25 mm, modified after Hartlaub (1914). (B) Manubrium with gonads, interradial view, modified after Russell (1953). (C-F) Variation of the branching pattern of the radial canals, from Kramp (1924), C-D in aboral view, E-F in lateral view, numbers and letters identify the radial canals and their branches. (G) Nematocysts: desmoneme and ? microbasic eurytele, for dimensions see text, from Russell (1940).

Colour of umbrella faint violet; gonad-covered part of stomach brick red; remainder of medusa colourless.

Polyp unknown.

Dimensions (Russell, 1940; 1953): Mature medusae 5-21 mm in height. ? Euryteles (17-20)x(10-11)μm; desmonemes (13-14)x(6)μm.

Distribution: Eastern Atlantic from Norway to South Africa; Mediterranean; north-western Atlantic; tropical parts of the Indian Ocean; Indonesia; Papua New Guinea, New Zealand (Hartlaub, 1914; Kramp & Damas, 1925; Russell, 1953; Kramp, 1968; Bouillon, 1980; Winkler, 1982; Van der Spoel & Bleeker, 1988; Pagès *et al.*, 1992; Schuchert, 1996). Type locality: 52.30167°N 15.89833°W (SW of Ireland).

Biology: *Bythothiara murrayi* is an oceanic medusa that is only rarely encountered in inshore waters. It can be caught at depths of several hundred meters only.

Remarks: The smallest medusa stages found by Russell (1953) measured 5 mm, but they already had mature gonads.

Genus ***Calycopsis*** Fewkes, 1882b

Type species: *Calycopsis typa* Fewkes, 1882b.

Diagnosis: Bythotiaridae medusae with four initially unbranched radial canals and with four or more centripetal canals arising from the ring canal, blind or joining the cruciform base of stomach or the perradial canals. Gonads interadial, usually with eight adradial rows of deep transverse furrows, alternatively transversely folded, or smooth, or with pits; basal portion of tentacles adnate to umbrella margin; tentacles hollow, usually tentacles all alike, rarely two types may be present, nematocysts only in terminal knobs. Without ocelli.

Remarks: The genus *Calycopsis* and its species are discussed in Kramp (1959) and Lindsay *et al.* (2008). The polyps remain unknown. Below follows an identification key to the *Calycopsis* medusae of the Atlantic north of the Equator (adapted from Kramp, 1959). A species not yet known from the ERMS zone has been included in brackets. It is not unlikely that it will ultimately also be found in the ERMS zone.

Key to the *Calycopsis* species of ghe ERMS zone:

1a umbrella with funnel-shaped apical depression; 3-4 centripetal canals in each quadrant . . . . . *C. typa*

1b umbrella without an apical depression 2

2a with only 4 perradial tentacles; one interradial centripetal canal; tentacle-base with adaxial appendage . . . . . *C. krampi*

2b with 8 or more tentacles, no adaxial appendages on tentacle bases 3

3a umbrella margin with exumbrellar papillae; 2 centripetal canals in each quadrant; 8-12 tentacles . . . . . [*C. papillata*]

3b marginal lobes of umbrella without papillae 4

4a gonads smooth or with few, irregular transverse folds; one centripetal canal in each quadrant; 8 tentacles; all alike . . . . . *C. simplex*

4b gonads with 8 adradial rows of deep, transverse furrows; more than 8 tentacles 5
5a 7 or more centripetal canals in each quadrant, most of them joining base of stomach or upper part of neighbouring canals; 16-32 tentacles . . . . *C. chuni*
5b 1 or 2 centripetal canals in each quadrant 6
6a one centripetal canal in each quadrant, blind; 8-16 long and several small tentacles . . . . . *C. bigelowi*
6b 1-2 centripetal canals in each quadrant, joining base of stomach; about 40 long tentacles . . . . . *C. gara*

Calycopsis typa Fewkes, 1882 Fig. 2

Calycopsis typa Fewkes, 1882b: 304, pl. 1 fig. 34. – Mayer, 1910: 131, fig. 70. – Hartlaub, 1914: 359: figs 293-294, 307. – Kramp, 1959: 21, 127, fig. 139, revision. – Kramp, 1961: 121, synonymy. – Van Soest, 1973: 121, fig. 2a.
Sibogita nuarchus Bigelow, 1909b: 206, pl. 1 figs 1-8. – Bigelow, 1913: 21, synonym of *C. typa*.
Not *Calycopsis typa*. – Vanhöffen, 1911: 214, pl. 22 fig. 6. [= *C. chuni* Vanhöffen, 1911]
Not *Calycopsis typa*. – Vanhöffen, 1912: 364 [?= *C. papillata*]
Sibogita typa. – Mayer, 1910: 491.
? *Calycopsis typa*. – Pagès *et al.*, 1992: 7, fig. 8A-C.

TYPE MATERIAL: United States National Museum, catalogue number 9727 (not seen).

DIAGNOSIS: *Calycopsis* medusa with a characteristic funnel-shaped depression at apex, 3-4 blind centripetal canals in each quadrant, 16 long tentacles.

DESCRIPTION: Medusa umbrella spherical to barrel-shaped, jelly thick, solid, with a characteristic funnel-shaped depression at apex, umbrella somewhat laterally flattened, plane in which flattening occurs is either radial or interradial. Umbrella margin lobed through embayments for the tentacles.

Manubrium large and voluminous, length 1/2 to 2/3 of bell cavity, urn-shaped, about two-thirds as broad as long, aboral end cruciform in section, mouth with four short perradial lips, mouth rim smooth or crenulated.

Gonads interradial, discontinuous in the perradii, with eight adradial rows of about 20 horizontal furrows, irregular, projecting lobes of gonads may be developed.

Four radial canals, widening near manubrium and forming short mesenteries, 3-4 blind centripetal canals in each quadrant, interradial centripetal canal the furthest developed, reaching nearly to the base of the manubrium, maximally usually around 16 canals in total, maximum number of canals observed 21.

Connected with each canal is a well-developed tentacle, thus around 16 in total, between long tentacles usually occur very small tentacles (16), long tentacles adnate to umbrella margin in furrows at the rim, long tentacles with club-like swollen ends, concentration of nematocysts at tip.

Colours: gonads deep brownish-red; terminal knobs pale yellowish.

DIMENSIONS: Up to 37 mm high and 40 mm wide. Bigelow (1909b, as *Sigogita nuarchus*) gives a table with measurements, tentacle- and canal numbers.

BIOLOGY: A deep-water species, usually occurring at depths of several hundred metres (Kramp, 1959).

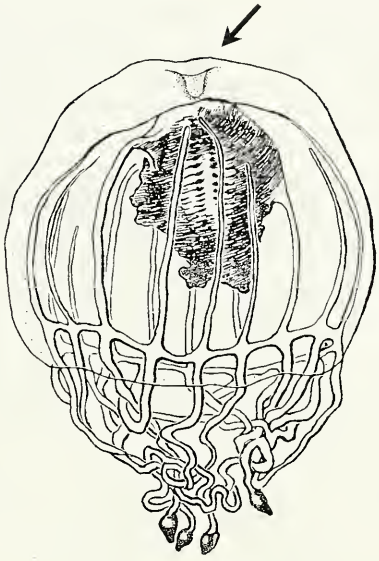

FIG. 2

Calycopsis typa Fewkes, 1882; modified after Bigelow (1909b) and Hartlaub (1914), note the characteristic apical funnel (arrow).

DISTRIBUTION: Atlantic Ocean, off the north-eastern coast of the USA, Cape Verde Islands (Kramp, 1959), Azores (Van Soest, 1973), ? South Africa (Pagès *et al.*, 1992). Type locality: Atlantic, off the New England, coast USA.

REMARKS: This species is rare in the ERMS area, it is only known from one specimen caught in deep waters NE of the Azores. The South African medusae described by Pagès *et al.* (1992) matched the description given above, but additionally they had knobs of nematocysts on the adaxial sides of the tentacle bases. Such knobs have never been mentioned for *C. typa* by other authors and perhaps the South African medusae belong to a new, unnamed species.

Calycopsis krampi Petersen, 1957 Fig. 3

Calycopsis krampi Petersen, 1957: 31, figs. 2-3. – Kramp, 1959: 126, fig. 135. – Kramp, 1961: 120. – Fraser, 1974: 13.

MATERIAL EXAMINED: ZMUC; holotype, without registration number; Dana Station 9806; 50.917°N 14.000°W; net tow with 120-200 m wire out; 21 August 1955.

DIAGNOSIS: *Calycopsis* medusa up to 4 mm high, 4 tentacles, 4 centripetal canals, at base of each tentacle an adaxial appendage pointing into bell cavity.

DESCRIPTION: Medusa spherical, jelly thick. Manubrium large and voluminous, length 3/4 of bell cavity. Four large interradial gonads leaving only mouth-region and perradial parts of manubrium visible; each gonad with very deep, vertical interradial furrow and three to four irregular transverse folds. The perradial surfaces of the stomach form four prominent longitudinal ridges, continued as short mesenteries where they join the radial canals.

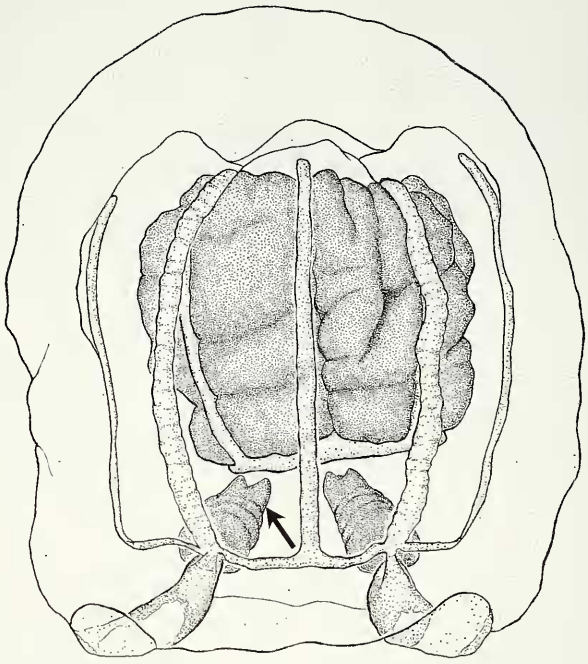

FIG. 3

Calycopsis krampi Petersen, 1957; modified after Petersen (1957), size 4 mm, the arrow points at one of the characteristic adaxial projections.

Four complete radial canals and four narrower, blind centripetal canals reaching almost to the top of the bell.

Four perradial tentacles without tentacular bulbs, proximal parts adnate to bell margin, structure of distal ends unknown. Four prominent adaxial appendages at the places where the radial canals join the ring canal, one in each perradius, projecting obliquely into bell cavity (arrow in Fig. 3). Each projection forms a direct adaxial continuation of the basal part of the tentacle attached to the exumbrella, the projection is about half the diameter of the bell opening long, nearly half as broad as long, tapering a little distally, drawn into two 'papillae' at the tip, aboral side with a longitudinal ridge.

DIMENSIONS: Umbrella 4 mm high and 3 mm wide.

BIOLOGY: Likely restricted to depths below 100 m, Fraser (1974) recorded it from deep waters east of Rockall.

DISTRIBUTION: A very rare species occurring west of the British Isles (Petersen, 1957; Fraser, 1974). Type locality: Porcupine Seabight SW of Ireland, 50.917°N 14.00°W, max. 200 m depth.

REMARKS: This species is known from only three specimens. Its perradial projections are unique and render the species quite distinct. The transversal folds of the gonads seen in the type specimen could be a fixation artifact.

Calycopsis simplex Kramp & Damas, 1925 Fig. 4

Calycopsis simplex Kramp & Damas, 1925: 282, figs 23-25. – Kramp, 1959: 126, fig. 133. – Kramp, 1961: 121. – Goy, 1973: 986, fig. 8. – Gili *et al.*, 1998: 116, fig. 2.

TYPE MATERIAL: Bergen Museum, Norway (not seen).

MATERIAL EXAMINED: MNHN1647; Mediterranean, France, Bay of Villefranche-sur-Mer; 16 December 1966; one medusa, material of Goy (1973).

DIAGNOSIS: *Calycopsis* medusa up to 9 mm, hemispherical; gonads smooth or with few, irregular transverse folds; 4 blind interradial centripetal canals; 8 tentacles all alike.

DESCRIPTION: Medusa globular to hemi-spherical, jelly moderately thick, umbrella margin with embayments for tentacles.

Manubrium conical, length 1/2 of bell cavity, cruciform cross-section, mouth small, corners not much drawn out. Gonads cover manubrium almost entirely as eight large adradial pads, adnate interradially but separated by deep vertical furrows, separated perradially, surface either smooth or with few, irregular transverse folds.

Four complete radial canals and four blind centripetal canals reaching to middle or top of the bell.

Eight tentacles, four perradial, four interradial, all alike, without tentacular bulbs, proximal parts adnate to bell margin, distal ends swollen, elongated club-like. No ocelli.

DIMENSIONS: Umbrella diameter 8-9 mm.

DISTRIBUTION: Norway (Kramp & Damas, 1925), Mediterranean (Goy, 1973; Gili *et al.*, 1998). Type locality: Hjørundfjord, Norway, deeper than 400 m.

BIOLOGY: Likely a deep water species, two of the three records were from more than 400 m depth.

Calycopsis chuni Vanhöffen, 1911 Fig. 5

Calycopsis chuni Vanhöffen, 1911: 217, pl. 22 fig. 8. – Bigelow, 1940: 290. – Kramp, 1959: 23, 127, fig. 140, revision. – Kramp, 1961: 119. – Kramp, 1968: 55, fig. 148.
Calycopsis valdiviae Hartlaub, 1914: 360. – Kramp, 1959: 23, synonym.
Calycopsis typa. – Vanhöffen, 1911: 214, pl. 22 fig. 6. [not *Calycopsis typa* Fewkes, 1882]

TYPE MATERIAL: Naturkundemuseum Berlin, Germany, syntypes ZMB Cni 14845 and ZMB Cni 14838 (not seen).

DIAGNOSIS: *Calycopsis* medusa around 30 mm high and wide, jelly thick, 32 or more radial canals, 16 long tentacles and up to 16 short ones; gonad in each quadrant with two vertical rows of 19-32 transverse clefts.

DESCRIPTION (Vanhöffen, 1911; Kramp, 1959): Umbrella spherical to somewhat oblong, jelly thick and rigid.

Manubrium about half as long as bell cavity, mouth rim crenulated, perradial corners of mouth drawn out into four simple lips, manubrium-base cruciform.

Gonad covering most of manubrium, with eight adradial rows of 19-32 parallel transverse furrows.

Four perradial canals and usually 28 centripetal canals, occasionally up to 60, all communicate with stomach in fully grown specimens, usually directly joining the

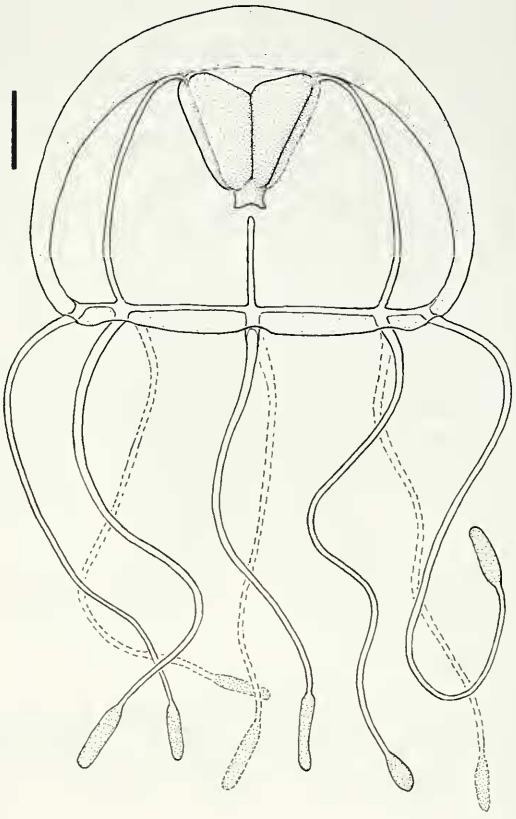

FIG. 4
Calycopsis simplex Kramp & Damas, 1925: after preserved material from the Mediterranean, scale bar 2 mm.

stomach and thus like radial canals, but sometimes fused with a neighbouring canal close to manubrium. In younger specimens some centripetal canals ending blindly.

16 large tentacles (max. 24) with terminal swellings and up to 16 small, hook-shaped tentacles, all tentacles in phase with radial and centripetal canals.

DIMENSIONS: Bell diameter 21-34 mm, height up to 38 mm (Kramp, 1959).

BIOLOGY: Occurs in deep and intermediate water layers (Kramp, 1959).

DISTRIBUTION: *Calycopsis chuni* has been recorded in the ERMS zone off the coast of Morocco and near the Canary Islands (Kramp, 1959). It is known to occur in the Indian Ocean from East Africa to the Malayan Archipelago, along the east coast of Australia, the Gulf of Panama, the West Indies, and the Atlantic coast of West Africa (Kramp, 1968). Type locality: Gulf of Aden, 1200 to 2000 m depth.

REMARKS: The high numbers of radial canals (including former centripetal canals that have joined the manubrium) characterize this rare species.

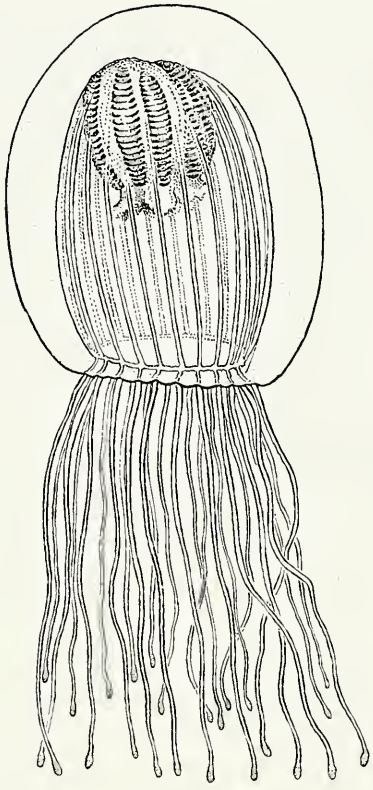

FIG. 5

Calycopsis chuni Vanhöffen, 1911; modified after Kramp (1959) and Vanhöffen (1911), bell size about 3 cm.

Calycopsis bigelowi Vanhöffen, 1911 Fig. 6

Calycopsis bigelowi Vanhöffen, 1911: 218, fig. 12. – Kramp, 1957: 21, map fig. 4. – Kramp, 1959:127, fig. 136. – Kramp, 1961: 119. – Kramp, 1968: 56, fig. 149. – Van der Spoel & Bleeker, 1988: 167, fig. 16. – Schuchert, 1996: 26, fig. 10a-b.

TYPE MATERIAL: Holotype in Naturkundemuseum Berlin, Germany, ZMB Cni 14837 (not seen).

MATERIAL EXAMINED: BMNH 1957.2.1.760-764; Discovery stations 100, 100c, 101, 983, west of Cape Good Hope; 6 mature medusae, some rather damaged, material described in Kramp (1957). – See also Schuchert (1996).

DIAGNOSIS: *Calycopsis* medusa 8-16 mm high and wide, jelly thick, 8-16 long tentacles and up to 40 short ones; four radial canals and four blind interradial centripetal canals; gonad in each quadrant with two vertical rows of up to 16 deep, regular, transverse clefts.

DESCRIPTION: Medusa umbrella ovoid to spherical, jelly thick, soft and adhesive. Velum somewhat shifted into subumbrella.

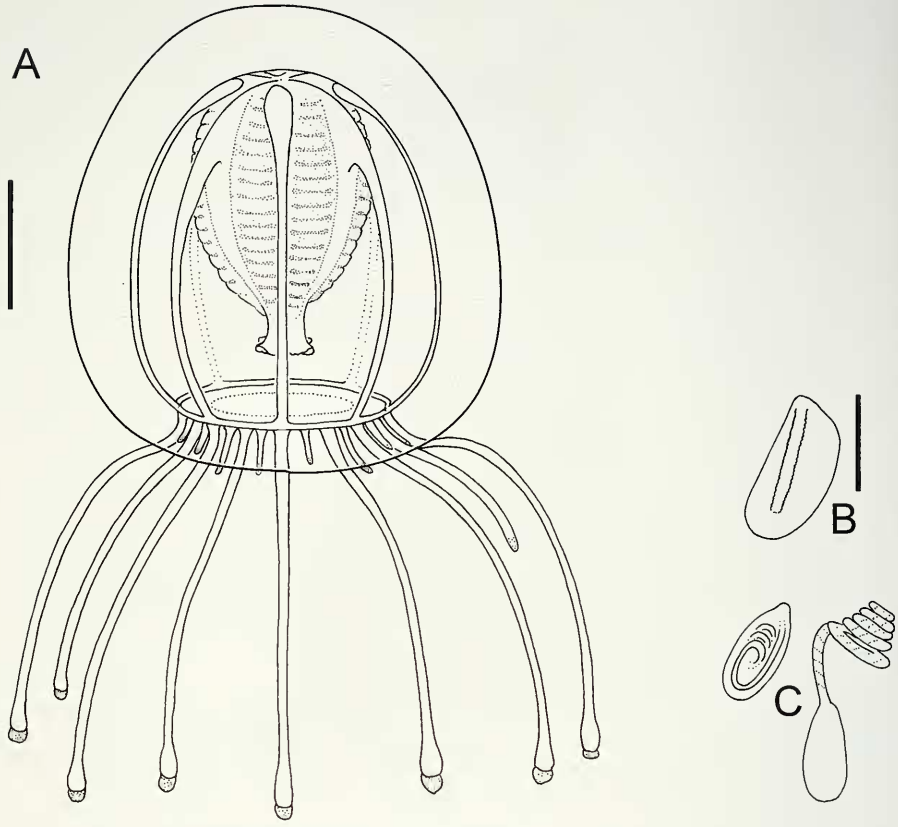

FIG. 6

Calycopsis bigelowi Vanhöffen, 1911; after Schuchert (1996). (A) Medusa, only frontal tentacles shown; scale bar 5 mm. (B) Heteroneme, scale bar 10 μm. (C) Intact and discharged desmonemes, same scale as B.

