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Two new species of *Chionodes* Hübner from Ecuador, with a summary of known Galapagos records of Gelechiidae (Lepidoptera)

Patrick SCHMITZ & Bernard LANDRY
Muséum d'histoire naturelle, C. P. 6434, CH-1211, Geneva, Switzerland.
E-mails: patrick.schmitz@ville-ge.ch / bernard.landry@ville-ge.ch

Two new species of *Chionodes* Hübner from Ecuador, with a summary of known Galapagos records of Gelechiidae (Lepidoptera). - Two new species of the genus *Chionodes* Hübner, 1825 (Lepidoptera, Gelechiidae) from Ecuador are described and illustrated. *Chionodes stefaniae* sp. n. occurs in the Galapagos on the islands of Floreana, Isabela, Pinta, Pinzon, Rabida, San Cristobal, and Santa Cruz, where it is believed to be endemic. *Chionodes manabiensis* sp. n. occurs on the Ecuadorian coast in Machalilla National Park. The previous Galapagos records of *Aristotelia howardi* Walsingham, 1909, and *Stegasta bosqueella* Chambers, 1875 were erroneous. *Stegasta zygotoma* Meyrick, 1917 is reported from the Galapagos for the first time. Altogether, five species records of Gelechiidae are now considered valid for the Galapagos.

Keywords: Lepidoptera - Gelechiidae - new species - *Chionodes* - endemic - Galapagos Islands - Manabi.

INTRODUCTION

The Gelechiidae represent one of the largest families of Lepidoptera with more than 4,530 species described (Hodges, 1998). Kaila (2004: 322) reported that the monophyly of the group is supported by 12 synapomorphies of which one is unique, i.e. the presence on the forewing of a row of narrow scales ventrally on vein R in females only. Genus *Chionodes* Hübner, 1825 is found throughout the Holarctic region and in the Neotropics. The largest number of species occurs in North America and in the mountain zones of the Palearctic region including the Arctic (Huemer & Sattler, 1995). An apparent apomorphy for *Chionodes* is the presence of a caecum on the phallus (Hodges, 1999: 15). In his revision of the North American species, Hodges (1999: 20, 24, 25) recognized and characterized six species-groups for the 187 species occurring in America North of Mexico and the 21 species in the Neotropical region. The two species described here belong to the phalacrus-group which already contains five described species in the Neotropics (i.e., south of the U.S.A.): *C. argosema* (Meyrick, 1917) described from the Ecuadorian Andes, *C. consona* (Meyrick, 1917) described from Peru, *C. donatella* (Walker, 1864) described from Jamaica, *C. eburata*

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(Meyrick, 1917) described from Colombia, and *C. phalacrus* (Walsingham, 1911) described from Mexico. Two undescribed species from Brazil were also recorded to belong to this group by Hodges (1999: 165). The known host plants of the group are in the Malvaceae: *Abutilon*, *Hibiscus*, *Malacothamnus*, *Malvastrum*, *Sida*, *Sidalcea*, *Sphaeralcea*, and *Wissadula* (Hodges, 1999).

As part of a project to document the entire microlepidopteran fauna of the Galapagos, dissected specimens of the Gelechiidae species collected by Bernard Landry (BL) in the Galapagos were critically examined by him with the help of Dr Klaus Sattler at the Natural History Museum, London, England (BMNH) in 2000. Among them was a new species of *Chionodes* which was used as an outgroup to study the evolution of the Galapagos endemic genus *Galagete* Landry (Autostichidae; Schmitz *et al.*, submitted). And while searching for potential taxa possibly related to *Galagete* at Machalilla National Park, on the coast of continental Ecuador, north of Guayaquil, Patrick Schmitz (PS) came upon another new species of *Chionodes* that proved to be different, yet very similar to the Galapagos species and to a few other described species. These two new species are described below.

So far only four valid species of Gelechiidae have been reported for the Galapagos. Schaus (1923) reported *Aristotelia howardi* Walsingham, 1909, and *Stegasta bosqueella* Chambers, 1875. However, we can report here that these two records were erroneous and respectively represent *Aristotelia naxia* Meyrick, 1926, described from the Galapagos, and *Stegasta zygotoma* Meyrick, 1917, described from Colombia, Ecuador, and Peru, and for which Clarke (1969) selected a lectotype from Ecuador, Huigra, 4,500 ft. The two erroneous records and *A. naxia* were subsequently listed also by Linsley & Usinger (1966) along with *Gelechia protozona* Meyrick, 1926 and *G. gnathodoxa* Meyrick, 1926, which Landry (2002) transferred to the Autostichidae. The other previous gelechiid records are those of the widespread invasives *Sitotroga cerealella* (Olivier, 1789) and *Tuta absoluta* (Meyrick, 1917) in Causton *et al.* (2006). Collections hold at least 12 more Gelechiidae species from the Galapagos, and they will be treated in a forthcoming paper.

MATERIAL AND METHODS

The 57 specimens forming the basis of this study were collected mostly by BL during three expeditions to the Galapagos in 1989, 1992, and 2002. Other specimens were collected by both of us during two more expeditions on the archipelago in 2004 and 2005, and by PS in the Galapagos and in Machalilla National Park in 2006. Seven additional specimens come from the collection of the Invertebrates Department of the Charles Darwin Research Station, Santa Cruz Island, Galapagos (CDRS). In addition to this institution, specimens will be deposited in the Natural History Museum, London, England (BMNH), the Canadian National Collection of Insects, Ottawa, Canada (CNC), and the Muséum d'histoire naturelle, Geneva, Switzerland (MHNG).

The manner of giving the label data of the holotypes and paratypes is presented in Landry (2006) and so are the methods used for specimen collecting, genital preparation, forewing length measurement, and illustrations. The terminology regarding genitalia follows Hodges (1999).

DESCRIPTIONS

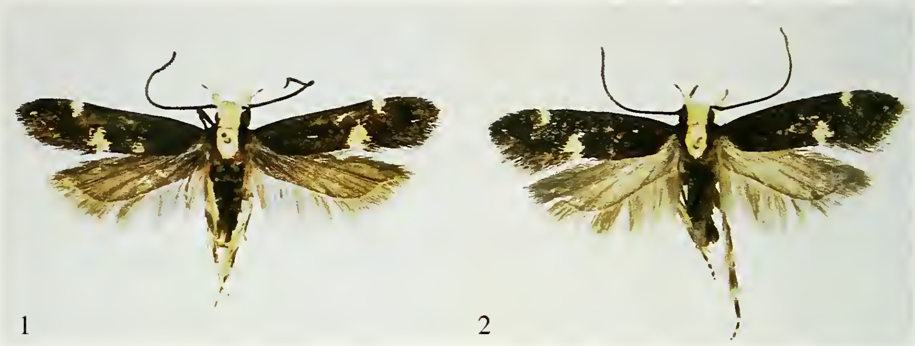
Chionodes stefaniae sp. n. Figs 1, 3-8

Material examined: Holotype ♂, [1] "ECU[ADOR]., GALAPAGOS/ Isabela, V[olcan]. Darwin/ 630 m[eters] elev[ation]., 17.v.1992/ M[ercury]V[apour]L[amp], *leg[it]*. B[ernard]. Landry". [2] "HOLOTYPE/ Chionodes/ stefaniae/ Schmitz & Landry". Specimen in perfect condition except for small hole in left forewing. Deposited in MHNG.

Paratypes, Ecuador: 19 ♂, 29 ♀, from the Galapagos Islands, collected with an ultraviolet light and by B. Landry, unless specified otherwise. – *Floreana*: 1 ♀, close to Loberia, G[lobal]P[ositioning]S[ystem]: S 01°17.002', W 90°29.460', 11.iv.2004 (P. Schmitz); 2 ♀, Las Cuevas, 23.iv.1992, M[ercury]V[apour]L[amp]; 1 ♂ (dissected, slide MHNG 3204), Zona arida, 300 m[e]t[er]s, Finca Las Palmas, 26.xii.1997, UVL-F.L. (L. Roque). – *Isabela*: 1 ♂, V[olcan]. Darwin, campamento base, 1.iii.2000, Malaise trap (L. Roque); 1 ♀, 1 km. W [of] Puerto Villamil, 3.iii.1989, MVL; 1 ♀, 11 km N Puerto Villamil, 9.iii.1989, MVL; 2 ♀, 11 km N Pto Villamil, 13.iii.1989, MVL; 1 ♂ (dissected, slide MHNG 3201), NE slope [Volcan] Alcedo, Los Guayabillos camp, GPS: elev[ation]. 869 m, S 00°24.976' W 91°04.617', 2.iv.2004, 4h00-5h30 (B. Landry, P. Schmitz); 1 ♀, [Volcan] Alcedo, lado NE, 200 m, camp arida alta, 14.iv.2002 (B. Landry, L. Roque); 2 ♀, [Volcan] Alcedo, lado NE, 400 m, camp pega-pega, 15.iv.2002 (B. Landry, L. Roque); 1 ♀ (dissected, slide MHNG 3208), [Volcan] Alcedo, lado NE, low arid zone, bosq[ue]. palo santo, 18.iv.2002 (B. Landry, L. Roque); 3 ♂, V. Alcedo, 570 m elev., 11.x.1998 (L. Roque). – *Pinta*: 1 ♂ (dissected, slide MHNG 3202), 1 ♀, 200 m elev., 16.iii.1992, MVL; 1 ♀, 400 m elev., 17.iii.1992, MVL; 1 ♀, N 00°34.476', W 90°45.102', 372 m elev., 16.iii.2006 (P. Schmitz, L. Roque); 1 ♂, 400 m elev., 18.iii.1992, MVL; 3 ♀, N 00°34.591', W 90°45.137', 421 m elev., 18.iii.2006 (P. Schmitz, L. Roque). – *Pinzon*: 1 ♀ (dissected, slide PS028), 01.v.2003 (L. Roque). – *Rabida*: 1 ♀, Tourist trail, 3.iv.1992, MVL. –*San Cristobal*: 1 ♀ (dissected, slide MHNG 3209), antiguo botadero, ca. 4 km SE Pto Baquerizo, GPS: 169 m elev., S 00°54.800', W 089°34.574', 25.ii.2005; 1 ♂ (dissected, slide MHNG 3203), near Loberia, GPS: elev. 14 m, S 00°55.149', W 89°36.897', 16.iii.2004 (B. Landry, P. Schmitz). – *Santa Cruz*: 1 ♂, Tortuga Res[erve]., W [of] Santa Rosa, 6.ii.1989, MVL; 1 ♀, NNW [of] Bella Vista, GPS: 225 m elev., S 00°41.293', W 090°19.665', 18.ii.2005 (B. Landry, P. Schmitz); 1 ♀, E[stacion]. C[ientifica]. C[harles]. D[arwin]., 7.iii.1992; 1 ♀, transition zone, recently cut road, GPS: S 00°42.528', W 90°18.849', 12.iii.2004 (B. Landry, P. Schmitz); 1 ♀, El Barranco, ECCD, 13.iii.2000, MVL Trap (L. Roque); 1 ♂, Finca S[teve]. Devine, 17.iii.1989, MVL; 1 ♂, ECCD, El Barranco, S 00°44.291', W 90°18.107', 22 m elev., 23. iii.2006 (P. Schmitz); 2 ♂, Finca Vilema, 2 km W [of] Bella Vista, 1.iv.1992, MVL; 1 ♀, C[harles] D[arwin] R[esearch] S[tation], [El] Barranco, 20 m elev., 30.iv.2002; 4 ♂ (one dissected, slide MNHG 3212), 3 ♀ (one dissected, slide MHNG 3207), Los Gemelos, 27.v.1992, MVL; 1 ♂, Barranco, CDRS, 23.x.2001 (L. Roque). Deposited in the BMNH, CDRS, CNC, and MHNG.

Etymology: We are pleased to name this species in honour of Stefania Bertoli-Schmitz for her love and support to PS through the last seven years.

Diagnosis: Among the species of *Chionodes*, *C. stefaniae* is similar in wing pattern to *C. argosema*, *C. donatella*, *C. manabiensis* sp. n., *C. mariona* (Heinrich, 1921), and *C. petro* Hodges, 1999 of the phalacrus-group of Hodges (1999). In male genitalia, *C. stefaniae* differs from *C. argosema*, *C. donatella*, *C. mariona*, and *C. petro* in having a shorter mesial projection of the uncus and short, curved and rather stout valval projections as opposed to long and thin projections in *C. argosema* (Clarke, 1969), and short and straight projections in the other three species (Hodges, 1999). Furthermore, *C. stefaniae* differs from *C. donatella*, *C. mariona*, and *C. petro* in having the male abdominal tergum VIII wider than long versus about twice as long as wide (Hodges, 1999: pl. W figs 16, 17, 20), and in the female, there is a modification at the posterior margin of tergum VII while modifications occur at the posterior margin of abdominal tergum VI and anterior margin of tergum VII in the other species (Hodges,



Figs 1-2
Holotypes of *Chionodes* spp. (1) *C. stefaniae*. (2) *C. manabiensis*.

1999: pl. VV figs 11-13). *Chionodes stefaniae* differs from *C. manabiensis* in several characters mentioned in the Diagnosis and Description of this species, below.

Description: *MALE* (n=20) (Figs 1, 3-5): Head off-white with yellowish orange scales on forehead. Haustellum dark brown; maxillary palpus off-white, 4-segmented. Labial palpus dark brown on first segment; second segment off-white to yellowish orange with broad scale brush; third segment off-white to yellowish orange, slender, dark brown on distal 1/3 to 1/2. Antennal scape dark brown with white scales ventrally; flagellum dark brown. Thorax off-white, tegula and metathorax dark brown. Foreleg coxa, tibia, femur and tarsomeres dark brown with white at apices of tarsomeres I and V. Midleg and hindleg femora and tibiae dark brown at base, apices 1/3 off-white; spurs white; tarsomeres I-V mostly dark brown with white at apex of each segment. Wingspan: 9.3-11.0 mm (Holotype: 11.0 mm). Forewing dark brown with pair of prominent off-white patches with yellowish orange scales on costal margin at 3/4 and on inner margin at end of fold; sometimes with slightly darker brown markings visible as two small spots submedially in middle, one above the other, and another spot post-medially above second off-white patch; with some scattered off-white scales between patches, on termen, and around both small spots; fringe dark brown. Hindwing dark greyish brown, fringe pale greyish brown. Abdomen dark brown dorsally, off-white ventrally; tergum VIII with more thickly sclerotized anterior margin a broad inverted V, with posterior margin broadly rounded; sternum VIII with lateral margins slightly convex and with conspicuous striae, anterior margin bearing pair of submesial lobes, posterior margin with broad and short rounded lateral lobes (apically folded on Fig. 5).

Male genitalia (n=4) (Figs 3, 4). Uncus with broadly rounded anterobasal lobes with stout setae ventrally and few hairlike setae on apical margins; with small, blunt, apicomesial projection. Median hook of gnathos rather long and thin, slender from base to apex, upturned and pointed apically. Dorsal connection of tegumen wide; pedunculi short and broad, shorter than vinculum. Valva with long and slender sickle-like projection of 1/2-1/3 X length of tegumen; with small recurved knob at lateral base of each projection; sacculus short, with few setae at base ventrally. Vinculum tapering to narrowly rounded saccus. Phallus narrow, with distinct, sclerotized rim around

Figs 3-5

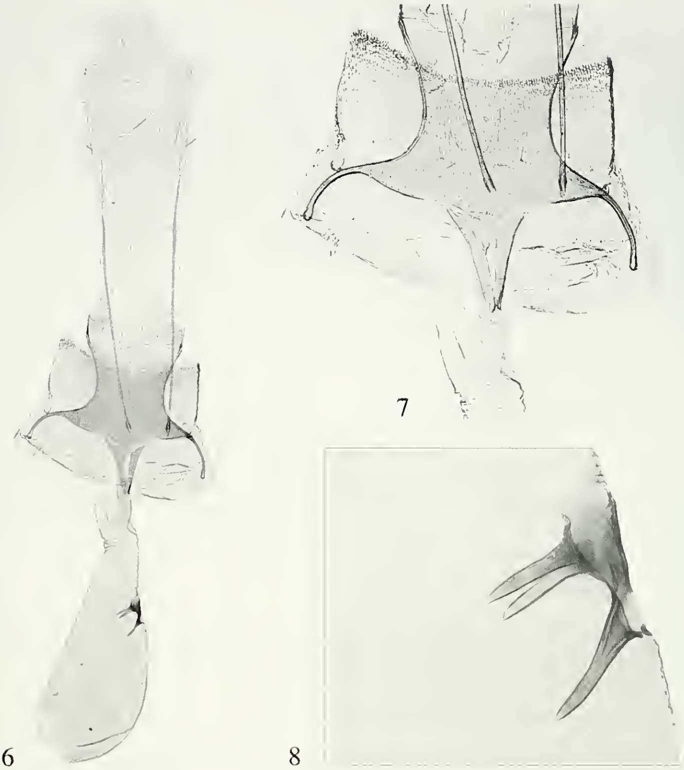
Male genitalia of *Chionodes stefaniae* from specimen on slide MHNG 3201. (3) Whole genitalia without phallus. (4) Phallus; (5) Abdominal segment VIII.

opening of ductus ejaculatorius, broadest at this point; slightly upturned at 5/6 of length; with long, rodlike caecum of about 1/3 X length of phallus; vesica without spines or cornuti.

FEMALE (n=29): Colour as in male. Antenna slightly thinner than that of male. Female wingspan: 8.7-10.9 mm. Tergum VII apically modified, with low, median depression associated with thin canal directed proximally.

Female genitalia (n=5) (Figs 6-8). Papillae anales slightly longer than wide. Posterior apophyses long, straight, very slightly enlarged at apex (about 2.4 X length of papillae), reaching base of antrum. Anterior apophyses partly fused with antrum, free proximal section arising from lateral margin of antrum near base, down curved with slightly enlarged apex. Antrum well developed with short, longitudinal sclerotized band in dorsal wall; also with heavily sclerotized lateral bands of about half length of ductus bursae and fused toward apex, with left band bent toward right one. Ductus bursae short, of medium girth (width = 0.2-0.25 X its length), slightly constricted at apex of lateral bands of antrum. Inception of ductus seminalis at base of corpus bursae. Corpus bursae elongate, widening and rounded at proximal end, with light scobination; signum situated posteriad middle of corpus bursae, triangular with heavily sclerotized, inwardly directed, large spine arising from each angle, sometimes with small extra spine.

Biology: The moths were collected at light in February, March, April, May, October, and December from sea level to 869 m.



FIGS 6-8

Female genitalia of *Chionodes stefaniae* from specimen on slide MHNG 3207. (6) Whole genitalia. (7) Segment VII. (8) Signum.

DISTRIBUTION: Currently known only from the Galapagos islands of Floreana, Isabela, Pinta, Pinzon, Rabida, San Cristobal, and Santa Cruz; presumed to be endemic to the archipelago.

REMARKS: This species and the following one are apparently more closely related to each other than to any of the other *Chionodes* species on the basis of the short mesial projection of the uncus, the curved and rather short valval projections, the wide abdominal tergum VIII of the male, and the modified posterior margin of tergum VII of the female.

Chionodes manabiensis sp. n. Figs 2, 9-14

MATERIAL EXAMINED: Holotype ♂, [1] "ECU[ADOR], Manabi, Parque nacional/ Machalilla, Los Frailes/ S 01°29.340', W 80°46.686/ 40 m[eters] elev[ation]., u[ltra] v[iolet] l[ight], 25.iv.2006/ *leg[it]*. P[atrick]. Schmitz". [2] "HOLOTYPE/ Chionodes/ manabiensis/ Schmitz & Landry". Specimen in perfect condition except for small notch in left hindwing. Deposited in MHNG.

Paratypes, Ecuador: 4 ♂, 3 ♀, from Manabi, collected at uvl by P. Schmitz. 1 ♀, Puerto Lopez, Hosteria Mandala, S 01°32.955', W 80°48.617', 10 m elev., 24.iv.2006; 3 ♂ (one dissected, slide MHNG 3187), with same data as holotype; 1 ♀ (dissected, slide MHNG 3210), Parque nacional Machalilla, Agua Blanca, S 01°31.421', W 80°46.081', 45 m elev., 26.iv.2006;

FIGS 9-11

Male genitalia of *Chionodes manabiensis* from specimen on slide MHNG 3187. (9) Whole genitalia without phallus. (10) Phallus. (11) Abdominal segment VIII.

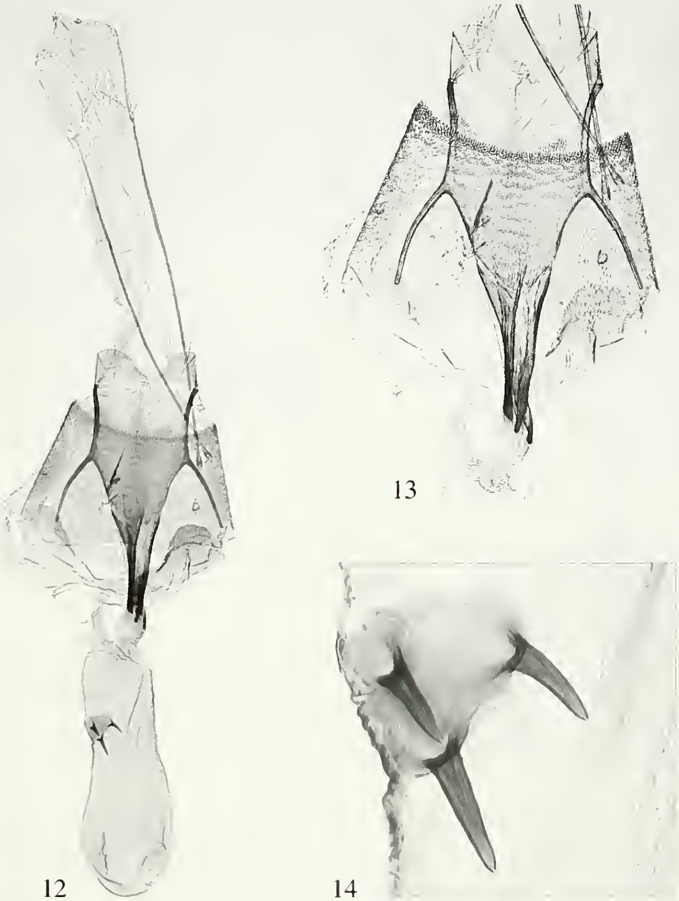
1 ♀, Parque nacional Machalilla, Los Frailes, S 01°29.369', W 80°46.805', 45 m elev., 27.iv.2006; 1 ♂, Parque nacional Machalilla, Los Frailes, S 01°29.053', W 80°47.064', 86 m elev., 28.iv.2006. Deposited in the BMNH and MHNG.

ETYMOLOGY: The name of *C. manabiensis* is derived from that of the type locality.

DIAGNOSIS: Based on wing pattern, *C. manabiensis* is impossible to distinguish from *C. argosema*, *C. donatella*, *C. mariona*, *C. petro*, and *C. stefaniae* of the phalacrus-group of Hodges (1999), but the same diagnostic characters mentioned under the diagnosis for *C. stefaniae* can be applied to separate *C. manabiensis* from *C. argosema*, *C. donatella*, *C. mariona*, and *C. petro*. *Chionodes manabiensis* differs from *C. stefaniae* in the slightly darker ground colour of the forewing, in the presence of a pair of patches of modified scales on abdominal tergum VIII of the males, in the female modification of tergum VII, which is located more medially and is associated with a low, elongate crest, and in genital characters as mentioned below.

DESCRIPTION: *MALE* (n=5) (Figs 2, 9-11): As *C. stefaniae*, except forewing and abdomen darker; wingspan: 9.0-10.0 mm (Holotype: 10.0 mm); abdominal tergum VIII more narrowly rounded apically, with pair of patches of modified scales, with anterior margins more rounded; abdominal sternum VIII slightly longer, less striated laterally, with lobes of anterior margin less heavily sclerotized.

Male genitalia (n=1) (Figs 9, 10). As in *C. stefaniae*, except uncus with more heavily sclerotized setae ventrally; tegumen longer than vinculum; long projection of valva less strongly bent and broader at base; small recurved lobe at base of projection slightly longer; sacculus shorter, with more setae ventrally; vinculum broader, especially at apex; phallus more broadly bent upward at 3/4 of length.



Figs 12-14

Female genitalia of *Chionodes manabiensis* from specimen on slide MHNG 3210. (12) Whole genitalia. (13) Segment VII. (14) Signum.

FEMALE (n=3): As in *C. stefaniae*, except colour as in male of *C. manabiensis*; wingspan: 9.5-11.9 mm; modification of tergum VII located more medially and associated with low, elongate crest.

Female genitalia (n=1) (Figs 12-14). As in *C. stefaniae*, except papillae anales longer (1.5 X longer than broad); posterior apophyses longer (about 3.4 X length of papillae); antrum with sclerotized band in dorsal wall much longer, apically reaching beyond margin of sternum VII, proximally reaching apices of lateral bands and more thickly sclerotized; lateral bands narrow, tapering gradually, at least 2 X length of those of *C. stefaniae*, with left one bending over right one, free apically.

Biology: The adults were attracted to light in April from sea level to 86 m.

Distribution: Currently known only from Machalilla National Park and the adjacent town of Puerto Lopez on the Ecuadorian coast (province of Manabi).

REMARKS: The divergence in a DNA fragment of the Cytochrome Oxidase mitochondrial gene (555 base pairs long) between *C. stefaniae* and *C. manabiensis* is 6.7% (GenBank accession numbers EF423724 and EF423725).

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APPENDIX

Resumen. Dos especies nuevas del género *Chionodes* Hübner en Ecuador con un resumen de las especies de Gelechiidae previamente reportadas para Galapagos (Lepidoptera). - Dos especies nuevas del genéro *Chionodes* Hübner, 1825 (Lepidoptera, Gelechiidae) de Ecuador son descritas e illustradas. *Chionodes stefaniae* sp. n. occurre en las Galápagos sobre las islas de Floreana, Isabela, Pinta, Pinzón, Rábida, San Cristóbal y Santa Cruz, donde parece ser endémica. *Chionodes manabiensis* sp. n. occurre en la costa ecuatoriana, Parque Nacional de Machalilla. Las menciónas anteriores de *Aristotelia howardi* Walsingham, 1909 y de *Stegasta bosqueella* Chambers, 1875 para Galapagos eran erróneas. *Stegasta zygotoma* Meyrick, 1917 es reportada en las Galápagos por la primera vez. En conjunto, cinco menciónas de especies de Gelechiidae ahora se consideran válidas para las Islas Galápagos.

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A new *Sapromyza* Fallén, 1810, from the Swiss Alps (Diptera, Lauxaniidae)

Bernhard MERZ
Muséum d'histoire naturelle, Département d'entomologie, C. P. 6434,
CH-1211 Genève, Switzerland.
E-mail: bernhard.merz@ville-ge.ch

A new *Sapromyza* Fallén, 1810, from the Swiss Alps (Diptera, Lauxaniidae). - A new Western Palaearctic *Sapromyza* with a rather well-developed presutural dorsocentral seta is described and illustrated. Its phylogenetic position is briefly discussed. Keys to the Western Palaearctic genera of the *Sapromyza-Lyciella* group of genera and to the Western Palaearctic species of the *Sapromyza obsoleta* group are given.

Keywords: Diptera - Lauxaniidae - *Sapromyza* - new species - Switzerland.

INTRODUCTION

Sapromyza Fallén, 1810, is a heterogeneous genus of Lauxaniidae which is widespread in the Old and New World. Some 600 species have been described so far as «*Sapromyza*», and over half of them are still placed in this genus. It belongs to the subfamily Lauxaniinae and is defined by negative characters, like the absence of a postsutural intra-alar seta, without a well-developed presutural dorsocentral seta, without setulae on the anepimeron, a flat face, bare veins, and antennae without particularities. Already Stuckenberg (1971, p. 570) pointed out that the species of *Sapromyza* are grouped together through a paraphyletic assemblage of characters and their separation from *Lyciella* Collin, 1948, and other genera is not always possible. *Lyciella*, for instance, differs from *Sapromyza* by the presence of a strong presutural dorsocentral seta and some fine setulae on the anepimeron (see Merz, 2003, for details) but some «intermediate» species of *Sapromyza* with 1-3 (smaller) presutural dorsocentral setae are known (best seen in the type-species of *Sapromyza*, *S. obsoleta* Fallén) and some *Lyciella* lack the fine setulae on the anepimeron (these species are now placed in two different genera: *Poecilolycia* Shewell, 1986, and *Pseudolyciella* Shatalkin, 2000). Stuckenberg (1971) observed also that most Australasian and Neotropical «*Sapromyza*» have a strong presutural dorsocentral seta but he did not propose new genera for them.

Recently, a pair of a «*Sapromyza*» with a distinct presutural dorsocentral seta was found in Switzerland. It is described here as a new species of the *S. obsoleta* group which includes in the Western Palaearctic Region the following species: *S. amabilis* Frey, 1930, *S. apicalis* Loew, 1847, *S. obsoleta* Fallén, 1820, *S. schnabli* Papp, 1987,

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S. setiventris Zetterstedt, 1847, and *S. simplicior* Hendel, 1908. The group is defined by the following characters: body subshining yellow brown (partly grey in *S. simplicior*), frons rather strongly shining; apex of postpedicel black; head in profile with higher gena than width of postpedicel and wide parafacial; postpedicel dorsally concave, about twice as long as wide; abdomen without black spots on tergites.

The two specimens from Switzerland differ from other Western Palaearctic genera superficially resembling *Sapromyza* (e. g., *Aulogastromyia*, *Cnemacantha*, *Eusapromyza*, *Lyciella*, *Mycterella*, *Neoparoecus*, *Poecilolycia*, *Pseudolyciella*, *Tricholauxania*) in diagnostic characters (Papp & Shatalkin, 1998; Shatalkin, 2000; Merz, 2003, and see key below). It is therefore reasonable to place this species in *Sapromyza* pending a cladistic analysis of the genera involved in this complex.

MATERIAL AND METHODS

The specimens of this study are deposited in the Muséum d'histoire naturelle Genève (MHNG). Terminology follows the first chapter in Papp & Darvas (2000), except for the terms of the antennae which are according to Stuckenberg (1999).

SYSTEMATIC PART

Sapromyza alpina sp. n. Figs 1-15

MATERIAL: Holotype ♂, **Switzerland**: VS, Jeitzinen, 1550 m, 26.VI.1999, Merz & Eggenberger (MHNG). Paratype: 1♀, **Switzerland**: VS, Visperterminen, 1400 m, 24.VII.1993, leg. B. Merz (MHNG).

The holotype is double mounted on a minutien pin on a polyporus block. It is in moderate condition, with some setae on head and mesonotum broken.

ETYMOLOGY

The name is derived from the Alps, the mountains of the type locality.

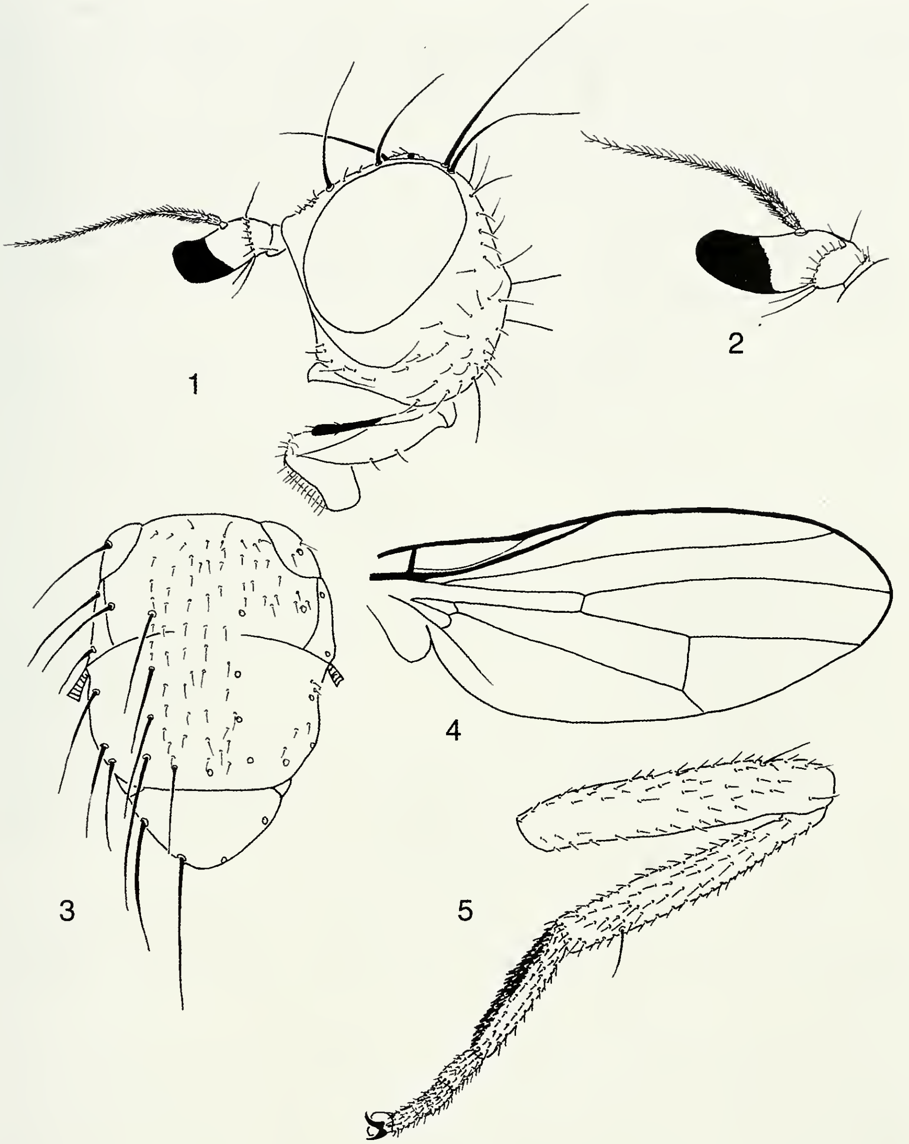
DIAGNOSIS

A yellow brown, rather strongly shining species which is placed despite the presence of a presutural (and 3 postsutural) dorsocentral setae in *Sapromyza*. Apical half of postpedicel and palpus black; 4-6 rows of short acrostichal setae present; no postsutural intra-alar seta; 2 katepisternal setae; no anepimeral setae or setulae; anterior tarsus contrastingly black; hind basitarsus in male ventrally along entire length with a brush of black setulae; wing hyaline, without setulae on veins; hind margins of tergites in female without longer setae or setulae; terminalia in both sexes characteristic.

DESCRIPTION MALE

Wing length: 4.1 mm.

Head: *Colouration* - Ground colour yellow brown, with strongly shining frons, fronto-orbital plates, and occiput; face paler yellowish, matte; parafacial and gena slightly microtrichose, dull; occiput dorsally of neck with a white, more or less shining patch; apical half of postpedicel, arista except for basal two segments, and apical half of palpus contrastingly black, sharply separated from yellow bases (especially in postpedicel). *Structure* - In profile 1.1 times higher than long, with strongly developed occiput; gena with 2 somewhat irregular rows of black setulae along ventral margin;



Figs 1-5

Sapromyza alpina sp. n. (1) Head, lateral view (female paratype). (2) Antenna in largest extension (female paratype). (3) Thorax, dorsal view (female paratype, setae only drawn on left side, setulae on right side). (4) Wing (male holotype, drawn in situ). (5) Hind leg of male holotype, anterior view.

1.2 times higher than width of postpedicel and about one third as high as compound eye; the latter about 1.3 times higher than long; parafacial about one third as wide as width of postpedicel; frons medially with a slight depression; about 1.7 times wider than compound eye and about 1.15 times wider than long (measured between posterior margin of posterior ocelli and lunule); in anterior third with about 15 black setulae; face more or less flat. *Antenna* – Scape shorter than wide, dorsally with few black setulae; pedicel about as long as wide, apically with the usual circle of black setulae and one stronger seta dorsally; postpedicel about twice as long as wide, dorsally slightly concave, tip apico-dorsally smooth; arista short setulose, longest rays about as long as diameter of arista at base. *Mouthparts* – Palpus with short, black, stiff setulae. *Chaetotaxy* – 2 probably reclinate fronto-orbital setae (all broken), 1 short ocellar seta reaching base of anterior fronto-orbital seta, inserted distinctly within the triangle of 3 ocelli; 1 inclinate medial vertical seta; 1 eclinate lateral vertical seta; postocellar seta inclinate, short, about as long as longest postocular setae; the latter in one row, and one additional row posterior on occiput.

Thorax: *Colouration* – Everywhere yellow brown, mesonotum very thinly microtrichose and therefore conspicuously subshining; pleura less shining. *Structure* – Mesonotum in lateral view almost flat, in dorsal view about 1.2 times longer than wide. *Chaetotaxy* – Acrostichal setae anterior to transverse suture in about 6 irregular rows, posterior to suture in 4 rows; setulae of medial two rows slightly longer than those of lateral rows; prescutellar acrostichal seta probably at most as long as presutural dorsocentral seta (judging from size of alveolus); 1+3 dorsocentral setae, the presutural seta distinct, but slightly shorter than anterior postsutural seta; 1 presutural intra-alar seta; 2 supra-alar setae; 1 postalar seta; no posterior intra-alar seta; 1 postpronotal seta; 2 notopleural setae, the posterior slightly shorter and weaker; 2 (pairs of) scutellar setae, no additional setulae between them; 1 proepisternal seta; 1 anepisternal seta (and some black setulae in posterior half); 2 katepisternal setae; anepimeron entirely bare, without setulae ventrally of wing base; prosternum with few black setulae.

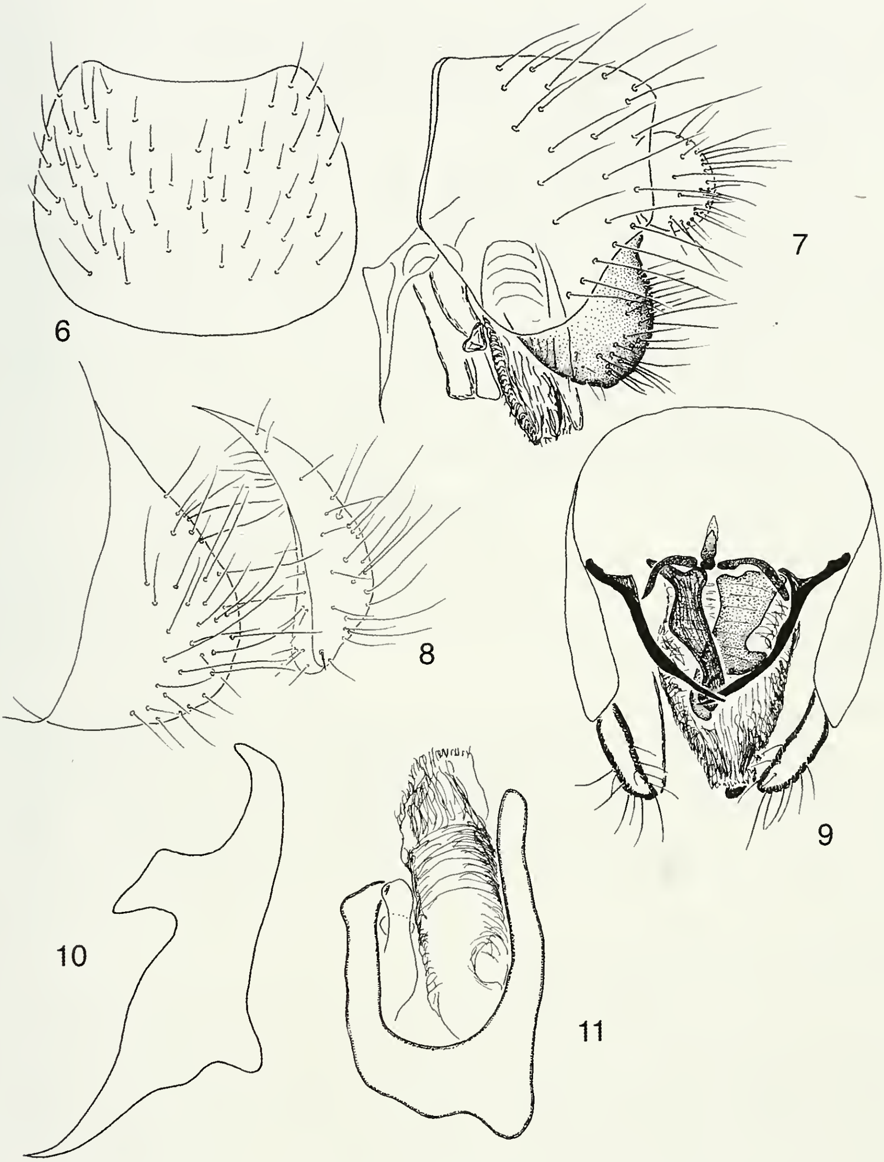
Wing (Fig. 4): Surface slightly yellowish, entirely hyaline; all veins bare; black setulae on costa ending halfway between R2+3 and R4+5; distance between R-M and DM-Cu on M1+2 about twice the length of DM-Cu; last section of M1+2 about 1.5 times longer than penultimate section (between crossveins).

Legs (Fig. 5): Yellow brown, but anterior tarsus contrastingly black; last 4 tarsal segments of mid and hind leg increasingly darker towards tip; all tibiae with a short black preapical dorsal seta; fore femur without ctenidium; hind femur with a subapical dorsal seta; mid tibia with one apical seta ventrally; hind basitarsus ventrally throughout length with a dense brush of short black setulae.

Male abdomen and terminalia (Figs 6-11): Yellow brown, less shining than mesonotum; tergites black setulose, without longer setulae at hind margins; sternite 5 (Fig. 6) posteriorly smoothly concave; epandrium in profile (Fig. 7) slightly higher than long; cercus distinctly protruding; surstylus (Fig. 8) free, setulose in ventral half, over twice as wide as high, evenly curved, without tooth on inner side; hypandrium (Fig. 9) not closed basally, with two acute clasps; pregonite (Fig. 10) of irregular shape, apically bilobate, the longer tooth apically slightly hooked; postgonite (Fig. 11) bare, consisting of two protuberances of different length; aedeagus as long as surstylus, apically with short, fine setulae.

DESCRIPTION FEMALE

Very similar to male, with following differences (condition in male in parentheses).



FIGS 6-11

Sapromyza alpina sp. n., male holotype. (6) Sternite 5. (7) Genitalia, lateral view. (8) Surstylus in largest extension. (9) Genitalia, ventral view. (10) Pregonite in largest extension. (11) Postgonite and aedeagus.

Wing length: 4.0 mm.

Head (Figs 1-2): Gena with only one distinct row of black setulae (two rows); frons about 1.25 times wider than long (1.15 times), in anterior half with about 20 black setulae (about 15 setulae); 2 reclinate fronto-orbital setae (broken off); ocellar seta ending slightly anterior of alveolus of anterior fronto-orbital seta (ending on level of alveolus of anterior fronto-orbital seta); postocellar seta about twice as long as longest postocular seta (as long as longest postocular seta).

Thorax (Fig. 3): Acrostichal setae throughout in 4 more or less regular rows (6 rows anterior to transverse suture).

Legs: Hind basitarsus with a row of short, rather wide-set blackish setulae ventrally, which do not form a brush as in the male.

Female abdomen and terminalia (Figs 12-15): Hind margins of tergites without stronger black setae; a small, intercalary pair of sclerotized plates present between tergite 7 and tergite 8 (Fig. 12); sternite 8 of complicated structure (Figs 13-14), ventrally an apically pointed, setulose plate reaching tip of sternite 9; this plate connected at base with a lateral plate which ends in a small tooth; dorsal of this tooth is a weakly sclerotized, setulose protuberance; at base of tooth with darker sclerotization, left and right tooth connected by a weakly sclerotized «bridge»; cercus about as long as wide at base; 3 spermathecae, with smooth surface, the unpaired egg-shaped, the paired spherical.

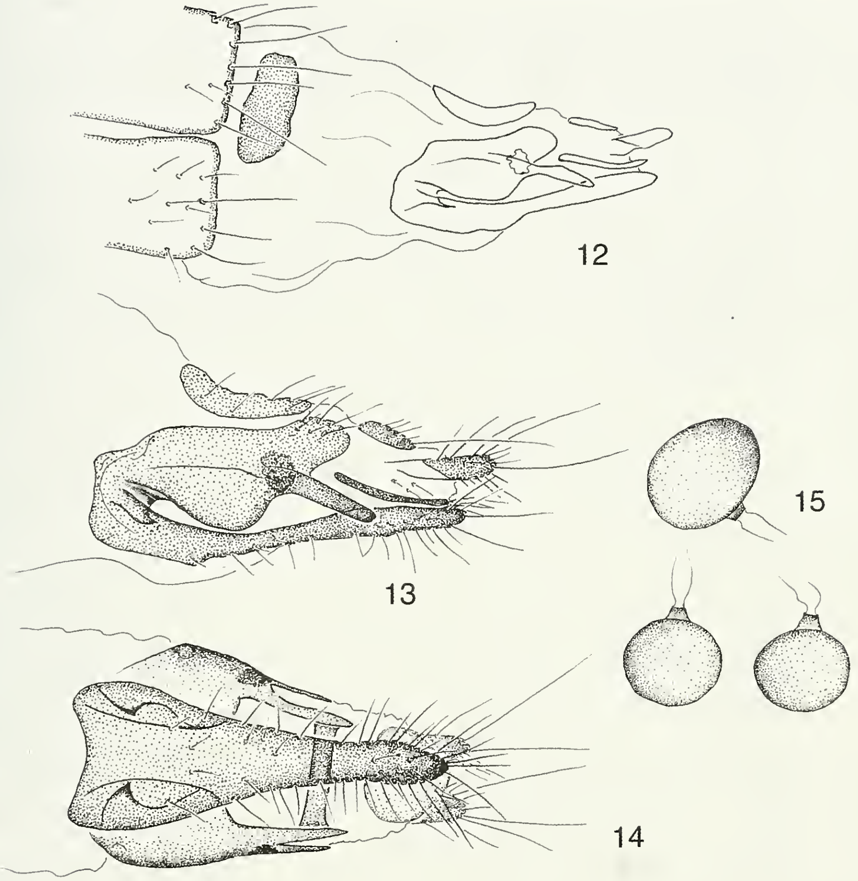
BIOLOGY

Both specimens were swept from vegetation in a dry habitat with shrubs, extensively managed meadows and open forests. They were collected between 1400 and 1600 m near the driest and hottest place in Switzerland. No further data about the biology of this species is available.

REMARKS

With the discovery of a new species with a short, but distinct presutural dorsocentral seta the separation of *Sapromyza*, as it is currently defined for the Palaearctic and Nearctic Regions (Stuckenberg, 1971; Papp, 1979; Papp & Shatalkin, 1998; Shatalkin, 2000; Merz, 2003) from *Lyciella* and related genera is even more problematic. Based on its combination of characters *S. alpina* is assigned to the *Sapromyza obsoleta* group of species. However, this placement is tentative because no cladistic anaylsis or comparative study of terminalia of the genera of the *Sapromyza-Lyciella* group has ever been carried out.

Sapromyza alpina can be separated from other species of the genus by the presence of a rather well-developed presutural dorsocental seta and by the combination of the entirely black anterior tarsus in both sexes, the presence of a dorsal preapical seta on hind tibia, and in the male by the ventral brush of black setulae on the hind basitarsus, but the hind tibia is unmodified. In external characters the new species can be confused with *S. obsoleta* which has the same colouration of antenna, palpus and fore tarsus, and often carries 1-3 longer setulae anterior of the 3 postsutural dorsocentral setae. *S. obsoleta* differs from the new species by the absence of the dorsal preapical seta on hind tibia (present in *S. alpina*). The male carries a brush of strong black setulae apicoventrally on hind tibia, and a curved apical spine anteriorly (no modifications of hind tibia in *S. alpina*). Another superficially similar species is *S. schnabli* with the same colouration of head and thorax, and which has also the fore tarsus darkened (but not distinctly black along entire length as in *S. alpina*). However, the hind basitarsus of the male is not modified, and the terminalia of both sexes are very different. In



Figs 12-15

Sapromyza alpina sp. n., female paratype. (12) Last segments (intercalary sclerite dotted). (13) Genitalia, lateral view. (14) Same, ventral view. (15) Spermathecae.

S. schnabli the male surstylus is armed with a tooth on inner surface and the postgonites are short and rounded apically. The female sternite 8 is shorter and has a different shape.

KEY TO WESTERN PALAEARCTIC GENERA OF THE *SAPROMYZA-LYCIELLA* GROUP

The following key allows a separation of the Western Palaearctic genera of Lauxaniinae with the combination of the following characters: Presutural intra-alar seta present; postsutural intra-alar seta absent; face straight without tubercle or rim; wing without horse-shoe like pattern.

Characters given in parentheses apply to all Western Palaearctic species of the couplet, but may also be present in some species of the alternative.

1a Either R2+3 or R4+5 with some setulae (always with 1+3 dorsocentral setae; at least along DM-Cu with brown infuscation) 2

1b Wing veins bare (Fig. 4) 3

2a R2+3 ventrally throughout length setulose; wing hyaline, but with brownish infuscation along DM-Cu; R4+5 bare . *Tricholauxania* Hendel, 1925

2b R2+3 bare, but R4+5 in basal half dorsally and ventrally with few setulae; wing with brown pattern on surface . . . . *Eusapromyza* Malloch, 1923

3a Mid tibia apico-ventrally with two setae (body black, 6 rows of acrostichal setae, 1+3 dorsocentral setae) . . . . *Cnemacantha* Macquart, 1835

3b Mid tibia apico-ventrally with one seta 4

4a Arista thick, covered with dense, white or brown to black rays 5

4b Arista slender, rays rather sparse, always dark (Fig. 2) 6

5a Postpedicel at most 2.5 times longer than wide; rays of arista brown to black . . . . *Neoparoecus* Özdikmen & Merz, 2006

5b Postpedicel at least 3 times longer than wide, rays of arista white . . . . *Mycterella* Kertész, 1912

6a Postpedicel almost entirely black. Male: hind basitarsus distinctly shorter than mid basitarsus; claws of hind leg asymmetrical: one claw almost as long as hind tarsus, the other claw as usual. Female: sternite 7 and tergite 7 fused, forming a sclerotized oviscape (body yellow brown; 1+3 dorsocentral setae; anepimeron with 1-3 setulae) . . . . *Aulogastromyia* Hendel, 1925

6b At least basal quarter of postpedicel yellow brown (Fig. 2); male and female without these modifications 7

7a Anepimeron with few fine, short setulae below wing base; always with 1+3 dorsocentral setae (mesonotum yellow brown, unstriped) . . . . *Lyciella* Collin, 1948

7b Anepimeron bare; with or without presutural dorsocentral seta 8

8a Ocellar setae inserted outside the triangle formed by the 3 ocelli (without presutural dorsocentral seta; body dull yellow brown including postpedicel and palpus; last 1-3 tergites of abdomen each with a pair of black spots laterally. Male: shape of postgonites very complicated, with black hooks and protuberances) . . . . *Sapromyzosoma* Lioy, 1864

8b Ocellar setae closer together, inserted inside ocellar triangle; combination of other characters different 9

9a Head and mesonotum grey, frons with a pair of brown vittae, mesonotum grey, with two pairs of brown longitudinal vittae; 1+3 dorsocentral setae which do not stand on darker spots . . *Poecilolycia* Shewell, 1986

9b Frons without a pair of brown vittae; combination of other characters different 10

10a Mesonotum usually grey, setae inserted on dark spots; always with 1+3 dorsocentral setae; 2-4 rows of acrostichal setae, those of the medial two rows almost as long as dorsocentral setae . . . . . *Pseudolyciella* Shatalkin, 2000

10b Mesonotum black, grey, or yellow brown; setae not on dark spots; medial two rows of acrostichal setae much shorter than dorsocentral setae (Fig. 3); usually without presutural dorsocentral seta, or, if present, then mesonotum yellow brown .... *Sapromyza* Fallén, 1810

KEY TO WESTERN PALAEARCTIC SPECIES OF THE *SAPROMYZA OBSOLETA* GROUP

The following key allows a separation of the Western Palaearctic species of the *Sapromyza obsoleta* group with the combination of the following characters: body subshining yellow brown (partly grey in *S. simplicior*), frons rather strongly shining; apex of postpedicel black; head in profile with higher gena than width of postpedicel and wide parafacial; postpedicel dorsally concave, about twice as long as wide; abdomen without black spots on tergites.

1a Palpus black in apical half (Fig. 1) 2

1b Palpus yellow brown, rarely slightly infuscated 6

2a Hind tibia without preapical dorsal seta. Male: hind tibia apicoventrally with brush of black setulae and with a curved, black spine at tip .... *S. obsoleta* Fallén, 1820

2b All tibiae with a preapical dorsal seta. Male: hind tibia without modifications 3

3a Fore basitarsus entirely black; presutural dorsocentral seta present (Fig. 3). Male: hind basitarsus ventrally on entire length with a brush of setulae (Fig. 5) .... *S. alpina* sp. n.

3b Fore tarsus yellow to dark brown, at least base of basitarsus and last tarsal segment paler (yellow brown to brown); sometimes some longer setulae anterior the anteriormost postsutural dorsocentral seta present, but they are not distinctly thicker than surrounding setulae. Male: hind basitarsus without modifications 4

4a More than apical half of postpedical black; border between black tip and yellow brown base not sharp. Male: genitalia large, surstyli converging, apically pointed (Scandinavia and North of Russia) .... *S. amabilis* Frey, 1930

4b At most apical half of postpedicel black; border between black tip and yellow brown base sharp. Male: genitalia small, surstylus not pointed apically... 5

5a Fore tarsus yellow; less than apical half of postpedicel black. Male: surstylus without tooth on inner side; both branches of postgonite sharply pointed, longer than aedeagus. Female: tergite 3 with some distinctly longer setae along posterior margin .... *S. apicalis* Loew, 1847

5b Fore tarsus brown to dark brown except for base of basitarsus and last tarsal segment; postpedical black in about apical half. Male: surstylus with a tooth on inner side; two branches of postgonite shorter, apically not distinctly pointed. Female: tergite 3 without longer setae along posterior margin .... *S. schnabli* Papp, 1987

6a Mesonotum light grey; frons with a linear dark patch medially .... *S. simplicior* Hendel, 1908

6b Mesonotum uniformly yellow brown; frons without darker patch medially .... *S. setiventris* Zetterstedt, 1847

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 2

Peter SCHUCHERT
Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland.
E-mail: Peter.Schuchert@ville-ge.ch

The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 2. - This study reviews all European species belonging to the filiferan families Bougainvilliidae, Cytaeididae, Rathkeidae, and Pandeidae. Updated diagnoses for the families and genera are provided and taxonomic problems solved or at least outlined. *Lizzia blondina* is removed from the Bougainvilliidae and transferred to the Rathkeidae based on results from 16S sequence data. *Dysmorphosa minuta* Mayer, 1900 is regarded as a synonym of *Lizzia blondina*; morphological and molecular evidence is provided. *Cytaeis minima* Trinci, 1903, formerly included in the Hydractiniidae, is transferred to a new genus *Podocorynoides* and included in the Rathkeidae as *Podocorynoides minima* (Trinci, 1903). *Perigonimus nanellus* Stechow, 1919 belongs to the genus *Dicoryne* and is likely a synonym of *Dicoryne conybearei* (Allman, 1864). *Perigonimus nudus* Stechow, 1919 is recognized as a new synonym *of Eirene viridula* (Péron & Lesueur, 1810). The Mediterranean records of *Rhizorhagium michaeli* and *R. arenosum* are most likely based on misidentifications of *Pachycordyle pusilla* (Motz-Kossowska, 1905). *Annatiara lempersi* Bleeker & van der Spoel, 1988 is a synonym of *Annatiara affinis* (Hartlaub, 1914).

Keywords: Cnidaria - Hydrozoa - Bougainvilliidae - Pandeidae - Cytaeididae - Ratkeidae - revision - taxonomy - northeastern Atlantic - Mediterranean.

INTRODUCTION

This study is the third in a series of taxonomic revisions of the European Anthoathecata (=Anthomedusae, Athecata). The previous ones being Schuchert (2004; Oceaniidae and Pachycordylidae) and Schuchert (2006; Acaulidae, Boreohydridae, Candelabridae, Cladocorynidae, Cladonematidae, Margelopsidae, Pennariidae, Protohydridae, and Tricyclusidae). The present publication treats the families Bougainvilliidae, Cytaeididae, Rathkeidae, and Pandeidae.

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MATERIAL AND METHODS

For morphological methods see Schuchert (1996; 2004) or Bouillon *et al.* (2004). Where possible, it was attempted to supplement the species descriptions with 16S DNA sequence information. This allows a much more precise evaluation of the specimens used and will facilitate the work of future revisors. The methods to obtain 16S DNA sequences are described in Schuchert (2005). All new sequences have been submitted to the EMBL database under the accession numbers **AM411408-AM411423**. Some of the sequences mentioned here have already been used in Schuchert & Reiswig (2006). Phylogenetic analyses were done as described in Schuchert (2005). Additionally, Maximum Likelihood analyses were performed using the program PHYML described by Guindon & Gascuel (2003).

Abbreviations

BMNH	The Natural History Museum, London, England
BELUM	Ulster Museum, Belfast, Northern Ireland
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
MNHN	Musée National d'Histoire Naturelle, Paris, France
NMNH	National Museum of natural History, Washington, USA
ICZN	International Code of Zoological Nomenclature
IRSN	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
ZMUC	Zoological Museum Copenhagen, Denmark
ZMHC	Zoological Museum of Harvard College, USA
ZSM	Zoologische Staatssammlung, Munich, Germany

TAXONOMIC PART

Family Bougainvilliidae Lütken, 1850

Synonyms (see Calder, 1988): Bougainvilleae, Lütken, 1850 (corrected to Bougainvilliidae by Allman, 1876). – Hippocrenidae McCrady, 1959. – Nemopsidae L. Agassiz, 1862. – Dicorynidae Allman, 1864a. – Atractylidae Hincks, 1868. – Bimeridae Allman, 1872. – Margelidae Haeckel, 1879. – Lizusidae Haeckel, 1879. – Thamnostomidae Haeckel, 1879. – Pachycordylini Cockerell, 1911. – Clavopsellidae Thiel, 1962.

Diagnosis: Hydroids solitary or colonial; hydranths stolonal, branched, or rarely sessile, arising from creeping hydrorhiza; erect colonies monopodial with terminal hydranths, stems monosiphonic or polysiphonic; perisarc terminating either at base of hydranths or forming a pseudohydrotheca; hydranths with one or more whorls of filiform distal tentacles, tentacles confined to narrow zone below hypostome; gonophores free medusae or fixed sporosacs developing either on hydrocauli, stolons, or blastostyles.

Medusae bell-shaped; mouth circular, with simple or dichotomously branched oral tentacles inserted distinctly above mouth rim, ending in nematocyst clusters; four radial canals and circular canal; marginal tentacles solid, contractile, either solitary or in clusters, borne on 4, 8, or 16 tentacular bulbs; gonads on manubrium, either forming a continuous ring or in adradial, interradial, or perradial position; adaxial ocelli absent or present.

Remarks: Although the genus *Bougainvillia* – the core-taxon of the family – is relatively well defined and easy to recognize, the family Bougainvilliidae as currently classified is difficult to delimit from several other families, notably the Cytaeididae

(Calder, 1988). The latter family and the Russellidae Kramp, 1957a possess oral tentacles that insert well above the mouth rim, a potential synapomorphy. While the medusa based genera are relatively easy to assess, this is much more difficult for the genera with gonophores reduced to sporosacs. The hydroids of many Bougainvilliidae and Pandeidae are very similar and show considerable intraspecific variation (Vannucci, 1960). If not provided with gonophores, they are often not objectively distinguishable. Pandeid species that have lost their medusa phase would thus become indistinguishable from bougainvilliid hydroids. Although it must be assumed that medusa reduction has also occurred in some species of the Pandeidae, they would presently be classified among the Bougainvilliidae. The classification of the genera without a medusa stage is therefore especially unsatisfactory and must be seen as provisional.

Contrary to my earlier view (Schuchert, 2004), I now think that the genera *Pachycordyle* and *Silhouetta* are closely related to the Bougainvilliidae and cannot be separated unambiguously from them with our present knowledge (comp. remarks under *B. muscus*). The two genera are thus included in the key to the genera of the Bougainvilliidae, but the *Pachycordyle* species are not treated again in the present paper (see Schuchert, 2004). As discussed in Schuchert (2004), the genus *Millardiana* Wedler & Larson, 1986 should not be included here.

The genus *Lizzella* Haeckel, 1879 is regarded as unrecognizable. Haeckel (1879) erected the genus *Lizzella* for *Lizzella octella* Haeckel, 1879 (= type species for the genus). *Lizzella octella* is not well characterized and Uchida (1927: 146, 233) referred it to a young *Spirocodon saltatrix* (Tilesius, 1818). This ambiguity renders the genus doubtful and useless. The genus *Lizella* should therefore not be used anymore. Also the other species included in this genus by Haeckel, *Lizella hyalina* (Haeckel, 1880), is a doubtful species.

In contradistinction to most taxonomic systems in use, *Lizzia blondina* Forbes, 1848 is here thought to be more closely related to the Rathkeidae Russell, 1953 than the Bougainvilliidae (see Remarks under family Rathkeidae).

Key to the genera of the Bougainvilliidae:

1a	gonophores sporosacs, medusoids, or adult medusa stage not yet known	8
1b	gonophores a free medusa, mature stages known	2
2a	four tentacular bulbs	3
2b	eight or more tentacular bulbs	6
3a	more than one tentacle per bulb	4
3b	one tentacle per bulb	5
4a	besides filiform tentacles also club-shaped or capitate ones	*Nemopsis*
4b	all tentacles identical in structure	*Bougainvillia*
5a	oral tentacles branched	*Thamnostoma*
5b	oral tentacles simple	*Nubiella*
6a	eight tentacular bulbs, these subdivided by cleft	*Chiarella**
6b	tentacular bulbs not subdivided by cleft	7
7a	8 tentacular bulbs with several tentacles	*Koellikerina*
7b	4 or 8 tentacular bulbs with a single tentacle	*Thamnostoma*
8a	hydroid occurring in freshwater of caves	*Velkovrhia*
8b	hydroid occurring in seawater, rarely in brackish waters	9
9a	gonophores on special blastostyles, released as swimming sporosacs	*Dicoryne*
9b	gonophores on hydrocauli or stolons	10

10a	gonophores a free medusa, adult not yet known	*Silhouetta*
10b	gonophores a sporosac or a medusoid (medusa without tentacles)	11
11a	hydranth with pseudohydrotheca, one or more whorls of tentacles	12
11b	hydranth without pseudohydrotheca, two or more whorls of tentacles	*Pachycordyle*°
12a	pseudohydrotheca sheathes also basal part of tentacles	*Bimeria*
12b	basal part of tentacles free of pseudohydrotheca	13
13a	one whorl of tentacles	14
13b	two or more whorls of tentacles	*Parawrightia**
14a	colonies erect	*Garveia*
14b	colonies stolonal	*Rhizorhagium*

* not treated here, as no species recorded in the area under investigation.
° see Schuchert (2004)

Genus *Bougainvillia* Lesson, 1830

TYPE SPECIES: *Bougainvillia macloviana* Lesson, 1830, by monotypy.

SYNONYMS: *Hippocrene* Brandt, 1835. – *Margelis* Steenstrup, 1850. – *Perigonimus* M. Sars, 1846. – *Atractylis* Wright, 1858 [type species = *Eudendrium ramosum* sensu Van Beneden, 1844 = *Bougainvillia muscus*, by designation of Totton, 1930]. – *Lizusa* Haeckel, 1879.

DIAGNOSIS: Hydroid colony stolonal or branched, more rarely hydranths sessile; perisarc terminating at base of hydranth or extending onto hydranth as pseudohydrotheca; hydranth cylindrical to spindle-shaped, tentacles in one or two closely approximated whorls, tentacle-bases never enveloped by pseudohydrotheca, tentacles alternately inclined up- and downward (amphicoronate). Gonophores develop into free medusae, arising singly or in clusters from stem, branches or stolons.

Medusa with four perradial marginal bulbs bearing two or more identical tentacles, with or without ocelli; four perradial oral tentacles, usually branched and ending in nematocyst clusters; gonads interradial or adradial on manubrium, sometimes also along basal perradial extensions of the manubrium.

REFERENCES: Kramp (1926, taxonomic history of genus); Vannucci & Rees (1961, synopsis); Edwards (1966, British species); Calder (1988, taxonomic history and synonymy).

KEY TO THE *BOUGAINVILLIA* HYDROIDS OF THE NE-ATLANTIC AND MEDITERRANEAN:

1a	colonies erect, branched several times	2
1b	colonies stolonal (= unbranched), or sparingly branched	4
2a	if polysiphonic, then all tubes roughly equal	3
2b	polysiphonic, central tube much thicker, medusae without ocelli	*B. muscoides*
3a	colony irregularly branched	*B. muscus*
3b	main axis and branches straight, medusa buds grouped on branched stalks	*B. pyramidata*
4a	hydranths sessile or with very short pedicel	5
4a	hydranths with distinct pedicels	6
5a	peduncle present in advanced medusa bud	*B. superciliaris*
5b	no peduncle present in advanced medusa bud	*B. principis*
6a	very long pedicels, buds in clusters on branched stalks	*B. britannica*
6b	pedicels not particularly long, buds not clustered	*B. macloviana*

KEY TO THE ADULT *BOUGAINVILLIA* MEDUSAE OF THE NE-ATLANTIC AND MEDITERRANEAN:

1a	gastric peduncle absent or short (much smaller than manubrium)	2
1b	distinct gastric peduncle present	8
2a	Without medusae budding from manubrium	3

2b With medusae budding from manubrium 7
3a With ocelli 4
3b Without ocelli 6
4a 1-4 mm, less then 8 tentacles per bulb . . . . *B. muscus*
4b > 4 mm, more than 8 tentacles per bulb 5
5a oral tentacles with long trunk, crescentic or oval ocelli on tentacles . . . . . *B. britannica*
5b oral tentacles with short trunk ocelli round and on bulbs . . . . *B. principis*
6a 3-5 mm high, 3-7 tentacles per bulb . . . . *B. muscoides*
6b < 2 mm, 2-3 tentacles per bulb . . . . *B. aurantiaca*
7a oral tentacles basal trunk absent, stomach flat . . . . *B. platygaster*
7b oral tentacles with long trunks, stomach flask-shaped . . . . *B. niobe*
8a Gonads also on perradial outgrowths of manubrium, ocelli on bulbs 9
8b no perradial outgrowths of manubrium, ocelli crescent-shaped on tentacles . . . . *B. superciliaris*
9a 4-9 tentacles per bulb, oral tentacles with moderately long basal trunk . . *B. pyramidata*
9b 30-65 tentacles per bulb, oral tentacles with short basal trunk . . . . *B. macloviana*

Bougainvillia muscus (Allman, 1863) Figs 1-3

Eudendrium ramosum. – Van Beneden, 1844: 56, pl. 4. figs 10-13.

[not *Eudendrium ramosum* (Linnaeus, 1758)]

Medusa octocilia Dalyell, 1847: 70, pl. 11. figs 9-10. – Edwards, 1966: 141, synonym.

Bougainvillia britannica. – Wright, 1859a: 108-109, pl. 1 figs 1-3.

[not *Bougainvillia britannica* (Forbes, 1841)]

Bougainvillia diplectanos Busch, 1851: 22, pl. 2, fig. 9. – Haeckel, 1879: 80, synomyn.

Atractylis ramosa. – Wright, 1859a: 108-109, pl. 1 figs 1-3.

Perigonymus muscus Allman, 1863: 12.

Podocoryne alderi Hodge, 1863: 82, pl. 2 figs 11-15 [medusa only, not hydroid]. – Calder, 1988: 27, synonym.

Corynopsis alderi. – Allman, 1864a: 354 [medusa, not hydroid].

Bougainvillia maniculata Haeckel, 1864: 327. – Haeckel, 1879: 89, pl. 5 figs. 4-5. – Mayer, 1910: 170, fig. 92. – Kramp, 1961: 78. – Vannucci & Rees, 1961: 71.

Bougainvillia fruticosa Allman, 1864b: 58. – Hincks, 1868: 110. – Allman, 1872: 314, pl. 9 figs 1-4.

Bougainvillia ramosa. – Hincks, 1868: 109, pl. 19 fig. 2. – Allman, 1872: 311, pl. 9 figs 5-74. – Hartlaub, 1911: 183, figs 162-167. – Broch, 1911: 17, fig. 13. – Brink, 1925a: 726. – Brink, 1925b: 126-203, text figs A-C, pls 6-71. – Kramp, 1926: 43. – Russell, 1938b: 152. – Vervoort, 1946: 135, figs 52a & 53. – Russell, 1953: 153, figs 74A-C, pl. 8 fig. 1, pl. 9 figs 4-5 – Kramp, 1959a: 109, fig. 91. – Kramp, 1961: 81. – Vannucci & Rees, 1961: 82. – Kramp, 1968: 34, fig. 87. – Morri, 1981: 50, fig 15. – Hirohito, 1988: 97, figs 34 b-f.

Bougainvillia muscus. – Hincks, 1868: 111. – Allman, 1872: 317, pl. 10 figs 1-3. – Calder, 1988: 24, figs 19-20. – Schuchert, 1996: 31, fig. 15a-e. – Peña Cantero & García Carrascosa, 2002: 22, fig. 3a-c.

Lizusa octocilia. – Haeckel, 1879: 80.

Bougainvillia autumnalis Hartlaub, 1897: 465, pl. 15 figs 11-13. – Hartlaub, 1911: 184, synonym. – Neppi & Stiasny, 1913: 29, pl. 2, figs 17-21. – Schmidt & Benovic, 1977: 636.

in part *Bougainvillia flavida* Hartlaub, 1897: 456, pl. 14 fig. 5 [female medusa only].

Bougainvillia benedenii Bonnevie, 1898a: 484, pl. 26 figs 34-35. – Brink, 1925b: 36, synonym. – Rees, 1956b: 113, synonym.

? *Bougainvillia obscura* Bonnevie, 1898b: 7, pl. 1 fig. 4. – Hartlaub, 1911: 184.

Lizusa octociliata. – Aurivillius, 1898: 114 [incorrect subsequent spelling].

Bougainvillia Gibbsi Mayer, 1900a: 5, pl. 4 figs 14-15.

Bougainvillia triestina Hartlaub, 1911: 154, fig. 138.

Bougainvillia ramosa var. *nana* Hartlaub, 1911: 189.

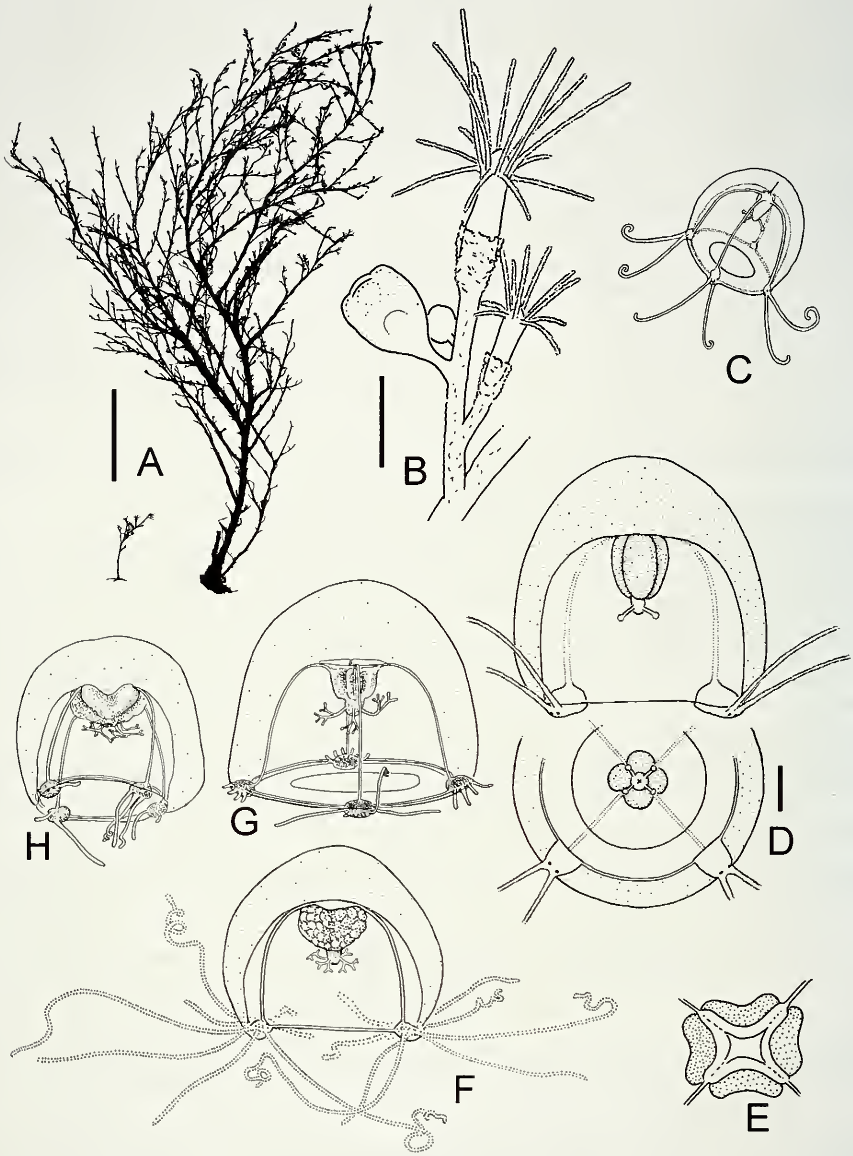


FIG. 1

Bougainvillia muscus (Allman, 1863). (A) Silhouettes of hydroid colonies, showing variability from small, monosiphonic (left) to large polysiphonic colony, scale bar 1 cm. (B) Hydranths with medusa buds, scale bar 0.5 mm. (C) Newly released medusa, about 0.8 mm high. (D) Lateral and oral view of a cultivated, mature medusa with low tentacle numbers and unbranched oral tentacles, scale bar 0.2 mm. (E) Manubrium seen from aboral of an older stage than shown in E (not same scale). (F-H) Mature medusae from plankton, note variation of manubrium and gonad shape, not to scale, bell heights are F=2.5 mm, G=2.2 mm, H= 1.8 mm. A, after preserved material; B-E, after living animals; F, modified after Hartlaub (1897); G-H, modified after Russell (1953).

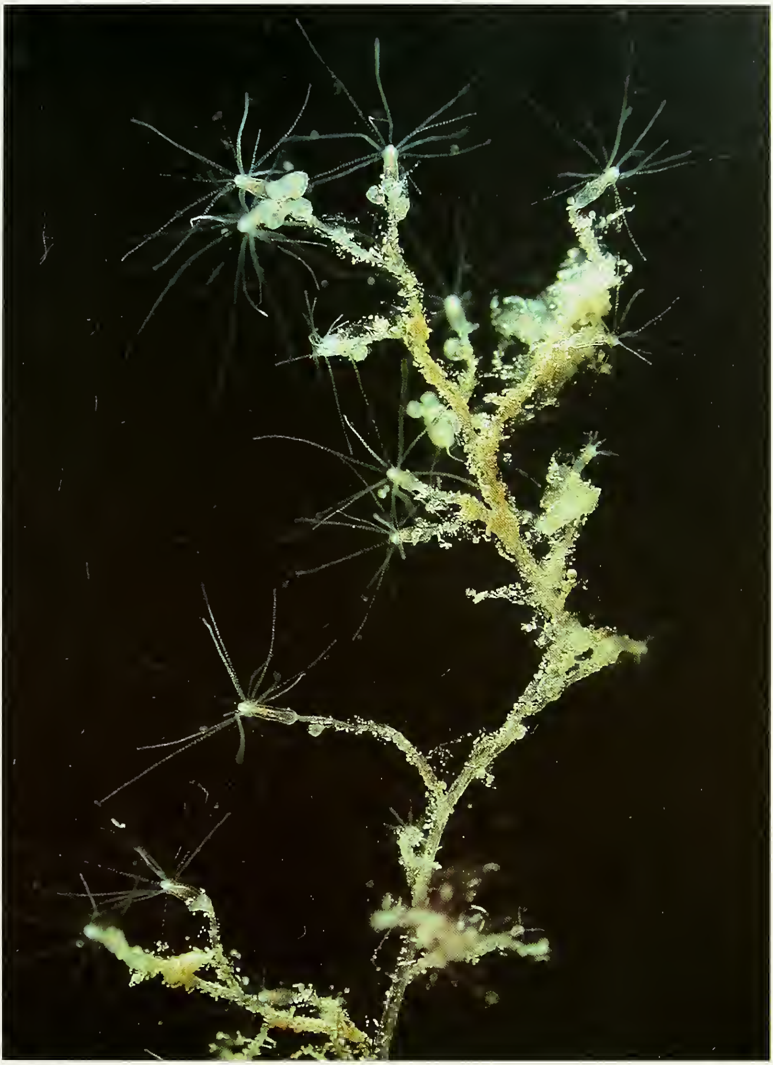


FIG. 2

Bougainvillia muscus (Allman, 1863), living colony from Villefranche-sur-Mer, Mediterranean.

Bougainvillia ramosa var. *minima* Kramp & Damas, 1925: 254, figs 5-7.
Bougainvillia autumnalis var. *magna* Babnik, 1948: 290, fig. 2. – Schmidt & Benovic, 1977: 636.
Bougainvillia ? *ramosa*. – Millard, 1975: 97, figs 33EH.
Bougainvillia ramosa f. *musca*. – Millard, 1975: 99.
Bougainvillia ramosa f. *fruticosa*. – Millard, 1975: 99.
Bougainvillia ramosa f. *ramosa*. – Millard, 1975: 99.
Bougainvillia ramosa f. *vanbenedeni*. – Millard, 1975: 99.

FIG. 3

Bougainvillia muscus (Allman, 1863), living colony from Norway, scale bar 5 mm, inset shows a higher magnification of a hydranth and medusa buds. This form with its straight stem, the clustered medusa buds, and unusually coloured hydranths was first mistaken for *B. pyramidata* (comp. Fig. 9A). Rearing experiments showed it to be *B. muscus*.

MATERIAL EXAMINED: MHNG INVE 29410, St. Pol de Leon, Brittany, 20 m; 6 June 2000, on *Ciona intestinalis*, examined alive, colonies 4 cm, polysiphonic, much branched (*ramosa-fruticosa* form), medusa grown to maturity, ocelli red; 16S sequence **AY787880**. – France, Brittany, Roscoff, under l'Estacade (pier of Île de Batz ferry), on algae; 15 September 2004, 1 cm colonies, monosiphonic (*muscus* form), branched; newly released medusae with dark-

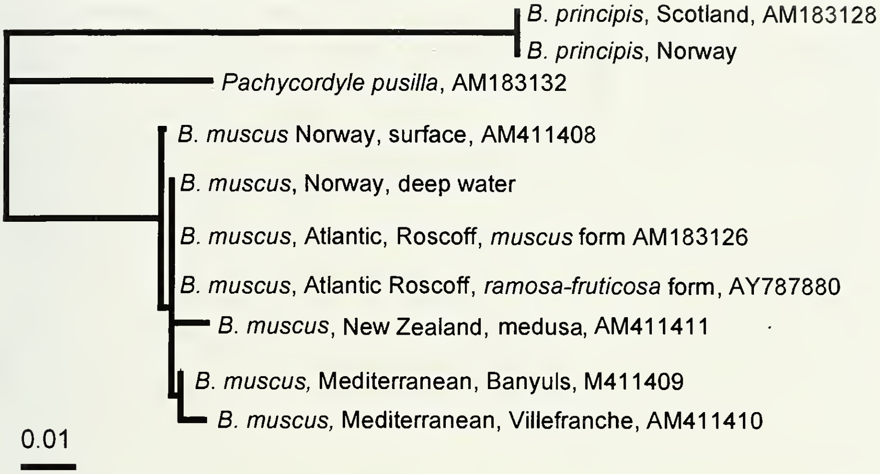


FIG. 4

16S sequence differences of *B. muscus* samples represented as a Neighbour-joining tree based on sequence divergences (HKY model, indels ignored). The length of the sum of the horizontal lines is a measure of the sequence difference.

crimson-red ocelli, 2 tentacles per marginal bulb, oral tentacles unbranched or branched once, jelly thin, cultivated medusae developed gonads within days, 16S sequence **AM183126**. – MHNG INVE48732, 48733, 48746, and 48750; Norway, Bergen, near Espeland marine station; growing on *Mytilus*, 0.5-1 m depth, June 2006, numerous large, polysiphonic colonies; examined alive, some colonies with medusa buds, others developed buds in culture; medusae of one colony (MHNG INVE 48746) grown to sexual maturity, marginal bulbs then with 2-3 tentacles and oral tentacles branched or not; extracted DNA, 16S sequence **AM411408**. – Norway, Korsfjord, great Skorpa Island; depth 80-160 m, collected by scraping almost vertical wall, 16 June 2006, infertile colony on bryozoan, used for DNA extraction, 16S sequence identical to **AY787880**. – Aquarium Zoological Institute Basel, 19 January 1991, 13°C, material originating from Banyuls-sur-Mer, examined alive, medusae cultivated to sexual maturity. – MHNG INVE32947, Mediterranean, marina of Banyuls-sur-Mer, 7 May 2002, 0 m, 1-5 cm colonies, polysiphonic, no medusa buds, 16S sequence **AM411409**. – Mediterranean, Villefranche-sur-Mer 4 April 2005, several colonies with medusa buds, on *Phallusia mammilata*, colonies monosiphonic, up to 2 cm, 16S sequence **AM411410**. – Several living medusae collected 6 July 2002 near Motutapu Island (Hauraki Gulf, New Zealand), up to five tentacles per marginal bulb, otherwise typical, 16S sequence **AM411411**. – MHNG INVE26550, Naples, collection pre 1900, large colonies. – BMNH 1957.3.2.129, Great Britain, Eddystone, 15 September 1897, slide labelled as *Bougainvillia ramosa*, 16 mm colony with buds. – BMNH 1957.3.2.137, Great Britain, Eddystone, 7 December 1897, slide labelled as *Bougainvillia ramosa*, 40 mm colony with buds. – BMNH 1957.3.2.163, Great Britain, Eddystone, 22 August 1898, slide labelled as *Bougainvillia ramosa*, 25 mm colony without buds. – BMNH 1957.3.2.134, Great Britain, Eddystone, 19 November 1897, slide labelled as *Bougainvillia ramosa*, 35 mm colony with buds. – BMNH 1985.9.10.22, Great Britain, Millport, Keppel Pier, 2 6 September 1940, labelled as *Bougainvillia ramosa*, 2 medusae in formalin, mature with 2 tentacles per bulb. – ZMUC without number, Denmark, July 1947, labelled as *Bougainvillia ramosa*, juvenile medusae, likely released from polyp, det. Kramp.

DIAGNOSIS: Hydroid colony erect, irregularly branched, mono- or polysiphonic, hydranth with 10-18 tentacles, medusa buds in rows on branches.

Medusa 1-4 mm, no distinct peduncle, usually two to four tentacles on each marginal bulb, oral tentacles branching zero to two times (rarely three times), ocelli round, on marginal bulbs, red or black.

Description: Hydroid colony varies in growth and form from monosiphonic, sparingly branched stems ('*muscus*' form) to tall irregularly and profusely branched tree-like forms with fascicled stems ('*ramosa*' and '*fruticosa*' forms); stolons tubular, forming a network; perisarc infested with detritus, corrugated at bases of branches but not regularly annulated, thinning out over hydranths, pseudohydrotheca usually present in animals from nature, absent in cultivated animals; hydranths terminal on branches and branchlets, with 10-18 tentacles, hypostome rounded to conical; gonophores pear-shaped, on unbranched stalks of variable length, arising singly, in rows, or in groups on the branches just below the hydranths. Especially in distal regions of colony regularly stolon-like, naked outgrowths that serve to attach the colony or broken parts of it to other substrata (apical stolons, tendrils). Nematocysts: microbasic euryteles and desmonemes. Colours: hydranths pink, red, orange, or greyish purple; colour depends on food items.

Medusa at release bell-shaped; jelly uniformly thin, a few nematocysts on exumbrella, apical canal may be present, no peduncle; two tentacles and two ocelli on each bulb, ocelli red or black; four oral tentacles unbranched. In females, small oogonia can be visible on the manubrium, but mostly these are not developed yet.

Medusa with mature gonads bell-shaped, jelly rather thick, thicker at apex, very low gastric peduncle sometimes present; radial canals narrow; bulbs rather small, oval; 2-6 tentacles per bulb (cultivated animals; when found in plankton usually 3-4); bulbs rounded, ocelli round, situated adaxially on bulbs near origin of tentacles; manubrium short (about $^1/_2$ of subumbrella), conical or in large specimens square- to slightly cross-shaped; oral tentacles divided dichotomously two times (rarely 3-4), basal trunks of moderate length, length variable; gonads interradial pads, sometimes extending slightly along radial canals. Nematocysts: microbasic euryteles and desmonemes. Colours: marginal bulbs and stomach reddish brown, red or yellowish; sometimes with greenish tinge; depends on food items.

Dimensions: Hydroid colonies with medusa buds variable from a few mm to 12 cm; hydranth length 0.7-0.9 mm; medusa buds up to 0.5 mm. Medusa at release about 0.7 mm wide and high. Adult medusa 1-4 mm wide and high. Nematocysts (Mediterranean material, polyps and young medusae): microbasic euryteles (7-8)x(3.5-5)μm; desmonemes (3-4)x(4-5.5)μm. For more nematocyst measurements see Russell (1938b), Millard (1975), and Schuchert (1996).

Distribution: A widely distributed species, perhaps also due to human activity. *Bougainvillia muscus* has been recorded in the eastern Atlantic from the Norwegian (Bonnevie, 1901; Rees, 1952; Christiansen, 1972) and Swedish coasts (Rees & Rowe, 1969), Denmark (Rasmussen, 1973), the Baltic Sea (Schönborn *et al.*, 1993); Germany (Hartlaub, 1911), Great Britain and Ireland (e. g. Hincks, 1868; Russell, 1953; Ballard & Myers, 2000), Holland (Vervoort, 1946; Tulp, 2005), Belgium (Leloup, 1947); France (Teissier, 1965; Fey, 1970); Portugal and Spain (Medel & López-González, 1996), Strait of Gibraltar (Peña Cantero & García Carrascosa, 2002), southwards to at least Morocco (Patriti, 1970) and Cape Verde Islands (Vanhöffen, 1912). Often also recorded in the Mediterranean (Peña Cantero & García Carrascosa, 2002), rarely in the Black Sea (Valkanov, 1957). The records from Iceland are uncertain, it is absent from Greenland (Schuchert, 2001). Also known to occur along the east coast of America (Mayer, 1910, as *B. autumnalis*; Vannucci, 1957; Calder, 1988), northern Pacific (Hirohito, 1988), tropical Pacific (Pictet, 1893; Bouillon, 1980), southern Pacific (Schuchert, 1996); South Africa (Millard 1975; Gili *et al.*, 1989). Type locality: Torquay, Devon, Great Britain, in tide pools near low-water mark.

BIOLOGY: *Bougainvillia muscus* hydroids have been found on a wide variety of substrata, e. g. seaweeds, hydrozoans, sponges, mollusc shells, polychaete tubes, and man made objects (Peña Cantero & García Carrascosa, 2002). In temperate waters, they seem to bud medusae from spring to autumn, planktonic medusa are sometimes also present in winter (Hartlaub, 1911). The hydroid of *Bougainvillia muscus* is a common, eurybathic form, found from tidal levels to about 100 m depth (Peña Cantero & García Carrascosa, 2002), but it can also occur in deep waters, e. g. 1193 m (Gili *et al.*, 1989). Usually it occurs in fairly wave sheltered conditions, often in slightly reduced salinity and also harbours. Considering the abundance of the hydroid along the European coasts, the medusa seems to be remarkably scarce in the plankton (Russell, 1953).

16S SEQUENCE DATA: A phylogenetic analysis of the available Filifera sequences always placed the various sequences of *B. muscus* within a well supported monophyletic lineage (results not shown, but see Schuchert & Reiswig, 2006). The closest relative being surprisingly *Pachycordyle pusilla,* followed by *B. principis*. The close relationship of *P. pusilla* hints at major discrepancies with our current macrotaxonomic system.

The available *B. muscus* sequences are not numerous enough for a serious phylogeographic analysis, but they nevertheless allow some interesting preliminary comparisons. Figure 4 shows a tree based on distance measures (due to the few shared differences other phylogenetic analyses like maximum parsimony make little sense). All *B. muscus* sequences are quite distant from *B. principis* (>10%, including base differences and insertions) and *P. pusilla* (>6.6%), while they are relatively similar to each other (max. 1.5% divergence). There are no obvious, distinct intraspecific lineages. The observed intra- and interspecific differences are comparable to those observed for some Corynidae (Schuchert, 2005; see also under *Lizzia blondina*). Polysiphonic and monosiphonic colonies from Roscoff – both mature and liberating medusae – had identical sequences, confirming earlier conclusions that they belong to the same species. The divergence of the two Mediterranean samples is 0.5%, those from Norway 0.34%. These values can be taken as a first estimate of the intra-population variation. Higher divergences are observed between the Mediterranean and Norwegian samples, reaching values of 1.2%. Comparing the European samples with one from New Zealand gives slightly higher divergence values, but the values overlap with what is seen for the differences between Atlantic and Mediterranean specimens.

This all suggests that the examined *B. muscus* likely belong to the same lineage and biological species, confirming its widespread, almost cosmopolitan distribution.

REMARKS: This species has a complicated synonymy which has been worked out by several authors, e.g. Hartlaub (1911), Brink (1925a, 1925b), Russell (1953); Vannucci & Rees (1961); Edwards (1964a, 1964b), Calder (1988), to cite only the most important.

I agree with Mayer (1910) and Vannucci & Rees (1961) that *Bougainvillia maniculata* is likely a degenerate form referable to *B. muscus*. The species has only been observed by Haeckel, despite its type locality being Villefranche-sur-Mer, one of the most thoroughly investigated localities, whose the plankton has been continuously observed for the decades (Trégouboff & Rose, 1978; Goy, 1973; Buecher & Gibbons, 1999).

Bougainvillia muscus is a very variable, in its polyp as well as in the medusa stage. Earlier authors attempted to attribute different forms to different species. In the hydroid phase, some authors distinguished a *muscus* and *fruticosus* form (see Russell, 1953; Millard, 1975). The former having small, monosiphonic colonies, the latter large, polysiphonic ones. The nominal species *B. vanbendeni* is characterized by its distal branches producing stolon-like tendrils (terminal search stolons). In a thorough analysis, Brink (1925a, 1925b) showed that these forms are not objectively separable and likely due to environmental influences.

Likewise for the medusa there are several specific and varietal names available. *Bougainvillia octocilia* (Dalyell, 1847), *Bougainvillia ramosa* var. *nana* Hartlaub, 1911 or *Bougainvillia ramosa* var. *minima* Kramp & Damas, 1925 represent mature medusa with only 2-3 tentacles per bulb and the oral tentacles are unbranched or branched once. Russell (1953: 158) thought it possible that two species might be involved, one producing black ocelli, the other red ones. Calder (1988) also considered the status of many nominal species as unclear and not resolvable. Here they are considered as variants of *B. muscus*.

Material from Norway, Roscoff and the Mediterranean was used to cultivate medusae to sexual maturity. Some medusae reached a stage with three tentacles per bulb, but often developed only to a stage with two tentacles per bulb and the oral tentacles remained unbranched. This does not conform with the commonly described planktonic adult (see above). It is likely that this growth retardation is due to the sub-optimal in-vitro cultivation conditions. Similar results were obtained by Schuchert (1996) and (Calder 1988), who assumed that the full size is only achieved under natural conditions in the sea, but similar adult medusae have also been observed in the plankton (Hartlaub, 1911; Kramp & Damas, 1925). Wright (1859a) was able to cultivate the medusa to a stage with six tentacles per bulb.

Reports of *Bougainvillia muscus* medusa with eight or more tentacles per bulb are likely due to a confusion with other similar species, notably *B. pyramidata* or *B. britannica*.

The polyp stages of polysiphonic *B. muscus* and *B. pyramidata* are very similar and may not always be distinguishable (see under *B. pyramidata*).

Bougainvillia britannica (Forbes, 1841) Fig. 5

Hippocrene britannica Forbes, 1841: 84, pl. 1 figs 2a-c.
Bougainvillia britannica. – Lesson, 1843: 291. – Forbes, 1848: 62, pl. 12 fig. 1. – Hartlaub, 1911: 160 & 162, figs 141-151. – Kramp, 1926: 43. – Russell, 1938b: 152, fig.s 23-25. – Russell, 1953: 158, figs 75A-B, 77A-B, 78A, 79A, pl. 8 figs 2-3, pl. 9 figs 1-3. – Vannucci & Rees, 1961: 61. – Edwards, 1964a: 1, figs 1-2. – Edwards, 1966: 147. – Tulp, 2005: 47, fig. 1.
Bougainvillia dinema Greene, 1857: 246, pl. 15 fig. 6a-f. – Edwards, 1966: 141, synonym.

