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Survey of the family Corynidae (Cnidaria, Hydrozoa)

Peter SCHUCHERT
Muséum d'histoire naturelle, route de Malagnou 1, CH-1208 Genève, Switzerland.
E-mail: Peter.Schuchert@mhn.ville-ge.ch

Survey of the family Corynidae (Cnidaria, Hydrozoa). - All genera and species of the family Corynidae are reviewed and the validity of some species discussed. Descriptions and figures for most valid species are given. The classification based on cladistic principles established by Petersen (1990) is discussed and modified. The family Corynidae encompasses the genera *Coryne*, *Sarsia*, *Dipurena*, *Nannocoryne*, *Cladosarsia*, *Bicorona*, and *Dicyclocoryne*. The family Dicyclocorynidae is not recognised and its members returned to the Corynidae. The genus *Bicorona* is redefined to accommodate *Coryne tricycla* Schuchert, 1996 as *Bicorona tricycla* comb. nov. The genus *Dicodonium* is excluded from the Corynidae because its type species is most probably an *Ectopleura* species and thus belongs to the Tubulariidae.

Key-words: Marine invertebrates - Cnidaria - Hydrozoa - Anthoathecata - Corynidae - worldwide survey - revision - descriptions - taxonomy.

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1. INTRODUCTION

Corynid hydroids and medusae are a regular component of many shallow water faunas of the world. This, and their relatively easy cultivation, has made them the preferred subject of a number of life-cycle studies and biological investigations. Numerous species have been described, but most information resides scattered in publications spanning more than 200 years of history. Identifications, especially at the species level, can often be very difficult. Therefore, the main incentive of this study was to provide a complete catalogue of the species, to discuss their status, to outline their distinguishing characters, and to summarise aspects of their biology. It was not intended to give a complete literature record for every species as Bedot (1901-1925) did. It is evident that many authors have misidentified their material or based their identification on a too small set of characters (e. g. non-reproductive polyps, juvenile medusae, damaged material). Simple records of species are therefore often unreliable if not supplemented by additional information. Simply listing all citations for a species might lead to the wrong implication that all identification were correct. Therefore, I mostly worked only with studies providing descriptions and figures. Wherever possible, material of the species concerned was examined and described.

The first corynids to be described were *Coryne muscoides* by Linnaeus in 1761 (as *Tubularia muscoides*) and shortly after *C. pusilla* by Gaertner (1774). Subsequently, new species were described regularly, although many older descriptions based on preserved material made distinction of species sometimes difficult. It was only after Rees, Edwards, and Brinckmann-Voss started to work with living specimens that the quality of information became more reliable. One important outcome of these studies was that in most cases knowledge of the complete life cycle is necessary to identify a species. It became evident that some species have nearly indistinguishable medusae, while their polyp stages were strikingly different, and likewise that some similar polyps produced medusae that sometimes even belonged to different families. New species of corynids continue to be described and it is evident that only a more careful search is needed to discover new species (see also below, discussion on distribution).

The limits of the family Corynidae have always been unclear and remain so even today. Some authors (e. g. Hincks, 1868; Naumov, 1969) also included members of the Zancleidae in this family (e. g. the genera *Zanclea* and *Halocoryne*). However, this group with medusae having partitioned gonads and macrobasic euryteles is only quite distantly related to the Corynidae (Petersen, 1990). Unexperienced students nevertheless may find it rather difficult to discriminate infertile hydranths of *Zanclea* and *Coryne*. *Zanclea* species, however, generally have many more tentacles and these are more scattered. More importantly, *Zanclea* species usually have a rather shallow hypostome and quite often it is completely flat. The resemblance of their polyps is probably a plesiomorphy. The most likely sister group of the Corynidae is the clade Eleutheriidae (the latter includes also the Cladonematidae, see Schuchert, 1996). Both groups are united by the presence of thin, filiform tentacles lacking nematocysts. Although this character has been lost in some species of both groups, it still remains a valid argument for a close affinity of both groups. Upon close examination, some Corynidae (e. g. *Sarsia lovenii*) without filiform tentacles have at the place of them a ring of epidermal sensory cells with long, stiff cilia. Similar cells are otherwise found on the filiform tentacles. However, as there is no good synapomorphy available for the Corynidae, the Eleutheriidae could as well be an ingroup of the Corynidae (see below).

The Solanderiidae are another group with a close affinity to the Corynidae. The former family has recently been revised by Bouillon *et al.* (1992) and the number of species was considerably reduced.

The position of the genera *Bicorona* and *Dicyclocoryne* are likewise problematic. Petersen (1979, 1990) united them in the family Dicyclocorynidae and synonymised *Bicorona* with *Dicyclocoryne*. Both genera are here retained in the family Corynidae, mainly because *Dicyclocoryne* has tentacle bulbs with high gastrodermal chambers and because *Bicorona tricycla* is intermediate between *Dicyclocoryne* and *Coryne*. For more details see the discussion on phylogeny and under genus *Bicorona*.

The difficulties in delimiting the family as a monophyletic taxon are due to the very limited number of characters that can be used for phylogenetic reconstructions. The macrotaxonomy of the aforementioned families appears thus only resolvable by using molecular techniques.

Like the limits of the family, the generic division of the family Corynidae is a longstanding controversy that is still not resolved satisfactorily (comp. Petersen, 1990). The main problem resides in the fact that many Corynidae have lost their medusa stage and the polyp phase does not offer enough characters to discriminate genera that are congruent with the system based on the medusae. Traditionally (e. g. Rees, 1957; Brinckmann-Voss, 1970; Bouillon, 1985a), the Corynidae were primarily subdivided based on the presence or absence of a medusa stage: *Coryne* had sessile gonophores, while *Sarsia* and *Dipurena* liberated free medusae. The distinction of *Sarsia* and *Dipurena* was based on the number of gonads. Several authors proposed an even finer subdivision and numerous synonyms are thus available. Mostly they are not worth being discussed further, perhaps with the exception of *Staurocoryne* and *Stauridiosarsia*, taxa occasionally still used by some non-taxonomists. *Staurocoryne* and *Stauridiosarsia* refer simply to *Coryne* or *Sarsia* species that have polyps with filiform tentacles. Numerous investigations have shown that the presence of these filiform tentacles is dependent on environmental conditions and they have likely been reduced several times during evolution. Furthermore, their presence is most probably a plesiomorphy and today's consensus is that they should not be used to delimit genera, but they are an important diagnostic trait to discriminate certain species.

The subdivision of the Corynidae into the three genera *Coryne, Sarsia*, and *Dipurena* has gained wide acceptance, although this classification is based on two characters only (loss of medusa stage, number of gonads). Both characters are apomorphies, but it is widely known from other hydrozoan families that the loss of the medusa stage has presumably occurred several times independently (e. g. Cunningham & Buss, 1993). Some corynids additionally present interpretational difficulties. *Sarsia occulta* forms liberable medusae, which however – depending on clone and environmental conditions – are retained on the polyp. To make the case even more perfid, the retained medusae also lose the long manubrium, another characteristic of most *Sarsia* medusae. *Sarsia occulta* thus clearly shows the shortcomings of this system (although, admittedly, it is very informative and practical!).

The only attempt to classify the Corynidae based on their phylogeny, meaning using cladistic methodology, was made by Petersen (1990). His findings will be discussed in detail below.

A cursory overview on the distribution of the Corynidae, in particular the species diversity, reveals that the best investigated sites like Great Britain, the Vancouver Island Region, and the Mediterranean also have the highest number of reported species. The investigations of Edwards (1978, 1983) and Brinckmann-Voss (1985; 1988; 2000) clearly show that life-cycle studies can reveal the existence of sibling species. Species diversity thus largely depends on search effort and many more species could likely be found. In particular the tropics are insufficiently examined.

The studies of Bouillon and co-workers at one restricted site in Papua New Guinea and using appropriate collecting methods (not general plankton samples) demonstrated the existence of an immense variety of small medusae and hydroids (Bouillon, 1978b-1985, Bouillon *et al.*, 1988-1991, Boero *et al.*, 2000).

It can therefore be expected that closer examinations of other localities will reveal the existence of considerably more species than known so far.

2. PHYLOGENY OF THE CORYNIDAE

Based on cladistic methodology, Petersen (1990) made a detailed analysis of the phylogeny of the Capitata and within them also the family Corynidae. Petersen used his findings to create a new classification. His classification has been accepted for some taxa (e. g. in Schuchert, 1996), but that of the Corynidae has attracted criticism (Kubota & Takashima, 1992; Pagès *et al.*, 1992; Schuchert, 1996; Brinckmann-Voss, 2000). The phylogeny of the Corynidae as interpreted by Petersen (1990) is shown in Figure 1.

Although Petersen's phylogenetic hypothesis must be regarded as an essential step towards a natural classification and his work is mostly well founded, there are indeed several points that need reconsideration. In the following, the transformation steps given by Petersen (in italic, see also Fig. 1) will be discussed in detail. Cladistic terms and methodology used here follow the general usage (e. g. as in Ax, 1984).

a) *tentacles homologous to aboral whorl in the Tubularoidea thin or completely reduced.*
Petersen postulates that the ancestor of the Corynidae and Eleutheriidae had a polyp with only one whorl of oral tentacles and one whorl of filiform tentacles, basically resembling the polyps of *Dipurena reesi* or *Cladonema radiatum.* The capitate tentacles below the oral whorl – here named lower capitate tentacles – were thus absent in the ground state of the Corynidae and Eleutheriidae. Outgroup comparisons (e. g., to the Solanderiidae, Pennariidae, Acaulidae, Zancleidae etc.), however, suggest that it is more parsimonious to assume the presence of these lower tentacles in the ground plan. It is more plausible that these lower tentacles were reduced in a few events (Eleutheriidae, Tubularoidea, some Corynidae) than to assume the independent appearance of these lower tentacles in several taxa. Prévot (1959) even mentions an unidentified *Cladonema* species from the Red Sea that had two whorls of capitate tentacles. The stem species of the Corynidae most probably had lower capitate tentacles reaching to or beyond the middle of the body, thus overlapping with the site of gonophore development. According to this view, species conforming with the ground plan of the Corynidae are *Coryne producta* or *C. japonica.*

b) *aboral tentacles thin and transformed into sense organs.*
This is a good synapomorphy uniting Corynidae and Eleutheriidae (sensu Petersen, 1990). The filiform tentacles, however, have been lost is some groups again. Some vestiges of them may remain as a ring of sensory cells (e. g. as in *Sarsia lovenii*).

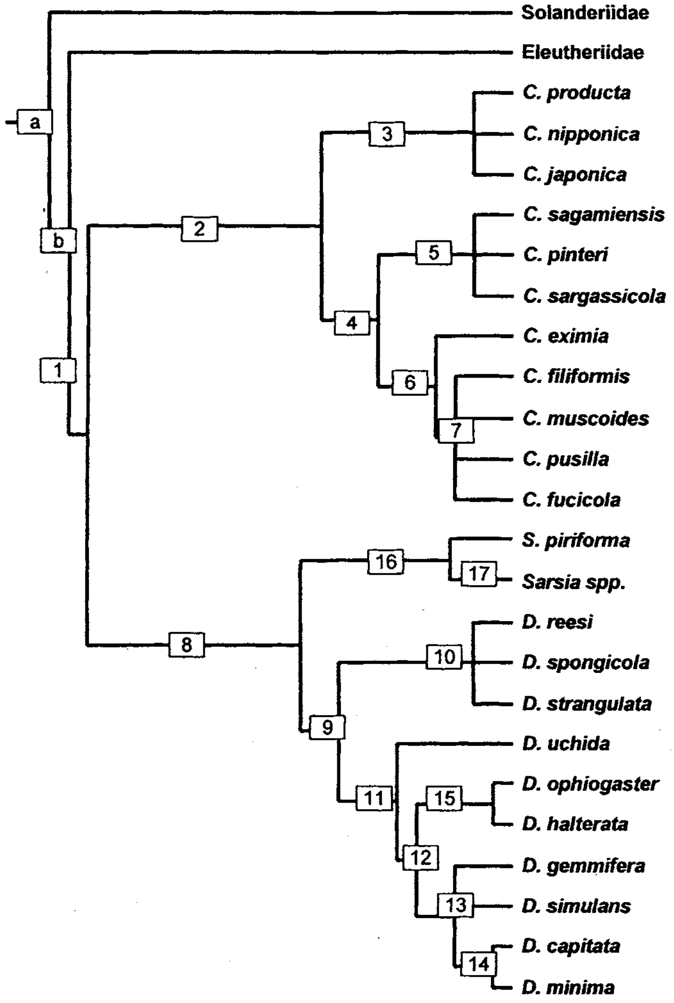

FIG. 1

Phylogeny of the Corynidae according to Petersen (1990). For the numbers and letters indicating character changes see text.

1) *marginal bulbs in medusa with bulbous gastrodermal chamber and nearly closed ring of thickened epidermis with nematocysts.*
This is perhaps a synapomorphy of the Corynidae, but some Eleutheriidae (e. g. *Cladonema radiata*) have comparable bulbs.

2) *gastrodermal chamber ovoid, laterally flattened, with tentacles issuing obliquely.*
This is invalid for several reasons. The shape of the gastrodermal chamber depends on the filling of the gastrodermal system and it is also otherwise highly variable. I was unable to find ovoid and laterally flattened chambers in the species

Coryne sensu Petersen. Furthermore, the shape is dependent on the state of contraction, and even in relaxed medusae it shows intra-specific variation.

Outgroup comparisons clearly show that the oblique direction of the tentacles is prevalent in out-groups like Eleutheriidae and Zancleidae and it is probably a plesiomorphic character. The vertically issuing tentacles occur also in *Coryne inabai* and most *Sarsia* and *Dipurena* species clearly issue their tentacles obliquely (see e. g. the photographs in Miller, 1982: fig. 3). Moreover, the direction is often variable and dependent on the state of contraction.

3) *medusae buds developed at location and instead of lowest whorl of lower capitate tentacles.*

This is a problematic character. The gonophores do not replace tentacles, but tentacles are reduced due to reproductive exhaustion (see e. g. Edwards, 1978: 309). This tentacle reduction starts with the lowest tentacles first. The location of the gonophores at the level of the lowest tentacles, meaning in the middle of the hydranth of the species concerned (*C. producta, C. japonica, C. nipponica*) is probably a plesiomorphic trait. Only the spreading of the gonophores towards the more distal tentacles is apomorphic.

In *Coryne japonica,* the gonophores are either independent from the tentacles or in their axils (Schuchert, 1996). Thus this character comes in mixed states in some species and furthermore they do not necessarily replace the lowest whorl of tentacles as asserted by Petersen (1990).

4) *medusae buds developed in the upper axils of the capitate tentacles.*

This is a clear and important apomorphy for a clade within the genus *Coryne.*

5) *perisarc transparent, wrinkled.*

A very problematic character which is most probably dependent on environmental conditions. Culture experiments (e. g. Brinckmann-Voss, 1970) have clearly shown that the morphology of the perisarc may depend on external factors.

6) *stems upright, regularly branched*

A weak apomorphy, very likely to show extensive homoplasia.

7) *medusae reduced to fixed sporosacs.*

A synapomorphy at this level only. Petersen strongly argues against using the reduction of the medusa phase as a synapomorphy for defining genera within the Corynidae. However, compared to the low complexity of the other characters recognised here as valid synapomorphies, the classification based on medusa reduction appears equally credible.

8) *manubrium of medusa with thin proximal part and swollen distal stomach.*

A good synapomorphy, although the transition between thin and swollen part can be rather gradual in some species (see also Pagès *et al.,* 1992).

9) *gonad developed around distal stomach; endodermal chamber of marginal bulbs regularly ovoid with radial canal and tentacle openings at top and bottom centre; button-shaped hypostomal gland field.*

The gonads covering the stomach region is certainly a plesiomorphic condition as it is also present in *Coryne* sensu Petersen. It is thus not useful to detect a monophyletic group.

The morphology of the gastrodermal chamber is too variable and was found to be of little significance for recognising clades.

The epidermal field of high gland cells around the mouth of the polyp is a problematic character, perhaps it is a plesiomorphy. Some infertile polyps collected by myself at Sandgerdi (Iceland) had all the characteristics of *S. tubulosa* and they also had a calotte of high epidermal cells. Likewise, *S. lovenii* has them too. Preserved material of *S. occulta* also quite clearly showed a calotte of high epidermal cells. According to Bouillon (1995), also *Coryne japonica*, *C. producta*, and *C. filiformis* have these cells. Furthermore, the same morphology is also found in *Zanclea* and *Asyncoryne*, genera only quite distantly related to Corynidae. In some Eleutheriidae these cells are also present, but they are so numerous that they form a pre-oral chamber. These facts taken into account, one can as well assume that the absence of such cells constitutes an apomorphy.

10) *gonad on stomach not reaching serpentine part of manubrium.*
    This is not correct for the species concerned, they do have additional gonad cylinders on the thin part.
11) *"oral tentacles" in hydroid spread over hydranth, independent of medusae buds.*
    Probably invalid, see remark under point a).
12) *gonad on distal stomach reaching serpentine manubrium section.*
    Invalidated under point 10.
13) *gonad forms one ring.*
    Is a plesiomorphic condition, thus not suitable for recognising a clade.
14) *medusae tentacles with stalked capitations.*
    A good synapomorphy. However, life-cycle information is still missing for the two species of *Cladosarsia*.
15) *gonad divided into separate cylinders.*
    A good synapomorphy uniting most members of the genus *Dipurena*.
16) *gonad developed on serpentine part of manubrium and not on stomach; gastrodermal chamber of bulbs saddle-shaped.*
    The gonad-free stomach is a good synapomorphy for the genus *Sarsia* sensu Petersen, while the shape of the gastrodermal bulb chamber is not generally applicable.
17) *oral tentacles in hydroid spread over distal part of hydranth above medusae budding zone.*
    Probably invalid as discussed under a) and 11).

We are thus left with the following more or less reliable synapomorphies summarised below and in Figure 2:

a) *most proximal tentacles very thin, without nematocysts, transformed into sense organs.*
b) *medusa with branched tentacles and sucker pads, more than four radial canals, polyp with preoral chamber.*
1) *marginal bulbs in medusa with large gastrodermal chamber and nearly closed ring of thickened epidermis with nematocysts.*

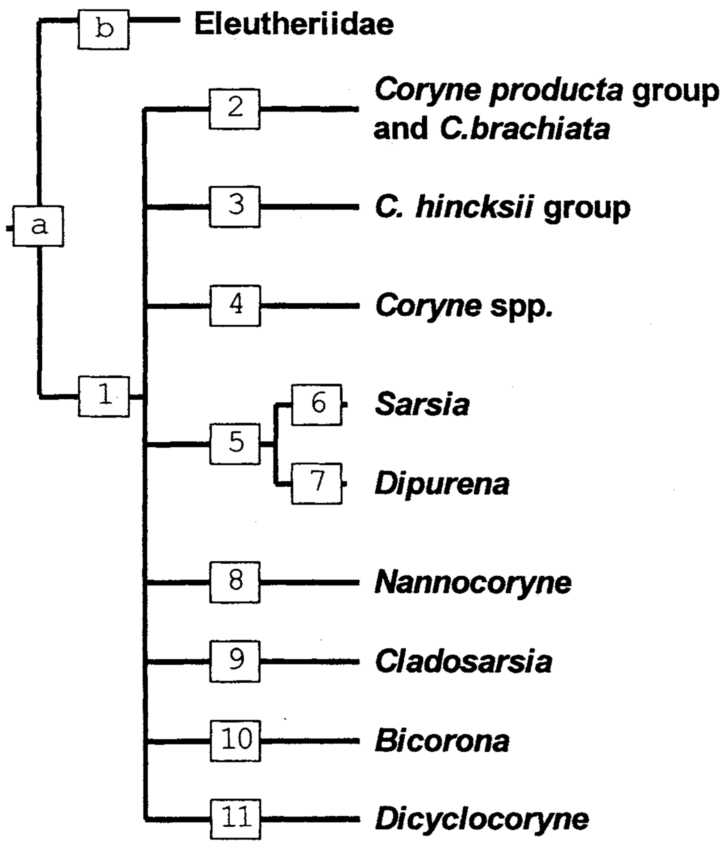

FIG. 2

Revised phylogeny of the Corynidae. For the numbers and letters indicating character changes see text.

The ground plan of the Corynidae comprises a polyp with an oral whorl of capitate tentacles, lower capitate tentacles reaching to the middle of the hydranth, gonophores developing in middle of hydranth among lowest capitate tentacles, one whorl of filiform tentacles. The medusa is small and has a short manubrium completely covered by one gonad. The ground plan of the Corynidae is thus best represented by species like *Coryne producta* and *C. japonica.*

2) no character available.

3) *medusa phase reduced to eumedusoids (sporosacs with radial canals), loss of filiform tentacles.*

4) *medusae buds develop in the upper axils of the capitate tentacles.*

5) *manubrium of medusa longer than bell, with thin proximal part and swollen distal stomach, cnidome comprises oblong isorhiza nematocysts* (lost in some species again).

6) *gonad only on thin part of manubrium, leaving swollen stomach region uncovered, lower capitate tentacles confined to zone above gonophore production.*
7) *gonad covers stomach nearly to distal end, gonad on serpentine part nearly always divided into several rings* (except *D. gemmifera*)*; lower capitate tentacles of polyp confined to zone above gonophore production for the majority of species.*
8) *gonophores completely reduced, gametes retained in gastrodermis.*
9) *medusa with branched tentacles* (perhaps shared with Eleutheriidae?).
10) *number of tentacles in lowest whorl twice or more the number found in oral whorl, gonophores reduced to sporosacs, sporosacs produced distal to aboral whorl of capitate tentacles; colonies large and branching, perisarc annulated throughout.*
11) *two whorls of tentacles, lower one with slightly more tentacles than upper one, medusae developing below tentacles, medusae released without ocelli.*

A useful character not mentioned by Petersen (1990) is the presence of oblong isorhiza capsules in the polyp or medusa. The cnidome is not known far all species of the Corynidae, but these oblong isorhizas are only present in members of the genera *Sarsia* and *Dipurena* (sensu lato, synapomorphy number 5).

Nevertheless, it is plainly evident that we do not have enough characters to resolve the phylogeny of the Corynidae and their relatives. In particular, there is no apparent synapomorphy for all members of the genus *Coryne* sensu Petersen. The genus *Coryne* as used here may thus be paraphyletic, but there is also no evidence that some of these *Coryne* groups are more closely related to the clade having long manubria (clade 5). The synapomorphies 4, 5, 6, and 7, however, must be used for a classification based on monophyletic groups and genus definition based on the cladogram given in figure 2 are used in this study. This system is largely congruent with the one of Petersen (1990), and it differs only in the generic placement of *C. uchidai* (see under this species for a discussion), and the provisional retention of the genera *Bicorona, Dicyclocoryne, Cladosarsia* and *Nannocoryne*. Contrary to Petersen (1990), both described species of *Cladosarsia* are here regarded as valid. Applying the synapomorphies outlined above, *Cladosarsia minima* would fall within the genus *Coryne*, *Cladosarsia capitata* to the genus *Dipurena*. I think it is advisable to keep both in the genus *Cladosarsia* until more data on their life cycle becomes available. Perhaps they are even a sister group of the Eleutheriidae, with which they share the branched tentacles. Likewise problematic is *Nannocoryne mammylia*, as its gonophores are totally reduced. Only molecular sequence analysis can give reliable data on its affinity.

Despite all this, the classification as used here is quite unambiguous and only the position of *Sarsia lovenii* is somewhat controversial. *Sarsia lovenii* is the only member of the clade *Sarsia* that has a medusa that is never released. Although *Sarsia occulta* medusae can remain fixed at the polyp stage, the liberated medusae are unequivocally related to otherwise typical *Sarsia* species.

Contrary to Petersen (1990), no clade Dicyclocorynidae is accepted and the group is here returned into the Corynidae. The medusa of *Dicyclocoryne* has tentacle bulbs with the characteristic, high gastrodermal chamber. This chamber is regarded as a weak synapomorphy for the Corynidae. Also Petersen used this synapomorphy to demonstrate the monophyly of the Corynidae. For further discussions see remarks under genus *Bicorona.*

Unclear remains also the position of the Solanderiidae with its sole genus *Solanderia* (Schuchert, 1996). *Solanderia* polyps resemble closely corynid polyps and its cnidome is identical to the one found in most *Coryne* species. Only their gonophore production on the branches and not hydranths sets them apart from most Capitata. The lack of comparable characters precludes any further discussions on their affinity.

These facts underline once more how important new approaches, like DNA sequencing, are for giving us a more accurate picture of corynid phylogeny. Additionally, further life-cycle observations, notably knowledge of the polyp stages of *D. gemmifera* and *Cladosarsia* spp., can help us to test the validity of the system proposed above.

3. MATERIAL AND METHODS

Corynid medusae and polyps are best studied alive. General collection methods for medusae and hydroids have been described by Russell (1953), Naumov (1969), Brinckmann-Voss (1970), and Bouillon & Barnett (1999). These authors also give a good introduction to the general morphology and terminology of these animals. The term "shoot" is here often used and it refers to a single, erect, polyp bearing stem arising from the stolons. All shoots and the stolons form the colony. Sometimes also the expression cormoid is used for this element (see Schuchert, 1996).

Ideally, medusae are caught by dipping a glass beaker. However, the densities are usually very low and the medusae hardly visible. Normally medusae are caught with a nylon plankton net. A mesh width of 0.25 mm is needed to collect also smaller forms and also to avoid damage by shearing. To further minimise damage the net should be dragged very slowly (up to 2 km/h). Due to the low abundance of these animals, large volumes of water must be filtered. Collection from long jetties and rowing boats give the best results, although even with slow filtration medusae will get damaged. Damaged medusae can sometimes be kept isolated in jars and they will regenerate. Many corynid medusae are seasonal, so samples must be taken at different dates. To account for diurnal migrations, samples must be taken at different depths or times of the day.

Polyps are best collected by examining pieces of rocks, shells, algae, sea-grass, sponges, etc. with the help of a stereomicroscope. The pieces can be obtained by diving or by dredging. Some polyps on rocks will become visible only after days or weeks in running sea-water. Feeding with planktonic crustaceans or *Artemia* nauplii hatched from dried egg may help to promote the growth of such colonies.

Examination of nematocysts is preferably done in living material. The size of nematocysts can also be measured in preserved material if it is immersed in 50 % lactic acid. Preserved nematocysts show about 10 % shrinkage, which is not much in view of the often considerable size variation of the capsules. Values given in this publication were usually obtained from preserved material.

4. ABBREVIATIONS

BCPM	Royal British Columbia Museum, Victoria, Canada
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
MHNG	Muséum d'Histoire Naturelle Genève, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMSZ	National Museums of Scotland, Zoology, Edinburgh, United Kingdom
NSMT	National Science Museum, Tokyo, Japan
ROMIZ	Royal Ontario Museum, Toronto, Canada
USNM	Unites States National Museum (Smithsonian Institution), Washington, USA
ZMA	Zoological Museum, University of Amsterdam, The Netherlands
ZMUC	Zoological Museum Copenhagen, Denmark
ZSM	Zoologische Staatssammlung München, Munich, Germany.

5. FAMILY CORYNIDAE, SYSTEMATIC PART

Diagnosis – Hydroids with colonial, monomorphic polyps having club-shaped to cylindrical or slightly vasiform bodies. With one whorl of capitate tentacles around mouth, with or without further capitate tentacles below them, with or without one whorl of filiform tentacles. Colonies upright, stolonal or branching, monosiphonic, stem and branches covered by perisarc. Stolons tubular. Nematocysts: stenoteles, with or without isorhizas or mastigophores, desmonemes absent. Gonophores in most species arising on hydranths, either liberated as free medusae or retained as medusoids or sessile sporosacs. Exceptionally gonophores completely reduced and gametes stored in hydranth wall. Free medusa if present with four radial canals, four tentacle bulbs, and four tentacles. Tentacle bulbs with a distinct gastrodermal chamber, epidermal part contains many nematocyst and forms a complete or nearly complete ring around tentacle base. Each bulb normally with one abaxial ocellus only. Manubrium cylindrical, without lips, gonads encircle manubrium without perradial interruptions. Exumbrella without nematocyst pouches. Nematocysts as in polyp stage, but additionally with desmonemes, macrobasic euryteles absent. Newly released immature medusae with manubrium always shorter than bell cavity.

5.1. Genus *Coryne*

Synonyms – (in part or fully) *Fistularia* Mueller, 1776; *Fistulana* Mueller, 1776; *Capsularia* Cuvier, 1798; *Stipula* M. Sars, 1829; *Syncoryna* Ehrenberg, 1834; *Hermia* Johnston, 1838; *Halybotrys* de Filippi, 1866; *Actinogonium* Allman, 1871 [not *Actinogonium* Schomburgk, 1847]; *Staurocoryne* Rotch, 1872; *Eucoryne* Broch, 1909 [not *Eucoryne* Leidy, 1855]; *Actigia* Stechow, 1921; *Perinema* Stechow, 1921.

Type species – *Coryne pusilla* Gaertner, 1774.

DIAGNOSIS – Hydroids colonial with creeping stolons, stems branched or unbranched. Hydranths with capitate tentacles either scattered, or in at least three whorls, whorls below oral one usually with four (rarely five or six in some hydranths) tentacles only; with or without filiform tentacles. Gonophores develop either in the upper axil of the lower capitate tentacles or among the lowest whorl of capitate tentacles. These proximal tentacles can be reduced with ongoing gonophore maturation. Isorhiza nematocysts absent from polyp stage. Gonophores remain fixed or are released as free medusae. Tentacles of medusa unbranched. Manubrium of free adult medusa not longer than bell, without thin proximal part. Gonads cover manubrium for most of its length.

REMARKS – The outline of this taxon has been discussed above in chapter 2 and corresponds closely to the concept of Petersen (1990).

Coryne tricycla Schuchert, 1996 is here excluded from the genus *Coryne* and placed in the genus *Bicorona* Millard, 1966. To account for this, only Corynidae with roughly equal numbers of tentacles per whorl (normally four, exceptionally up to six) are here accepted in the genus *Coryne*.

With one exception (*Sarsia lovenii*), the genus *Coryne* as conceived here comprises all the Corynidae with fixed gonophores as well as those producing free medusae with a short manubrium. The genus *Sarsia* as seen here, and in agreement with Petersen (1990), comprises only Corynidae with a long manubrium.

The development of gonophores in the upper axil of the capitate tentacles is a good synapomorphy that unites several *Coryne* species to a clade of their own. A future revision based on the discovery of new characters might exclude the remaining *Coryne* species which produce gonophores independent from the tentacles. Some of them show a mixed character state, e. g. *Coryne japonica* and *C. cliffordi* develop medusae buds in the axil of tentacles as well as independent of them (Schuchert, 1996). Some species are only provisionally allocated to *Coryne* as they are not adequately known and new data may necessitate removing them from here. *Coryne* thus serves also as default genus for hydroids with incomplete life-cycle information. The order of the species given in the following is approximately as sketched in figure 2. The groupings made within the genera do not necessarily correspond to clades and are only made to allow easier comparisons. The groups are formed by grouping similar species around a well known or easily identifiable species. The groups are as follows: *Coryne producta* group, *Coryne hincksii* group, *Coryne brachiata* group, *Coryne pintneri* group, and *Coryne eximia* group.

5.1.1. *Coryne* species with non-axillary gonophores

This is a paraphyletic or polyphyletic grouping.

5.1.1.1. *Coryne producta* group

This group comprises the species *Coryne producta, C. cliffordi, C. japonica,* and *C. nipponica.* Important differences between these similar species them are tabulated in table 1.

TABLE 1. Differences of the species resembling *Coryne producta*

character	*C. producta*	*C. cliffordi*	*C. japonica*	*C. nipponica*
size of adult medusa, mm	6-10	5.5	3-6	1.2 - 2.4
tentacles of medusa	long	long	long	short
nematocyst clusters on tentacles of medusa	>50	>50	>50	<13
egg size in µm	11-46	about 200	105±14	127±10
radial canals very fine	no	yes	no	no
exumbrellar nematocysts in young medusa	scattered	variable	8 adradial rows	scattered
polyp size in mm	0.8-1.5	1.4-1.7	1.3-2.7	1.3-1.9
filiform tentacles of polyp	always present	absent	frequently present	ephemeral
polyp capitate tentacles	12 (8-16 range)	16-20	18 (12-24 range)	16-18
lower capitate tentacles	2 whorls	scattered	3 whorls	scattered
number of medusa buds	1-5	3-20	up to 14	2 (max. 4)
buds clustered	never	possible	possible	no
stems branched	no	occasionally	no	no

Coryne producta (Wright, 1858) Fig. 3A-C

Coryne cerberus Gosse, 1853: 222, pl. 14 figs 4-6; Rees, 1938: 37.
? *Oceania thelostyla* Gegenbaur, 1856: 224, pl. 8 fig. 9.
Stauridia producta Wright, 1858: 283, pl. 7, figs 6-8; Hartlaub, 1895: 142, pl. 7 figs 1-19, pl. 8 figs 1-8, pl. 9 figs 1-2, 6.
not *Coryne producta* Hargitt, 1902: 551 [=*Sarsia hargitti* Mayer, 1910]
Sarsia producta – Kramp, 1959: 80, fig. 19; Brinckmann-Voss, 1970: 67, figs 77-78; West, 1974: 5, figs 1-2; Brinckmann-Voss, 1989: 688, tables 2-3, fig. 7; Altuna Prados, 1993: 30; Orlov, 1996: 329, figs 8.
Stauridium productum – Hincks, 1868: 68, pl. 12 fig. 1; Allman, 1871: 371, pl. 17 figs 11-12; Hartlaub, 1907: 53, figs 48 50; Rees, 1938: 37, fig. 11.
Stauridiosarsia producta – Russell, 1953: 64, figs 26A-C, 27A-B; Kramp, 1961: 33; Kramp, 1968: 8, fig. 10.
Coryne producta – Petersen, 1990: 211; Schuchert, 2001: 49, Fig. 35.
? *Sarsia* sp. – Altuna Prados, 1993 : 35, fig. 4a-d.
not *Coryne producta* – Migotto, 1996: 21, fig. 5d-g, [=*Coryne nipponica*].
TYPE LOCALITY – Firth of Forth, Scotland.
MATERIAL EXAMINED – ZMUC, north of Frederikshavn harbour, Denmark, 0.2 m depth, on *Halichondria* (Porifera), 11. 08.1972, polyps and young medusae – Sandgerdi, Iceland, 0.5 m, May 2000, infertile polyps, cultivated for 10 months, no gonophores formed, described also in Schuchert (2001).

DESCRIPTION – (combined from various sources) Hydroid stolonal, cauli short, perisarc smooth or slightly wrinkled, thin. Hydranths clavate, height 0.8-1.5 mm when relaxed, diameter 0.15-0.23 mm, hypostome dome shaped, short. One whorl of 4-6 oral tentacles, 1-3 additional whorls of lower capitate tentacles, whorls distinct, normally 4 tentacles per whorl but 3-6 possible in some hydranths, tentacle positions alternate in adjacent whorls. Total number of capitate tentacles 12-16. At lower third of hydranth a single whorl of 3-6 filiform tentacles. The filiform tentacles are a constant feature of this species. They are produced during development just after the oral whorl of tentacles, thus before the lower tentacles. Gonophores develop among or below the lowest whorl of capitate tentacles and are set free as medusae, 1-5 buds per hydranth. Colour: reddish gastrodermis. Nematocysts: stenoteles, (23-27) x (20-21) μm and (15-16) x (11-12) μm.

Newly released medusa 0.8-1.1 mm high, slightly less in diameter, with scattered nematocysts on exumbrella, apical canal present.

Adult medusa 6-10 mm in height, diameter 5-8 mm, umbrella bell shaped to spherical, top rounded, jelly thick, jelly at apex about 1/4 of total height. Velum spans 1/2 of its radius. Manubrium 2/3 to 1/1 as long as bell cavity, tubular, with long apical canal spanning at least 1/2 of the mesogloea, base of apical canal may be enlarged to a conical apical knob. Gonad encircles manubrium for nearly its entire length, leaving short free parts near base and mouth. Radial canals and circular canal of similar thickness. Radial canals well visible, entering gastrodermal chamber of bulbs in middle. Gastrodermal chamber of bulbs high. One black or deep-brown ocellus on abaxial side of epidermal ring of tentacle bulb. Tentacles long (<1.5 bell height), covered with many crescent shaped nematocyst clusters, terminal cluster spherical, not or only slightly enlarged. Colours: apical canal and bulbs reddish or brown. Nematocysts: stenoteles as in polyp; desmonemes (6-7) x (9-10) μm.

DISTRIBUTION – European Atlantic coast from Bay of Biscay to White Sea and Iceland; North American coast along New England region. The presence in the Mediterranean is uncertain (Brinckmann-Voss, 1970).

BIOLOGY – The polyp was found growing on *Tubularia indivisa* (Rees, 1938), on *Spartina* spec. (Salt Marsh Grass: West, 1974), shells (Orlov, 1996), and probably on many other solid objects, just below the low water line. The medusa has only rarely been collected from nature (e. g. by West, 1974). Orlov (1996) describes prey capture and preference. The most common prey items were copepod nauplii, protists, and larvae of gastropods and polychaetes. Aspects of its ecology and feeding behaviour were also studied by Orlov (1996).

REMARKS – The adult medusa of *Coryne producta* resembles *C. eximia*, but living specimens should be distinguishable. *Coryne producta* is considerably larger (5-10 mm versus 3-4 mm) and has a distinct apical canal or chamber. Their polyp phases are very different.

Coryne producta in both polyp and medusa phase differs only little from *Coryne japonica*. Differences between the two are discussed under the latter species and in table 1 (see also Kubota & Takashima, 1992).

The medusae of *C. producta* and *C. cliffordi* are likewise similar, although their polyp phases differ. The medusae – they are apparently not sympatric – can be distinguished by the much thinner radial canals in *C. cliffordi*.

West (1974) tabulates an egg size of 11-46 μm for this species. This seems unusually small and needs reconfirmation.

Naumov (1969) reported this species also from the Sea of Okhotsk. He had only a juvenile medusa and therefore his identification must be considered uncertain. Moreover, *Coryne japonica* is not readily distinguishable from this species.

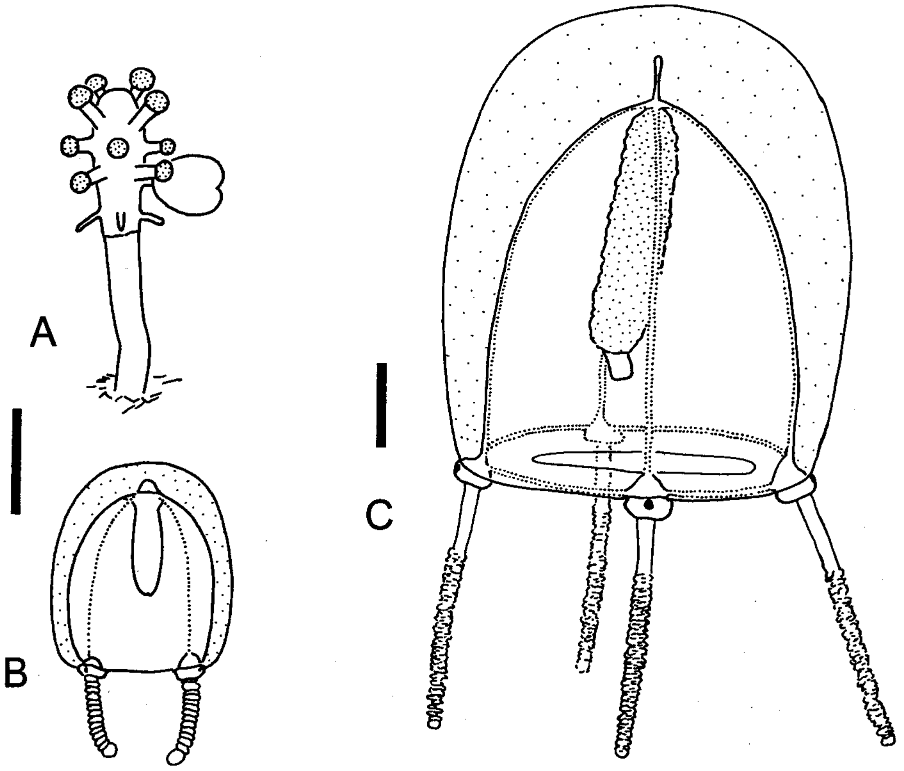

FIG. 3

Coryne producta (Wright, 1858). A-B, after preserved material from Denmark, C, modified after Russell (1953). A) Somewhat contracted polyp with medusa bud, scale bar 0.5 mm. B) Newly released medusa, same scale as A. C) Mature medusa, scale bar 1 mm.

The ultrastructure of receptors in the filiform tentacles was investigated by Golz & Thurm (1994). Vannucci (1949) and Migotto (1996) identified a corynid polyp from Brazil as *C. producta.* They were able to rear the medusa. The polyp had more than the usual two whorls of lower tentacles and the mature medusa reached only 3 mm in height, had no apical canal, and short tentacles covered by only a dozen nematocyst clusters. These are all characteristics of *Coryne nipponica* and the Brazilian records are here referred to this species (in a personal communication Dr. A. Migotto agreed with this view).

Coryne cliffordi (Brinckmann-Voss, 1989) Fig. 4

Sarsia sp. I Arai, 1987: 187, pl. 4.
Sarsia cliffordi Brinckmann-Voss, 1989: 685, figs 1-4.
TYPE LOCALITY – Sooke Harbour, British Columbia, depth 0.2 m (hydroid).
MATERIAL EXAMINED – ROMIZ B934, paratypes, 2 female medusae raised from holotype colony by A. Brinckmann-Voss, August 1984 – MHNG INVE 29807, Canada, Quadra Island near Vancouver Island, hydroid colony with medusae buds growing on other hydroid, from floating dock, 0.2-0.5 m, coll. 10.06.1999 by A. Brinckmann-Voss.