Manubrium large and voluminous, length 2/3 of bell cavity, with cross-shaped base. Mouth with slightly undulating margin and with four small perradial lips. Four large, interradial gonads leaving only perradial parts of manubrium visible. Gonads with eight adradial rows of up to 16 horizontal furrows, occasionally some additional pits.

Four complete radial canals, widening near manubrium and forming mesenteries. Four additional centripetal canals which reach almost to the manubrium top, likely ending blindly, terminal region somewhat broadened. All radial canals are rather broad and are connected to the equally broad circular canal. No tentacular bulbs present.

Up to 16 long tentacles, four perradial, four interradial, and up to eight adradial ones. Perradial and interradial tentacles usually fully developed in mature animals and longer than bell height, most of the adradial tentacles are also fully developed but some are shorter and in mid-development. In addition to these 16 long tentacles, 16-40 short

tentacles. All tentacles hollow and with bases adnate to the umbrella margin. Long tentacles end in a terminal swelling with a concentration of nematocysts. Shorter tentacles without terminal swelling, but with a concentration of nematocysts. Without ocelli.

Nematocysts: rare heteronemes (Fig. 6B) and frequent, elongated desmonemes (Fig. 6C). Desmonemes on tentacle tips, discharged with five coils, thread with spiral pattern of small bristles

Colours: gonads yellow-green colour (Kramp, 1957) or red (Vanhöffen, 1911).

Dimensions Mature medusa 9-16 mm high and wide, umbrella wall 3 mm. Desmonemes (11-12)x(5-6)μm, heteronemes (14-15)x(7-8)μm (Schuchert, 1996).

Biology: Oceanic species, prefers deep waters down to 2500 m (Kramp, 1957), usually around 400-600 m.

Distribution: Gulf of Aden; South Africa; Indo-Malayan region; tropical Indian Ocean; New Zealand; Scotland, ? British Columbia (Kramp, 1965, Van der Spoel & Bleeker, 1988; Fraser, 1974; Schuchert, 1996; Brinckmann-Voss & Arai, 1998). Type locality: Gulf of Aden, depth 1100 m.

Remarks: This is a rare species and in the ERMS region it is only known from a single specimen collected in deep water west of Scotland (Fraser, 1974). A very similar species is *Calycopsis gara* Petersen, 1957. It differs from *C. bigelowi* in having more (up to 46) long tentacles and four to eight centripetal canals. As only very few specimens of *C. bigelowi* and *C. gara* are known, their morphological variation is not sufficiently known and the status of *C. gara* is somewhat uncertain.

Calycopsis gara Petersen, 1957 Fig. 7

Calycopsis gara Petersen, 1957: 29, fig. 1. – Kramp, 1959: 127, fig. 137. – Kramp, 1961: 120. – Winkler, 1982: 37. – Bleeker & Van der Spoel, 1988: 231, fig. 17.

Type material: ZMUC (not seen).

Diagnosis: *Calycopsis* medusa 10-20 mm high, 8 radial canals, sometimes a few additional centripetal canals, gonads with 15-16 transverse clefts in eight vertical rows, 40-50 tentacles.

Description (Petersen, 1957): Medusa umbrella ovoid to spherical, evenly rounded, somewhat laterally compressed along two interadii, jelly thick.

Manubrium large and voluminous, length 2/3 of bell cavity, half as wide as long, with cross-shaped base. Mouth rim smooth, four small perradial lips. Four large, interradial gonads leaving only perradial parts of manubrium visible. Gonads with eight vertical, adradial rows of up to 16 horizontal furrows, some can be irregular. The perradial edges of the stomach form meridional ridges which in their uppermost parts connect with the radial canals to form short funnels (=mesenteries).

Four radial canals, rather wide, usually four centripetal canals joining the base of the manubrium, sometimes additional blind centripetal canals. No tentacular bulbs present.

40-50 tentacles, some short, ending in a terminal swelling with a concentration of desmonemes.

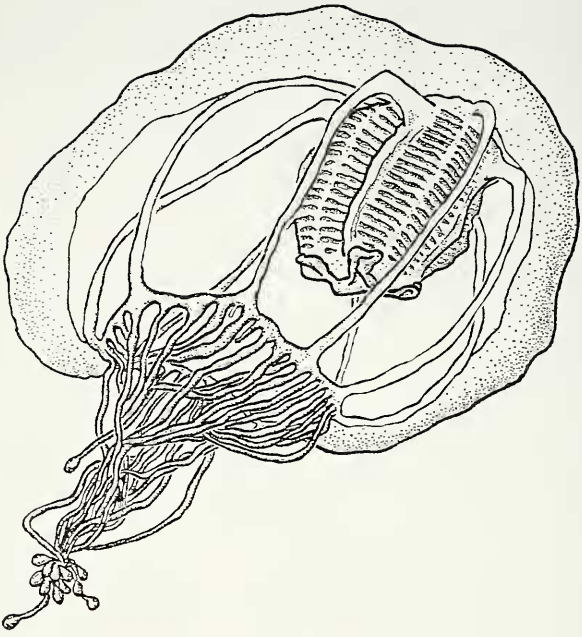

FIG. 7
Calycopsis gara Petersen, 1957; modified after Petersen (1957), bell size 11 mm.

DIMENSIONS: Bell diameter 11-21 mm, height 10-22 mm (Winkler, 1982).

BIOLOGY: All known records are from less than 200 m depth.

DISTRIBUTION: Central North Atlantic Ocean (Petersen, 1957; Winkler, 1982; Bleeker & Van der Spoel, 1988). Type locality: 50.883°N 34.417°W, 0-100 m.

REMARKS: See above under *C. bigelowi*.

Genus ***Sibogita*** Maas, 1905b

TYPE SPECIES: *Sibogita geometrica* Maas, 1905b.

DIAGNOSIS: Bythotiaridae with four primary radial canals which branch repeatedly at various levels; no centripetal canals, gonads with eight rows of transverse furrows. No ocelli. Polyps unknown.

REMARKS: This is currently a monotypic genus. Bigelow (1919) assumed that the side branches of the radial canals were actually centripetal vessels that arose from the ring canal and only later in life joined the radial canals. He therefore synonymized the genus with *Calycopsis*. Kramp (1959) outlined the taxonomic history of the genus and contested Bigelow's view of the growth direction of the radial canals. Kramp thinks that the branching radial canals arise indeed through branching during ontogeny and he thus has an argument to maintain the genus. The diminution of the canal width towards the periphery is a good argument in favour of this view. Nevertheless, the

difference to *Bytothiara* is not so clear-cut and *Sibogita* can admittedly be seen as a synonym of the former. As we neither know the polyp stage of *Bythotiara murrayi* nor of *Sibogita geometrica*, further discussions on the validity of *Sibogita* are premature.

Sibogita geometrica Maas, 1905b Fig. 8

Sibogita geometrica Maas, 1905b: 17, pl. 3 figs 16-18. – Mayer, 1910: 186, fig. 99. – Kramp, 1965: 49. – Kramp, 1968: 57, fig. 151a-b. – Van Soest, 1973: 121, fig. 2c. – Winkler, 1982: 37, figs 9-11. – Bleeker & van der Spoel, 1988: 234, figs 18-19. – Pagès *et al.*, 1992: 9, fig. 9.
Sibogita geometrica occidentalis Kramp, 1959: 28, 129, pl. 2 figs 2-3, text-figs 4-5.
Calycopsis geometrica. – Bigelow, 1919: 290, pl. 40 fig. 5-7, pl. 41 fig. 2.

TYPE MATERIAL: ZMA COEL no 3853 (not seen).

DIAGNOSIS: See genus diagnosis.

DESCRIPTION: Medusa umbrella globe- to pumpkin-shaped, top rather flat or even slightly concave, walls straight, thick, bell can be laterally compressed, without gastric peduncle, bell-margin undulated through embayments for tentacles.

Manubrium relatively short, square to cross-shaped in section, 1/4 to 1/2 of the height of the subumbrellar cavity, mouth with four more or less distinct lips, mouth rim undulated. Four large, interradial gonads with eight adradial rows of 6-19 horizontal furrows.

Four primary radial canals divided irregularly at different levels giving rise to a total of 16-43 radial canals joining the ring-canal, anastomoses of radial canals rarely present, no centripetal canals. Radial canals widening somewhat where they join the ring-canal, intersection containing dark pigment granules.

About half as many to as many long tentacles as there are radial canal endings, originating in line with radial canals, base adnate, highly contractile, distal end swollen, club-like. Between successive pairs of long tentacles usually a short, inward-directed tentacle.

Living specimen colourless except for faintly yellow manubrium (Kramp, 1959).

DIMENSIONS: Bell height usually around 2 cm (max. 4 cm), diameter 2 cm. Winkler (1982) gives the following data for Atlantic specimens: height 15 mm, diameter 21 mm, jelly 3 mm, manubrium 8 mm long and 5 mm wide. Kramp (1965) gives a table with the correlation of the bell-size and the number of radial canals.

BIOLOGY: A quite rare, oceanic species, usually found at depths of some 100 metres. Bleeker & van der Spoel (1988) found evidence for diel vertical migration as all night samples taken were above and all day samples below 200 m depth.

DISTRIBUTION: Malayan Archipelago and tropical Indian Ocean (Maas, 1905b; Bigelow, 1919), Bay of Biscay, Azores and Mid-Atlantic (Kramp, 1959; Van Soest, 1973; Winkler, 1982; Bleeker & van der Spoel, 1988), Benguela Current off South Africa (Pagès *et al.*, 1992) Type locality: northeast of Sulawesi, 1.633°N 124.46°E, 0-900 m.

REMARKS: Kramp (1959) thought that the Atlantic population differs slightly from the Pacific one and he introduced for the former the subspecies *Sibogita geo-*

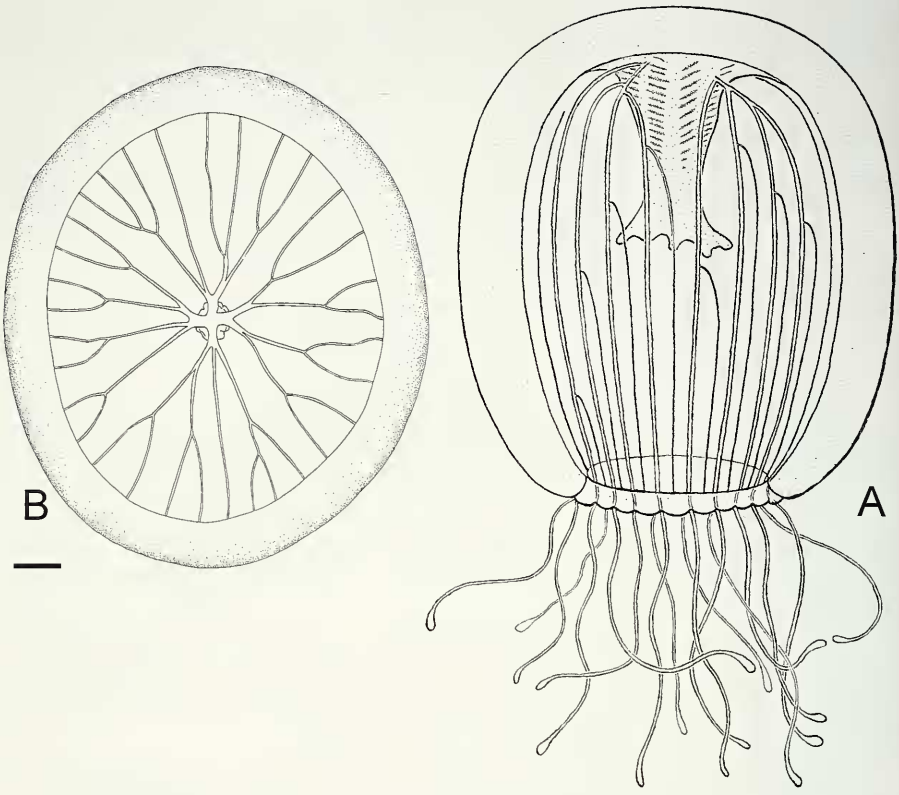

Fig. 8

Sibogita geometrica Maas, 1905b. (A) Medusa from Pacific in side-view, bell height 38 mm, modified after Maas (1905) and Mayer (1910). (B) Aboral view of medusa from Atlantic showing branching pattern of radial canals, from Winkler (1982), scale bar 3 mm.

metrica occidentalis. The differences to the nominal Pacific species were given as a smaller bell-size, fewer gonadal folds, and radial canals dividing already close to the centre. After having seen more specimens from the Pacific, Kramp (1965) then synonymized the subspecies *occidentalis* with the nominal Pacific species. Also other authors (e. g. Winkler, 1982; Bleeker & van der Spoel, 1988) confirmed this. Both forms occur in the Atlantic and the Pacific and they are connected by intermediate forms.

Family Proboscidactylidae Hand & Hendrickson, 1950

Synonyms: Willsiadae Forbes, 1848 [family name incorrectly derived from genus *Willsia*]. – Laridae Hincks, 1868 [preoccupied by Laridae Rafinesque, 1815, Seagulls]. – Hydrolaridae Allman, 1872 [type species *Lar sabellum* Gosse, 1857 by monotypy]. – Williadae Haeckel, 1879 [invalid emendation of original name]. – Williadi Mayer, 1910. – Willsiidae Stechow, 1913 [correct derivation of name].

Diagnosis (Bouillon *et al*., 2006): Hydroid usually on rim of sabellid polychaete tubes, with creeping, naked stolons; hydranths almost sessile, polymorphic;

gastrozooid with rounded hypostome, separated from body by a constriction; hypostome with large pad of nematocysts somewhat displaced onto one side, two filiform tentacles arising close together beneath hypostomial constriction, opposite to nematocyst cluster; gonozooids and dactylozooids without tentacles, mouth-less and smaller than gastrozooids; medusa buds close to gonozooid tip.

Medusa umbrella mostly hemispherical; with exumbrellar nematocyst buttons or bands alternating with tentacles; radial canals branched, obliterated canals sometimes present; usually instead of circular canal a solid gastrodermal marginal strand; manubrium base with four, six or more radial gastric lobes, extending along proximal portions of radial canals, lobes in some species inconspicuous; gonads surrounding manubrium and extending onto gastric lobes; tentacles hollow, with swollen hollow base connected to the lumen of radial canals.

Remarks: For the taxonomic history and naming of this family see e. g. Browne (1905), Maas (1905a), Bigelow (1909a), Hartlaub (1917), Stechow (1923), Kramp (1939), and Hand & Hendrickson (1950).

Hand and Hendrickson (1950) argued that the family name must be changed to Proboscidactylidae because Uchida & Okuda (1941) had previously synonymized *Willsia* with *Proboscidactyla*. But this renaming was not necessary, and the correct and valid name of this family would have been Willsiidae, as was argued by Stechow (1923). The name Willsiidae has, however, hardly been used and after 1950 many general treatises (e. g. Russell, 1953; Kramp, 1961) adopted the name Proboscidactylidae. Later authors exclusively used this name. In the interest of nomenclatural stability, the usage of the name Proboscidactylidae should thus be continued. This is explicitly endorsed by article 40.2 of the ICZN, because Hand and Hendrickson (1950) replaced the name Willsiidae with Proboscidactylidae before 1961.

Kramp (1939) referred the family to the Limnomedusae (subclass Trachylinae). The occurrence of desmonemes, the gonads on the manubrium, and the lack of statocysts argue strongly against this. It is nowadays again included in the Anthomedusae (=Anthoathecata = Athecata). Molecular phylogenies confirmed that they do not belong to the Trachylinae but to the Hydroidolinae, although the precise relationships within the latter subclass are not yet resolved (Cartwright *et al.*, 2008).

This family currently comprises only the genus *Proboscidactyla* (see Bouillon *et al.*, 2006). Schuchert (1996) also included the genus *Fabienna* Schuchert, 1996 in this family, replacing in part *Pochella* Hartlaub, 1917, a genus that had originally been included in the Proboscidactylidae by Russell (1938a) (now in Trichydridae). Although *Fabienna* has a close affinity with the family Proboscidactylidae (Schuchert & Reiswig, 2006; Cartwright *et al.*, 2008), it is here in the interim kept separate in the family Magapiidae (former Laingiidae) following Bouillon *et al.* (2006). See also the remarks for this family.

The medusae of the Proboscidactylidae have reportedly a solid strand instead of a radial canal. It is not clear if is true for all species. A detailed histological of several species would be most helpful.

Genus ***Proboscidactyla*** Brandt, 1835

Synonyms: *Willsia* Forbes, 1846 [type species *Willsia stellata* Forbes, 1846 by monotypy]. – *Lar* Gosse, 1857. – *Willia* Agassiz, 1862 [invalid emendation]. – *Dyscannota* Haeckel,

1879 [type species *Dyscannota dysdipleura* Haeckel = *P. ornata*]. – *Dicranocanna* Haeckel, 1879 [type species *Dicranocanna furcillata* Haeckel, 1879 = ? *P. ornata*]. – *Willeta* Haeckel, 1879. – *Misakia* Uchida, 1927 [type species *Misakia typica* Uchida, 1927, synonym of *Proboscidactyla ornata*]. – *Psythia* Agassiz & Mayer, 1902 [type species *Psythia prolifera* Agassiz & Mayer, 1902].

TYPE SPECIES: *Proboscidactyla flavicirrata* Brandt, 1835.

DIAGNOSIS: As for family.

KEY TO THE GENERA OF THE *PROBOSCIDACTYLA* SPECIES OF THE ERMS ZONE:

1a medusa with 4 primary radial canals, occurring in Mediterranean . . . *P. ornata*
1b medusa with 6 primary radial canals, occurring in northern Atlantic . *P. stellata*

Proboscidactyla ornata (McCrady, 1859) Figs 9-10

Willsia ornata McCrady, 1859: 149, pl. 9 figs 9-11.
Willia ornata. – Agassiz, 1865: 171, figs 274a-279. – Fewkes, 1882b: 299, pl. 1 figs 22-24.
Dyscannota dysdipleura Haeckel, 1879: 152.
? *Dicrocanna furcillata* Haeckel, 1879: 156.
Willetta ornata. – Haeckel, 1879: 157.
Willia gemmifera Fewkes, 1882b: 300, pl. 1 fig. 24.
Proboscidactyla ornata. – Browne, 1905: 726. – Mayer, 1910: 189, fig. 100, pl. 20 figs 1-10. – Neppi & Stiasny, 1913: 35, pl. 2 fig. 24, pl. 3 fig. 25. – Hartlaub, 1917: 368, figs 316-323. – Menon, 1932: 12, pl. 2 fig 18. – Kramp, 1957: 13, pl. 3 fig. 7. – Kramp, 1961: 235, synonymy. – Kramp, 1962: 342, figs 7-10, synonymy. – Kramp, 1959: 178, fig. 255. – Kramp, 1965: 103. – Kramp, 1968: 108, fig. 290. – Calder, 1970: 130, fig. 1. – Calder, 1971: 44, pl. 3 fig. A, pl. 7 Fig. A. – Brinckmann & Vannucci, 1965: 357, figs 2-6. – Bouillon *et al.*, 2004: 74, fig. 43C-D. – Goy, 1973: 997.
Proboscidactyla tropica Browne, 1905: 727.
Proboscidactyla gemmifera. – Browne, 1905: 727.
Proboscidactyla varians Browne, 1905: 728, pl. 54 figs 1-2.
Proboscidactyla flavicirrata var. *stolonifera* Maas, 1905b: 21, pl. 4 figs 24-28.
Proboscidactyla ornata var. *stolonifera*. – Bigelow, 1909a: 220, pl. 6 figs. 1-2; pl. 41 figs. 1-7. – Mayer, 1910: 191, fig. 101.
Proboscidactyla ornata var. *gemmifera*. – Mayer, 1910: 192, fig. 101a, pl. 21, figs 1-3.
Misakia typica Uchida, 1927: 237, fig. 15.
? *Proboscidactyla conica* Menon, 1932: 13, pl. 2 fig. 18.
Proboscidactyla mutabilis. – Nair, 1951: 57. [not *Proboscidactyla mutabilis* Browne]
? *Proboscidactyla ornata*. – Goy *et al.*, 1991: 118, fig. 46.

TYPE MATERIAL: Based on a single medusa, not located.

MATERIAL EXAMINED: MHNG INVE 54619; Indonesia, Moluccas, Ambon; as *Proboscidactyla flavicirrata* var. *stolonifera*, material of Maas (1906), one medusa, umbrella shrunken.

DIAGNOSIS: *Proboscidactyla* medusa with square- to cross-shaped stomach base, without distinct gastric lobes, 4 primary radial canals, branching 1-2 times, 12-16 tentacles, medusa-buds may arise from corners of stomach or radial canals. Medusa buds on polyps with 4 tentacle bulbs.

