Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae

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Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. - This paper reviews the European Hydrozoa species belonging to the families Oceanidae and Pachycordylidae. Emended diagnoses for the Oceanidae, the Pachycordylidae, and for some of their genera are provided. Due to the paucity of suitable characters, the macrotaxonomy of the two families is unsettled and must be regarded as provisional. The family Oceanidae includes the genera *Cordylophora*, *Corydendrium*, *Merona*, *Oceania*, *Rhizogeton*, *Turritopsis*, *Turritopsoides*, and the new genus *Similomerona* gen. n. The family Pachycordylidae includes the genera *Pachycordyle* and *Silhouetta*. *Turritopsis polycirrha* and *T. dohrnii* are both regarded as valid species and distinct from *T. nutricula* of the western Atlantic. Histological sections confirmed that *Turritopsis polycirrha* is hermaphroditic and larviparous, while *T. nutricula* is dioecious and oviparous. *Turritopsis rubra* (Farquhar, 1895) comb. n. from New Zealand is also regarded as a valid species and removed from synonymy with *T. nutricula*. The known distribution of *Corydendrium dispar* is extended to include the Faroe Islands. A former record of *C. dispar* from Denmark is referred to *Pachycordyle navis* (Millard, 1959) comb. n. *Pachycordyle fusca* Müller, 1913 is regarded as a likely synonym of *Pachycordyle pusilla* (Motz-Kossowska, 1905) comb. n.

Key-words: Marine invertebrates - Cnidaria - Hydrozoa - Antoathecata - Oceanidae - Pachycordylidae - Clavidae - descriptions - revision - taxonomy.

INTRODUCTION

Although the athecate hydroids and anthomedusae of the European coasts have a long taxonomic history, with some species going back to Linnaeus, we lack a comprehensive, up-to-date treatise like the one by Cornelius (1995) for the thecate hydroids of North-West Europe. Some groups are covered by good monographs. The Stylasteridae have been monographed by Zibrowius & Cairns (1992). The European *Hydra* species are treated by Holstein (1995). The monograph of Brinckmann-Voss

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(1970) covers the Capitata, but is restricted to the Mediterranean fauna only. Naumov's (1969) book on the Hydrozoa of the USSR includes also the Baltic Sea, but its scope is not European for the most part. Russell's (1953) work on the British medusae is certainly still very valuable, but treats only species with a medusa phase. There are also some recent worldwide reviews of single families which also include European species, e. g. by Segonzac & Vervoort (1995) for the genus *Candelabrum*, Boero *et al.* (2000) for *Zanclea*, or Schuchert (2001b) for the Corynidae. Some similar, older publications, e. g. Vannucci & Rees (1961), Rees (1962), also offer much valuable information. However, the scattered information makes it desirable to review all species. The author therefore aims at bringing together in a series of publications all important taxonomic information on the European Anthoathecata.

All European species belonging to the order Anthoathecata (Cornelius, 1995) will be revised, as will the supraspecific taxa where necessary. Taxa for which there exist recent revisions will, however, not be treated in detail. Wherever possible, taxa will be redefined so that most of them are plausibly monophyletic. However, these animals offer only few morphological characters and they tend to be insufficiently complex. Many shared characters are thus very prone to be homoplasies. A comprehensive phylogenetic analysis based exclusively on morphology was therefore considered unreliable and only a few suitable characters could be used to delimit some genera and families.

The geographic region covered in this revision reaches from the North Cape to the Canary Islands and the European parts of the Mediterranean. It excludes the Azores and Iceland. The hydroid species of the Azores are listed in Rees & White (1966) and Cornelius (1992). The hydroid fauna of Iceland has recently been reviewed by Schuchert (2001a).

In the present paper, the families Oceanidae and Pachycordylidae have been revised. The macrotaxonomy of both families, as well as their genera, is particularly unsettled and disputed. It can therefore only be regarded as provisional.

MATERIAL AND METHODS

Standard histological techniques were used to obtain serial thin sections. Animals fixed in formaldehyde were embedded in paraffin and serial sections of 8-10 μm thickness were made. Staining was with Hematoxilin and Eosin. All slides have been deposited in the MHNG.

ABBREVIATIONS

BMNH   The Natural History Museum, London, England
ICZN   International Code of Zoological Nomenclature, 4th Edition
IRSNB   Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
MHNG   Muséum d'histoire naturelle de Genève, Switzerland
RMNH   Naturalis, Leiden, The Netherlands
ZMUC   Zoological Museum Copenhagen, Denmark
ZSM   Zoologische Staatssammlung, Munich, Germany

TAXONOMIC PART

OCEANIDAE Eschscholtz, 1829

SYNONYMS – Cordylophoridae von Lendenfeld, 1885.

DIAGNOSIS – Anthoathecata Filifera with monomorphic or polymorphic polyps. Gastrozooids bearing filiform tentacles scattered over at least distal third of hydranth body, not concentrated in a narrow band. Gonophores developing either below the hydranth body, or directly on stolons, or from stolonal blastostyles with perisarc-covered pedicels. Gonophores either free medusae or fixed sporosacs. Free medusa, where present, with four mouth lips, mouth margin fringed with numerous spherical nematocyst clusters; four simple radial canals, without centripetal canals, juveniles with four or more tentacles, adults with numerous tentacles, these not grouped, their nematocysts evenly distributed. Ocelli present on adaxial bases of tentacles. Gonads on interradial walls of manubrium.

REMARKS – The name Oceanidae Eschscholtz, 1829 is here revived and it replaces the junior synonym Cordylophoridae von Lendenfeld, 1885 as well as the name traditionally used for the present group: Clavidae McCrady, 1859.

If the genus *Oceania* Péron & Lesueur, 1810 is regarded as valid, then auto-matically also the family name Oceanidae Eschscholtz, 1829 becomes available. If the genera *Oceania* and *Cordylophora* are placed within the same family, then *Oceania* is a senior synonym of Cordylophoridae von Lendenfeld, 1885. The latter name was recently re-introduced by myself (Schuchert 2001a, 2003a, 2003b) without being aware of the name Oceanidae Eschscholtz, 1829.

The scope of the family Oceanidae as used here corresponds largely to what was until recently known as Clavidae (comp. Millard, 1975; Bouillon, 1985; Calder, 1988a; Schuchert, 1996; Bouillon & Boero, 2000). The possession of scattered filiform tentacles was usually considered a diagnostic trait of the family Clavidae. However, also other filiferan families, like the Pandeidae or Hydractiniidae, have polyps with scattered tentacles. The hydroid of *Stomotoca atra* L. Agassiz, 1862, a member of the family Pandeidae, has scattered filiform tentacles (Boero & Bouillon, 1989) and in the absence of information on the medusa phase would certainly have been classified among the former Clavidae. Scattered tentacles are also prevalent in the sister group of the Filifera, the Capitata (see Petersen, 1990 for diagnoses for both taxa). The character "scattered filiform tentacles" must thus be used with necessary caution, although it is potentially a synapomorphy for the family Oceanidae. The isolated occurrences of scattered filiform tentacles in the Pandeidae and Hydractiniidae must then be explained as homoplasies.

The genus *Clava* does not belong to the Oceanidae. Schuchert (2001a) showed that the genus *Clava* Gmelin, 1791 must be transferred to the family Hydractiniidae. Although *Clava multicornis* (Forsskål, 1775), the type species of *Clava*, has scattered tentacles similar to many Oceanidae, its gonophores develop on the hydranth body directly below the tentacles. This gonophore position is the plesiomorphic condition within the Anthoathecata and it is found in filiferan families such as the Hydractiniidae and Eudendriidae, as well as in many other hydroids, e. g. Corynidae, most Zancleidae, some Limnomedusae, and some Leptothecata lacking a gonotheca. In some Filifera,

however, the site of gonophore development has been shifted towards proximal, either to the hydranth pedicels, branches, or even stolons. This downward shift is an apomorphy found in the Oceanidae, Bougainvilliidae, Pandeidae, Cytaeididae and some other minor groups. In the Calycopsidae, the site of the gonophores is somewhat unclear because they are produced at the insertion of the naked pedicel with the hydranth body (comp. Brickmann-Voss, 1979; Schuchert, 1996).

Because the genus *Clava* shows the plesiomorphic condition of gonophore position, and because there are no evident synapomorphies, it cannot be included in the Oceanidae as defined here. *Clava* is better transferred to the Hydractiniidae. Some Hydractiniidae have similarly scattered filiform tentacles (comp. Millard, 1975; Schuchert, 1996; Bouillon *et al.* 1997) and there are actually no significant morphological differences that would distinguish *Clava multicornis* from the Hydractiniidae, particularly when compared to *Clavactinia*. The similarity of *Clava* with the Hydractiniidae has also been noted by Boero *et al.* (1998), but they regarded it as distinct on account of its monomorphic polyps. This is, however, not convincing as also several hydractiniids lack a polymorphism and gonophores develop on gastrozooids that remain otherwise unchanged (e. g. *Hydractinia sarsii*; see Schuchert, 2001a). Gonophore producing hydranths generally reduce their size and tentacle numbers, an effect named reproductive exhaustion. This reproductive exhaustion should not be confounded with a true, pre-determined polymorphism, in which gonozooids differ from gastrozooids even before they develop gonophores.

Because *Clava*, the genus to which Clavidae is anchored, must be transferred to the Hydractiniidae, the taxon name Clavidae is not available anymore for the remaining genera of this family (Clavidae actually becomes a senior synonym of Hydractiniidae, see Schuchert 2001a). The name Oceanidae is therefore proposed for these remaining genera.

The original scope of Oceanidae Eschscholtz, 1829 was very broad and encompassed genera now allocated to several families. This is certainly due to the original broad meaning of the genus *Oceania*, but this should not be seen as an argument against its usage. Many other old hydrozoan names that are still in use have a similar history (e. g. the Linnean genera *Tubularia* and *Sertularia*). The family Oceanidae is tied to the genus *Oceania* and applies to the family that contains this genus, irrespective of the original scope of the family. The historical usage of *Oceania* is summarized under remarks for the genus *Oceania*.

The family Oceanidae thus comprises the following previously known genera: *Cordylophora*, *Corydendrium*, *Merona*, *Oceania*, *Rhizogeton*, *Turritopsis*, and *Turritopsoides*. Additionally, the new genus *Similomerona* is proposed.

The family Oceanidae as defined here lacks a clear synapomophy, hence its delimitation from other families like the Bougainvilliidae and Calycopsidae is not strict (Millard, 1975; Calder, 1988a expressed similar thoughts). It is possible that the family Oceanidae is not a monophyletic group and future results of sequence phylogenies might require a regrouping. The taxonomy of the Oceanidae must thus be regarded as provisional only.

It was necessary to re-define some of the genera included in this family, both to accommodate some recently described species which do not entirely fit formerly

provided diagnoses and to use as much phylogenetic information as possible to delimit monophyletic groups. Nearly all species described as belonging to these genera were considered for the diagnoses, although not all are discussed here. Unfortunately, the available synapomorphies are very limited and I failed to produce a convincing phylogenetic analysis. The genera were therefore delimited in a way that minimizes name changes and maximizes to some degree the possible monophyly. The synapomorphies and some important problems of the genera are discussed in the following sections.

Considering only the life-cycle, species with a medusa phase like *Turritopsis nutricula* or *Oceania armata* must represent the least derived condition because a medusa was present in the ground plan of the Anthoathecata (see Petersen, 1990; Schuchert, 1993; Boero *et al.*, 1998).

The current usage of *Turritopsis* is unmistakable and the genus is well delimited. The vacuolated gastrodermal cells forming a peduncle on top of the manubrium represents a clear apomorphy.

The genus *Oceania*, although in current usage quite well defined, poses taxonomic problems. They are outlined under remarks for the genus. *Oceania* auct. is only gradually different form *Turritopsis* and both genera should perhaps be merged, as it has been done by Haeckel (1879). Also McCrady (1857) thought that *Turritopsis* is very closely related to *Oceania* auct., and he initially considered *Turritopsis* to be only a subgenus of *Oceania*. To maintain nomeclatural stability, both genera are here employed. Traditionally, *Turritopsis* was kept separate from *Oceania* auct. on account of its manubrial peduncle formed by vacuolated cells (Mayer, 1910; Kramp, 1961). *Oceania* has a gelatinous peduncle, but the most proximal parts of the radial canals are also dilated and composed of large cells, exactly as in *Turritopsis*. In *Oceania* and in large *Turritopsis* medusae, these vacuolated cells are continued along the manubrium as four perradial ribs, resembling claws that clasp the manubrium (Figs 2C, 3B, 5). The vacuolated cells and the radial ribs could be a synapomorphy of the two genera. *Oceania* differs from *Turritopsis* in having stalked nematocyst clusters along it mouth, while they are without a distinct stalk in *Turritopsis*. Adult *Turritopsis* and *Oceania* medusae also resemble medusae of the family Pandeidae (comp. Kramp, 1959), but the lining of the mouth margin with nematocysts clusters separates them from the latter family (see Fig. 5C). These nematocyst clusters are, however, not a unique synapomorphy, as also at least some medusae of the family Calycopsidae have them (see e. g. *Bythotiara* spec. in Schuchert, 1996: fig. 9e). Medusae of the family Calycopsidae are, however, easily separable on account of their tentacle morphology.

Corydendrium parasiticum, type species of its genus, has gastrodermal gonads developing within the perisarc tubes of the hydranth pedicels and they are only extruded when mature. This is a clear apomorphy. The same internal gonads are also found in *Corydendrium brevicaulis* Hirohito, 1988, although this species forms variably either branched or stolonal colonies. *Corydendrium parasiticum* possesses another apomorphy: the side-branches remain within the perisarc tube of the original branch and they emerge only after a certain distance (Weismann, 1883). The perisarc of the side-branch is already formed within the tube of the original branch, leading to a typical nested structure of the perisarc tubes, best seen in cross-sections (well visible even in hand-made sections). This clear apomorphy is also found in *Corydendrium*

dispar Kramp, 1935 (see Kramp, 1935: fig. 2). However, *C. dispar* has external gonophores, although the structure of the male ones resemble that of *C. parasiticum*. *Turritopsis nutricula* hydroids also form erect, branching colonies with adnate side-branches. The perisarc tubes of *Turritopsis*, however, are not nested. This was verified in hand-made cross-sections of colonies from the Mediterranean and the Andaman Sea. The adnate side branches of *T. nutricula* represent perhaps only the first steps of a development that lead to the nested tubes seen in *Corydendrium parasiticum*. Because *Turritopsis* does not possess any of the two apomorphies found in *Corydendrium*, Kramp's (1935) proposal of merging *Turritopsis* and *Corydendrium* is here not adopted. This would also cause very troublesome name changes.

Merona has very obvious apomorphies: the nematophores in perisarc tubes and the sporosacs on blastostyles. The genus thus corresponds very likely to a clade. Antsulevich & Polteva (1986) described a new *Merona* species from the Kurile Islands which they named *Merona nematophorum*. It has naked nematophores resembling modified hydranths and it produces sporosacs issuing directly from the stolons. These combined differences suggest that *M. nematophorum* has perhaps attained its superficial similarity to other *Merona* species by convergence. Unfortunately, all these animals offer too few morphological characters to substantiate this with the aid of a reliable phylogenetic analysis and we have to wait for a molecular phylogenetic investigation. Meanwhile, it seems appropriate to follow Calder's (1988a) opinion that *M. nematophorum* should be transferred to a new genus. Therefore, the new genus *Similomerona* proposed.

The diagnosis for **Similomerona gen. n**. is as follows: "Anthoathecata Filifera with polymorphic polyps; feeding zooids stolonal, with scattered filiform tentacles; defensive zooids with rudimentary tentacles, not in perisarc tubes; gonophores sporosac developing on stolons." Type species is *Merona nematophorum* Antsulevich & Polteva, 1986. The species name will thus become *Similomerona nematophorum* (Antsulevich & Polteva, 1986) comb. n. The genus is currently monotypic. It is not represented in the European fauna.

Rhizogeton, with its sporosacs on the stolons and the stolonal or sessile hydranths, is easily distinguished from other members of the family. Both characters are apomorphies, but they are not independent and the *Rhizogeton*-like morphology can be imagined to have easily originated from various other genera. It is thus very prone to be polyphyletic.

Turritopsoides brehmeri Calder, 1988b, the type species of the genus, normally forms purely stolonal colonies, but infrequently some shoots bear a side-branch. These side-branches are adnate to the branch of origin, an apomorphy also found in *Turritopsis nutricula*. This, and the branched spadix of the female sporosacs, justify keeping the genus separate from *Rhizogeton*. The genus *Turritopsoides* is not represented in the European fauna.

The genus *Cordylophora* is difficult to define in terms of evident apomorphies, and the delimitation to *Pachycordyle*, here placed in a separate family, is based primarily on the tentacle arrangement of the hydroids (for an opposing view see Morri, 1980; or Stepanjants *et al.*, 2000). In the Pachycordylidae, the tentacles are confined to a small band below the hypostome, while in the Oceanidae they are more scattered.

Some genera that have at times been assigned to the Clavidae sensu Bouillon (1985) are either invalid or do not belong to the Oceanidae as defined here:

Campaniclava Allman, 1864: referred to the Pandeidae (Picard, 1956).

Clava Gmelin, 1791: see above and Schuchert (2001a), referred to Hydractiniidae.

Cnidostoma Vanhöffen, 1911: this genus was referred to the Clavidae sensu Bouillon, 1985 by Picard (Picard in Kramp, 1961: 444), a proposal accepted by Bouillon (1985). Kramp (1959, 1961) allocated it to the Cytaeididae. Examination of *Cnidostoma fallax* from the Ivory Coast (MHNG INVE 27133) confirmed the accurate description of Vanhöffen (1911). The overall habit, but especially the manubrium ending in four clusters of stalked nematocytes, bring this species very close to medusae of the Hydractiniidae and *Cnidostoma* is here provisionally allocated to that family.

Hataia Hirai & Yamada, 1965 is excluded from the Oceanidae because its sole species (*Hataia parva*) possesses stenoteles and must thus be transferred to the Capitata (see Yamada & Kubota, 1991).