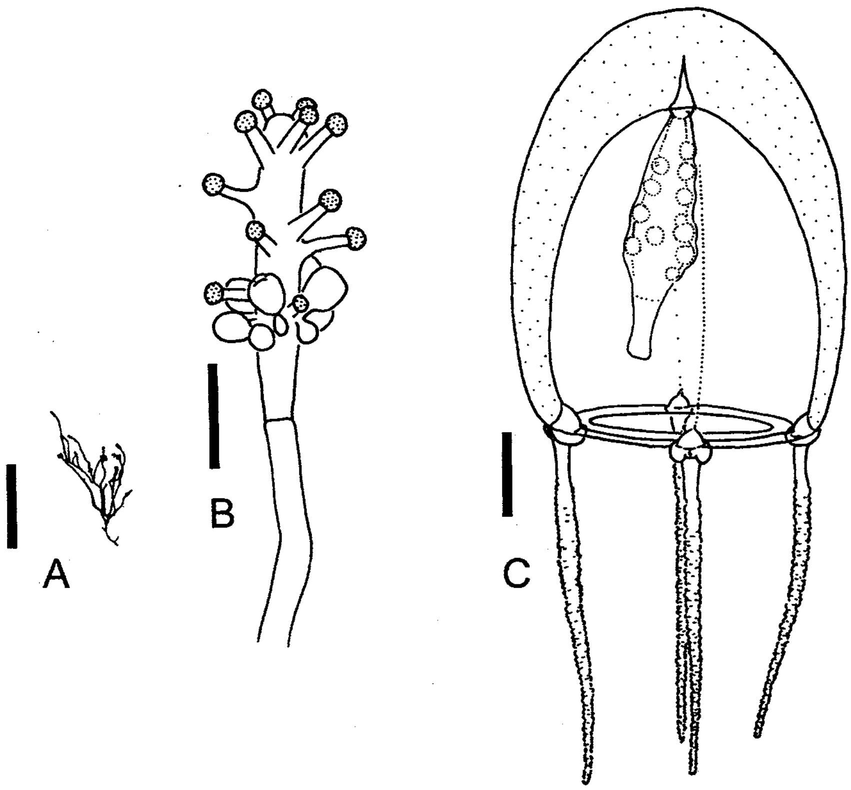

FIG. 4
Coryne cliffordi (Brinckmann-Voss, 1989). A) Hydroid colony, scale bar 1 cm. B) Hydranth with medusae buds, scale bar 0.5 mm. C) Female medusa, scale bar 0.5 mm.

DESCRIPTION – (partly after Brinckmann-Voss, 1989) Hydroid forms bushy colonies up to 2 cm high, stolons tangled but not anastomosed, transition between stolons and caulus indistinct, larger stems usually branched a few times. Stems and stolons enclosed in clear, transparent perisarc. Perisarc often wrinkled and undulated, rarely annulated. Hydranths fusiform, 1.4-1.7 mm in height, with an oral whorl of 4-5 capitate tentacles, oral tentacles 0.2-0.3 mm long, slightly shorter than lower tentacles, stalks not much tapering. Lower capitate tentacles present in 2-4 whorls, each with 4-5 tentacles, whorls sometimes indistinct and tentacles thus scattered. Filiform tentacles absent. Lowest fourth of hydranth free of tentacles. Gonophores develop in clusters of 1-3 among, above, or slightly below the lowest tentacles, 3-20 per hydranth. Gonophores develop mostly independent from tentacles, perhaps by mere coincidence they are sometimes in their upper axils. Colours: hypostome and capitulae white, gastrodermis of body pink, gonophores brown, yellow, or pink. Nematocysts: stenoteles, (18-19) x (12-13) μm and (11-12) x (7-8) μm.

Gonophores are released as free medusae. Newly released medusa 1 mm in height and diameter, exumbrellar nematocysts scattered or in rows, tentacles with about 10 nematocyst clusters, terminal one not enlarged. Nematocysts: stenoteles (10-11.5) x (7-8) µm; desmonemes (8-9) x (4) µm; round heteronemes on the exumbrella, (11-12) x (9-11) µm.

Mature medusa up to 5.5 mm high, diameter 2.5 mm, bell thus higher than wide, bullet-shaped, jelly thick, thicker at apex. Manubrium shorter than height of subumbrella, with large conical apical chamber spanning up to $^1/_2$ of apical mesogloea. Gonad covers nearly the whole manubrium but leaves distal 1/5 free, females with few (10-20) eggs. Radial canals very fine, much thinner than ring canal, barely visible in preserved material. Bulbs with ocellus, epidermal nettle ring thick, not completely encircling bulb. Tentacles issued obliquely or vertically, when extended longer than 1.5 times the bell height, covered by clasping nematocyst clusters, terminal cluster spherical and not enlarged. Colours: manubrium yellow to orange. Nematocysts: stenoteles (12) x (9) µm.

DISTRIBUTION – Pacific coast of Canada.

BIOLOGY – The polyp occurs on mussels, barnacles, and logs. It can tolerate reduced salinity. The life span of medusa is about 5 weeks and it can spawn several times.

REMARKS – *C. cliffordi* medusae resemble *C. eximia*, *C. producta* and *C. japonica.* The very thin radial canals are a characteristic of this species. For further discussions see under these species and table 1.

The reported occurrence of macrobasic euryteles in the newly released medusae (Brinckmann-Voss, 1989) is erroneous (A. Brinckmann-Voss, pers. com.). My own examinations revealed the occurrence of a spherical heteroneme on the exumbrella of the young medusa.

Coryne japonica (Nagao, 1962) Fig. 5A-C

Stauridiosarsia japonica Nagao, 1962: 176, figs 1-5; Kubota, 1976: 231. fig 1.9-12, nematocysts.
[not *Sarsia japonica* Maas, 1909 = *Euphysa japonica*]
Sarsia japonica – Arai & Brinckmann-Voss, 1980: 21, fig. 10; Brinckmann-Voss, 1989: table 2 & 3; Kubota & Takashima, 1992: 371, figs 1-14; Schuchert, 1996: 128, fig. 79a-g.
TYPE LOCALITY – Akkeshi, Hokkaido, Japan.
MATERIAL EXAMINED – see Schuchert (1996), New Zealand material, in part also deposited at MHNG as INVE 27293 (slide).

DESCRIPTION – (after Nagao, 1962; Kubota, 1976; Kubota & Takashima, 1992) Hydroids mostly stolonal, occasionally branched once or twice, height 5-10 mm. Perisarc thin, transparent, entirely smooth. Hydranths 1.3-2.7 mm, diameter 0.3-0.44 mm, cylindrical to slightly clavate, with short dome-shaped hypostome; one oral whorl of 4-5 (max. 6) capitate tentacles, below them 3 whorls of lower tentacles, 4-5 per whorl, total number of capitate tentacles 12-24 (average 18), all tentacles of roughly equal length, stalks only slightly tapering. All capitate tentacles confined to distal half of hydranth. At lower third one whorl of 2-5 filiform tentacles. Gonophores develop among lowest whorls of capitate tentacles or below them, they are inde-

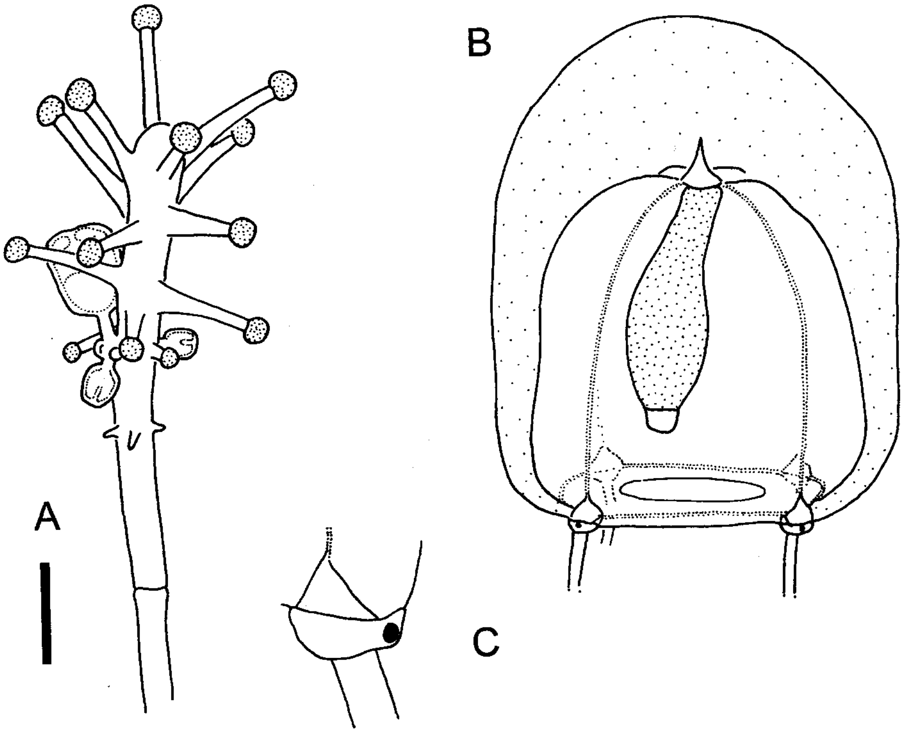

FIG. 5

Coryne japonica (Nagao, 1962), modified after Kubota (1992). A) Cultivated polyp with clusters of medusae buds, scale bar 0.5 mm. B) Mature medusa, (after 48 days), tentacles truncated, bell height 5.2 mm. C) Tentacle bulb, about three times larger than in B.

pendent of the tentacles, on relative long stalks, in clusters of usually up to 4, maximal observed number of gonophores per hydranth 14. Gonophores are released as free medusae. Colour: pink. Nematocysts: stenoteles of two size classes (for measurements see Kubota & Takashima, 1992).

Newly released medusa 1.1-1.4 mm, with exumbrellar nematocysts in eight adradial rows, radial canal wider than ring canal, with apical canal. Maturity in culture is reached after 2-3 weeks.

Mature medusa 3- 6 mm, bell nearly as wide as high, jelly thick, much thicker at apex where jelly is about as thick or thicker than 1/4 of bell height. Umbrella bell-shaped, top rounded. Velum spanning about 1/2 of its radius. Manubrium cylindrical, length about 2/3 to 1/1 of bell cavity, with or without shallow conical apical knob, shape of knob variable. Gonad covers manubrium nearly along its entire length. The radial canals are broader than the ring canal, entering the gastrodermal chamber of the bulb in the adaxial half. Gastrodermal chamber of bulbs triangular in side view. Epidermal nettle ring of bulb complete, abaxial ocellus black or red, tentacles issue bulbs obliquely. Tentacles very long, covered by clasps of nematocyst clusters, terminal cluster globular but not particularly enlarged. Egg size: 105±14 μm, more than 100 eggs per medusa. Nematocysts: two size classes of stenoteles; desmonemes; aberrant stenoteles on exumbrella of young medusa, resembling mastigophores (for measurements see Kubota & Takashima, 1992).

DISTRIBUTION – Coasts of Japan, British Columbia (Canada), New Zealand (Schuchert, 1996).

BIOLOGY – The polyps grow on shells, rock; from the intertidal to depths of 5 m.

REMARKS – *Coryne japonica* and *C. producta* resemble each other very closely. The differences, here considered significant, are listed in table 1. *Coryne nipponica* also resembles these species and the differences are discussed under *C. nipponica.*

Coryne japonica has so far been recorded from Japan (Nagao, 1962; Hirohito, 1988; Kubota & Takashima, 1992), British Columbia (Arai & Brinckmann-Voss, 1980) and New Zealand (Schuchert, 1996). A record from California was regarded as doubtful by Brinckmann-Voss (1989). The only records of the medusa were made by Arai & Brinckmann-Voss (1980) who found the medusa on the coast of British Columbia.

The population from New Zealand identified by myself (Schuchert, 1996) differed in some details from the Japanese one. The polyps had smaller nematocysts, their tentacles were occasionally scattered, gonophores developed also among the second lowest whorl of capitate tentacles. The medusae were slightly smaller, reached maturity in less time, lacked an apical knob, had a less thick jelly, and the nematocyst clusters of the tentacles were arranged like beads. The New Zealand medusae additionally had characteristic tufts of stiff cilia which were so far not observed in Japanese animals. As previous workers might have overlooked these cilia, not too much emphasis can be placed on this difference. If, however, these cilia are absent in medusae from the type locality, the population of New Zealand is probably a separate species.

Coryne nipponica (Uchida, 1927) Fig. 6

Sarsia nipponica Uchida, 1927: 183, pl. 10 fig. 1; Uchida, 1940: 222, fig. 4; Chow & Huang, 1958: 174, pl. 1 fig. 1; Kramp, 1961: 29; Kramp, 1968: 7, fig. 7; Kubota, 1991: 17, figs 1-9; ? Gravier Bonnet & Mioche, 1996: 173, fig. 2E.
Syncoryne nipponica – Nakamura, 1940: 255, figs 1-12; Nakamura, 1941: 185, fig. 1.
? *Sarsia producta* – Vannucci, 1949: 223, pl. 1 figs 1-2.
? *Coryne producta* – Migotto, 1996: 21, fig. 5d-g [not *Sarsia producta* (Wright, 1858)].
TYPE LOCALITY – Seto Marine Biological Laboratory, Misaki Tanabe Bay, Kishu, Japan.
MATERIAL EXAMINED – NSMT-Hy R2690, Japan, Sagami Bay, colony described by Hirohito (1988).

DESCRIPTION – (mainly after Kubota, 1991) Hydroid stolonal, cauli 0.4-1.6 mm, covered by thin periderm without annulations. Hydranths cylindrical to slightly clavate, 1.3-1.9 mm in height, with one oral whorl of 4-5 capitate tentacles, additionally 14-18 lower capitate tentacles scattered over distal 2/3 of hydranth. At lower third there may be a transient whorl of 4 filiform tentacles, these mostly absent in colonies from nature. Gonophores are formed among but independent of the lowest capitate tentacles, mostly two per hydranth, but a few more possible. Gonophores are

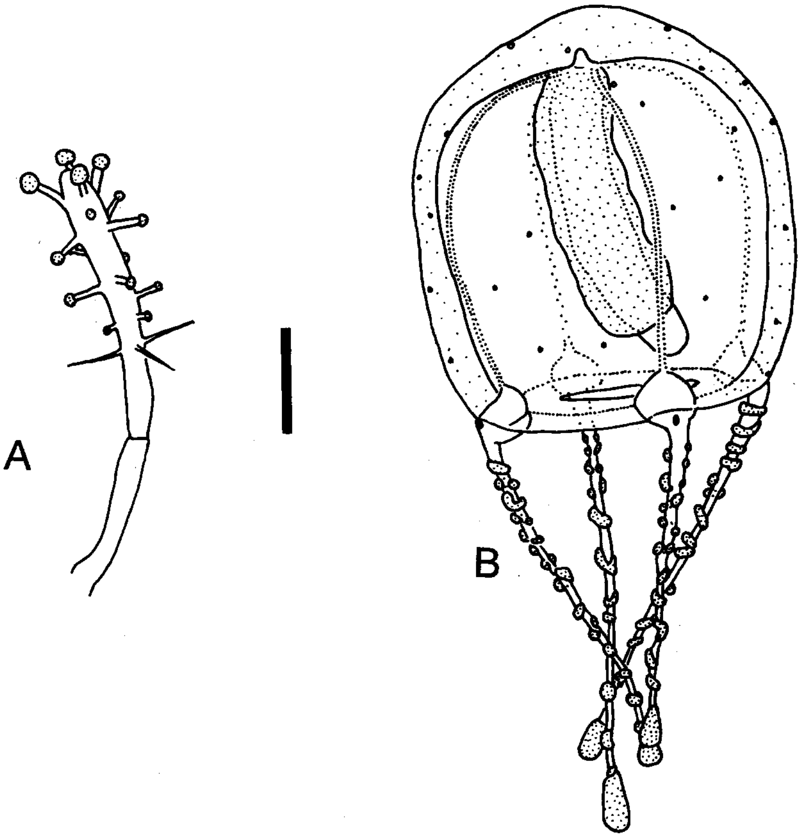

FIG. 6

Coryne nipponica (Uchida, 1927), modified after Kubota (1991), scale bar for both sections equals 0.5 mm. A) Hydranth from culture. B) Mature, cultivated medusa (after 8 days), note short tentacles and low number of nematocyst clasps.

released as free medusae. Colour: pink, reddish brown below hypostome. Nematocysts of polyp: stenoteles, (15-17) x (21-22) µm and (7-8) x (10-11) µm.

Newly released medusa 0.6 mm high, with scattered nematocysts on exumbrella, four short tentacles with only four nematocyst clusters, with or without brown ocelli. Medusa matures within 6 days.

Adult medusa 1.2 mm (nature) to 2.4 mm (culture), only slightly higher than wide, umbrella bell shaped, jelly of moderate thickness, thickness nearly even, only at top slightly thicker. Velum spans 1/2 of its radius. Manubrium nearly as long as height of bell cavity, tubular, with or without a small apical knob, no apical canal. The gonads encircle nearly the whole manubrium, leaving free only a small part near the mouth. Radial canals enter the gastrodermal chamber of the bulbs in the adaxial half. Gastrodermal chamber triangular in side view, abaxial side concave. Each bulb with a brownish-crimson ocellus and a short tentacle, tentacle fully extended only 0.5 to 1.1

times as long as bell size. Tentacles are stout, covered by maximally 13 clasping nematocyst clusters, terminal cluster slightly enlarged and elongated. Egg size: 127 ±10 µm. Nematocysts (see Kubota, 1991 for measurements): stenoteles of various sizes, desmonemes, aberrant stenoteles resembling mastigophores on exumbrella.

DISTRIBUTION – Coasts of Japan, Chefoo (China), ? Brazil, La Réunion.

BIOLOGY – The polyp is known to occur in the intertidal to subtidal region on submerged bamboo, *Mytilus*, floats of a net, and red algae.

REMARKS – *Coryne nipponica* was first described by Uchida (1927) based on mature medusae found in the plankton. Later, Uchida (1940) described its polyp, although he did not observe the full life cycle. The full life cycle was elucidated by Kubota (1991).

Nakamura (1940; 1941) carried out regeneration experiments with hydranths of *S. nipponica*. As a most surprising result he found that regeneration of cut hydranths is strictly dependent on light. No regeneration was observed in the dark. Nakamura's regeneration experiments also showed that *S. nipponica* transiently forms filiform tentacles. The ephemeral character of these filiform tentacles was later confirmed by Kubota (1991).

Sarsia nipponca closely resembles *S. producta* and *S. japonica*. The best character to separate it from the other two species are the short tentacles of the medusa (Fig. 6B). The tentacles are also covered by few nematocyst clusters only. For further differences see table 1.

The material of Sagami Bay examined here lacked filiform tentacles, which, however, is not surprising due to their ephemeral character. This material was also described by Hirohito (1988) and he noted that the newly released medusae had no ocelli. The same observations were made by Uchida (1940). This is in contrast with the observations made by Kubota (1991), who obtained slightly larger medusae with ocelli present even at the earliest stages. Perhaps these are only clone-specific differences or differences due to culture conditions.

Vannucci (1949) and Migotto (1996) identified a corynid polyp from Brazil as *S. producta*. They were able to rear the medusa to maturity. The polyp had more than the usual two whorls of lower capitate tentacles and the mature medusa reached only 3 mm in height, had no apical canal, and had short tentacles covered by only a dozen nematocyst clusters. These are all characteristics of *Sarsia nipponica* and the Brazilian records are here referred to this species (see also under *C. producta*).

Recently, Gravier Bonnet & Mioche (1996) recorded *Sarsia nipponica* from La Réunion (Indian Ocean).

5.1.1.2. ***Coryne hincksii*** group

This group comprises the species *C. hincksii*, *Coryne sagamiensis*, and *C. crassa*. Although perhaps not a clade, they all have gonophores with a ring canal. Distinguishing characters are given in table 2.

TABLE 2. Distinguishing characters of the *Coryne hincksii* group

character	*C. hincksii*	*C. crassa*	*C. sagamiensis*
colony	branched	branched	stolonal
gonophore oblong	yes	no	variable
gonophore with velum	no	yes	yes

Coryne hincksii Bonnevie, 1898 Fig. 7A-C

Coryne hincksii Bonnevie, 1898a: 492, pl. 27, fig. 48-49; Rees, 1956: 109; Calder, 1972: 222, pl. 1 fig. 6; Schuchert 2001: 46, fig. 32A-C.

? *Dipurena uchidai* – Petersen, 1990: 212

TYPE LOCALITY – Hammerfest, Norway 183 m.

MATERIAL EXAMINED – ZMUC, Greenland, Hellefiskebanke, 21.08.1976 – ZMUC, Greenland, 59.99°N 43.93°W, 30-40 m, 19.08.1970 – ZMUC, Greenland, 59.88°N 43.53°W, 225 m, 20.08.1970 – ZMUC, labeled *Coryne uchidai*, Russia, Vladivostok, 42.27°N 130.73°E, 130-225 m, on cable, mentioned in Petersen (1990) – ROMIZ B562, Canada, Frozen Strait, 66°13'N 85°09'W, 85-92 m, 29.08.1961, material described by Calder (1972) as *C. pusilla*, branched colony, with annulated perisarc, but some sporosacs seem to have radial canals and the sporosacs appear not to be in the axils of the tentacles, thus this material is perhaps also *C. hincksii*, however, contraction of the material does not allow a detailed investigation.

DESCRIPTION – Hydroid up to 2 cm, stems branching 1-3 times, 0.25-0.3 mm in diameter, perisarc thick, mostly smooth, occasionally corrugated, rarely annulated. Hydranths 1.5-2.2 mm in height, 0.4 mm in diameter, spindle-shaped, 16-22 scattered capitate tentacles, oral tentacles 4-6, without filiform tentacles. Gonophores are sessile sporosacs, 4-12 developing among but independently of the tentacles in lower half of hydranth, sometimes up to three sporosacs clustered, stalk of sporosacs longer than in other species. Sporosacs oblong, up to 1 mm length and 0.7-0.75 mm wide when fully developed, at distal end a clearly visible ring canal of narrow diameter, radial canals only occasionally visible, spadix distinct, without bulbs or tentacle rudiments. Nematocysts: stenoteles of two size classes, (16-18) x (11-12) µm and (28-29) x (18-20) µm.

REMARKS – *Coryne hincksii* differs from *Coryne pusilla* in developing its gonophores independently from the tentacles. *Coryne pusilla* carries them in the upper axils of the tentacles. Furthermore, *Coryne hincksii* has sporosacs with a distinct circular canal and the sporosacs are longer and more elongated. Additionally, the perisarc of *Coryne pusilla* is usually annulated. However, this is not a diagnostic trait.

The radial canals of *C. hincksii* could only be seen in a minority of the sporosacs. There were not always four canals present in these cases. It appears that the radial canals in this species are only occasionally formed. More likely, they are so narrow that they often cannot be seen properly using a stereomicroscope or unsectioned material. Bonnevie (1898a) described this species as having radial canals. Rees (1956) re-examined her type material and was unable to find the radial canals. Calder (1970) examining Canadian material found radial canals only occasionally, just like my own observations on material from Greenland. This variability certainly explains the discrepancy of Bonnevie's and Rees' observations.

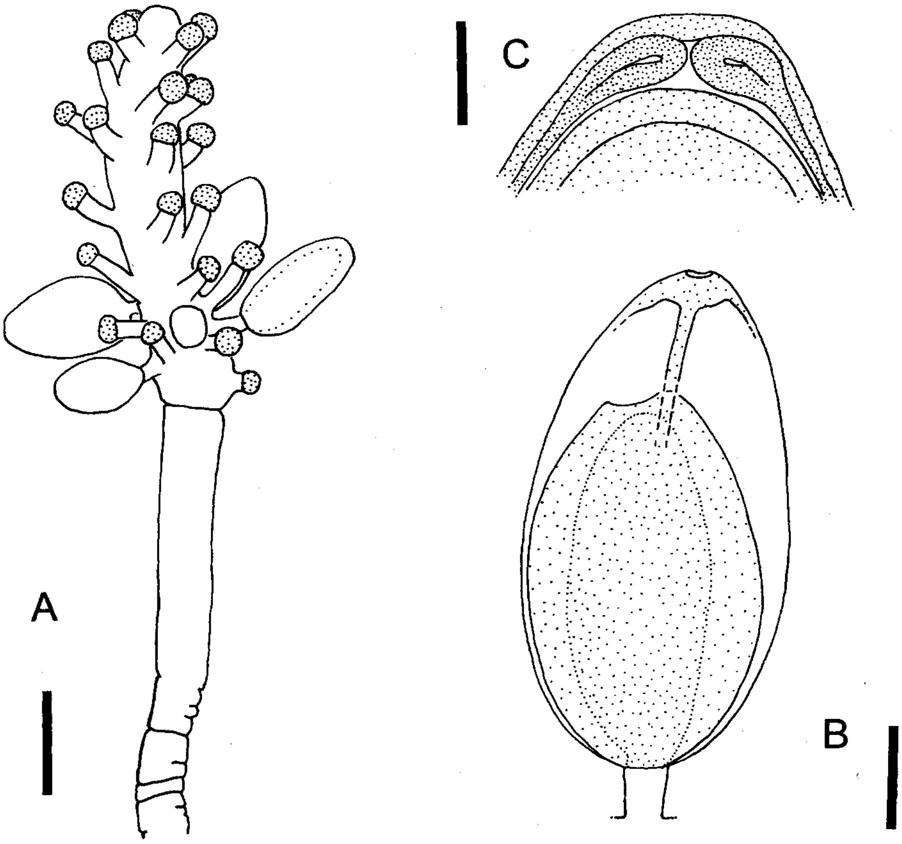

FIG. 7
Coryne hincksii Bonnevie, 1898 from Cape Farewell, Greenland. A) Hydranth with sporosacs, scale bar 0.5 mm. B) Male sporosac, note presence of radial canals, scale bar 0.2 mm. C) Optical section of a young sporosac showing circular canal, scale bar 0.1 mm.

In the examined material it was not possible to see a button of high gland cells around the mouth. However, for a reliable investigation histological sections must be made.

Material from Vladivostok identified as *C. uchidai* by Petersen (1990) was reexmined by me and I think it belongs to *C. hincksii*, although radial canals could not be seen reliably and it forms larger and more robust colonies than *C. hincksii* from the Atlantic.

DISTRIBUTION – An Arctic species known from the coasts of Norway, Canada, Greenland, perhaps also off Vladivostok, Russia.

Coryne crassa **Fraser, 1914** Fig. 8A-B

Coryne crassa Fraser, 1914: 113, pl. 2 fig. 3; Fraser, 1937: 27, fig. 10; Brinckmann-Voss, 1996: 96.
[not *Syncoryne crassa* Pictet, 1893 = *Pteroclava crassa* (Pictet, 1893)]
TYPE LOCALITY – Friday Harbour, Washington, USA.
MATERIAL EXAMINED – original material of Fraser from Friday Harbour, possibly type material (see Arai, 1976), BCPM 976-129-2, slide, with gonophores.

DESCRIPTION – (in part after Fraser, 1914) Hydroid slightly and irregularly branched, reaching a height of 15 mm. Branches originate at wide angle, stem and branches of same diameter, perisarc corrugated or with occasional annulations. Perisarc ends at base of hydranths without dilation. Hydranths 1.5-2 mm, fusiform, with an oral whorl of 4 tentacles and below them additional 10-15 tentacles scattered over nearly the whole length of the hydranth. Hypostome comparatively long, mouth without button of high gland cells. Several gonophores develop in clusters below or above the proximal tentacles, often on one side of the hydranth only. Gonophores 0.7 mm to 1 mm (uninflated), seated on relatively long stalks. Gonophores remain presumably fixed as sporosacs, but at maturity perhaps with umbrella. Almost mature gonophores have a truncated distal end with a velum-like structure as well as a broad ring canal. Tentacles are absent (Fig. 8B). The manubrium with the gonad fills nearly the whole subumbrellar cavity. Colours: stem and branches horn colour, hydranths and sporosacs pink, spadix red to pink.

DISTRIBUTION – Known from type locality only.

REMARKS – Some medusa-like gonophores in the type slide suggest that the mesogloea of mature gonophores swells like that of a free medusa before it is released. The presence of a circular canal as well as a velum-like structure (Fig. 8B) are quite evident. Radial canals or rudimentary bulbs could not be seen, but their presence in fully mature gonophores is possible. Radial canals can be invisible in slide preparations. Also in slides of *C. lovenii* and *C. sagamiensis*, which definitely have these canals, they are often invisible. Further observations on living material or histological cross-sections are needed to reveal more details on the gonophore morphology *C. crassa.*

Coryne crassa resembles closely *C. hincksii*, however, a velum is absent in the latter species. Differences to *C. sagamiensis* are also minimal and consist in the branched stems and occasional perisarc annulation of *C. crassa.*

Coryne sagamiensis **Hirohito, 1988** Fig. 9A-D

Coryne sagamiensis Hirohito, 1988: 33, fig. 10d-f.
TYPE LOCALITY – Amadaiba, Sagami Bay, Japan, 90 m.
MATERIAL EXAMINED – Type material, NSMT-Hy numbers 648 to 652, Sagami Bay (see Hirohito, 1988), slides and alcohol material.

DESCRIPTION – Hydroid stolonal, cauli 1-1.5 mm high, perisarc cover doubles diameter towards distal, smooth or slightly and irregularly undulated, never annulated, transparent, some with very fine longitudinal striations. Hydranth about 1.5 mm in height, spindle-shaped, tentacles confined to distal 2/3, just below them an annular thickening of the epidermis. Tentacle number about 16-21, one oral whorl of 4-5

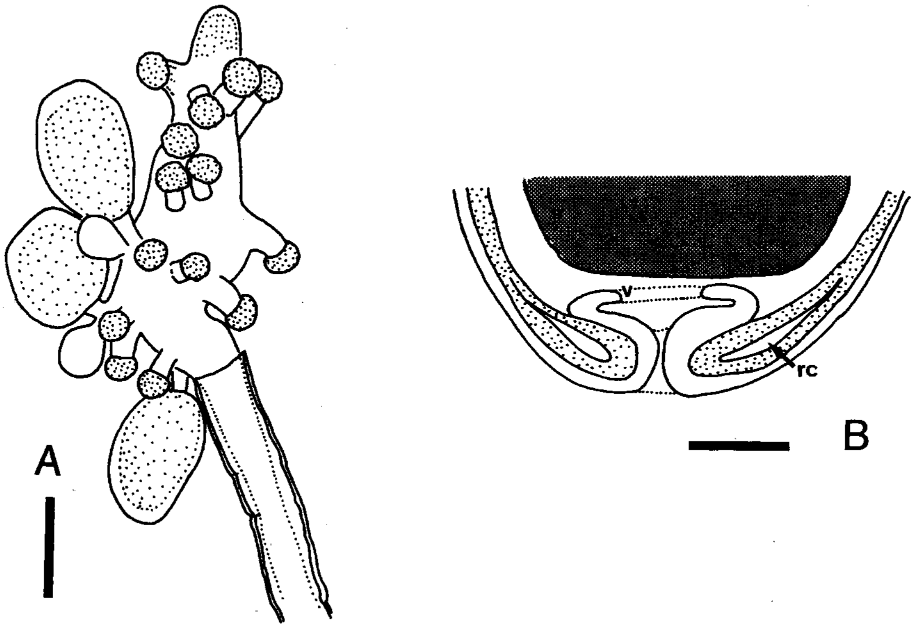

FIG. 8

Coryne crassa Fraser, 1914, syntype material. A) hydranth with gonophores, *camera lucida* drawing, this might be the same hydranth as depicted by Fraser (1914), scale bar 0.5 mm. B) distal end of advanced gonophore in optical section, scale bar 0.1 mm, gastrodermal tissue lightly stippled, manubrium and gonads dark, v velum, rc ring canal.

tentacles, 10-16 lower capitate tentacles scattered or in indistinct whorls, length of tentacles rather uniform except for the oral ones which are shorter than the lower tentacles. Hypostome rounded, without button of high gland cells.

Gonophores develop around middle of hydranth body, about 1-3 per hydranth, in upper axil or independent of tentacles. Gonophores remain fixed as medusoids, umbrella spherical to oblong, 1.1 mm, jelly thin and even, distal opening narrow, with four distinct radial canals, circular canal, four marginal bulbs with nematocysts, no ocelli and no tentacles. Manubrium bulbous, size about 2/3 of bell cavity. Gonads completely cover manubrium and nearly fill bell cavity. Eggs numerous (>100), in one layer, high, polygonal. Distal half of exumbrella studded with nematocysts.

Nematocysts: stenoteles of two sizes, (19-21) x (12-17) µm and (11-13) x (6-7) µm.

DISTRIBUTION – Known from type locality only.

BIOLOGY – The polyps grows on other hydroids in depths of 60-100 m.

REMARKS – Although the formal differences from other species of this group appear minimal, *Coryne sagamienesis* is likely a distinct species. It is characterised by the purely stolonal colonies, the smooth and dilated perisarc of the caulus, the relatively long basal part of the hydranth that is free of tentacles, and the annular epidermal thickening. Its gonophores are more rounded than the ones of *C. hincksii*.

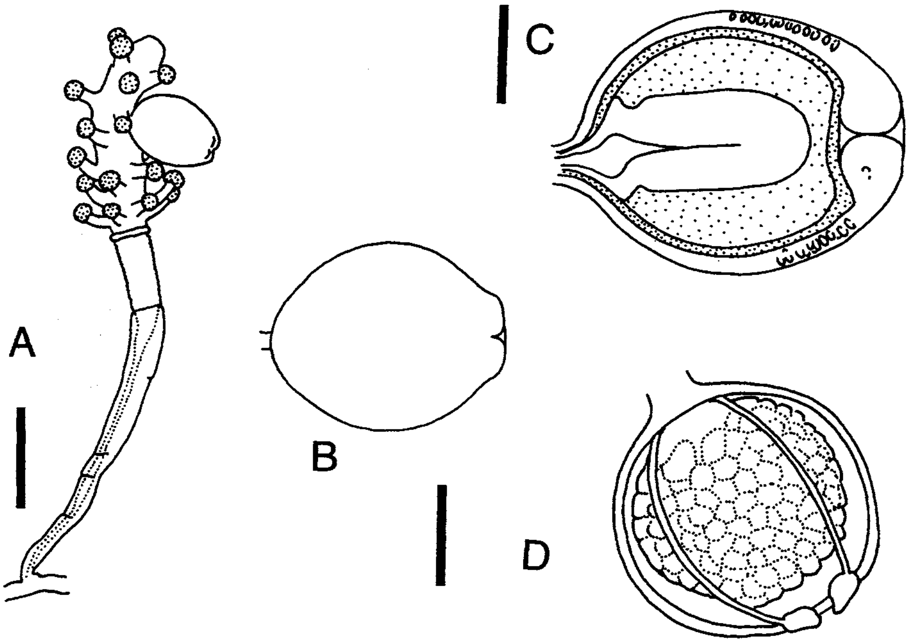

FIG. 9

Coryne sagamiensis Hirohito, 1988. A) Single stem with gonophore-bearing hydranth, scale bar 0.5 mm. B) Outline of medusoid from ethanol material, scale bar 0.2 mm. C) Optical cross-section of a immature male medusoid, scale bar 0.1 mm. D) Schematic drawing of a mature female medusoid, drawn from slide preparation, shape may be distorted, same scale as B.

Contrary to the view of Petersen (1990), perhaps inspired by the figures of Hirohito (1988), the gonophores of *C. sagamiensis* do not exclusively develop in association with tentacles, although some may be found in their proximity by mere coincidence.

5.1.1.3. *Coryne brachiata* group

This group comprises at present only one species. The peculiar brachioles (nematophores?) distinguish this species from all the other members of the Corynidae.

Coryne brachiata Nutting, 1901 Fig. 10A-B

Coryne brachiata Nutting, 1901: 159, 165, pl. 14 figs 1-2; Fraser, 1937: 26, pl. 2 fig. 8.
TYPE LOCALITY – Yakutat, Alaska, USA.
MATERIAL EXAMINED – syntype material, USNM no. 71384 and no. 70508, Yakutat, Alaska.

DESCRIPTION – Hydroid branched, 1 cm, straggling, branches originate at very acute angles, shoots thus slender, branching up to fourth degree. Perisarc annulated throughout. Hydranths typical for genus, with 20-35 scattered capitate tentacles, without filiform tentacles. Gonophores develop between the capitate tentacles. Gonophores sessile sporosacs, spherical, without radial canals, females with 12-20 eggs.

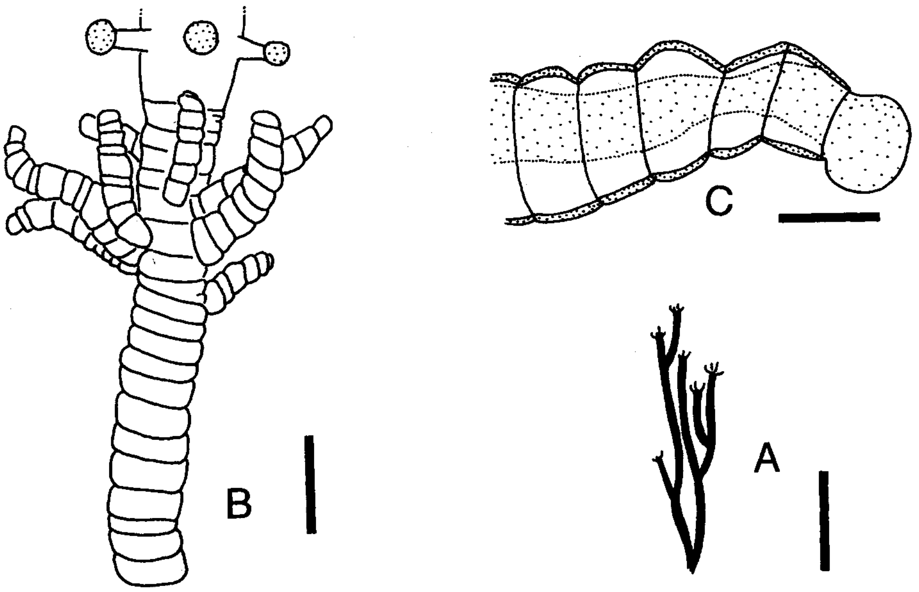

Fig. 10
Coryne brachiata Nutting, 1901, after type material. A) Colony form, scale bar 5 mm. B) Distal part of caulus with brachioles (perisarc covered tentacles), scale bar 0.5 mm. Brachiole in higher magnification, note that coenosarc protrudes at tip, scale bar 0.1 mm.

With numerous arms at distal end of caulus in perisarc covered zone, scattered in a small band. These arms mostly unbranched, but some branched once, diameter at origin about 1/3 to 1/2 of caulus diameter, tapering towards distal, covered by perisarc which is annulated throughout, distal end with opening where a small spherule of coenosarc protrudes.

Distribution – Known from type locality only.

Remarks – *Coryne brachiata* is unique among the Capitata in having tentacle-like appendages (brachioles) covered by perisarc (comp. Fig. 10B). Although it was not possible to see nematocysts in the capitae of these arms in the available material, they might normally be present. The function of these arms remains enigmatic, but possibly they are defensive and correspond to nematophores. The origin of the gonophores could not be seen reliably in the available material. Thus it is uncertain whether they are associated with tentacles or not.

5.1.2. ***Coryne*** species with axillary gonophores

As mentioned in the introduction, this clade is revealed by the synapomorphic trait of gonophores that develop solely in the upper axil of the lower capitate tentacles.

5.1.2.1. *Coryne pintneri* group

This group comprises *Coryne pintneri*, *C. filiformis*, and *C. uchida*. They form stolonal or sparingly branched colonies, have sessile sporosacs in the axil of the tentacles, and possess filiform tentacles. Distinguishing characters are given in table 3.

TABLE 3. Distinguishing characters of the *Coryne pintneri* group

character	*C. pintneri*	*C. filiformis*	*C. uchidai*
tentacle numbers	15-26	28-36	25-30
filiform tentacles	present	present	transiently present
eggs in one whorl	no	no	yes
viviparous	no	no ?	yes

Coryne pintneri Schneider, 1898 Fig. 11A

Coryne pintneri Schneider, 1898: 476; Brinckmann-Voss, 1970: 53, text-figs 59-64, pl. 3 fig. 3; Edwards & Harvey, 1983: 37, fig. 1.

Staurocoryne pintneri – Rees, 1936: 140.

Staurocoryne spec. – Swedmark, 1975, figure in obituary, Cah. biol. Mar., vol 16.

TYPE LOCALITY – Rovigni, Adriatic Sea.

MATERIAL EXAMINED – BMNH 1974.11.21.15, Naples, from *Posidonia*, cultivated for 6 months, preserved November 1962, material described in Brinckmann-Voss (1970), infertile, not well preserved – BMNH 1956.10.24.10, as *Staurocoryne filiformis*, identified by W. J. Rees, collected 12.9.1956 at Roscoff (Brittany), single hydranth with filiform tentacles, without gonophores, growing on white unidentified substrate, is better referred to *C. pintneri* but may also be *C. producta*. – IRSNB 27.838 as *C. filiformis*, Roscoff, coll. J. Bouillon Sept. 1965 and 1966, infertile, growing on *Bugula* together with *Zanclea* spec. – Villefranche-sur-Mer, Ligurian Sea, Mai 2001, several small, infertile colonies growing on rock in a depth of about 1 m, cultivated, sporosacs and filiform tentacles formed in secondary hydranths.

DESCRIPTION – (in part after Brinckmann-Voss, 1970) Hydroid mostly stolonal, occasionally sparingly branched with two hydranths, rarely up to five side branches, maximally 1-2 cm in height. Perisarc mostly smooth, not thick, yellowish, annulated for occasional stretches at origin of side branches and cauli or at other places. Cauli perisarc-covered, up to 3 mm high. Hydranths cylindrical, 1.2-1.6 mm from filiform tentacles to mouth. With 15-21 tentacles, either scattered or in whorls each with 3-4 tentacles. Oral capitate tentacles with 14-17 gastrodermal cells. Below capitate tentacles one whorl of 2-6 filiform tentacles, often absent, especially in colonies from agitated waters. Gonophores develop in two whorls in upper axils of tentacles in middle of hydranth body, often two gonophores of different developmental stage per tentacle. Gonophores remain fixed as sporosacs. Sporosacs spherical, about 0.3 mm, without radial or circular canals. Females with numerous eggs. Sexual products are shed into the water, development takes place in the free water. Nematocysts: stenoteles of two size classes.

After Edwards & Harvey (1993) there is often also an annular thickening at the base of the hydranth, possibly associated with caulus elongation.

DISTRIBUTION – Mediterranean, coasts of Brittany (France) and Scotland.

BIOLOGY – The polyp grows on *Posidonia oceanica* (sea grass), on *Peysonnellia* (red algae), and also on rock in depths of 1-30 m. Sporosacs are formed from March to end of May (Brinckmann-Voss, 1970). Tardent & Stössel (1971) and Tardent & Schmid (1972) described the morphology of mechano-receptors in the filiform tentacles. The reactions to mechanical stimulation is described in Stössel & Tardent (1971).

REMARKS – The filiform tentacles are often missing, especially in colonies from agitated waters (see Brinckmann-Voss, 1970; Edwards & Harvey, 1983). Such colonies are indistinguishable from juvenile *Coryne pusilla* and a culture is necessary for a correct identification. In culture, the filiform tentacles are always formed by *C. pintneri* and mature *C. pusilla* form branched colonies with several hydranths. It is likely that many earlier authors misidentified *C. pintneri* lacking these filiform tentacles as *C. pusilla* (Brinckmann-Voss, 1970).