DESCRIPTION (Mayer, 1910; Brinckmann & Vannucci, 1965; Calder, 1970): Hydroid colonial, arising from creeping, apparently naked stolons, polyps usually confined to end of polychaete tube, polyps polymorphic with gastrozooids and gonozooids (blastostyles). Gastrozooids in a single circle around the rim of the worm tube, almost sessile, body near base somewhat constricted and thus forming an indistinct

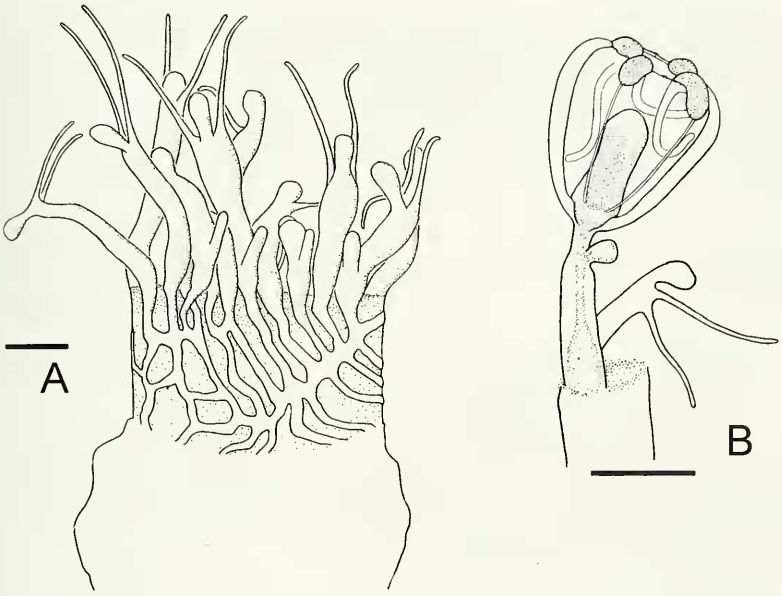

FIG. 9

Proboscidactyla ornata (McCrady, 1859); from Brinckmann & Vannucci (1965). (A) Hydroid on rim of polychaete tube, some incipient gonozooids (blastostyles) at bases of gastrozooids are visible; scale bar 0.5 mm. (B) Gonozooid with advanced medusa bud, at rear a gastrozooid; scale bar 0.25 mm.

pedicel, oral end enlarged to form a head-like proboscis separated from the rest of body by a constriction (neck). Two smooth tentacles arise close together from base of neck, tentacles arise on side facing the opening of the polychaete tube and give the hydranths a bilateral symmetry. Apex of proboscis with a cap-like nematocyst cluster containing white pigment granules.

Gonozooids usually smaller than gastrozooids (max 3/4), arising near base of gastrozooid on the side opposite the tentacles, body thin and tentacle-like, terminating in a small, spherical nematocyst cluster, without mouth. Gonozooids of more advanced stages can also be isolated from gastrozooid, occasionally several mm down the worm tube, but remaining in contact with the rest of the colony via the hydrorhiza. Gonozooids with up to four medusa buds in a single whorl located in upper half of polyp, buds in more advanced stages with four large tentacle bulbs. Nematocysts: desmonemes, microbasic euryteles of two size classes, and large macrobasic euryteles with indistinct swelling of shaft and thus difficult to distinguish from mastigophores.

Newly liberated medusa bell-shaped, with umbilical canal, stomach cylindrical and about half the length of the subumbrellar cavity, lips simple, four unbranched radial canals, no gonads present. Alternating with the tentacles are small clusters of nematocysts, evenly spaced on the exumbrella just above the margin. Nematocysts: macrobasic euryteles and desmonemes with unusually long threads in many loops, discharged with up to 15 loops.

Mature medusa bell-shaped, slightly higher than wide; jelly thick, rigid, shallow gastric peduncle can be present, near rim of exumbrella up to 16 small nematocysts clusters, one in-between each tentacle-pair, connected to rim of umbrella by meridional line on exumbrella. Manubrium flask-shaped, height 1/2 to 1/1 of subumbrellar height, base square- to cross-shaped, four perradial recurved lips, mouth margin with some crenulations. Gonads on sides of stomach, may extend onto radial canals, surface smooth.

Four primary radial canals, narrow, branching up to two times in well spaced branching points so that normally 16 canals reach the bell margin, rarely up to 20 canals, some populations with only up to 12 canals. No ring canal, but instead a solid strand of gastrodermal cells.

Usually as many tentacles as radial canals (around 16, range when mature 4-20), with relatively large marginal bulbs containing a brownish pigment.

Some populations have medusae that form stolon-like blastostyles bearing medusa buds, these blastostyles may arise from the corners of the stomach (= *gemmifera* form) or the branching points of the radial canals (= *tropica* form). Colours of Eastern Atlantic form: gastrodermis ochre-yellow or greenish-yellow, bulbs brown. Nematocysts: not described, but likely as in young medusa.

Dimensions: Gastrozooids in nature 0.35-1.3 mm high, tentacles up to 1.5 mm long (Brinckmann & Vannucci, 1965; Calder, 1970). In culture, the polyps get larger (up to 1.8 mm, Brinckmann & Vannucci, 1965). The gonozooids are smaller (max. 3/4 of gastrozooids). Polyp nematocysts (Mediterranean form, Brinckmann & Vannucci, 1965): small microbasic euryteles (5-6)x(2-2.5)μm; large microbasic euryteles (7.5-9.5)x(2.5-3.5)μm; macrobasic euryteles (16-19)x(9-12.5)μm. For data of a Western Atlantic population see Calder (1970).

The newly liberated medusa is about 1 mm in height and 0.8 mm wide (Brinckmann & Vannucci, 1965). The mature medusa can reach bell diameters of up to 5 mm (Kramp, 1968), but in the Mediterranean they remain much smaller (about 1 mm, Goy, 1973; Goy *et al.*, 1991; 3.4 mm Neppi & Stiasny, 1913) and they reach rarely or never the 16 tentacle stage. They can even have mature gonads at the four-tentacle stage. For nematocyst dimensions see Brinckmann & Vannucci, (1965) and Calder (1970).

Biology: The polyps occur exclusively on the tubes of sabellid polychaetes. Calder (1970; east coast of the USA) found it on *Sabella microphthalma* Verrill living in somewhat brackish waters (salinities from 18ppt to 23ppt). In the Mediterranean, Brinckmann & Vannucci (1965) found it on the tubes of *Branchiomma vesiculosum* (Montagu) and other sabellids. In the Bay of Naples, the polyps are locally quite abundant (in depths of about 100 m), but the medusa is very rare (Brinckmann & Vannucci, 1965). It is also rare in other regions of the Mediterranean (Mediterranean (Neppi & Stiasny, 1913; Goy, 1973; Goy *et al.*, 1991). The liberated medusa develops gonads rather rapidly (after 2-6) days and is fully grown within 3-4 weeks (Brinckmann & Vannucci, 1965; Calder, 1970).

The medusa seems not to tolerate temperatures below 17-18°C (Brinckmann & Vannucci, 1965). It can be found close to the surface (Kramp, 1965).

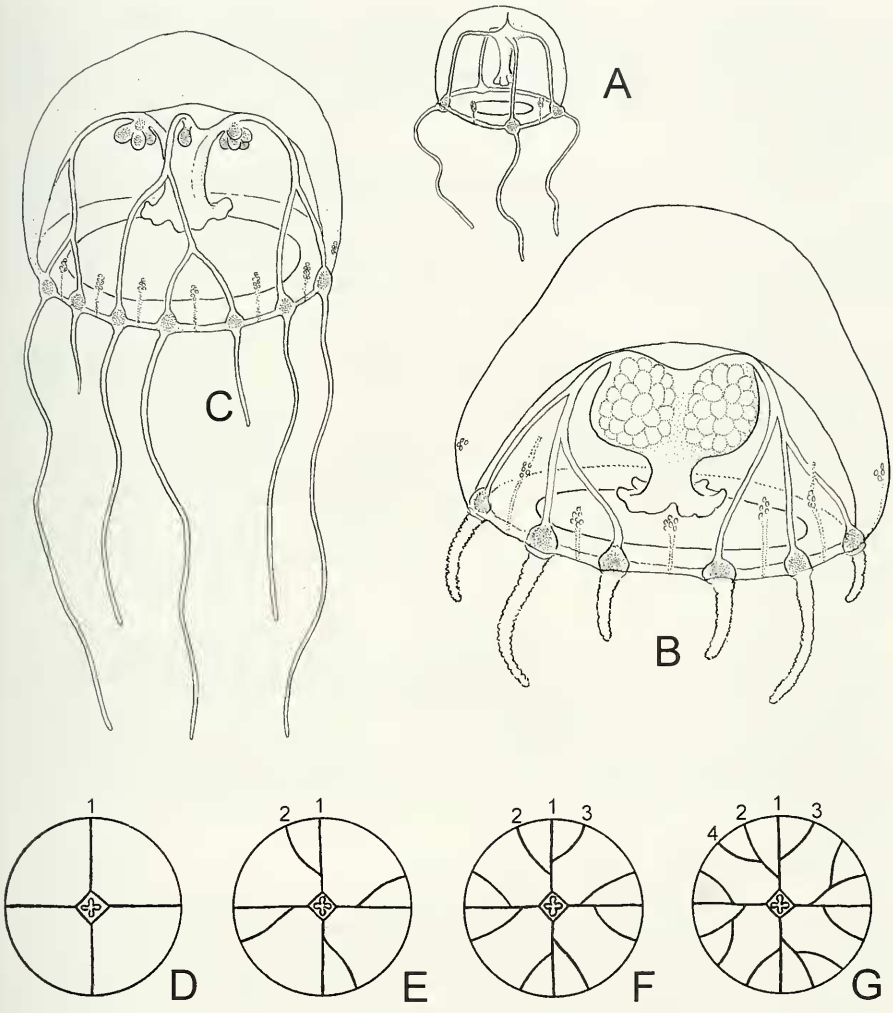

FIG. 10

Proboscidactyla ornata (McCrady, 1859); modified after Mayer (1910), see text for dimensions. (A) Young medusa. (B) Mature female medusa. (C) Immature medusa with medusa buds on the corners of the stomach. (D-G) Sequence of the branching of the radial canals.

Uchida & Sugiura (1975) examined the medusa budding. Kawamura & Kubota (2008) investigated the influence of temperature and salinity on the asexual budding of the medusa.

Many biological observations made by Hand & Hendrickson (1950) on a Californian *Proboscidactyla* species are certainly also valid for *P. ornata* (see also Hand, 1954).

DISTRIBUTION: The medusa has a circumglobal distribution in warm and coastal waters (Kramp, 1965). In Europe it occurs only in the Mediterranean (Bouillon *et al.*, 2004). The polyp stage is known from the Chesapeake Bay, USA (Calder, 1970) and the Mediterranean (Brinckmann & Vannucci, 1965). Type locality: Charleston Harbor, South Carolina, USA.

REMARKS: The life cycle of this species has been observed by Brinckmann & Vannucci (1965) for Mediterranean animals and by Calder (1970) for hydroids from Virginia, USA. Calder tabulates also differences between the two populations, mainly concerning the size of the nematocyst capsules. He interpreted the small differences as due to intraspecific variation and different culture conditions.

The medusae of *P. ornata* are quite variable and a number of species and subspecies have been proposed, mainly based on the presence and position of vegetative medusa buds. Kramp (1957; 1965) found good evidence that all these variants likely belong to the same species. Kramp (1962) also found a single medusa in Vietnam with a polyp growing out of the manubrium. This polyp had a dome-shaped hypostome surrounded by a whorl of 18 tentacles, thus is very much unlike all other *Proboscidactyla* polyps known so far. The hydroids of the Pacific *P. ornata* have never been observed and it remains to be shown that they are identical to the Atlantic and Mediterranean ones. It could well be that our current concept of *P. ornata* nevertheless comprises several species.

The Mediterranean *P. ornata* medusae are relatively small and develop fewer tentacles and radial canals (max. 12). Gonads can even be present at the four tentacle stage and with unbranched radial canals (Neppi & Stiasny, 1913; Goy, 1973). The medusa from Lebanese waters described by Goy *et al.* (1991) also had these characteristics, in addition to medusa buds on the manubrium. This location of the medusa buds has so far never been observed in other populations.

Proboscidactyla stellata (Forbes, 1846) Figs 11-12

Willsia stellata Forbes, 1846: 268. – Mayer, 1910: 193.
Lar sabellarum Gosse, 1857: 113, pl. 20. – Hincks, 1868: 36, fig. 2. – Hincks, 1872: 313, pl. 19. – Browne, 1896: 468, pl. 16 figs 3-4, synonym. – Browne, 1897: 818, figs 1-9.
Willia stellata. – L. Agassiz, 1862: 346. [incorrect subsequent spelling]
Willia stellata. – Browne, 1905: 725, 729. – Hartlaub, 1917: 374, figs 324-328. – Ranson, 1937: 323, fig. 1. – Russell, 1938b: 154, fig. 45. – Kramp, 1939: 503, figs 1-5.
Willisa cornubica Peach, 1867: 355, pl. 1 figs 1-2. – Russell, 1953: 393, synonym.
Willia furcata Haeckel, 1879: 158. – Russell, 1953: 393, synonym.
? *Proboscidactyla brooksi* Mayer, 1910: 194, fig. 101C-F. – Russell 1953: 393, ? synonym.
Proboscidactyla stellata. – Russell, 1953: 386, figs 250-256, pl. 23 figs 3-4. – Hand, 1954: 64. – Kramp, 1959: 178, fig. 256. – Kramp, 1961: 236, bibliography. – Pagès *et al*,. 1992: 37, fig. 41. – Galea, 2007: 29, pl. 1 fig. J. – Buecher *et al.*, 2005: 44.

TYPE MATERIAL: Not located, likely lost.

MATERIAL EXAMINED: France, Roscoff; living medusae, used for DNA extraction; 2 April 1998; plankton in 10 m depth; 16S sequence accession number **AM183138**. – BMNH 1962.11.7.34, polyps with medusae buds; Norway, Bergen, Espegrend; 30 m depth; collected 09.08.1962; on *Pseudopotamilla reniformis* (curled tube). – BMNH 1985.9.1.13 polyps with medusae buds; Great Britain, Plymouth; collected 28.06.1937; leg. & det. W. J. Rees.

DIAGNOSIS: *Proboscidactyla* medusa with star-shaped stomach with 6 lobes and 6 primary radial canals, 24 tentacles. Medusa buds on polyps have 6 tentacle bulbs.

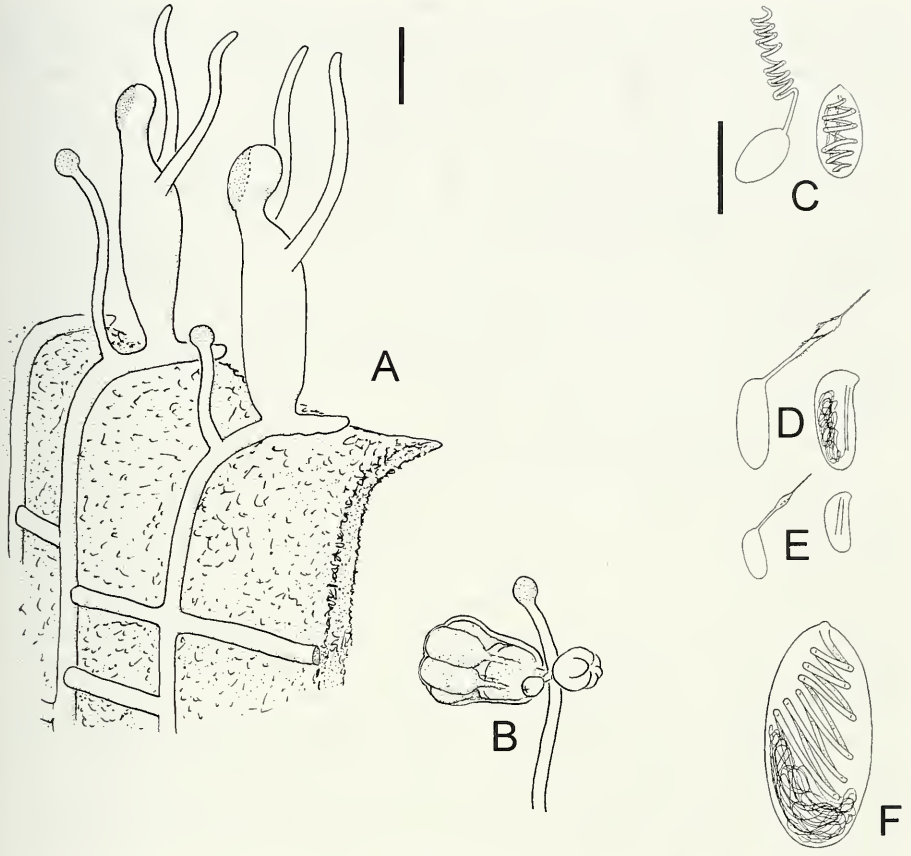

FIG. 11

Proboscidactyla stellata (Forbes, 1846); A-B, after preserved material from Norway, C-F modified after Russell (1938b). (A) Gastrozooids and gonozooids without medusa buds on the rim of a polychaete tube. Note that the tentacles are directed towards the opening of the tube, while the nematocyst clusters on the heads are directed in the opposite direction, scale bar 0.2 mm. (B) Gonozooid with medusa buds of different developmental stages. (C) Discharged and intact desmoneme, scale bar 10 μm. (D) Discharged and intact large microbasic eurytele, same scale as C. (E) Discharged and intact small microbasic eurytele, same scale as C. (F) Intact macrobasic heteroneme, same scale as C.

DESCRIPTION (Russell, 1938b, 1953; own observations): Hydroid colonial, arising from creeping, apparently naked stolons, covering region near rim of polychaete tube, stolons net-like, more or less parallel to worm tube and with connections at right angles. Polyps usually confined to end of polychaete tube, polyps polymorphic with gastrozooids and gonozooids (blastostyles), gonozooids without medusa buds often present, can be interpreted as dactylozooids.

Gastrozooids in a single circle around the rim of the worm tube, almost sessile, body near base somewhat constricted and thus forming an indistinct pedicel, oral end enlarged to form a head-like proboscis separated from the rest of body by a constric-

tion (neck). Two smooth tentacles arise close together from base of neck, tentacles arise on side facing the opening of the polychaete tube. Proboscis with a cap-like nematocyst cluster on side opposite to the tentacles. The nematocyst cluster and the two tentacles give the hydranths a bilateral symmetry.

Gonozooids usually smaller than gastrozooids (1/2), arising on stolons close to gastrozooid on the side opposite the tentacles, body thin and tentacle-like, terminating in a small, spherical nematocyst cluster, without mouth. Medusa buds in upper part of gonozooids, up to four in one whorl, buds not covered by membrane, buds in more advanced stages with six large tentacle anlagen (bulbs). Some gonozooid-like polyps without medusa buds can be present and may act as defensive dactylozooids.

Nematocysts of polyp stage: large macrobasic heteronemes (mastigophores or euryteles with faint swelling of shaft end), present only on proboscis; microbasic euryteles of two size classes; desmonemes with unusually long threads in many coils, discharged with up to seven coils.

Newly liberated medusa bell-shaped, with umbilical canal, velum broad, stomach cylindrical and about half the length of the subumbrellar cavity, attached to a very short gastric peduncle, gonads not yet developed, base with six short prolongations or lobes from which six primary radial canals start, radial canals unbranched. Six marginal tentacles, equal in size, on margin of umbrella, one opposite termination of each radial canal. Base of each marginal tentacle large and conspicuous, containing dark brown or blackish pigment. Alternating with marginal tentacles are small clusters of nematocysts, evenly spaced on exumbrella just above bell-rim. During the ensuing growth of the medusa the radial canals branch three times.

Umbrella of mature medusa dome-shaped, slightly wider than high; jelly thick. Velum narrow. On exumbrella near rim small pads of nematocysts, usually one per tentacle and one in-between each tentacle-pair (around 24 in total), the two series at different levels, usually a number of pads lost, all connected to margin of bell by a thin, meridional line of thickened epidermis.

Stomach short, six-sided, with six basal lobes prolonged for a short distance over the subumbrellar surface resulting in star-shaped base. Mouth with six folded lips. Very short gastric peduncle. Gonads situated at base of stomach wall and continued along the six lobes of stomach.

Six primary radial canals, each giving rise to three additional branches making twenty-four in all; all branching subject to considerable variation. Radial canals narrow. No ring canal, but instead solid strand of gastrodermis.

Twenty-four rather short marginal tentacles, each situated at end of a radial canal branch, filiform, hollow, with adaxial basal nematocyst cushion.

Colour of tentacle bases yellowish brown, dark purple-brown or black; colour of stomach and gonads yellow or reddish yellow. Nematocysts: not described.

VARIATION: Rarely only four primary canals are present. The population of Japan shows more variability (Uchida, 1927).

DIMENSIONS: Medusa when full grown 8 mm high and 9 mm wide. Newly liberated medusa about 1 mm high. Gastrozooids 0.6-2.5 mm high. Nematocysts of polyp stage (Russell, 1938b): large macrobasic heteronemes (24-33)x(9-13)μm; euryteles (9-13)x(4-5)μm, and (6.5-7)x(2.5-3)μm; desmonemes 10x5μm.