Tubiclava Allman, 1863: Allman (1872: 256) wrote: "...since I do not at this distance of time feel absolutely certain as to the identity of the Dublin Bay and Torquay hydroids, the gonosome of *Tubiclava* must still be regarded as in some respects hypothetical, and the genus itself as defined above must be accepted with just so much of a provisional element." The type species of the genus *Tubiclava* is *T. lucerna* (by monotypy). Allman (1863, 1872) described *Tubiclava lucerna* based on infertile material. He thought that he had observed similar colonies a few years earlier that had gonophores, but which he previously thought to be an aberrant *Clava multicornis*. Rees (1956: 505) maintained that *Tubiclava lucerna* is a problematic species and he doubted whether Allman had actually observed sporosacs. *Tubiclava* is a doubtful genus and should therefore not be used anymore. Although occasionally other authors mention findings of *Tubiclava lucerna*, this species remains doubtful and no material could be located in any museum. All other species allocated to *Tubiclava* are either not recognizable or must be referred to other genera. *Tubiclava fruticosa* Allman, 1872 was based on infertile material and is not recognizable. Picard (1958: 189), referred all Mediterranean records of *T. fruticosa* to *Pachycordyle napolitana*, but some in Riedl (1959) are evidently *Turritopsis dohrnii*. Also *Tubiclava rubra* Farquhar, 1895 belongs to the genus *Turritopsis* (see Schuchert, 1996). *Tubiclava laxa* Fraser, 1938 must be referred to the genus *Merona*, while *Tubiclava triserialis* Fraser, 1938 is not recognizable. In his diagnosis of *Tubiclava* Allman (1872) stated that the sporosacs develop on the hydranth body immediately below the tentacles, just as in *Clava multicornis*. This renders the genus incompatible with the concept of the Oceanidae as used here. The theoretical genus *Tubiclava* sensu Allman has some resemblance to *Millardiana* Wedler & Larson, 1986. *Millardiana longitentaculata* Wedler & Larson, 1986, presently the only species of its genus, is not known from the region under investigation, but Cornelius (1992) reported it from the Azores and it is conceivable that this species could also be found along the coasts of southern Europe.

Millardiana Wedler & Larson, 1986 has sporosacs on the hydranth body. Therefore, using the same arguments as given above for *Clava*, it can neither be included in the Oceanidae nor the Bougainvilliidae as proposed by Calder (1988a). At present, the affinities of *Millardiana* are unclear. It should preferably be placed in a new family.

Pachycordyle Weismann, 1883: this genus is here placed in a separate family, the Pachycordylidae. For more details see under remarks for this family (includes also *Thielia* Stepanjants *et al.*, 2000).

Rhizodendrium Calder, 1988a: it might be necessary to use this genus for some stolonal Oceanidae to separate them from *Rhizogeton fusiformis* L. Agassiz, 1862 (type species of the genus). It is not used here because we do not yet know the gonophores of the type species of *Rhizodendrium* (see under genus *Rhizogeton*).

The order of the genera given below has no phylogenetic meaning. It merely attempts to group resembling genera to facilitate comparisons.

Turritopsis McCrady, 1857

SYNONYMS – *Clavula* Wright, 1859; *Dendroclava* Weismann, 1883.
TYPE SPECIES – *Turritopsis nutricula* McCrady, 1857.

DIAGNOSIS – Erect, branching hydroid colonies, side-branches and hydranth pedicels adnate to for some distance, perisarc tubes not nested. Hydranths spindle- to club-shaped; filiform tentacles scattered over much of hydranth body. Gonophores develop on the hydrocauli in perisarc covered region and are liberated as medusae. Medusae with proximal portion of radial canals swollen through vacuolated gastrodermals cells, forming a peduncle-like mass on top of manubrium, in larger animals continued on manubrium as perradial ribs. Tentacles numerous and evenly distributed. Mouth four-lipped, fringed with numerous spherical nematocyst clusters, these without distinct stalk. Ocelli adaxial, at tentacle base.

REMARKS – For the taxonomic history of this genus see Calder (1988a). For the publication date of McCrady's works see Calder *et al.* (1992).

Large *Turritopsis* and *Oceania* medusae resemble each other quite closely. Both have large cells at the proximal end of their radial canals which are continued along the manubrium as four perradial ribs, resembling claws that clasp the manubrium (Figs 2C, 3B, 5). *Oceania* differs from *Turritopsis* in having stalked nematocyst clusters along it mouth, while they are without a distinct stalk in *Turritopsis*. In addition, the manubrium base of *Oceania armata* is somewhat constricted. This allows to distinguish even badly preserved material (Kramp, 1965).

Turritopsis polycirrha (Keferstein, 1862)   Figs 1 & 2C-D

? *Medusa sanguinolenta* Modeer, 1791: 26.
? *Cyanea coccinea* Davis, 1841: 236, pl. 2 figs 1-3.
? *Oceania globulosa* Forbes, 1848: 29, pl. 3 fig. 3.
Turris neglecta – Wright, 1859: 106; Hincks, 1868: 13, pl. 3 fig. 1.
[not *Turris neglecta* Lesson, 1843].
Clavula Gossii Wright, 1859: 106, pl. 8 fig. 1.
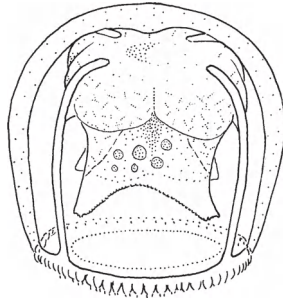*Oceania polycirrha* Keferstein, 1862: 26, pl. 2 figs 11-13.

FIG. 1

Turritopsis polycirrha (Keferstein, 1862), sketch after preserved material from The Netherlands, note that the radial canals overtop the mass of vacuolated cells, a few eggs are visible on the lower part of the manubrium, tentacles are lost, scale equals 1 mm.

? *Tubiclava fruticosa* Allman, 1872: 257, pl. 2 figs 5-6.
Turritopsis polynema Haeckel, 1879: 66, new name.
Turritopsis polycirrha – Hartlaub, 1897: 480, pl. 16c fig 2; Hartlaub, 1911: 202, figs 179-180.
Turritopsis nutricula – Kramp, 1930: 13, map 5; Russell, 1953: 115, figs 54A-C, 55, 56, pl. 5
    figs 1-5, pl. 29.
[not *Turritopsis nutricula* McCrady, 1857].

MATERIAL OF *T. POLYCIRRHA* – ZMUC, as *T. nutricula*, North Sea, 50° 59' N 1° 37'5 E, collected 23 August 1904, about 5 medusae, some with planulae, bells not so well preserved, one used for serial sectioning, deposited as MHNG INVE 33967 – RMNH Coel 10345, as *T. nutricula*, Texel, The Netherlands, North Sea, coll. 1973; 19 medusae, 18 clearly with oocytes or embryos, two specimens with visible oocytes were used to make serial sections, deposited as MHNG INVE 34417 and 34418 – IRSNB, hydroids as *T. nutricula*, coll. J. Bouillon June 1964 Roscoff, 2 lots, one small colony on microscopic slide, overgrowth of *Fosliella farinosa* indicates that it has been cultivated for quite some time; the second lot is a small polyp with gonophores growing on a piece of an unidentified gelatinous animal.
MATERIAL OF *T. NUTRICULA* FOR COMPARISONS – ZMUC, Beaufort Inlet, North Carolina, USA, > 100 medusae, collected August to September 1962 and 1964 by J. Allwein, many mature animals, sexes clearly distinguishable, no brooding, 2 females and 2 males used for serial sections, deposited as MHNG INVE 33963 to 33966.
MATERIAL OF *T. RUBRA* FOR COMPARISONS – see also Schuchert (1996), as *T. nutricula* – About 50 living medusae collected around Rangitoto Island (Hauraki Gulf, New Zealand), July 2002, some deposited as MHNG INVE 33469, 2 males and 2 females used for serial sections (MHNG INVE 33968 to 33971).
TYPE MATERIAL – There presumably exists no type material of *T. polycirrha*.

DIAGNOSIS – Typical *Turritopsis* medusae, adults 4-5 mm in height and diameter, 80-90 tentacles, tentacle tips not inflated, umbrella top rounded, manubrium without gelatinous peduncle, on top of manubrium four blocks of vacuolated cells fused into a single compact mass, radial canals overtop this mass. Vacuolated cells continued downward on manubrium as bulging, perradial rib. Radial canals broad. Simultaneous hermaphrodites and larviparous. Colour: stomach and gonads brilliant red to dark crimson. Nematocysts of medusa (Russell, 1940): microbasic euryteles

(8-10) x (4) μm; desmonemes (6-7) x (4-4.5) μm. Polyp phase inadequately known from nature, likely a stolonal or only sparingly branched colony, hydranths with scattered filiform tentacles, hydranth colour: red.

DESCRIPTION – See Russell (1953), who also provides good colour drawings.

BIOLOGY – Neritic species. Medusa present in autumn and winter months, occasionally until April; most abundant in September and October (Russell, 1953). Along the coast of The Netherlands, Van der Baan (1980) found it in December and January only. According to Kramp (1930), the medusae are presumably liberated from the hydroid during June or July. Teissier (1965) indicates August as the month of medusa liberation. Medusae present in the North Sea are considered to originate from the English Channel (Russell, 1953; Edwards, 1968).

DISTRIBUTION – English Channel; Great Britain, up to Firth of Forth in the east, up to Bristol Channel in the west; southern parts of the North Sea, sometimes as far east as Heligoland. Type locality: St. Vaast, Normandy, France.

COMPARISON OF REPRODUCTIVE STRATEGIES – The European *Turritopsis polycirrha* and *T. dohrnii*, as well as other nominal *Turritopsis* species from the Pacific have been synonymized with the American *T. nutricula* (although McCrady (1857) did not mention where he had collected *T. nutricula*, it can be inferred from McCrady (1859) that Charleston Harbor must be the type locality). Particular attention was therefore paid to *Turritopsis* medusae from the east coast of the USA and they were compared to *Turritopsis* medusae from other regions. The morphology of more than 100 medusae originating from the USA were examined. They all matched the description of *T. nutricula* given by Mayer (1910) and Brooks (1886). Together with the proximity of the type locality, there is no doubt about their specific identification. Even cursory examination with a stereomicroscope reveals that the sexes must be separate as eggs are easily discernible in mature females. None of the females had larvae or developing embryos attached to the manubrium. Histological examination of two males and two females confirmed that individuals produced either sperms or eggs, but never both together (Figs. 2A-B). The spermatogenic cells are small cells with little cytoplasm and a strongly staining nucleus. They differentiate distally into spermatogonia and finally into spermatozoa (comp. Tardent, 1978). In clusters of mature or nearly mature sperms, their aligned tails become visible even under light microscopy by producing a filamentous structure. The American *T. nutricula* is thus clearly dioecious and oviparous. This has been noted by other authors as well (Brooks, 1886; Brooks & Rittenhouse, 1907).

About 24 *Turritopsis polycirrha* medusae from the eastern Atlantic (North Sea) were obtained. No unambiguously identifiable males were found among them, but almost all specimens had eggs and some even had attached planulae. Due to the limited number of animals, only three medusae could be used for serial sectioning. The histological organization of the three proved to be clearly different from that observed in the American *T. nutricula*. Besides oocytes of all developmental stages, there often are pockets containing small cells with little cytoplasm that show differentiation into typical spermatozoa (Figs. 2C-D). Comparison with male *T. nutricula* from the USA
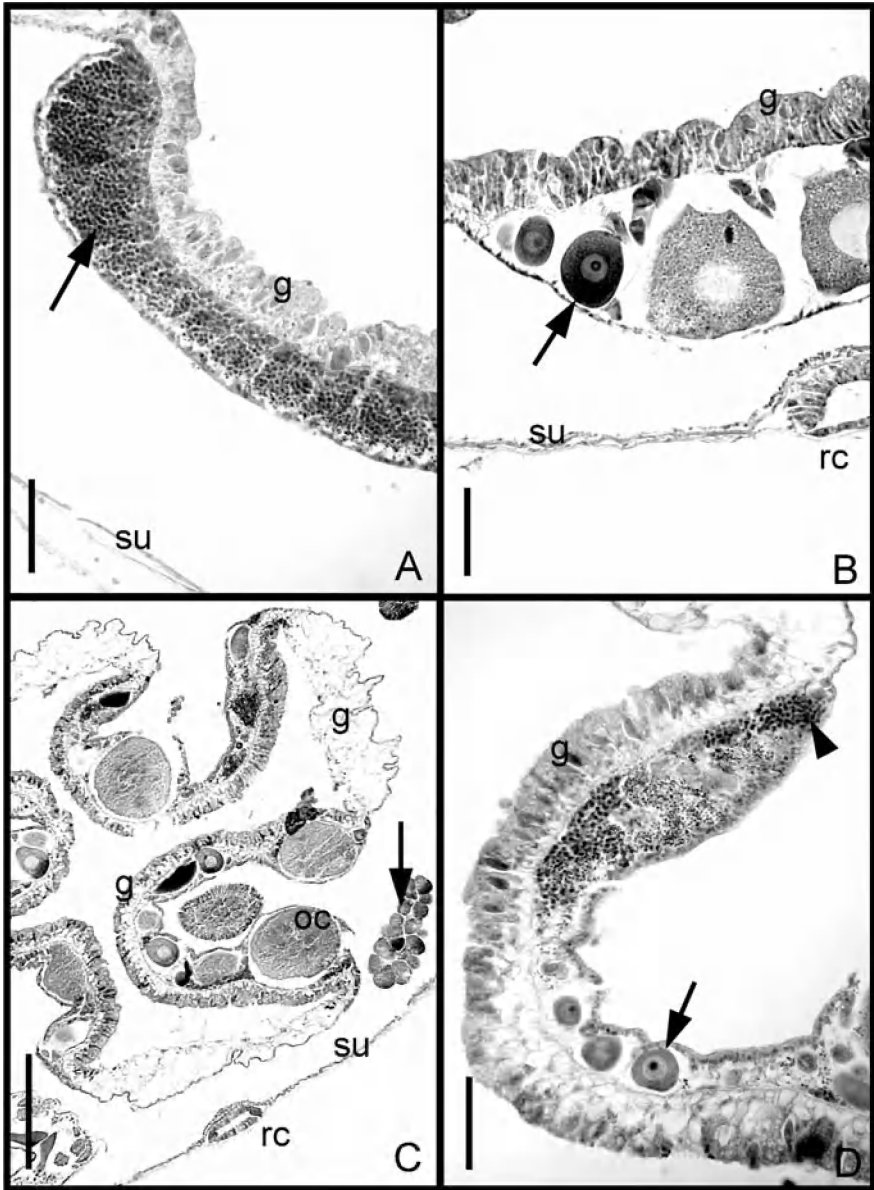
Fig. 2. Horizontal thin sections in region of gonads. A) Male *Turritopsis nutricula* medusa from the USA, arrow points to spermatogenic cells, scale equals 50 μm. B) Female *Turritopsis nutricula* medusa from the USA, arrow points to a developing oocyte, scale equals 50 μm. C) *Turritopsis polycirrha*, mature hermaphroditic medusa from the North Sea, overview, arrow points to a developing embryo, the gonad contains oocytes as well as pockets of spermatogenic cells. Note the perradial vacuolated cells of the gastrodermis. Scale equals 20 μm. D) Higher magnification of animal depicted in C, arrowhead points towards spermatogenic cells, arrow points to an oocyte, scale equals 50 μm. Abbreviations: g = gastrodermis, oc = oocyte, rc = radial canal, su = subumbrellar musculature.

leaves no doubt that these must be spermatogenic cells as well as mature spermatozoa. The presence of eggs, developing embryos, and sperms in various stages of differentiation makes the European *T. polycirrha* a simultaneous hermaphrodite. This confirms similar observations by Hartlaub (1911), which, however, have largely been ignored. The fertilized eggs are brooded and released as fully formed planula larvae, a fact that has already been observed by several authors (Mayer, 1910; Russell, 1953).

     Turritopsis medusae from New Zealand, until recently attributed to *T. nutricula* (see Schuchert, 1996), appear to be almost indistinguishable from *T. polycirrha* (Fig. 3A-B). Both have the same morphology and colour, and the same morphological arguments can be used to distinguish them from *T. nutricula* (table 1). However, in contrast to *T. polycirrha*, the New Zealandic *Turritopsis* is gonochoristic. Examination of more than 100 living, mature *Turritopsis* medusae from New Zealand (see also Schuchert, 1996) clearly showed that males and females can be distinguished using a stereomicroscope (10 x magnification). The females brood their larvae, sometimes even to the primary polyp stage (Fig. 3A-B; see also Schuchert, 1996). The examination of histological serial sections (2 females and 2 males) confirmed that the two sexes are clearly separate and that there are no differentiating sperm cells in the female medusae (results not shown). Because *Turritopsis* from New Zealand is thus distinct from both *T. nutricula* and *T. polycirrha*, it is preferable to regard it as a distinct species, namely *Turritopsis rubra* (Farquhar, 1895) new. comb.

     TAXONOMIC HISTORY – Because the medusa of *T. polycirrha* is quite conspicuous due to its red colour, it was possibly mentioned by several early naturalists (see synonymy above and Russell, 1953) but it was Keferstein (1862) who gave the first reliable description. Due to the great similarity to the American *Turritopsis nutricula*, Mayer (1910) considered *T. polycirrha* to be only a synonym of the former. Kramp (1930) and Russell (1953) followed the arguments of Mayer, although Russell acknowledged the differences between the European and the American forms. Hartlaub (1911, 1917) and Browne (1916), both of whom presumably had seen living European material, did not agree and kept *T. polycirrha* separate from *T. nutricula*. Browne (1916: 179) kept both species distinct based on the following arguments:

    T. nutricula: "... the radial canals, by a considerable thickening of their walls and coalescence, form a kind of endodermal peduncle upon which the stomach hangs."

    T. polycirrha: "... a further development of the endoderm takes place, it is no longer confined to the walls of the radial canals, but grows across the top of the umbrella cavity and forms a homogenous mass of cells. This extension also grows downward and takes in the radial canals in the uppermost part of the subumbrella. The extension of the endoderm is recorded by the leaving of the outer half of the radial canal wall in situ alongside the umbrella. In adult specimens, the radial canals run alongside this mass of endoderm nearly to the top of the subumbrella and there they curve sharply inside to the stomach."

Browne's arguments translate into the observation that in *T. polycirrha* the four masses of vacuolated cells are completely fused and the outer portions of the radial

canals reach higher up and overtop the mass of vacuolated cells. The difference in the radial canals was also observed in the examined preserved material (comp. Figs 1 and 3D-E). In addition, the American *Turritopsis nutricula* has its mass of vacuolated cells more clearly split into four blocks, while in the European *T. polycirrha*, the four blocks are tightly fused into one mass, although the fusion lines remain visible. Hartlaub (1917: 407) also noted this difference. As shown in Fig. 3, in living medusae these differences are quite obvious (although Figs 3A-C and 3D-E compare *T. rubra* and *T. nutricula*, but the former species from New Zealand closely resembles *T. polycirrha*). Fixation and contraction, though, may largely obliterate the morphological differences. The observed differences of the three compared species are summarized in table 1.