Edwards & Harvey (1983) found *C. pintneri* also in Scotland, thus the distribution of *C. pintneri* and *C. filiformis* overlap. Both species resemble each other extraordinarily and can only be distinguished by their tentacle numbers and the hydranth size. *Coryne pintneri* has 15-26 capitate tentacles and the hydranth is about 1.5 mm high, while *C. filiformis* has 28-36 capitate tentacles and the hydranth reaches a size of 3.5 mm. *Coryne pintneri* seems also to prefer more warmer temperatures than *C. filiformis* (Edwards and Harvey, 1983). Tentacle number is otherwise not considered to be a criterion of much use in distinguishing *Coryne* species. Further studies are clearly needed to prove that *C. filiformis* is separate from *C. pintneri*.

It is well possible that the higher tentacle number of *C. filiformis* as described by Rees (1936) was just a population-specific trait. Rees (1938) later described a finding of a colony from near Plymouth, the only description of *C. filiformis* hydranths from nature. These hydranths were smaller than his previous cultivated ones and his figure shows 22 tentacles (but some might be hidden). These polyps seem indistinguishable from *C. pintneri* as depicted in Edwards & Harvey (1983: fig. 1). Rees also deposited a corynid in the British Museum which he collected at Roscoff (see material examined). This single, infertile polyp was only 1.2 mm high and had only about 18 tentacles. It thus conforms better with *C. pintneri*. This can be interpreted that Rees perhaps did not consider the tentacle number as decisive for separating his *C. filiformis* from *C. pintneri*. However, at the time of Rees' publication, he could not know the gonophores of *C. pintneri* as they were only described in 1970 by Brinckmann-Voss. Material from Roscoff collected by J. Bouillon in 1965 and 1966, now held by the IRSNB, was likewise identified as *C. filiformis*, despite being infertile. The tentacle numbers of these specimens varied between 16 and 24 (7 hydranths examined) and the hydranths measured about 1.5 mm in height, the tentacle whorls were distinct only in the lower half. Both Rees' and Bouillon's material from Roscoff is here assigned to *C. filiformis*. Identical material was also found by myself at Roscoff in June 2000. The infertile polyps were growing on a holdfast of a laminarian alga and they grew reasonably well in culture, although they did not produce gonophores (after 3 months). The colony was surprisingly sensitive to low temperatures (12 °C). It immediately reduced all hydranths at this temperature and did not form them again. However, the colony grew at 20-25 °C, although few new hydranths were formed. The filiform tentacles appeared after 2 whorls of capitate tentacles had developed. This thus makes it less probable that it might have been *C. producta*.

Coryne filiformis (Rees, 1936) Fig. 11B

Staurocoryne filiformis Rees, 1936: 135, figs 1-11; Rees, 1938: 38.
Coryne filiformis – Edwards & Harvey, 1983: 41; Petersen, 1990: 211.
TYPE LOCALITY – Stoke Point, Plymouth, England.

DESCRIPTION – (after Rees, 1936 and Rees, 1938) Hydroid stolonal or slightly branched, several mm high. Perisarc mostly smooth, annulated at origin of branches and cauli. Hydranths on caulus, fully grown hydranths 3.0 to 3.5 mm in height, with 28-36 tentacles, these either scattered or in 7-9 whorls with four tentacles arranged cross-like and tentacles of adjacent whorls often in alternate positions. Below capitate tentacles 4-5 filiform tentacles that are often vestigial or reduced in older hydranths. Filiform tentacles of secondary polyps develop only after several whorls of capitate tentacles are present. Filiform tentacles may have few nematocysts. Gonophores develop in axils of tentacles in middle of hydranth, mostly one, sometimes two or three, in one whorl. Gonophores remain fixed as sporosacs. Female sporosacs lack circular and radial canals, spherical, size 0.35 mm. Initially they contain a large number of eggs that are later reduced to about 10-20. Male gonophores unknown.

DISTRIBUTION – Coasts of Great Britain.

BIOLOGY – Reported to grow on dead *Eunicella verrucosa* (Pallas) and on *Pecten* shells.

REMARKS – For the distinction of the closely resembling *Coryne pintneri* see under this species.

Coryne uchidai Stechow, 1931 Fig. 12A-E

Coryne uchidai Stechow, 1931: 178; Stechow & Uchidai, 1931: 546, fig'd; Kakinuma, 1960: 137-140, figs. 1-2.
not *Dipurena uchidai* – Petersen, 1990: 212
TYPE LOCALITY – Tsuchia, Asamushi, Mutsu Bai, Japan.
MATERIAL EXAMINED – material identified and processed to slide by Stechow, putative holotype, ZSM, as *Coryne uchidai*, Japan, Mutsu Bay, one slide with two hydranths; the red framing of the label also indicates this being the holotype.

DESCRIPTION – (in part after Kakinuma, 1960) Hydroid stolonal or sparingly branched. Perisarc corrugated or wrinkled, but not annulated. Hydranths clavate, 1.6 mm high, 0.36-0.48 mm diameter, with 25 to 30 scattered capitate tentacles. Tentacles quite long, length of tentacles and size of capitulum decreasing towards proximal. Oral tentacles with 12-15 gastrodermal cells. Young hydranths have four aboral filiform tentacles, which are later reduced to a ring-shaped vestige or are completely lost. Numerous gonophores develop in the upper axils of the lower tentacles, either singly or two to three gonophores of different developmental stages closely grouped together. Gonophores are fixed sporosacs, without canal system. Mature male gonophores about 0.4 mm, with a short stalk, broadest near base, then conical with pointed

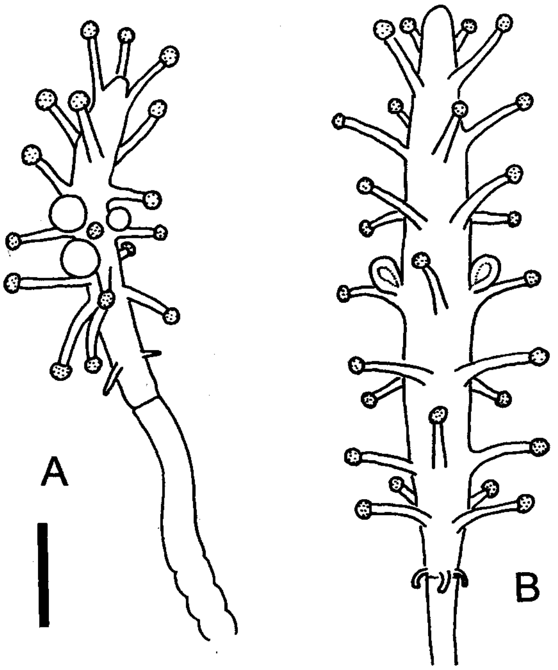

FIG. 11
A) *Coryne pintneri* Schneider, 1898, combined from various sources, scale bar 0.5 mm. B) *Coryne filiformis* (Rees, 1936), modified after Rees (1936), scale approximately like in A.

distal end (drop-shaped). Spermatozoa are ejected through hole at the pointed end. Mature female gonophores about the same size as male ones, spherical, with short stalk, with 4-5 eggs (up to 9 possible), arranged in one ring around spadix, egg size 0.1-0.15 mm. Eggs are fertilised while still within the sporosac and the planulae develop within the sporosac or remain attached to the spadix after rupture of the sporosac casing.

BIOLOGY – Colonies grow on rocks and seaweeds and show periods of dormancy in summer, with gonophores present from March to April. The polyps feed on copepods, amphipods and annelids (Kakinuma, 1960). Kakinuma (1961) and Hirai & Kakinuma (1960) described more morphological details of this species.

DISTRIBUTION – Mutsu Bay, Japan.

REMARKS – Stechow (1931) based his initial description on two hydranths only. Stechow & Uchida (1931) provided a figure of this very material, which is still kept in the ZSM. The figure of the colony fragment in Stechow & Uchida (1931, fig. 1B), corresponds exactly to the fragment present on the slide. This material must therefore be the material on which the first description was based, hence the holotype. Later, Kakinuma (1960) described the male gonophores and life cycle using material

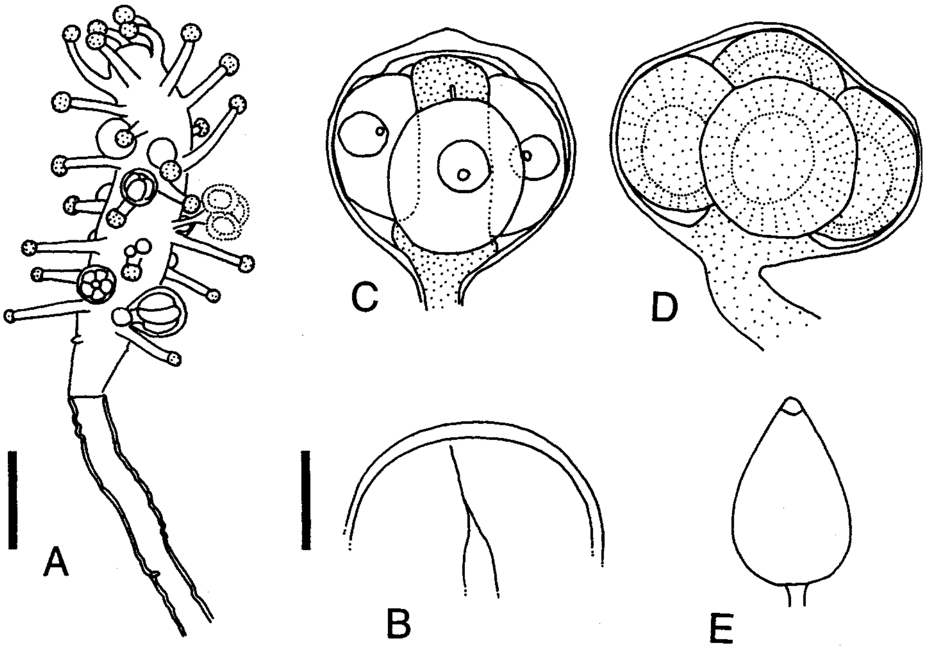

FIG. 12
Coryne uchidai Stechow, 1931. A-D, after possible type material. A) hydranth with gonophores, scale bar 0.5 mm. B) Optical longitudinal section through mouth region, scale bar 0.1 mm. C) Mature female gonophores, note large pronuclei, same scale as B. D) Female sporosacs with planulae, same scale as B. E) Shape of male gonophores, redrawn from Kakinuma (1960).

from the same region. Kakinuma (1960) described the female gonophores as having a transient discoidal structure at their distal end. Such a structure was not found in the present material, but the distal half of the mature female gonophores had a thickened epidermis (Fig. 12) with an even thicker margin. This structure certainly corresponds to the one observed by Kakinuma. Perhaps this thickening forms a discoidal end in living material only (see figures in Kakinuma, 1960). Kakinuma (1960) noted that the gonophores develop in the upper axils of the capitate tentacles. This was also observed in the present material. *Coryne uchidai* appears not to have high gland cells around the mouth opening. Petersen (1990) placed this species in the genus *Dipurena* owing to the gonophores that are independent from the tentacles. Petersen's material (ZMUC, as *Dipurena uchidai*, Vladivostok, 130-225 m, coll. 9.03.1895) was reexamined for this study. The colonies are large and branched. The sporosacs develop indeed independently from the tentacles. They are oblong and arise in clusters of up to 3 sporosacs. I am convinced that this colony is not *C. uchidai* and it is better referred to *C. hincksii*.

Coryne uchidai resembles *C. pusilla*, but clearly differs by its filiform tentacles (often absent), by vivipary, by the low number of eggs arranged in one ring around the spadix, by the thickened epidermis of the female gonophore, and by the pointed male gonophore.

5.1.2.2. *Coryne eximia* group

This group contains only *C. eximia*, but *C. gracilis* most probably belongs also to this group, if it is not altogether conspecific with *C. eximia*. Differences are discussed below.

Coryne eximia Allman, 1859 Figs 13A-D & 18B-C

Coryne eximia Allman, 1859: 141; Petersen, 1990: 211, fig. 43A-C.
Syncoryne eximia – Allman, 1871: 262, fig; Haeckel, 1879: 17, pl. 1 fig. 5; Fraser, 1944: 41, pl. 4 fig. 14.
Coryne tenella Farquhar, 1895: 208, pl. 13 fig. 5.
Sarsia bretonica Hartlaub, 1904: 99, *nomen nudum*; Hartlaub, 1907: 10, fig. 2a-b.
Syncoryne tenella – Bale, 1924: 228; Ralph, 1953: fig. 15, Schuchert, 1996: 125.
Sarsia eximia – Browne, 1905: 756; Mayer, 1910: 57, fig. 20; Hartlaub, 1907: 8, figs 1-2; Vanhöffen, 1913b: 4, fig. 1, pl. 1 fig. 1, pl. 2 fig. 1; Russell, 1938: 150, figs 8-12; in part Berrill, 1953: 281, figs 4-5 (not others); Russell, 1953: 50, text fig. 17A, 18A-B, plate 2 fig. 3; Kramp, 1959: 79, fig. 15; Kramp, 1961: 27; Kramp, 1966: 2; Bodo & Bouillon, 1968: 83, fig. 4; Brinckmann-Voss, 1970: 68; Russell, 1970: 232; Millard, 1975: 52, fig. 20A-D; Brinckmann-Voss, 1989: 688, figs 5-6; Altuna Prados, 1993: 28, fig. 1; Schuchert, 1996: 125, figs 77a-h, 78; Watson, 1997: 506, fig. 2A.
? *Sarsia eximia* – Goy, Lakkis & Zeidane, 1991: 101, fig. 3.
? *Sarsia tubulosa* – Goy, Lakkis & Zeidane, 1991: 102, fig. 5.
TYPE LOCALITY – British Isles.
MATERIAL EXAMINED:
France – MHNG INVE 25126, Roscoff, France, tonne du pot de fer, 15.4.1919, preserved, large polyp colony on *Mytilus edulis*, with medusae buds, height up to 25 mm – Roscoff, several living colonies collected by author underneath pier of Île de Batz ferry, 31.5.2000, young medusae reared until incipient gonads visible (3 days), one colony preserved as NHMG INVE 29982 – Roscoff, 5.6.2000, living, adult medusae from plankton of 10-20 m depth.
Great Britain – ZMUC, Plymouth, 4.10.1906, det. E. Browne, polyps, 3 cm colony, with medusae buds, some hydranths with thin perisarc cup at base.
New Zealand – Wellington and Goat Island, see Schuchert (1996).
Chile – ZMUC, 31°51.5'S 71°35'W, 25.02.1960, coll. E. Fagetti, det Kramp, 2-3 mm high medusae, bell cylindrical, terminal tentacle cluster small.

DESCRIPTION – (after examined European material) Hydroid erect, 1-5 cm, branching. Shoots irregular, no main stem, often forming tufts, up to 20 hydranths per shoot. Perisarc of branches smooth with some annulated stretches. Hydranths 1.5-1.8 mm high, diameter 0.3 mm, spindle-shaped or cylindrical, on pedicels of 1-2 mm length or at end of branches, occasionally perisarc funnel shaped at base of hydranths (collar, sheath). Hydranth with up to 20 capitate tentacles, 4-5 oral tentacles, remaining lower tentacles scattered over nearly entire hydranth leaving only at base about 1/6 of height free, hypostome large, rounded. Oral tentacles attached obliquely, length 1-1.5 times the diameter of the hydranth body, most proximal tentacles shorter. Tentacles not much tapering, diameter of capitulum about two times diameter of tentacle stalk. Gonophores develop in upper axils of lower tentacles, up to 3 per tentacle, released as free, immature medusae. Colours: hydranths orange-red, some greenish. Nematocysts: stenoteles, (18-20) x (11-15) µm and (11-13) x (6.5-7) µm.

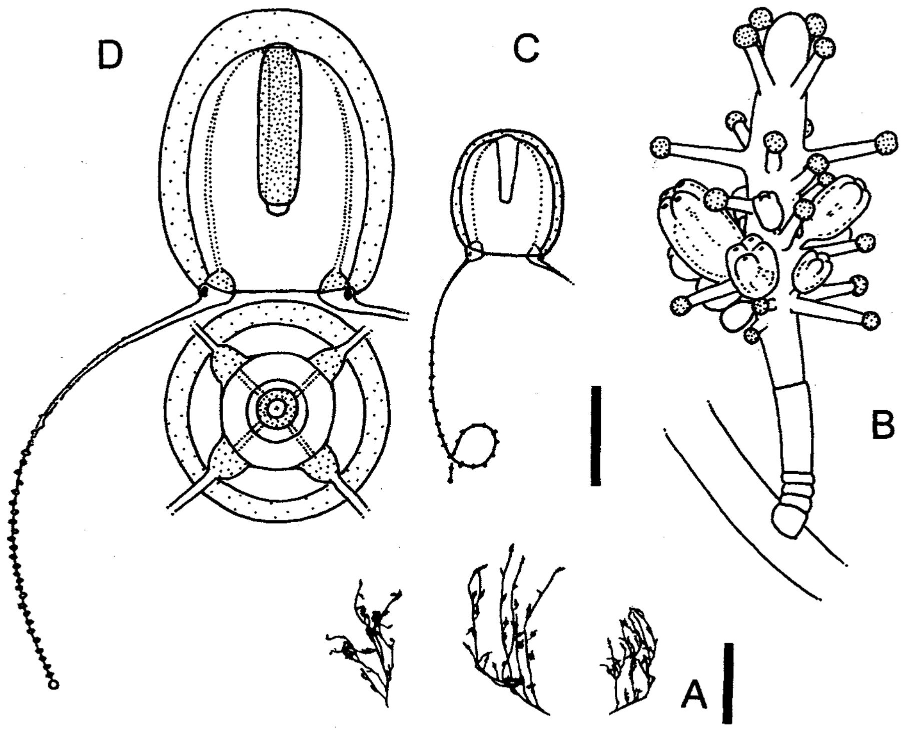

FIG. 13
Coryne eximia Allman, 1859; after living material from Roscoff, France. A) Three different shoots, scale bar 1 cm. B) Hydranth with medusae buds, scale bar 0.5 mm. C) Newly released medusa, only one tentacle shown, scale bar 1 mm. D) Mature male in side view (top) and seen from below (bottom), same scale as C.

Newly released medusa 1.2 mm high, exumbrella with scattered stenoteles, ocelli dark brown-red, no gonads visible, tentacles with approx. 30 nematocyst clusters, cnidocils short and fine, no tufts of cilia on tentacles.

Adult medusa 2-3 mm (reportedly up to 10 mm), normally bell-shaped, diameter slightly less than height, jelly evenly thick or slightly thicker at apex. Four radial canals, broader than ring canal, ending in four large marginal bulbs. Bulbs with rounded red gastrodermal chamber, entry of radial canal at top, epidermal pad studded with nematocysts on adaxial side and on abaxial side a large dark-brown ocellus. Relaxed tentacles issued obliquely, 2-3 times as long as bell height, tapering, proximal part smooth, otherwise studded with about 30 clasping nematocyst clusters, terminal cluster spherical, diameter about 1.5 times as large as other clusters. Manubrium spans 2/3 of subumbrella, cylindrical, without apical chamber, greenish. Gonads encircle manubrium for almost its complete length, leaving free only a small part near mouth. Egg size 0.18-0.20 mm. Nematocysts: stenoteles, (12-14) x (8.5-10) µm and (10-10.5) x (6-7) µm; desmonemes (8-10) x (4-5) µm.

ADDITIONAL DATA – Russell (1938) reported slightly larger stenoteles for the hydroid: (21.5-26) x (15-18) µm and (12-13) x (7.5-9) µm. Schuchert (1996) recorded for hydroids from New Zealand (20-24) x (13.5-15) µm and (11-13) x (6.5-7) µm.

DISTRIBUTION – All European coasts from Norway to Galicia; east coast of Canada and USA; coasts of South Africa; Alaska to California (but some records may refer to *C. cliffordi*), Chile; New Zealand; Western Australia. The medusa has also been reported from the Mediterranean, as well the coasts of Brazil and Papua New Guinea. However, these records need reconfirmation.

BIOLOGY – The hydroids occur in shallow waters (max. 25 m, Fey, 1965) up to the low water mark, growing on rocks, mussels, seaweed, floating objects like buoys and rafts. Perhaps due to the small size of the medusa, it's seasonality is not clearly established. At Roscoff (Brittany), colonies with medusae buds appear in May, but fertile medusae can already be found in April. According to Russell (1953) and Fey (1970), medusae are produced from April to September. Around Wellington (New Zealand), Schuchert (1996) found mature medusae and colonies with medusae buds all year round. Young medusae are positively phototactic. Although corynid hydroids might be eaten by numerous nudibranchs, one of them seems to feed exclusively on *C. eximia*: *Doto sarsiae* (see Morrow, Thorpe & Picton, 1992). The gastropods seem to feed by puncturing the stem of hydroids and sucking out the sap - just like aphids (B. Picton, pers. comm.). The early development has been described by Bodo & Bouillon (1968).

REMARKS – *Coryne eximia* is a well known and common species. Despite this, our knowledge of its ecology is very limited.

The diameter of spawned eggs observed in material from Brittany was 0.18 to 0.2 mm. This compares favourably with values from New Zealand (0.19 mm; Schuchert, 1996). Brinckmann-Voss (1989) tabulated only 0.11 mm for material from western Canada, however, the eggs shown in her figure 6 have a diameter of about 0.2 mm.

Schuchert (1996) observed some large variants of the medusa (up to 7 mm) that had a more cylindrical umbrella. This variant was connected to the normal form by a continuous row of intermediates. Crosses of both forms resulted in viable planulae. Similarly large forms were also mentioned by Hartlaub (1894) to occur in the North Sea.

Some hydranths of *C. eximia* may bear a thin cup of dilated perisarc at their base, similar to *C. muscoides*. This was observed in colonies from New Zealand (Schuchert, 1996) as well as in material from Great Britain (this study).

Sarsia bretonica Hartlaub, 1904 was only mentioned as a name without description nor figure. Later, Hartlaub (1907) mentioned this species again and even figured it, but he acknowledges it to be *Sarsia eximia*. Considering his figures, which are indistinguishable from *C. eximia* and the frequent occurrence of this species at Roscoff, it is obvious that *Sarsia bretonica* must in fact be *C. eximia*.

Coryne gracilis Browne, 1902 closely resembles *C. eximia* and both could be conspecific. For further details see under *C. gracilis*.

Coryne cliffordi Brinckmann-Voss, 1989 from British Columbia may be mistaken for *C. eximia*. But contrary to *C. eximia*, in *C. clifffordi* stolons and branches or cauli are not clearly distinguishable, the branches lack any annulation, and the perisarc is thin and transparent. More importantly, the medusae buds of *C. cliffordi* are never in the upper axils of the tentacles as in *C. eximia.*

I think that Berrill (1953) misidentified a colony of *S. lovenii* from Guernsey as *S. eximia.* The position of the medusoid below the tentacles as well as the shape and maturity of the medusoid clearly agree with *S. lovenii.* Berrill's two colonies from the Gulf of Maine are also not referable to *C. eximia.* One is perhaps also *S. lovenii* (figure 10 in Berrill, 1953), while the colony depicted in his figure 9 has gonophores independent of the tentacles and could belong to several species of Corynidae.

The distribution of *C. eximia* is not entirely clear. *Coryne eximia* medusae have been reported for the Mediterranean by Kramp (1957), Goy (1970), and Goy *et al.* (1991). None of these authors, however, had mature animals or provided evidence of medusae with developed gonads. Furthermore, the extensive survey of Brinckmann-Voss (1970) did not find this species. The Mediterranean occurrence of *C. eximia* thus needs re-confirmation. The medusa of *C. eximia* have also been recorded from warm or tropical waters like the Gulf of Mexico, Florida, Brazil and Papua New Guinea (Deevey, 1950; Vannucci, 1957; Bouillon, 1978). Deevey's (1950) hydroid from Texas had no medusae buds and thus was not reliably identifiable. Berrill (1953: 281, fig. 3) probably depicted material of this population as *Syncoryne* spec. (see under *C. angulata* and 5.9 for further discussions). The record for *C. eximia* from Brazil was regarded as rather uncertain by Vannucci herself. As the polyp phase is only known from temperate waters, both records must be regarded cautiously and they need confirmation by life-cycle observations. Likewise, the records from Greenland and Iceland need reconfirmation, as they were based on non-reproductive polyp material (see Schuchert 2001).

5.1.2.3. *Coryne pusilla* group

This group comprises *C. pusilla* and *C. muscoides.* Differences between them are discussed under *C. pusilla.*

Coryne pusilla Gaertner, 1774 Fig. 14A-B

Coryne pusilla Gaertner, 1774: 40, pl. 4 fig. 8; Johnston, 1847: 39, pl. 2; Hincks, 1868: 39, pl. 7 fig. 1; Allman, 1871: 266, fig. 60, pl. 4 figs 1-7; Vanhöffen, 1910: 275; Stechow, 1919: 5, fig. A; Da Cunha, 1944: 11; van de Vyver, 1967 : 500 ; ? in part Calder, 1972: 223, pl. 1 fig. 7; Brinckmann-Voss, 1970: 51, fig. 57; ? Millard, 1975: 51, figs 19F-G; Boero, 1981: 187, fig. 1C-D; Hirohito, 1988: 33, fig. 10a-e; Schuchert, 1996: 119, fig. 72a-d.

Hydra ramosa Fabricius, 1780: 348 (synonym after Bedot, 1901).

Stipula ramosa – Sars, 1829: 4, pl. 1 fig. 1; Allman, 1871: 269; Bonnevie, 1898b: 492.

Coryne glandulosa Dujardin, 1845: 1276; Bedot, 1905: 119.

Coryne fruticosa Hincks, 1861: 158, pl. 6 figs 5-6; Hincks, 1868: 44, pl. 7 fig. 2; Allman, 1871: 269; Koch, 1873: 467, pl. 23 figs 6-7.

Coryne vermicularis Hincks, 1866: 296; Hincks, 1868: 42, pl. 8 fig. 2; Allman, 1871: 267; Jäderholm, 1909: 39, pl. 1 fig. 4; Broch, 1916: 16; Fraser, 1944: 39, pl. 3 fig. 9.

TYPE LOCALITY – possibly Cornwall (after Allman, 1871).

MATERIAL EXAMINED:

French Atlantic coast – MHNG INVE 29386, Roscoff, coll. 31.5.2000 below pier of Île de Batz ferry, low water level, examined alive – MHNG INVE 29385, Roscoff, coll. 1.6.2000

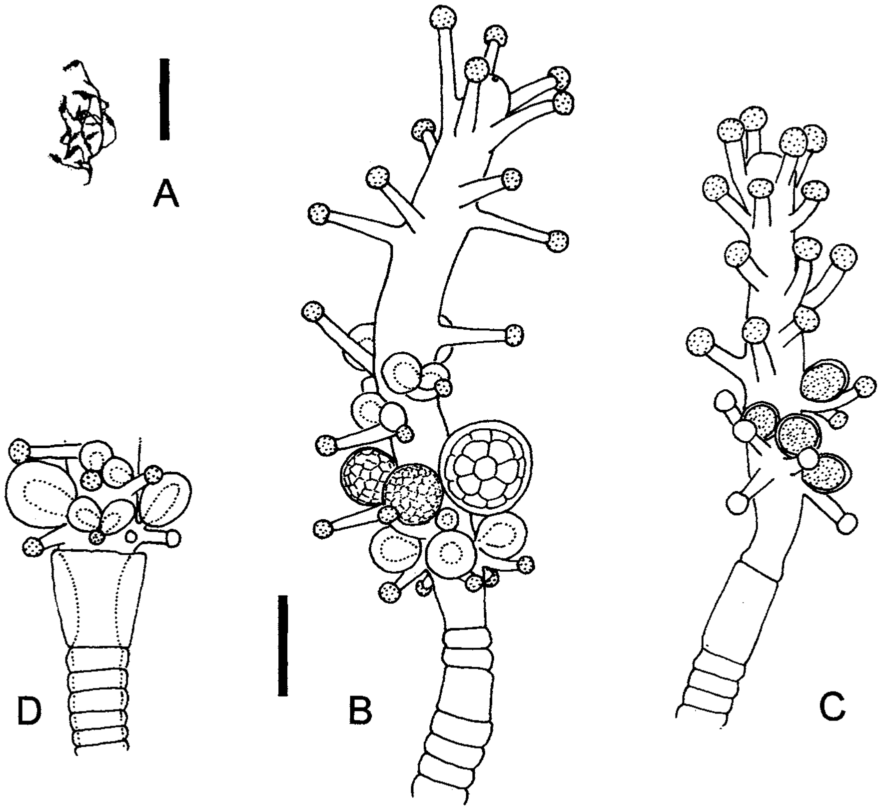

FIG. 14

Coryna pusilla Gaertner, 1774; all from Roscoff, France. A) Typical form of single shoots, scale bar 1 cm. B) Extended hydranth with female sporosacs, after life, note that it represents a hydranth of maximal size, much smaller hydranths with less tentacles are also possible, scale bar 0.5 mm. C) More contracted hydranth with male sporosacs, preserved material, same scale as B. D) Base of hydranth with perisarcal collar formation, MHNG INVE 29387, same scale as B.

on *Ascophyllum nodosum*, well above low water level, examined alive, some hydranths with perisarc collars – MHNG INVE 29387, Roscoff, coll. 4.6.2000 by author on *Ascophyllum nodosum*, well above low water level, examined alive – IRSNB, Wimereux, coll. J. Bouillon 1965 – IRSNB, Roscoff, coll. J. Bouillon June 1966.

Norway – ZMUC, loc. Bergen, det. Kramp.

Denmark – ZMUC, Frederikshavn, July 1899, leg. Th. Mortensen, 3 cm high fertile colonies – ZMUC, Frederikshavn, 27.07.1981, 2 cm colony, typical flabellate form of shoots, with female sporosacs, hydranths with perisarc funnels.

Iceland – ZMUC, Reykjavik, leg. Saemundson, id. Broch, 2 cm colony.

United Kingdom – NMSZ 1993-065-161, Kentra Bay Narrows, Millport, 5.5.1989 – NMSZ 1993-065-166, Loch Sunart, mid- to eulittoral, on *Ascophyllum nodosum* – NMSZ 1993-065-163, Loch Ewe, littoral, 9.6.1990 – NMSZ unregistered, Plymouth Marine Biological Station, on fucoid alga, no date, det. Rees & Thursfield – NMSZ 1993-065-162, Loch Ewe, 9.6.1990 – NMSZ 1976.64.64, South of Fintray Bay, Great Cumbrae, under rock overhang LWM, 24.5.1976 – NMSZ 1997-130-143, south of Pincushion

Rock, Seaham, 10.6.1993 – NMSZ 1993-065-165, Loch Tarbert, mid- to low shore, 21.8.1990 – NMSZ 1997-130-142, as *C. muscoides*, south side of Newbiggia Point, NE England, 6.6.1992 – NMSZ 1974-72-10, as *C. muscoides*, Shetland, 25.7.1974 – NMSZ 1974-72-3, as *C. muscoides*, Bay of Okraquoy, Shetland, 26.7.1974.
New Zealand – see Schuchert (1996).

DESCRIPTION – (after Atlantic material) Hydroid erect, branching several times, shoots 1-3 cm in height, 5-15 hydranths per shoot, colony shape typically rather broad and bushy, occasionally more elongated, branches and stems often curved irregularly, sometimes also straight. Perisarc of stems and cauli either annulated throughout or with annulated stretches interrupted by smooth regions, annulation can be quite irregular and indistinct, diameter of stem and branches variable. Perisarc of distal end of some cauli may rarely end in funnel-like dilation (perisarc collar). Hydranths 1.5-2.5 mm long, cylindrical in relaxed animals, more spindle-shaped in contracted animals, with 18-28 tentacles. All tentacles capitate, oral whorl of 4-5 tentacles inserted obliquely, stalk only slightly tapering, stalk less than 2 times as long as hydranth body diameter, lower tentacles scattered, held at right angle to hydranth body, lowest tentacles somewhat shorter; capitae spherical, diameter about two times the diameter of the stalk. Gonophores arise in upper axil of the tentacles along lower 1/2 to 2/3 of hydranth, 1-3 per tentacle. Gonophores remain fixed as sporosacs, without canal system, spadix present, sporosac spherical to egg-shaped, size max. 0.45 mm, size of mature sporosacs variable. Mature female sporosacs with 15-25 eggs, younger ones with many more eggs, number reduced during maturation. Sporosac casing of males sometimes thickened at distal end. Nematocysts: stenoteles, (18-23) x (11-15) µm and (12-16) x (6.5-10) µm. Colours: observed living hydranths were white, brownish or greenish, mature male and female sporosacs white. Red hydranths are also known.

FURTHER DATA – Stenotele sizes in Japanese populations: (21.7-26.5) x (13.0-16.2) µm and (13.4-16.1) x (6.8-10) µm (Kubota, 1976). Stenotele sizes in New Zealand populations: (21-23) x (13-15) µm and (10-12) x (5.5-6.5) µm.

DISTRIBUTION – All European coasts, Mediterranean, coasts of South Africa, Kerguelen, Seychelles, Korea, Japan, New Zealand, eastern Canada.

BIOLOGY – Grows on a variety of substrates, also on man-made floating objects (Schuchert, 1996). The population from the English Channel tolerates exposure to air. These colonies often grow on *Ascophyllum nodosum* which remains above the water line for several hours during low water. The hydroid is mostly protected from drying out by the wet sea-weeds covering it. Colonies mature in May and June in the English Channel. Colonies from Brittany apparently harbour endosymbiotic zooxanthellae (visible in living hydranths only).

REMARKS – Many authors (e. g. Allman, 1871; Brinckmann-Voss, 1970) thought that Gaertner's original description was insufficient to recognise the species correctly. While this is certainly the case, it is nevertheless very likely that Gaertner's material, probably originating from the English Channel coast, coincides with our present concept of the species. *Coryne pusilla* is frequently found on seaweeds exposed to air at low tide and it is the most abundant corynid of the English Channel. It is thus highly probable that Gaertner's material belonged to what we know today as

C. pusilla. Roscoff lies close to this putative type region and the living material described here can therefore be seen as representative for the species.

Coryne pusilla and *C. muscoides* were usually separated by the occurrence of a perisarc collar (basal beaker, sheath) in the latter species. However, some otherwise typical colonies of *C. pusilla* from Brittany and Denmark also had occasional hydranths with a perisarc collar. This collar formation can also be observed in other branching corynids, e. g. *Coryne eximia* (see above and Schuchert, 1996). The presence of such a collar alone is thus not diagnostic for *C. muscoides*. *Coryne pusilla* and *C. muscoides* occur sympatrically and both species are normally easily separable in the north-eastern Atlantic. The differences found in material from Roscoff are as follows: *Coryne pusilla* differs from *C. muscoides* by its smaller colonies (3 cm versus 5-12 cm); the more straggling, bushy habit versus the elongate form; the general absence of a long main stem; differences in hydranth colour (brown-green versus red); the more irregular and broader annulation; the perisarc collar which is only occasionally present; the longer hydranths and higher tentacle numbers (18-28 versus 16-22); the smaller size of the large stenoteles (18-23 µm versus 25-32 µm). Comparing mature female colonies (Figs 15A and 16 A), I also found that the maximal number of mature eggs per sporosac of *C. pusilla* is only half to one third of the one of *C. muscoides* (table 4). However, this trait needs careful use as a taxonomic character. On one hand, immature female sporosacs of *C. pusilla* contain many more eggs than mature ones and their number is reduced during maturation (see Weisman, 1884; Rees, 1936; van de Vyver, 1967). On the other hand, the numbers of apparently mature eggs in sporosacs of *C. muscoides* was found to be very variable, even in sporosacs of the same hydranth (20-70) and the number also decreases during maturation.

Contrary to the Atlantic, the Mediterranean populations resembling *C. muscoides* or *C. pusilla* pose considerable difficulties by showing all possible intermediate forms between the forms found in the Atlantic (see below). No Mediterranean material unequivocally attributable to *C. pusilla* could be examined.

Coryne pintneri often lacks its characteristic filiform tentacles and such colonies are hardly distinguishable from smaller colonies of *C. pusilla*. Because *C. pintneri* is quite frequent in the Mediterranean, some earlier authors may have mistaken *C. pintneri* for *C. pusilla* (Brinckmann-Voss, 1970).

Coryne fruticosa is here seen as conspecific with *C. pusilla*. Hincks (1868) distinguished it from *C. pusilla* on account of its dense growth and larger sporosacs. Notably Allman (1871) commented "it is plainly very nearly allied to *Coryne pusilla*...I feel much tempted to regards it as a mere variation of that species..." The figures of Hincks (1861) leave no doubt that *Coryne fruticosa* belongs to *C. pusilla* as it is seen today.

Coryne vermicularis Hincks, 1866 was also regarded as a possible synonym of *C. pusilla* by Allman (1871). Broch (1916) regarded both species as conspecific, a view also adopted here. *Coryne vermicularis* was probably based on a completely extended hydranth as shown in Fig. 15A.

Bonnevie (1898b) examined the type material of *Stipula ramosa* Sars, 1829 and found that it must belong to *C. pusilla*.

TABLE 4. Differences of examined independent colonies of *C. muscoides* and *C. pusilla*

species	material (see material examined)	perisarc collar	colony size in cm	length of large stenotele in µm	st. dev	number of measurements	eggs per sporosac
Atlantic material							
C. muscoides	Roscoff, coll. 1998	present	5	28.3	2.3	3	nd
C. muscoides	Roscoff, MHNG INVE 29383	present	6	32.0	0.6	5	20-70
C. muscoides	Roscoff, MHNG INVE 29384	present	10	27.1	0.0	6	male
C. muscoides	Isle of Man, NMSZ1910.174.5	absent, ? lost	7	24.9	0.3	7	50
Mediterranean material							
C. muscoides	Naples, MHNG INVE 25125	present	3	28.8	1.7	12	20-25
C. muscoides	Naples, MHNG INVE 27202	absent	4.5	20.8	0.8	8	nd
C. muscoides	Villefranche, MHNG INVE 31743	present	3.5	24.6	1.5	6	male
C. muscoides	Cala Murada, MHNG INVE 27129	present	2	18.5	0.6	5	15-20
C. muscoides	Cala Murada, MHNG INVE 27129	present	2	20.3	0.8	8	nd
C. muscoides	Cala Murada, MHNG INVE 27129	present	2	19.8	0.5	5	nd
C. muscoides	Cala Murada, MHNG INVE 27129	present	2	20.5	0.6	8	nd
C. muscoides	Cala Murada, coll. 2000	mostly absent	2	21.3	0.6	8	25-30
C. muscoides	Otranto, MHNG INVE 31742	absent	1-2	22.7	0.3	8	nd
C. muscoides	Otranto, coll. 2000	absent	1	23.9	1.8	6	nd
C. muscoides	Lecce, coll. 1997	absent	1-2	21.0	-	2	15-20
Atlantic and Pacific material							
C. pusilla	Frederikshavn, coll. 1899	absent	3	18.4	1.8	6	male
C. pusilla	Frederikshavn, coll. 1981	few present	2	18.4	0.8	7	10-20
C. pusilla	Roscoff, coll. 1966	absent	3	18.4	0.3	13	male
C. pusilla	Roscoff, MHNG INVE 29386	absent	2	18.9	0.6	7	15-25
C. pusilla	Roscoff, MHNG INVE 29385	absent	2	21.4	0.8	13	male
C. pusilla	Roscoff, MHNG INVE 29387	some present	2	19.3	0.9	8	male
C. pusilla	Wimereux, coll. 1965	absent	3	17	-	2	nd
C. pusilla	Shetland, NMSZ 1974-72-3	absent	1	17.8	1	6	male
C. pusilla	Kentra Bay, NMSZ 1993-065-161	absent	1-2	19.0	0.6	6	nd
C. pusilla	Loch Sunart, NMSZ 1993-065-166	absent	2	18.3	1.5	6	nd
C. pusilla	Loch Ewe, NMSZ 1993-065-163	absent	1-2	18.5	0.6	6	male
C. pusilla	Seaham, NMSZ 1997-130-143	absent	1-2	19.1	0.5	6	nd
C. pusilla	Loch Tarbert, NMSZ 1993-065-165	some indistinct	1	17.8	1.2	6	nd
C. pusilla	NMSZ 1997-130-142	absent	1-2	18.5	1.0	6	male
C. pusilla	Auckland, coll. 1994	absent	2	22.0	0.5	10	20-25

Coryne pusilla is most probably restricted to temperate waters. Results of a re-examination of Canadian material identified by Calder (1972) as *C. pusilla* suggest that it could also belong to *C. hincksii* (see there).

Coryne muscoides (Linnaeus, 1761) Figs 15A-B & 16A-F

Tubularia muscoides Linnaeus, 1761: 539.

Coryne ramosa – Johnston, 1847: 42, pl. 6 figs 4-7 (plate as *Coryne pusilla* var. *muscoides*).

Coryne muscoides – Bedot, 1910: 275; ? not Mammen, 1963: 45, figs 12-13; van de Vyver, 1967: 501, figs 14-18, development; Brinckmann-Voss, 1970: 49, figs 54-56; Boero, 1981: 187, fig. 1A-B.

Coryne vaginata Hincks, 1861: 295; Hincks, 1868: 41, pl. 3 fig. 1; Allman, 1871: 268, pl. 4 figs 8-9; Da Cunha, 1944: 11, fig. 12.

Coryne pusilla – Weisman, 1883: 49.

? *Coryne pusilla* var. *Napolitana* Weisman, 1883: 49, pl. 13, fig. 3, 5-8, 12, 15, 17-18.

TYPE LOCALITY – Linnaeus (1761) states: "*Habitat in Oceano Bahusiam alluente*", which translates to coast of Bohuslan (west coasts of Sweden).

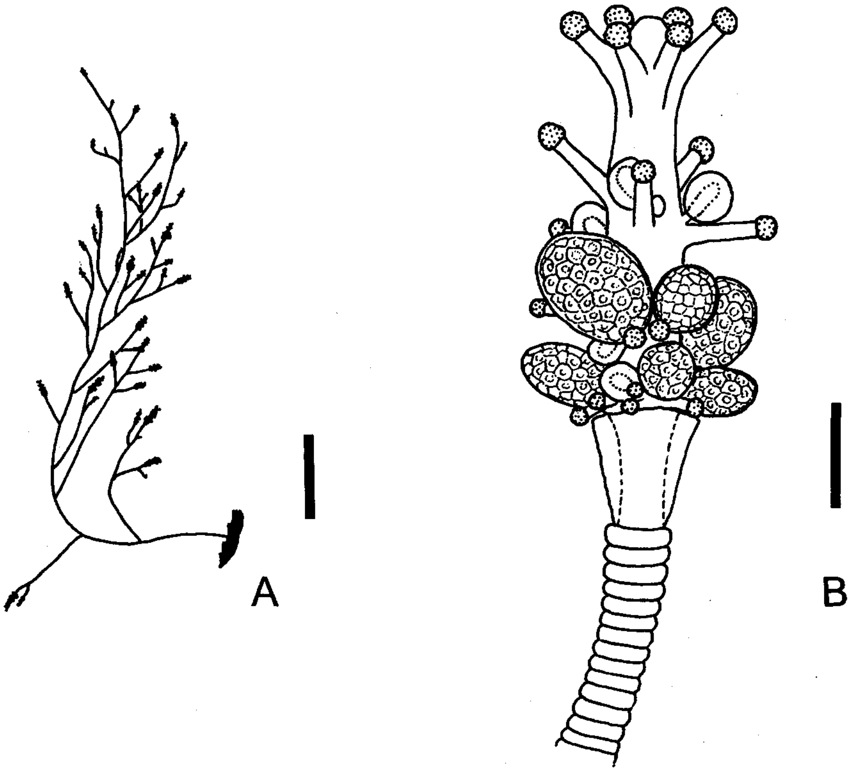

FIG. 15
Coryne muscoides (Linnaeus, 1761), after living material from Brittany. A) One typical shoot, scale bar 1 cm. B) Hydranth with female sporosacs of different developmental stages, scale 0.5 mm.