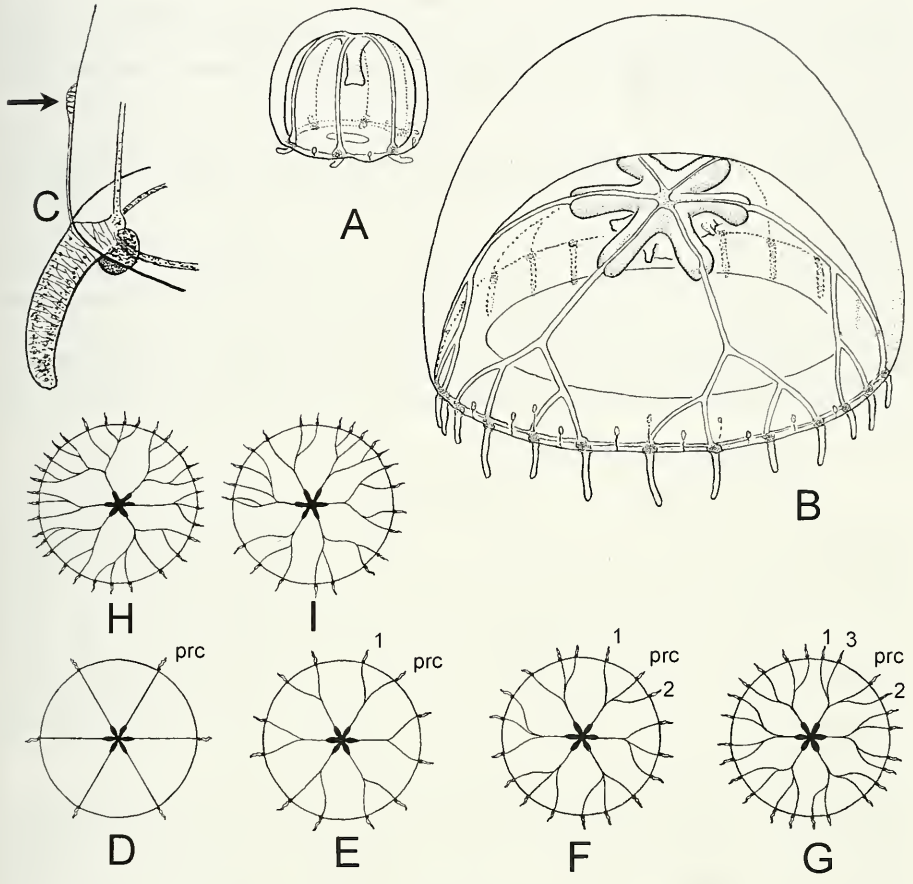

FIG. 12

Proboscidactyla stellata (Forbes, 1846); A-C, modified after Russell (1953); D-I, modified after Browne (1897). (A) Newly liberated medusa, bell height approx. 1 mm. (B) Mature medusa, bell diameter 4.2 mm. (C) Rim of medusa in side view showing tentacle and exumbrellar nematocyst clusters (arrow). (D-G) Development of the tentacles and the branching of the radial canals, prc = primary radial canal, 1 = first side-branch, 2 = second side branch, etc. (H-I) Irregular canal branching.

BIOLOGY: The life cycle of this species was elucidated by Browne (1896). The hydroid occurs exclusively on the tubes of sedentary polychaetes like *Megalomma vesiculosum* (Montagu), *Potamilla torelli* (Malmgren), *Pseudopotamilla reniformis* (Müller), or *Sabellaria* spec. The known depth range is from subtidal to about 50 m. (Gosse, 1857; Hincks, 1872; Russell, 1957; own data).

In the British Isles, the medusa may be found in any month of the year (Russell, 1953; Ballard & Myers, 2000). It occurs in the upper water layers.

DISTRIBUTION: In Europe from the northern part of the Bay of Biscay over the British Isles to Norway (Hartlaub, 1917; Rees, 1952; Russell, 1953; Russell, 1957;

Kramp, 1959; Teissier, 1965; Fraser, 1974; Ballard & Myers, 2000). The medusa has also been reported from Japan (Uchida, 1927), South Africa (Pagès *et al.*, 1992; Buecher *et al.*, 2005), and the Fjords of Chile (Galea, 2007). Perhaps also present along the Atlantic coast of the USA (Kramp, 1961, as *P. brooksi*). Type locality: Bay of Oban, Scotland.

Remarks: Russell (1938b) identified the large heteronemes of the polyp as mastigophores, although he depicted one shaft that is clearly a eurytele. Hand & Hendrickson (1950) concluded that there are likely only euryteles in *P. stellata* and that Russell's mastigophores were a fixation artefact. In other *Proboscidactyla* hydroids the large heteronemes are of the eurytele type (Hand & Hendrickson, 1950; Brinckmann & Vannucci, 1965). Some heteronemes of hydrozoans can have a faint, variable swelling of the shaft and cannot be classified unambiguously as mastigophores or euryteles. Similar observations were made by Brinckmann & Vannucci (1965).

Family Magapiidae Schuchert & Bouillon, 2009

Diagnosis (modified after Bouillon *et al.*, 2006): Medusa umbrella almost hemispherical, margin lobed through furrows for tentacles; four radial canals; four tentacles with nematocysts concentrated terminally; no typical circular canal but a solid strand of gastrodermis; tentacles solid, issuing on exumbrellar surface above bell margin; alternating with tentacles there may be narrow exumbrellar nematocyst bands or triangular ciliated fields; manubrium simple, tubular or with cruciform base, mouth opening quadrangular to circular, no lips; gonads in four masses on the manubrium or on interradial pockets of the manubrium; no sense organs; cnidome: macrobasic mastigophores or macrobasic euryteles. Hydroid stage unknown.

Remarks: This family was previously known as Laingiidae. Because the genus name *Laingia* is preoccupied, Schuchert & Bouillon (2009) introduced the replacement names *Magapia* and Magapiidae. The family Magapiidae is here placed in the order Anthoathecata and not in a subclass Laingiomedusae of its own as suggested by Bouillon (1978b). The medusae of the Magapiidae have a lobed umbrella margin and tentacles originating more or less on the exumbrellar side of the bell. They thus exhibit some characters otherwise found in the Narcomedusae. However, a similar situation is also found in *Thecocodium quadratum* (Anthoathecata, family Ptilocodiidae; see Jarms, 1987). In any case, with their gonads on the manubrium and the fully developed radial canals they match more typically anthomedusae rather than Narcomedusae and they are thus here classified as Anthoathecata Filifera. Molecular analyses (Collins *et al.*, 2006; Cartwright *et al.*, 2008) have shown that *Fabienna*, a genus placed in Laingiomedusae by Bouillon & Barnett (1999), does not belong to the Trachylinae and is closely related to some *Proboscidactyla* species. Admittedly, a final decision on the status of the Laingiomedusae can only be made once the position of its name-giving species, *Laingia jaumotti* Bouillon, 1978b, has been determined by a molecular phylogenetic analysis.

KEY TO THE LAINGIIDAE GENERA:

1a with exumbrellar nematocyst bands . . . . . *Kantiella*
1b without exumbrellar nematocyst clusters 2
2a bell margin with interradial ciliated fields; marginal bulbs only slightly displaced from bell rim . . . . . *Fabienna*
2b no ciliated fields, tentacles shifted high up to exumbrella . . . . . [*Magapia*]*

* not in ERMS zone

Genus ***Kantiella*** Bouillon, 1978

TYPE SPECIES: *Kantiella enigmatica* Bouillon, 1978.

DIAGNOSIS: Magapiidae medusa with radial exumbrellar nematocyst bands; gonads on four interradial pouches of manubrium; four short marginal tentacles with terminal cluster of nematocysts, tentacle bulbs not on bell margin but on exumbellar side at some distance from margin.

REMARKS: The genus is currently monotypic.

Kantiella enigmatica Bouillon, 1978a Fig. 13

Kantiella enigmatica Bouillon, 1978a: 158, fig. 13-14. – Bouillon, 1978b: 477, fig. 2, pl. 1. figs 1-3. – Goy *et al.*, 1991: 116, fig. 43.

HOLOTYOPE: In IRSN (Bouillon *et al.*, 1995), not seen.

MATERIAL EXAMINED: IRSN, Papua New Guinea, Laing Island; 20 medusae collected July 1978 by J. Bouillon.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION: Medusa umbrella hemispherical, mesogloea thick at apex (ca. 1/3 of total height), margin lobed through deep perradial embayments where tentacles originate, 4-8 short radial exumbrellar nematocyst bands originating from margin; short and broad gastric peduncle present.

Manubrium quadrangular, reaching almost to level of velum, mouth margin quadrate or circular, without marked lips, mouth rim with nematocysts. With or without medusa buds at apex of radial canals. Gonads covering interradial sides of manubrium, bulging, separated perradially by cleft.

Four simple radial canals, instead of circular canal a solid strand of gastrodermis.

Four short, solid tentacles, bulbs large, placed on exumbrellar side at some distance from margin, with short radial connection to circular strand, mesogloea of bell reduced below tentacles; nematocysts of tentacles confined to tip, initially in a terminal and an adaxial subterminal cluster, later both clusters fused. Nematocysts: ovoid holotrichous macrobasic mastigophores, on mouth rim, tentacle tips, tentacle bulbs, and exumbrellar bands.

Polyp stage unknown.

DIMENSIONS: Umbrella 3-4 mm wide, 2-3 mm high (Bouillon *et al.*, 2004). Macrobasic mastigophores (11-23)x(7-18) μm (Bouillon, 1978b).

BIOLOGY: A coastal species occurring in shallow depths.

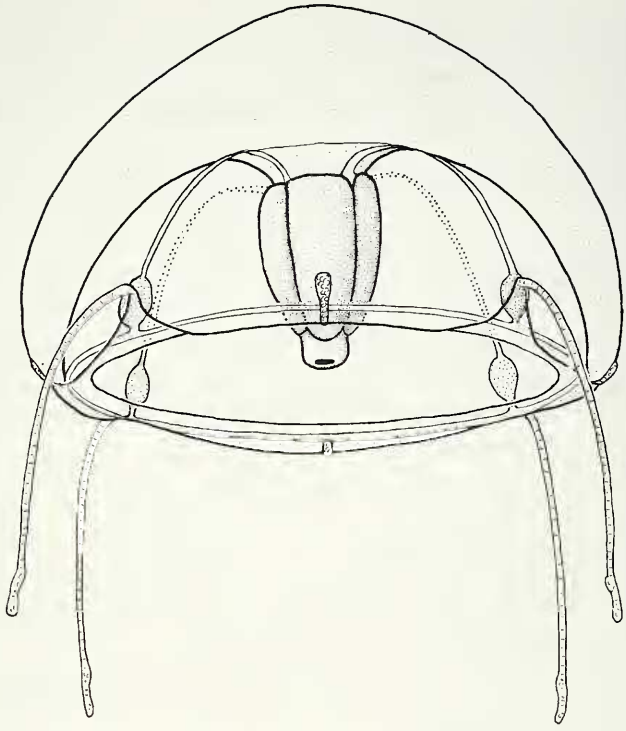

FIG. 13

Kantiella enigmatica Bouillon, 1978a; after preserved material from Papua New Guinea, bell diameter 4 mm.

DISTRIBUTION: Seychelles (Bouillon, 1978a), Papua New Guinea (Bouillon, 1978b), South Africa (Pages *et al.*, 1992), eastern Mediterranean (Goy *et al.*, 1991), Taiwan Strait (Xu & Huang, 2004). Type locality: Seychelles.

REMARKS: This species does not occur along the European coasts, but it has been found in the eastern Mediterranean (Lebanon; Goy *et al.*, 1991), thus within the ERMS zone.

Genus ***Fabienna*** Schuchert, 1996

TYPE SPECIES: *Fabienna sphaerica* Schuchert, 1996 by original designation.

DIAGNOSIS: Medusae with slightly lobed umbrella margin, four perradial tentacles that have their origin slightly displaced away from the bell margin, without exumbrellar nematocyst bands but instead interradial ciliary fields near umbrella margin. Manubrium with cruciform base, mouth simple. Nematocysts of tentacles concentrated in tip in one terminal cluster immediately followed proximally by a second adaxial cluster, the two clusters usually fused in older animals. Radial canal replaced by solid strand of gastrodermis. Cnidome includes macrobasic euryteles, no desmonemes. Gonads four large, interradial pads on manubrium.

REMARKS: The genus *Fabienna* shares with *Kantiella* the peculiar structure of the tentacles and to some degree also the cnidome (macrobasic heteronemes, absence of desmonemes). Species of both genera also show a strong overall similarity. The tentacle structure is likely a synapomorphy and the inclusion of *Fabienna* in the family Magapiidae by Bouillon & Barnett (1999, as *Laingiidae*) is therefore correct. Only one *Fabienna* species occurs in the ERMS zone.

Fabienna oligonema (Kramp, 1955)

Pochella oligonema Kramp, 1955: 270, fig. 7, pl. 2, fig. 2. – Kramp, 1959: 179, fig. 259. – Kramp, 1961: 233. – Goy *et al.*, 1991:118. – Daly Yahia *et al.*, 2003: 650.
Fabienna oligonema. – Schuchert, 1996: 87. – Bouillon *et al.*, 2004: 115, fig. 60A.

MATERIAL OF *F. OLIGONEMA* EXAMINED: ZMUC, syntypes; Accra, Goldcoast, Atlantide station 77; 3 specimens examined for Schuchert (1996). The type material is lost as it dried out after it was returned to Copenhagen (observation made in 2005).

MATERIAL OF *F. SPHAERICA* FOR COMPARISON: MHNG INVE 33453; few medusae collected in surface plankton near Narrow Neck Beach, Devonport, New Zealand; 31 June to 2 July 2002; DNA sample taken from one specimen, 16S sequence GenBank accession number **AM183133**, 18S **AY920767**, 28S **AY920797**.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION (Kramp, 1955; own data): Umbrella spherical to dome-shaped, jelly thick, especially at apex (about 1/3 of total height), with broad and shallow gastric peduncle (1/4 of manubrium height), margin somewhat lobed through shallow perradial embayments where tentacles originate; exumbrella with scattered nematocysts, some interradial ciliated fields may be present near bell margin. Velum narrow.

Manubrium pyramidal, base cruciform, mouth simple, opening cruciform to quadrangular, perradial corners of mouth with nematocysts. Gonads four large, bulging, interradial pads covering large part of manubrium, shape ovoid, the four gonads separated perradially.

Four simple radial canals, ending in relatively large gastrodermal bulbs, bulbs somewhat displaced away from umbrella margin towards exumbrella, sometimes even with a short canal linking them to circular canal (strand?).

Tentacles about as long as bell height, bases adnate to umbrellar margin, solid, single row of gastrodermal cells, tentacle tips sometimes hook-shaped, nematocysts of tentacles concentrated in tip, in younger animals in one terminal and one adaxial, subterminal cluster, later both clusters fused, some additional nematocysts distributed along rest of tentacle. Nematocysts: unknown. Hydroid: unknown.

DIMENSIONS: Umbrella 2 mm high and wide.

DISTRIBUTION: Occurs in shallow depths.

DISTRIBUTION: A very rare species, known from waters off Lebanon and Algeria (Goy *et al.*, 1991; Daly Yahia *et al.*, 2003) and the Gulf of Guinea (western Africa, Kramp, 1955). Type locality: Accra, Ghana.

REMARKS: *Fabienna oligonema* is a very rare medusa, only a few specimens have been reported so far. It does not occur along the European coasts, but it has been found in the ERMS zone. Its currently known distribution suggests that it could also

occur in southern Spain, Italy, or Greece. It is well possible that it has been confounded repeatedly with *Hydractinia exigua* (see Schuchert, 2008a). This is easily possible for specimens that have lost their tentacles, as it is often the case for plankton-net samples.

This species was originally attributed to the genus *Pochella* Hartlaub, 1917. After the life cycle of the hydroid *Trichydra pudica* Wright, 1858 had been revealed (Rees, 1941; Edwards, 1973), it became evident that *Pochella polynema* Hartlaub, 1917 is the medusa stage of *Trichydra pudica*. Because *Pochella polynema* is also the type species of the genus, *Pochella* thus became a synonym of *Trichydra* Wright, 1858. Based only on its superficial similarity and pending more information on its life cycle, *P. oligonema* was provisionally also transferred to *Trichydra* by Edwards (1973a). Schuchert (1996) then regarded *Pochella oligonema* Kramp, 1955 as sufficiently distinct from *Trichydra* to be placed in a genus of its own, namely *Fabienna*.

The genus *Fabienna* comprises currently only two species, *F. sphaerica* Schuchert, 1996 and *F. oligonema*. Both are very similar and with the current state of knowledge hardly distinguishable. Schuchert (1996) lists the following differences: *F. oligonema* has a gastric peduncle, the tentacle bulbs get narrower towards the circular strand and are more displaced towards the exumbrella than in *F. sphaerica*, the gonads are more oval in shape compared to triangular in *F. sphaerica*. Unfortunately, a thorough comparison of the species was hampered by the suboptimal preservation of the syntypes of *F. oligonema*. It seems however that in one of the syntypes there were ciliated fields as in *F. sphaerica*. It was not possible to examine the nematocysts, nor could it be seen if the circular canal is solid or hollow.

Since my first description of *F. sphaerica* in 1996, I have seen more specimens, notably also fully mature living medusae (Fig. 14). The new observations make distinction of the two species even more difficult as fully grown *F. sphaerica* can also have a shallow gastric-peduncle as in *F. oligonema* (the gastric-peduncle of *F. oligonema* in the type specimens is much smaller than given in the figure of Kramp (1955).

Although *F. oligonema* and *F. sphaerica* could be conspecific, it seems better to retain both names for the time being, if only for biogeographic reasons. We do not know the polyp stage of both species (the youngest stages of *F. sphaerica* had an apical funnel and umbilical canal, thus were very likely budded from a polyp stage) and the cnidome of *F. oligonema* remains unknown. There is thus potential to find more and better defined differences. Evidently, we need a more detailed re-description of *F. oligonema* based on living animals.

Family Ptilocodiidae Coward, 1909

Diagnosis: Polyps arising from reticular stolons or encrusting hydrorhiza without apparent perisarc. Polyps stolonal, naked, polymorphic; gastrozooid without tentacles; dactylozooids with four or more capitate tentacles, sometimes filiform tentacles. Gonophores on gonozooids or gastro-gonozooids; developing into fixed sporosacs, eumedusoids, or free medusae.

Mature medusa with more or less bell-shaped umbrella, with or without radial exumbrellar furrows, with marginal nematocyst ring from which usually arise several centripetal nematocyst bands or exumbrellar rows of refringent spots. With four marginal tentacles or tentacles absent. Manubrium with perradial nematocyst clusters,

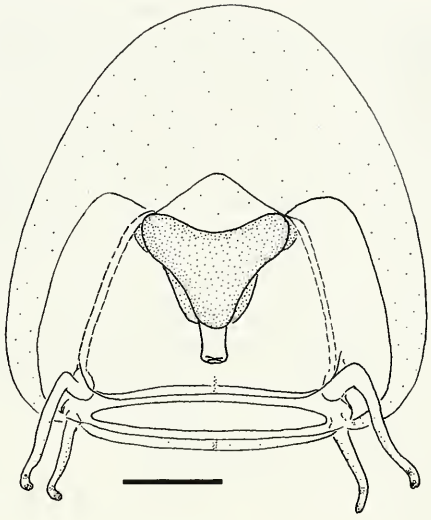

FIG. 14
Fabienna sphaerica Schuchert, 1996; drawn after a living, mature male medusa from New Zealand; scale bar 0.5 mm.

clusters may be on oral arms; gonads four interradial or eight adradial masses on manubrium; no ocelli.

REMARKS: For a recent revision of the family see Bouillon *et al.* (1997) or Bouillon *et al.* (2006).

KEY TO THE PTILOCODIDAE HYDROIDS:

1a	dactylozooids of two types	[*Hydrichthella*]*
1b	dactylozooids of one type	2
2a	hydrorhiza crust-like, not covered by visible perisarc	[*Ptilocodium*]*
2b	hydrorhiza a network of perisarc-protected tube-like stolons	*Thecocodium*

KEY TO THE PTILOCODIDAE MEDUSAE:

1a	no marginal tentacles	*Tregoubovia*
1b	with marginal tentacles	2
2a	four interradial gonads	*Thecocodium*
2b	eight adradial gonads	[*Hansiella*]*

* not represented in ERMS zone

Genus ***Thecocodium*** Bouillon, 1967

TYPE SPECIES: *Thecocodium brieni* Bouillon, 1967 by monotypy.

DIAGNOSIS: Hydroid with reticulate, tubular hydrorhiza, covered by perisarc. Polyps on stolons, sessile, naked, polymorphic, usually with gastro-gonozooids and dactylozooids. Gastro-gonozooids cylindrical or club-shaped, without tentacles, hypo-

stome with nematocysts. Dactylozooids thin, solid gastrodermis, terminal group of capitate tentacles. Gonophores fixed sporosacs or free medusae developing in a single whorl on gonozooids. Cnidome of polyp includes desmonemes.

Medusa with lobed bell margin, with marginal nematocyst ring from which usually arise several centripetal nematocyst bands or exumbrellar rows of refringent spots. Four radial canals and hollow circular canal, short mesenteries. Four marginal tentacles with bases embedded in umbrellar furrows, no ocelli. Manubrium with short, perradial mouth arms ending in nematocyst clusters; gonads interradial on manubrium.

Remarks: For descriptions of fully developed *Thecocodium* medusa see Jarms (1987) and Kubota (1993). The ring circular canal of the medusa of *Thecocodium quadratum* is hollow (own unpublished observations on young medusae), unlike the Proboscidactylidae which have reportedly a solid circular strand.

Key to the *Thecocodium* species of the ERMS zone:

1a dactylozooids with up to 5 capitate tentacles 2
1b dactylozooids with more than 7 capitate tentacles, gonophores liberated as medusae . . . . . *T. penicillatum*
2a gonophores fixed sporosacs, shallow water form . . . . . *T. brieni*
2b gonophores a medusa or medusoid, deep water form . . . . . *Thecocodium* spec.