Hartlaub (1911) and Russell (1953) regarded *Turris neglecta* Lesson, 1843 as a questionable synonym of *T. polycirrha* or *T. nutricula*. According to Lesson (1843), *Turris neglecta* has a size of about 12-15 mm and only 16 tentacles. This is incompatible with *Turritopsis polycirrha* and the identity of *Turris neglecta* remains unresolved. The *Turris neglecta* described by Gosse (1853), Wright (1959), and Hincks (1868), however, are without doubt referable to *Turritopsis polycirrha*.

TABLE 1: Differences of the Turritopsis species discussed in this publication.

character	T. nutricula (eastern Atlantic)	T. polycirrha (North Sea)	T. rubra (New Zealand)	T. dohrnii (Mediterranean)
embryo brooded	no	yes	yes	no
reproduction	gonochoristic	hermaphroditic	gonochoristic	gonochoristic
outer portion of radial canals	does not appear to overtop mass of vacuolated cells	appears to overtop mass of vacuolated cells	appears to overtop mass of vacuolated cells	appears to overtop mass of vacuolated cells
mass of vacuolated cells	split into four blocks	four blocks fused into one mass	four blocks fused into one mass	split into four blocks
colour of stomach	yellow to orange	red-orange to red	red-orange to red	?brownish
bell size	3-4 mm, max. 6 mm	4-5 mm	3-7 mm	1.8-2.7 mm
umbrella top	rather flat	rounded	rounded to conical	conical
swelling of tentacle tips	distinctly swollen	not swollen	sometimes slightly swollen	swollen
tentacle number	40-100	up to 90	up to 120	14-32
manubrial pads in young medusae	not reported	unknown	present	present
hydroid colony	branched, mono- or polysiphonic	? stolonal or sparingly branched	branched, mono- or polysiphonic	branched, mono- or polysiphonic

REMARKS ON POLYP STAGE – Although *Turritopsis polycirrha* medusae can be quite common in the English Channel (Russell, 1953, as *T. nutricula*), the hydroid stage has only rarely been reported. Actually, the only records appear to be by Billard (1912) and Teissier (1965), who found it at Roscoff. Teissier recorded it on pebbles in the intertidal zone and on old shells in subtidal regions. Billard (1912, as *T. neglecta*) found the hydroid in aquaria. He did not mention gonophores. In addition, it is very likely that *Tubiclava fruticosa* Allman, 1872 is the polyp phase of *T. polycirrha*. Especially worth mentioning is its reddish colour, a characteristic trait of several *Turritopsis* hydroids. However, Allman's hydroid from Wales did not bear medusae buds and remains of uncertain identity.

The hydroid has been reared several times from planulae released by the medusa (e. g. Gosse, 1853 as *Turris neglecta*; Wright, 1859 as *Clavula Gossi*; Russell, 1953 as *T. nutricula*). Cultivated hydroids and colonies from nature collected by Prof. J. Bouillon near Roscoff (Brittany) were deposited in the IRSNB and were examined for this study. However, the state of conservation did not permit extraction of information beyond that indicated above under "characteristics". Nevertheless, *Turritopsis polycirrha* appears to form only small, sparingly branched colonies. It seems quite unlikely that *T. polycirrha* forms large colonies as seen e. g. in *T. dohrnii* or *T. rubra*. Such conspicuous colonies would certainly have been discovered along the coasts of Europe, one of the regions of the world that has been searched for hydroids very intensively.

CONCLUSIONS – Although quite similar in morphology, *Turritopsis* medusae from the western and north-eastern Atlantic differ in reproductive strategy. While the American medusae spawn their eggs into the free water (oviparity), their European counterparts brood fertilized eggs and release fully formed planula larvae (larviparity). There is also a significant difference in the gonad structure: the European medusae are simultaneous hermaphrodites, while American medusae are dioecious. Whether there exist also purely male medusae in the European Atlantic cannot be said at present, because not enough specimens could be examined. None of the prominent authors (e. g. Hartlaub, 1911; Russell, 1953) mentions male medusae, but Keferstein (1862) noted that he had observed male and female medusae. It is also not known whether autofertilization is possible. Hermaphroditic hydromedusae are not common, but the phenomenon is known to occur e. g. in *Eleutheria dichotoma* (see Müller, 1908).

The brooding behaviour and the hermaphroditism make the *Turritopsis* medusae of the north-eastern Atlantic quite distinct from *T. nutricula* found in the western Atlantic. Although Russell (1953) attributed only varietal character to this difference, it seems unlikely that animals with such different reproductive strategies form a single biological species. Because there are also other, unrelated differences (table 1), it is justified to regard *T. polycirrha* as a valid species and distinct from *T. nutricula*.

The medusa of *Turritopsis polycirrha* is very similar to *T. rubra* from New Zealand inasmuch both species brood their embryos, share the same intense red colour, the tightly fused blocks of vacuolated cells, and the high insertion point of the radial canals (Fig. 3A-B). *Turritopsis rubra* differs, however, in being gonochoristic and presumably also in forming large, polysiphonic hydroid colonies (see also table 1).
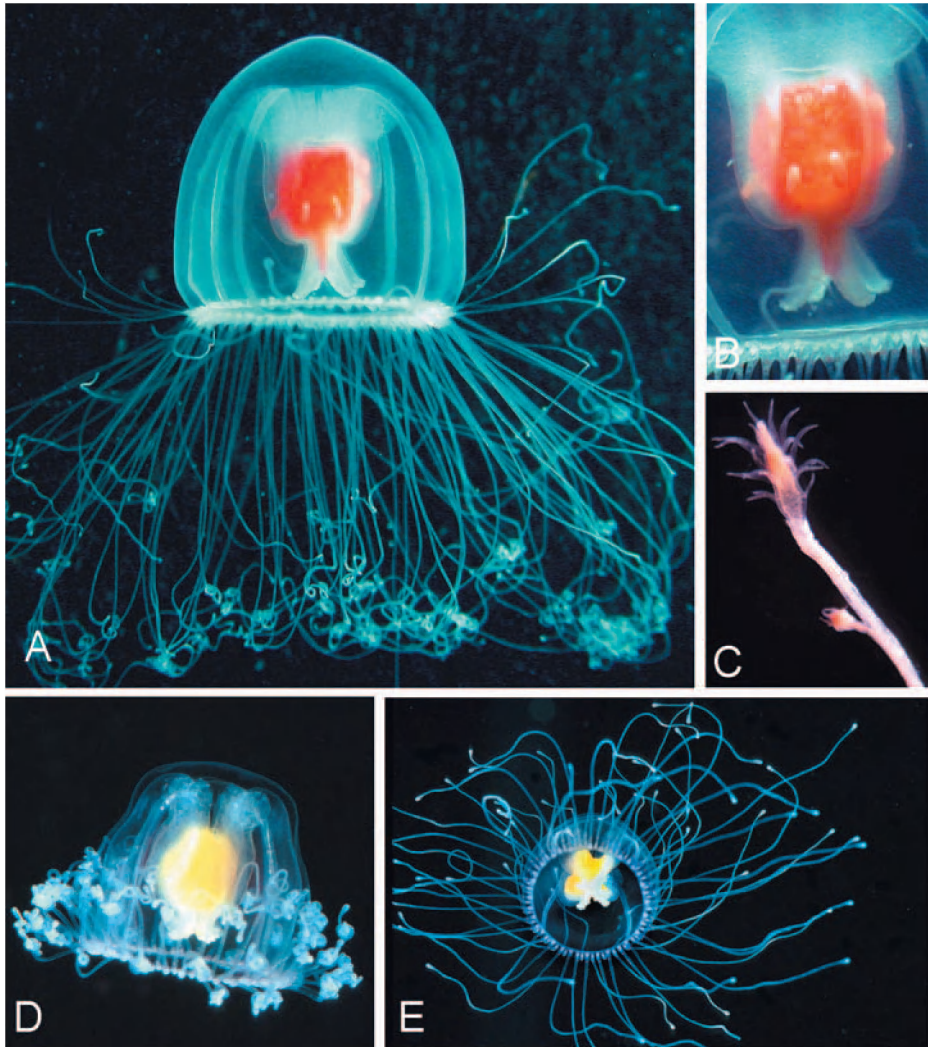
Fig. 3

A-C, *Turritopsis rubra* from New Zealand; this species has almost the same morphology and colour as the European *T. polycirrha*. D-E, *Turritopsis nutricula* from Brazil (photographs D-E kindly provided by Dr A. Migotto, São Paulo). A) Brooding female medusa, bell height 4 mm. B) Higher magnification of manubrium with planula larvae. C) Hydroid stage, tentacles somewhat contracted, height of hydranth body about 1 mm. D-E) Medusa, bell size approx. 3 mm, note the difference to *T. rubra* in bell shape, manubrium colour, shape of the vacuolated masses, the swollen tentacle tips, and the entry point of the radial canals.

Another European *Turritopsis* species is the Mediterranean *T. dohrnii*, the status of which is discussed below.

Further potentially valid nominal species within the genus *Turritopsis* are: *Turritopsis fascicularis* Fraser, 1943; *Turritopsis pleurostoma* (Péron & Lesueur,

1810); *Turritopsis chevalense* (Thornely, 1904); *Turritopsis lata* von Lendenfeld, 1885; *Turritopsis pacifica* Maas, 1909; and *Turritopsis minor* (Nutting, 1905). Their reproductive strategies and life-cycles must all be re-evaluated.

Turritopsis dohrnii (Weismann, 1883) Fig. 4

Dendroclava dohrnii Weismann, 1883: 26; Zoja, 1892: 409; Neppi, 1917: 42, pl. 4 fig. 14.
Tubiclava fruticosa – Riedl, 1959: 611.
[not *Tubiclava fruticosa* Allman, 1872 = ? *Turritopsis polycirrha*].
Turritopsis nutricula – Neppi & Stiasny, 1913: 25; Ramil & Vervoort, 1992: 17; Piraino *et al.*, 1996: 304, figs 4-5; Carla *et al.* 2003: 213, figs 1-3.
[not *Turritopsis nutricula* McCrady, 1857].

MATERIAL EXAMINED – Several living polyp colonies collected at Mallorca, depth 2-4 m, July-August 1999 and 2000, initial stages of medusa phase cultivated; some material deposited as MHNG INVE 27123 – Living material from Ischia, Italy, collected July 1993, medusae cultivated for 7 days – Natural History Museum of Vienna, as *Tubiclava fruticosa*, coll. Riedl, Tyrrhenia Expedition, 31.7.1956, on sponge, medusae buds present although tissue somewhat deteriorated (material mentioned in Riedl, 1959).
TYPE MATERIAL – There presumably exists no type material of *T. dohrnii*.

DIAGNOSIS – Hydroid colony of variable height, either sparingly branched with shoots only a few mm high to much branched and polysiphonic colonies up to 35 mm high. Hydranths with 12-20 tentacles. Periderm two-layered (see Schuchert, 1996: fig. 5d). Hydranths in life colourless or pinkish. Newly released medusa with 8-12 tentacles, manubrium with yellow-fluorescent interradial pads (paler to colourless in cultivated animals), vacuolated cells visible. Adult medusa (after Neppi & Stiasny, 1913; Piraino *et al.*, 1996) up to 2.7 mm in height, diameter 3.2 mm, mature specimens with 14-32 tentacles, manubrium reaching to bell margin, tentacles sometimes with terminal swellings, ocelli rust-coloured, gonads brownish, with 4 interradial rust-coloured dots, proximal ends of radial canals swollen through vacuolated gastrodermal cells, the four swellings not fused into a single mass. Sexes separate and females oviparous (Dr. S. Pirano, pers. comm.). Medusa can metamorphose back into polyp stage (Piraino *et al.*, 1996; Carla *et al.*, 2003).

DISTRIBUTION – Western Mediterranean, Adriatic Sea. Type locality: Naples, Mediterranean.

REMARKS – Weismann (1883) used the name *Dendroclava dohrnii* for this species. The spelling of the specific epithet ending with –*ii* is correct and must be maintainted (ICZN, 1999: § 31.1.1 and §31.1.3. The name is meant as a dedication to Anton Dohrn, latinized as *Dohrnius*, which gives in genitive case *dohrnii*).

The initial description of *Turritopsis dohrnii* was based on the hydroid phase only. It was synonymized with *T. nutricula* by Neppi (1917) and her opinion was adopted by nearly all subsequent authors. The only life-cycle studies resulting in mature medusae are described by Piraino *et al.* (1996, as *T. nutricula*) and Carla *et al.* (2003, as *T. nutricula*).

I consider *T. dohrnii* to be a distinct species differing from the European *T. polycirrha* and the American *T. nutricula*. *Turritopsis dohrnii* is oviparous and dioecious and thus clearly distinct from the hermaphroditic and larviparous *T. polycirrha*. Other differences from the latter species are more gradual: colony size (large polysiphonic
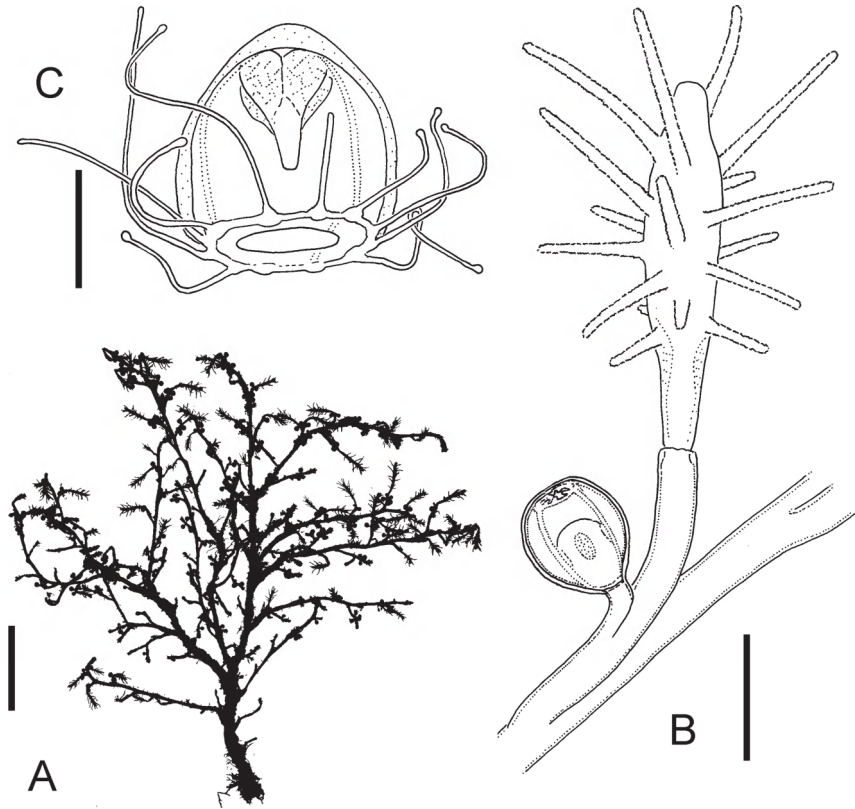
FIG. 4

Turritopsis dohrnii (Weismann, 1883). A) Silhouette of colony, preserved material from Mallorca, scale equals 5 mm. B) Hydranth and medusa bud, tentacles somewhat contracted, after living material from Ischia, scale bar 0.4 mm. C) Young medusae, drawn after photograph in Piraino *et al.* (1996), scale bar 1 mm.

versus small monosiphonic), number of tentacles of the medusa (16-32 versus up to 90), the colour of the gonads (brown versus red), and possibly also the brown spots on the gonads in *T. dohrnii* (the latter detail needs a re-evaluation).

The differences of *T. dohrnii* and the American *T. nutricula* are significant, although they are mostly only gradual. The medusae differ in tentacle numbers, bell size, and the size of the vacuolated masses. The newly released medusae have conspicuous manubrial pads, which have never been reported for *T. nutricula* (comp. Brooks 1886; Brooks & Rittenhouse, 1907; Migotto, 1996). The polyp stage seems to be indistinguishable, although *T. dohrnii* may form larger colonies. According to Migotto (1996), *T. nutricula* forms either monosiphonic or polysiphonic colonies, as in *T. dohrnii*. It seems prudent to regard *T. dohrnii* as separate from *T. nutricula* until more detailed life-cycle studies prove otherwise. Preliminary molecular investigations confirmed that the two belong to two separate lineages (M. P. Miglietta, Duke University, pers. comm.).

While the hydroid phase is relatively common on rocky substrates of the western Mediterranean, *Turritopsis* medusae are much less known. *Turritopsis* medusae have has been reported from the Mediterranean by: Hartlaub (1911, Sète, as *T. polycirrha*), Neppi & Stiasny (1913, Trieste, as *T. nutricula*), Schmidt (1973, as *T. nutricula*), Dowidar (1984, Egyp, as *T. nutricula*), Goy *et al.* (1991, Lebanon, as *T. nutricula*).

Another record of a Mediterranean *Turritopsis* medusa is *T. pacifica* by Browne (1927). Browne's medusa from Port Said at the Suez Canal was 3.5 mm in size and had 120 tentacles, a number which is significantly higher than observed by Neppi & Stiasny (1913) or Piraino *et al.* (1996). I believe that this medusa was probably not *T. dohrnii* and that it was perhaps an invader from the Red Sea or Indian Ocean. Kramp (1959: 246) likewise stated that *T. nutricula* might have invaded the eastern Mediterranean via the Suez Canal, but is unclear to what morphotype he was referring to or on which evidence he based his assumption.

The records of *T. nutricula* by Schmidt (1973), Dowidar (1984), and Goy *et al.* (1991) from the eastern Mediterranean do not provide sufficient data to evaluate the taxonomic status of their animals.

Oceania Péron & Lesueur, 1810

Type species – Mayer (1910) designated *Oceania armata* Kölliker, 1853 as type species, a species not originally included in the genus *Oceania* by Péron & Lesueur (1810). Mayer's designation is thus currently not valid.

Diagnosis – Anthoathecate medusae with eight or more marginal tentacles not grouped in clusters. Manubrium upon a simple, solid, gelatinous peduncle not formed by vacuolated cells. Manubrium ovoid, diameter at base smaller than in middle, mouth rim studded with a row of spherical nematocyst clusters, each cluster on a short stalk. Ocelli adaxial, on tentacle base. Polyp phase forming stolonal colonies, hydranths with scattered filiform tentacles.