MATERIAL EXAMINED:

Atlantic – Roscoff, France, living colonies coll. 31.3.1998 by myself on fucoid algae, 0 m, several stems, up to 3 cm, young gonophores present – Roscoff, 4 colonies collected 1-4.06.2000 by myself on diverse algae, all at low water mark but immersed, males and females, examined alive, some preserved as MHNG INVE 29383 and MHNG INVE 29384 – NMSZ1910.174.5, as *C. pusilla*, coll. J. Ritchie, Isle of Man, 5.8.1910, det. Rees & Thursfield 1964, apparently dried out at some stage (reconstituted 1992), typical 7 cm colony but no perisarc collars visible, perhaps collapsed.

Mediterranean – MHNG INVE 25125, Naples, coll. 10.4.1911, on brown algae, 3 cm, elongated colony, with perisarc collars – MHNG INVE 27202, Naples, Italy, coll. 20.2.1892, infertile, 4.5 cm colonies, without perisarc funnels – MHNG INVE 27129, Mallorca, Cala Murada, coll. 22.08.1999 by author, numerous male and female colonies growing on *Corallina* spec. at 0.2 to 0.5 m depth on vertical rock coast, up to 2 cm, with perisarc collars – MHNG INVE 29759, labelled *C. pusilla*, Mallorca, Cala Murada, coll. 21.08.2000, same locality and substrate as MHNG INVE 27129, with and without perisarc collars – MHNG INVE 31743, Villefranche-sur-Mer, Ligurian Sea, 0-0.5 m, coll. by author 8.5.2001, fertile male, 3.5 cm high, very elongate, with collars – MHNG INVE 31742, Italy, Otranto, Torre del Serpe, coll. S. Piraino 13.3.2001, 1-2 m on algae, mass occurrence, infertile, several shoot per colony, without perisarc collars or with fine membrane only, elongate colony form – Italy, Otranto, coll. A. Frese 10.3.2000, infertile, appears identical to previous material – near Lecce, Italy, coll. A. Faucci 1997 on *Cystoseira*, infertile.

DESCRIPTION – (after Atlantic material) Hydroid large, 5-15 cm, shape of shoots usually very elongate, with long, straight main stem and shorter side branches (Fig. 15A), diameter of stem and branches similar, about 0.3 mm, branches and stems regularly straight; stem and branches regularly and sharply annulated throughout, rings narrow, height of rings less than half of diameter. Perisarc usually ends at base of hydranth in a funnel-shaped perisarc collar (Fig. 15B), distal diameter of collar about twice the caulus diameter, collar regularly present in examined undamaged material, but can be missing in some hydranths, can also be collapsed in preserved material. The collar has thin, filmy walls and is a dilation of the perisarc, sometimes with indistinct annulation, it is not a gelatinous addition. Hydranths about 2 mm in height, spindle shaped, with 16-22 tentacles. Tentacles all capitate, arranged in an oral whorl of 4-6 tentacles and lower tentacles scattered or in 3 indistinct whorls. Oral tentacles attached very obliquely to hydranth, up to 40 gastrodermal cells in stalk. Tentacle stalks not much tapering, capitae spherical, relatively small, most proximal tentacles short and their capitae small. Gonophores develop in upper axils of lower tentacles, 2-3 per tentacle, 10-16 in total, all of variable developmental stages. Gonophores are sessile sporosacs without any canal system, with spadix, shape oblong, max. 0.6 mm long, size of mature sporosacs variable, female sporosacs with 20-70 eggs, depending also on stage of maturity. Nematocysts: stenotele (25-33) x (14-22) µm and (17-21) x (8-12) µm. Colours: hydranths orange, capitae of tentacles red, stems yellow-orange, mature male and female sporosacs white.

ADDITIONAL DATA – Van de Vyver (1967) examined the early development and gives an egg size of about 0.1 mm.

DISTRIBUTION – Coast of Sweden, south-western Britain, France, Portugal, Mediterranean.

BIOLOGY – The Atlantic forms occurs on brown algae in depths of 0-2 m, mature animals can be found from March to June, perhaps also later.

REMARKS – For notes on the taxonomic history see Bedot (1910).

Colonies of *C. muscoides* from the Atlantic are normally easily distinguishable from *C. pusilla.* The differences are given above under *C. pusilla.* As mentioned, the presence of a few perisarc collars alone is not diagnostic of *C. muscoides.* Some hydranths of *C. muscoides* can lack it and *C. pusilla* and other corynids like *S. eximia* can have hydranths with such collars. In the examined Atlantic material, however, nearly all hydranths of *C. muscoides* had this collar (one dried out specimen excepted), while the collar is only present in some hydranths of *C. pusilla*, if at all.

Contrary to the Atlantic populations, the Mediterranean forms here allocated to *C. muscoides* are difficult to evaluate and they could belong to a separate species or subspecies. The Mediterranean forms are very variable and are in many respects intermediate between the Atlantic forms of *C. muscoides* and *C. pusilla.* This perhaps lead Picard (1960) to synonymise *C. pusilla* with *C. muscoides.* His opinion was not shared by Brinckmann-Voss and I also regard both species as valid. The Medi-

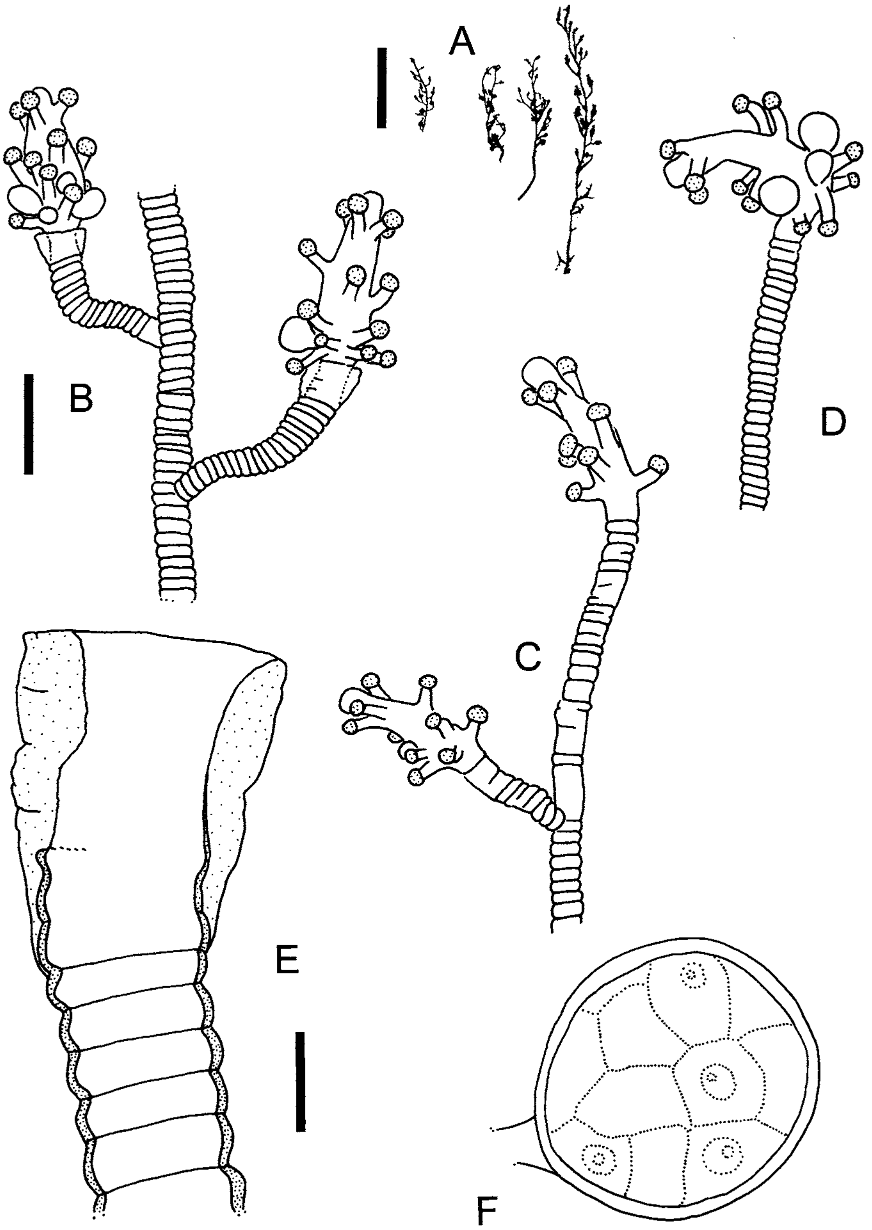

FIG. 16

Coryne muscoides (Linnaeus, 1761), Mediterranean form, all after preserved samples associated with *Corallina* spec. A) Silhouettes of typical colonies, scale bar 1 cm. B) MHNG INVE 27129, part of shoot with two hydranths, note presence of perisarc collars, scale bar 0.5 mm. C-D) Parts of one colony (MHNG INVE 29759), note absence of perisarc collars, same scale as B. E) Distal end of caulus with perisarc collar, scale bar 0.1 mm. F) Female sporosac, same scale as E.

terranean form resembling *C. muscoides* is well documented by Brinckmann-Voss (1970). I found abundant identical material on Mallorca and at Villefranche-sur-Mer (Fig. 16A-F). The colonies are frequently found immediately below the water surface growing in association with a species of the calcareous red algae *Corallina*. They form mostly solitary, elongate shoots with a main stem like typical *C. muscoides*. A perisarc collar is frequently present in these colonies, but some lack it. Especially in colonies from deeper waters (1-3 m), these collars can be entirely absent or they are only formed as a adhering perisarc film. Some of the perisarc collars found in the Mediterranean material were like a gelatinous additional layer on the outside of the annulated periderm (Fig. 16E), something not observed in the Atlantic material.

The Mediterranean material here examined was reluctantly allocated to *C. muscoides* and not *C. pusilla* following Brinckmann-Voss (1970). This decision was based on the elongated colony shape, the frequent occurrence of a perisarc collar, the tentacle numbers, and the often regular and complete annulation. Admittedly, these are all characters often acknowledged as prone to variation due to environmental factors, but sometimes the overall similarity of specimens from both populations was quite striking. The Mediterranean material usually differs from the Atlantic *C. muscoides* in forming smaller colonies measuring 1-4.5 cm in height; the female sporosacs have fewer eggs (10-30); and the length of the large stenotele is usually smaller. These characteristics match better *C. pusilla*. The length of the larger stenotele was found to be very variable, but without forming two separate groups (see table 4). Boero (1981) used nematocyst size to separate Mediterranean *C. muscoides* and *C. pusilla*. With the material observed here, this was not evident.

Nevertheless, I am inclined to regard the Mediterranean *Coryne* growing in association with *Corallina* as a species separate from both *C. pusilla* and *C. muscoides*. The differences from the Atlantic *C. muscoides* and *C. pusilla* have been listed above, but are considered insufficiently reliable to be of diagnostic value. New investigations using genetic methods must address the problem.

Mostly for biogeographic reasons I doubt that Mammen's (1963) material from the tropical Indian Ocean identified as *C. muscoides* belongs to this species. Mammen's colonies were only 5 mm high, but they had perisarc collars.

5.1.3. Incompletely known *Coryne* species

This set comprises all species of which we have only incomplete information. Some of them are nevertheless distinct and well recognisable species. They are listed in alphabetical order.

Coryne epizoica Stechow, 1921 Fig. 17

Coryne spec. P – Graeffe, 1884: 352
Coryne epizoica Stechow, 1921: 248; Stechow, 1923b: 41, fig. C; ? not Riedl, 1959: 603; Brinckmann-Voss, 1970: 48, figs 52-53.
TYPE LOCALITY – Naples, Italy, Mediterranean.
MATERIAL EXAMINED – Naples, coll. J. Bouillon June 1962, IRSNB IG27.838, three hydranths.

DESCRIPTION – Hydroid stolonal, 2-3 mm high, stolons creeping on shells of *Rissoa* spec. (Gastropoda), hydranths with perisarc-covered caulus (1-3 mm),

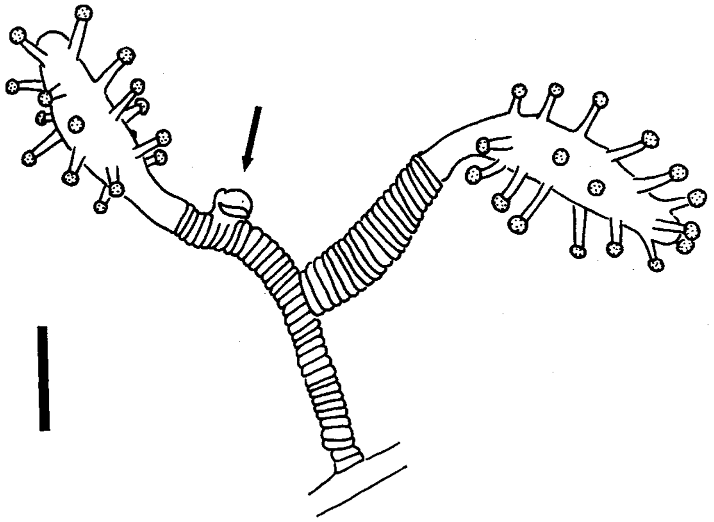

FIG. 17
Coryne epizoica Stechow, 1921, after preserved material from Naples, arrow points at residue of a gonophore-like outgrowth, scale bar 0.5 mm.

hydranth body 1-2 mm. Perisarc of caulus always narrowly annulated throughout. Hydranth body cylindrical, with about 15-20 tentacles, 4-6 oral tentacles in one whorl, others scattered or in indistinct whorls. Gonophore-like outgrowths develop on caulus in perisarc covered zone. Mature gonophores unknown. Colours: hydranth reddish brown, perisarc light to dark brown.

DISTRIBUTION – Naples, Villefranche, Trieste (Mediterranean).

BIOLOGY – This species grows exclusively on shells of *Rissoa* spec. living in *Posidonia* beds in 20-40 m depth (Brinckmann-Voss, 1970).

REMARKS – The outgrowths from the perisarc-covered region of the caulus were interpreted by Brinckmann-Voss (1970) as incipient gonophores, although she never found spermatids or oocytes. It is thus probable that these outgrowths are a structure of unknown function. New life-cycle studies on this species are needed.

Coryne gracilis (Browne, 1902) Fig. 18A

Sarsia gracilis Browne, 1902: 275; Browne & Kramp, 1939: 271, pl. 14 figs 1-2, pl. 15 fig. 1; Kramp, 1957: 4; Kramp, 1959: 79, fig. 16; Kramp, 1961: 28; Schuchert, 1996: 128.
? *Syncoryne sarsi* – Hartlaub, 1905: 525, fig. F.
TYPE LOCALITY – Falkland Islands.
MATERIAL EXAMINED – ZMUC, Falkland Islands, Stanley Harbour, several medusae collected at various dates in 1901 and 1902 by Vallentin, id. Kramp, mature specimens 1.5-2 mm – IRSNB IG27.838, South Africa, Cape Town, Table Bay, coll. J. Bouillon 1969, 1 medusa 1.4 mm with few eggs on manubrium.

DESCRIPTION – (after Browne & Kramp, 1939; Kramp, 1959) Medusa 5 mm high, 3 mm wide, cylindrical bell, wall moderately thick, margin quadrangular; manu-

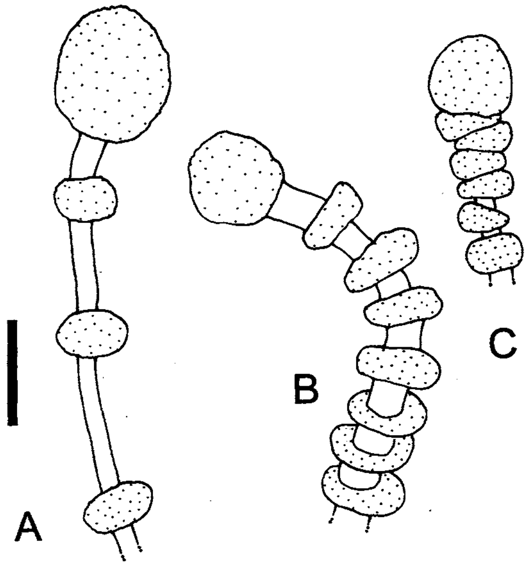

FIG. 18
A) *Coryne gracilis* from South Africa, terminal tentacle tip of medusa, scale bar 0.1 mm. B) *Coryne eximia* from Brittany, same scale as A, but more contracted. C) *Coryne eximia* tentacle tip from New Zealand, same scale as A, but more contracted.

brium two-thirds as long as bell cavity, nearly whole length surrounded by gonad; tentacles with large oval terminal knob. Juvenile medusae with bell wall much thickened in interradial position.

DISTRIBUTION – Falkland Islands, ? South Africa.

REMARKS – Medusae from the type locality (ZMUC, Stanley Harbour) examined here seem to be identical to the form of *C. eximia* with cylindrical bell described by Schuchert (1996). However, they are smaller and do not reach the size given by Browne & Kramp (1939). The medusae look like *C. eximia* with a thicker apex and the terminal nematocyst clusters of the tentacles are somewhat larger. The South African medusa was also quite small (1.4 mm), but already had a few eggs (diameter 0.2 mm), its terminal cluster was also somewhat larger than in *C. eximia* and resembled the ones from the Falkland Islands. Browne & Kramp (1939) described juvenile stages of this species with the interradial portion of the subumbrella bulging towards the axis. This seems at first to be the only considerable difference to *C. eximia*; however, such a bulging of the subumbrellar ectoderm is often seen in small medusae due to mechanical stress (e. g. caused by the collecting procedure with a plankton net). I have seen it too in *C. eximia* from the English Channel. Thus, it might well be that the interradial bulges described for the young *C. gracilis* are an artifact only.

The cylindric shape of *C. gracilis* is also not unique to this species, as some *C. eximia* have it too (Schuchert, 1996). The only consistent difference to *C. eximia* remains thus the larger terminal tentacular cluster (Fig. 18A-C). I suspect that *C. gracilis* belongs to *C. eximia*, but life-cycle observations at the type locality must be made before a closer comparison is possible.

Coryne inabai Uchida, 1933 Fig. 19

Sarsia inabai Uchida, 1933: 126, fig. 2, Bouillon, 1978a: 131, fig. 3; Bouillon, 1985b: 248, fig. 1.
Plotocnide borealis – Kramp, 1968: 91.
TYPE LOCALITY – South West of Kamchatka, 51°33'N 156°20'E, 0-30 m.
MATERIAL EXAMINED – Laing Island, Papua New Guinea, IRSNB IG 27.828, coll. J. Bouillon 1978 and 1981, two lots with two medusae, some mature.

DESCRIPTION – Medusa bell height 3 mm (reportedly up to 8.5 mm), higher than wide, jelly very thick, especially at top where about 2/5 of total height, maximal diameter of bell in middle of height or above. Manubrium short, about 3/5 of bell cavity, with or without very shallow apical knob, gonads encircle manubrium for nearly its whole length, leaving manubrium visible only at the top and near the mouth. Velum narrow. Ring canal broader than radial canals, these narrow, ending in large tentacular bulbs. Gastrodermal chamber of marginal bulbs high, epidermal ring complete, with distinct ocellus. Each bulb with one short tentacle, for most part with few nematocysts, distal part swollen and studded with nematocysts (2 sizes of stenoteles, desmonemes). Shape of distal tentacular swelling spherical or oblong. Polyp phase unknown.

DISTRIBUTION – Kamchatka, Mozambique, Papua New Guinea.

REMARKS – *Coryne inabai* is a very rare species. Kramp (1942) doubted its validity and referred it to *Plotocnide borealis*, a morphologically similar species but one which lacks ocelli. Bouillon (1978a) thought he had found the species again at the Seychelles (1 medusa). However, his medusa – although mature – measured only 1.3 mm as opposed to 3-8.5 mm given by Uchida (1933) and it had a slight peduncle. Perhaps this is a different species. Later, Bouillon (1985b) recorded this medusa also from Papua New Guinea. These specimens – re-examined for this study – fit Uchida's description rather well, except for the more oblong tentacular swellings (Fig. 19A). Some smaller, juvenile specimens from Papua New Guinea had distinctly spherical capitae (Fig. 19D) and it seems that the tentacle tips undergo some changes during development.

Although not unusual for hydrozoans, the occurrence in the cold northern Pacific as well as in the tropical Pacific and Indian Ocean is somewhat surprising. New investigations have to prove that all medusae assigned to *S. inabai* in fact belong to one species.

Coryne prolifera (Forbes, 1848) Fig. 20A-D

Sarsia prolifera Forbes, 1848: 59, pl. 7 fig. 3; Hartlaub, 1907: 15, figs 7-8; Russell, 1953: 52, pl. 2 fig. 1, text-figs 17B, 19, 20, 25D; Kramp, 1959: 79 fig. 14; Kramp, 1961: 30; Brinckmann-Voss, 1970: 66; Bouillon, 1974: pl. 6.
? *Codonium codonoforum* Haeckel, 1879: 14, pl. 1 fig. 3; Mayer, 1910: 61.
? *Sarsia prolifera* – Goy, 1972: 971, fig. 2
Coryne prolifera – Petersen, 1990: 211, fig. 43E.
TYPE LOCALITY – Penzance Bay, Cornwall, England.

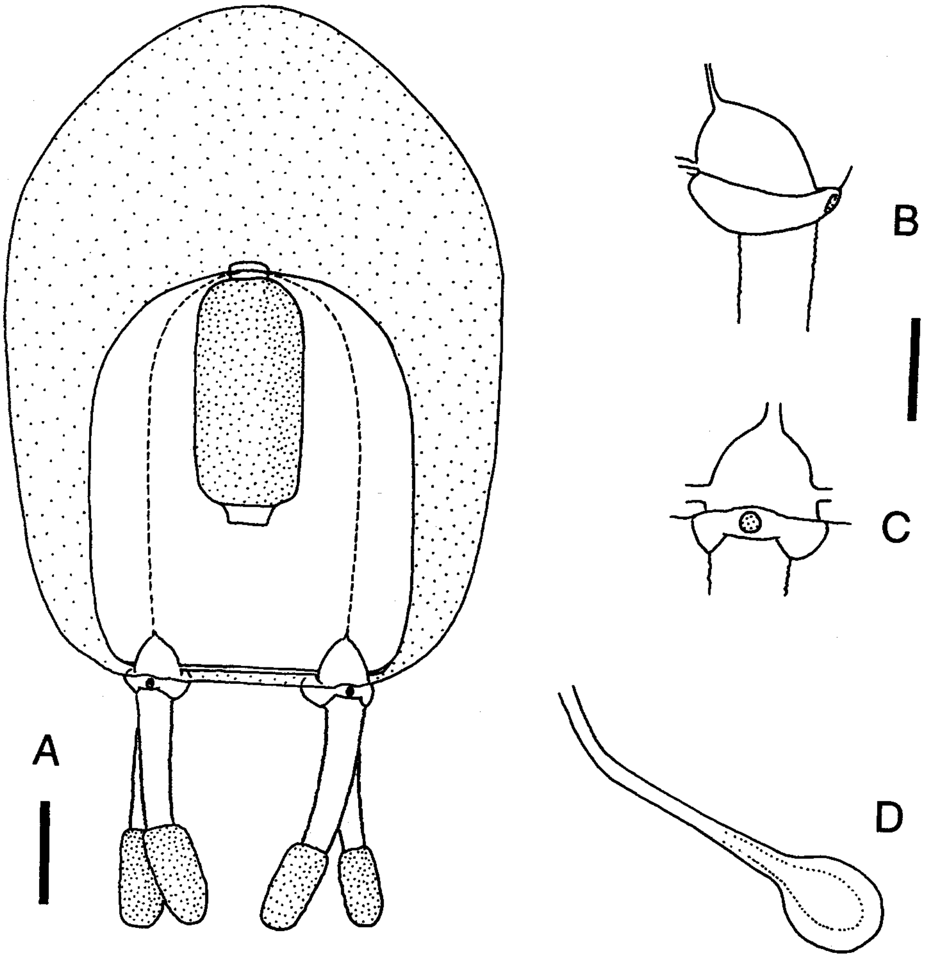

FIG. 19

Coryne inabai Uchida, 1933, material from Papua New Guinea. A) Whole mature, medusa, scale bar 0.5 mm. B) Lateral view of tentacle bulb, scale bar 0.2 mm. C) Frontal view of tentacle bulb, same scale as B. D) Distal end of relaxed tentacle of a smaller specimen, same scale as B.

MATERIAL EXAMINED – IRSNB IG27.838, Roscoff, France, coll. J. Bouillon 1961, 1971, several medusae, young polyps -ZMUC, SW British coasts, leg. E. T. Browne, 3 medusae – ZMUC, Plymouth, 25.11.1907, leg. & det. E. T. Browne, nice medusa of 2 mm.

DESCRIPTION – Medusa up to 3 mm in height, usually smaller than 2 mm, bell diameter as large or slightly larger than height, umbrella broadly bell-shaped, jelly somewhat thickened at apex. Four thin radial canals, tentacular bulbs quite broad, extended tentacles as long or longer than two times bell height, issuing obliquely, covered by numerous clasping nematocyst clusters, terminal cluster not enlarged. Manubrium spans 1/2 of bell cavity, cylindrical, with or without apical chamber,

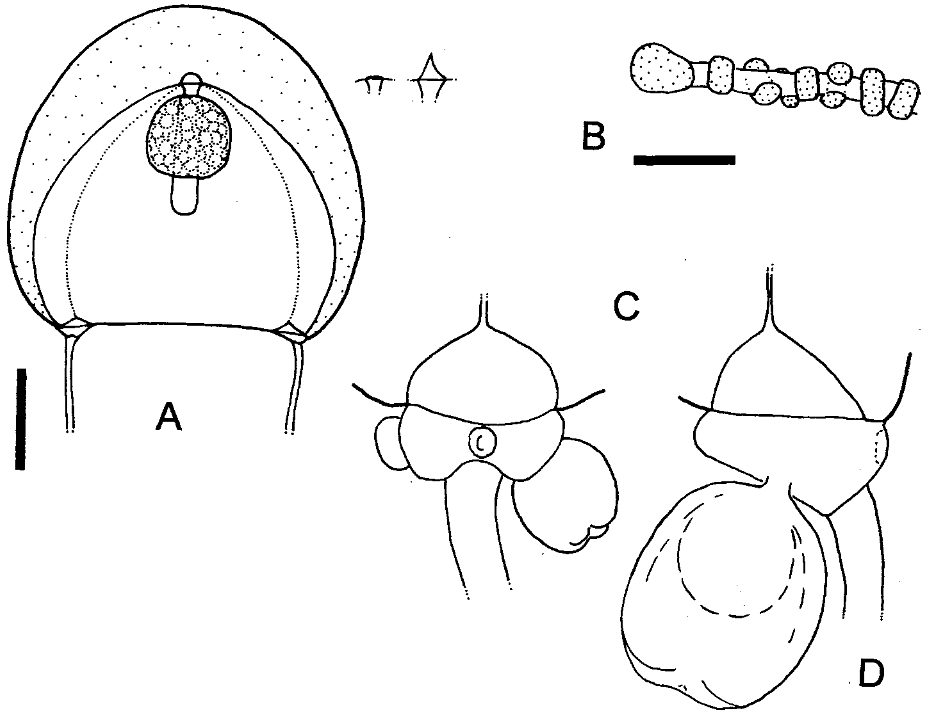

Fig. 20

Coryne prolifera (Forbes, 1848) from Roscoff. A) Side view of mature female with variation of apical chamber (right), scale bar 0.5 mm. B) Tentacle tip of medusa, scale bar 0.1 mm. C) Tentacle bulb with two medusa buds in frontal view, same scale as B. D) Side view of tentacle bulb with one advanced medusa bud, same scale as B.

apical chamber if present rounded or conical. Gonad encircles upper part of manubrium only and leaves distal fourth of stomach free. Nematocysts: stenoteles and desmonemes. Egg size: 45-60 µm. Immature medusae bear characteristic medusae buds on the epidermal part of the tentacle bulbs, up to two buds per bulb.

Biology – The medusa is present along the south-western coast of the British Isles from June to October. Some specimens may also be found as early as March and as late as November (Russell, 1953).

Distribution – British Isles, France, ? Mediterranean.

Remarks – The immature medusae with their medusae buds on the tentacle bulbs are very characteristic and immediately identifiable. Fully mature animals may cease medusae production. Such animals can be difficult to distinguish from *C. eximia* or *C. producta*. The smaller size, the flatter bell, and the shorter gonads are a trait that could help to identify mature, non-budding medusae. Additionally, *C. producta* always has an apical canal or chamber, *C. prolifera* occasionally, and *C. eximia* never.

The polyp stage of *C. prolifera* is so far unknown. However, the IRSNB holds a small polyp collected by Prof. Jean Bouillon that is likely the polyp stage of *C. prolifera*. It is a typical, although small, corynid with scattered capitate tentacles. Filiform tentacles could not been seen. A young stage is probably depicted in Bouillon (1974a, plate 6). Prof. J. Bouillon informed me that he collected this material at Roscoff on sponges. One of the polyps released a medusa with the characteristics of *C. prolifera*, but the medusae buds on the bulbs were only just starting to grow before the animal was lost. Also the polyp colony could not be kept for a longer time. The polyp shown in Bouillon (1974a) clearly has high epidermal cells around the mouth. The polyp stage of *C. prolifera* must nevertheless be considered as insufficiently known and new investigations are required.

Brinckmann-Voss (1970) regarded all Mediterranean records of this species doubtful. Goy (1972) found one specimen in the western Mediterranean, but because the manubrium protruded from the bell she was not sure about her identification.

Haeckel's *Codonium codonoforum* was described from a single medusa from Corfu (Adriatic, Mediterranean) and was much larger (8 mm) compared to Atlantic *S. prolifera* (max. 4 mm, normally 2 mm) and it had an apical canal. It has never been found again, but its size could make it recognisable. Following Mayer (1910), it is here treated as a questionable synonym of *S. prolifera*.

Coryne sargassicola Calder, 1988

Sarsia mirabilis – Fraser, 1912: 347, fig. 3.
[not *Sarsia mirabilis* L. Agassiz, 1849]
Sarsia decipiens – Stechow, 1919: 3.
Coryne sargassicola Calder, 1988: 64, figs 48-49.
TYPE LOCALITY – Natural Arches Beach, Bermuda, on *Sargassum*.
MATERIAL EXAMINED – Slide from ZSM, collection Stechow, labelled *Syncoryna mirabilis*, Gulf of Mexico, Dr. Heitz 1904; colonies grow on algal substrate, most probably material described in Stechow (1919).

DESCRIPTION – (after Fraser, 1912 & Calder, 1988) Stolonal colonies on *Sargassum*, 3 mm high cauli arising from creeping hydrorhiza. Perisarc of moderate thickness, thinning out distally, smooth or with a few wrinkles, not annulated. Hydranth elongate-oval, 1 mm long and 0.3 mm wide, with 2-5 whorls of 4-6 capitate tentacles. Below capitate tentacles one whorl of filiform tentacles that may be reduced. Nematocysts: two types of stenoteles. Gonophores arise from axils of proximal tentacles (Calder, 1988) or below them (Fraser, 1912), developing presumably into sessile sporosacs, perhaps sessile medusoids (Fraser, 1912).

DISTRIBUTION – Bermuda, western Atlantic.

REMARKS – *Coryne sargassicola* is only insufficiently known and especially its mature gonophores are unknown. However, its association with *Sargassum* make it recognisable.

Material that most probably corresponds to material described by Stechow (1919) as *Sarsia decipiens* was examined for this study. Calder (1988) is certainly right in stating that *S. tubulosa* (=*S. decipiens*) does not occur in warm waters and thus Fraser's and Stechow's identifications must be erroneous. Stechow's material

TABLE 5. Distinguishing characters of the *Dipurena* species

characters	*D. gemmifera*	*D. baukalion*	*D. bicircella*	*D. halterata*	*D. ophiogaster*	*D. reesi*	*D. simulans*	*D. strangulata*	*D. spongicola*
number of gonad rings	1	2	2	2-4	3-9	2, occ. 3-4	2-3	2	min. 2
most proximal gonad adjacent to manubrium base	no	yes	no	no	no	no	no	no	no
swellings along radial canal	0	0	0	1-3	0	0	1	0	unknown
apical chamber	present	present	present	present	present	present	small or absent	small	unknown
bell size mm	5	3.8	1.6-2.1	4-8	3-5	2-3	5	2-4	unknown
number of nematocyst clusters	many	many	many	3-6	many	many	1	1	unknown
haploneme in medusa	no?	yes?	no	yes	occasionally	no	yes	no	unknown
polyp associated with sponges only	unknown	unknown	no	yes	no	no	yes	yes	yes
hydranth size in mm	unknown	unknown	0.3 - 0.4	1-1.7	1-2	1-1.5	0.5	0.8-1.0	0.4-0.8
number of capitate tentacles	unknown	unknown	8-10	15-24	10-18	4-5	10-13	4-5	4-5
whorls of capitate tentacles	unknown	unknown	2	3-5 or scattered	4 or scattered	1	2-3	1	1
gastrodermal cells in oral tentacles	unknown	unknown	12?	7-10	unknown	13 -18	6-8	7 - 11	6-8
gonophores below or among capitate tentacles	unknown	unknown	below	among	below	below	below	below	below
filiform tentacles	unknown	unknown	present	absent	present	present	absent	present	present
length of filiform tentacles	unknown	unknown	medium	-	short	long	-	short	short
haploneme in polyp	unknown	unknown	no	yes	no	no	yes	no	present

consists of a few small stolonal stems that might correspond to *Coryne sargassicola* Calder, 1988. It differs from the latter in having an irregularly corrugated perisarc and no filiform tentacles. It bears some immature gonophores, which develop among the tentacles.

5.2. Genus ***Dipurena***

SYNONYM – *Slabberia* Forbes, 1846 (pre-occupied, Mayer, 1910).
TYPE SPECIES – *Dipurena strangulata* McCrady, 1859.

DIAGNOSIS – Colonial hydroids with one or several whorls of capitate tentacles, with or without one whorl of aboral filiform tentacles. Gonophores released as free medusae. When mature the manubrium is distinctly longer than bell height. Gonad in two or more cylinders around manubrium (except *D. gemmifera* which has only one gonad). Gonads also cover distal, swollen stomach region. Tentacles unbranched. Cnidome without or with isorhiza nematocysts.

REMARKS – A summary of the distinguishing characters of the better known species of this genus is given in table 5.

Dipurena baukalion Pagès, Gili & Bouillon, 1992 Fig. 21A-B

Dipurena baukalion Pagès, Gili & Bouillon, 1992: 15, figs 15-16.
TYPE LOCALITY – 34° 51'S 19° 55'E, 0-40 m, Benguela Current, South Atlantic.
MATERIAL EXAMINED – South Africa, INSNB IG27.828, coll. 1978, part of original material used for first description.

DESCRIPTION – (in part after Pagès *et al.*, 1992) Medusa bell-shaped, about twice as high as wide, height up to 3.2 mm, jelly thickened at apex. With rounded apical chamber. Manubrium protruding from bell in adult specimens, with distal swelling. Gonad divided into two cylinders and enveloping the manubrium. Proximal ring short, located just below apical chamber, distal gonad long, covering the distal half of the manubrium except for the mouth region. Four narrow, hardly visible radial canals without dilations. Tentacle bulbs large, oval, with red abaxial ocellus. Four tapering tentacles with a proximal portion free of nematocysts followed by nematocysts clusters, ending in a not significantly enlarged spherical nematocyst cluster. Nematocysts: stenoteles (length 15-22 µm), desmonemes, perhaps also a haploneme. Polyp phase unknown.

DISTRIBUTION – Cape of Good Hope (South Africa).

REMARKS – *Dipurena baukalion* resembles *D. ophiogaster*, but has a different arrangement of the gonads. While *S. ophiogaster* usually has more than two gonad rings of equal size that are at placed far away from the origin of the manubrium, *D. baukalion* has only two unequal ones, the upper beginning just at the origin of the manubrium.

Dipurena bicircella J. T. Rees, 1977 Fig. 22

Dipurena bicircella Rees, 1977: 198, figs 1-2; Pagès *et al., 1992*: 16.
TYPE LOCALITY – Horseshoe Cove, Bodega Bay, California, USA (38°19' N 123°04'W).

DESCRIPTION – (after Rees, 1977) Hydroid stolonal, stems including hydranths up to 5 mm. Hydranths small (0.3-0.4 mm in height), clavate, with one oral whorl of

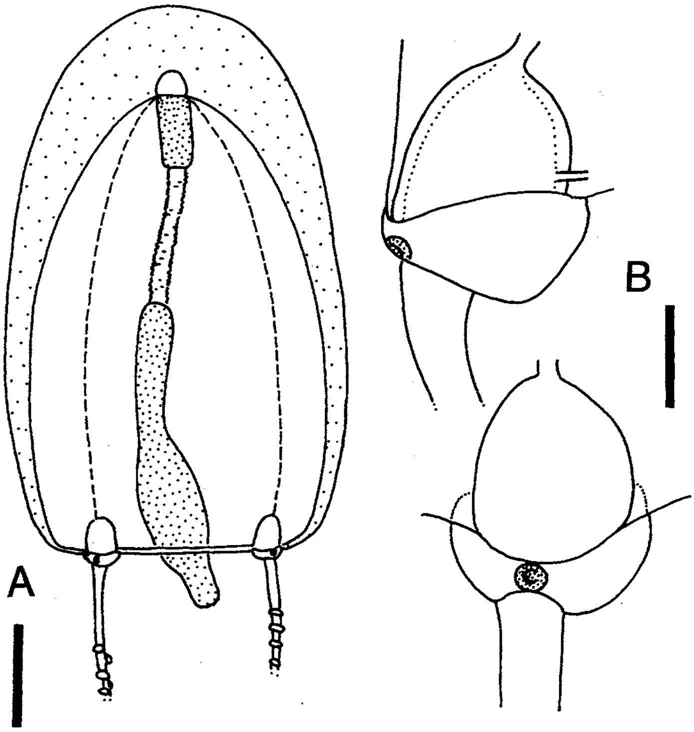

FIG. 21
Dipurena baukalion Pagès, Gili & Bouillon, 1992. A) mature medusa, composite picture after preserved material, scale bar 0.5 mm. B) Tentacle bulbs, scale bar 0.2 mm, top in in frontal view, below in side view.

4-5 capitate tentacles and a single whorl of 4-5 lower capitate tentacles, at lower fourth one whorl of filiform tentacles (present also in colonies from nature). Gonophores develop in middle of hydranth below capitate tentacles and above the filiform tentacles, 1-6 gonophores in one whorl. Gonophores are released as free medusae. Nematocysts: stenoteles, (20-22) x (14-15) µm and (14-16) x (10) µm.

Newly released medusa 0.5 mm high, with red ocelli, with 22 nematocyst clusters on tentacles, exumbrella with scattered nematocysts of microbasic mastigophore type, size (12) x (14-15) µm.

Adult medusa 1.6 to 2.1 mm high, as wide as high, bell-shaped, jelly moderated thick, jelly at apex about 1/4 of bell height. Manubrium with bullet-shaped apical chamber, extended manubrium about two times as long as bell height, with thin serpentine part and distal stomach. Gonads in two rings, distal one on swollen stomach region, more proximal one at lower third of manubrium. Tentacles short, length when extended equals about bell height, with small nematocyst clusters and a slight terminal knob. Ocelli red, gastrodermal system orange-yellow. Nematocysts: stenoteles (12-13) x (9) µm; desmonemes (10-11) x (5) µm.

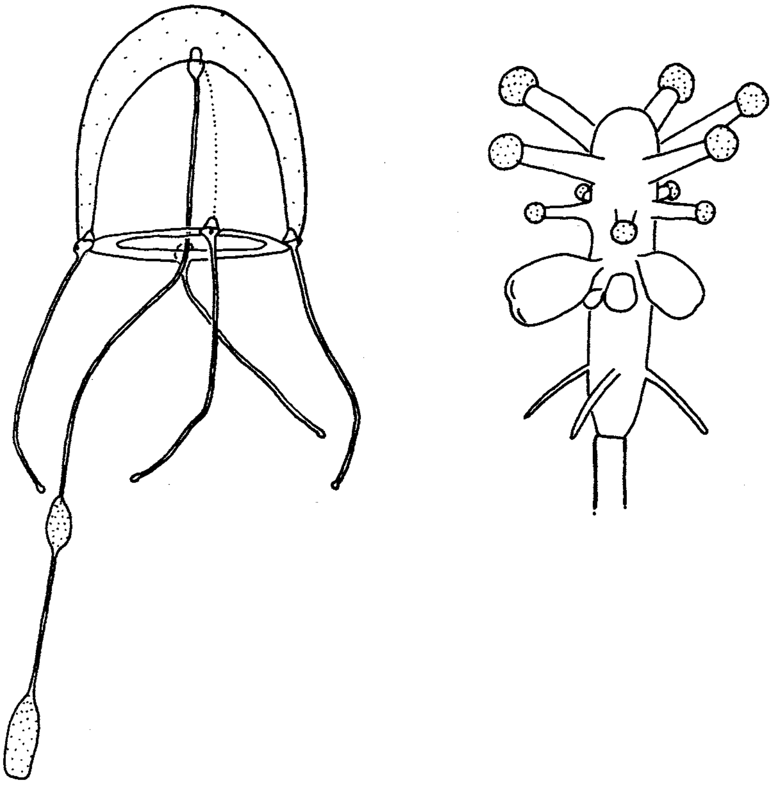

FIG. 22
Dipurena bicircella Rees, 1977, modified after Rees (1977), mature medusa and polyp with medusa buds.

DISTRIBUTION – Only known from type locality in California.

BIOLOGY – The hydroids grow on rock and bivalve shells, depth 3-10 m. The medusa is not known from nature. In the laboratory it matured within two weeks.