Thecocodium brieni Bouillon, 1967 Fig. 15

Ptilocodium repens. – Teissier, 1965: 13. [not *Ptilocodium repens* Coward, 1909]
Thecocodium brieni Bouillon, 1967: 1106, figs 1-11. – Brinckmann-Voss, 1970: 85, figs 100-106. – Edwards & Harvey, 1983: 41, fig. 2. – Boero & Fresi, 1986: 139. – Bouillon *et al*., 2004: 76, fig. 44B. – Calder, 1998: 1849.

Material examined – IRSNB IG 27.838, holotype and paratype colonies; type colony collected 1961, Naples, on barnacle (sponge covered?) growing on piece of rock, second small colony on algae; paratype colonies on sponge covered rock, fertile.

Diagnosis: *Thecocodium* with dactylozooids having 4-5 tentacles, gastrozooids without pedicel, gonophores sessile sporosacs, males styloid, females with radial canals reduced to pouches.

Description (Bouillon, 1967; Brinckmann-Voss, 1970; own observations): Colonies small, hydranths stolonal, issuing from creeping, mesh-like hydrorhiza formed by round stolons, these covered by very thin perisarc. Polyps polymorphic, with gastro-gonozooids and dactylozooids.

Gastrozooids without tentacles, bottle-shaped, sessile, with ovoid base tapering distally into neck-like hypostome, base without distinct pedicel, polyp thus sessile, gastrodermis of hypostome forming four thickened longitudinal ridges visible from outside, apical epidermis studded with nematocysts, lower part of hydranth sac-like.

Dactylozooids much more frequent than gastro-gonozooids, contractile, composed of slightly tapering or isodiametric stem ending in a whorl of capitate tentacles, usually four tentacles, occasionally five, rarely three, trunks of tentacles radiate from end of stem, held either horizontally or directed upwards depending on contraction, base of stem with shallow perisarc collar, gastrodermis of stem and tentacles chordoid.

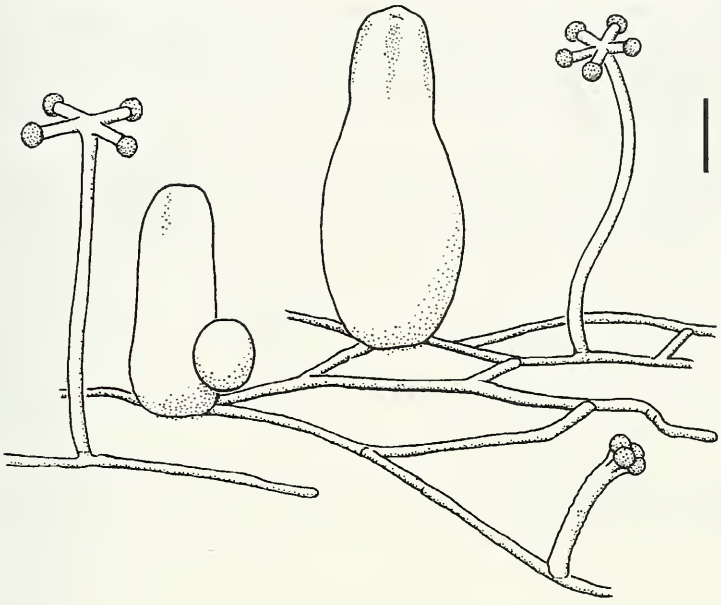

FIG. 15

Thecocodium brieni Bouillon, 1967; after preserved type material; part of colony with three dactylozooids in different states of contraction and two gastrozooids, the left one bearing a gonophore at its side, scale bar approximately 0.2 mm.

Gonophores develop singly near base of gastrozooids, the latter can get reduced in size while gonophores mature. Gonophores are sessile sporosacs, male ones a simple bulbous evagination of body wall (styloid type), female gonophores with vestiges of radial canals forming four pouches surrounding the spadix, occasionally female gonophores also containing spermatogonia, several oogonia develop, but usually only two mature to eggs, eggs develop to planula in situ, animal thus larviparous.

Nematocysts: microbasic euryteles, discharged shaft about as long as capsule; desmonemes with relatively long capsules.

Colours: gastro-gonozooids pink with opaque white hypostomes, dactylozooids translucent colourless with white capitula, stolons pink (Edwards & Harvey, 1983).

DIMENSIONS (Bouillon, 1967; Brinckmann-Voss, 1970; own observations): Colony diameter usually smaller than 10 mm; gastrozooids 0.3-1.3 mm high, diameter up to 0.4 mm; dactylozooids up to 0.9 mm, diameter 0.05-0.1 mm (contractile), capitula diameter up to 65 μm, tentacle length up to 0.2 mm (contractile); sporosacs ca. 0.2 mm or more. Microbasic euryteles 15.4x5.6 μm, desmonemes 11.2x4.2 μm.

OTHER DATA: The histology of the polyps and gonophores has been described by Bouillon (1967) and Brinckmann-Voss (1970). Bouillon (1967) also depicts the nematocysts.

BIOLOGY: Occurs on stones, rocks, oyster shells, calcareous tubes of polychaete worms, algae, and tunics of ascidians, depth range 2-200 m (Brinckmann-Voss, 1970;

Calder, 1998). In the Mediterranean, fertile animals have been observed from April to November (Brinckmann-Voss, 1970; Boero & Fresi, 1986). The feeding behaviour was described in detail by Brinckmann-Voss (1970) and Edwards & Harvey (1983). Prey is caught by the dactylozooids, the gastrozooids then elongate towards them and swallow the prey.

Distribution: Mediterranean (Naples: Bouillon, 1967; Brinckmann-Voss, 1970), northern Brittany (Bouillon, 1967); Western Scotland (Oban: Edwards & Harvey, 1983); Bermuda (Calder, 1998). Type locality: Naples (designation of type specimen by J. Bouillon).

Thecocodium penicillatum Jarms, 1987 Fig. 16

Thecocodium penicillatum Jarms, 1987: 62, figs 8.5-8.6.

Type material: The type material is likely lost (pers. com. P. Stiewe, Zoological Museum of the University of Hamburg).

Diagnosis: *Thecocodium* with dactylozooids having 7-11 tentacles, gastrozooids with long pedicel. Gonophores free medusae, stomach with large vacuolated cells, exumbrella with meridional tracks of refractive spots, four tentacles.

Description (after Jarms, 1987; from in vitro culture): Colonies with stolonal hydranths issuing from creeping, mesh-like hydrorhiza formed by tubular stolons, covered by thin perisarc. Polyps polymorphic, with gastro-gonozooids and dactylozooids, without perisarc envelope.

Gastrozooids without tentacles, club-shaped, with stalk (pedicel), pedicel thin and cylindrical, distal part bottle-shaped, tapering distally into neck-like hypostome, up to five gonophores developing in a single whorl at junction of pedicel and hydranth-body.

Dactylozooids much more frequent than gastro-gonozooids, contractile, without mouth, composed of thin, slightly tapering or isodiametric stem ending in a radiating tuft of capitate tentacles, 7 to 11 (average 10) capitate tentacles with thin stalk, gastrodermis of stem and tentacles chordoid.

Newly released medusa bell-shaped, distinctly higher than wide, umbrella rather thick, without gastric peduncle, margin lobed through perradial embayments, exumbrella with perradial and interradial meridional furrows, interradial ones shallow, on exumbrella four interradial lines of refractive spots, some nematocysts scattered on exumbrella. Velum broad.

Manubrium conical, gastrodermis composed of remarkably large (vacuolated?) cells, mouth small and surrounded by many nematocysts, without any visible primordial gonads. Four radial canals, widening where entering manubrium and thus forming short mesenteries, narrow circular canal. Four short perradial tentacle stumps, slightly swollen near origin.

Adult medusa unknown.

Nematocysts: microbasic euryteles on polyp and medusae; desmonemes; holotrichous macrobasic euryteles occurring only on dactylozooids.

Dimensions (Jarms, 1987): Gastrozooids including pedicels 2-3 mm high, pedicels 1.6-2 mm; dactylozooids up to 1.6 mm high, capitate tentacles 0.1-0.3 mm

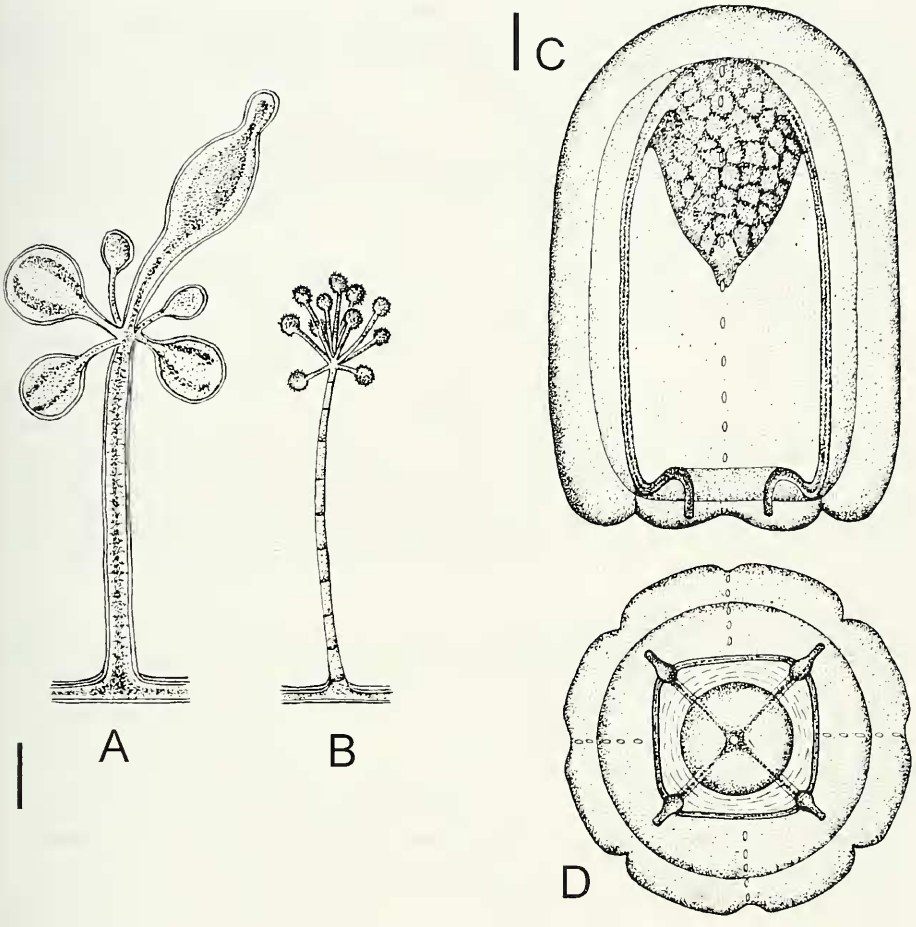

FIG. 16

Thecocodium penicillatum Jarms, 1987; from Jarms (1987). (A) Gastro-gonozooid, scale bar 0.25 mm. (B) Dactylozooid, same scale as A. (C) Newly released medusa in side view, scale bar 0.1 mm. (D) Same as C but oral view.

long; gonophores before liberation 0.45 mm in diameter; newly liberated medusa 0.8-0.95 mm high and 0.64 mm wide.

BIOLOGY: Deep water hydroid found on slag (clinker?).

DISTRIBUTION: Only known from type locality, Canary Islands, 25.4006°N 16.2342°W, 810 m depth.

REMARKS: See *Thecocodium* spec. below.

Thecocodium spec. Fig. 17

MATERIAL EXAMINED: MHNG INVE 62870; Norway, Jan Mayen, Trollveggen vent field, 71.298°N 05.773°W, 574 m, 25.07.2008; coll. by 2008 G.O. Sars Cruise of the University of Bergen, growing on *Sertularella tenella*, gonozooids and dactylozooids present, stolons covered by orange-red mineral precipitate (iron oxide?); 16S sequence accession number **FN422378**.

Description: Gastro-gonozooids and dactylozooids identical to *T. brieni* (comp. Fig. 15), but gonophores are medusoids or medusae with a manubrium composed of large vacuolated cells, no tentacles or bulbs, stolons covered by thicker perisarc, deep water occurrence.

Nematocysts: elongated desmonemes in dactylozooids; large almond-shaped microbasic euryteles around mouth of gastrozooids and in capitula of dactylozooids, discharged shaft about as long as capsule and only faintly swollen; smaller ovoid microbasic heteroneme on gonophores.

Dimensions: Desmonemes (18.5-19)x(5.5-6.5)μm, large microbasic eurytele (21-23)x(6.5-8.5)μm, small microbasic heteroneme (8.5-9)x(5.5)μm.

Distribution: Deep water (>500m), Jan Mayen, North Atlantic.

Remarks: During the "GO Sars 2008 Expedition" of the Centre for Geobiology of the University of Bergen, some hydroids were collected in the vicinity of a deep-water hydrothermal vent area near the island of Jan Mayen. Among these hydroids was also a *Thecocodium* colony growing on *Sertularella tenella*. The colony consists of convoluted stolons bearing gono-gastrozooids and dactylozooids. The polyps of this *Thecocodium* colony resembles in almost all aspects *Thecocodium brieni* (Fig. 15). The dactylozooids have 4-5 capitate tentacles and the gono-gastrozooids are sessile with a whorl of gonophores in the lower region. However, the gonophores seem to be medusoid and not sessile sporosacs (Fig. 17). The most advanced gonophores (0.35 mm long, 0.2 mm wide) have a large spadix with vacuolated gastrodermal cells, but lack any traces of gametes. At the distal end of the manubrium/spadix there is a small zone with more dense tissue. There were no tentacles or bulbs visible. They thus resemble the medusoids of *T. penicillatum* described by Jarms (1987) (see Fig. 16C). The gonophores were covered by ovoid heteronemes which are smaller and rounder than the normal microbasic euryteles of the polyp. This type of nematocyst capsule is unknown in *T. brieni* (Bouillon, 1967). All these differences, together with its unusual habitat, suggest that this colony likely belongs to an undescribed species. However, it could also be a form of *T. penicillatum*, a deep-water *Thecocodium* species that produces medusoids or medusae. According to our current knowledge, *T. penicillatum* has dactylozooids with 7-10 tentacles and stalked gastro-gonozooids. Unfortunately, this species is only known from a single, in vitro culture. As we have no idea of its intraspecific variability, especially in material collected from nature, it is not possible to relate the present sample to this species.

As the only available sample did not permit to obtain sufficient information on the nature of the mature gonophores, the species is here not named in order to avoid the creation of further, ambiguous hydroid species. The 16S sequence will perhaps allow it to be identified in the future.

Genus ***Tregoubovia*** Picard, 1958

Type species: *Tregoubovia atentaculata* Picard, 1958 by monotypy.

Diagnosis: Medusa small, spherical, without tentacles, bell margin with nematocyst ring from which originate centripetal, flat, nematocyst containing bands running meridionally on exumbrella. Manubrium large, cruciform base, the four perradial

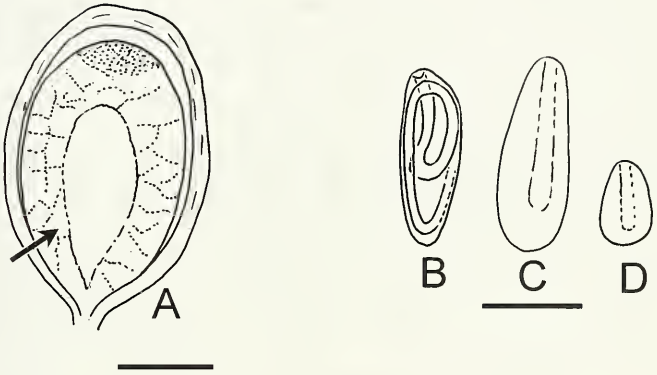

Fig. 17

Thecocodium spec. MHNG INVE 62870, preserved material from the North Atlantic. (A) Optical section of the most advanced gonophore; the gastrodermis of the manubrium is composed of very large, apparently vacuolated cells (arrow), only at the distal end there is some more dense tissue; scale bar 0.2 mm. (B) Desmoneme. (C) Large microbasic eurytele. (D) Small microbasic heteroneme. The scale bar for B-D equals to 10 μm.

corners of mouth margin drawn into distinct oral tentacles with terminal nematocyst clusters. Gonads interradial on manubrium wall. Without desmonemes.

Remarks: This is currently a monotypic genus. The polyp stage remains unknown.

Tregoubovia atentaculata Picard, 1958 Fig. 18

Tregoubovia atentaculata Picard, 1958: 185, fig. – Goy, 1973: 979. – Bouillon *et al.*, 2004: 77, fig. 44C.

Material examined: MHNG INVE 39476, supposed holotype, collected 1955, ex. Picard collection.

Diagnosis: See genus diagnosis.

Description: Medusa umbrella spherical to ovoid, mesogloea moderately thick, bell margin slightly lobed, without gastric peduncle, exumbrella with scattered nematocysts, velum rather narrow.

Manubrium large and voluminous, reaching to level of velum, base square to cross-shaped, the four perradial corners of mouth margin drawn into distinct oral arms, oral arms with chordoid gastrodermis, ends swollen and studded with nematocysts.

Gonads four large, oblong interradial pads on manubrium, well separated perradially.

Four relatively thick radial canals, widening where entering manubrium and thus forming short mesenteries. Diameter of ring canal and bell opening relatively narrow.

Without free tentacles. Along bell margin a ring of thickened tissue with nematocysts from which originate up to 16 centripetal bands (4 perradial, 4 interradial, 8 adradial) running meridionally on the surface of the exumbrella towards aboral pole,

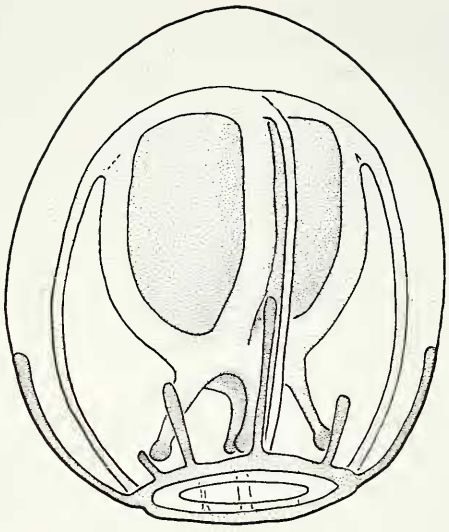

FIG. 18
Tregoubovia atentaculata Picard, 1958; redrawn from (Picard, 1958), male medusa, bell size about 1.5 mm.

reaching maximally to mid umbrella; these tentacle-like structures contain nematocysts and are like flat bands pressed into the surface of the exumbrella so that they are flush with the exumbrellar epithelium, but they are not covered by the exumbrellar epithelium.

Nematocysts: microbasic euryteles, desmonemes absent.

Polyp stage unknown.

DIMENSIONS: Umbrella 1.5-3.2 mm high when mature, euryteles 8x4μm.

BIOLOGY: Deep water species.

DISTRIBUTION: Only known from the type locality: Mediterranean, Villefranche-sur-Mer.

REMARKS: This is a very rare species; so far only two or three specimens have been reported in the literature. *Tregoubovia atentaculata* lacks tentacles but has flat centripetal nematocyst bands originating from a nematocyst band at the bell margin. Similar structures are present in *Thecocodium quadratum* (Werner, 1927) and *Hansiella fragilis* Bouillon, 1980 (Bouillon *et al.*, 1997), which justifies its inclusion in the Ptilocodidae. Picard (1958) regarded these nematocyst bands as being derived from tentacles that developed inside the mesogloea. He claims to have seen that they are composed of a gastrodermal core enveloped by epidermal tissue with nematocysts. The presence of a gastrodermal core could not be verified with the available material. It was evident, however, that these bands are not covered by the normal exumbrellar epithelium, thus they are not really tentacles that have grown into the mesogloea. They more resemble flattened tentacles pressed into and fused to the surface of the exum-

brella. More details can only be obtained through new material and a histological examination using electron microscopic methods.

Family **Eucodoniidae** Schuchert, 1996

Diagnosis: Anthomedusae without pointed apical projection, exumbrella without nematocyst tracks or clusters, with gastric peduncle; manubrium tubular; mouth quadrangular, with four inconspicuous nematocyst-clusters, with medusa budding on manubrium wall; gonads encircle manubrium without radial interruptions; four radial canals and circular canal present; four small perradial marginal bulbs and four tentacles; tentacles with a single terminal swelling; no ocelli; cnidome comprises microbasic euryteles and desmonemes.

Remarks: This is a monotypic family, the polyps are unknown. See also the remarks under *Eucodonium brownei*.

Genus ***Eucodonium*** Hartlaub, 1907

Type species: *Eucodonium brownei* Hartlaub, 1907 by monotypy.

Diagnosis: See family diagnosis.

Eucodonium brownei Hartlaub, 1907 Fig. 19A-B

Dipurena sp. Browne 1896: 473, pl. 16 fig. 2.
Eucodonium brownei Hartlaub 1907: 71, fig. 67. – Neppi & Stiasny, 1913: 14, pl. 1 fig. 6. – Kramp, 1937: 28, fig. 8c. – Russell, 1953: 93, fig. 40. – Picard, 1955: 95. – Vannucci, 1957: 43, figs 2-3. – Kramp, 1959: 91, fig. 44. – Kramp, 1961: 36. – Brinckmann-Voss, 1970: 19, figs 16-19, pl. 2 fig. 4. – Goy, 1973: 972. – Petersen, 1990: 217. – Schuchert, 1996: 89, fig. 53a-b. – Bouillon *et al.*, 2006: 56, fig. 33C.