Remarks – *Oceania* Péron & Lesueur, 1810 originally included species of medusae now referred to several different families and orders (Goy, 1995). First attempts to restrict the scope of the genus *Oceania* were made by Lesson (1843), who used it more in the sense of *Clytia* of present-day authors, thus falling within the order Leptothecata. Forbes (1848), on the contrary, used *Oceania* so that its species would today either fall within the Pandeidae or the Oceanidae as delimited in this publication. Forbes's usage was adopted by Kölliker (1853) when he described *Oceania armata*, and by Gegenbaur (1856) in his taxonomic system of the medusae. Agassiz (1862) returned to the usage of Lesson (1843) and with some ambiguity he even designated a type species. He noted for a conglomerate of species nowadays allocated to several families (Agassiz, 1862: 346, footnote 2): "I see, however, no reason why the name Nucleiferae, which he [Lesson] proposed for the old Forskalian type, should not be retained for this family, and the name Oceania and Oceanidae applied specifically, as Lesson has done, to Oceania phosphorica, which Péron & LeSueur place in the first section of the genus. This corresponds to the genus Thaumantias of modern writers." The sentence is somewhat ambiguous and it is debatable whether this must be seen as

a valid type-species designation (comp. ICZN § 67.5.3), but in the following taxonomic overview, Agassiz (1862) used the genus *Oceania* approximately in the sense of the present-day usage of *Clytia. Oceania phosphorica* Péron & Lesueur, 1810, the species which Agassiz considered typical for the genus, is likely a synonym of *Clytia hemisphaerica* (see Goy, 1995). Following authors adopted either Forbes's or Lesson's view of the genus. This caused so much confusion that Haeckel (1879) abandoned the genus *Oceania*. In order to settle the dispute, and in order to stabilize the prevailing usage, Mayer (1910: 147) designated *Oceania armata* Kölliker, 1853 as type species for the genus *Oceania*. This settled the dispute and all following authors, notably also Kramp (1959, 1961, 1968) in his influential synopses, used *Oceania* as proposed by Mayer (1910). However, Mayer's type species designation is not in accordance with provisions of the ICZN currently in use (Calder, 1988b). The designation is invalid because *O. armata* was not one of the originally included species (ICZN § 69.1). This contrasts with the usage of the genus *Oceania* which was employed almost exclusively for the species *Oceania armata*, a circumglobal species that is well known and has regularly been reported in the literature of the last 150 years. Nomenclatural stability is thus severely threatened if the genus *Oceania* were to be replaced by a new name, or even worse, if recognized as a senior synonym of the leptomedusan genus *Clytia* Lamouroux, 1812. Therefore, after the publication of this study, a case will be made to conserve *Oceania* in its current meaning by asking the International Commission on Zoological Nomenclature to rule that *Oceania armata* is the type species of the genus, notwithstanding the fact that it was not an originally included species and overruling the potential type-designation of Agassiz.

If the genus *Oceania* Péron & Lesueur, 1810 is accepted as valid, then automatically also the family group name Oceanidae Eschscholtz, 1829 becomes available.

Turritopsis and *Oceania* medusae resemble each other quite closely, but they can be distinguished (see remarks under genus *Turritopsis*).

Oceania armata Kölliker, 1853 Fig. 5

Oceania armata Kölliker, in Gegenbaur *et al.*, 1853: 323; Metschnikoff, 1886: 78, pl. 1 figs 32-39; Mayer, 1910: 147, figs 80-81; Uchida 1927: 219; Kramp, 1959: 99, fig. 63; Kramp, 1961: 65; Kramp, 1968: 27, fig. 67; Brinckmann-Voss, 1970: pl. 4 fig. 2; Bouillon, 1980: 308; Bleeker & Van der Spoel, 1988: 230, fig. 6; Bouillon, 1995: 224; Schuchert, 1996: 15, fig. 4a-c.
Oceania flavidula – Gegenbaur, 1856: 223, pl. 7: fig. 4.
[not *Oceania flavidula* Péron & Lesueur, 1810 (= *Laodice undulata* (Forbes & Godsir, 1851))].
Turritopsis armata – Haeckel, 1879: 65.
Callitiara polyophtalma Haeckel, 1879: 67, pl. 3 figs 1-5.
Conis cyclophthalma Haeckel, 1879: 55, pl. 4 fig. 1; Hartlaub, 1913: 342, synonym; Kramp, 1955: 152, synonym.
Tiarella parthenopia Trinci, 1906: 208, figs.

MATERIAL EXAMINED – MHNG INVE 32787, Naples, coll. 1892 – MHNG INVE 34177, Naples, det. Hartlaub, 1 medusa – MHNG INVE 31178, Villefrance-sur-Mer, France, det. Hartlaub, 5 medusae.
TYPE MATERIAL – There presumably exists no type material of *O. armata*.

DESCRIPTION – Mature medusa 5-10 mm high, maximal bell diameter about the same as height, umbrella bell-shaped with flat top, jelly uniformly thin. Manubrium on
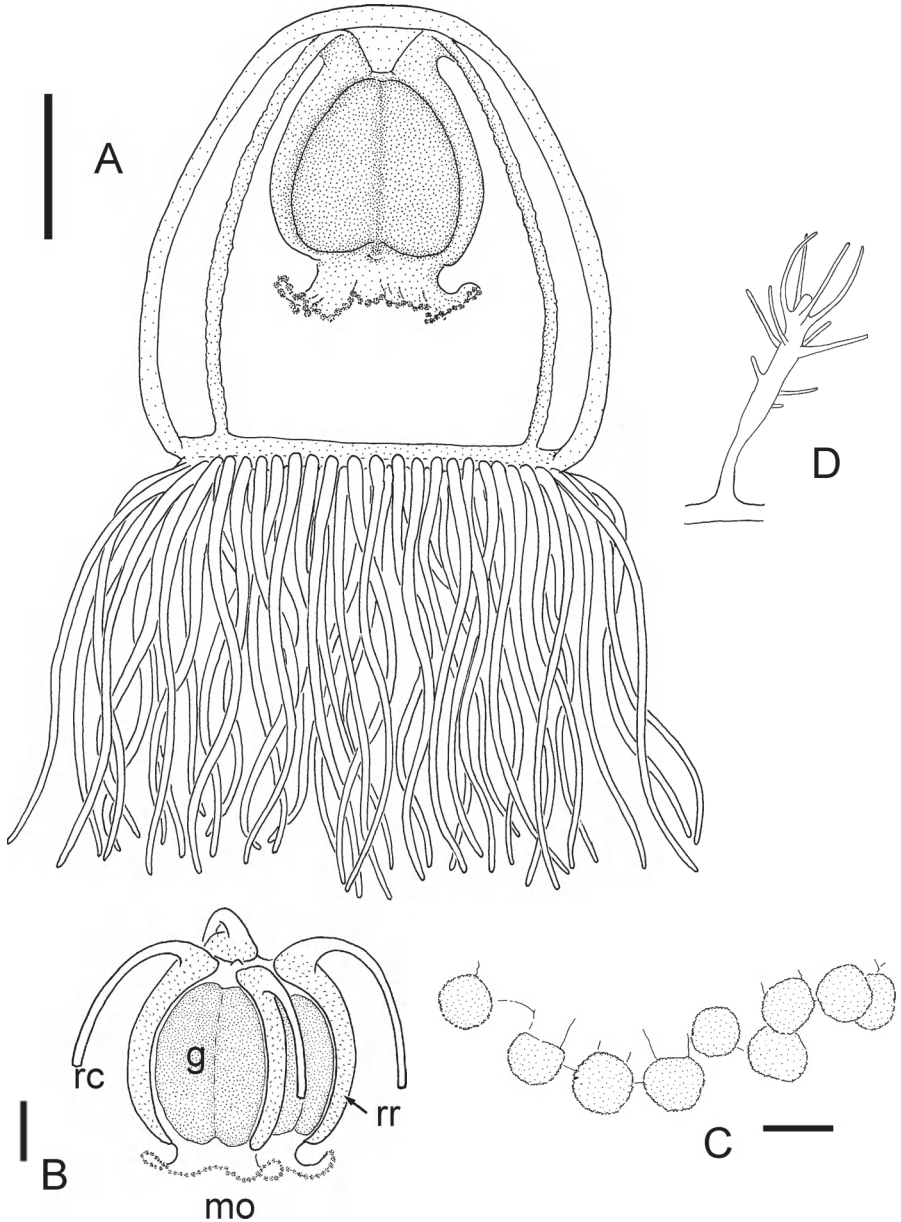
FIG. 5

Oceania armata Kölliker, 1853, A-C, after preserved material from Naples; D, modified after Metschnikoff (1886). A) Mature medusa, scale equals 2 mm. B) Manubrium with parts of radial canals, scale equals 1 mm, g = gonad, mo = mouth, rc = radial canal, rr = radial rib. C) Higher magnification of mouth rim fringed with pedicellate nematocyst clusters, scale 0.1 mm. D) Young hydranth, no scale available.

a transparent, shallow peduncle without vacuolated cells. Manubrium large, up to 2/3 of subumbrellar height, ovoid, manubrium base constricted, with funnel-shaped mouth region. Stomach and mouth region distinctly cruciform in cross-section. Radial canals where joining manubrium funnel-like dilated and composed of large cells, continued on manubrium as radial ribs like four clasping claws (Fig. 5B). Mouth rim crenulated, with four prominent perradial lips. Margin of mouth with a continuous row of spherical nematocyst clusters, these usually on short pedicels. Gonads smooth, on interradial surface of stomach. Four quite broad radial canals, margins occasionally jagged, circular canal broad. Marginal tentacles tapering, 80-120 in number, longer than bell (preserved sample), gastrodermis chordoid. Origins of tentacles somewhat alternately displaced adaxially and abaxially. Each tentacle with a slight proximal swelling beginning shortly after origin. Adaxial ocellus near tentacle base. Nematocysts: microbasic euryteles, desmonemes. Colours (after Haeckel, 1879): Manubrium and gonads yellow or brown-yellow, mouth-lips orange or red, radial canals, ring canal and tentacles yellow, ocelli brown-red. Egg size about 0.27 mm. Polyp stage (after Metschnikoff, 1886) colonial, with creeping, ramified stolons. Hydranths on short, periderm-covered pedicel. Hydranth spindle-shaped with conical hypostome. With around 13 filiform tentacles in up to four whorls.

BIOLOGY – Usually occurring in depths of less than 200 m, but not at surface (Kramp, 1965).

DISTRIBUTION – Mediterranean, coasts of Senegal and Gambia, Canary Islands, Cape Verde, Azores, Portugal, Spain; West Indies; Japan, New Zealand, Tasman Sea. The northern limit in Europe seems to be Portugal. Type locality: Mediterranean.

REMARKS – The polyp *Oceania armata* is known only from the rearing experiments of Metschnikoff (1886) and has never been found in nature. The origin of medusae buds is also not known.

Bleeker & van der Spoel (1988) described the morphologically similar *Oceania tydemani* based on a single medusa taken south-west of the Azores. *Oceania tydemani* differs from *O. armata* in having more tentacles (180) and the nematocyst clusters of mouth margin are absent over four short interradial stretches.

The identity of *Oceania flavidula* Péron & Lesueur, 1810 is pertinent to the question of the valididity of the genus *Oceania* (see remarks under genus *Oceania*). Gegenbaur (1856) believed *O. flavidula* and *O. armata* to be conspecific. The plates of Péron & Lesueur published by Goy (1995) now allow to identify *O. flavidula* as a synonym of *Laodice undulata* (Forbes & Godsir, 1851). Thus, the genus *Oceania* sensu Péron & Lesueur, 1810 did not originally include *Oceania armata* Kölliker, 1853.

Corydendrium van Beneden, 1844 (emended)

SYNONYM – *Soleniopsis* Ritchie, 1907.
TYPE SPECIES – *Sertularia parasitica* Linnaeus, 1767.

DIAGNOSIS – Erect, branching or stolonal hydroid colonies, monosiphonic or polysiphonic. In branching colonies, branches and hydranth pedicels adnate to other branches over part or almost all their length. Perisarc firm, terminating near hydranth base, tubes of sister-branches nested. Hydranths spindle- to club-shaped; filiform

tentacles scattered over much of hydranth body. Gonads formed within perisarc tubes of branchlets or at the end of branchlets and thus replacing a hydranth. Gonads gastrodermal.

REMARKS – The taxononomic history of this genus was reviewed by Calder (1988a). Kramp (1935) has not been followed in merging *Corydendrium* with *Turritopsis* (see discussion above). As mentioned in the introduction to the family, the genus *Corydendrium* is here restricted to Oceanidae which have at least one of the following synapomorphies: (I) gonads within the perisarc tubes of hydranth pedicels or branchlets, (II) nested perisarc tubes.

Clearly also a member of the genus *Corydendrium* in the sense of the author is the Japanese *C. brevicaulis* Hirohito, 1988. This species is quite important in discussions of the scope of the genus as it forms either stolonal or branched colonies. In its morphology, this species otherwise resembles *C. parasiticum* so closely that it could arguably seen only as a variant of it. The generic diagnosis was therefore modified to include stolonal colonies to permit the inclusion of *C. brevicaulis* Hirohito, 1988.

Hirohito (1988) also described another *Corydendrium*, namely *C. album*. It resembles closely *Turritopsoides brehmeri* Calder, 1988b and should be transferred to the genus *Turritopsoides* if the so far unknown female gonophores of *C. album* will prove to be identical.

Fiorini (1977) argued that the reproductive organs of *C. parasiticum* are probably not homologous to a gonophore and thus to a vestigial medusa. They are most likely a composite structure derived from a polyp with several gonophores (the term gonophore must be restricted to gonad-bearing structures that can be homologized with a single medusa bud). Such a composite gonad-bearing organ is thus better referred to as a gonangium (see also discussion in Thiel, 1962). Contrary to most other hydrozoans, the germ cells of *Corydendrium parasiticum* and of the males of *C. dispar* remain in the gastrodermis (Weismann, 1883; Fiorini, 1977; Kramp, 1935). Other species referred here to *Corydendrium* should be examined if they have similar gonangia, which would consolidate it as an additional synapomorphy for the genus. Germ cells located in the epidermis represent a synapomorphy for the Hydrozoa (Schuchert, 1993). The gastrodermal gonads of some *Corydendrium* species must be seen a character reversal. All other related taxa have epidermal gonads.

Corydendrium corrugatum Nutting, 1905 from Hawaii likely also belongs to the genus *Corydendrium*, although its reproductive structures remain unknown (see Schuchert, 2003b). The same holds true for *C. flabellatum* Fraser, 1938 from the tropical eastern Pacific and *C. fruticosum* Fraser, 1914 from Vancouver Island (northeastern Pacific). *Corydendrium splendidum* Boone, 1938 is a synonym of *Pennaria disticha* Goldfuss, 1820 (see Cooke, 1977).

The European fauna includes only two species, namely *Corydendrium parasiticum* (Linnaeus, 1767) and *Corydendrium dispar* Kramp, 1935.

Corydendrium parasiticum (Linnaeus, 1767)   Fig. 6

Sertularia parasitica Linnaeus, 1767: 1315.
? *Solenopsis dendriformis* Ritchie, 1907: 495, figs 142-143, pl. 26 fig. 1.
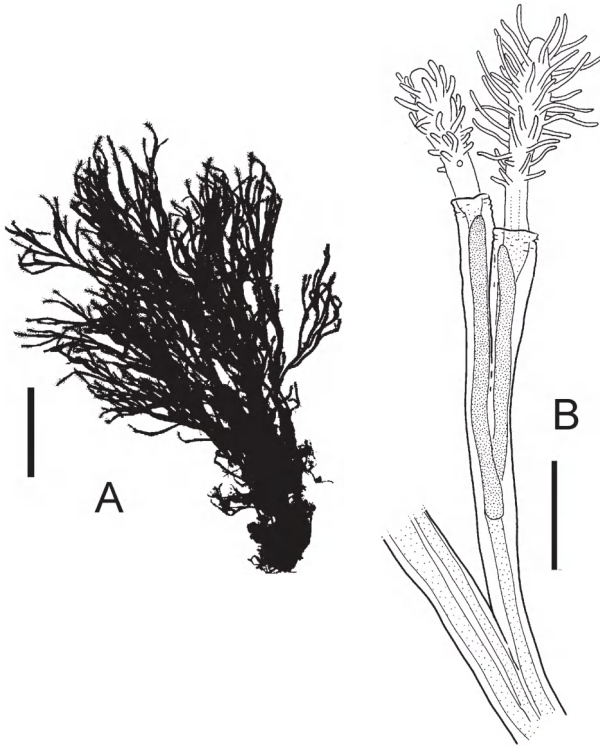? *Corydendrium sessile* Ritchie, 1910a: 802, pl. 76 figs 1-2.

Fig. 6

Corydendrium parasiticum (Linnaeus, 1767), after preserved material from Naples. A) Colony silhouette, scale equals 1 cm. B) Distal branches with two hydranths, note gonads (stippled) in perisarc tube of pedicels and adnate braches, scale equals 1 mm.

not *Clava (Corydendrium) parasiticum* – Bonnevie, 1899: 39 [= *Corydendrium dispar* Kramp, 1935].
Corydendrium parasiticum – Weismann, 1883: 34, fig. 7, pl. 14 figs 1-9, pl. 15 figs 1-5, pl. 16 figs 1-2, 4; Neppi, 1917: 43, figs 7-8; Rossi, 1971: 20, fig. 6L; Millard, 1975: 72, fig. 24B-D; Wedler & Larson, 1986: 82, fig. 5C; Rees & Vervoort, 1987: 12, bibliography; Calder, 1988a: 6, figs 3-4; Hirohito, 1988: 66, fig. 21 a-c, pl. 2 fig. B; Migotto, 1996: 11, fig. 2e; Watson, 1999: 2, fig. 2A-E; Calder *et al*. 2003: 1176, fig. 2.

MATERIAL EXAMINED – MHNG INVE 25127, Naples, Italy, fertile males, very profuse colony – MHNG INVE 31489, Naples, Italy, coll. 1892 – MHNG INVE 31490, Naples, Italy, coll. 1896.
TYPE MATERIAL – No type material was localized.

DESCRIPTION – Colonies bushy, much branched, polysiphonic, 2-5 cm in height (reportedly up to 16 cm). Perisarc stiff, smooth or encrusted with silt, not annulated, terminating below hydranths, sometimes terminal part slightly dilated and wrinkled. Branches adnate for some distance, then diverging at acute angle. Perisarc tubes of side-branches nested at their origins. Diameter of branches 0.4-0.5 mm, terminal tubes 0.3 mm. Hydranths elongated, cylindrical to fusiform, 1-3 mm long, diameter up to 0.35 mm, with 20-40 filiform tentacles scattered over most of hydranth body.

Hypostome prominent, dome-shaped. Sexual organs tubular structures, length 3 mm and more, arising as side branches of hydranth pedicels, initially wholly contained within perisarc tube, mature eggs extruded from perisarc but remaining attached near end of tube until developed into planulae, thus larviparous (Neppi, 1917; Wedler & Larson, 1986). Structure of sexual organs simple, bi-layered, gametes in gastrodermis. Nematocysts: microbasic euryteles and desmonemes.