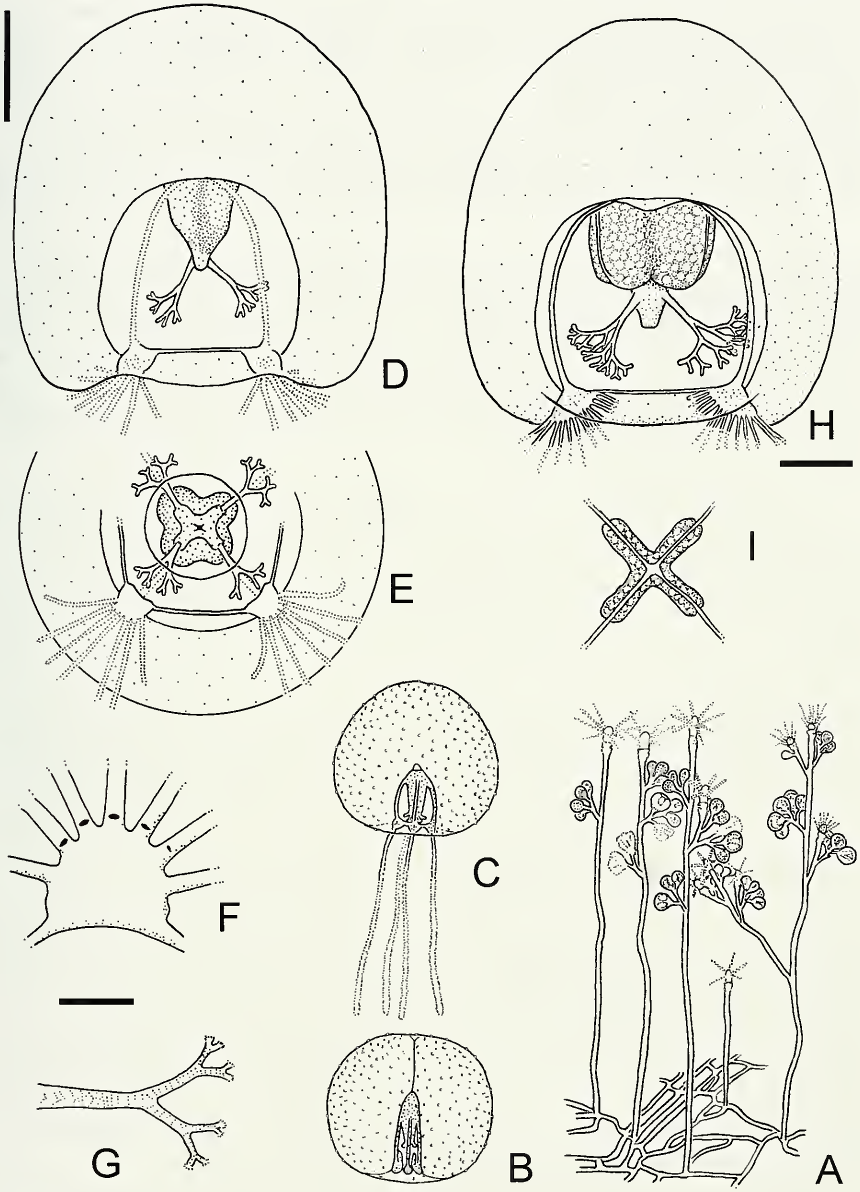


Fig. 5

Bougainvillia britannica (Forbes, 1841). (A) Hydroid colony with medusa buds. (B) Newly released medusa. (C) Two days old medusa, size ca. 1 mm. (D) Subadult medusa, scale bar 1 mm. (E) Same as D, oral view, same scale. (F) Marginal bulb of medusa shown in D, note oblong ocelli on tentacles, scale bar 0.2 mm. (G) Oral tentacle of medusa shown in D, note long basal trunk, same scale as F. (H) Mature medusa, scale bar 1 mm. (I) Aboral view of manubrium of medusa shown in H, same scale as in H. A-C, redrawn after Edwards (1964a); D-G, after living medusa from Dunstaffnage; H-I, schematic reconstruction based on several preserved medusae.

Margelis zygonema Haeckel, 1880: 635. – Edwards, 1966: 141, synonym.
Atractylis linearis Alder, 1862b: 313, pl. 14 figs 1-3. – Edwards, 1964a: 9, synonym. – Cornelius & Garfath, 1980: 278.
Bougainvillia xantha Hartlaub, 1897: 461, pl. 15 figs 2-3, pl. 16 fig. 3, pl. 16b fig. 19. – Hartlaub, 1911: 169, synonym.
Bougainvillia bella Hartlaub, 1897: 470, pl. 15 fig. 7. – Hartlaub, 1911: 162, synonym.
? *Bougainvillia britannica* var. *coeca* Hartlaub, 1911:168.
in part *Bougainvillia flavida* Hartlaub, 1897: 456, pl. 14 figs 1-4, 7-10 (non 5-6). – Edwards, 1964a: 8, synonym.

MATERIAL EXAMINED: Dunstaffnage Bay, Scotland, May 2004, several subadult medusae from surface plankton, examined alive, one used to extract DNA and to determine 16S sequence, EMBL/GenBank accession number **AM183127**. – BMNH 1982.11.30.1; Ireland, Lough Ine, Skibberean; collected July 1939. – BMNH 1955.11.23.198-231, 232-288; Great Britain, Plymouth; 20.04.1934. – BMNH 1956.1.1.5-7; Great Britain, Clyde; 24.05.1955; W. J. Rees collection. – BMNH 1955.11.23.23; Great Britain, Plymouth; 25.05.1934; figured in Russell 1953, pl. 8 fig. 2. – BMNH 1955.11.23.1-3; Great Britain, Plymouth; 03.05.1935. – BMNH 1954.11.13.106-114; Ireland, Valentia Island; 10.08.1899; label: *Margelis bella*. – ZMUC, no number; Germany, Helgoland; about 50 medusae, 26 May 1931, det. P. Kramp.

DIAGNOSIS: Medusa 5-12 mm, jelly thick; no gastric peduncle, basal trunk of oral tentacles long, ocelli crescentic or oval, often appearing almost linear in oral view, situated adaxially on bases of tentacles, not on bulbs, 12-17 tentacles per bulb, oral tentacles branch 4-5 times; polyp stolonal or sparingly branched, long pedicels, medusa buds in clusters on branched stalks, young medusa with very narrow subumbrella.

DESCRIPTION (after examined material, Russell, 1953, and Edwards, 1966): Hydroid colonies forming erect shoots, not much branched, branching at acute angles; stems arising from a large-meshed irregular network of tubular stolons; stems relatively tall; stems and branches monosiphonic; perisarc of stems wrinkled transversely to slight degree only, not annulated; perisarc expands around larger hydranths to form cup-like pseudohydrotheca; hydranths terminal on stems and branches, 6-10 tentacles (max. 14) in a single whorl; gonophores thick-jellied and globular at maturity, in clusters on fairly long branched stalks arising from stems and branches, several clusters on one stem may occur, buds completely invested in a delicate perisarcal sheath, which remains attached to the colony after rupture and the release of the medusa.

Newly released medusa almost spherical; jelly very thick, exumbrella with scattered nematocysts, subumbrellar cavity very small and narrow, thin apical canal; one tentacle on each bulb, without ocelli, tentacles retained in subumbrella, four oral tentacles unbranched, velum rudimentary. The apical canal disappears rapidly during the further growth, the tentacles are extended towards the outside,

Adult medusa with very thick jelly; no gastric peduncle, the jelly of the umbrella overhangs the margin of the subumbrellar cavity and the marginal tentacles emerge from channel-shaped depressions in this jelly; radial canals rather broad; bulbs triangular to kidney-shaped, about half as wide as intervals, but can be contracted very much; up to 30 tentacles on each bulb, usually 12-17, very contractile; ocelli lenticular or oval, often appearing almost linear in oral view, situated adaxially on bases of tentacles and not on bulbs; oral tentacles fairly long, dichotomously divided up to 4-6 times, with long basal trunks; stomach broad-based, in form of perradial cross. Gonads eight adradial pads, confluent interradially, separated by perradial cleft even in fully mature animals. Nematocysts: microbasic euryteles and desmonemes. Colours of polyp white, of medusa: bulbs orange to brown-red, ocelli dark purple to black.

VARIATION: The thickness of the jelly varies considerably, in some specimens the apical jelly takes up half of the total bell-height, while in others it is not much thicker than the lateral bell-wall. Likewise, the breadth of the radial canals, the size of the manubrium, and the size and shape of the marginal bulbs are very variable.

DIMENSIONS: Stems of polyps up to 15 mm, hydranths 0.3-0.55 mm, gonophores 0.55 mm in diameter, newly released medusa 0.52 mm wide (Edwards, 1964a). Adult medusa 5-8 mm, exceptionally up to 12 mm; egg size 0.14-0.15 mm, planulae 0.36 mm (Russell, 1953). Microbasic euryteles (10-11)x(3.5-4)μm, desmonemes (6-6.5)x(3.5-4)μm (Russell, 1938b). More data on dimensions, the development of bell size, tentacle numbers, and branching of the oral tentacles can be found in Russell (1953) and (Edwards, 1964a).

DISTRIBUTION: North-eastern Atlantic and North Sea in coastal areas, with the English Channel as southern limit and Norway as northern limit. Also present west of Iceland (Fraser, 1953). There is also a record from Maine (USA) based on a single medusa (Mayer, 1910). Absent from the Baltic Sea, Mediterranean, snd Black Sea. There are also a records from China (Chow & Huang, 1958), Papua New Guinea (Bouillon, 1980), and Northern Alaska (see Vannucci & Rees, 1961). In view of its rather restricted distribution in the cool temperate waters of the NE Atlantic, records outside this regions, especially in warm or tropical waters, need reconfirmation by life-cycle studies as they could be due to a confusion with other, similar species. No exact type locality has been specified, Forbes (1841) had medusae from North of Ireland and East of Scotland.

BIOLOGY: Edwards (1964a) found the polyp on shells of *Aporhais pespelecani* (L.) at depths of 60-80 m on a mud bottom. Colonies collected from end of March to mid May had medusa buds. Other authors found the polyp on a variety of bivalve- and gastropod-shells. The medusa can be found in the plankton from April to October (Russell, 1953; Edwards, 1964a; Ballard & Myers, 1996). The life span of the medusa is likely not much more than two months; at day-time, it lives usually in 20-30 m depth (Plymouth: Russell, 1953; Lough Hyne: Ballard & Myers, 1996). Some data indicate a diel vertical migration (Russell, 1953).

REMARKS: The synonymy and taxonomic history of this species has been worked out by Russell (1953) and Edwards (1964a, 1966). The latter also described the life-cycle in detail. The polyp had been previously been known as *Atractylis linearis* Alder, 1862 and as *Bougainvillia flavida* Hartlaub, 1897.

The medusa of *Bougainvillea britannica* can be difficult to distinguish from *B. principis*. The following differences help to differentiate them. In *B. britannica* the jelly is usually much thicker and hence the subumbrellar cavity is smaller than in *B. principis*. The basal attachment of the stomach is usually quite horizontal in *B. britannica* whereas in *B. principis* there is a tendency towards a shallow peduncle. The basal trunks of the branches of the oral tentacles are long in *B. britannica*, while they are rather short in *B. principis*, but contraction can obliterate the difference. In *B. britannica* the ocelli are oblong and they are situated on the tentacles, while they are more rounded in *B. principis* at the junctions of the tentacles with the bulb (appearing on the bulbs in contracted specimens).

Bougainvillea britannica is also incorrectly listed as occurring in the Mediterranean (Bouillon *et al.,* 2004). The record goes back to Thiel (1935) who listed it for the Black Sea based on a literature record of the polyp stage of *B. muscus* (recorded as *Eudendrium ramosum*). Thiel incorrectly assumed that *B. britannica* is the medusa stage of this polyp, a frequent error going back to Wright (1858, 1859a) and repeated by several other prominent authors (see Kramp, 1926: 42).

Bougainvillia principis (Steenstrup, 1850) Fig. 6-7

Margelis principis Steenstrup, 1850: 35. – Haeckel, 1879: 88, pl. 6 figs 14-16.
? *Medusa duodecilia* Dalyell, 1847: 70, pl. 11 figs 11-12. – Edwards, 1966: 138, questionable synonym.
? *Hippocrene simplex* Forbes & Goodsir, 1853: 313, pl. 10, fig. 6a-e. – Edwards, 1966: 140, questionable synonym.
Bougainvillia fruticosa. – Romanes, 1876: 526. – Haeckel, 1879: 88, synonym.
[not *Bougainvillia fructicosa* Allman, 1864, = *B. muscus*]
Bougainvillia allmanii Romanes, 1877: 190. – Haeckel, 1879: 88, synonym.
Nemopsis heteronema Haeckel, 1879: 93, pl. 5 figs 6-9. – Kramp, 1926: 48, synonym.
In part *Margelis principis*. – Haeckel, 1879: 88, pl. 6 figs 14-16. – Kramp, 1955a: 154.
Hippocrene aurea Linko, 1905: 216. – Hartlaub, 1911: 179.
Bougainvillia superciliaris. – Hartlaub, 1897: 466, pl. 16a figs 5, 8, 12.
[not *Bougainvillia superciliaris* (L. Agassiz, 1849)]
Bougainvillia principis. – Mayer, 1910: 160. – Hartlaub, 1911: 177, fig. 158. – Le Danois, 1914b: 307, figs 5-6. – Kramp, 1926: 48, chart VIII. – Russell, 1953: 164, figs 76A-B, 78B, 79B.– Kramp, 1959a: 108, fig. 88. – Vannucci & Rees, 1961: 79. – Edwards, 1966: 129, figs 1-2. – Kramp, 1968: 32, fig. 83. – Naumov, 1969: 216, fig. 85. – Russell, 1970: 238, figs 4s-5s. – Pagès *et al.*, 2006: 371, fig. 5B-E
in part *Bougainvillia superciliaris*. – Hartlaub, 1911: 174, figs 154-156 [polyp and young medusae].

MATERIAL EXAMINED: MHNG INVE35768, Scotland, Dunstaffnage Bay, 7-13 May 2004, several mature medusae from surface plankton, examined alive, DNA made of one individual, 16S sequence **AM183128**. – MHNG INVE48763; Norway, Raunefjord, 0-35m, June 2006, 2 living medusae from plankton, DNA made from one specimen, 16S sequence was identical to **AM183128**. – BMNH 1955.11.23.23-33, Great Britain, Plymouth, 12-14 April 1937, few badly preserved mature medusae, leg. & det. F.S. Russell. – ZMUC (without number), Denmark, NW of Hanstholm, 200 m wire, 27.09.1930, 3 medusae, leg & det P. Kramp. – ZMUC (without number), Denmark, NW of Lodbjerg, 60 m wire, 27 September 1930, 3 medusae, leg. & det. P. Kramp.

DIAGNOSIS: Medusa 7-8 mm, with 20-30 tentacles per bulb, oral tentacles branching 5-6 times, basal trunk of oral tentacles short, ocelli round and mostly on bulb and not tentacle; hydroid stolonal, sessile or with very short pedicels, small, medusa buds on stolons, released without peduncle, with three tentacles and three ocelli on each bulb.

DESCRIPTION (polyp and newly released medusa after Edwards, 1966): Hydroid stolonal, arising singly at intervals from fine creeping stolons, which form a very open

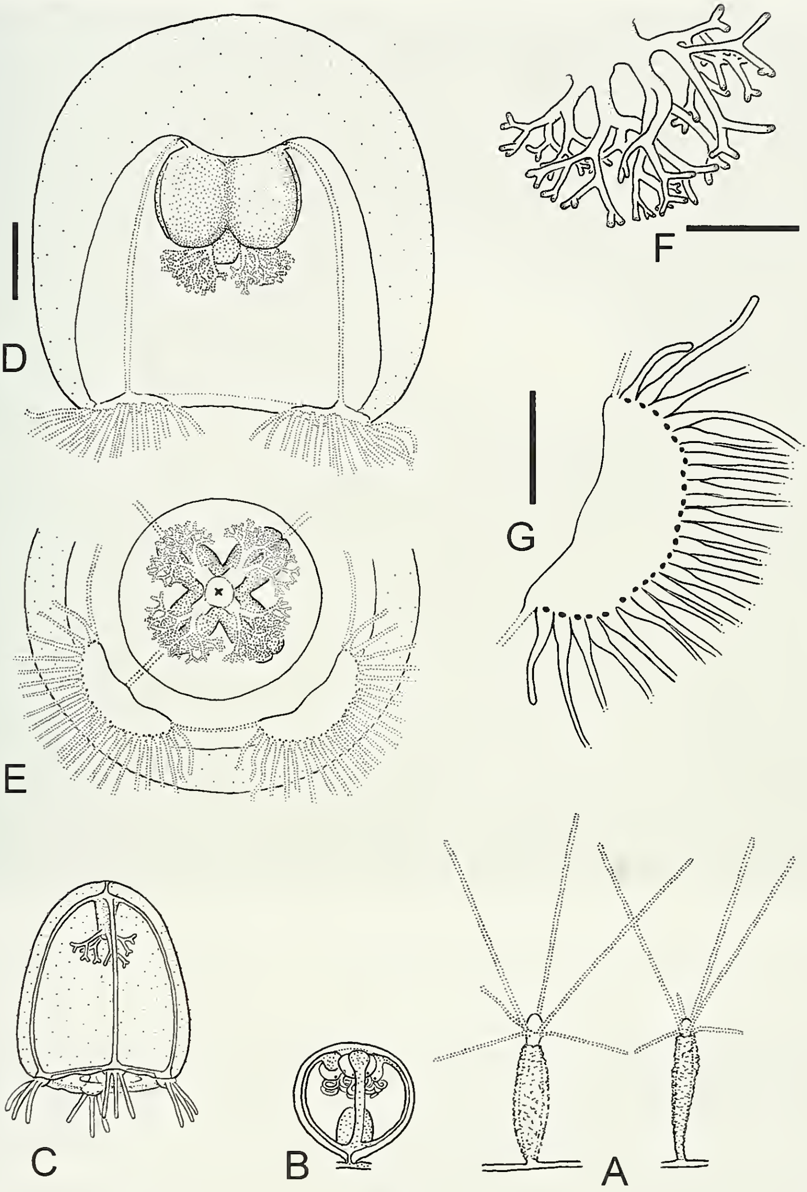


FIG. 6

Bougainvillia principis (Steenstrup, 1850). (A) Two polyps, note that the left one has no pedicel, while the right one has an indistinct one, for dimensions see text. (B) Medusa bud issuing from stolon, same scale as A. (C) Newly released medusa, size about 1 mm, note the presence of three tentacles per bulb as well as branched oral tentacles. (D) Mature medusa in side view, tentacles truncated, scale bar 1 mm. (E) Same animal and scale as in D, oral view. (F) Oral tentacles of one quadrant, note the very short basal trunk, scale bar 0.5 mm. (G) Marginal bulb, the ocelli are at the junctions of the tentacles with the bulb, scale bar 0.5 mm. A-C, modified after Edwards (1966); D-E, after living medusa from Dunstaffnage; F-G, after preserved material.

FIG. 7

Bougainvillia principis (Steenstrup, 1850), photograph of a living medusa, bell height about 1 cm

network; hydranths have very short stems or are sessile; perisarc of stolons smooth, the one investing lower part of hydranth often wrinkled, it thins out distally; hydranths spindle-shaped, hypostome short and rounded, 5-8 tentacles in a single whorl; gonophores globular, borne singly on very short stalks arising from the stolons. Colour: hypostome opaque white, gastrodermis dull pink.

Newly released medusa deep bell-shaped; jelly thin, thickness uniform, exumbrella with numerous nematocysts, four moderately deep interradial longitudinal furrows and four slight perradial longitudinal furrows in umbrella; without peduncle; three tentacles and three ocelli on each bulb; manubrium tubular, with four oral tentacles divided dichotomously 1-2 times, trunk long. Colours: gastrodermis of manubrium and bulbs brick-red.

Adult medusa wider than high or globular; jelly moderately thick, rather thicker above than at sides, umbrellar interradial furrows very shallow and perradial ones slight; with or without broad shallow peduncle; four radial canals moderately broad; bulbs long, epaulette-shaped, as long or longer than intervals; 20-40 tentacles per bulb; round adaxial ocelli at the junctions of the tentacles with the bulb (appearing on the bulbs in contracted specimens); oral tentacles rather short, dichotomously divided 5-8 times, basal trunks very short or absent and thus sometimes like two independent oral tentacles per perradial position (Fig. 6F), tips with nematocyst clusters, but not swollen; stomach broad-based, in form of perradial cross; gonads in form of eight adradial pads, confluent interradially, clearly separated by perradial cleft even in fully mature animals, in subadults separated perradially by gonad-free stripe. Colours: centre of bulbs with a red to darkish brown or orange pigment that forms radiating stripes on the abaxial side of the bulb; ocelli black; gonads orange-pink.

DIMENSIONS: Adult medusa usually 5-8 mm wide, maximally 10-11 mm. Newly released medusa 1.1 mm wide and 1.3 mm high. Hydranths up to 1.1 mm high, diameter 0.18 mm; diameter gonophores 0.63 mm; more measurements are given in Edwards (1966).

VARIATION: Edwards (1966) gives more details on the growth of the medusa and the variation of tentacle numbers and the branching of the oral tentacles.

DISTRIBUTION: A northern boreal medusa occurring in coastal areas from the Barents Sea to the English Channel and the North Sea. Also present around Iceland, western Greenland and New England (Hartlaub, 1911; Kramp, 1927; Russell, 1953; Kramp, 1961; Zelickman, 1972; Pages *et al.*, 2006). Chow & Huang (1958) recorded it in the East China Sea. The records for NE Pacific were referred to the very similar *B. multitentaculata* Foerster, 1923 by Arai & Brinckmann-Voss (1980), but later changed to *B. principis* (Cairns *et al.*, 2002). Type locality: Sandvaag, The Faroe Islands.

ADDITIONAL DATA: The ultrastructure of the ocelli is described by Singla (1974).

BIOLOGY: The polyp was found on the surface of pieces of clinker, coal and stone dredged at 30 m depth. Gonophores were observed from March to May. The life span of the medusa is about two to three months (Edwards, 1966). The seasonal occurrence of the medusa has been summarized or examined by Kramp (1926), Russell (1953), Edwards (1966), Ballard & Myers (1996). It is a summer species and can be found in the plankton from April to September. In more northern localities it will appear later than in the south. In a sea-lough SW of Ireland, Ballard & Myers (1996, 2000) found it usually in depths of 20-30 m. Although they could not detect any diel vertical migration, *B. principis* might migrate at other places.

REMARKS: A distinct species, although sometimes it can be difficult to separate from *B. britannica* (see there). Its synonymy and life cycle has been well worked out by Edwards (1966). *Bougainvillia multitentaculata* Foerster, 1923 from the NE Pacific resembles very closely *B. principis* and has been confounded with this species (see Arai & Brinckmann-Voss, 1980). *Bougainvillia multitentaculata* differs from *B. principis* in having no perradial interruption of the gonads.

Bougainvillia muscoides (Sars, 1846) Fig. 8

Perigonimus muscoides M. Sars, 1846: 8, pl. 1 figs 19-21. – Jäderholm, 1909: 46, pl. 1 fig. 18.
Bougainvillia nigritella Forbes, 1848: 63, pl. 12, fig. 2a-f. – Edwards, 1966: 139, synonym.
Margelis nordgaardii Browne, 1903: 14, pl. 2, fig. 1, pl. 3 figs 5-6. – Mayer, 1910: 168, fig. 91. – Kramp & Damas, 1925: 256, figs 11-12. – Kramp, 1926: 43. – Rees, 1938: 2, synonym. – Kramp, 1959a: 110, fig. 94. – Kramp, 1961: 79.
Bougainvillia obscura Bonnevie, 1898b: 7, pl. 1 fig. 4. – Rees, 1956b: 113, synonym.
Thamnitis sp. Browne, 1905b: 758. – Edwards, 1964b: 741, synonym.
Bougainvillia muscoides. – Rees, 1938: 2, fig. 1. – Rees, 1956b: 113. – Edwards, 1964b: 730, figs 5-6. life cycle. – Rasmussen, 1973: 24, fig. 8.
Thamnostoma spec. – Russell, 1953: 150, fig. 73A-E. – Edwards, 1964b: 741, synonym.

MATERIAL EXAMINED: MHNG INVE48760 and INVE48761; Norway, Raunefjord, Flesland beacon, 20-100 m, 26 June 2006, on tubes of *Sabella* spec., hydroid colonies with medusa buds, release of medusae observed, newly released medusa without ocelli, orange; DNA extracted, 16S sequence **AM411412**. – MHNG INVE48764; Norway, Fanafjord, 0-150 m, 22 June 2006; one mature female medusa from plankton, examined alive. – BMNH 1965.1.14.39+62; Sweden, Kosterfjord, Sächen Reef; polyp colonies without medusa buds; depth 80-100 m; 23 September 1964. – BMNH 1965.1.14.74+75; polyp colony on slides; Sweden, Kosterfjord, Sächen Reef; 80-100 m; 23 September 1964. – BMNH 1985.9.12.12 Norway, Bognøstrømmen; polyp colonies without medusa buds from *Ascidia mentula;* 14 August 1937; coll. W. J. Rees, labelled as *Perigonimus muscoides*. – BMNH 1985.9.11.5; Norway, Bognøstrømmen; polyp colonies with medusa buds; 18 August 1937; coll. W. J. Rees. – BMNH 1969.12.2.93; Norway, Bognøstrømmen; polyp colony on slides, with medusa buds; 6 September 1937; coll. W. J. Rees. – BMNH 1985.9.12.10; Norway, Herdla and Brattholmen; medusae and polyps, medusa from plankton; August 1937; coll. W. J. Rees. – BMNH 1949.2.1.41; Norway, Mofjord; 1 May 1903; 3 medusae from plankton; labelled as *Bougainvillia nordgaardi*, leg. E. T: Browne. – BMNH 1949.2.1.42; Norway, Mofjord; 2 May 1903; several medusae from plankton; labelled as *Margelis nordgaardi*, leg. E. T: Browne. – ZSM, Stechow collection, 20000639 and 2000641, two slides as *Perigonimus muscoides*, loc. Capri, most likely material described in Stechow (1923a). – MHNG INVE38775; Chile, Huinay marine station, February 2006; several mature medusae from plankton; leg. H. Galea; 16S sequence **AM411413**.

DIAGNOSIS: Medusa without ocelli, 3-5 mm high, oral tentacles up to four times branched, 3-7 tentacles per bulb, tentacle bases swollen, stomach narrowed at base, gastric peduncle short. Hydroid colony erect, branched polysiphonic, with thin auxiliary tubes creeping over thick central tube, hydranths on short pedicels, medusa buds single.

DESCRIPTION (own observations; Kramp & Damas, 1925; Edwards, 1964b): Hydroid forming erect, polysiphonic stems arising at intervals from a network of tubular stolons; stem fairly thick and not much branched, secondary branches short, rather few; stem composed of a thicker central tube covered by up to seven thinner auxiliary tubes originating as stolons, towards distal the number of auxiliary tubes gets reduced and the distal-most parts are only formed by central tube; perisarc of central tube undulated, sometimes multilayered. Hydranths arise from central tube and auxiliary tubes, pedicels often very short and hydranths thus close to stem, many almost adnate; hydranths of very variable size, terminal ones larger than lateral ones; perisarc of polyp pedicel thin, wrinkled and forming cup around proximal part of hydranth like a short pseudohydrotheca; hydranth with 8-12 tentacles. Gonophores abundant, pear-shaped, arising singly on short stalks on central tube, auxiliary tubes, hydranth pedicels, and sometimes the stolons, frequently in rows on auxiliary tubes,

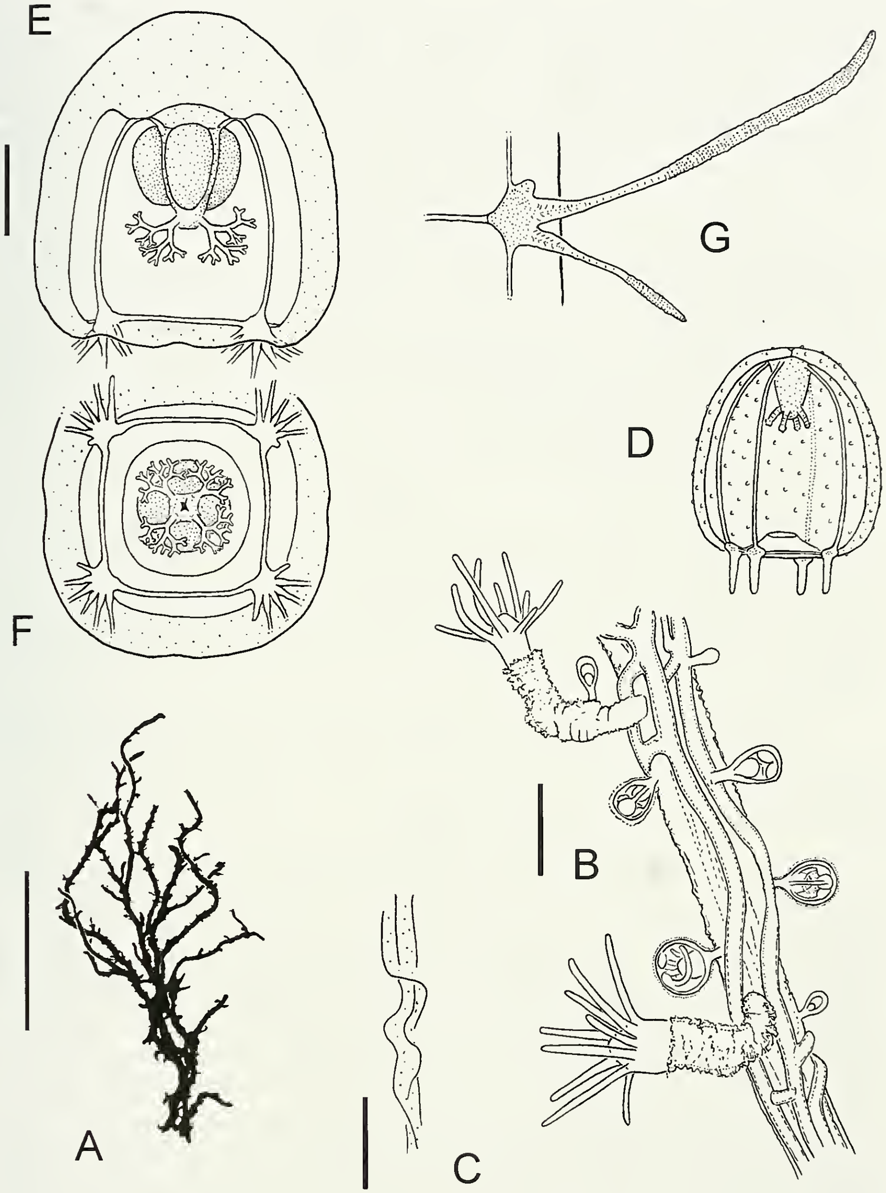


FIG. 8

Bougainvillia muscoides (Sars, 1846). (A) Colony silhouette, scale bar 1 cm. (B) Part of branch with polyps and medusa buds, note thick central tube and thinner auxiliary tubes, scale bar 0.5 mm. (C) Higher magnification of perisarc of central tube, scale bar 50 μm. (D) Newly released medusa. (E) Side view of mature medusa, tentacles truncated, scale bar 0.4 mm. (F) Oral view of medusa, same scale as E. (G) Tentacle bulb of juvenile medusa in adaxial view, note absence of ocelli and basal swelling of tentacle. A-C, E-F, after preserved material from Norway; D & G, modified after Edwards (1964b).

covered by filmy perisarc. Colours: polyps orange or reddish, medusa buds red and white.

Newly released medusa with uniformly thin jelly, bell relatively opaque, with four shallow perradial longitudinal furrows in exumbrella, exumbrellar nematocysts present; no peduncle, manubrium short; no ocelli, only one tentacle on each bulb, tentacle bases swollen or not; four oral tentacles unbranched. Colours: manubrium reddish, less brilliant than in the buds; tentacle bulbs with reddish brown pigment.

Adult medusa about as wide as high; bell relatively angular and opaque; jelly moderately thick, thicker apically than at sides; exumbrella with four interradial and four perradial furrows; rather shallow gastric peduncle present; radial canals moderately wide; bulbs rather large, rounded triangular; 3-7 tentacles on each bulb, tentacles swollen at base, distal end also thickened, bulbs without ocelli; oral tentacles divided dichotomously 4-7 times ending in weak capitations, basal trunks of oral tentacles short or of moderate length (1/5 or more of total length). Stomach relative small, spanning about $^1/_2$ of subumbrellar cavity, ovoid, narrowed at base; gonads form bulging interradial pads on stomach wall. Colour of manubrium and bulbs red-orange.

DIMENSIONS (Kramp & Damas, 1925; Edwards, 1964b; Rasmussen, 1973; own observations): Mature polyp colonies up to 2-7 cm, central tube 0.25-0.35 mm diameter, auxiliary tubes 0.08-0.1 mm in diameter; hydranths up to 1 mm long and 0.3 mm wide. Medusa buds 0.4 mm high, diameter 0.3 mm. Newly released medusa 0.55-0.7 mm. Height of adult medusa 3-5 mm. Egg size about 0.2 mm (Norwegian medusae).

VARIATION: In the north of the British Isles, the medusae are about 3 mm in height and have up to three tentacles per bulb. In Norway, the medusae reach sizes of 4-5 mm and can have up to seven tentacles per bulb. In preserved material, the basal swelling of the tentacles is not always present.

BIOLOGY: The polyp is found on *Tubularia indivisa*, *Ascidia mentula*, *Mytilus, Sabella pavonia, Sertularella gayi*, in depths of 4-200 m, mostly around 40 m (Edwards, 1964b; Rasmussen, 1973). Rasmussen (1973, Denmark) observed newly settled hydroids in October-November. Medusa buds in Norwegian, Scottish and Danish colonies were observed in June and August (Edwards, 1964b; Christiansen; 1972; Rasmussen, 1973; own data). The medusa is found in the plankton from June to November, mostly in deeper waters (around 100 m) but sometimes also at the surface (Kramp & Damas 1925; Edwards, 1964b; own data). The colonies are dioecious.

DISTRIBUTION: Reliable records of both polyp and medusa phase are restricted to a relatively narrow region reaching from Trondheimsfjord in Norway south to Scotland (Edwards, 1964b). Also present along the west coast of Sweden (Jäderholm, 1909; Allwein, 1968; Rees & Rowe, 1969, Christiansen, 1972) and Denmark (Rasmussen, 1973). Records from Chile and British Columbia (NE Pacific) were thought to be erroneous (Kramp, 1952; Arai & Brinckmann-Voss, 1980). However, recently Dr Horia Galea (MHNG INVE38775) has found and documented medusae in a Chilean Fjord that are indistinguishable from *B. muscoides*. A sequence comparison of about 590 base-pairs of the 16S gene of the Chilean specimens with polyp material from Norway gave only a difference of a single base pair, suggesting that they are conspecific (see also under *B. muscus*). There are also records from the Mediterranean (Stechow, 1923a), Red Sea (Schmidt, 1973a, Papua New Guinea (Bouillon, 1980) and New Zealand (Bouillon, 1995). The records from warm or tropical regions are probably misidentifications of closely related species (see also Schuchert, 1996). In the Mediterranean, the medusa has never been seen, and the presence of the polyp stage in the Mediterranean is not certain (see below). Type locality: Mangerfjord, Norway, polyp on *Ascidia mentula* and *Tubularia indivisa*, 36-55 m.

REMARKS: Stechow (1923a: 75) reported an infertile colony of *Bougainvillia muscoides* from near Capri in 200 m depth, but he admitted that it was only tentatively identified. Although Stechow's material appears indistinguishable from Atlantic material (material re-examined for this study), the presence of *B. muscoides* in the Mediterranan is not certain as long the medusa has not been found or cultivated. Stechow also noted the similarity of his material to *Bimeria biscayana* Browne, 1907 (here referred to *Amphinema bicayana*), and it is possible that it belongs to this species

Due to the absence of ocelli, the medusa of *B. muscoides* is easily distinguishable from all other *Bougainvillia* species of the region (note that in formalin fixed specimens the pigment of ocelli fades rapidly). However, Goy *et al.* (1991) described a *Bougainvillia* medusa originating from Lebanon in the eastern Mediterranean. They assigned it to *Bougainvillia aurantiaca* Bouillon, 1980, a species originally described from Papua New Guinea. The Lebanese medusa closely resembles *B. muscoides*, but it is distinctly smaller (1.5 mm), has only two tentacles per bulb and its oral tentacles branch only two times. More life cycle information is needed for the Lebanese populations in order to evaluate their status and to provide more diagnostic characters to distinguish it more reliably from *B. muscoides*.

Bougainvillia pyramidata (Forbes & Goodsir, 1853) Fig. 9

Hippocrene pyramidata Forbes & Goodsir, 1853: 312, pl. 10 fig. 4.
? *Medusa ocilia* Dalyell, 1847: 64, pl. 11 figs 1-10. – Edwards, 1966: 138, questionable synonym.
in part *Bougainvillia flavida* Hartlaub, 1897: 456, pl. 14 fig. 6 [male medusa only]. – Hartlaub, 1911: fig. 168. – Edwards, 1964b: 734, synonym.
Bougainvillia pyramidata. – Mayer, 1910: 168. – Hartlaub, 1911: 180, fig. 159. – Russell, 1953: 167, fig. 82A-C. – Kramp, 1959a: 108, fig. 86. – Kramp, 1961. – Edwards, 1964b: 725, figs 1-4. – Russell, 1970: 236, fig. 6s.

MATERIAL EXAMINED: BMNH 1971.5.11.10, Great Britain, Isle of Cumbrae, Millport, 36 m, 24 September 1970, polyp on *Tubularia* and reared young medusae, det. C. Edwards. – BMNH 1967.12.1.7, Great Britain, Little Cumbrae, off Lighthouse, 82 m, 08 July 1966, polyp on *Tubularia*, hydranths lost, coll. W. J Rees. – BMNH 1966.1.4.13+24, Sweden, Gullmarfjord, 50 m, 13 October 1964, polyp on ascidian, coll. W. J. Rees. – BMNH 1966.1.4.38, Sweden, Gullmarfjord, Skär, 80 m 3 October 1964, polyp colony, det. W. J. Rees. – BMNH 1985.9.10.23, Great Britain, Millport, Keppel Pier, one medusa, 30 September 1940, det. W. J. Rees. – BMNH 1985.9.4.12, Ireland, Kerry county, Valentia Island, 27 July to 5 August 1938, 7 medusae, coll. W. J. Rees.

DIAGNOSIS: Medusa with cone-shaped gastric peduncle, 4-9 tentacles per bulb, oral tentacles 3-4 times branched, with moderately long basal trunk; gonads adradial on perradial outgrowths of stomach; ocelli round on bulbs. Hydroid erect, branching, polysiphonic, with distinct and straight main axis, medusa buds in groups.

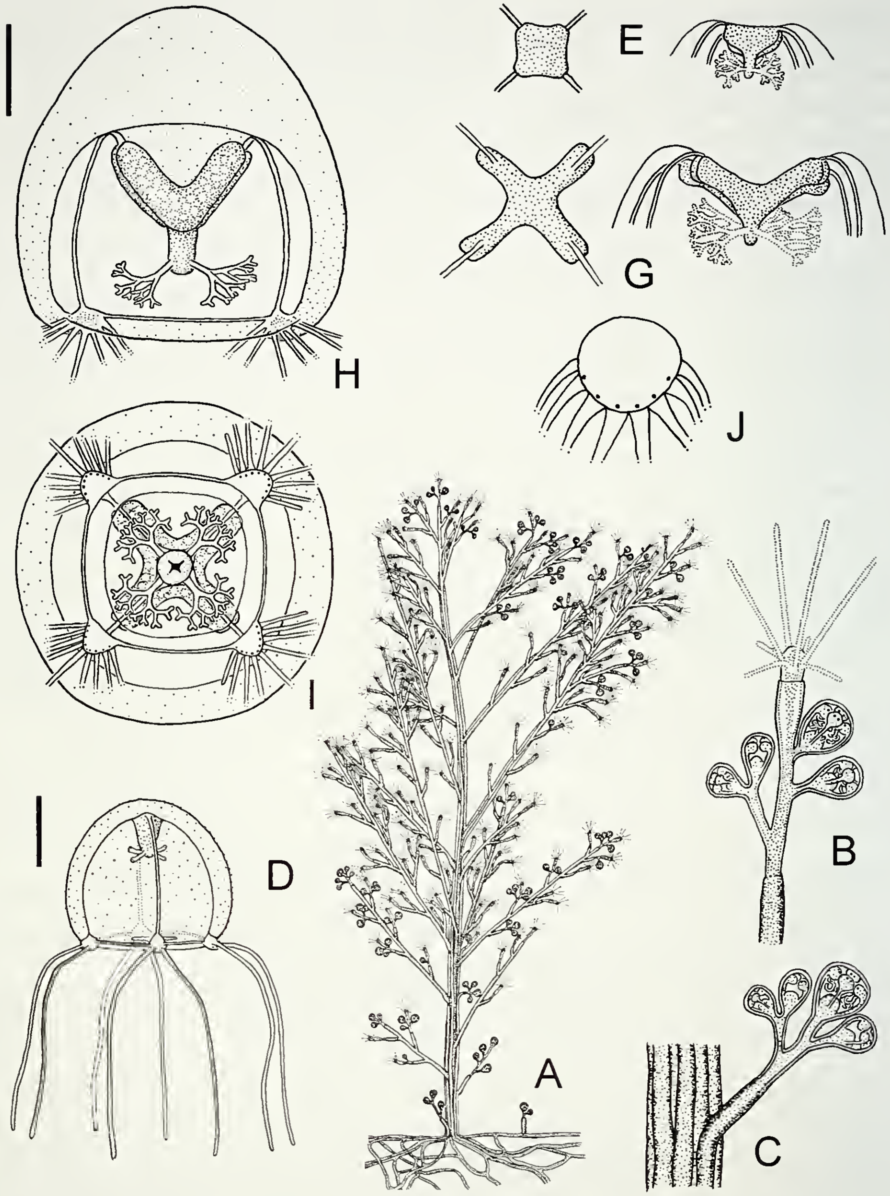


FIG. 9

Bougainvillia pyramidata (Forbes & Goodsir, 1853). (A) Colony, size about 4 cm. (B) Hydranth with medusa buds, for sizes see text. (C) Part of polysiphonic stem with cluster of medusa buds. (D) Newly released medusa, note absence of peduncle, unbranched oral tentacles, two tentacles per bulb, scale bar 0.3 mm. (E) Manubrium of juvenile medusa, left aboral view, right lateral view. (G) Manubrium of mature, cultivated medusa, left aboral view, right side-view. (H) Mature medusa from plankton, side view, scale bar 0.5 mm. (I) Same as in H, oral view. (J) Adaxial view of tentacle bulb. A-G, modified from Edwards (1964b); H-I, schematic composite picture from several preserved medusae; J, after Russell (1953).

DESCRIPTION (after own observations; Russell, 1953; Edwards, 1964b): Hydroid forming erect stems with a distinct, straight, central primary axis, primary, secondary and tertiary branches present. Stolons creeping, tubular, branching and forming meshwork, sometimes polysiphonic, stem and primary branches polysiphonic, branches straight and regular; perisarc corrugated at bases of branches, thins out over hydranths to pseudohydrotheca; hydranths terminal on the branches and stem, cylindrical and quite long, with 6 to 13 tentacles in one whorl; medusa buds egg-shaped, on distinct stalks, arising in clusters on the branches just below the hydranths, on stem or on short stems arising from the stolons, stalks of medusa buds can be branched. Colours: hypostome white, gastrodermis pink.

Medusa at release subglobular; jelly uniformly thin, exumbrella with numerous scattered nematocysts and with four shallow interradial longitudinal furrows; no peduncle; two tentacles and two ocelli on each bulb; four oral tentacles unbranched.

Adult medusa subglobular; jelly thick, especially apically; manubrium on a conical peduncle, height of peduncle variable; radial canals narrow; bulbs oval, much smaller than space between them; 7-9 tentacles per bulb; ocelli round, situated adaxially on bulbs at bases of tentacles; oral tentacles divided dichotomously 3-4 times. Perradial lobes of the stomach extend along radial canals on peduncle and gonads lie in the walls of these lobes and adjacent basal part of stomach walls, appearing V-shaped in side-view and cross-shaped in axial view. Colours: marginal bulbs reddish brown or yellow; stomach yellowish brown; ocelli black.

VARIATION: The development of the medusa is described in Russell (1953) and Edwards (1964b). The peduncle is only fully formed in mature medusae.

DIMENSIONS: Hydroid colony up to 4 cm high, hydranths up to 0.66 mm long and 0.1 mm wide, gonophores 0.45 mm in diameter (after Edwards, 1964b, for more measurements see this publication). Medusa at release about 0.72 mm wide and 0.63 mm high. Adult medusa 2-5 mm wide and high, exceptionally up to 8 mm.

DISTRIBUTION: *Bougainvillia pyramidata* appears to be restricted to the northeastern Atlantic along the western coasts of Scotland, the Irish Sea, the western coast of Ireland, and the western coast of Sweden (Russell, 1953; Rees & Rowe, 1969; Boyd *et al.,* 1973; Ballard & Myers, 1996). Type locality: Loch Laigh, Mull, Scotland.

BIOLOGY: The polyp was found in depths of 30-80 m on stems of *Tubularia indivisa* and *Virgularia mirabilis* and on tests of *Ascidiella aspersa*. Along the Scottish coast, the medusa is present in the plankton (Scotland) from June to begin of November, with a clear maximum towards the end of August. The medusa seems to be associated with moderately deep waters, it is purely neritc, it has been taken commonly near the surface and there is no evidence that it lives in deep layers (Edwards, 1964b). Ballard and Myers (1996, 2000) observed it in a lough in SW Ireland in low numbers from April to November, depths of 10-20 m. No diel vertical migration was observed.

REMARKS: The hydroid of *Bougainvillia pyramidata* is prone to be mistaken for *B. muscus* (Edwards, 1964b; Rees & Rowe, 1969). According to Edwards (1964b) *Bougainvillia pyramidata* is distinguished by its erectness and straightness of the stems, the straightness of the branches and their regularity of arrangement. It does not appear tree-like as in large *B. muscus* colonies, but has a conspicuous, more or less straight central main stem running to the top of the colony. Branched pedicels of the medusa buds (Fig. 9B-C) are so far only known in *B. pyramidata*. Although they may not always be present, they are likely a diagnostic difference. The tentacle number may also be lower with a maximum of 13 (*B. muscus* 18), and its occurrence seems to be restricted in depths below 30 m, while *B. muscus* can also be found immediately below the water surface. Whatsoever, the morphologies of both species – both medusa and polyp – intergrade and they are sometimes not objectively separable. Some Norwegian colonies (MHNG INVE48746) were initially taken for *B. pyramidata* as they differed markedly from other nearby colonies of typical *B. muscus* (comp. Figs. 2 and 3). The colonies had a straight central axis and clustered medusa buds. They also differed in colour from the more typical *B. muscus* colony. However, the rearing of the medusa and the 16S data proved that these colonies were *B. muscus*. The hydroid stage of both species can thus sometimes not be distinguished morphologically, but the medusa clearly separates the two species.

Bougainvillia superciliaris (L. Agassiz, 1849) Fig. 10

Hippocrene superciliaris L. Agassiz, 1849: 273, pl. 1-3.
? *Hippocrene Bougainvillii*. – Brandt, 1835: 29 [pagination of reprint]. – Brandt, 1838: 393, pl. 20.
[not *Cyanea Bougainvillii* Lesson, 1830 = *B. macloviana*]
? *Bougainvillia Mertensii* L. Agassiz, 1862: 344, new name for *Hippocrene Bougainvillei* Brandt.
Not *Bougainvillia Mertensii*. – A. Agassiz, 1865: 152, hydroid. – Allman, 1872: 318.
Bougainvillia paradoxa Mereschkowsky, 1879: 177, pl. 20 figs 1-5. – Hartlaub, 1911: 176, synonym.
in part *Bougainvillia superciliaris*. – Mayer, 1910: 162, figs 87-88, 162, pl 17 fig. 1. – Hartlaub, 1897: 466, pl. 16a figs 5, 8, 12. – Hartlaub, 1911: 171, figs 153 [not polyp and young medusae].
Bougainvillia superciliaris. – Bigelow, 1909: 305, pl. 31 fig. 2. – Russell, 1953: 169, figs. 83-85. – Kramp, 1959a: 108, fig. 87. – Uchida & Nagao, 1960: 249, figs 1-4. – Vannucci & Rees, 1961: 85. – Kramp, 1961: 82. – Werner, 1961: 206, figs 1-5. – Edwards, 1966: 148. – Kramp, 1968: 32, fig. 80. – Russell, 1970: 236, 243. – Arai & Brinckmann-Voss, 1980: 38, fig. 18.
Not *Bougainvillia superciliaris*. – Naumov, 1969: 215, figs 83-84.

MATERIAL EXAMINED: IRSNB, collection IG 27838, collected by J. Bouillon 1970, Atlantic Ocean, 4 females and one male. – BMNH 1970.1.4-7 and 12-15, Great Britain, Wales, Dale Fort Field Centre, 25-26 March 1963, several medusae collected W. J. Rees. – BMNH 1931.12.21.16-19, Canada, Hudson Strait, Port Burnwell, collected 1931, medusae. – ZMUC, Denmark, Aggersund, 6 May 1929, 6 medusae. – ZMUV, Denmark, Hvalpsund, 21 m depth, 22 April 1924, 2 medusae.

DIAGNOSIS: Medusa jelly moderately thick, with distinct gastric peduncle, 11-15 tentacles per bulb, oral tentacles branched 4-5 times, basal trunk very short; crescent-shaped ocelli on base of tentacles (not on bulbs). Hydroids small, sessile, medusa buds on stolons, peduncle visible in buds, more than two ocelli and tentacles per bulb.

DESCRIPTION (after Russell, 1953; Werner, 1961; own data): Polyps arising from a network of creeping tubular stolons; hydranth small, without distinct pedicel hence sessile, body covered by very thin, tightly adhering, membranous perisarc (pseudohydrotheca), expanded polyp fusiform to cylindrical, rounded hypostome, 7-13

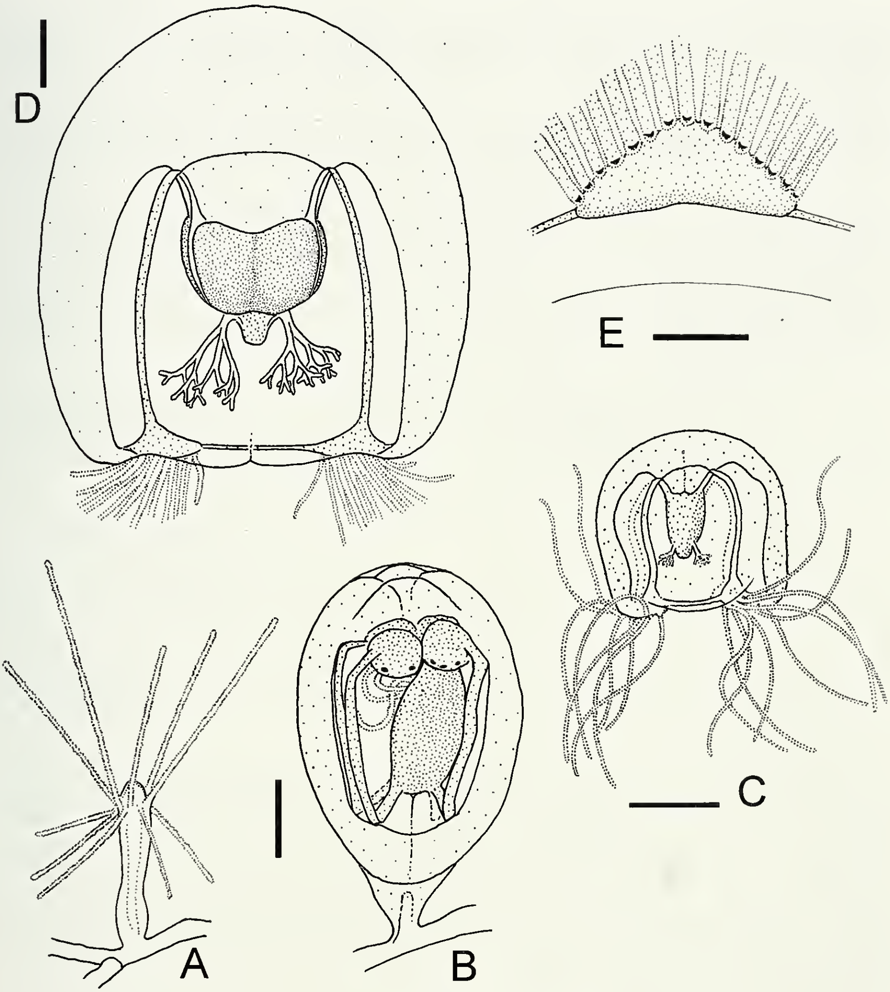


FIG. 10

Bougainvillia superciliaris (L. Agassiz, 1849). (A) Polyp stage, scale bar 0.4 mm. (B) Advanced medusa bud, same scale as A. (C) Newly released medusa, note presence of peduncle, scale bar 1 mm. (D) Mature medusa, scale bar 1 mm. (E) Marginal bulb seen from oral side, note position of crescent shaped ocelli on tentacle bases, scale bar 0.4 mm. A-C, modified after Werner (1961); D-E, after preserved material.

tentacles in one whorl. Gonophores arise singly on short stalks from the stolons, egg- or pear-shaped, larger than polyps. Nematocysts: desmonemes and microbasic euryteles.

Newly released medusa bell-shaped; jelly of moderate thickness, thicker apically than at sides; usually with well developed peduncle; four rather shallow interradial longitudinal furrows in umbrella, exumbrella with numerous nematocysts in groups of 2-4; 5-9 tentacles and about 5 ocelli to each bulb, ocelli on bases of tentacles; four oral tentacles divided dichotomously 2-3 times.

Adult medusa almost globular; or rather higher than wide; jelly thick, thicker at top than at sides; interradial furrows variably developed, umbrella cross-section rather quadrangular; well-developed gastric peduncle; radial canals relatively broad; bulbs triangular, less wide than intervals; 11-15 (exceptionally up to 22) tentacles per bulb, ocelli large, crescentic-round, adaxial, on bases of tentacles; oral tentacles divided dichotomously 4-5 times (exceptionally up to 6-8 times), basal trunks short, distal ends beset with nematocyst but not distinctly swollen; stomach broad-based, in form of perradial cross; gonads interradial, in mature specimens covering the whole surface of the stomach, but separated perradially; eggs without nematocysts, most planulae develop enveloped in capsules and attached to gonad by a short stalk (larviparous). Colour of stomach reddish brown, marginal bulbs chestnut brown, ocelli black. Nematocysts: desmonemes and microbasic euryteles of two size classes.

VARIATION: The presence of a gastric peduncle in the newly released medusa is a characteristic trait of this species, but it can be absent in a minority of individuals, mostly due to pathological development (Werner, 1961). The Pacific medusae are larger than the Atlantic ones (up to 12 mm; Uchida & Nagao, 1960).

DIMENSIONS: Polyp stage (Werner, 1961) height up to 1.0 mm, usually 0.5-0.7 mm; gonophores up to 2.2 mm high, 1.4 mm wide. Newly liberated medusa (Werner, 1961) 1.9-2.5 mm wide, 1.6-2.5 mm high. Mature medusa bell height 4-9 mm. See Werner (1961) for the sizes of nematocysts of hydroid and medusae.

ADDITIONAL DATA: Linko (1900) examined the histological structure of the ocelli. Gerd (1892) describes the early embryology. The diploid chromosome number is 30 (Werner, 1961).

DISTRIBUTION: An Arctic species penetrating into colder boreal regions. Originally described from Massachusetts, also present along northern New England, Canada, and Western Greenland. In Europe resident on the coasts of Iceland, Spitsbergen, Norway, Denmark, Germany, and Holland. In British waters the medusa has been reported on the North Sea coasts. Further occurrences are known from the Bering Sea, Hokkaido, Yellow Sea, Aleutian Islands, British Columbia, perhaps as far south as San Francisco (for references see Hartlaub, 1911; Kramp, 1926; and Arai & Brinckmann-Voss, 1980).

BIOLOGY: In Arctic waters, the medusa of *Bougainvillia superciliaris* is present during summer from May to July or September, in the southern parts of its distribution (North Sea, south of Cape Cod) it is only found in early spring, mainly from February to April (Kramp, 1926; but see Zelickman, 1972).

Werner (1961) examined in detail the ecology and development of *Bougainvillia superciliaris* for the population of the North Sea. In culture, the polyp is eurytherm (2-15°C) and can even be maintained at room temperature, but medusae budding takes place only at low temperatures (5-7 °C). In contradistinction to the polyp, the medusa is stenotherm and it dies at temperature above 11-14°C. It takes very long for the medusa buds to develop (8 weeks), but the liberated medusa matures within four weeks. Females are able to produce eggs in several rounds. The fertilized eggs remain attached to the stomach wall and develop there, although some may detach and develop in the subumbrella.

The medusa uses its oral tentacles to capture herring larvae, euphausid nauplii and polychaete trochophores in preference to various other crustaceans (see refs in Arai & Brinckmann-Voss, 1980).

Nagao (1964) found the hydroid in nature growing on a shell of a gastropod belonging to the genus *Neptunea*. Orlov (1995) examined the settling behaviour of the larvae.

REMARKS: This species has a complicated taxonomic history partially described by Edwards (1966: 136). Also Vannucci & Rees (1961) provide a synonymy. Some comments concerning *Bougainvillia mertensii* L. Agassiz, 1862 are nevertheless needed. Brandt (1835, as *Hippocrene Bugainvillii*) attributed a medusa from the Bering Sea to *Cyanea Bougainvillii* Lesson, 1830, which he supplemented later (1838) by a figure. However, *Cyanea Bougainvillii* Lesson, 1830 is as synonym of *Bougainvillia macloviana* Lesson, 1830. As Brandt's medusa is evidently not referable to *B. macloviana,* L. Agassiz (1862) gave it the new name *Bougainvillia mertensii*. Haeckel (1879) indicated the close similarity of *Bougainvillia mertensii* to *B. superciliaris* and Vannucci & Rees (1961) listed it as a questionable synonym of *B. superciliaris*. This view is also adopted here.

The knowledge of the life-cycle of *B. superciliaris* has also an intricate history. Agassiz (1865) associated an erect, branched, 5 cm high *Bougainvillia* colony from Massachusetts to this species. He observed the release of the medusae and followed their development. Of the obtained medusa he says (Agassiz, 1865: 155), «it assumes all the principal features of the adult, as in Fig. 232, with the exception of the simpler character of the tentacles of the actinostome». In other words, the oral tentacles did not branch as much as in the medusae found in the plankton. Although Agassiz's account appears plausible, Hartlaub (1911) doubted his results and attributed Agassiz's hydroid to *B. muscus*. He did so because he believed that he had found the true polyp of *B. superciliaris*, a colony of sessile hydranths found in an aquarium of the Helgoland station. Hartlaub also claimed to have followed the development of the medusa until its identity was evident. Others continued to iterate Agassiz's version (e. g. Mayer, 1910; Fraser, 1937, 1944; Berrill, 1948; Vannucci & Rees, 1961). The life cycle was then re-investigated in detail by Uchida & Nagao (1960) for the Japanese population and by Werner (1961) for European animals. Both studies started with planulae released by the medusa stage and found a sessile hydroid, but did not discuss the discrepancy of their and Agassiz's observations. There were also some discrepancies in Werner's and Hartlaub's observations, which were resolved by Edwards who realized that Hartlaub had in fact found the hydroid of *B. principis* and not *B. superciliaris*.

Unfortunately, Agassiz did not depict the medusae he obtained from his rearing experiments, so we are unable to decide how reliable his identifications are. Although it is more probable that Agassiz indeed mistook another *Bougainvillia* hydroid for the one of *B. superciliaris* (unlikely *B. muscus* as the medusae had at least seven tentacles per bulb), there remains the possibility that *B. superciliaris* as currently perceived is composed of at least two species differing in their polyp stage only. New life-cycle studies on *B. superciliaris* from Massachusetts should be made to resolve this.

Bougainvillia macloviana Lesson, 1830 Fig. 11

Bougainvillia macloviana Lesson, 1830: 118, pl. 14 fig. 3. – Mayer, 1910: 160.– Hartlaub, 1911: 156, fig. 139. – Künne, 1933: 249, fig. 1. – Browne & Kramp, 1939: 284, pl. 14 fig. 6, pl 15 figs 7-14. – Russell, 1953: 173, figs 86-88B. – Kramp, 1959a: 108, fig. 85. – Kramp, 1961: 78. – Vannucci & Rees, 1961: 69. – Edwards, 1966: 147. – Kramp, 1968: 32, fig. 78. – Millard, 1975: 96, fig. 33A-C. – O'Sullivan, 1982: 38, fig. 16, map 15. – Pagès *et al.*, 1992: 3, fig. 1. – Schuchert, 1996: 30, fig. 14a-c.

Cyanea Bougainvillii Lesson, 1830: 118, pl. 14 fig. 3, simultaneous synonym.

Hippocrene macloviana. – Haeckel, 1879: 90, pl. 5 figs 1-2.

Perigonimus maclovianus. – Vanhöffen, 1910: 284, fig. 10a-d.

MATERIAL EXAMINED: BMNH 1939.6.8.1009-1025, Falkland Islands, collected 1898, young, mature medusae, collection Vallentin, leg. E. T. Browne. – See also Schuchert (1996).

DIAGNOSIS: Medusa up to 8-15 mm, jelly moderately thick, large gastric peduncle present, bell margin quadrangular, 30-65 tentacles per bulb, ocelli on marginal bulbs, oral tentacles branching 5-7 times, basal trunk short; stomach forms perradial lobes extending upwards onto peduncle and bearing the gonads. Hydroid small, stolonal, medusa buds singly on stolons and hydranth pedicels.

DESCRIPTION (Vanhöffen 1910, Browne & Kramp, 1939; Edwards, 1966; and own observations): Hydroid forming stolonal colonies, hydranths arising from tips of creeping tubular stolons which form an open network; perisarc much wrinkled, not annulated, extending as thin membrane over body of hydranth; up to 16 tentacles; medusa-buds pear-shaped, borne singly on short annulated stalks arising from stolons and pedicels.

Newly released medusa bell-shaped; jelly very thin, exumbrella even, but early in development deep interradial furrows and shallow adradial ones appear; no peduncle; bulbs globular, each with 2-5 tentacles and 2-3 ocelli; ocelli round, on bulbs at bases of tentacles; four oral tentacles unbranched or with one division.

Adult medusa with bell as high as wide or slightly higher than wide, with quadrangular cross-section; jelly fairly thick, thickened at apex; deep interradial longitudinal furrows in umbrella, bell-margin with perradial lobes; large conical peduncle that can span 1/2 to 2/3 of the subumbrella. Radial canals moderately broad; tentacle bulbs crescentic or V-shaped, about half as wide as intervals; about 30 tentacles per bulb in European animals (up to 65, usually 40-55 in Southern Ocean), when more than 18-20 tentacles then in a double row, sometimes three rows, young and old tentacles mixed; ocelli large, round or crescentic, on bulbs near bases of tentacles. Manubrium short, conical, with four long narrow perradial lobes running along peduncle; oral tentacles divided 5-7 times and with up to 80 ends ending in only slightly swollen nematocyst clusters, branching not always dichotomous, basal trunks very short. Gonads pad-like on adradii of stomach and along its perradial lobes, separated perradially and usually also interradially. Eggs covered with euryteles. Nematocysts: microbasic euryteles, on tentacles and eggs; desmonemes. Colours: stomach, gonads and marginal bulbs bright red, reddish brown, or orange-rose, ocelli red or black.

DIMENSIONS: Hydroid up to several millimetres high, medusa buds reach 1 mm in diameter. Newly released medusa 0.5-0.75 mm high. Gonad maturation starts at a size of 2-4 mm (Browne & Kramp, 1939). Adult medusa up to 8.5 mm in the NE

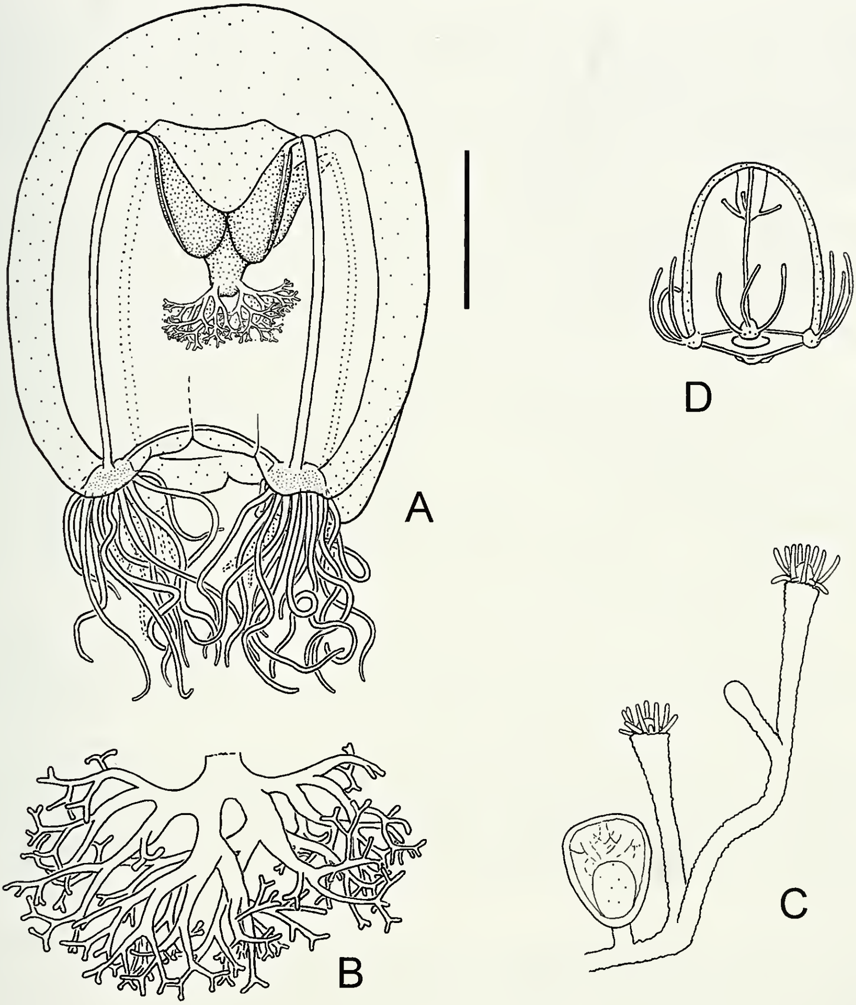


FIG. 11
Bougainvillia macloviana Lesson, 1830. (A) Mature, but not fully grown medusa, scale bar 2 mm. (B) Oral tentacle of fully grown medusa. (C) Hydroid with medusa bud. (D) Very young medusa, height about 0.6 mm. A, after preserved material from the Falkland Islands; B & D; modified after Browne & Kramp (1939); C, modified after Vanhöffen (1910).

Atlantic, 15 mm in Southern Ocean. Nematocysts (Schuchert, 1996): microbasic euryteles (7-8)x(3-4)μm; desmonemes, (6-7)x(4-4.5)μm.

DISTRIBUTION: Originally a species of the Southern Ocean, it has been known since 1895 to be resident in the North Sea and is believed to have been introduced there in the hydroid stage on ships. It is rare in European waters, but in its native region it can reach very high densities. The medusa was also found off the Isle of Cumbrae, Firth of Clyde, and the Mull of Kintyre (Edwards, 1966). The polyp has not been detected in Europe, it is only known from the Kerguelen Islands and South Africa (Millard, 1975). The medusa is also present in the coastal waters of the Kerguelen Islands (Vanhöffen, 1910); South Africa and Mozambique (Millard, 1975); Benguela Current (Pagès *et al.,* 1992); southern tip of New Zealand, Campell and Auckland Islands (Schuchert, 1996). Type locality: Soledad Bay, Falkland Islands, South Atlantic.

BIOLOGY: A coastal species. In the South Atlantic, mature medusae are present from November to March (austral summer, Browne & Kramp, 1939). In the North Sea, they occur from April to June (Russell, 1953). Buecher & Gibbons (2003) examined the dial vertical migration and found that *Bougainvillia macloviana* was largely confined to surface waters and did not appear to display any vertical migration.

OTHER DATA: The development of the medusa is described by Browne & Kramp (1939) and Russell (1953). Contrary to most other *Bougainvillia* species which add tentacles only at both sides of the bulbs, in *B. macloviana* young tentacles also develop among the older ones, causing an overcrowding which results in a displacement of the tentacles, so that they become arranged in two rows, both of which contain old and new tentacles (Browne & Kramp, 1939). According to Künne (1933), the North Sea specimens have black ocelli black, orange-rose gonads and manubrium, and a rusty brown zig-zag band on each bulb.

REMARKS: In the present fauna, *Bougainvillia macloviana* medusae can potentially only be confounded with *B. pyramidata*, but mature animals differ considerably in size and the number of tentacles per bulb.

There has been some confusion on the date and name of the first description of this species, because Lesson (1830) used the names *Cyanea Bougainvillii* as heading for a species, which he considered incorrect and he named it on the same page *Bougainvillia macloviana*. As explained by Calder (1988), both names are simultaneous synonyms and later Lesson (1836), acting as first reviser, chose *B. macloviana* as name.

Vanhöffen (1910) observed mature medusae of *B. macloviana* in high densities while his ship was in the Observatory Bay of Kerguelen Island. Later he found that polyps had settled on the ship hull, which he then attributed to *B. macloviana*. Although there remains some uncertainty because a direct link of the adult medusae and the observed was not established, it is very probable that Vanhöffen's conclusions were correct.

Bougainvillia platygaster (Haeckel, 1879) Fig. 12

Hippocrene platygaster Haeckel, 1879: 91.
Bougainvillia platygaster. – Kramp, 1957a: 9, text. fig. 1, pl. 3 figs 1-6. – Kramp, 1959a: 109, fig. 89. – Kramp, 1961: 80. – Vannucci & Rees, 1961: 78. – Kramp, 1968: 34, fig. 86. – Winkler, 1982: 30, fig. 3. – Bleeker & van der Spoel, 1988: 230, figs 8-9. – Pagès *et al.*, 1992: 4, fig. 2. – Bouillon, 1995: 227, fig. 1. – Schuchert, 1996: 33, fig 16. – Bouillon *et al.*, 2004: 44, fig. 26D. – Pagès *et al.*, 2006: 372, fig. 5F.
not *Bougainvillia platygaster.* – Goy *et al.*, 1991: 108, fig. 20.

MATERIAL EXAMINED: ZMUC, Neotype designated by Kramp (1957a), det. E. Haeckel, 25.067°S 27.433°W, off Brazil, collected 1869, 1 medusa, bell torn. – ZMUC, Dana station

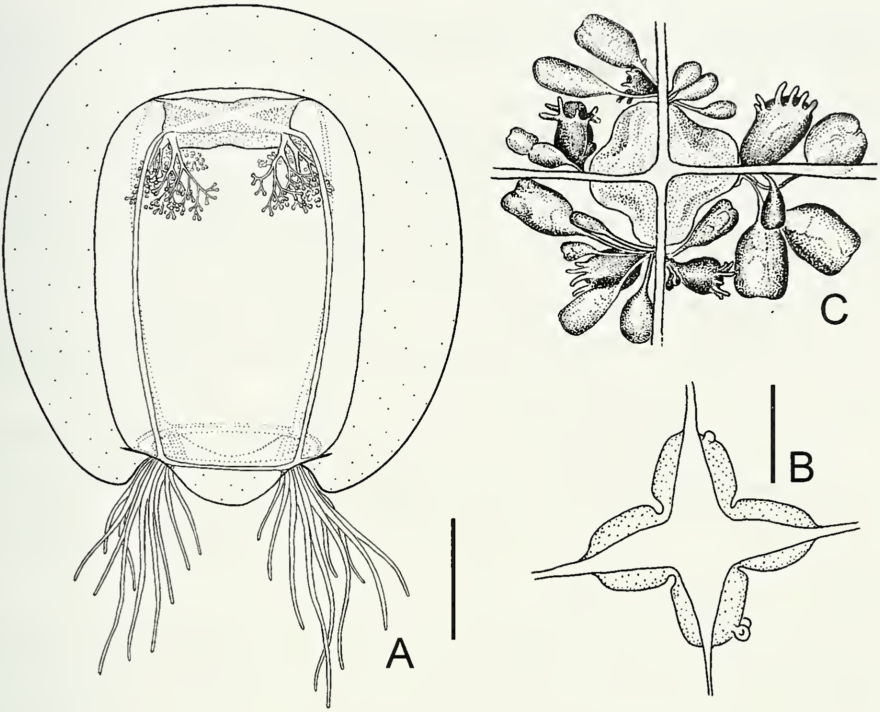


FIG. 12

Bougainvillia platygaster (Haeckel, 1879). (A) Medusa, the widely open mouth is likely a fixation artefact, scale bar 2 mm. (B) Stomach seen from aboral, note small medusa buds, scale bar 1 mm. (C) Immature specimen, aboral view of stomach with medusa buds and polyp formations. A, modified from Schuchert (1996); B, after preserved material from W Atlantic; C, from Kramp (1959a).

3547, 11.000°N 77.480°W, western Atlantic, 0-300 m, collected 24 August 1927, 1 medusa. – ZMUC, Dana station 3544, 18.417°N 56.050°W, western Atlantic, 14 August 1928, 1 medusa. ZMUC, Dana station 3543, 21.833°N 50.200°W, western Atlantic, 12 August 1928, 1 medusa. – BMNH 1957.12.29.148-151, Discovery station 680, 22.600°S 30.025°W, tropical western Atlantic, 0-260 m, 30 April 1931 several medusae, material mentioned in Kramp (1957).

DIAGNOSIS: Medusa 4-12 mm, globular, thick jelly, no peduncle, manubrium flat, with medusa buds, oral tentacles divided up to six times, basal trunk absent, up to 14 tentacles per marginal bulb, with ocelli.

DESCRIPTION: Medusa with globular umbrella, slightly flattened apex, jelly very thick, subumbrella cylindrical, the jelly of the umbrella overhangs the margin of the subumbrellar cavity and the marginal tentacles emerge from channel-shaped depressions in this jelly; without gastric peduncle. Radial canals rather thin, ending in small but broad triangular marginal bulbs with 7 - 14 short tentacles, ocelli crescent-shaped with concavity turned outwards. Manubrium very broad and flat, in younger specimens more cross-shaped, in older ones more quadrangular, in preserved specimens mouth often widely gaping and quadratic. Gonads four interradial flat pads, not divided interradially. Oral tentacles arising rather close to radial canals and branching dichotomously up to six times immediately from their point of origin, thus no basal trunk present, each distal end of oral tentacles with a nematocyst cluster. Immature animals regularly with medusa buds arising from the adradial stomach walls; medusae may be budded in clusters directly from manubrium or from polypoid structures, polyps sometimes also with stolons.

Hydroid only known from vegetative buds on the corners of the medusa manubrium, with, short pedicel, 10-12 filiform tentacles, medusa buds on stalks immediately below the hydranths or on pedicels from stolons.

DIMENSIONS: Medusa normally 4-7 mm, maximally 12 mm.

OTHER DATA: The medusa- and polyp-budding of the medusa is described in detail by Kramp (1957a).

BIOLOGY: The depth distribution of the medusa in the North Atlantic is spanning the upper 300 m, with concentrations in the 100-200 m interval during daytime and 0-50 at night, isolated specimens at depths greater than 500 m (Pagès *et al.*, 1992). Diurnal vertical migration seems to take place (Winkler, 1982; Bleeker & van der Spoel, 1988). The medusa is often parasitized by the narcomedusa *Pegantha triloba* Haeckel, 1879 (Winkler, 1982).

DISTRIBUTION: Widely distributed in tropical and subtropical waters of the Atlantic and Indian Oceans: Canary Islands, Cape Verde Islands, western Mediterranean, Brazil, Sargasso Sea, Benguela Current, South Africa, Bismarck Sea, Malayan Archipelago, Fiji Islands, New Zealand. (Pages *et al.* 1992; Schuchert, 1996; Bouillon *et al.*, 2004). It is clearly a species restricted to warmer waters and thus it does normally not occur north of the 40° latitude. An exception seems to be the find in the Gulf of Maine by Pages *et al.* (2006). Type locality: Island of Trinidade, Brazil (Neotype designated by Kramp, 1957a).

REMARKS: Although characteristic and regularly encountered in preserved material of this species, the widely open mouth is certainly a fixation artefact (Pagès *et al.*, 2006). I concur with Bouillon *et al.* (2004) that the record of *B. platygaster* for Lebanese waters by Goy *et al.* (1991) is a misidentification. Bouillon *et al.* (2004) refer this record to *Bougainvillia niobe* Mayer, 1894. The Lebanese record is based on a single specimen without tentacles and ocelli. The paucity of the material and discrepancies in the shape of the manubrium makes it preferable not to assign this material to a nominal species. More and better specimens are needed to confirm the presence of *B. niobe* for the Mediterranean. *Bougainvillia niobe* and *B. platygaster* both produce medusa buds on the manubrium, but *B. niobe* can easily be distinguished as it has a flask-shaped manubrium, its buds not in groups, the oral tentacles have a long trunk, there are only about eight tentacles per bulb, and sexually mature animals have eight adradial gonads (Kramp, 1959a: 12).

Bougainvillia aurantiaca Bouillon, 1980

Bougainvillia aurantiaca Bouillon, 1980: 309, fig. 1. – ? Goy *et al.*, 1991: 107, fig. 19. – ? Schuchert, 1996: 28, fig. 11. – Bouillon *et al.*, 2004: 43, fig. 25D.

Diagnosis: Mature medusa < 2 mm, without ocelli, 2-3 tentacles per bulb, oral tentacles with long basal trunks, divided 2-3 times, weak peduncle, large interradial gonads.

Description (Bouillon, 1980): Adult medusa slightly higher than wide; jelly moderately thick, thicker apically than at sides; rather shallow gastric peduncle present. Radial and circular canal thin, bulbs rather small, hemispherical, without ocelli; 2 or rarely 3 tentacles on each bulb; tentacles with swollen distal end; oral tentacles divided dichotomously 2-3 times and ending in weak capitations, basal trunks of oral tentacles long (1/2 or more of total length). Stomach spanning about $^1/_2$ of subumbrellar cavity, conical. Gonads voluminous bulging interradial pads on stomach wall. Colours: distal end of tentacles green, inner side of gonads orange. Nematocysts: microbasic euryteles and desmonemes. Polyp stage unknown.

Dimensions (Bouillon, 1980): Height of adult medusa max 1.8 mm high, gonads visible even in specimens of 0.5 mm size.

Distribution: Papua New Guinea (Bouillon, 1980), ? Lebanon (Goy *et al.*, 1991), ? New Zealand (doubtful record, see Schuchert, 1996). Type locality: Laing Island, Papua New Guinea.

Remarks: This species resembles strongly *Bougainvillia muscoides*, notably through the absence of ocelli. However, it remains much smaller (1.8 mm versus 3-5 mm), has fewer tentacles (2-3 versus 3-7), and the trunks of the oral tentacles are longer. The so far unknown polyp stage might perhaps present more distinguishing characters.

The Mediterranean records of *Bougainvillia aurantiaca* are based on a single medusa from Lebanon reported by Goy *et al.* (1991). The animal depicted by them has no gonads despite it is 1.5 mm high. According to Bouillon (1980), animals of this size should have developed gonads. As the life cycle of this species is not known, I think that the presence of *B. auriantiaca* in the Mediterranean is not reliably proven.

Bougainvillia niobe Mayer, 1894

Bougainvillia niobe Mayer, 1894: 236, pl. 1 fig. 2. – Mayer, 1910: 166, pl. 18 figs 1-3, text fig. 90. – Kramp, 1959a: 110, fig. 93. – Bouillon *et al.*, 2004: 44, fig. 26C.
? *Bougainvillia platygaster*. – Goy *et al.*, 1991: 108, fig. 20.

Remarks: This species is not present in European waters, but perhaps in the eastern Mediterranean, thus still in the region covered by the European Register of Marine Species (ERMS, Costello *et al.*, 2001). See comments under *B. platygaster*.

Bougainvillia multicilia (Haeckel, 1879)

Lizusa multicilia Haeckel, 1879: 81, pl. 6 fig. 13.
Bougainvillia multicilia. – Kramp, 1955b: 249. – Kramp, 1961: 78. – Vannucci & Rees, 1961: 72. – Bouillon *et al.*, 2004: 44.

Remarks: A doubtful species, perhaps based on a misinterpretation. Haeckel (1879) erected this species based on a medusa he saw near Algeciras (Gibraltar). The combination of unbranched oral tentacles, 10-12 tentacles per marginal bulb, and the abaxial ocelli is highly unusual. The species has never been seen again and the verdict of Kramp (1955b) is still valid: «...one can hardly suppress a doubt about the correctness of the description of this medusa.»

Genus ***Koellikerina*** Kramp, 1939

SYNONYM: *Koellikeria* L. Agassiz, 1862 [preoccupied by *Koellikeria* Cobbold, 1860 (Trematoda)].

TYPE SPECIES: *Melicerta fasciculata* Péron & Lesueur, 1810, by designation of Kramp (1939).

DIAGNOSIS: Hydroids colonial, stolonal or branching, covered by perisarc infested with foreign material; filmy perisarc also envelops hydranth body and basal part of tentacles; hydranths with one whorl of filiform tentacles; gonophores arise singly from hydranth pedicels, liberated as free medusae.

Medusa with eight clusters of marginal tentacles, all tentacles similar in structure; with or without ocelli; with four dichotomously branching oral tentacles; gonads in perradial or adradial position.

REMARKS: See Kramp (1939) for the taxonomic history. A tabular comparison of all species is given in Xu & Huang (2004).

Koellikerina fasciculata (Péron & Lesueur, 1810) Fig. 13

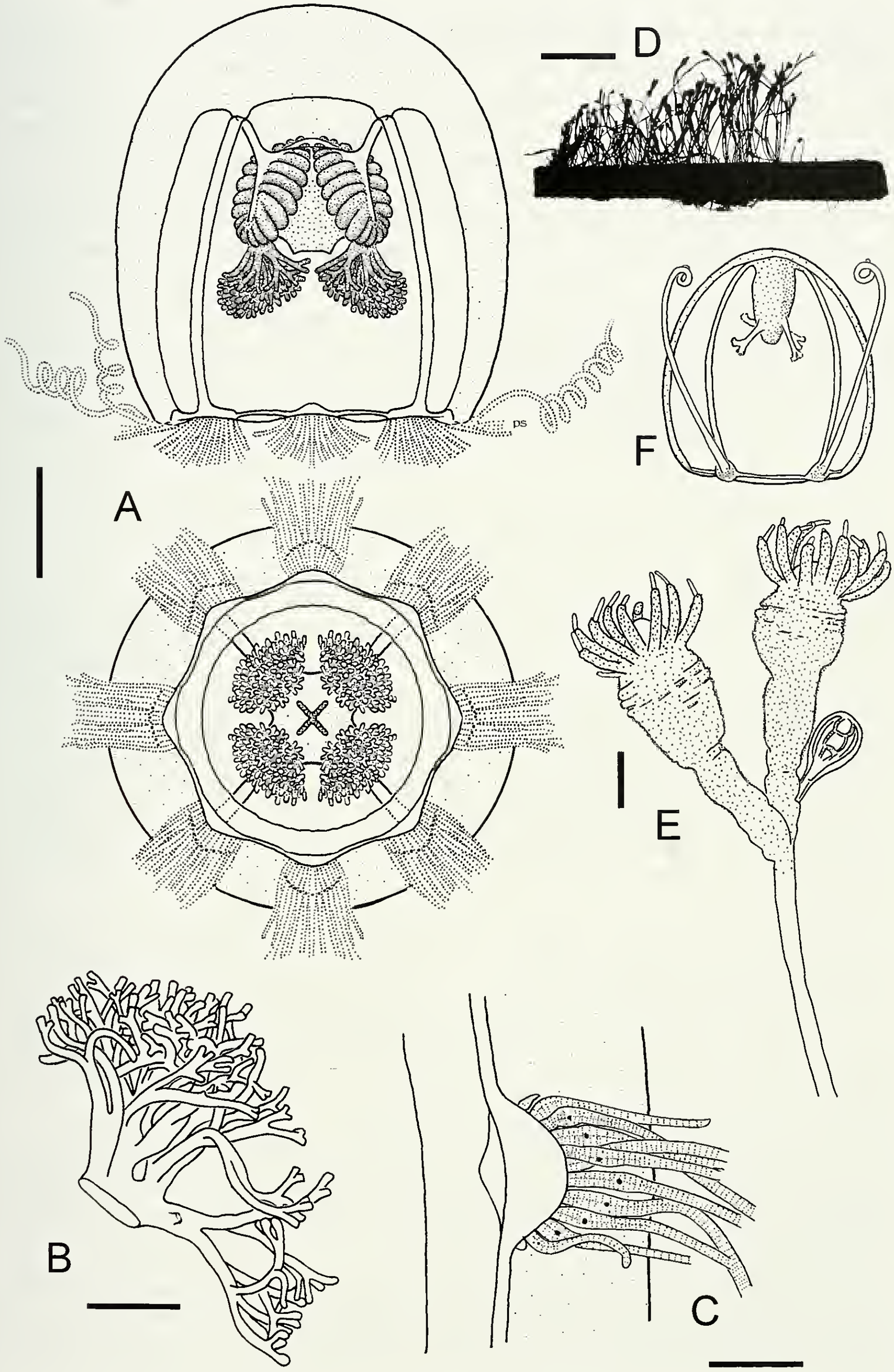
Melicerta fasciculata Péron & Lesueur, 1810: 353.
Rathkea fasciculata. – Mayer, 1910: 179, fig. 94.
Lizzia koellikeri Gegenbaur, 1854: 176, pl. 2 figs 1-9.
Perigonimus cidaritis Weismann, 1883: 117. – Motz-Kossowska, 1905: 73, fig. 7. – Brückner, 1914: 448, figs 1-6, pl. 8 figs 1-2.
Thamnitis dichotoma Brückner, 1914: 460.
Thamnostoma russelli Rees, 1938: 22, fig. 7. – Kramp, 1959a: 106, fig. 83. – Petersen & Vannucci, 1960: 486, synonym.
Not *Thamnostoma* spec. – Russell, 1953: 151, fig. 73C-E [= *B. muscoides*].
Koellikerina fasciculata. – Kramp, 1959a: 112, fig. 98. – Petersen & Vannucci, 1960: 473, figs 1-14. – Kramp, 1961: 85. – Brinckmann-Voss, 1970: pl. 9, figs 1-3. – Pagès *et al*., 1992: 5, fig. 3. – Bouillon *et al*., 2004: 46, fig. 27H-L.

MATERIAL EXAMINED: One living medusa collected at Villefranche-sur-Mer, 0-70 m, May 2001, not preserved, used to make DNA, 16 S sequence **AM183129**. – One living medusa collected at Villefranche-sur-Mer 6 April 2005, 0-70 m. – ZSM, Stechow collection, two slides with numbers 20000703 and 20000704, as *Thamnitis cidaritis*, Naples, April 1879, with young medusa buds, mentioned in Stechow (1919). – MHNG INVE29033, as *Thamnostoma cidaritis*, Naples, on spines of cidarioid sea-urchin, no medusa buds. – MHNG INVE32788, Naples 1892, 7 mature medusae. – ZMUC, type material of *Thamnostoma russelli*.

DESCRIPTION: Polyp growing on polychaetes and spines of cidaroid sea urchins. Stolons creeping, branched, giving off shoots of variable height, shoots with a long thin basal part widening distally into hydranth, shoots unbranched or occasionally branched

FIG. 13

Koellikerina fasciculata (Péron & Lesueur, 1810). (A) Mature medusa in lateral and oral view, scale bar 2 mm. (B) Oral tentacles, scale bar 0.5 mm. (C) Cluster of marginal tentacles seen from adaxial side, scale bar 0.5 mm. (D) Silhouette of a colony growing on sea urchin spine, scale bar 5 mm. (E) Polyps with medusa bud, scale bar 0.5 mm. (F) Newly released medusa, height about 0.8 mm. A-E, after preserved material; F, modified from Petersen & Vannucci (1960).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once or twice. Perisarc smooth, occasionally with corrugated stretches, perisarc continued as detritus infested gelatinous layer over hydranth and also investing lower parts of tentacles, wrinkled on hydranth body. Hydranths quite broad and therefore appearing club-like, with 14-18 tentacles in two very closely set whorls, hypostome conical. Medusa buds arise below hydranths, never on stolons, not detritus covered, pear-shaped, with pedicel. Nematocysts: microbasic euryteles and desmonemes.

Newly released medusa with four bulbs, each with one tentacle, no ocelli, oral tentacles branched once, manubrium height about 1/4 of bell cavity, manubrial peduncle absent. Colour: manubrium light orange, with brick-red interradial bands, bulbs orange.

Adult medusa nearly as broad as high, barrel-shaped bell, flatly rounded apex and relatively thick walls, velum narrow. Radial canals broad, mostly smooth. Four perradial and four interradial bulbs, bulbs broadly triangular and flat, about as broad as intermittent free bell margin; each of the eight bulb with up to 19 tentacles, tentacles issuing nearly parallel from bulb, getting slightly thicker after origin, then tapering again, where thickest with one adaxial ocellus, thus ocelli rather far away from bulb. Tentacles with chordoid gastrodermis, developing continuously, the youngest and shortest ones being the outermost ones, sometimes being mere stumps only, ocelli of youngest tentacles often not formed yet. Manubrium on a short broad peduncle, manubrium short, about 1/3 to 1/2 of bell cavity, cruciform cross-section; mouth cruciform, without lips, smooth; four perradial sets of oral tentacles, these inserting high above mouth level under protruding gonads, oral tentacles branched many times and with numerous ends (>100), ends with a concentration of euryteles but only indistinctly capitate; branching pattern of oral tentacles resembling a tight bush when tentacles contracted, oral tentacles can be expanded very much and the ends form a cloud in lower part of subumbrella. Oral tentacles with parenchymatic gastrodermis. Gonads adradial, U-shaped, lower ends free and overarching bases of oral tentacles; gonad partitioned by radiating furrows, thus forming up to ten lappets on each side. Nematocysts: microbasic euryteles and two types of desmonemes differing in their morphology. Colours: Oral tentacles and gonads intensively red.

OTHER DATA: Petersen & Vannucci (1960) described and depicted the development of the medusa in great detail.

Mayer (1910) observed that whenever the medusa is disturbed by a mechanical shock, the oral suddenly expand to their full extent, forming a network of filaments around the mouth. Such a reaction is remarkable, for in common with other medusae all other parts of the animal contract when disturbed.

DIMENSIONS: Polyp pedicels 4-6 mm, basal diameter 0.07 mm, hydranths about 0.5 mm high (preserved material). Mature medusa 7-13 mm high, egg size 110 μm (Petersen & Vannucci, 1960). Detailed nematocyst measurements can be found in Petersen & Vannucci (1960).

DISTRIBUTION: Mediterranean; Black Sea; Cape Verde Islands; Red Sea (Schmidt, 1973a); polyp and medusae also in Scotland and Norway, but perhaps not reproducing there (Petersen & Vannucci, 1960; Fraser, 1973). Type locality: Mediterranean (Péron & Lesueur, 1810).

BIOLOGY: The medusa lives for seven months or more and it requires temperatures above 8°C for maturation. The periods with sufficiently warm water temperatures in the NE Atlantic are perhaps too short to allow the medusa to mature. In the Mediterranean, the medusa is found from autumn to spring (Petersen & Vannucci, 1960). The medusae are most abundant in late autumn and winter, occasional specimens may be found as late as April or May. The medusae can tolerate reduced salinities down to 28 ppt. The polyps lives in deeper waters (20-270 m) on the spines of sea urchins (*Stylocidaris affinis*, *Dorocidaris papillata*) and on the parapodia of polychaetes (*Aphrodite aculeate, Hermione hystrix*). They prefer colder waters and are therefore not found above 20 m depth (Petersen & Vannucci, 1960).

REMARKS: The blood-red colour and the eight tentacle clusters make this medusa very conspicuous and it is easy to recognize. The life cycle was revealed by Brückner (1914) and Petersen & Vannucci (1960). For the synonymy see also the latter publication.

Genus ***Thamnostoma*** Haeckel, 1879

SYNONYM: *Thamnitis* Haeckel, 1879.
TYPE SPECIES: *Lizzia dibalia* Busch, 1851 [designation by Kramp, 1959a].

DIAGNOSIS: Bougainvilliidae medusa with four to eight solitary marginal tentacles and with four branched oral tentacles inserting above mouth rim; four interradial gonads; with ocelli. Polyp stage not reliably known, similar to genus *Koellikerina*.

REMARKS: The gender of *Thamnostoma* is neuter (ICZN 30.1.2). No polyp stage of an unambiguously identifiable (mature) *Thamnostoma* medusa is known. Hirohito (1988) described some polyps that released young medusae referable to the genus *Thamnostoma*. However, also *Koellikerina fasciculata* medusae go through a *Thamnostoma* stage during their development (Petersen & Vannucci, 1960; described as a distinct species, *Thamnostoma russelli* Rees, 1938).

Thamnostoma dibalium (Busch, 1851) Fig. 14

Lizzia dibalia Busch, 1851: 23, pl. 1 figs 7-9.
Thamnostoma dibolia. – Haeckel, 1879: 86. – Neppi & Stiasny, 1913: 27, pl. 2, fig. 15. – Bouillon *et al*,. 2004: 49, Fig. 29D. [incorrect spelling].
Thamnostomum dibalium. – Kramp, 1959a: 106, fig. 82. – Kramp, 1961: 91.

DIAGNOSIS: See genus.

DESCRIPTION (Busch, 1851; Neppi & Stiasny, 1913): Umbrella bell-shaped, somewhat higher than wide; manubrial peduncle short, conical; eight marginal tentacle bulbs, each with one tentacle, all tentacles of the same length in mature animals, at tentacle base an adaxial adnate spur-like process which bears an ocellus at its end. Manubrium cylindrical to ovoid, spanning about half of the bell cavity; four thick oral tentacles, two to three times dichotomously branched (the third division incipient only). Gonads as four bulging interradial pads along almost the whole length of the manubrium, eggs large, conspicuous. Colour: stomach and marginal bulbs dark-brown.

DIMENSIONS: Bell height 3.5-7 mm, 3-6 mm wide.