Type material: Not located (not found in BMHN).

Material examined: MNHN1618; France, Villefranche-sur-Mer; plankton 50-100 m; 3 medusae collected October 1963 and July 1964; material of Goy (1973). – See also Schuchert (1996).

Diagnosis: See family diagnosis.

Description (Russell, 1953; Brinckmann-Voss, 1970; own observations): Medusa umbrella nearly hemispherical, sometimes slightly higher than wide, lateral walls thin, apex with thickened jelly, manubrium attached to a broad, well developed gastric peduncle, velum broad.

Manubrium cylindrical, 1/2 as long as bell cavity, tube-like, mouth quadrangular with four inconspicuous perradial lips, each containing a group of nematocysts. Immature animals produce secondary medusae via medusae buds on middle region of stomach. Mature animals without buds, gonads encircle the manubrium without radial interruptions.

Four very narrow radial canals and circular canal present. Four small marginal bulbs containing blackish pigment granules, without apparent ocelli.

Four equally developed tentacles with a conspicuous terminal swelling, swelling spherical to ovoid; tentacle gastrodermis chordoid; terminal swellings with enlarged gastrodermis and epidermis with fibrous structure. Nematocysts not only

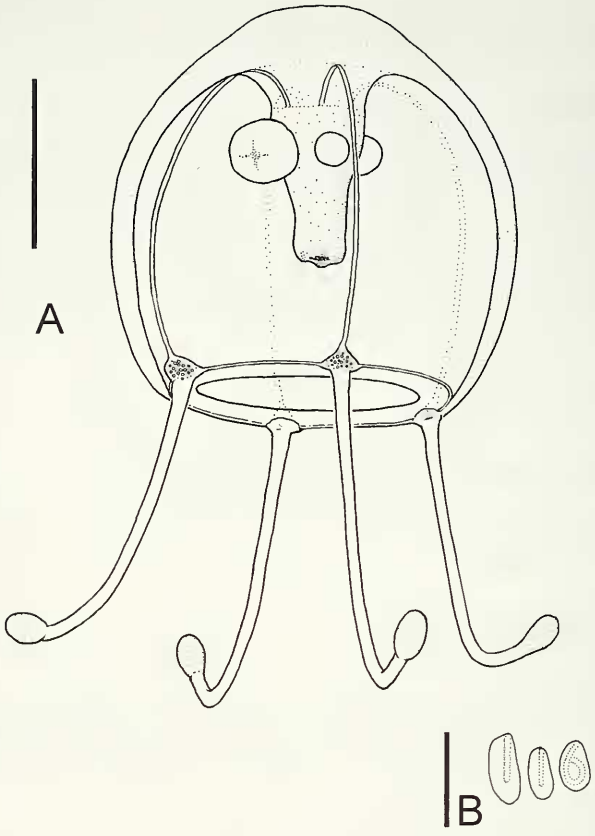

FIG. 19

Eucodonium brownei Hartlaub, 1907; preserved material from New Zealand, modified after Schuchert (1996). (A) Medusa with medusa-buds on manubrium, scale bar 0.3 mm. (B) Undischarged nematocysts: microbasic eurytele from tentacles, heteroneme from manubrium, desmoneme, scale bar 10 μm.

present in terminal swelling but also along the tentacles, nematocysts in terminal swelling not so dense.

Nematocysts: microbasic euryteles on tentacles, heteronemes (microbasic euryteles?) from lips, desmonemes on tentacles.

Colour of marginal tentacles bulbs blackish, stomach blackish brown, terminal knob of marginal tentacles brownish.

DIMENSIONS: Bell diameter and height usually 0.8-1 mm. For nematocyst dimensions see Schuchert (1996).

BIOLOGY: The medusa can be found close to the water surface. In the Atlantic it is very rare, but Brinckmann-Voss (1970, 1987) found it in relatively high numbers near Naples from September to October. Also Daly *et al.* (2003) found it off Tunis in elevated numbers. Likewise, it was found in comparatively high numbers in northern

New Zealand during the summer months. Brinckmann-Voss (1970) observed that lowering the temperature from 20 to 13°C stopped the medusa budding irrespective of the season. The gonad maturation likely also depends on falling temperatures.

DISTRIBUTION: English Channel (Browne, 1896; Hartlaub, 1907; Franc, 1951; Russell, 1957), Faroe-Shetland Channel (Fraser, 1974), Denmark (Kramp, 1927), Mediterranean (Neppi & Stiasny, 1913; Picard, 1955 ; Brinkmann-Voss, 1970, 1987; Goy, 1973; Daly *et al.*, 2003; Medel & López-González, 1996), Brazil (Vannucci, 1957), SW Atlantic (Genzano *et al.*, 2008), New Zealand (Schuchert, 1996; Bouillon & Barnett, 1999). Type locality: Plymouth, England.

REMARKS: With its swollen tentacle ends combined with the medusa buds and the gastric peduncle this is quite a characteristic medusa (Fig. 19A). The tentacle swellings in European animals seem to be larger than in those observed in New Zealand.

The polyp stage of *Eucodonium* remains unknown, which makes it difficult to relate it to other species of Filifera. *Eucodonium* was initially placed among the Capitata, but the cnidome makes it obviously related to the Filifera (Picard, 1955; Schuchert, 1996). Picard (1955) thinks that is could be close to *Podocorynoides minima* (Trinci, 1903) (see Schuchert, 2007 for redescription). Indeed, both medusae are quite similar, except for the tentacle tips of *Eucodonium* and the oral tentacles of *Podocorynoides*, and Picard's suggestion could be correct.

FAMILY RUSSELLIIDAE KRAMP, 1957

DIAGNOSIS: Medusa umbrella with apical projection. Manubrium on gastric peduncle, four unbranched oral filiform tentacles attached above mouth margin, mouth simple, lips indistinct. Marginal tentacles in eight groups, four perradial and four interradial, each group with one large tentacle flanked by two small tentacles; large tentacles hollow, without basal swellings, basal part adnate to umbrella and sunk into deep furrows of umbrella margin, adaxial ocellus at base of free portion of each tentacle. Gonads in eight large adradial pads on manubrium wall.

REMARKS: The polyp stages of the Russellidae are unknown. The family comprises only one genus.

Genus ***Russellia*** Kramp, 1957

TYPE SPECIES: *Russellia mirabilis* Kramp, 1957 by original designation.

DIAGNOSIS: As for family.

REMARKS: The genus is currently monotypic.

Russellia mirabilis Kramp, 1957 Fig. 20A-D

Russellia mirabilis Kramp, 1957: 24, pl. 4 figs 1-6, text-fig. 4. – Kramp, 1959: 30, 129, fig. 142. – Kramp, 1968: 58, fig. 154. – Pagès *et al.*, 1999: 2431, fig. 1. – Bouillon *et. al.*, 2004: 78, fig. 45A.

TYPE MATERIAL: BMNH (not seen).

DIAGNOSIS: See family diagnosis.

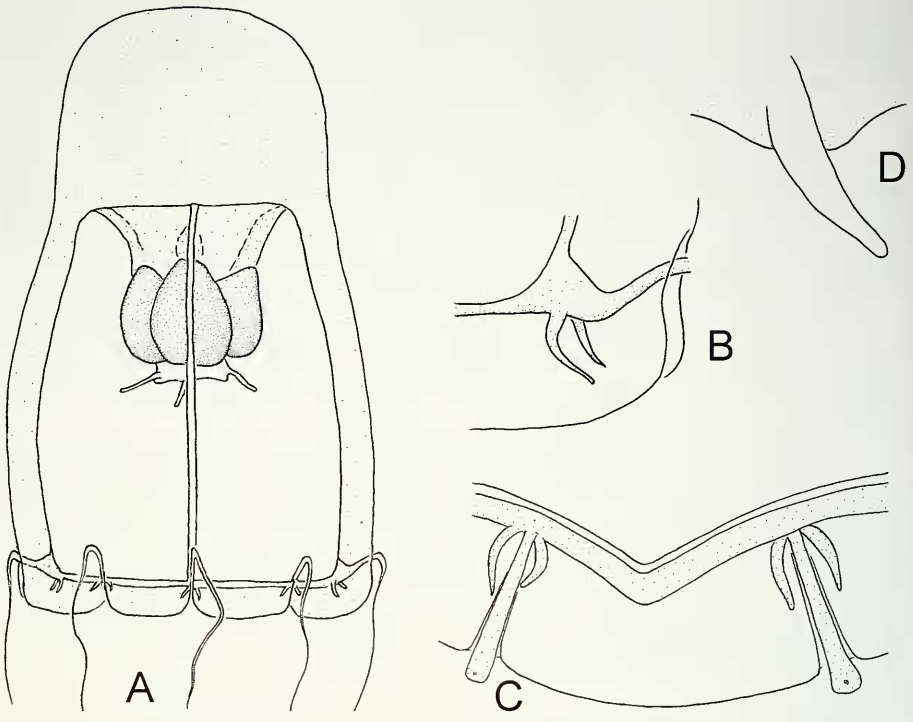

FIG. 20

Russellia mirabilis Kramp, 1957; redrawn from Kramp (1957). (A) Lateral view of medusa, bell height 13 mm. (B) Higher magnification of tentacle base in lateral view. (C) Oral view of a sector of the bell margin showing radial canal and two tentacle bases flanked by a pair of dwarf-tentacles. (D) Perradial corner of the mouth with an oral tentacle.

DESCRIPTION (Kramp, 1957): Umbrella distinctly higher than wide, with broad, dome-shaped apical projection measuring about 1/3 of total height, lateral walls moderately thick, bell-margin hanging in lobes somewhat below the level of the ring-canal, stomach mounted on a broad, conical peduncle, extending partly into the cavity of the stomach, peduncle about as high as stomach, which spans somewhat less than one fourth the height of the bell cavity. Velum narrow.

Base of stomach cross-shaped; stomach itself deeply folded inward in the interradii, and sometimes also in the perradii. In the preserved condition stomach slightly wider than long, the interior surface of the stomach densely wrinkled transversally and along each interradius a narrow, prominent ridge thrown into regular transverse folds, indicating that in living specimens the stomach may be extended to a greater length. Mouth quadrangular with very short and simple perradial lips, mouth rim smooth and entire, slightly thickened, without concentration of nematocysts in the rim itself, but with some scattered in the wall above it. At a short distance above the perradial corners of the mouth four oral tentacles, finger-shaped, tapering towards their distal end, without terminal cluster of nematocysts, but numerous nematocysts evenly scattered

throughout the entire length of the tentacle, not more concentrated towards the tip than in the basal part.

Gonads in eight adradial pads, occupying almost the entire length of the stomach, separated in the perradii and interradii by narrow lines, surface smooth, without transverse folds.

Tentacles in eight clusters, each consisting of one large and two small tentacles. Eight large tentacles of equal size, four perradial and four interradial, basal part (root) of each tentacle directed upward and outward and deeply sunken into a narrow cleft between two prominent lobes of the umbrella-margin; in the interradial tentacles ascending root directly adnate to the gelatinous tissue of the exumbrella, in the perradial tentacles root fused to the terminal part of the corresponding radial canal by a triangular connection (Fig. 20B). Distal to the adnate root, tentacles becoming free and very thin; with one adaxial, red ocellus where tentacles become free; terminal tentacle-structure unknown. At the base of each of the eight large tentacle-roots a pair of much smaller tentacles, structure similar to larger ones (Fig. 20B-C).

Four radial canals, their ascending part on the peduncle fairly wide, in transverse section like an equilateral triangle; descending portion along subumbrella narrow and flat, with smooth edges. Ring-canal narrow.

Polyp stage and cnidome unknown.

Dimensions: Bell height up to 15 mm, diameter up to 9 mm, manubrium about 3 mm high.

Biology: The medusa *Russelia mirabilis* lives mainly in the 0–300 m depth range (Pagès *et al.*, 1999). Outside its main distribution (Antarctica) it occurs usually in deeper waters (200-1000 m: Kramp, 1959; Pagès *et al.*, 1999).

Distribution: Antarctica; West Indies; Mediterranean (Kramp, 1959; Navas-Pereira & Vannucci, 1990; Pagès *et al.*, 1999). Type locality: 66.475°S 71.27083°W, Antarctica, West of Graham Land, 0-165 m.

Remarks: The disjunct and rather surprising distribution pattern of this medusa is difficult to explain. Pagès *et al.* (1999) suspect that transport in the ballast water of a cargo ship is the most plausible explanation for its occurrence in the Mediterranean, but oceanic currents could have brought it to the Caribbean.

Family Niobiidae Petersen, 1979

Diagnosis: Anthomedusae with two opposite simple and two opposite bifurcated radial canals, so that six canals reach the circular canal; gonads interradial on manubrium; marginal tentacular bulbs developing into secundary medusae; no ocelli, no gastric peduncle, no mesenteries.

Remarks: This family currently comprises only one genus. The polyps of the Niobiidae are unknown and thus the systematic position of the family remains unsolved.

Genus *Niobia* Mayer, 1900

Type species: *Niobia dendrotentaculata* Mayer, 1900 by monotypy.

DIAGNOSIS: As for family.

REMARKS: This genus is currently monotypic.

Niobia dendrotentaculata Mayer, 1900 Fig 21A-E

Niobia dendrotentaculata Mayer, 1900: 36, pl. 42 figs 141-144, pl. 43 fig. 144. – Mayer, 1910: 187, pl. 19 figs 1-5. – Brinckmann, 1959: 334, figs 1-2. – Kramp, 1959: 115, fig. 104. – Kramp, 1961: 110, fig. 103. – Kramp, 1968: 41, fig. 103. – Bouillon *et al.*, 2004: 66, fig. 40a.

TYPE MATERIAL: Location not investigated.

DIAGNOSIS: As for family.

DESCRIPTION (Mayer, 1910; Brinckman, 1959): Medusa umbrella hemispherical or slightly flatter than a hemisphere, no apical projection, no gastric peduncle, jelly uniformly thin, relatively rigid.

Manubrium of mature medusa tubular, about as long as height of bell, with four simple but well developed lips, mouth cruciform, gonads in four interradial patches in upper part of manubrium, gonads usually – but not always – mature only after medusa budding from bulbs has stopped.

Four radial canals arise from the four corners of the stomach, but two opposite canals bifurcate closely to manubrium so that six radial canals reach the circular canal at the margin, each pair of radial canals about 60° apart.

Up to twelve marginal tentacles or bulbs present, one for each radial canal and one intermediate between each successive pair of radial canals. The tentacles develop successively and they are arranged in a bilaterally symmetrical manner in accordance with age. The oldest and the youngest tentacles are opposite, situated at the ends of the two simple radial canals, the remaining 10 tentacles are arranged in a bilaterally symmetrical manner in accordance with their various ages, the axis being in the diameter of the unbranched radial-canals and the oldest and youngest tentacles (Fig. 21E). Tentacle bulbs and tentacles transform successively into small medusae which detach from the parent (Fig. 21A-B).

Colours: gastrodermis of manubrium, bulbs, circular canal brownish-yellow, other parts transparent.

Newly-released medusa with 3-5 tentacles, radial canals and unevenly developed marginal tentacles render the medusa bilaterally symmetric (Fig. 21C).

Nematocysts: microbasic euryteles and microbasic mastigophores.

DIMENSIONS: Diameter of mature medusa 2.4-4 mm, height only about 0.6 times the width. Newly released medusa 1.2 mm wide. Microbasic euryteles 7x2.5μm, microbasic mastigophores 5x2.5μm (Brinckmann, 1959).

BIOLOGY: The medusa occurs close to the surface. It thrives well in culture (Mayer, 1910).

DISTRIBUTION: Rare, circumglobal in warm and temperate waters, recorded from Florida (Mayer, 1900); New England (Bigelow, 1915); Vietnam (Dawydoff, 1936); Mediterranean (Brinckmann, 1959); India (Nair, 1951); Argentina (Goy, 1979); Papua New Guinea (Bouillon, 1980). Type locality: Tortugas, Florida, USA.

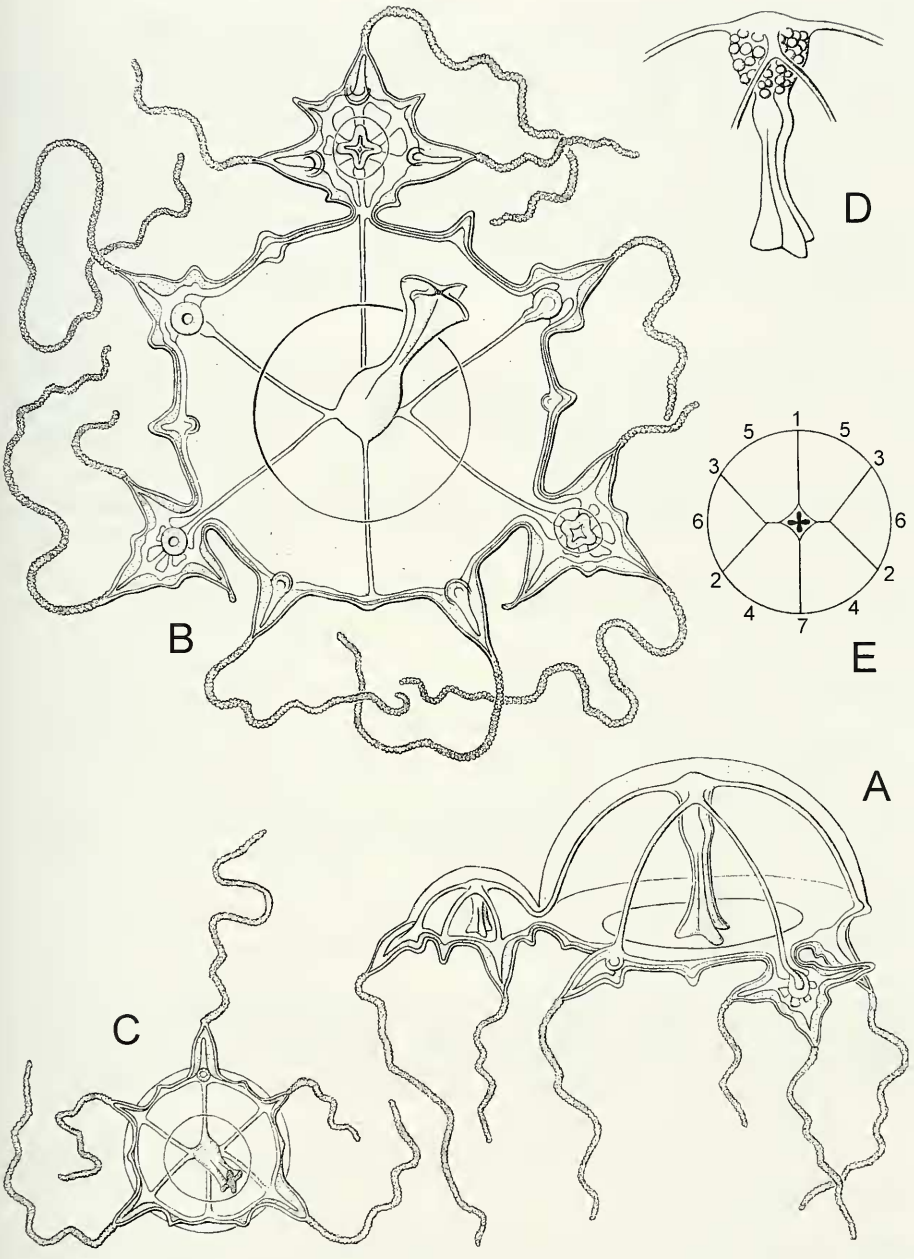

FIG. 21. *Niobia dendrotentaculata* Mayer, 1900; modified after Mayer (1910). (A) Side view of medusa showing the development of secondary medusae from the tentacle bases. (B) Oral view of a medusa, note the characteristic six radial canals and the bulbs that develop into small medusae. (C) Newly released medusa, note bilateral symmetry (mirror symmetry). (D) Manubrium of mature medusa with eggs. (E) Symmetry and sequence of tentacle development of medusa shown in section A, 1 denotes the most advanced, 7 the least developed tentacle.

Family Protiaridae Haeckel, 1879

Diagnosis (Bouillon *et al.*, 2006): Hydroid colonial, arising from creeping, tubular stolons; hydranths issued from short hydrocaulus; hydrorhiza and hydrocaulus covered by perisarc, forming a hydrotheca-like tube; hydranth with one whorl of filiform tentacles, large nematocysts alternating with tentacles.

Medusa with four fully developed marginal tentacles arising from large, hollow tentacular bulbs; four simple radial canals and a circular canal, mouth with four simple lips; gonads interradial, with smooth surface; with or without mesenteries; without rudimentary bulbs; margin with or without cirri-like tentacles; exceptionally with ocelli.

Remarks: The medusae of the Protiaridae and the Pandeaidae (see Schuchert, 2007) appear very similar and the differences in the diagnoses are minimal. Both families have nevertheless rather dissimilar polyps. Protiaridae polyps resemble those of *Trichydra* (see p. 495) and the cnidome comprises merotrichous isorhizas, capsules otherwise only found in some leptomedusae (i.e., Eirenidae, Eucheilotidae, Haleciidae, Lovenellidae and Tiaropsidae; Bouillon, 1985; Bouillon *et al.*, 1988). The development of the medusae and the gonozooids are insufficiently known in this family. Dr. Brinckmann-Voss, however, has found and reared the polyps of *Halitiara formosa* (pers. com., unpublished) and she observed that the medusae are produced in gonothecae. The family could thus be more closely related to the order Leptothecata.