BIOLOGY – Grows most often on rock. The fertile period in the Mediterranean is from August to September, while colonies are present from June to October (Lo Bianco, 1909). Motz-Kossowska (1905) obtained fertile colonies from the Balearic Archipelago in August. Neppi (1921) found colonies during June and August, and they were also fertile during this period. In the Mediterranean, the species seems to be only locally abundant, with most records coming from Naples. Intensive searches for it at localities near Banyuls-sur-Mer (Motz-Kossowska, 1905), Island of Medes (Gili, 1982) and near Genoa (Boero & Fresi, 1986) were unseccussful.

OTHER INFORMATION – The microscopic structure was investigated in detail by Weismann (1883) and Fiorini (1977). The ultrastructure of the planula and the oocytes were investigated by Glätzer (1970, 1971). The early development was examined by Neppi (1917) and Glätzer (1971).

DISTRIBUTION – Perhaps circumglobal in tropical and subtropical seas: along the European coasts confined to the Mediterranean (Weismann, 1883; Neppi, 1917), also coasts of western and southern Africa (Ritchie, 1907; Millard, 1975), tropical western Atlantic (Wedler & Larson, 1986; Calder, 1988a; Migotto, 1996), Indian Ocean (Millard & Bouillon, 1973; Rees & Vervoort, 1987), Indonesia (Vervoort, 1941; Schuchert, 2003b), coasts of northern Australia (Watson, 1999), tropical western Pacific (Leloup, 1937, as *C. dendriforme*), north-western Pacific (Hirohito, 1988), ? tropical eastern Pacific (Fraser, 1938, as *C. flabellatum*). Depth range about 1-90 m.

REMARKS – The taxonomic history and synonymy of this species are given by Calder (1988a) and need not be repeated here in detail. Vervoort (1941), Millard (1975), and Calder (1988a) considered *Corydendrium dendriforme* (Ritchie, 1907) from the Cape Verde Islands conspecific with *C. parasiticum*. This contrasts with Rees & Thursfield (1965) who re-examined the type material of *C. dendriforme* and kept it distinct. Both species reportedly differ in the more arborescent colony of *C. dendriforme* versus the more bushy one of *C. parasiticum* (see fig. 6). Although the arguments in favour of a conspecificity appear more convincing, a definite answer is not possible at the moment. A detailed comparison of the populations from the Cape Verde Archipelago with those from adjacent regions is needed to provide the necessary arguments. *Corydendrium dendriforme* (and also *C. sessile*) are thus treated as questionable synonyms of *C. parasiticum*. The material from the Strait of Gibraltar reported by Ramil & Vervoort (1992) as *C. parasiticum* is somewhat atypical and perhaps does not belong to this species.

Corydendrium dispar Kramp, 1935   Fig. 7

Clava (Corydendrium) parasiticum – Bonnevie, 1899: 39.
[not *Corydendrium parasiticum* (Linnaeus, 1767)].

Corydendrium dispar Kramp, 1935: 1, figs 1-4.
not *Corydendrium dispar* – Rasmussen, 1973: 22 [= *Pachycordyle navis* (Millard, 1959)].

TYPE MATERIAL EXAMINED – ZMUC, holotype, Kungsbackafjord, Sweden, coll. 26 Jun 1928, 26
    m – ZMUC, paratype, Kvittingsøy, Norway.
OTHER MATERIAL EXAMINED – BIOFAR collection (Nørrevang *et al.*, 1994), kept by Kaldbak
    Marine laboratory, The Faroes: Station 8 (62.29°N 5.40°E, 171 m, 17 Jul 1987, on bi-
    valve shell); station 165 (62.18 °N 4.97°E, 184 m, 07 May 1988), slides of this material
    deposited as MHNG INVE 33555; station 204 (62.16°N 5.88°E, 158 m, 11 May 1988,
    on *Abietinaria fusca*).

DESCRIPTION – (after Kramp, 1935 and examined material) Colonies forming delicate, erect shoots, less profuse than *C. parasiticum*, 0.5 - 2 cm in height, reportedly up to 6.5 cm. Stolons creeping, ramified, anastomosing. Shoots irregularly branched, entirely monosiphonic or polysiphonic in lower parts of the shoots, branches adnate to each other over variable distances, diameter of single branch up to 0.2 mm, perisarc tubes at origin of branches nested, perisarc wrinkled, generally double-layered, inner layer thick and firm, outer layer membranous. Hydranths spindle-shaped, 0.6 mm in preserved material, hypostome dome-shaped, 16-20 filiform tentacles scattered over most of hydranth body. Reproductive organs not within perisarc tubes of branchlets, arising like hydranths at end of side-branches, covered by very thin perisarc membrane. Male sexual organs are sessile sporosacs, oblong-elliptic or -ovoid, length 0.7 mm, diameter 0.4 mm, on short pedicels; structure sac-like, with thin epidermis and thick gastrodermis containing the gametes. Mature female organs insufficiently known, likely sessile sporosacs, spherical, diameter up to 1.2 mm.

BIOLOGY – Known substrates are shells and hydroids (Kramp, 1935; this study). Occurs in fully marine environments only. Depth range: 26 to 184 m.

DISTRIBUTION – Along Swedish and Norwegian coast north to Trondheim Fjord (Kramp, 1935), The Faroes. Type locality: Kungsbackafjord, south of Gothenburg, Sweden, 26 m (Kramp, 1935).

REMARKS – *Corydendrium dispar* Kramp, 1935 is recorded here for the first time in waters of the Faroe Islands. The samples contained only male specimens and the mature female reproductive structures are still imperfectly known. While the male structures are only simple sacs without any recognizable vestiges of a medusa structure, the initial developmental stages of female ones suggest a medusoid origin (Kramp, 1935).

The material recorded by Rasmussen (1973) as *C. dispar* was re-examined and identified as *P. navis*. See remarks under this species.

Merona Norman, 1865

TYPE SPECIES – *Tubiclava cornucopiae* Norman, 1864 by monotypy.

DIAGNOSIS – Stolonal hydroid colonies, polyps polymorphic with gastrozooids, gonozooids and nematophores. Hydranths with scattered filiform tentacles and perisarc-covered caulus. Gonozooids reduced, without mouth or tentacles, thus blastostyle-like, bearing numerous gonophores. Gonophores sessile sporosacs. Defensive zooids small, arising from stolons, in funnel-shaped perisarc tube.
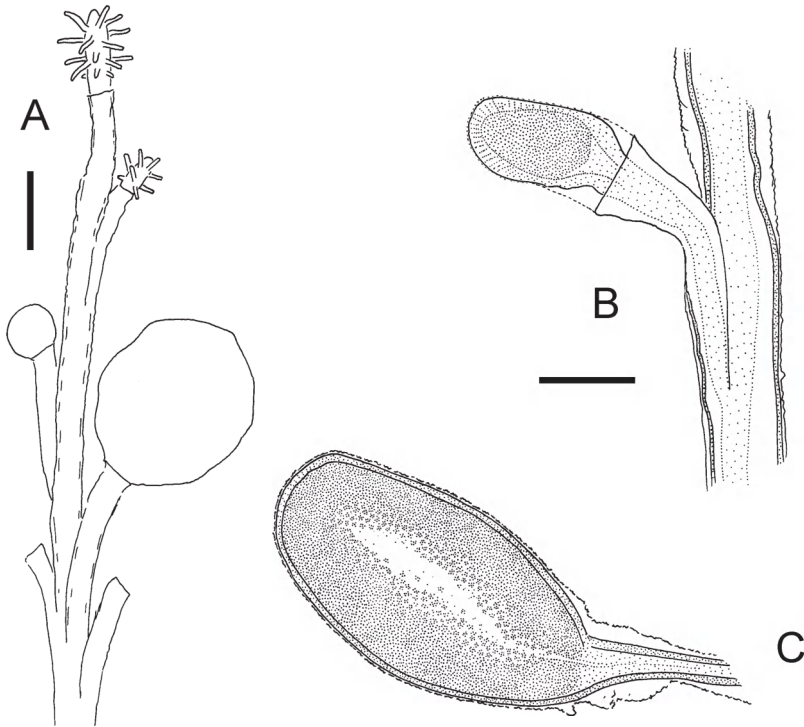
Fig. 7

Corydendrium dispar Kramp, 1935; A, after paratype material; B-C, after preserved material from The Faroes. A) Part of shoot, the putative female sporosacs were empty in this material, scale equals 0.5 mm. B) Branch with young male reproductive structure, optical section, scale bar 0.2 mm. C) Mature male reproductive organ, optical section, same scale as B.

REMARKS – The gonophores of *Merona* arise on blastostyles that can either be interpreted as being derived evolutionary from a hydranth or from a hydranth pedicel. Their simple structure does not lend itself to an easy answer. If the blastostyles are derived from a hydranth body, this would be problematic because in all other Oceanidae the gonophores arise on the pedicels or stolons (see above). The alternative interpretation that the gonozooids are homologous to hydranth pedicels only is much better compatible with the scope of the family as outlined in this publication.

Merona cornucopiae (Norman, 1864)   Fig. 8

Tubiclava cornucopiae Norman, 1864: 82, pl. 9 figs 4-5; Hincks, 1868: 11, pl. 2 fig. 2; Allman, 1872: 258; Fraser, 1937: 23, fig. 4; Fraser, 1944: 36, fig. 4.
Merona cornucopiae – Broch, 1916: 40, pl. 2 fig. 17, fig. L; Rees, 1956: 499, figs 1-3; Cabioch, 1965: 401, figs 1-3; Millard & Bouillon, 1973: 28, fig. 3H-J; Millard, 1975: 74, fig. 25; Medel, Garcia-Gómez & Bouillon, 1993: 515, figs 1-2B; Ramil *et al.*, 1998: 184, fig. 2a-b.

MATERIAL EXAMINED – ZMUC, Denmark, Groves Flak, 25 m, 17 May 1923, on scaphopod, det. Kramp, infertile – ZMUC, Faroe Islands, Skalbünd, 7 Jun 1899, on bivalve shell, much
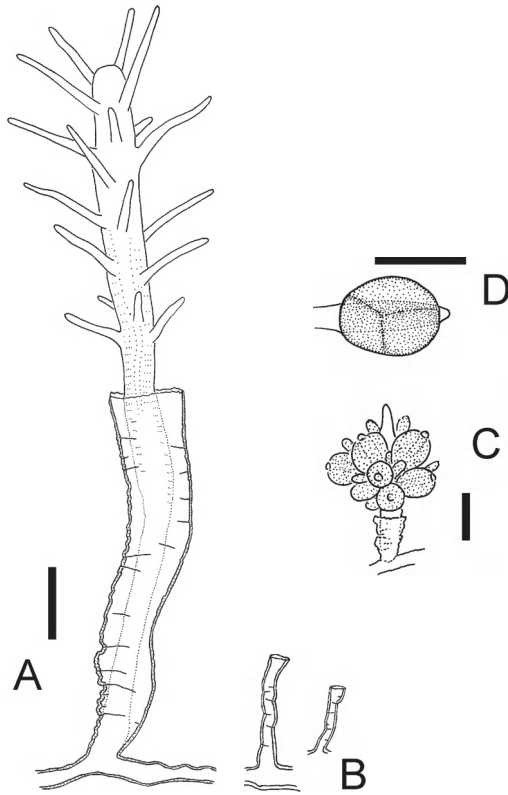
FIG. 8

Merona cornucopiae (Norman, 1864), after preserved material from Roscoff. A) Hydranth, quite expanded, scale equals 0.2 mm. B) Nematothecae on stolons, same scale as A. C) Blastostyle with female gonophores, scale equals 0.2 mm. D) Female gonophore, scale equals 0.1 mm.

damaged, with blastostyles – IRSNB, France, Brittany, Roscoff, numerous colonies on shells of *Turritella* spec. and *Nassarius* spec. inhabited by *Phascolion* spec., not well preserved, one blastostyle seen – BMNH 1956.11.7.1, Brittany, Baie de Morlaix, off. Callot, 22-23 Jun 1955, 15-25 m, on bivalve and *Turritella*, coll. W. J. Rees (material of Rees, 1956), one colony with female gonophores – BMNH 1941.3.20.516, English Channel, Eddystone, 4 Jun 1898, coll. E. T. Browne (material described in Rees, 1956), soft tissues quite damaged, several blastostyles with female gonophores present.

TYPE MATERIAL – The type material of *M. cornucopiae* is kept by the BMNH (Rees, 1956).

DESCRIPTION – (after examined material, and Rees, 1956) Colonies stolonal, never branched, stolons creeping, reticulated or coalesced into mat. Gastrozooids consisting of a perisarc-covered pedicel and a terminal hydranth. Living tissue of hydranth pedicels not well demarcated from hydranth body. Pedicels in wide perisarc tube, the latter 1-5 mm in height, diameter at distal end double or more the basal diameter (0.1-0.14 mm), perisarc thus cone-shaped, often slightly bent or curved, irregularly corrugated, often coated by mud and fine sand grains. Contracted hydranth able to withdraw almost completely into perisarc tube. Relaxed hydranths 1-5 mm,

rod- to slightly spindle shaped, with 16-20 long, filiform, tapering tentacles scattered over distal half or more. Hypostome dome-shaped. High gastrodermal cells in proximal half of hydranth body, apparently vacuolated. Colonies dioecious. Gonophores arise on blastostyles with a short basal perisarc cone as in the hydranths. Gonophores in a dense cluster at distal end of blastostyle. In females, blastostyles with pointed tip that may slightly overtop gonophore cluster, 15-20 gonophores per blastostyle. Gonophore ovoid when mature, length up to 0.2 mm, with distinct stalk, continued through gonophore as spadix, distal part of spadix slightly protruding like nipple, up to six eggs per gonophore. Male blastostyles (after Medel *et al.*, 1993) shorter, gonophores more dense, spherical, spadix perhaps (?) not protruding. Nematophores facultatively present, arising from stolons, about 0.3 mm in height, simple tentacle-like, within thin perisarc tube, the latter at distal end widening funnel-like, tip of nematophore with concentration of large euryteles. Nematocysts (after Cabioch, 1965): large microbasic eurytele (19-22) x (5) μm, discharged shaft about two times as long as capsule; medium sized microbasic eurytele (13-14) x (5) μm, shaft as long as capsule, mainly on tentacles; small microbasic eurytele, (8) x (3) μm, shaft as long as capsule, mainly on tentacles; desmonemes (5) x (3) μm. Colours in life: Hypostome intense white, gastrodermis of hydranth body-orange brown to scarlet, fading in non-tentacular portion into a uniformly pale tint.

BIOLOGY – *Merona cornucopiae* grows predominantly on shells of molluscs such as *Glycimeris*, *Aporrhais*, *Dentalium*, *Turritella* and others, very often on *Turritella* shells inhabited by the sipunculid *Phascolion strombi*. Occurrence is on sediment bottoms in depths of 10-274 m. Fertile specimens were collected at Plymouth in May and June (Rees, 1956), at Roscoff June-July (Teissier, 1965), at Oslofjord end of April (Christiansen, 1972), at Trieste January-February (Graeffe, 1884).

DISTRIBUTION – British Isles (Rees, 1956), Brittany (Rees, 1956; Cabioch, 1965), Faroes (Broch, 1916), Norway (Christiansen, 1972), Spain (Ramil *et al.*, 1998; Medel & López González, 1996), Mediterranean (Graeffe, 1884), north-western Atlantic (Fraser, 1944), north-eastern Pacific (Fraser, 1937), South Africa (Millard, 1975), Seychelles (Millard & Bouillon, 1973). Type locality: Shetland Islands.

REMARKS – Medel *et al.* (1993) described what they considered a sexual dimorphism of the blastostyles of *Merona cornucopiae*. They found that the female blastostyles are longer and they have their gonophores distributed over a larger area, resulting in a less dense arrangement than in males. In the present study, only females were observed and the findings of Medel *et al.* could therefore not be verified. It nevertheless appears that some of the differences are probably only due to different states of contraction and different ages. Rees (1956: figures 1 and 2) shows both types of blastostyles, but both are females (a re-examination of Rees's material confirmed this). The apparent density of the female sporosacs also depends also on how many eggs there are present. A partial spawing results in an apparent reduction of the density of sporosacs, because only the thin spindle-shaped spadices remain of the initially oviform sporosacs.

Merona ibera Medel, Garcia-Gomez & Bouillon, 1993 and *M. cornucopiae* can be distinguished only by their female gonophores. At least for the Mediterranean, it is

therefore not possible to reliably identify *Merona* species without female gonophores. Some of the records of *Merona cornucopiae* from the Mediterranean (e. g. Motz-Kossowska, 1905) are thus perhaps referable to *M. ibera*. Graeffe's (1884, as *Tubiclava cornucopiae*) material from Trieste had four eggs per gonophore. It thus corresponds more with *M. cornucopiae* than with *M. ibera*.

Merona ibera Medel, Garcia-Gomez & Bouillon, 1993

Merona ibera Medel *et al.*, 1993: 513, figs 2C-D & 3A-C.

TYPE MATERIAL – The type material of *M. ibera* is kept by the Museo Nacional de Historia Natural (Madrid) and the RMNH.

DIAGNOSIS – Similar to *Merona cornucopiae*, but female blastostyles smaller and gonophores placed more distally, eggs smaller (37-60 μm), more eggs per gonophore (>12 per gonophore), female gonophore spindle-shaped, distal end of spadix with button of nematocysts.

DISTRIBUTION – Known from type locality only: Algecirras Bay, Strait of Gibraltar, Mediterranean, 21 m, on bivalve *Gouldia minima*.

REMARKS – See under *M. cornucopiae*.

Rhizogeton L. Agassiz, 1862

TYPE SPECIES – *Rhizogeton fusiformis* L. Agassiz, 1862.

DIAGNOSIS – Stolonal hydroid colonies, polyps monomorphic, hydranths either sessile or with a perisarc-covered caulus. Hydranths with scattered filiform tentacles covering at least half of hydranth body. Nematophores absent. Gonophores sessile sporosacs arising from stolons.