REMARKS – *Dipurena bicircella* is so far the only known *Dipurena* species with polyps having constantly two whorls of capitate tentacles only. The relatively short tentacles of the medusa combined with its small size might render this species recognisable also in the medusa stage, although it is very prone to be confounded with *D. ophiogaster*, a medusa known from waters of nearby Mexico. The medusa is also hardly distinguishable from *D. reesi*, a species also known to occur in California (Bullivant, 1970). Perhaps the long cnidocils of *D. reesi* can be used to distinguish them, but the cnidocils of *D. bicircella* remain uninvestigated.

Dipurena gemmifera (Forbes, 1848) Fig. 23A-D

Sarsia gemmifera Forbes, 1848: 57, pl. 7 fig. 2; Sverdrup, 1921: 14, pl1 fig. 3; Kramp, 1927: 35, chart 4; Russell, 1938: 150, figs 13-18; Berrill, 1950: 306, figs 7B-C; Russell, 1953: 61, figs 24 & 25a-c, pl. 1 figs 1 & 4; Kramp, 1959: 79, fig. 12; Kramp, 1961: 27; Brinckmann-Voss, 1970: 64, text-figs 75-76, pl. 3 fig. 1; Goy, Lakkis & Zeidane, 1991: 102, fig. 4.

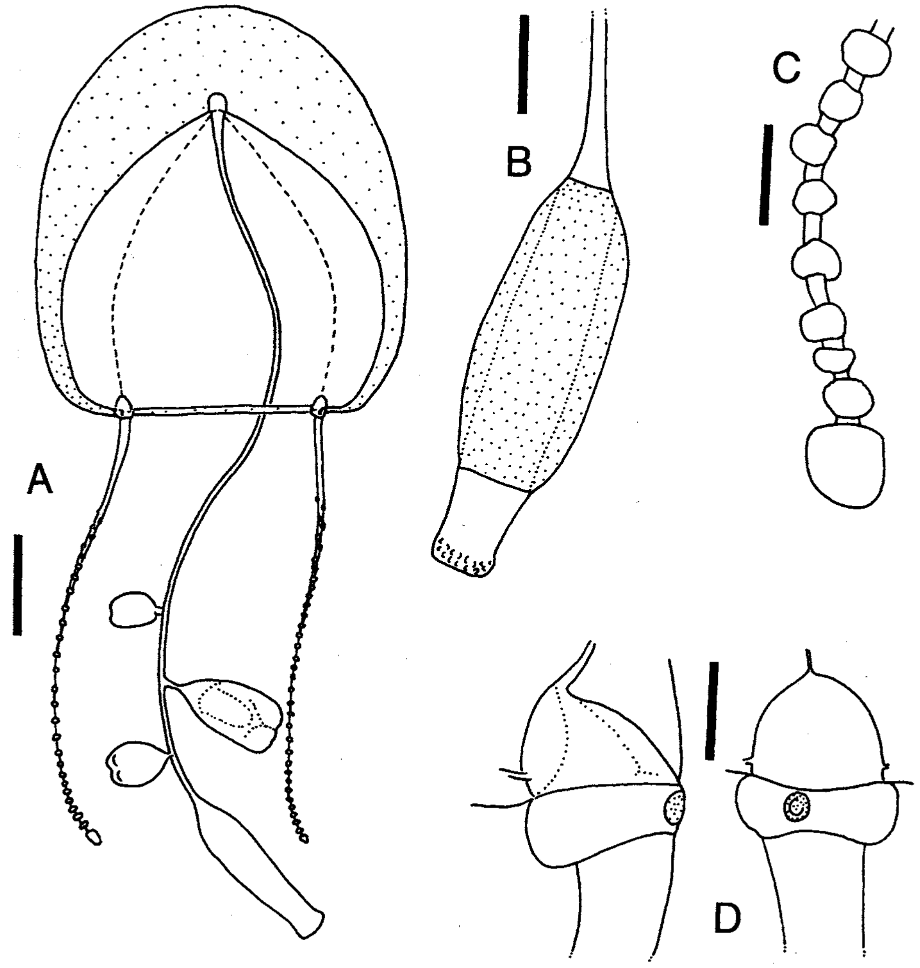

FIG. 23

Dipurena gemmifera (Forbes, 1848), after preserved material. A) Medusa with medusae buds on manubrium, scale bar 0.5 mm. B) Manubrium covered by gonad tissue, scale bar 0.2 mm. C) Tentacle tip, scale bar 0.1 mm. D) Marginal bulbs in side- and frontal view, scale bar 0.1 mm.

Sarsia clavata Keferstein, 1863: 63; Hartlaub, 1907: 51, fig. 46.
Dipurena fertilis Metschnikoff, 1871; synonym after Hartlaub, 1907: 59.
Sarsia siphonophora Haeckel, 1879: 20, pl. 1 fig. 4; Kramp, 1959: 307; Kramp, 1961: 31.
Purena gemmifera – Hartlaub, 1907: 58, figs 54-58, Le Danois, 1913: 305, fig. 2.
Dipurena gemmifera – Petersen, 1990: 212.
TYPE LOCALITY – British Isles.
MATERIAL EXAMINED – IRSNB IG 27.838, Roscoff, France, coll. J. Bouillon 1965 and August 1968, several medusae, one with gonads, several with medusae buds – ZSM, Bergen, Norway, collection Stechow, 1 slide, coll 1905, number E628/15 – ZMUC, 51°43.5N 2°06', 23.08.1906, id. Kramp, badly damaged – ZMUC, British Coasts, leg. & det. E. T. Browne, one medusa – ZMUC, Frederikshavn, Denmark, 27.07.1981, 2 nice medusae – Roscoff, France, 1 juvenile medusa collected by author 5.6.2000, examined alive.

DESCRIPTION – Adult medusa 2-3 mm high, somewhat higher than wide, jelly moderately thick, thicker at apex, exumbrella rounded, subumbrella rounded or pointed. Manubrium with a bullet-shaped apical knob. Extended manubrium at least two times as long as bell height, composed of a long, thin proximal part (serpentine part) and a distal swollen stomach. Along distal part of serpentine manubrium develop spirally arranged medusae buds (normally 1-4, max. 13). The gonad develops only on the distal, swollen stomach. Radial canals very thin, thinner than circular canal, entering gastrodermal chamber of bulb at its top. Gastrodermal chamber of bulbs high, walls bulging, nettle ring of bulb nearly complete, with ocellus. Tentacles issued mostly parallel to main axis of animal, relatively short (1.5 times bell height when relaxed), with 15-30 nematocyst clusters and a slightly enlarged, bullet-shaped terminal cluster. The contracted tentacle has its proximal half free of nematocyst clusters. According to Russell (1953) the tentacles bear cilia confined to the nematocyst clusters. The tentacles make vibrational movements through these cilia. Nematocysts (Russell, 1938): stenoteles (16) x (12) µm and (13) x (9-10) µm; desmonemes (13-14) x (6-7) µm. Colours: stomach, apical chamber, bulbs pale orange-red, ocelli black. Development: daughter medusae released from their host medusa may already have the next generation of medusae buds on their manubrium. Egg size 125 µm, embryo encysts (Brinckmann-Voss, 1970). Polyp stage unknown.

BIOLOGY – In the north-western Mediterranean, the medusa is present in the plankton from February to August, with a maximum in April (Goy, 1997), at Naples it is present from April to June (Brinckmann-Voss, 1987). In British and Irish waters it is present from May to September with a maximum in August and September (Russell, 1953).

DISTRIBUTION – British Isles; European coasts as far north as Bergen, Mediterranean.

REMARKS – Due to the gonad that covers the distal stomach, this medusa is here placed in the genus *Dipurena* as proposed by Petersen (1990). It is the only *Dipurena* species with an undivided gonad. The ciliated tentacles are also unique. Such cilia and a similar vibrational tentacle movement have been observed for *Coryne japonica* medusae of New Zealand (Schuchert, 1996).

Sarsia clavata Keferstein was regarded as different from *D. gemmifera* by Hartlaub (1907) on account of its flatter bell and thinner jelly. This, however, is not convincing as Keferstein's medusa might have been in bad condition. Graeffe (1884) gave a description of a polyp which he believed to be the hydroid stage of *D. clavata*. Graeffe's polyps from the Adriatic grew on *Suberites massa* and released medusae with a terminal nematocyst cluster and some incipient nematocyst rings, some already with one such ring. As he gave no figures it is difficult to evaluate his findings, particularly the proportion of the terminal clusters would have been important to know. Graeffe's polyp probably was *Dipurena halterata*.

Also Picard (1960) claims to have identified the polyp stage. However, Picard neither observed medusae buds on the manubrium of the released medusae nor did he cultivate the medusae to maturity. Therefore, his identification is here considered somewhat doubtful and it needs reconfirmation. Picard basically identified his material as belonging to *S. gemmifera* based on the enlarged terminal nematocyst cluster of the newly released medusae. His figure (1G), however, does not show a particularly large cluster. The presumed polyp of *S. gemmifera* formed mostly stolonal colonies, had 3-4 whorls of 4-6 capitate tentacles, developed a whorl of filiform tentacles in culture, and the medusae developed among the capitate tentacles, but not in their axils. The oldest medusa stage obtained had a manubrium that just protruded out of the bell.

Sarsia siphonophora Haeckel, 1879 was described based on a single specimen from the Canary Islands. It was synonymised by Mayer (1910: 62) with *D. gemmifera*, however Hartlaub (1917: 391) and Kramp (1955b; 1961) disagreed without discussing their opinion. Kramp (1959) kept both species separate mainly on account of the tentacles without a terminal nematocyst cluster and possibly also the increased number of medusae buds. The terminal nematocyst clusters are often missing in plankton catches due to mechanical damage. The higher number of medusae buds is here also not seen as sufficient to separate the species. It is thus very likely that *S. siphonophora* is nothing but *S. gemmifera* and I follow Mayer here in uniting it with *D. gemmifera*.

Dipurena halterata (Forbes, 1846) Fig. 24A-E

Slabberia halterata Forbes, 1846: 286; Forbes, 1848: 53, pl. 6 fig. 1; Mayer, 1910: 75; Neppi, 1912: 716, pl. 1 fig. 3, not figs 1-2 = *D. gemmifera*.
Slabberia catenata Forbes & Goodsir, 1851: 311, pl. 10 fig. 3; Haeckel, 1879: 655; Browne, 1900: 704, synonym; Mayer, 1910: 77, pl. 8 figs 8-9; Russell, 1953: 71, synonym.
Dipurena halterata – Browne, 1897: 816, pl. 49 fig. 2, 2a, 2b; Browne, 1900: 704; Rees, 1939: 343, figs 1-3; Russell, 1953: 67, figs 28, 29a-c, pl. 1 fig. 3, pl. 2 fig. 2; Kramp, 1959: 82, fig. 21; Kramp, 1961: 22; Kramp, 1968: 9, fig. 12; Goy, 1972: 970; Bouillon, 1971: 327, fig. 2, pl. 2; ? Christianson, 1972: 284, fig. 2; Petersen, 1990: 212; Goy, Lakkis & Zeidane, 1991: 101, fig. 1; Pagès *et al.*, 1992: 14, fig. 14.
Dipurena picta Mayer, 1900b: 29, pl. 18 fig. 45-46; Mayer, 1910: 77, synonym.
? *Syncoryne clavata* – Graeffe, 1884: 352.
Gemmaria implexa – Stechow, 1919: 5.
[not *Zanclea implexa* (Alder, 1857)]
Sarsia pulchella – Stechow, 1923b: 35, fig. A.
[not *S. pulchella* Allman, 1865 = *S. tubulosa*]
? *Syncoryna pulchella* – Rossi, 1950: 197, fig. 2.
Sarsia halterata – Brinckmann-Voss, 1970: 57, fig. 65.
TYPE LOCALITY – Mount's Bay, Cornwall, England.
MATERIAL EXAMINED – Roscoff, France, living non-reproductive polyp colonies on *Haliclona simulans* and living subadult medusae from plankton samples, polyp colonies preserved as MHNG INVE 29388 – IRSNB IG27.838, La Toreau, Roscoff, leg. & det. J. Bouillon 1963, on sponge, with *Cladonema radiatum* and *D. simulans*, one hydranth with gonophores – ZMUC, U. K., Eddystone Fyr, 19.05.1914, id. Kramp, several medusae – ZSM, Naples, Mediterranean, collection Stechow, 5 slides, material described by Stechow (1923b) as *S. pulchella*, polyps on sponge – MHNG INVE 31741, Villefranche-sur-Mer, Mediterranean, Mai 2001, living colony on sponge *Petrosia ficiformis*, cultivated until medusae released.

DESCRIPTION – Hydroid stolonal, stolons deeply embedded in sponge tissue. Stolons and cauli covered by thin, wrinkled or smooth perisarc. Hydranths 1.0-1.7 mm, diameter about 0.15 mm, slightly clavate to cylindrical, with 15-24 capitate tentacles, without filiform tentacles. Capitate tentacles distributed either over entire

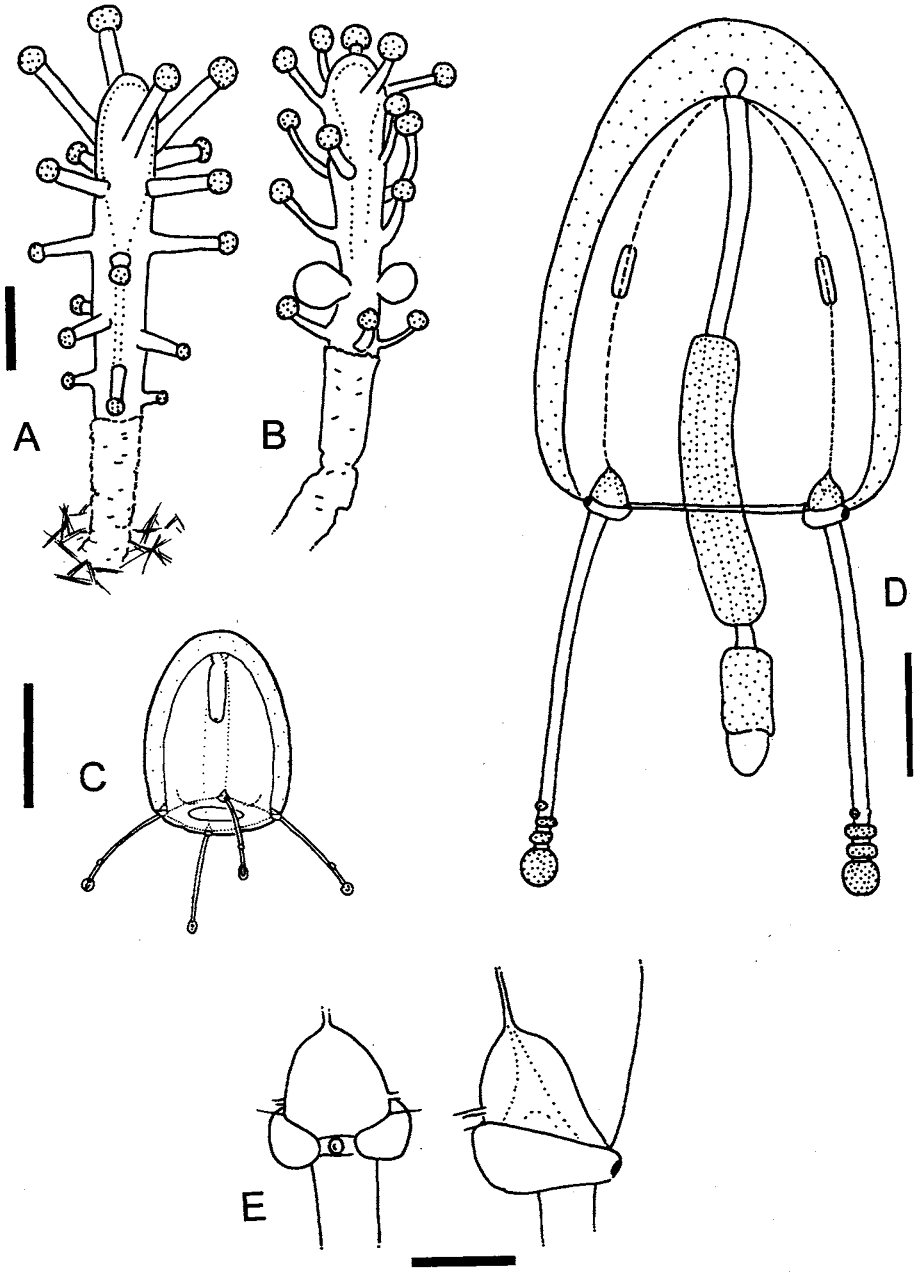

FIG. 24

Dipurena halterata (Forbes, 1846). A) polyp after life material, scale bar 0.2 mm. B) Hydranth with medusae buds, after photograph in Bouillon (1971). C) Newly hatched medusa, after life, scale bar 1 mm. D) Adult medusa, scale bar 1 mm. E) Tentacle bulbs in frontal and side view, scale bar 0.2 mm.

hydranth down to perisarc or covering distal 2/3 of hydranth only, organised in one oral whorl of 4-5 oral tentacles and scattered lower capitate tentacles. Oral tentacles of usual length (1-2 times diameter of hydranth), with 7-10 gastrodermal cells. Stalks of all capitate tentacles slightly tapering, length of stalk and diameter of capitulae decreasing or not towards proximal. Around mouth a button of high epidermal gland cells. Gonophores develop in middle of hydranth, 1-10 per hydranth in one to several whorls, among but independent of tentacles, released as free medusae. Fertile hydranths may reduce their tentacles (reproductive exhaustion). Nematocysts: stenoteles (19-20) x (15.5-16) µm and (10-13) x (6-9) µm; basitrichous isorhizas (17-20) x (8-10) µm.

Newly released medusa 1.5-1.6 mm high and 1.1-1.3 mm wide, exumbrella with interradial furrows, a few scattered exumbrellar nematocysts, radial canals narrow and without swellings, ocelli dark-red, tentacles with a large spherical terminal nematocyst cluster and some smaller clasping clusters on the distal half of the tentacles. Apical knob or canal absent.

Adult medusae 4-8 mm high, higher than wide, umbrella bell-shaped, apex rounded, jelly thick, slightly thickened at apex. Top of manubrium with rounded apical knob. Manubrium 2-3 times as long as bell height, with long thin serpentine part and an swollen stomach at its end. Gonads in 2-4 rings, most distal one may either only cover swollen stomach-region or may be very long and covering stomach as well as end of serpentine part, additional rings along distal half of manubrium may be present. Four radial canals with at least one linear swelling in its middle, sometimes flanked by two smaller swellings. Radial canal enters gastrodermal chamber of bulb at the centre of its top, bulbs large, with dark red ocellus. Tentacles somewhat longer than bell height, smooth for most of their length, at end 2-4 closely set annular nematocyst clusters and one large spherical terminal cluster. Colours: bulbs and terminal tentacular clusters orange to brown, apical knob red to green. Nematocysts: stenoteles; isorhizas; desmonemes.

DISTRIBUTION – Great Britain, Ireland, France, Mediterranean, western and southern Africa, Florida.

BIOLOGY – The polyps grow in and on the sponges *Haliclona cinerea* (Grant) (Rees, 1938, as *Chalina montagui), Haliclona simulans* (Johnston), and *Petrosia ficiformis* (Poiret). Rees (1938) observed medusae buds in May (Rees, 1939). The medusa is only occasionally found in the plankton of the Atlantic from April to September (Russell, 1953). In the Mediterranean, reproductive colonies were found in April to June, colonies occurred in depths of 0.5-5 m (Boero & Fresi, 1985). In the north-western Mediterranean, the medusa is present in May (Goy, 1997).

REMARKS – A complete taxonomic history of this species is given by Russell (1953). Forbes (1848) described and depicted *D. halterata* with a single terminal nematocyst cluster per tentacle. Later Forbes & Goodsir (1851) described *S. catenata* which had several additional nematocyst rings. Browne (1900) and Russell (1953) assumed that *Slabberia catenata* was just a more advanced and mature stage of *D. halterata*. However, as the young medusa *D. halterata* sensu Russell has several nematocyst clusters even just after its release, Forbes' *Slabberia halterata* with its single terminal cluster might actually have been the species we call today *D. simulans* Bouillon, 1965. Forbes' medusa was about 3.5 mm high and probably subadult. Perhaps Forbes overlooked the sometimes small additional clusters. The manubria figured by Forbes (1848) apparently had an apical chamber or projection, a feature which is very prominent in *D. halterata* sensu Russell, but rare or small in *D. simulans*. Nevertheless, it remains highly uncertain whether *Dipurena halterata* as we see it today really corresponds to Forbes' *Slabberia halterata*. Because it is unlikely that any of Forbes' medusae are left (pers. com. Susan Chambers, National Museums of Scotland), any taxonomic revision cannot be based on sufficient evidence. As the concept of *D. halterata* sensu Russell is now well established and widely used, and the synonymising of Bouillon's *D. simulans* with *Slabberia halterata* Forbes would certainly generate considerable confusion, I oppose any attempt to do so.

Dipurena picta Mayer, 1900 differs from *D. halterata* by the absence of swellings along the radial canals. These may have been overlooked by Mayer and in his monograph of 1910 he treated it as a synonym of *Slabberia catenata*.

The polyp of *Dipurena halterata* is rather unique for the genus as it develops its gonophores among the tentacles and not below them. For further distinguishing traits see under *D. simulans* and table 5.

Christiansen (1972) identified fertile polyps from Oslofjord as *D. halterata*. His polyps were 6 mm high and had more than 33 tentacles. The unusual size in particular leads me to somewhat doubt this identification.

Material collected by Stechow and identified by him first as *Gemmaria implexa* and then as *Sarsia pulchella* (Stechow, 1919; 1923b) was re-examined for this study. The medusae buds of this material arise among, but independently of the capitate tentacles and thus rule out *S. pulchella*, a putative synonym of *S. tubulosa*. The material was found growing on sponges. Some of the medusae are quite advanced and have tentacles with one large, spherical terminal nematocyst cluster. This is also indicated in Stechow's (1923b) figure, but not clearly enough. The buds also have an elongate nematocyst capsule like an isorhiza. It seems therefore very probable that Stechow's polyps belong to *D. halterata*. Likewise, the material of Rossi (1950) could belong to here, but it is not clearly identifiable. I found *Dipurena halterata* colonies growing on the sponge *Petrosia ficiformis* in shallow waters at Villefranche-sur-Mer (Ligurian Sea). The polyps were absolutely identical to material seen in Brittany. Also the types and sizes of nematocysts were the same. The Mediterranean colony was kept in running seawater and fed regularly with planktonic copepods. The colony proliferated and started to produce many medusae. The medusae budding hydranths often showed reproductive exhaustion and reduced all tentacles. A young medusa is shown in figure 24C.

Dipurena ophiogaster Haeckel, 1879 Fig. 25A-E

Dipurena ophiogaster Haeckel, 1879: 25; Uchida, 1927: 187, fig. 27; Rees, 1941: 131, fig. 2; Russell, 1953: 71, pl. 1 fig. 5, pl. 2 fig. 4; text figs 25e, 30a-b, 31; Kramp, 1959: 82, fig. 22; Kramp, 1961: 23; Kramp, 1966: 2; Kramp, 1968: 8, fig. 11; Bouillon, 1971: 334, table 1; Goy, 1972: 970; Petersen, 1990: 212, fig. 44E; Goy, Lakkis & Zeidane, 1991: 101, fig. 2; Pagès *et al.*, 1992: 16; Schuchert, 1996: 123, fig. 76a-d.

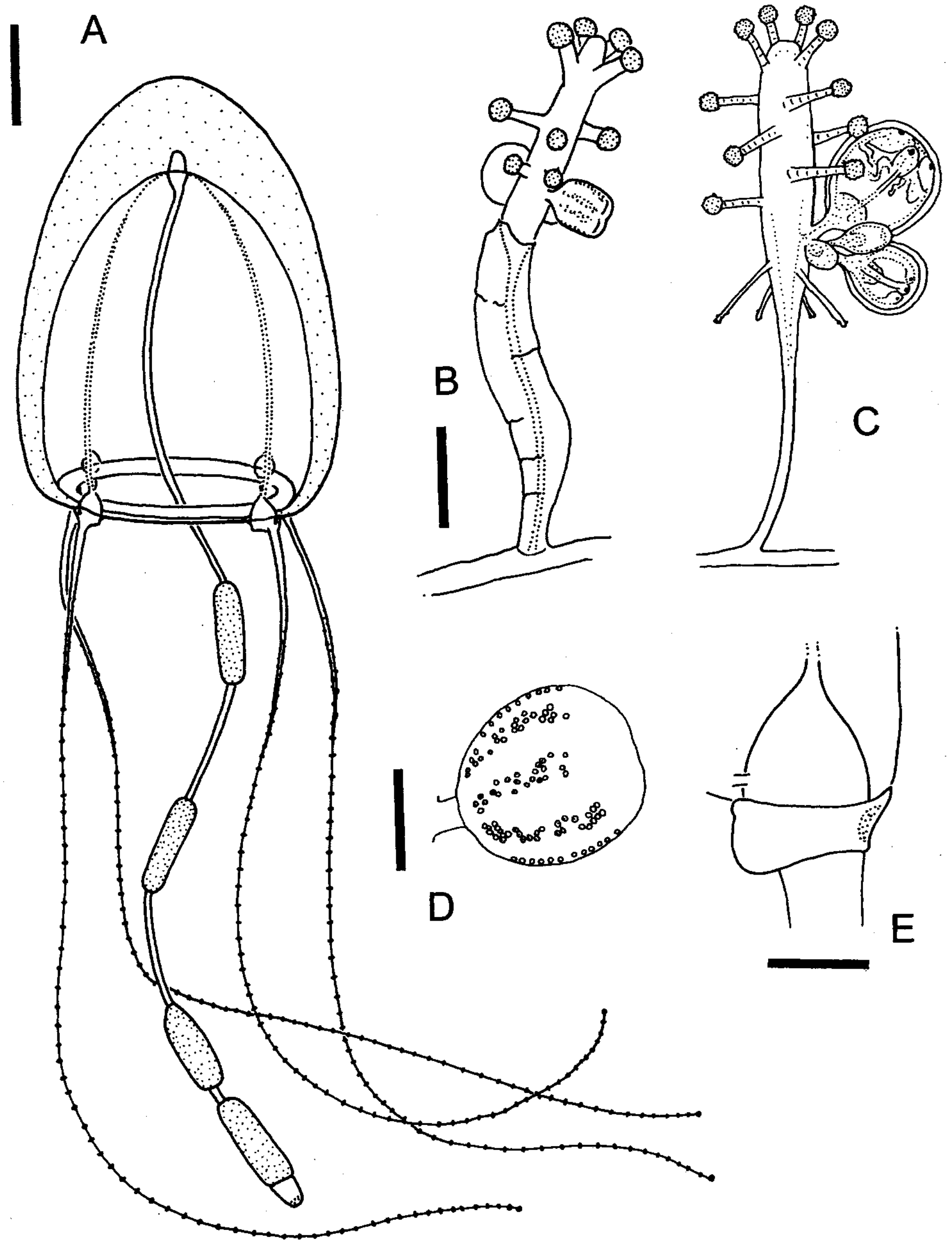

FIG. 25
Dipurena ophiogaster Haeckel, 1879. A) Mature medusa from New Zealand, scale bar 1 mm. B) Polyp stage with medusae buds immediately after collection from the sea (Mediterranean), note absence of filiform tentacles and the characteristic, loose perisarc of the caulus, scale bar 0.5 mm. C) Cultivated polyp with medusae buds, figure modified after Rees (1941). D) Medusa bud with characteristic rows of nematocysts, scale bar 0.1 mm. E) Lateral view of tentacle bulb of mature medusa, scale bar 0.2 mm.

Sarsia strangulata – Allman, 1871: 46, fig. 17.
Dipurena spec. – Browne, 1905: 133, pl. 2 figs 1-2.
Slabberia ophiogaster – Mayer, 1910: 79, figs 36-37.
Sarsia ophiogaster – Brinckmann-Voss, 1970: 59, pl. 3 fig. 4; text figs 66-71.
Purena brownei Bigelow, 1909: 183, pl. 7, fig. 7, pl. 44 figs 8-9; Uchida, 1927:187; Russell, 1953: 71; Kramp, 1959: 82; Kramp, 1961: 22.

TYPE LOCALITIES – Coasts of Great Britain and Ireland.

MATERIAL EXAMINED:
France – INSNB IG 27.838, Roscoff, coll. J. Bouillon 1967, two badly preserved medusae.
Mediterranean – INSNB IG 27.838, Naples, Nisida, coll. J. Bouillon 1962, several polyps, some with medusae buds – MHNG INVE 31740, Torre del Serpe, Otranto, Italy, 0-5 m, on rock, collected 13.3.2001 by S. Piraino, polyps with medusae buds and newly released medusae.
New Zealand – 5 medusae from Auckland and Leigh, collected February 1997 by A. Freudenthal; more material was examined for the study Schuchert (1996).
Chile – ZMUC, Valparaiso Bay, 17.03.1959, leg Fagetti, det. Kramp.
Papua New Guinea – ZMUC, 1 mile E of Port Moresby, Galathea stat. 532, 25.10.1951, det. Kramp, damaged medusa.
Vietnam – ZMUC, Nhatrang, May 1938, several medusae, some mature, tentacles very short, ? det. Kramp; is probably not *Dipurena ophiogaster*.

DESCRIPTION – Hydroid stolonal, cauli only very rarely branched once, height of caulus and hydranth up to 4 mm, stems occasionally with short stolons given away at some distance from the substratum. Perisarc thin, soft, not annulated, some wrinkles present. In colonies from nature the periderm of the stem widens distally and the basal portion of the stem is able to retract into the perisarc (Fig. 25B). Regenerating colonies in culture do not develop this wide perisarc. Hydranth clavate to cylindrical, 1-2 mm in height and 0.25-0.35 mm in diameter. With about 10-18 capitate tentacles and at lower third one whorl of 2-6 filiform tentacles. Capitate tentacles organised in one oral whorl of 4 tentacles and below them scattered lower capitate tentacles. The capitulae may decrease in size towards proximal. The filiform tentacles can be absent in material from nature, sometimes they bear a few nematocysts. Gonophores develop in 2-3 clusters of 2-6 buds below the capitate tentacles and above filiform tentacles. Advanced gonophores have on their outside eight meridional tracks of nematocysts. The gonophores are released as free, immature medusae. Nematocysts of polyp: stenoteles (Bouillon, 1971).

The newly released medusa has eight distinct, broad, adradial rows of spherical nematocysts on its exumbrella, tentacles bear 18 and more nematocyst clusters.

Adult medusa 3-6 mm high, 2-4 mm in diameter, jelly thick, thickened at apex, umbrella bell-shaped, top of bell rounded. At top of manubrium a bullet-shaped apical chamber. Manubrium very long (>2 times bell height), with long, thin serpentine part and cylindric, swollen stomach. Gonads in 2-4 cylinders (max. 9) encircling manubrium, most distal one covering the stomach, the others on distal half of serpentine part. Four radial canals and circular canal present. Gastrodermal chamber high. Epidermal nettle ring of bulbs not complete, in side view with at double curvature at adaxial side (Fig. 25E). Tentacles very long, covered by numerous nematocyst clusters, terminal one spherical and not enlarged. Cnidocils on nematocytes of tentacular clusters normal, about $^1/_2$ as long as stenotele capsule. Ocelli black. Colour of bulbs and apical chamber yellowish brown or reddish yellow. Nematocysts: stenoteles and rarely a few isorhizas along the radial canals (Bouillon, 1971).

DISTRIBUTION – British Isles to Mediterranean, Skagerak, Sri Lanka, Japan, Palau Islands, Papua New Guinea, Pacific Coast of Mexico, Chile, New Zealand.

BIOLOGY – The hydroid is known to occur in shallow depths on algae (Rees, 1941), barnacles and rocks (Brinckmann-Voss, 1970). In British and Irish waters, the medusae are present in the plankton between May and September, with a maximum in July (Russell, 1953). In the north-western Mediterranean, the medusa is present in the plankton from May to July, with a maximum in April (Goy, 1997). Development: the medusa matures within 10 to 15 days (Brinckmann-Voss, 1970).

REMARKS – The adult medusa of *Dipurena ophiogaster* is not readily distinguishable from *D. reesi* (see Brinckmann Voss, 1970), and the widespread occurrence of the latter species makes many records for *D. ophiogaster* medusae questionable and some records might in fact relate to *D. reesi*.

Dipurena ophiogaster can be distinguished from *D. reesi* by the higher and more dome shaped bell (versus triangular and as wide as high), the higher number of gonadal rings (3-9, versus 2, occ. 3), and the cnidocils of the tentacles (fine versus stout and long). For further differences see also table 5.

Material from Vietnam identified by Kramp (1962) as *D. ophiogaster* was re-examined for this study and I think it probably does not belong to this species. The medusae were rather small (2 mm), had one to four thick, rounded gonads, and characteristically short tentacles (0.8 mm) with less than 10 nematocysts clusters. The short tentacles make these medusae very distinct and I am convinced that they do not belong to *D. ophiogaster*. The medusae show a strong resemblance to *Euphysa problematica* Schuchert, 1996. The allocation to the genus *Euphysa* of this species has recently been criticised by Bouillon & Barnett (1999), as the ocelli of the preserved material might have had faded. I must admit this possibility and *E. problematica* could as well be a *Dipurena* species. New investigations on living material from new Zealand must be made before further conclusions can be drawn.

Dipurena reesi Vannucci, 1956 Fig. 26A-F

Dipurena reesi Vannucci, 1956: 479, text-figs 1-2, pls 1-2; Kramp, 1959: 82; Brinckmann & Petersen, 1960: 386, figs 1, 3-5, 6b; Kramp, 1961: 24; Bullivant, 1970: 112, figs 2-3; Bouillon, 1971: 333; Moreira et al, 1978: 161; Petersen, 1990: 212; Pagès *et al.*, 1992: 16.

Sarsia reesi – Brinckmann-Voss, 1970: 62, text-figs 72-74, pl. 3 fig. 2; Altuna Prados, 1993: 31, figs 2 - 3.

TYPE LOCALITY – São Paulo, Brazil.

MATERIAl EXAMINED – hydroids probably coming from Banyuls-sur-Mer, collected 1990 and 1996, cultivated in aquarium of zoological institute of Basel, examined alive, observed young medusa – IRSNB IG 22.838, Naples, coll. J. Bouillon, several medusae released from polyps, some cultivated to maturity – ZMUC, Naples, leg M. Vannucci, 4.06.1959, several young medusae.

DESCRIPTION – Hydroid stolonal, stolons creeping, but may detach in cultured colonies. Stems of variable length. Hydranths 1-1.5 mm, slightly clavate, with only one oral whorl of 4-5 capitate tentacles and at lower third one whorl of 4-5 filiform tentacles. Capitulum of oral tentacles slightly flattened, nematocysts confined to outer half, stalk with 13-15 gastrodermal cells. Gonophores develop singly or in pairs

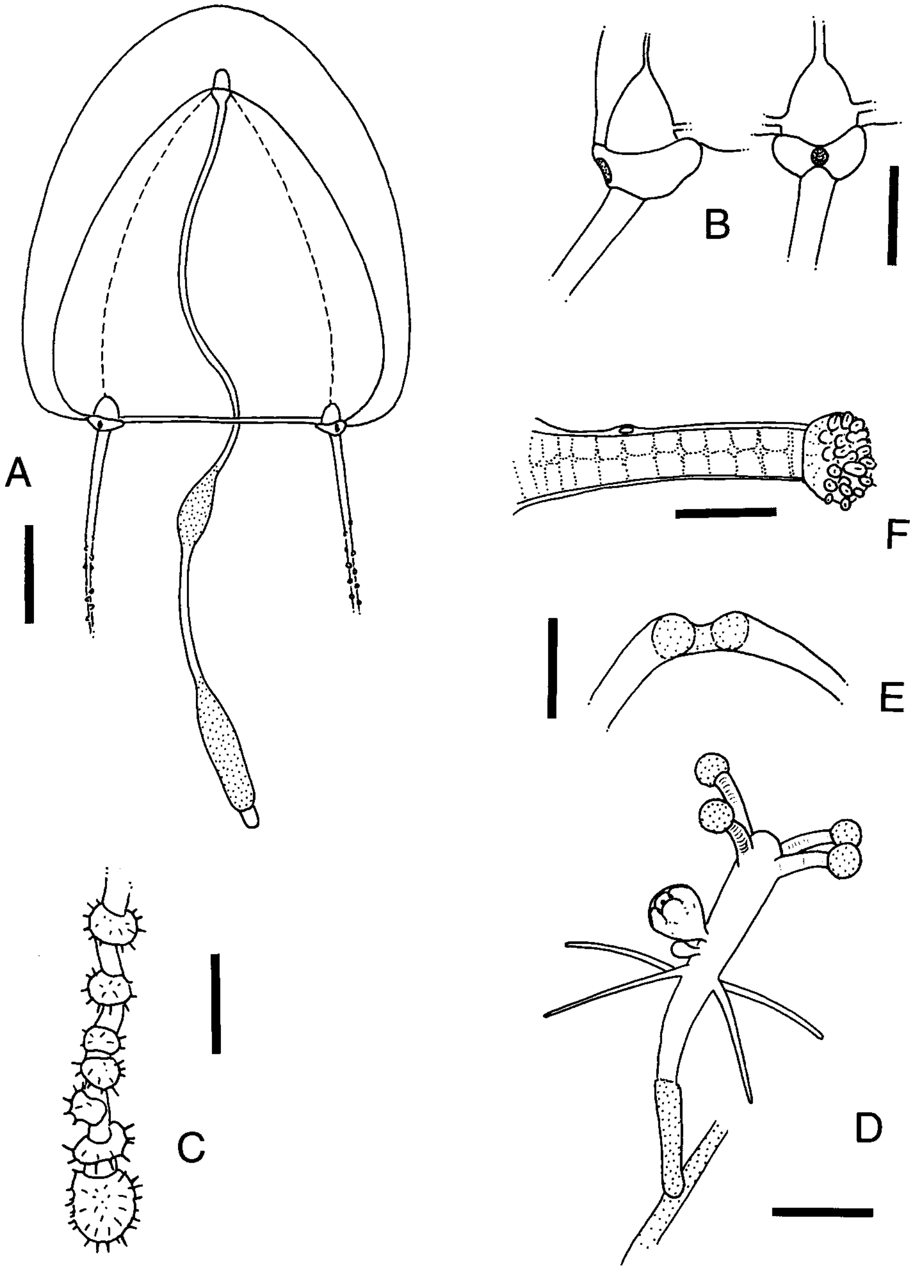

FIG. 26

Dipurena reesi Vannucci, 1956, medusa after preserved material, polyp after living material. A) Mature medusa, scale bar 0.5 mm. B) Lateral and frontal view of tentacle bulbs, scale bar 0.2 mm. C) Tip of medusa tentacle, note long spiny, cnidocils, scale bar 0.1 mm. D) Polyp with medusae buds, scale bar 0.5 mm. E) Optical section through hypostome of polyp, mouth open, note button of high gland cells (shaded), scale bar 50 µm. F) Capitate tentacle, scale bar 0.1 mm.

somewhat above the filiform tentacles and are released as free medusae. Nematocysts of polyp stage: stenoteles of two size classes, (22-29) x (20-21) µm and (16-17) x (10-11) µm, discharged stenoteles with three stilettos.

Newly released medusa 0.8-1 mm, exumbrella with 16 indistinct meridional rows of nematocysts or nematocysts scattered, no apical chamber, tentacles with less than 10 nematocyst clusters. Cnidocils stout and long.

Adult medusa normally 2-3 mm (max. 5 mm), diameter only slightly less, bell somewhat conical but with rounded top, subumbrella rather conical, jelly moderately thick. Manubrium with a bullet-shaped apical chamber. Manubrium at least two times as long as bell height. Divided into a long, thin serpentine part and a thicker cylindrical stomach at its end. Gonads in 2-3 rings, one on stomach region, the others short and on the serpentine part, end of gonad rings taper gently. Radial canals fine, narrower than ring canal, entering gastrodermal chamber of bulbs at centre-top. Epidermal nettle ring of bulb not complete, with ocellus. Tentacles long, issuing either vertically or obliquely (smaller specimen). Tentacles covered by up to 100 nematocyst clusters, terminal cluster not much thicker. Nematocytes bear long, thorn-like cnidocils, much more robust than in other species of the family. Nematocysts: stenoteles and desmonemes.

DISTRIBUTION – Brazil; Mediterranean; Bay of Biscay; California.

BIOLOGY – The hydroid occurs on a variety of solid substrates in shallow water, but is hardly detectable. Brinckmann-Voss (1970) found the polyps on shells at a depth of 20-50 m, Günzl (1964) in 1-2 m depth on rock. Most observations of the polyp were made from aquarium cultures. The polyp is quite invasive and readily establishes colonies in aquaria. The medusa has not yet been identified in material from the sea. Development: gonad maturation in cultivated animals begins 16-18 days after release (Brinckmann-Voss, 1970). Günzl (1964) investigated the factors that induce the formation of medusae buds. He found that a temperature shift from 18 to 24 °C could trigger medusae production provided that the colony had reached a certain size. Günzl (1964) also described the histology of the initial medusa bud formation. Nematocyst development is described in Günzl (1968; 1973). Tardent & Stössel (1971) described the morphology of mechanoreceptors in the filiform tentacles. The reactions to mechanical stimulation are described in Stössel & Tardent (1971).

REMARKS – The polyp of *D. reesi* resembles closely the polyps of *D. strangulata, D. spongicola, Sarsia marii, S. piriforma,* and *Cladonema radiatum* Dujardin, 1843. *D. reesi* differs from all of them by having longer filiform tentacles, which is, however, much dependent on culture conditions. All, except perhaps *S. piriforma,* also have fewer gastrodermal cells in their capitate tentacles (comp. table 5). Further differences to *Cladonema radiatum* have been outlined by Brinckmann & Petersen (1960), although the difference between the armature of the stenoteles is probably incorrect (see Bouillon, 1971: 333).

The medusa of *Dipurena reesi* resembles *D. ophiogaster*. This makes many records of *D. ophiogaster* medusae rather questionable, notably as both species have overlapping distributions (e. g. Bay of Biscay; Altuna Prados, 1993). The medusa of

D. reesi can be distinguished from *D. ophiogaster* by its more pointed form, the fewer gonad rings, and the stouter cnidocils on the tentacles. Brinckmann-Voss (1970) found also differences in the shape of the tentacle bulbs.

Brinckmann & Petersen (1960) found 18 gastrodermal cells in the tentacles of their *D. reesi* polyps. However, in the two colonies examined by me I could find only 13-15 cells. This is still more than in other similar polyps. The exumbrellar nematocysts of the newly released medusa were described by Brinckmann-Voss (1970) as scattered. In my animals they were in 16 radial rows, although some of the rows were indistinct.