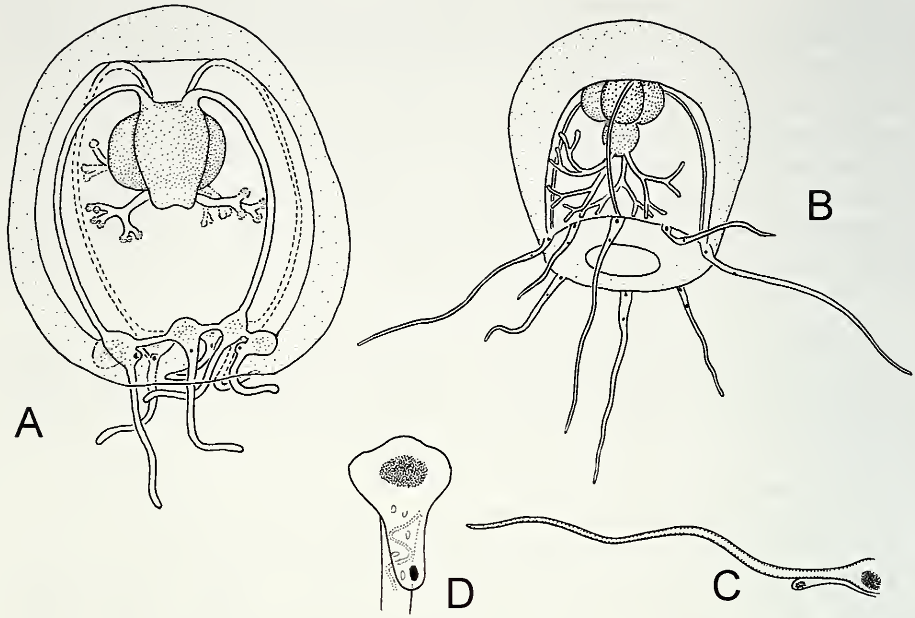

FIG. 14

Thamnostoma dibalum (Busch, 1851). (A-B) Medusae, no scale given. (C) Tentacle seen from side, note process with ocellus. (D) Tentacle bulb, base of tentacle and adaxial spur with ocellus seen from adaxial side. A, modified after Neppi & Stiasny (1913); B-D, after Busch (1851).

BIOLOGY: A rare species, observed in September and October.

DISTRIBUTION: Adriatic Sea (Benovic & Lucic, 1996), Mediterranean coast of Spain (Riera *et al.,* 1986). Type locality: Trieste, Adriatic Sea.

REMARKS: The gender of *Thamnostoma* is neuter, therefore the specific epithet must be *dibalium*. Haeckel (1879) proposed the name *dibolia*, which is incorrect (see Russell, 1953: 152). According to Neppi & Stiasny (1913), there is only one ocellus per tentacle. Haeckel (1879) mentioned two ocelli, one on a process, the other not. Busch (1851) describes that there is a pigment in the bulb as well as on a process of the tentacles like a stalked eye, but he also explicitly states that he could not decide whether both spots were really functional eyes.

Genus ***Nemopsis*** L. Agassiz, 1849

TYPE SPECIES: *Nemopsis bachei* L. Agassiz, 1849, my monotypy.

DIAGNOSIS: Hydroids, solitary, small, club-shaped, with pedal disk, hydrocaulus not distinctly delimited from hydranth body, large medusa buds in basal region. Medusa with four clusters of marginal tentacles, in each cluster a median pair of club-shaped or capitate tentacles flanked by a number of simple, filiform tentacles; with adaxial ocelli; with four perradial dichotomously branched tentacles; manubrium with four radial lobes extending outwards along the radial canals; gonads on these lobes.

Nemopsis bachei L. Agassiz, 1849 Fig. 15

Nemopsis bachei L. Agassiz, 1849: 289, fig. 1. – A. Agassiz, 1865: 149, figs. 227-231. – Mayer, 1910: 173, pl. 17, figs 5-6. – Hartlaub, 1911: 194, fig. 174. – Tiffon, 1956; 550, fig. 1. – Kramp, 1959a: 111, fig. 97. – Kramp, 1961: 89. – Kühl, 1962: 221, figs 11, pls 5-6. – Thiel, 1969: 71, fig. 3. – Kühl, 1972: 250, figs 18-22. – Denayer, 1973: 290, fig. 7. – Dumoulin, 1997: 102, figs 3-6. – Faasse & Ates, 1998: 72, figs 1-2. – Tulp, 2002: 89, figs. 1-2, photo 1.
Nemopsis gibbesii McCrady, 1859: 160, pl. 10, figs 1-3 [medusa only, not hydroid].
? *Hippocrene crucifera* Forbes & Goodsir, 1853. – Edwards, 1966: 143, synonym.
? *Hippocrene cruciata* Forbes & Goodsir, 1853 [in legend to figures, incorrect spelling].
Nemopsis heteronema Haeckel, 1879: 93, pl. 5 figs 6-9. – Hartlaub, 1911: 197, fig. 174.
Bougainvillia charcoti Le Danois, 1914a: 15, figs 1-3. – Kramp, 1959a: 111. – Edwards, 1966: 142, synonym.
Nemopsis crucifera. – Hartlaub, 1911: 195, fig 173.
Bougainvillia charkoti. – Hartlaub, 1917: 406 [subsequent incorrect spelling].
? not *Nemopsis Bachei*. – Brooks, 1883: 468 [hydroid].

MATERIAL EXAMINED: BMNH 1967.10.20.12-20; USA, North Carolina, Morehead City; 18.03.1964; 50 mature medusae. – BMNH 1982.11.30.2; Germany, Weser Estuary; 22.02.1961; 6 mature, badly preserved medusae, up to 1 cm in size.

DIAGNOSIS: Medusa up to 12 mm, four marginal bulbs, each with 14-34 filiform tentacles and a pair of capitate or clavate tentacles in middle; stomach base with large perradial basal lobes rendering it cruciform, gonads on these lobes; four oral tentacles branched up to eight times. Polyp very small, solitary, club-shaped, indistinct pedicel, large pedal disc, one whorl of long tentacles, medusa buds large.

DESCRIPTION: Polyp stage (after Kühl, 1962; 1972), small, solitary, with a relatively large pad-like attachment disc; hydranth body club-shaped, thick distal end turning into thinner pedicel without clear transition. Primary polyps with 2-4 tentacles, mature polyps with a single whorl of 8-14 tentacles, these much longer than the size of the polyp, often curled up; hydranth body enveloped by detritus. The medusa buds develop below the tentacles (likely at junction of hydranth body and pedicel), up to four buds in one whorl.

Newly released medusa spherical, jelly thick, 2-3 tentacles per marginal bulb, club-shaped tentacles not formed yet, oral tentacles not branched, no manubrial lobes present.

Adult medusa bell-shaped, higher or as high as wide, jelly very thick, apical jelly about 1/3 of bell-height, top and sides curved, margin lobed through perradial embayments, no manubrial peduncle. Four radial canals ending in broad marginal bulbs, ring canal thin, bulbs usually contracted to U-shape, outline in oral view irregular, each bulb with 8-28 filiform tentacles, ends sometimes swollen in living animals, ocelli on bulb at origin of tentacles, in addition to filiform tentacles a median pair of short club-shaped to capitate tentacles, in younger animals this pair of shorter tentacles more club-shaped (depending on state of contraction) or even absent, ocelli of capitate tentacles on adaxial side of tentacles on a swelling and not on bulb. Manubrium conical, ending in a mouth with four short lips, base of manubrium with very large perradial lobes, lobes extend along the radial canals for up to 5/6 of the canals, lobes render stomach large and cruciform; four perradial oral tentacles arising well above mouth margin, branching 5-8 times, basal trunk long, termini slightly

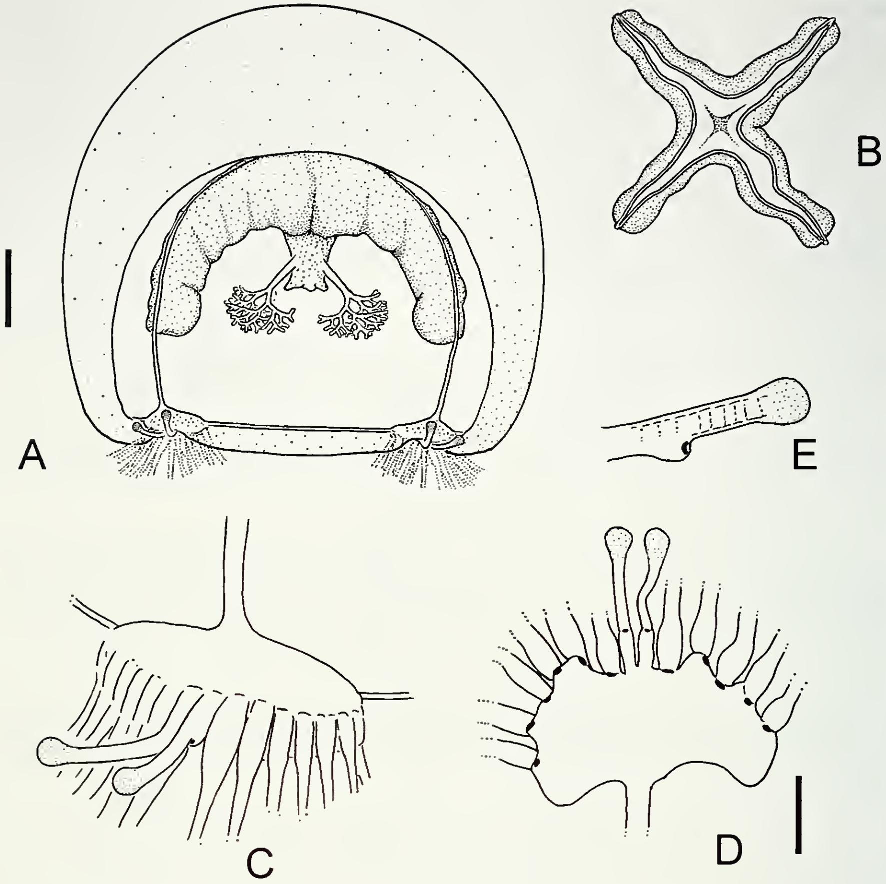

FIG. 15

Nemopsis bachei L. Agassiz, 1849; after preserved material. (A) Medusa, scale bar 1 mm. (B) Stomach seen from aboral, same scale as in A. (C) Tentacle bulb with the characteristic capitate tentacles. (D) Flattened tentacle bulb from adaxial, note that in living animals the bulb is usually contracted to a U-shape, scale bar 0.2 mm. (E) Capitate tentacle in side view, note ocellus on basal swelling.

swollen with concentration of nematocysts. Gonads a thick layer on the manubrium and its basal outgrowths, with vertical folds. Colours: Manubrium and gonads milky white to yellow. Nematocysts: microbasic euryteles and desmonemes

VARIATION: Thiel (1969) made a detailed investigation on the correlation of bell-size, tentacle number, and branching order of the oral tentacles. The German population may have up to 36 filiform tentacles per bulb (Kühl, 1962), but the usual range is about 14-27 tentacles. The American population seems to have less (14 acc. to Mayer, 1910), while the Japanese *N. dofleini* has about 40 (Kramp, 1968). Hargitt (1901) described the variations and aberrations found in the American population.

Dimensions: Adult medusa around 10 mm, usually not larger than 12 mm, but very rarely up to 14-18 mm (Thiel, 1969). Newly hatched polyps about 0.15-0.18 mm high, mature polyps about 0.5-0.6 mm, tentacle 0.9 mm long, newly released medusa diameter 1.5 mm (Kühl, 1962; 1972).

Distribution: In the western Atlantic occurring from Woods Hole to Florida and the northern Gulf of Mexico (Kramp, 1959a; Moore, 1962), in the NE-Atlantic occurring from Norway to the Bay of Biscay, usually in estuaries. European records are e. g.: Norway (*Nemopsis heteronema* Haeckel, 1879; Sognefjord); Scotland (Edwards, 1966; Fraser, 1973); Germany (Kühl, 1962, 1972; Thiel, 1968, 1969); Holland (Faasse, & Ates, 1998; Tulp, 2002); Belgium (Dumoulin, 1997); France, Loire Estuary (Denayer, 1973); France, Gironde (Tiffon, 1956). Type locality: Nantucket, Vineyard Sound, Massachusetts, USA.

Biology: *Nemopsis bachei* prefers reduced salinities and high plankton densities, it is thus often found in estuaries. Kühl (1972) reports that the medusa occurs from May to October in great quantities in the Elbe Estuary. *Nemopsis bachei* is thought to have been introduced several times to Europe through its polyp stage. The history of these introductions is analyzed in Thiel (1968). Aspects of the ecology of *N. bachei* were investigated by Purcell & Nemazie (1992) and Purcell *et al.* (1994). The polyp grows very slowly and it takes 9-12 months to attain its full size. Also the medusa-bud development is very slow, taking up to two months (Kühl, 1972).

Remarks: Among the medusa of the present fauna, *Nemopsis bachei* is an easily identifiable species due to its very long stomach lobes in combination with clustered tentacles. The pair of small capitate tentacles makes this species even more unique, but these capitate tentacles are often missing or not visible in preserved plankton samples.

The synonymy of this species has been discussed by several authors, e. g. by Mayer (1910), Nagao (1964) and Thiel (1969). Current opinion is that there are only two valid *Nemopsis* species, namely *N. bachei* and *N. dofleini* Maas, 1909. *Nemopsis dofleini* from Japan has more tentacles per bulb (about 40) and is larger (13 mm) (Kramp, 1968). Thiel (1968) showed that the Japanese medusae have an elevated tentacle number at all size stages and he interpreted this as a good argument that *N. dofleini* is a separate species. The present author has nevertheless some doubts, as local populations of introduced species like *Nemopsis* medusae often have reduced genetic variability due to founder effects and they can be quite distinct from other populations because of the absence of intermediate genotypes. Although tentacle numbers seem indeed lower in *N. bachei*, the maximal tentacle number of 36 filiform tentacles per bulb of the European population seems not so drastically different from *N. dofleini*. The American medusae seem to have fewer tentacles per bulb (14 after Mayer, 1910).

In his study on medusae of Charleston Harbor, McCrady (1859) also described *Nemopsis gibbesii*. His description was mainly based on a series of medusae that are clearly referable to *Nemopsis bachei*. But McCrady also found a polyp in the plankton which he erroneously associated with this medusa. The polyp closely resembles the polyp of *Margelopsis haeckelii* and Hartlaub (1899) pointed out that McCrady's medusae were actually *Nemopsis bachei* and the polyp belonged to the genus

Margelopsis. Similar conclusions concerning the medusa were already formulated by A. Agassiz (1865) and Brooks (1883). Brooks (1883) seems to have made another error when describing the hydroid stage of *N. bachei*. The hydroid was found at a place where *N. bachei* occurred abundantly. The colony was about 2.5 cm high and branched. The hydranths had funnel-shaped hypostomes, 24 tentacles, six to eight gonophores developed on the hydranth body. Brooks noted that the hydroid looked in fact much more like a *Eudendrium* than a *Bougainvillia*. Nevertheless, he claimed to have found newly released bougainvilliid medusae which he could keep for a short time until they had formed stage with four tentacles per bulb. To me, the presented data are insufficient to prove that Brooks indeed observed the medusa of *N. bachei* as he did not follow the medusae to a stage were they are unambiguously identifiable. The hydroid is most peculiar and perhaps he had in fact a *Eudendrium* species that had some epizoic *Nemopsis* hydroids. The hydroid of *N. bachei* was described by Kühl (1962; 1972) and shortly afterwards also the hydroid of *N. dofleini* became known (Nagao, 1964). Both authors found a very small, solitary hydroid and it is thus easily conceivable that Brooks had perhaps overlooked these polyps in his sample.

The hydroids of both nominal species *N. bachei* and *N. dofleini* appear very similar, again suggesting that both species might in fact be conspecific. As the figures in Kühl (1962; 1972) are not suitable for reproduction, the polyp of *N. dofleini* is shown instead (Fig. 16).

The position of the gonophores in *Nemopsis* is quite remarkable. The gonophores of the Bougainvilliidae and Pandeidae are never on the hydranth body as e. g. in the Hydractiniidae and most other hydroids (= plesiomorphic condition). In *Nemopsis*, the gonophore position is not entirely clear, it could be on the hydranth body or at the junction of the body and the pedicel. The pedicel is, however, now well distinguishable from the hydranth body. This reversal, or near-reversal, of the gonophore position is certainly linked to the modification of the polyp to a solitary, almost sessile form.

Genus ***Nubiella*** Bouillon, 1980

Type species: *Nubiella mitra* Bouillon, 1980.

Diagnosis: Bougainvilliidae medusae with four unbranched oral tentacles; umbrella with four marginal bulbs, each with a single tentacle.

Nubiella mitra Bouillon, 1980

Nubiella mitra Bouillon, 1980: 314, fig. 4. – Goy *et al.*, 1991: 109, fig. 22. – Bouillon *et al.*, 2004: 47, fig. 28G.

Diagnosis: Medusa bell with conical apex, apical jelly about 1/3 of total height, bell height 1.7 mm, 1.2 mm diameter; no gastric peduncle; manubrium cylindrical, spanning more than half of the bell cavity, with four simple capitate oral tentacles attached above mouth rim; four marginal bulbs each with one tentacles, without ocelli; gonads encircling manubrium; several medusa buds can be present on the upper part of the manubrium.

Distribution: Papua New Guinea; eastern Mediterranean. Type locality: Laing Island, Papua New Guinea.

FIG. 16

Nemopsis dofleini Maas, 1909; modified from Nagao (1964). The polyp stage of *N. bachei* is practically indentical. (A) Polyp stage with two medusa buds, scale bar 0.2 mm. (B) Newly released medusa, scale bar 0.5 mm.

REMARKS: This species, the only one in its genus, has not been recorded in European waters. The Mediterranean records are based on two medusae found off Lebanon by Goy *et al.* (1991). In the figure given by Goy *et al.* (1991), the oral tentacles arise at the mouth margin and not above it as it is typical for this species.

Genus ***Silhouetta*** Millard & Bouillon, 1973

TYPE SPECIES: *Silhouetta uvacarpa* Millard & Bouillon, 1973.

DIAGNOSIS: Colonial hydroids, stolonal or erect, with firm perisarc terminating at hydranth base; hydranths broad, ovoid to club-shaped, tentacles filiform, in two or more whorls concentrated in a band below hypostome, tentacles of one whorl alternating with those of adjacent whorls.

Gonophores free medusae, arising in clusters from stem and branches. Medusae at liberation with four simple or dichotomously branched oral tentacles attached above mouth rim; four tentacle bulbs, each with a single tentacle; ocelli present.

REMARKS: The hydranths of *Silhouetta* appear identical to those of *Pachycordyle napolitana* (see Schuchert, 2004).

Silhouetta uvacarpa Millard & Bouillon, 1973 Fig. 17

Silhouetta uvacarpa Millard & Bouillon, 1973: 25, figs 3A-D, pls 2-3. – Millard & Bouillon, 1975: 3. – Calder, 1988: 17, figs 13-14.

MATERIAL EXAMINED: Holotype, Musée Royal de l'Afrique centrale, Tervuren, Belgium; reg. No 2808; loc. Seychelles, Silhouette, 1966; several colonies, with medusa buds, leg. Millard and Bouillon. – BMNH 1990.5.2.7 and 1990.5.2.9, labelled *Clavopsella navis*, later added *Silhouetta uvacarpa*; Azores Faial, on *Mytilus galloprovincialis*, 0.3 m depth, 26.07.1989, coll. P. F. S. Cornelius, some with medusa buds.

DIAGNOSIS: As for genus.

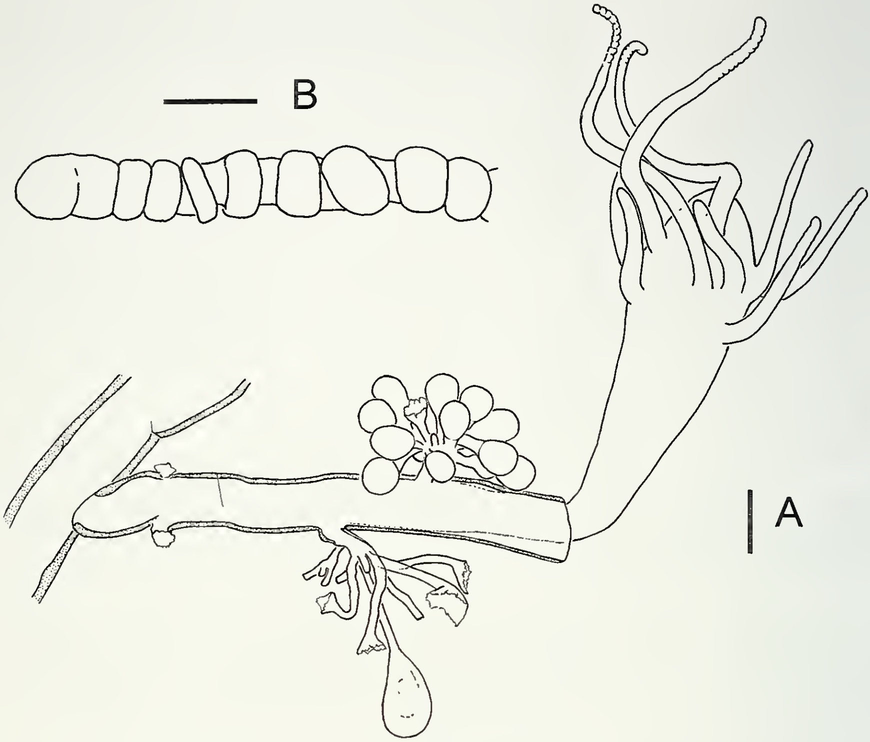

FIG. 17

Silhouetta uvacarpa Millard & Bouillon, 1973; after type material. (A) Terminal branch with hydranth and two typical clusters of medusa buds, the lower one almost completely spent, scale bar 0.2 mm. (B) Tip of semi-extended tentacle, note moniliform arrangement of nematocyst clusters, scale bar 0.05 mm.

DESCRIPTION: Colonies initially stolonal, later erect, arising from creeping hydrorhiza; older colonies can be polysiphonic (Calder, 1988). Perisarc wrinkled in certain areas, smooth in others, no annulation, perisarc ends below hydranth body, no pseudohydrotheca. Hydranths terminal on stem and branches, large, club-shaped, widest diameter in terminal third, evenly tapering towards proximal, hypostome conical, with 16-26 tentacles in 2-4 closely alternating whorls immediately below the hypostome. The youngest hydranths have only two whorls and new tentacles appear to arise proximal of them, thus increasing the number of whorls with age. Extended tentacles moniliform. Nematocysts: microbasic euryteles and desmonemes.

Gonophores free medusae, developing in grape-like clusters on stem or branches, 12-20 to a cluster, pedicels long and thin, originating as a common trunk with a distal arborescent branching carrying terminal medusa buds. Each bud completely surrounded by transparent perisarc.

Newly released medusa with four marginal bulbs, each with one black ocellus and one tentacle; four unbranched oral capitate tentacles arising just above the mouth margin.

Mature medusa unknown.

DIMENSIONS (Millard & Bouillon, 1973, 1975; Calder, 1988): Colonies reaching 2.3 cm in height, diameter of branches 0.29 mm; hydranth up to 1.5 mm high and 0.9 mm wide. Newly released medusa up to 0.3 mm high and 0.23 mm wide. Nematocysts see Calder (1988).

BIOLOGY: The hydroid has been found in shallow waters (1-30 m) of tropical seas on *Pecten* shells and sponges.

DISTRIBUTION: Tropical seas, reported from the Seychelles (Millard & Bouillon, 1973), Puerto Rico (Wedler & Larson, 1986), Bermudas (Calder, 1988), and Guam (Kirkendale & Calder, 2003). Type locality: Île Silhouette, Seychelles Islands.

REMARKS: Cornelius (1992) briefly mentioned that this species also occurs in the region of the Azores. Cornelius's material could be re-examined for this study and it was compared with the type material. The colony is growing on a *Mytilus* shell and there can be no doubt that it is the material Cornelius was referring to. However, the specimens could not convince me that this is *Silhouetta uvacarpa* because they lack some of the characteristic features of this species, namely the clustered gonophores on arborescent pedicels, the tentacles in several whorls, and the large, club-shaped hydranth. There are if fact only few medusa buds and the whole colony resembles more a *Bougainvillia* colony, despite that some hydranths are thicker than usual. It is possible that Cornelius had based his identification on the released medusae, but these could not be re-examined.

Considering its wide distribution, *Silhouetta uvacarpa* could perhaps occur in the Azores, but currently its presence there must be taken as unproven.

Genus ***Dicoryne*** Allman, 1859

TYPE SPECIES: *Dicoryne stricta* Allman, 1859b [= *D. conferta* (Alder, 1856)].
SYNONYM: *Heterocordyle* Allman, 1864a [type species *Heterocordyle conybearei* Allman, 1864].

DIAGNOSIS: Colonial hydroids, branched or not, perisarc not ensheathing bases of tentacles; hydranth with one whorl of filiform tentacles; gonophores on specialized blastostyles replacing a hydranth, numerous, released as swimming ciliated sporosacs provided with one or two tentacle-like processes at their proximal end (tentaculoids).

REMARKS: See Ashworth and Ritchie (1915) for a first important revision of the genus.

KEY TO THE SPECIES:

1a	sporosacs with mostly 2 tentaculoids, females 2 eggs	*Dicoryne conferta*
1b	sporosacs with mostly 1 tentaculoid, females 1 egg	*Dicoryne conybearei*

Dicoryne conferta (Alder, 1856) Fig. 18

Eudendrium confertum Alder, 1856: 354, pl. 12 figs 5-8. – Cornelius & Garfath, 1980: 278.
Dicoryne stricta Allman, 1859b: 369. – Allman, 1861: 168, synonym.
Dicoryne flexuosa Sars, 1874: 128, pl. 5 figs 21-26. – Fraser, 1944: 56, pl. 6 fig. 26.
Dicoryne conferta. – Allman, 1861: 168, fig'd. – Hincks, 1868: 105, pl. 18 fig 1. – Allman, 1872: 293, pl. 8. – Goette, 1907: 66, pl 6. – Ashworth & Ritchie, 1915: 266, pl. 8 fig. 16. – Fraser, 1944: 55, pl. 6 fig. 25. – Naumov, 1969: 218, fig. 86. – Millard, 1975: 101, fig. 34E-J. – Schuchert, 2001: 24, fig. 13. – Bouillon *et al.*, 2004: 45, fig. 26E-G.
Bougainvillia conferta. – Broch, 1916: 50, fig. O.
Perigonimus conferta. – Vervoort, 1946: 144, figs 52b & 56.

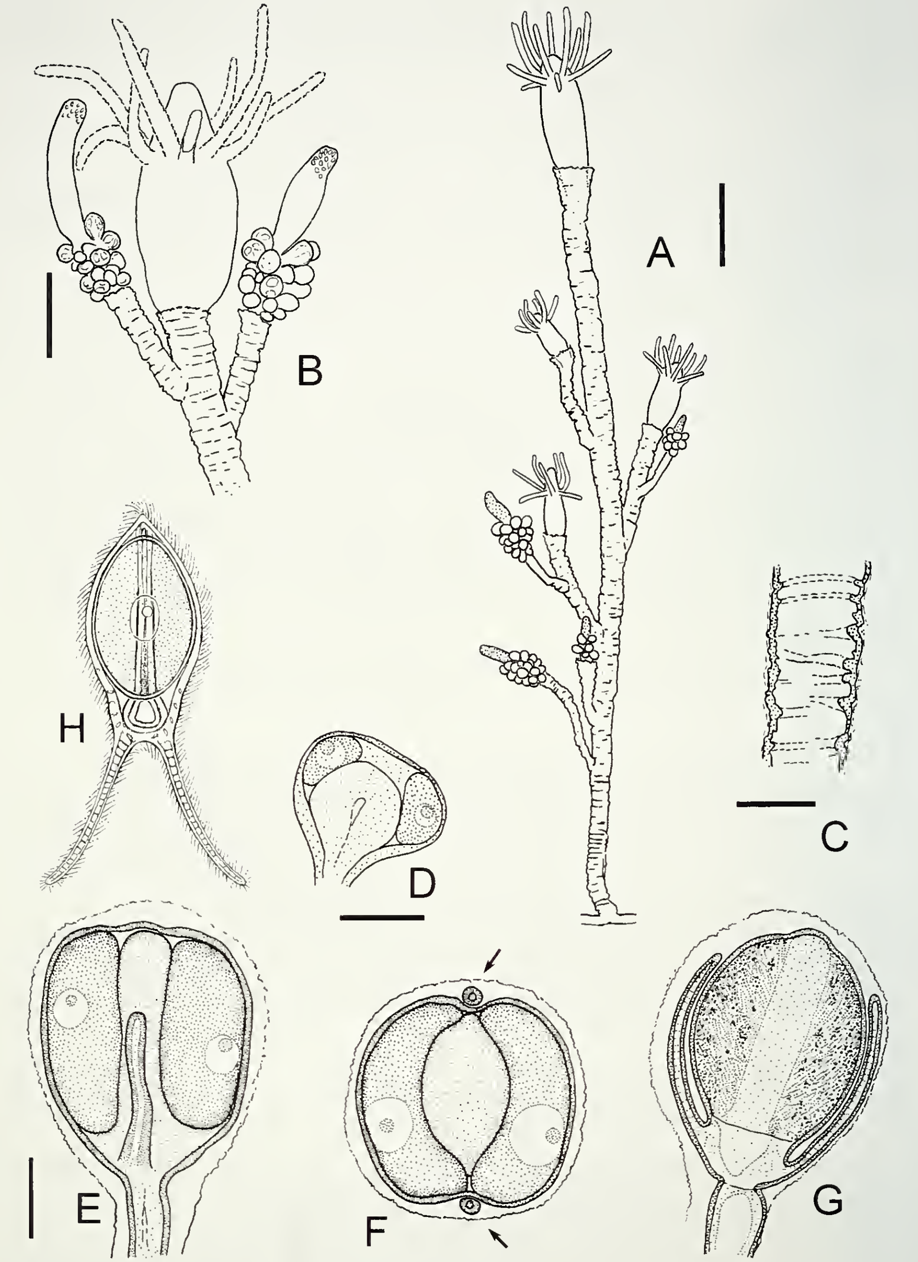

FIG. 18

Dicoryne conferta (Alder, 1856). (A) A single stem with hydranths and blastostyles, scale bar 0.5 mm. (B) Hydranth and blastostyles with sporosacs, scale bar 0.2 mm. (C) Stem perisarc, note the internal corrugation, scale bar 0.1 mm. (D) Young female sporosacs with two eggs, scale bar 0.05 mm. (E) Mature, but still attached sporosacs in side view, the rear tentaculoid is not visible, Material examined: MHNG INVE33562; Iceland, 65.35°N 13.61°W, 65 m, 19 July 1991, large colony on 5 cm hermit crab shell, fertile female, two eggs per sporosac. – MHNG INVE27337; Iceland, 65.35°N 13.33°W, 173-177 m, 18 July 1987, fertile male. – BMNH 1965.1.14.15; Sweden, Kosterfjord, Ramsö, coll. W. J. Rees 1 October 1964, on shell with *Eupagurus berhardus,* luxurious female colony, often two eggs per sporosac, some confirmed with 2 tentaculoids. – BMNH 1912.12.21.157; Great Britain, Shetland; Norman collection; on gastropod shells used by hermit crabs, female with 2 eggs per sporosac, some 1. – BMNH 1957.10.24.32; Italy, Naples, off Santa Lucia; coll. W. J. Rees, October 1957, on *Aporrhais pespelicani,* female 1-2 eggs per sporosac, not well preserved. – BMMN 1962.11.8.7 and 1962.11.8.6 (slide); Sweden, Gullmarfjord, Gåsö, Ranna; 20-30 m; on bucciniid shell with hermit crab; coll. 27 August 1962 by W. J. Rees, males and females, among 19 examined female sporosacs 18 with two eggs, one with one egg, two tentaculoids were visible. – BMNH 1964.8.7.17 slide; Sweden, Kristineberg; male colony, 3-4 times branched, sporosacs with 2 tentaculoids. – BMNH 1964.8.7.19-20, slides; North Sea, stems up to 8 mm, branched several times, male, at least one sporosac seen with two tentaculoids – ZMUC; Denmark, Frederikshavn, Mellum; 8 m, 24 June 1939; fertile. – ZMUC; Denmark, Frederikshavn, Blanetbund; 15 m, 14 August 1972, fertile. – ZMUC, Denmark, North of Haustholm; 33 m, 26 September 1930, fertile female with 2 eggs per sporosacs. – ZMUC, without number; Denmark, Frederikshavn; liberated sporosacs from polyp growing on *Aporrhais pespelecani.* – ZSM, Stechow collection, Helgoland, slides 2000523 & 2000524, fertile males, identity not clear.

Diagnosis: *Dicoryne* species with predominantly two eggs and two tentaculoids per sporosac

Description: Colonies growing on gastropod shells, stems numerous and dense, arising from reticulate, perisarc covered stolons. Individual stems unbranched or variably branched with up to 20 hydranths, monosiphonic, height depending on environment, all branches ending with hydranths or blastostyles, stems increasing slightly in diameter towards distal, often with distinct primary axis and shorter side-branches. Perisarc outside wrinkled and infested with detritus, inner wall strongly and irregularly corrugated throughout, in terminal region filmy and variably continued or not on hydranth body as pseudohydrotheca, usually short and only covering basal part of the hydranth. Hydranth fusiform, conical hypostome, 10-16 (usually 10-12) tentacles in one or two very closely set whorls. Blastostyles arise either as side branches from stems or directly from stolons, their caulus perisarc covered, blastostyle spindle-shaped, often lower part bearing the sporosacs thinner, no tentacles, no mouth, terminal region densely studded with large euryteles giving a strong refringency and thus well visible, lower 2/3 densely covered by numerous sporosacs on short stalks; the blastostyle - especially the upper part without sporosacs - can make worm-like movements, the shape is thus not fixed. Colonies gonochoristic. Perisarc colour brown.

Gonophores released when mature as swimming sporosacs of the styloid type, when attached covered with a very thin perisarc membrane, released sporosacs ovoid, covered by cilia, with two tentaculoids at its base directed away from the sporosacs, sometimes only one tentaculoid present, the tentaculoids develop only in the final maturation phase of the sporosac; female sporosacs predominantly with two eggs, a

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scale bar 0.05 mm. (F) Optical horizontal cross section of sporosac shown in E, note the two tentaculoids and the two eggs, same scale as E. (G) Optical section of an attached male sporosacs, note the two tentaculoids, same scale as E. (H) Free, swimming sporosacs, note that the posterior egg is hidden by the anterior one. A-G, after preserved material from Iceland and Sweden; H, after Allman (1861).

minority of sporosacs with one egg or eggs unequally developed, eggs in a plane perpendicular to the two tentaculoids.

Nematocyst: large microbasic euryteles, only on tip of blastostyles; smaller microbasic euryteles; desmonemes, only on tentacles of gastrozooids.

DIMENSIONS: Stems up to 25 mm high, usually less than 12 mm; stem diameter 0.1-0.12 mm; hydranths 0.4-0.9 mm high, terminal hydranth usually largest, other hydranths 0.4-0.6 mm. Sporosacs 0.13-0.15 mm long, diameter 0.10-0.12 mm, tentaculoids 0.10-0.12 mm. Nematocyst: large microbasic euryteles of blastostyle (13-16)x(5.5-6.5)μm; microbasic euryteles of hydranth (6-8)x(3-5)μm; desmonemes 3x2.5 μm.

FURTHER DATA: Histological section of the sporosacs and their development are show in Goette (1907) and Ashworth & Ritchie (1915).

BIOLOGY: Grows on gastropod shells, either inhabited by the gastropod or hermit crabs, sometimes on spider crabs, usually in depths of 5 to 300 m. In the Atlantic, mature sporosacs have been observed from March to October, in the Mediterranean in summer and autumn.

DISTRIBUTION: Widely known in the eastern Atlantic from the Barents Sea to the Strait of Gibraltar and likely also western Mediterranean (e. g. Sars, 1874; Hincks, 1868; Allman, 1872; Motz-Kossowska, 1905; Robson, 1914; Vervoort, 1946; Leloup, 1947; Naumov, 1969; Vervoort, 1985; Medel & López-González, 1996; Bouillon *et al.*, 2004); also in the North Sea (Hartlaub, 1894; Jäderholm, 1909; Rees & Rowe, 1969 Christiansen, 1972); Iceland and the Faroes (Broch, 1916; Schuchert, 2001), Atlantic Canada to Massachusetts Bay (Calder, 2003), and South Africa (Millard, 1975). Type locality: Cullercoats, England.

REMARKS: *Dicoryne conferta* and *Dicoryne conybearei* are relatively easy to recognize, even when infertile, due to the characteristic internal perisarc corrugation and their epizoic growth on gastropod shells. However these two species are by now means easily separable. The table provided by Ashworth and Ritchie (1915) is only partially correct and I have not found characteristics of the trophosome that would permit distinguishing the two. The same view has already been expressed by Allman (1864b) himself when describing *D. conybearei*. The only reliably observable difference is found in the sporosacs. *Dicoryne conferta* has usually two tentaculoids and the female sporosacs have two eggs. Although for a given colony this seems to hold true, there is nevertheless some variation known. There may be one or two tentaculoids in *Dicoryne conybearei* (Ashworth & Ritchie, 1915; Schuchert, 1996), leaving only the egg number as a diagnostic character. But also this character shows some variation in *D. conferta*. In 18 examined sporosacs of one colony, one had only one egg, the others two. Also Millard (1975) observed such a variation for *D. conferta*. The same variation was observed for nominal *D. conybearei* samples: 2 out of 20 sporosacs had two eggs instead of one only (see below). This makes it arguable whether these two species should be regarded as distinct. They might be just two morphotypes of the same biological species, the one of *D. conferta* apparently more prevalent in northern regions. Because the egg number is either predominantly one or two, which correlates rather well with the number of tentaculoids, I prefer to keep them separate for the moment. More detailed studies are clearly needed.

Because many authors based their identification on unreliable differences of the trophosome, many records are not trustworthy. Especially the Mediterranean records need re-confirmation.

An important revision of the genus was made by Ashworth & Ritchie (1915). Sars (1874) depicted the female sporosacs of his *Dicoryne flexuosa* and they have clearly two eggs. So, this name is obviously a synonym of *D. conferta*. The differences in the trophosome as given in Fraser (1944) are not diagnostic.

Dicoryne conybearei (Allman, 1864) Fig. 19

Heterocordyle conybearei Allman, 1864a: 366. – Allman, 1864b: 59, pl. 2. – Hincks, 1868: 107, pl. 18 fig. 2. – Allman, 1872: 307, pl. 10 figs 4-7.
Heterocordyle conybeary – Weismann, 1883: 84, pl. 11 figs 7-9 [subsequent incorrect spelling].
Dicoryne conybeari. – Motz-Kossowska, 1905: 76. – Philbert, 1935: 19, fig. 2. – Bouillon *et al*., 2004: 45, fig. 17A. [incorrect spellings].
Dicoryne conybearei. – Ashworth & Ritchie, 1915: 257, fig. 3, pl. 6.
? *Perigonimus* (?) *nanellus* Stechow, 1919: 14, fig. C. – Rees, 1956a: 342.
? *Heterocordyle conybearei* – Neppi, 1921: 21.
Heterocordile conibeari. – Bavestrello, 1985: 351, fig. 1-a-b, [subsequent incorrect spelling].

Material examined: ZSM 2000643 & 20000644, holotype material of *Perigonimus* (?) *nanellus*, 2 slides, from *Dorocidaris papillata* spines. Blastostyles without gonophores present. – MHNG INVE32949, Banyuls-sur-Mer, examined alive, 8 May 2002, on *Hinia incrassata*, fertile female, 16S sequence **AM183141**.– Ischia, Naples, 17 November 1992, examined alive, on *Murex* spec., fertile female with one egg per sporosac. – ZSM 20000526 and 20000527, as *Dicoryne conferta*, two slides, Stechow collection, Villefranche-sur-Mer, May 1909, fertile females; sporosacs with 1 tentaculoid, one egg per sporosac but rarely (2 in 20) two eggs. – IRSNB, Roscoff, coll. J. Bouillon, fertile male on small gastropod shell inhabited by hermit crab, almost exclusively stolonal, one tentaculoid per sporosac. – BMNH 1957.10.24.29 as *Dicoryne conferta*; Italy, Naples, off Stazione Zoologica, October 1957, on *Cerithium vulgaris* shell, coll. W. J. Rees, female, one egg per sporosac seen, but not well preserved, thus more likely *D. conybearei*.

Diagnosis: *Dicoryne* species with predominantly one egg and one tentaculoid per sporosac.

Description: See under *Dicoryne conferta*, the only differences are given in the diagnosis.

Other data: Ashworth & Ritchie (1915) provide many histological details of the sporosac and its development. Philbert (1935) observed terminal stolons that are used for spreading to other substrata.

Dimensions and other data: Up to 8 hydranths per stem seen, stems up to 10 mm; hydranths 0.3-0.6 mm, 8-16 tentacles. Sporosacs about 0.12 mm long and 0.1 mm wide. Nematocysts (living capsules in material from Ischia): gonozooids have small microbasic euryteles (9-10)x(5-5.5) μm and large microbasic euryteles (21-23)x(7.5-8.5)μm. Gastrozooids have microbasic euryteles (7.5-8.5)x(3.5)μm and desmonemes (3.5-4)x(2-3)μm.

Biology: Grows on gastropod shells either inhabited by the mollusc or hermit crabs (Allman, 1864b; Weismann, 1883; Motz-Kossowska, 1905; Russell, 1957;

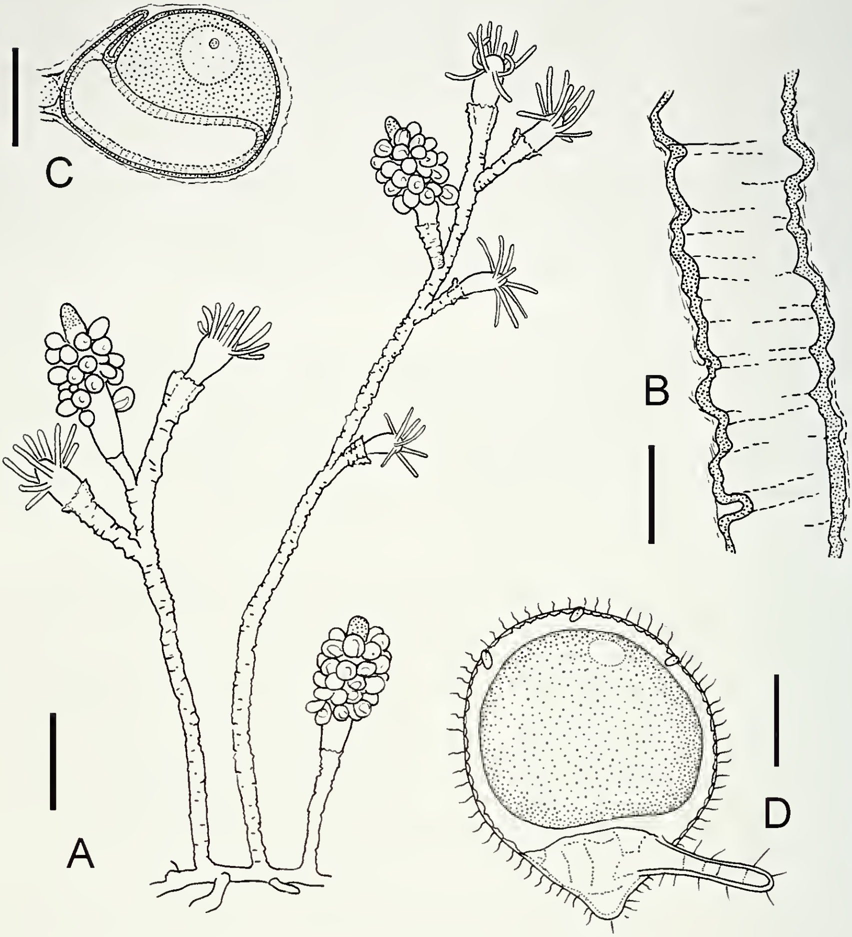

FIG. 19

Dicoryne conybearei (Allman, 1864). (A) Stems with hydranths and blastostyles bearing sporosacs, scale bar 0.5 mm. (B) Stem perisarc magnified, note corrugation, scale bar 0.05 mm. (C) Young female sporosac, scale bar 0.05 mm. (D) Liberated sporosac. All after living material, A-C Mediterranean material; D, New Zealand.

Bavestrello, 1985; Schuchert, 1996). Likely also epizoic on spines of cidaroid sea-urchins. In the Mediterranean, mature colonies were observed from March to the end of autumn (Weismann, 1883; Motz-Kossowska, 1905; Ashworth & Ritchie, 1915), in the British Isles at least from August to October (Allman, 1872; Russell, 1957).

DISTRIBUTION: North-eastern Atlantic from Ireland and English Channel to Iberian Peninsula (e. g. Allman, 1864b; Philbert, 1935; Teissier, 1965; Medel & López-González, 1996); widespread in the Western Mediterranean (Weismann, 1883; Motz-Kossowska, 1905; Bavestrello, 1985). The northernmost record is perhaps Oban, Scotland (Hincks, 1868), though this identification is uncertain. Also recorded from

Japan (Hirohito, 1988) and New Zealand (Schuchert, 1996). Type locality: Ireland, Cork, Glengariff Harbour, on hermit crab shells.

REMARKS: As discussed above, *Dicoryne conybearei* could be only a variety of *D. conferta*. The species is diagnosed through its sporosac with one egg, although occasionally some sporosacs contain two eggs (observed in 2 of 20 sporosacs of one colony). There is usually only one tentaculoid present, but this trait is even more variable (Ashworth & Ritchei, 1915; Schuchert, 1996).

The type material of *Perigonimus* (?) *nanellus* Stechow, 1919 was re-examined for this study and it became evident that this must be a *Dicoryne* species. The colony has some tentacle free polyps, these are also depicted Stechow (1919), which have a cap of large heteronemes at their tips. It is quite obvious that these are identical to blastostyles of *Dicoryne*, but without the sporosacs. These have either been spent or not developed yet. Moreover, the perisarc has the same irregularly corrugated structure and also the size of the hydranths matches well. However, in the absence of sporosacs it is impossible to attribute it either to *D. conferta* or *D. conybearei*. *Dicoryne conybearei* appears more plausible, as this is the more frequent of the two in the Mediterranean. The only unusual feature of *Perigonimus nanellus* is its occurrence on sea urchin spines.

Genus ***Bimeria*** Wright, 1859

TYPE SPECIES: *Bimeria vestita* Wright, 1859b by monotypy.
SYNONYM: *Manicella* Allman, 1859a: 51.

DIAGNOSIS: Colonies stolonal or erect, with perisarc enveloping hydranth and extending as a sheath over proximal ends of tentacles. Hydranth ovoid to vasiform; hypostome dome-shaped; tentacles in single whorl or in two close whorls. Gonophores fixed sporosacs on hydrorhiza and branches.

REMARKS: See Calder (1988) for taxonomic details concerning this genus.

Bimeria vestita Wright, 1859 Fig. 20

Bimeria vestita Wright, 1859b: 109, pl. 8 fig. 4. – Hincks, 1868: 103, pl. 15 fig. 2. – Allman, 1872: 297, pl. 12 figs 1-3. – Hamond, 1957: 297, figs 3-4. – Millard, 1975: 95, fig. 32C-H. – Calder, 1988: 21, figs 17-18, synonymy. – Hirohito, 1988: 94, fig. 33d-f, 34a. – Ramil & Vervoort, 1992: 14, bibliography. – Migotto, 1996: 9, figs 2a-b. – Genzano & Zamponi, 1999: 63, figs 4-5. – Marques *et al.*, 2000: 322, figs 1-3. – Bouillon *et al.*, 2004: 42, fig. 25A-C. – Vervoort, 2006: 196, fig. 5.2.
Eudendrium vestitum Allman, 1888: 3, pl. 1 figs 1 & 1a. – Marques *et al.*, 2000: 322, synonym.
Manicella fusca Allman, 1859a: 51. – Hincks, 1868: 104, synonym. – Calder, 1988: 22, synonym.
Bimeria humilis Allman, 1877: 8, pl. 5 figs 3-4. – Marques *et al.*, 2000: 322, synonym. – Fraser, 1944: 49, fig. 17.
? *Bimeria amoyensis* Hargitt, 1927: 492, fig. 1. – Hirohoto, 1988: 96, ? synonym.
Bimeria vestita f. *nana* Leloup, 1932: 142, fig. 14.
Bimeria corynopsis Vanhöffen, 1910: 287, fig. 12.
Bimeria (? Garveia) humilis. – Wedler & Larson, 1986: 89, fig. 9B.
not *Bimeria vestita*. – Annandale, 1907: 141, fig. 3 [= *Garveia franciscana* (Torrey, 1902)].

MATERIAL EXAMINED: Roscoff, 8 June 2000, infertile colonies, all used to extract DNA, 16S sequence **AM183130**. – MHNG INVE32957, Banyuls-sur-Mer, 11 May 2002, 2 m, on algae, infertile. – MHNG INVE35920 Spain, Alboran Sea, 36.522°N 2.837°E, 107, 12 April

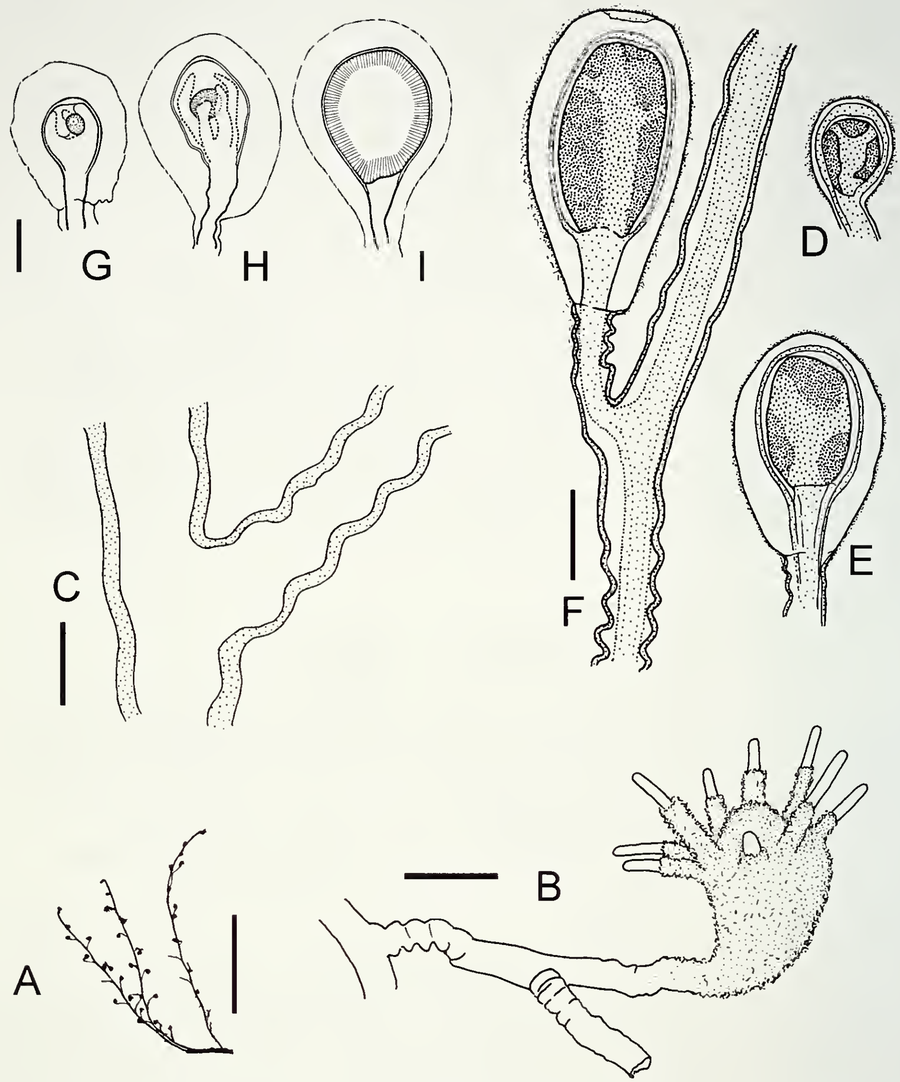

FIG. 20

Bimeria vestita Wright, 1859. (A) Silhouette of colony, scale bar 5 mm. (B) Part of stem with side branch bearing a hydranth, note sheathed tentacles, scale bar 0.2 mm. (C) Optical section of stem perisarc with annulated branching point. (D-F) Male sporosacs of different developmental stages, last stage is likely mature, note branched spadix, scale bar 0.1 mm. (G-I) Developmental stages of female sporosac, last stage likely with planula, scale bar equals 0.1 mm. A-C, after preserved material from the Mediterranean; D-F, after preserved material from Devon, England; G-I modified after Hirohito (1988).

2004, leg. H. Zibrowius, infertile, on *Lafoea dumosa*. – IRSNB, coll. J. Bouillon Roscoff, Brittany, 1964, small infertile colony on *Abietinaria abietina*. – BMNH 1957.3.2.122, England, Devon, Start Bay, 20 August 1898, with male sporosacs, growing on *Abietinaria abietina*, slide preparation. – BMNH 1957.3.2.123, Bay of Biscay, 07 March 1916, 137 m, infertile, on *Sertularella* spec., slide preparation.

DIAGNOSIS: Branching hydroid colony, proximal part of tentacles ensheathed with soft perisarc, gonophores sporosacs.

DESCRIPTION (after examined material and literature): Colonies erect, monosiphonic, arising from creeping tubular stolons. Shoots branched, when fully grown with central main axis and shorter side-branched, irregularly pinnate with alternate branches, all ends with hydranths; stem and branches covered by firm perisarc, single-layered, smooth or annulated over stretches, frequently annulated or spirally corrugated at the origin of side branches, perisarc continued on hydranths as soft pseudohydrotheca, covering also hypostome and forming tubular sheaths around basal part of tentacles, perisarc of hydranth encrusted with detritus and fine sand. Hydranth vasiform, merging below almost imperceptibly into pedicel, pedicels quite long; hypostome conical; 10-12 tentacles (reportedly up to 16) in one whorl or two very close whorls, amphicoronate. Gonophores fixed sporosacs on stem and branches, ovoid to oblong, without radial canals, enveloped in loose filmy perisarc infested with detritus; spadix in younger sporosacs irregularly branched or with irregular lateral processes, female with sporosac with one egg only, planula developing in situ, colonies likely gonochoristic. Colour: perisarc yellowish. Nematocysts: microbasic euryteles, and desmonemes.

DIMENSIONS: Stems from a few mm to 25 mm, stem diameter 60-80 μm; hydranth 0.25-0.5 mm high; sporosac up to 0.35 mm long and 0.2 mm wide (incl. perisarc covering); egg size 0.2 mm (Millard, 1975). Microbasic euryteles (6.5-7)x(3-3.5) μm; desmonemes 3 x 2 μm. More measurements are given in Millard (1975), Calder (1988), Genzano (1992), and Migotto (1996).

DISTRIBUTION: *Bimeria vestita* is reportedly a cosmopolitan species (Ramil & Vervoort, 1992), but it is unlikely to occur in cold and Arctic waters. Along the European coasts it has been reported from Scotland, western and eastern England, the English Channel, the southern North Sea, Bay of Biscay, the Iberian Peninsula, and the Mediterranean (e. g. Allman, 1872; Motz-Kossowska, 1905; Browne, 1907; Hamond, 1957; Teissier, 1965: Fey, 1970; Patriti, 1970; Ramil & Vervoort, 1992; Medel & López-González, 1996; Faasse, 2003; this study). Scotland seems to be its northern limit. It has also been reported from the Black Sea (Manea, 1980); western and southern Africa (Leloup, 1937; Buchanan, 1957; Millard, 1975; Vervoort, 2006), Argentina (Genzano & Zamponi, 1999); western Atlantic (Fraser, 1944, as *Bimeria humilis*; Calder, 1988; Vervoort, 1968), Indian Ocean (Mammen, 1963; Millard, 1975), western Pacific (Leloup, 1932; Hirohito, 1988); eastern Pacific (Fraser, 1938). Type locality: Firth of Forth, Scotland.

BIOLOGY: Occurs frequently on hydroids, but also algae, pebbles and other unspecific hard substrata in depths of 0-200 m. Aspects of its ecology in Argentinean waters were investigated by Genzano & Zamponi (1999). They found that the colonies were present all year round and they produced gonophores in the austral summer. In the NE Atlantic, the fertility period is likely also early summer, but here are not enough data available. In the Mediterranean (Boero & Freesi, 1986), reproductive colonies occur from October to May, they are found frequently on *Eudendrium* species in 10-20 m, and the reproduction takes place from October to February.

Remarks: The synonymy and history of this species have been treated by Calder (1988) and Marques *et al.* (2000a). Hirohito (1988) thought that also *Bimeria amoyensis* Hargitt, 1927 could be a synonym with this species. The type material of this species must be re-examined to come to a reliable conclusion. Hirohito (1988) included also *Bimeria corynopsis* Vanhöffen, 1910, an Antarctic species, in the synonymy of *B. vestita*. Although Vanhöffen's material was infertile and thus not reliably identifiable, he kept it apart from *Bimeria vestita* on account of the swollen tentacle tips. The biogeographic differences argue also in favour of the two being separate species.

With its ensheathed tentacles this is a very characteristic species. *Koellikerina fasciculata*, a species with a medusa phase, has a similar hydroid (Fig. 13F).

Genus ***Garveia*** Wright, 1859

Type species: *Garveia nutans* Wright, 1859b.

Synonyms: *Corythamnium* Allman, 1859a [type species *Eudendrium bacciferum* Allman, 1859a = *G. nutans*]. – *Calyptospadix* Clarke, 1882 [type species *Calyptospadix cerulea* Clarke, 1882]. – *Pruvotella* Motz-Kossowska, 1905 [type species *Pruvotella grisea* Motz-Kossowska, 1905].

Diagnosis: Colonial hydroids with branched stems, monosiphonic or polysiphonic; hydranth fusiform, hypostome dome-shaped or conical, usually one distal whorl of tentacles, rarely two; pseudohydrotheca covering polyp base but not ensheathing tentacles; gonophores fixed sporosacs, borne on pedicels on hydrocauli or on hydrorhiza.

Remarks: The genus *Perigonimus* M. Sars, 1846 is sometimes still incorrectly used as a synonym of *Garveia* Wright, 1859 or *Rhizorhagium* M. Sars, 1874. Because the type species of *Perigonimus* – *P. muscoides* – is currently placed in the genus *Bougainvillia* as *B. muscoides*, *Perigonimus* becomes a synonym of *Bougainvillia* (see Rees, 1938).

The *Garveia* species are quite heterogeneous and the genus is unlikely a clade. But following most recent authors and for the sake of nomenclatural stability, *Pruvotella grisea* Motz-Kossowska, 1905 is here also kept in the genus *Garveia*, despite several features of this species might warrant to place it in a separate genus: the double layered perisarc, the somewhat unusual sporosacs with high, vacuolated cells, the adnate side-branches, the large heteroneme, and the extraordinarily contractible hydranth body and tentacles. See also the discussion under *Rhizorhagium* M. Sars, 1874.

Key to the *Garveia* species treated here:

1a	mature colonies monosiphonic	2
1b	mature colonies polysiphonic	3
2a	several sporosacs clustered on hydranth pedicels, branches not adnate	*Garveia franciscana*
2b	sporosac large and solitary, branches adnate	*Garveia grisea*
3a	branches adnate, perisarc double layered, tentacles in several whorls	*Garveia grisea*
3b	branches not adnate, perisarc single layered, one whorl of tentacles	4
4a	hypostome conical, broadly arborescent, deep water species	*Garveia arborea*
4b	hypostome rounded to spherical, colonies elongate, shallow water species	*Garveia nutans*

Garveia nutans Wright, 1859 Fig. 21

Garveia nutans Wright, 1859b: 109, pl. 7, fig 5. – Hincks, 1868: 102, pl. 14 fig. 4. – Allman, 1871: 44, fig. 15B. – Allman, 1872: 295, 4, pl. 12 figs 4-11. – Philbert, 1935: 18. – Fraser, 1937: 36, pl. 5 fig. 22. – Leloup, 1952: 19, fig. 57. – Ramil & Vervoort, 1992: 15. – Bouillon *et al.*, 2004: 46, fig. 27F-G.

Eudendrium bacciferum Allman, 1859a: 53. – Hincks, 1868: 102, listed as synonym.

MATERIAL EXAMINED: BMNH 1948.9.8.52; Great Britain, Plymouth; collected 1898, infertile. – BMNH 1969.11.29.1-3; Great Britain, Menai Bridge, Church I; 22 May 1963; fertile female. – BMNH 1985.9.1.22; Great Britain, Plymouth; May 1936; fertile female, no hydranths. – BMNH 1957.3.2.170 slide; Great Britain, Plymouth; 17 October 1898; fertile female. – ZSM, as *Bimeria nutans*, Plymouth, slides 20000453, 20000454, and 20000455, Stechow collection, material mentioned in Stechow (1919), fertile male. – The Faroes 62.317°N 06.833°W (BIOFAR station 370); 66 m; 25 July 1988, infertile.

DIAGNOSIS: Hydroid colony with polysiphonic stem, stem tubes more or less equal: Hydranths yellow, broad, hypostome very large and often spherical, one whorl of tentacles, pseudohydrotheca present, gonophores large sessile sporosacs resembling a medusoid, mature without radial or circular canal, spadix present, large subumbrellar cavity, females with several eggs.

DESCRIPTION: Colonies elongate, with conspicuous central main axis and thinner, short, straggling side branches, main stem strongly polysiphonic, thinning out to monosiphonic, side branches mostly monosiphonic. Stolons creeping, ramified. Perisarc usually one-layered, smooth or irregularly corrugated or wrinkled, expanding at distally as filmy pseudohydrotheca onto hydranth body, not infesting tentacles. Hydranths at end of long branches, rather broad, urn-shaped, reminiscent of the genus *Eudendrium*, hypostome very large, up to 1/3 of total hydranth height, spherical to high dome-shaped, one whorl of 10-14 tentacles, these evenly covered by nematocysts, gastrodermis chordoid. Gonophores arising from main stem, ovoid, on tapering pedicel of about same length, pedicel covered by conical perisarc sheath that gets gradually thinner towards distal. Gonophores fixed sporosacs, in younger stages reminiscent of medusoids, oval shape, mature without radial canals, circular canal, or velum, with spadix projecting into spacious subumbrellar cavity. Females with up to 10 eggs, these relatively large, sporosac not covered by perisarc film in older stages, eggs developing in situ, thus larviparous. Colours: hydranths and eggs have an intense yellow-orange colour, may be red, tentacles yellow. Disturbed hydranths bend themselves towards below (see Fig. 21B, lowest hydranth).

DIMENSIONS: Colony up to 3 cm, polyps up to 0.8 mm high, diameter 0.35 mm. Diameter of distal branches 0.16 mm. Sporosacs 0.9 mm long, diameter 0.65 mm. Egg size ca. 0.25 mm.

ADDITIONAL DATA: The Gonophores possess rudimental radial canals during their early developmental stages (Allman, 1872).

BIOLOGY: Occurs at sites with strong or very strong tidal streams, attached to stones, bed-rock, hydroids, seaweeds and other hard substrata. Mature February to October, but perhaps also in other months. Usually in shallow water of a few metres depth (laminarian zone) and even at the low water mark, but there is also a record from 580 m (Ramil & Vervoort, 1992).

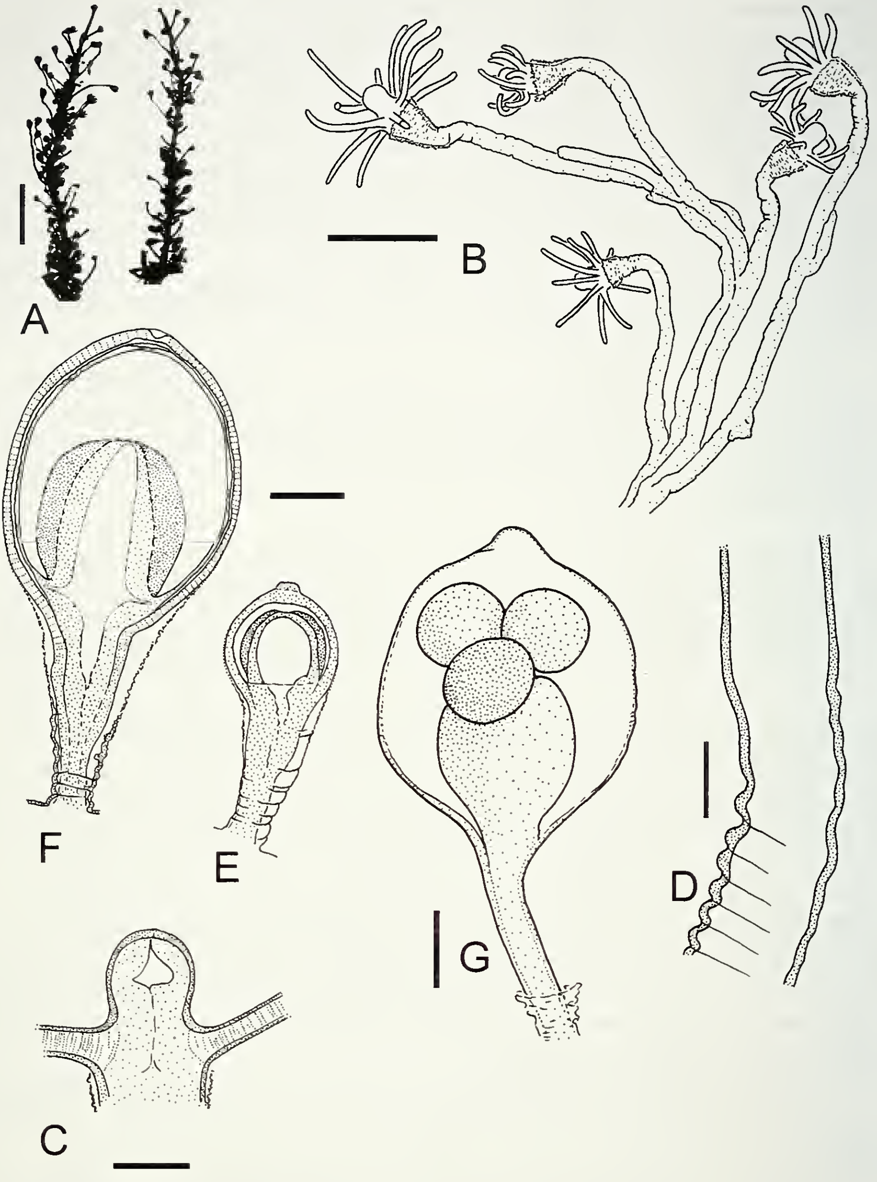

FIG. 21

Garveia nutans Wright, 1859; after preserved material from Plymouth. (A) Colony silhouette, scale bar 5 mm. (B) Part of colony, note pseudohydrothecae on hydranth bodies, scale bar 1 mm. (C) Optical section of hypostome, note its spherical shape, scale bar 0.1 mm. (D) Perisarc of hydranth pedicel, note transition of corrugated to smooth perisarc, scale bar 0.1 mm. (E) Young male sporosac in optical section, scale bar 0.1 mm. (F) Mature male sporosac in optical section, note spadix with spermatids (dark) projecting onto spacious cavity (subumbrella), same scale as E. (G) Mature female sporosac with developing embryos, scale bar 0.2 mm.

DISTRIBUTION: Great Britain, The Faroe Islands, English Channel, Belgium, Bay of Biscay, Strait of Gibraltar. (Allman, 1872; Browne, 1907; Philbert, 1935; Leloup, 1952; Hammond, 1957; Russell, 1957; Cabioch, 1976; Ramil & Vervoort, 1992). The record from Alaska (Nutting, 1901) is somewhat doubtful. Type locality: Inch Garvie, Firth of Forth, Shetland Islands, United Kingdom.

REMARKS: With its straggling colonies and yellow hydranths having spherical hypostomes, *Garveia nutans* Wright, 1859 can easily bee mistaken for a *Eudendrium* species. However, the pseudohydrotheca and the sporosacs immediately distinguish it from the genus *Eudendrium*.

Garveia franciscana (Torrey, 1902) Fig. 22

Bimeria franciscana Torrey, 1902: 28, pl. 1 fig. 4. – Weill, 1934a: 77, fig. 71a-b. – Weill, 1934b: 386. – Fraser, 1937: 31, fig. 14.
Bimeria Monidi Billard, 1927: 467, figs 1-2a. – Vervoort, 1964: 125, synonym.
Bimeria tunicata Fraser, 1943: 76, pl. 15 fig. 2. – Fraser, 1944: 5, fig. 18. – Vervoort, 1964: 125, synonym.
Perigonimus megas Kinne, 1956: 257, figs 1-7. – Vervoort, 1964: 125, synonym.
in part *Cordylophora lacustris* – Pennycuik, 1959: 165, pl. 2 figs 4-5.
[not *Cordylophora lacustris* Allman, 1844]
Garveia franciscana. – Vervoort, 1964: 127, figs 1-4. – Morri, 1981: 53, fig. 16, pl. 1 fig. 2. – Morri, 1982: 381, figs 1-5, pl. 1. – Barnes, 1994: 62, fig. – Calder & Maÿal, 1998: 73. – Schönborn *et al.*, 1993: 220, pl. 4 fig. 2. – Bouillon *et al.*, 2004: 45, fig. 27B-D.

MATERIAL EXAMINED: ZSM, slide 20000536, The Netherlands, Zuiderzee, Vuile Gat, WN 77, 29 September 1926, ex. Zool. Mus. Amsterdam, det W. Vervoort, fertile female colonies. – BMNH 1966.10.8.30 and 37, 39, 40; Nigeria, Port Harcourt; 10 September 1957; fertile, several male and female colonies from raft, also 3 slides. – BMNH without registration number; Germany, Kiel-Kanal, near Rendsburg, 13 September 1961, male and female colonies; collected Hjalmar Thiel, labelled as *Perigonimus megas*. – BMNH 1981.11.4.3 alcohol plus slide material, as *Dicoryne conferta*, Alexandria, Egypt, 20 November 1980, leg. A. Shoukr, not well preserved, 5 cm polysiphonic stems, sporosacs on hydranth pedicels, likely belongs to *Garveia franciscana*.

DIAGNOSIS: Occurring in brackish waters, colonies branching, tall, monosiphonic; one whorl of tentacles; several sporosacs on hydranth pedicels, one egg per sporosac, larviparous.

DESCRIPTION: Occurs only in brackish waters, colonies erect, monosiphonic throughout, much branched, bushy to irregularly pinnate, branches long; root-like hydrorhiza. Branches arise at an angle of about 60°, not adnate. Perisarc one-layered, smooth or irregularly corrugated, at origin of side-braches an annulated stretch of variable length. Hydranth body covered by thin pseudohydrotheca; hydranth fusiform, hypostome conical, 8-12 filiform tentacles in one whorl. Colonies are dioecious, sporosacs concentrated on hydranth pedicels, usually several ones present, up to 20 possible.

Sporosacs ovoid, enveloped in filmy perisarc, in advanced stages loose. Sporosacs without radial or circular canals, no velar opening, spadix present. Female sporosacs with usually one egg only, spadix remains below egg, egg develops in situ to planula (larviparous). Male sporosacs slightly larger, spadix present, spermatozoa develop on spadix.

Nematocysts: desmonemes and microbasic euryteles.

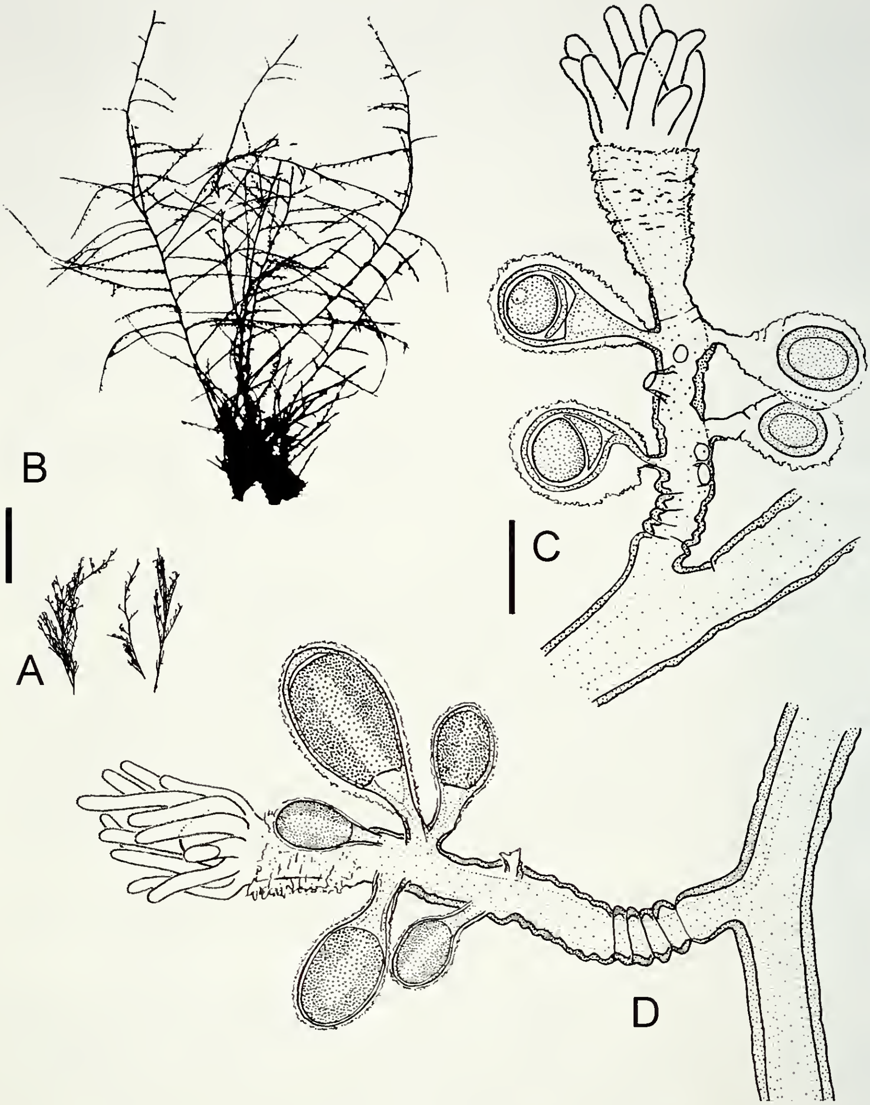

FIG. 22

Garveia franciscana (Torrey, 1902). (A-B) Colony silhouettes, scale bar 1 cm. (C) Branch with hydranth and female sporosacs, some sporosacs broken off, scale bar 0.2 mm. (D) Branch with hydranth and male sporosacs, same scale as C. All after preserved material, A & C from Holland, B & D from Nigeria.

DIMENSIONS: Colony heights 1-20 cm; branch diameters 0.15-0.3 mm; hydranth about 0.5 mm high; female sporosacs about 0.3 mm long, diameter 0.2 mm. Desmonemes 4 μm long, microbasic euryteles 7 μm (Morri, 1982).

BIOLOGY: Tolerates a wide range of salinity, but occurs only in brackish waters in very shallow depths down to a few meters, can withstand elevated temperatures of above 30°C, but regresses below 9°C (Crowell & Darnell, 1955). Morri (1982) gives a preferred salinity range of 20-30 ppt. Schönborn *et al.* (1993, Baltic Sea) found it in 1-18 ppt salinity, mostly below 6 ppt; reproduction was observed from June to September if temperatures remained above 14°. The polyps fed on copepods and oligochaetes. The hydranths remain smaller in reduced salinities.

DISTRIBUTION: California; Atlantic coast of America from Brazil up to Virginia; east and west coasts of India; Andaman Sea; west coast of Africa; eastern Australia; Holland (now extinct), North Sea; Baltic Sea; Mediterranean lagoons (Fraser, 1937; Vervoort, 1964; Morri, 1982; Schönborn *et al.*, 1993; Barnes, 1994; Calder & Maÿal, 1998). Type locality: San Francisco, California, intertidal.

REMARKS: The synonymy of this species has been worked out by Vervoort (1964) and his view is here adopted. *Garveia franciscana* can easily be confounded with *Pachycordyle navis* (Millard, 1959), a species also occurring in brackish waters (see Schuchert, 2004 and Fig. 29). The latter, however, has hydranths with tentacles in several whorls (though sometimes close set), forms smaller colonies, has often a bi-layered perisarc, the sporosacs are not clustered on the hydranth pedicels, and the female sporosacs contain several eggs (comp. Fig. 29C).

Garveia arborea (Browne, 1907) Fig. 23

Bimeria arborea Browne, 1907: 15, pl. 1 figs 1-3, pl. 2.
Garveia arborea. – Vervoort, 1985: 273, pl. 2. – Ramil & Vervoort, 1992: 15.
? *Bimeria arborea*. – Hirohito, 1988: 94, fig. 331a-c.

MATERIAL EXAMINED: Holotype, BMNH 1948.10.1.117, as *Bimeria arborea*, alcohol and slide preparations; Bay of Biscay; 752 m; August 1906; fertile. – MHNG INVE36661 (part of CARACOLE collection station KGS 11); 53.779°N 13.938°W (west of Ireland), 793 m, collected by Usnel corer; date 9 August 2001; on mud/polychaete tube; fertile male.

DIAGNOSIS: Deep-sea *Garveia* species with polysiphonic, irregularly arborescent colonies, central main tube larger than peripheral auxiliary tubes; hydranths with small, conical hypostome, tentacles in one whorl; sporosacs small, not in clusters, on stem, branches and rarely on hydranth pedicels and stolons; males without vestige of subumbrellar cavity.

DESCRIPTION: Colonies erect, polysiphonic, branching tree-like, composed of a branching, central main tube covered by many thinner, parallel auxiliary tubes, number of auxiliary tubes decreasing towards distal until only main tube is left at distal branch tips, main tube of branches originates from main tube of stem, perisarc of main tube and auxiliary tubes mostly smooth. Stolons tubular, root-like or creeping. Hydranths arise from the main tube on stems and branches, with pedicels of variable length, perisarc smooth, corrugated or wrinkled, continued over hydranth body as filmy pseudohydrotheca terminating below tentacles, detritus infested. Hydranths typical for Bougainvilliidae, spindle shaped, slender, with short conical hypostome, one whorl of 8-12 filiform tentacles, strongly contractible. Gonophores develop on stems and branches, issuing from the main tube, occasionally also on hydranth pedicels and even stolons. Gonophores are sessile sporosacs of the cryptomedusoid type. Male sporosacs ovoid to spherical, tapering proximally into a short pedicel; mature sporosacs with a

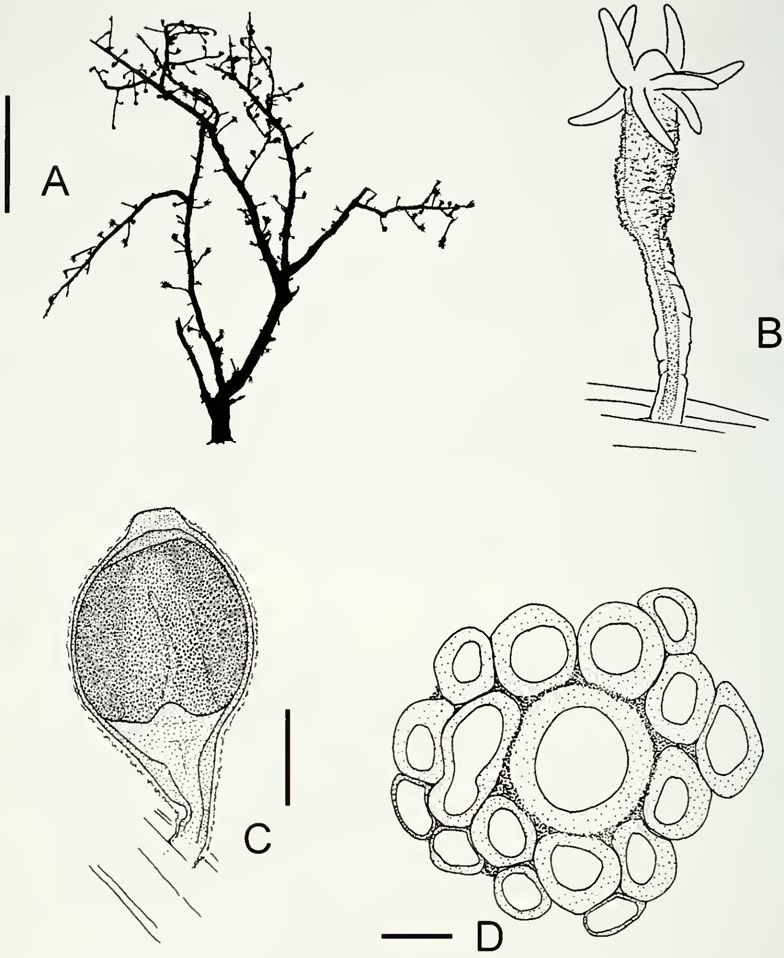

FIG. 23

Garveia arborea (Browne, 1907); after preserved material (MHNG INVE36661). (A) Colony silhouette, scale bar equals 5 mm. (B) Hydranth, scale bar equals 0.1 mm. (C) Male sporosac, scale bar equals 0.1 mm. (D) Cross-section of a branch, note central primary tube, the dotted region around the main tube represents detritus particles, scale bar equals 50 μm.

thickening of distal epidermis; simple central spadix covered by a thick layer of germ cells filling cavity entirely, this round mass of gametes with four shallow embayments at its base. At least in younger sporosacs four short, pouch-like vestiges of radial canals. Female sporosacs unknown. Nematocysts: larger heteronemes (likely microbasic euryteles) on sporosacs and in coenosarc; smaller microbasic euryteles and desmonemes abundant on tentacles.

DIMENSIONS (after Browne, 1907; Vervoort, 1985; own data): Stems 1-3 cm (max. 8.75 cm), basal stem diameter up to 3 mm (Vervoort, 1985); main tube 0.1-0.25

mm, auxiliary tubes 0.05-0.1 mm; hydranth pedicels up to 1 mm, hydranth body up to 0.2-0.25 mm high; sporosacs 0.2-0.3 mm. Larger heteroneme (6.5-8.5)x(3.5-4)μm, smaller microbasic euryteles (5-6.5)x(2.5-3)μm, desmonemes (3.5-4.5)x(2.5-3)μm.

BIOLOGY: A deep water species, known from depths of 420-3100 m. Can grow on solid substrata like polychaete tubes worms (this study) or anchored in soft substrates by a root-like hydrorhiza (Ramil & Vervoort, 1992).

DISTRIBUTION: Continental margins from west of Ireland to Strait of Gibraltar (Browne, 1907; Vervoort, 1985; this study), perhaps also Somalia (Stechow, 1925; as *B. crassa*), South Africa (Millard, 1977; as *G. crassa*), and Japan (Hirohito, 1988). Type locality: Bay of Biscay, 48°7'N 8°13'W, 412 fathom (= 752 m), sand, mud and hard ground (Browne, 1907).

REMARKS: This is a rare, deep water species. Hirohito's (1988) identifications are based on infertile material and should therefore be considered with some reservations (see also Vervoort, 2006).

Vervoort (1985) suggested that *Garveia crassa* (Stechow, 1923b) could be conspecific with *G. arborea*. A re-examination of the type material of *Bimeria crassa* (ZSM 20000436 & 20000437, slides) indicated that this species has different gonophores. The gonophores in the slide material are not fully mature and no gametes could be seen. They are oblong, usually about two times as long as wide, thus clearly different from those of *G. arborea*. Furthermore, their internal structure appears also different. The gastrodermal layers form a cup-like structure and no spadix is present (although the lumen of the cup-like structure feigns a spadix). If these differences are not due to a sexual dimorphism, then it is unlikely that *B. crassa* is conspecific with *G. arborea*.

The presence of stenoteles could not be confirmed in the available material, this in contradistinction to Vervoort (1985).

Concomitantly with *Bimeria arborea*, Browne (1907) also described the similar *Bimeria biscayana*. The latter species produces medusae and was transferred provisionally to the genus *Amphinema* (see below). Fertile material of both species is easily separable, but also infertile material has a different habitus and in *B. arborea* the main tubes of the branches originate from main tubes of the stem.

Garveia grisea (Motz-Kossowska, 1905) Figs 24-25

Pruvotella grisea Motz-Kossowska, 1905: 77, fig. 9, pl. 3 figs 10-15.
Bimeria fragilis Stechow, 1919: 28, fig. E. – Picard, 1958:190, synonym.
Garveia grisea. – Picard, 1951: 339. – Morri, 1982: 389, fig. – Boero & Freesi, 1986: 140. – Morri *et al.*, 1991: 31. – Medel & López-González, 1996: 193. – Bouillon *et al.*, 2004: 46, fig. 27E.

MATERIAL EXAMINED: Syntype series of *Bimeria grisea,* ZSM, microslides 20000442, 20000443, 20000438, 20000439, Stechow, 1919. – MHNG INVE34436, France, Calanque Port d'Alon near Bandol, 22 April 2003, 0-2 m depth in shaded places and caves, examined alive, several infertile colonies up to 2 cm height, 16S sequence **AM183131**. – Ligurian Sea, Villefranche-sur-Mer 5 April 2005, 6 infertile colonies, some cultivated for 3 weeks, hydranths regenerated well although they did not feed on *Artemia*, no gonophores.

DIAGNOSIS: Hydroid forming branching colonies, polysiphonic or not, double-layered perisarc, branches adnate, hydranths very contractile, with macrobasic

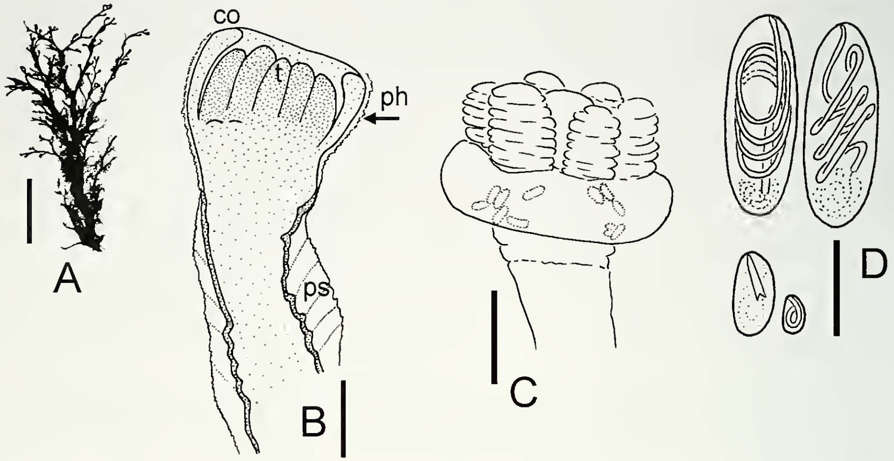

FIG. 24

Garveia grisea (Motz-Kossowska, 1905). (A) Colony silhouette, note that in shallow waters the colony can be stolonal, scale bar 5 mm. (B) Optical section of a contracted hydranth, note the collar-like membrane (co) into which the tentacles can retract, the pseudohydrotheca (ph), and the double layered perisarc (ps); scale bar 0.1 mm. (C) Strongly contracted cultivated hydranth, note large heteronemes on the bulging hydranth-wall, scale bar equals 0.1 mm. (D) Undischarged nematocysts, in the upper row the large macrobasic heteronemes in two views, lower row microbasic eurytele and desmoneme, scale bar equals 10 μm. A-B, after preserved material; C-D, after life.

heteronemes, tentacles can be in two whorls or scattered. Gonophores large styloid sporosacs with one egg and thick vacuolated epidermis; larviparous.

DESCRIPTION: Colonies branching or not, sometimes stem and major branches polysiphonic, but stolonal colonies occur also. Stolons creeping, ramified. Side-branches adnate for some distance, perisarc in older parts double layered, inner layer thicker and undulated, outer layer filmy, the latter continued onto hydranth body as pseudohydrotheca, both layers connected by lamellar membranes. Hydranth spindle shaped, hypostome dome-shaped, in colonies from nature 7-12 tentacles in two whorls, distance of whorls variable, some hydranths with tentacles scattered in upper part of hydranth. The hydranth can contract very strongly, so that the tentacles disappear in a collar-like epidermal fold (seen in preserved material) or the hydranth gets very short and the body-wall forms a bulge. Colour of hydranths: milky-white.

Gonophores relatively large, developing on stem; fixed sporosacs, oblong ovoid, broader end distal; with distinct pedicel. Pedicel covered by firm perisarc, gonophore enveloped by filmy perisarc. Structure of sporosac of styloid type, but atypical and complex. Epidermis very thick, composed of high, vacuolated cells, below these vacuolated cells a sac-shaped inner lining. Mature females contain inside this second lining an ovoid egg or planula enveloped by two layers of cells. Young female sporosacs with one oocyte in epithelium of inner cell layer. Larviparous. Male sporosacs with spermatogenesis in gastrodermal layer.

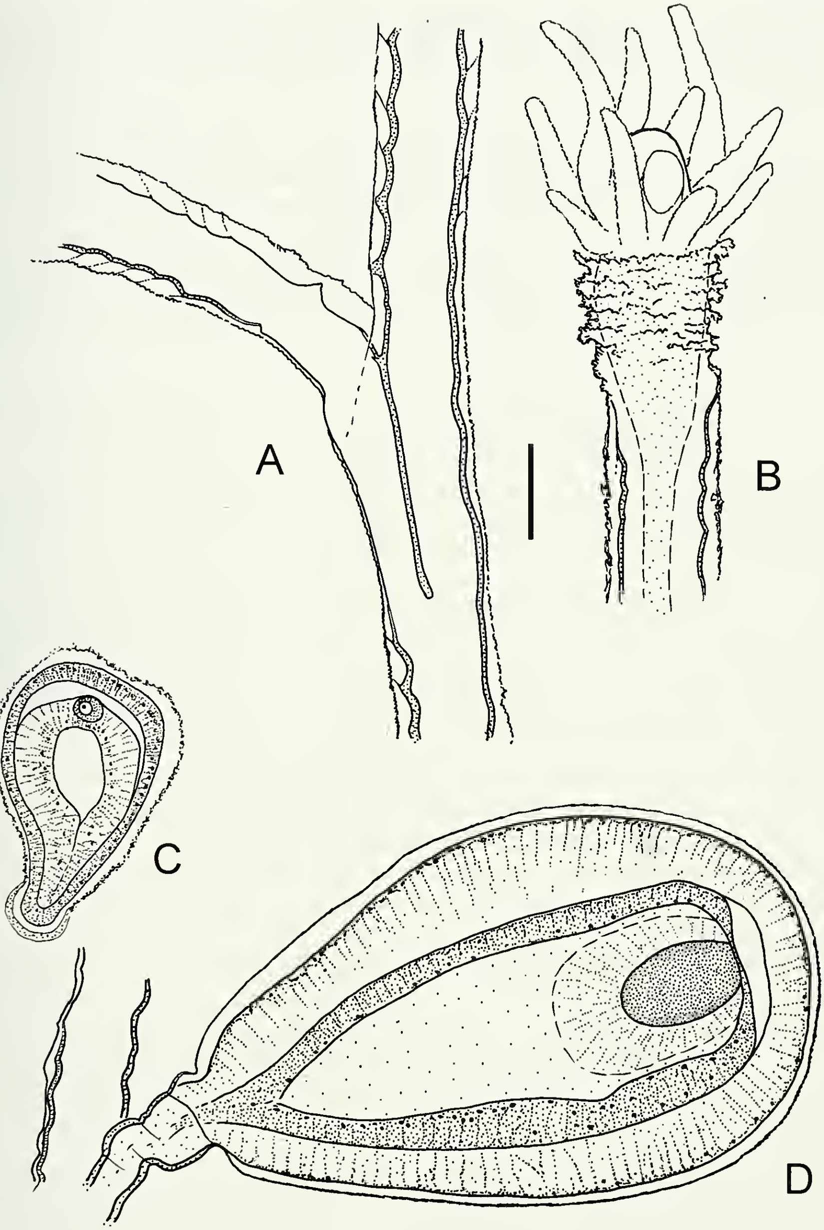

Fig. 25

Garveia grisea (Motz-Kossowska, 1905), after type material of *Bimeria fragilis* (see page 260), scale bar equals 0.1 mm, valid for all figures. (A) Stem with side-branch, note adnate base of branch and double layered perisarc. (B) Semi-relaxed hydranth, same scale as A. (C) Young female sporosac. (D) Fully grown female sporosac, note the large vacuolated cells.

Nematocysts: (1) microbasic euryteles, shaft discharged about 0.8-0.9 times as long as capsule, abundant on tentacles. (2) desmonemes, abundant on tentacles. (3) macrobasic heteroneme, on hydranth body, shaft in with 3-4 coils, coiling pattern variable, not seen discharged.

DIMENSIONS (Motz-Kossowska, 1905; own observations): Colonies 3 mm in shallow waters, up to 3 cm in deeper waters. Diameter of branches 0.1-0.13 mm. Hydranth about 0.3 mm. Female sporosacs 0.7 to 1 mm long and 0.4-0.6 mm wide. Nematocysts (living material): microbasic euryteles, (8-10)x(4.5-5.5) μm, shaft discharged about 0.8-0.9 times as long as capsule, abundant on tentacles; desmonemes, (4-5)x(2.5-3.0) μm, abundant on tentacles; macrobasic heteroneme, on hydranth body, shaft in with 3-4 coils, coiling pattern variable, not seen discharged, (19-21)x(8-9.5) μm.

ADDITIONAL DATA: Motz-Kossowska (1905) describes the development of the female sporosacs. Already Motz-Kossowska (1905) noted that the hydranths of *Garveia grisea* are able to contract very strongly. This contraction can lead to the formation of a collar-like epidermal membrane that covers and hides the tentacles (Fig. 24B). The living material observed for this study confirmed this extraordinary contractility. The collar like membrane, however, was not always observed. Its presence may depend on the degree of contraction of the hydranth. The hydranths of *Garveia grisea* are very sensitive and they deteriorated very rapidly in freshly collected material. It was very difficult to get them relaxed with 7% $MgCl_2$ solutions. Despite their initial sensitiveness, they regenerated well in culture, though not the pseudohydrotheca. Surprisingly, in the regenerated hydranths the tentacles grew in one whorl and not scattered in a narrow band as was often seen in hydranths collected in the sea. If disturbed – e. g. by squeezing a tentacle by tweezers – the hydranth contracts strongly so that the body forms a ring-like bulge (Fig. 24C). The large heteroneme capsules on the hydranth body are thus brought into an exposed position. It is very suggestive to regard this as a defensive reaction. The large heteroneme could not be identified more precisely as their discharge could not be induced, this despite numerous native capsules were examined.

DISTRIBUTION: Western Mediterranean*. Type locality: Mediterranean, France, Banyuls-sur-Mer.

BIOLOGY: A winter species, being present from September to May, occurs along rocky shores in depths of 0-80 m, reproduction: September to November (Motz-Kossowska, 1905), or October-January (Boero & Freesi, 1986). Occurs often on large *Eudendrium* colonies.