REMARKS – Calder (1988a) thought that it might be necessary to split this genus and proposed the new genus *Rhizodendrium*. He held the genus *Rhizodendrium* distinct from *Rhizogeton* on account of the following characters: the hypostome is short and dome-shaped instead of very elongate and conical, it has 20 or more tentacles instead of about 10, its gonophores are more rounded than fusiform. The gonophores of *Rhizodendrium sterreri* Calder, 1988, the type species of the genus *Rhizodendrium*, are so far unknown. The difference in the shape of the gonophores was therefore based on *Rhizogeton nudus* and *R. eozense* Yamada, 1964, which according to Calder (1988a) should be transferred to the genus *Rhizodendrium*. Although the differences in the shape of the gonophore are not so apparent (Dons, 1912), *Rhizogeton fusiformis* appears otherwise to be distinct from *R. nudus* (comp. Fig. 9 and figure 3 in Fraser, 1944). The proposal of Calder (1988a) to separate them into two genera could therefore be justified. If the gonophores of *R. sterreri* are discovered and independent data including DNA sequences show that *Rhizogeton* and *Rhizodendrium* species do not form a monophyletic group, then Calder's proposal should be followed. But because the gonophores of the type species of *Rhizodendrium* are so far unknown, and in order to maintain nomenclatural stability, only the genus *Rhizogeton* is used here.

Rhizogeton nudus Broch, 1909   Fig. 9

Rhizogeton nudum Broch, 1909: 137, fig. 1; Antsulevich & Polteva, 1986: 967, fig. 2; Jones, 1992: 721, fig. 1; Schuchert, 2001a: 20, fig. 10A-C.

Rhizogeton fusiformis – Browne, 1897: 243.
[not *Rhizogeton fusiformis* L. Agassiz, 1862].
Rhizogeton nudus – Dons, 1912: 53, fig. A-C; Calder, 1972: 223, pl. 2 fig. 1.
Rhizodendrium nudum – Calder, 1988a: 11.

MATERIAL EXAMINED – Material from Greenland and Iceland, see Schuchert (2001a).
TYPE MATERIAL – The type material of *R. nudus* could not be located.

DESCRIPTION – Colonies stolonal, stolons creeping, ramified. Hydranths appearing sessile, without distinct pedicel, at base a short beaker of very thin perisarc, usually invisible. Hydranths up to 2-5 mm in height, rod-shaped, with 14-19 tentacles, these scattered in distal half to distal third of hydranth. Tentacles with chordoid gastrodermis, tentacles smooth, tapering, quite long and thin, lengths unequal, proximal ones shorter. Hypostome dome-shaped. High gastrodermal cells in proximal half of hydranth body, apparently vacuolated. Gonophores arising from stolons and developing into sessile sporosacs without canal system or velum but with spadix; with short pedicel enveloped by perisarc, young sporosacs also enveloped by very thin, filmy perisarc. Female sporosacs ovoid to spindle-shaped, diameter 0.35-0.45 mm, length 0.6-0.7 mm, with 3-5 eggs, at maturity the sporosac envelope disappears but eggs and developing embryos stick to the spadix. Male sporosacs oblong ellipsoids, about the same size as female sporosacs. Nematocysts: microbasic euryteles, 7 x 3 μm; desmonemes 5 x 3 μm. Colour in life: pinkish.

VARIATION – Females sporosacs from Britain may contain up to 15 eggs, hydranths are orange (Jones, 1992). According to Dons (1912) the male sporosacs become ovoid with a pointed distal end when fully mature.

BIOLOGY – Grows on a variety of substrates such as mussels, hydroids, bryozoans, and holdfasts of macroalgae. Depth range 0-100 m.

DISTRIBUTION – Greenland (Kramp, 1914; Schuchert, 2001a), Iceland (Schuchert, 2001a), Spitsbergen (Broch, 1909), White Sea (Antsulevich & Polteva, 1986), Norway (Dons, 1912), British Isles (Jones, 1992), north-eastern Canada (Calder, 1972). Type locality: Bismarck Sound, Spitsbergen, 35 m, on *Grammaria abietina*.

REMARKS – In his first description, Broch (1909) used the specific name *nudum*. In a footnote, Dons (1912) mentioned that Broch had asked him through a letter to change this to *nudus* because the gender of *Rhizogeton* is masculine ("geton" is derived from the Greek word γεῖτων for neighbour, which is masculine). Following the rules of the ICZN (ICZN, 1999: § 31.2 and 34.2), the specific epithet must have an ending matching the gender of the genus. The correct name is thus *Rhizogeton nudus* Broch, 1909.

Broch (1909) and Dons (1912) described the hydranths as devoid of a basal perisarc. Careful examination with the help of a compound microscope nevertheless revealed the presence of a fine perisarc in the material examined here.

The development of the sporosacs is well documented by the study of Dons (1912).

The sporosacs depicted by Millard (1975) had no pedicels and were directly attached to the stolons. This material from the tropical Indian Ocean as well as the
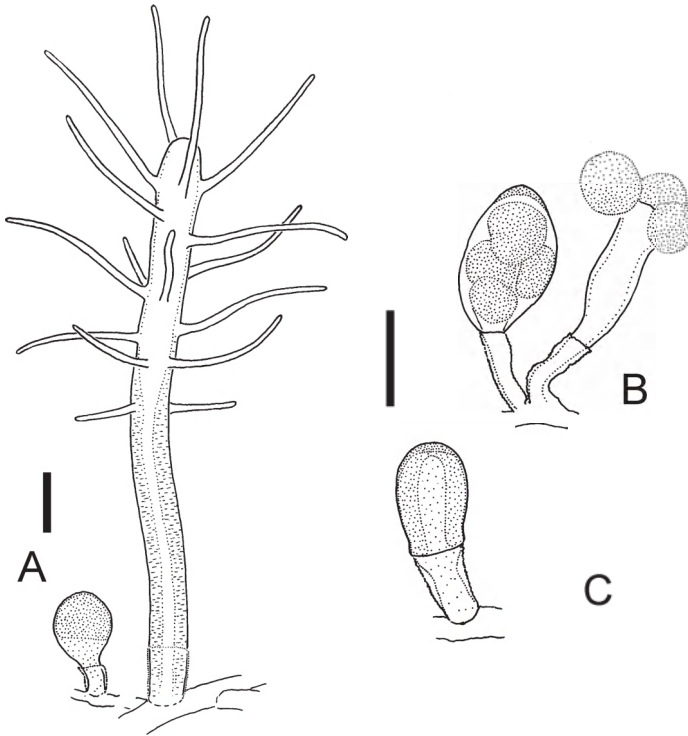
FIG. 9

Rhizogeton nudus Broch, 1909, after preserved material from Iceland (A) and Greenland (B-C). A) Hydranth and presumed gonophore, scale equals 0.3 mm. B) Female sporosacs, right with shed envelope and eggs still sticking to spadix, scale equals 0.5 mm. C) Young male sporosac, same scale as B.

records of Mammen (1963) and Ritchie (1910b) may therefore belong to separate species. Mammen (1963), Rees & Thursfield (1965) and Antsulevich & Polteva (1986) made similar suggestions. The male sporosacs described by Genzano (1993) in material from Argentina likewise lacked a pedicel and may therefore also belong to another species. *Rhizogeton nudus* is probably restricted to arctic and cool-temperate waters of the North Atlantic.

Park (1997) suggested that *R. fusiformis* L. Agassiz, 1862 and *R. nudus* are conspecific. Although Dons (1912) kept both species apart, he found that there is little difference in the morphology of the gonophores. Calder (1988a) re-examined the type material of *R. fusiformis* and he confirmed that this species has a pointed hypostome and only about 10 tentacles. The differences even prompted Calder (1988a) to place the two species in different genera (see remarks under genus *Rhizogeton*). I therefore think that *R. fusiformis* and *R. nudus* of the north-west Atlantic should be kept distinct.

In his report on hydroids of Valencia Harbour (western Ireland), Browne (1897) also described material which he attributed to *R. fusiformis* L. Agassiz, 1862, although he noted marked differences to Agassiz's description. The most critical difference was

the number of tentacles, which was around 20 and not 10-12. The data given by Browne (1897) closely match *R. nudus* as described above and it is very likely that his specimens belonged to this species. This interpretation is supported by the finding of *R. nudus* in the Morecambe Bay (Irish Sea, England; Jones, 1992).

Cordylophora Allman, 1844

TYPE SPECIES – *Cordylophora lacustris* Allman, 1844 by monotypy.

DIAGNOSIS – Erect, branching hydroid colonies, side-branches and hydranth pedicels not adnate, perisarc tubes not nested. Relaxed hydranths spindle-shaped, hypostome well delimited from hydranth body, filiform tentacles scattered in distal half of hydranth body. Gonophores oblong, borne on pedicels of hydranths and on branches, sessile sporosacs with branched spadix.

REMARKS – *Cordylophora* resembles somewhat to the genus *Pachycordyle* and could as well belong to the Pachycordylidae (comp. Morri, 1980; Stepanjants *et al.*, 2000). Unfortunately, there are no convincing synapomorphies that would link it unambiguously to either the Oceanidae or the Pachycordylidae. Mainly for historic reasons, it is here kept in the Oceanidae. It shares with this family the tentacles that are scattered over much of the hydranth body, while in the Pachycordylidae they are concentrated in the distal part.

Cordylophora caspia (Pallas, 1771)   Fig. 10

Tubularia caspia Pallas, 1771: 479.
Tubularia cornea Agardh, 1816: 258.
Cordylophora lacustris Allman, 1844: 330; Allman, 1853: 367, pls 25-26; Schulze, 1871: 1-52,
    pls 1-6; Hincks, 1868: 16, pl. 3 fig. 2; Allman, 1872: 252, pl. 3; Nutting, 1901: 327, fig.
    2; Roch, 1924a: 350, footnote 1.
Cordylophora albicola Kirchenpauer, in Busk, 1861: 284, pl. 9 figs 12-14; Allman, 1872: 254.
Cordylophora lacustris var. *otagoensis* Fyfe, 1929: 813, figs 2-10.
Cordylophora americana Leidy, 1870: 113.
Cordylophora whiteleggi von Lendenfeld, 1886: 97, pl. 6 figs 11-12.
Cordylophora lacustris otagoensis – Ralph, 1953: 64 fig. 6.
Cordylophora caspia – Vervoort, 1946: 119, fig. 47b & 48a (not others); Naumov, 1969: 196, fig.
    66; Rossi, 1971: 20, fig. 6I; Morri, 1980: 155, figs 1-3; Morri, 1981: 45, fig. 13, pl. 1 fig.
    3, pl. 2 fig. 3; Morri & Boero, 1986: 34, figs 14-15a-b; Barnes, 1994: 60, fig; Holstein,
    1995: 95 figs 49-50; Schuchert, 1996: 15, fig. 3a-e.

MATERIAL EXAMINED – MHNG INVE 34179, Rostock, Germany, Baltic Sea (not well preserved,
    no hydranths left) – ZMUC, Randers Fjord, Mellerup, Denmark, 1.5 m, 25.05.1916 –
    ZSM, as *C. lacustris*, Elbe estuary, Germany, fertile – ZSM, as *C. lacustris*, Brunsbüttel,
    Germany, fertile – ZSM, as *C. lacustris*, Woltersdorf near Berlin, Germany, fertile,
    3.08.1920 – ZSM, as *C. lacustris*, Heringsdorf, Germany, fertile – ZSM, as *C. lacustris*,
    Greifswald, Germany, June 1902 – New Zealand, see Schuchert (1996).
TYPE MATERIAL – There presumably exists no type material of *C. caspia*.

DESCRIPTION – Erect, branching hydroid colonies, stems up to 3 cm high (reportedly up to 10 cm), arising from reticulate stolons. Occasional autoepizooism possible. Erect shoots with monopodial growth, branching several times irregularly at various angles, ending in up to 40 hydranths. Shoots often composed of a long main stem and shorter side branches, branches not adnate, stem diameter about 0.2 mm.
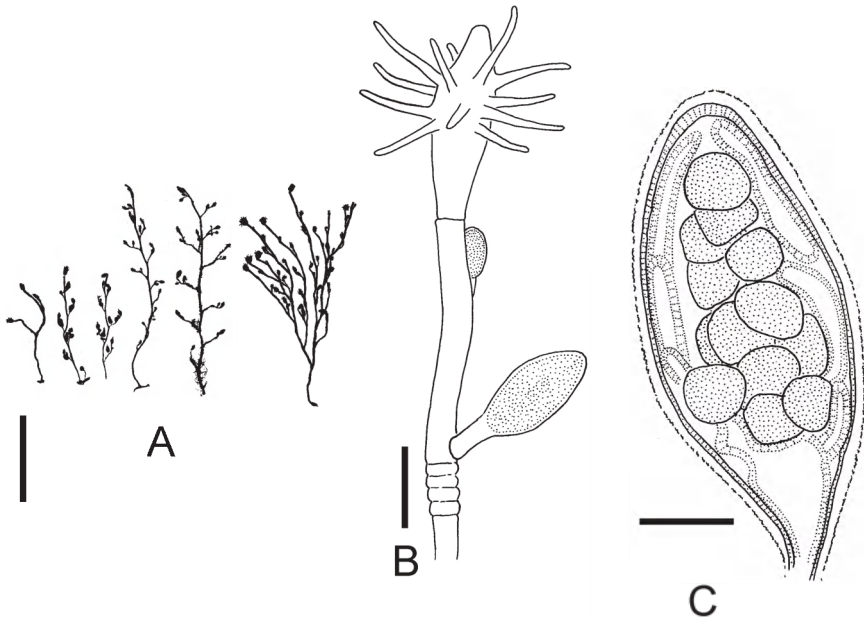
FIG. 10

Cordylophora caspia (Pallas, 1771), A samples from Germany, B-C from Denmark. A) Colony silhouettes demonstrating variability, scale equals 5 mm. B) Hydranth with two gonophores on its pedicel, scale equals 0.2 mm. C) Schematic optical section of a mature female gonophore, eggs are shown stippled and surrounded by solid line, note branched spadix, scale equals 0.2 mm.

Colonies living under unfavourable conditions remain stolonal with hydranths on a simple perisarc covered pedicel. Perisarc smooth with occasional annulated stretches, perisarc ends below hydranths. Relaxed hydranths spindle-shaped, contracted ones ovoid, 1-2 mm high, size variable even within a single shoot, with prominent hypostome, the latter bullet-shaped to conical. Scattered filiform tentacles, usually around 14-16 (up to 27 possible), proximal third of hydranth body free of tentacles. Tentacles of varying length (up to 1.4 mm), tapering slightly to 3/4 of basal diameter, gastrodermis composed of chordoid cells. Colours: hydranths white or pale pink, perisarc brown. Nematocysts: microbasic euryteles and desmonemes. Colonies dioecious. Gonophores ellipsoid, arising at pedicels of hydranths, branches and stems, covered with perisarc, mature about 0.7-1 mm long, diameter about half the length. Initially with a branched spadix, reduced in later development, gametes released through distal hole. Females with 7-16 eggs (fewer also possible), 0.07-0.12 mm in diameter, developing to planulae in situ.

OCCURRENCE – Circumglobal in temperate and subtropical regions, usually in brackish waters as in estuaries, river deltas and lagoons. Absent from fully marine environments. Sometimes penetrating into completely fresh water, but there usually a reduced development. When occurring in inland rivers and lakes, these water bodies

are generally characterized by elevated concentrations of some ions (Arndt, 1984). However, it has recently also been found that *C. caspia* can successfully invade pure freshwater biotopes (Smith *et al.*, 2002). Depth range 0-85 m (Naumov, 1969), usually in very low waters, on rock, under stones, on *Dreissena* spec. (Bivalvia). Type locality: Caspian Sea.

REMARKS ON VARIATION, MORPHOLOGY AND ECOLOGY – There is a vast body of literature on this species and it is impossible to review it here completely. Only the most important works are therefore mentioned. The morphology was studied in detail by Allman (1853), Schulz (1871), and Weismann (1883). The embryology was examined by Van de Vyver (1967). Roch (1924a, 1924b) reviewed all records of this species and examined the influence of chemical and physical parameters on the morphology. These studies were later extended by Kinne (1956, 1957) and Arndt (1984). The morphology of the colony and the hydranths correlates strongly with salinity. Near fresh-water conditions causes low colonies and stolonization, low salinities produce spherical hydranths with short, stubby tentacles, while in water with high salinity hydranths are elongated and their tentacles long and thin. A salinity of 16.7 ‰ at 20 ° and 10 ‰ at 10 °C was found to be optimal for growth in the population examined by Kinne (1957, North Sea to Baltic Sea Channel). Arndt (1984) found a salinity optimum of 6-10 ‰ for populations of the Baltic and Arabian Sea. Sexual reproduction started when water temperatures rose above 10 °C. The temperature optimum was 11-18 °C. Smith *et al.* (2002) found the species in fresh-water and demonstrated that it has successfully invaded this biotope by adjusting its physiology and ecological needs. *Cordylophora caspia* is able to survive long periods without food. This is especially pronounced in fresh water, where it has lived without feeding up to six months (Kinne, 1956). Bouillon (1963) found that this species can be either larviparous or viviparous. For more references see also Holstein (1995), Folino (2000), and Smith *et al.* (2002).

TAXONOMIC REMARKS – Although the original description of *Tubularia caspia* by Pallas (1771) is too vague to allow an unambiguous recognition, most contemporary authors have followed Roch (1924b) in considering it a senior synonym of *C. lacustris* Allman, 1844. Stepanjants *et al.* (2000) disagree, however, without providing arguments. A good review, and remarks on the taxonomic status, can be found in Folino (2000), who also considers the possibility that more than one species might be included in the present concept of *C. caspia*. It is certainly possible that C. *caspia* and *C. lacustris* – the latter referring to populations confined to nearly or fully freshwater conditions – are morphologically inseparable, but nevertheless represent two separate biological species. Genetic methods must be used to clarify the status of the various *Cordylophora* ecomorphs.

Vervoort (1964) examined type material of *Bimeria* (?) *baltica* Stechow, 1923 and found it indistinguishable from *C. caspia*.

PACHYCORDYLIDAE Cockerell, 1911
SYNONYM – Clavopsellidae Thiel, 1962.

DIAGNOSIS – Anthoathecata Filifera, polyp phase forming stolonal or branching colonies, hydranths pedicellate, perisarc terminating at base of hydranth, without

pseudohydrotheca. Hydranths club-shaped, spindle-shaped, or amphora-shaped; hypostome nipple- to dome-shaped. Tentacles in two or more whorls restricted to a narrow band below hypostome, spreading over less than one third of the hydranth body only. Gonophores arising on stems or pedicels. Gonophores free medusae, medusoids that can be liberated, or fixed sporosacs. Medusae at liberation with four simple or branched oral tentacles arising above mouth, four tentacle bulbs with one tentacle each, ocelli present.