In the preserved medusa it was noted that the nematocyst clusters of the tentacles bear long and coarse cnidocils. Their length equalled the length of the stenotele capsule. They were very characteristic and differed markedly from the ones seen in *D. ophiogaster*.

Dipurena simulans Bouillon, 1965 Fig. 27A-D

Dipurena simulans Bouillon, 1965: 323; Bouillon, 1971: 323, figs 1 & 3.1, pl. 1.

TYPE LOCALITY – Roscoff, Britanny, France, Atlantic Ocean.

MATERIAL EXAMINED – Living polyps on *Haliclona simulans* and subadult medusae from plankton collected near Roscoff (Brittany), June 2000, several polyp colonies with medusae buds, the released medusae were cultivated a few days – INSNB IG 27.838, Roscoff, coll. J. Bouillon 1963 & 1965, polyps embedded in sponge, one young medusa – ZMUC, Roscoff, medusa grown from hydroid stage, leg. & det. J. Bouillon, 2 specimen.

DESCRIPTION – Hydroid stolonal, with stolons deeply embedded in sponge tissue, perisarc very thin and only visible at high magnifications, hydranths protrude at sponge surface and into exhalent canals. Hydranths 0.5-0.6 mm in height, sessile, cylindrical, with prominent dome-shaped hypostome. Near mouth a button of high epidermal gland cells. Polyps on sponge surface with 10-13 capitate tentacles, hydranths in oscula with up to 16 tentacles. Tentacles arranged in one oral whorl of 3-4 tentacles and lower tentacles scattered or in indistinct whorls. No filiform tentacles present. Oral tentacles very long (0.4 mm), with 6-8 gastrodermal cells, capitulum relatively large (70-80 µm), stalk tapering to half of its original diameter. Lower capitate tentacles shorter than oral ones, stalk length and size of capitulae decreases towards proximal. Gonophores develop below tentacles in one whorl of 3-6 buds, released as free medusae. Colour: pale orange. Nematocysts, (7-11) x (4.5-7) µm and (16-17) x (12.5-13) µm; basitrichous isorhizas (17-20) x (8-10) µm.

Newly released medusae 0.7 mm, four radial canals without linear swellings, with slight apical chamber, ocelli dark red, tentacles issue vertically, short, smooth, only with one terminal swelling containing nematocysts, exumbrella with scattered nematocysts.

Adult medusa 3-5 mm high, 3.5-4.5 mm in diameter, umbrella bell-shaped, jelly thick, spanning at apex 1/4 of bell height, subumbrella with flat top, occasionally with shallow apical subumbrellar pockets. Apical chamber absent or shallow. Manubrium up to two times as long as bell height, with long and thin proximal part and a terminal swollen stomach, limits of both parts often indistinct. Gonads usually in one ring (up to 3 rings possible acc. Bouillon, 1971), initial gonad covering swollen

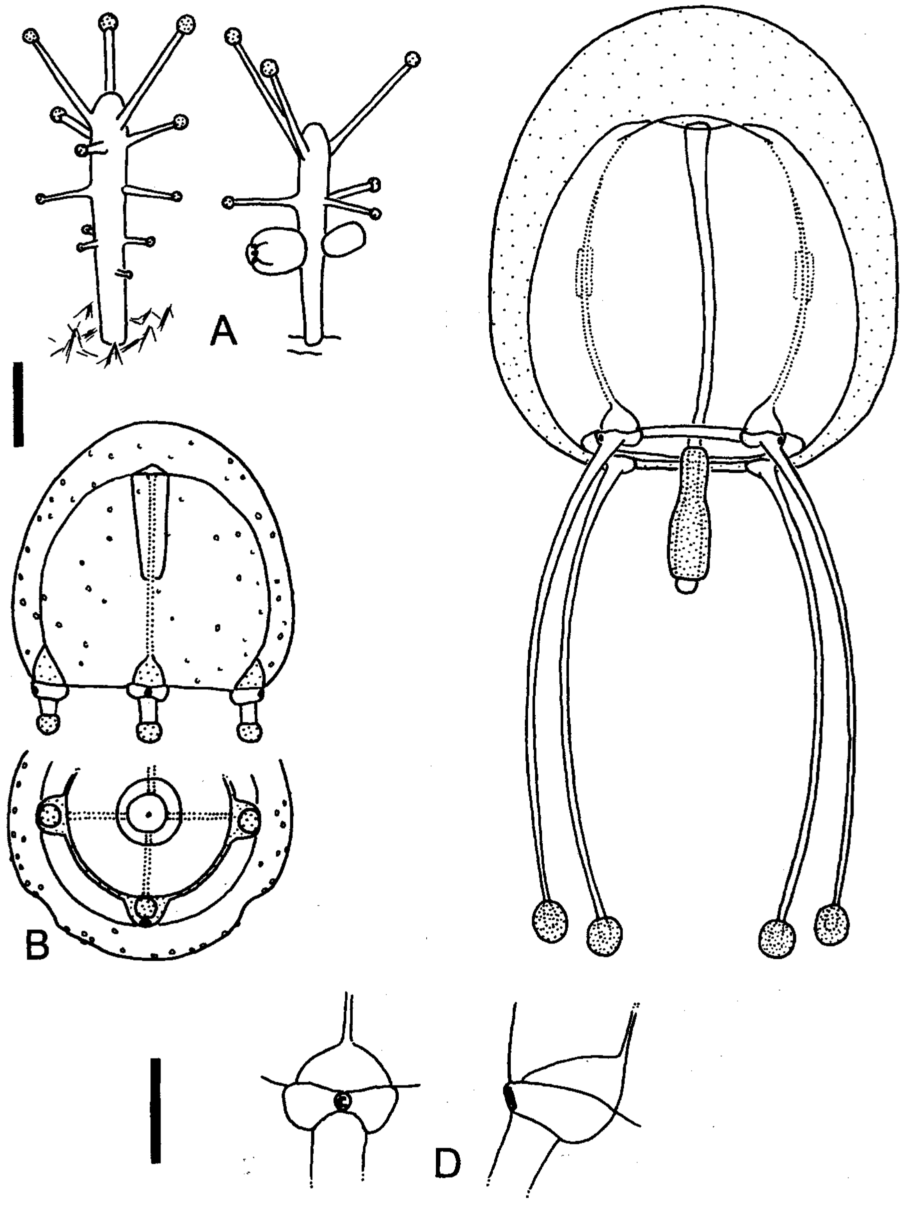

FIG. 27
Dipurena simulans Bouillon, 1965. A) Polyps after living material, right one with medusae buds, scale bar 0.2 mm. B) Newly released medusa in side view (top) and view from below, same scale as A. C) Mature medusa, scale bar 0.5 mm. D) Tentacle bulbs in frontal and side view, scale bar 0.2 mm.

stomach, later ones – if formed – on serpentine part of manubrium. Each radial canal with a single linear swelling in its middle part. Tentacles issue obliquely, somewhat longer than bell height, smooth except for a large, spherical terminal swelling covered by nematocysts. Nematocysts: stenoteles; isorhizas (rare and sometimes absent); desmonemes.

DISTRIBUTION – The hydroid and the medusae are only known from near the type locality, but they could be more wide-spread (see under *D. halterata*).

BIOLOGY – The polyps grows in and on the sponge *Haliclona simulans* (Johnston), medusae are released at Roscoff in May to August, with a maximum in July (Bouillon, 1971).

REMARKS – Although the hydroid of *D. simulans* can occur together with *D. halterata* on the same sponge, even non-reproductive hydranths can be distinguished. *Dipurena halterata* polyps are larger, accumulate detritus, and have their base ensheathed in perisarc. They develop their gonophores among the capitate tentacles. Polyps of *D. simulans* also occur on the surface of the sponge, but they are able to retract into the sponge as they have their base not covered by perisarc, they are not smothered with detritus (comp. also figures 24A and 27A). The gonophores of *D. simulans* develop below the capitate tentacles. Gonophore-bearing polyps are preferentially found in the oscular system of the sponge, although dense colonies will also form them on the surface of the sponge. The medusa of *D. simulans* with its single terminal nematocyst cluster and the single linear swelling of the radial canals is quite distinct (see also table 5). For a possible taxonomic problem see discussion under *D. halterata*.

Contrary to the observations of Bouillon (1971), some medusae of *D. simulans* observed by myself had a slight apical chamber (Fig. 27B-C). The newly released medusae also had no visible swelling of the radial canals.

Dipurena strangulata McCrady, 1859 Fig. 28A-D

Dipurena strangulata McCrady, 1859: 135, pl. 9 figs 1-2; Kramp, 1955: 243, fig. 2; Kramp, 1959: 81, fig. 20; Kramp, 1961: 24; Calder, 1970: 109, fig. 1; Pagès *et al.*, 1992: 16, table 2.

Dipurena cervicata McCrady, 1859: 136; Mayer, 1910: 76, synonym.

Dipurena conica L. Agassiz, 1862: 341; Mayer, 1910: 76, synonym.

Slabberia strangulata – Mayer, 1910: 76, pl. 7 figs 1-2, not 3.

Dipurena fragilis Mayer, 1900b: 28, pl. 17 fig. 41.

Slabberia strangulata var. *fragilis* – Mayer, 1910: 77, pl. 7 fig. 4.

TYPE LOCALITY – Charleston Harbor, South Carolina, USA.

MATERIAL EXAMINED – IRSNB IG 27.838, USA, Virginia, Gloucester Point, coll. D. Calder 28.08.1970, numerous polyps on sponge, some with medusae buds – ZMUC, St. Andrews Bay, Florida, July 1961, medusae det. Kramp – ZMUC, 5°27'N 07'E, 1700 mW, 29.01.1946, Atlantide st. 82, much damaged medusae – ZMUC, Accra, Atlantide station 77, damaged medusae – ZMUC, 4°50'N 1°17W, Atlantide station 76, 23.01.1946, 1 damaged medusa – ZMUC, 8°22'N 14°08'W, Atlantide station 144, 1 mature medusa – USNM 58646, Laurel Reef, Puerto Rico, coll. R. Larson 15.03.1975, 3 mature and 1 juvenile medusa, max. bell size 1.2 mm.

DESCRIPTION – (in part after Calder, 1970) Hydroid stolonal, stolons embedded in sponge tissue, perisarc thin, smooth. Hydranths 0.5-0.8 mm high, clavate to cylin-

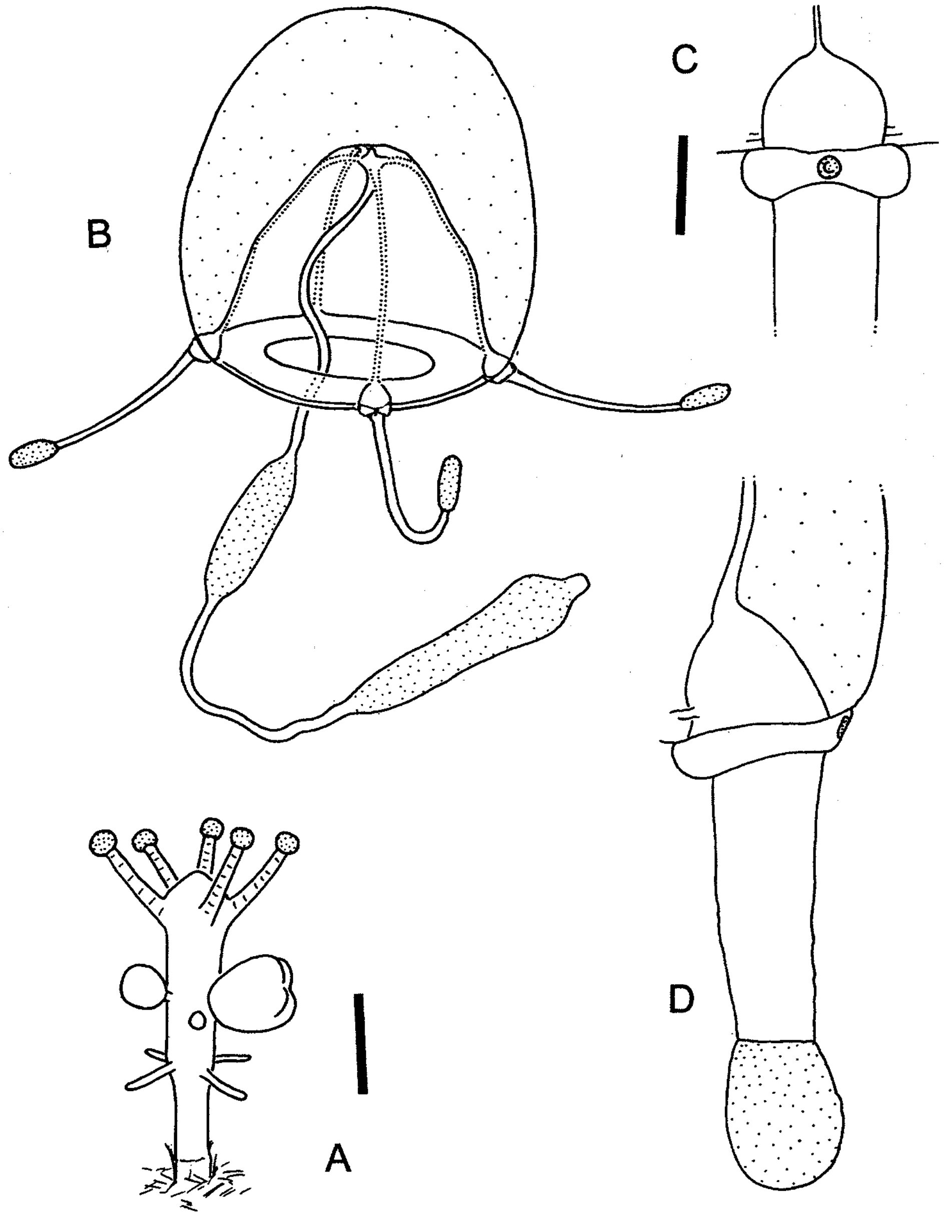

FIG. 28
Dipurena strangulata McCrady, 1859. A) Polyp with medusa buds, drawn after preserved material. B) Adult medusa, modified after Mayer (1910). C) Tentacle bulb in frontal view, scale bar 0.1 mm. D) Contracted tentacle and bulb in lateral view (material from Puerto Rico), same scale as C.

drical, hypostome a flat cone, with one oral whorl of 4-5 capitate tentacles and at lower third one whorl of 4-5 short filiform tentacles. Capitate tentacles short (0.2 mm), with 8-11 gastrodermal cells. A button of high epidermal gland cells is present (Bouillon, 1971: 333). Gonophores develop in middle of hydranth, 1-2 buds per hydranth, released as free medusae. Nematocysts: stenoteles (8-11) x (12-17) µm and (14-18) x (21-25) µm.

Newly released medusa about 0.5 mm in size, with a few scattered exumbrellar nematocysts, ocelli dark red, tentacles short, stout, nematocysts concentrated in a single large spherical cluster at end of tentacle.

Adult medusa 1.5-4 mm high, bell shape variable, often spherical, jelly thick, at apex thicker and jelly reaching 1/4 to 1/3 of total bell height. Manubrium with or without a shallow, conical apical knob. Manubrium about two times as long as bell height, with a long, thin serpentine part an a swollen stomach region at its end. Gonads encircle distal stomach region and there is an additional ring of gonad tissue somewhat more proximal to the former. Radial canals smooth, without linear swellings, entering gastrodermal chambers in middle, gastrodermal chamber high, epidermal nettle ring thick, with one dark red ocellus. Tentacles short, as long or shorter than bell height, stiff, with a single large terminal nematocyst cluster, this one either spherical or elongated. Nematocysts: stenoteles and desmonemes. Colours: gastrodermis is green or yellowish-green (Mayer, 1910).

DISTRIBUTION – Cape Cod to Florida (USA), Puerto Rico, Gulf of Guinea.

BIOLOGY – Can tolerate reduced salinity, the polyp occurs in the sponge *Microciona prolifera*.

REMARKS – Mayer (1910) mentions an abaxial spur of the tentacle bulbs on which the ocellus is placed. In the examined material no distinct spur could be seen, only sometimes a very small one (Fig. 28D). Calder (1970) also did not describe such a spur. The bulbs thus do not differ from other species of the genus.

The life cycle of *Diprena strangulata* was described by Calder (1970). Calder also noted that the young stages of *D. strangulata* described by Mayer (1910) were probably misidentified *Sphaerocoryne agassizii*. Young medusae of *D. strangulata* have four tentacles as all other members of the family and not two as depicted by Mayer.

Mayer (1910) examined numerous *Dipurena* medusae from Charleston Harbor and found that *Dipurena cervicata* McCrady, 1859 and *Dipurena conica* Agassiz, 1862 are only slight variants of *Dipurena strangulata*. The forms differ only in bell-shape and length of the manubrium. Both characters are subject to considerable variation even in one population and Mayer's opinion is adopted here too. Mayer himself (1900b) described also another similar species, *Dipurena fragilis*, which he later (Mayer, 1910) considered as a variant only. The variant differs from the normal form by its more slender tentacles and the dull-yellow colour of its gastrodermis. Further details on the synonymy of this species can be found in Calder (1970).

Polyps of *D. strangulata*, *D. reesi*, *Sarsia piriforma*, *Sarsia marii*, and *Cladonema radiatum* are difficult to distinguish. Some of their differences are discussed under *D. reesi*.

Bigelow (1904) described a medusa from the Maldive Islands as "closely allied or identical" to *D. fragilis*, a synoynym of *D. strangulata*. For biogeographic reasons I doubt that Bigelow's medusa belonged to *D. strangulata*.

Dipurena spongicola Anger, 1972

Dipurena spongicola Anger, 1972: 80, figs 1-11.
TYPE LOCALITY – Langeland Island, Germany.
MATERIAL EXAMINED – holotype material, ZMUC, on *Halichondiria*, leg. K. Anger – Roscoff, 30.3.98, few living polyps in (?) *Suberites domuncula*.

DESCRIPTION – (after Anger, 1972) colonies in sponge tissue, hydranths in cavities of sponge, stolonal, perisarc very thin and loose, short cauli covered with perisarc, hydranth fusiform, 0.4-0.8 mm, diameter 0.12-0.35 mm, one oral whorl of 4-6 short capitate tentacles with 6-8 gastrodermal cells, one aboral whorl of 5-7 filiform tentacles with few nematocysts. Nematocysts: stenoteles and very variable isorhizas. Stenotele with three stylettos. Gonophores unknown, probably a *Dipurena* like medusa with split gonad rings.

DISTRIBUTION – Germany, Sweden (Baltic Sea).

BIOLOGY – The polyp occurs within the canal system of the sponge *Halichondria panicea*, in depths of 9-10 m.

REMARKS – This species is not sufficiently described because the medusa stage was not cultivated. The occurrence within sponges, the absence of lower capitate tentacles, and the presence of the haploneme in the polyp stage, however, should render this species recognisable. It resembles *D. reesi* and *D. strangulata*, although both lack haplonemes.

5.3. Genus ***Sarsia***

SYNONYMS – *Sthenyo* Dujardin, 1845; *Codonium* Haeckel, 1879; *Sarsiella* Hartlaub, 1907; *Stauridiosarsia* Mayer, 1910; *Syndiction* A. Agassiz, 1862.
TYPE SPECIES – *Sarsia tubulosa* (M. Sars, 1835).

DIAGNOSIS – Hydroid with one oral whorl of capitate tentacles and with or without lower capitate tentacles, with or without filiform tentacles. Tentacles usually longer and thinner than in other Corynidae. Gonophores develop below capitate tentacles and over filiform tentacles. Gonophores either released as free medusae or retained at hydranth. Cnidome with or without isorhiza nematocysts. Adult medusa with manubrium extending beyond umbrella margin, thin and serpentine proximally, distally with wide stomach; gonad forming cylinder around thin part of manubrium only, leaving distal stomach free of gonad. Tentacles unbranched.

5.3.1. ***Sarsia tubulosa*** group

Comprises the species: *S. tubulosa, S. densa, S. occulta, S. striata, S. piriforma, S. viridis, S. apicula, S. princeps, S. bella*. Important characters to distinguish the species are given in table 6.

TABLE 6. Distinguishing characters of the *Sarsia tubulosa* group

character	*S. tubulosa*	*S. apicula*	*S. bella*	*S. densa*	*S. occulta*	*S. piriforma*	*S. princeps*	*S. striata*	*S. viridis*
bell pointed	no	sometimes	variable	no	no	yes	yes	no	no
subumbrella pointed	no	yes	no	no	no	no	yes	no	no
apical knob or canal	knob small, present or absent	knob present, size variable	knob short, conical	knob present	knob small, conical	knob rounded to conical	long, thin canal, occ. branched	small knob	conical knob
bell height in mm	6-10	9-12	6-9	6-8	max. 3.4	5-8	15-25	<11	5-8
gonad-free part of manubrium	short	short	more than half	more than half	very short	very short	very short	short	half of manubrium
exumbrellar nematocysts in young medusae	scattered	scattered	concentrated in 16 adradial patches	scattered	scattered	8 adradial groups	8 loose adradial groups	few scattered	unknown
subumbrellar pockets	transient	none	none	none	none	none	none	yes	?none
ridged pockets	no	no	no	no	no	no	no	yes	no
radial canal enters jelly	yes	yes	no	unknown	no	no	no	yes	yes
gastrodermal chamber of bulbs	high	high, abaxial side straight or concave	low	high	high	high, abaxial side concave	very flat	small knob	high, abaxial side straight or concave
colour bulbs	variable	yellow	reddish	red	orange to red	orange to red	intensively orange	red	brilliant green
colour apical knob	variable	red	reddish	red	orange to red	orange to red	orange	red	brilliant green
size of hydranth in mm	0.8-2.6	1.3-2	<1.5	>1.5 mm	1.6	1.0-1.8	0.7-0.8	1.3	unknown
number of capitate tentacles in polyp	12-20	12-15	8	12-20	12-17	4-6	8	8-10	unknown
whorls of capitate tentacles	scattered	3 very closely set	2 very closely set	scattered	3	1	2 closely set	2	unknown
filiform tentacles	absent	present	absent or rudimentary	absent	absent	short	present	present or absent	unknown
colony branched	stolonal or branched	stolonal	stolonal	much branched	stolonal	stolonal or slightly branched	stolonal	stolonal, occasionally branched	unknown
special	-	red tentacles	-	-	medusa sometimes fixed, jelly thin	-	hydranth club shaped, manubrium orange colour	-	green

Sarsia tubulosa (M. Sars, 1835) Fig. 29A-F

Oceania tubulosa M. Sars, 1835: 25, pl. 5 fig. 11.
Syncoryne decipiens Dujardin, 1845: 275, pl. 14-15, medusa named *Sthenyo*; Hartlaub, 1907: 30, figs 21-22b.
Medusa proboscidea Dalyell, 1847-48: 248, pl. 53 fig. 1-2, pl. 52 fig. 3 (after Bedot, 1905).
Sarsia mirabilis L. Agassiz, 1849: 224, pls 4-5; in part Berrill, 1953: 273, fig. 1A-C, (not others, = *S. occulta*).
Coryne mirabilis – in part L. Agassiz, 1862: 189, pl. 17-18.
? *Syndiction reticulatum* L. Agassiz, 1862: 340.
Sarsia tubulosa – Forbes, 1848: 55, pl. 6 fig. 2; Schulze, 1873: 14, pl. 1-3; Browne, 1903: 9; Hartlaub, 1907: 19, figs 10-14; Mayer, 1910: 53, pl. 3 figs 2-5, pl. 4 figs 1-2; in part Kramp, 1926: 8, figs 6-16, pl. 1 figs 5-7; in part Kramp, 1927: 24, chart 3; Russell, 1953: 55, figs 21-23; Kramp, 1959: 78, fig. 10; Kramp, 1961: 32; Kakinuma, 1966: 206, figs 1-5; Kramp, 1968: 6, fig. 2; Brinckmann-Voss, 1970: 66; Russell, 1970: 232; Calder, 1972: 223, pl. 1 fig. 8; Edwards, 1978:301, figs 4-5; Arai & Brinckmann-Voss, 1980: 25, fig. 12; Miller, 1982: 153, figs 3A, 4A, 4C.
Syncoryna Sarsi Lovén, 1836: 276, pl. 8 fig. 7-10.
Syncoryne sarsii – Schulze, 1873: 2, pls 1-3, not Genzano & Zamponi, 1994 [= ? *S. eximia*].
Sarsia macrorhynchia Busch, 1851: 10, pl. 3 fig. 7-10, pl. 4 fig. 1-2.
Sarsia pattersoni Haddon, 1886: 6.
Sarsia barentsi Linko, 1905: 214; Hartlaub, 1907: 14; Mayer, 1910: 53; Kramp, 1959: 207.
Sarsia litorea Hartlaub, 1907: 32, figs 23-24; Mayer, 1910: 53, fig. 13; Kramp, 1926: 15.
Sarsia pulchella – Hartlaub, 1907: 34, fig. 27.
Sarsia reticulata – Hartlaub, 1907: 45, figs 41-43; Kramp, 1961: 31.
Sarsia tubulosa var. *mirabilis* Mayer, 1910: 57, pl. 4 figs 3-4, pl. 5 fig. 6, figs 13-18.
Syncoryne mirabilis — in part Fraser, 1944: 41, pl. 4.
Coryne tubulosa – Werner, 1963: 468, figs 5-12; Naumov, 1969: 252, figs 36, 122, 123, pl. 29 fig. 6.

TYPE LOCALITY – Florø Island, Norway, summer and fall (Sars, 1835).

MATERIAL EXAMINED – ZMUC, Hirtshals, Denmark, 11.05.1931, several medusae, well preserved – ZMUC, Nyborg Biological Station, Denmark, 17.5.1915, several medusae, 6-8 mm, mature – ZMUC, Dana Station 3047, 17.05.1923, 2 medusae, det. Kramp as blue variant – ZMUC, Dana station 3078, 17.05.1923, several medusae det. Kramp – ZMUC, hydroid labeled as *Coryne sarsii*, Greenland, 67°13N 53°54W, on *Fucus*, intertidal, with gonophores below tentacles – ZMUC, hydroid labeled as *Syncoryne mirabilis*, Woods Hole, Massachusetts, USA, colony 1 cm high, in dense lawn, long stems, fertile– Woods Hole, Massachusetts, USA, living hydroid colony obtained through Annette Frese, cultivated at 16 °C until medusae buds developed – MHNG INVE 29805, Sooke, British Columbia, Canada, three medusae collected 18.4.1999 by A. Brinckmann-Voss – NMSZ 1976.64.66, Marine Station Millport, Scotland, coll. 26.5.1976, 2 mature medusae, manubrium blue-green – NMSZ 1908.151.1, Dunbar, Scotland, coll. 1908, 2 ill preserved medusae – NMSZ 1910.34.7, Heligoland, North Sea, 2 ill preserved medusae, manubrium contracted, gonad free portion very short – ZMA Coel 3969, Helder Harbour, Netherlands, coll. 1928, 3 mature medusae, one with 5 radial canals and bulbs.

DESCRIPTION – (in part after Russell, 1953 and Edwards, 1978) Hydroid stolonal or sparingly branched (up to 2 times), reaching maximal heights of 13 mm. The cauli and stolons are covered by perisarc which may be corrugated but not truly annulated. Hydranths spindle shaped, 0.8-2.6 mm in height. Capitate tentacles confined to the distal half of the hydranth, about 12-20, scattered or in indistinct whorls, length up to 0.9 mm. Filiform tentacles absent. In the lower half of the hydranth an annular thickening of the epidermis, from which a very thin and filmy periderm is secreted that covers the basal part of the hydranth. Gonophores arise in an

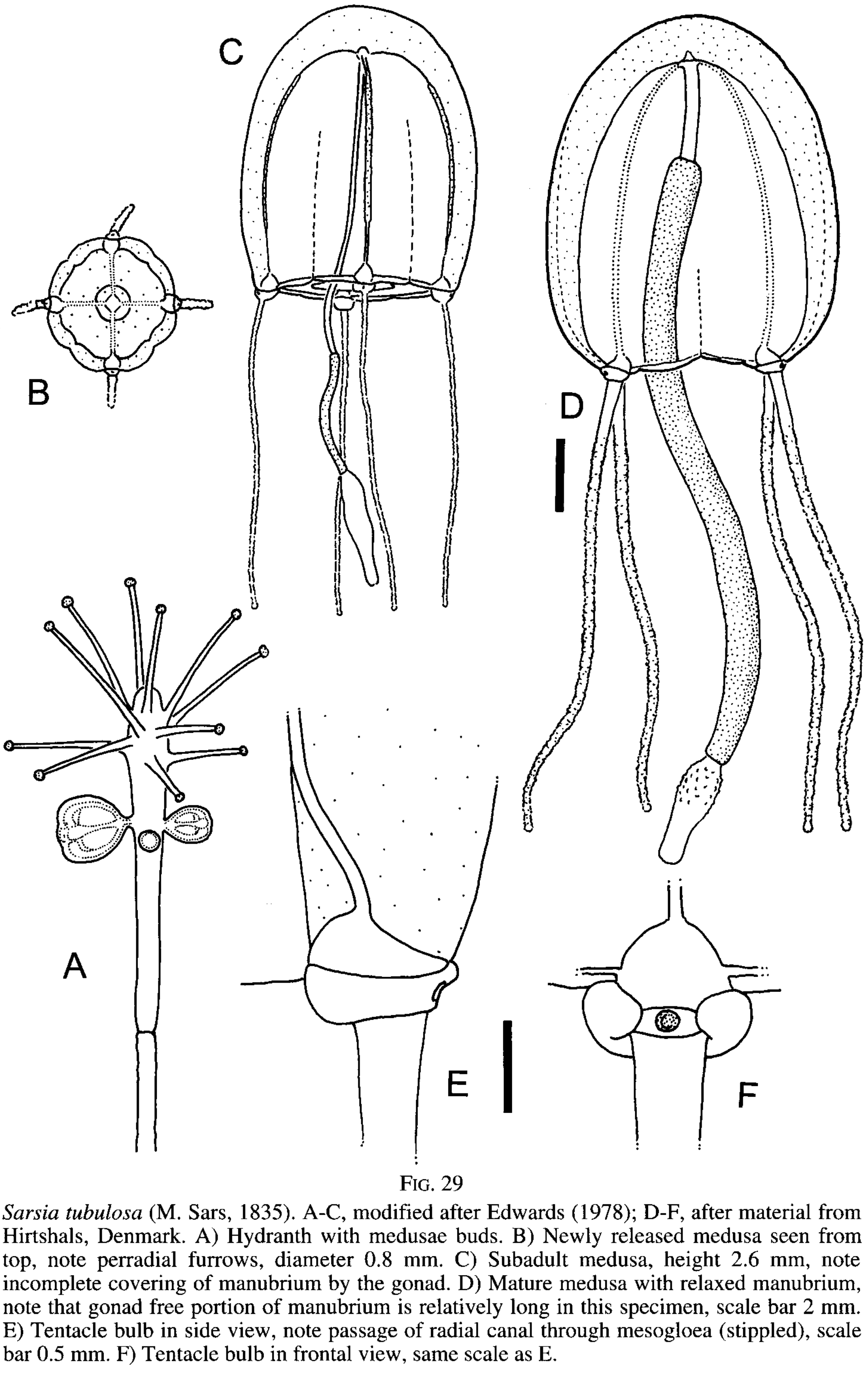

FIG. 29

Sarsia tubulosa (M. Sars, 1835). A-C, modified after Edwards (1978); D-F, after material from Hirtshals, Denmark. A) Hydranth with medusae buds. B) Newly released medusa seen from top, note perradial furrows, diameter 0.8 mm. C) Subadult medusa, height 2.6 mm, note incomplete covering of manubrium by the gonad. D) Mature medusa with relaxed manubrium, note that gonad free portion of manubrium is relatively long in this specimen, scale bar 2 mm. E) Tentacle bulb in side view, note passage of radial canal through mesogloea (stippled), scale bar 0.5 mm. F) Tentacle bulb in frontal view, same scale as E.

irregular whorl in the middle of the hydranth below the lower tentacles, 1-8 per hydranth. Gonophores are released as free, immature medusae. Hydranths producing medusae often reduce their tentacles (reproductive exhaustion). Nematocysts of polyp (Woods Hole material): stenoteles, (18-20) x (12.5-14) µm and (15-16) x (10-11) µm; isorhizas in pedicels, (13-15) x (3) µm.

Newly released medusa 0.8 mm wide and high, with scattered nematocysts on umbrella, with umbilical canal, with deep interradial and shallow perradial furrows in the exumbrella, four radial canals with glandular thickenings along part of their course, black ocelli, tentacles with several rings of nematocyst clusters. Glandular thickenings grow longer during further development, but are absent in mature animals.

Adult medusa 6-10 mm in height (in arctic waters reportedly up to 18 mm), higher than wide, bell-shaped, shape variable, jelly moderately thick, with interradial exumbrellar furrows. Manubrium very long, 2-3 times as long as bell. Apical chamber or apical knob of variable shape usually present, apical canal mostly lacking. Manubrium composed of a long, thin proximal part and a spindle shaped swelling at the distal end (stomach). Stomach at upper end covered by warts with nematocysts. Gonads encircle manubrium along thin part, leaving at top of manubrium a region of the manubrium uncovered (less than 1/4 of bell height in mature animals). Gonad ends distally at beginning of stomach. Four thin radial canals, glandular swellings diminish with adulthood. Radial canals enter gastrodermal chamber of bulbs on abaxial side and pass through mesogloea. Tentacle bulbs large, gastrodermal chamber high, epidermal nematocyst ring incomplete, with on abaxial black or red ocellus. Each bulb with a very long tentacle, leaving bulb vertically to slightly obliquely, covered by nematocyst clusters in patches or spiral rings, terminal cluster spherical but not enlarged. Colours of bulbs and apical knob very variable, blue to green, orange to yellow, ocelli black to crimson. Sars (1835) described the colours of the manubrium and tentacles as a pale brown-grey, red-yellow to faintly greenish. Nematocysts of medusa (Bouillon, 1974): desmonemes, basitrichous isorhizas, stenoteles. The young medusa has also microbasic mastigophores on its exumbrella (Nagao, 1969).

BIOLOGY – The hydroids grow on rocks, stones and weeds, chiefly near low water (Edwards, 1978). The medusa appears in British waters at the beginning of April and commences to disappear by the end of June in the south. In the North it persists into August. Similar observations were given for British Columbia by Arai & Brinckmann Voss (1980). Kramp & Damas (1925) state that off the Norwegian coast *S. tubulosa* comes to the surface on calm days in May, but usually keeps at depths of 20-100 m.

Edwards (1978) cultivated the polyp between 2 and 20 °C and it produced medusae within this temperature range. These findings contrast with results obtained by Werner (1963), who was able to induce medusae buds by lowering the temperature to 2-6 °C. At 14 °C medusae budding stopped, while at 6-8 °C medusae developed irregularly, sometimes the medusae bud were transformed into polyp buds. Perhaps Werner's material was in fact *S. densa*, which could explain the differences.

Sarsia tubulosa is able to tolerate reduced salinity. Christiansen (1972) found the polyp in Oslofjord only during winter and spring. It was rare or absent in summer. Polyps with buds were found in November.

The medusa is known to feed on copepods, mysids, amphipods, nauplii of cirripedia and euphausiids, chaetognaths, fish larvae and occasionally other medusae such as *Aurelia* (Arai & Brinckmann-Voss, 1980). Food intake, growth and ecology of the species have recently been investigated by Daan (1986). The ecological and potentially economic impact on commercially important fish larvae has been investigted by van der Veer (1985) and Purcell (1986).

Sarsia tubulosa has been the subject of numerous morphological, behavioural and physiological studies. References were compiled by Arai & Brinckmann-Voss (1980). Some more recent investigations are Leonard (1980 through 1984), Singla & Weber (1982) and Weber (1982).

DISTRIBUTION – Boreal Atlantic coasts of Europe and North America, penetrating into arctic regions. Its southern limit in Europe is the English Channel, in the western Atlantic it occurs from Chesapeake Bay to Greenland. In the Pacific it is also present along North America from San Francisco to Alaska. In the Eastern Pacific it occurs in Japan and further north. It is absent from the Mediterranean (Brinckmann-Voss, 1970). Occurrence in arctic waters is known, but some records are doubtful. Apparently it is rarer in cold waters. In view of the existence of several closely resembling species, not all records of *Sarsia tubulosa* may in fact relate to this species.

REMARKS – The life cycle of *Sarsia tubulosa* has been examined several times, commencing with Schulze (1873). Edwards (1978) gives a particularly detailed and valuable account.

Sarsia tubulosa is a variable species with a complicated synonymy, discussed extensively among others in Hartlaub (1907), Kramp (1926), Russell (1953), Edwards (1978; 1983), and Arai & Brinckmann-Voss (1980). Particularly confusing was that Agassiz apparently lumped two or three species with differing life cycle into his *S. mirabilis* (see Edwards, 1978). There is no need to repeat all the discussions here, but some ambiguities remain up to now, in particular in relation to the different colour morphs of the medusa stage. New genetic investigations are urgently needed to assess the status of this important species.

Kramp (1926; 1927) found that Danish waters are inhabited by three forms differing in colour:

> The 'blue *Sarsia*' has a manubrium and tentacles in an intensive sky-blue colour without intermixture of any other colours, especially without a tinge of green. It is usually smaller than 10 mm. This form was found widely in the Kattegat and Belt Sea, but it was absent from the North Sea.
>
> The 'brown *Sarsia*' had a manubrium and bulbs ranging from emerald-green to yellowish-brown or brown. Every shade of intermediate colour was present. This form was present in the North Sea and along Norway. Kramp considered this form to correspond to Sars' original morphotype.

The 'scarlet *Sarsia*' had manubria that were either colourless or with a faint yellowish or greenish hue, but the apical chamber and the bulbs were of a brilliant scarlet. The population was also present along the west coast of Denmark and the distribution overlapped with the brown form. At some places the two forms were found together in the same catch (see Kramp, 1927, chart 3).

Kramp examined these three colour variants for morphological differences and found a few microanatomical differences, but considered them mostly not significant or consistent enough to distinguish separate species. Only the 'scarlet' variant had a nearly filled apical chamber and a relatively long part of the manubrium not covered by gonad tissue, and it thus stood somewhat apart from the other two. Kramp related the 'scarlet' form to *Sarsia densa* Hartlaub, 1897. The 'brown' form he related to the *Sarsia tubulosa* Sars sensu stricto. Colour in hydromedusae can be significant, however, more often it is only due to the type of ingested food (Edward, 1978; Brinckmann-Voss, 1980). The apical canal may be absent or present in individuals from any geographic area without correlation to the size of the medusa. The shape of the apical chamber is also very variable, sometimes it is also missing (see Kramp, 1926: fig. 15). The shape is additionally also correlated with the degree of contraction of the medusa. Some of the medusae for which Kramp recorded the colour (blue, brown, and red) when alive are still kept by the ZMUC and they were examined for this study. It was evident that some of the brown variant had distinct subumbrellar pockets with angular ridges (e. g. Dana station 2999) and I would identify them without hesitation as *Sarsia striata* Edwards, 1983. However, it must clearly be stated that not all brown *S. tubulosa* of Kramp can be attributed to *S. striata*. Kramp's red medusae are too contracted to be of any good use, but it s evident that they are all smaller than usual *S. tubulosa*. Perhaps they are juvenile.

Kramp (1926) concludes that his red medusae and hence *Sarsia densa* might be a distinct species, but that it could also be a mere local variant. Similar conclusions were reached by Russell (1953). Hartlaub (1907) distinguished *Sarsia densa* from *S. tubulosa* mainly by the long gonad free portion of manubrium. This gonad free portion is longer than the bell height and covers about half of the tubular part of the manubrium. Further distinguishing traits are the smaller size and it is reportedly a less active swimmer than *S. tubulosa*. The polyp of *S. densa* is similar to the one of *S. tubulosa*, but the colonies are more dense and the stems more branched. The validity of the long gonad free portion of the manubrium was questioned by Edwards (1983), as he noted that also *S. tubulosa* goes through such a stage during its development (see Fig. 29C). In view of the results obtained by Miller (1982) discussed below, *S. densa* is here kept separate from *S. tubulosa* until other methods help to clearify the situation.

Miller (1982) made a close examination of the "*Sarsia tubulosa*" complex present at Friday Harbour (USA, Washington, Pacific Ocean). He noted consistent differences in egg sizes between individual female medusae. This difference correlated with other minute morphological details that permitted him to distinguish also morphotypes among the male medusae. He was able to distinguish three morphotypes, but one was rare. Miller named the two main types S and L forms (small and large egg-size). The L-form differed from the S-form in having a longer gonad free proximal portion of the manubrium, extending to the bell margin or beyond (shorter than bell in S-form), thus corresponding to *S. densa.* The L-Form also had four adradial nematocyst patches on the exumbrella (completely absent in S-form). Both forms also differ in the timing of their spawning. Miller (1982) then used cross-fertilisation to further investigate whether these morphotypes belong to reproductively isolated populations. Cross-fertilisation between the two forms indeed resulted in only a few viable hybrids and it is now clear that the two forms must belong to two different species. The S-form was initially attributed to *S. tubulosa sensu stricto*, but recently Brinckmann-Voss (2000) referred it to *S. apicula* (Murbach & Shearer, 1902) (although this is difficult to see in Miller's (1982) figures). The L-form was described by Brinckmann-Voss (2000) as a new species, *Sarsia bella.*

Synoryna sarsii Lovén, 1836 was most probably based on a polyp of *S. tubulosa* showing reproductive exhaustion (Edwards, 1978). Although Loven's species is not sufficiently recognisable, most contemporary authors accepted the synonymy of the the two names. Only Genzano & Zamponi (1994) contested this view. Their supposed material of *S. sarsii*, however, was more likely *S. eximia* (they could not cultivate the medusa to maturity). Whatever it was, it obviously does not match Lovén's (1836) description and figures.

S. mirabilis Agassiz, 1849 seems to form dense polyp colonies with considerably branched stems. Mayer (1910: 49) tabulates further differences, although most of them are not appropriate to distinguish *Sarsia* species. Most subsequent authors treated *S. mirabilis* as a synonym of *S. tubulosa.* Even Mayer (1910) gave *S. mirabilis* only a status of a variety of *S. tubulosa. Syndyction reticulata* Agassiz, 1862 is seen by most authors as conspecific with *S. mirabilis.* According to Mayer (1910), it differs from *S. mirabilis* in having a smaller medusa (3 mm) with a bell covered by reticulated clusters of nematocysts. The nematocytes seem to have characteristically long cnidocils (Mayer, 1910 : pl. 4 fig. 4, pl. 5 fig. 6). The polyp is smaller and less branched. The colour of the medusa is constantly brick-red in contradistinction of the more variable *S. mirabilis. Sarsia reticulata* is here treated as questionable synonym of *S. tubulosa*, while *S. mirabilis* is regarded as subjective synonym of *S. tubulosa.*

Sarsia barentsi Linko, 1905 was described without figures and the observations were based on four specimens only. Linko (1905) considered it a separate species due to the s-shaped manubrium. This may, however, have been an artifact (fixation). No further records of this species are known and it seems very likely that it is referrable to *S. tubulosa*, an opinion already expressed by Mayer (1910, synonym to *S. tubulosa* var. *mirabilis*).