SYNONYMY AND TAXONOMY: Picard (1958) synonymized *Bimeria fragilis* Stechow, 1919 with *Garveia grisea* without further discussion. A re-examination of the type material of *Bimeria fragilis* Stechow, 1919 confirmed that it is indistinguishable from *G. grisea* in nearly all aspects, except for the contracted hydranths. The type material of *B. fragilis* showed moderately expanded hydranths identical to those observed in cultivated material of *G. grisea*. I suspect that Stechow has either treated his material with muscle-relaxing chemicals or he had colonies with regenerated

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* Note added in proof: also West of Ireland, MHNG INVE53151.

hydranths. Because *B. fragilis* is otherwise identical to *G. grisea*, notably sharing the same unique sporosacs, the double-layered-perisarc, the colony form, the adnate side-branches, and the large supplementary nematocysts, it is here regarded as conspecific with *G. grisea*.

REMARKS: *Garveia grisea* is one of the few bougainvilliid hydroids that can also be identified in the absence of gonophores. The adnate branches, the double-layered perisarc, the strongly contractile hydranths, and the large heteroneme make it distinct from all other bougainvilliids. The colonies resemble quite *Turritopsis dohrnii*, with which they can easily be confounded. However, the hydranths of the latter species are not as contractile, they have their tentacles scattered over most of the hydranth body, and they never have a pseudohydrotheca (see Schuchert, 2004).

Genus ***Rhizorhagium*** M. Sars, 1874

TYPE SPECIES: *Rhizorhagium roseum* M. Sars, 1874 by monotypy.

SYNONYMS: *Wrightia* Allman, 1872 [type species *Atractylis arenosa* Alder, 1862 by monotypy; invalid junior homonym of *Wrightia* L. Agassiz, 1862]. – *Gravelya* Totton, 1930 [type species is *Perigonimus antarcticus* Hickson & Gravely, 1907 by designation of Totton, 1930]. – *Aselomaris* Berrill, 1948 [type species *Atractylis arenosa* Alder, 1862, designation by Calder, 1988].

DIAGNOSIS: Hydroids forming stolonal colonies, hydranths on perisarc covered hydrocauli, rarely some shoots with one or two side branches; hydranth fusiform; hypostome dome-shaped, conical, or nipple-shaped, surrounded by one distal whorl of tentacles; pseudohydrotheca covering polyp base but not sheathing tentacles; gonophores fixed sporosacs, borne on hydrocauli and/or on stolons.

REMARKS: Rees (1956b) outlines the taxonomic history of this genus, although he erroneously attributed it to a later publication of M. Sars.

In its prevailing usage (Millard, 1975; Bouillon, 1985), the scope of *Rhizorhagium* is only gradually different from *Garveia* Wright, 1859 and not well separable from the latter. Its scope should therefore be modified, an opinion already put forward by Bouillon *et al.* (2004). The stolonal colony organisation is always a growth stage in erect forms and it is likely that it can evolve quite easily from an erect form. Stolonal hydroids of the families Bougainvilliidae or Pandeidae that produce a medusa stage can also relatively easily evolve into *Rhizorhagium* through a simple medusa reduction. It is therefore very likely that the current concept of *Rhizorhagium* is polyphyletic. However, due the paucity of morphological characters, only a molecular phylogeny can resolve the relationships. As it seems unwise to make not well founded provisional changes that might prove obsolete once molecular phylogenies are available, and in order to maintain taxonomic stability, the current classification is retained here. This compromise was already proposed by Ree (1938: 6), although he did not include *R. arenosa* in this genus. He gave no arguments for this, but likely excluded it because it has its gonophores on the hydrocauli and not the stolons. Likewise, also Calder (1988) proposed to restrict *Rhizorhagium* to species with a nipple shaped hypostome.

KEY TO THE *RHIZORHAGIUM* SPECIES TREATED HERE:

1a	gonophores on stolons	2
1b	gonophores on hydrocauli	*R. arenosum*
2a	hypostome nipple-shaped, long hydrocauli	*R. roseum*
2b	hypostome conical or dome-shaped, hydranths subsessile	*R. album*

Rhizorhagium roseum M. Sars, 1874 Fig. 26

? *Atractylis coccinea* Wright, 1861: 130.
? *Atractylis miniata* Wright, 1863: 351. – Rees, 1956a: 341.
Rhizorhagium roseum M. Sars, 1874 (in G. O. Sars, 1874: 129). – M. Sars, 1877: 28, pl. 2 figs 37-43. – Jäderholm, 1909: 46, pl. 3 fig. 7. – Broch, 1911: 16, fig. 12. – Broch, 1916: 54. fig. R. – Rees, 1938: 8. – Rees, 1956b: 113. – Calder, 1972: 225, pl. 2 fig. 4. – Schuchert, 2001: 25, fig. 14A-B.
Perigonimus coccineus. – Hincks, 1871: 77.
Perigonimus sarsii Bonnevie, 1898b: 6, pl. 1 fig 3. – Rees, 1956b: 113, synonym.
Garveia groenlandica Levinsen, 1893: 155 . – Kramp, 1911: 263. – Broch, 1916: 55, synonym. – Fraser, 1937: 35, fig. 21.
Wrightia coccinea. – Russell, 1907: 53, fig.
Perigonimus roseus. – Naumov, 1969: 205, fig. 73.

MATERIAL EXAMINED: MHNG INVE28734, Greenland, Akuliaruseq, 60.16°N 44.16°W, 40-60 m, 11 August 1966; male; dense colony on *Abietinaria abietina*. – MHNG INVE27654, Iceland, 66.42°N 23.83°W, 138-152 m, 12 July 1989 (BIOICE station 2530); female colony on hydroid. – MHNG INVE33554, Faroes, 62.18°N 04.97°W, 184 m, 07 May 1988 (BIOFAR station 165), female colony on hydroid. – BMNH 1967.12.1.3; identified by W. J. Rees as *Perigonimus coccineus* (label); Great Britain, Little Cumbrae, off Lighthouse, 82 m; 8 July 1966; female. – BMNH 1969.12.2.1966; identified as ? *R.roseum* by W.J. Rees, is clearly this species; on *Tubularia*; female; origin and date not known. – BMNH 1965.7.21.1; as *Perigonimus coccineus*; Scotland, Bute, Firth of Clyde, Mount Stuart; 20 June 1962; on *Tubularia indivisa*; male.

DIAGNOSIS: Stolonal hydroid, hydrocauli long and well demarcated from hydranth, hydranths with pseudohydrotheca, hypostome nipple-shaped, one whorl of tentacles; sporosacs arising from stolons, on relatively long pedicels.

DESCRIPTION: Colonies stolonal or stems rarely branched once; stolons creeping, ramified to reticulate. Hydrocauli long, enclosed in perisarc that is mostly smooth but can have some corrugated regions; perisarc continues distally as thin, wrinkled membrane over body of hydranth as a pseudohydrotheca. Hydranth spindle- to urn-shaped, diameter about 1/3 of height, appearing relatively broad, 6-12 (normally 8) filiform tentacles. Hypostome high, thin, characteristically nipple-shaped. Gonophores develop from stolons, on pedicels, covered by perisarc, perisarc may be loose. Young female sporosacs oblong, later spherical, main body enclosed by wrinkled membrane, with a club-shaped spadix on which eggs develop, 2-6 eggs per sporosac. The eggs are fertilized in situ and develop within the membrane into planulae (larviparous). Male sporosacs oblong, tightly packed with spermatozoids. Colour of hydranth: rose to red. Upon disturbance, the hydranth bends back towards the pedicel.

DIMENSIONS (Rees, 1956b; own observations): Hydrocauli 2-8 mm high (according to Broch (1916) up to 12 mm), hydranth 0.4-0.45 mm height, diameter of hydranth 0.3-0.35 mm, hydrocaulus diameter 0.12-0.2 mm, length of female sporosac 0.6-1.2 mm, diameter of gonophores 0.5-0.75 mm, length of sporosac stalk 0.35-0.7 mm, male sporosacs up to 0.6 mm, diameter 0.45 mm.

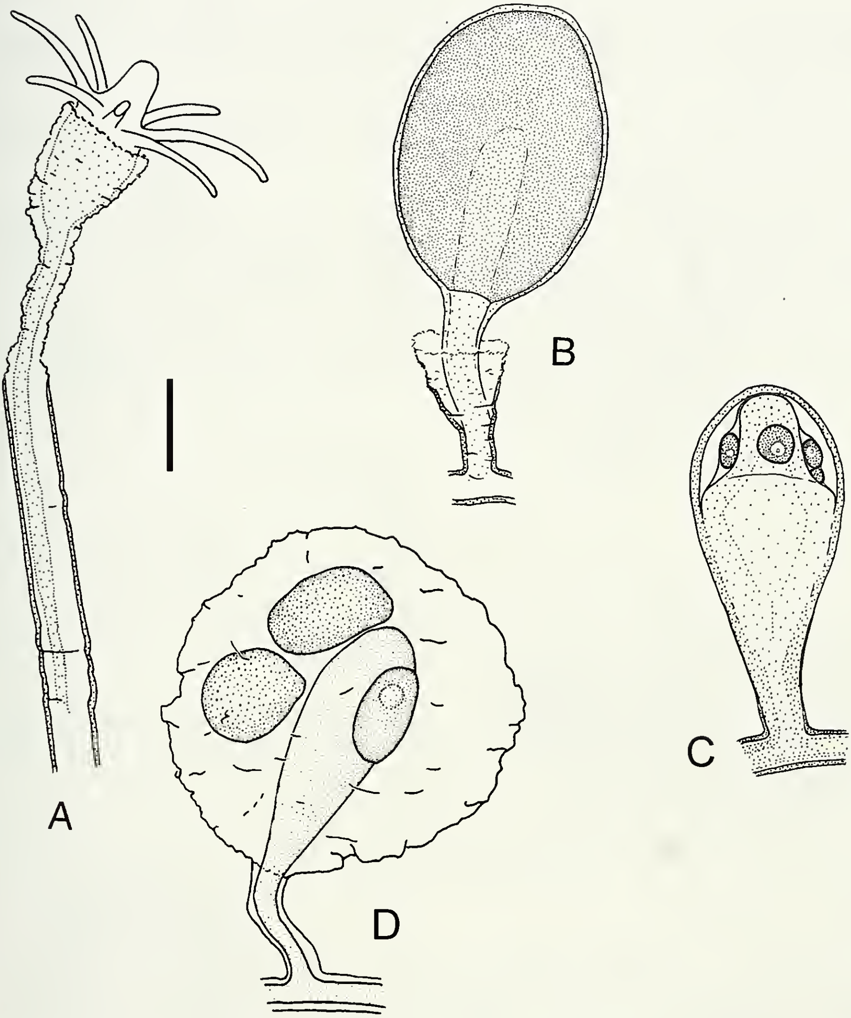


FIG. 26

Rhizorhagium roseum Sars, 1874, after preserved material, scale bar 0.2 mm. (A) Hydranth with pseudohydrotheca and distal part of caulus. (B) Male sporosac. (C) Younger female sporosac sporosac. (D) Female sporosac with spadix bearing one egg and two developing embryos.

DISTRIBUTION: A circumpolar Arctic-boreal species. Its southern limit seems to be western Scotland (Firth of Clyde; Russell, 1907; this study). Known from Norway (Jäderholm, 1909; Christiansen, 1972), western Sweden (Jäderholm, 1909; Rees & Rowe, 1969); the Faroe Islands (this study); western Scotland; Greenland (Schuchert, 2001); Iceland (Schuchert, 2001); Barents Sea; White Sea (Naumov 1969); north-eastern Canada (Calder, 1972); western Canada (Brinckmann-Voss, 1996); Alaska (Fraser, 1937). Type locality: Norway, Mangerfjord, Bongnestrømmen, on *Tubularia indivsa* (Rees, 1956b).

BIOLOGY: Found mostly on other hydroids, mainly on *Tubularia indivisa* and *Abietinaria abietina* at a depth of 15-200 m. Fertile colonies have been observed from May to October, but a longer period is possible.

REMARKS: The synonymy of this species as elaborated by Broch (1916) and Rees (1938, 1956b) is adopted here. *Atractylis coccinea* Wright, 1861, is not recognizable, but likely belongs to this species.

The characteristic hypostome makes this hydroid quite easy to identify, even for infertile material. The unique shape of the hypostome was also the reason why Calder (1988) excluded from the genus *Rhizorhagium* all similar species that have a dome-shaped hypostome (see also Schuchert, 1996).

As noted by Rees (1956b), the reaction of the hydranths if disturbed or fixed is to bend back towards the stem. This reaction also often seen in the hydroids of the genus *Amphinema* (Schuchert, 1996: 62).

The size of the sporosacs observed in this study was smaller than those observed by Rees (1938, 1956b).

Rhizorhagium arenosum (Alder, 1862) Fig. 27

Atractylis arenosa Alder, 1862a: 144. – Alder, 1862b: 313, pl. 13 figs 5-7. – Wright, 1863: 47, pl. 4 figs 7-10. – Hincks, 1868: 88, pl. 16 fig 1. – Cornelius & Garfath, 1980: 277.
Wrightia arenosa. – Allman, 1872: 300.
Rhizorhagium arenosum. – Bouillon *et al*., 2004: 49, Fig. 29A.
? not *Aselomaris arenosa*. – Pennycuick, 1959: 163, pl. 2 fig. 6.
Aselomaris arenosa. – Hamond, 1964: 662, fig. 1.

MATERIAL EXAMINED: MHNG INVE3666, slide; 51.433°N 11.755°E (station: CARACOLE 125-03), Porcupine Seabight, 890 m, collected by submersible robot arm, 3 August 2001, male colony, covered by bacteria, epizoic on other hydroid, may belong to this species.

DIAGNOSIS: Stolonal hydroid, hydrocauli short and not well demarcated from hydranth, hydranths with pseudohydrotheca, hypostome dome-shaped to conical, one whorl of tentacles, sporosacs on hydrocauli, females with 30 and more eggs, embryos develop in acrocyst.

DESCRIPTION (after literature and own data): Hydroids arising from ramified, creeping stolons; stolons covered by perisarc, hydrocauli unbranched, often not distinctly delimited from hydranth body which tapers towards base; conical pseudohydrotheca into which the hydranth can completely withdraw, covered by mud and particles. Hydranth spindle-shaped, hypostome conical to dome-shaped, 6-12 tentacles in one whorl. Gonophores are sporosacs of the styloid type; one or two sporosacs on hydrocaulus, likely also stolons. Female sporosacs oblong (two times as long as wide, but ratio may vary), covered by filmy perisarc; mature with many eggs (>30), embryonic development takes place in a gelatinous mass (acrocyst) to the planula stage, thus larviparous. Male sporosacs similar to female ones. Colours: milky white.

DIMENSIONS: Hydranth up to 1 mm (estimation), hydrocaulus and pseudohydrotheca up to 1.4 mm; female sporosac up to 0.5 mm (measured in Hamond, 1964), male sporosacs 0.3 mm long, 0.15 mm wide.

OTHER DATA: Wright (1863) described the maturation of the sporosac (Fig. 27E-G). When mature, the thin periderm envelope ruptures and the sporosac

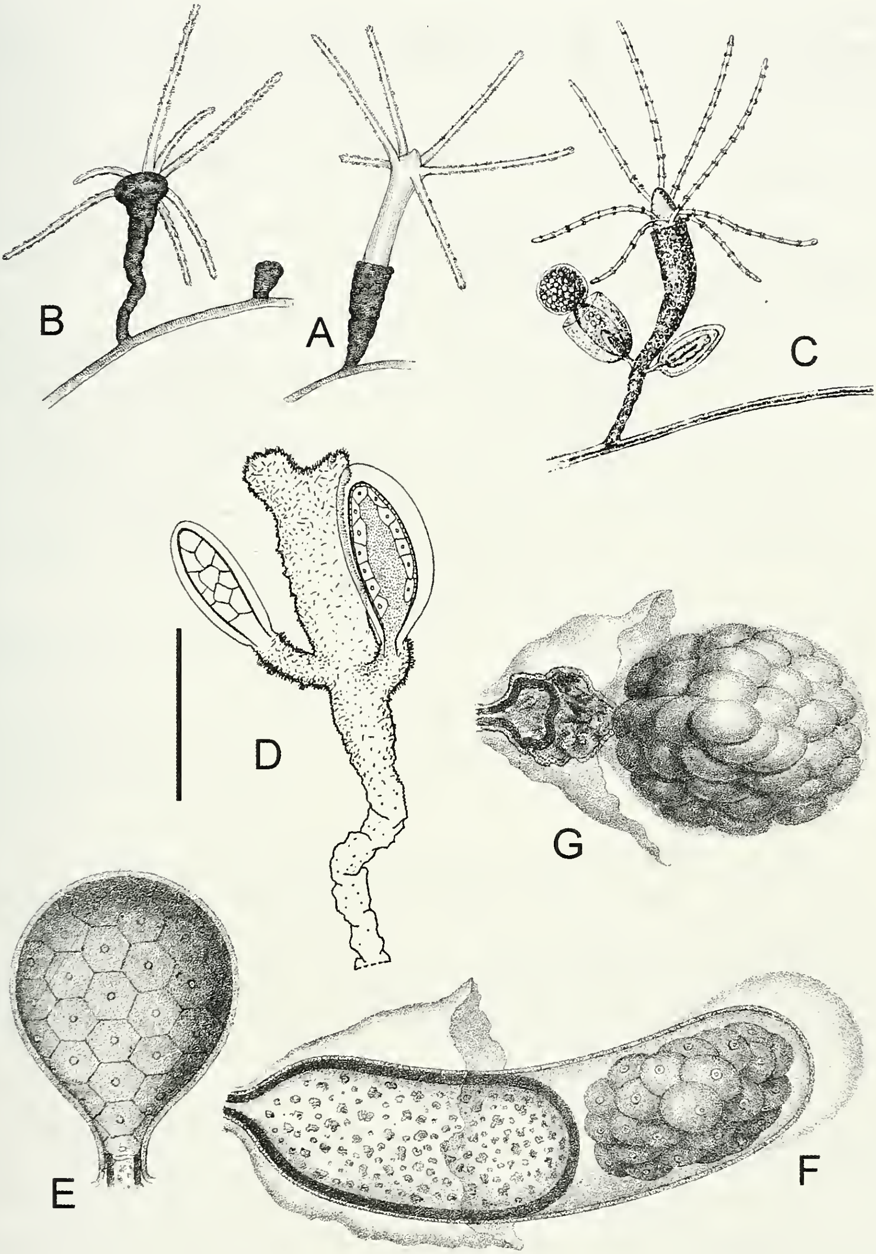


FIG. 27

Rhizorhagium arenosum (Alder, 1862). (A) Expanded hydranth. (B) Contracted hydranth. (C) Hydranth with two sporosacs. (D) Hydrocaulus with two young female sporosacs, scale bar 0.5 mm. (E) Mature female sporosac before extrusion of eggs. (F) Female sporosac in process of extruding its eggs. (G) Same as F, eggs are in gelatinous acrocyst. A-B, from Alder (1862b); C, from Hincks (1868); D, modified after Hamond (1964), E-G, from Wright (1863).

emerges in a long cylindrical form, it contracts like a medusa bell. Concomitantly, the apical part of the sporosac secretes a gelatinous substance and further contractions let the sporosac rupture, so that the eggs are pushed into the gelatinous acrocyst where they develop into planulae.

Biology: Predominantly an intertidal species occurring on algae, stones and other substrates.

Distribution: North Sea coast of Britain (Allman, 1872), perhaps also SW Ireland (Duerden, 1893; this study). Type locality: Tynemouth and Cullercoats, Northumberland, intertidal, on stones and *Laminaria* holdfasts.

Remarks: This is a rather poorly documented species, which may be more frequent than reflected by its few records. As remarked by Hamond (1964), infertile colonies of this species are indistinguishable from immature *Bougainvillia muscus*.

The examined material from deep waters SW of Ireland differs from the existing descriptions in that the sporosacs arise from the stolons. In combination with its occurrence in deep waters, this identification is therefore somewhat doubtful.

The Mediterranean record of this species (Lo Bianco, 1909) must be a misidentification of *Pachycordyle pusilla* (Motz-Kossowska, 1905) (see Schuchert, 2004). Lo Bianco (1909) states: «occurs on *Posidonia* in shallow waters».

Rhizorhagium album (Rees, 1938) Fig. 28

? *Eudendrium pudicum* Van Beneden, 1867: 116, pl. 8 figs 1-2.
Rhizorhagium album Rees, 1938: 9, fig. 2a-c.

Diagnosis: Stolonal hydroid, hydrocauli very short or absent, hydranths with pseudohydrotheca, hypostome conical, one whorl of tentacles, styloid sporosacs on stolons, ovoid shape.

Description (after Rees, 1938): Colonies small, stolons creeping, covered by thin, irregularly wrinkled perisarc. Hydranths with very short hydrocauli, sometimes hydranths subsessile, pedicels covered by wrinkled perisarc continued as thin, filmy pseudohydrotheca over hydranth body; hydranths tubular, hypostome conical, 6-10 filiform tentacles in a single whorl. Colour of polyps white. Gonophores ovoid, developing from stolons on relatively long stalks, sporosacs of the styloid type, spadix present, only males known.

Dimensions (after Rees, 1938): Stolon diameter 0.1 mm, hydrocauli maximally 0.3 mm high, hydranths 0.35-0.55 mm high, diameter 0.1-0.14 mm. Pedicels of sporosacs 0.3-1.0 mm, sporosac diameter 0.4 mm.

Biology: The original colony was found on filamentous algae in a rock pool.

Distribution: Known from the type locality only, Newquay (Cornwall, England).

Remarks: This species is only known from its original description based on cultivated material. The principal difference to *R. arenosum* is the location of the sporosacs on the stolons. This could be, however, a cultivation artefact as cultivated hydroids can differ from those grown under natural conditions. I strongly suspect that

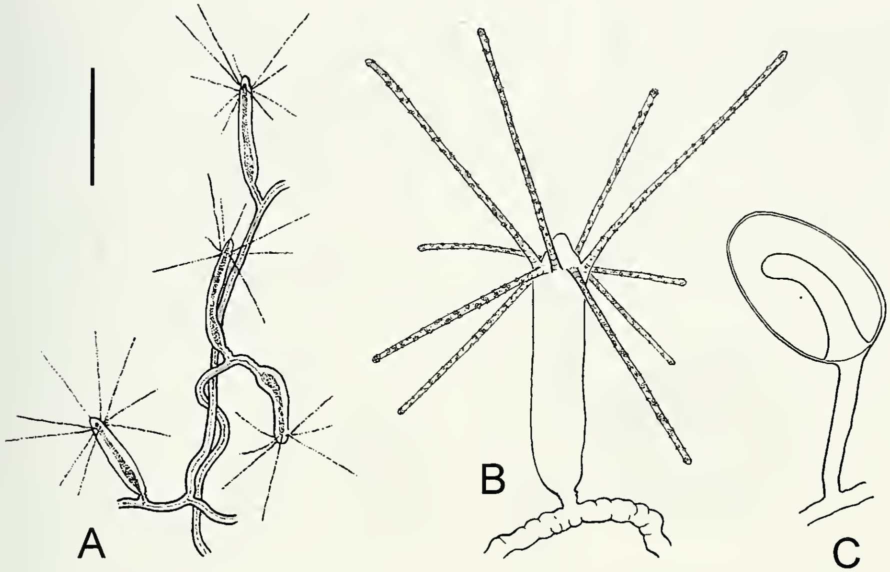


FIG. 28

Rhizorhagium album (Rees, 1938), modified after Rees (1938), scale bar 0.3 mm. (A) Part of cultivated colony. (B) Single hydranth. (C) Sporosac.

R. album is only a form of *R. arenosum*. Also the similar *Rhizorhagium antarcticum* (Hickson & Gravely, 1907) can have its sporosacs either on the hydrocauli or the stolons (Schuchert, 1996).

Genus ***Pachycordyle*** Weismann, 1883

TYPE SPECIES: *Pachycordyle napolitana* Weismann, 1883 by monotypy.

SYNONYMS: *Clavopsella* Stechow, 1919; *Thieliana* Stepanjants *et al.*, 2000 [type species *Clavopsella quadranularia* Thiel, 1962].

DIAGNOSIS: Stolonal or branching hydroid colonies, hydranths pedicellate, perisarc terminating at base of hydranth. Hydranths club-shaped, hypostome dome- to nipple-shaped, tentacles in two or more whorls. Gonophores borne on stems or pedicels. Gonophores fixed sporosacs or degenerated medusae lacking mouth, marginal tentacles, oral tentacles, radial canals, and ocelli.

REMARKS: See Schuchert (2004) for a more information on the species *Pachycordyle napolitana* Weismann, 1883, *Pachycordyle navis* (Millard, 1959), and *Pachycordyle pusilla* (Motz-Kossowska, 1905).

Pachycordyle michaeli (Berrill, 1948) n. comb. Fig. 30

Aselomaris michaeli Berrill, 1948: 289, figs 1-4.

not *Clavopsella michaeli*. – Piraino, 1992: 241, figs 1-13, [= *Pachycordyle pusilla* (Motz-Kossowska, 1905)].

not *Rhizorhagium michaeli*. – Bouillon *et al.*, 2004: 49, fig. 29B-C.

MATERIAL EXAMINED: Paratypes BMNH 1985.9.13.9, as *Aselomaris michaeli* Berrill, 1948, USA, Boothbay Harbour, Maine, leg. N. Berrill, large colonies, male and females present.

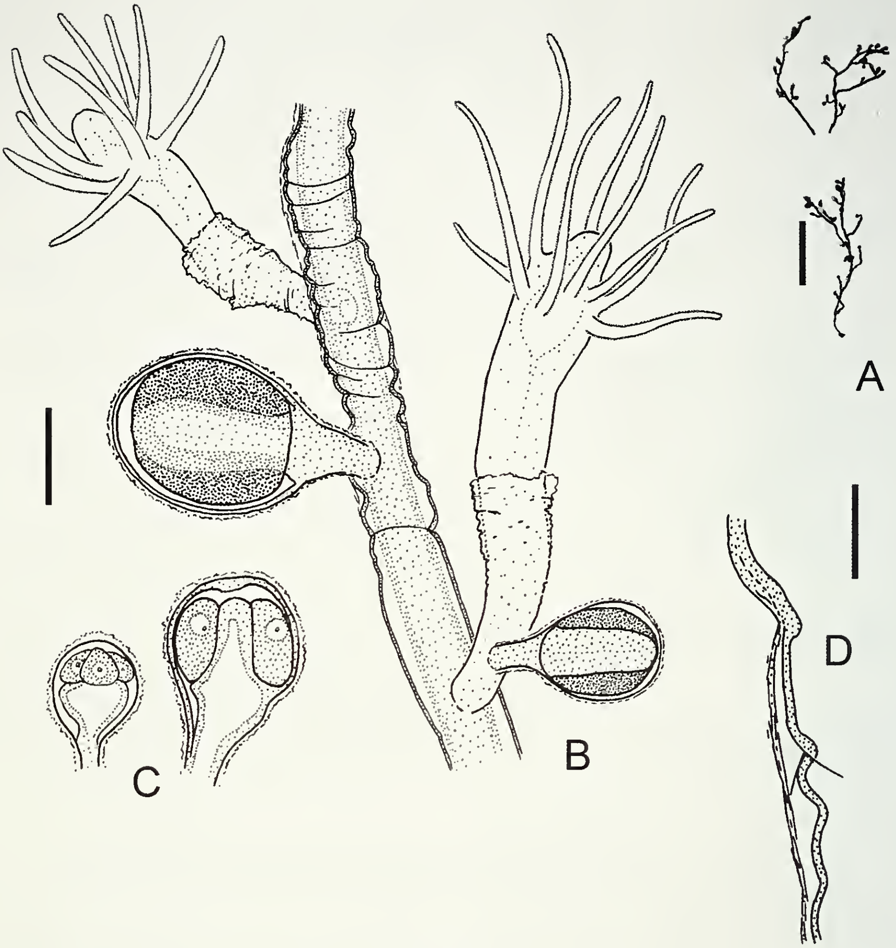


FIG. 29

Pachycordyle navis (Millard, 1959). (A) Colony silhouettes, scale bar 0.4 mm. (B) Part of branch with two male sporosacs, scale bar 0.2 mm. (C) Young female sporosacs, right one as optical section, same scale as B. (D) Perisarc of branch, outside is left, note transition from single- to double layered perisarc, scale bar 50 μm. After preserved material from Widewater, Lancing, Sussex, UK, BMNH 1959.10.4.2.

DESCRIPTION: Colony stolonal or occasionally sparingly branched. Hydrocauli and stems covered by perisarc, terminating below hydranth, thus without pseudohydrotheca. Perisarc mostly corrugated, sometimes smooth. Hydranths club-shaped, hypostome high, conical to dome-shaped; tentacles 12-20, in 2-3 closely approximated, alternate whorls. Gonophores fixed sporosacs (heteromedusoid type), numerous on hydranth pedicels, spherical to ovoid, with conspicuous spadix, stalks distinct and usually relatively long, but length variable. Colonies dioecious. Female sporosacs with about 6-10 eggs, when mature with nematocysts on surface. Eggs develop into planulae in situ.

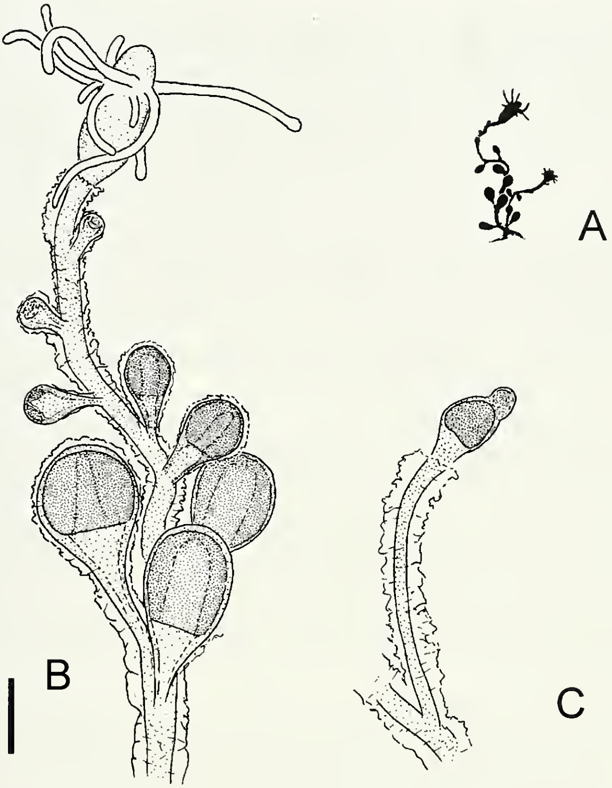


FIG. 30

Pachycordyle michaeli (Berrill, 1948), after preserved paratype material. (A) Colony silhouette, height approx. 3 mm. (B) Hydranth and several male sporosacs, scale bar 0.2 mm. (C) Spent male sporosac in more proximal region of shoot shown in B, note the very long stalk, same scale as B.

DIMENSIONS: Stems up to 4 mm, hydranths 0.4 mm high. Sporosacs up to 0.5 mm long and 0.35 mm wide, pedicels sporosacs length very variable 0.07-1.2 mm.

BIOLOGY: Shallow water species, growing on wooden floats and *Fucus*. Light induces spawning (Berrill, 1948).

DISTRIBUTION: Presumably only known from region of type locality, Boothbay Harbour (Maine, USA). The Mediterranean record likely refers to *P. pusilla*.

REMARKS: Piraino (1992) described the nematocyst-covered eggs of a Mediterranean bougainvilliid species which he named *Clavopsella michaeli* (Berrill, 1948). The hydroid was cultivated in the laboratory and Dr Piraino kindly furnished me with some preserved material of this colony, part of which was deposited in the MHNG (as INVE38150). This material was compared to the type material of *Aselomaris michaeli* Berrill, 1948 (see above), material of *Pachycordyle pusilla* (Motz-Kossowska, 1905) (MHNG INVE36202; INVE32953, both Mediterranean) and *P. navis* (Millard, 1959) (MHNG INVE31852 and INVE34226, both from Denmark;

BMNH 1959.10.4.2, UK material, Fig. 29). The material of Piraino appears indistinguishable from *Pachycordyle pusilla* (Motz-Kossowska, 1905) (see review in Schuchert, 2004), the only unusual trait being its original substrate. Piraino (1992) found his hydroid on the tubes of the polychaete *Sabella spallanzani* (Gmelin, 1791), while *Pachycordyle pusilla* was so far only known to occur on seagrasses (*Posidonia* and *Cymodocea*). It is nevertheless possible that *P. pusilla* can also grow on other substrates. Müller (1913, as *Pachycordyle fusca*) cultivated *P. pusilla* over long periods and he observed that the colonies also spread onto lead blocks. I am therefore convinced that the hydroid described in Piraino (1992) should be assigned to *P. pusilla*. The higher number of sporosacs and the nematocysts on the eggs cannot be used to keep it separate. In the original description of *P. pusilla*, Motz-Kossowska (1905) mentions that there can be 2-5 sporosacs per hydrocaulus and there are nematocysts on the egg surface.

The re-examination of the type material of *Aselomaris michaeli* showed that the description of Berrill (1948) must be modified somewhat. The hydrocauli bear mostly only one hydranth, but rarely some branching occurs. More important is that the tentacles are not in a single whorl, but in two close-set whorls, sometimes even in three well separated whorls. The hydroid resembles very closely *Pachycordyle navis* (Millard, 1959) (see Fig. 29) and I suspect that they are conspecific. The very long pedicels of the sporosacs are not unique to *R. michaeli*, similarly long pedicels of the sporosacs have also been depicted by Thiel (1962) for *Clavopsella quadanularia*, a synonym of *P. navis* (Millard, 1975).

As already mentioned in Schuchert (2004), *P. navis* resembles also *P. pusilla*, the differences being mainly the longer hydrocauli that can also be branched, the long gonophore pedicels, and its preference for reduced salinities. There remains, however, the possibility that even *P. pusilla* is only a form of *P. navis* growing in fully marine environments. Detailed investigation using molecular methods are needed to re-evaluate the status of *P. pusilla, P. navis*, and *R. michaeli*. Some preliminary results (Fig. 4) show that *P. pusilla* is in fact closely related to some *Bougainvillia* species, indicating that even the inclusion in the genus *Pachycordyle* is incorrect.

Genus ***Velkovrhia*** Matjašič & Sket, 1971

TYPE SPECIES: *Velkovrhia enigmatica* Matjašič & Sket, 1971.

DIAGNOSIS: Colonial, stolonal freshwater hydroids occurring in caves. Hydranth pedicels covered by irregularly corrugated, multi-layered perisarc, hydranth body urn-shaped, without pseudohydrotheca, filiform tentacles in two whorls, hypostome nipple-shaped. Gonophores arise on hydranth pedicels, fixed sporosacs, females with branched gastrodermal system, larviparous.

REMARKS: The genera *Parawrightia* Warren, 1907 and *Velkrovhria* appear very similar. There are some small differences in their sporosacs (*Parawrightia* has sporosacs with radial canals (comp. Warren, 1907; Wedler & Larson, 1986; Velikonja, 1994). Additionally, *Parawrightia* has a pseudohydrotheca and is a marine species. Although these traits are normally not considered to be important enough to separate genera, the genus name *Velkrovhria* should be retained until it is clear whether its type species might not belong to *Cordylophora* (see below).

Velkovrhia enigmatica Matjašič & Sket, 1971 Fig. 31

Velkovrhia enigmatica Matjašič & Sket, 1971: 139, figs 1-4. – Kuštor, 1977: 51. – Sket & Matjašič, 1977: 263-265, figs 1-2. – Velikonja, 1986: 123, fig. 2. – Velikonja, 1994: 39, fig 1. – Holstein, 1995: 99, fig. 52. – Bouillon *et al.*, 2004: 49, fig. 29E.

MATERIAL EXAMINED: No material was available, but Dr B. Sket kindly provided some good colour photographs of living animals.

DIAGNOSIS: As for genus.

DESCRIPTION (after literature data): Small stolonal colonies, stolons creeping on substrate, perisarc covered. Hydranths on perisarc covered pedicels, perisarc multilayered, irregularly corrugated, terminating below hydranth. Hydranth urn-shaped, with high, nipple-shaped hypostome, up to 10 tentacles in two close set whorls, alternating. Gonophores are sessile sporosacs, developing on hydrocauli, spherical to ellipsoid, covered by filmy periderm, colonies dioecious; female sporosacs with about 5 eggs, planulae develop in situ, gastrodermal system (spadix?) branched, adnate to wall. Colour milky white, periderm yellowish-brown. Nematocysts: desmonemes and microbasic euryteles (Kuštor, 1977).

DIMENSIONS: Hydrocauli 1.3-1.7 mm, hydranths 0.4 mm, hydrocaulus diameter 0.25 mm. Sporosacs about 0.4 mm, planula size 0.2 mm.

BIOLOGY: A freshwater species living in carstic caves. The hydranth density is dependant on the season, with a summer minimum and a winter maximum (Velikonja, 1986).

DISTRIBUTION: Slovenia, Croatia, and Hercegovina. Type locality: Rake Passage, Cave of Planina, Slovenia.

REMARKS: Although Matjašič & Sket (1971, in English summary) describe this species as having one whorl of tentacles only, their figures show two whorls. Sket & Matjašič (1977) describe the hydranth as having two tentacle whorls. The spadix of the female sporosac is branched as suggested by Figure 31B and also colour photographs of living animals (given as black and white photographs in Sket & Matjašič, 1977).

Velkovrhia enigmatica shares many traits with *Cordylophora caspia* (Pallas, 1771) (for a review see Schuchert, 2004): the hydranth shape, the female sporosacs with the branched spadix, and its occurrence in fresh-water. Kinne (1956; 1957) has shown in extensive experiments that *Cordylophora caspia* changes drastically its morphology in varying salinities. In freshwater, the colonies remain stolonal, the hydranths get small and broad, and the tentacle number is reduced, approaching thus the morphology of *V. enigmatica*. But even in freshwater the colonies could form gonophores. It could thus be that *V. enigmatica* is nothing but a subdued form of *Cordylophora caspia*. However, at this stage this stage this is only an assertion that has to be proven by either by cultivating *V. enigmatica* in water with varying salinities, or by comparisons of 16S sequence data.

INDETERMINATE BOUGAINVILLIDAE OR SPECIES REFERABLE TO OTHER FAMILIES

Atractylis bitentaculata Wright, 1867

Atractylis bitentaculata Wright, 1867: 45, pl. 1 fig. 5.
Perigonimus bitentaculatus. – Hincks, 1968: 98, fig. 9. – Rees, 1956a: 338.

TYPE LOCALITY: Firth of Forth, near Inch Keith, on a *Pecten* shell.

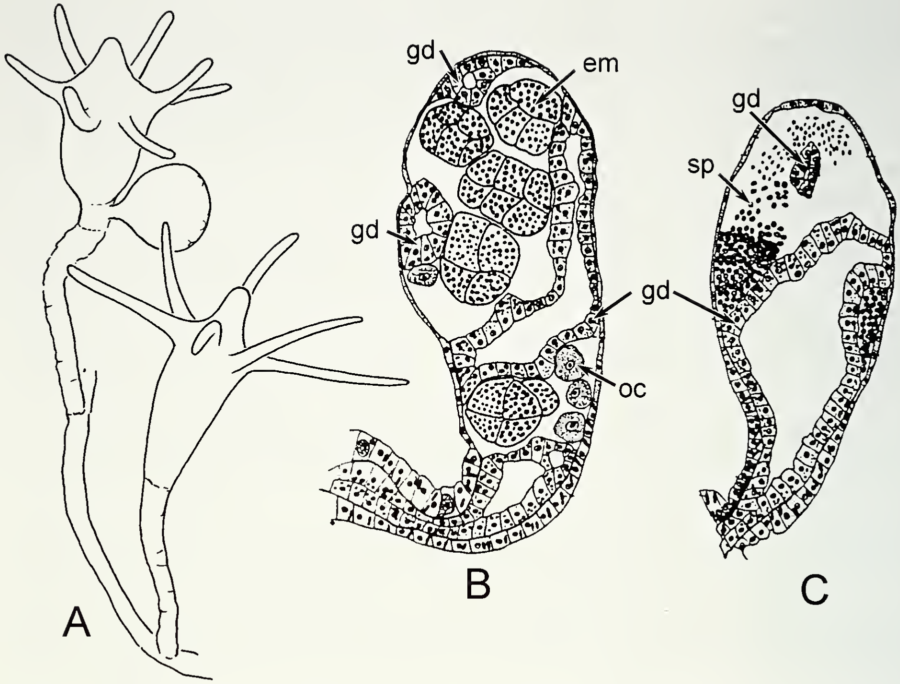


FIG. 31

Velkovrhia enigmatica Matjašič & Sket, 1971. (A) Two hydranths issuing from a common stolon, rear polyp with sporosac, after photograph in Velikonja (1994), some tentacles imaginary (not clearly visible in photo). (B-C) Histological sections of female and male sporosacs; em developing planula, gd gastrodermis, oc oocyte, sp spermatids; from Velikonja (1986).

REMARKS: Rees (1956a) thought that this species, the gonophores of which are unknown, might belong to the genus *Proboscidactyla*. Because the members of this genus occur exclusively around the openings of the tubes sabellid polychaetes and Wright's species grew on a *Pecten* shell, this appears less likely. Moreover, the figures in Hincks (1868, reproduction of Wright, 1867?) shows polyps with distinct pedicels and a conical hypostome. Allman (1872: 329) regarded it as an immature form of an indeterminate hydroid.

Atractylis quadritentaculatus Wright, 1867

Atractylis quadritentaculatus Wright, 1867: 45, pl. 1 fig. 6.

REMARKS: An indeterminate species.

Perigonimus georginae Hadzi, 1913

Perigonimus georginae Hadzi, 1913: 98, figs 7, 10-11. – Rees, 1956a: 340.

REMARKS: An indeterminate species, could be *Amphinema rugosum* or *A. dinema* (Rees, 1956a).

Perigonimus inflatus Duerden, 1895
Perigonimus (?) *inflatus* Duerden, 1895: 329, pl. 14 fig. 4. – Rees, 1956a: 340.

REMARKS: An indeterminate species, could be *a Rhizorhagium* species (Rees, 1956a).

Perigonimus nutans Hincks, 1877
Perigonimus ? *nutans* Hincks, 1877: 149, pl. 12 fig. 1. – Rees, 1956a: 342.

REMARKS: An indeterminate species, could be *Amphinema rugosum* or *A. dinema* (Rees, 1956a).

Perigonimus decorans Schneider, 1898
Perigonimus decorans Schneider, 1898: 479. – Rees, 1956a: 340.

REMARKS: An indeterminate species, it is unclear to which family it belongs (Rees, 1956a).

Perigonimus steinachi Jickly, 1883
Perigonimus steinachi Jickly, 1883: 617, pl. 27 figs 1-9. – Rees, 1956a: 344.

REMARKS: An indeterminate species, it is unclear to which family it belongs (Rees, 1956a). Perhaps referable to *Perarella schneideri*.

Eirene viridula (Péron & Lesueur, 1810)
Oceania viridula Péron & Lesueur, 1810: 346.
Perigonimus nudus Stechow, 1919: 16, fig. D. **new synonym**
Eirene viridula. – Cornelius, 1995: 223, fig. 51.

REMARKS: The type material of *Perigonimus nudus* Stechow, 1919 could be examined (ZSM, 20000646 and 20000647, 2 slides, loc. Trieste, leg. Maas 1908). The material is obviously *Eirene viridula* (for description see Cornelius, 1995).

Lizzella hyalina (Van Beneden, 1867)
Circe hyalina Van Beneden, 1867: 95, pl. 3 fig 14.
? *Lizzella hyalina*. – Haeckel, 1880: 634.
Lizzella hyalina. – Hartlaub, 1911: 151, fig. 137. – Kramp, 1959a: 86, doubtful species.

REMARKS: Van Beneden (1867) described a medusa from the Belgian coast that resembled closely *R. octopunctata*, but it had eight radial canals and lacked medusa buds. He named it *Circe hyalina*. Haeckel (1880) thought that he had found the same species at the coast of Normandy. Because *Circe* is a preoccupied name for a mollusc genus, Haeckel referred it to the genus *Lizzella*, a genus he had proposed earlier for *Lizzella octella* Haeckel, 1879. However, Haeckel's (1880) and Van Beneden's (1867) descriptions differ in some important aspects (colour, number of radial canals) that it appears improbable that both had observed the same species. Van Beneden (1867) described and depicts eight radial canals for his *Circe hyalina*. This was contested by Haeckel (1880) who dismissed the radial canals of Van Beneden as longitudinal muscles. This, however, appears unlikely for a bougainvilliid medusa. A quite similar medusa but without oral tentacles has been described from Japan, namely *Octorathkea onoi* Uchida, 1927.

If the description of Van Beneden was accurate, then his species should be recognizable. Because the species has never been found again, despite of it originating in one of the best explored waters the world, it is more likely that Van Beneden had an abnormal *Rathkea octopunctata*, a view already expressed by Russell (1953).

FAMILY **CYTAEIDIDAE** L. AGASSIZ, 1862

TYPE GENUS: *Cytaeis* Eschscholtz, 1829.

DIAGNOSIS: Hydroids forming mostly non-polymorphic colonies, rarely polymorphic, arising from reticulate stolons covered by perisarc. Hydranths without distinct caulus (sessile), with one whorl of filiform tentacles below conical hypostome. Base of hydranths often with a perisarc collar. Gonophores develop from stolons and are liberated as medusa, medusoids, or remain fixed as sporosacs. Medusa with simple, circular mouth, with four or more non-branching oral tentacles near mouth. Gonads develop in interradial position on manubrium or encircle manubrium. With four, rarely eight, solid marginal tentacles without lumen. Ocelli lacking.

REMARKS: Although the original name was Cytaeidae, the correct name formation following the provisions of the ICZN is Cytaeididae (Kramp, 1961). The latter spelling must be used as it is now the prevalent one.

Rees (1962) provides a taxonomic review of the hydroids of this family. Also Calder (1988) gives important taxonomic details. However, the scope of the family remains problematic. See also remarks under the genus *Perarella*.

KEY TO THE GENERA OF THE CYTAEIDIDAE:

1a	gonophores medusae having 4 or 8 marginal tentacles	2
1b	gonophores medusoids or sporosacs	*Perarella*
2a	medusa with eight marginal tentacles	*Paracytaeis*
2b	medusa with four marginal tentacles	*Cytaeis*

Genus ***Cytaeis*** Eschscholtz, 1829

TYPE SPECIES: *Cytaeis tetrastyla* Eschscholtz, 1829 by monotypy.

SYNONYMS (after Calder, 1988): *Cytactis* de Blainville, 1834: 284 [incorrect spelling]. – *Cyteis* Van Beneden, 1867: 18 [incorrect spelling]. – *Cytheis* Van Beneden, 1867: 18 [incorrect spelling]. – *Nigritina* Haeckel, 1879: 73. – *Cytaeidium* Haeckel, 1879: 75 [type species *Cytaeis pusilla* Gegenbaur, 1856]. – *Cytaesis* Bouillon, 1978a: 129 [incorrect spelling].

DIAGNOSIS: Hydroids monomorphic, arising from reticulate stolons covered by perisarc. Hydranths sessile, with one whorl of filiform tentacles below conical hypostome; base of hydranths often with a perisarc collar. Gonophores develop from stolons, liberated as medusa with four tentacles.

Medusa with four or more capitate oral tentacles arising well above mouth margin, medusa budding from manubrium. With four marginal tentacles.

REMARKS: Calder (1988) gives the taxonomic history of this genus. There are several nominal *Cytaeis* species, but their status remains unclear (Kramp, 1961; Rees, 1962; Calder, 1988; Pagès *et al.*, 1992; Schuchert, 1996; Bouillon *et al.*, 2004). Bouillon *et al.* (2004) included in this genus also forms with sporosacs or medusoids. As it is not clear that these forms are really members of the Cytaeididae, I did not follow this. The arguments are discussed under the genus *Perarella*.

Currently there is only one accepted species known in the region of investigation.

Cytaeis tetrastyla Eschscholtz, 1829 Fig. 32

Nigritina atlantica Steenstrup. – Kramp, 1961: 64, name not available.
Cytaeis tetrastyla Eschscholtz, 1829: 104, pl. 8 fig. 2. – Will, 1844: 67. – Haeckel, 1879: 73. – Mayer, 1910: 133. – Hartlaub, 1911: 139, figs 127-129. – Vanhöffen, 1911: 204, fig. 6. – Bigelow, 1918: 367. – Kramp, 1953: 263. – Kramp, 1959a: 99, fig. 62, pl. 1 figs 3-6. – Kramp, 1965: 9. – Kramp, 1961: 63. – Rees, 1962: 382. – Kramp, 1968: 26, fig. 64. – Brinckmann-Voss, 1970: pl. 7 fig. 4. – Goy, 1973: 976. – Bouillon, 1980: 318. – Bleeker & van der Spoel, 1988: 230, fig. 5.– van der Spoel & Bleeker, 1988: 168, fig. 4.– Goy *et al.*, 1991: 106, fig. 13.
? *Bougainvillia mediterranea* Busch, 1851: 21, pl. 2 figs, 10-11. – Haeckel, 1879: 73, synonym.
Cytaeis pusilla Gegenbaur, 1856: 228, pl. 8 fig. 8. – Keferstein & Ehlers, 1861: 84, pl. 13 figs 8-9. – Haeckel, 1879: 75. – Kramp, 1959a: 99, doubtful synonym. – Kramp 1961: 63.
Cytaeis macrogaster Haeckel, 1879. pl. 6 fig. 1. – Kramp, 1955a: 153, synonym.
Cytaeis nigritina Haeckel, 1879: 74, pl. 6 figs 2-5. – Maas, 1904: 8, pl. 1 figs 3-4. – Kramp, 1955a: 154, synonym.
? not *Cytaeis vulgaris* Agassiz & Mayer, 1899: 161, pl. 2 figs 3-5. – Mayer, 1910: 134. – Kramp, 1968: 27, perhaps valid.
Cytaeis herdmani Browne, 1905a: 135, pl. 1 fig. 1, pl. 4 fig. 12. – Mayer, 1910: 135. – Browne, 1916: 177, synonym.
Cytaeis vulgaris. – Bigelow, 1909: 190, pl. 6 fig. 3, pl. 40 figs 2, 5, pl. 43 fig. 4.
Cytaeis atlantica. – Mayer, 1910: 133, figs 71-72 [invalid combination].
? not *Cytaeis pusilla*. – Neppi & Stiasny, 1913: 23.
Cytaeis japonica Uchida, 1927: 215, fig. 39. – Kramp, 1959a: 99, synonym.
[not *Cytaeis japonica*. – Komai, 1931, = *Cytaeis uchidae* Rees, 1962]
? *Cytaeis vulgaris*. – Kramp, 1928: 44, fig. 19.
Cytaeis. spp. – Pages *et al.*, 1992: 5, fig. 4. – Bouillon *et al.*, 2004: 55, fig 33A. – Pages *et al.*, 2006: Fig. 7G (colour photograph).
Cytaeis cf. *tetrastyla*.– Schuchert, 1996: 61, fig. 35a-b.

MATERIAL EXAMINED: BMNH 1970.10.8.55; Brit. Terra Nova Expedition 1910-1913, station H28(59); 0° N 25.25°W, equatorial Atlantic; 16 May 1913; 7 medusae. – MNHN1625; France, Villefranche-sur-Mer; 03 January 1967; material of Goy (1973); 2 medusae, with and without gastric peduncle, immature, 1.4 mm high.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION (after own data and various sources): Fully grown medusa with bell-shaped umbrella, widest near base, jelly not thick, apical jelly sometimes slightly thicker than lateral walls, with or without short peduncle. With four broad radial canals and thin circular canal. With four tentacles of about bell length when contracted, thick, tapering. Epidermis of tentacle bulbs triangular, flat, attached to exumbrella around tentacles (not in juveniles). Manubrium very voluminous, pear-shaped, length up to 4/5 of bell cavity; manubrium with 8-32 (max. 50) simple, capitate tentacles scattered in a band slightly above mouth rim, adnate at origin. Stomach with medusa buds in animals without gonads, irregularly scattered, usually more towards top, some animals with large number of buds spreading over almost entire manubrium. Gonads interradial pads. Colour (Kramp, 1955b, eastern Atlantic): stomach light brown with darker coloured perradial edges, central part of tentacle bulb black, epidermis brown or bright reddish brown. Younger stages likely not coloured.

DIMENSIONS: Medusa usually not larger than 2-4 mm (rarely up to 6 mm high after Kramp, 1961), 3 mm wide. Nematocyst dimensions are given in Bouillon (1980) and Schuchert (1996).

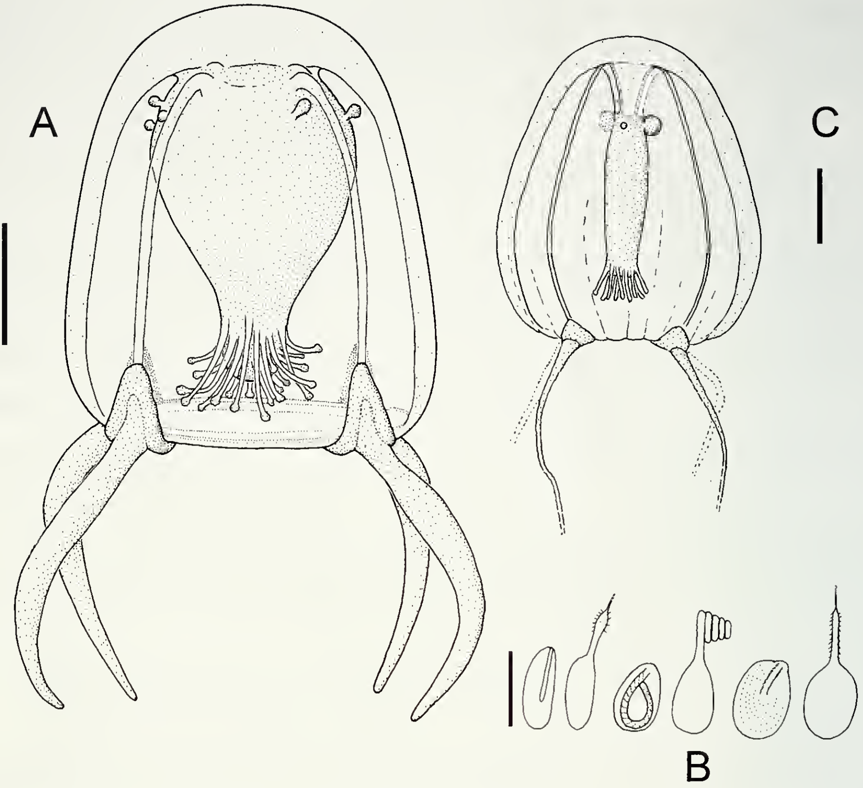


FIG. 32

Cytaeis tetrastyla Eschscholtz, 1829; after preserved material. (A) Fully grown medusa with medusa buds from near the Fiji Islands, modified after Schuchert (1996), scale bar 1 mm. Note that future investigations might show that this Pacific medusa belong to a separate species (B) Cnidome of medusa shown in A, microbasic euryteles, desmonemes, microbasic mastigophores, scale bar 10 μm. (C) Juvenile medusae from the Ligurian Sea (Mediterranean), note the presence of a gastric peduncle, the exumbrella has weak longitudinal furrows, scale bar 0.4 mm.

OTHER DATA: Polyp buds on the manubrium were described by Kramp (1959a).

BIOLOGY: Prefers depths of 0-100 metres depth (Bigelow, 1909). Bleeker & van der Spoel (1988) give a range 0-520 m.

DISTRIBUTION: Occurs circumglobally in tropical to subtropical seas, partly oceanic (Kramp, 1959a; 1965). In the eastern Atlantic it occurs from the Strait of Gibraltar to South Africa (Maas, 1904; Vanhöffen, 1911; Kramp, 1955b; Bleeker & van der Spoel, 1988; Pages *et al.*, 1992). It is also present in the Mediterranean (Will, 1844; Goy, 1973; Brinckmann-Voss, 1970 & 1987; Dallot *et al.*, 1988; Goy *et al.*, 1991; Benovic & Lucic, 1996). Type locality: Atlantic Ocean, south of Equator.

REMARKS: Eschscholtz's (1829) description and figure of *Cytaeis tetrastyla* clearly permit to recognize the medusa as a *Cytaeis* species. His medusa was certainly based on a juvenile medusa of about 1 mm size and with only eight oral tentacles. This caused some problems when later adult forms were described as distinct species. Kramp (1953) gives a good overview on the taxonomic history and situation of this species. He thinks that there is only one valid species, but later (Kramp, 1968) he apparently changed his mind and kept *Cytaeis vulgaris* sensu Agassiz & Mayer, 1899 distinct (not other records assigned to this species). The taxonomy of *Cytaeis tetrastyla* from the Indian- and Pacific Ocean remains unsatisfactory. Experienced students like Vanhöffen, Bigelow, and Kramp, who have seen numerous specimens and from different oceans, tended lump all nominal *Cytaeis* medusa into *C. tetrastyla*. Rees (1962) working with the hydroid phase found several distinct species and suspected that *Cytaeis tetrastyla* sensu Kramp (1961) represents an aggregate of species. This view was also adopted by e. g. Bouillon (1980) and Pagès *et al.* (1992). The latter authors and also Bouillon *et al.* (2004) thought that the *Cytaeis tetrastyla* medusae *sensu* Kramp (1961) should not be given a specific name until the taxonomy has been sorted out properly. We could indeed be faced with a situation as in many *Clytia* and *Obelia*, where the species can only be distinguished in the hydroid phase. However, at least for the eastern Atlantic, no distinct *Cytaeis* polyps are known and there is so far no indication that there are distinct morphotypes of the medusa phase. The mature form as described here has been regularly found in the same region (see under Distribution). *Cytaeis tetrastyla* is partly an oceanic form and it can be expected to have a widespread distribution. We can thus be reasonably sure that for the eastern Atlantic, *Cytaeis tetrastyla* is the correct name.

The situation of the Mediterranean is more difficult to evaluate because only few authors documented the fully grown form as described above (e. g. Goy *et al.*, 1991). The uncertainty mainly relates to the status of *Cytaeis pusilla*. Gegenbaur (1856) described this species based on a juvenile *Cytaeis* he found near Messina (Sicily). It was about 2 mm high and had a gastric peduncle. In his figure he depicted the medusa with a peduncle of about the same length as the manubrium itself, but in the text he qualifies it as short. Haeckel (1879) used the presence of a peduncle to separate this species from all other *Cytaeis*, placing it even in a separate subgenus *Cytaeidium*. Gegenbaur did not discuss why he regarded *C. pusilla* as distinct from *C. tetrastyla*, but from his discussion on the genus one can deduce that he erroneously assumed that *C. tetrastyla* has ocelli, while there are none in his *C. pusilla*. Keferstein & Ehlers (1861) found *C. pusilla* again and described the peduncle as short. Haeckel (1879) had again material from Messina with a long peduncle (umbrella 2-3 mm). Goy (1973, Ligurian Sea, see Fig. 32C) found both forms, with and without a peduncle, in the same catch. I think that not too much weight should be placed on this character as it is likely variable and in later growth the peduncle might be obliterated by the massive growth of the manubrium. I therefore regard *C. pusilla* as a questionable synonym of *C. tetrastyla*. The medusa identified by Neppi & Stiasny (1913) as *C. pusilla*, however, could be a different species. Their single medusa from the Adriatic Sea was very small, measuring only 0.62 mm in height, but nevertheless it had mature gonads.

The polyp stage of *C. tetrastyla* remains unknown. The polyp described by Calder (1988) as *Cytaeis* spec. could belong to *C. tetrastyla*.

More developmental and life-cycle studies of various *Cytaeis* medusae and polyps are evidently needed to clarify the situation. Above all, a neotype of *Cytaeis* *tetrastyla* should be designated, this based on a medusa from the tropical Atlantic and whose 16S and COI gene sequences are known.

Genus ***Perarella*** Stechow, 1922

TYPE SPECIES: *Perigonimus schneideri* Motz-Kossowska, 1905 by monotypy.

DIAGNOSIS: Hydroids with perisarc-covered, reticulate stolons. Hydranths naked, sessile or nearly so, sometimes with a basal collar of perisarc, one whorl of filiform tentacles. Gonophores arise from stolons, developing either into medusoids or fixed sporosacs.

REMARKS: Following the idea of Petersen (1990) that genera should not be delimited based on the degree of gonophore reduction, Bouillon *et al.* (2004) synonymized *Perarella* with *Cytaeis*. This approach is certainly correct in cases where a hydroid can be attributed unambiguously to a certain family, as e. g. in the Corynidae or Tubulariidae. But in the case of the genus *Perarella* this is not so. *Perarella schneideri*, the type species of *Perarella,* could as well belong to the Bougainvilliidae or Pandeidae. Comparing it with some *Rhizorhagium* species (see above), one is even tempted to synonymize *Perarella* with this genus. It is therefore advisable to retain the genus *Perarella* until a reliable molecular phylogenetic analysis has revealed its true affinities.

Perarella schneideri (Motz-Kossowska, 1905) Fig. 33

Perigonimus schneideri Motz-Kossowska, 1905: 72, fig. 6i. – Rees, 1956a: 344.
? *Perigonimus steinachi* Jickeli, 1883: 617, pl. 27 figs 1-9. – Rees, 1962: 393.
Stylactella (*Hydractinia*) *else-oswaldae* Stechow, 1921: 251.
Clavopsis schneideri. – Stechow, 1921: 252.
Stylactella elsae-oswaldae. – Stechow, 1923a: 64, fig. E. – Picard, 1958: 190, synonym.
Perarella schneideri Stechow, 1922: 145. – Rees, 1962: 393. – Bavestrello *et al.*, 2000: 141, figs 1, 4-5.
Cytaeis schneideri. – Bouillon *et al.*, 2004: 55, fig. 32I.

MATERIAL EXAMINED: MHNG INVE49086, Italy, Portofino, coll. June 2006, infertile, on *Schizoporella longirostris* (Hincks) growing on glass bottles, leg. & det. S. Puce, 16S sequence **AM411414**.

DIAGNOSIS: Hydroid growing on bryozoan, two types of hydranths, larger ones with many tentacles and smaller hydranths with few short tentacles; gonophores free medusoids released with mature gonads.

DESCRIPTION (Bavestrello *et al.*, 2000; own data): Hydroid colonies stolonal, growing on the cheilostomate bryozoan *Schizoporella longirostris* (Hincks), stolons reticulate, running along the zooid margins of the bryozoan, often embedded in the skeleton of the host. Hydranths dimorphic with a larger form with long tentacles and a slender form with only 4-5 stubby tentacles; both forms of hydranths without distinctly demarcated pedicel, base in a short perisarc tube that usually widens somewhat towards distal, perisarc thin, not annulated. Larger hydranths club-shaped, high conical hypostome, one whorl of 8-14 long, filiform tentacles. Smaller hydranths thinner, very contractile, hypostome short, one whorl of 4-5 short, stubby tentacles. Gonophores develop on stolons, with distinct pedicel enclosed in perisarc that widens like a funnel, gonophores released as medusoids with fully developed gonads. Free medusoid with

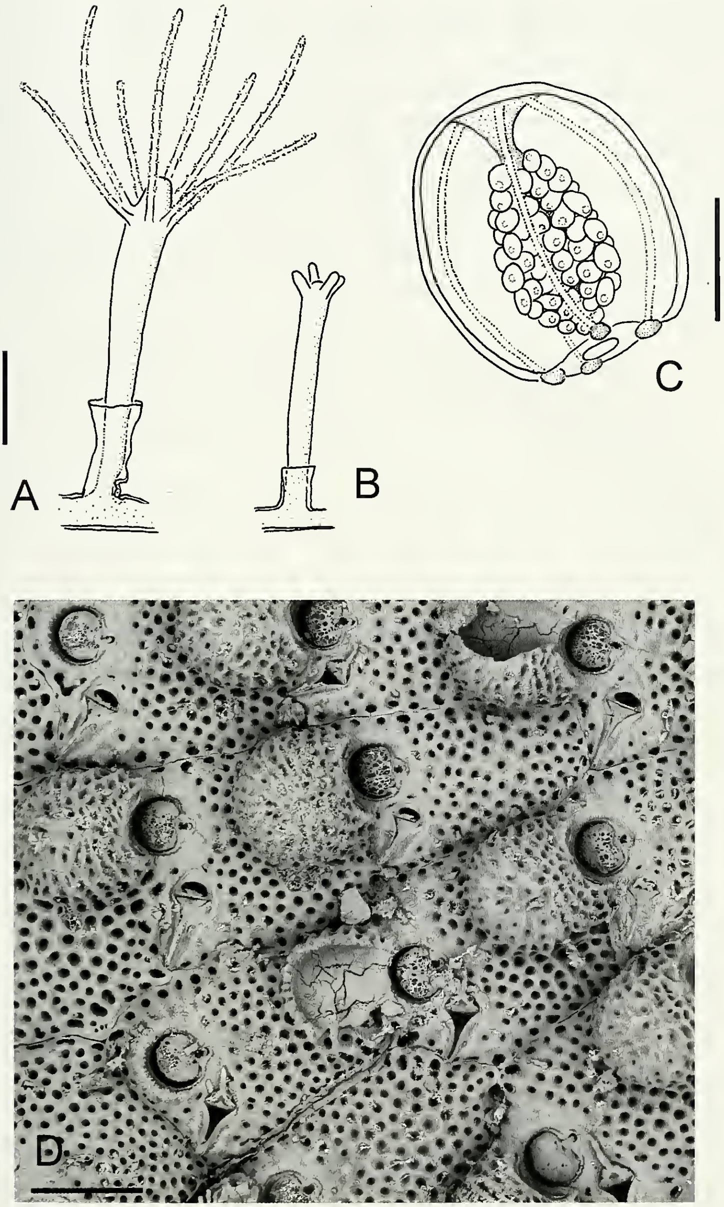


FIG. 33

Perarella schneideri (Motz-Kossowska, 1905). (A) Hydranth form with long tentacles, scale bar 0.2 mm. (B) Hydranth type with few short tentacles, same scale as A. (C) Free female medusoid, scale bar 0.5 mm. (D) Scanning electron microscopic photo of the skeleton of *Schizoporella longirostris*, scale bar 0.3 mm. A-B, after preserved material; C, modified after Bavestrello *et al.* (2000).

bell-shaped umbrella, slightly higher than wide, jelly thin, four radial canals ending in marginal bulbs, ring canal, no tentacles, velum present; manubrium long, non-functional, reaching almost to velum level, encircled by voluminous gonad filling subumbrella cavity, females with 80 or more eggs; only female medusoids swim, males inactive. Nematocysts: microbasic euryteles and desmonemes. Colours (Motz-Kossowska, 1905): hydranths red, male gonophores whitish with red gastrovascular canals.

DIMENSIONS (Bavestrello *et al.*, 2000; Stechow, 1923a; own data): Hydranth with long tentacles about 0.7 mm, pedicel (as delimited by perisarc) about 0.2 mm; gonophores 0.64 mm high and 0.4 mm wide; medusoids 1.1 mm high; egg size 80-100 μm; for nematocyst sizes see Bavestrello *et al.* (2000).

BIOLOGY: The biology of this species is described by Bavestrello *et al.* (2000). The colonies can be found from 1 to more than 100 m depth (Motz-Kossowska, 1905), always on *Schizoporella longirostris* growing on hard substrata like rock or the bivalve *Pinna nobilis*. The hydroid is most easily collected by examining discarded glass bottles lying on sandy bottoms. Female medusoids can swim from five days before spawning. Male medusoids remain inactive. The two types of hydranths show two different trophic strategies. The larger ones feed preferably on meiobenthic organisms like nematodes and polychaetes, but also the larvae of the bryozoan host. The slender hydranths with few short tentacles in turn engulf the tentacles of the bryozoan host and feed on its collected small food particles. The tentacles of the bryozoan seem not to be harmed, though.

Perarella schneideri hydroids show a marked seasonality, being present from September through June with a maximum in February. No hydroids can be found during summer. The period of medusoid production is between the second half of May to the end of June.

DISTRIBUTION: Endemic to the Mediterranean. Type locality: Motz-Kossowska (1905) did not explicitly specify a type locality, but the only locality mentioned is Pollensa (island of Mallorca).

REMARKS: The hydranth size of 15 mm given in the original description is likely a misprint for 1.5 mm as it does not match the size of the hydranth shown in figure.

Picard (1958) listed *Stylactella else-oswaldae* Stechow, 1921 as a synonym of *P. schneideri* and I concur. In his description, Stechow (1923a) did not mention the substrate his colony was growing on. The type specimen of *Stylactella else-oswaldae* is kept by the ZSM and Dr. Ruthensteiner told me that the hydroid is indeed growing on an encrusting bryozoan which adheres to a piece of stone. *Perigonimus steinachi* Jickeli, 1883 was described as growing on a bryozoan, but Jickli's description is inadequate and the species remains indeterminate.

The hydranths of *Perarella schneideri* have no clearly demarcated hydrocaulus, but the basal part in a perisarc tube (Fig. 33A) must be homologized to a hydrocaulus.

Perarella propagulata Bavestrello, 1987 Fig. 34

Perarella propagulata Bavestrello, 1987: 19, figs 5.1-5.4.
Cytaeis propagulata. – Bouillon *et al.*, 2004: 55, fig. 32F-H.

MATERIAL EXAMINED: Holotype, Museum of natural History of Genoa, C. E. 47716-a; Italy, Bay of Paraggi; 21 April 1983, depth 10 m, female; soft tissues quite macerated.

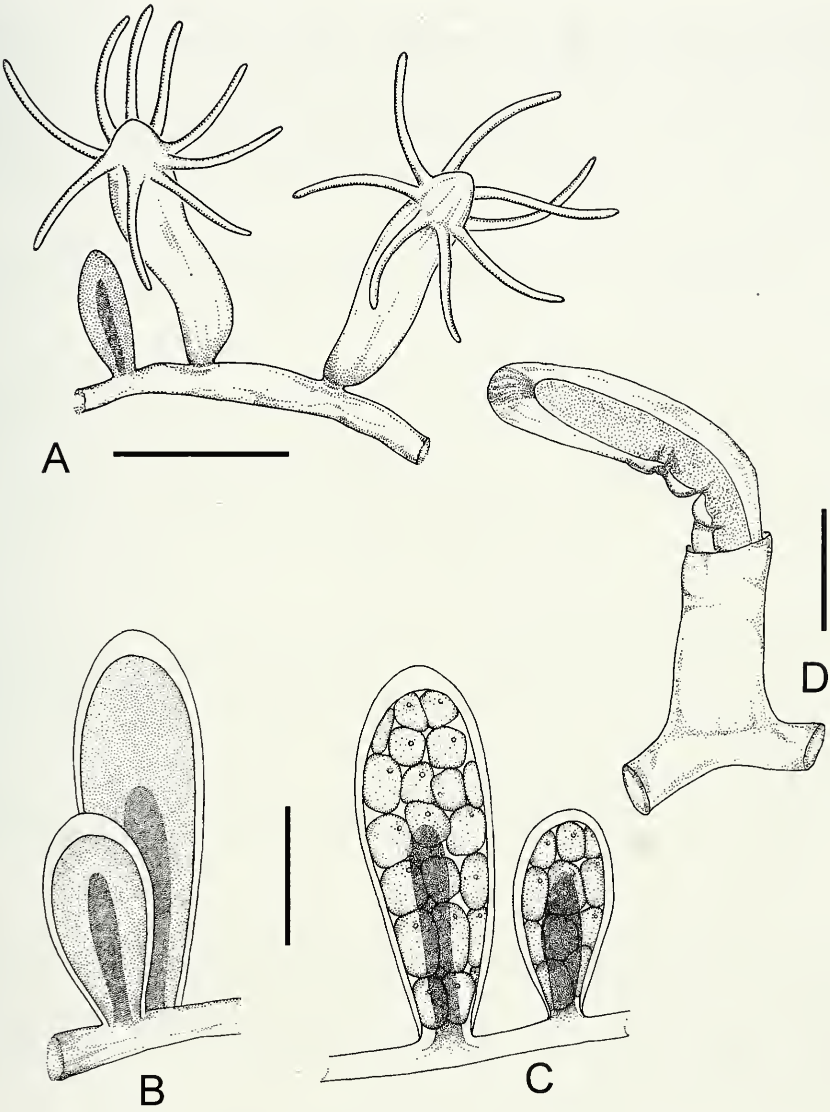


FIG. 34

Perarella propagulata Bavestrello, 1987; modified from Bavestrello (1987). (A) Two hydranths and a male sporosac, scale bar 0.5 mm. (B) Male sporosacs, scale bar 0.1 mm. (C) Female sporosacs, same scale as B. (D) Propagule issuing from stolon, scale bar 0.1 mm.

DIAGNOSIS: *Perarella* with sessile hydranths lacking basal perisarc collar; sporosacs rather elongate, spindle shaped, no radial canals; propagule formation from stolons.

DESCRIPTION (Bavestrello, 1987): Hydroid living on *Hinia incrassata* shells, colonies stolonal, creeping reticulate stolons forming hydrorhiza, stolons in thin membranous perisarc. Hydranths monomorphic, without pedicels (sessile), without basal perisarc collar, spindle shaped, hypostome conical, 7-15 filiform tentacles in one whorl. Gonophores on stolons, without pedicels; sporosacs without radial canals, bulbs, and velar opening, very elongate, spadix spanning about two-thirds of the total height, spadix disappears after liberation of gametes; colonies gonochoristic, female sporosacs with 15-25 eggs. Some colonies produce propagules from stolons, tubes of naked coenosarc, surrounded at base by perisarc tube. Nematocysts: microbasic euryteles and desmonemes.

Dimensions: Hydranths approximately 0.6 mm high; sporosacs up to 0.3 mm high and 0.1 mm wide; propagules 0.3-0.5 mm; microbasic euryteles 6 x 3 μm, desmonemes 4.5 x 3 μm.

Biology (Bavestrello, 1987): This species grows on shells of *Hinia incrassata* (Müller), either inhabited by the gastropod or by hermit crabs. Only a small fraction (1-2%) of the investigated shells had the hydroid. It occurs in depths of 5-10 m. Hydranths are present from April to May. Colonies kept in the laboratory released numerous propagules which can spread the hydroid to other suitable substrates.

Distribution: Only known from the region near the type locality. Type locality: Paraggi Bay, Liguria, Italy, Mediterranean, 10 m.

Genus ***Paracytaeis*** Bouillon, 1978

Type species: *Paracytaeis octona* Bouillon, 1878, by monotypy.

Diagnosis: Cytaeididae with eight marginal tentacles; with four opaque interradial exumbrellar spots.

Paracytaeis octona Bouillon, 1978

Paracytaeis octona Bouillon, 1878: 149, fig. 8. – Bouillon, 1980: 319, fig. 6. – Bouillon *et al.*, 1988: 95, pl. 1 figs 1-2. – Goy *et al.*, 1991: 106, fig. 14. – Bouillon *et al.*, 2004. 56, fig. 33B.

Diagnosis: See genus diagnosis.

Description: Umbrella bell shaped, with four opaque interradial exumbrellar spots of vacuolated cells; velum narrow; eight marginal tentacles, with large tentacular bulbs, adaxial epidermal nematocyst pad clasping bulb. Manubrium conical, half as long as umbrellar height, mouth circular with up to 20 oral adnate capitate tentacles; with medusa buds in four interradial clusters in upper part of manubrium. Gonads interradial, covering manubrium almost entirely.

Dimensions: Umbrella up to 2.5 wide and 3 mm high.

Distribution: Seychelles, Papua New Guinea, Mediterranean. Type locality: Ternay Bay, Mahe Island, Seychelles, Indian Ocean.

Remarks: This species has not yet been recorded in European waters. The Mediterranean records are based on medusae found in the eastern Mediterranean near Lebanon by Goy *et al.* (1991). The hydroid of this species is unknown.

FAMILY **RATHKEIDAE** RUSSELL, 1953 emended

Type genus: *Rathkea* Brandt, 1835.
Synonym: Lizzinae Russell, 1953. **new synonym**

Diagnosis: Medusa bell-shaped, manubrium either with four elongated lips forming simple or branched oral arms with terminal knobs, or perradial unbranched oral tentacles inserted vertically or very oblique at level of mouth margin; immature animals with or without orthogonally arranged interradial medusa buds. With four or eight radial canals and a circular canal. Usually eight bulbs, interradial ones with more than one tentacle, rarely only four bulbs and four tentacles. Ocelli absent. Gonads encircle manubrium completely

Hydroids (where known) colonial, arising from ramified stolons. Hydranths monomorphic, without pedicel, with one whorl of filiform tentacles. Medusa buds arise from stolons, or more rarely from base of hydranths.

Remarks: In contradistinction to most taxonomic systems in current use, *Lizzia blondina* Forbes, 1848 is here thought to be more closely related to the Rathkeidae Russell, 1953 than the Bougainvilliidae. This decision is primarily based on the 16S phylogeny given in Fig. 39, but there is also a potential synapomorphy shared by *Lizzia blondina* and *Rathkea octopunctata* (M. Sars, 1835): the highly ordered, orthogonally arranged medusae budding from the interradial manubrium wall (Chun, 1896; Berrill, 1952; Werner, 1956). Furthermore, both species resemble each other so closely (symmetry, size, form, manubrial peduncle) that they are easily confounded, although these traits are difficult to see as synapomorphies. Despite the polyp of *Lizzia* remains unknown, the genus was usually included in the Bougainvilliidae (Russell, 1953) due to the presence of perradial oral tentacles. This view was thereafter adopted in virtually all important subsequent works (e. g. Kramp, 1961; Bouillon, 1985; Bouillon & Boero, 2000b), although Mayer (1910) regarded *Lizzia* and *Rathkea* as synonyms (which is correct in the formal sense, see below). It was generally asserted that the oral tentacles of *Lizzia* originate above the mouth like in *Bougainvillia*, which is not true. A closer examination shows that the position and attachment of oral tentacles of *Lizzia blondina* are slightly different from those found in the Bougainvilliidae. They become free at the level of the lips and not at some distance above the rim. They are also attached very obliquely and remain adnate to the manubrium for quite some distance, being continued as ridges along the manubrium accompanied by underlying vacuolated gastrodermal cells (Fig. 36D). The same situation is also found in *Rathkea* species (Fig. 35E). The same arguments also apply to *Hydractinia minuta* (Mayer, 1900) and *H. minima* (Trinci, 1903), which will be removed from the Hydractiniidae. *Hydractinia minuta* is regarded as a conspecific with *Lizzia blondina* and the new genus *Podocorynoides* is proposed to accommodate *Cytaeis minima* Trinci, 1903. The diagnosis was therefore adapted to fit the new scope of the family.

Key to the genera:

1a four radial canals 2
1b eight radial canals . . . . *Allorathkea**
2a obliquely or vertically inserted oral tentacles with a distinct, round pedicel 3
2b oral arms are elongated corners of the mouth . . . . *Rathkea*
3a eight marginal bulbs, perradial ones sometimes with more than one tentacle . . . . *Lizzia*
3b four bulbs, each with one tentacle only . . . . *Podocorynoides*

* not present in area under investigation

Genus ***Rathkea*** Brandt, 1838

TYPE SPECIES: *Oceania blumenbachii* Rathke, 1835.

SYNONYMS: *Margellium* Haeckel, 1879. – Currently also *Lizzia* Forbes, 1846 [type species *Cytaeis octopunctata* M. Sars, 1835, by monotypy and original designation].

DIAGNOSIS: Rathkeidae medusa with four radial canals; eight marginal tentacle bulbs, all with two or more tentacles; the four perradial corners of the mouth drawn out so as to form oral arms with clusters of nematocysts. Hydroid colonial, small, sessile, with long filiform tentacles, medusa buds arise from stolons.

REMARKS: There is only one species of *Rathkea* medusa known in the region under investigation, but a second *Rathkea*-like polyp occurs. O'Sullivan (1984) gives an overview on all known species.

Rathkea octopunctata (M. Sars, 1835) Fig. 35

Cytaeis octopunctata M. Sars, 1835: 28, pl. 6 figs 14a-g.
Oceania Blumenbachii Rathke, 1835: 21, pl. 1 figs 1-4.
Lizzia octopunctata. – Forbes, 1848: 64, pl. 12 fig. 6.
Lizzia grata A. Agassiz, 1862: 100, figs 28-29.
Rathkia Blumenbachii. – L. Agassiz, 1862: 345 [incorrect spelling].
? *Circe hyalina* Van Beneden, 1867: 95, pl. 3 fig 14.
Margellium octopunctatum Haeckel, 1879: 95.
Margellium gratum. – Haeckel, 1879: 95.
Lizzia shimiko Kishinouye, 1910: 25, pl. 5.
Rathkea Blumenbachii. – Brandt, 1838: 353. – Neppi & Stiasny, 1913: 34, pl. 2, figs 23. – Hartlaub, 1911: 229, figs 196-199. – Hartlaub, 1917: 408.
Rathkea octopunctata. – Haeckel, 1879: 97. – Mayer, 1910: 177, pl. 20 fig. 11. – Kramp, 1926: 58, chart X. – Rees & Russell, 1937: 71, figs 7-8. – Russell, 1938b: 153, figs 26-32. – Russell, 1953: 137, pl. 7 figs 3-4, text figs 65A-E, 66, 67A-B. – Werner, 1958: 138, figs 1-13. – Kramp, 1959a: 103, fig. 75. – Kramp, 1961: 72. – Kühl, 1962: 218, figs 7-9. – Kramp, 1968: 30, fig. 74. – Naumov, 1969: 212, figs 80-81. – Russell, 1970: 236. – Goy, 1973: 979. – Arai & Brinckmann-Voss, 1980: 33, fig. 16. – O'Sullivan, 1984: 868, tab. 2. – Schuchert, 1996: 59, fig. 34a-c. – Bouillon *et al*., 2004: 77, fig. 44D-H.

MATERIAL EXAMINED: BMNH 1985.9.2.15; Great Britain, Plymouth; May 1937, coll. W.J. Rees; ca. 50 medusae. – France, Brittany, Roscoff; April 1998; few living medusae from plankton; not preserved; 16S sequence accession number **AM183140**. – Roscoff; few living medusae, not preserved; 10-20 m; 5 June 2000. – Norway, Raunefjord, living medusae, not preserved; 0-3 m; 14 June 2006; 5 medusae; 16S sequence **AM411415.** – MHNG INVE 33454; New Zealand, Hauraki Gulf, Devonport, Narrow Neck Beach 0-1 m; 2-3 July 2002; several medusae, examined alive; 16S sequence **AM411416**.

DIAGNOSIS: Four radial canals; eight marginal tentacular bulbs, four perradial bulbs each with 3-5 tentacles, four interradial bulbs with 2-3 tentacles; black pigment in manubrium and bulbs; oral tentacles bifid, terminal and lateral nematocyst clusters.

DESCRIPTION (Werner, 1958; own observations): Hydroids arising from creeping, reticulate stolons, stolons enclosed in thin perisarc. Hydranths small, uniform, without pedicel, cylindrical to spindle-shaped, base with thin gelatinous perisarc, one whorl of 4-6 tentacles, hypostome conical. Tentacles very thin and long. Medusa buds arise from stolons or rarely from base of hydranth, pear shaped, larger than hydranths, advanced stages with relatively long pedicel. Nematocysts: microbasic euryteles, desmonemes.

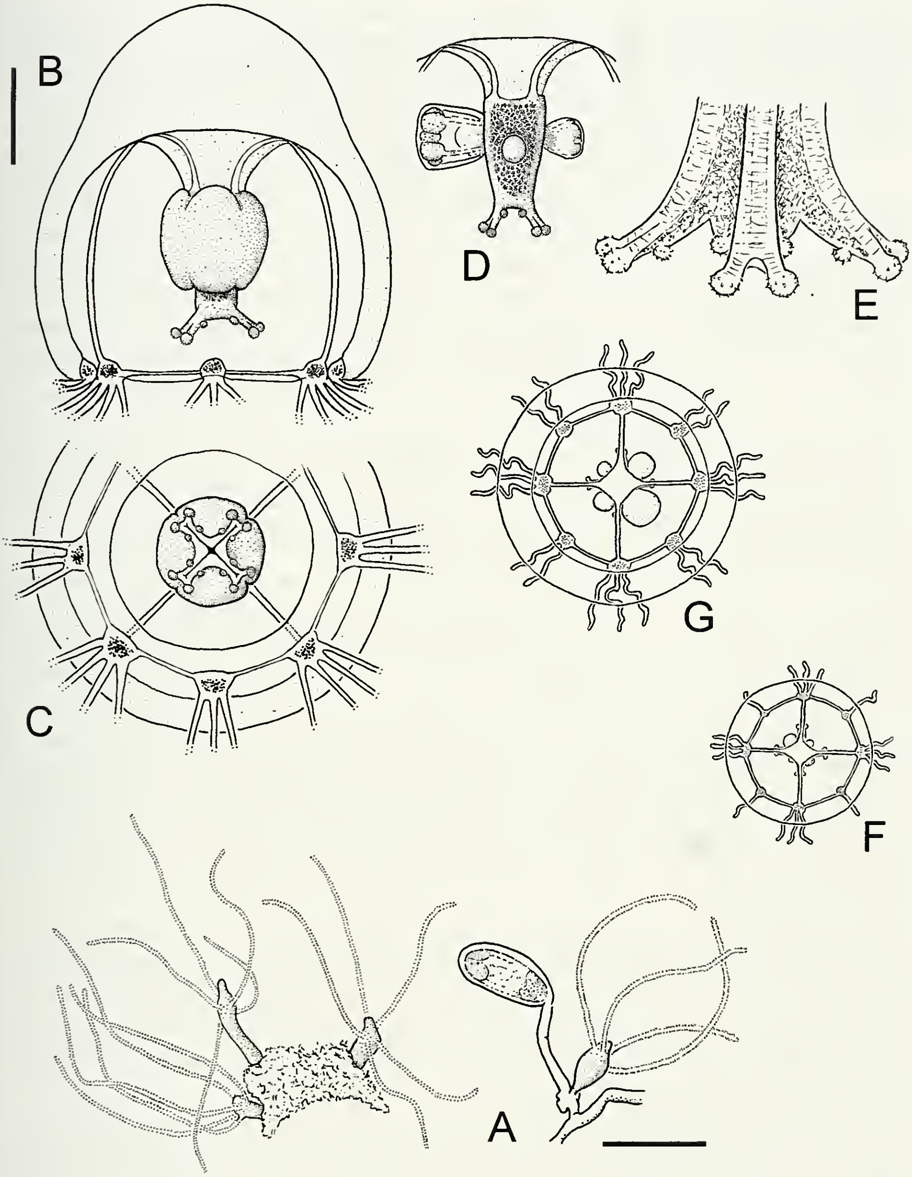


FIG. 35

Rathkea octopunctata (M. Sars, 1835). (A) Hydroid colonies, right one with stolonal medusa bud; scale bar 0.5 mm; redrawn from Kühl (1962). (B) Lateral view of sexually mature medusa, scale bar 0.4 mm, combined after living and preserved animals. (C) Oral view of animal depicted in B. (D) Manubrium with medusa buds of a medusa of the same size as shown in B. (E) Enlarged mouth region in perradial view, from Russell (1953). (F-G) Aboral view of younger stages with fewer tentacles than shown in B, from Russell (1953).

Primary medusae (newly liberated medusae originating from polyp stage) similar to adults, eight bulbs, three tentacles per perradial bulb, 1-2 tentacles per interradial bulb, manubrium with up to 4 medusa buds, oral lips not branched, terminal capitula not much developed. The primary medusae have a more elongate bell than the secondary medusae budded from the manubrium of a medusa.

Mature medusa with globular bell, slightly higher than wide or as wide as high; jelly relatively thick, thickened at apex (up to 1/3 of total umbrella height); with gastric peduncle of variable length, shorter than manubrium length; dilated velum spanning 1/2 of radius. Four radial canals and ring canal narrow. Eight marginal tentacular bulbs with long filiform tentacles, four perradial bulbs, each with three to five tentacles, four interradial bulbs, each with two to three tentacles; bulbs with dark pigment in gastrodermis but no ocelli. Manubrium cylindrical, not reaching beyond umbrella margin in full extension; gastrodermis with dark pigment. Mouth with four lips, each divided at its extremity into two short arms, both ends with a spherical nematocyst cluster, in fully developed animals also a pair of lateral nematocyst knobs on common trunk of oral arms; bases of oral arms continued along manubrium for some distance as perradial ridges with vacuolated gastrodermal cells. Perradial medusa buds, appearing in regular opposite succession, up to 16 buds per manubrium, usually fewer; budding stops with the onset of gonad maturation. Gonads completely surrounding stomach, some indication of perradial separation. Colour of marginal tentacular bulbs pale yellowish, dark yellowish brown or deep brown, appearing black by transmitted light. Colour of stomach brownish or black, persists even when fed on carotenoid rich *Artemia* nauplii. Nematocysts: euryteles and desmonemes.

DIMENSIONS: Hydranth size 0.15-0.5 mm, tentacle length up to 3 mm (Rees & Russell, 1937; Werner, 1958; Kühl, 1962). Newly liberated medusa 0.9 mm (Kühl, 1962). Sexually mature medusa usually 2-3 mm high and about as wide, height of up 4 mm have been reported. Eggs 0.14 mm in diameter, planulae 0.2-0.24 mm long and 80-90 μm wide (Rees & Russell, 1937). For nematocyst sizes see Russell (1938b) and Schuchert (1996).

ADDITIONAL DATA: The medusa budding process on the manubrium has been investigated by several authors (e. g. Chun, 1896; Berrill, 1952; Bouillon, 1962). The buds are derived from epidermal cells only. They develop in an ordered succession. The medusa buds of the hydroid stage derive as in other species from both epidermal and gastrodermal cells (Bouillon & Werner, 1965). The sexes are usually separate but hermaphroditic medusae are known to occur (Kulikova, 1957).

DISTRIBUTION: North-western Europe from Norway to Strait of Gibraltar; Mediterranean; Black Sea; Barents Sea and White Sea; Iceland; Greenland; Hudson Strait; Newfoundland; New England; Bermuda; Aleutian Islands; Kamchatka; northern Japan; British Columbia; Victoria, Australia; New Zealand (Kramp, 1959a; Arai & Brinckmann-Voss 1980; O'Sullivan 1984; Schuchert, 1996). Kramp (1926) reviews all European records. Type locality: Bergen, Norway.

BIOLOGY: Due to its small size, the polyp has only rarely been found in nature (Kühl, 1962; Teissier, 1965; Karlsen, 1980; ? Watson, 1998). Kühl (1962) found it in shallow pools on *Mytilus* shells and stones; Teissier (1965) reports oyster shells as substrate.

The medusa occurs in coastal waters, sometimes also in lagoons and brackish waters (Kühl, 1962; Barnes, 1994). It may also survive in polluted waters (Beyer, 1968) and can occur in long lasting mass aggregations (Zelickman *et al.,* 1969).

Being quite a common medusa, there exist a number of investigations on its seasonality (Kramp, 1926; Russell, 1953; Werner, 1958, 1962; Kühl, 1962; Rasmussen, 1973; Ballard & Myers, 2000).

In the North Sea and most of the adjacent areas, the occurrence of the medusa is limited to the cold seasons of the year. It appears during the months of October to December, and is always to be found in small numbers in the winter plankton. In the spring, from April to May, there is a great increase in numbers, then within a brief time the medusa disappears almost entirely. In the Mediterranean and the Black Sea, the medusa was described as occurring during the spring, whereas it is a distinct summer form in the Arctic boreal area.

The medusa has the ability to reproduce asexually by budding medusae. Two different generations of medusae are therefore to be recognized, i.e. a) the primary medusae originating from medusa buds of the hydroid, b) the secondary medusae produced by the budding process on the manubrium of the primary medusa. The secondary medusae are also able to reproduce asexually in the same way and give rise to more generations. It is because of the asexual reproduction of the medusae that there is a rapid increase medusa numbers during the spring.

Werner (1956, 1958, 1962) made detailed experiments to demonstrate how the temperature influences the budding of medusae from the polyp and medusa stage. The life cycle of *R. octopunctata* is determined by seasonal temperature changes. Rapidly falling temperatures in autumn induce the polyps to develop medusae which then appear in the winter plankton. The young medusae multiply by budding more medusae until rising water temperatures in spring induce the development of gonads and later sexual reproduction. The medusae then disappear from the plankton by late summer (North Sea).

Rathkea octopunctata is a nonselective polyphage which has been observed feeding on a number of animals including *Clytia, Pleurobrachia,* rotifers, Cladocora, copepods, nauplii, trochophores, crab zoeae and eggs, *Sagitta,* appendicularians, fish larvae (for references see Arai & Brinckmann-Voss, 1980).

As an abundant species it is an influential consumer of other planktonic organisms (Zelickman *et al.*, 1969; Matsakis & Conover, 1991).

REMARKS: The synonym and taxonomic history of this species is outlined in Kramp (1926) and Russell (1953). Kramp (1926) also provided arguments why the name *R. octopunctata* M. Sars, 1835 is to be preferred over *R. blumenbachii* (Rathke, 1835).

The three available 16S sequences of *R. octopunctata* did not form a monophyletic group, the sequence from New Zealand being quite distant (Fig. 39). The animals from New Zealand differ also slightly in their morphology: the oral tentacles are about two times as long and they have a distinct, round trunk inserted at the mouth rim. The oral tentacles are paired and they resemble more those of *Lizzia octostyla* than those of *Rathkea octopunctata* from the Atlantic. It is possible that the New Zealand *Rathkea* medusae belong to a separate species.

Rathkea spec.

MATERIAL EXAMINED: Living hydroids observed in June 1998, September 2004, and September 2006; originating from Île de Callot, Baie de Morlaix, France, English Channel; always embedded in *Haliclona simulans* (Johnston).

DIAGNOSIS: Hydroid 0.1-0.2 mm high, *Rathkea*-like but tentacles shorter, predominantly four tentacles, polyp embedded in surface of the sponge *Haliclona simulans* (Johnston), colonial, stolons without perisarc. Nematocysts: heteronemes, 6 x 2.5 μm; desmonemes 4 x 2.5 μm.

REMARKS: This hydroid occurs regularly in the sponge *Haliclona simulans* colonized by the hydroids *Dipurena simulans* Bouillon, 1965 and *D. halterata* (Forbes, 1846). There are usually hundreds of hydranths per sponge. They are extraordinary small and possess four tentacles only. The hydroid lives immediately below the sponge surface and only the short tentacles protrude beyond the surface. It can withdraw completely into the host tissue and apparently it is able to retract its tentacles completely into the hydranth body. The polyps are very difficult to observe and I only became aware of them when I tried to feed small *Artemia* nauplii to the *Dipurena* hydroids and the nauplii were efficiently captured by the almost invisible hydroid. The *Artemia* diet rendered the hydroids orange and better observable. Gonophores could not be found (June, and September). The shorter tentacles and the host species make it unlikely that this is *Rathkea octopunctata*. It could potentially belong to *Lizzia blondina*, a common medusa in the southern English Channel.