Protiaridae genera of the ERMS zone:

1a with cirri (= small free-hanging tentacles on bell margin, in addition to normal tentacles) . . . . . *Halitiara*
1b without cirri 2
2a without mesenteries, marginal tentacles without abaxial spurs . . . . . *Protiara*
2b with short mesenteries, marginal tentacles with abaxial spurs . . . . . *Paratiara*

Genus ***Halitiara*** Fewkes, 1882a

Type species: *Halitiara formosa* Fewkes, 1882a by monotypy.

Diagnosis: Medusa with four straight radial canals; four perradial marginal tentacles; with marginal cirri between long tentacles; mouth simple, cruciform; with or without mesenteries; gonads interradial, smooth, sometimes extending along mesenteries; without ocelli; cnidome where known including merotrichous isorhizae.

Hydroid diagnosis as for family.

Remarks: Gershwin & Zeidler (2003) provide a table with the characteristics of all known *Halitiara* species.

Key to the *Halitiara* medusae of the ERMS zone:

1a with apical process . . . . . *H. formosa*
1b without apical process . . . . . *H. inflexa*

Halitiara formosa Fewkes, 1882a Figs 22A-B, 23A-B

? *Dissonema gaussi* Vanhöffen, 1912: 361, pl. 24 fig. 2. – Kramp, 1965: 27, possible synonym.

Halitiara formosa Fewkes, 1882a: 267, pl. 4 fig. 2. – Kramp, 1959: 115, fig. 103. – Uchida, 1927: 203. – Menon, 1932; 7, pl. 1 fig. 4. – Kramp, 1961: 102. – Kramp, 1968: 40, fig. 102. – Brinckmann-Voss, 1970: pl. 11 fig. 1. – Goy, 1973: 983, fig. 7. – Bouillon, 1980; 332. – Goy *et al*., 1991: 110, fig. 26. – Schuchert, 1996: 76. – Gershwin & Zeidler, 2003: table 3. – Bouillon *et al*., 2004: 75, fig. 43E.
Protiara formosa. – Mayer, 1910: 107, pl. 6 figs 4-6, pl. 13 figs 1-2.
in part *Halitiara formosa*. – Kramp, 1965: 27. [some = *Leuckartiara simplex*]

Type material: Location not investigated.

Material examined: ZMUC, without registration number; USA, Florida, St Andrews Bay; collected August 1959, 2 medusae, det. Kramp, leg. M. Hopkins. – MHNG INVE 63285 ; Mediterranean, France, Villefranche-sur-Mer, surface plankton; 10 April 1972; one mature, contracted medusa, one medusa without manubrium; specimens collected and identified by A. Brinckmann-Voss.

Diagnosis: Medusa up to 3 mm high, with solid apical projection, manubrium about half as long as bell cavity; mouth opening cruciform; with indistinct mesenteries. Four long and 24-35 short, tightly coiled, cirrus-like tentacles; no ocelli.

Description: Polyp stage similar to *H. inflexa* and *Trichydra pudica* (A. Brinckmann-Voss, pers. comm.). Gonozooids are reduced hydranths without tentacles (=blastostyles) enclosed in a filmy, soft perisarc tube like a gonotheca, budding one or two medusae at a time.

Newly liberated medusa with 3-4 perradial tentacles and 1-3 cirri between each pair of successive perradial tentacles.

Mature medusa with bell-shaped umbrella, slightly higher than wide, with distinct, solid apical projection of somewhat variable shape; without gastric peduncle; velum narrow.

Manubrium pyriform to cruciform in section, about half as long as the depth of the bell-cavity, with simple, cruciform mouth. Gonads on interradial sides of the manubrium, large, covering most of manubrium, separated perradially, ova large and conspicuous.

Four straight, narrow radial canals and a slender circular canal, radial canals with elongated opening where joining manubrium, thus forming mesenteries, but these inconspicuous, shorter than half the manubrium height, may be absent in specimens with less developed gonads.

Four long perradial tentacles, with long, hollow, tapering basal bulbs, without exumbrellar spurs, without ocelli; in addition to long tentacles 24-35 short, solid, cirri-like tentacles, independent of long tentacles, often tightly coiled, gastrodermal cells chordoid.

Colours: gastrodermis of the manubrium and tentacle bulbs in the female green, but in the males light-brown (Mayer, 1910).

Dimensions: Bell height of mature medusa 1-3 mm. Nematocysts of preserved Mediterranean specimen: large ovoid capsules, one long side more straight than other, (16-17)x(9-10)μm; smaller elongate almond-shaped capsules (8-8.5)x(2.5-3)μm. The capsule types could not be identified, but the undischarged capsules resemble those of *H. inflexa* depicted in Bouillon *et al*. (1988).

Biology: A coastal medusa occurring in shallow depths. The medusa is rare in the Mediterranean, but Mayer (1910) reported it as being very abundant at the

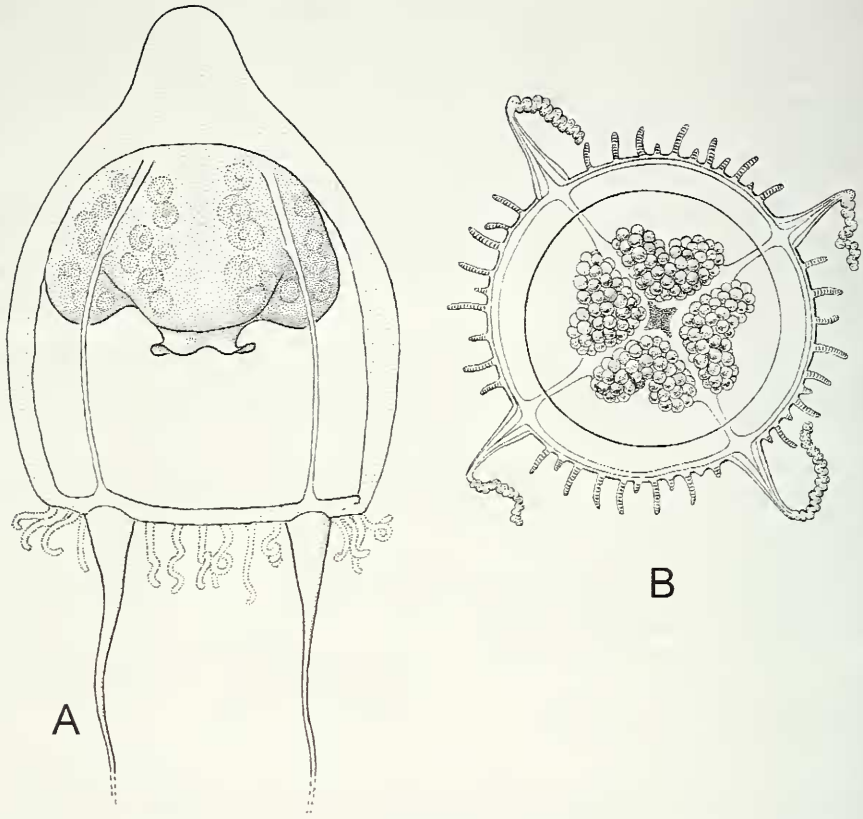

FIG. 22

Halitiara formosa Fewkes, 1882. (A) Lateral view of mature, female medusa, manubrium somewhat contracted, composite image drawn after several preserved specimens from Florida, height about 1.2 mm (B) Oral view of medusa, from Mayer (1910).

Tortugas, Florida. In the Mediterranean, the medusae were observed from August to November (Goy, 1973; Brinckmann-Voss, 1987; Goy *et al.*, 1991). Polyps budding medusae were observed in September (Brinckmann-Voss, 1987). They occur on oyster shells (A. Brinckmann-Voss, pers. com.).

DISTRIBUTION: Tortugas, Bahamas (Mayer, 1910); Mediterranean (Goy, 1973; Brinckmann-Voss, 1987; Goy *et al.*, 1991); Argentina (Genzano *et al.* 2008); tropical parts of the Indo-Pacific Ocean (Menon, 1932; Kramp, 1965; Bouillon, 1980); NW Pacific (Uchida, 1927; Kramp, 1965); records from New Zealand are likely erroneous (Schuchert, 1996). Type locality: Tortugas, Florida, USA.

REMARKS: Descriptions or illustrations of the polyp stage of *H. formosa* have not yet been published. Dr Anita Brinckmann-Voss found the polyp repeatedly near Naples and she was able to rear the medusa released from these colonies. Dr Brinckmann-Voss was so kind to send me her drawings and notes and they were here used for the description and the figure of the gonotheca (Fig. 23A-B).

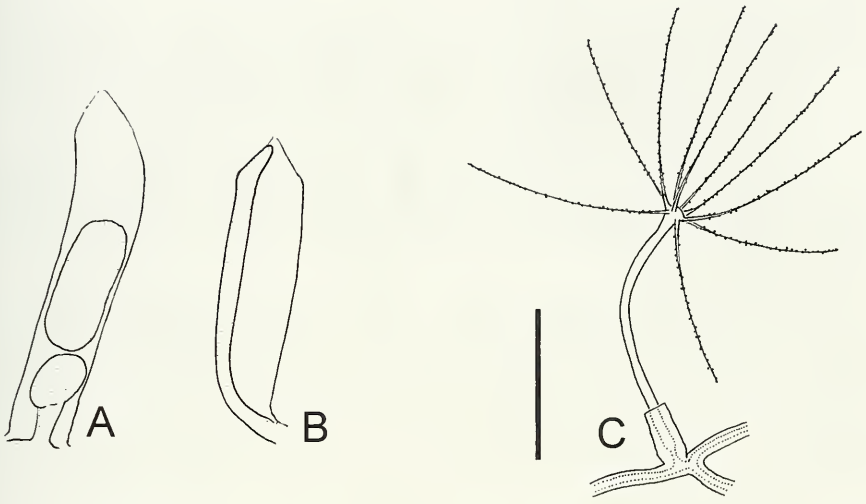

FIG. 23

(A-B) *Halitiara formosa* Fewkes, 1882; lateral view of gonothecae, living material from the Mediterranean, after unpublished sketches of Dr. A. Brinckmann-Voss. Note that the images are not represented at the same scale as C.
(A) Gonotheca with a developing medusa (oval mass). (B) Gonotheca after release of medusa, blastostyle drawn stippled.
(C) *Halitiara inflexa* Bouillon, 1980; polyp stage, modified from Bouillon (1985).

According to Kramp (1959), the medusa of this species has no mesenteries. Some authors (e. g. Goy, 1973) nevertheless described it as having mesenteries (but in the accompanying figure they are not apparent). The specimens examined for this study – coming from the same biogeographic region as the type material – clearly had mesenteries (Fig. 22A), although they were rather short and inconspicuous. The length is less than half of the manubrium height. The original figure given by Fewkes (1882a) also suggests slight mesenteries, but it is possible that their full development is correlated with the age or size of the animal and also the size of the manubrium and gonads.

Some specimens from the NE Pacific identified by Kramp (1965) as *H. formosa* (in ZMUC) were re-examined for this study and they turned out to be *Leuckartiara simplex* Bouillon, 1980.

The related species *Halitiara inflexa* Bouillon, 1980 has been reported from the eastern Mediterranean by Goy *et al.* (1991) (see also Bouillon *et al.*, 2004: 76, fig. 43F-G). This species differs from *H. formosa* by the absence of an apical process. The other purported difference, namely the presence of mesenteries, is likely incorrect or unreliable (see above). As also the apical process shows some variation, the Mediterranean records of *H. inflexa* could be just a variant of *H. formosa*. *Halitiara inflexa* is otherwise only known from Papua New Guinea and this population is likely distinct from *H. formosa* (see also Gershwin & Zeidler, 2003).

Halitiara inflexa Bouillon, 1980 Fig. 23C

Halitiara inflexa Bouillon, 1980: 324, fig. 9. – Bouillon, 1985: 259, fig. 7. – Bouillon *et al.*, 1988: 211, fig. 8. – Goy *et al.*, 1991: 110, fig. 27. – Bouillon, 1995: 230, fig. 6. – Schuchert, 1996: 77, fig. 46a-b. – Bouillon *et al.*, 2004: 43F-G.

TYPE MATERIAL: IRSN Bruxelles (not seen).

DIAGNOSIS: Medusa up to 3 mm high and 2.4 mm wide, bell conical without apical projection, manubrium about half as long as bell cavity; mouth opening cruciform; with distinct mesenteries. Four long and 28-40 short, cirrus-like tentacles; no ocelli.

DESCRIPTION (Bouillon, 1980; Bouillon, 1985; Schuchert 1996): Hydroid colonies arising from creeping, perisarc-covered stolons. Polyps with a very short caulus, a long, narrow cylindrical body and a short conical hypostome. Below hypostome one whorl of ten long, filiform tentacles with irregular clusters of nematocysts. Alternating with the tentacles are large nematocysts. Caulus and base of polyp body are covered by a perisarc cup into which the polyp can almost completely retract. Gonozooids unknown.

Medusa umbrella bell-shaped, rather conical, jelly moderately thick, gradually thickening towards top to about two times the thickness of the lateral walls. Manubrium voluminous, quadrangular, length about 2/3 of bell cavity, joined to radial canals by mesenteries for 1/2 of their length. Mouth with four simple lips.

Gonads large, bulging, filling interradial position completely, leaving only a small perradial band of stomach and the mouth region free.

Four radial canals and circular canal, all narrow and with smooth margins.

Four long perradial tentacles, with broad conical base then tapering, base not laterally compressed. Nematocysts evenly distributed on tentacles. Between each pair of long tentacles 3 to 10 short, cirri-like tentacles, without bulbs, often coiled, with chordoid gastrodermis, tips with nematocysts (haplonemes). Nematocysts: atrichous isorhizas of two size classes, merotrichous isorhizas, mastigophores.

DIMENSIONS: Bell height up to 3 mm, diameter up to 2.4 mm. For nematocyst dimensions see Bouillon (1980) and Bouillon *et al.* (1988). Polyps up to 1 mm, with a very short caulus (80 μm),

DISTRIBUTION: Papua New Guinea, New Zealand, Mediterranean (Bouillon, 1980; Bouillon, 1995; Goy *et al.*, 1991; Schuchert, 1996).

REMARKS: This species does not occur along the European coasts, but it has been found in the eastern Mediterranean (Lebanon; Goy *et al.*, 1991), thus within the ERMS zone. For figures see Bouillon (1980, 1985) and Schuchert (1996). See also remarks under *H. formosa*.

Genus ***Paratiara*** Kramp & Dumas, 1925

TYPE SPECIES: *Paratiara digitalis* Kramp & Dumas, 1925.

DIAGNOSIS: Protiaridae medusae without marginal cirri, four marginal tentacles with abaxial spurs, no ocelli, with smooth, interradial gonads, manubrium more or less twisted, four simple oral lips, with short mesenteries.

REMARKS: This is a monotypic genus.

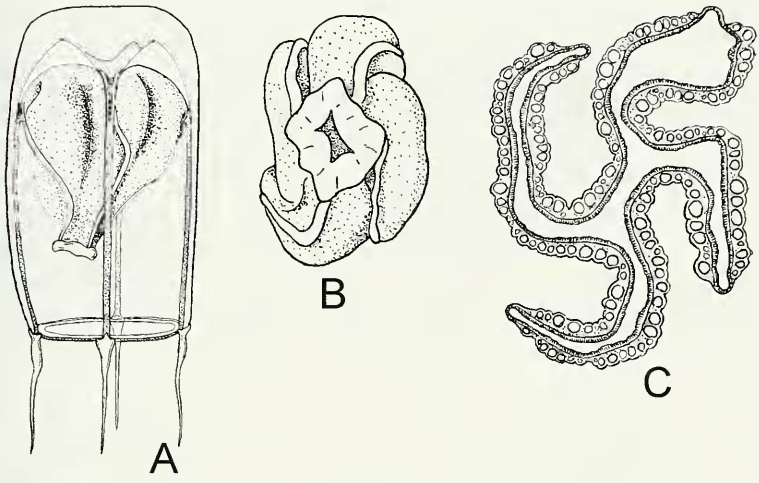

FIG. 24

Paratiara digitalis Kramp & Dumas, 1925; from Kramp & Dumas (1925). (A) Medusa in side view, bell height about 1 cm. (B) Oral view of manubrium, note characteristic torsion of its perradial wings. (C) Horizontal section of manubrium of a female medusa.

Paratiara digitalis Kramp & Dumas, 1925 Fig. 24A-C

Paratiara digitalis Kramp & Dumas, 1925: 273, figs 18-20. – Kramp, 1926: 66, chart XI. – Kramp, 1961: 114s. – Fraser, 1974: 12.

TYPE MATERIAL: Location not investigated.

MATERIAL EXAMINED: ZMUC, DANA station 851 (NE of Bahamas), 22.3833°N 60.7667°W, 50 metres wire, 05.06.1920; one damaged medusa, material of Kramp (1959). – ZMUC, DANA station 891 (West-Indian Islands), 29.4667°N 69.4167°W, 50 metres wire, 24.07.1920; one much damaged medusa, material of Kramp (1959).

DIAGNOSIS: See genus diagnosis.

DESCRIPTION: Medusa bell higher than wide, cylindrical shape with thin walls and rather flat top, roof of subumbrella with four interradial pockets.

Manubrium flask-shaped, 2/3 of length of bell cavity, with short mesenteries (1/4 of manubrium height); four simple lips; manubrium cruciform in cross-section, sometimes twisted (Fig. 24B-C), the perradial edges all turned towards one side.

Gonads smooth, interradial, completely covering the stomach walls except in the perradii.

Four perradial tentacles with conical basal bulbs, each with a well developed, epidermal, abaxial spur; no ocelli.

Four radial canals, smooth, straight, joining manubrium in upper fourth and forming mesenteries; ring canal thin.

Polyp stage and nematocysts unknown.

DIMENSIONS: Bell height up to 10 mm, in tropical waters 4.5 mm high and 4 mm wide.

BIOLOGY: A rare medusa usually found close to the water surface, mostly caught during summer time.

DISTRIBUTION: Rockall (Fraser, 1974); between Shetland and Iceland (Kramp, 1926); North Cape (Kramp & Damas (1925); Sargasso Sea (Kramp, 1959). Type locality: Vardø, North Cape, Norway, North Atlantic Ocean, near surface.

REMARKS: The presence of mesenteries is a feature that distinguishes this species and genus from *Protiara tetranema*. A re-examination of some specimens identified by Kramp and also the figures in Kramp & Damas (1925, reproduced in Fig. 24) showed that they are rather short, spanning only about 1/4 of the manubrium height. The torsion of the manubrium is a unique feature of this species, but this seems not to be a constant feature as some examined medusae had a straight manubrium.

Genus ***Protiara*** Haeckel, 1879

TYPE SPECIES: *Oceania tetranema* Péron & Lesueur, 1810 by monotypy.

DIAGNOSIS: Protiaridae medusae without marginal cirri, four marginal tentacles, with or without ocelli, with four or eight smooth, vertical gonads in the adradial-interradial region, four simple oral lips, without mesenteries.

REMARKS: This genus is likely invalid as its type species is indeterminate. See the remarks below.

Protiara tetranema (Péron & Lesueur, 1810) Fig. 25

zweyte karminrothe Beroe Slabber, 1775: 64, pl. 14, Fig. 1. [nomenclature not binomial]
Oceania Tetranema Péron & Lesueur, 1810: 347.
in part *Protiara beroe* Mayer, 1910: 106.
Protiara tetranema. – Haeckel, 1879: 47. – Hartlaub, 1914: 250, Fig. 206. – Kramp, 1959: 114, diagnosis. – Kramp 1961: 114. – Bouillon *et al*., 2004:76, fig. 44A.

TYPE MATERIAL: Likely lost.

TYPE LOCALITY: Coast of The Netherlands.

REMARKS: This species is based on the description of a medusa given in Slabber (1775). Slabber describes and depicts a microscopically small, carmine-red medusa of which he had collected two living specimens from the Dutch coast (Fig. 25). It is characterized by four tapering tentacles, a cylindrical bell, and a short manubrium with four perradial lips. The most conspicuous trait is the carmine-red colour of the manubrium. Although Slabber's description and figure are quite accurate, it seems nevertheless impossible to relate this obviously immature medusa to any species known today.

Maybe Slabber had a young pandeid medusa (cf. also Vanhöffen (1891) who had similar thoughts), although the red manubrium remains problematic. *Neoturris pileata* can also have an intensively red manubrium and its youngest stages have four tentacles only, but it is rare in this region. A conspicuous red medusa of the region is *Turritopsis polycirrha* (see Schuchert, 2006; or Russell, 1953 as *T. nutricula*), but most young *Turritopsis* medusae are released with eight tentacles (although the newly liberated medusae of *T. polycirrha* has never been described). Slabber (1775) also describes another carmine-red medusa with 18 tentacles, which was almost certainly

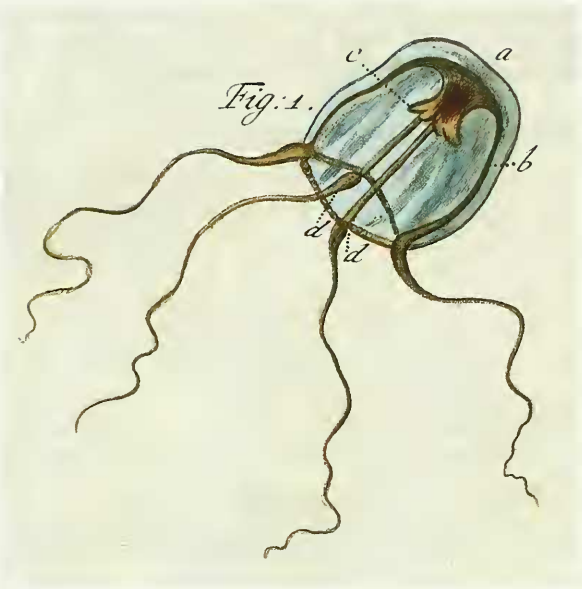

FIG. 25

Protiara tetranema (Péron & Lesueur, 1810); original illustration of Slabber (1775) depicting the type specimen. Size given as "microscopic"; Slabber indicates: a = flat top of body [umbrella], b = inside of body [subumbrella], d = tubes which transport digested food [radial canals], c = stomach.