Infertile hydroids of *S. lovenii* have often been misidentified as *S. tubulosa* (see also under *S. lovenii*). The hydranths of the latter species are larger and the stems can be quite branched and tall.

Sarsia apicula (Murbach & Shearer, 1902) Fig. 30A-C

Codonium apiculum Murbach & Shearer, 1902: 72; Murbach & Shearer, 1903: 165, pl. 17 fig. 1, pl. 22 figs 4-5.

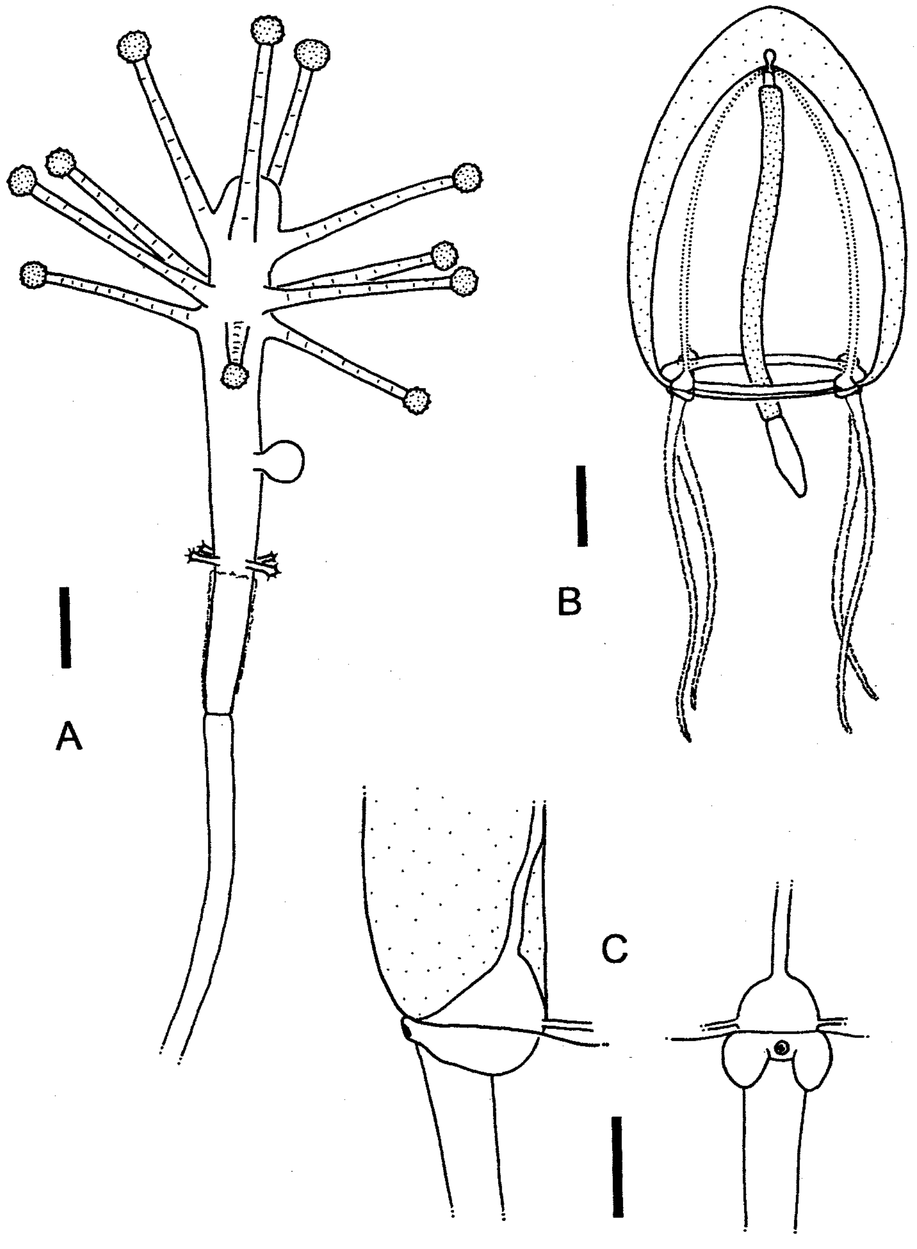

FIG. 30
Sarsia apicula (Murbach & Shearer, 1902), after preserved material from Sooke, British Columbia. A) Polyp with medusa bud, scale bar 0.2 mm. B) Mature medusa with contracted manubrium and tentacles, scale bar 2 mm. C) Tentacle bulbs in lateral and frontal view, note that radial canal passes through mesogloea (stippled, figure left), scale bar 0.2 mm.

Sarsia apicula – Hartlaub, 1907: 17, fig. 9; ? not Sverdrup, 1921: 14, pl. 1 fig. 2; Arai & Brinckmann-Voss, 1980: 18, fig. 8, 9a; Brinckmann-Voss, 1985: 673, figs 1-5.

TYPE LOCALITY – Puget Sound and Victoria, Canada.

MATERIAL EXAMINED – Sooke, British Columbia, one medusa collected 22.5.1999 by A. Brinckmann-Voss, damaged – MHNG INVE 29806, Sooke, polyps with medusae buds raised from mature medusae by A. Brinckmann-Voss, Nov. 1999.

DESCRIPTION – (in part after Brinckmann-Voss, 1985) Hydroid mostly stolonal, rarely branched once. Stems and stolons covered by thin, flexible, smooth perisarc, no annulations. Hydranths up to 1.3-2 mm high, club-shaped, distal end slightly swollen. Normally with three, rarely two, very closely set whorls of long capitate tentacles. Tentacles confined to distal third of hydranth. Each whorl with four, rarely five tentacles, mostly in alternate position to tentacles of adjacent whorls. Distance between oral whorl and middle whorl larger than distance between the two lower whorls. Lowest whorl of tentacles slightly shorter than other ones. Tentacle stalks tapering somewhat. At lower third of hydranth one whorl of small filiform tentacles, number variable from 0 to 4, with accumulation of sensory bristles at end. Filiform tentacles often absent in material from the sea. Hydranth base from end of perisarc up to level of filiform tentacles covered by very fine, filmy layer (visible in compound microscope only). Gonophores develop in middle of hydranth above filiform tentacles in one or two indistinct whorls. Normally 1-4 gonophores, but up to 10 possible. Colours: gastrodermis pink, hypostome white. Nematocysts: stenoteles (11-17) x (7-11) µm.

Gonophores are released as free medusae. Newly released medusa 1.0-1.1 mm, with scattered exumbrellar nematocysts, tentacles with six to eight nematocyst clusters, terminal one not thickened. Subadult medusa (5-8 mm) is rounded, thick jelly and with subumbrellar pockets that disappear in the adult. Newly released medusa with mastigophores on exumbrella.

Adult medusa 9-12 mm high, diameter 7.5-9 mm, bell top pointed to rounded, jelly thick. Subumbrella quite conical (Fig. 30B). Extended manubrium about two times as long as bell height, with apical knob. Apical knob variable in form from high cone or bulb to a flat cap. Manubrium with long, thin serpentine part and distal swollen stomach. Gonad covers nearly entire serpentine part, thickness near top in extended manubrium tapering evenly. Radial canals enter the gastrodermal chamber at its top, passing a very short distance through the mesogloea. Epidermal part of bulbs with an incomplete nematocyst ring, sometimes a light exumbrellar spur, with black ocellus. Tentacles at least two times as long as bell, covered densely by nematocyst clusters, terminal cluster not thickened. Colours: tentacles in adults characteristically red, epidermal parts of the bulbs yellow, gastrodermal part of bulbs orange to red, apical knob red. Nematocysts: stenoteles, (15-16) x (10-11) µm and (11-12) x (8) µm; desmonemes (9-11) x (4-5) µm. Egg size less than 100 µm.

DISTRIBUTION – North eastern Pacific, Puget Sound, Sooke and Victoria Harbour, Friday Harbour, San Juan Islands (Brinckmann-Voss, 2000).

BIOLOGYY – The polyp grows on rock scallops [*Himnites multirugosus* (Gale)], 20-30 m, the medusa was present in the surface plankton from end of March to middle of August.

REMARKS – The medusa of *Sarsia apicula* is characterised by the red tentacles, by its somewhat conical subumbrella, and the tapering of the gonad towards its base (not visible in Fig. 30B). Preserved medusae are hardly distinguishable from *S. tubulosa* and *S. princeps* in the region of sympatry (Vancouver Island region). *Sarsia apicula* is distinguished from *S. tubulosa* through its triangular bell, which is a rather constant feature in living specimens. The pinkish colour of the tentacles and manubrium also distinguishes it from the typical blue *S. tubulosa* of their sympatric range. It is distinguished from *S. princeps* through its shorter apical canal, the relation of height to width of the bell, the shape of the tentacular bulbs and the radial canal that passes through the mesogloea (comp. Figs 30C and 35B).

They are, however, clearly different in their polyp stage. Hydranths of *Sarsia tubulosa* have no filiform tentacles, and those of *S. princeps* have only two whorls of tentacles and they are two times smaller.

Colour in most corynid medusae such as *S. tubulosa* is dependent on their diet (Edwards, 1978), but a colour difference in animals from the same locality is very indicative for that different species are present.

Sarsia bella Brinckmann-Voss, 2000 Fig. 31A-C

Polyorchis penicillatus – Brinckmann-Voss, 1977: 93, figs 1-2.
Sarsia L – Miller, 1982: 157, figs 3B and 4B-D.
Sarsia bella Brinckmann-Voss, 2000: 190, figs 2-6.
TYPE LOCALITY – Becher Bay, off Vancouver Island, Canada.

DESCRIPTION – (after Miller, 1982 and Brinckmann-Voss, 2000) Hydroid stolonal, without clear separation of caulus and stolons, hydranths relatively small (<1.5 mm), with an oral whorl of 4-5 capitate tentacles and an additional whorl of capitate tentacles very close below, lower tentacles only half the length of the oral ones. With about 10 gastrodermal cells in oral tentacles. Filiform tentacles absent or very small. Gonophores develop below capitate tentacles in middle region of hydranth, released as free, immature medusae. Nematocysts: stenoteles (12-18) x (7-12) µm; homotrichous isorhizas (14-15) x (5-7) µm.

Newly released medusa 1 mm high and wide. Exumbrella with 16 distinct adradial nematocyst patches, two patches per adradius, each pair on one meridian, each patch consisting of 6-11 densely packed microbasic mastigophores. During growth, the nematocysts become more scattered and often disappear. Manubrium shorter than bell, without visible gonads.

Mature medusa 6-9 mm high, diameter slightly less, bell rounded to conical. Exumbrella thicker at apex than at side, adradial exumbrellar nematocyst patches faintly visible or absent. Manubrium with short, conical apical chamber. Manubrium about three times as long as bell height, divided into long, thin serpentine part and distal, swollen stomach. Gonads restricted to serpentine part and covering only distal half of it. Four radial canals, stout, clearly visible, not entering mesogloea above gastrodermal chamber of tentacle bulb. Gastrodermal chamber of bulbs shallow, epidermal part prominent, with abaxial ocellus. Tentacles issue obliquely to almost horizontal in living specimen. Tentacles several times as long as bell height, with numerous nematocyst clusters. Nematocysts: stenoteles (9-12) x (7-9) µm; desmo-

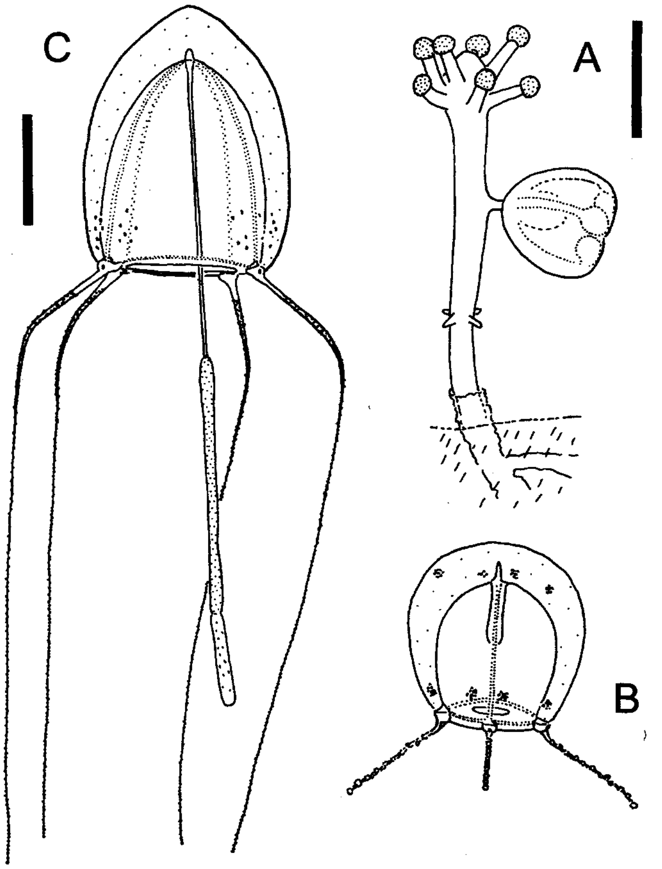

FIG. 31

Sarsia bella Brinckmann-Voss, 2000; combined and modified after Brinckmann-Voss (1977; 2000) and Miller (1982). A) Hydroid with contracted tentacles and medusa bud, embedded in sponge, scale bar 0.2 mm. B) newly released medusa, note characteristic clusters of nematocysts, height about 1 mm. C) Mature medusa, scale bar 4 mm.

nemes (7-9) x (4-5) µm; mastigophores on umbrella (11-12.5) x (8-10) µm. Egg size: 110-130 µm.

BIOLOGY – The polyp was found partially embedded in a sponge growing on the margin of the rock scallop *Hinnites multirugosus* (Gale). Medusae buds were observed in May at sea temperatures of 9 °C.

DISTRIBUTION – Vancouver Island region and Friday Harbor.

REMARKS – Medusae of *Sarsia bella* are best distinguished from other similar medusae by their long gonad free portion of the serpentine part of the manubrium. Only *Sarsia densa* and *Sarsia viridis* have such long portions of the manubrium free of gonads. Another characteristic of *S. bella* are the 16 nematocyst patches on the exumbrella. The patches are in adradial position and form an upper and a lower circle. Mature animals, however, may have lost most of the exubrellar nematocysts. For further differences see table 6. The polyp of this species has previously been misidentified as *Polyorchis penicillatus* (Brinckmann-Voss, 1977; corrected in Brinckmann-Voss, 2000).

Sarsia bella is one of the few hydrozoans that have been investigated for possible mechanisms for reproductive isolation. It is – although perhaps not completely – reproductively isolated from other similar, sympatric species by a difference in the time of spawning and in differences of the sperm attractant (Miller, 1982). However, especially the time difference of spawing might be of minor importance and additional other factors, like species specific sperm binding, are likely to prevent most hybridisations.

Sarsia densa Hartlaub, 1897 Fig. 32

Syncoryne sarsi – Hartlaub, 1895: 165.
Syncoryne densa Hartlaub, 1897: 452, pl. 15b figs 4 & 11, pl. 6c fig. 7; Mayer, 1910: 51, 55, fig. 18; Hartlaub, 1907: 26, figs 17-19; Kramp, 1926: 15; Russell, 1953: 57; Edwards, 1983: 59.
? *Syncoryne pulchella* Allman, 1865: 1; Allman, 1871: 279, pl. 6 figs 1-3.
[not *Sarsia pulchella* Forbes, 1848]
? *Sarsia coacta* Hartlaub, 1918: 386, fig. 333.
TYPE LOCALITY – Heligoland, North Sea.
MATERIAL EXAMINED – ZSM, collection Stechow, several slides originating from Heligoland, identified as *Sarsia decipiens*, collected begin of century, may belong to this species – ZMUC, as *Sarsia tubulosa* red variant, Dana station 3022, north of Bulbjerg, 09.05.1923, id. Kramp, 3 medusae, 2 mm, may belong to here.

DIAGNOSIS – Medusa like *S. tubulosa*, but smaller (6-8 mm, max. 10 mm), gonad free portion of proximal manubrium as long as gonad and longer than bell height, radial canals narrow, colours: bulbs and apical knob dark reddish-brown or scarlet, gonad region yellow-brown or yellow-grey, ocelli red. The polyp phase is similar to *S. tubulosa*, but forms dense colonies and the stems are more branched (shoots with up to 6 hydranths). According to Hartlaub (1897), the perisarc is characteristically yellow.

DISTRIBUTION – North Sea. Due to the difficulties in distinguishing this species from *S. tubulosa*, many records must be seen as doubtful.

BIOLOGY – The medusa is present in Heligoland from February to April.

REMARKS – Hartlaub (1907) distinguishes the medusa of *Sarsia densa* from *S. tubulosa* mainly by the long gonad-free portion of manubrium. This gonad free portion is longer than the bell height and covers about half of the tubular part of the manubrium. The validity of the long gonad free portion of the manubrium was questioned by Edwards (1983), as he noted that also *S. tubulosa* goes through such a stage during its development. Further distinguishing traits are the smaller size and Hartlaub considered it to be a less active swimmer than *S. tubulosa*. The polyp of *S. densa* is similar to the one of *S. tubulosa*, but the colonies are more dense and the stems much more branched (Fig. 32). For more discussions see also under *S. tubulosa*. More work is clearly needed to resolve the status of the various *S. tubulosa*-like

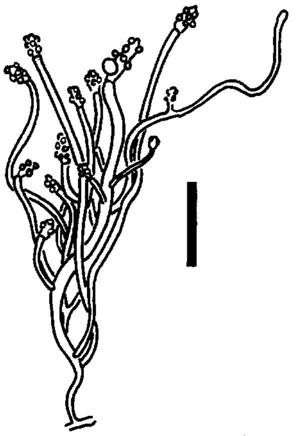

FIG. 32
? *Sarsia densa* Hartlaub, 1897, colony from Heligoland, scale bar 2.5 mm.

species in the North Sea. In view of the results of Miller (1982), *S. densa* is here kept separate from *S. tubulosa* until genetic studies will prove the contrary.

Several hydroid colonies from Heligoland identified by Stechow as *S. decipiens* and now held by the ZSM might perhaps belong to this species. The hydranths and the position of the medusae buds are exactly as described by Edwards (1978) for *S. tubulosa,* but the stems branch much more. One stem has more than 12 hydranths. The diameters of the branches varies considerably (factor 2), the oldest branches increase their diameter towards distal (Fig. 32). Hartlaub (1897) depicts a colony of his *S. densa* with a stem that has 6 terminal hydranths. This is much more than in Scottish material of *S. tubulosa* (Edwards, 1978) or North American colonies (Fraser, 1944, as *S. mirabilis*). The material from Heligoland has a very fine adhering periderm membrane that covers the basal region of the hydranth from the end of the caulus to the origin of the gonophores, however, such a membrane can occur in all *Sarsia* species.

Sarsia frutescens (Allman, 1871) also resembles *Sarsia densa* in forming large colonies and perhaps belongs also to here.

Sarsia coacta Hartlaub, 1917 is only known from its polyp phase. It produces very dense, much branched colonies. The gonophores develop below the tentacles. Kramp (1961) thought that *S. coacta* is conspecific with *S. tubulosa.* The profuse growth of the colonies argues somewhat against this. Material identified by Hartlaub as *S. coacta* is still in the collection of the ZSM (several slides and alcohol material) and was examined for this study. It differed from the above mentioned *S. densa* material in being more gracile. It is here included as a questionable synonym of *S. densa*, although it might also belong to *S. lovenii.*

Sarsia occulta Edwards, 1978 Fig. 33A-B

Coryne mirabilis - in part L. Agassiz, 1862: 189, pls 17-18; Edwards, 1978: 293.
Sarsia occulta Edwards, 1978: 293, figs 1-3; Edwards, 1983: 59.

Syncoryne mirabilis – Berrill, 1953: 277, figs 1E, 2B (not others); Edwards, 1978: 293.
TYPE LOCALITY – Near Dunstaffnage Marine Laboratory, Oban, Scotland.
MATERIAL EXAMINED – USNM 58288, Keppel, Millport, Scotland, large colony with subadult medusae, collected C. Edwards 8.5.1978, colony was cultivated 1 month.

DESCRIPTION – (in part after Edwards, 1978 & 1983) Hydroid mostly stolonal, rarely branched once. Cauli may reach 9 mm in height, mostly shorter, perisarc smooth, irregularly corrugated, or annulated, annulations present especially in lower part of stem. Hydranths up to 1.6 mm, club- to spindle-shaped, tentacles confined to upper half of polyp, at lower third often an annular thickening. Mouth surrounded by high epidermal gland cells. Tentacles capitate, in three not so distinct whorls, tentacle number up to 17, may be reduced in gonophore producing hydranths, tentacle length up to 0.85 mm. Filiform tentacles absent. Gonophores develop below lower tentacles in middle of hydranth, normally one only, occasionally two per hydranth. Gonophores develop into medusae that are either released or retained at the hydranth, the degree of development at release depends on environmental conditions. Nematocysts: stenoteles, (17-18) x (11-12) µm and (13-14) x (7-8) µm; haplonemes, slightly curved, numerous, (14-15) x (3) µm. Colour of hydranth is pink, perisarc translucent pale horn-coloured.

Young medusa 1.1-1.8 mm in height, manubrium variably developed, exumbrella covered with scattered nematocysts. Maturation of gonads starts already when medusa is still attached to hydroid.

Free, adult medusa up to 3.4 mm, diameter only sightly less, bell-shaped, jelly of even thickness, rather thin, velum breadth about 1/2 of radius. Manubrium with an apical knob and an umbilical canal. Manubrium about two times as long as bell height, with a long thin proximal part and a thicker, spindle shaped stomach at distal end. Mouth region covered by nematocysts. Gonad encircles thin part of manubrium and extends from nearly the base of the manubrium to the begin of the swollen stomach. Radial canals and circular canal narrow, glandular thickenings of radial canals very slight, radial canal enters at top of tentacular bulbs without passing through mesogloea. Tentacular bulbs small, gastrodermal chamber conical, epidermal ring complete, with large deep violet to black ocellus. Each bulb with a tentacle originating in vertical direction, about 1.5 times as long as medusa, with many scattered nematocyst clusters, distal ones ring-shaped, terminal cluster spherical but not enlarged. Nematocysts: stenoteles (11-13) x (7-8) µm; desmonemes (8-9) x (3-4) µm. Colours: gastrodermal system orange, brownish-red or scarlet.

DISTRIBUTION – Coasts of Scotland, Massachusetts, and Maine.

BIOLOGY – Medusae are produced in late winter and in spring within a temperature range of about 7-11 °C (Edwards, 1978). Polyps grow on stones and seaweeds near low water.

REMARKS – With the discovery of *Sarsia occulta*, Edwards (1978) resolved a longstanding confusion between *Sarsia tubulosa* and *S. lovenii* going back to Agassiz (1862) and other authors (see Edwards, 1978). With detailed experiments Edwards (1978) was able to show that all three species are distinct, but that gonophore maturity in *Sarsia* may nevertheless be influenced by environmental conditions. Although the medusa of *S. occulta* is often released, Edwards (1978; 1983) found conditions and

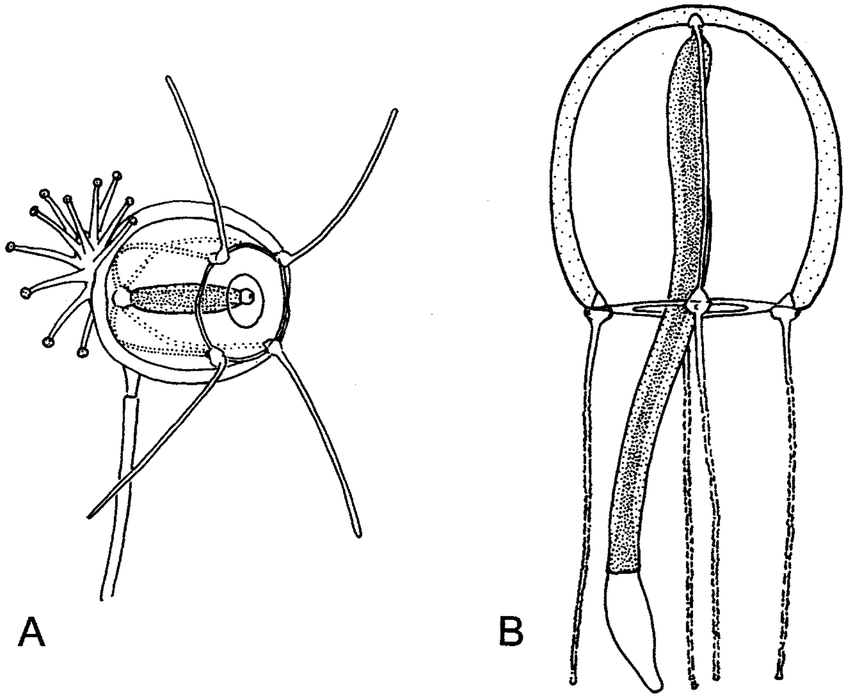

FIG. 33

Sarsia occulta Edwards, 1978, modified after Edwards (1978). A) Polyp with medusa immediately before release, development of gonads is fairly advanced. B) Free, mature medusa; bell height 3.4 mm.

clones that kept the mature medusa fixed at the polyp. Release or retention of the medusa depend on the interplay of environmental factors, particularly food supply and temperature. Development at higher temperatures seemed to favour the retention.

The medusa of *S. occulta* is not known from the sea. It is a very inactive swimmer and may remain near the sea bottom. It closely resembles *S. tubulosa*, but can be distinguished on account of the following details. *Sarsia occulta* differs from *S. tubulosa* by its smaller dimensions (half the size), the advanced stage of the gonads at release, the very short gonad free portion at the base of the manubrium, the retention of the apical canal throughout its life, the indistinct interradial exumbrellar furrows, the indistinct glandular swellings of the radial canals and the radial canal that does not enter the mesogloea before joining the marginal bulb (valid for fully grown animals only).

Sarsia piriforma Edwards, 1983 Fig. 34A-B

Sarsia piriforma Edwards, 1983: 49, figs 1-2.
TYPE LOCALITY – Near Oban, Argyll, Scotland.

DESCRIPTION – (after Edwards, 1983) Hydroid stolonal or stems long and branched 1-3 times. Perisarc of stolons and stems mostly smooth, not annulated,

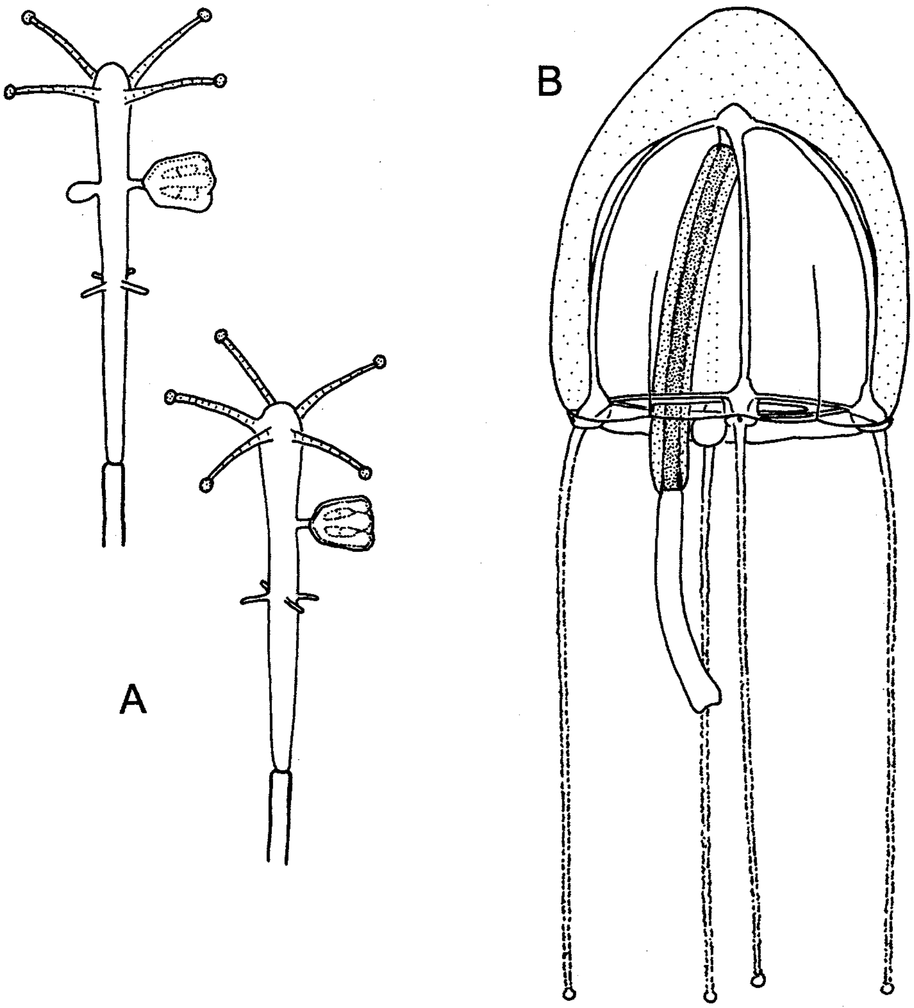

FIG. 34
Sarsia piriforma Edwards, 1983; modified after Edwards (1983). A) Two hydranths with differing tentacle numbers and medusae buds. B) Mature medusa, bell height 7.3 mm.

occasionally somewhat corrugated. Hydranths 1.0-1.8 mm in height, nearly cylindrical, with a single whorl of oral capitate tentacles (4-6) and one whorl of 3-5 short filiform tentacles in the middle of the body. About 10 gastrodermal cells in the oral tentacles. Hypostome short and rounded. Gonophores are formed halfway between filiform and capitate tentacles, one or two per hydranth, released as free medusae. Colours: hypostome white, gastrodermis pink or orange.

Newly released medusae 0.9 mm, with a few rather large exumbrellar nematocysts in eight adradial groups, with umbilical canal, ocelli black, tentacles with spirally arranged nematocyst clusters, terminal cluster not enlarged.

Adult medusa 5-8 mm in height, diameter slightly less than height, jelly moderately thick, much thickened at apex which gives a conical shape to the upper half of the bell, interadial exumbrellar furrows shallow. Manubrium about two times as long as height of bell cavity, with a conical to rounded apical knob. The manubrium has no distinct thin serpentine part, the gonad encircles the manubrium from nearly its origin along the proximal 2/3 of its length. Four radial canals of variable breadth (perhaps not in nature), entering gastrodermal chambers of bulbs at top. Gastrodermal chamber with abaxial side concave. Tentacles about two times as long as height of bell, with spirally arranged nematocyst clusters along nearly its whole length, ending in a slightly enlarged, hollow globular cluster. Colours: apical knob and gastrodermal chambers of bulbs orange or scarlet, ocelli black.

DISTRIBUTION – Type locality only.

BIOLOGY – The polyp was found on clinker in a depth of 15-20 m.

REMARKS – The medusa of *Sarsia piriforma* is not known from the sea. During its cultivation Edwards (1983) noted that it is an inactive swimmer often resting at the bottom of the culture vessel. This suggests that in nature it may also live close to the bottom and does not inhabit the surface layers, which may explain why it has never been found in the plankton. Edwards (1983) further noted that during cultivation, the majority of the medusae died, only 1-3 of hundred and more survived. He suspected that some interaction killed them (nematocyst stings?).

The hydroid of *Sarsia piriforma* is almost indistinguishable from *Dipurena reesi*, but the latter has longer filiform tentacles. The medusa has a characteristic, thick apical jelly which distinguishes it from the similar *S. tubulosa*. In cultivated specimens, the manubrium is also shorter and the gonad-free stomach not much swollen. However, it is not known whether this also holds true for medusae from nature. The medusa of *Sarsia apicula* from the North Pacific is even more similar. *Sarsia apicula* differs from *S. piriforma* by the more pointed subumbrella. The polyps are easily separable (see table 6 and Figs 30 and 34).

Sarsia princeps (Haeckel, 1879) Fig. 35A-E

Codonium princeps Haeckel, 1879: 13, pl. 1 figs 1-2; Grönberg, 1898: 458, pl. 27 figs 1-2.
Sarsia princeps – Browne, 1903: 8, pl. 1 fig. 1, pl. 3 fig. 4; Hartlaub, 1907: 47, fig. 44; Mayer, 1910: 60, fig. 22; Sverdrup, 1921: 14, fig. 1; Kramp, 1926: 2, figs 1-5, pl. 1 figs 1-4; Kramp, 1959: 79, fig. 13; Kramp, 1961: 29; Kramp, 1968: 7, fig. 3; Naumov, 1969: 255, fig. 124, pl. 29 fig. 7; Arai & Brinckmann-Voss, 1980: 23, fig. 11; Brinckmann-Voss, 1985: 676, figs 5-9, tables 1-3.
not *Sarsia princeps* – Uchida, 1933: 126, fig. 1 [? = *S. tubulosa*].
TYPE LOCALITY – Western Greenland.
MATERIAL EXAMINED – Holotype, as *Codonium princeps*, ZMUC, loc. Greenland, leg. Fleischer, 2.10.1865, 22 mm high, Haeckel no. 12 – paratypes, ZMUC, as *Codonium princeps*, loc. Greenland, det. Haeckel, several medusae all > 1 cm – IRSNB IG27.838, 2 medusae, coll. J. Bouillon, loc. arctic, size 22-25 mm – Sooke, British Columbia, collection A. Brinckmann-Voss no. 1740, one 13 mm high male medusa, coll. 10.5.99; hydroid grown from such medusae, without medusae buds as already released, preserved 2.3.2000; 3 young medusae released from mentioned polyp colonies.

DESCRIPTION – (hydroid after Pacific material) Hydroid mostly stolonal, one times branched stems rarely present. Stolons and stems enclosed in thin, soft, wrink-

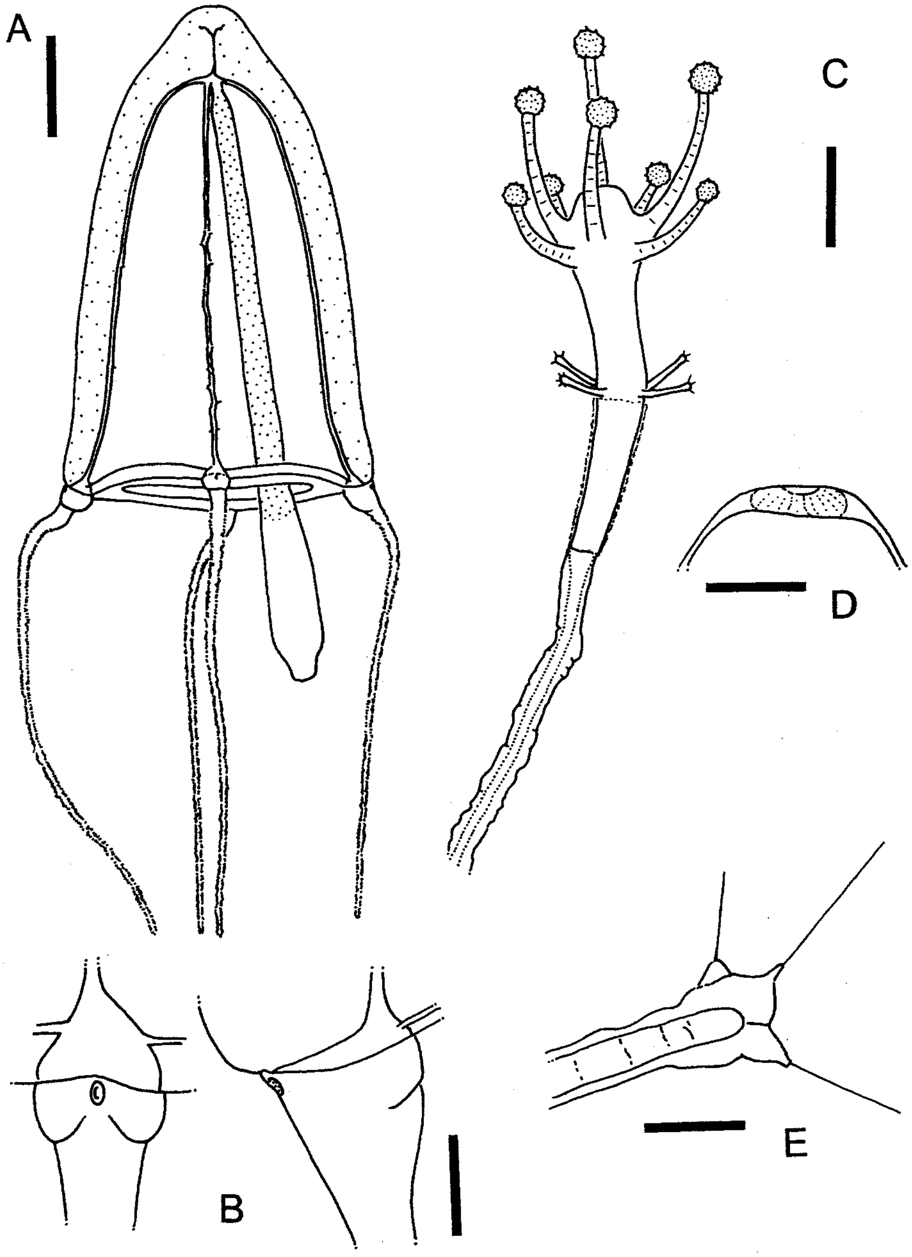

FIG. 35

Sarsia princeps (Haeckel, 1879). A) Fully grown medusa, scale bar 5 mm. B) Tentacle bulbs in frontal and side view, the oblique view makes the gastrodermal chamber in left figure appear higher than it actually is, scale bar 1 mm. C) Polyp stage, material from British Columbia, scale bar 0.2 mm. D) Hypostome of polyp in optical section, high epidermals cells are clearly present, scale bar 50 μm. E) Tip of filiform tentacles with presumed sensory cilia, scale bar 10 led perisarc, without regular annulations. Base of hydranth up to filiform tentacles enclosed in very fine, filmy perisarc, visible only in compound microscope. Hydranths 0.7-0.8 mm high, slender, club shaped, distal end swollen. With two closely set whorls of long capitate tentacles, 4 per whorl, in alternate positions, lower tentacles shorter than oral ones, all capitate tentacles taper to half the diameter towards distal. Hypostome short, with button of high epidermal cells. Below middle of hydranth one whorl of 4-5 small filiform tentacles of equal length, always present, distal end somewhat swollen and provided with long, stiff sensory cilia. Gonophores develop halfway between capitate and filiform tentacles, 1-5 per hydranth, at different levels but not in whorls. Colours: gastrodermis pink, capitulae white. Nematocysts: stenoteles, (16.5-18) x (11-12) μm and (11.5-13) x (7-9) μm; haplonemes (isorhizas?) (13-16) x (4.5-5) μm.

Gonophores are released as free medusae. Newly released medusa after Brinckmann-Voss (1985) as high as wide, about 1 mm, with eight adradial concentrations of exumbrellar cnidocysts in the lower part of the umbrella.

Adult medusa of Atlantic populations normally 15-25 mm (12-15 mm in southern regions, may reach 40 mm in high arctic waters), bell distinctly conical and about two times as high as wide, jelly quite thick, thickened at apex. Manubrium 1.5 to 2 times as long as height of bell, proximal part thin and tapering, distally swollen to stomach, but limits may be indistinct. Gonads encircle the manubrium from nearly its base to the beginning of the swollen stomach region, the thickness tapers gently towards proximal. At top of manubrium a long, thin, often branched, apical canal. Radial canals broader than circular canal, often jagged and provided with lateral diverticulae. Radial canal enters gastrodermal chamber of bulbs in its adaxial half without entering mesogloea. Tentacular bulbs large, in frontal view quite narrow compared to tentacle width, gastrodermal chamber very shallow, abaxial side straight or more often concave in side view (Fig. 35B, right). Epidermal part high, with large black ocellus. Tentacles long, contracted as long as height of medusa, tightly covered by crescent-shaped to disc shaped (more distal) nematocyst clusters. Colours: manubrium, apical canals, bulbs are light to intensively red-orange. Nematocysts: stenoteles (12-15) x (11-12) μm; desmonemes.

BIOLOGY – Brickmann-Voss (1985) found the polyp in depths of 15 to 25 m on shells and she thinks that light plays a role in the triggering of gonophore production. Kramp (1926) found the medusae in arctic waters during the summer months. The medusa ocurrs in the upper strata, often immediately below the surface. Along the Murmansk coast, medusae may also occur during wintertime. Aspects of feeding ecology of the medusa were examined by Matsakis & Conover (1991).

DISTRIBUTION – A circumpolar arctic species. Southern limits in the Atlantic are the south coast of Newfoundland, Angmagssalik in eastern Greenland, Spitzbergen, Bear Island, and Kola Peninsula; in the Pacific Sea south to Sea of Okhotsk and Hokkaido, in the east Vancouver Island. Kramp (1926) and Arai & Brinckmann-Voss (1980) give more details on the distribution.

REMARKS – *Sarsia princeps* is the largest medusa of the Corynidae and fully grown specimens are normally easy to identify. The orange colour, the shallow gastrodermal chamber of the bulbs, the radial canals entering near the adaxial side of the bulbs, the jagged radial canals, the long thin and often branched apical canal, and the characteristic high and pointed bell make this species distinct. The radial canals, however, may not always be jagged, and jagged radial canals may also occur in deteriorating medusae of other species like *S. tubulosa.*

Sarsia princeps is sympatric with *S. apicula* along the coast of British Columbia and it is sometimes difficult to distinguish them, in particular from preserved material. *Sarsia princeps* medusae are normally very large (up to 40 mm), but apparently get smaller (12-15 mm) towards the limits of their distribution. Vancouver Island is close to the southern limit of *S. princeps,* therefore the size of *S. princeps* there comes close to *S. apicula.* The bullet-shaped, more elongated bell, the long apical canal, and the radial canals that enter the bulbs quite adaxially and without entering the mesogloea help to distinguish *S. princeps* from *S. apicula.* Both hydroids are similar, but there are differences in size and in tentacle numbers and whorls. *Sarsia apicula* has maximally 14 capitate tentacles in three whorls, while *S. princeps* has maximally 8 in two whorls. However, it seems unwise to identify polyps from nature down to species level withouth life-cycle information. Newly released medusa of *S. apicula* have scattered nematocysts on their exumbrella, while those of *S. princeps* and *S. piriforma* have eight adradial patches on the lower part of the exumbrella.

Linko (1900) described the microscopic anatomy of the ocelli. Kramp (1926) describes the microscopical anatomy of the manubrium and found an unusual sexual dimorphism of the mesogloea.