Genus ***Lizzia*** Forbes, 1846

TYPE SPECIES: Currently *Cytaeis octopunctata* Sars, 1835, see below.

DIAGNOSIS: Medusae with four or eight simple, unbranched perradial oral tentacles inserting at level of mouth rim; with manubrial peduncle; eight or exceptionally 16 tentacle bulbs, each with one or more simple tentacles, usually with more tentacles on the perradial than the interradial bulbs; interradial medusa buds develop on manubrium; gonads enveloping manubrium.

REMARKS: When Forbes (1846: 286) defined the genus *Lizzia* he stated «..founded for *Cytaeis octopunctata* of Sars...». This type species designation was iterated in Forbes (1848) when he added *Lizzia blondina* Forbes, 1848 to this genus. The type species of *Lizzia* is thus *Rathkea octopunctata* (M. Sars, 1835) by original designation as well as by monotypy. This leads to the awkward situation that *Lizzia* Forbes, 1846 is actually a junior synonym of *Rathkea* Brandt, 1838. As the genus *Lizzia* is well known and it has been used consistently for the rather common species *Lizzia blondina* Forbes, 1848, it is in the interest of nomenclatural stability to maintain this usage. After the publication of this study, a case to the International Commission on Zoological Nomenclature will be made asking them to use their plenary power to overrule Forbes's type species designation and select *Lizzia blondina* instead.

The polyps are not known.

KEY TO THE *LIZZIA* SPECIES RECORDED FOR EUROPE:

1a	four solitary oral tentacles	2
1b	eight oral tentacles in four perradial pairs	*Lizzia octostyla*
2a	without ocelli, interradial bulbs normally with one tentacle only	*Lizzia blondina*
2b	with adaxial ocelli, interradial bulbs with two tentacles	*Lizzia elisabethae*

Lizzia blondina Forbes, 1848 Figs 36-38

Lizzia blondina Forbes, 1848: 67, pl. 12 fig. 4a-f. – Browne, 1895: 265. – Hartlaub, 1911: 145, figs 131-135. – Kramp & Damas, 1925: 266, figs 13-14. – Kramp, 1926: 52, chart IX. – Russell, 1938b: 153, figs 33-36. – Russell, 1953: 145, figs 69-71, not 72, pl. 7 figs 1-2, pl. 34 figs 5-6. – Kramp, 1959a: 105, fig. 78. – Kramp, 1961: 87. – Brinckmann-Voss, 1970: plate 8 fig. 2. – Goy, 1973: 980. – Bouillon *et al.*, 2004: 47, fig. 28A-D.
Lizzia spec. Claparède, 1860: 401, pl. 32, fig 1-2.
? *Dysmorphosa fulgurans* A. Agassiz, 1865: 163, figs 259-260.
Cubaster gemmascens Haeckel, 1879: 76, pl. 6 figs 8-12. – Kramp & Damas, 1925: 266, synonym.
Dysmorphosa minima Haeckel, 1879: 78, pl. 6 fig. 7. – Browne, 1895: 261. – Browne, 1897: 148. – Hartlaub, 1911: 145, synonym.
[not *Cytaeis minima* Trinci, 1903 = *Podocorynoides minima* (Trinci, 1903)]
Lizzia claparèdei Haeckel, 1879: 82.– Hartlaub, 1911: 145, synonym.
? *Lizzia minuta* McIntosh, 1893: 344.
Lizzia claparèdei. – Chun, 1896: 36, figs 2-4. – Braem, 1908: 795, figs 4-5
Dysmorphosa minuta Mayer, 1900b: 41, pl. 18 fig. 42. **new synonym**
[not *Hydractinia minuta* Bonnevie, 1898a = *H. carica* Bergh, 1887]
Podocoryne minuta. – Mayer, 1910: 140, pl. 14 fig. 1. – Kramp, 1959a: 102, fig. 68. – Kramp, 1961: 69. – Goy, 1973: 978. – Goy *et al.*, 1991: 107, fig. 18.
In part *Podocoryne minuta*. – Neppi & Stiasny, 1913: 24, pl. 2 fig. 13a-b.
Lizzia fulgurans. – Brinckmann-Voss, 1970: plate 8 fig. 1.
Podocoryna minuta. – Schuchert, 1996: 50, fig. 28a-b.
Hydractinia minuta. – Bouillon *et al.*, 2004: 66, fig. 39F-G.

Material examined: BMNH 1985.9.11.10; Ireland, Valentia Harbour; 05 August 1938; few medusae. – BMNH 1985.9.12.16; Great Britain, Plymouth; 7 June 1937; >200 mature medusae, 1-3 perradial tentacles. – Atlantic, France, Roscoff, 20 September 2006, 5 medusae, depth 5-15 m, with 2 tentacles per perradial bulb (stumps when collected), 16 S sequence made of 2 medusae gave identical sequence **AM411423**; some cultivated for 3 weeks, secondary medusae mostly with eight tentacles only. – MHNG INVE48742, Norway, Ranefjord, 0-3 m, 16.06.2006, about 10 fully grown medusae, examined alive, all with 8 tentacles only, cultivated for two weeks to sexual maturity, not further tentacles developed, colour changed to orange when fed with *Artemia* nauplii; 16S sequence **AM411417**. – Mediterranean, France, Villefranche-sur-Mer, 7 April 2005, 6 medusae, initially identified as *Hydractinia minuta*, all specimens used to extract DNA, direct sequencing of amplified the 16S gene showed it to be polymorphic, the fragments were therefore cloned using standart techniques and then sequenced again, **AM183124** and **AM411419**. – ROMIZ B775, as *Lizzia fulgurans;* Italy, Naples, 28 June 1961, collected by A. Brinckmann-Voss (mentioned or depicted in Brinckmann-Voss, 1970; 1987); about 20 medusae. – USNM 58065; as *Hydractinia minuta*; Belize, Carrie Cay lagoon; coll. 1977; 7 medusae; det. R. J. Larson. – USNM 58063; as *Hydractinia minuta*; Belize, Carrie Cay Lagoon; 16 May 1977; 7 medusae; det. R. J. Larson. – USNM 58064; as *Hydractinia minuta*; Belize, Carrie Cay Lagoon; 23 May 1976; 7 medusae; det. R. J. Larson. – New Zealand, Wellington Harbour, Seatoun; several medusae, examined alive, from surface plankton collected 11-12 July 2002, all with 8 tentacles only, therefore identified initially as *Hydractinia minuta*, 16S sequence determined from several animals **AM411418**.

Diagnosis: *Lizzia* with four oral tentacles, each perradial bulb with 1-3 tentacles, four interradial bulbs each with a single tentacle only, rarely two; medusa buds on manubrium, with manubrial peduncle; no ocelli.

Description: Umbrella spherical, sometimes a little higher than wide, usually with a shallow, rounded apical process; jelly moderately thick, especially in apical region; gastric peduncle present, slim, usually shorter than manubrium. Four radial canals and ring canal narrow, radial canals along manubrial peduncle with enlarged gastrodermal cells. Eight marginal bulbs, without ocelli, adaxial side with nematocyst

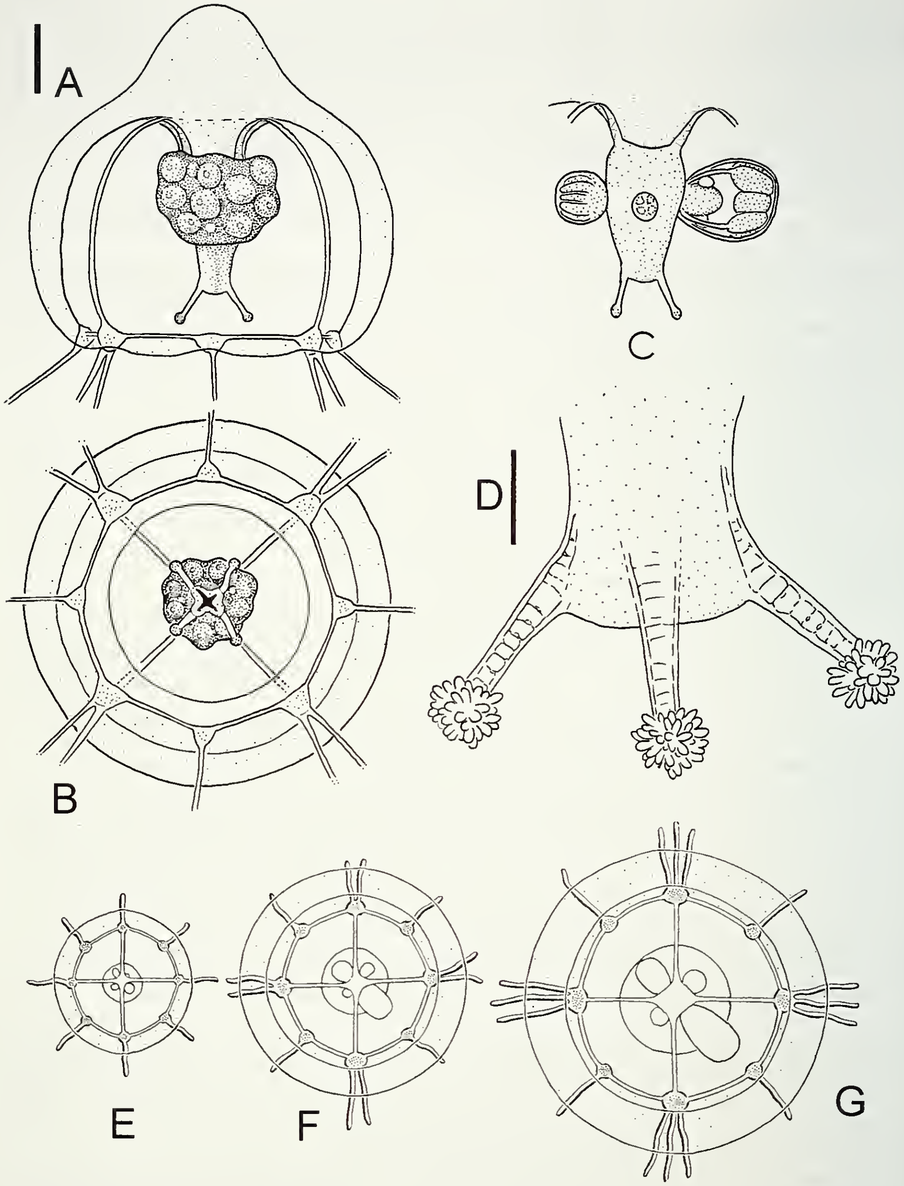


FIG. 36

Lizzia blondina (Forbes, 1848). A) Diagrammatic reconstruction of sexually mature female medusa in side view, scale bar 0.2 mm. (B) Oral view of medusa shown in A. (C) Manubrium of medusa before gonad maturation and with medusa buds. (D) Oral region in side view, note the origin of the oral tentacles very close to the margin of the manubrium, scale bar 50 μm. (E-G) Growth stages in aboral view. A-D, after preserved material; E-G, modified from Russell (1953).

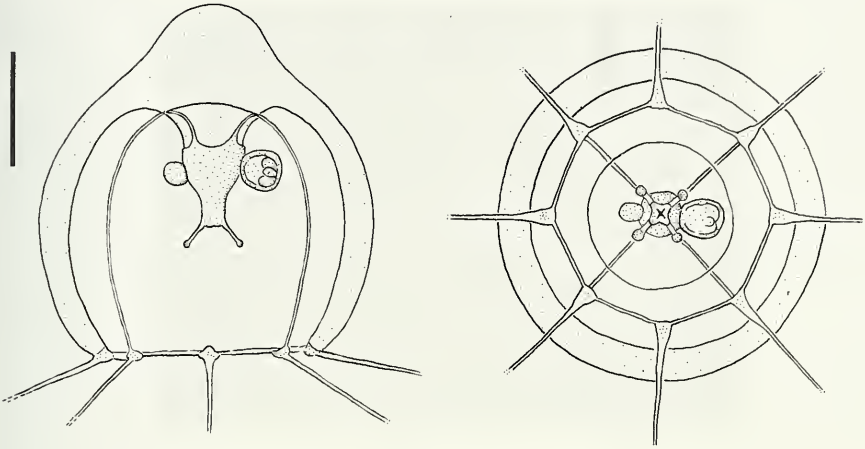


FIG. 37

Lizzia blondina (Forbes, 1848), after living material from Norway, lateral and oral view, scale bar 0.4 mm. Note that this form with one tentacle per bulb has previously often been named *Hydractina/Podocoryne minuta* or *Lizzia fulgurans*.

cushion, four perradial ones each with one to three tentacles, four interradial bulbs with a single tentacle, rarely two. Manubrium short, not reaching beyond umbrella margin in full extension, cone-shaped, either with broad quadrangular base attached to peduncle or perradial corners somewhat extending along peduncle, gastrodermis thickened interradially; medusae budding from stomach wall in interradial position, medusa budding phase overlaps with gonad maturation phase; four unbranched oral tentacles, attached very obliquely and adnate for some distance, lower axils at level of mouth-margin, oral tentacles relatively long but contractile, each with one terminal nematocyst cluster. Gonads completely surrounding stomach in a form of ring-shaped cushion. Colour of marginal tentacle bulbs and stomach pale straw, yellow, or yellowish brown, depends on food items. Nematocysts (Russell, 1938b): microbasic euryteles and desmonemes.

DIMENSIONS: Sexually mature medusa height around 1 mm, maximally 2 mm; earliest stages of vegetatively produced medusa 0.5-0.7 mm. Eggs measure 0.08-0.12 mm in diameter (Chun, 1896). Nematocysts see Schuchert (1996).

VARIATION: The perradial bulbs can have 1-3 tentacles. Mature medusae with three perradial tentacles are quite rare. Medusae budded from a medusa are released with one tentacle per bulb, therefore there are regularly also representatives of this stage in a population. Also the eight-tentacled medusae can have gonads. The size of mature medusae is quite variable.

The interradial bulbs of *Lizzia blondina* have mostly only one tentacle, but occasionally some of the bulbs may have two tentacles, but never all of them.

FURTHER DATA: The earliest known stages of medusa have already eight marginal bulbs, each with one tentacle; scattered nematocysts on exumbrella; medusa buds are present at a very early stage, they are borne in two, or rarely three series and in each

FIG. 38
Lizzia blondina (Forbes, 1848), living medusa with buds from Roscoff.

series there are four interradial buds approximately at right angles; the proximal series, nearest the base of the stomach, is the first to develop and the buds in each series show a graded order of development in that the two oldest buds stand opposite one another. The gonads start to ripen towards the termination of asexual reproduction and ripe sexual cells may be present while some buds still remain unliberated.

The histology of the vegetative medusa budding was investigated by Chun (1896, as *Lizzia claparèdei*) and Braem (1908). The sexes are separate (Chun, 1896).

DISTRIBUTION: *Lizzia blondina* occurs from Norway to the Mediterranean as well as in the NW Atlantic (Allwein, 1967; Russell, 1970). It has been recorded from Norway as far north as Bergen (Kramp & Damas, 1925; Rees, 1952), around Denmark (Hartlaub, 1911; Kramp, 1926; Rasmussen, 1973); North Sea (Hartlaub, 1911); all round the British Isles, being scarcest in the eastern end of the English Channel and the southern North Sea (Russell, 1953; Fraser, 1973; Russell, 1970); Iceland (northernmost record), The Faroes, and Faroe-Shetland Channels (Hartlaub, 1911; Kramp, 1926); France (Hartlaub, 1911; Teissier, 1965); Iberian Peninsula from the Bay of Biscay to the Mediterranean (Medel & López-González, 1996); western Mediterranean (Hartlaub, 1911; Goy, 1973). Under the name *Podocoryne minuta* it has also been recorded along the coast of western Africa (Thiel, 1938), Florida (Mayer, 1900b, as *Dysmorphosa minuta*), and New Zealand (Schuchert, 1996). Type locality: Originally described from the Shetland Islands (Sound of Brassay and Fitful Head).

BIOLOGY: *Lizzia blondina* is a summer species found in nearshore waters. Owing to the rapid proliferation by asexual budding this species may at times be exceedingly abundant. It occurs in the plankton around the British Isles from March to December, but more abundantly in May to October (Russell, 1953; Ballard & Myers, 2000). In Norway, the medusae appear in June and last until end of October (Kramp & Damas, 1925; own data). In the Kattegat, they are present from at least July to

November or December (Kramp, 1926). In the Mediterranean, the species can be found all year round (Goy, 1973; Riera *et al*., 1986).

REMARKS: The life cycle of this otherwise relatively common medusa is not known. Kramp (1926) suspected that the polyp lives mainly along the southern and western coasts of the British Isles and the distribution in the Danish waters let Kramp think that the polyp lives only in areas with soft, clayey bottoms. Perhaps the polyp described above as *Rathkea* spec. is its polyp.

The synonymy and history of this species is treated by Russell (1953) but new data suggest that at least also *Dysmorphosa minuta* Mayer, 1900 must be added to the synonymy.

Since the medusae may be found mature at any stage of the tentacle development, the identity of the species was at first not certain and three separate species were described (see Fig. 36E-G, *Dymorphosa minima* one tentacle per bulb, *Lizzia claparedei* two perradial tentacles, *Lizzia blondina* three tentacles per radial bulb). Asexually produced *Lizzia blondina* are always liberated with eight bulbs and eight tentacles and will typically develop more perradial tentacles. However, also the eight tentacles stage can become sexually mature. As these forms co-occurred with the normal *blondina* form, they could quite easily synonymized (Browne, 1897; Hartlaub, 1911).

Kramp & Damas (1925) and Kramp (1926), however, also attributed populations from Norway and Denmark to this species, despite that the animals of these populations always have one perradial tentacle only. Such pure eight-tentacled *Lizzia* populations (Fig. 37) would otherwise be identified as *Podocoryne/Hydractinia minuta* (Mayer, 1900b) or *Lizzia fulgurans*. Kramp (1961) already suspected that the Mediterranean records of *Podocoryne minuta* by Neppi & Stiasny (1913) were actually *L. blondina*. A careful comparison of *Hydractinia minuta* material from the Mediterranean (see Material examined) confirmed that it is indistinguishable from eight-tentacled *Lizzia blondina* originating from Great Britain. Likewise, eight-tentacled *Lizzia* from Norway were otherwise indistinguishable from *Lizzia blondina* from the English Channel. This similarity was also confirmed by their 16S sequence data (Fig. 39), the two sequences differed in a single base pair only.

The purported (Hartlaub, 1911: 144) difference of the insertion site of the oral tentacles of *Lizzia blondina* and *Hydractinia minuta* does not exist. The oral tentacles in *Lizzia* insert very close to the mouth margin, they are very oblique (Fig. 36D) and filled with chordoid gastrodermal cells. They thus insert lower than usually seen in adult *Bougainvillia* spec. (but also in young *Bougainvillia* spec. the insertion can be quite close to the mouth rim).

Also material from New Zealand, previously identified by myself (Schuchert, 1996) as *Podocoryne minuta,* conforms with the eight-tentacle-stage of *Lizzia blondina*.

Some preliminary comparisons of 16S sequence data confirm the hypotheses outlined above (Fig. 39). *Lizzia blondina* from the English Channel (specimens with two perradial tentacles) is part of a well supported clade that includes also the samples referable to the *Hydractinia minuta* morphotypes. *Lizzia blondina* from the Channel showed only a single base pair difference to the Norwegian specimens. Likewise, *Lizzia blondina* differed in only one or two positions (of 570 compared base pairs)

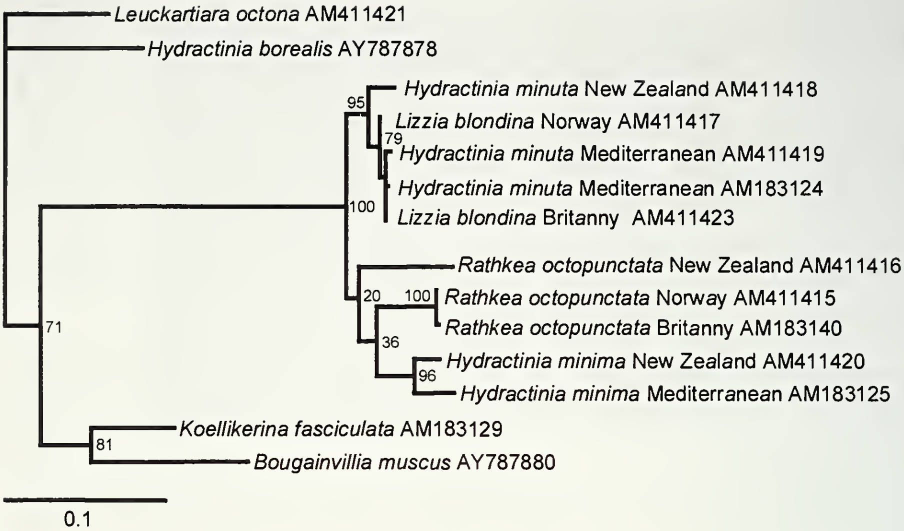


FIG. 39

Molecular phylogeny of some Rathkeidae based on partial 16S sequences and Maximum Likelihood analyses using the software PHYML (HKY model, default parameters). The numbers near some nodes indicate the percentage of bootstrap support (1000 replicates nonparametric bootstrap analysis as implemented in PHYML). Initial analyses included many other 16S sequences of a variety of Filifera species (see also Schuchert & Reiswig, 2006), but no significant relationship of the Rathkeidae could be detected. In the analysis shown here, only a few selected outgroup taxa were used in order to improve the readability. The topology of the *Rathkea* clade did not change significantly by reducing the number of outgroup taxa.
The accession numbers of the sequences are given after the species name. In order to better visualize the revision made in the text, the initial species identifications are given. *Hydractinia minuta* must be synonymized with *Lizzia blondina*, *Hydractinia minima* is referred to *Podocorynoides minima*.

from Mediterranean medusae initially identified as *H. minuta*. These differences are certainly attributable to intraspecific variation (comp. also Fig. 4 and remarks for *B. muscus*). The *Lizzia* clade also includes the sequence of *H. minuta* from New Zealand, although it is more distant (14 bp difference). The good support of the *Lizzia* clade and the relative minor sequence differences suggest that *H. minuta* is nothing but a form of *Lizzia blondina*.

This raises the question whether also the original descriptions of *Dysmorphosa fulgurans* A. Agassiz, 1865 and *Dysmorphosa minuta* Mayer, 1900 were actually based on *L. blondina*. There is nothing in Agassiz's description that would make his *D. fulgurans* distinguishable from eight-tentacled *Lizzia blondina,* except for the presumably lower number of tentacles in newly liberated medusae. This seems to be an error. Agassiz (1865: fig. 260) depicts a manubrium with an advanced bud that has at least eight bulbs and tentacles. Because Mayer (1910) mentions that it can have occasionally up to 16 bulbs, I somewhat hesitate to synonymize it with *L. blondina*. It is possible that the form with 16 bulbs belongs to a different species.

Mayer (1900b) kept his *Dysmorphosa minuta* distinct from *Dysmorphosa fulgurans* A. Agassiz, 1865 based on colour and size differences (bell size of 0.3 mm for *D. minuta*). His *Dysmorphosa minuta* were not sexually mature and could thus well be small, newly liberated medusae. The colour of the bulbs of *Lizzia blondina* depends on food items.

I tried to locate the type material of both *D. fulgurans* and *D. minuta* but could neither find them in the HCZH nor the NMNH. The type material of both species is likely lost. Medusae identified as *Podocoryne minuta* originating from Belize, which can be considered as belonging to the same biogeographic region as Florida (type locality of *D. minuta*), were indistinguishable from European *Lizzia blondina* with eight tentacles. I therefore think that *Dysmorphosa minuta* Mayer, 1900b and likely also *Dysmorphosa fulgurans* A. Agassiz, 1865 are nothing but eight-tentacled *L. blondina*.

Cytaeis minima Trinci, 1903, which Mayer (1910) considered to be only a young stage of *D. minuta*, is clearly a distinct species that always has four tentacles only.

Lizzia octostyla (Haeckel, 1879) Fig. 40

Dysmorphosa octostyla Haeckel, 1879: 78, pl. 6 fig. 6.
Podocoryne octostyla. – Mayer, 1910: 140.
Lizzia octostyla. – Neppi & Stiasny, 1913: 32, pl. 2, fig 22. – Kramp, 1959a: 106, fig. 81. – Kramp, 1961: 88. – Brinckmann-Voss, 1970: plate 8, fig 3. – Bouillon *et al*., 2004: 47, Fig. 28F.
Koellikerina fasciculata. – Kramp, 1957c: 118, fig. 1.

MATERIAL EXAMINED: ROMIZ B773, Naples, Mediterranean, 6 medusae collected by A. Brinckmann-Voss, 22 February to 24 March 1961, damaged.

DIAGNOSIS: Medusa 0.5-1 mm, low apical apex, with peduncle, eight oral tentacles in perradial pairs, medusa buds on manubrium, eight marginal bulbs, 8-12 tentacles.

DESCRIPTION: (Neppi & Stiasny, 1913; own observations) Adult medusa spherical; jelly thin, shallow apical process; manubrium on a conical peduncle; radial canals narrow; eight rather small marginal bulbs, interradial ones slightly smaller, no ocelli but dark pigment in bulbs; in younger specimens one tentacle per bulb, in older ones perradial bulbs with paired tentacles; tentacles long, very expandable; eight unbranched adradial oral tentacles inserting slightly above mouth margin, oral tentacles in pairs, ends with distinct capitulum (nematocyst cluster); interradial medusa buds on middle of manubrium; gonads as flat pads on manubrium wall, medusae budding can continue after gonad maturation.

DIMENSIONS: Medusa bell 0.4-1.3 mm high and wide, usually around 0.5 mm.

BIOLOGY: Recorded in the months February, March, and August to October.

DISTRIBUTION: Mediterranean only; Ligurian Sea (Kramp, 1957d, as juv. *Koellikerina fasciculata*); Tyrrhenian Sea (Brinckmann Voss, 1970); Adriatic Sea (Neppi & Stiasny, 1913; Benovic & Lucic, 1996); Ionian Sea (Haeckel, 1879). Type locality: Island of Corfu, Greece.

REMARKS: This is perhaps only a form of *Lizzia blondina*.

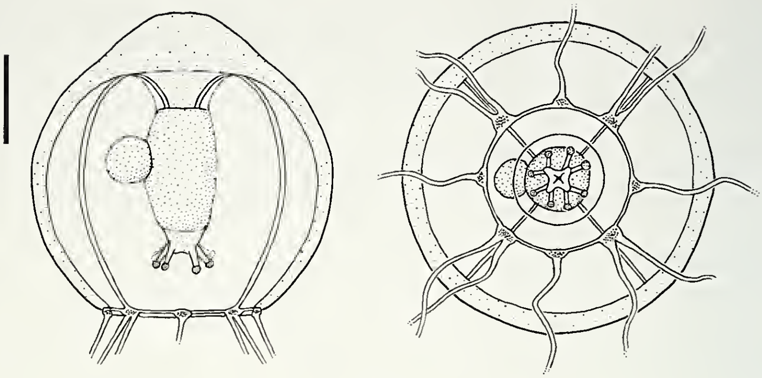


FIG. 40
Lizzia octostyla (Haeckel, 1879), schematic reconstruction after preserved material, scale bar 0.2 mm. (A) Lateral view. (B) Oral view.

Lizzia elisabethae Haeckel, 1879 Fig. 41

Lizzia Elisabethae Haeckel, 1879: 83, pl. 6 fig. 12. – Hartlaub, 1911: 149, fig 136. – Russell, 1953: 150. – Kramp, 1959a: 105, fig. 70. – Kramp, 1961: 88.

DIAGNOSIS (Kramp, 1959a): Umbrella 6 mm high, 4 mm wide, with thick apex, perradial bulbs with four, interradial bulbs with two tentacles; an ocellus at the base of each tentacle; medusa buds not observed.

DISTRIBUTION: Type locality only: Jersey, English Channel.

REMARKS: *Lizzia elisabethae* has never been seen again since its original description by Haeckel (1879). Its size and ocelli would make it certainly quite distinct,

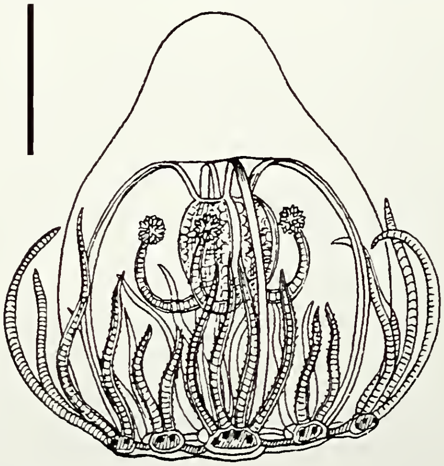


FIG. 41
Lizzia elisabethae Haeckel, 1879, after Hartlaub (1911) from Haeckel (1879), originally drawn after life, scale bar 2 mm.

however some doubts on its validity remain. Russell (1953: 153) thought that it might have been an abnormal *L. blondina* while Kramp (1959a, 1961) kept it as valid.

Genus ***Podocorynoides*** n. gen

TYPE SPECIES: *Cytaeis minima* Trinci, 1903.

DIAGNOSIS: Medusae with four vertical, unbranched oral tentacles inserting at level of mouth rim; with manubrial peduncle; four bulbs, each with one simple tentacle; interradial medusa buds on manubrium; gonads enveloping manubrium.

REMARKS: The 16S sequence data (Fig. 39) indicate that *Podocorynoides minima* (Trinci, 1903) is closely related to *Lizzia* and *Rathkea* and it does not belong to the Hydractiniidae as usually assumed (Mayer, 1910; Kramp, 1959a, 1961). Referring it to the Rathkeidae made it necessary to transfer it to the new genus *Podocorynoides*. The name gives an allusion to its similarity to medusae formerly included in the genus *Podocoryna*.

Podocorynoides minima (Trinci, 1903) n. comb. Fig. 42

Cytaeis minima Trinci, 1903: 26, pl. 1 figs 1-30.
[not *Dymorphosa minima* Hackel, 1879: 78, pl. 6 fig 7. – Hartlaub, 1911: 145 = *Lizzia blondina*]
Podocoryne simplex Kramp, 1928: 45, fig. 20. – Russell, 1953: 136, synonym. – Kramp, 1968: 28, fig. 70.
Podocoryne minima. – Russell, 1953: 134, figs 63-64. – Kramp, 1961: 69. – Chow & Huang, 1958: 176, pl. 1 figs 10-11. – Kramp, 1968: 28, figs 69-70. – Brinckmann-Voss, 1970: pl. 7 fig. 1. – Uchida & Sugiura, 1977: 53, figs 1-2. – Goy *et al.*, 1991: 107, fig. 17.
In part *Podocoryne minuta*. – Neppi & Stiasny, 1913: 24, pl. 1 fig 12 (not others).
[not *Dysmorphosa minuta* Mayer, 1900]
Podocoryna minima. – Schuchert, 1996: 50, fig. 27.
Hydractinia minima. – Bouillon *et al.*, 2004: 65, 39D-E. – Chaplygina & Dautova, 2005: 142, fig. 1.

MATERIAL EXAMINED: Mediterranean, Ligurian Sea, Bay of Villefranche-sur-Mer; depth 0-70 m; 6 April 2005; 6 medusae; no material preserved, DNA made from 4 medusae, 16S sequence accession number **AM183125**. – New Zealand, Hauraki Gulf, Motutapu Island; 0-3 m; 30 June 2002; plankton; no material preserved, DNA made from several medusae, 16S sequence accession number **AM411420**.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION: Medusa with globular bell; apical jelly slightly thickened in fully grown animals; relatively long gastric peduncle present (up to 1/3 of bell cavity). With four radial canals and ring canal, rather narrow. With four perradial tentacle bulbs and tentacles, without ocelli, adaxial epidermis of bulbs thickened and pad-like, gastrodermis with brown pigment, tentacles very contractile. Manubrium length 1/2 of bell cavity, cylindrical, dark pigment in interradial gastrodermis, perradial lip margins elongated to short oral tentacles terminating in a spiny, spherical knob of nematocysts. Interradial medusa buds on manubrium with ordered budding sequence. Gonads surrounding stomach completely. Nematocysts (Chaplygina & Dautova, 2005): microbasic euryteles and desmonemes.

DIMENSIONS: Bell size 0.3-0.9 mm (Uchida & Sugiura, 1977; own data). For nematocyst dimensions see Chaplygina & Dautova (2005).

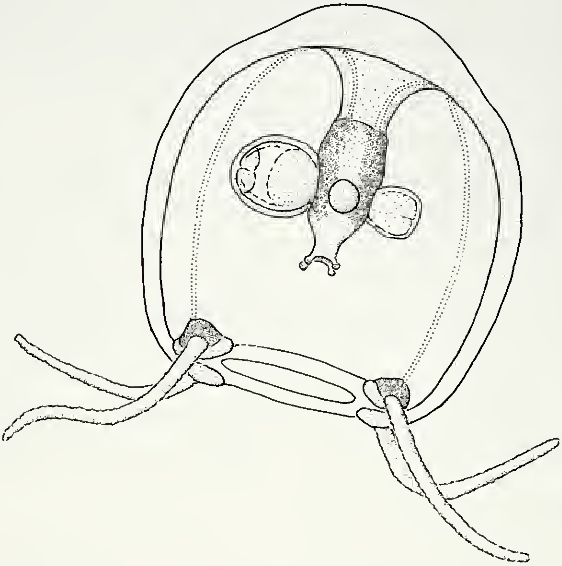


FIG. 42

Podocorynoides minima (Trinci, 1903) n. comb., mouth gaping, size about 1 mm, after photographs and living material from the Mediterranean.

OTHER DATA: The buds on the manubrium are of epidermal origin (Trinci, 1903). The medusae are gonochoristic. The development of the secondary medusa is described by Uchida & Sugiura (1977). There are no significant differences in size and general structure between medusae with gonads and those without them. Even animals with gonads can continue to bud medusae.

BIOLOGY: In the Mediterranean, the medusa is present at least during the months March to September (Trinci, 1903; Goy, 1973; Brinckmann-Voss, 1987).

DISTRIBUTION: Mediterranean (e. g. Trinci, 1903; Goy, 1973; Brinckmann-Voss, 1987; Goy *et al.*, 1991; Benovic & Lucic, 1996); English Channel (Russell, 1953); Brazil (Vannucci, 1957); North Carolina (Allwein, 1967); Red Sea (Schmidt, 1973a); New Zealand (Schuchert, 1996); Papua New Guinea (Bouillon, 1980); north-western Pacific (Kramp, 1928; Chow and Huang, 1958; Uchida & Sugiura, 1977). Type locality: Gulf of Naples, Mediterranean.

REMARKS: Although they have a distinct, round trunk, the oral tentacles of this species resemble much the *Podocoryna* (=*Hydractinia*) type and it is quite surprising to find this species more closely related to the Rathkeidae than the Hydractiniidae. The oral tentacles are mostly held in a nearly vertical position, thus somewhat unlike the oblique tentacles of *Lizzia blondina*.

FAMILY **PANDEIDAE** HAECKEL, 1879

DIAGNOSIS: Hydroid stage normally stolonal, exceptionally branching. Hydranths bearing one whorl of filiform tentacles (exceptionally two whorls, scattered tentacles or no tentacles). Perisarc developed to a variable degree, occasionally missing completely, but often also enveloping hydranth as a filmy pseudohydrotheca. Reproduction is by free medusae (except in some genera of questionable affinity).

Medusae with or without an apical projection; manubrium large, mounted or not on a peduncle; mouth with either four simple, or crenulated, or complexly folded lips. With four (rarely eight as in *Octotiara*) radial canals, often broadened to a band; exceptionally centripetal canals can be present; with or without mesenteries. Gonads either with a smooth surface or complexly folded; on the manubrium in adradial or interradial position; in a few species extending onto the radial canals. Tentacles hollow, originating from conical tentacle bulbs tapering gradually into tentacles; tentacles never with terminal nematocyst clusters (capitation). Sometimes with rudimentary tentacles, cirri-like tentacles, or marginal protuberances. Ocelli present or not.

REMARKS: The Pandeidae comprise a large number of genera and some need a revision. Therefore, the key below relates only to medusa based genera used in this study. For a complete key of the Pandeidae genera see Bouillon & Boero (2000).

KEY TO THE ADULT PANDEIDAE MEDUSAE OF THE NE ATLANTIC AND MEDITERRANEAN:

1a	eight radial canals	*Octotiara*
1b	four radial canals	2
2a	two large perradial tentacles	3
2b	four or more tentacles	4
3a	four interradial gonads that extend onto subumbrella and forming a bell like cavity	*Codonorchis*
3b	gonads unlike above	*Amphinema*
4a	gonads not on folds or in pits, surface smooth or rugose	*Merga*
4b	gonads on stomach folds, or in pits	5
5a	manubrium short, perradial stomach corners drawn out into a large cross-like form	*Annatiara*
5b	stomach large, flask-shaped	6
6a	with mesenteries (elongated connection of stomach and radial canals)	7
6b	mesenteries absent	*Halitholus*
7a	gonads forming a reticulated network of pits	*Pandea*
7b	gonads with folds only, or folds and pits combined	8
8a	gonads in long folds that tend to be vertical in interradial region, some pits	*Catablema*
8b	adradial rows of gonad folds	9
9a	no or very few pits, gonad folds directed towards perradial, with ocelli	*Leuckartiara*
9b	with many interradial pits, gonad folds directed towards interradial, without ocelli	*Neoturris*

Genus ***Pandea*** Lesson, 1843 emended

TYPE SPECIES: *Dianaea conica* Quoy & Gaimard, 1827, designation by Mayer, 1910.

SYNONYM: *Campaniclava* Allman, 1864a: 352 [type species *Syncoryne cleodorae* Gegenbauer, 1854].

DIAGNOSIS: Hydroids, where known, forming stolonal colonies with naked hydranths on very short pedicels; with filiform tentacles. Dactylozooids may be present. Medusa buds arise from stolons.

Medusa with or without apical projection, with or without longitudinal ridges and nematocyst tracks on exumbrella; lips large and much folded; gonads at first in the adradii and eventually covering the manubrium, forming a complex reticulated network; radial canals band-like; more than eight tentacles, without rudimentary marginal tentacles or marginal warts; with or without abaxial ocelli.

KEY TO THE *PANDEA* SPECIES TREATED HERE:

1a	with exumbrellar ribs and nematocyst tracks, gonad network coarse, marginal bulbs laterally compressed, ocelli present, subumbrella colourless	*Pandea conica*
1b	without exumbrellar ribs and nematocyst tracks, gonad network close meshed, marginal bulbs not much laterally compressed, ocelli absent, manubrium and radial canals deep red	*Pandea rubra*

Pandea conica (Quoy & Gaimard, 1827) Figs 43-44

Dianaea conica Quoy & Gaimard, 1827: 182, pl. 6 figs 3-4.
Oceania sedecimacostata Kölliker, 1853: 324.
Syncoryne cleodorae Gegenbauer, 1854: 166, pl. 1 fig 3. – Picard, 1956: 1, synonym.
Campaniclava cleodorae. – Allman, 1872: 261.
Tiara reticulata Haeckel, 1879: 60, pl. 3 fig. 11. – Vanhöffen, 1911: 209, synonym. – Hartlaub, 1914: 340, synonym.
Tiara pileata var. *ampullacea* Haeckel, 1879: pl. 3 fig. 7.
Pandaea conica. – Haeckel, 1879: 54 [incorrect subsequent spelling].
Pandea conica. – Mayer, 1910: 118, fig. 63. – Hartlaub, 1914: 339, figs 283-287, synonymy. – Uchida, 1927: 214, fig. 38. – Kramp, 1924: 8, fig. 7. – Ranson, 1936: 84, pl. 1 figs 1-6. – Russell, 1953: 207, figs 107-110. – Picard, 1956: 1, figs 1-3. – Kramp, 1961: 111. – Brinckmann-Voss, 1970: pl. 11 fig. 2. – Russell, 1970: 250, figs 14s-15s. – Winkler, 1982: 34, fig. 6. – Lalli & Gilmer, 1989: 127, fig. 47b. – Pagès *et al*., 1992: 14, fig. 13. – Schuchert, 1996: 71, fig. 42a-c. – Bouillon *et al.*, 2004: 74, fig. 43A-B.

MATERIAL EXAMINED: MHNG INVE35427, polyp colonies on two specimens of *Clio cuspidata*, Villefranche-sur-Mer, with numerous medusa buds. – MHNG INVE35433, about 7 medusae from Villefranche-sur-Mer, identified 1911 by C. Hartlaub. – MHNG INVE35434, Naples, 2 badly preserved medusae. – Serial sections of *Campaniclava cleodorae* from the Picard collection (kept by Station Marine d'Endoume, Marseille), leg & det. J. Picard, coll. 1933, Villefranche-sur-Mer France.

DIAGNOSIS: *Pandea* medusa with exumbrellar ribs bearing nematocyst tracks, marginal tentacles laterally compressed, with ocelli, subumbrella colourless, 16-24 tentacles. Polyps on *Clio cuspidata*, polymorphic, feeding zooid almost sessile, two whorls of tentacles, with tentaculozooids, medusa buds stolonal, medusae released with two tentacles.

DESCRIPTION: Polyp stage living on the pelagic gastropod *Clio cuspidata*; polyps polymorphic, with gastrozooids and tentaculozooids, arising from creeping stolons. Stolons fine, covered by thin perisarc, long straight stretches, not much ramified, bifurcations usually coincide with polyp positions. Polyps with a very short pedicel, almost sessile, base in membranous perisarc cup, body spindle shaped, diameter about 1/3 of height, hypostome high (about 1/5 of total height), conical to nipple-shaped, 8-10 filiform tentacles in two closely set whorls, distal tentacles longer, gastrodermis chordoid. Tentaculozooids present but infrequent, usually near gastrozooids, about as high as gastrozooids, with slightly swollen tip. Medusa buds arise directly from stolons, short pedicel, buds covered with thin perisarc. Nematocysts: microbasic euryteles and desmonemes.

Newly liberated medusa (Picard, 1956) as high as wide, bell-shaped with moderately thick jelly. Jelly at apex interrupted by remains of the gonophore stalk. Manubrium length 1/2 of bell cavity, conical with four very inconspicuous lips, no gonads visible. With four broad, smooth radial canals and circular canal. Two opposite larger and two smaller tentacle bulbs present. Only larger bulbs bear a tentacle. Ocelli

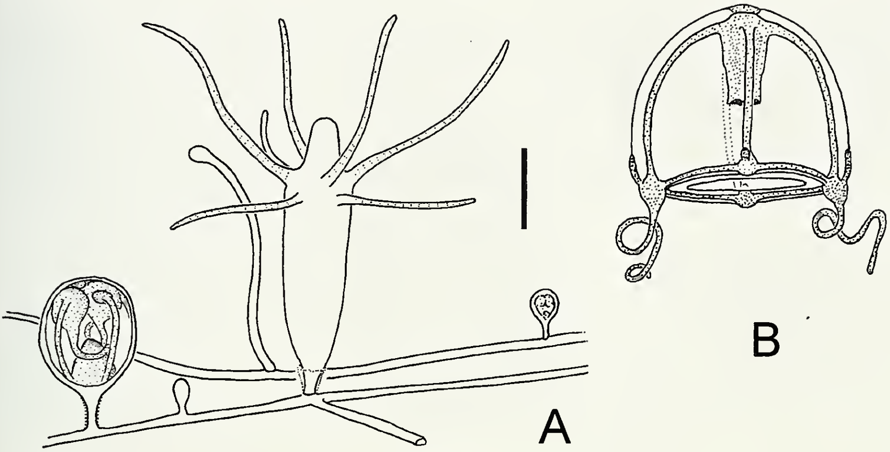


FIG. 43

Pandea conica (Quoy & Gaimard, 1827). (A) Part of hydroid colony on *Clio cuspidata*, with gastrozooid, medusa buds on stolons, and tentaculozooid, scale bar 0.3 mm. (B) Newly released medusa. A, after preserved material from the Mediterranean; B, redrawn from Picard (1956).

not present, but a dispersed red pigment present in bulbs. Above bulbs on exumbrella patches of tissue with nematocysts that later grow towards top.

Mature medusa bell-shaped to conical, usually higher than wide, with small rounded or conical apical projection covered by opaque epidermis; with longitudinal keel-like exumbrellar ribs, corresponding to number of marginal tentacles, crest of ribs with a line of thickened epidermis studded with nematocysts (nematocysts tracks) originating from marginal tentacle; jelly fairly thick. Four radial canals fairly broad, with smooth or jagged outlines, forming mesenteries; ring canal narrower, with smooth outlines. Sixteen to 24 (sometimes as many as 45) smooth, marginal tentacles, each with a conical, laterally compressed bulb that clasps umbrellar margin, with one abaxial ocellus, abaxial spur continued as nematocyst track up to top of bell, no rudimentary marginal tentacles. Stomach voluminous, almost filling upper half of subumbrellar cavity, length variable, usually about half of subumbrella cavity in length, attached to subumbrella along perradii for about 2/3-4/5 of its length (mesenteries). Mouth with four perradial lips with much folded or crenulated margins, beset with nematocysts but these not in clusters. Gonads interradial, in fully grown specimens covering upper 2/3 of the manubrium wall, not continuous as separated perradially by mesenteries, gonad forming coarse-meshed network of ridges with pits between. Colour of stomach and gonads, reddish, brownish or yellowish; mouth-lips reddish or pink; tentacles milky yellow; ocelli red or reddish brown; subumbrella colourless (in part after Russell, 1953). Nematocysts of medusa: microbasic euryteles.

DIMENSIONS: Mature medusa 10-20 mm high; polyps about 1 mm. For nematocyst sizes see Picard (1956) and Schuchert (1996).

OTHER DATA: Ranson (1936) describes the growth and development of the medusa (summarized in Russell, 1953). Also Mayer (1910) depicts young medusae. In younger stages the gonads have an interradial cleft (= horse-shoe shaped).

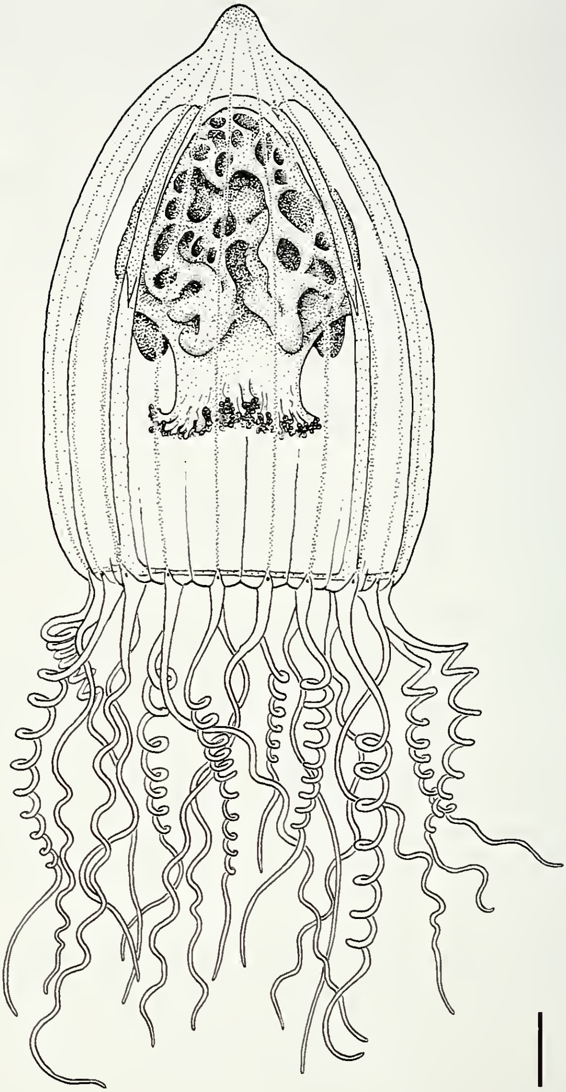


FIG. 44

Pandea conica (Quoy & Gaimard, 1827); adult medusa, after preserved material from the Mediterranean, scale bar 2 mm.

BIOLOGY: The polyps of this species occur on the shell of the pteropod *Clio cuspidata* (see Picard, 1956; Lalli & Gilmer, 1989). In the Mediterranean, Kramp (1924) recorded the medusa from January to September. Bleeker & van der Spoel (1988) found the medusa at night in depths of 45-95 m, during the day in 50-300 m.

DISTRIBUTION: An oceanic medusa recorded from the Mediterranean; the Atlantic Ocean from Scotland to Bermuda, South Africa and Patagonia; East Africa;

Sri Lanka; Central North Pacific, California; southern Japan; China; Vietnam; Philippines; Rarotonga; Papua New Guinea; east of Australia; New Zealand (Ranson, 1936; Russell, 1953; Kramp, 1968; Bleeker & van der Spoel, 1988; Pagès *et al.* 1992; Schuchert, 1996). The polyp phase has been recorded from the Mediterranean, South Atlantic and Indian Ocean (Picard, 1956). However, its host *Clio tricuspidata* has a much wider distribution and probably also the polyp stage of *Pandea conica*. Type locality (medusa): Strait of Gibraltar.

REMARKS: The correlation of the polyp stage, previously known as *Campaniclava cleodorae* (Gegenbauer, 1854), and *Pandea conica* was established by Picard (1956). Picard observed only the newly released medusa and he apparently did not cultivate it to older, more distinctive stages. The only character that allow a tentative identification of the young medusa were incipient exumbrellar nematocyst tracks. Although *Campaniclava cleodorae* is very likely the polyp stage of *Pandea conica*, it seems desirable that this is proven again by more conclusive data.

The tentaculozooids observed in the present material have not been reported so far. It could be that they are not formed in all colonies, a phenomenon also observed in several other hydroids.

There seems to be a difference in the cnidome between *Pandea conica* of Europe and New Zealand (comp. Schuchert, 1996). The large isorhiza found in animals from New Zealand could not be found in Mediterranean medusae (this study and Picard, 1956). It could be that the New Zealand *Pandea* belongs to a separate species.

There are two other *Pandea* species in the Atlantic: *Pandea rubra* Bigelow, 1913 and *Pandea cybeles* Alvarino, 1988. *Pandea rubra* lacks an apical projection and the exumbrellar nematocysts. *Pandea cybeles* from the Sargasso Sea differs more gradually from *P. conica*, mainly in having about twice as many tentacles, a broader bell, and a larger manubrium. Alvarino (1988) tabulates more differences of these three species.

Pandea rubra Bigelow, 1913 Fig. 45

Pandea rubra Bigelow, 1913: 14, pl. 2, figs 1-7. – Kramp, 1926: 96, pl. 2 fig. 15, chart XVII. – Bigelow, 1938: 107. – Russell, 1953: 211, figs 11-112. – Kramp, 1961: 112. – Naumov, 1969: 207, fig. 75. – Kramp, 1968: 51, fig. 135. – Arai & Brinckmann-Voss, 1980: 61, fig. 34. – Bleeker & van der Spoel, 1988: 231, fig. 14, map fig. 15. – Brinckmann-Voss & Arai, 1998: 50, fig. 5.

MATERIAL EXAMINED: ZMUC; Discovery station 1889; 55.887°S 32.780°W, South Atlantic; 1200-1500 m; 10 March 1937; 1 much damaged medusa. – ZMUC; 54.083°N 26.133°W, North Atlantic; 0-1000 m; 15 July 1913; 1 fragmented medusa (material of Kramp, 1926). – ZMUC; 6.867°N 79.500°E, Indian Ocean; 300-1000 m; 24 Nov. 1929; 1 much damaged medusa. – Photograph of living medusa kindly provided by Dr K. Rascoff, medusa observed in June 2001 near Oceanographers Canyon (off Massachusetts), depth about 700 metres.

DIAGNOSIS: *Pandea* species without exumbrellar nematocyst tracks; gonad forming fine-meshed network of pits, no ocelli, manubrium and radial canals deep-red.

DESCRIPTION (Russell, 1953): Umbrella bell-shaped, as high as or slightly higher than wide; with rounded summit without marked apical process; without exumbrellar nematocyst tracks; jelly very soft and fragile. Four radial canals, broad, with wavy or jagged outlines; ring canal broad, with smooth outlines. Radial canals

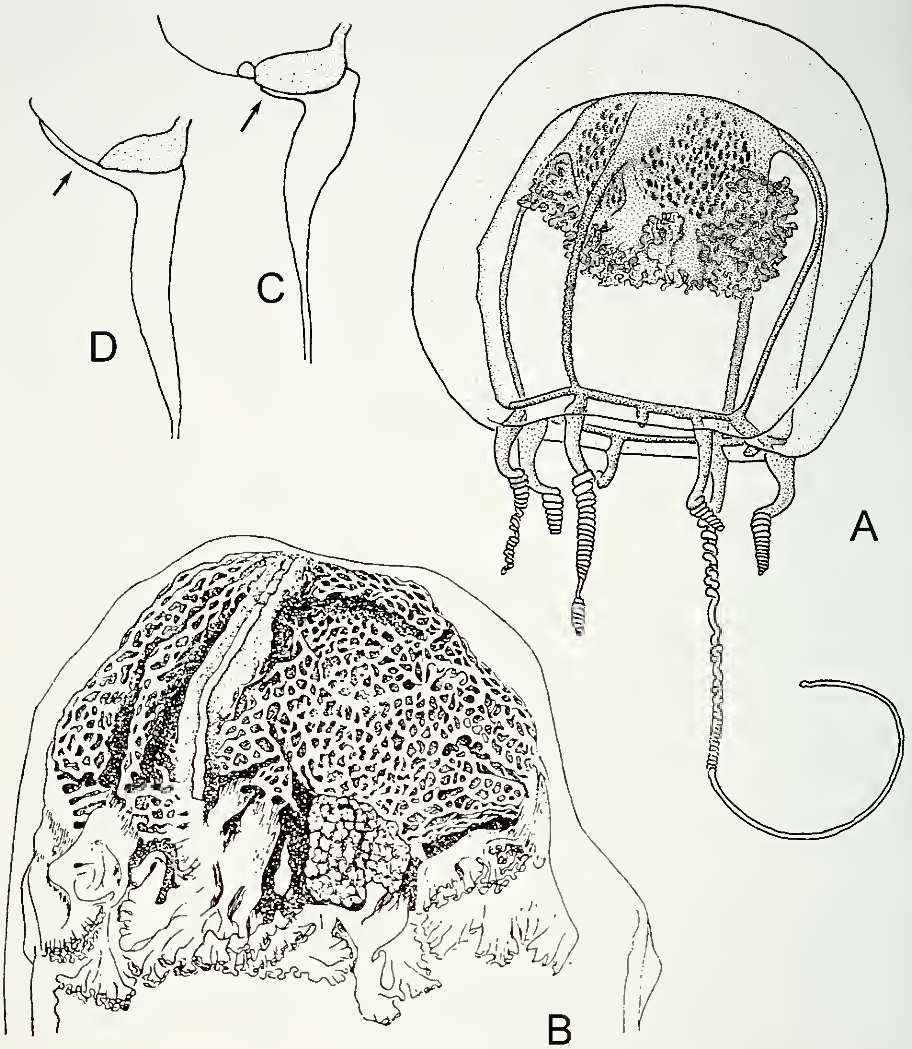


FIG. 45

Pandea rubra Bigelow, 1913. (A) Young, though fertile medusa. (B) Manubrium of a larger specimen. (C-D) Lateral views of tentacle bulbs, arrow points at abaxial spur, in C it is partially embedded in the jelly. A, after photograph of living animal kindly provided by Dr. K. Raskoff; B, from Hartlaub (1914); C-D, redrawn from Kramp (1926) and Brinckmann-Voss & Arai (1998).

narrow proximal, wider distal. Seven to twenty-four marginal tentacles of varying sizes, much extensible, hollow, smooth, each with large conical basal bulb, not much laterally compressed, with distinct abaxial spur clasping margin of exumbrella. Abaxial spurs of bulbs either pigmented or not, may be embedded in the jelly of the exumbrella. No rudimentary tentacles. No ocelli. Stomach large, with broad base, about half height of subumbrellar cavity in length; attached to subumbrella along perradii for about 1/2 or more of its length (mesenteries). Mouth with four lips with much folded and crenulated margins. Gonads situated interradially on stomach, forming very close-meshed irregular network of ridges with pits between. Colour stomach, mouth, gonads, radial and circular canals, and marginal tentacles deep brownish red to chocolate brown. In older or larger specimens, the red pigment spreads also over the subumbrella so that it can get opaque (Bigelow, 1913).

Polyp stage unknown.

VARIATION: The abaxial spurs of bulbs can either be pigmented or not, they may be embedded in the jelly of the exumbrella (Fig. 45C). A table with sizes and tentacle numbers of growth stages is given in Bigelow (1913) and Russell (1953). The smallest known specimens measured 5 mm (Brinckmann-Voss & Arai, 1998). The maximal number of tentacles so far observed is 32 (Brinckmann-Voss & Arai, 1998), usually there are only 12-24.

DIMENSIONS: Medusa bell height rarely up to 75 mm, usually 30-40 mm.

DISTRIBUTION: North and north-east Pacific (Bigelow, 1938; Arai & Brinckmann-Voss, 1980; Brinckmann-Voss & Arai, 1998); India (Vannucci *et al.,* 1970); Bermuda (Bigelow, 1938); north-eastern Atlantic (Kramp, 1920; Kramp, 1926; Fraser, 1973; Bleeker & van der Spoel, 1988); north-western Atlantic (K. Raskoff, pers. comm.); South Atlantic (Kramp, 1957a; Bleeker & van der Spoel, 1988). Type locality: Albatross Station 4797, NE Pacific, off south-east coast of Kamtchatka, 0-548 m.

BIOLOGY: A deep water species, occurring in all oceans, usually far away from the continents, maximal recorded depths 1750 m, usually in depths of several hundred meters. The specimens of the Atlantic were taken in July (Russell, 1953), May and July near Bermuda; in the autumn near the Azores (Bleeker & van der Spoel, 1988) As deep water species it is likely not much seasonal.

REMARKS: A rare, though distinct and easily recognizable species. The mesogloea is very fragile, thus specimens taken with a plankton net are often much damaged.

Genus ***Amphinema*** Haeckel, 1879

TYPE SPECIES: *Oceania dinema* Péron & Lesueur, 1810, by designation of Rees & Russell (1937).

DIAGNOSIS: Medusae with two large opposite tentacles; with or without ocelli; gastric peduncle absent; mostly with a considerable apical projection; with or without marginal small tentaculae or marginal warts; with or without mesenteries; four simple oral lips, not or not much crenulated. Gonads on manubrium in adradial or interradial position, occasionally extending to the radial canals.

Hydroid colonies usually stolonal (except for one species of uncertain affinity), hydranths with a well developed caulus, caulus longer than hydranth, covered by perisarc; hydranths without pseudohydrotheca, spindle-shaped, conical hypostome, one whorl of filiform, amphicoronate tentacles. Polyps bend over when disturbed. Gonophores arise either from cauli, stolons or both, released as free medusae.

REMARKS: See Rees & Russell (1937), Russell (1953), and Bouillon *et al.* (2000) for important revisions and the taxonomic history of the genus. The last mentioned publication gives also a tabular overview on most *Amphinema* medusae known at that time. Two species have to be added, namely *Amphinema tsingtauensis* Kao, Li, Chang & Li, 1958 and *Amphinema cheshirei* Gershwin & Zeidler, 2003. The gender of the name is neuter (ICZN article 30.1.2.) It is possible that not all endings of the specific epithets are correct, but it seems more desirable to maintain taxonomic stability and to use the names as given in Kramp (1961).

KEY TO THE *AMPHINEMA* MEDUSAE TREATED IN THIS STUDY:

1a	without conspicuous apical chamber	2
1b	with conspicuous apical chamber above manubrium	*A. rubrum*
2a	gonads not extending along radial canals	3
2b	gonads extending along radial canals	*A. turrida*
3a	red-brown manubrium, gonad surface rugose, cellular strands issuing from radial canals	*A. krampi*
3b	not as above	4
4a	with ocelli, with aboral processes of manubrium projecting into mesogloea	*A. bouilloni*
4b	not as above	5
5a	folded gonads, with small tentaculae, tentacle bulbs brownish-yellow	*A. rugosum*
5b	gonads smooth, no tentaculae, tentacles purple, manubrium green	*A. dinema*

Amphinema dinema (Péron & Lesueur, 1810) Fig. 46

Oceania dinema Péron & Lesueur, 1810: 346. – Goy, 1995: 255, plate.
? *Oceania diadema* Lamarck, 1817: 506. – Haeckel, 1879: 50, synonym.
Perigonimus serpens Allman, 1863: 10. – Allman, 1872: 327, pl. 11 figs 7-9.
Saphenia apicata McCrady, 1859: 129, pl. 8 figs 2-3.
Stomotoca apicata. – Fewkes, 1881: 152, pl. 2 figs 1, 4, 9. – Rittenhouse, 1910: 333, figs 1-32.
Saphenia titania Gosse, 1853: 387, pl. 26, figs 7-9.
Dinematella cavosa Fewkes, 1881: 151, pl. 2 figs 2-3, pl. 4 fig. 3.
Amphinema titania. – Haeckel, 1879: 50, pl. 4 figs 8-9.
Amphinema apicatum. – Haeckel, 1879: 50.
Tiarula coeca Hartlaub, 1914: 261, fig. 215.
Stomotoca dinema. – Mayer, 1910: 109, pl. 9 figs 8-10, pl. 10 figs 1-4. – Neppi & Stiasny, 1913: 18, pl. 1 fig. 8.
in part *Amphinema dinema*. – Hartlaub, 1914: 259, fig. 215 [others = *A. rugosum*].
Amphinema dinema. – Rees & Russell, 1937: 62, figs 1-4. – Russell, 1938b: 153, figs 37-40. – Russell, 1953: 180, text-fig. 89, pl. 10, figs 1, 2, 4, pl. 11 figs 1, 3. – Kramp, 1959a: 117, fig. 109. – Kramp, 1961: 93. – Kramp, 1968: 42, fig. 108. – Goy *et al.*, 1991: 109, fig. 24. – Schuchert, 1996: 63, fig. 36a-d. – Bouillon *et al.*, 2004: 68, fig. 40B-C.

MATERIAL EXAMINED: France, Brittany, Roscoff; 10-20 m; 06 June 2000; 1 medusa, examined alive, 16S sequence **AM183136**. – BMNH 1985.9.2.20; Great Britain, Plymouth; 11 October 1938; 50 medusae from plankton. – BMNH 1985.9.1.16; Great Britain, Plymouth; 25 June 1937; hydroid colonies on *Scalpellum* from rearing experiments, leg. W. J. Rees. – BMNH 1985.9.1.15; Great Britain, Plymouth; 5 July 1937; cultivated hydroid on glass, with medusa buds, from rearing experiments of W. J. Rees. – BMNH 1969.12.2.128; Great Britain, Plymouth; 18 February 1937; hydroid reared from medusa, material of Rees & Russell (1937).

DIAGNOSIS: *Amphinema* with simple, not folded gonads on each of the eight adradial surfaces of stomach; fourteen to twenty-four small marginal bulbs without tentacles; manubrium intensively green, tentacles purple. Hydroid stolonal, medusa buds only on stolons. Newly liberated medusa without apical process.

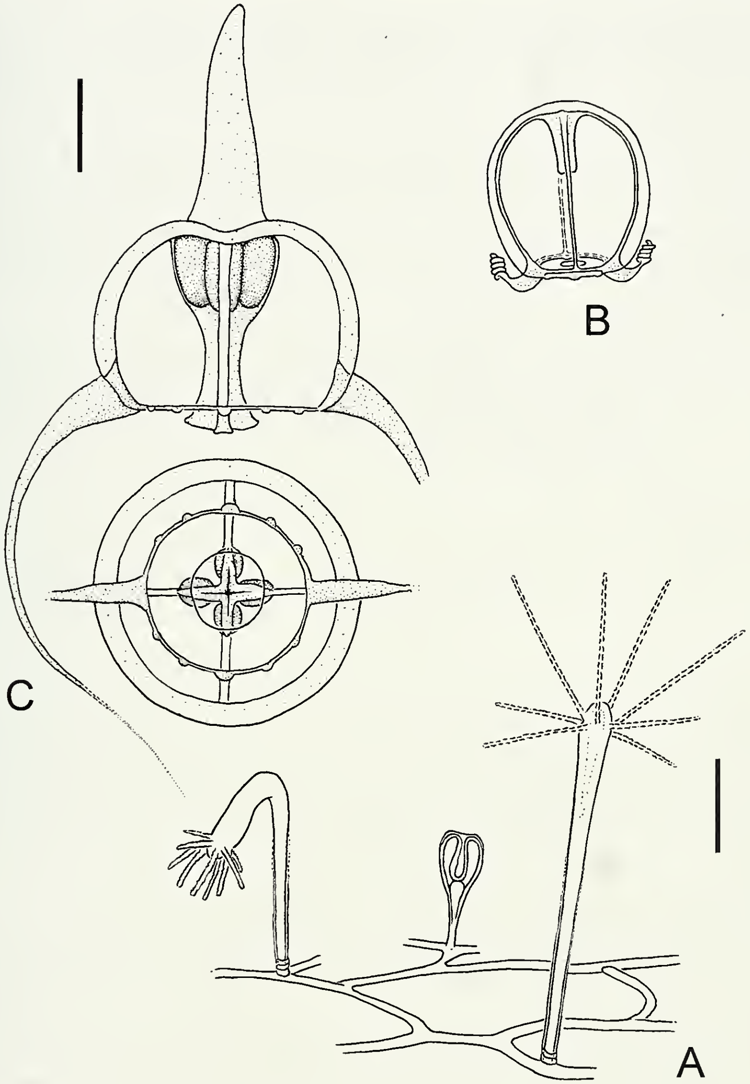


FIG. 46

Amphinema dinema (Péron & Lesueur, 1810). (A) Part of hydroid colony with a medusa bud, scale bar 0.5 mm. (B) Newly liberated medusa, size about 0.7 mm. (C) Mature medusa in lateral and oral view, the gonads are not yet fully developed. A, after preserved material; B, modified from Rees & Russell (1938); C, after life.

DESCRIPTION (Rees & Russell, 1937; Russell, 1953; own observations): Stolonal hydroid colonies arising from creeping, ramified stolons; hydrocauli not branched, enclosed in perisarc, perisarc at base with or without annulated region, perisarc becoming very thin distally and end is difficult to observe, perisarc can be infested with detritus. Hydranth spindle shaped with a dome shaped hypostome, tapering below gradually into hydrocaulus, below hypostome one whorl of 8-10 (max. 14) amphicoronate tentacles. Medusa buds arise from stolons only, ovoid to pear-shaped, tapering below into short pedicel, pedicel shorter than bud, bud enclosed in thin perisarc membrane. Nematocysts: microbasic euryteles, desmonemes. Colour of hydranth brilliant orange-red.

Newly liberated medusa spherical, jelly thin, no apical process present, scattered nematocysts on exumbrella, only two opposite tentacles, rather long, at place of other tentacles only small swellings (marginal warts); manubrium cylindrical, about 1/3 of height of bell cavity; colour of tentacle bulbs and stomach reddish orange, developing soon into a vivid emerald green manubrium and violet tentacles.

Mature medusa bell slightly wider than high, jelly of uniform thickness, with a large conical, solid apical process, shape and size of process very variable, process height usually depassing bell size, bell top with slight perradial furrows; dilated velum spanning 1/2 of radius. With four broad radial canals, no mesenteries, only two diametrically opposed tentacles with thick base, hollow, tentacles tapering evenly and very long (ten times bell size), additionally with 6-12 marginal warts, but no short tentacles. Manubrium intensively green, manubrium length 3/4 of subumbrella to reaching slightly beyond velum, cross-shaped in section, mouth with four prominent, slightly recurved lips. Eight gonads in adradial pads with smooth surface. Ocelli absent. Colours: proximal part of tentacles intensively purple. Nematocysts: only microbasic euryteles.

DIMENSIONS (Rees & Russell, 1937; Russell, 1953; own observations): Hydroid total height 1.6-4 mm, hydranth body about 0.8-1.0 mm (transition to hydrocaulus gradual), hydrocaulus diameter 0.05-0.10 mm, stolons 0.04-0.08 mm; medusa buds ready for liberation 0.30-0.33 mm long and 0.20-0.23 mm wide. Newly liberated medusae 0.6-0.7 mm high. Bell size of mature medusa 1-2.3 mm, total height maximally up to 6 mm and 4 mm wide; the apical process develops at a bell size of about 1 mm; eggs 0.15 mm diameter; planulae 0.25 mm long and 0.09 mm wide. For nematocyst sizes and shapes see Russell (1938b) and Schuchert (1996).

DISTRIBUTION: The medusa is widespread, it occurs in the eastern Atlantic from the Shetland Islands (Kramp, 1926) to the Gulf of Guinea in western Africa (Kramp, 1955b) (see also Russell, 1953; Kramp, 1961; Russell, 1970; Fraser, 1973); Western Mediterranean (e. g. Neppi & Stiasny, 1913; Goy, 1973; Benovic & Lucic, 1996; Bouillon *et al.*, 2004); Eastern Mediterranean (Goy *et al.*, 1991); North America from Cape Cod to Florida (Mayer, 1910); Brazil (Vannucci, 1957); Indian Ocean (Ganapati & Nagabhushanam, 1958); Tropical Pacific Ocean (Kramp, 1953; Bouillon, 1980); New Zealand (Schuchert, 1996). The hydroid is known from British Isles (Allman, 1872; Rees & Russell, 1937; Russell, 1957); the Atlantic coast of Spain (Medel & López-González, 1996) and Morocco (Patriti, 1970), New Zealand (Schuchert, 1996); Mediterranean (e. g. Motz-Kossowska, 1905). Type locality: English Channel.

BIOLOGY: The medusa is widespread but usually only few specimens can be caught. In the English Channel, the hydroid has been found on stems of *Eunicella verrucosa* and frequently on the stalked barnacle *Scalpellum* in the months March to September (Rees & Russell, 1937; Russell, 1957). In the western Mediterranean, Motz-Kossowska (1905) found the polyp fixed on the bryozoan *Cellaria fistulosa* on muddy bottoms, medusae were produced during winter the months. Brinckmann-Voss (1987) reports that medusae are budded from May to August. Boero & Fresi (1986) give a depth range of 0.5-20 m, and as substrates algae, sponges and barnacles. The medusae mature in the Mediterranean from September onward (Neppi & Stiasny, 1913). In the English Channel, the medusa appears in the plankton in late summer, being most abundant in September and October (Russell, 1953). Lebour (1922) describes how the medusa eats other planktonic organisms like *Obelia* and *Eutima* medusae, *Calanus* and *Sagitta* species. Rittenhouse (1910) attempted to cross *A. rugosum* and *A. dinema* without success.

REMARKS: The life cycle of this species has been investigated by Rittenhouse (1910), Rees & Russell (1937), and Schuchert (1996).

Contrary to the opinion of Rees & Russell (1937), the hydroid pedicel can also be annulated at its base (own observations and Russell, 1953).

Amphinema rugosum (Mayer, 1900) Fig. 47

Stomotoca rugosa Mayer, 1900a: 4, pl. 2 fig. 5.
Saphenia dinema. – Forbes, 1848: 25, pl. 2 fig. 4. – Le Danois, 1914a: 18, fig. 5.
[not *Amphinema dinema* (Péron & Lesueur, 1810)]
In part *Amphinema titania*. – Haeckel, 1879: 50, pl. 4 figs 8-9.
[not *Saphenia titania* Gosse, 1853 = *Amphinema dinema*]
? *Amphinema apicatum*. – Brooks, 1883: 711.
Stomotoca rugosa. – Mayer, 1910: 112, pl. 10 figs 5-6, pl. 11 figs 1-2. – Uchida, 1927: 202, fig. 32.
in part *Amphinema dinema*. – Hartlaub, 1914: 259, fig. 214, 216-217, not 215.
Amphinema rugosum. – Rees & Russell, 1937: 67, figs 5-6. – Russell, 1938a: 423. – Russell, 1953: 183, figs 90A-B, pl. 10 fig. 3, pl. 11 figs 2 & 4. – Kramp, 1959a: 117, fig. 110. – Kramp, 1961: 94. – Kramp, 1968: 43, fig. 110. – Wedler & Larson, 1986: 96, fig. 7Aa-b. – Migotto, 1996: 15, figs 2f-g. – Schuchert, 1996: 64, fig. 37a-d. – Goy *et al*., 1991: 109, fig. 25. – Bouillon *et al*., 2004: 69, fig. 40E-F.

MATERIAL EXAMINED: BMNH 1985.9.1.14; Great Britain, Plymouth; 15 May 1937; infertile hydroid colony on floating cork. – BMNH 1969.12.2.135; Great Britain, Plymouth; June 1937; slide preparation, part of material of Rees & Russell (of BMNH 1985.9.1.14). – BMNH 1955.11.23.77-105; Great Britain, Plymouth; 1930-1934; about 15 medusae from plankton; coll. F. S. Russell.

DIAGNOSIS: *Amphinema* medusa with folded gonads on each of the eight adradial surfaces of stomach; besides two large tentacles 14-15 reduced, small tentaculae; manubrium and tentacles brownish-yellow to orange. Hydroid mostly stolonal, medusa buds only on stolons and hydrocauli. Newly liberated medusa with apical process.

DESCRIPTION (Rees & Russell, 1937; Russell, 1953; own data): Hydroid stolonal or very rarely some hydrocauli branched once or twice, arising from creeping, ramified stolons; stolons covered by perisarc. Hydrocauli long, gradually expanding their diameter about two times from proximal to distal, without distinct demarcation of hydranth body and coenosarc of hydrocaulus; hydrocaulus covered by thin perisarc, at junction to stolons with annulated stretch (2-5 rings), upper end distinct, not forming a pseudohydrotheca, the perisarc can be infested with detritus. Hydranth cylindrical,

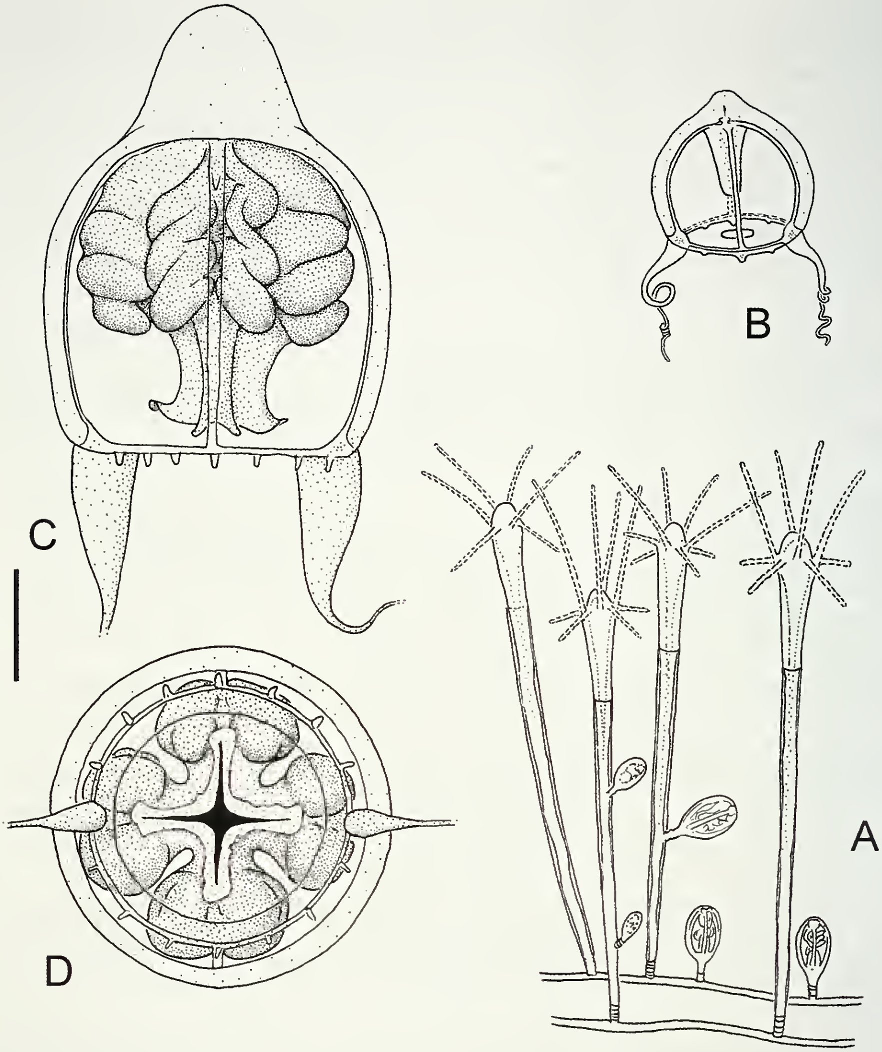


FIG. 47

Amphinema rugosum (Mayer, 1900). (A) Part of hydroid colony with medusa buds. (B) Newly liberated medusa, note presence of small apical process. (C) Mature male medusa in side view, scale bar 1 mm. (D) Same as in C, oral view. A-B, modified from Rees & Russell (1937); C-D, after preserved material from Plymouth.

with a dome-shaped hypostome; below hypostome one whorl of 8 to 12 amphicoronate tentacles. Medusa buds arise from stolons and from hydrocauli, 1-3 buds per hydrocaulus can be present, pedicels of medusa buds shorter than bud height; bud is covered by thin perisarc. Nematocysts microbasic euryteles and desmonemes. Colour: hydranths and coenosarc possess a bright reddish orange in European specimens, perisarc horn coloured.

Newly liberated medusa spherical, with small apical process and usually the remains of an apical canal, exumbrella with scattered nematocysts; manubrium half the length of the subumbrellar cavity; two opposite tentacles, with or without two small opposite perradial tiny tentacles (tentaculae). Colour of tentacle bulbs reddish-orange, with faint tinge of yellow, stomach bright ochreish yellow.

Adult medusa with bell slightly higher than wide, jelly uniformly thin besides top, on top a conical to hemispherical apical process, size variable; top of umbrella with slight perradial furrows. With four broad radial canals with jagged and smooth margins, normally without mesenteries, sometimes with short mesenteries. Two diametrically opposed tentacles with thick bases, tapering and very long (ten times bell size), bulbs conical, hollow; additionally 14-24 small, reduced tentaculae. Manubrium reaching almost to velum, cross-shaped in section, mouth with four prominent, slightly recurved lips. Eight gonads in adradial pairs, each with three to four oblique folds sloping downwards towards the interradii. The gonad can be fused perradially in the more oral part, while there can be an interradial connection at the top. Ocelli not present. Nematocysts: microbasic euryteles. Colour of marginal tentacle bulbs and stomach rich brownish yellow to orange, with central masses of deep purple-brown pigment; cores of two marginal tentacles ochre; marginal tentaculae colourless.

Dimensions (after Rees & Russell, 1937; Russell, 1953; own data): Total height of medusa when fully grown 5-6 mm, usually smaller. Newly liberated medusa 0.42-0.65 mm in height. Hydroid stems up to 2.0-3.5 mm (total height), hydranths 0.5-0.75 mm; stolons 0.05-0.06 mm wide; diameter of hydrocaulus at base 0.10-0.15 mm, hydrocaulus distal end 0.2 mm; medusa buds up to 0.35 mm high and 0.25 mm wide, pedicels 0.13-0.15 mm. For nematocyst dimensions, see Russell, (1938b), Migotto (1996) and (Schuchert (1996).

Further data: Russell (1953) provides tables with details of the medusa development. The medusa is prone to abnormalities. The radial canals may be connected to the stomach by short mesenteries. It is not possible to distinguish the hydroids of *A. dinema* and *A. rugosum* if no medusa buds are present. There is no significant size difference and the perisarc annulation can also be present in *A. dinema*.

Biology: The medusa of *Amphinema rugosum* occurs in the plankton at Plymouth usually from April to July, it has occasionally been seen as late as October (Russell, 1953). In daytime, the medusa lives generally in the deeper water layers below 20 m, but may migrate right to the surface at night. In south-western Ireland, Ballard & Myers (2000) recorded the medusa from July to September.

The polyp stage occurs on a variety of hard substrata. In the Mediterranean, Boero & Freesi (1986) found it regularly in depths of 0.5-20 m. It was present all year round but more abundant during the winter months. It grew on algae, sponges, hydroids, bryozoans, and polychaete tubes.

Rittenhouse (1910) attempted to cross *A. rugosum* and *A. dinema* without success.

Distribution: The medusa occurs circumglobally, it has been recorded along the American coasts from New England to Florida (Mayer, 1910); Caribbean Sea (Kramp, 1959a); in the eastern Atlantic from the Shetland Isles and the British Isles to the Azores (Hartlaub, 1914; Russell, 1953; Russell, 1957; Cornelius, 1992); rarely in the North Sea (Allwein, 1968); western and eastern Mediterranean (Brinckmann-Voss, 1987; Goy *et al.*, 1991); Red Sea (Schmidt, 1973a); Madagascar (Kramp, 1965); Japan (Uchida, 1927); New Caledonia, Sumatra, South China Sea (Kramp, 1965); New Zealand (Kramp, 1965; Schuchert, 1996); Papua New Guinea (Bouillon, 1980).

The polyp has been found in the British Isles (Rees & Russell, 1937), Bay of Biscay (Medel & López-González, 1996); Mediterranean (Boero & Fresi, 1986); Puerto Rico (Wedler & Larson, 1986); Brazil (Migotto 1996); and New Zealand (Schuchert, 1996). No type locality was specified by Mayer (1900a). He based his description on medusae from Newport (Rhode Island), Charleston (South Carolina) and the Tortugas (Florida).

REMARKS: *Amphinema rugosum* has frequently been confused with *A. dinema* until the life cycle was investigated by Rees & Russell (1937) who provided criteria to distinguish it from *A. dinema*. At least for the European fauna, the medusae and polyps with medusa buds are unambiguously distinguishable. In other regions this might be not more difficult.

Migotto (1996) observed a hydroid colony and newly liberated medusae. The latter lacked an apical process. It is thus possible that this process is not always present in all newly liberated medusae. A similar observation was made by Schuchert (1996).

There might be more *Amphinema* species that resemble *A. rugosum* and *A. dinema*. Rees (2000) describes a hydroid from California that had polyps matching *Amphinema rugosum*, but the immature and adult medusae resembled *A. dinema*.

Amphinema rugosum var. *shantungensis* Chow & Huang, 1958 from Chefoo (China) differs from the typical form in lacking marginal tentaculae and being larger.

Amphinema rugosum var. *tsintanensis* Kao, Li, Chang & Li, 1958 has ocelli and thus deviates significantly from the typical form. This variant was therefore justly raised to species level by Xu (1993) as *Amphinema tsintanensis* Kao, Li, Chang & Li, 1958.

Amphinema turrida (Mayer, 1900) Fig. 48

Dissonema turrida Mayer, 1900b: 44, fig. 3-4. – Mayer, 1910: 116, pl. 10 fig. 1, pl. 22 fig. 1.
Amphinema turrida. – Bigelow, 1909: 200, pl. 7 fig. 2, pl 40, fig. 6, pl. 43 fig 3, pl. 44 figs 3-4. – Kramp, 1959a: 118, fig. 112. – Kramp, 1961: 95. – Kramp, 1968: 42, fig. 106. – Goy, 1973: 982, fig. 6. – Bouillon, 1980: 322, fig 8. – Bouillon *et al.*, 2004: 69, fig. 40G.
Stomotoca turrida. – Mayer, 1915: 199, pl. 1 fig. 1.

MATERIAL EXAMINED: MNHN No. 1638; Bay of Villefranche-sur-Mer, Ligurian Sea, France; part of material described by Goy (1973), one much damaged two-tentacled medusa and two medusae with four perradial tentacles.

DIAGNOSIS: *Amphinema* species with elongated, folded gonads that extend along 1/2 of radial canals; two opposite tentacles and many small tentaculae or rudimentary bulbs, most with ocelli.

DESCRIPTION (Mayer, 1900b; Bigelow, 1909; Bouillon, 1980): Umbrella bell-shaped, somewhat higher than wide; with relatively small apical projection; above stomach a clear gastric chamber. Two opposite perradial tentacles, hollow, basal bulbs elongated, conical, laterally compressed; between the single pair of tentacles 12-16

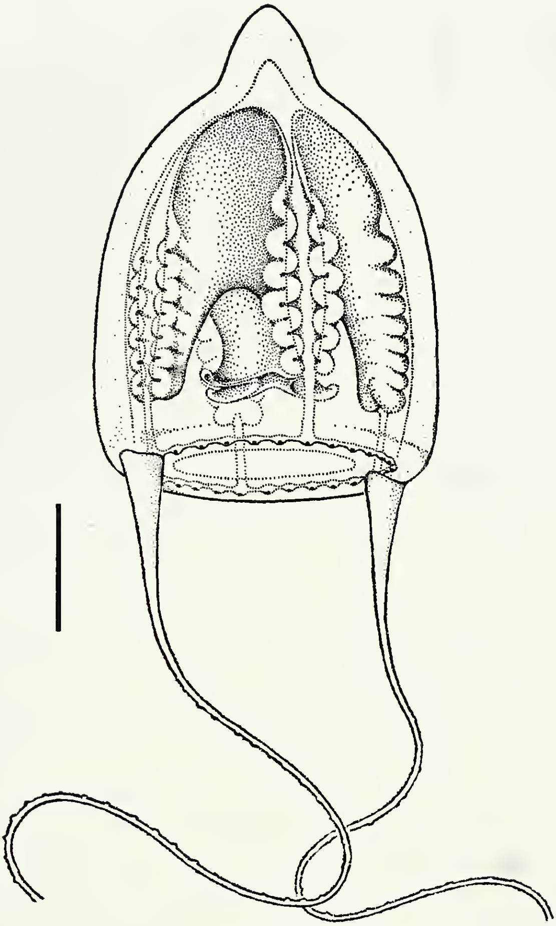


FIG. 48

Amphinema turrida (Mayer, 1900), modified after Bouillon (1980), note that this figure represents the prevailing Pacific form which has no tentaculae but only rudimentary bulbs; scale bar 2 mm.

small, solid tentaculae (Atlantic and Mediterranean), or up to 28 rudimentary bulbs (Pacific); all with red ocelli. Manubrium large, reaching nearly to velum level or beyond it, pyriform, mouth cruciform, lips simple, recurved. Gonads as adradial pairs, folded, extending along 3/4 of the subumbrella and manubrium thus forming long mesenteries.

DIMENSIONS: Bell height 2-7 mm (Bigelow, 1909; Goy, 1973).

OTHER DATA: Mayer (1910) reports that females have 4-7 eggs in each of the four gonads.

VARIATION: Most Pacific animals lack the tentaculae and have rudimentary bulbs only (Bigelow, 1909; Mayer, 1915; Bouillon, 1980). Bigelow (1909) observed rudimentary bulbs and tentaculae in the same animal. It is thus a variable character. Some animals may have four perradial tentacles, although one pair remains small (Bigelow, 1909). Goy (1973) observed animals with four equally developed perradial tentacles (see below). At least in younger stages, the gonads are connected interradially on the manubrium by a thin layer (Bigelow, 1909).

DISTRIBUTION: Florida and Bahamas (Mayer, 1910); Mediterranean (Goy, 1973); Torres Strait (Mayer, 1910); Papua New Guinea (Bouillon, 1980); Japan (Uchida, 1938a); Pacific Side of Mexico (Bigelow, 1909); Chile (Kramp, 1966). Type locality: Tortugas, Florida, USA.

REMARKS: This species is very rare along the European coasts, being known only from four specimens found in the Mediterranean. While the medusa depicted in Goy (1973) is evidently *A. turrida*, other specimens collected by Goy had four equally developed perradial tentacles instead of two only. These specimens could be reexamined for this study. The gonads of these specimens are smooth and unlike the ones in Fig. 48. The gonads are rather large and bulging, enveloping and almost completely hiding the rest of the manubrium (see also *Codonorchis*). It is not clear whether this represents only a fixation artefact. New Mediterranean material is needed for a further evaluation of the status of this form.

Amphinema krampi Russell, 1956 Fig. 49

Amphinema krampi Russell, 1956a: 371, figs 1-2. – Russell, 1958: 81, figs 1-3f. – Kramp, 1959a: 118, fig. 113. – Kramp, 1961: 93. – Russell, 1970: 245, fig. 8s.

MATERIAL EXAMINED: Holotype BMNH 1956.1.10.1, 47.20°N 07.67°W, west of Brittany, 0-821m; 21.07.1955; one badly damaged medusa.

DIAGNOSIS: Medusa oblong; two opposite perradial tentacles, 6-8 small tentaculae; gonads interradial, rugose; manubrium reddish brown and with long mesenteries, several fine cellular strands connecting radial canals and exumbrella.

DESCRIPTION (Russell, 1956a; 1970): Medusa with bell-shaped umbrella, distinctly higher than wide, with a small apical process; jelly moderately thick. Four radial canals and ring canal moderately broad, with smooth margins; radial canals attached to stomach along half of its length, thus forming mesenteries; up to 17 strands of tissue running from each radial canal to the umbrella surface. Two opposite perradial tentacles with swollen elongated basal bulbs; 6-8 marginal tentaculae with nematocysts. No ocelli. Manubrium cross-like in section, about two-thirds length of umbrella cavity, without peduncle; mouth with four simple perradial lips, not crenulated. Four cushion-like gonads, one on each interradial wall of stomach, female gonads irregularly folded and much corrugated, male ones perhaps smooth. Colour of stomach and gonads rich reddish brown, ring canal brownish. Nematocysts: likely two sizes of microbasic euryteles.

DIMENSIONS: Medusa 5-7 mm high, diameter 4 mm.

DIMENSIONS: See Russell (1958) for more histological details of the tentaculae and the tissue strands.

BIOLOGY: A rare deep water medusa, taken with wire lengths of 800 to 1600 m.

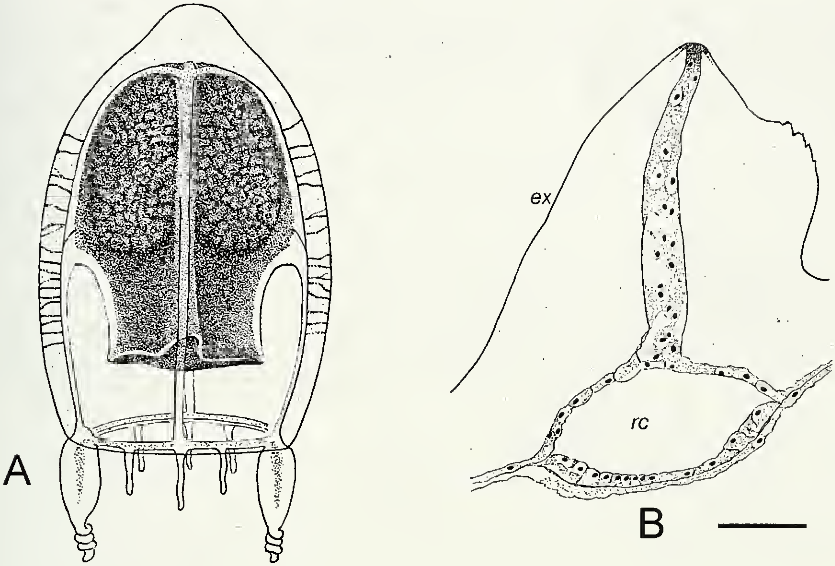


FIG. 49
Amphinema krampi Russell, 1956; from Russell (1958). (A) Female medusa, size 7 mm. (B) Histological section depicting a cellular strand connecting the radial canal (*rc*) with the exumbrella (*ex*).

DISTRIBUTION: Deep waters west of Brittany. Type locality: 47.20°N 07.67°W, max. 821 m.

REMARKS: This species resembles *Amphinema rubrum* (Kramp, 1957), but lacks the characteristic apical chamber. The tissue strands connecting the radial canals and the exumbrella have also not been observed in *A. rubrum*. It is not entirely clear whether the male gonads are smooth or also rugose as in the female. In Russell (1956a) they are depicted with a smooth surface.

Amphinema rubrum (Kramp, 1957) Fig. 50

Merga rubra Kramp, 1957a: 14, pl. 2 fig. 4.
Amphinema rubra. – Kramp, 1959a: 118, fig. 114.
Amphinema rubrum. – Kramp, 1961: 94. – Goy, 1973: 982, fig. 5. – Gili *et al.*, 1998: 117. – Bouillon *et al.*, 2004: 68, fig. 40D.

MATERIAL EXAMINED: MNHN No 1737, 43°39.5'N 07° 17.4'E, 7 Aug. and 1 Oct. 1964; 2 specimens; material of Goy (1973); bell height up to 4.8 mm.

DIAGNOSIS: *Amphinema* species with apical process and large apical chamber, manubrium red-brown, bell margin with tentaculae, gonads smooth.

DESCRIPTION (Kramp, 1957a; own data): Umbrella of medusa higher than wide, moderately thick wall, with pointed apical projection; broad apical chamber above stomach. Two opposite perradial tentacles with large, conical bulbs; no ocelli observed; two perradial and four interradial tenon-like tentaculae. Stomach large, round or cruci-

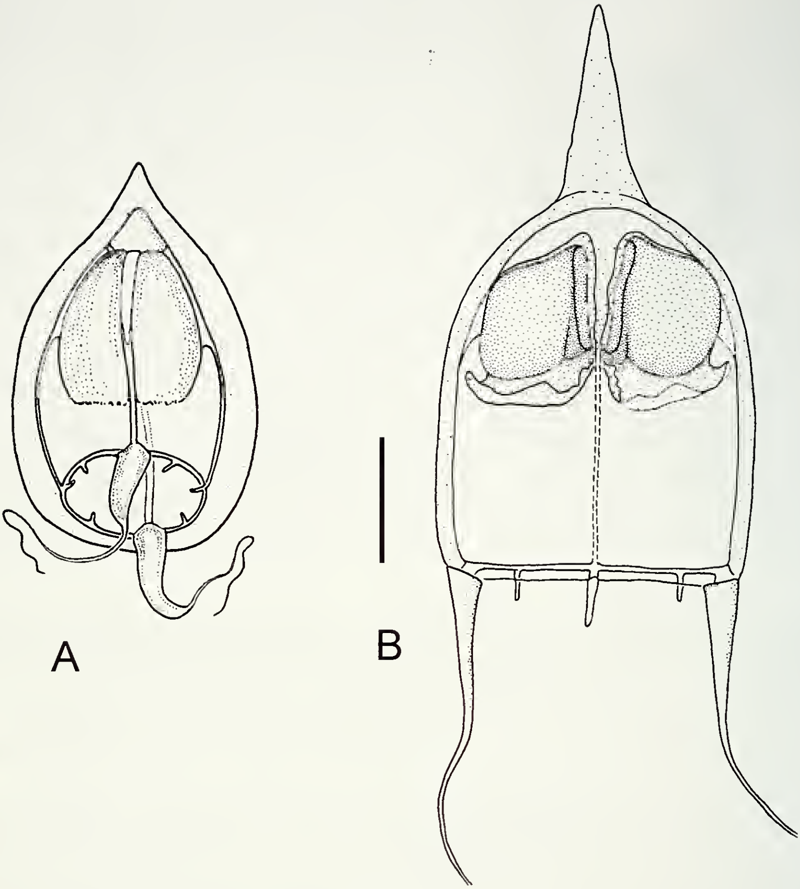


FIG. 50

Amphinema rubrum (Kramp, 1957a). (A) From Kramp (1959a). (B) Schematic drawing after preserved medusae from the Mediterranean, scale bar 1 mm.

form in section, connected to radial canals by relatively long mesenteries (1/2 of manubrium height), mouth likely simple and cruciform. Four smooth gonads completely covering adradial-interradial walls of stomach. Stomach deep reddish-brown.