REMARKS – The family Pachycordylidae comprises the genera *Pachycordyle* and *Silhouetta*. Thiel (1962) proposed the new family Clavopsellidae comprising the genera *Clavopsella*, a synonym of *Pachycordyle*, and *Balella* Stechow, 1919. The latter genus has hydranths with two widely separated whorls of tentacles and it produces gonophores on gonozooids. Schuchert (2003b) argued that *Balella* has closer affinities with the Hydractiniidae and must be placed into a family of its own (Tubidendridae, although the valid name is Balellidae, see Calder 1988a: 13). Thiel was probably unaware that there was already a family group name available that included *Pachycordyle*, namely Pachycordylini Cockerell, 1911. Calder (1988a) raised it to subfamily level as Pachycordylinae and he provided arguments why it must be preferred over Clavopsellidae and why *Silhouetta* should be included in the group. Here, the taxon Pachycordylinae is raised to family level, becoming thus Pachycordylidae. I think this is necessary because *Pachycordyle* is so intermediate between Oceanidae and Bougainvilliidae that it threatens the scope of both families.

The affinities of *Pachycordyle*, or its synonyms *Clavopsella* and *Thieliana*, are disputed even by contemporary authors. Some authors, including Millard (1975), Bouillon (1985), and Calder (1988a), place *Pachycordyle* in the Bougainvilliidae, while Morri (1980) and Stepanjants *et al.* (2000) firmly associate it with *Cordylophora* and the Clavidae sensu Bouillon (1985). To the present author its affinities with the Bougainvilliidae appear to be more evident. *Pachycordyle navis* and *Pachycordyle pusilla* sometimes approach the bougainvilliid species *Aselomaris michaeli* Berrill, 1948 so much, that they could be easily confused. Also, the hydranths of the genera *Parawrightia* Warren, 1907, *Velkovrhia* Matjašič & Sket, 1971 or *Pruvotella* Motz-Kossowska, 1905 are intermediate between *Pachycordyle* and *Bougainvillia*. All of them have two or more whorls of tentacles. Even *Bougainvillia muscus* (Allman, 1863), certainly a typical representative of the Bougainvilliidae, may have two whorls of tentacles, although quite closely approximated (own observations on living Mediterranean material). But most importantly, *Silhouetta uvocarpa* Millard & Bouillon, 1973 has a trophosome identical to that of *Pachycordyle*, but it produces medusae with branched oral tentacles. This definitely indicates a closer relationship to the Bougainvilliidae. The occurrence of nematocysts on the eggs of *Pachycordyle navis* (see Thiel, 1962, as *Clavopsella quadranularia*) and in many other bougainvilliids as well (Russell, 1953 for *B. macloviana*; Szollosi, 1969 for *B. multitentaculata*; Calder, 1971 for *B. rugosa*; Piraino, 1992 for *A. michaeli*; Calder 1993 for *B. abberans*; Schuchert, 1996 for several species) could be interpreted as a synapomorphy. However, the distribution of such "stinging eggs" (Piraino, 1992) among the Filifera is too insufficiently known to draw a well supported conclusion. The few Oceanidae examined for this study apparently lack a conspicuous nematocyst layer on their egg surface.

Contrary to the view of Calder (1988a), the genus *Millardiana* is not included in the Pachycordylidae because it develops gonophores on the hydranth body (see under family Oceanidae, discussion relating to *Tubiclava*).

The genus *Silhouetta* is thus far not known to occur in the region under investigation, but Cornelius (1992) recorded *Silhouetta uvocarpa* Millard & Bouillon, 1973 from the nearby Azores. Considering its wide occurrence, ranging from the Seychelles to the western tropical Atlantic (Calder, 1988a), it might also occur along the coasts of southern Portugal or Spain.

Pachycordyle Weismann, 1883

SYNONYMS – *Clavopsella* Stechow, 1919; *Thieliana* Stepanjants *et al.*, 2000.
TYPE SPECIES – *Pachycordyle napolitana* Weismann, 1883 by monotypy.

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 close whorls. Gonophores borne on stems or pedicels. Gonophores fixed sporosacs or degenerated pyriform medusae lacking mouth, marginal tentacles, oral tentacles, radial canals, or ocelli.

REMARKS – *Clavopsella* Stechow, 1919 is clearly a junior synonym of *Pachycordyle* Weismann, 1883 (Calder, 1988a; Stepanjants *et al.*, 2000). The definition of *Pachycordyle* adopted in this work follows that used by Thiel (1962) and Millard (1975) for *Clavopsella*. This definition also includes *Pachycordyle navis* and other similar species. Calder (1988a) did not agree with this and considered *P. navis* as belonging to the subfamily Bougainvilliinae rather than the Pachycordylinae and he referred *Pachycordyle navis* to the genus *Aselomaris* Berrill, 1948. Stepanjants *et al.* (2000) again placed *P. navis* in the same subfamily as *Pachycordyle napolitana*, but in the new genus *Thieliana*. *Thieliana* differs from *Pachycordyle* only in the degree of reduction of its gonophores. While *Pachycordyle* sensu Stepanjants *et al.* (2000) has either radial canals or a circular canal, they are absent in *Thieliana*. In the remarks relating to *Pachycordyle napolitana*, I will show that there is probably no real circular canal present in this species. The radial canals of *Pachycordyle kubotai* Stepanjants *et al.*, 2000 are additionally somewhat unusual in that they are not between layers of epidermis. Perhaps they are better homologized with a branched spadix. Generic distinction based on the degree of gonophore reduction have been shown to lead to artificial taxa in many cases (e. g. Petersen 1990, Bouillon *et al.* 1997, Boero *et al.* 1998, Schuchert 2001b). The degree of gonophore reduction, notably if it is only so slight as in the case for *Thieliana*, should therefore not be used to distinguish genera if this trait does not concord with other, independent characters. *Thieliana* is here thus treated as a synonym of *Pachycordyle*.

Kramp (1959, 1968) allocated a number of degenerate medusae to *Pachycordyle*. Kramp himself considered these medusae as possibly belonging to very different taxa and they are placed only temporarily in *Pachycordyle* pending forthcoming information on their polyp phase.

In the region under investigation, there are three known species referable to the genus *Pachycordyle*: *P. napolitana*, *P. navis*, and *P. pusilla*. Piraino (1992) reported

Clavopsella michaeli (Berrill, 1948) from the Mediterranean. This species has a single whorl of tentacles and is here seen as belonging to the Bougainvilliidae. It should therefore not be included in the genus *Clavopsella*, or its senior synonym *Pachycordyle*.

Pachycordyle napolitana Weismann, 1883   Fig. 11

Pachycordyle napolitana Weismann, 1883: 87; Neppi, 1921: 5, fig. 1; Calder, 1988a: 15, figs
        11-12.
Cordylophora annulata Motz-Kossowska, 1905: 66, fig. 5; Stechow, 1923: 56.
Perigonimus neapolitanus – Motz-Kossowska, 1905: 75, fig. 8 [incorrect subsequent spelling].
[not *Perigonimus napolitanus* Hargitt, 1904 = *Leuckartiara octona* (Fleming, 1823)].
Pachycordyle weismanni Hargitt, 1904: 553, pl. 21 figs 1-8; Kramp, 1959: 94; Kramp, 1961: 52.
Tubiclava annulata – Stechow, 1912: 343, pl. 13 fig. 8.
? *Tubiclava fruticosa* – Neppi, 1917: 47, fig. 9.
Clavopsella weismanni – Stechow, 1923: 55.
Clavopsella annulata – Wedler & Larson, 1986: 86, fig. 8Aa-f, 9.
? not *Cordylophora neapolitana* – Morri, 1980: 159, figs 4-5; Morri & Boero, 1986: 34, fig. 15c;
        Morri, 1981: 47, fig. 14, pl. 1 fig. 4 [incorrect subsequent spelling].

MATERIAL EXAMINED – IRSNB, Italy, Naples, young female colony collected by J. Bouillon, June
        1962 – ZSM, Stechow collection, as *Clavopsella weismanni* several colonies from
        Naples collected 1897-1904 as alcohol preparation and slide material, includes male and
        female colonies, gonophores of variable developmental stages, all colonies on *Fusinus
        rostratus*.
TYPE MATERIAL – There presumably exists no type material of *P. napolitana*.

DESCRIPTION – Colony stolonal, or rarely pedicels branched once. Pedicels of very varied length (1-15 mm, usually below 5 mm), usually widening distally, bearing a terminal hydranth. Perisarc moderately thin, irregularly corrugated throughout, not distinctly double-layered, terminating at base of hydranth, not forming pseudohydrotheca. Hydranths club-shaped, 1-2 mm long, diameter about 0.3 mm if expanded, when contracted much thicker, in distal third 12-24 tentacles, in larger hydranths distinctly scattered in a broad band (3 whorls), in smaller hydranths more concentrated into a narrow band and almost appearing as one whorl only, proximal tentacles often smaller than distal ones, contracted tentacles filiform, well expanded tentacles moniliform. Hypostome dome- to nipple-shaped. Gonophores arise from hydranth pedicels at some distance below hydranth, 1-3 per pedicel, on short stalk, completely infested with soft, wrinkled, detritus-covered perisarc, shape ovoid, length up to 1.6 mm, diameter 0.8-1 mm. Mature gonophore medusoid, with a distinct subumbrella and a short collar projecting into subumbrella resembling a velum (Fig. 11I). Radial canals absent, circular canal presumably absent. Vestigial manubrium simple, large. Below manubrium a bubble-like gastrodermal chamber (Fig. 11G-I). Gonads encircling manubrium in a thick layer so that it is completely covered. Females with 100-150 eggs, oocytes with relatively large pronucleus, eggs shed and developing free in the water. Egg size about 0.07 mm. Immature male gonophores resembling sporosacs, manubrium large and with pointed diverticulae, mature male sporosacs also medusoid and identical to female ones.

FURTHER DATA – Shoots may have up to three hydranths (Weismann, 1883). Hydranth body orange or reddish, hypostome whitish (Hargitt, 1904). Nematocysts are microbasic euryteles and desmonemes (Calder, 1988a).
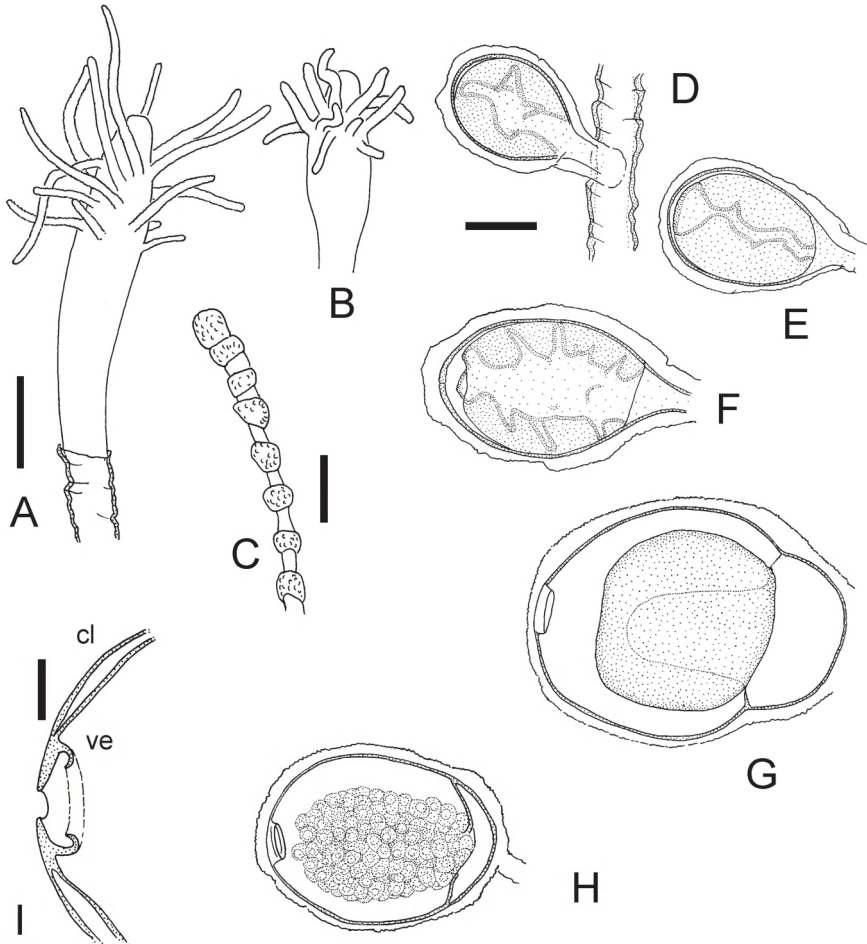
Fɪɢ. 11. *Pachycordyle napolitana* Weismann, 1883, after preserved material from Naples. A) Hydranth with somewhat contracted tentacles, scale equals 0.4 mm. B) Hydranth, note that tentacles are less scattered than in specimen shown in A, same scale as A. C) Tip of a fully expanded tentacle, note moniliform arrangement of nematocyst clusters, scale equals 50 μm. D-F) Successive developmental stages of a male gonophore, note branched spadix (manubrium), scale equals 0.3 mm. G) Fully mature male medusoid, it is still enveloped by perisarc film, same scale as D. H) Mature female medusoid, note that there is no more tissue connection to the polyp stage, but the medusoid is still within the perisarc envelope, same scale as D. G) Higher magnification of the distal opening of the female medusoid, ve = velum-like collar, cl = cleft, a possible fixation artefact and likely not a circular canal, scale equals 0.1 mm.

Bɪᴏʟᴏɢʏ – Reliable identifications are from fully marine conditions only. Colonies usually grow on gastropod shells (*Fusinus rostratus*, *Murex* spec.), either inhabited by mollusc or hermit crabs, mostly on muddy bottoms; known to occur in depths from a few metres to perhaps 40 m; mature from spring to October. Boero & Fresi (1986) also found it growing on algae and *Eudendrium* spec. (fully marine conditions).

DISTRIBUTION – Western Mediterranean (Weismann, 1883; Hargitt, 1904; Motz-Kossowska, 1905; Lo Bianco, 1909; Stechow, 1919; Neppi, 1921; Stechow, 1923; Boero & Fresi, 1986), Adriatic Sea (Stechow, 1912), Bermuda (Calder, 1988a), Puerto Rico (Wedler & Larson, 1986). Type locality: Mediterranean, Naples, 40 m, on empty *Murex* shell.

REMARKS – Weismann (1883) described *P. napolitana* only summarily, as he was more interested in its histology and in the development of the gonophores. The gonophores he described were male, appeared like sessile sporosacs, and had a characteristic, branched spadix. Hargitt (1904), also studying material from Naples, found similar colonies which were all female. Although he noted the close resemblance to *P. napolitana*, he assigned his material to a separate species and named it *P. weismanni*, based mainly on the medusoid gonophores he observed. Shortly afterwards, Motz-Kossowska (1905) published her findings of athecate hydroids from the western Mediterranean. Motz-Kossowska, most probably unaware of Hargitt's publication, also described a new species with several whorls of filiform tentacles and female medusoid gonophores and named it *Cordylophora annulata*. A similar, male colony with sporosacs identical to Weismann's material was allocated by her to *P. napolitanus* under the name *Perigonimus neapolitanus* (Weism.) (not to be confounded with *P. neapolitanus* Hargitt, 1904, presumably a synonym of *Leuckartiara octona*). Mayer (1910) concluded that *P. napolitana* and *P. weismanni* belonged to the same species and that the differences of the two nominal species were attributable only to differences of the sex. Neppi (1921) put forward the same thoughts and substantiated this by observations. She demonstrated that the male gonophores of *P. napolitana* are also medusoid and have intermediate developmental stages resembling those described by Weismann. Stechow (1923) vehemently rejected the idea of Mayer and insisted that *P. napolitana* and *P. weismanni* are separate species. Additionally, he also kept *C. annulata* distict from *P. weismanni*, although without giving arguments. A re-examination of Stechow's material, today kept by the ZSM, makes it difficult to understand Stechow's opinion, as the material clearly shows several developmental stages of male gonophores (Fig. 11D-G). It is especially important to note the development of the spadix, which initially has very characteristic lateral diverticulae, resembling a branched spadix (Fig. 11F). Such a spadix was also described by Weismann (1883). There can thus be no doubt that *C. napolitana* and *P. weismanni* are conspecific, although they were initially recorded on different gastropod shells (*Murex* spec. versus *Fusinus rostratus*). Thiel (1962) continued to use *P. weismanni*, and he kept *P. annulata* Motz-Kossowska, 1905 separate on account of the absence of a circular canal and the different branching degree, although Motz-Kossowska did not explicitly mention the absence of such a ring canal. Hargitt (1904) made histological sections of the medusoids and found a cleft-like space encircling the bell opening which he interpreted as a circular canal, although it lacked an epithelial lining. In the slide material made by Stechow, a similar cleft can be seen (Fig. 11I), but it is very likely that it is only a fixation artifact as in Hargitt's material. Thus, *Pachycordyle napolitana* very likely has no real circular canal.

Pachycordyle napolitana has usually been reported growing on gastropod shells in waters of normal salinity, both in the Mediterranean and elsewhere (Wedler &

Larson, 1986, as *C. annulata*; Calder, 1988a). Boero & Fresi (1986) recorded it also on algae and *Eudendrium* spp., also in a fully marine environment. Morri (1980, 1981) reported *P. napolitana* on seagrasses growing in brackish waters. It seems, however, that medusoid gonophores were never observed in these animals (see comment in Morri, 1980: 163). Because this is an essential character in distinguishing them from other similar species, like *P. navis* (Millard, 1959) (see Stepanjants *et al.*, 2000), I think that the identity of Morri's material is not reliably established and needs confirmation. The difference of biotopes – fully marine versus reduced salinity and different substrata – are also arguments for two different species being involved. *Pachycordyle navis* is quite similar and is well known to occur in brackish waters.

As already noted by Stechow (1923), the tentacles in fully grown hydranths of *P. napolitana* are clearly arranged in several whorls, but this may not be the case in smaller or younger hydranths. In preserved and contracted material it can also be quite difficult to recognize more than one tentacle whorl.

Hargitt (1904) observed in aquarium cultures that the mature gonophores are released as free medusoids. As noted by Stechow (1923), this may not necessarily be the case under natural conditions, and some gonophores may spawn even while still attached to the hydranth.

Pachycordyle navis (Millard, 1959) **comb. n.**   Fig. 12

Rhizorhagium navis Millard, 1959: 244, fig. 2.
Clavopsella quadranularia Thiel 1962: 228, figs 1-28; Schönborn *et al.*, 1993: 217, pl. 2 fig 3.
Corydendrium dispar – Rasmussen, 1973: 22.
[not *Corydendrium dispar* Kramp, 1935].
Clavopsella navis – Millard, 1975: 100, fig. 3A-D.
? *Cordylophora neapolitana* – Morri, 1980: 159, figs 4-5; Morri & Boero, 1986: 34, fig. 15c; Morri, 1981: 47, fig. 14, pl. 1 fig. 4.
[not *Pachycordyle napolitana* Weismann, 1883].
Cordylophora inkermanica Marfenin, 1983: 1732, fig'd; Stepanjants *et al.* 2000: 226.
Thieliana navis – Faasse & Vervoort, 2001: 181, figs 1-3.