T. polycirrha, and which he had collected only four days earlier. They were the size of sand grains, thus presumably not more than 2 mm. A similar size or more likely smaller must also be assumed for Slabber's second red medusa, now called *Protiara tetranema*.

As Slabber's account did not use a binomial nomenclature, he named it his "*second carmine-red Beroe*", Péron & Lesueur (1810) gave it the name *Oceania tetranema*. They also noted the presence of numerous wart-like protrusions along the inside of the ring-canal. These knobs were not mentioned in Slabber's description, but they can be seen in his figure (Fig. 25). Could they be remnants of lost tentacles or incipient tentacles?

Haeckel (1879) then thought that he could recognize the species again in a medusa he collected in the English Channel. He had a relatively large medusa (4 mm high and wide), which had four tentacles with abaxial ocelli. A very unique feature of Haeckel's medusa was that it had four perradial gonads. He describes them as smooth, elongate, cylindrical bodies attached along the four perradial edges of the stomach. Unfortunately he provided no figure. Perradial gonads are rare in the Filifera, only in advanced stages of *Merga* species they can get fused perradially (see Bouillon, 1980; Schuchert, 2007). Formally, Haeckels's medusa resembles thus *Merga tregoubovi* Picard, 1960 (see Schuchert, 2007). In contrast to Haeckel's medusae, *Merga tregoubovi* has no ocelli, but Haeckel sometimes misinterpreted dark pigments in the tentacle bulbs as ocelli. Whatsoever, it is by no means convincing that Haeckel had the same species as Slabber.

The uncertainty of the scope of *Protiara tetranema* is also reflected in Mayer (1910), who erroneously also associated *Plotocnide borealis* Wagner with this species.

Hartlaub (1914) thought that Haeckel must have misinterpreted the gonads. He thinks that they were more likely the result of a perradial fusion of adradial bulges of very advanced gonads in a *Merga* species.

The species was not seen after Haeckel except for Pell (1938) who gives an uncommented record of a single medusa in the Adriatic Sea. It remains unclear what Pell used as criteria to identify the medusa and later intensive searches (Benovic & Lucic, 1996) never found it again. Pell perhaps mistook a *Merga* species for *Protiara tetranema*.

A second species of the genus *Protiara* was described by Hargitt (1902) as *Protiara haeckeli*, occurring in the Vineyard Sound, Massachusetts. This species has an apical process, lacks ocelli, and the manubrium is white. Hargitt remains somewhat vague concerning the position and form of the gonads. *Protiara haeckeli* has apparently also never been reported again and as its morphology remains incompletely known it is thus of limited help in elucidating the genus *Protiara*. A rather distinct, third *Protiara* species was described by Bigelow (1912) as *P. tropica*. Bouillon (1980) removed it from the genus *Protiara* to *Pseudotiara* (Family Bythotiaridae).

Summarizing, *Protiara tetranema* is a doubtful, unrecognizable species. Because the only other species of the genus, *P. haeckeli*, is also somewhat doubtful, this undermines seriously the usefulness and validity of the genus *Protiara* and the family Protiaridae.

Family Trichydridae Hincks, 1868

Diagnosis: Hydroid colonial, colony stolonal, stolons covered by thin perisarc; hydranths with a hydrotheca-like tube of perisarc at base into which polyp can withdraw, hydranths very small, sessile, with one amphicoronate whorl of filiform tentacles. Gonozooids are reduced hydranths without tentacles (blastostyles) enclosed in a filmy, soft perisarc-tube like a gonotheca.

Medusa bell-shaped, with apical process, without gastric peduncle; manubrium with four large, folded lips; four radial canals; numerous fine, branched, anastomosing centripetal canals connecting non perradial marginal bulbs to radial canals; gonads interradial pads; marginal tentacles solid, with relatively large marginal bulbs; no ocelli.

Remarks: The systematic position of this family and its sole genus is somewhat unclear. The majority of current authors (e. g. Bouillon *et al.*, 2006) place it among the Anthoathecata based on its medusa, which is undeniably typical for this order. Werner (1984), however, classified it under Leptothecata. This was likely a conclusion he derived from his knowledge of the gonotheca of the hydroid stage (briefly mentioned in Werner, 1984 and pers. comm. Dr Anita Brinckmann-Voss). *Trichydra* and *Halitiara* share identical polyp stages and both are likely more closely related than previously thought. The cnidome of *Trichydra* remains imperfectly known, but the one of *Halitiara* is rather unique and resembles more the cnidomes found in the Leptothecata (i.e., Eirenidae, Eucheilotidae, Haleciidae, Lovenellidae and Tiaropsidae; Bouillon, 1985; Bouillon *et al.*, 1988). The taxonomic position of *Trichydra* and *Halitiara*

remain thus unsettled and intriguing. Hopefully, molecular phylogenetic investigations will soon address the problem.

Genus ***Trichydra*** Wright, 1858

SYNONYM: *Pochella* Hartlaub, 1917 [type species *Pochella polynema* Hartlaub, 1917].

TYPE SPECIES: *Trichydra pudica* Wright, 1858 by monotypy.

DIAGNOSIS: See family diagnosis.

REMARKS: This is currently a monotypic genus. See also the remarks under *Fabienna oligonema*.

Trichydra pudica Wright, 1857 Fig 26-28

? *Oceania pusilla* Gosse, 1853: 384, pl. 13 figs 11-14.
not *Eudendrium pudicum* Van Beneden, 1867: 116, pl. 7 figs 1-2. – Rees, 1941:135.
Trichydra pudica Wright, 1857: 168. – Wright, 1858: 257, pl. 15. Fig. 1. – Wright, 1863: 440, pl. 22 figs 1-6. – Hincks, 1868: 216, fig. 26. – Rees, 1941: 135, figs 4-5. – Hamond, 1957: 296. – Edwards, 1973: 87, Fig. 1A-E. – Fraser, 1974: 19. – Arai & Brinckmann-Voss, 1980: 75, fig. 42. – Werner, 1984: 187, fig. 116.
Pochella polynema Hartlaub, 1917: 414, figs 344-346. – Russell, 1938a: 425, figs 1-3. – Russell, 1953: 394, figs 257-262. – Kramp, 1959: 179, fig. 258. – Kramp, 1961: 233. – Kramp, 1968: 109, fig. 296.
Proboscidactyla polynema. – Foerster, 1923: 30, pl. 3 figs 5-7, pl. 4 fig. 1.
? *Pochella polynema*. – Goy *et al*., 1991: 118, fig. 45.

TYPE MATERIAL: Not located, likely lost.

MATERIAL EXAMINED: BMNH 1954.11.13.383; as *Pochella oligonema*; England, Plymouth; mature medusa collected 30 April 1898; material depicted in Russell (1953: fig. 260). – BMNH 1955.11.23.1938; as *Pochella oligonema*; England, Plymouth; mature medusa collected 25.05.1934; material depicted in Russell (1953: fig. 258). – BMNH 1954.11.13.126, slide preparation, as *Trichydra pudica*; Ireland, Valentia; hydroid collected April 1900, reared colony from aquarium of M. J. Delap; donated by E. T. Browne, likely the material mentioned in Rees (1941: 335).

DIAGNOSIS: See family diagnosis.

DESCRIPTION (Rees, 1941; Edwards 1973; own observations): Hydroid colonial, hydranths very small, connected by ramified, creeping, tubular stolons covered by thin perisarc. Hydranth with a basal hydrotheca-like tube of filmy perisarc into which the hydranth can partially or entirely contract, no operculum, the slightest disturbance makes them retract, hydranth very extensible, rather flexible, distal part can droop like a flower, hydranth body cylindrical, thin, hypostome conical, one whorl of 6-8 tentacles, tentacles thin, irregularly disposed nematocysts give spiny appearance to extended tentacles, fully extended often longer than polyp height.

Reproductive polyps reduced to blastostyles producing one to two medusae at a time, contained in a perisarc tube resembling hydrotheca of the hydranths, these gonothecae without distinct operculum, blastostyle a simple rod-like process without tentacles.

Newly liberated medusae very small, cup-shaped, jelly fairly thin, without umbilical canal; four short tentacles with conspicuous bulbs, four radial canals and a ring canal, radial canals without side-branches, stomach relatively large but without lips, velum broad, numerous nematocysts scattered over the exumbrellar surface; stomach and bulbs tinged with pale pinkish yellow.

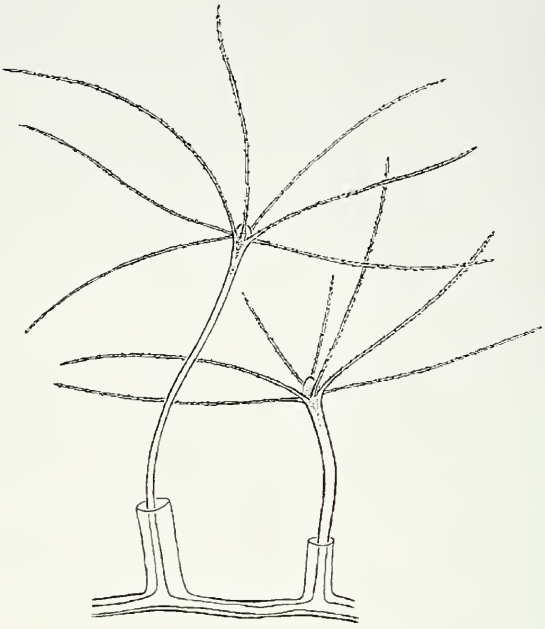

FIG. 26
Trichydra pudica Wright, 1857; living polyps, modified after Rees (1941).

Adult medusa with bell-shaped or hemispherical umbrella, slightly wider than high, jelly fairly thick, with broad, rounded apical process, without exumbrellar nematocyst tracks. Velum fairly broad. Stomach large, four-sided to cruciform in section, length about 1/2 to 2/3 the height of subumbrellar cavity; mouth cruciform through four rather large perradial lips, mouth-margin undulated. Four interradial gonads on stomach wall, cushion-like, each gonad when fully developed covering almost entirely the interradial wall of stomach. Thirty to forty or more solid marginal tentacles with large rounded basal swellings, without ocelli. Four straight smooth perradial canals fairly broad, usually also numerous fine, branched, anastomosing centripetal canals connecting non-perradial marginal bulbs to radial canals, connections of fine centripetal canals to perradial canals occurring at varying levels.

Colour of stomach and marginal tentacle bases brown.

Nematocysts inadequately known, almond-shaped capsules resembling macrobasic heteronemes or merotrichous isorhizas, desmonemes most probably absent.

DIMENSIONS: Polyps hydranths up to 1 mm, tentacles when expanded may reach a length of 1.2 mm, basal perisarc collar (hydrotheca) 0.15-0.35 mm high and 0.1-0.14 mm wide (Rees, 1941). Gonothecae 0.3-0.55 mm high and 0.15-0.2 mm wide. Newly liberated medusae from 0.15-0.2 mm in diameter and height (Edwards, 1973) to 0.3 mm wide and 0.4 mm high (Rees, 1941). Mature medusae may reach 3.85 mm in diameter and 3.47 mm in width (Edwards, 1973), mature medusae in the plankton have a diameter of 2-3 mm (Russell, 1953).

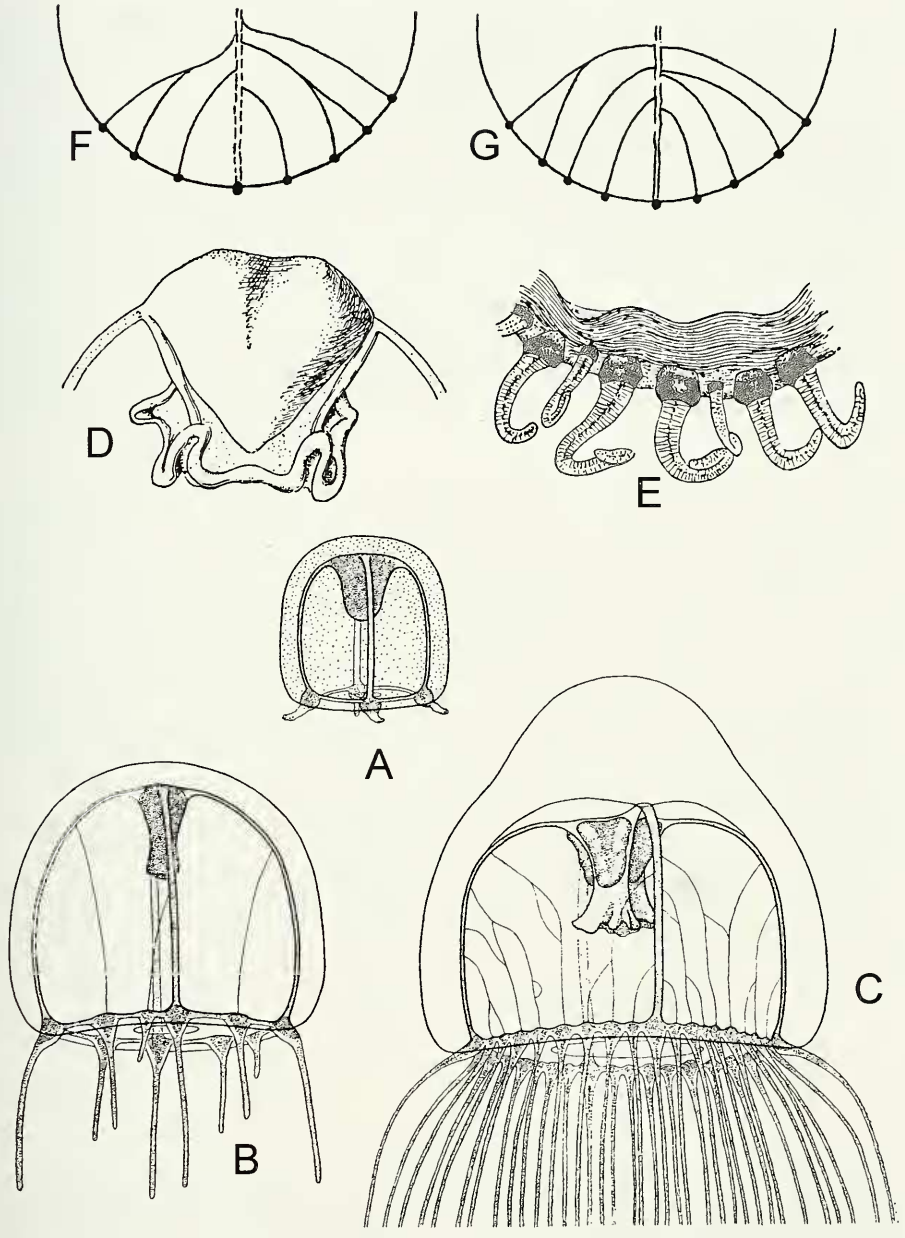

FIG. 27

Trichydra pudica Wright, 1857; medusa stage. A-C from Edwards (1973), D-E after Hartlaub (1917), F-G from Russell (1953). (A) Newly liberated medusa, height 0.15 mm. (B) Intermediate growth stage, diameter 1.2 mm. (C) Mature male medusa, bell height 3.3 mm, diameter 3.6. (D) Manubrium with mature gonads, medusa from plankton. (E) Bell rim with tentacle bases, note bulb-like swelling when the tentacles are contracted. (F-G) Schemata showing the variation of the branching pattern of the fine, centripetal canals.

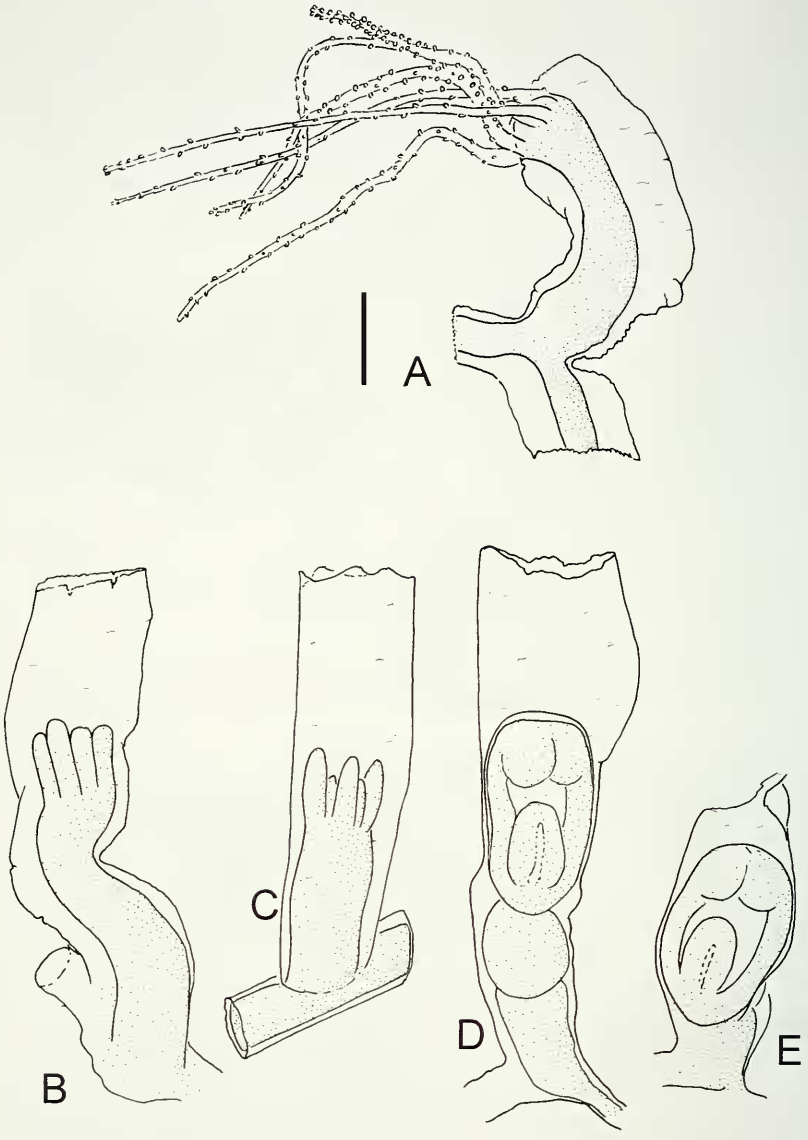

FIG. 28

Trichydra pudica Wright, 1857; after material from Ireland (BMNH 1954.11.13.126, permanent slide-preparation); scale bar valid for all section, equals 0.1 mm. (A) Polyp with extended tentacles. (B-C) Polyps that are completely retracted into perisarc tube. (C-D) Gonothecae with blastostyles and maturing medusae.

OTHER DATA: The development of the medusae and the correlation of size and tentacle number are described by Russell (1953) and Edwards (1973).

BIOLOGY: The hydroid was found on shells and stones (Wright, 1857; Hammond, 1957), clinker (=coal burning waste; Rees, 1941; Edwards, 1973), and the

ascidian *Microcosmos claudicans* (Savigny) (Hamond, 1957). The observations of Edwards (1973) indicate that medusae are liberated from April to June, becoming mature by July or August (Firth of Clyde). The length of life is about 2 months.

DISTRIBUTION: The hydroid is known from the British Isles (English Channel, North Sea, western and eastern Scotland, western Ireland; Wright, 1857; Hincks, 1868; Rees, 1941; Hamond, 1957; Russell, 1957; Edwards, 1973; this study). The medusa occurs in the British Isles (Russell, 1953; Fraser, 1974), the northern part of the North Sea (Hartlaub, 1917), and in the north-eastern Pacific along the coast of British Columbia (Foerster, 1923; Arai & Brinckmann-Voss, 1980). Goy *et al.* (1991) also reported it from the eastern Mediterranean, but their single medusa had only eight tentacles and the identification is not convincing. The occurrence in the Mediterranean needs reconfirmation. The remaining records of both medusae and polyp suggest a more northern Boreal distribution. Type locality: North Sea, Scotland, Firth of Forth; on shells and stones.

REMARKS: Most unusual for an Anthoathecata, this species has gonozooids in gonothecae, just like *Halitiara formosa*. The gonothecae of *Trichydra pudica* were first mentioned in a brief species diagnosis given by Werner (1984), presumably based on unpublished observations. The gonothecae observed in this study were found in a sample identified as *T. pudica* by M. J. Delap and E. T. Browne. As there is no information on the mature medusa connected to this sample, the identification remains somewhat uncertain. The polyps of *Halitiara formosa* are identical, but the medusa does not occur in the region. Some small Campanulinidae are also similar, though their hydrothecae usually have a pedicel and an operculum formed by perisarc flaps (comp. Cornelius, 1995a).

The medusa of *T. pudica* was first described as *Pochella polynema* by Hartlaub (1917) and it was Edwards (1973) who linked it unambiguously with the hydroid *T. pudica*. The hypothetical linking of *T. pudica* with *Lizzia blondina* by Rees (1941) thus proved to be incorrect. The medusa is very rare and at first glance, or in damaged material from net catches, can be mistaken for a *Podocoryna* species (see Schuchert, 2008a). The cruciform mouth and the absence of oral nematocyst clusters however allow them to be distinguished easily. Also the cnidome could be different, but unfortunately the cnidome of *Trichydra* remains inadequately known.

ACKNOWLEDGEMENTS

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