DIMENSIONS (Kramp, 1957a): Medusa bell up to 7 mm high, 4.5 mm wide.

BIOLOGY: The medusa occurs in depths below 250 m.

DISTRIBUTION: Antarctica, Mediterranean. Type locality: 57.60°S 29.908°W, 500-250 m, North of South Orkney Islands, Antarctica.

REMARKS: Kramp (1957a) based his description on a preserved, damaged specimen that lacked the mouth region. As ocelli are usually rapidly lost in preserved material, it is also not known whether they were originally present. The species has also been recorded for the Mediterranean by Goy (1973) and Gili *et al.* (1998). A re-examination of the material of Goy (1973) confirmed her identification. The manubrium is attached below the highest point of the subumbrella, thus creating a transparent, chamber-like cavity above the upper level of the manubrium (but which is not separated from the gastric cavity).

Amphinema biscayana (Browne, 1907) Fig. 51

Bimeria biscayana Browne, 1907: 21, fig. 1, pl. 1 figs 4-5.
Garveia biscayana. – Vervoort, 1985: 277.
Amphinema biscayana. – Schuchert, 2000: 415, fig. 3. – Schuchert, 2001: 21, fig. 11A-D.

MATERIAL EXAMINED: Syntypes BMNH 1948.10.1.118, slides and alcohol material; Bay of Biscay (Allen's station XIII); 752 m; August 1906; infertile. – MHNG INVE25967, alcohol and slide material; 62.340°N; 16.997°W; Iceland; 2074 m; 27 August 1991; with medusa buds. – MHNG INVE36665 (ex CARACOLE 132-10 KGS 15); 55.544°N 15.687°W (Rockall Plateau); 865 m; 13 August 2001; infertile.

DESCRIPTION: Colonies erect, when fully grown stem and branches stout, may be covered by silt particles. Very thin stolons forming a dense rooting structure (rhizoid) for anchoring in soft substrata. Alternatively, stolons can be creeping on solid substrata. Colony highly polysiphonic, branching profusely, distal part monosiphonic. Polysiphonic part, composed of a thick-walled axial tube surrounded by thinner, tightly packed, parallel auxiliary tubes. Axial tubes of side branches originate from an auxiliary tube of main branch and not from axial tube. Only in distal monosiphonic parts, the axial tube is branching. Distal monosiphonic outgrowths as thick as axial tubes, composed of long main branches with mostly short side branches, all with hydranths. Some hydranths on short pedicels also grow out of auxiliary tubes on lower polysiphonic parts of colony. Hydranths covered by adhering pseudohydrotheca that ends below tentacle whorl, can be infested with fine silt particles. Hydranth cylindrical, one whorl of 10-12 filiform tentacles, hypostome conical or dome-shaped. Some hydranths bent at base. Gonophores arise singly, far below hydranths in perisarc covered zone. Young gonophores pear-shaped, older ones spherical, enclosed in thin perisarc membrane. Gonophores develop into medusa. Oldest medusae observed had a simple manubrium without appendages, four broad radial canals, two opposite tentacle bulbs were strongly developed and large, elongated, conical, presumably without ocelli, each large bulb with one long tentacle without desmonemes. Other pair of perradial bulbs small or absent. Between larger tentacles (presumably at interradial positions) at least two very small tentaculae (totally at least 4), their tips provided with desmonemes. Nematocysts of polyp: desmonemes; asymmetric microbasic euryteles. Nematocysts of young medusa: like polyp plus an additional egg-shaped heteroneme (for figures see Schuchert, 2000).

DIMENSIONS: Colonies up to 4 cm high, rhizoid length may reach 2 cm; diameter of stems up to 3 mm; axial tubes about 0.4 mm, auxiliary tubes 0.1 mm.

BIOLOGY: A deep water species recorded in depths of 752-2074 m.

DISTRIBUTION: Bay of Biscay (Browne, 1907); Rockall Plateau (this study); south of Iceland (Schuchert, 2000). Type locality: 48.117°N 08.217°W.

REMARKS: The axial tubes of the side branches are normally produced by a tube that grows out of an auxiliary tube of the original branch, and not by a branching axial

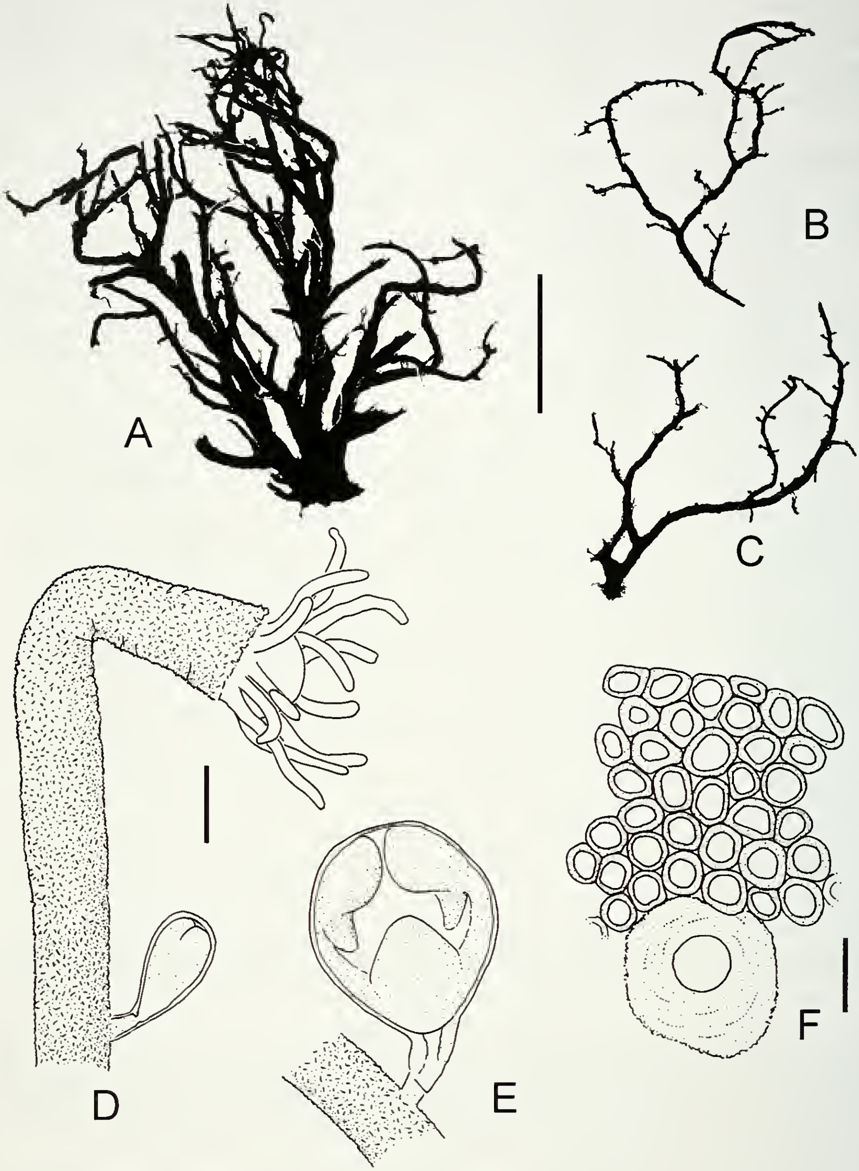


FIG. 51

Amphinema biscayana (Browne, 1907). (A-C) Silhouettes of colony forms, scale bar 1 cm. (D) Hydranth with pseudohydrotheca and young medusa bud, scale bar 0.2 mm. (E) Advanced stage of medusa bud, same scale as D. (F) Segment of a cross-section of the stem showing central axial tube and peripheral auxiliary tubes (not all shown), scale bar 0.2 mm. After preserved material from Iceland (A, D-F) and the Rockall Plateau (B-C).

tube itself. This latter, more common branching pattern, is known from the similar e.g. *Garveia arborea* (Browne, 1907).

This species cannot yet be allocated to the correct genus, as information on the mature medusa is not available. The genus *Amphinema* used is only a guess, the colonies could belong to several other member of the family Pandeidae. Speculating on the possible adult medusa of *A. biscayana,* and considering only pandeid medusae known from the North Atlantic having no ocelli and possessing tentaculae, *Amphinema krampi* Russell, 1956a and *Merga reesi* Russell, 1956b seem to be good candidates. Both are deep water medusae first discovered close to the type locality of *Amphinema biscayana*.

Amphinema bouilloni n. spec. Fig. 52

Codonorchis octaedrus. – Boero *et al.*, 1997: 359, figs 1-3.
[not *Codonorchis octaedrus* Haeckel, 1879]

TYPE MATERIAL: Not examined, according to Bouillon *et al.* (1997) an adult male medusa has been deposited as type specimen at the Institut Royal des Sciences naturelles de Belgique, Bruxelles, IG 27838.

DIAGNOSIS: *Amphinema* species with ocelli, up to 14 rudimentary bulbs present, apical process present, aboral processes of manubrium penetrating into mesogloea; gonads interradial on manubrium, horse-shoe shaped, with slight folds. Hydroid sessile, medusa buds on stolons, with pedicels.

DESCRIPTION (Boero *et al.,* 1997): Hydroid colonial, stolons tubular; hydranths sessile (without pedicel); hydranth body naked, yellow, white hypostome, single whorl of 4-6 filiform tentacles; hydrant contracts longitudinally and not sideways. Medusa buds orange, ovoid, arising singly from stolons, on pedicel of variable length. Nematocysts: microbasic euryteles and desmonemes.

Newly released medusa higher than wide, with small apical projection, exumbrella with numerous nematocysts; four ribbon-like radial canals and ring canal; with four perradial marginal bulbs, each with a red ocellus, one opposite pair of bulbs larger, conical, with a short tentacles on each. Manubrium tubular, orange, reaching $1/4$ of subumbrellar height, mouth quadratic with four small lips.

Mature medusa higher than wide, lateral wall relatively straight, with well formed apical projection, no gastric peduncle; four radial canals ribbon-like, broad, jagged, forming short mesenteries where entering stomach. Margin with 16 bulbs, all with abaxial ocelli; one perradial opposite bulb-pair large and tapering into long tentacles, other bulbs small, conical, sometimes with a short tentacle rudiment. Manubrium relatively small, reaching about $1/2$ of the height of the subumbrellar cavity, with quadratic base, with one big and several small apical processes penetrating into apical mesogloea, mouth-region cruciform in section, four simple lips. Gonads on interradial wall of manubrium only, separated perradially, large, horse-shoe shaped, with some interradial folds. Nematocysts: microbasic euryteles and desmonemes.

DIMENSIONS (Boero *et al.,* 1997): Polyp 0.25 mm; newly liberated medusa 0.65 mm wide and 1 mm high; bell height of mature medusa 2.2 mm, apical projection 0.7 mm.

TYPE LOCALITY: Mediterranean Sea near Otranto. Apulia. Italy; depth 25 m.

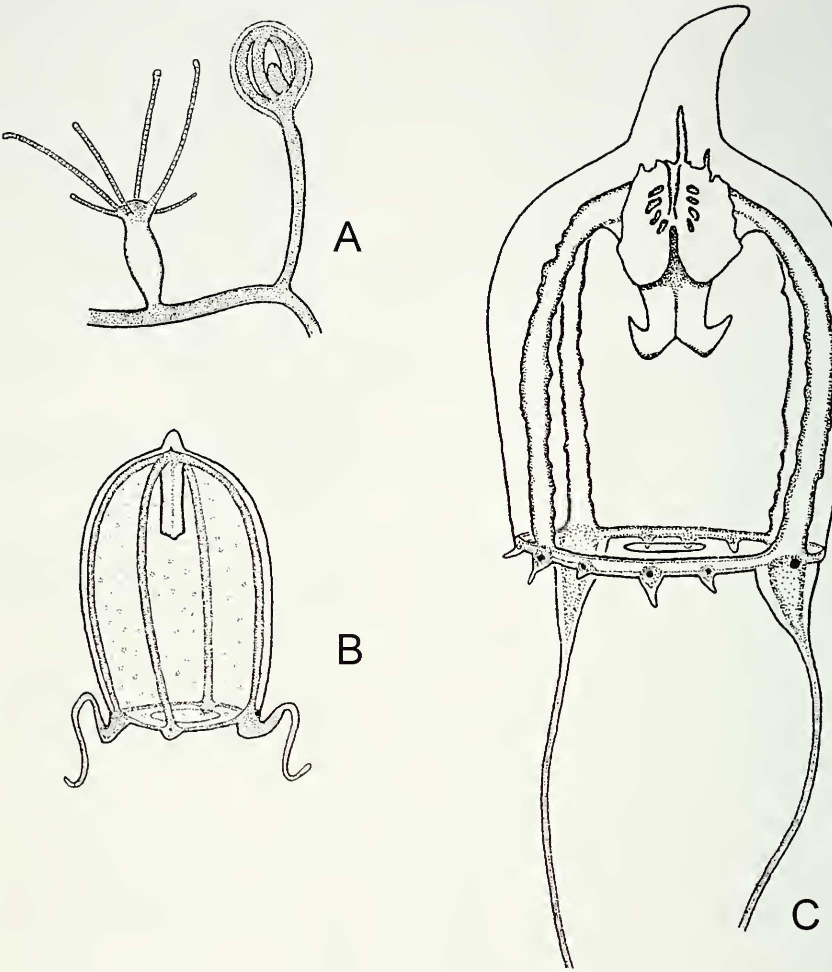


FIG. 52
Amphinema bouilloni new species; from Boero *et al.* (1997), for dimensions see text. (A) Hydroid with medusa bud. (B) Newly released medusa. (C) Mature medusa.

REMARKS: This species is based on material originally attributed to *Codonorchis octaedrus* by Boero *et al.* (1997). The arguments why I disagree with this identification are given in the remarks under the genus *Codonorchis*. The species is therefore described as new. It resembles closely *Amphinema australis* (Mayer, 1900b) and *Amphinema tsingtauensis* Kao *et al.*, 1958, two other *Amphinema* species with ocelli. *Amphinema turrida* also has ocelli, but its unique gonads make it quite distinct. *Amphinema australis* differs from *A. bouilloni* in the following details (Bigelow, 1909; Mayer, 1910): no aboral processes of manubrium, only 8 marginal bulbs and not 16, the bell-shape is relatively wide and not so high, the gonads are smooth and bulging. *Amphinema tsingtauensis* from China appears even more similar, but differs in the following traits (Kao *et al.*, 1958): no aboral processes of manubrium, the size is 2-3 times larger, 22 bulbs instead of 16, gonads in marked oblique folds. Admittedly, these differences relate to somewhat variable characters that can be considered as not so suitable to distinguish species. However, as long as the life cycle of the *A. australis* and *A. tsingtauensis* remain unknown, a more detailed comparison with *A. bouilloni* is impossible and it is therefore preferable to have it named as a new species.

Genus ***Leuckartiara*** Hartlaub, 1914

TYPE SPECIES: *Geryonia octona* Fleming, 1823 [designation by Kramp, 1959a].

SYNONYM: *Dinema* Van Beneden, 1867 [type species *Dinema slabberi* Van Beneden, 1867, = *L. octona*].

REFERENCES: Hartlaub (1914: 282), Kramp (1926: 76), Ranson (1936: 70), Rees (1938: 11); Kramp (1959a: 120), Russell (1953: 187), Schuchert (1996: 68), Pagès *et al.* (1992: tab. 1), Bouillon & Boero (2000: 107).

DIAGNOSIS: Hydroids colonial, arising from creeping stolons; hydrocauli covered by perisarc, not or only sparingly branched, stems monosiphonic. Perisarc extends onto hydranth body as a more or less gelatinous pseudohydrotheca which does not envelop the tentacles. Hydranths with a conical hypostome and one whorl of filiform tentacles. Gonophores develop on cauli or stolons, liberated as medusae. Medusa mostly with an apical projection of variable size. Manubrium voluminous, connected to radial canals by mesenteries. Mouth with extensively folded and crenulated margin. Gonads on interradial walls of manubrium, bipartite but with broad connection in upper half, with with various degrees of folding, no or only few interradial pits. Radial canal very broad, often jagged. With many tentacles arising from elongated bulbs, laterally compressed; small bulbs or growth arrested tentacles often present. With or without ocelli.

REMARKS: See also under *Neoturris*. Pagès *et al.* (1992) provided a tabular review on all known *Leuckartiara* species. A key to all species is provided by Xu & Huang (2004).

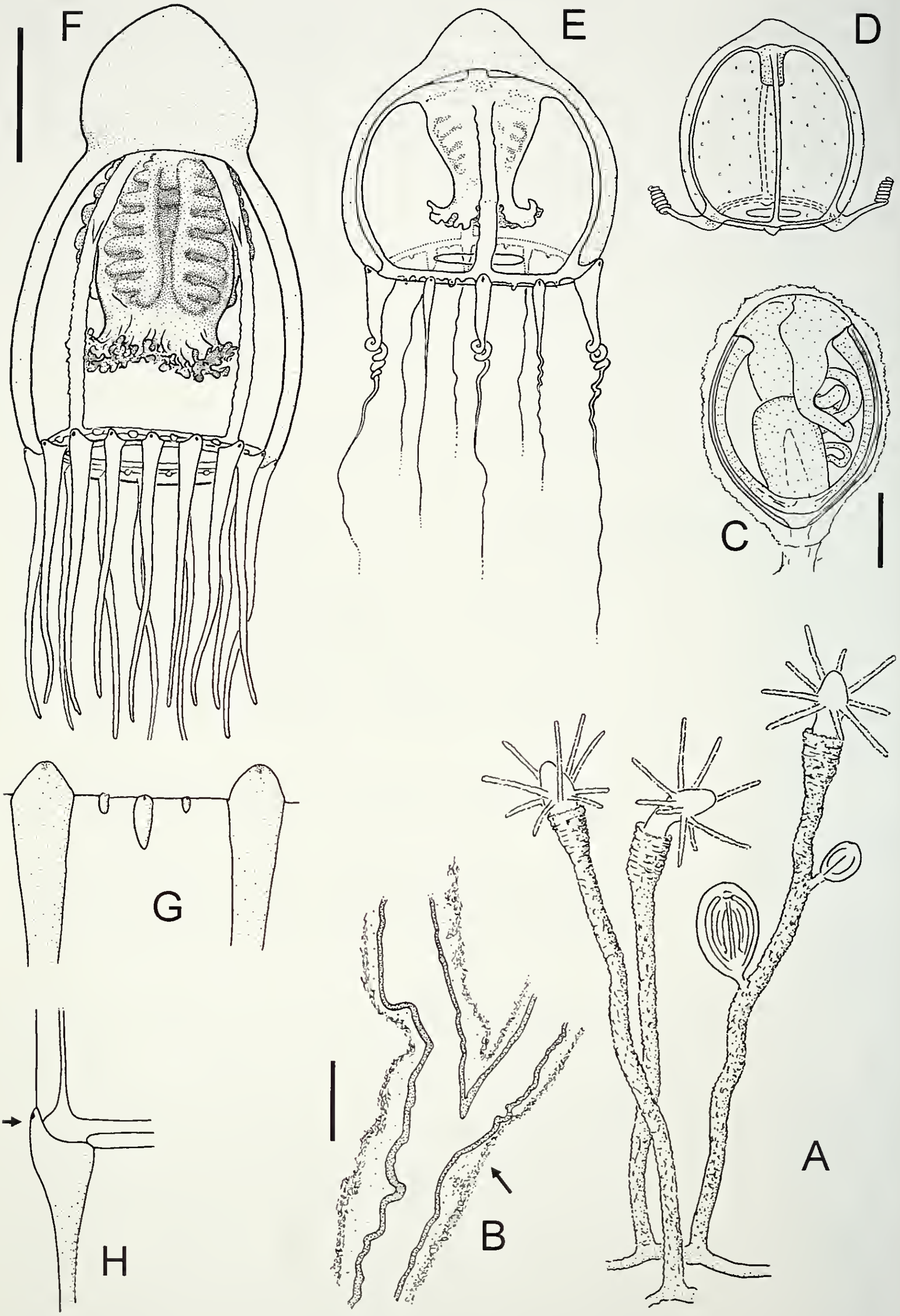
Even for a restricted region like the north-eastern Atlantic, juvenile and subadult medusae of the genera *Leuckartiara* and *Neoturris* can be very difficult to identify. There is also quite a lot of variation in fully mature specimens that renders identifications not an easy task.

KEY TO THE *LEUCKARTIARA* MEDUSA TREATED HERE:

1a more than four fully developed tentacles 2
1b only four perradial tentacles fully formed, others small; no ocelli . . . . *L. brownei*
2a mesenteries along entire stomach . . . . *L. grimaldi*
2b mesenteries shorter than stomach 3
3a mature with 1-3 rudimentary bulbs between fully formed tentacles, with abaxial spurs . . . . *L. octona*
3b few rudimentary bulbs but majority of tentacles not fully grown, no abaxial spurs . . . . *L. nobilis*

Leuckartiara octona (Fleming, 1823) Fig. 53

Geryonia octona Fleming, 1823: 299.
Oceania pileata. – Ehrenberg, 1837: 190, pl. 8 figs 2-4.
[not *Neoturris pileata* (Forsskål, 1775)]
? *Turris neglecta* Lesson, 1843: 284.


F
E
D
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H

Oceania episcopalis Forbes, 1848: 27, pl. 2 fig. 1.
Oceania turrita Forbes, 1848: 28, pl. 2 fig 2.
Eudendrium sessile Wright, 1857: 60, pl. 3 figs 16-17.
Eudendrium pusillum Wright, 1857: 84, pl. 2 figs 8-9.
Atractylis repens Wright, 1858: 450, pl. 22 figs 4-5. – Wright, 1859a: 108, pl. 1 figs 4-5.
Atractylis palliata Wright, 1861: 129, pl. 4 fig. 6.
Perigonimus minutus Allman, 1863: 11.
Perigonimus vestitus Allman, 1864b: 57. – Allman, 1872: 326, pl. 11 figs 1-3. – Rees, 1956a: 345, synonym.
Tiara smaragdina Haeckel, 1864: 336. – Hartlaub, 1914: 294, synonym.
Dinema slabberi Van Beneden, 1867: 130, pls 9-10.
? *Oceania gaedii* Van Beneden, 1867: 95.
Perigonimus repens. – Hincks, 1868: 90, pl. 16 fig. 2.
Oceania coronata Allman, 1871: 33, fig. 8.
Tiara octona. – Haeckel, 1879: 57.
Perigonimus Jonesii Osborn & Hargitt, 1894: 27, fig. 1-12. – Rees, 1956a: 340, synonym.
? *Perigonimus gelatinosus* Duerden, 1895: 327, pl. 14 figs 2-3. – Rees, 1956a: 340, possible synonym.
Perigonimus pugetensis Heath, 1910: 74, figs 1-2. – Rees, 1956a: 343, synonym.
? *Perigonimus napolitanus* Hargitt, 1904: 571, pl. 22 fig. 25.
Tiara papua. – Maas, 1909: 9 pl. 1 fig. 3.
[not *Neoturris papua* (Lesson, 1843)]
Perigonimus vestitus f. *radicans* Vanhöffen, 1910: 286, fig. 11a-c.
Turris vesicaria. – Mayer, 1910: 126, pl. 12 figs 2-3, pl. 13 fig. 7.
[not *Catablema vesicarium* (A. Agassiz, 1862)]
Perigonimus repens. – Broch, 1911: 14, fig.11. – Broch, 1916: 52, fig. P. – Vervoort, 1946: 141, figs 54-55.
Leuckartiara octona. – Hartlaub, 1914: 285, figs 238-214, figs 244-253. – Kramp, 1926: 76, pl. 2 figs 5-7, text fig. 35. – Uchida, 1927: 211, fig. 37. – Ranson, 1936: 75. – Rees, 1938: 11, fig. 3-5. – Russell, 1938b: 153, figs 41-44. – Russell, 1953: 188, pl. 11 figs 5-6, pl. 12. fig. 3, pl. 30-31, text figs 91-96. – Kramp, 1959a: 121, fig. 119. – Kramp, 1961: 105. – Kramp, 1968: 47, fig. 121. – Millard, 1975: 123, figs 41a-d. – Arai & Brinckmann-Voss, 1980: fig. 29. – Hirohito, 1988: 106, fig. 38f-g. – Pagès *et al.,* 1992: 10, 12, fig. 11. – Ramil & Vervoort, 1992: 21. – Migotto, 1996: 16, fig. 3e-g. – Schuchert, 1996: 68, fig. 40a-b. – Bouillon *et al*., 2004: 70, fig. 41D-F. – Pages et al., 2006: Fig. 7F.
Leuckartiara octona var. *minor* Ling, 1937: 353: fig. 2.

MATERIAL EXAMINED: Mediterranean, Ligurian Sea, Bay of Villefranche-sur-Mer, 70 m; 4 April 2005; 1 fertile medusa, examined alive, used for DNA extraction, 16S sequence **AM411421**. – MHNG INVE49100, hydroid culture obtained from Prof. G. Plickert, Cologne, originally isolated from hermit crab shells from the North Sea, grew well and produced many medusa, these cultivated to a size of 3-4 mm, 6-8 tentacles plus 8 bulb rudiments, with abaxial spurs, some hydroids preserved and deposited in MHNG; 16S sequence **AM411422.** – MHNG INVE35728, large colony on *Aporrhais pespelecani* Italy, Naples, Palazzo Donn'Anna; 30

FIG. 53

Leuckartiara octona (Fleming, 1823). (A) Hydroid colony with medusa buds; for sizes see text; modified from Hincks (1868). (B) Optical section of hydrocaulus with branching point, note detritus infested outer perisarc layer (arrow), scale bar 0.1 mm, after preserved material from Helgoland. (C) Advance medusa bud, scale bar 0.1 mm; after preserved material from Helgoland. (D) Newly liberated medusa, bell height 1.2 mm; modified after Russell (1953). (E) Young medusa with beginning gonad formation, bell height 4 mm; modified from Russell (1953). (F) Mature medusa after preserved material from Denmark, scale bar 3 mm. (G) Magnified section of bell margin with the bases of a pair of normal tentacles flanking three rudimentary bulbs, the middle one is club-shaped. (H) Lateral view of a tentacle base showing abaxial spur (arrow), after preserved material.

March 1911. – ZMUC; Denmark, Frederikshavn, inner side of harbour; 0 m; 27 July 1981; mature medusae. – BMNH 1982.11.30.5; Great Britain, Eddystone; 4 June 1925; coll. F. S. Russell, numerous mature medusae. – BMNH, slide with no registration number, Loch Striven, Clyde, 55 m, 19 September 1931, several polyps with medusa buds. – BELUM Md643, Ireland, Donegal, St Johns point, Portnagh Rock; 2 mature medusae. – ZSM, slides 20000635 and 20000636, as *Perigonimus gelatinosus*, Duerden, on *Pagurus*, loc. Helgoland, Stechow collection, mentioned in Stechow (1919).

DIAGNOSIS: *Leuckartiara* medusa with 8-23 fully developed marginal tentacles, one to three rudimentary marginal bulbs between adjacent pairs of tentacles; tentacle bulbs with distinct abaxial spur bearing an ocellus; without exumbrellar nematocyst tracks, with apical process. Mature 10-15 mm in height.

DESCRIPTION (Kramp, 1926; Rees, 1938; Russell, 1953; own observations): Hydroids arising from creeping, branching to reticulate hydrorhiza. Shoots either unbranched or sparingly branched; sister-branches not adnate for some distance; hydranth pedicels can be relatively long, but variable and depending on environment, sometimes almost subsessile. Perisarc often two-layered with a particle infested outer gelatinous layer and a solid inner layer, solid perisarc smooth or variable corrugated, transparent or horn coloured with a distinct membranous dilatation reaching to base of tentacles (pseudohydrotheca). Hydranths spindle-shaped, with a single whorl of 6-12 tentacles. Medusa buds borne on short stalks arising from stolons or the hydranth pedicels. Advanced medusa buds ovoid, covered by thin perisarc membrane, medusa structure well visible, only two tentacles developed. Nematocysts: desmonemes and microbasic euryteles (Bouillon, 1985).

Newly liberated with or without small apical process, with scattered exumbrellar nematocysts. Stomach cylindrical, about one-third the height of subumbrella cavity in length, mouth simple, without lips. Two opposite perradial tentacles and two opposite perradial rudimentary marginal bulbs, without ocelli; the marginal tentacle bulbs, rudimentary marginal bulbs and stomach are pale straw to ochreish in colour. The first ocelli appear on the second perradial pair of tentacles when the bell reaches a size of about 2 mm. At the eight tentacle stage, with a height of about 4 mm, the mouth is already considerably crenulated and the gonads begin to form on the adradial surfaces of the stomach. Sixteen tentacles are reached at about 7-12 mm bell height.

Mature medusa umbrella bell-shaped, higher than wide, with conical or spherical solid apical process varying much in size; jelly thin; velum narrow. Four radial canals broad, with smooth or jagged outlines; ring canal broad, with smooth outlines; radial canals joined to stomach by long mesenteries. Eight to 23 (usually around 16) marginal tentacles, hollow, smooth, with large, laterally compressed, elongated conical basal bulbs, clasping umbrella margin and forming pronounced abaxial spurs on exumbrellar surface, nematocysts of tentacle concentrated in adaxial clasps. Usually one to three rudimentary marginal bulbs between adjacent tentacles (temporarily growth arrested), either simply hemispherical buttons or pine-cone shaped appendage, not tapering into short tentacle. One small abaxial ocellus on each tentacular and rudimentary marginal bulb. Stomach flask shaped, not extending beyond umbrella margin in full extension, with broad base; mouth with four crenulated lips. Gonad situated interradially on folds of stomach wall, in two tiers, joined by transverse bridge, with several folds directed outwards to each perradius. Nematocysts: microbasic euryteles and microbasic mastigophores (Russell, 1938b). Colour of marginal tentacles and stomach a deep flesh-pink to crimson or yellowish; ocelli crimson.

DIMENSIONS: Mature medusa 5-20 mm, usually around 10 mm; medusa when first liberated from its hydroid about 1.1 mm in height. Nematocysts of medusa (Russell, 1938b): microbasic euryteles (8-10.5)x(3-4.5)μm; microbasic mastigophores (7)x(3.5-4)μm. Hydroid dimensions (Rees, 1938): stolons diameter 0.05-0.07 mm; total height of stems 1.5-3.8 mm; hydrocaulus diameter 0.08-0.12 mm; hydranths up to 0.5-0.7 mm, diameter of hydranths 0.25-0.3 mm; length of medusa buds 0.6 mm, diameter of medusa buds 0.45-0.5 mm, stalk of medusa bud 0.1-0.3 mm.

DISTRIBUTION: A neritic, circumglobal species occurring in subtropical to temperate seas. The medusa is common and widely distributed on the north-western European coasts (see summaries in Hartlaub, 1914; Kramp, 1926; Russell, 1953; Kramp 1959a; Kramp, 1965): coasts of the British Isles; west coast of Norway to Lofoten; Skagerrak and Kattegat but not the Baltic Sea; south of Iceland; Rockall; France and Iberian Peninsula; western Mediterranean; east coast of North America from Newport to Labrador; western Africa (Kramp (1959a); South Atlantic (Pages *et al.*. 1992); Red Sea (Schmidt, 1973a); Indian- and Pacific Ocean (Hartlaub, 1914; Kramp, 1965; Schuchert, 1996). Arai & Brinckmann-Voss (1980) do not include the medusa in the fauna of British Columbia. The polyp has also been widely reported (usually as *Perigonimus repens*) along coast of the north-eastern Atlantic and Mediterranean (Rees, 1938); also South Africa (Millard, 1975), Brazil (Migotto, 1996), and the Pacific and Indian Ocean (Rees, 1938).

ADDITIONAL DATA: For more structural and developmental details see Kramp (1926), Rees (1938), and Russell (1953). The shape and size of the apical process is variable. The hydroid morphology and dimensions are also variable and depend on food and substrate (Rees, 1938). The ultrastructure of the ocelli is described by Singla (1974) (species identity perhaps not clear, see Arai & Brinckmann-Voss, 1980).

BIOLOGY: The hydroid is nearly always living in association with other animals, it occurs in association with many species of crustacean and molluscs, in particular also on the parapodia of the polychaete *Aphrodite* (Leloup, 1934; Latham, 1963). Also known to occur on fish (Rees, 1938). Depth distribution 10-400 m (Christiansen, 1972). In Norway, Christiansen (1972) observed medusa budding from May to October. Kramp (1930) says that medusa liberation stops in August or somewhat later. Robson (1914) records the hydroid as liberating medusae from September to February on the Northumberland coast.

As summarized by Kramp (1926), the medusa is found at the British coasts from April or May (young individuals) to October or November. In Danish waters, the young individuals appear first in May or June; during autumn *L. octona* is one of the most abundant medusa of the region; in certain years a number of individuals may surpass the winter and be observed in the plankton as late as March or April the next year. At the coast of Norway, the medusa appears in June and occurs at least until November. In the Mediterranean, the medusa is less frequent than in the Atlantic, it has been observed from February to November (Goy, 1973; Brinckmann-Voss, 1987). The depth range of the medusa is about 0-300 m (Kramp, 1965), occasionally also caught in deeper waters.

The medusa makes daily vertical migrations, it is present at the surface only during night-time (Buecher & Gibbons, 2003). Feeding habits have been described by (Lebour, 1922, 1923). The medusa is highly voracious, eating almost everything given to them.

Vannucci (1960) observed that a female medusa was able to spawn eggs almost daily for a period of two months.

REMARKS: *Leuckartiara octona* is a common and well known species, but it has a complicated taxonomic history that has been worked out by several authors (e. g. Hartlaub, 1914; Rees, 1938; Russell, 1953; Rees, 1956a; Kramp, 1961). There is thus no need to discuss it here again. The list given above may be not complete as there are also several doubtful cases. The species has repeatedly been confounded with other similar species like *Leuckartiara nobilis*, *Catablema vesicarium*, and *Neoturris pileata*. Only after the thorough revision of Hartlaub (1914), the taxonomy became more or less stable. However, as indicated in Arai & Brinckmann-Voss (1980: 56), the situation might be more complicated.

Leuckartiara octona var. *minor* Ling, 1937 is about 5 mm high and has only eight tentacles. It falls well within the range of variation seen in other populations and is therefore here considered a synonym.

Leuckartiara nobilis Hartlaub, 1914 Figs. 54-55

Leuckartiara nobilis Hartlaub, 1914: 308, figs 257-260. – Kramp, 1926: 83, fig. 36a-e, pl. 2 fig. 9. – Russell, 1953: 195, pl. 12 fig. 4, text-fig. 97. – Kramp, 1959a: 120, fig. 120. – Kramp, 1961: 104. – Kramp, 1968: 47, fig. 123. – Arai & Brinckmann-Voss, 1980: 54, fig. 28. – Pagès *et al.*, 1992: 12.

MATERIAL EXAMINED: BMNH 1954.11.13.85; Ireland, Valentia; several medusae collected 1898 [by E. Browne ?], could be paratype material. – BMNH 1954.11.13.b3; France, Villefranche; 13 March 1913; labelled as ? paratype, leg. & det. C. Hartlaub (comment: material is not mentioned by Hartlaub (1914), paratype status unclear. – Scotland, Firth of Lorn, Dunstaffnage Bay; 0 m; 7 May 2004; one medusa, identity not entirely clear (see Fig. 55); 14 mm high, 8 tentacles of varying size, 8 tentacles and 8 rudiments; tentacles without abaxial spurs, with ocelli, gonad and manubrium not fully developed, apical process 1/2 of total height, 16S sequence **AM183135**. – BMNH 1952.2.20.71; France, Villefranche, Cap Ferrat; 0 m; 15 April 1949; ca. 16 specimens; collected A. K. Totton. – ZMUC; 57.050°N 11.333°W, eastern Atlantic; 65 m wire; 28 May 1908; Thor Station 12(8), 1 medusa, det. Kramp. – ZMUC Thor station 181; 61.567°N 18.750°W, eastern Atlantic; 20 m wire; 10 July 1904; 1 medusa.

DIAGNOSIS: Up to 40 relatively widely spaced tentacles, of these only up to 8-23 fully developed, others small, in variable stages of development, but with thin, pointed ends; only few rudimentary bulbs; bulbs without distinct abaxial spurs, with ocelli.

DESCRIPTION (after Kramp, 1926; Russell, 1953; own data): Umbrella bell-shaped, higher than wide, with pointed or rounded solid apical process of variable size; jelly thin. Velum narrow. Four radial canals very broad, with irregular jagged outlines; ring canals broad with smooth outlines; radial canals joined to stomach by mesenteries.

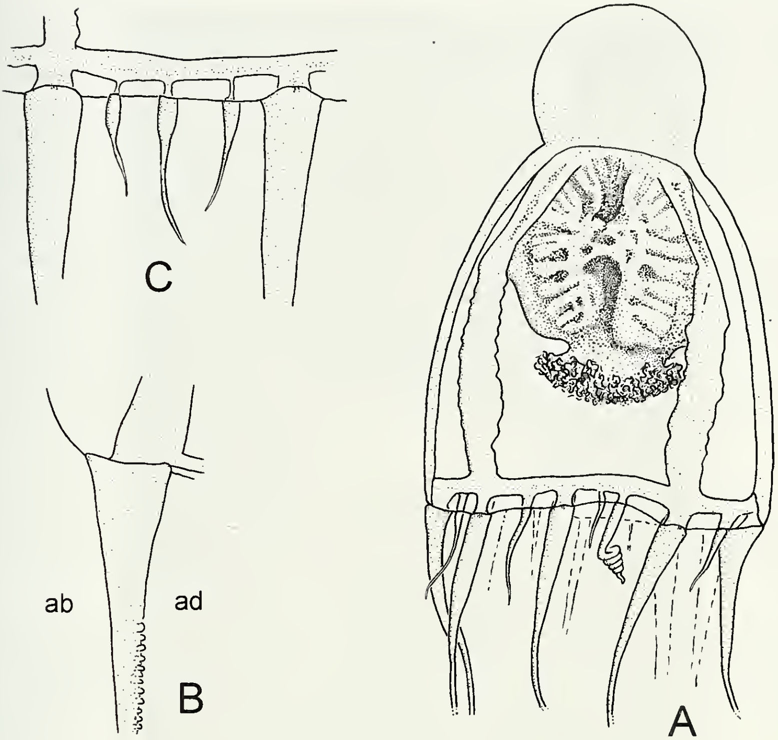

FIG. 54

Leuckartiara nobilis Hartlaub, 1914; after preserved material from the Mediterranean. (A) Mature medusa, about 23 mm high. (B) Perradial tentacle in side view, note absence of abaxial (ab) spur on bulb and the nematocyst clasps on the abaxial side (ab). (C) Part of bell margin with characteristic tentacle arrangement: two fully formed tentacles flank three smaller, not fully developed tentacles.

Up to forty or more marginal tentacles, hollow, smooth, with elongated, conical, laterally compressed basal bulbs which clasp the umbrella margin but do not form well-developed abaxial spurs; marginal tentacles fairly widely spaced; only about 8-23 tentacles are fully developed, the intercalated remaining tentacles are much smaller and less developed, ending in a pointed tip (unlike club or pine-cone); with only a few scattered rudimentary bulbs. One small ocellus on each tentacle bulb, at abaxial side close to exumbrella. Tentacles have nematocysts concentrated on adaxial side, forming clasps, also gastrodermis has an irregular outline. Stomach flask-shaped, constricted near mouth, not extending beyond umbrella margin in full extension, with broad base; mouth with much folded lips. Gonads interradial on folds of stomach, bipartite with transverse connection in upper half, adradial parts with many folds directed outwards to each perradius, there are regularly a few pits in the interradial region of the gonads. Colour: stomach, i.e. gonad, orange red; tentacle bases bright yellowish-brown or white.

FIG. 55

Leuckartiara nobilis Hartlaub, 1914, living medusa from Dunstaffnage, Scotland, about 14 mm high. This plate illustrates the difficulty to identify subadult *Leuckartiara* species. The medusa has 8 tentacles and adradial rudiments, the typical gonad-folds are clearly visible. It was identified as *L. nobilis* and not *L. octona* because there are no abaxial tentacle spurs and at this size *L. octona* should have more tentacles. However, there remains some ambiguity. The shape and size of the apical process is highly variably in both species.

DIMENSIONS: Total height of medusa when fully grown 20-27 mm, apical process up to 1/5 of total height, in younger specimens up to $^1/_2$.

VARIATION: Apparently fully grown medusae from the Atlantic can have 12-23 maximally developed tentacles, while Mediterranean medusae have only 8-12.

DISTRIBUTION: In the North Atlantic found usually rather far off the coast. Recorded from the western Mediterranean, SW of Ireland, Atlantic Ocean west of Scotland, Rockall, at Iceland, New Foundland, one exceptional finding at Denmark (Hartlaub, 1914; Kramp, 1926; Goy, 1973); also in the Pacific near Japan and British

Columbia (Kramp, 1965; Arai & Brinckmann-Voss 1980). Type locality: Not designated, Hartlaub (1914) had material from the Ligurian Sea (Monaco, Villefranche-sur-Mer) and from western Ireland (Valencia, now spelled Valentia).

BIOLOGY: A species that seems to prefer oceanic regions. There are only few records, these indicate an occurrence during the summer months in the Atlantic and in spring for the Mediterranean (Goy, 1973; Brinckmann-Voss, 1987). Fraser (1969) describes the feeding behaviour.

REMARKS: This is a relatively little known species of which the polyp stage remains to be discovered. Some Atlantic specimens identified by Hartlaub (1914) and Kramp (1926) as *L. breviconis* appear only gradually different from *L. nobilis* (see discussion under *N. breviconis*).

The sample from Scotland (Fig. 55) was rather young and it was not possible to identify it with the desirable reliability. Its 16S sequence was quite different (7.9% bases) from an unambiguously identified *L. octona* (AM411421).

Leuckartiara grimaldii Ranson, 1936 Fig. 56

Leuckartiara grimaldii Ranson, 1936: 78, pl. 1 figs 7-8. – Kramp, 1961: 104. – Kramp, 1959a: 120.

DIAGNOSIS: 16 mm high, 12 mm wide; bell-shaped, thin walls, no apical projection. Stomach very large, smooth, filling 2/3 or more of subumbrella, mesenteries along entire length of stomach; gonads not observed; mouth folded. Radial canals short, broad, slightly jagged. 24 tentacles and 32 small bubs. Presence of ocelli unknown.

DISTRIBUTION: Known from type locality only: 37.467°N 25.117°W (near Azores), 0-1000 m.

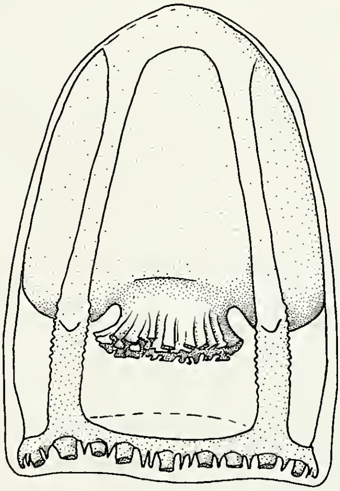

FIG. 56

Leuckartiara grimaldii Ranson, 1936, redrawn from Ranson (1936).

REMARKS: This species is based on a single, damaged specimen. Gonads were not observed by Ranson (1936) and the ocelli could not be observed as the material had been conserved for more than 30 years when it was described. The inclusion into the genus *Leuckartiara* was based solely on the tentacles which resemble those of *L. nobilis* or *N. breviconis* as described by Hartlaub (1914). However, other genera are also possible, e. g. *Pandea* or *Merga*. Ranson (1936) evokes the possibility that the specimen was a senescent animal with spent gametes. The species remains insufficiently known.

Leuckartiara abyssi (G.O. Sars, 1874) Fig. 57

Perigonimus abyssi G.O. Sars, 1874: 126, pl. 5 figs 27-30. – Broch, 1916: 53, fig. Q. – Rees, 1956a: 338. – Naumov, 1969: 202, fig. 70.
Leuckartiara abyssi. – Rees, 1938: 19, fig. 6a-d. – Rees, 1956b: 114. – Edwards, 1965: 446.

DIAGNOSIS: Stolonal hydroids on bivalves and scaphopods, medusa buds on hydrocauli and stolons, with pseudohydrotheca, newly liberated medusa with four tentacles.

DESCRIPTION (Rees, 1938): Hydroid epizoic on bivalves and scaphopods, colonies stolonal hence hydrocauli unbranched. Stolons form an open network, colour light brown. Perisarc of stems with adhering mud particles; perisarc often irregularly wrinkled throughout, but never ringed at the hydrocaulus base, becoming dilated around the base of the hydranth to form a pseudohydrotheca, reaching almost to the base of the tentacles where it thins out and disappears. Hydranth fusiform to flask-shaped, with a well developed conical hypostome and one whorl of six to eight filiform tentacles, the long ones held almost vertical and the shorter ones at right angles to the hydrocaulus. The limits of the hydranth and the hydrocaulus are not clearly marked, the transition being gradual. Gonophores develop on short stalks from the stolons and the hydrocauli.

Newly liberated medusa deeply bell-shaped, no apical process, jelly fairly thin and of uniform thickness, scattered nematocysts on exumbrella. Velum present. Four radial canals and ring canal fairly broad. With four perradial tentacles with elongated hollow conical bulbs; of these two opposite tentacles were better developed than the other two; without ocelli. Manubrium short, quadrangular in section, reaching about 1/3 the height of the umbrella cavity, mouth without lips. Colour of bulbs pale yellowish green.

DIMENSIONS (Rees, 1938; Rees, 1956b): Total height of stems up to 1.1 mm, perisarc covered part 0.7 mm, hydranth body 0.35 mm, diameter of hydranth 0.175 mm, stem diameter 0.05 mm, stolon diameter 0.05-0.07 mm, tentacle length up to 1.2 mm, medusa bud 0.45-0.50 mm long, stalk of medusa bud 0.05 mm, newly liberated medusa 1.15 mm high and 1.05 mm wide.

DISTRIBUTION: A northern boreal to Arctic species, but, because of the likely confusion with other species, most records outside Norway should be regarded with reservation. Recorded from Norway (Sars, 1874; Bonnevie, 1901; Rees, 1938; Christiansen, 1972), western Sweden (Jäderholm, 1909); Greenland (Kramp, 1911, 1914, 1943); Bear Island (Bonnevie, 1899), Spitsbergen (Broch, 1910); Barents Sea

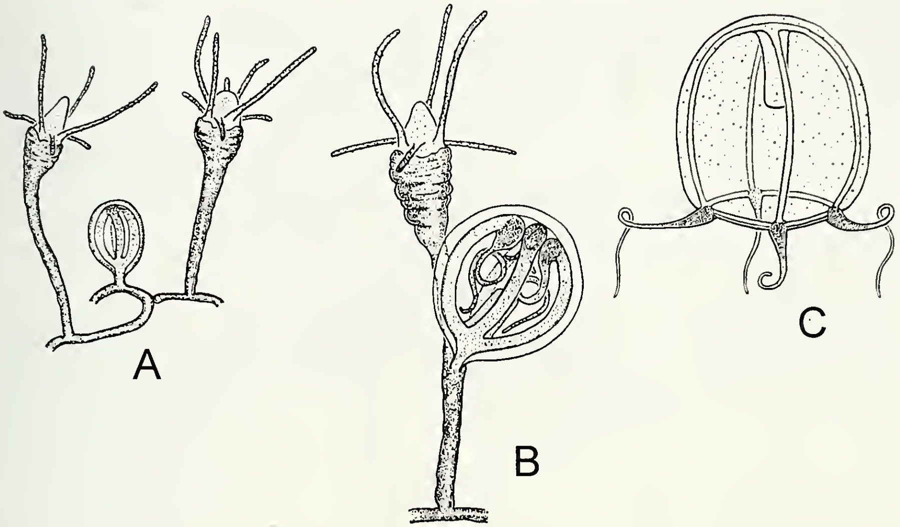

FIG. 57
Leuckartiara abyssi (G.O. Sars, 1874), from Rees 1938, for dimensions see text.

(Spassky, 1929). A record from western Ireland by Ritchie (1913) has been regarded as doubtful by Edwards (1965). Type locality: Norway, Hvitingsø (= Kvitsøya, island near Stavanger), 146-365 m, on *Dentalium dentale* (Linnaeus), designation by Rees (1956b).

BIOLOGY: The hydroid grows on scaphopods (*Dentalium dentale*) and bivalve shells of the genus *Nucula* and *Nuculana* occurring normally in depths of 100-600 m (range 20-1600 m). Medusa buds were observed from July to September (Rees, 1938; Christiansen, 1972).

REMARKS: All morphological and biological traits of *L. abyssi* from Norway appear identical to the hydroid of *Neoturris pileata* described by Edwards (1965) based on material from Scotland. Although it is likely that also the Norwegian hydroid belongs to this species – the medusa of *N. pileata* also occurs there – Edwards correctly refrained from synonymizing the two species because more life cycle information for the Norwegian hydroid is needed. Because many pandeid hydroids are very similar, *L. abyssi* could also correspond to other medusae known from the region, e. g. *Neoturris breviconis* or *L. nobilis*.

Leuckartiara brownei Larson & Harbison, 1990 Fig. 58

Perigonimus sp. Browne, 1910: 16.
Leuckartiara brownei Larson & Harbison, 1990: 20, fig. 1. – Pagès *et al.*, 1992: 12. – Bouillon *et al.*, 2000: 89, fig. 2. – Bouillon *et al.*, 2004: 70, fig. 41B.

DIAGNOSIS: Medusa up to 10 mm, four normal perradial tentacles and up to 28 much smaller tentacles; no ocelli; gonad on two longitudinal interradial folds, no transverse connection.

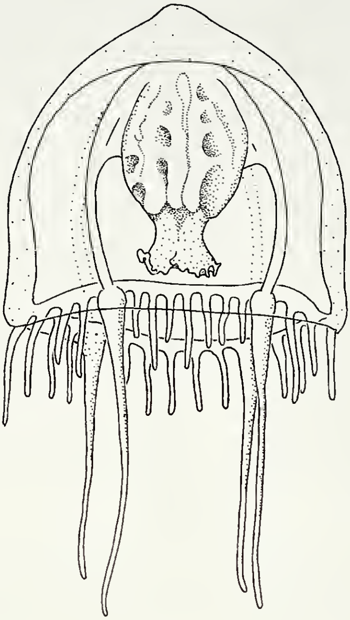

FIG. 58
Leuckartiara brownei Larson & Harbison, 1990; modified from original publication, bell height 10 mm.

DESCRIPTION: Umbrella with a small pointed apical projection of variable height; mesogloea moderately thick, velum narrow. Radial canals four, fairly broad, mostly smooth outlines. Only the four perradial tentacles are fully formed, tapering, not laterally compressed, coiled when contracted; additionally up to 28 short rudimentary tentacles (= juvenile tentacles), number variable, developing in succession; all tentacles without ocelli and abaxial spurs. Manubrium relatively large, more than half of the bell cavity height; mesenteries well developed; lips somewhat folded. Gonads occupy the interradial areas of the manubrium, each gonad with a pair of longitudinal folds adjacent to the interradii forming a continuous interradial groove, additionally a few isolated folds in the adradii mostly oriented perradially. Coloration in life: gonads orange-brown, tentacles pink-orange.

The youngest specimens show that the medusa is probably released with two tentacles only.

DIMENSIONS: Umbrella up to 10 mm high and 9 mm wide.

BIOLOGY: In the Antarctic occurring from the surface to depths of several hundred meters (Bouillon *et al.*, 2000), this always at sub-zero temperatures (Larson & Harbison, 1990).

DISTRIBUTION: Antarctica, Mediterranean. Type locality: McMurdo Sound, Ross Sea, Antarctica.

REMARKS: It is somewhat surprising to find a cold water medusa in the relatively warm waters of the Mediterranean. The Antarctic *Leuckartiara brownei* medusae occur in waters of sub-zero temperatures, while the Mediterranean waters remain always warmer than 12°C at all depths (Klein & Roether, 2001).

Genus ***Neoturris*** Hartlaub, 1914

TYPE SPECIES: *Medusa pileata* Forsskål, 1775, designation by Kramp (1959a).

SYNONYMS: *Turris* Lesson, 1843 for *Turris papua* Lesson, 1843: 283, name preoccupied. – *Tiara* Lesson, 1843, for *Tiaria papalis* Lesson, 1843 = *Neoturris pileata,* name preoccupied.

DIAGNOSIS: Hydroids colonial, arising from creeping stolons; hydrocauli covered by perisarc, not or only rarely sparingly branched, stems monosiphonic. Perisarc extends onto hydranth body as a more or less gelatinous pseudohydrotheca which does not envelop the tentacles. Hydranths with a conical hypostome and one whorl of filiform tentacles. Gonophores develop on cauli or stolons, enclosed in thin perisarc membrane. Gonophores liberated as free medusae.

Medusa mostly with an apical projection of variable size. Manubrium voluminous, connected to radial canals by mesenteries. Mouth with extensively folded margin. Gonads on interradial walls of manubrium, each quadrant with two adradial longitudinal rows of transverse folds, interradial region depressed, with numerous gonadal pits. Radial canal very broad, often jagged. With many tentacles arising from elongated bulbs, laterally compressed, without rudimentary tentacles or marginal warts. Without ocelli.

REMARKS: Following the opinion of Arai & Brinckmann-Voss (1980), this genus also includes *N. breviconis* (Murbach & Shearer, 1902).

The polyp stage of *Neoturris pileata,* the only one known, is indistinguishable from those found in the genus *Leuckartiara*. The main differences to *Leuckartiara* medusae are the adradial rows of gonadal folds, typically directed towards interradial, flanking a region with pits. Also the absence of ocelli is quite characteristic, although *Leuckartiara brownei* also lacks them.

KEY TO THE *NEOTURRIS* MEDUSAE TREATED HERE:

1a eight adradial rows of gonads folds, folds directed towards interradial, many gonadal pits (>20) .... *N. pileata*

1b gonad folds arranged like horseshoe, folds directed towards perradial and aboral, relatively few interradial gonadal pits (<20) .... *N. breviconis*

Neoturris pileata (Forsskål, 1775) Fig. 59-60

Medusa pileata Forsskål, 1775: 110. – Forsskål, 1776: pl. 33, fig. D.
Oceania Lesueurii Péron & Lesueur, 1810: 345. – Goy, 1995: 244, plate
Carybdea pisifera Oken, 1815: 125.
Oceania pileus de Blainville, 1830: 258.
Oceania ampullacea Sars, 1835: 22, pl. 6 fig. 8. – Haeckel, 1879: 58, synonym.
Tiaria papalis Lesson, 1843: 287. – Haeckel, 1879: 58, synonym.
Turris digitale Forbes, 1846: 286. – Hartlaub, 1914: 324, synonym.
Turris digitalis. – Forbes, 1848: 21, pl. 3 fig. 1. – Haeckel, 1879: 61, pl. 4 figs 2-3.
Oceania episcopalis Forbes, 1848: 27, pl. 2 fig. 1. – Haeckel, 1879: 58, synonym.
Oceania cocciniea Leuckart, 1856: 20, pl. 2 fig. 3.– Haeckel, 1879: 58, synonym.
Oceania constricta Patterson, 1859: 279, figs.

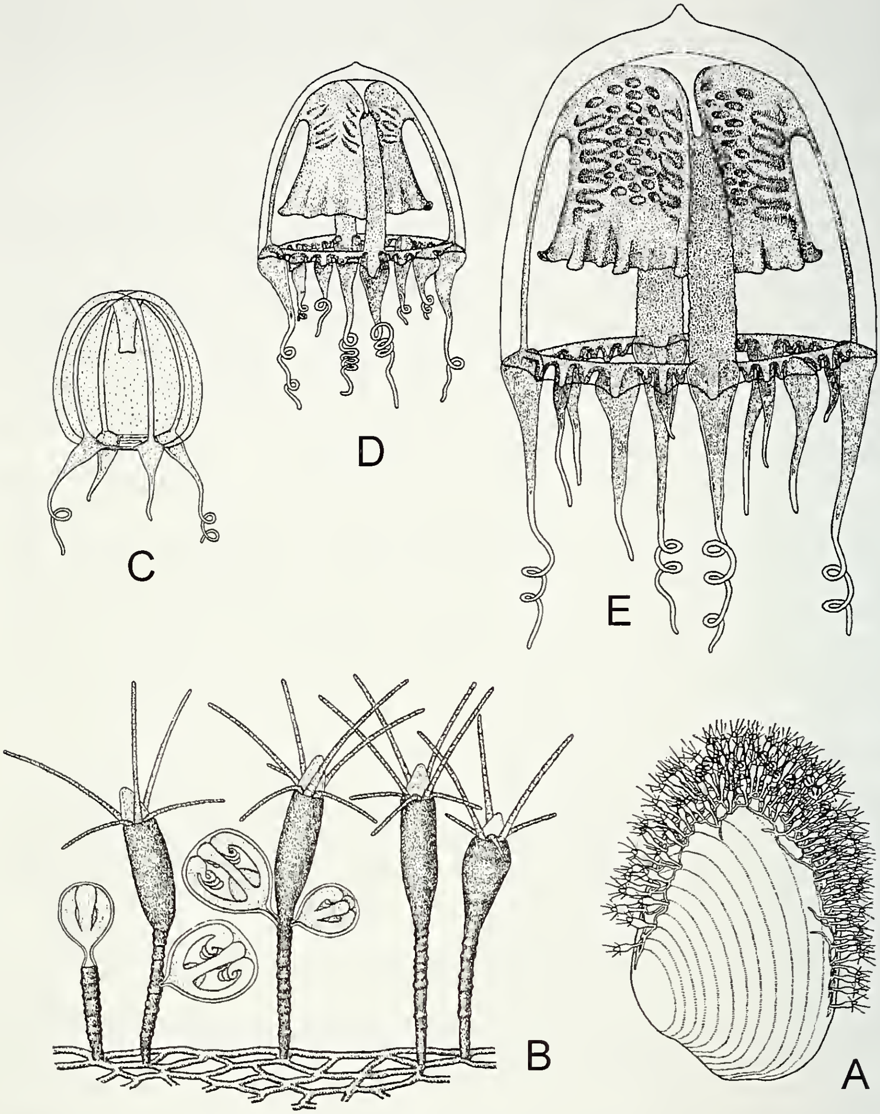

FIG. 59

Neoturris pileata (Forsskål, 1775); from Edwards (1965). (A) Typical distribution of the hydroid colony on a bivalve. (B) Part of hydroid colony bearing medusa buds), for dimensions see text. (C) Newly liberated medusa, height 1.2 mm. (D) Juvenile medusa (2.7 mm) with beginning formation of gonadal ridges. (E) Young medusa of about 5 mm height, a small apical process is present and more gonad-folds and pits have formed.

Tiara pileata. – Haeckel, 1879: 58, pl. 3 figs 6-8.
Turris coeca Hartlaub, 1892: 19, fig. 1. – Hartlaub, 1914: 329, synonym.
in part *Turris pileata*. – Mayer, 1910: 123, pl. 12 fig. 4, pl. 13 fig. 6.
Tiara pileata. – Le Danois, 1914a: 17, fig. 4.

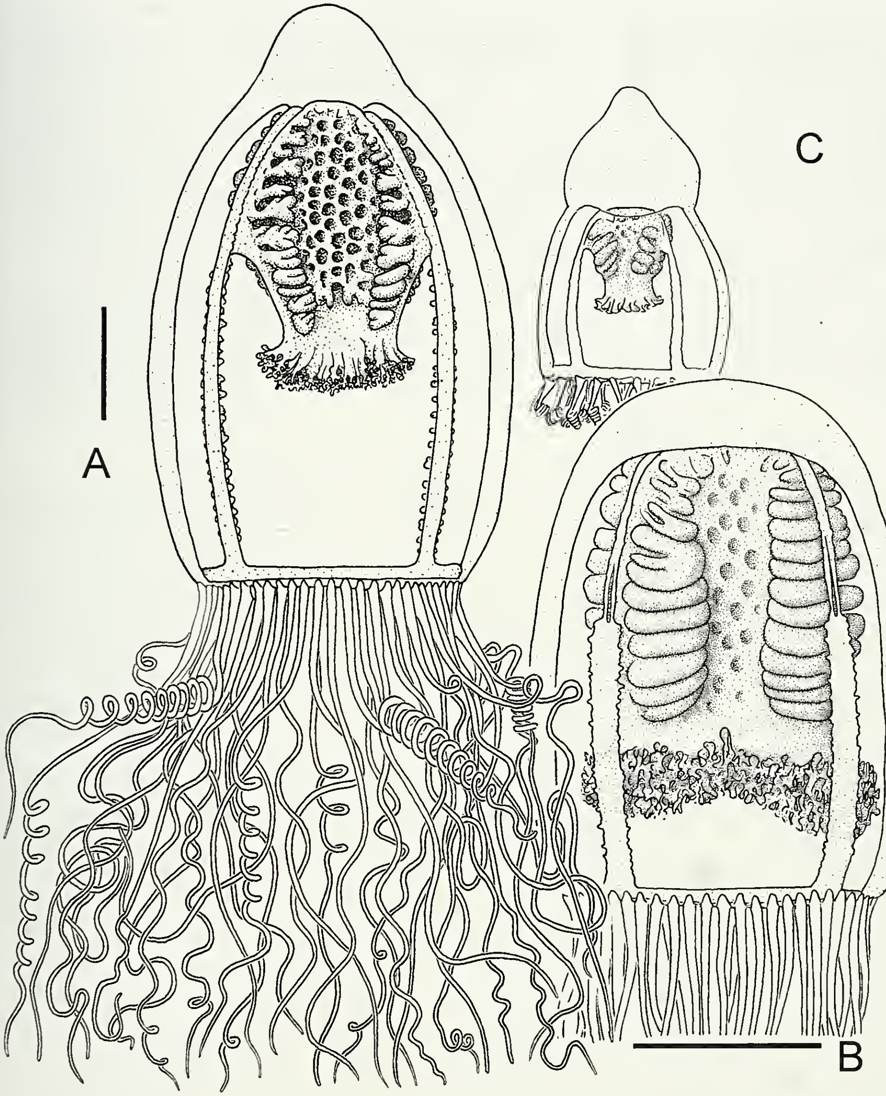

FIG. 60

Neoturris pileata (Forsskål, 1775). (A) Mature medusa from Villefranche-sur-Mer, preserved material, scale bar 5 mm. (B) Mature medusa from off Mauritania, preserved material, scale bar 10 mm. This form lacks an apical process and differs in other details from the typical form shown in A. It could belong to a different, unnamed species. (C) Subadult medusa from Scotland, after photograph of living specimen, approximately same scale as B.

Neoturris pileata. – Hartlaub, 1914: 326, figs 270, 273, 274-281. – Kramp, 1926: 92, fig. 37, pl. 2 figs 13-14, chart XVIII. – Russell, 1953: 203, figs 104-106, pl. 12 fig. 1. – Kramp, 1959a: 122, fig. 124. – Kramp, 1961: 109. – Edwards, 1965: 461, figs 1-4. – Kramp, 1968: 50, fig. 131. – Russell 1970: 247, figs 10s-13s.– Bouillon *et al.*, 2004: 73, fig. 42C-E.

Material examined: MHNG INVE35522; Mediterranean, Villefranche-sur-Mer; 6 mature medusae, 2-3 cm, leg. and det. C. Hartlaub 1911, material mentioned in Hartlaub (1914). – MHNG INVE47956, Scotland, Great Cumbrae Island, 0 m, 15 May 1992, 3 subadult medusae, colour photographs made before fixation. – ZMUC, Dana station 4007, off Mauritania, 18.367°N 18.233°W, 600 m wire length, 15 March 1930, 10 medusae 1.5-3 cm, id. P. Kramp. – BELUM Md645, Ireland, Donegal, St. Johns Point, Portnagh Rock; one mature medusa. – BMNH 1985.9.2.25; England, Plymouth; July 1937; 3 medusa from plankton. – BMNH 1985.6.13.1; medusa misidentified as *Leuckartiara nobilis* Great Britain, Northern Ireland, Strangford Lough. – BMNH 1965.1.14.1-10; Sweden, Kosterfjord, Ulvillarna; 100 m; 1 Oct 1964; polyps on *Nucula* shells, with medusa buds. – BMNH 1962.11.8.1; Sweden, Gullmarfjord, Gåsö, Ranna; 20-30 m; 27 August 1962; polyps on *Dentalium* (Scaphopoda), with medusa buds

Diagnosis: Bell higher than wide, height 2-4 cm, no exumbrellar nematocyst ridges, with or without apical projection, no apical canal, with about 60-80 tentacles, interradial gonad region large and without folds but with many gonadal pits (>20), eight adradial rows of gonads folds, folds directed towards interradial; no papillae on gonads, radial canals jagged.

Description (Edwards, 1965; own observations): Hydroid phase forming dense colonies on shells of *Nucula* bivalves. Hydrorhiza a close network of creeping stolons. Hydranths stolonal, stems rarely branched once; perisarc of pedicels irregularly or spirally corrugated but not annulated, continued over hydranth as filmy pseudohydrotheca ending below tentacles. Hydranth spindle-shaped, clearly set apart from the thin pedicel, with prominent conical hypostome, 6-7 (range 4-9) filiform tentacles in a single whorl, longer and erect tentacles alternating with shorter and depressed ones. Medusa buds borne on the hydranth pedicels, less frequently on the stolons; pear-shaped to spherical, short pedicel, enclosed in filmy perisarc. Mature buds with four large tentacle bulbs, each bearing a tentacle.

Newly released medusa bell-shaped, with scattered exumbrellar nematocysts, umbilical canal; manubrium conical, simple, 1/4 to 1/3 of subumbrellar depth; radial canals smooth, thick; four perradial tentacles, each with a conical base not laterally compressed, of these tentacles two opposite ones well developed and the two others less developed, no rudiments of further bulbs, no ocelli. During subsequent growth, tentacles are intercalated between existing ones, the manubrium increases its size, after a size of 2 mm the mesenteries form, when about 2.7 mm high the gonadal bulges commence their development, later followed by the pits, the mouth margin gets frilled.

Adult medusa bell- to bullet-shaped, higher than wide, with solid apical process varying much in size, sometimes lacking; jelly relatively thin but firm. Velum narrow. Four broad radial canals, with short lateral diverticles; ring canal broad, with smooth outlines. Proximal parts of radial canals joined to stomach my mesenteries for about 1/3 of their length. Marginal tentacles numerous, usually about sixty, up to ninety possible, hollow, with large, laterally compressed, elongated conical basal bulbs clasping the umbrella margin but not forming conspicuous abaxial spurs; without ocelli; nematocysts concentrated in crescent-shaped clasps, in distal regions confined to adaxial side of tentacle. Tentacles bases directed towards below. Developing tentacles or bulbs can be present, but usually rare in mature animals. Manubrium flask-shaped, of variable length (1/3 to 5/6 of subumbrellar height), with broad base, intensive red colour, mouth with strongly folded lips. Gonads interradial in two adradial series of folds directed towards the interradius (in region of mesenteries only) and a depressed interradial portion with numerous round pits, rendering this region reticulated. Nematocysts: microbasic euryteles, abundant on tentacles; perhaps also an additional, much rarer, smaller capsule.

DIMENSIONS (Edwards, 1965; own data): Hydroid stems 1.6-2.2 mm, occasionally up to 4 mm, hydranths 0.5-1.1 mm high, medusa buds up to 0.7 mm long, stalks of buds 0.11-0.18 mm. Newly released medusa about 1.2 mm high. Adult medusa 2-3.5 cm high, diameter 1.5 cm; microbasic euryteles (7-8)x(3) μm.

VARIATION: Certain characters of the fully-grown medusa show considerable variation. The apical process may vary very much in size: it may be a large almost spherical mass comprising over a third of the total height of the medusa, or it may be completely absent. The stomach also varies considerably in length, in some reaching almost to the umbrella margin while in others it is not even half the height of the subumbrellar cavity.

DISTRIBUTION: The medusa is present in the north-eastern Atlantic as far north as 64°N, occurring along the Norwegian coast, British Isles, northern North Sea, Skagerrak and northern Kattegat, Bay of Biscay, off southern Portugal, western Mediterranean; north-west, west and south-west Africa. Also present in the mid-Atlantic and at Iceland. Absent in southern parts of the North Sea and the eastern English Channel. There is no certain evidence that the species is present in the Pacific and Indian Ocean (see also Kramp, 1968; Arai & Brinckmann-Voss, 1980). Edwards (1965) reviews all records of the medusa. The polyp stage is known from western Scotland, Norway, and Sweden. The preferred host of the polyp phase, *Nucula sulcata* Bronn, 1831 has a similar distribution like the medusa of *Neoturris pileata* (Edwards, 1965). Type locality: Mediterranean.

BIOLOGY (Edwards, 1965): The polyps occur exclusively on shells of the bivalve genus *Nucula*, preferably on *Nucula sulcata* Bronn, 1831, in depths of 40-180 m. Gonophore production in the Atlantic starts in January to February, apparently at the annual minimum of the water temperature and the maximum of oxygen concentration. The polyp is adapted to live buried within the mud. Polyps of *Leuckartiara octona* and *N. pileata* polyps can co-occur on the same shell. In favourable years, fully grown medusae appear in the Atlantic in May. The length of life of the medusa appears to be 3-4 months. The medusae are rare and it is only in occasional seasons that fully grown, mature medusae are present, they may be seen in numbers swimming at and near the surface, in more northerly waters and in the Skagerrak and Kattegatt the medusae persist longer, some to October. In the Mediterranean, the medusae occur earlier than in the Atlantic. They are absent during the summer month.

FURTHER DATA: Krasińska (1914) examined some histological details of the medusa.

REMARKS: The synonymy established by Haeckel (1879), Bedot (1901, 1905), Le Danois (1914a), Hartlaub (1914) was here fully adopted. Hartlaub (1914) was able to examine some of the type specimens.

The correct spelling of the author of this species is apparently Forsskål, despite in the title of the original publication of 1775 the spelling Forskål was used (Cernohorsky *et al.*, 1991).

In the distal portions of the tentacles, the nematocysts are all on one side and concentrated in crescent-shaped bulges. This has already been mentioned by Kramp (1926) and he states that the clusters lie on the adaxial side. Kramp (1926) maintains that the cross-section of the tentacles is triangular, but this was not the case in the present material.

Neoturris pileata differs from *N. breviconis* in the more slender shape of the umbrella, the higher number of interradial pits, and the lower number of tentacles (Arai & Brinckmann-Voss, 1980).

The hydroid resembles much *L. octona*, but according to Edwards (1965) the stems are less branched and shorter, as well as the hydranths and medusa buds are larger. The newly liberated medusa offers better traits to distinguish the colonies (*N. pileata* four tentacles, *L. octona* two tentacles).

Neoturris breviconis (Murbach & Shearer, 1902) Fig. 61

Turris breviconis Murbach & Shearer, 1902: 73. – Murbach & Shearer, 1903: 170, pl. 18 figs 1-2. – Mayer, 1910: 127.
Leuckartiara brevicornis. – Hartlaub, 1914: 304, figs 254-256 [subsequent incorrect spelling].
Leuckartiara breviconis. – Kramp & Damas, 1925: 280. – Kramp, 1926: 80, pl. 2 fig. 8. – Uchida, 1938b: 49, fig. 1. – Russell, 1953: 198, pl. 12 fig. 2. – Kramp, 1959a: 120, fig. 121. – Kramp, 1961: 103. – Kramp, 1968: 4, fig. 124.
Perigonimus breviconis. – Naumov, 1969: 204, fig. 72.
Neoturris breviconis. – Arai & Brinckmann-Voss 1980: 57, figs 30- 33.

MATERIAL EXAMINED: MHNG INVE35729, British Columbia, Malcolm Island, Mitchell Bay, 5 June 2002, coll. & id. A. Brinckmann-Voss, 1 medusa of about 1 cm, subadult, ca. 80 tentacles mostly equally developed, gonad folds and pits weakly developed, pits numerous. – BMNH 1954.11.13.68; North Sea; 14 March 1913; 1 medusa badly preserved, could also be *L. nobilis*, leg. & det. C. Hartlaub. – ZMUC, Thor station 241(04); 64.583°N 11.750°W; eastern Atlantic; 8 August 1904; 5 medusae; material described in Kramp (1926). – ZMUC, no number; Iceland, Vestmanaeyjar; 12 July 1904; 5 medusae; material described in Kramp (1926).

DIAGNOSIS (Atlantic form): Height 2-4 cm, as broad as high, with up to 140 tentacles, no exumbrellar nematocyst ridges, with shallow apical projection, no apical canal, gonad folds arranged like horseshoe, folds directed towards perradial and aboral, relatively few interradial gonadal pits (<20), no papillae on gonads; radial canals jagged; mesenteries rather short.

DESCRIPTION (Atlantic form): Medusa bell relatively wide, as broad as high or slightly higher, with apical rounded dome-shaped process of variable height, lateral jelly relatively thin. Four broad radial canals with much jagged outlines, ring canal smooth; radial canals joined to stomach by mesenteries, these relatively short (1/2 or less of manubrium length), abaxial side with transverse ridges. Marginal tentacles up to 105, one row, many not fully developed, sizes thus very variable, no or very few rudimentary bulbs, tentacles hollow, laterally compressed, clasping umbrella but not forming abaxial spurs. Manubrium flask-shaped, relatively large (2/3 of bell cavity), broad base, mouth with much crenulated lips. Gonads folds, arranged like a horseshoe, folds relatively irregular, directed mostly towards perradial, central interradial region somewhat depressed and in large animals with up to 20 gonadal pits and also some folds. Polyp stage unknown.

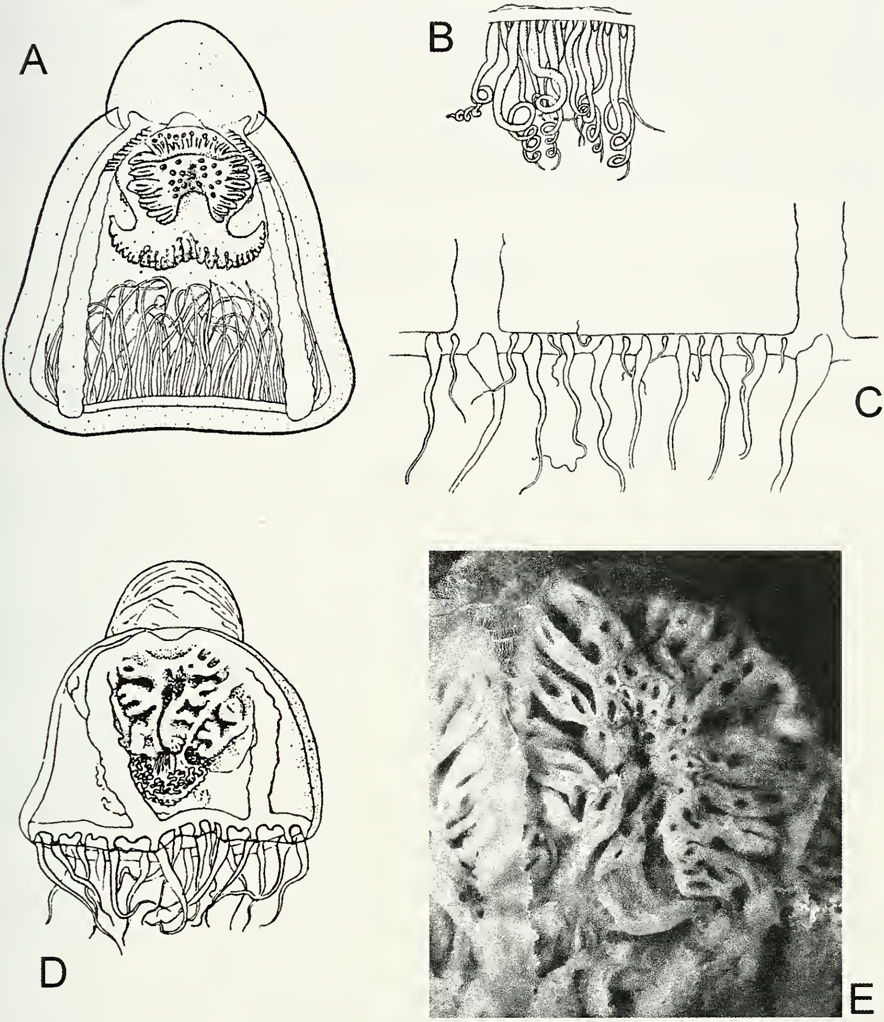

FIG. 61

Neoturris breviconis (Murbach & Shearer, 1902). (A) Pacific form, about 20 mm high, from Uchida (1938b). (B) Bell margin and tentacles of medusa shown in A. (C) Bell margin with tentacles of an Atlantic medusa, modified from Hartlaub (1914). (D) A relative young specimen from the North Sea, height about 15 mm, from Hartlaub (1914). (E) Typical gonad of a mature Atlantic medusa from east of Iceland, 20-30 mm wide and about 60 tentacles.

VARIATION: Derived from data and material of Kramp (1926), the following approximate correlation of bell diameter and tentacle number can be given for the Atlantic form: bell diameter 4 mm 16 tentacles; 5 mm 12-32 tentacles, 7 mm 16-46 tentacles; 10 mm 40-68 tentacles, 11 mm 38-65 tentacles; 20-30 mm 60-64 tentacles; 30 mm 89 tentacles.

The Pacific form differs in the following details: tentacle number is higher (up to 140; Uchida (1938) had an animal of 15 mm diameter with 120 tentacles; the examined specimen was about 10 wide and had around 80 tentacles), the tentacles are more equally developed, the bell margin is very densely beset with tentacles so that it get crowded and the tentacles may appear in two rows; the lateral mesogloea thicker; stomach with gonads distinctly shorter (1/3 of bell cavity), mouth part about as long as stomach part; gonad folds short, pitted region larger, with more pits (about twice or more).

Dimensions: Atlantic form 10-40 mm high and up to 30 mm wide; Pacific medusa 45 mm high and 35 mm broad.

Other Data: Kramp (1926) reported that the large tentacles have abaxial transversal folds in the distal region, contrary to many other Pandeidae which have adaxial folds (could not be confirmed for Pacific specimen). Nematocysts: microbasic euryteles and mastigophores (Mackie & Mackie, 1963).

Distribution: Currently seen as a circumpolar Arctic to northern boreal species. In the eastern Atlantic, the southern limits are the northern North Sea, Firth of Clyde, western Ireland, and the south of Iceland (Kramp & Damas, 1925; Kramp, 1926; Naumov, 1969; Russell, 1953; Russell, 1970; Zelickmann, 1972; Boyd *et al.*, 1973). In the Pacific it occurs as far south as British Columbia and Japan (Uchida, 1938b; Arai & Brinckmann-Voss 1980). Type locality: St. Paul Island, Pribyloff Islands, Bering Sea.

Biology: A quite rare medusa, recorded in the NE Atlantic during the summer months (Russell, 1953; Boyd *et al.*, 1973).

Remarks: The examined specimen from the north-eastern Pacific, likely a good representative for the typical form, differs somewhat from the Atlantic specimens (see Variation). Uchida (1938b) gives a good figure of the Pacific variant and it is here reproduced in Fig. 61A. A good colour photograph of a living medusa from the Pacific is given in Heeger (1998) and also Arai & Brinckmann-Voss (1980) show a photograph. It is evident that the Pacific form corresponds much more to a *Neoturris* than the Atlantic specimens and the species is here left in this genus following Arai & Brinckmann-Voss (1980). The Atlantic specimens have gonads that resemble more those of *Leuckartiara* species (Fig. 61E). I therefore suspect that the Atlantic *N. breviconis* (sensu Hartlaub, 1914; Russell, 1953; Kramp 1959a) belongs to a different species than the Pacific *N. breviconis*. It could even be that the Atlantic form of *N. breviconis* is actually *L. nobilis* with exceptionally high tentacle numbers and much developed gonads. It must also be noted that most of the so far described Atlantic specimens had been in preservative for years or decennia. As the pigment the ocelli fades rapidly in formalin, it is therefore not certain whether they really lacked ocelli originally. New investigations using living animals are needed to re-evaluate the status of the Atlantic population of *N. breviconis*.

Genus ***Halitholus*** Hartlaub, 1914

Type species: *Halitholus pauper* Hartlaub, 1914, designation by Kramp (1959a).

Diagnosis: Pandeid medusae with four or more tentacles, large dome-shaped apical projection, quadrangular manubrium without mesenteries, gonads adradial with or without horizontal interradial connection, gonad folds directed towards perradial, mouth margin moderately folded; with or without ocelli.

Hydroid stolonal, hydranths on short pedicels, with pseudohydrotheca, hypostome conical, filiform tentacles, number relatively low (around six); medusa buds on stolons.

REMARKS: The genera *Halitholus* and *Leuckartiara* are quite similar, but the absence of mesenteries makes *Halitholus* quite easily separable.

KEY TO THE *HALITHOLUS* SPECIES OF THE NORTH ATLANTIC:

1a 30-40 tentacles, gonads without interradial connection, without ocelli . . . . . *H. cirratus*

1b 4-8 tentacles, adradial portions of gonads with interradial connection, with ocelli . . . . *H. pauper*

Halitholus cirratus Hartlaub, 1914 Fig. 62

? *Perigonimus yoldia-arcticae* Birula, 1897: 88, pl. 10 fig. 3. – Naumov, 1969: 200, fig. 67.
Perigonimus cirratus Hartlaub, 1914: 274, fig. 234. – Arndt, 1964: 332, figs 1-3.
Halitholus cirratus Hartlaub, 1914: 274, figs 225-234. – Kramp, 1926: 74, pl. 2 fig. 4, chart XII. – Kramp, 1959a: 119, fig. 117. – Kramp, 1961: 101. – Kramp, 1968: 45, fig. 116.
? *Halitholus yoldiaarcticae*. – Schuchert, 2001: 22, fig. 12.

MATERIAL EXAMINED: BMNH 1950.3.1.203; Baltic Sea; 14 March 1913; 12 medusae; leg. and det. C. Hartlaub. – ZMUC, Dana Station 2965; Denmark, SW of Bagenkop; 30-80 m wire; 21 April 1923; 50 damaged medusae. – ZMUC, Dana Station 3050; Denmark, N of Anholt; depth 15 m; 18 May 1923; 7 medusae. – IRSNB; Baltic Sea; 3 damaged medusae; coll. J. Bouillon.

DIAGNOSIS: Medusa 5-16 mm high, large apical projection; with shallow manubrial peduncle; lips only weakly folded; 30-40 tentacles; no ocelli; gonads irregular and variable, often in eight vertical rows of folds. Polyp stolonal, on bivalves, with pseudohydrotheca, about six tentacles, medusa buds on stolons.

DESCRIPTION (after Hartlaub, 1914; own data): Polyp stage resembles closely *L. octona* (Figs. 53A; 62B and D), about six tentacles, stems shorter but length variable, medusa buds so far only observed on stolons. Newly released medusa with two tentacles.

Mature medusa with wide bell, apical process of variable size and shape, may be half the total height of the medusa. Mesogloea of lateral wall relatively thin, manubrium on a shallow peduncle. Four radial canals moderately broad, smooth or with wavy outlines, not forming mesenteries, at top recurved due to shallow manubrial peduncle; ring canal smooth. Marginal tentacles 30-40, rarely up to 50, no rudimentary bulbs, bulbs gradually tapering into tentacles, laterally compressed, without abaxial spurs, without ocelli, nematocysts concentrated on adaxial side. Manubrium voluminous, cross-shaped in section, reaching almost down to level of velum, mouth region relatively short; mouth wide, rim only weakly folded: Gonads very irregular, usually in eight adradial series, usually with transverse folds directed towards perradius, gonads widely separated perradially; interradial region depressed and wide, rather smooth, only occasionally with folds, interradial connecting fold absent, usually no pits present, sometimes isolated pits on gonadal folds; sometimes gonads without folds and upper ends fused interradially. Colours: Manubrium brick-red.

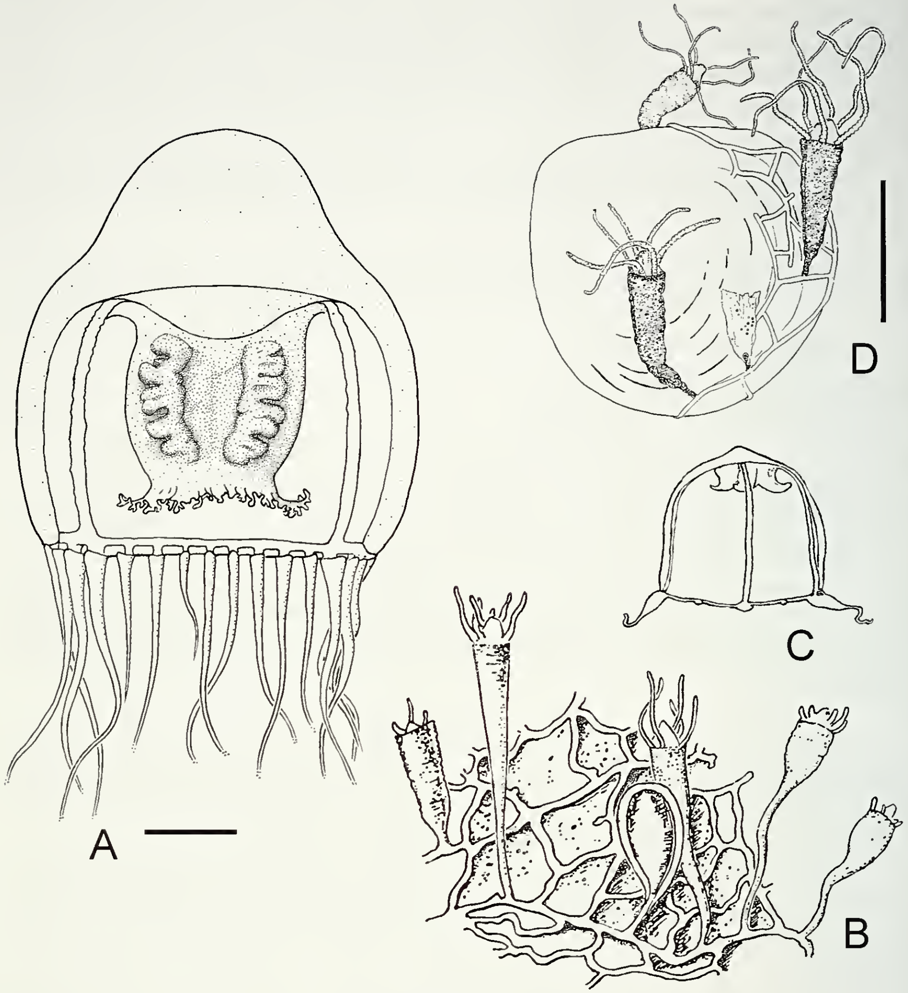

FIG. 62

Halitholus cirratus Hartlaub, 1914. (A) Mature medusa, scale bar 2 mm. (B) Hydroid, size of polyps about 2 mm in height. (C) Newly liberated medusa. (D) Hydroid on the bivalve *Astarte borealis* (Schumacher), note the empty envelope of a medusa bud (lower right), scale bar 1 mm. A, after preserved material; B-C, from Hartlaub (1914); D, modified after Arndt (1964).

DIMENSIONS: Mature medusa up to 16 mm high, diameter up to 14 mm, usually smaller (10 mm), in Baltic Sea 5-11 mm high. Hydroid up to 2 mm high (Hartlaub, 1914), hydranth body 0.8-0.8 mm, pedicel 0.2 mm (Arndt, 1964).

DISTRIBUTION: A costal Arctic species occurring along the northern coasts of Eurasia and America, western Greenland; frequent at Spitsbergen (Kramp, 1926; Naumov, 1969; Kramp 1961); present also in the Baltic Sea and the Kattegat. Type locality: not specified, Hartlaub had material from Svalbard, the Barent Sea, the Baltic Sera and the North Sea.

BIOLOGY: At Spitsbergen, the medusa is common from June to August (Kramp, 1926). The putative hydroid phase described by Arndt (1964) and Schönborn *et al.* (1993) occurred on shells of Nuculidae and Astartidae and other bivalve shells, down to 100 m, it supported reduced salinities down to 8 ppt, medusa budding was observed in March and April. The polyps fed on nematodes.

REMARKS: The putative polyp of this species was first described by Hartlaub (1914) based on colonies growing on an isopod collected in the Baltic Sea. Hartlaub did not rear the medusa to maturity, but concluded from the absence of any other pandeid medusa in the Baltic Sea that this must be the hydroid of *Halitholus cirrata*. Although Hartlaub's conclusion is likely correct, there remains an element of uncertainty and the life cycle of this species should be reinvestigated. The hydroids of many pandeids and bougainvilliids are exceedingly similar and offer few or no reliable traits to distinguish them securely. The only trait that distinguishes Hartlaub's polyp from similar ones like *L. octona* is its lower tentacle number (about 6). The polyp was also described and depicted by Arndt (1964), but without providing information on the medusa stage. Arndt (1964) also found the medusa at the same locality where he had collected the hydroid. It is thus very likely that they had the polyp of *H. cirratus*.

The hydroid *Perigonimus yoldiaarcticae* Birula, 1897, growing preferably on shells of the Arctic bivalve *Yoldiella*, is at present not sufficiently described as its life cycle is unknown (see also Naumov, 1969; Schuchert, 2001). Birula's polyp could belong to several other Arctic Bougainvilliidae or Pandeidae species. Birula's polyp had also only few tentacles and Naumov (1969) thought that it is conspecific with *Halitholus cirratus* Hartlaub, 1914. Although this appears plausible, Naumov's claims were apparently not based on rearing experiments starting with polyps on *Yoldiella* shells. I therefore hesitate to synonymize *H. cirratus* and *P. yoldiaarctica*.

Halitholus pauper Hartlaub 1914 Fig. 63

in part *Tiaria conifera* Levinson, 1893: 144. – Mayer, 1910: 128.
[not *Tiara conifera* Haeckel, 1879]
Halitholus pauper Hartlaub, 1914: 272, figs 223-224. – Kramp, 1926: 71, pl. 2 figs 1-3, chart XI. – Uchida, 1933: 128, figs 4-5. – Kramp, 1926: 71 pl. 2 figs 1-3. – Kramp, 1959a: 119, fig 116. – Kramp, 1961: 101. – Kramp, 1968: 45, fig 115. – Arai & Brinckmann-Voss, 1980: 46, fig. 22. – Schuchert, 1996: 67, fig. 39.

MATERIAL EXAMINED: Holotype, ZMUC, loc. Greenland, Egedesminde; four fully formed tentacles, interradial tentacles only rudiments. – IRSN Bruxelles, IG 27.838, loc. Greenland, 3 medusae.

DIAGNOSIS: Medusa with 4-8 tentacles, with small ocelli, adradial portions of gonads connected interradially by transverse fold.

DESCRIPTION: Umbrella broad, with low rounded apical projection, no or very shallow manubrial peduncle; four radial canals, rather broad, margins smooth or sometimes partly jagged, entering stomach at its top; ring canal smooth. With four perradial tentacles, these with thick base, then tapering, not much laterally compressed, clasping bell margin, abaxial ocelli; four interradial tentacles can be present, these often small or only as rudimentary bulbs; usually also several rudimentary adradial bulbs. Manubrium massive, reaching 2/3 of subumbrellar height, cross-shaped in section, mouth

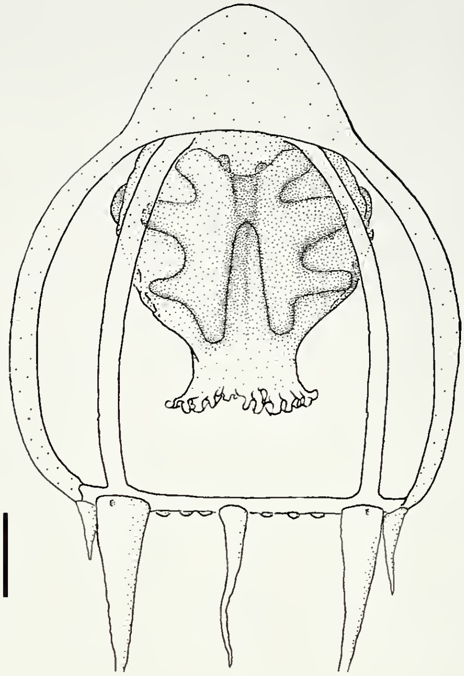

FIG. 63

Halitholus pauper Hartlaub, 1914; after preserved material from Greenland, scale bar 1 mm.

margin moderately folded; gonads adradial with a distinct transverse interradial connection in the upper part giving a horse-shoe shape, folds and openings directed towards perradial and upwards. Colours: gonads orange or reddish-orange (Arai & Brinckmann-Voss, 1980).

Polyp stage unknown.

DIMENSIONS : Medusa 5-12 mm high.

DISTRIBUTION: Iceland, western and eastern Greenland, Arctic waters of Canada, British Columbia, southern Kamchatka, northern Japan, New Zealand (Arai & Brinckmann-Voss, 1980; Schuchert, 1996). Type locality: Western Greenland, Egedesminde (Aasiaat).

REMARKS: This species is so far not known to occur along the continental coasts of Europe, but it could be present in the Arctic regions of Eurasia.