TYPE MATERIAL EXAMINED – Type of *Clavopsella quadranularia* Thiel, 1962, Zoological Museum Hamburg, registration number C7434, loc. Kiel, Aussenhafen, Holtenauer Schleuse. The type material of *P. navis* is kept by the South African Museum in Capetown, but was not examined during this study.

OTHER MATERIAL EXAMINED – Material described by Rasmussen (1973) as *Corydendrium dispar*; Denmark, Isefjord, on *Mytilus* in the strong currents of the intake of the power station Kyndbyvaerket, fertile female, material kept by "The Isefjord Laboratory" at Vellerup Vig (University of Roskild, Denmark), part of this material also deposited as MHNG INVE 34226.

DESCRIPTION – (After Thiel, 1962 and examined material) Colony stolonal or variably branched, height 7-30 mm, 1-30 hydranths per shoot. Stolons ramified, initially creeping on substrate, in larger colonies detached and forming tangled masses, sometimes also growing along stems of older shoots. Pedicels and stems covered by perisarc, terminating below hydranth. Perisarc mostly smooth, some annulated stretched in European colonies. Perisarc often double-layered, inner layer may be annulated while outer layer is smooth (Fig. 12C). Pedicel length variable but relatively long, diameter 0.1-0.15 mm. Hydranth body 1.0-1.8 mm high (1.4 mm mean), diameter about 0.35 mm, spindle-shaped. Hypostome high, dome-shaped. Tentacles 12-24, in a
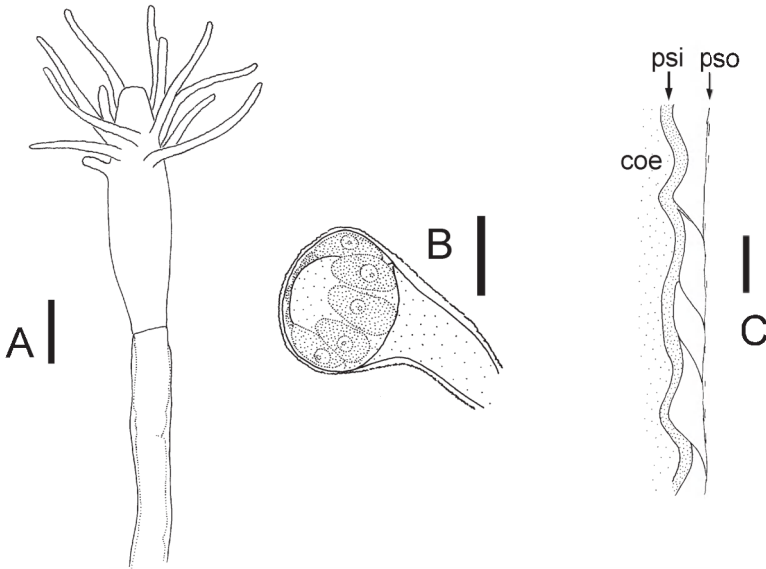
FIG. 12

Pachycordyle navis (Millard, 1959), A-B, after type material of *Clavopsella quadranularia*; C, after material from Denmark. A) Hydranth with part of pedicel, scale equals 0.2 mm. B) Female sporosac, scale equals 0.2 mm. C) Higher magnification of double-layered perisarc, coe = coenosarc, psi = inner perisarc layer, pso = outer perisarc layer, note the thin lamellae connecting both layers, scale equals 50 μm.

narrow band below hypostome, 2-4 closely approximated alternating whorls. Gonophores about 0.4 mm, borne in irregular spiral on stem or hydranth pedicels. Gonophores with relatively long pedicel, completely sheathed in perisarc. Gonophores fixed sporosacs (heteromedusoids) with distinct spadix, lacking tentacle rudiments, radial canals, circular canal, or velum. Colonies dioecious. Male sporosacs spherical to spindle-shaped. Female sporosacs club-shaped, distal end obtuse, containing a very variable number of eggs, 5-20, if up to 12 eggs then these in one tier, but arrangement can also be irregular, eggs about 0.1 mm in diameter, covered with a few nematocysts only. Eggs develop into planulae in situ. Nematocysts: microbasic euryteles, desmonemes. Colour: perisarc clear to brown, coenosarc white to reddish, hydranths red (depends on food).

BIOLOGY – Euryhaline. European colonies known from brackish waters only, the minimal salt concentration is perhaps 8 ‰; experimental cultures in seawater of normal salinity kept well over long time (Thiel, 1962). The South African colony was growing on a ship hull that had never left South Africa. Grows on algae, wood, iron constructs, *Mytilus*, and other solid substrata. Thiel (1962) observed two periods of reproductive activity: in spring and late summer to autumn.

DISTRIBUTION – South Africa (Millard, 1975), Baltic Sea (Thiel, 1962, as *C. quadranularia*), southern England (Barnes, 1994), The Netherlands (Faasse & Vervoort, 2001), Denmark (this study), Black Sea (Marfenin, 1983, as *Cordylophora inkermanica*). Type locality: Table Bay, South Africa, on hull of ship.

REMARKS – This species was initially described as *Rhizorhagium navis* Millard, 1959. Later Millard (1975) placed it in the genus *Clavopsella*. Because *Pachycordyle* Weismann, 1883 has priority over *Clavopsella* Stechow, 1919, this species is here referred to the former genus as *Pachycordyle navis* (Millard, 1959) new comb.

Millard (1975) reported that she had compared material of *P. navis* with Thiel's *Clavopsella quadranularia* and both authors agreed that they were very likely conspecific.

As put forward by Stepanjants *et al.* (2000), *Cordylophora inkermanica* Marfenin, 1983 appears indistinguishable from *P. navis* and it is here regarded as a synonym of the latter.

Material identified by Rasmussen (1973) as *Corydendrium dispar* was re-examined during this study. Although not well preserved, it is obviously referrable to *P. navis*. Some preserved hydranths have the typical tentacle arrangement of this species. The side branches arise at acute angles, but remain not adnate as in *C. dispar*. Also, the well preserved female sporosacs were rather typical. The double-layered perisarc seen in both *C. dispar* and *P. navis* may have mislead Rasmussen to identify his material as *C. dispar*.

Pachycordyle navis resembles *P. pusilla* Motz-Kossowska, 1905, but the latter is smaller, is stolonal, has fewer eggs per sporosac, and has a funnel-shaped perisarc dilation at the distal end of the pedicel. Furthermore, their ecology is different, with *P. pusilla* occuring only on sea-grasses in fully marine environments. European records of *P. navis* are all from sites with reduced salinities. There is an interesting similarity in the structure of their perisarc (comp. figs. 12C and 13D). The perisarc is often doubled with a thicker, corrugated inner layer and a thin outer layer. Both layers are connected by thin lamellae. In *P. pusilla*, this double layered-structure is confined to the distal part of the pedicels.

Pachycordyle pusilla (Motz-Kossowska, 1905) **comb. n.**   Figs 13 & 14

Cordylophora pusilla Motz-Kossowska, 1905: 63, fig. 4, pl. 3 fig. 3-9; Morri, 1980: 164, fig. 6; Boero, 1981: 188, fig. 2; Schuchert 2003a: 540, fig'd.
? *Pachycordyle fusca* Müller, 1913: 357, figs 3-7, figs 14-23.
Tubiclava pusilla – Stechow, 1919: 10; Leloup, 1930: 24, figs 1-3.
Merona pusilla – Picard, 1951: 349.

TYPE MATERIAL EXAMINED – ZSM, syntype material of *Pachycordyle fusca*, Stechow collection, one slide labelled as "*Clavopsella (Pachycordyle) fusca* (H. G. Müller) Neapel Cotypus !!" (cotypus in red ink), 2 hydranths with young gonophores (stage 1 acc. Müller, 1913: 399), gastrodermal zooxanthellae clearly visible. The type material of *P. pusilla* could not be located.

OTHER MATERIAL EXAMINED – IRSNB, Mediterranean, Monaco, coll. E. Leloup 1929, on *Posidonia oceanica* (material of Leloup, 1930) – IRSNB, Mediterranean, Villefranche-sur-Mer, coll. E. Leloup 24 Mar 1934, depth 15 m, on *Posidonia oceanica* – ZSM, Naples, as *Clavopsella fusca*, coll. Bedot no. 186, on *Cymodocea nodosa*, with young gonophores – ZSM, as *Clavopsella fusca*, Naples, coll. Splettstösser, fertile females – MHNG INVE 32953, Banylus-sur-Mer, on *Posidonia oceanica*, 10 May 2002, examined alive, fertile female.

DESCRIPTION – Colony stolonal or rarely branched once, stolons creeping, smooth, mostly linear, growing on seagrasses. Hydranths pedicellate, pedicel 0.4-2 mm high, with perisarcal sheath, perisarc annulated in lower region, at distal end often
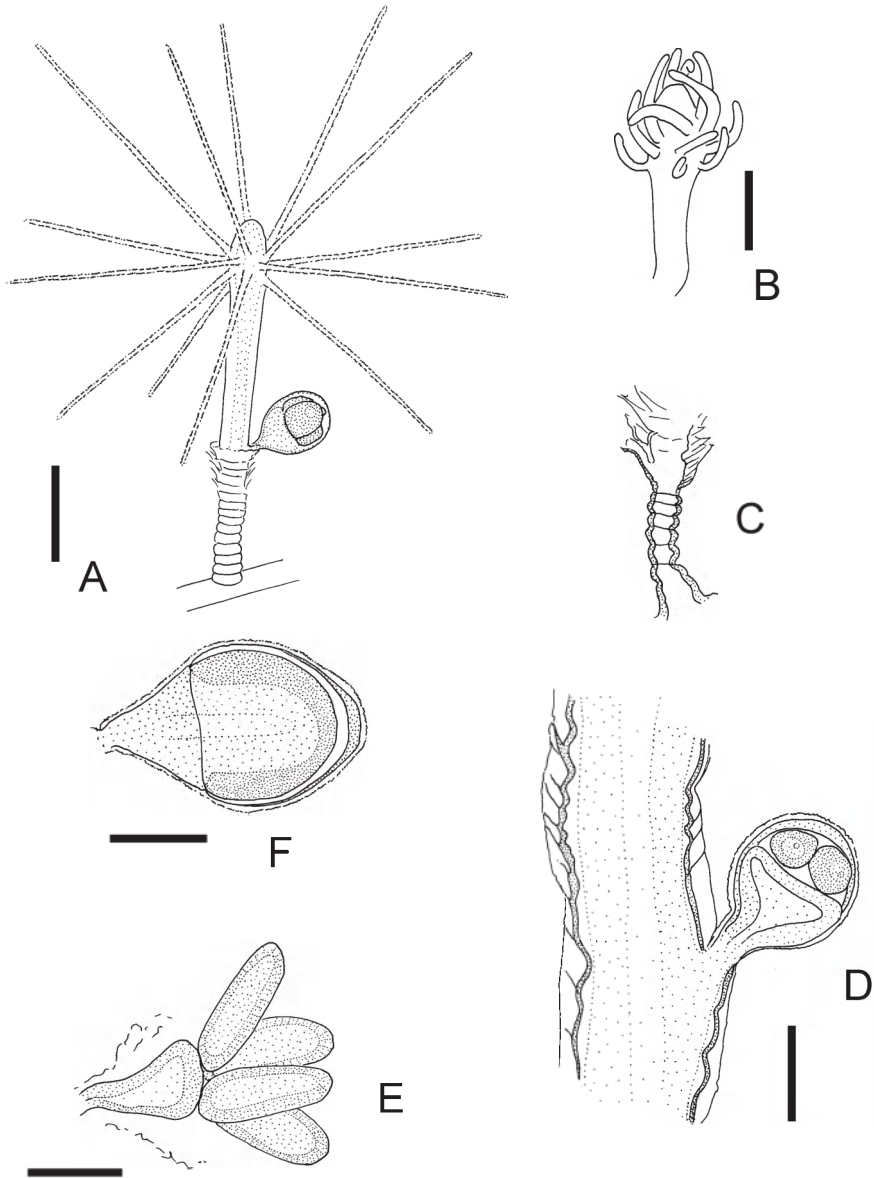
FIG. 13

Pachycordyle pusilla (Motz-Kossowska, 1905). A) hydranth with female sporosac, drawn after living material from Banyuls-sur-Mer, scale equals 0.4 mm. B) Hydranth with contracted tentacles, note scatter of tentacles, preserved material from Monaco, scale equals 0.4 mm. C) Optical section of hydranth pedicel, note double-layered, lamellar structure of distal end, same scale and material as in B. D) Optical section of hydranth pedicel with young female sporosac, preserved material from Naples, scale equals 0.2 mm. E) Final developmental stage of female sporosacs with three fully developed planulae, same material as D, scale equals 0.2 mm. F) Male sporosac in optical section, preserved material from Villefranche, scale equals 0.1 mm.
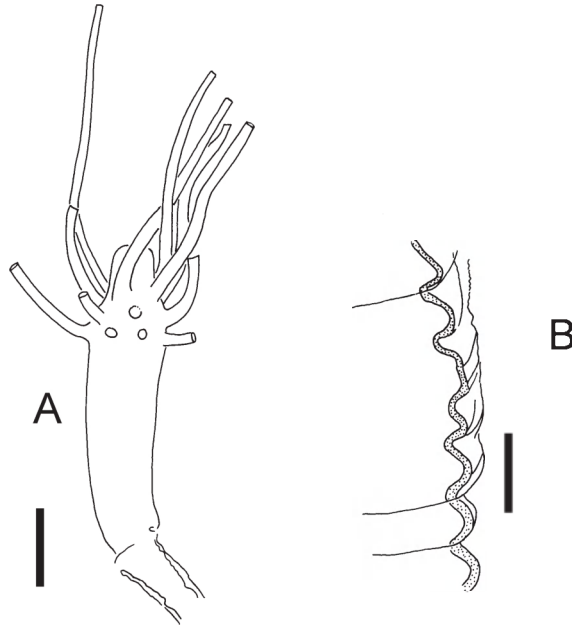
Fig. 14

Pachycordyle fusca Müller, 1913, after type material. A) Hydranth, some tentacles are broken off, note their scattered arrangement, scale equals 0.2 mm. B) Higher magnification of pedicel perisarc in optical section, note annulation and double-layered periderm, the inner thicker and the outer layer are connected by lamellae, scale equals 50 μm.

expanding and fuzzy, double-layered, the two layers connected by lamellae (Figs 13D), sometimes resembling nested funnels. Hydranth 0.7-1.2 mm, fully relaxed hydranths slightly club-shaped with swelling in region of tentacles (Fig. 13A), hypostome high, dome-shaped. Tentacles radiating from a narrow band below hypostome, 12-16 in number, either in 3 whorls or scattered, expanded very thin, up to 1.4 mm long. Size of tentacle-bearing region quite variable, in some hydranths very narrow, giving the impression of only one whorl being present. Gonophores borne on the hydranth pedicels, usually near the distal end, 1-4 per pedicel. Gonophores sessile sporosacs, without radial or circular canals, no velum, simple spadix present, proximal gastro-dermal chamber large, taking up almost the same volume as the gametes. Gonophores surrounded by loose, thin periderm. Females with 4, occasionally 5, eggs in a single tier, eggs uncoloured, clear. Development takes place in sporosacs, planulae remain attached to spadix even after periderm casing has been shed. Nematocysts: microbasic euryteles and desmonemes.

BIOLOGY – Grows on *Posidonia oceanica* or *Cymodocea nodosa* in sea water of normal salinity. Mature colonies found from June to August (Motz-Kossowska, 1905), March to April (Leloup, 1930), October (Boero & Fresi, 1986). Reproduction leads to reduction of hydranths (reproductive exhaustion; Leloup, 1930).

DISTRIBUTION – Mediterranean. Records: Banyuls-sur-Mer (Motz-Kossowska, 1905); Marseille (Stechow, 1919); Monaco (Leloup, 1930); Algeria (Picard, 1955); Genoa (Boero, 1981; Boero & Fresi, 1986); Cabo de Creus, Spain (Gili & Castello, 1985). Type localities: *Pachycordyle pusilla*, near Arago Laboratory, Banyuls-sur-Mer, France, Mediterranean, on *Posidonia oceanica*; *Pachycordyle fusca*, Bay of Naples, on *Cymodocea nodosa*, 2-4 m.

REMARKS – Contemporary authors placed this species in the genus *Cordylophora*. The tentacle arrangement, however, is identical to that of *Pachycordyle napolitana* and *P. navis*. All three species resemble each other quite closely, although they are certainly distinguishable. Therefore, this species is here used in the new combination *Pachycordyle pusilla* (Motz-Kosowska, 1905).

Most hydranths have their tentacles scattered in a band below the hypostome, but in some hydranths they are so close that they can be taken as one whorl only. These polyps look very much like bougainvilliid hydranths.

Motz-Kossowska (1905) mentioned that the eggs are covered by nematocysts. In the examined material from Banyuls, though, only very few nematocysts were present on the egg surface.

Zooxanthellae could not be detected reliably in the examined living hydranths, but they may have been present in low numbers.

Pachycordyle fusca Müller, 1913 very much resembles *P. pusilla* in all aspects, but its gastrodermal tissue contains many zooxanthellae. The zooxanthellae give the hydranth a brown colour. The species has apparently not been mentioned by other authors since its original description. Müller (1913) described *P. fusca* quite precisely, especially the gonophores and their development. In one respect, however, he might have been wrong: the tentacles are not in a single whorl as shown in his figure (Müller 1913: fig. 3). The ZSM collection contains a slide that is very likely syntype material because it is clearly labelled "Cotypus". It was presumably donated by Müller to Stechow, who initiated the hydroid collection of the ZSM (these authors must have been in contact because they also published together, e. g. Stechow & Müller, 1923). This slide preparation contains two hydranths that clearly match Müller's figure, including the double layered perisarc (Fig. 14B). The tentacles, however, are clearly in three whorls (see Fig. 14A). The zooxanthellae are visible in the preparation. Besides the zooxanthellae, and perhaps the host plant, there is thus nothing that distinguishes *P. fusca* reliably from *P. pusilla*, and I suspect that both are conspecific. *Pachycordyle fusca* is therefore listed as a questionable synonym of *P. pusilla*.

Müller (1913) primarily investigated the development of the gonophores and the regeneration of the hydranths and gonophores. He also kept his colonies in the dark which considerably reduced the zooxanthellae, but which had no adverse effect on the hydroid.

Picard (1955) identified hydroids as *Cordylophora pusilla* that were growing on *Cymodocea*. He noted that the gastrodermis contained a small number of zooxanthellae.

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