Genus *Catablema* Haeckel, 1879

TYPE SPECIES: *Turris vesicaria* A. Agassiz, 1862 [designation by Kramp, 1959a].
REFERENCES: Haeckel, 1879; Hartlaub, 1914; Kramp, 1961; Bouillon & Boero, 2000.

DIAGNOSIS: Medusa with large apical projection; radial canals broad and strongly jagged; mesenteries relatively short; tentacles numerous, with or without rudimentary tentacle-bulbs between normal tentacles; with abaxial ocelli; manubrium large with broad base; mouth large with much folded rim; gonads in long folds that tend to be vertical in the interradial region, gonadal pits may be present on and between the folds; gonads separated perradially.

REMARKS: The gonads on long, oblique to almost vertical stomach folds is the main characteristic of this species. To Haeckel (1879) they resembled to a theatre-curtain and he created the name *Catablema* – meaning curtain in Greek – as an allusion to this character. The gender is neuter. Only one species is present in area of investigation, *Catablema vesicarium*.

Catablema vesicarium (A. Agassiz, 1862) Fig. 64

Turris vesicaria A. Agassiz, 1862: 97. – A. Agassiz, 1865: 164, figs 261-268.
Catablema campanula Haeckel, 1879: 63. – Maas, 1904: 13, synonym.
Catablema eurystoma Haeckel, 1879: 63. – Maas, 1904: 13, synonym. – Hartlaub, 1914: 319, synonym.
? *Tiara conifera* Haeckel, 1879: 59. – Hartlaub, 1914: 284, likely synonym.
Catablema vesicarium. – Haeckel, 1879: 64. – Maas, 1904: 12, pl. 1 fig. 8, pl. 2 fig. 10. – Bigelow, 1909: 304, pl. 30 figs 3-4, pl. 31 fig. 6. – Hartlaub, 1914: 315, figs 263-267. – Kramp, 1926: 87, pl. 2 figs 10-11, chart 17. – Kramp, 1959a: 122, fig. 125. – Kramp, 1961: 96. – Kramp, 1968: 50, fig. 132.
in part *Turris vesicaria*. – Mayer, 1910: 126, pl. 12 figs 2-3, not pl. 13. fig 7.
not *Catablema vesicarium* var. *nodulosa* Bigelow, 1913: 17, pl. 1 figs 8-9 [= *C. nodulosa* Bigelow, 1913].
in part *Perigonimus vesicarius*. – Naumov 1969: 202, fig. 69 [some perhaps *C. nodulosa*].

MATERIAL EXAMINED: ZMUC; Greenland, Godthaab Station 50, 69.740°N 57.367°W; 200 m wire; 13 July 1928; 10 medusae; det. Kramp. – ZMUC; Dana Station 2362, Greenland, 63.583°N 57.183°W; 50-320 m; 320; 27 June 1925; 5 damaged medusae.

DIAGNOSIS: Medusa up to 25 mm wide and 30 mm high, including the large, globular apical projection; gonads in long, irregular folds, oblique in lateral parts, almost perpendicular in middle part of each gonad, with or without densely reticulate surfaces; about 32 tentacles; mesenteries short.

DESCRIPTION (Hartlaub, 1914; own data): Medusa with rather broad umbrella bearing a large globular or dome-shaped apical process, lateral bell walls relatively thin. Four radial canals, very broad and with lateral diverticules; ring canal broad, with undulated to jagged outlines. Proximal parts of radial canals joined to stomach my mesenteries for up to 1/4 of their length, thus relatively short mesenteries. Marginal tentacles up to about 32, rarely more, with large conical basal bulbs, laterally compressed, clasping the umbrella margin, forming slight abaxial spurs; with red ocelli, can be inconspicuous; nematocysts concentrated on adaxial side of tentacle, adaxial side in contracted tentacles corrugated; between tentacle pairs often a wart-like tentacle-rudiment. Gastrodermal chamber of some tentacle bulbs has finger-like protrusion reaching upward into the mesogloea (Fig. 64B). Manubrium flask-shaped, voluminous, size variable, sometimes reaching nearly to velum level, with broad base, mouth with strongly folded lips. Gonads on interradial wall of stomach, in irregular folds, oblique in lateral parts, almost perpendicular in middle part of each gonad, giving impression of radiating from a centre; in many larger specimens also with numerous pits on and between the folds, producing a reticulate surface. Colour of manubrium yellow-orange (after living specimens from Spitsbergen seen by Hartlaub, 1914).

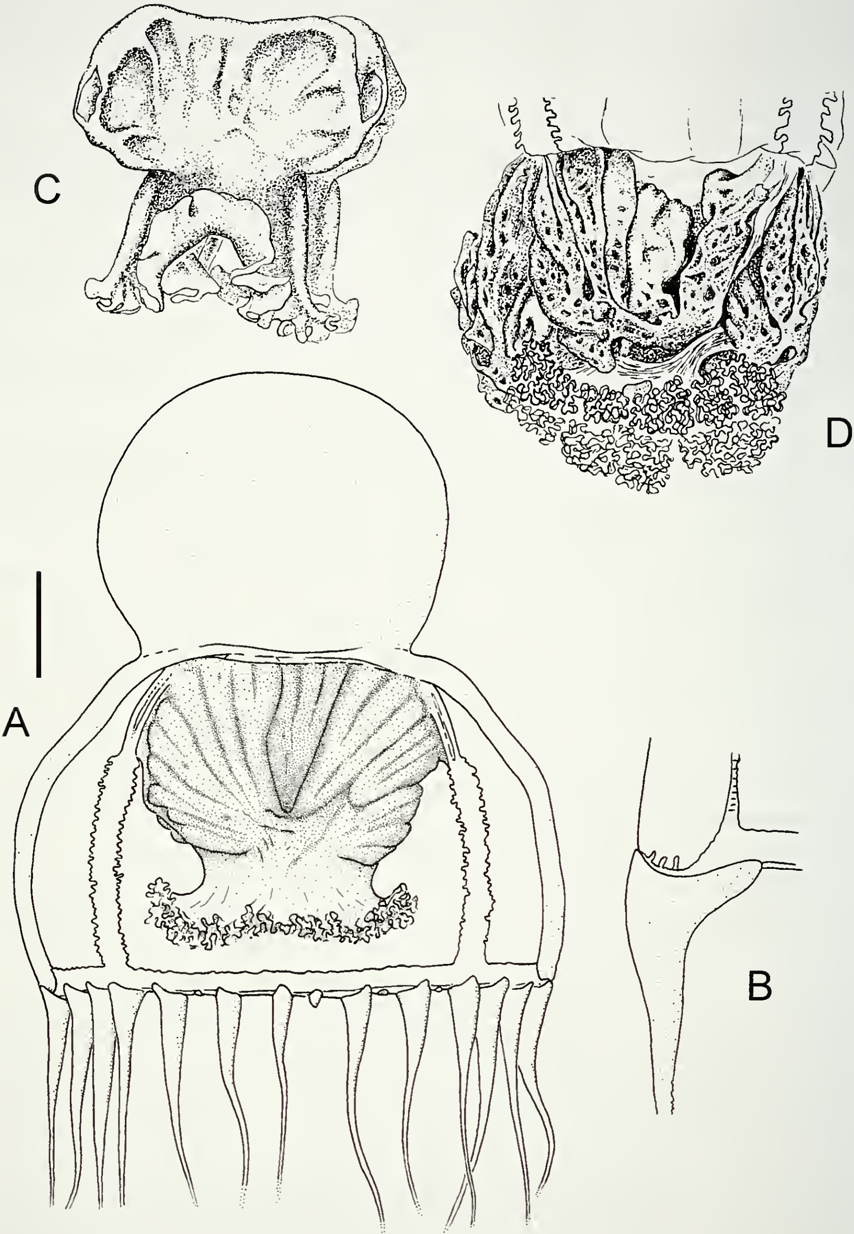

FIG. 64

Catablema vesicarium (A. Agassiz, 1862). (A) Mature medusa, specimen without gonadal pits, schematic reconstruction after several preserved medusa from Greenland, scale bar 0.4 mm. (B) Enlarged lateral view of tentacle base, note villi of gastrodermal chamber that project into mesogloea. (C) Manubrium of young medusa (5 mm high, 11 tentacles) with beginning formation of the gonadal folds, from Hartlaub (1914). (D) Manubrium of large specimen that also have numerous pits on the gonadal folds; from Hartlaub (1914).

Polyp stage unknown, the smallest known medusae (3.5 mm diameter; Kramp, 1926) had four large perradial tentacles, four somewhat smaller interradial tentacles, eight adradial very short tentacles, and 16 tentacular rudiments. The radial canals were already jagged at this stage.

DIMENSIONS: Medusa up to 25 mm wide and 30 mm high (including the large, globular apical projection), size at maturity is very variable (diameters 12-25 mm, Kramp, 1926).

DISTRIBUTION: An Atlantic medusa confined to Arctic regions, rarely penetrating into boreal regions. There is a record from northern Norway from the region south of The Faroes (Fraser, 1973). It is also known from north of Iceland and at Greenland; coast of North America from Cape Cod northward (Hartlaub, 1914; Kramp, 1926; 1959a; Zelickman, 1972). Pacific records are uncertain (Arai & Brinckmann-Voss, 1980). Type locality: Nahant, Massachusetts Bay, USA.

BIOLOGY: A cold water species, usually collected during the summer months (Zelickmann, 1972). The polyp stage is unknown.

REMARKS: The synonymy of this species has been discussed by Maas (1904) and Hartlaub (1914). Haeckel placed this species in the genus *Catablema* and changed the ending of original specific epithet *vesicaria* to *vesicarium*. This was spelling was also used by most subsequent authors.

Hartlaub (1914: 321) and Kramp (1926: 88) regarded *Catablema vesicarium* var. *nodulosa* Bigelow, 1913 as a synonym of *C. vesicarium*. This view was contested by Brinckmann-Voss (1980) who raised the variant to full species level (*Catablema nodulosum* Bigelow, 1913). The latter species has only 8-16 tentacles, rarely 32. The shape of the gonads cannot be used to distinguish the two species.

Catablema multicirratum Kishinouye, 1910 from the North Pacific and the north-western Atlantic is similar to *C. vesicarium*, but larger (up to 60 mm high) and it has more than 80 tentacles (see Arai & Brinckmann-Voss, 1980).

Genus ***Merga*** Hartlaub, 1914

TYPE SPECIES: *Pandea violacea* Agassiz & Mayer, 1899 by designation of Hartlaub (1914).

SYNONYMS: *Tiarula* Hartlaub, 1914 [type species *Tiarula tergestina* Neppi & Stiasny, 1912]. – *Mergintha* Hartlaub, 1914 [type species *Mergintha lobianci* Hartlaub, 1914].

DIAGNOSIS: Pandeid medusae with smooth or granulate adradial or interradial gonads, with mesenteries, stomach with cross-shaped base, manubrium not twisted, with simple or faintly folded oral lips; four, eight, or more tentacles, with or without rudimentary bulbs or tentaculae, with or without ocelli.

Hydroids where known colonial, arising from tubular, ramified hydrorhiza, cauli slightly branched or not, with or without pseudohydrotheca, when present not enveloping tentacles, one whorl of filiform tentacles. Medusa buds arise from stems or stolons.

REMARKS: The genus is discussed by e. g. Hartlaub (1914), Russell (1953), Kramp (1959a), Vannucci & Yamada (1959), Picard (1960), Arai & Brinckmann-Voss (1989). Hartlaub established this genus to accommodate pandeid medusae that resemble *Leuckartiara* or *Halitholus* species but that have gonads without folds. However, some (*M. tergestina*) can have variably some folds in their gonads, which somewhat compromises the usefulness of this genus. The species *Merga reesi* Russell, 1956b has gonads with a warty-granulated surface and therefore fits not well into the genus. In order to keep this species within *Halitholus*, Kramp (1959a) modified the definition by allowing also granulated gonad surfaces. Arai & Brinckmann-Voss (1989) proposed that it should be removed from this genus and united it together with *Amphinema krampi*, a species with similarly structured gonads. Although this appears very reasonable, I refrained from doing so as this should be made based on a comprehensive phylogenetic analysis of all Pandeidae genera.

KEY TO THE EUROPEAN *MERGA* SPECIES:

1a with distinct apical process, at least some bulbs with abaxial spurs 2
1b without apical process, no abaxial spurs on marginal bulbs 3
2a 4-8 tentacles, up to 8 rudimentary bulbs, mesenteries short . . . . *Merga tergestina*
2b 8-16 tentacles, perradial bulbs with band-shaped ocelli, mesenteries long *Merga galleri*
3a gonad rough by warts and groves, red-brown manubrium, with tentaculae . *Merga reesi*
3b gonads smooth, no tentaculae 4
4a 4 perradial tentacles, no rudimentary bulbs, no tentaculae, no ocelli . *Merga tregoubovi*
4b 8-12 tentacles, 24-36 rudimentary bulbs, all with ocelli . . . . *Merga violacea*

Merga tergestina (Neppi & Stiasny, 1912) Fig. 65

Tiaria tergestina Neppi & Stiasny, 1912: 556. – Neppi & Stiasny, 1913: 21, pl. 1 fig. 10.
Merga tergestina. – Kramp, 1959a: 116, not fig. 107 [= *Amphinema dinema*]. – Vannucci & Yamada, 1959, 320, figs 1-7. – Vannucci, 1960: 393, figs 1-17. – Kramp, 1961: 107. – Brinckmann-Voss, 1970: pl. 10, fig. 1. – Goy *et. al.*, 1991: 110, ? fig. 28. – Bouillon *et al.*, 2004: 72, fig. 41I-J.
in part *Tiarula tergestina*. – Hartlaub, 1914: 253, fig. 208, not 209.

MATERIAL EXAMINED: BMNH 1959.6.8.1-5; Italy, Naples; coll. 1959; some; young medusae reared from polyp by M. Vannucci, not well preserved. – ZMUC; Italy, Naples; coll. 5 June 1959; 5 well preserved medusae, mature; leg. M. Vannucci, likely grown from hydroid.

DIAGNOSIS: *Merga* medusa with distinct apical projection, 4-8 tentacles, up to 8 rudimentary bulbs, with simple ocelli on abaxial spurs, spurs also on interradial tentacle-bulbs, no tentaculae, mouth margin not much folded, mesenteries short.

DESCRIPTION (Vannucii & Yamada, 1959; Vannucci, 1960; own data): Polyp stage resembles *L. octona* (Figs 53A, 65B) and several other Pandeidae; colonies stolonal, hydrorhiza creeping, reticulate stolons, hydrocaulus of variable length from short to almost sessile to relatively long, hydrocaulus covered by thin, corrugated, horn-coloured perisarc that may or may not continue as pseudohydrotheca over hydranth body; 6-9 tentacles (normally 8); hypostome conical. Medusa buds arise from stolons and hydrocauli, often with relatively long pedicel but also short ones occur, bud ovoid, enclosed in thin perisarc membrane. Hydranth colourless. Nematocysts: two types of microbasic euryteles and desmonemes.

Newly liberated medusa with apical process, umbrella oval, umbilical canal present, radial canals wide, abaxial side irregular, adaxial side smooth, two long perradial tentacles (extended up 25 times bell height), ocelli develop rapidly on abaxial spurs of the bulbs.

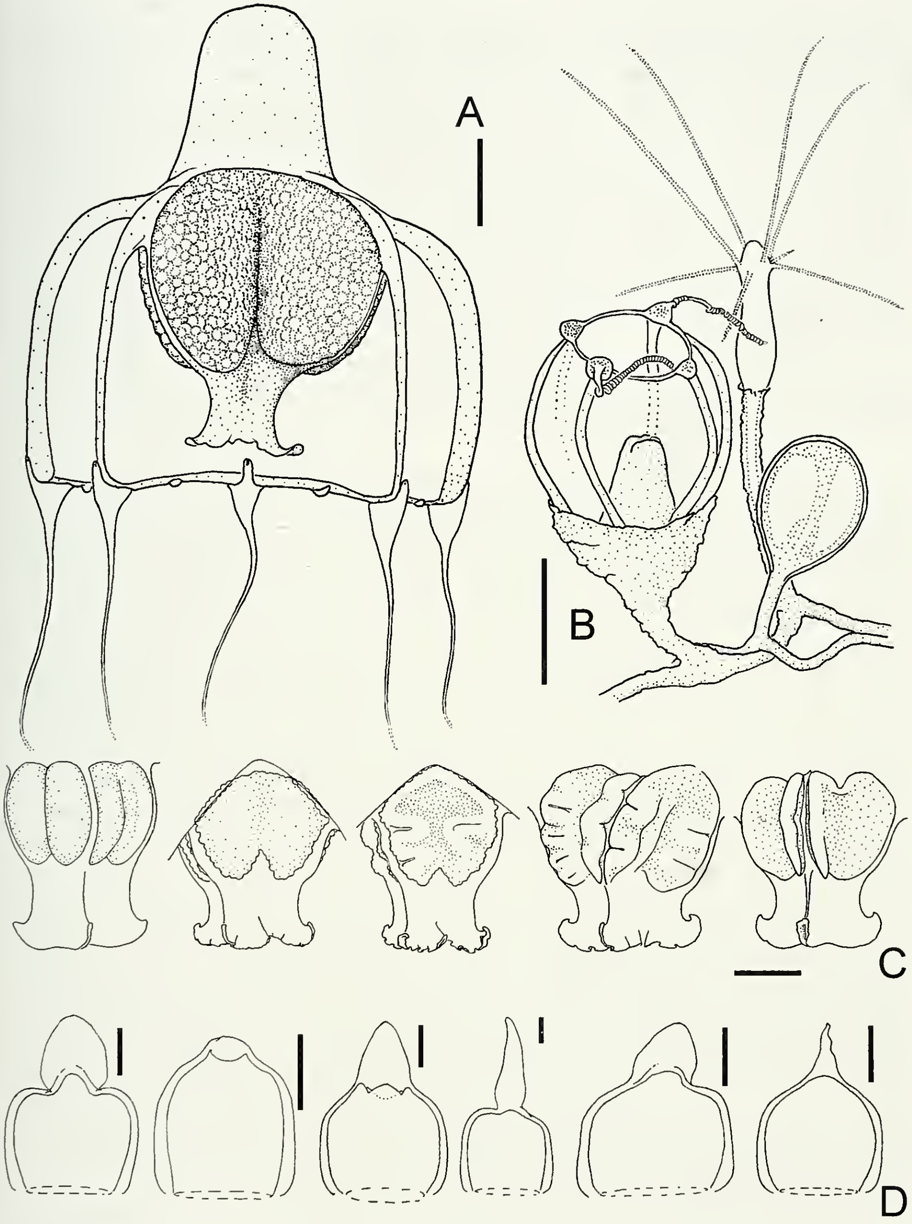

FIG. 65

Merga tergestina (Neppi & Stiasny, 1912). (A) Schematic drawing of a medusa, scale bar 0.5 mm. (B) Polyp with two medusa buds, scale bar 0.5 mm. (C) Variability of gonad form and lip folds; scale bar 0.5 mm, valid for whole series. (D) Variability of apical process and bell-shape, scale bars equal 1 mm. A, after preserved material; B, modified from Vannucci & Yamada (1959); C-D, from Vannucci (1960).

Mature medusa with bell-shaped umbrella bearing a distinct apical projection of variable size and form, lateral walls relatively thin; four radial canals moderately broad, mostly smooth, attached to manubrium through short mesenteries (about 1/6 or less of manubrium height). With 4-9 long marginal tentacles plus about the same number of small intercalated rudimentary bulbs, no tentaculae; tentacle bases laterally compressed and forming long abaxial spurs bearing an ocellus at its end, length of spurs variable; bulbs taper quite abruptly into thinner part of tentacle; rudimentary bulbs small, with or without ocelli. Manubrium large, in fully grown animals reaching almost to velum level, cruciform in section, mouth region relatively small, mouth margin with a few folds. Four large interradial gonads reaching to perradial, forming bulging adradial pads, surface usually smooth, but in very advanced specimens with up to five irregular folds (may also depend on state of contraction). Nematocysts: microbasic euryteles. Colour of manubrium and bulbs in animals from nature brownish (Neppi & Stiasny, 1913).

DIMENSIONS (Vannucci & Yamada, 1959; Vannucci, 1960): Hydranth 0.24-0.62 mm high; mature medusa buds 0.5-0.68 mm wide and 0.7-0.8 mm long; newly liberated medusa bell height 0.98-1.05 mm, apical process up to 0.3 mm. Mature medusa up to 7 mm high and 4 mm wide, more usually 3-4 mm high; egg size 68-84 μm. More data and dimensions of nematocysts are given in Vannucci (1960).

OTHER DATA: The polyp and young medusa were first described by Vannucci & Yamada (1959). The morphological variation of the polyp and medusa has been investigated in detail by Vannucci (1960). Hydroids from different substrates differ considerably in habitus so that they appear to belong to different species, but in culture they become more similar. The hydroids differed in hydranth size, tentacle number, perisarc development, length of hydrocaulus, and also nematocysts. This paper also reports upon the early embryology. Growth stages of the medusa are also tabulated in Neppi & Stiasny (1913).

BIOLOGY (Vannucci, 1960): The hydroid has been found on spines of the sea urchin *Stylocidaris affinis* (Philippi), regularly on the parapodia of large specimens of the polychaete *Laetmonice hystrix* (Savigny, 1820)(= *Hermione hystrix*), on shell of *Murex* spec., and on tube of the polychaete *Spirorbis* sp. Depth range: 15-60 m. The medusa lived up to 145 days in vitro. They started to spawn eggs when 14-26 days old and continued to do so almost daily for a period of up to 24 days. Eggs of *L. octona* could rarely be fertilized with sperms of *M. tergestina* and a hybrid planula developed. Neppi & Stiasny (1913) found the medusa in the plankton near Trieste from July to October, mature animals were present from August onwards.

DISTRIBUTION: Mediterranean and Papua New Guinea (Bouillon, 1980). The only record for the Atlantic (Kramp, 1955b; Gulf of Guinea) has been attributed to *Ampinema dinema* by Vannucci (1960). In the Mediterranean, it has been reported from the Adriatic Sea (Neppi & Stiasny, 1913; Benovic & Lucic, 1996; medusa phase), the Tyrrhenian Sea (Vannucci & Yamada, 1959; Brinckmann-Voss, 1970; polyp), Ligurian Sea (Vannucci, 1960; polyp), and off Lebanon (Goy *et al.*. 1991; medusa). Type locality: Trieste, Mediterranean.

Remarks: The interclonal and intraclonal variation of the polyp was investigated by Vannucci (1960). The morphology of the polyps is considerably influenced by the environment. In view of the variation encountered, Vannucci found that it is impossible to identify many pandeid and bougainvilliid hydroids down to the genus and species level whenever gonophores are absent.

Merga galleri Brinckmann, 1962 Fig. 66

Merga galleri Brinckmann, 1962: 1, figs 1-3. – Brinckmann-Voss, 1970: pl. 10 fig. 3. – Bouillon *et al.*, 2004: 71, fig. 41G-H.

Material examined: Syntype; ZMUC; Italy, Naples, Mergellina, 6 m; 13 July 1961; hydroid on *Cerithium vulagatum*; soft tissues almost completely macerated. – Syntype; ZMUC; one medusa, leg. A. Brinckmann; 27 Sept. 1960.

Diagnosis: *Merga* medusa reaching 8 mm, with 16 bulbs and 8-16 tentacles, large apical process, only perradial tentacle-bulbs with long abaxial spurs and band-shaped ocelli, lips much folded.

Description (Brinckmann, 1962; own observations): Polyp stage resembles *Dicoryne* spec. (Figs 18A, 19A, 66A) and other moderately branched Bougainvilliidae; hydranths stolonal or on sparingly branched shoots with up to four polyps; hydrorhiza creeping, reticulate stolons; stolons and shoots covered by thin perisarc, perisarc infested with detritus, widening distally into a wrinkled pseudohydrotheca; hydranth with conical hypostome, one whorl of four to six filiform tentacles. Medusa buds arise on the hydrocauli, ovoid with short pedicel, surrounded by thin perisarc. Nematocysts: microbasic euryteles and desmonemes.

Newly liberated medusa with apical process and two perradial tentacles, ocelli on bulbs bearing no tentacles.

Mature medusa with bell-shaped umbrella, nearly as wide as high, bearing a large apical projection; four broad, jagged radial canals, ring canal also jagged on upper side, radial canals attached to manubrium via mesenteries of moderate length (about 1/3 of manubrium height). Bell margin with 16 large conical bulbs bearing 8-16 tentacles, lengths unequal; four perradial bulbs with long abaxial spurs and reddish ocelli in a semi-circular band, other bulbs without spurs and with dot-like ocelli. Manubrium large (1/2 of subumbrella depth) and broad, cruciform in section, mouth region separated by a neck, mouth margin strongly folded; gonads in eight bulging adradial pads, rarely with an interradial connection, surface smooth or one or two weak folds. Nematocysts: microbasic euryteles and desmonemes.

Dimensions (Brinckmann, 1962): Hydroid up to 1 cm, newly liberated medusa 0.9-1.2 mm high and 0.9-1.3 mm wide. Adult medusa 9-11.5 mm total height, 3.5-4.5 mm bell diameter. Dimensions of the nematocysts are also given in Brinckmann (1962).

Biology: The polyp was found on shells of the gastropod *Cerithium vulgatum* Bruguière in a depth of 6-10 m. The medusa is only known from rearing experiments. It took 24-28 days to reach sexual maturity (Brinckmann, 1962).

Distribution: Known from type locality only, outside Mergellina Harbour, Naples, Italy.

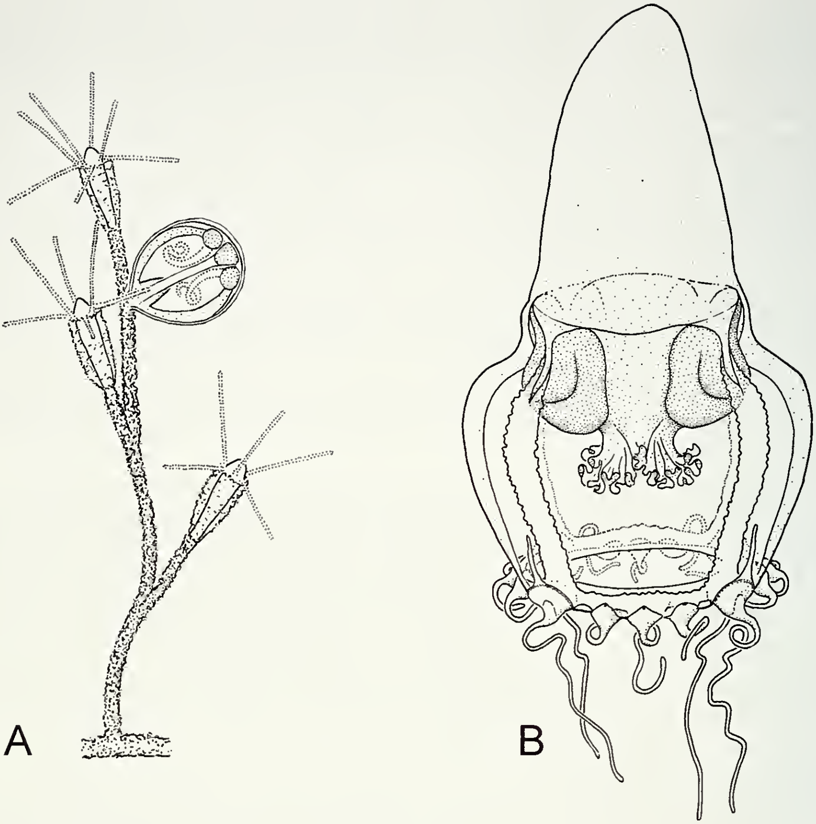

FIG. 66

Merga galleri Brinckmann, 1962; modified after Brinckmann (1962). (A) Shoot of hydroid colony, with medusa buds. (B) Mature medusa, total height about 8 mm.

Merga reesi Russell, 1956 Fig. 67

Merga reesi Russell, 1956b: 493, fig. 1. – Kramp, 1959a: 116, fig. 108. – Kramp, 1961: 105. – Russell, 1970: 246, fig. 9s. – Brinckmann-Voss & Arai, 1998: 48, fig. 4.

MATERIAL EXAMINED: Holotype, BMNH 1956.4.14.1; Bay of Biscay 47.20°N 07.67°E, 821m wire out; coll. 21 July 1955; on medusa, badly damaged and macerated, almost useless.

DIAGNOSIS: *Merga* medusa without apical process, four perradial tentacles and four interradial tentaculae, red-brown gonad, surface with warts and grooves.

DESCRIPTION (Russell, 1956b; Brinckmann-Voss & Arai, 1998): Umbrella bell-shaped, higher than wide, jelly thin, no apical process; four radial canals smooth, attached to manubrium for more than half their length via mesenteries, ring canal smooth, narrower than radial canals. Four large perradial tentacles and four small interradial tentaculae, without ocelli; perradial tentacles with swollen basal part through enlarged gastrodermis, narrowing towards bell margin. Manubrium large, spanning more than $3/4$ of subumbrella, flask-shaped with broad base; mouth with

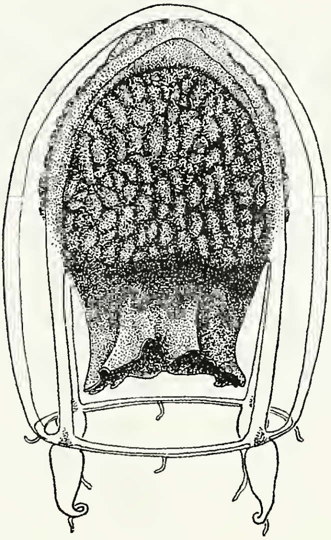

FIG. 67
Merga reesi Russell, 1956; from Russell (1970).

slightly crenulated lips armed with a band of nematocysts. Gonads large, interradial, only separated perradially by mesenteries, surface irregularly corrugated by warts and grooves. Colour of stomach and gonads dark reddish brown.

Polyp stage unknown.

DIMENSIONS (Brinckmann-Voss & Arai, 1998): Bell height up to 10 mm, diameter up to 8 mm.

OTHER DATA: Brinckmann-Voss & Arai (1998) depict the tentacle base with its enlarged proximal part.

BIOLOGY: A very rare medusa occurring in depths of several hundred meters.

DISTRIBUTION: Atlantic Ocean, off Brittany (Russell, 1956b); Indian Ocean, Bay of Bengal (Navas, 1971; Navas-Pereira & Vannucci, 1991); north-eastern Pacific Ocean (Brinckmann-Voss & Arai, 1998). Type locality: 47.20°N 07.67°E.

REMARKS: *Merga reesi* shows many similarities with *Amphinema krampi,* notably both have the same peculiar gonad surface. Although the latter species is currently clearly separable on account of its tentacle number, the apical process, and the tissue strands in the mesogloea, the possibility that both are actually only forms of the same species should not be disregarded entirely. See also comments under *Amphinema biscayana*.

Merga tregoubovii Picard, 1960 Fig. 68

Merga tregoubovii Picard, 1960: 333, fig. 1. – Kramp, 1961: 444. – Goy, 1973: 985. – Bouillon, 1980: 334. – Bouillon *et al.*, 2004: 72, fig. 42A.

DIAGNOSIS: *Merga* without apical process, four perradial tentacles, no rudimentary bulbs or tentaculae, no ocelli.

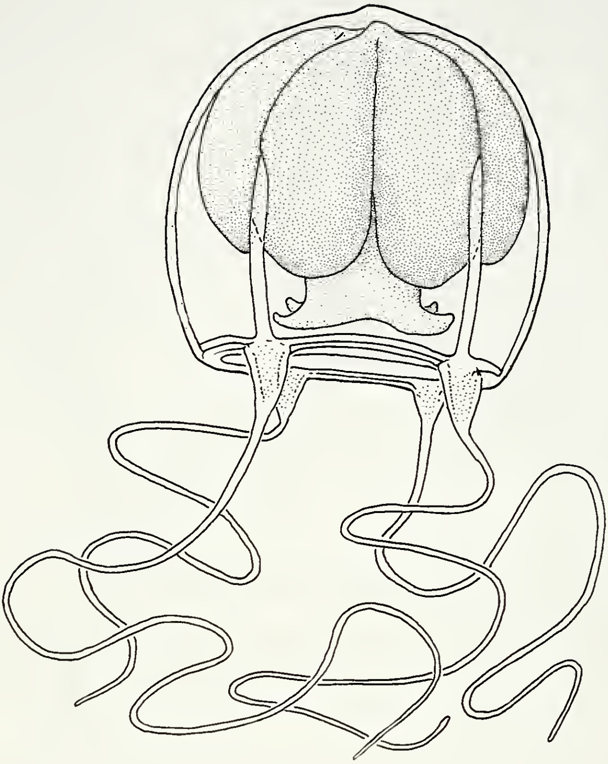

FIG. 68

Merga tregoubovii Picard, 1960; after Picard (1960) based on preserved material, the bell could thus be more voluminous in living animals.

DESCRIPTION (Picard, 1960; Bouillon, 1980): Umbrella of mature medusa rather spherical, jelly very thin, without apical process, without manubrial peduncle; four moderately broad radial canals, smooth, radial canals attached to manubrium via mesenteries that run along about 1/2 of the manubrium height. Bell margin with four large conical bulbs bearing four tentacles, no abaxial spurs, no ocelli. Manubrium large, quadrangular, reaching almost to velum level, four lips without folds. Gonads very voluminous, in eight bulging adradial masses with an interradial connection at the top, surface smooth; in very advanced animals the gonads are connected over the entire interradial surface. Nematocysts: microbasic euryteles.

DIMENSIONS (Picard, 1960): The preserved medusae had a height and diameter of about 2.5 mm.

DISTRIBUTION: A very rare medusa, only known from a few specimens from the Ligurian Sea (Picard, 1960; Goy, 1973) and more than hundred specimens from Papua New Guinea (1980). Type locality: Villefranche-sur-Mer, France, Mediterranean.

Merga violacea (Agassiz & Mayer, 1899) Fig. 69

Pandea violacea Agassiz & Mayer, 1899: 160. – Bigelow, 1909: 205, pl. 41, figs 10-11. – Mayer, 1900b: 34, pl. 1 fig. 1. – Mayer, 1910: 119, pl. 11 fig. 7, pl. 12 fig. 1, text fig. 64.
Pandea spec. – Lo Bianco, 1903: 217, pl. 7 fig. 1. – Mayer, 1910: 119, synonym.
Mergintha lobianci Hartlaub, 1914: 250, fig. 205. – Kramp, 1953: 265, synonym.
Merga violacea. – Hartlaub, 1914: 249, fig. 204. – Menon, 1932: 7, pl. 1 fig. 10. – Kramp, 1953: 265. – Kramp, 1959a: 116, fig. 106. – Kramp, 1961: 107. – Kramp, 1962: 313. – Kramp, 1968: 41, fig. 104. – Goy, 1973: 985. – Schmidt, 1973a: 21. – Bouillon *et al.*, 2004: 72, fig. 42B.
? not *Merga violacea.* – Goy *et al.*, 1991: 111, fig. 28.

MATERIAL EXAMINED: ZMUC, as *Merga lobianci*, Thor station 147; 31.583°N 19.150°E; southern Mediterranean; 25 July 1910, det. Kramp. – ZMUC, as *Merga lobianci*, Thor station 200; 39.300°N 10.183°E; Tyrrhenian Sea; 25 m; 26 Aug. 1910; 2 damaged medusae, det. Kramp. – ZMUC, as *Merga lobianci*, Thor station 142; 35.733°N 15.117°E; southern Mediterranean; 25 m; 22 July 1910; 1 damaged medusa, det. Kramp. – ZMUC, as *Merga lobianci*, Thor station 147; 31.583°N 19.033°E; southern Mediterranean; 25 m; 25 July 1910; 1 damaged medusa, det. Kramp. – ZMUC, as *Merga lobianci*, Thor station 184; 38.167°N 22.550°E; SE Mediterranean; 10 m; 17 Aug. 1910; 2 medusae, det. Kramp. – ZMUC, Dana station 3809; 6.367°S 105.200°E; Indonesia; 0-100 m; 04 Sept. 1929; 2 medusae. – ZMUC; Vietnam, Nhatrang; 29 June 1936; 1 medusa, det. Kramp.

DIAGNOSIS: Bell 4-11 mm high, with thick walls and dome-like apex, no apical process; four slightly folded lips, mesenteries very long; 8-12 long tentacles and 24-36 rudimentary tentacles, all with ocelli.

DESCRIPTION: Medusa umbrella bell-shaped, top relatively flat, walls thick, very thick at apex, no gastric peduncle; four radial canals, margins smooth, attached to manubrium by long mesenteries (about $^1/_2$ of total length); ring canal smooth. With 8-12 fully formed tentacles, their bases laterally flattened, without abaxial spurs, thinning quite abruptly into round tentacles after some distance; between pairs of fully formed tentacles normally three rudimentary marginal bulbs; all tentacle bases and rudimentary bulbs with a small ocellus. Manubrium 1/2 to 3/4 as long as bell cavity, cross-shaped in section; mouth margin slightly crenulated. Gonads large adradial bulges, surface smooth, with deep interradial fold but gonad may also cover interradial position. Colours: the manubrium and bulbs of the Atlantic forms are light pink to red-pink (Mayer, 1910); Menon (1932) observed a light-greenish tint.

Polyp stage unknown.

DIMENSIONS : Bell height up to 11 mm, usually less (4-6 mm).

BIOLOGY: Occurs in tropical to subtropical seas, usually in less than 100 m depth, but some Mediterranean specimens (Lo Bianco, 1903) came from 900-1100 m depth. According to Mayer (1900), the medusa is common at the Tortugas throughout the summer.

DISTRIBUTION: Mediterranean, Florida, Bahamas, Brazil, Red Sea, India, Nicobars, Vietnam, Sunda Strait, NE Australia, Fiji Islands, Papua New Guinea, Pacific coast of Mexico Pacific, Chile (Kramp, 1966, 1968; Goy, 1973; Schmidt, 1973a; Bouillon, 1980). Type locality: The first description was based on material from the Dry Tortugas (Florida) and Suva Harbour (Fiji Islands).

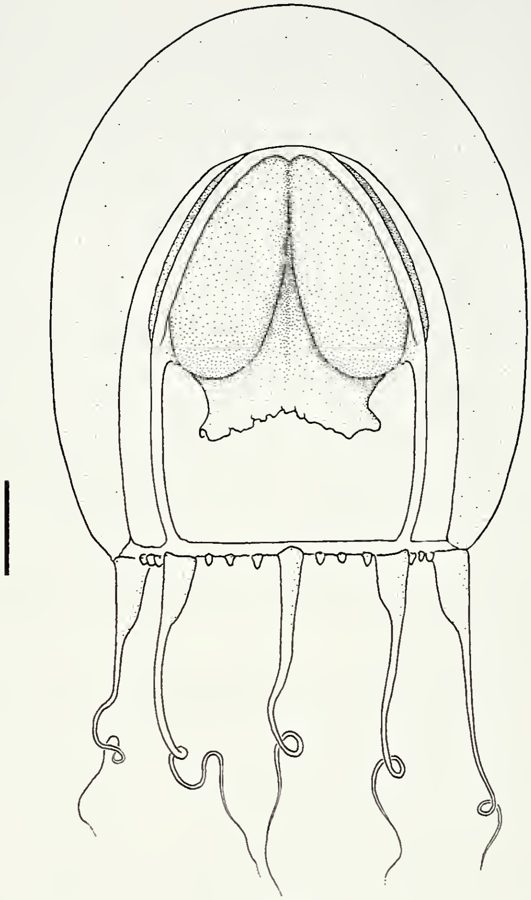

FIG. 69

Merga violacea (Agassiz & Mayer, 1899); schematic drawing after several preserved Mediterranean specimens, scale bar 1 mm.

REMARKS: In preserved material, the gonad can have some irregular folds. The animal depicted in Goy *et al.* (1991) has an apical process and short mesenteries and is unlikely *M. violacea*. Perhaps the legend is wrong and it should depict *M. tergestina*.

Genus ***Annatiara*** Russell, 1940

TYPE SPECIES: *Tiaranna affinis* Hartlaub, 1914 by monotypy.

DIAGNOSIS: Medusa bell without apical process, with exumbrellar nematocyst tracks. With four radial canals. Manubrium short and wide, cruciform through four long perradial lobes, mouth rim folded. Gonads on stomach lobes and interradial walls. Many hollow marginal tentacles, elongated conical bases, without well developed abaxial spurs; alternating with tentacles rudimentary tentacles or bulbs. With abaxial ocelli.

REMARKS: The genus is regarded as monotypic (see below).

Annatiara affinis (Hartlaub, 1914) Fig. 70

Tiaranna affinis Hartlaub, 1914: 269, figs 220-221. – Kramp, 1920: 6, pl. 1 fig. 1. – Kramp, 1926: 68, pl. 1 figs 15-17, map 11. – Ranson, 1934: 436.
Annatiara affinis. – Russell, 1940: 518. – Russell, 1953: 200, figs 101-103. – Kramp, 1955b: 251, fig. 3. – Kramp, 1959a: 121, fig. 123. – Kramp, 1961: 96. – Kramp, 1968: 48, fig. 125. – O'Sullivan, 1982: 41, fig. 18, map 17. – Bleeker & van der Spoel, 1988: 231, figs 10-12. – Schuchert, 1996: 66, fig. 38.
Annatiara lempersi Bleeker & van der Spoel, 1988: 249, fig. 13. **new synonym**

MATERIAL EXAMINED: ZMUC, Thor Station 178, 48.067°N 12.667°W, eastern Atlantic, 1000 m wire; 2 Sept. 1906; det. Kramp; 2 damaged medusae. – ZMUC, Dana Station 855, 29.008°N 59.750°W, western Atlantic, 500 m wire; 9 June 1920; det. Kramp; 1 much damaged medusa. – ZMUC, 46.967°N 19.100°W, eastern Atlantic, 300 m wire; 21 July 1910; 1 much damaged and macerated specimen.

DIAGNOSIS: As for genus.

DESCRIPTION (Russell, 1953; own data): Umbrella bell-shaped, about as high as wide; jelly relatively thick, thickest at top; no apical projection: exumbrella with numerous meridional nematocyst tracks originating from the tentacle bases. Velum narrow. Four straight radial canals issuing at ends of stomach lobes, narrow at first, widening somewhat distally with uneven margins, entering by wide orifice into narrow ring canal. No centripetal canals. Usually with 24-32 large hollow smooth tentacles (up to 44 observed), with elongated laterally compressed conical bases which clasp umbrella margin but do not form well-developed abaxial spurs. One very small or rudimentary tentacle between adjacent large tentacles. One small abaxial ocellus on bases of large and rudimentary tentacles. Stomach short, cross-shaped trough four long triangular perradial lobes, extending along more than half of the subumbrella meridian in fully grown animals; walls thin; mouth very large, cruciform, with folded margins. Gonads on irregular folds and pits on inter- and adradial walls of stomach, more developed adradially, gonad pits bulge into stomach, pits sometimes in rows along stomach base. Colour of ocelli brown; gonads yellowish or colourless. Polyp stage unknown.

VARIATION: Younger medusae have a square shaped stomach, which later develops its cruciform shape. Russell (1953) provides a table correlating bell diameter and tentacle number.

DIMENSIONS: Mature medusa usually around 12 mm high and 14-15 mm wide (Kramp, 1961), maximal diameters 23 mm (Ranson, 1934).

BIOLOGY: Occurs in depths of several hundred meters, but apparently not a typical deep water species.

DISTRIBUTION: Rare, usually off-shore in deeper waters. Atlantic Ocean between the Faroes and the equator; south-western Africa to South Africa; central Indian Ocean; Sri Lanka; east of Australia; New Zealand; Indonesia; Papua New Guinea; north-eastern Pacific (Ranson, 1934; Kramp, 1959a, 1961, 1965; Bouillon, 1980; Fraser, 1973; Bleeker & van der Spoel, 1988; Schuchert, 1996; Wrobel & Mills, 1998). Type locality: southwest of Ireland, 48.483°N 13.917°W, 300 m wire out.

REMARKS: The jelly of this rare species is rather delicate and specimens taken by plankton nets are almost invariably severely damaged.

FIG. 70

Annatiara affinis (Hartlaub, 1914). (A) A medusa from the Pacific, bell slightly contracted as in repulsion phase, drawn after photograph of living animal kindly provided by Dr D. Wrobel. (B) Interradial view of stomach with mature gonads, from Hartlaub (1914).

Besides reporting details on *Annatiara affinis*, Bleeker & van der Spoel (1988) described also the new species *Annatiara lempersi* based on a single medusa from the mid North-Atlantic. They admit that their medusa was perhaps not fully mature, but they distinguished it from *A. affinis* on account of the lower tentacle number (24) and the stomach being square shaped instead of cruciform. It is quite clear that *Annatiara lempersi* is only based on a younger stage of *Annatiara affinis*. It matches rather perfectly the description of the type material in Hartlaub (1914), who also had animals with 24 tentacles and a square-shaped stomach.

The polyp stage of *A. affinis* remains unknown. A potential candidate with a similar distribution in the north-eastern Atlantic is *Hydrichthys sarcotretis*.

Genus ***Hydrichthys*** Fewkes, 1887

TYPE SPECIES: *Hydrichthys mirus* Fewkes, 1887.

SYNONYMS: ? *Nudiclava* Lloyd, 1907 [type species *Nudiclava monocanthi* Lloyd, 1907]. – *Ichthyocodium* Jungersen, 1913 [type species *Ichthyocodium sarcotretis* Jungersen, 1913].

DIAGNOSIS: Hydroid parasitic on fishes or parasitic copepods of fishes, hydrorhiza reticular or forming a naked, encrusting plate; polyps dimorphic or not, club-shaped or tubular, without tentacles, hydrocaulus indistinct and without perisarc covering; gonophores either growing at base of feeding zooids or on special gonostyles; gonostyles branched or not. Gonophores develop into medusa or fixed sporosacs. Newly liberated medusa with two opposite tentacles only.

REMARKS: The first complete life cycle of a *Hydrichthys* hydroid was revealed by Larson (1982). He could identify the resulting medusa as *Stomotoca pterophylla* Haeckel, 1879. Because his hydroid showed little host specificity and many other *Hydrichthys* polyps are rather similar, Larson concluded that they will also produce medusae referable to the genus *Stomotoca* L. Agassiz, 1862. Therefore, he suggested to synonymize *Hydrichthys* and *Stomotoca*. This was contested by Arai (1989) and Boero & Bouillon (1989). The latter authors could show that the type species of *Stomotoca* – *S. atra* L. Agassiz, 1862 – had a polyp stage that was completely different from *Hydrichthys* (free living, with scattered tentacles). Moreover, the polyp of a tentatively identified *Hydrichthys mirus* Fewkes, 1887 – type species of the genus *Hydrichthys* – produced a *Leuckartiara*-like medusa (Boero *et al*., 1991). Because *Stomotoca pterophylla* and *Stomotoca atra* have different polyps, Boero *et al*. (1991) proposed the new genus *Larsonia* for *S. pterophylla*.

More life-cycle information on various other *Hydrichthys* hydroids could show an even larger array of medusa morphologies and some might be referred to known medusa based genera.

Because the *Hydrichthys* polyps produce medusae belonging to different genera, it must be assumed that the *Hydrichthys*-like polyp evolved several times convergently through a simplification and adaptation to the parasitic mode of life. Just like for many *Bougainvillia* hydroids, the *Hydrichthys* hydroids offer few morphological traits to distinguish reliably separate species. The host specificity seems not to be very strict neither (Millard, 1975; Larson, 1982). *Hydrichthys* species identification is therefore difficult and assignments to nominal species should generally only be made when the material comes from approximately the same geographic region as the type specimen. It remains thus not beyond any doubt that the medusa of *Hydrichthys mirus* Fewkes, 1887 corresponds to the medusa described by Boero *et al*. (1991) based on a colony from Papua New Guinea, whereas *H. mirus* was originally described from New England. Further clarification of the genus depends on the rearing and identification of mature medusae of each nominal *Hydrichthys* species based on material from the original biogeographic region.

Following Arai (1989), the morphological differences of *Hydrichthys sarcotretis* (Jungersen, 1913) and *H. mirus* are considered not sufficient to warrant a generic separation. *Nudiclava* Lloyd, 1907 was based on a hydroid which fixed sporosacs. The affinities of this genus are thus not clear, but it could be a synonym of *Hydrichthys*.

KEY TO THE EUROPEAN *HYDRICHTHYS* SPECIES :

1a on copepods parasitizing fish, medusa buds not on hydrorhiza . . . . *H. sarcotretis*

1b on fins of fish, medusa buds on hydranths and hydrorhiza . . . . *H. cyclothonis*

Hydrichthys sarcotretis (Jungersen, 1913) Fig. 71

Ichthyocodium sarcotretis Jungersen, 1913a: 1, figs. 5-6, pls. 1. figs 1-6. – Jungersen, 1913b: 211. – Kramp, 1921: 13, figs 7-8. – Jones, 1966: 173, figs 1-2. – Templeman, 1973: 1355, figs 2-5.

Hydrichthys sarcotretis. – Arai, 1998: 94, figs 1-2.

MATERIAL EXAMINED: ZMUC, holotype colony; loc. SW of Ireland; coll. 1906. – ZMUC, W Greenland; 64.010°N 55.300°W; 8 May 1909; det. W. Jungersen (material not part of Jungersen, 1913a but mentioned in Jones, 1966). – ZMUC; E Greenland; 60.933°N; 45.766°W; 550 m wire; 22 August 1953; det. P. Kramp.

DIAGNOSIS: *Hydrichthys* growing on copepod parasites of deep-sea fishes, polyps not dimorphic, medusa buds not on hydrorhiza.

DESCRIPTION (Jungersen, 1913a; own observations): Hydroid growing on parasitic copepods of fish. Stolons thin and not well visible, without perisarc, forming a tight meshwork and often coalescing into a plate-like hydrorhiza. Polyps dense, naked, non-reproductive polyps club-shaped but form variable, usually with an indistinctly demarcated pedicel widening distally into hydranth body, subterminally a slight neck and thus delimiting a head-like hypostome, contraction can obliterate this regionalization, mouth region without or with very few nematocysts, no tentacles. Medusa buds develop at lower part of normal hydranths (pedicels), hydranths can get gradually atrophied to mere stumps with ongoing budding, buds in several whorls (3-4), up to 20 buds can be present.

Advanced medusa buds are elongate (nearly two times longer than wide); two large opposite perradial bulbs, tapering into a short tentacle, abaxial fold in bulbs, other pair of bulbs small or not yet developed; many exumbrellar nematocysts; no sex cells visible in medusa buds.

DIMENSIONS (Jungersen, 1913a; Jones, 1966; own data): Non-reproductive polyps 1-8 mm, diameter 0.05-0.2 mm; advanced medusa buds 0.4-0.84 mm long.

ADDITIONAL DATA: Some hydranths can be branched, the gastrodermis has 6-11 (usually 8) longitudinal ridges (Templeman, 1975).

BIOLOGY: This hydroid lives on copepods (*Sarcotretes scopeli, Sphyrion lumpi*) parasitizing different fish species (*Benthosema glaciale, Sebastes mentella*) (Jungersen, 1913a; Jones, 1966; Templeman, 1973). The host fish occur in depths of several hundred meters, usually over very deep water. Jungersen (1913a) collected the hydroid in depths of 100-450 m.

Microscopic examination of the stomach content showed that the hydroid likely feeds on blood and tissues of the host fish (Jones, 1966).

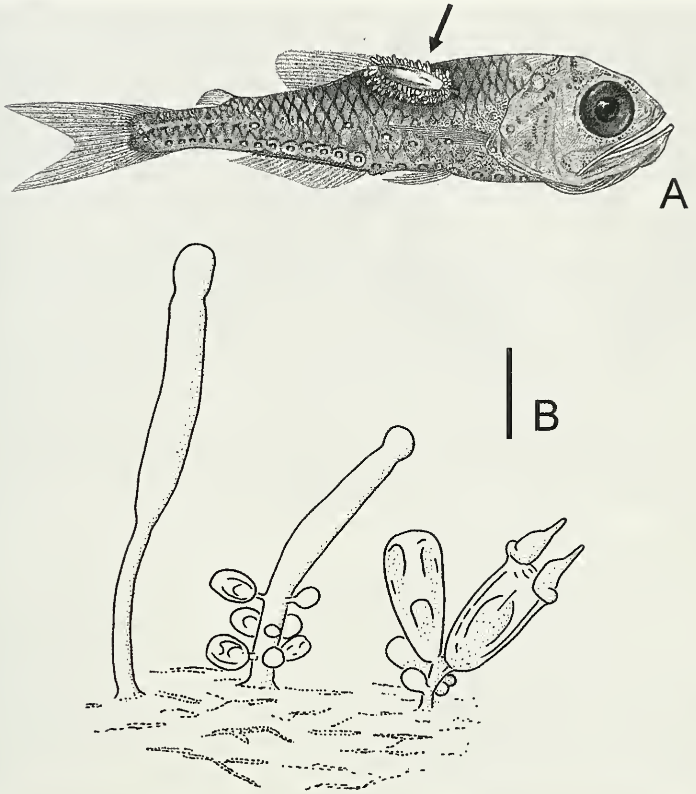

FIG. 71
Hydrichthys sarcotretis (Jungersen, 1913). (A) *Benthosema glaciale* (Reinhardt) with the parasitic copepod *Sarcotretes scopeli* (Jungersen) (arrow) bearing the hydroid colony; about two times magnified. (B) Schematic drawing of hydroid colony (polyp density reduced) with non-reproductive hydranth (left) and two hydranths producing medusae, hydranth at right much reduced or lost and with a medusa ready to be released, scale bar 0.2 mm. A, from Jungersen (1913); B, after preserved material.

DISTRIBUTION: Subarctic to boreal Atlantic, recorded from The Faroes to southwest of Ireland (Jungersen, 1913a); between Greenland and Iceland (Jungersen, 1913a, 1913b; Jones, 1966); western Greenland (Jungersen, 1913b; this study); Atlantic coast of Canada (Templeman, 1973). Type locality: southwest of Ireland.

REMARKS: The publication date of Jungersen's work is usually given as 1911, but according to the volume cover it was published in 1913.

Kramp (1921) re-examined Jungersen's material and he also made histological sections. He doubted that the gonophores are liberated as free medusae and he interpreted the infolded tentacles in the subumbrella as thickened gastrodermal tissue. Having also examined Jungersen's and additional material, I think that Kramp was wrong, a conclusion also put forward by Damas (1934) and Jones (1966). There were clearly some medusa buds with everted tentacles in the examined material (Fig. 71B).

The adult medusa of *Hydrichthys sarcotretis* (Jungersen, 1913) is unknown. The distribution of this species overlaps with two other congeners, *H. mirus* and *H. cyclothonis*. *Hydrichthys mirus* Fewkes, 1887 was originally described as parasitizing a coastal fish of New England. It grows directly on the fish and differs also morphologically as it has dimorphic polyps. The gonozooids have many side branches bearing the medusa buds. *Hydrichthys cyclothonis* Damas, 1934 occurs immediately south of *H. sarcotretis*, ranging from the Gulf of Biscay to the Morocco and Madeira. It grows directly on the fins of the host. Apart from the host organism, the morphological differences are very not pronounced: the basal plate digesting the host tissues has a wide cavity; the medusa buds occur on the hydranth bases, the basal plate, and on blastostyles; the nematocysts on the medusa bud are evenly distributed. The first two differences could be linked to the different substrate and the blastostyles seem to be reduced hydranths in this case too. The nematocyst distribution on the medusa bud is variable in *H. sarcotretis* (Jones, 1966). As at least some *Hydrichthys* species can grow on copepods and fish simultaneously (McCormick *et al.*, 1967), *Hydrichthys cyclothonis* is thus perhaps a form of *H. sarcotretis* (Jungersen, 1913).

Hydrichthys cyclothonis Damas, 1934 Fig. 72

Hydrichthys cyclothonis Damas, 1934: 1, figs 1-4.

Diagnosis: *Hydrichthys* growing on fish of the genus *Cyclothone*, medusa buds at base of polyps and on hydrorhiza.

Description (Damas, 1934): Hydroids growing on epidermis of fish of the genus *Cyclothone*. Hydrorhiza plate-like, with large gastrodermal cavity, without perisarc, without processes infiltrating host tissue («haustoria»). Polyps dense, non-reproductive polyps club-shaped, widening distally, without distinct pedicel, without tentacles, their epidermis with few nematocysts only, mostly around mouth opening. Medusa buds develop either at base (pedicels) of feeding zooids, or from hydrorhiza, or from blastostyle-like polyps (likely reduced hydranths); numerous medusa buds give a grape-like appearance to the colony.

Advanced medusa buds elongate (nearly two times longer than wide); with two large opposite perradial tentacle-bulbs; no sex cells visible; nematocysts of exumbrella evenly distributed.

Dimensions (Damas, 1934): Non-reproductive polyps 0.6 mm high and 0.2 mm wide (preserved material); advanced medusa buds 0.64 mm long and 0.25 mm wide.

Biology: Grows on fins of *Cyclothone* species. It digests and destroys the tissue, it is thus a true parasite. Damas (1934) caught his fish with nets using cable lengths of 300-2120 m. According to Froese & Pauly (2006), *Cyclothone alba* has a depth range of 300-600 m.

Distribution: Gulf of Biscay: off Portugal, between Morocco and Madeira, Azores (Damas, 1934) Type locality: Not specified.

Remarks: For the differences to *H. sarcotretis* see under remarks for this species. Damas (1934) gives as host species *Cyclothone signata* (Garman). This species is currently seen as restricted to the Pacific Ocean (Froese & Pauly, 2006), but

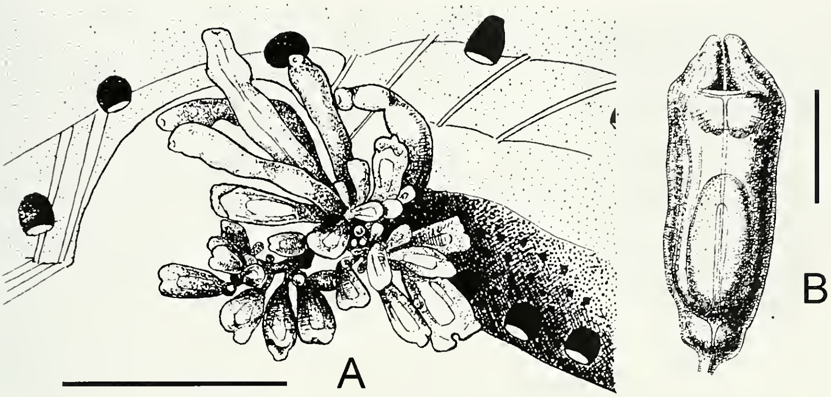

FIG. 72
Hydrichthys cyclothonis Damas, 1934; figures from Damas (1934). (A) Colony on ventral fin, the black dots are the luminescent organs of the fish, scale bar 1 mm. (B) Advanced medusa bud, scale bar 0.2 mm.

was earlier regarded as a cosmopolitan species. It is likely that Damas's fish belonged to the very similar *Cyclothone alba* Brauer, a nominal species initially described as subspecies of *C. signata*.

McCormick *et al.* (1967) examined more than 2000 specimens of *Cyclothone* originating from the north-eastern Pacific, among them *C. signata*, but they found no parasitic hydroids. They found them only on other genera and also on parasitic copepods. In a few cases the *Hydrichthys* polyps grew on both the parasitic copepod and the fish.

Genus ***Octotiara*** Kramp, 1953

TYPE SPECIES: *Octotiara russelli* Kramp, 1953 by monotypy.

DIAGNOSIS: Pandeid medusa with eight simple radial canals in adults, manubrium reaching far beyond velum level, with eight transversely folded gonads; without mesenteries, no ocelli, eight or more tentacles, with or without gastric peduncle.

Hydroid on bryozoans, colony stolonal, hydrocaulus covered by thin perisarc, hydranth with a single whorl of filiform tentacles, medusa buds on stolons.

REMARKS: The genus is currently monotypic.

Octotiara russelli Kramp, 1953 Fig. 73

Octotiara russelli Kramp, 1953: 266, pl. 1 figs 1-3. – Kramp, 1961: 111. – Kramp, 1965: 38. – Kramp, 1968: 44, fig. 114. – Boero & Bouillon, 1989: 1, figs 1-3, 4A. – Bouillon *et al.*, 2004: 73, fig. 42F-H.
Octotiara violacea Kramp, 1959b: 234, fig. 8a-c. – Kramp, 1965: 38, synonym.

MATERIAL EXAMINED: MNHN, No 1645, coll. April 1954; Bay of Villefranche-sur-Mer, Ligurian Sea; material of Goy (1973), 1 damaged infertile medusa, bell diameter ca. 2 mm.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION (Russell, 1968; Boero & Bouillon, 1989): Hydroid colonial, growing on specific cheilostomate bryozoans; colony stolonal, hydrorhiza tubular,

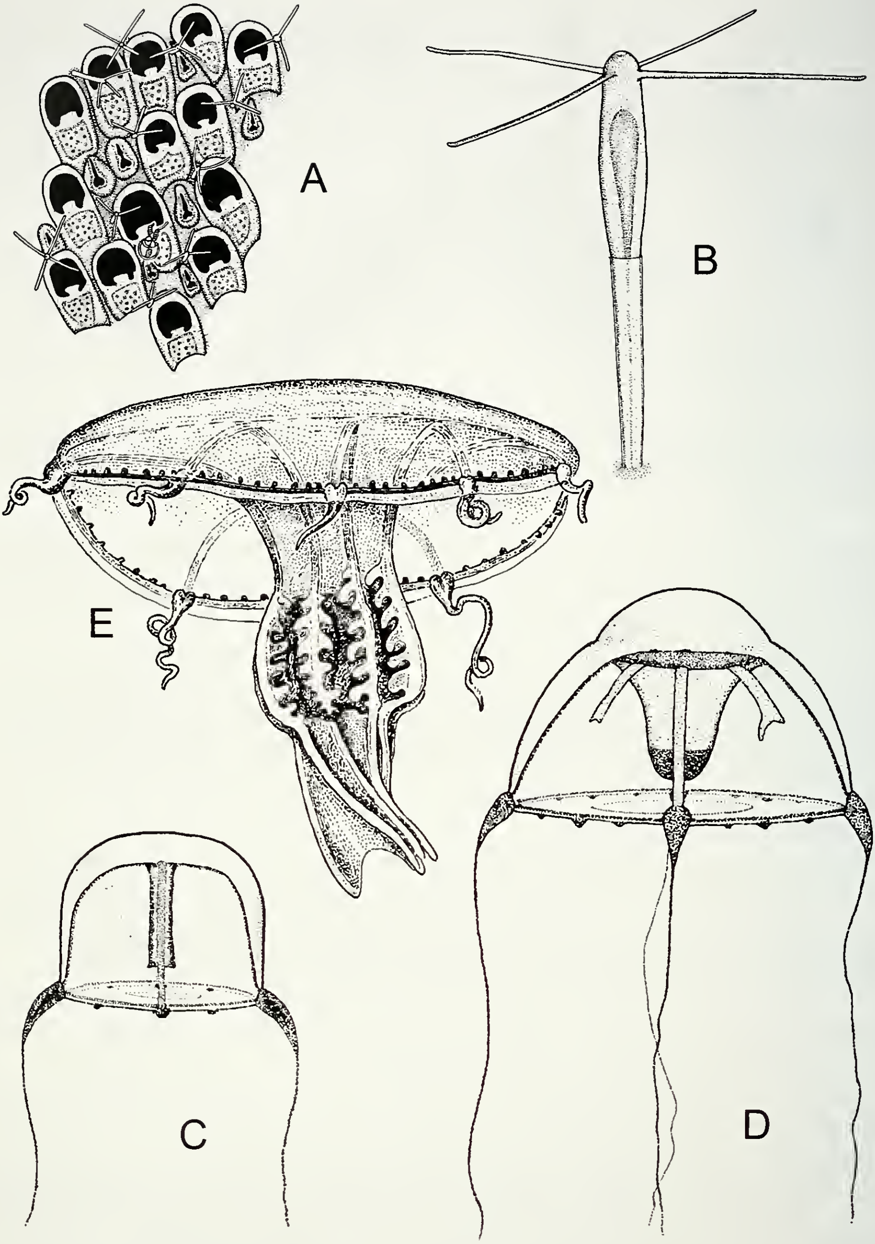

FIG. 73
Octotiara russelli Kramp, 1953. (A) The bryozoan *Steginoporella mandibulata* with the hydroid of *Octotiara russelli*, one medusa bud is present. (B) Higher magnification of the hydroid. (C) Newly released medusa. (D) Fifteen-day-old medusa, the second set of radial canals has not yet reached the ring canal. (E) Mature medusa. A-D, from Boero & Bouillon (1989); E, from Kramp (1968).

embedded in skeleton of host, hydranths arising between bryozoan zoecia; hydrocaulus short, covered by thin perisarc; hydranth with a single whorl of 3-4 filiform tentacles, rounded hypostome, reddish body. Medusa buds arise singly from stolons.

Newly liberated medusa roundish to quadratic, exumbrella green; small apical projection present in some individuals; four radial canals only. Two long opposite marginal tentacles originating from triangular-elongate perradial tentacular bulbs, two small atentaculate perradial bulbs; four smaller interradial bulbs; all bulbs reddish. Manubrium reddish, cylindrical, reaching 2/3 of height of subumbrellar cavity, mouth with four simple lips.

Umbrella of mature medusa flatter than hemisphere, sometimes with a large and broad gastric peduncle; eight radial canals fairly narrow, with smooth edges, in younger individuals only the four perradial canals may reach the ring canal, interradial ones shorter; circular canal narrow; velum narrow. Usually eight large tentacles but occasionally up to 32, additionally 8-64 rudimentary bulbs or tentacles; nematocysts of tentacles evenly distributed. Manubrium long, reaching far beyond velum level, along its entire length eight deep longitudinal furrows; mouth part and stomach part approximately same length, mouth part with eight sharp edges terminating in eight pointed lips. Gonads usually beyond level of velum along each of the eight perradial edges of the stomach, each with 6-10 deep irregular transverse folds. Nematocysts: microbasic euryteles. In living specimens the wall of the stomach between the gonads have a dark, almost black violet colour.

DIMENSIONS: Hydranths about 0.5 mm high; newly liberated medusa 0.5-0.7 mm; diameter of mature medusa 7-11 mm.

BIOLOGY: The hydroid was found in 10-20 m depth on the Indo-Pacific cheilostomate bryozoan *Steginoporella mandibulata* Harmer. This bryozoan genus is not known to occur in the Mediterranean or Atlantic (Costello *et al.*, 2001). If the polyp is present in the Mediterranean, then it likely occurs on other bryozoans species. Boero & Bouillon (1989) found that the medusa was abundant near the water surface at Wuvulu Island, Papua New Guinea. Kramp (1953, 1965) collected it from near the surface to more than 400 m depth.

DISTRIBUTION: Great Barrier Reef (Kramp, 1953); Sri Lanka (Kramp, 1959b); Malayan Archipelago and east coast of Africa (Kramp, 1965); Papua New Guinea (Bouillon 1980; Boero & Bouillon, 1989); Mediterranean (Goy, 1973). Type locality: Papuan Pass, Great Barrier Reef, Australia, depth more than 400 m.

REMARKS: The only European record of this species was published by Goy (1973). She found one mutilated and infertile medusa in the Ligurian Sea (Mediterranean) which she attributed to *O. violacea*. This name has been synonymized with *O. russelli* by Kramp (1965). Goy's specimen could be re-examined for this study. Although the identification may be correct, the state of preservation precludes a reliable identification. The presence of this species in the Mediterranean is therefore somewhat uncertain.

Genus ***Codonorchis*** Haeckel, 1879

TYPE SPECIES: *Codonorchis octaedrus* Haeckel, 1879 by monotypy.

Diagnosis: Pandeidae medusa with only two opposite tentacles; no manubrial peduncle; no mesenteries, with ocelli. The gonad are composed of four large flat interradial leaves that extend from the stomach surface onto the subumbrella, their margins are adnate to the radial canals, thus forming a bell-like structure within the subumbrella.

Remarks: This is a problematic genus based on single specimen of which there is no illustration available. Haeckel promised to provide an illustration in a subsequent paper, but he never did so. The genus is characterized by a unique form of the gonad. This was, however, not made very clear in the synopsis of Kramp (1961). Haeckel (1879) gives more details on this genus (translated from German, my additions in brackets): «I establish the genus *Codonorchis* for a peculiar Tiaridae which differs from all other genera of this group by its peculiar formation of the gonads. The gonads form four large interradial lappets which do not only cover most of the four sides of the tetraedric stomach, but they are continued onto the subumbrella where they cover its upper half; the thickened margins of the gonads are adnate to the radial canals and the gonads occupy completely the space between the proximal [upper] halves of the radial canals. By this, the four gonads form a bell-like cavity within which the stomach dangles. This peculiar formation arose probably when the eight gonadal ridges, which in turn originated through a cleavage of the four original perradial bulges, grew from the stomach base along the margins of the radial canals and got a connection through interradial lamellae.»

The name *Codonorchis* is composed of the Greek words for bell and gonad. The interradial leaf-like gonads that extend halfway to the subumbrella are unique and should render the genus very distinct, if it is not based on a misinterpretation. The only Pandeid species that shows some resemblance to this species is *Amphinema turrida* (Mayer, 1900) (see Fig. 48). Also in this species the gonads extend to the subumbrella, but in this species they are adradial to perradial and not interradial. Picard (1960: 336) thought that *C. octaedrus* could actually be *A. turrida*. Also Bigelow (1909: 200) and Hartlaub (1914: 264) thought that *Codonorchis octaedrus* is related to *A. turrida*.

For more problems associated with this genus, see the remarks under *C. octaedrus*.

Codonorchis octaedrus Haeckel, 1879

Codonorchis octaedrus Haeckel, 1879: 51. – Picard, 1960: 336. – Kramp, 1961: 98.
Not *Codonorchis octaedrus*. – Boero *et al.*, 1997: 359, figs 1-3.

Description (Haeckel, 1879): Umbrella highly arched, shape quite octaedric through longitudinal exumbrellar perradial edges and one equatorial edge, with high cylindrical apical process, umbrella almost twice as high as wide. Two opposite tentacles, much longer than umbrella, conical bulbs; along bell margin ten bulbs, all bulbs with ocelli. Manubrium tetraedric, attached with broad quadratic basis, spanning half of the subumbrellar height; mouth-lips simple, short. Gonads four interradial lappets which cover the upper half of the subumbrella. Colours: stomach, gonad and tentacles yellowish; ocelli brown-red.

Dimensions: Diameter of bell 2.5 mm, bell-height 4 mm.

Distribution: Type locality only, Croisic (Brittany, France), depth 20 m.

REMARKS: Although its peculiar gonads and the ocelli should render this species distinct, it has never been found again. There exists very likely no type material. It must be regarded as a doubtful species

Although the medusae of the region of the type locality – close to the mouth of the Loire – have not been investigated ever since, it is quite unlikely that *C. octaedrus* should be confined to this region. As the medusae of the nearby coasts are otherwise relatively well investigated, it is difficult to imagine why it has never been seen again. It could well be that Haeckel misinterpreted his specimens or he had shrunken and damaged material. As Haeckel repeatedly mistook some diffuse pigments for ocelli, it could also be that his medusa did not have true ocelli. Perhaps *C. octaedrus* was a well grown *A. rugosum* as shown in Fig. 47. Some authors linked *O. octaedrus* to *Amphinma turrida* (see above); Kramp (1961) considered it a doubtful species.

Recently, Boero *et al.* (1997) thought that they have found this species again. They described adult medusae reared from a hydroid collected in the Ionian Sea. Their medusa shares several features with *O. octaedrus*, like the bell-shape, the apical process, tentacle number, the ocelli, and the bulb rudiments. However, it lacks the crucial feature of the genus *Codonorchis*, the gonad that extends to the subumbrella. I therefore hesitate to accept that this was *O. octaedrus* and consider it to represent a new, undescribed *Amphinema* species. In accordance with Dr. F. Boero and following his suggestion, it is therefore here described as the new species *Amphinema bouilloni*. The details are given under the *Amphinema* species.

Boero *et al.* (1997) also designated neotype material for *C. octaedrus*. This designation can be regarded as invalid as it does not met the provision of article 75.3.5 of the ICZN («evidence that the neotype is consistent with what is known of the former name-bearing type from the original description and from other sources...»). It might nevertheless be necessary to have a formal ruling of the International Commission on Zoological Nomenclature.

PANDEIDAE *INCERTA SEDIS*:

Genus ***Perigonella*** Stechow, 1921

TYPE SPECIES: *Perigonimus sulfureus* Chun, 1889, by monotypy.

DIAGNOSIS: Hydroid on shells of pelagic gastropods; colony stolonal, stolons tubular, hydranth with very short pedicel, one whorl of very short tentacles. Perhaps also dactylozooids. Gonophores borne on hydrorhiza, with pedicels, giving rise to free medusae. Advanced buds with four perradial tentacles, manubrium simple.

REMARKS: According to Stechow (1921), this genus belongs to the Hydractiniidae. This is quite unlikely and following Bouillon (1985) it is placed among the Pandeidae. It shows many similarities with other Pandeidae, e. g. *Pandea*.

Perigonella sulfurea (Chun, 1889) Fig. 74

Perigonimus sulfureus Chun, 1889: 524. – Steche, 1907: 30, figs. 1-2.
Perigonella sulfurea. – Stechow, 1921: 250. – Stechow, 1923a: 57. – Rees, 1956a: 344.

DIAGNOSIS: See genus diagnosis.

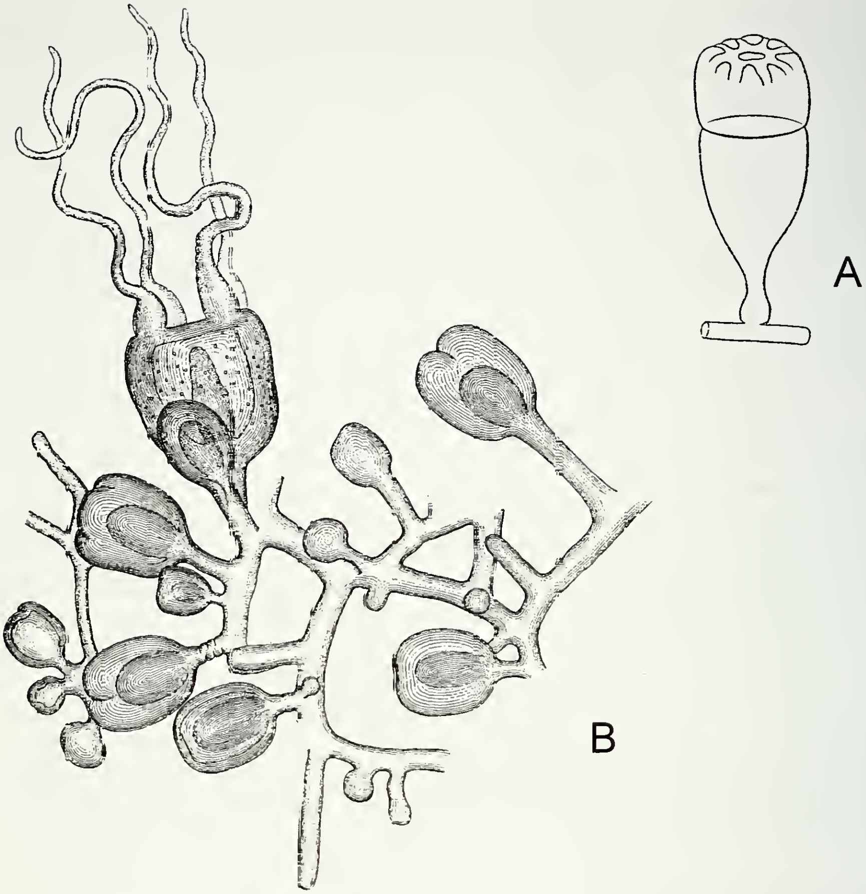

FIG. 74

Perigonella sulfurea (Chun, 1889). (A) Feeding zooid, the constriction in the middle of the hydranth body is exceptional; the tentacles are very short, figure from Steche (1907). (B) Hydrorhiza with medusa buds, from Steche (1907) after drawings of C. Chun.

DESCRIPTION: Hydroid colony stolonal, growing on shells of the pteropod *Cavolinia tridentata* (Forsskål, 1775), hydrorhiza formed by reticulate stolons, covered by perisarc. Hydranths thick club-shaped, hypostome short, surrounded by 6-9 thick and very short tentacles; hydranth tapers rapidly near base into a pedicel with a hinge-joint, likely covered by perisarc. Gonophores are free medusae, developing singly from the stolons, pedicel a variable length present. Most advanced medusa buds known with four long tentacles and large conical bulbs, exumbrella with nematocysts, manubrium without oral tentacles. Colours: Gastrodermis of polyp and manubrium of medusa sulphur-yellow in living colonies.

OTHER DATA: Steche (1907) observed an unusual hydranth with a horizontal constriction (Fig. 74A).

BIOLOGY: This species occurs on shells of *Cavolinia tridentata* (Forsskål, 1775), the original identification of Chun (1889) was corrected by Steche (1907). Steche (1907) also mentions the stomach content: molluscan eggs. They are most likely the eggs of the host.

DISTRIBUTION: Only known from the Canary Islands (type locality).

REMARKS: No type material of *P. sulfurea* could be located. It is perhaps lost, although Steche (1907) could re-examine it.

This species has perhaps also dactylozooids. They were mentioned by Steche (1907) as «conical processes that represent modified zooids with a defensive function». These were interpreted by Stechow (1923a) as spines, but more likely they correspond to what Kramp (1921) identified as incipient gonophores in *Kinetocodium danae*, but later recognized as dactylozooids. The account of Steche (1907) is somewhat ambiguous concerning the perisarc covering of the hydrocaulus, but it seems that there is perisarc on the pedicel. He mentions that the perisarc of the pedicel forms a constriction that serves as a hinge-joint.

The hydranth tentacles were short and knob-like, this also while the colony was still alive. Although Steche (1907) interpreted this as the natural condition, it could also be a reduction due to mechanical and thermal stress.

Kramp (1921) thought that this species is perhaps congeneric with his *Kinetocodium danae*. As the latter species produces a medusa with only three tentacles this seems not very likely and both genera should be retained until more is known on the mature medusae.

In the absence of more life-cycle information, this species is difficult to classify. As the medusa has apparently no oral tentacles, it is best placed among the Pandeidae *incerta sedis*.

Genus ***Kinetocodium*** Kramp, 1921

TYPE SPECIES: *Kinetocodium danae* Kramp, 1921.

DIAGNOSIS: Hydroid colony stolonal, living on pelagic gastropods; polyps polymorphic with gastrozooids and dactylozooids; gastrozooids sessile, simple, with few short tentacles below rounded hypostome; dactylozooids filiform, nematocysts evenly distributed; gonophores on stolons, with pedicels, liberated as free medusae.

Juvenile medusae with flask-shaped manubrium, mouth with oral nematocyst ring; four radial canals; three bulbs and three marginal tentacles, one perradial bulb rudimentary and without tentacle.

Kinetocodium danae Kramp, 1921 Fig. 75

Kinetocodium danae Kramp, 1921: 1, figs 1-8, pl. 1. – Kramp, 1957b: 47, figs 1-5. – Lalli & Gilmer, 1989: Fig. 8.

MATERIAL EXAMINED: Holotype, ZMUC, polyps on *Diacra trispinosa* (Lesueur).

DIAGNOSIS: See under genus.

DESCRIPTION (Kramp, 1921, 1957b; own data): Hydroid growing on shells of the pelagic gastropod *Diacra trispinosa* (Lesueur). Stolons reticulate, flattened tubes, covered by very thin perisarc, stolons widened where bearing hydranths. Polyps

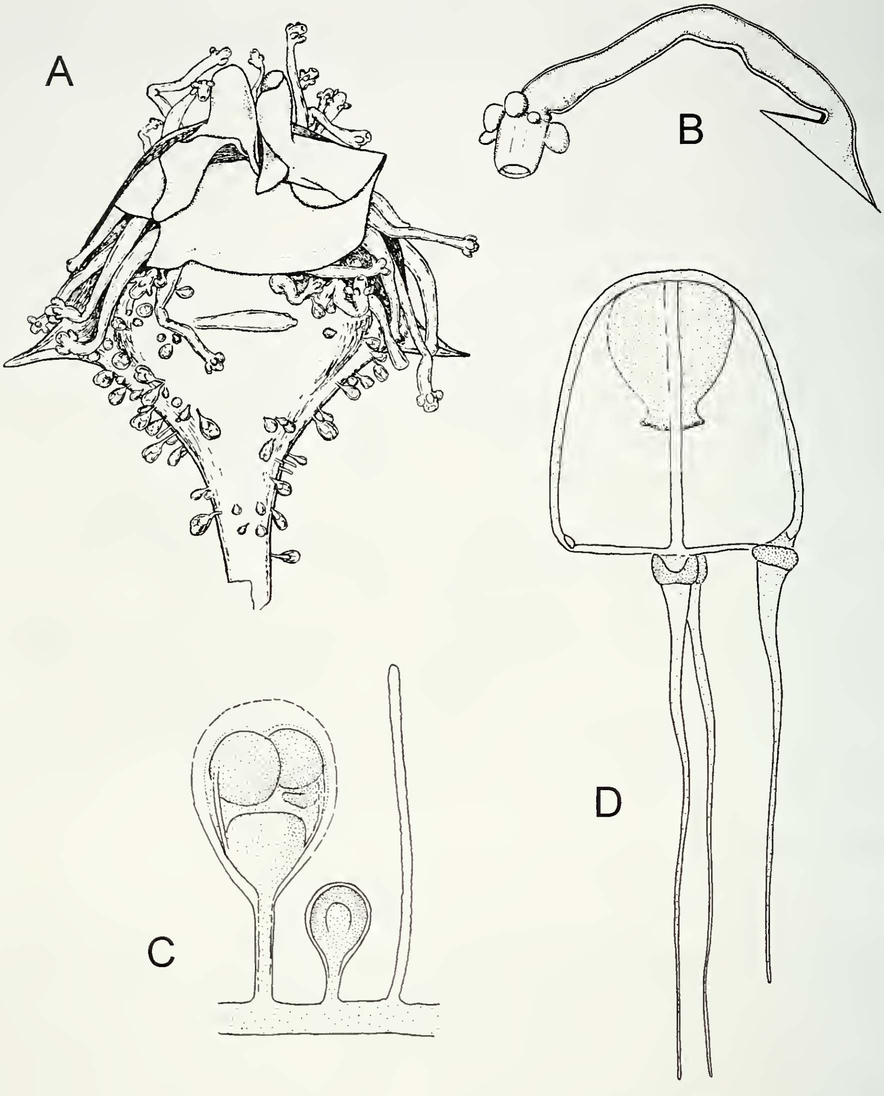

FIG. 75

Kinetocodium danae Kramp, 1921; modified from Kramp (1921, 1957), for dimensions see text. (A) Colony on the pteropod *Diacra trispinosa* (Lesueur). (B) Single hydranth, note sharp bend near base and short tentacles, which are reportedly a natural feature of this species. (C) Stolon with two medusa buds and a dactylozooids. (D) Newly released medusa, note that there are only three tentacles.

dimorphic, gastrozooids and dactylozooids present. Gastrozooids naked, without distinct pedicels, long and slender, cylindrical, widened base, often sharply bend immediately above base, some polyps nevertheless straight; hypostome large, dome-shaped, below it one whorl of up to seven very short oval tentacles, usually four tentacles, some hydranths without tentacles. Dactylozooids about as high as gonophores, filiform and very thin, nematocysts evenly distributed, dactylozooids do not coil but can contract. Gonophores develop from stolons on pedicels of variable length, ovoid, surrounded by a delicate perisarc, developing into free medusae. Colour: gastrodermis of hydranths brownish-orange.

Newly liberated medusa bell-shaped, slightly higher than wide, jelly very thin, thickness uniform, exumbrella with nematocysts. Radial canals and ring canal narrow, velum well developed; only three perradial bulbs developed and bearing a tentacle, fourth rudimentary and without tentacle; tentacle bulbs broad, surrounded by a thick transverse band of nematocysts, broad on adaxial, narrow on abaxial side, without ocelli; tentacles covered evenly and densely with nematocysts throughout their length, gastrodermis parenchymatic; two opposite tentacles of same length (five time the bell size when expanded), third tentacle slightly shorter. Manubrium roundly flask-shaped and half as long as the bell cavity, or more elongated and reaching nearly to the velar opening, without mesenteries, radial canals enter at the top, mouth quadrangular, margin beset with nematocysts, not particularly concentrated perradially, no lips, no oral tentacles or oral arms. Colours: gastrodermis of manubrium brightly orange.

Mature medusa unknown.

DIMENSIONS (Kramp, 1921; 1957b): Polyps up to 3 mm high, 0.2 mm wide, stolons 40 μm wide. Medusa buds without pedicels 0.4 mm high and 0.25 mm wide. Newly released medusa 0.5 mm high and 0.3-0.4 mm wide.

OTHER DATA: The bends of polyps are accompanied by a unilateral thickening of the mesogloea and gastrodermis. More histological details are given in Kramp (1921, 1957b).

BIOLOGY: Kramp (1957b) thinks that the hydroid parasitizes on its host, but he could not provide solid evidence for this.

DISTRIBUTION: A rare species known from the West Indies, mid-Atlantic, Azores, Portugal, Madagascar (Kramp, 1957b). Type locality: 20.65° 61.80°W, 300 m wire out, between the Bermudas and the West Indies.

REMARKS: With its three-tentacled medusa *Kinetocodium* does not fit in any family of the Filifera. It may be that this is only a feature of the juvenile medusa and the adult has more tentacles. Kramp (1921, 1957b) though that *Kinetocodium* might be a synonym of with *Perigonella*. Because of the dactylozooids and the manubrium mouth with nematocysts, Kramp (1957b) associated the genus *Kinetocodium* with the Hydractiniidae. This seems unlikely as the medusa buds are on the stolons and not on the hydranths as in typical Hydractiniidae (Schuchert, 2001). The medusa does likewise not correspond to a *Hydractinia* species. In order to allow a comparison and with *Perigonella* and *Hydrichthys, Kinetocodium* is here provisionally placed among the Pandeidae as incerta sedis, awaiting more information on its mature medusa. Admittedly, the tentacle bulbs with their nematocyst rings are atypical for the Pandeidae. The nematocysts could give some important cues to the affinities of *Kinetocodium*, but they could not be examined in the available material (holotype).

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A new species of *Lygosoma* (Squamata: Sauria: Scincidae) from the Central Truong Son, Vietnam, with notes on its molecular phylogenetic position

Thomas ZIEGLER[1], Andreas SCHMITZ[2], Astrid HEIDRICH[1,3], Ngoc Thanh VU[4] & Quang Truong NGUYEN[5]

[1] AG Zoologischer Garten Köln, Riehler Straße 173, D-50735 Köln, Germany.
E-mail: tziegler@zoo-koeln.de

[2] Muséum d'histoire naturelle, Department of Herpetology and Ichthyology, C.P. 6434, CH-1211 Geneva 6, Switzerland. E-mail: andreas.schmitz@ville-ge.ch

[3] Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany. E-mail: astrid_heidrich@web.de

[4] Centre for Natural Resources and Environmental Studies (CRES), Vietnam National University, Hanoi, University of Science, Faculty of Biology, Department of Vertebrate Zoology, Zoological Museum, 334 Nguyen Trai Str., Thanh Xuan, Hanoi, Vietnam. E-mail: vnthanh@fpt.vn

[5] Institute of Ecology and Biological Resources (IEBR), Vietnamese Academy of Science and Technology, 18 Hoang Quoc Viet St., Hanoi, Vietnam.
E-mail: truong@iebr.vast.ac.vn

A new species of *Lygosoma* (Squamata: Sauria: Scincidae) from the central Truong Son, Vietnam, with notes on its molecular phylogenetic position. - A new *Lygosoma* species is described from the Central Truong Son (Annamite mountain range) of Quang Binh Province, Vietnam. The description is based on a single female specimen, collected during the dry season in the karst forest of Phong Nha – Ke Bang National Park. The new *Lygosoma* differs from any other congener by the dorsal scales with pseudokeels in combination with a pair of frontoparietals; a scaly lower eyelid; seven supralabials; seven infralabials; 32 midbody scale rows; 66 middorsal (paravertebral) scales; smooth ventral scales, arranged in 81 transverse rows; 108 smooth, not enlarged median subcaudal scales; the fourth toe with 14 keeled subdigital lamellae; a reddish brown to brownish black dorsum and an orange-yellowish to greyish ventral side in life; as well as greyish black edged sutures of anterior supra- and infralabials. The new *Lygosoma* species is the third karst-adapted scincid species that has been described from Phong Nha - Ke Bang National Park since 2005. A first molecular positioning of the new species within the genus *Lygosoma* is given as well as a key to the Vietnamese *Lygosoma* species.

Keywords: Sauria - Scincidae - *Lygosoma boehmei* sp. n. - taxonomy - phylogeny - Central Truong Son - Vietnam.

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INTRODUCTION

During recent herpetofaunal investigations in the Phong Nha – Ke Bang National Park, Central Truong Son (Annamite mountain range) of Quang Binh Province, in Central Vietnam (e.g., Ziegler & Herrmann, 2000; Ziegler & Le, 2005, 2006; Ziegler *et al.,* 2004, 2005, 2006) a remarkable scincid lizard was collected. At first glance, the specimen appeared with its apparently keeled dorsal scales to be another representative of *Lygosoma carinatum*, that was described a decade ago by Darevsky & Orlova (1996) based upon two specimens from the "Tau Nguen (sic)" (= Tay Nguyen) plateau in Kon Tum Province, Vietnam. However, as is pointed out in detail below, our investigations showed the dorsal keels to be pseudo-keels in fact. In addition, the single specimen found by us showed a distinctly differing pholidosis, i.e. larger body scales, resulting in distinctly lower midbody, middorsal, and ventral scale counts compared to *L. carinatum*, and differed as well from the remaining *Lygosoma* (and *Riopa*) species listed in Nguyen *et al.* (2005) for Vietnam. It must be noted that there exists quite some confusion concerning the assignment of species to the genera *Lygosoma* Hardwicke & Gray, 1827 and *Riopa* Gray, 1839, respectively. While *Riopa* was long considered as a valid genus (e.g., Smith, 1937; Mittleman, 1952), Greer (1977) carried out a careful morphological revision and as a result has synonymized the genus *Riopa* with *Lygosoma*. This author gave a missing "close ecological and morphological continuity among [the genus] own species and sharp ecological and morphological discontinuity from its near relatives" as the main reason to place *Riopa* (together with other proposed skink genera) into the synonymy of *Lygosoma*. But this assignment has not been unambiguously followed since. Some more recent authors such as Manthey & Grossmann (1997) again list specimens that bear supranasals under *Riopa*, while others either follow Greer (1977) and accept the synonymization of *Riopa* with *Lygosoma* or simply do not distinguish between both genera (e.g., Honda *et al.,* 2003). A solution to this problem cannot be provided in the framework of this paper and should be treated in a comprehensive phylogenetic approach, preferably based on modern molecular analyses. We preliminarily follow in this paper the definition of Greer (1977) and consider *Riopa* as a synonym of *Lygosoma*. As our specimen was neither assignable to any of the other scincid genera listed by Nguyen *et al.* (2005) for Vietnam (*Dasia*, *Emoia*, *Eumeces*, *Leptoseps*, *Lipinia*, *Eutropis* [see Mausfeld *et al.,* 2002 and Mausfeld & Schmitz, 2003 on the split of *Mabuya* sensu lato and the resulting nomenclatural changes], *Paralipinia*, *Scincella*, *Sphenomorphus*, *Tropidophorus*, and *Vietnascincus*), nor to any of the described *Lygosoma* (or '*Riopa*') species from Vietnam or its neighbouring countries (Bourret, unpubl.; Manthey & Grossmann, 1997; Darevsky & Orlov, 1994, 1997, 2005), we describe it herein as new.

MOLECULAR METHODS

To support our morphological results molecular data were collected to identify the phylogenetic position of the new species in a general framework of related species of the genus *Lygosoma* (including its supposed synonym *Riopa*). We sequenced a portion of the mitochondrial 16S rRNA gene and compared it with the following species, some of which are also present in the key to the Vietnamese species (see below): *Lygosoma quadrupes* (type species of the genus *Lygosoma*), *L. albopunctatum*, and *Lygosoma* sp. (India). Further, we included specimens from several localities of *L. koratense* (2), *L. lineolatum* (2; used as outgroups), and the widespread *L. bowringii* species-complex (3). For GenBank accession numbers see Table 1.

DNA was extracted from the tissue samples using QuiAmp tissue extraction kits (Quiagen) or a modified Chelex-Protocol (Walsh *et al.,* 1991; Schmitz, 2003). The primers 16sar-L (light chain; 5' - CGC CTG TTT ATC AAA AAC AT - 3') and 16sbr-H (heavy chain; 5' - CCG GTC TGA ACT CAG ATC ACG T - 3') of Palumbi *et al.* (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure followed Schmitz *et al.* (2005). PCR products were purified using Qiaquick purification kits (Qiagen). Sequences (including complimentary strands for assuring the accuracy of the sequences) were obtained using an automatic sequencer (ABI 377). The obtained sequences (lengths referring to the aligned sequences including gaps) comprised 548 bp. Sequences were aligned using ClustalX (Thompson *et al.,* 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall, 1999). We used PAUP* 4.0b10 (Swofford, 2002) to compute the uncorrected pairwise distances for all sequences.

We performed maximum parsimony (MP), maximum likelihood (ML), Neighbor-joining (NJ) and Bayesian (PP) reconstructions. For ML and Bayesian analysis parameters of the model were estimated from the data set using Modeltest 3.7 (Posada & Crandall, 1998) and MrModeltest 2.2 (Nylander, 2005), respectively. The NJ-analysis used the uncorrected 'p-distances'. Additionally, we used bootstrap analyses with 2000 (MP and ML) and 20000 (NJ) pseudoreplicates to evaluate the relative branch support in phylogenetic analysis. For the MP analysis, we used the "heuristic search" with the "random addition" option of PAUP* (Swofford, 2002) with 10 replicates, using the TBR (tree bisection-reconnection) branch swapping option. All Bayesian analyses were performed with MrBayes, version 3.0b4 (Huelsenbeck & Ronquist, 2001). We ran two MCMC analyses for 10^6 generations each. The initial 100000 (10%) trees were disregarded as "burn-in". We consider probabilities of 95% or greater to be significantly supported. The exact parameters used for the Bayesian analyses followed those described in detail by Reeder (2003).

RESULTS AND DISCUSSION

Lygosoma boehmei sp. n.

HOLOTYPE: Zoologisches Forschungsmuseum Alexander Koenig, ZFMK 86359: female (Figs 1-8), from the karst forest of Cha Noi, 350-400 m a.s.l., Phong Nha – Ke Bang National Park, Quang Binh Province, Vietnam; collected by Astrid Heidrich and Thomas Ziegler at the end of the dry season (21 June) 2006.

ETYMOLOGY: We name this new species in honor of Professor Dr Wolfgang Böhme, vice director of the Zoological Research Museum Alexander Koenig in Bonn, head of the vertebrate section and curator for herpetology, in recognition of his outstanding contributions not only towards lizard systematics throughout the last three decades.

DIAGNOSIS: The new species can be distinguished from any other *Lygosoma* / *Riopa* currently known by the following combination of characters: (1) Body elongate

FIGS 1-2

(1) Female holotype of *Lygosoma boehmei* sp. n. (ZFMK 86359) in life. (2) Portrait of the holotype of *Lygosoma boehmei* sp. n. (ZFMK 86359) in life.

(SVL 86.0 mm), the distance between axilla and groin being slightly more than 3 times the length of the forelimb; (2) forelimb and hindlimb short, pentadactyl, fingers and toes widely separated when adpressed, the distance between them corresponding to the length of the hindlimb; (3) dorsum reddish brown in life, brownish grey in preser-

TABLE 1. List of samples used for genetic analysis (geographic origin, locality and GenBank accession numbers). Acronyms are as follows: KUZ for Herpetological Collection of the Department of Zoology, Kyoto University, Japan; MHNG for Muséum d'histoire naturelle, Geneva, Switzerland; ZFMK for Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

Species	Geographic origin	Locality	Voucher	Accession number
L. albopunctatum	India	Near Ajur, Peryar-Trivandrum	ZFMK 73430	AY308262
L. boehmei n. sp.	Vietnam	Cha Noi, Phong-Nha Ke Bang NP	ZFMK 86359	EF193650
L. bowringii	Indonesia	Pondok Sari, Permuteran, Bali	ZFMK 78822	AY308263
L. bowringii (I)	Thailand	Khao Chong	KUZ 37884	AB028786
L. bowringii (II)	Thailand	Tha Uthen	MHNG 2679.72	EF193649
L. koratense	Malaysia	locality unknown	ZFMK 71715	AY308269
L. koratense	Thailand	locality unknown	KUZ 27358	AB028817
L. lineolatum	Myanmar	Rakhine State, Gwo Township	CAS 206647	AY308270
L. lineolatum	Myanmar	Mandalay Div., Popa Mountain Park	CAS 210669	AY308271
L. quadrupes	Thailand	Bankok	KUZ 40033	AB028818
Lygosoma sp.	India	Ooty-Bandypur	ZFMK 77814	AY308272

vative, the surfaces of the limbs and tail being brownish black; ventral side yellowish beige to greyish below the tail in preservative, with some indistinct dark marbling; in life, chin and throat are light orange and the remaining ventral side of the body cream to light brownish, turning to greyish at the underside of the tail; sides of body and neck with irregular dark flecking; sutures of anterior supra- and infralabials edged by greyish black; (4) rostral separated from undivided frontonasal by supranasals (5) prefrontals widely separated; (6) parietals forming a suture behind interparietal, no enlarged nuchals; (7) four supraoculars; bordered by six supraciliaries; posteriorly, the fourth supraocular is bordered by a small scale (postsupraocular); (8) lower eyelid scaly; (9) two loreals; (10) seven supralabials, fifth right below the eye; (11) seven infralabials; (12) postmental undivided; (13) first pair of chinshields in broad contact, bordered by six scales; (14) ear opening small, ovoid to roundish; (15) 32 midbody scale rows; (16) 66 middorsal (paravertebral) scales (from the posterior end of parietals to insertion of hindlimb); (17) dorsal and dorsolateral scales notched, appearing as three longitudinal (pseudo-)keels on neck, body, and anterior half of tail; (18) ventral scales smooth, arranged in 81 transverse rows from first gular row between third pair of chinshields to preanals; (19) six slightly enlarged preanals; (20) 108 median subcaudal scales, not enlarged, smooth; (21) fourth toe with 14 keeled subdigital lamellae.

DESCRIPTION OF HOLOTYPE: Female specimen, for measurements see Table 2. Body elongate, the distance between axilla (end of forelimb) and groin (insertion of hindlimb) slightly more than 3 times the length of the forelimb. Forelimb and hindlimb short, pentadactyl. Fingers and toes widely separated when adpressed, the distance between them corresponding to the length of the hindlimb. Head only slightly set-off from neck, snout rounded. Rostral wider than high, visible from above. A pair of

TABLE 2. Measurements (taken by a caliper, in mm) and some scalation features of the female holotype of *Lygosoma boehmei* sp. n. compared to the female holotype of *Lygosoma carinatum* (ZIN 20482) from Kannack, Kon Tum province, Vietnam, studied by us (* = data from Darevsky & Orlova, 1996). SVL: snout-vent length (from snout tip to cloaca); TaL: tail length (from cloaca to tail tip); TL: total length; HL: head length (distance from snout tip to posterior margin of interparietal); HW: maximum head width; SL: maximum snout length (from tip to anterior margin of the eye); ET: maximum eye to tympanum length (from hind margin of the eye to anterior border of tympanum); TW: maximum tympanum width; SFl: maximum snout to forelimb length; AG: maximum axilla to groin length; FlL: maximum forelimb length (from body insertion to beginning of claw of fourth finger); HlL: maximum hindlimb length (from body insertion to claw of fourth toe); IL: Infralabials; MB: midbody scale rows; MD: middorsal scale rows (from posterior end of parietals to insertion of hindlimb / to centre of thigh / and to posterior hindlimb); V: transverse rows of ventral scales (from first gular row subsequent to first pair of chinshields to preanals); MSS: median subcaudal scales; L4T: Lamellae beneath fourth toe.

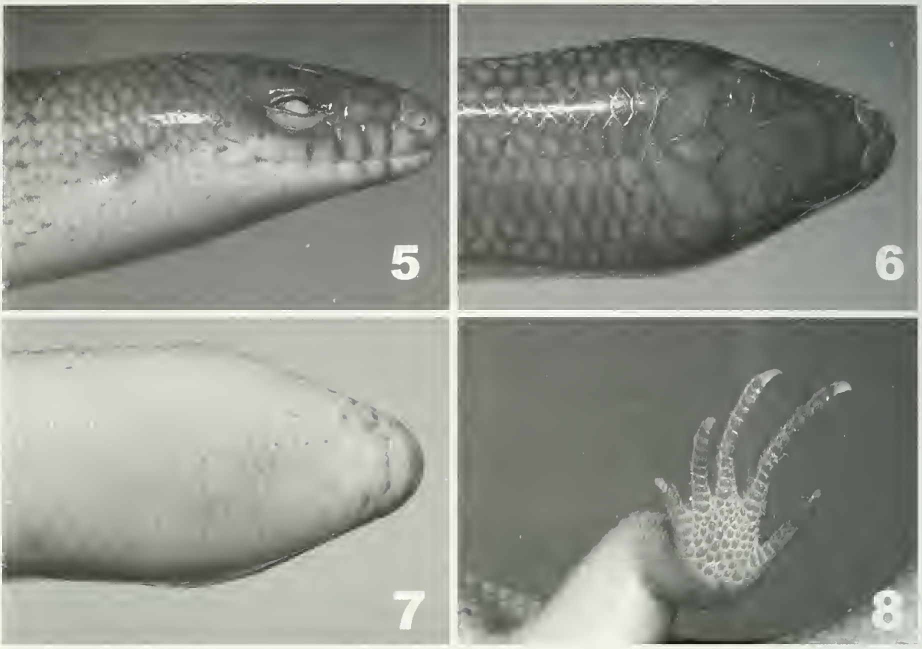
	Lygosoma boehmei sp. n. ZFMK 86359	*Lygosoma carinatum* ZIN 20482
SVL	86.0	*71.0
TaL	91.0	*77.0
TL	177.0	*148.0
HL	12.3	10.0
HW	10.5	8.9
SL	6.1	5.5
ET	6.4	5.6
TW	1.3	1.1
SFl	29.4	23.1
AG	47.0	40.3
FlL	14.7	12.2
HlL	19.0	15.0
IL	7	6-7
MB	32	38
MD	66 / 70 / 72	80 / 82 / 85
V	81	92
MSS	108	115
L4T	14	16

supranasals, somewhat wider than long, forming a distinct median suture, touching nasals and anterior loreal laterally. Prefrontals widely separated, touching both loreals laterally. Frontonasal wider than long, in contact with supranasals, anterior loreals, prefrontals, and frontal. Frontal large, longer than its distance to tip of snout, narrowing posteriorly, in contact with frontonasal, prefrontals, first supraciliary, first and second supraoculars, and frontoparietals. A pair of frontoparietals, about as wide as long. Parietals forming a suture behind the interparietal, that is longer than wide, smaller than frontal and narrowing posteriorly. Small transparent spot on interparietal, showing location of parietal foramen. No distinctly enlarged nuchal scales. Nostril piercing nasal, that is in contact with rostral, first supralabial, anterior loreal, and supranasal. Two loreals, anterior the higher (bordering nasal, first and second supralabials, posterior loreal, prefrontal, frontonasal, and supranasal), posterior the longer. The posterior loreal is in contact with the first supraciliary, the prefrontal, the anterior loreal, the second and third supralabials, and is bordered behind by two large preoculars. The upper one of these large preoculars is posteriorly bordered by a somewhat

Figs 3-4

(3) Lateral view of the holotype of *Lygosoma boehmei* sp. n. (ZFMK 86359) in life. (4) Ventral view of the holotype of *Lygosoma boehmei* sp. n. (ZFMK 86359) in life.

smaller preocular, that touches the first and second supraciliary above; the lower one of the large precoculars is posteriorly bordered by a somewhat smaller, more elongated preocular (presubocular), that is in broad contact below with the fourth supralabial and further touches the corner of the fifth supralabial. Lower eyelid scaly. Supraoculars four, plus one small posterior supraocular (postsupraocular: small scale posterior to the supraocular series). Supraoculars laterally bordered each by six supraciliaries. Three large postoculars, the upper one bordering the postsupraocular above, the lower one (postsubocular) borders the fifth and sixth supralabials below. Ear opening small, ovoid to roundish. Seven supralabials, fifth right below the eye. Mental in contact with first infralabials and postmental. Undivided postmental in contact with mental, first and



Figs 5-8

Lygosoma boehmei sp. n. (ZFMK 86359), preserved holotype. (5) Lateral view of the head. (6) Dorsal view. (7) Ventral view. (8) Underside of the left foot.

second infralabials, and first pair of chinshields. First pair of chinshields in broad contact, posteriorly bordered by six scales. Seven infralabials. 32 midbody scale rows. 66 middorsal (paravertebral) scales from posterior end of parietals to insertion of hindlimb (70 to centre of thigh, 72 to posterior hindlimb). Dorsal and dorsolateral scales smooth, appearing as three longitudinal (pseudo-)keels on neck, body, and anterior half of tail. Although visual inspection and the macro-photograph of the dorsal midbody scales of the holotype indicates a keeled appearance of the scale surfaces (Fig. 9), the SEM (scanning electron microscopy) pictures revealed that the scales bear in fact only pseudo-keels (Fig. 10). Contrary to its naming by Darevsky & Orlova (1996), the same is actually true for the holotype of *L. carinatum* (Fig. 11).

Dorsal body scales of the holotype of *L. boehmei* sp. n. as large as ventrals. Ventral scales smooth, arranged in 81 transverse rows from first gular row subsequent to first pair of chinshields to preanals. Six slightly enlarged preanals. 108 median subcaudal scales (without tail tip), not enlarged, smooth. Fourth toe with 14 keeled subdigital lamellae.

Colour in preservative brownish grey on dorsal and dorsolateral surfaces of head and body, the surfaces of the limbs and tail appear brownish black. Especially the dorsal scales are distinctly edged by brownish black. Except for the somewhat darker tail, the lateral parts of the tail base, body, neck and head become lighter. The light ventral side is yellowish beige (lightest below head and neck) to greyish below the tail with

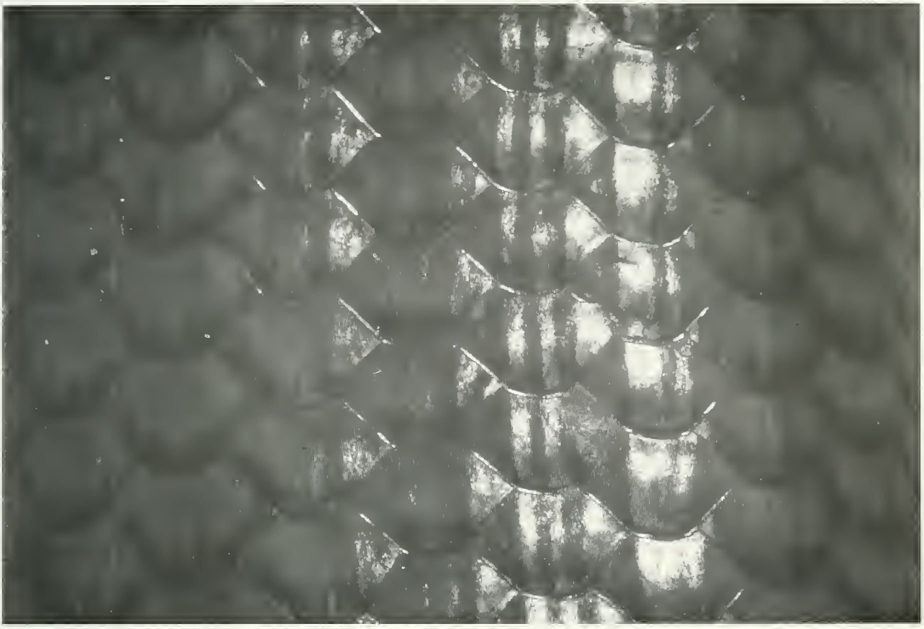


FIG. 9

Macro-photograph of the apparently keeled dorsal midbody scales in the preserved holotype of *Lygosoma boehmei* sp. n. (ZFMK 86359).

some indistinct dark marbling. Sides of body and neck with irregular dark flecking. Sutures of anterior supra- and infralabials edged by greyish black. In life, the dorsal colour is reddish brown. Chin and throat are light orange and the remaining ventral side of the body is cream to light brownish, turning to greyish at the underside of the tail.

COMPARISONS: The new species is easily distinguishable from the skink species listed in the genera *Lygosoma* and *Riopa* known to occur in Vietnam (Darevsky & Orlova, 1996, Nguyen *et al.,* 2005) by a combination of proportions, coloration and scalation features (Table 3). The new species differs:

from *Lygosoma carinatum* by having seven infralabials instead of six lower labials, 32 midbody scale rows instead of 38-40, and only 66 middorsal (paravertebral) scales instead of 81-85 according to Darevsky & Orlova (1996). However, our study of the holotype of *L. carinatum* revealed that the specimen only bears 6 infralabials on the right side, but 7 on the left (see Table 2); the holotype of *L. carinatum* further had 92 transverse rows of ventrals (instead of 81 in the new species), 115 median subcaudal scales (instead of 108), 16 keeled subdigital lamellae beneath the fourth toe (instead of 14), and the holotype of *L. carinatum* had an enlarged nuchal scale on the left side;

from *L. quadrupes* by lacking an extremely elongate body (the length of the forelimb is not contained twelve to fourteen times in the distance between the fore- and hindlimbs), by the rostral not being in contact with the frontonasal, by having 32 midbody scale rows instead of 24-26, by having 14 instead of 5 lamellae beneath the fourth

TABLE 3. Overview of supralabial (SuL), midbody scale (MbS), and middorsal (MdS) scale counts, as well as presence of dorsal keels or pseudo-keels (DK: +/-) and number of lamellae beneath fourth toe (L4T) for the *Lygosoma* / *Riopa* species recorded from Vietnam (after Bourret, unpubl.; Smith, 1935; Taylor, 1963; Darevsky & Orlova, 1996; Manthey & Grossmann, 1997, and own data).

	SuL	MbS	MdS	DK	L4T
albopunctatum	7	26-28	63-72	-	12-15
angeli	?	30	110-115	-	5
boehmei sp. n.	7	32	66	+	14
bowringii	7	26-32	52-58	-/+	10-15
carinatum	7	38-40	80-85	+	15-16
corpulentum	6	36-38	?	-	13-14
punctatum	7	24-28	62-76	-	11-14
quadrupes	6-7	24-26	104-121	-	5

toe, and by lacking the tail being as thick as the body for a considerable part of its length (Smith, 1935);

from *L.* (‘*Riopa*’) *punctatum* by lacking a lower eyelid with an undivided semi-transparent disc, smooth dorsal scales, by having 32 midbody scale rows instead of 24-28, and by lacking dorsal scales with a dark basal spot, usually confluent into four to six longitudinal lines down the back in the young (Smith, 1935).

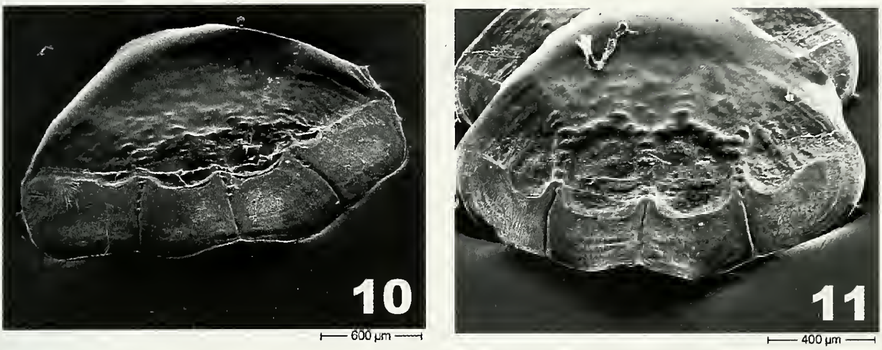
from *L.* (‘*Riopa*’) *albopunctatum* by having 32 midbody scale rows instead of 26-28, lacking dark brown or black sides of neck and anterior part of the body, and by lacking smooth dorsal scales with a dark spot, forming longitudinal series (Bourret, unpubl.; Smith, 1935);

from *L. angeli* (as ‘*Riopa angeli*’ in Bourret, unpubl.; Nguyen *et al.*, 2005) by lacking a single frontoparietal, having 32 midbody scale rows instead of 30, having pseudo-keeled dorsal scales, 66 middorsal (paravertebral) scales instead of 110-115 scales down the middle of the back, and by having 14 instead of 5 lamellae beneath the fourth toe (Bourret, unpubl.; Darevsky & Orlova, 1996).

from *L. bowringii* (as ‘*Riopa bowringi*’ in Smith, 1935, and as *Riopa bowringii* in Nguyen *et al.,* 2005) in lacking a single frontoparietal and a pair of nuchals, by having 66 middorsal (paravertebral) scales instead of 52-58 scales down the middle of the back, by lacking smooth dorsal scales with a darker spot forming more or less continuous longitudinal lines, and by lacking a dark brown or black dorso-lateral stripe of variable thickness, light-edged above (Bourret, unpubl.; Smith, 1935; Darevsky & Orlova, 1996);

from *L. corpulentum* (as ‘*Riopa corpulenta*’ in Smith, 1935; Nguyen *et al.*, 2005) in having seven supralabials (vs. six in *corpulentum*), pseudo-keeled dorsals (vs. smooth body scales in *corpulentum*), 32 midbody scale rows instead of 36-38, and in coloration and pattern (*Lygosoma corpulentum* is light yellowish-brown and thickly mottled on the back and sides with dark brown) (Smith, 1935; Darevsky & Orlova, 1996).

From the *Lygosoma* / *Riopa* species of the neighbouring countries, the new species differs [e.g. comp. Bourret (unpubl.); Werner (1909); Smith (1935); Taylor (1963); Manthey & Grossmann (1997)] by lacking lower eyelids with disc in combi-



FIGS 10-11

(10) *Lygosoma boehmei* sp. n. (ZFMK 86359), preserved holotype. SEM (scanning electron microscopy) picture of a dorsal midbody scale; the externally visible scale surface is smooth, showing the "keels" being in fact pseudo-keels. (11) SEM picture of a dorsal midbody scale of the holotype of *Lygosoma carinatum* (ZIN 20482); the externally visible scale surface is smooth, showing the "keels" being in fact pseudo-keels.

nation with 22 smooth midbody scale rows, only 6-10 lamellae under the fourth toe, and more or less developed dorso-lateral line (as in the species *anguinum* and *lineolatum*), by lacking a single frontoparietal in combination with a) supranasals fused anteriorly with nasals, and 88-98 middorsal scales (as in *isodactylum*), b) in combination with 40-42 midbody scale rows, and 143 middorsal scales (as in *haroldyoungi*), or c) in combination with 28-30 midbody scale rows, 56-60 middorsal scale rows, 78 slightly enlarged median subcaudal scales, and dorsolateral lines (as in *frontoparietale*), by lacking a combined nasal-supranasal scale in combination with eight supralabials and smooth dorsals (as in *koratense*), by lacking a midbody scale count of 26-30 in combination with six infralabials, 55-57 middorsal scales and a more or less developed stripe from eye along side of body (as in *herberti*), and by having different midbody scale counts from the Indonesian species *bampfyldei* (38-40) and *opisthorhodum* (30), the latter of which has in contrast a light lateral stripe and a blackish brown anterior dorsum, which is getting paler backwards and turning to a light reddish brown tail.

DISTRIBUTION: Currently, the new species is only known from its type locality, the karst forest of Cha Noi, 350-400 m a.s.l., within Phong Nha - Ke Bang National Park in Quang Binh province, central Vietnam (Fig. 12).

NATURAL HISTORY: The female holotype of *Lygosoma boehmei* sp. n. was discovered at night on the forest ground in a steep primary karst forest area (compare Fig. 13). We did not find any water courses in the immediate vicinity, however, the discovery took place at the end of the dry season. The skink was found crawling at the base of a tree stump in the surrounding of karst rock outcrops (Fig. 14).

The stomach content of the holotype of *Lygosoma boehmei* sp. n. contained brown earth-like masses, plant and tissue remains which most probably come from an earth-worm.

FIG. 12
At present, *Lygosoma boehmei* sp. n. is only known from its type locality in the Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam.

Lygosoma boehmei sp. n. is the third scincid species that has been described from the karst forests of Phong Nha - Ke Bang National Park since 2005 (Darevsky & Orlov, 2005; Ziegler *et al.*, 2005); the discovery of the new species took place at the locus typicus of the recently discovered water skink species *Tropidophorus noggei* (see Ziegler *et al.*, 2006).

MOLECULAR PHYLOGENETIC POSITION OF *LYGOSOMA BOEHMEI* SP. N.

Since *L. carinatum*, the supposed closest relative of *L. boehmei* sp. n. could not be included in the molecular data set (the former species is only known from the type series), we could not make a direct genetic comparison of all Vietnamese *Lygosoma* species (but compare the morphological discussion). Therefore, we decided to analyze the phylogentic position of *L. boehmei* sp. n. within the general framework of the taxa of the genus *Lygosoma*.

All molecular analyses produced an almost identical tree topology shown in Figure 15; the only difference was found in the MP-tree (not shown) where *L. albopunctatum* was not directly clustered within the clade containing *Lygosoma* sp. and the 3 included members of the *L. bowringii* species complex. The heuristic search of the MP analysis produced 2 most-parsimonious tree (tree length = 194; CI = 0.680; RI = 0.682; RC = 0.464). The comparison between the different likelihood scores for each

FIGS 13-14
(13) The steep karst forests of Cha Noi: habitat of *Lygosoma boehmei* sp. n. in the Phong Nha - Ke Bang National Park. (14) Microhabitat of *Lygosoma boehmei* sp. n.: the female holotype was collected at night crawling at the base of this tree stump.

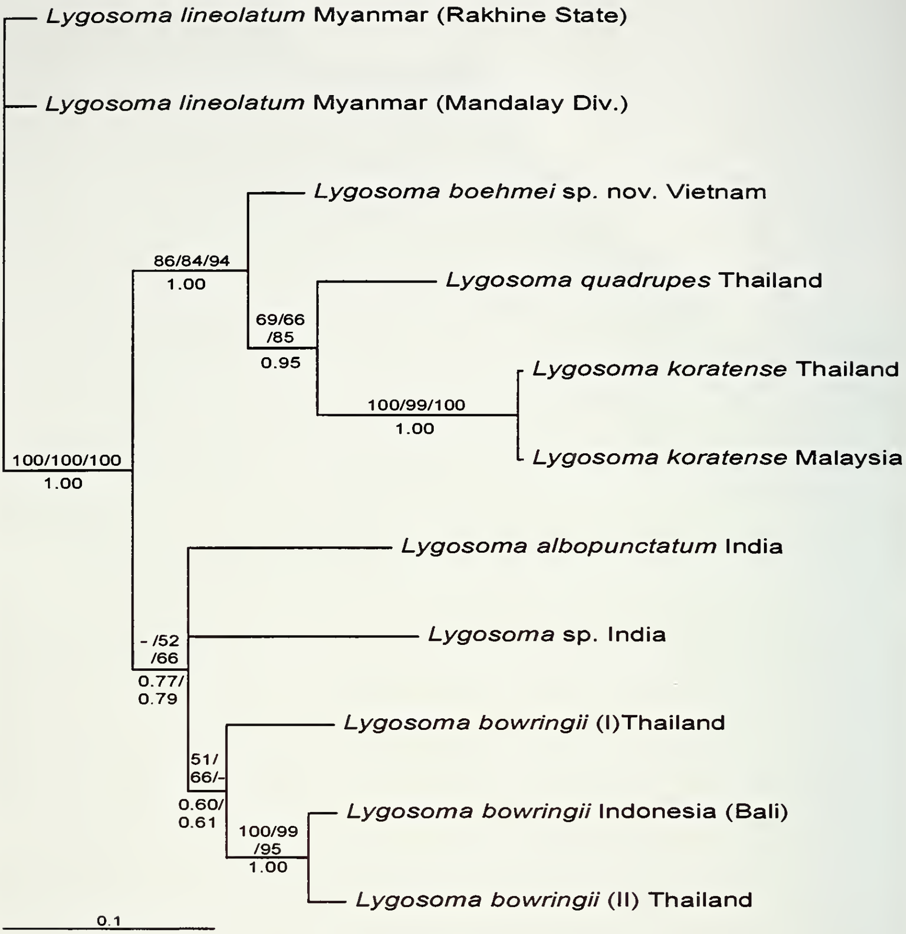


FIG. 15

Phylogram based on 548 bp of the mitochondrial 16S ribosomal RNA gene sequences. Values above the nodes represent bootstrap values in percent for maximum parsimony, neighbor-joining and maximum likelihood analyses, respectively; lower values are Bayesian posterior probabilities. Values below 50% (or 0.50 for the Bayes analyses) not shown.

model showed that the TRN+I+G model (Tamura & Nei, 1993) was determined to be the optimal ML model for data set. This model incorporates unequal base frequencies [$\pi_{(A)} = 0.3461, \pi_{(T)} = 0.2335, \pi_{(C)} = 0.2448, \pi_{(G)} = 0.1756$], a proportion of invariable sites ($I = 0.4165$), and a gamma distribution shape parameter ($\alpha = 0.2513$). The optimal ML tree had a log-likelihood of -lnL = 1766.91104.

The resulting tree shows three clearly separated groups with the two specimens of *L. lineolatum* genetically well separated from the rest of the included species; this was true even when these two OTUs were included as ingroup taxa and a different outgroup was used. The newly described *Lygosoma boehmei* sp. n. is consistently placed

TABLE 4. Summary of the uncorrected p-distances for the 16S data set.

Taxa	1	2	3	4	5	6	7	8	9	10	11
1 *Lygosoma lineolatum* (Rakhine State)	-										
2 *Lygosoma lineolatum* (Mandalay Div.)	0.0204	-									
3 *Lygosoma albopunctatum* India	0.0987	0.0947	-								
4 *Lygosoma quadrupes* Thailand	0.0988	0.0988	0.0944	-							
5 *Lygosoma boehmei* sp. n. Vietnam	0.0744	0.0705	0.0892	0.0684	-						
6 *Lygosoma koratense* Thailand	0.1170	0.1108	0.1174	0.0847	0.0767	-					
7 *Lygosoma koratense* Malaysia	0.1101	0.1025	0.1131	0.0845	0.0726	0.0000	-				
8 *Lygosoma* sp. India	0.0993	0.1006	0.0955	0.1013	0.0923	0.1176	0.1107	-			
9 *Lygosoma bowringii* (I) Thailand	0.1006	0.0984	0.0942	0.1125	0.0861	0.1169	0.1166	0.0962	-		
10 *Lygosoma bowringii* Indonesia (Bali)	0.0675	0.0691	0.0875	0.0949	0.0805	0.1106	0.1027	0.0817	0.0741	-	
11 *Lygosoma bowringii* (II) Thailand	0.0786	0.0824	0.0836	0.0931	0.0826	0.1191	0.1130	0.0808	0.0640	0.0211	-

into a second clade, which also includes the type species of the genus *Lygosoma* (*L. quadrupes*), as well as the two *L. koratense* specimens from Thailand and Malaysia (whose sequences showed a 100% identity despite coming from two different countries). This whole clade is strongly supported in all used analyses methods (MP: 86 / NJ: 84 / ML: 94 /PP: 1.00) and shows that *L. boehmei* sp. n. is a true member of the genus *Lygosoma*, regardless of the ongoing discussion on the validity of the genus *Riopa* (see Introduction). *Lygosoma boehmei* sp. n. stands basal to the other OTUs of this clade, but a definitive polarity decision cannot be made with our data set. The genetic differences between the different species of this clade varied from 6.8%-8.5%. *L. boehmei* sp. n. is also well separated from the members of the third recovered clade, which includes all three specimens of the *L. bowringii* species complex as well as *Lygosoma* sp. and *L. albopunctatum* (both from India). The genetic differences between the taxa of this third clade were similar to those found in the second clade and varied from 6.4%-9.5%. Regarding the distances between the two clades one finds that they are normally slightly higher than the distances within the two clades (9.4%-11.7%), but this is not completely consistent since the genetic distance of one of these species (*L. boehmei* sp. n.) towards the taxa of the third clade is in the range of or even slightly lower (8.1%-9.2%) than the maximum inter-clade differences mentioned above. Also we found that in some cases the genetic differences between geographically close taxa are not necessary lower than those living in far-away habitats (e.g. *L. boehmei* sp. n.-*L. lineolatum* and *L. boehmei* sp. n.-*L. koratense*; Table. 4). This shows that a subdivision of the genus *Lygosoma* would need to be based on a rather complete taxon sampling, since our preliminary molecular data already indicate a rather complicated intrageneric structure within *Lygosoma*. One further notable result is that (equal as shown in our key to the Vietnamese *Lygosoma* species where the *L. bowringii* species complex is found on two different positions in the key) the genetic analyses also strongly support that *L. bowringii* is a species-complex which comprises at least 2 different taxa. The recovered genetic difference between the two different specimens from Thailand is 6.4% and therefore has about same amount of genetic divergence as between other *Lygosoma* species, and the new *L. boehmei* sp. n. is about equidistant with all three included *L. bowringii* taxa (8.1%-8.6%).

KEY TO THE VIETNAMESE *LYGOSOMA* SPECIES

1a	Dorsal scales appearing smooth	2
1b	Dorsal scales with keels or pseudo-keels	7
2a	5 lamellae beneath fourth toe	3
2b	10-15 lamellae beneath fourth toe	4
3a	24-26 midbody scale rows	*quadrupes*
3b	30 midbody scale rows	*angeli*
4a	36-38 midbody scale rows, six supralabials	*corpulentum*
4b	24-32 midbody scale rows, seven supralabials	5
5a	52-58 middorsal scales	*bowringii* (species complex)
5b	62-76 middorsal scales	6
6a	lower eyelid scaly (central scales may be enlarged)	*albopunctatum*

6b lower eyelid with undivided semitransparent disc . . . . *punctatum*
7a 26-32 midbody scale rows, 52-66 middorsal scales 8
7b 38-40 midbody scale rows, 80-85 middorsal scales . . . . *carinatum*
8a 52-58 middorsal scales . . . . *bowringii* (species complex)
8b 66 middorsal scales . . . . *boehmei* sp. n.

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Five new European species of the *Rhamphomyia* (s. str.) *albosegmentata* group (Diptera: Empididae)

Miroslav BARTÁK
Czech University of Agriculture, Faculty of Agrobiology, Food and Natural Resources, Department of Zoology and Fishery, 165 21 Praha 6 - Suchdol, Czech Republic.
E-mail: bartak@af.czu.cz

Five new European species of the *Rhamphomyia* (s. str.) *albosegmentata* group (Diptera: Empididae). - *Rhamphomyia* (s. str.) *bellinosetosa* sp. n. (Italy), *Rhamphomyia* (s. str.) *piedmontensis* sp. n. (Italy), *Rhamphomyia* (s. str.) *ponti* sp. n. (Austria), *Rhamphomyia* (s. str.) *saintbaumensis* sp. n. (France), and *Rhamphomyia* (s. str.) *sellacrinita* sp. n. (Italy, Switzerland), are described and illustrated. The key to the Palaearctic species of the *Rhamphomyia* (s. str.) *albosegmentata* group is updated.

Keywords: *Rhamphomyia* - new species - Europe - taxonomy - key.

INTRODUCTION

The species of the *Rhamphomyia* (s. str.) *albosegmentata* group are usually medium-sized (wing size from 3.2 to 8.9 mm), with characteristic shape of genitalia (cercus [= dorsal genital lamella] simple, without «subcercal process», with finger-like projection near base of its upper margin, phallus broadened apically), proepisternal depression setose, axillary angle acute, anal vein (A1) complete, prosternum bare, costal seta present, haltere dark and hind femur with ventral setae. Females are sometimes difficult to distinguish from other groups and species complexes of the subgenus *Rhamphomyia* (s. str.).

Palaearctic species of the group were revised by Barták (1981), however, three species were described more recently (Barták, 1998) and five additional species are described here as new to science, and this necessitates revision of the earlier key (Barták, 1981).

MATERIAL AND METHODS

The material studied is deposited in the following collections:

CNC	Canadian National Collection, Ottawa
CUA	Czech University of Agriculture, Prague
MHNG	Muséum d'histoire naturelle, Geneva
NHM	Natural History Museum, London
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UMO	University Museum, Oxford

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The genitalia were macerated in 10% KOH (24 hours, room temperature) and they are stored together with specimens in plastic microvials with glycerine. The morphological terms used here follow Merz & Haenni (2000) and Sinclair (2000). Abbreviations: T1l,T2l,T3l = length of fore, mid, hind tibia; B1l,B2l,B3l = length of fore, mid, hind basal tarsomere; B1w,B2w,B3w = width of fore, mid, hind basal tarsomere; M2/D = length of vein M2: greatest length of discal medial cell (discal cell); M3/Db = length of apical: preapical sections of vein CuA1; lw: ww = greatest length of wing: greatest width of wing. Ratio of antennal segments = length of first: 2nd: 3rd: style (in 0.01 mm scale).

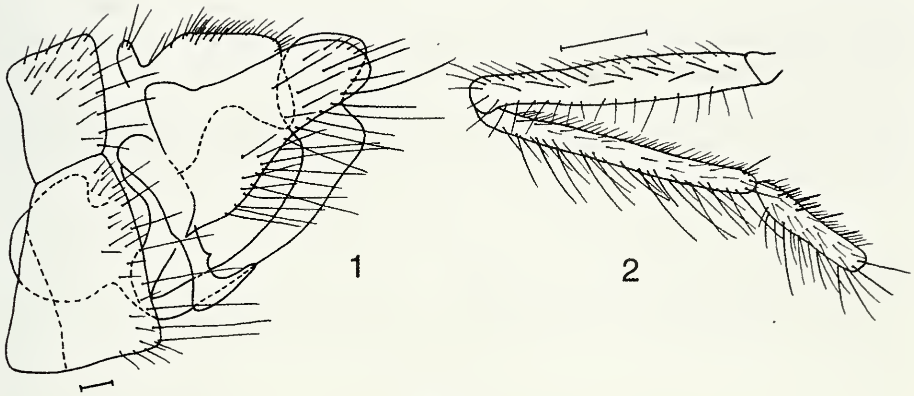
SYSTEMATIC TREATMENT

***Rhamphomyia* (s. str.) *bellinosetosa* sp. n.** Figs 1, 2

HOLOTYPE MALE: Italy: Piedmont, Celle de Bellino, 11.-12.vii.1974, Malaise trap, W. Baker leg. (CNC).

DESCRIPTION

Male: Eyes holoptic, facets in lower half of eye much smaller than upper ones. Frons black, grey pruinose, bare. Ocellar setae black, fine, 2/3 as long as frons, ocellar triangle with single pair of additional slightly smaller setulae. Face black, grey pruinose, about 0.35 mm broad below and 0.20 mm long, bare. Occiput black, light grey pruinose, medium densely black setose, dorsal setae quite strong, postocular row incomplete. Antennae black, ratio of antennal segments = 17: 10: 55: 11, both basal segments covered with long setae, longest ones about 0.25 mm long. Labrum brownish black, polished, subequally long as head is high. Palpus brown, long, densely covered with very long bristly setae (the longest 0.50 mm long). Genae narrow and mostly polished, clypeus pruinose. Thorax black, light grey pruinose, mesoscutum light grey without distinct stripes. All setae and setulae black. Chaetotaxy: about 15 setulae on proepisternum; prosternum bare; proepisternal depression with one setula; 20 biserial acrostichals; 20-25 irregularly 2-3 serial dorsocentrals ending in 4 strong prescutellars (both acrostichals and dorsocentrals rather strong and up to 0.40 mm long); 1-2 intrahumeral; 1-2 posthumeral; about 20 additional setulae lateral of dorsocentrals in presutural area; 1 postpronotal seta and about 12 additional shorter setae; 2-3 notopleurals (2-4 setulae in front part of notopleura, some of them quite strong); a line of 4-5 strong setae in supraalar and prealar areas, 1-2 prealar and 6-7 additional setae in unusual position between supraalars and dorsocentrals (even between hindmost supraalars and hind dorsocentrals); 1 long, 1 shorter and several additional small postalar; 3 pairs of scutellars; laterotergite (metapleura) with black setae. Coxae brownish black and pruinose, concolorous with pleura. Legs blackish brown and pruinose, black setose. A long seta present in comb at tip of hind tibia. Fore femur (Fig. 2) with sparse and irregular rows of anteroventral, posteroventral and posterior setae slightly longer than femur is deep, dorsal setulae very short, but several anterodorsal and nearly complete row of anterior setae are somewhat longer. Fore tibia (Fig. 2) with row of (8) very strong anterodorsal and irregular row of (greater number) similarly strong posterodorsal and posterior setae up to 3 times as long as diameter of tibia (up to 0.45 mm long with many much smaller and finer setulae between them), very fine



FIGS 1-2
Rhamphomyia (s. str.) *bellinosetosa* sp. n. (1) Male terminalia (macerated), lateral view. Scale 0.1 mm. (2) Male fore femur, tibia and basitarsus, posterior view. Scale 0.5 mm.

ventral ciliation consists of setulae subequally long as diameter of tibia. Mid femur with anteroventral row of setae slightly longer than femur is deep, posteroventral setae much shorter and finer, only a single strong posteroventral present on basal third. Mid tibia with two rows of anterodorsal and posterodorsal setae (about 6 in each row) almost 4 times as long as diameter of tibia and with anteroventral and posteroventral setae (3 in each row) twice as long as diameter of tibia. Hind femur with 5 anteroventral, a single long submedian posteroventral seta and 2-3 subapical anterodorsal setae at least as long as femur is deep, several fine posterior setae on base of femur long, other ciliation short. Hind tibia with anterodorsal and posterodorsal setae (6-8 in each row) twice as long as diameter of tibia (small setulae between them are much shorter), ventral setulae short. Basal tarsomere of fore leg thin, with several strong setae dorsally up to 3 times as long as diameter of this tarsomere and with short ventral spines, T1l: B1l = 2.1, B1l: B1w = 5.0; basal tarsomere of mid leg short and thin, short setose and with short ventral spines, T2l: B2l = 2.8, B2l: B2w = 5.0. Basal tarsomere of hind leg thin, dorsally with some 6 setae three times as long as diameter of this tarsomere and with long ventral spines, T3l: B3l = 2.2-2.3, B3l: B3w = 7.7. Wing clear or slightly brownish, stigma light brown, veins brown, anal vein (A_1) complete. Costal seta long, axillary angle sharply acute (30°). M2/D = 1.3, M3/Db = 1.8, lw: ww = 3.0. Haltere brown, calypter yellow with dark fringes. Abdomen black, light grey pruinose (light grey in dorsal view). Setae and setulae all black. Hind marginal setae on sides of tergites 2-5 strong and slightly longer than their segments, on segments 6-7 fine and slightly shorter than their segments, discal setulae shorter than hind marginals. The first sternite with several setulae on sides. Terminalia as in Fig. 1; apical angle of cercus slightly obtuse. Length of body: 5.7 mm, wing: 6.1 mm.

Female: Unknown.

DIFFERENTIAL DIAGNOSIS: *Rhamphomyia* (s. str.) *bellinosetosa* sp. n. is similar to *R. hirtimana* Oldenberg, 1922, however, the latter species has fore tibia with almost homogeneously fine dorsal ciliation, more sparsely setose mesoscutum (about 10 setae on presutural area of mesoscutum lateral of dorsocentrals), labrum longer than head is high and palpi sparsely setose (less than 15 setae on each palpus, whereas more than 20 in the new species described above).

DERIVATIO NOMINIS: The species name is derived in part from the type locality denomination (bellino-) and -setosa which refers to the strongly setose fore tibia.

DISTRIBUTION: Italy.

DATES OF OCCURRENCE: July.

***Rhamphomyia* (s. str.) *piedmontensis* sp. n. Fig. 3**

HOLOTYPE MALE: Italy: Celle de Bellino, Piedmont, July 11-12, 1974, W. Baker - Mal. Trap (CNC).

DESCRIPTION

Male: Eyes holoptic, facets in lower half of eye smaller than upper ones. Frons black, grey pruinose, bare. Ocellar setae black, about as long as upper postocular ciliae, ocellar triangle with 4-5 pairs of additional slightly shorter setulae. Face black, grey pruinose, about 0.45 mm broad below and 0.30 mm long, bare. Occiput black, grey pruinose, rather densely and long black setose. Antenna black, ratio of antennal segments = 24: 13: 60: 15, both basal segments covered with very long setae (longest about 0.45 mm long). Labrum brownish black, polished, slightly longer than head is high. Palpus brown, long, very densely covered with very long bristly setae (longest up to 0.60 mm long). Genae narrow and pruinose, clypeus pruinose. Thorax black, dark grey or slightly brownish grey pruinose, mesoscutum without stripes. All setae and setulae black. Chaetotaxy: about 40 setulae on proepisternum; prosternum bare; about 15 setulae on proepisternal depression; great number of 4-5 serial acrostichals; great number of multiserial dorsocentrals, ending in 3-4 strong prescutellars, spreading down sides of mesoscutum in both pre- and postsutural area (whole mesoscutum is densely covered with setulae, leaving only very narrow stripes between acrostichals and dorsocentrals bare, stripes much narrower than space occupied by acrostichal setae, areas just around postalar callus and notopleuron behind notopleural setae bare), setae on mesoscutum about 0.40 mm long; intrahumeral and posthumeral setae not differentiated; postpronotal scarcely differentiated from many similar setulae; 4 notopleurals (many long setulae in front part of notopleuron); supraalar and prealar area densely covered with setulae, 2-3 supraalars stronger and longer; 1 long and 1 short postalars; 4 pairs of scutellars; laterotergite (metapleura) with black setae. Coxae and legs concolorous with pleura, pruinose, black setose. Long seta present in comb at tip of hind tibia. Fore femur with rather sparse anteroventral and more dense posteroventral and posterior setulae about as long as femur is deep, dorsal setulae shorter. Fore tibia with almost equally long but unequally strong setae and setulae dorsally only slightly longer than diameter of tibia, ventral setulae very short. Mid femur with anterodorsal, anteroventral and posteroventral setae slightly longer than femur is deep, other ciliation short. Mid tibia with 4-5 pairs of setae dorsally at most twice as long as diameter of tibia, anteroventral and posteroventral setae shorter. Hind femur with ventral, anterodorsal and posterior setae slightly longer than femur is deep. Hind tibia very slightly flattened, with 7-8 pairs of closely inserted anterodorsal and posterodorsal setae slightly longer than diameter of tibia, ventral setulae very short.

Basal tarsomere of fore leg thin and short setose, ventral spines not prominent, T1l: B1l = 2.5, B1l: B1w = 7.1, basal tarsomere of mid leg short and thin, with several ventral spines, T2l: B2l = 2.6, B2l: B2w = 5.0. Basal tarsomere of hind leg thin, dorsally with several setae more than twice longer than diameter of this tarsomere, ventral spines slightly longer than ciliation, T3l: B3l = 2.4, B3l: B3w = 5.7. Wing slightly brownish, stigma brown, veins brown, anal vein (A_1) complete. Costal seta long, axillary angle sharply acute. M2/D = 1.4, M3/Db = 2.4, lw: ww = 3.0. Haltere brownish-black, calypter brown with dark fringes. Abdomen black, dark brownish-grey pruinose (brown in dorsal view). Setae and setulae black. Hind marginal setae on sides of tergites 2-5 1.5 times longer than their segments, on tergites 6-7 shorter, discal setulae shorter than hind marginals. Dorsum of tergites with unusually long setae (marginals about as long as their segments). The first sternite setulose on sides. Terminalia as in Fig. 3. Length of body: 6.0 mm, wing: 6.5 mm.

Female: Unknown.

DIFFERENTIAL DIAGNOSIS: *Rhamphomyia* (s. str.) *piedmontensis* sp. n. differs from all other known species of *R. albosegmentata* group by multiserial acrostichal setae. In spite of female remaining unknown, I believe it could be very easily identified according to the following combination of characters: multiserial acrostichals, long costal seta, dark haltere, axillary angle sharply acute and complete anal vein. These characters are usually not sexually dimorphic and are unique among the Palaearctic fauna of *Rhamphomyia*.

DERIVATIO NOMINIS. The species is named after the type locality.

DISTRIBUTION: Italy.

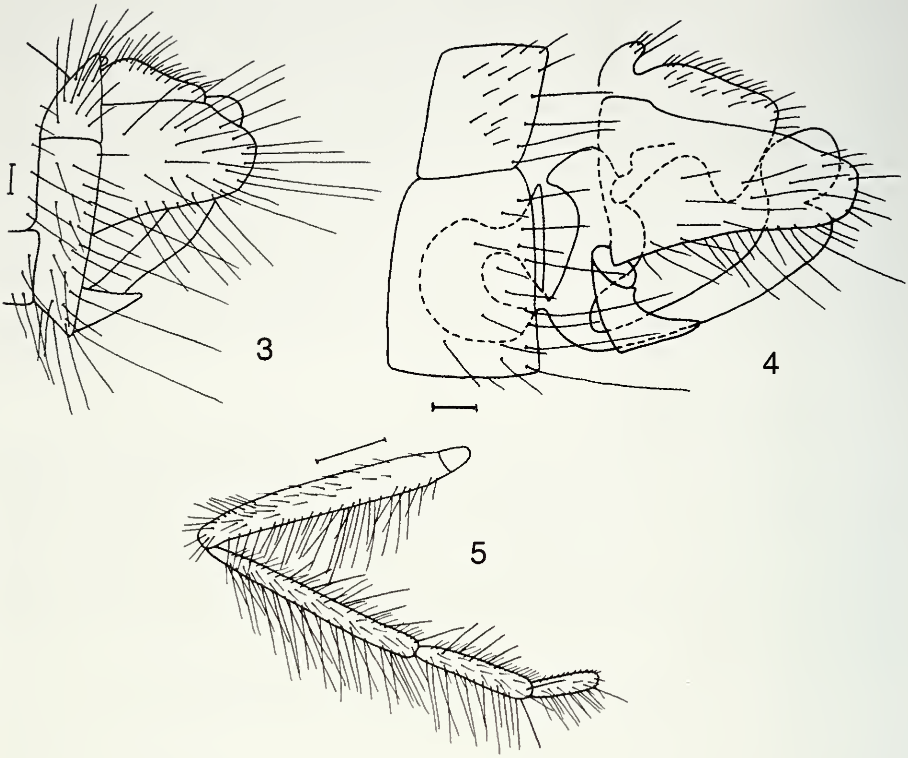
DATES OF OCCURRENCE: July.

***Rhamphomyia* (s. str.) *ponti* sp. n.** Figs 4, 5

HOLOTYPE MALE: Austria: Tyrol, Oetztal, Obergurgl, Gaisbergertal to Hohe Mut, heath, 2400 - 2600 m, 7.viii.1981, leg. A.C. Pont (NHM). - Paratype. Trögeralm, Glockner, 16.vii.1941, “Rhamphomyia hirtimana Loew, Lindner det.”, 1 male (SMNS).

DESCRIPTION

Male: Eyes holoptic, facets in lower half of eye much smaller than upper ones. Frons black, grey pruinose, bare. Ocellar setae black, fine, 2/3 as long as frons, ocellar triangle with 2-3 pairs of additional slightly smaller setulae. Face black, grey pruinose, about 0.30 mm broad below and 0.20 mm long, bare. Occiput black, light grey pruinose, medium densely and medium long black setose, postocular row incomplete and distant from eye margin in middle. Antenna black, ratio of antennal segments = 18: 11: 55: 14, both basal segments covered with long setae (longest about 0.25 mm long). Labrum brownish black, polished, slightly longer than head is high. Palpus brown, long, sparsely covered with long bristly setae (longest are 0.40 mm long). Genae narrow and mostly polished, clypeus pruinose. Thorax black or brownish black, mesoscutum with distinct brownish tinge, without stripes or with three darker stripes under rows of acrostichals and dorsocentrals visible only in sharp caudal view. All setae and setulae black. Chaetotaxy: 10-15 setulae on proepisternum; prosternum bare; 1-3 setulae on proepisternal depression; 24-26 biserial acrostichals; 25-30 irregularly



FIGS 3-5

Rhamphomyia (s. str.) *piedmontensis* sp. n. (3) and *Rhamphomyia* (s. str.) *ponti* sp. n. (4-5). (3-4) Male terminalia, lateral view. Scale 0.1 mm. (5) Male fore femur, tibia and basitarsus, posterior view. Scale 0.5 mm.

triserial dorsocentrals ending in 1-2 strong prescutellars (both acrostichals and dorsocentrals moderately strong and about 0.30 mm long); 0-2 intrahumeral; 0-1 posthumeral; about 10 additional setulae lateral of dorsocentrals in presutural area; 1 postpronotal scarcely differentiated from 15 setulae; 3-4 notopleurals (3-5 setulae in front part of notopleuron); 1 long supraalar, 3-4 prealars and 2-3 other setae in line between them; 1 long and 1 short postalars; 2 pairs of strong and 1 pair of fine scutellars; laterotergite (metapleura) with black setae. Coxae brownish black and pruinose, concolorous with pleura. Legs blackish brown and pruinose, black setose. Long seta present in comb at tip of hind tibia. Fore femur (Fig. 5) densely covered with irregularly arranged posteroventral setae and less numerous anteroventrals both at least twice as long as femur is deep, also anterior and posterior setae longer than femur is deep, dorsal setae subequally long as femur is deep. Fore tibia (Fig. 5) densely covered with long setae along dorsal and posterior surfaces (almost 0.70 mm long, i.e. 4-5 times as long as diameter of tibia), dense ventral ciliation consists of setulae subequally long as diameter of tibia and between these setulae with irregular row of 6-8 ventral setae 2-3 times as long as diameter of tibia. Mid femur with two rows of ventral setae at least

1.5 times as long as femur is deep, other ciliation short. Mid tibia with two irregular rows of anterodorsal and posterodorsal setae, 4-5 of them in each row about as long as those on fore tibia (0.70 mm), and with two rows (3-4 setae in each row) of unusually long anteroventral and posteroventral setae (0.50 mm long). Hind femur with 3-8 anteroventrals (8 strong in holotype and 3 fine in paratype), single long submedian posteroventral and 2 subapical anterodorsal setae at least as long as femur is deep, also several fine posterior setae on base of femur long, other ciliation short. Hind tibia with anterodorsal and posterodorsal setae (4-8 in each row) up to three times as long as diameter of tibia, ventral setulae contrastingly short. Basal tarsomere of fore leg thin, densely covered with setae dorsally only slightly shorter than the length of this tarsomere, also ventral spines unusually long, longer than diameter of this tarsomere (long dorsal setae occur also on second tarsomere), T1l: B1l = 1.9-2.0, B1l: B1w = 5.0-5.5; basal tarsomere of mid leg short and thin, with several long dorsal setae and long ventral spines, T2l: B2l = 2.4-2.6, B2l: B2w = 5.0-6.1. Basal tarsomere of hind leg thin, dorsally with some 6 setae three times as long as diameter of this tarsomere and with long ventral spines, T3l: B3l = 2.1-2.2, B3l: B3w = 5.8-6.1. Wing clear, stigma light brown, veins brown, anal vein (A_1) complete. Costal seta long, axillary angle sharply acute (35°). M2/D = 1.3-1.5, M3/Db = 2.1-2.2, lw: ww = 2.8-3.1. Haltere brown, calypter yellowish brown with dark fringes. Abdomen black, light grey pruinose (light grey in dorsal view). Setae and setulae all black. Hind marginal setae on sides of tergites 2-5 strong and slightly longer than their segments, on segments 6-7 fine and slightly shorter than their segments, discal setulae shorter than hind marginals. Dorsum of tergites with short setae in midline but longer just outside this line. The first sternite with several setulae on sides. Terminalia as in Fig. 4; apex of cercus right-angled. Length of body: 5.7-6.4 mm, wing: 5.9-6.7 mm.

Female: Unknown.

DIFFERENTIAL DIAGNOSIS. *Rhamphomyia* (s. str.) *ponti* sp. n. is somewhat similar to *R. ursina* Oldenberg, 1915 or *R. kreischi* Barták, 1998 (due to several long setae ventrally on fore tibia), however, the new species differs from both in many characters, e.g. mid tibia in both *R. ursina* and *R. kreischi* covered along dorsal side with numerous long setae not forming rows and abdomen is brown viewed from above. In several characters this new species is somewhat smilar to *R. hirtimana*, however, the latter species has short setose second fore tarsomere, mesoscutum light bluish-grey without brownish tinge and sparse posterodorsal setae on fore femur forming nearly a row.

DERIVATIO NOMINIS. The species named after the collector of the holotype, the leading world specialist on Muscidae, Dr Adrian C. Pont (Oxford).

DISTRIBUTION: Austria.

DATES OF OCCURRENCE: July-August.

***Rhamphomyia* (s. str.) *saintbaumensis* sp. n.** Figs 6-8

HOLOTYPE MALE. France: Provence, Saint Baume, 30.?.1945, deposited in UMO.

DESCRIPTION.

Male: Eyes holoptic, facets in lower half of eye smaller than upper ones. Frons black, grey pruinose, bare. Ocellar setae rather weak, black, about as long as dorsal postocular ciliae, ocellar triangle with 2 additional slightly shorter setulae. Face black, grey pruinose, about 0.30 mm broad below and equally long, bare. Occiput black, grey pruinose, densely and long black setose. Antenna black, both basal segments brown, ratio of antennal segments = 19: 11: 50: 14, longest setulae on basal two segments about 0.30 mm long. Labrum brown, polished, about as long as head is high. Palpus brown, long, densely covered with long bristly setae. Genae narrow and polished, clypeus pruinose. Thorax black, grey pruinose, mesoscutum dark brownish grey, with somewhat darker stripes below rows of acrostichals and dorsocentrals visible in sharp caudal view. All setae and setulae black. Chaetotaxy: proepisternum with about 30 setulae; prosternum bare; proepisternal depression with 8 setulae; about 35 biserial, fine acrostichals; great number of multiserial dorsocentrals, ending in 2 strong prescutellars, spreading down the sides of mesoscutum in presutural area (both acrostichals and dorsocentrals about 0.30 mm long); intrahumeral seta not differentiated from setulae, 1 posthumeral accompanied with several setulae, postpronotal scarcely differentiated from many similar setulae; 3 notopleurals (4-5 long setulae in front part of notopleuron); 2 supraalars and about 10 setulae in prealar area; 1 long and 1 short postalars; 3 pairs of scutellars; laterotergite (metapleura) with black setae. Coxae concolorous with pleura, pruinose, black setose. Legs brown, pruinose, black setose. Long seta present in comb at tip of hind tibia. Fore femur densely covered with long posteroventral and posterodorsal setae longer than femur is deep, anteroventral ones sparser and shorter, posteroventrals do not form row. Fore tibia with dense and almost homogeneous setae in posterodorsal area more than 3 times as long as diameter of tibia (also at least basal two fore tarsomeres with similar setae), ventral setulae very short. Mid femur with rows of anteroventral and posteroventral setae slightly longer than femur is deep, other ciliation short. Mid tibia with 4-5 long and strong anterodorsal and posterodorsal setae up to 4 times as long as diameter of tibia, and 4 almost equally long posteroventrals. Hind femur with 4-5 rather fine anteroventral setae about as long as femur is deep and with equally long two subapical anterodorsals and 1 posteroventral near middle of femur. Hind tibia thin, with 6-7 pairs of anterodorsal and posterodorsal setae, longest setae twice as long as diameter of tibia, ventral setulae short. Basal tarsomere of fore leg slightly swollen, densely covered with long setae dorsally (also at least second tarsomere long setose), T1l: B1l = 2.3, B1l: B1w = 3.5, basal tarsomere of mid leg slightly swollen, covered with rather long spines ventrally, T2l: B2l = 3.0, B2l: B2w = 3.5. Basal tarsomere of hind leg thin and short setose, T3l: B3l = 2.3, B3l: B3w = 6.7. Wing clear to slightly yellowish, stigma brown, veins brown, anal vein (A_1) complete. Costal seta long, axillary angle sharply acute. M2/D = 1.3-1.4, M3/Db = 2.0, lw: ww = 3.2. Haltere dark brown, calypter brownish-yellow with dark fringes. Abdomen black, light grey pruinose even in dorsal view. Setae and setulae all dark. Hind marginal setae on sides of tergites 2-3 slightly shorter than their segments, on tergites 4-5 shorter than their segments and very short on tergites 6-7, discal setulae shorter than hind marginals. Dorsum of tergites with slightly shorter setulae. The first sternite with several setulae on sides. Terminalia as in Figs 6-8; hypandrium slightly bifurcated apically; phallus with lateral «wing», apical swelling irregular. Length of body 6.4 mm, wing 6.0 mm.

Female: Unknown.

DIFFERENTIAL DIAGNOSIS. *Rhamphomyia* (s. str.) *saintbaumensis* sp. n. is allied to several species of the *R. albosegmentata* group (e.g. *R. curvinervis* Oldenberg, 1915, *R. tristriolata* Nowicki, 1868, *R. hirtimana* Oldenberg, 1922) sharing with them the following characters: densely and long setose fore femur and light grey abdomen. However, it differs from all these species in swollen fore basal tarsomere covered (together with the following tarsomere) with very long setae dorsally. Moreover, the new species has peculiarly shaped phallus (with lateral «wings») and dark and rather brownish mesoscutum.

DERIVATIO NOMINIS: The species is named after the type locality.

DISTRIBUTION: France.

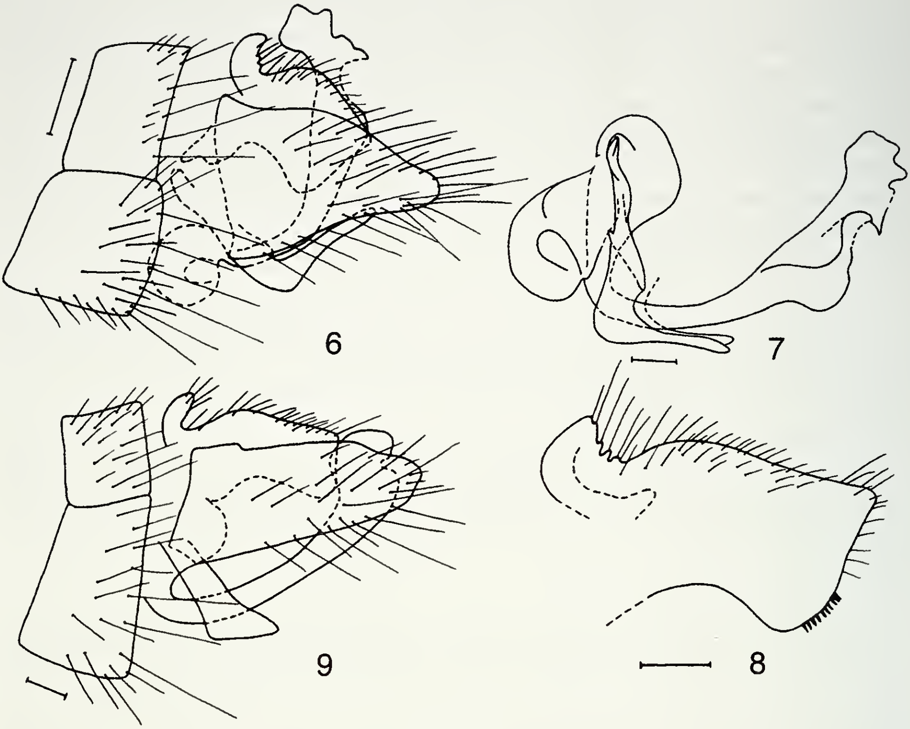
DATES OF OCCURRENCE: Unknown (it is impossible to read the month of collecting which is illegibly hand-written on the label - March?).

***Rhamphomyia* (s. str.) *sellacrinita* sp. n.** Fig. 9

HOLOTYPE MALE. Italy: Passo Sella, forest boundary, 1800 m, 46°26'N, 11°46'E, 8.viii.1988, leg. M. Barták (CUA). - Paratypes. Same data as the holotype, 1 male (CUA); Switzerland, VS Visperterminen, ob. Dorf, 1550 m, 27.viii.2001, Merz and Landry leg., 1 male (MHNG).

DESCRIPTION

Male: Eyes holoptic, facets in lower half of eye much smaller than upper ones. Frons black, grey pruinose, bare. Ocellar setae black, very fine, hardly 1/3 as long as frons, ocellar triangle with 1-2 pairs of additional nearly equally long setulae. Face black, grey pruinose, about 0.18 mm broad below and 0.40 mm long, bare. Occiput black, dark grey pruinose, rather sparsely and short black setose (uppermost postocular setae only about 0.10 mm long). Antenna black, ratio of antennal segments = 15: 10: 39: 12, both basal segments covered with medium long setae (longest about 0.20 mm long). Labrum brownish black, polished, slightly shorter than head is high. Palpus brown, long, sparsely covered with long bristly setae (longest 0.25 mm long). Genae very narrow and mostly pruinose, clypeus pruinose. Thorax black or brownish-black, mesoscutum deep black and slightly subpolished, without stripes. All setae and setulae black. Chaetotaxy: proepisternum with about 10 setulae; prosternum bare; 1-3 setulae on proepisternal depression; about 12 narrowly biserial acrostichals; 12-15 irregularly 2-3 serial dorsocentrals ending in 2-3 strong prescutellars (both acrostichals and dorsocentrals medium strong and about 0.20 mm long); 2 intrahumeral; 0-2 posthumeral setae (inserted in unusual lateral position, almost in area of notopleuron), 6-8 fine additional setulae lateral of dorsocentrals in presutural area; 1-2 postpronotals in addition to several shorter setulae; 3 notopleurals (5-8 setulae in front part of notopleura, some of them quite strong); 2 supraalars and 2-3 prealars; 1 long and 1 short postalars; 2 pairs of strong and 0-1 pair of fine scutellars; laterotergite (metapleura) with black setae. Coxae brown and pruinose, legs brown and mostly polished, black setose. Long seta present in comb at tip of hind tibia. Fore femur with rather sparse anteroventral and posteroventral rows of setae about twice as long as femur is deep one third before tip of femur but absent in basal half of femur, dorsal setulae very short. Fore tibia with almost homogeneous dorsal and posterodorsal ciliation subequally long as diameter of tibia, ventral setulae short. Mid femur with very short and fine setulae,



FIGS 6-9

Rhamphomyia (s. str.) *saintbaumensis* sp. n. (6-8) and *Rhamphomyia* (s. str.) *sellacrinita* sp. n. (9). (6) Male terminalia (macerated), lateral view. Scale 0.1 mm. (7) Male phallus and hypandrium (macerated), lateral view. Scale 0.1 mm. (8) Male cercus (macerated), lateral view. Scale 0.1 mm. (9) Male terminalia (macerated), lateral view. Scale 0.1 mm.

both anteroventrals and posteroventrals at most 1/3 as long as femur is deep. Mid tibia with 4-5 very long anterodorsals almost 4 times as long as diameter of tibia (up to 0.50 mm long), and with 3-4 shorter posterodorsal; anteroventrals and posteroventrals (1-3 in each row) up to twice as long as diameter of tibia. Hind femur with 8 strong anteroventral and one submedian strong posteroventral setae slightly longer than femur is deep and with 1-2 subapical anterodorsal and several posterior setae in basal part of femur, other ciliation short (setulae between anteroventral setae much shorter than strong anteroventrals). Hind tibia with anterodorsal and posterodorsal setae (5-7 in each row) twice as long as diameter of tibia, ventral setulae short as well as setulae between strong anterodorsals and posterodorsal. Basal tarsomere of fore leg thin and short setose, with short ventral spines and with peculiar long, fine and curved ventral setulae (these setulae distinct but shorter also on following tarsomeres), T1l: B1l = 2.3-2.5, B1l: B1w = 4.2-5.0, basal tarsomere of mid leg short and thin, with short ventral spines and also with several curved ventral setulae, T2l: B2l = 2.8-3.0, B2l: B2w = 4.5-5.0. Basal tarsomere of hind leg thin, dorsally with 2-3 pairs of setae twice longer than diameter of this tarsomere and with short ventral spines, T3l: B3l = 2.4-2.5, B3l: B3w = 5.6-5.7. Wing brownish, stigma brown, veins brown, anal vein (A_1) complete. Costal seta long, ax angle sharply acute. M2/D = 1.6-1.7, M3/Db = 2.9-3.0, lw: ww = 2.9-3.1. Haltere brownish black, calypter brownish yellow with dark fringes. Abdomen brownish black, grey pruinose (brown in dorsal view). Setae and setulae all black. Hind marginal setae on sides of tergites 2-5 1.5 times as long as their segments, on tergites 6-7 very short, discal setulae shorter than hind marginals. Dorsum of tergites with short setae. The first sternite with single setula on each side. Terminalia as in Fig. 9; epandrium (=lateral genital lamella) oblong-ovate, with only fine setulae at dorsal part apically, strong setae occur in middle part; apical angle of cercus slightly obtuse. Length of body: 4.4-4.6 mm, wing: 5.2 mm.

Female: Unknown.

DIFFERENTIAL DIAGNOSIS: *Rhamphomyia* (s. str.) *sellacrinita* sp. n. is most allied to *R. crinita* Becker, 1887 (and also to at least three other still undescribed species) sharing with them a single row of posteroventral setae on fore femur confined to apical third of femur. However, it differs from all of them in the following combination of characters: fore basal tarsomere ventrally with a few peculiar, long and fine, upright setulae with bent tip; mesoscutum deep black (as in *R. montana* Oldenberg, 1915); wing brownish and fore tibia with homogeneous ciliation dorsally about as long as diameter of tibia.

DERIVATIO NOMINIS. The species name is composed of: sella- (after type locality) and -crinita (stresses the similarity with *R. crinita*).

DISTRIBUTION: Italy, Switzerland.

DATES OF OCCURRENCE: August.

KEY TO PALAEARCTIC SPECIES OF *RHAMPHOMYIA* (S. STR.) *ALBOSEGMENTATA* GROUP

Notes: "additional characters" are useful for distinguishing keyed species from still undescribed species or species with which they can be confused or (in the case of females) from species of other *Rhamphomyia* (s. str.) species groups. Abbreviation: "M2/D" is not used in the key, instead of it, expressions like "vein M2 1.2-1.3 times as long as discal cell" are used. The key should be used together with the previously published keys and descriptions of Barták (1981, 1982, 1998) for checking illustrations, detailed descriptions and further remarks.

1a Acrostichals multiserial (unknown female probably keys here) .... *R. piedmontensis* sp. n.

1b Acrostichals biserial 2

2a (1) Dorsocentrals almost uniserial and 2-3 times longer and stouter than ac. (Additional characters: mesoscutum deep black, without any stripes; female with several anteroventral setae on hind tibia at least half as long as diameter of tibia; male fore femur with 1-5 strong posterior setae; male tergites 2-8 and female tergites 2-5 polished, other parts of abdomen pruinose) .... *R. anthracina* Meigen, 1822

2b Dorsocentrals 2-4 serial, at most slightly longer and stronger than acrostichals 3

3a (2) Mesoscutum with four longitudinal polished stripes. Female hind tibia slightly swollen, with anterior surface virtually bare .... *R. luridipennis* Nowicki, 1868

3b Mesoscutum uniformly pruinose. Female hind tibia with another ciliation 4

4a (3) Male 5

4b Female (of *R. lautereri, R. saintbaumensis, R. sellacrinita, R. ponti, R. erecta,* and *R. bellinosetosa* unknown) 32

5a (4) Posteroventral setae on fore femur absent. Mid femur with a group of small setae subbasally .... *R. parvicellulata* Frey, 1922

5b Posteroventral setae on fore femur present. Mid femur without any group of setae 6

6a (5) Fore femur with a tuft of long anteroventral setae subapically on distinct protuberance .... *R. armimana* Frey, 1922

6b Anteroventral setulae on fore femur spread subequally, they do not form tuft 7

7a (6) Fore tibia with setae ventrally at least twice as long as tibia is thick. (Additional character: basal tarsomere of mid leg with setae dorsally at least 4/5 as long as its length) 8

7b Fore tibia ventrally with homogeneous setulae shorter than diameter of tibia 10

8a (7) Mid tibia with setae dorsally arranged in two rows of. Abdomen grey when viewed from above. Hind femur with a few setae ventrally about as long as femur is deep .... *R. ponti* sp. n.

8b Mid tibia with very long setae both dorsally and ventrally not forming rows. Abdomen brown when viewed from above. Hind femur at least in basal two thirds with short setae ventrally 9

9a (8) Mid femur with long anterodorsal and posterodorsal setae, the longest setae at least twice as long as femur is deep. Fore tibia not swollen, uniformly setose on posterior surface .... *R. ursina* Oldenberg, 1915

9b Mid femur with very short anterodorsal, dorsal and posterodorsal setulae, about one third as long as femur is deep. Fore tibia swollen, with bare pruinose stripe on posterior surface ...... *R. kreischi* Barták, 1998

10a (7) Posteroventral setae on fore femur form a single row, which may be confined to apical half of femur only. Posteroventral (posterior) surface of fore femur polished at least above posteroventral setae or posteroventrals absent in basal half of femur 11

10b Posteroventral surface of fore femur covered with setae and setulae not forming row or this row is irregular. Posteroventral area of fore femur pruinose and simultaneously posteroventrals present in basal half of femur 15

11a (10) Posteroventral row of setae on fore femur incomplete, confined to apical half of femur 12

11b Posteroventral row of setae on fore femur complete, these setae are almost equally long throughout all length of femur 13

12a (11) Basal tarsomere of fore leg ventrally with a few peculiar, long and fine, upright setulae with bent tips. Mesoscutum deep black. Wings brownish. (Additional characters: fore tibia with homogeneous ciliation dorsally about as long as diameter of tibia; abdominal tergites 6-7 with very short hind marginals) . . . . *R. sellacrinita* sp. n.

12b Basal tarsomere of fore leg with normal setulae ventrally. Mesoscutum mostly light or brownish grey. Wing clear. (Additional characters: both fore tibia and basitarsus dorsally with heterogeneous setae much longer than diameter of these tarsomeres) . . . . *R. crinita* Becker, 1887

13a (11) Hind femur slightly bent in anterior view, with ventral «pilosity» confined to basal half only . . . . *R. lautereri* Barták, 1981

13b Hind femur straight as usual, with ventral «pilosity» throughout its length. (If mid tibia with only one ventral row of setae, fore tibia with posterodorsal setulae about as long as tibia is thick, abdomen somewhat subpolished, and apical angle of cercus slightly acute, compare *R. subdolomitica*) 14

14a (13) Anteroventral setae on mid femur 1/3 as long as femur is deep or even shorter. (Additional characters: discal cell short, vein M2 1.4-1.6 times as long as discal cell; abdomen brown viewed from above; epandrium with short spines near the tip) . . . . *R. montana* Oldenberg, 1915

14b Anteroventral setae on mid femur nearly as long as femur is deep. (Additional characters: posteroventral setae on mid femur subequally long as corresponding anteroventral - about as long as femur is high; posteroventral seta on hind femur present; proepisternum with normal setulae; discal cell slightly elongated; abdomen light grey viewed from above). (If discal cell about 1.1 times as long as vein M2, compare *R. aucta*; if vein M2 more than 1.4 times as long as discal cell, acrostichals and dorsocentrals more than twice as long as the distance between their rows, and apical angle of cercus obtuse, compare *R. hirtimana*; if dorsal setae on mid tibia short, about twice as long as tibia is thick, compare *R. sanctimauritii*)
. . . . *R. albosegmentata* Zetterstedt, 1838

15a (10) Discal cell elongated and narrow, about as long as vein M2. Apical angle of cercus obtuse. Fore femur short setulose dorsally. Hind femur with 1 long and strong posteroventral. Abdomen light grey viewed from above. (If discal cell elongated and other characters disagree, compare *R. serpentata* or *R. nubigena*) . . . . *R. aucta* Oldenberg, 1917

15b Discal cell shorter, vein M2 usually more than 1.1 times as long as discal cell. Other characters disagree 16

16a (15) Abdomen grey when viewed from above. In difficult cases simultaneously: basal tarsomere of fore leg above with setae longer than half of its length, mid tibia with two ventral rows of setae, discal cell short - vein M2 more than 1.3 times as long as discal cell, the longest dorsal setae on mid tibia at least three times as long as tibia is thick and face always bare 17

16b Abdomen brown when viewed from above. In difficult cases basal tarsomere of fore leg above mostly with setae shorter than half of its length and: either mid tibia with one ventral row of setae or discal cell elongated - vein M2 less than 1.2 times as long as discal cell or face with a few setulae or mid tibia with short setae dorsally 23

17a (16) Hind femur with at most 1-2 fine anteroventral setae shorter than femur is deep. Posteroventral setae on hind femur present or absent 18

17b Hind femur with 3 or more strong anteroventral setae about as long as femur is deep. Posteroventral seta on hind femur always present 19

18a (17) Mesoscutum light grey when viewed from above, often with darker longitudinal stripes between rows of setae. Posteroventral setae on mid femur up to twice as long as femur is deep. Abdominal tergites 4-7 with very short setulae. Costal seta often short and fine. Base of wing somewhat milky white . . . . *R. chionoptera* Bezzi, 1904

18b Mesoscutum brown when viewed from above. Wings not milky white. Posteroventral setae on mid femur shorter than femur is deep. Other characters disagree . . . . *R. crassimana* Strobl, 1898

19a (17) Basal tarsomere of fore leg swollen, 3.5 times as long as broad (and 0.21 mm broad), densely covered with long setae dorsally. Also the 2nd fore tarsomere dorsally with setae longer than this tarsomere. Phallus of unusual shape, with lateral «wings». (Additional characters: larger species - wing 6.0 mm; scutum dark brownish grey) . . . . *R. saintbaumensis* sp. n.

19b Basal tarsomere of fore leg not swollen, more than 4 times as long as broad (and usually about 0.15 mm broad), sparsely covered with shorter setulae dorsally. The 2nd fore tarsomere dorsally short setulose (only preapicals may be longer). Phallus of usual «albosegmentata» type 20

20a (19) Apical angle of cercus right to obtuse. Acrostichals and dorsocentrals shorter and stronger, about twice as long as the distance between their rows (rarely up to 2.5 times as long). Dorsocentrals sparsely spreading down sides of mesoscutum (10-20 setae in presutural area of mesoscutum lateral of dorsocentrals) 21

20b Apical angle of cercus acute. Acrostichals and dorsocentrals long and fine, about three times as long as the distance between their rows and setae densely cover even the area lateral from dorsocentrals in front of suture 22

21a (20) Fore tibia with strong anterodorsal, posterodorsal and posterior setae clearly differentiated from nearby setulae. About 20 setae in presutural area of mesoscutum lateral of dorsocentrals. Labrum shorter than head is high. Palpi densely long setose (more than 20 strong setae on each palpus) . . . . *R. bellinosetosa* sp. n.

21b Fore tibia with almost homogeneous dorsal ciliation. About 10 setae in presutural area of mesoscutum lateral of dorsocentrals. Labrum longer than head is high. Palpi sparsely setose (less than 15 strong setae on each palpus). (If fore tibia with rather short setae dorsally, palpi densely setose and apical angle of cercus very obtuse, compare *R. janovensis*) . . . . *R. hirtimana* Oldenberg, 1922

22a (20) Apical angle of cercus about 45° . . . . *R. curvinervis* Oldenberg, 1915

22b Apical angle of cercus about 80° . . . . *R. tristriolata* Nowicki, 1868

23a (16) Posterodorsal setae on fore tibia almost homogeneous, about as long as diameter of tibia. Discal cell short, vein M2 1.6-1.8 longer than discal cell (if discal cell elongated, compare *R. sanctimauritii*). Apical angle of cercus sharply acute. (If nearly right, compare *R. subdolomitica*). Both acrostichals and dorsocentrals relatively short, not much longer than the distance between their rows
. . . . *R. brevipila* Oldenberg, 1922

23b Fore tibia with heterogeneous setae dorsally longer than tibia is thick. Other characters disagree 24

24a (23) Fore femur dorsally and anterodorsally with only short setulae. (Additional characters: abdomen light grey in lateral view, pruinose; face and frons bare) 25

24a Fore femur with setulae dorsally or anterodorsally at least as long as femur is deep 27

25a (24) Mid tibia with short setulae dorsally, at most twice as long as tibia is thick. Larger species (wing more than 7.5 mm). (Additional characters: apical angle of cercus obtuse; discal cell slightly elongated, vein M2 1.1 - 1.3 times as long as discal cell; mesoscutum with distinct stripes; posteroventral setae on mid femur strong and about 0.20 mm long) . . . . *R. sanctimauritii* Becker, 1887

25b Mid tibia with longer setulae dorsally, at least three times as long as diameter of tibia 26

26a (25) Apical angle of cercus slightly acute. Discal cell short (vein M2 usually more than 1.4 times as long as discal cell)
. . . . *R. subdolomitica* Barták, 1981

26b Apical angle of cercus very obtuse. Discal cell slightly elongated (vein M2 1.2-1.3 times as long as discal cell) . . . . *R. janovensis* Barták, 1981

27a (24) Apical angle of cercus acute. Abdominal tergites pruinose, light grey in lateral view. Mid tibia with two ventral rows of setae. Eyes meet on frons. Face bare. Discal cell slightly elongated, vein M2 less than 1.2 times as long as discal cell. (If discal cell short, acrostichals and dorsocentrals twice as long as the distance between their rows and only 1 posteroventral on f3 present, compare *R. luridipennis*)
. . . . *R. serpentata* Loew, 1856

27b Apical angle of cercus right or slightly obtuse. Abdominal tergites at least moderately subpolished (if pruinose, follow couplets 13 or 20). Face often with a few setulae. Other characters in another combination . . . 28

28a (27) Basal tarsomere of fore leg dorsally with setae longer than half the length of basitarsus. Mid femur with anteroventral and posteroventral setae longer than femur is deep. Mid tibia with two complete rows of setae ventrally. (Additional character: mesoscutum pruinose, without stripes) 29

28b Basal tarsomere of fore leg dorsally with setae shorter than half of its length. Mid femur with at least anteroventral setae shorter than femur is deep. Mid tibia usually with only one ventral row of setae 30

29a (28) Abdominal tergites subpolished, not glossy polished. The 8th tergite without "brush" of erect setae dorsally . . . . . *R. lindneri* Barták, 1998

29b Abdominal tergites glossy polished at least partly. The 8th tergite with peculiar "brush" of erect setae . . . . . *R. erecta* Barták, 1998

30a (28) Hind femur with dense and long anteroventral setulae, subequally long as strong setae. Tergites 2-7 polished, other parts of abdomen pruinose. Acrostichal setae distinctly shorter and finer than dorsocentrals . . . . . *R. loewi* Nowicki, 1868

30b Hind femur with short and sparse anteroventral setulae in addition to much longer and stronger setae. Tergites at most subpolished, with distinct microchaetae. Acrostichal and dorsocentral setae subequal 31

31a (30) Mesoscutum subpolished, without traceable stripes. Epandrium equally rounded at tip. Apical angle of cercus slightly obtuse . . . . . *R. discoidalis* Becker, 1889

31b Mesoscutum pruinose, with two distinct darker stripes between rows of setae. Epandrium not rounded at tip, but with distinct dorsal constriction. Apical angle of cercus exactly right one. (Additional characters: abdominal tergites 2-6 pruinose) . . . . . *R. morio* Zetterstedt, 1938

32a (4) Discal cell elongated almost to wing margin, more than 2.5 times as long as vein M2 33

32b Discal cell shorter, at most twice as long as vein M2 34

33a (32) Discal cell of unusual shape, vein bordering its lower side clouded . . . . . *R. serpentata* Loew, 1856

33b Discal cell of usual shape. Hind femur anteriorly with an irregular row of setae nearly as long as femur is deep . . . . . *R. aucta* Oldenberg, 1917

34a (32) Wing partly clouded, at least along apical sections of veins M2 and CuA1 35

34b Wing uniformly coloured, clear to brown. (If the whole posterior margin of wings clouded, compare *R. discoidalis*) 36

35a (34) Apical section of vein M1 clouded . . . . . *R. tristriolata* Nowicki, 1868

35b Apical section of vein M1 without clouding . . *R. curvinervis* Oldenberg, 1915

36b (34) Both acrostichals and dorsocentrals shorter than 1/3 of the distance between their rows. Hind femur without any strong anterior setae in basal half 37

36b Acrostichals or dorsocentrals longer than 1/3 of the distance between their rows or hind femur with strong anterior setae even in basal half 38

37a (36) Hind femur somewhat dilated, covered with short and almost pennate ciliation both above and beneath in addition to 4-6 strong anteroventral setae. Discal cell not elongated, vein M2 1.3-1.7 times as long as discal cell. (Additional characters: mesoscutum dark black; acrostichals and dorsocentrals stout, spinose). (If acrostichals and dorsocentrals fine and hair-like, compare *R. brevipila*) .... *R. montana* Oldenberg, 1915

37b Hind femur not dilated and without subpennate ciliation. Discal cell elongated, vein M2 less than 1.2 times as long as discal cell. (Additional character: wings brownish, discal cell and the area behind it and second basal cell conspicuously lighter than other parts of wing membrane) .... *R. discoidalis* Becker, 1889

38a (36) Basal three fore tarsomeres somewhat dilated, covered with fine, silver pilosity .... *R. crassimana* Strobl, 1898

38b Front tarsi shaped and setose as usually. (Additional character: mid femur straight, not bent) 39

39a (38) Discal cell elongated, vein M2 less than 1.2 times as long as discal cell . . 40

39b Discal cell short, vein M2 more than 1.2 times as long as discal cell. (Additional characters: face bare; ocellar setae long and strong, usually longer than 2/3 of frons) 44

40a (39) Face with a few long fine setulae. (Additional character: abdomen pruinose). (If mesonotum subpolished and without stripes, acrostichals short and posterior margin of wings dark and discal cell much paler, compare *R. discoidalis*) .... *R. morio* Zetterstedt, 1938

40b Face bare 41

41a (40) Abdomen light grey. (If fore femur pruinose and not at least polished, follow couplet 44) .... *R. albosegmentata* Zetterstedt, 1838

41b Abdomen brown, at least on tergites 42

42a (41) Fore tibia without rows of setae ventrally. Mid femur with setae ventrally 1/3 as long as femur is deep. Abdominal tergites subpolished . ... *R. lindneri* Barták, 1998

42b Fore tibia with distinct rows of ventral setae (sometimes very short). Mid femur short setulose ventrally. Abdominal tergites 2-7 polished 43

43a (42) Both tergites and sternites of abdomen polished, at least sides of sternites 3-6 .... *R. ursina* Oldenberg, 1915

43b Sternites pruinose, at most last segments slightly subpolished. (If fore tibia with very short ventral setulae and fore coxa with anterior and anterodorsal setulae longer than diameter of fore tibia, compare *R. loewi*) .... *R. kreischi* Barták, 1998

44a (39) Hind femur somewhat dilated, with short and almost subpennate ciliation above and sometimes also beneath, in addition to 2-5 strong anteroventral spines 45

44b Hind femur without subpennate ciliation and not at least dilated 46

45a (44) Many (usually more than 20) setulae lateral of dorsocentrals in presutural part of mesoscutum. Both acrostichals and dorsocentrals usually shorter than half of the distance between their rows. Mid femur with short subpennate posteroventral ciliation. Abdomen grey dusted .... *R. brevipila* Oldenberg, 1922

45b Almost no setulae lateral of dorsocentrals. Both acrostichals and dorsocentrals usually longer than half of the distance between their rows. Posteroventral surface of mid femur sparsely covered with simple (not flattened) setulae shorter than half of depth of femur. Tergal part of abdomen slightly polished . . . . *R. subdolomitica* Barták, 1981

46a (44) Marginal setae on abdominal segment 3 about 1/4 as long as this segment, following segments almost bare. Costal seta short and fine, almost absent. Hind femur almost bare ventrally . *R. chionoptera* Bezzi, 1904

46b Abdominal segment 3 with hind marginal setae longer, also the following segments with considerable pubescence. Costal seta long. Hind femur with ventral setae 47

47a (46) Tergites 2-7 polished, sternites pruinose. Mid and hind femora with very short setulae and very short ventral spines . . . . *R. loewi* Nowicki, 1868

47b Not as above. (Additional character: hind femur with long and strong setae ventrally) 48

48a (47) Hind femur with a complete row of strong anterior (or anterodorsal) setae. Both acrostichals and dorsocentrals usually shorter than half of the distance between their rows. (Additional character: large species, wing more than 6.9 mm) . . . . *R. sanctimauritii* Becker, 1887

48b Strong anterior or anterodorsal setae absent at least in basal half of hind femur. Both acrostichals and dorsocentrals usually longer than the distance between their rows 49

49a (48) Hind femur thickened apically. Mid femur and tibia covered with peculiar, rather adhered and thick pubescence. (Additional character: posteroventral surface of fore femur bare and polished)
. . . . *R. parvicellulata* Frey, 1922

49b Hind femur not thickened. Mid leg with ordinary pubescence. (Additional characters: both acrostichals and dorsocentrals less than twice as long as the distance between their rows; tergites uniformly pruinose) 50

50a (49) Usually more than 30 acrostichal setae. Hind femur usually with 3 or more anterodorsal setae or fore femur with strong anterior seta. Haltere dark 51

50b Usually less than 30 acrostichal setae. Hind femur with at most 2 anterodorsal setae and fore femur usually without anterior seta. Haltere yellow to dark. (Additional characters: femora pruinose; fore femur with distinct posteroventral setulae; scutum usually with more than 10 setulae in presutural area beside intrahumeral and posthumeral; dorsocentrals multiserial; hind tibia with ordinary ciliation) 52

51a (50) Mid femur with one strong posterior seta in apical third
. . . . *R. armimana* Frey, 1922

51b Mid femur without strong posterior seta in apical third
. . . . *R. janovensis* Barták, 1981

52a (50) Acrostichals rather stout. Haltere pale, often almost yellow. Abdomen grey viewed from above . . . . *R. hirtimana* Oldenberg, 1922

52b Acrostichals fine. Haltere dark. Abdomen brown viewed from above. (Additional character: fore femur pruinose). (If acrostichals reach far into presutural area, compare *R. janovensis*) .... *R. crinita* Becker, 1887

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ERRATUM

Georgiev, Boyko B. & Mariaux, Jean 2007. Cestodes of the genus *Bluterina* Fuhrmann, 1902 (Cyclophyllidea: Paruterinidae) from passeriform and piciform birds in the Ivory Coast, with a key to the species of the genus. *Revue suisse de Zoologie* 114 (1): 141-174.

Due to a technical problem, the symbol ≥ was rendered incorrectly in the key to the species of the publication cited above. The correct key is therefore printed again below.

KEY TO THE SPECIES OF *BIUTERINA*

1a. Parasites of Paradisaeidae in the Australian Region 2
1b. Parasites of other birds 3
2a. Testes ~30 in number. Genital atrium without distinct dilatory muscles . . . . . *B. clavula*
2b. Testes ~15 in number. Genital atrium with distinct dilatory muscles . . . . . *B. mertoni*
3a. Anterior rostellar hooks ≤ 17 long; if anterior rostellar hooks 17 long then total number of rostellar hooks ≤ 32 4
3b. Anterior rostellar hooks ≥ 17 long; if anterior rostellar hooks 17 long or slightly longer then total number of rostellar hooks ≥ 40 5
4a. Rostellar hooks 24 in number . . . . . *B. globosa*
4b. Rostellar hooks 30-32 in number . . . . . *B. motacillabrasiliensis* and *B. motacillacayanae*
5a. Uterus entirely embedded in paruterine organ in pregravid proglottides 6
5b. Paruterine organ situated anterior to uterus in pregravid proglottides, not entirely embedding it 8
6a. Developing uterus horseshoe-shaped, with posteriorly directed lateral extremities 7
6b. Developing uterus consisting of two rounded lateral chambers connected anteriorly by narrow, branched isthmus . . . . . *B. passerina*
7a. Rostellar hooks 26-30 in number; anterior hooks ≥ 56 long . . . . . *B. cordifera*
7b. Rostellar hooks 56-62 in number; anterior hooks 24-25 long . . . . *B. pogoniuli*
7c. Rostellar hooks 40-42 in number; anterior hooks 20 long . . . . . *B. chlorurae*
8a. Anterior rostellar hooks > 35 long 9
8b. Anterior rostellar hooks < 35 long 21
9a. Number of rostellar hooks ≤ 20 10
9b. Number of rostellar hooks ≥ 26 11
10a. Number of rostellar hooks 14; anterior rostellar hooks 56-60 long; cirrus sac ~140 long . . . . . *B. erithaci*
10b. Number of rostellar hooks 18-20; anterior rostellar hooks 44-48 long; cirrus sac ~90 long . . . . . *B. fallax*
11a. Anterior rostellar hooks 75-85 long . . . . . *B. africana*
11b. Anterior rostellar hooks ≤ 70 long 12

12a. Anterior rostellar hooks 58-66 long 13
12b. Anterior rostellar hooks 38-49 long 14
13a. Rostellar hooks 34-36 in number; testes 15-18 in number; cirrus sac 86-105 long .... *B. morgani*
13b. Rostellar hooks 40-44 in number; testes 6-9 in number; cirrus sac > 120 long .... *B. triangula*
14a. Rostellar hooks spine-like .... *B. lansdowni*
14b. Rostellar hooks triangular, of typical shape for *Biuterina* 15
15a. Rostellar hooks ≤ 30 in number 16
15b. Rostellar hooks > 35 in number 17
16a. Rostellar hooks 26 in number, anterior rostellar hooks 43-46 long; paruterine organ wide, occupying almost entire width of median field .... *B. campanulata*
16b. Rostellar hooks ~30 in number; anterior rostellar hooks 41 long; paruterine organ in middle of median field .... *B. trapezoides*
17a. Anterior rostellar hooks < 45 long 18
17b. Anterior rostellar hooks > 45 long 19
18a. Gravid strobila consisting of ~180 proglottides; cirrus sac crosses poral osmoregulatory canals and substantial part of it situated in median field .... *B. macrancistrota*
18b. Gravid strobila consisting of ~50-60 proglottides; cirrus sac in lateral field .... *B. petroniae*
19a. Posterior rostellar hooks not longer than 55% of length of anterior rostellar hooks .... *B. planirostris*
19b. Posterior rostellar hooks longer than 60% of length of anterior rostellar hooks 20
20a. Blade of rostellar hooks 4-5 times shorter than handle .... *B. diversihamata*
20b. Blade of rostellar hooks slightly longer than handle or of same length .... *B. sobolevi*
21a. Rostellar hooks ~20 in number .... *B. distincta*
21b. Rostellar hooks > 30 in number 22
22a. Anterior rostellar hooks > 30 long .... *B. reynoldsi*
22b. Anterior rostellar hooks < 30 long 23
23a. Rostellar hooks > 56 in number 24
23b. Rostellar hooks ≤ 52 in number 27
24a. Rostellum consists of weak musculature and strongly developed glandular tissue .... *B. quelea*
24b. Rostellum consists of strongly developed musculature, with no glandular tissue or glandular tissue weakly developed 25
25a. Paruterine organ in pregravid proglottides occupies entire width of median field .... *B. ugandae*
25b. Paruterine organ distinctly narrower than width of median field 26
26a. Parasite of Furnariidae in the Neotropics (Brazil) .... *B. trigonacantha*
26b. Parasite of Dicruridae in India .... *B. singhi*
26c. Parasite of Laniidae in the Palaearctic .... *B. collurionis*

27a. Rostellar hooks 40 in number 28
27b. Rostellar hooks ≥ 48 (possibly, as exception, 42 in *B. fuhrmanni*) 29
28a. Anterior rostellar hooks 27 long . . . . *B. meropina*
28b. Anterior rostellar hooks < 20 long . . . . *B. dicruri*
29a. Testes number ≥ 12 . . . . *B. fuhrmanni*
29b. Testes number ≤ 10 30
30a. Rostellar hooks 52 in number; anterior rostellar hooks 23-25 long . . . . *B. cylindrica*
30b. Rostellar hooks 48 in number; anterior rostellar hooks 19-22 long . . . . *B. zambiensis*

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MERTENS, R. & WERMUTH, H. 1960. Die Amphibien und Reptilien Europas. *Kramer, Frankfurt am Main*, XI + 264 pp.

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Revue suisse de Zoologie, Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland.
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