In the specimen examined for this study, the manubrium was not clearly divided into a thin serpentine part and a distant large stomach. The thin part rather increased constantly its diameter to reach the diameter of the stomach.

The first stages of the polyp phase were already described by Naumov (see Naumov, 1969), but the complete cycle was revealed by Brinckmann-Voss (1985). Contrary to most other related species, filiform tentacles are always present in *Sarsia princeps* polyps (Brinckmann-Voss, 1985). However, life-cycle investigations on the Atlantic populations should be made to prove that the Atlantic and Pacific populations have identical polyps.

Sarsia striata Edwards, 1983 Fig. 36A-C

Sarsia striata Edwards, 1983: 54, figs 3-4.

TYPE LOCALITY – Near Oban, Argyll, Scotland.

MATERIAL EXAMINED – ZMUC, as *Sarsia tubulosa* brown variant, Dana station 2999, 10 mm high medusa, with distinctly ridged subumbrellar pockets.

DESCRIPTION – (after Edwards, 1983) Hydroid normally stolonal, occasionally branched once or twice, height up to 2-3 mm. The perisarc of stolons and stems is irregularly corrugated and translucent pale horn-coloured. Hydranths are spindle to club-shaped, up to 1.3 mm high, with one oral whorl of 4-5 capitate tentacles and one whorl of 4-5 lower tentacles in alternate positions. Near middle of hydranth one whorl of 4 short filiform tentacles, may be missing or rudimentary. Gonophores develop

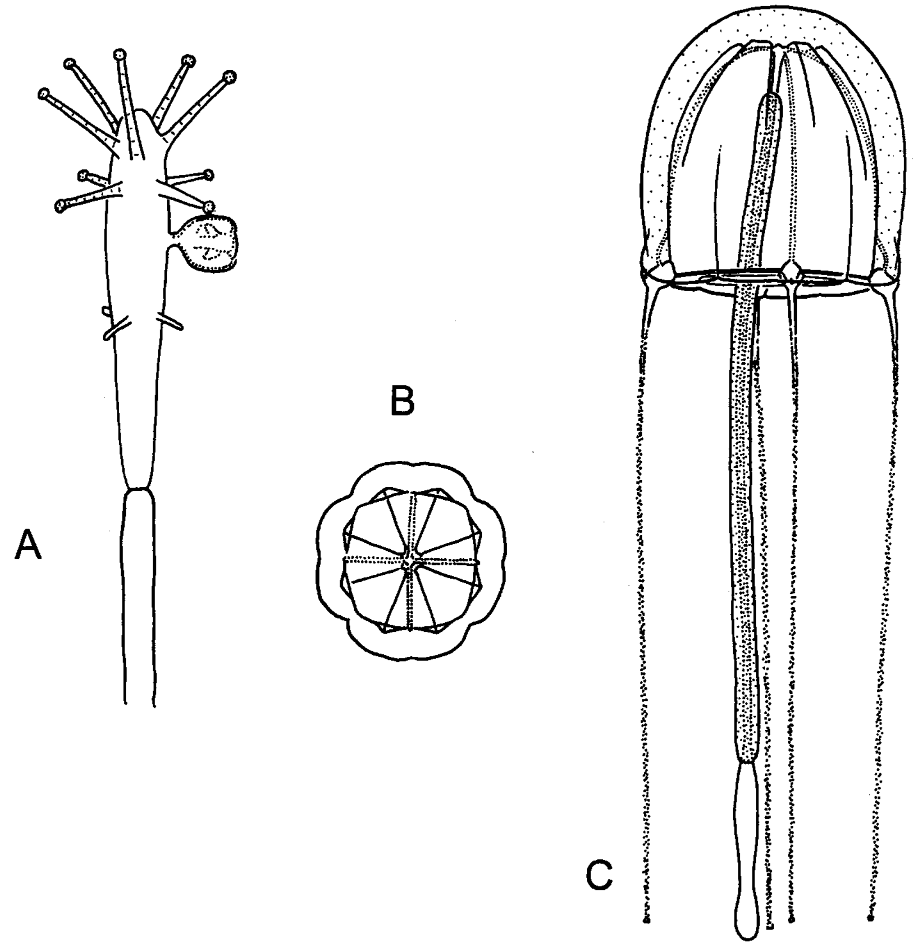

FIG. 36
Sarsia striata Edwards, 1983; modified after Edwards (1983). A) Hydranth with medusa bud. B) Bell of mature medusa seen from above. C) Mature male medusa, note the characteristic ridged subumbrellar pockets, bell height 11 mm.

halfway between capitate and filiform tentacles, 1-2 per hydranth, released as free medusae. Colours: hypostome white, gastrodermis and gonophores pink.

Newly released medusa 1.2 mm, uniformly thick jelly of moderate thickness, umbilical canal present, with few scattered nematocysts on exumbrella, black ocelli, manubrium short and base raised conically.

Adult medusa up to 11 mm in height, bell shaped, as high as broad, jelly relatively thick, more so at apex, top of bell rounded, exumbrella with deep interradial and shallower perradial furrows, subumbrella at top with interradial pockets marked with angular ridges. The velum spans about 1/2 of its radius. The manubrium can attain four times the length of the bell height, with a long and thin serpentine part and a terminal swelling functioning as stomach. The gonad encircles the serpentine part of the manubrium only, leaving uncovered only the stomach and at the base a part of the tubular section (about 1/5 of the height of the bell cavity). Manubrium often with a small apical knob. The radial canals are narrow, without glandular swellings. At maturity (not before), the radial canals pass through the mesogloea to enter the gastrodermal chambers of the bulbs at their abaxial side. Bulbs well formed, gastrodermal chamber large, epidermis with a black ocellus. Tentacles very long and hollow, leaving bulbs obliquely, thickly covered with spirally arranged clusters of nematocysts, ending in a slightly enlarged terminal hollow cluster. Gastrodermal part of bulbs and apical knob are scarlet.

DISTRIBUTION – Firth of Lorn, Scotland.

BIOLOGYY – At the type locality, the polyp was common on clinker in depths of 15-20 m. The medusa was present in the plankton from April to end of May. It is an active swimmer.

REMARKS – While the polyps are quite different – *Sarsia striata* has filiform tentacles and is much smaller – the medusae of *S. striata* closely resembles *S. tubulosa*. It is entirely possible that both have been confounded in earlier publications (e. g. by Kramp (1926; 1927), some of his material of *S. tubulosa* proved to be clearly *S. striata*, see under *S. tubulosa*). *Sarsia striata* can be distinguished from *S. tubulosa* mainly by its characteristic subumbrellar pockets with angular ridges, the thicker jelly, and the longer shorter gonad free portion at the base of the manubrium. The ecology of the two is also slightly different. While the polyps of *S. tubulosa* occur near low water, the polyps of *S. striata* were found in depths of 15-20 m. In Scotland, the medusa of *S. tubulosa* occurred more in sheltered coastal places, while that of *S. striata* was common in more open waters.

Sarsia viridis Brinckmann-Voss, 1980 Fig. 37A-B

Sarsia viridis Brinckmann-Voss, 1980: 2, figs 1-2; Arai & Brinckmann-Voss, 1980: 29, fig. 13.
TYPE LOCALITY – Sooke Harbour, Vancouver Island, Canada, surface water.
MATERIAL EXAMINED – ROMIZ B96, paratype, Ucluelet Inlet, Vancouver Island, 25.05.1977, one medusa.

DESCRIPTION – (in part after Brinckmann-Voss, 1980) Adult medusa 5-8 mm high, maximal diameter slightly less than height, deep bell shaped, umbrella rounded. Manubrium about twice as long as bell, with conical apical chamber, manubrium divided into long and thin serpentine part and a distal swollen stomach part. Stomach part with nematocysts near mouth. Gonad on serpentine part of manubrium only, leaving the upper half of it free of gonad cover. Radial canals enter gastrodermal chamber of bulb at top, passing a short stretch through mesogloea. Gastrodermal chamber of bulb with concave or straight abaxial wall. Epidermal part of bulb relatively shallow, evenly thick, ocellus black in colour. Radial canals rather thick and clearly visible, thicker than ring canal. Tentacles with nematocyst clusters over most of their length, terminal cluster not much larger. Colours: marginal bulbs and apical knob brilliant green, manubrium paler green, umbrella slightly green. Polyp phase unknown.

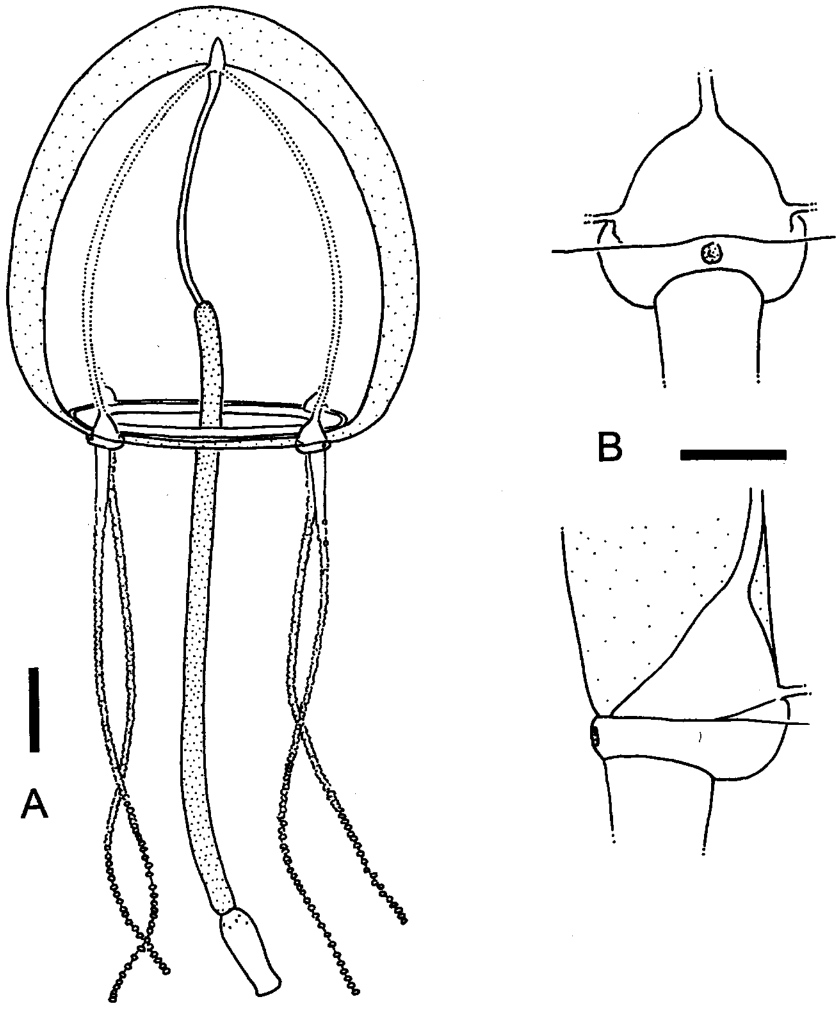

FIG. 37
Sarsia viridis Brinckmann-Voss, 1980. A) Mature medusa, the manubrium is perhaps somewhat contracted, scale bar 1 mm. B) Tentacle bulbs in lateral and frontal view, scale bar 0.2 mm.

DISTRIBUTION – British Columbia and Puget Sound, rare.

REMARKS – *Sarsia viridis* owes its name to the intense green colour of the bulbs and the apical knob. With its long gonad-free portion of the manubrium it resembles *S. bella* and *S. densa* from the North Sea. The characteristic green colour and the smaller size may help to distinguish it. More information on the life cycle of *Sarsia viridis* is needed.

5.3.2. *Sarsia* species with sessile gonophores

This group contains at present only *S. lovenii*, characterised by medusoids that remain attached to the hydroid. The inclusion of this species in the genus *Sarsia* is discussed below.

Sarsia lovenii (M. Sars, 1846) Fig. 38A-D

Syncoryne ramosa – Lovén, 1836: 275, pl. 8 figs 1-6.
Syncoryne lovenii M. Sars, 1846: 2 footnote.
[not *Syncoryne loveni* van Beneden, 1866]
Coryne gravata Wright, 1858: 33, pl. 19 fig. 5.
Syncoryne gravata – Hincks, 1868: 53, pl. 10 figs 1c-f, not e.
Coryne mirabilis – in part L. Agassiz, 1860: pl. 17 figs 10, 11, 13-16.
Syncoryne loveni – Allman, 1871: 276; Jäderholm, 1909: 8, pl. 1 fig. 7; Broch, 1916: 15, fig. A, pl. 1 fig. 2, pl. 2 fig. 13; Hartlaub, 1916: 91, figs 6-10, 12; Russell, 1953: 61, text fig. 23B, pl. 2 fig. 5.
? *Sarsia eximia* – in part Berrill, 1953: 286, figs 6B-D, 7A-C, (not others).
[*Coryne loveni* Allman, 1859]
Coryne lovenii – Naumov, 1969: 257, fig. 12; Schuchert 2001: 47, fig. 33.
Sarsia loveni – Edwards, 1978: 310, fig. 6; Petersen, 1990: 213.
TYPE LOCALITY – coast of Norway.
MATERIAL EXAMINED – IRSNB 27.838, Denmark, Middlefort Harbour, coll. P. Kramp 21.05.1915, dense, 3 x 2.5 cm colony on mussel, with mature male medusoids – ZMUC, Greenland, Godthaab, 26.06.1895, material of Broch (1916), fertile – MHNG INVE 29592, Iceland, Sandgerdi, living colonies collected 7.5.2000 by author, cultivated at 12 °C until medusoids matured (4 weeks).

DESCRIPTION – Hydroid either stolonal or irregularly branched a few times, reaching 3 cm in height. Fertile colonies can form dense mats or consist of few hydranths only. Branches arise at acute angles, mostly growing vertical and giving the stem a slender appearance (Fig. 38A). Length of branches very unequal, but mostly comparatively long. Perisarc annulated over stretches, especially at origin of branches, otherwise smooth or corrugated, not thick, yellowish colour. Perisarc terminates at base of hydranth normally without dilation, very rarely funnel-like dilation present. Hydranth 0.8-1.3 mm in length, spindle-shaped to club-shaped, hypostome large, near lower third a slight annular thickening of the epidermis or a ring of sensory cells with long, stiff cilia. With about 12-18 capitate tentacles arranged in more or less distinct whorls. One oral whorl of 4-6 tentacles, and normally two (occasionally three) additional whorls of lower tentacles, tentacle positions in each whorl alternate with the ones of adjacent whorls, tentacles of most proximal whorl often shorter than more distal ones. Oral tentacles with 8-12 gastrodemal cells, capitae spherical (diameter about 0.14 mm), nematocytes cover entire surface. No filiform tentacles, these replaced by sensory cells. Mouth encircled by button of high epidermal cells.

Gonophores arise just below lowest whorl of tentacles, mostly one per hydranth, but up to three are possible. Some hydranths are reduced with continued growth of gonophore and only a mere blastostyle may remain (reproductive exhaustion). Gonophores remain fixed as medusoids, reaching 0.8-1.0 mm in length. Gonophore much longer than broad in living material, attached by thick peduncle, jelly thin. Gonophores have four distinct radial canals, a ring canal, and four rudi-

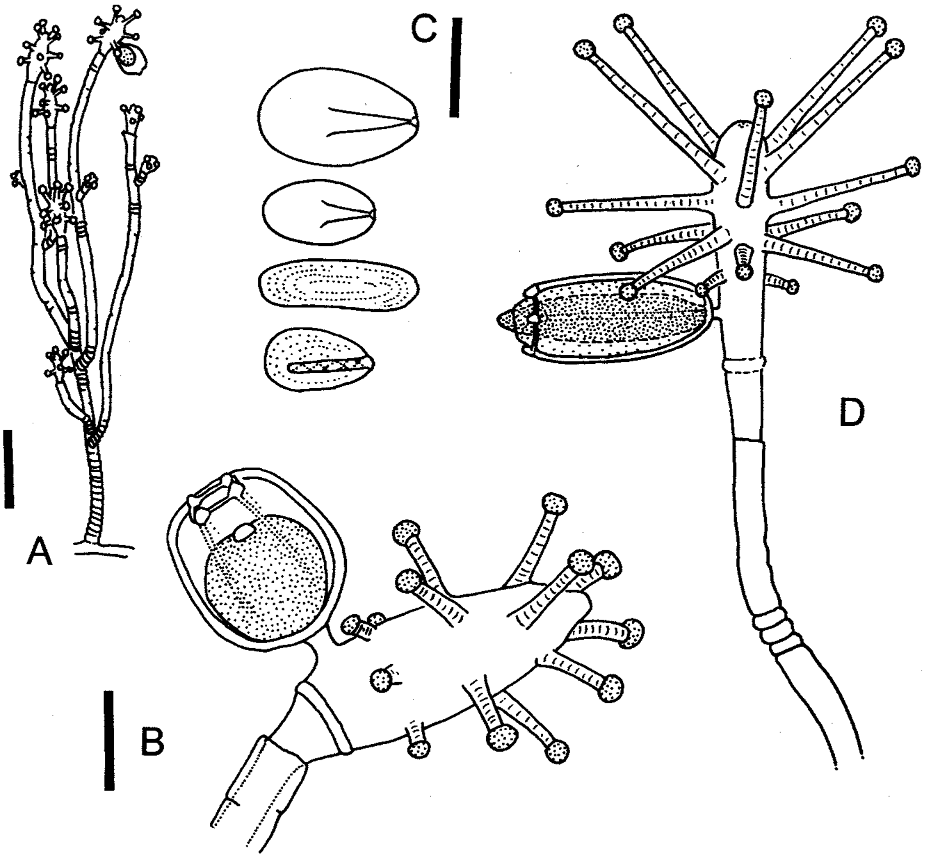

FIG. 38
Sarsia lovenii (M. Sars, 1846); A-C after preserved material from Denmark, D, after living material from Iceland. A) Single stem, scale bar 1 cm. B) Hydranth with mature medusoid, scale bar 0.5 mm. C) Cnidome: stenotele 1, stenotele 2, isorhiza, microbasic mastigophore, scale bar 10 µm. D) Hydranth with mature medusoid, note shape difference to preserved material, same scale as B.

mentary bulbs without ocelli or tentacles. Manubrium present, slightly longer than bell in living animals. Gonads voluminous, encircling manubrium completely and filling nearly bell cavity. Colours hydranth opaque white to pink, canals and manubrium of gonophores red.

Nematocysts: stenoteles, (16-17) x (10) µm and (10-11) x (6-7) µm; isorhizas, at hypostome and in marginal bulbs of gonophores, (14-16) x (5) µm, r ~ 3; microbasic mastigophores, in gonophores only, (10-12) x (6-7) µm, s < 1.

DISTRIBUTION – Cooler waters of the Atlantic (northern boreal to arctic regions). White Sea, Barents Sea, Norwegian Sea, North Sea, Great Britain, western part of Baltic Sea to Kattegat Strait, Davis Strait, Iceland, Atlantic Canada and northern New England (USA).

BIOLOGY – In aquaria with seawater kept at the temperature of circulating sea water, gonophores developed from April to June (Edwards, 1978). *Sarsia lovenii* can tolerate reduced salinity. The polyp grows on stones and other solid object, low water mark to 200 m.

REMARKS – There has been a considerable confusion of this species and others in the older literature, principally going back to Agassiz (1860). The hydroid has often been confounded with *S. tubulosa*. Hartlaub (1916) and Edwards (1978) clarified the status of this species. Edwards (1978) also added new data on behaviour, ecology and occurrence. He noted that the gonophore bell pulsates like a free medusa, although it is never released. The eggs are released into the water and develop into ciliated planulae.

I think that Berrill (1953) misidentified a colony of *S. lovenii* from Guernsey as *S. eximia*. The position of the medusoid below the tentacles as well as the shape and maturity of the medusoid clearly agree with *S. lovenii*. The two colonies from the Gulf of Maine are also not referable to *C. eximia*. One is perhaps also *S. lovenii* (figure 10 in Berrill, 1953), while the colony depicted in his figure 9 has gonophores independent of the tentacles. The identity of this species is unclear and most probably it is a so far unknown species.

The cnidome of *Sarsia lovenii* comprises also an ovoid microbasic mastigophore and an isorhiza. This makes the species quite distinct. The button of high epidermal cells around the mouth opening, the location of the gonophores below the capitate tentacles, the long manubrium, the long and tapering tentacles, and the occurrence of haplonemes associates this species with *Sarsia* or *Dipurena* (see cladogram in figure 2). It is here provisionally placed into the genus *Sarsia*. Molecular investigations must be made to find the correct genus for this species.

5.4. Genus *Nannocoryne*

TYPE SPECIES – *Nannocoryne mammylia* Bouillon & Grohmann, 1994.

DIAGNOSIS – Corynid hydroids with one oral whorl of capitate tentacles and one whorl of filiform tentacles. Gonophores absent, gametes mature in gastrodermis.

REMARKS – *Nannocoryne* has completely suppressed all gonophore development as in *Hydra* species. In Hydrozoa, gamete precursor cells develop in the gastrodermis and are then transferred and stored into the epidermal layer (a synapomorphy for the Hydrozoa, see Schuchert, 1993). In *Nannocoryne mammylia* they remain in the gastrodermis of the hydranth body, which must be interpreted that even the transfer from the epidermal layer has been abolished in this species, an altogether complete reduction of all gonophore development.

Nannocoryne mammylia Bouillon & Grohmann, 1994 Fig. 39

Nannocoryne mammylia Bouillon & Grohmann, 1994: 431, figs 1-2, pl. 1.
TYPE LOCALITY – Rio de Janeiro, Brazil, interstitial.

DESCRIPTION – Hydroid stolonal, stems including hydranths reach 1.1 mm in height, stolons and caulus covered by perisarc. Hydranths fusiform, up to 0.5 mm, with one oral whorl of four (3-5) short capitate tentacles, at lower third 4-7 filiform

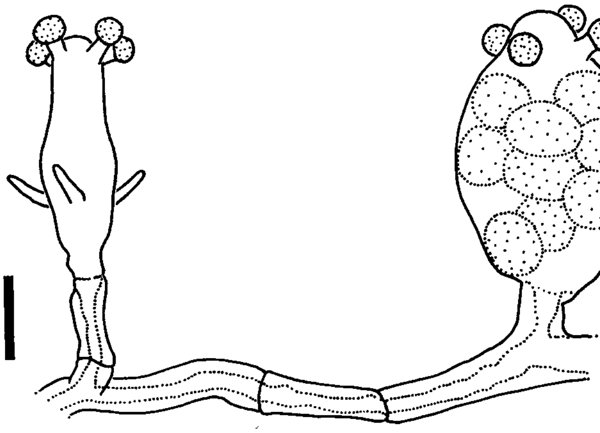

FIG. 39
Nannocoryne mammylia, figure modified after Bouillon & Grohmann (1994), scale bar 0.1 mm.

tentacles, some containing nematocysts. Gametes are formed and stored in the gastrodermis of a hydranth, only females known, with up to 13 eggs. Nematocysts: stenoteles of two sizes; perhaps also rare heteronemes.

DISTRIBUTION – Type locality.

BIOLOGY – Occurs in coarse sand.

REMARKS – The filiform tentacles of *N. mammylia* may contain some nematocysts. This is not unusual for the Corynidae. The hypostome has some slightly enlarged secretory cells, which Bouillon & Grohmann (1994) interpreted as related to the button of high gland cells in the genus *Dipurena*. These gland cells, however, are not characteristic for the genus *Dipurena* only (see phylogeny).

5.5. Genus *Cladosarsia*

TYPE SPECIES – *Cladosarsia minima* Bouillon, 1978a.

DIAGNOSIS – Corynidae producing medusae with branched capitate tentacles.

REMARKS – Bouillon (1978a) erected the new family Cladosarsiidae to accommodate *Cladosarsia minima*. Later, Bouillon (1978b) added a new species, *C. capitata,* to this family. Both medusae closely resemble other corynid medusae except for the branched tentacles. In his phylogenetic analysis Petersen (1990) included *Cladosarsia* in the Corynidae due to the following synapomorphies: (i) tentacular bulbs with large gastrodermal chamber, (ii) nearly complete ring of thickened epidermis studded with nematocysts. Petersen even went further and synonymised *Cladosarsia* with *Dipurena*. In view of the lack of knowledge on the polyp phase and the few *Cladosarsia* specimens examined so far, this synonymisation with *Dipurena* appears premature. However, Petersen (1990) is followed here in including the genus in the Corynidae. Future life cycle investigations have to confirm this. Perhaps *Zanclea indica* Mammen, 1963 belongs to this genus. *Zanclea indica* is at present not recognisable and might as well belong to the Corynidae. Its medusae with tentacles having a large terminal cluster is certainly more compatible with a member of the Corynidae than with a *Zanclea* species (see also Boero *et al.*, 2000).

Cladosarsia capitata Bouillon, 1978b Fig. 40

Cladosarsia capitata Bouillon, 1978b: 253, figs 2-3.
TYPE LOCALITY – Laing Island, Papua New Guinea.
MATERIAL EXAMINED – holotype, ZMUC, Dec. 1976, leg. & det. J. Bouillon, well preserved – paratypes, IRSNB IG 27.838, Papua New Guinea, Laing Island, coll. J. Bouillon 1976-1983, two jars with 4 medusae in total, not well preserved.

DESCRIPTION – Medusa small, 0.5-1 mm, bell nearly globular, jelly moderately thick, thicker at top. Manubrium in fully grown medusae about 1.5 times as long as bell, cylindrical, with shallow apical knob. Gonads thick, restricted to distal half of manubrium and encircling it completely. Proximal portion of manubrium thin. Mouth simple, circular, hardly visible in fully mature individuals. Gonad maturation apparently starts before the manubrium has developed its full length, thus when still shorter than bell cavity. Four radial canals, ending in large tentacle bulbs. Gastrodermal chamber of bulbs high and large, epidermal ring complete and with a distinct ocellus. Each bulb with one slender tentacle, length extended about 1.5 times the size of the bell, distal end with up to 5 short branches in one row, each ending in a spherical nematocyst cluster like at end of main tentacle. Side branches becoming shorter towards proximal so that most proximal clusters are nearly sessile. Juvenile medusae have only nearly sessile capitae. Tentacles except for the capitations with few nematocysts. Colours: ocelli red or brown. Nematocysts: stenoteles and desmonemes.

DISTRIBUTION – Type locality only.

REMARKS – A small but distinctive medusa. For the distinction from *Cladosarsia minima* see below.

Cladosarsia minima Bouillon, 1978a Fig. 41

Cladosarsia minima Bouillon, 1978a: 135, fig. 4.
TYPE LOCALITY – Seychelles, Indian Ocean.

DESCRIPTION – (after Bouillon, 1978a) Medusa small (0.4 mm high, 0.5 mm diameter, tentacles 0.3 mm), bell nearly globular, with small apical process. Velum very broad. Manubrium cylindric, length about half the height of the bell cavity, mouth simple, circular. Gonads encircle the whole manubrium without interruptions. Four radial canals ending in four large tentacle bulbs. Gastrodermal chamber of bulbs higher than wide, epidermal ring complete, adaxial side thickened and studded with nematocysts, at abaxial side a red ocellus. Four tentacles, conical, distal end branched once and each end with a spherical nematocyst cluster, proximal to the branching point there is a further, sessile spherical cluster and the proximal half of the tentacle is covered by nematocysts.

DISTRIBUTION – Type locality only.

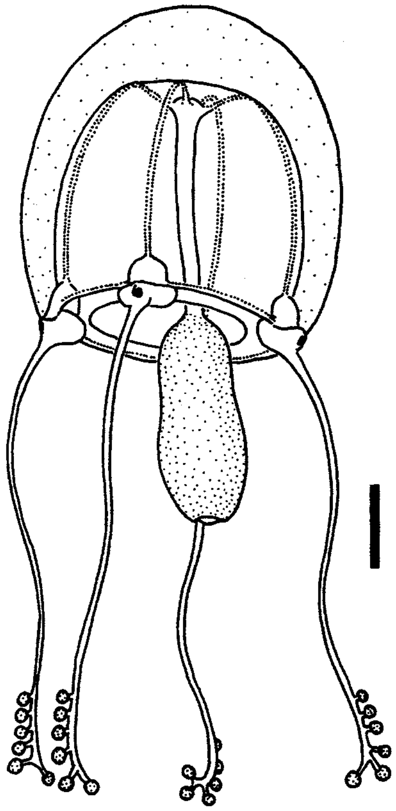

FIG. 40
Cladosarsia capitata Bouillon, 1978b, adult medusa, modified after Bouillon (1978b), scale bar 0.25 mm.

REMARKS – *Cladosarsia minima* is known from one specimen only. Petersen (1990) hypothesized that *C. minima* is nothing but a younger *C. capitata*. While subadult *C. capitata* indeed have a short manubrium like *C. minima*, the latter differs from *C. capitata* in having a differently shaped bell and in having the proximal part of the tentacles covered by nematocysts. However, more material and information is clearly needed.

5.6. Genus *Bicorona*

TYPE SPECIES – *Bicorona elegans* Millard, 1966.

DIAGNOSIS – Corynidae forming large, branching colonies. Hydranth body vasiform, all tentacles capitate, with one oral whorl of four tentacles and one basal whorl of seven or more tentacles. With or without one whorl of four tentacles between distal and proximal whorl. Gonophores fixed sporosacs developing above aboral whorl of tentacles. Nematocysts: stenoteles only.

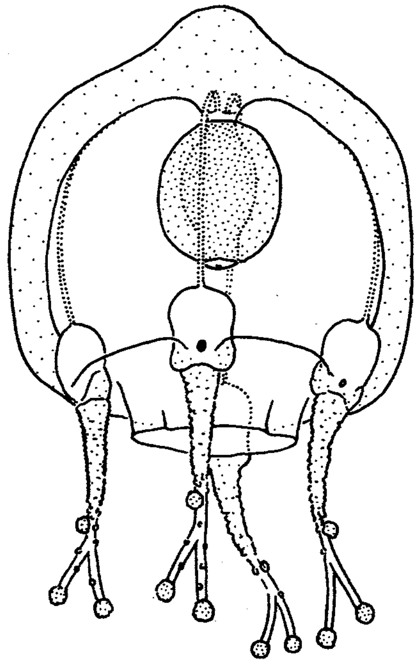

FIG. 41
Cladosarsia minima Bouillon, 1978a, medusa, modified after Bouillon (1978a), bell diameter about 0.5 mm.

REMARKS – The genus is here redefined to accommodate *Coryne tricycla* Schuchert, 1996. Millard (1966) proposed the new genus *Bicorona* for her species *Bicorona elegans*. She thought this necessary as the hydranths of *B. elegans* differ somewhat from all other Corynidae: the body is somewhat vase-shaped and the tentacles are in two clearly separate sets. The hydranth thus attains some resemblance to the ones of the genus *Pennaria*. However, the simple cnidome composed only of stenoteles precludes any affinity with *Pennaria*. The gap between *Bicorona* and *Coryne* was somewhat filled by the discovery of *Coryne tricycla*. *Coryne tricycla* resembles *C. elegans* in having a vasiform hydranth body and an aboral whorl of capitate tentacle having more than the usual four tentacles. Both species also form large colonies, have a completely annulated perisarc, both have the base of their hydranths covered by a gelatinous funnel of perisarc, and both occur in the intertidal region of the southern hemisphere. Also their overall appearance (*habitus*) is quite similar. In contradistinction to *B. elegans*, *B. tricycla* has an additional whorl of tentacles, which is, however, formed quite late in development, even after the onset of gonophore development. Another important difference is found in the site of gonophore production: while it is in the upper axils of the tentacles in *B. elegans*, the sporosacs of *B. tricycla* develop independently from the tentacles. I regard the development of the sporosacs in the upper axils in *B. elegans* and in some *Coryne* species as a homoplasy.

Although the combination *Bicorona tricycla* is somewhat of an oxymoron, the undeniable shared apomorphies of vasiform hydranth and increased number of tentacles in the most proximal whorl prompted me to unite *Bicorona elegans* and *Coryne tricycla* in a common genus.

Petersen (1990) synonymised *Bicorona* Millard, 1966 with *Dicyclocoryne* Annandale, 1915 based on the argument that the degree of gonophore reduction cannot be used to distinguish genera. In view of the scant knowledge of the type species of the genus *Dicyclocoryne* and the notable differences of the polyp stages both species are here kept separate. *Bicorona elegans* forms large, much branched colonies and develops its sporosacs above the aboral whorls, while *Dicyclocoryne* is mostly stolonal, liberates medusae which originate below the most proximal tentacles of the polyp. Any speculations concerning on the phylogenetic relationship of *Bicorona* and *Dicyclocoryne* are better postponed until more details of *D. filamentata* – especially the cnidome – become known. Petersen (1979) also placed *Dicyclocoryne* including *Bicorona* in a separate family. The discovery of *Bicorona tricycla*, however, made it difficult to draw a clear separation line between the Corynidae and the Dicyclocorynidae. The high gastrodermal chamber of the tentacle bulbs of *Dicyclocoryne* strongly suggests that this is also a member of the Corynidae. Until additional evidence to the contrary is forthcoming, I continue to regard *Bicorona* and *Dicyclocoryne* as members of the Corynidae.

Bicorona elegans Millard, 1966 Fig. 42

Bicorona elegans Millard, 1966: 441, fig. 3; Millard, 1975: 49, frontispiece, fig. 19A-E.
Dicyclocoryne elegans – Petersen, 1990: 204.
TYPE LOCALITY – Saldanha Bay, South Africa.

DESCRIPTION – (after Millard, 1975) Hydroid reaching 58 mm in height, stem monosiphonic, monopodial, one main stem with long side branches that can be branched again, all endings bearing hydranths. Perisarc closely annulated throughout except for a smooth area at the base of each branch. Perisarc terminates as a gelatinous, compact funnel covering base of hydranth. Hydranths 1-2 mm in length, vasiform, with one oral whorl of 4-7 capitate tentacles and one aboral whorl of 10-21 capitate tentacles in middle of hydranth. Aboral tentacles longer than oral ones, held alternately elevated and depressed in life, usually shorter and longer ones alternating. Oral tentacles held erect. Aboral set of tentacles of young hydranths in up to three alternating whorls. Gonophores on seven short blastostyles in the upper axils of the aboral tentacles. Each blastostyle unites 2-4 gonophores. Gonophores develop into fixed sporosacs. Sporosacs oval to oblong, without radial or circular canals, females 0.4 mm in diameter and containing 29-84 small eggs, males 0.6 mm. Nematocysts: stenoteles, (13.5) x (7) µmn and (26) x (17) µm. Egg size 0.05-0.10 mm. Colours: dark red ("plum-colour" after Millard).

DISTRIBUTION – Endemic to South Africa.

BIOLOGY – Grows at lower intertidal level, stems embedded in sponges.

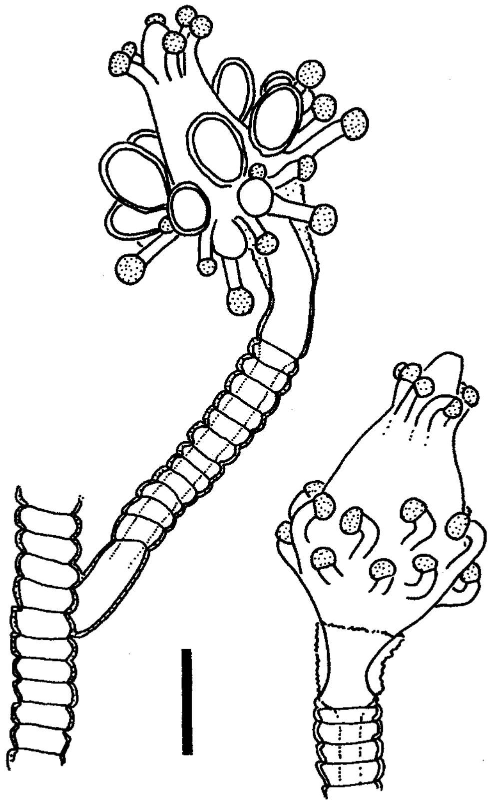

FIG. 42
Bicorona elegans (Millard, 1966), part of colony with hydranth bearing sporosacs, and infertile hydranth with two aboral tentacle whorls, scale bar 0.5 mm, modified after Millard (1966).

Bicorona tricycla (Schuchert, 1996) **comb. nov.** Fig. 43A-D

Coryne vaginata – Ralph, 1953: 66, fig. 13; misidentification.
Coryne tricycla Schuchert, 1996: 120, fig. 73a-d.
TYPE LOCALITY – North-east of Te Raekaihau, Lyall Bay, Wellington, New Zealand, intertidal.

DESCRIPTION – Colonies arising from creeping, ramified stolons. Stems up to 45 mm high and with up to 30 hydranths. With monopodial growth and branching in all planes. Perisarc soft and elastic, sharply annulated throughout. At base of hydranths the perisarc dilates to a thick, gelatinous funnel into which hydranth is unable to retract. Hydranths up to 2 mm long (free part), cylindrical to slightly pear shaped; with one oral whorl of 4 short, adnate capitate tentacles, one median whorl of four capitate tentacles in alternate positions to oral tentacles, and one aboral (proximal) whorl of eight capitate tentacles. These 8 tentacles all originate at the same level from a slightly thickened region of the hydranth body. They are all held in the same plane. The median whorl is either exactly in the middle of the body or closer too

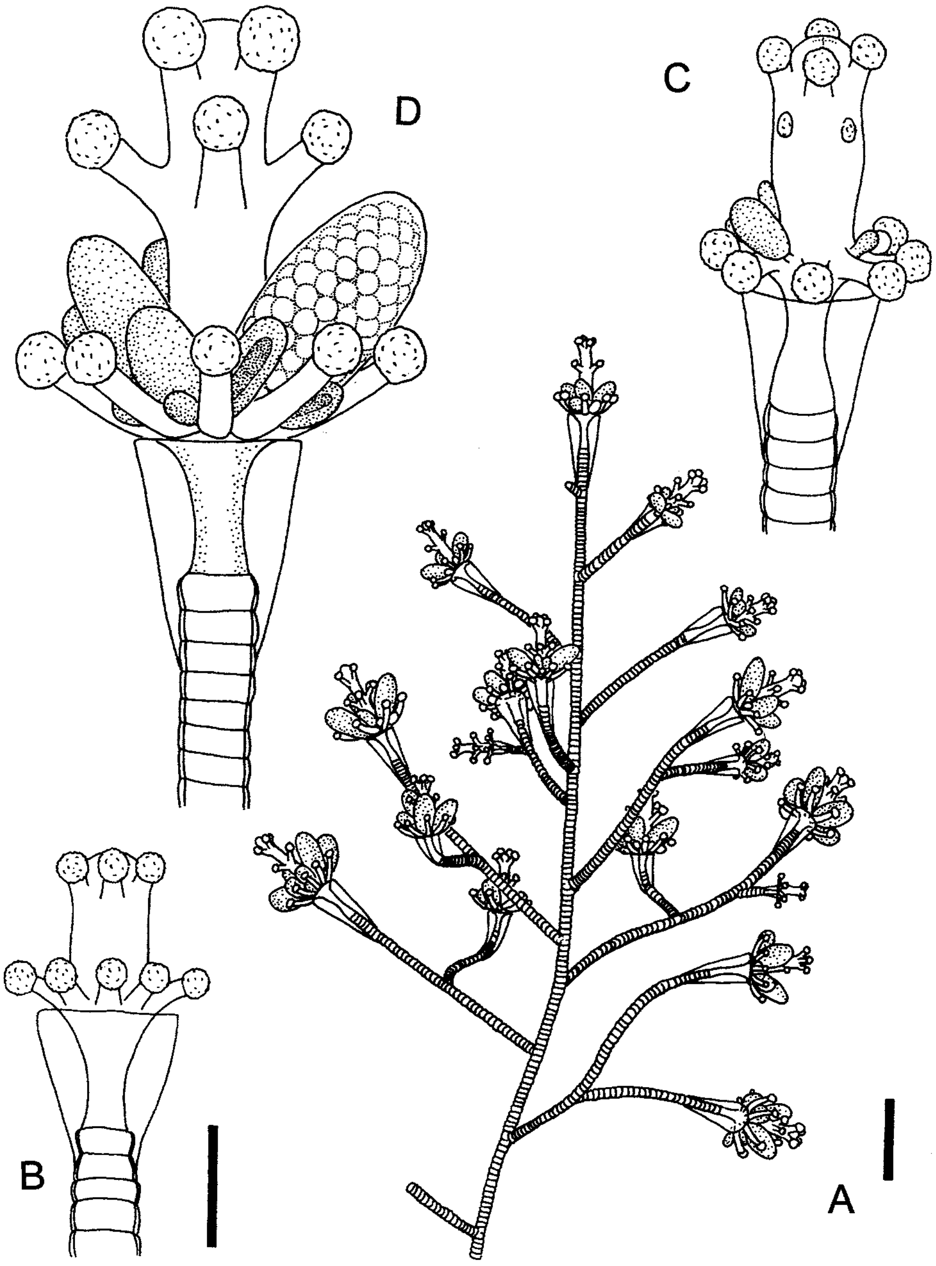

FIG. 43
Bicorona tricycla (Schuchert, 1996); drawn after living holotype. A) Colony, scale bar 2 mm. B) Young hydranth with two whorls of tentacles, scale bar 0.5 mm. C) Hydranth with beginning gonophore development, same scale as B. D) Fully mature hydranth with ripe sporosacs, same scale as B.

the oral whorl of tentacles. Median whorl of tentacles develop last, even after onset of gonophore development. Gonophores arise just above the aboral whorl of tentacles and alternate in position with these. There are up to 3 gonophores per position, all in various stages of development. The mature female gonophores are oblong and remain fixed as sporosacs with up to 100 eggs; a spadix is present but radial or circular canals are absent. Male gonophores unknown. Nematocysts: Only stenoteles of very variable size, (19-36) x (9-22)mm. Colour: brown, especially gonophores. Stem diameter 0.20-0.23 mm, gonophores up to 1 mm long, size of spawned eggs 114 µm (s. dev. = 6 µm, n=6).

BIOLOGY – Occurs on rock and macroalgae at low waterline.

DISTRIBUTION – Wellington and Makara Beach, New Zealand.

5.7. Genus ***Dicyclocoryne***

TYPE SPECIES – *Dicyclocoryne filamentata* (Annandale, 1907).

DIAGNOSIS – Hydroid colonial, hydranth with one oral whorl of four capitate tentacles and one aboral whorl of six capitate tentacles. Gonophores borne below aboral tentacles. Gonophores released as medusae. Medusae known only as newly liberated. Umbrella evenly rounded, manubrium stout, shorter than subumbrellar cavity, simple circular mouth, four tentacle bulbs with epidermal ring and ovoid gastrodermal chamber. Four short tentacles. Ocelli not present.

REMARKS – Complete life-cycle information of *Dicyclocoryne filamentata* and knowledge of its cnidome is needed before the affinities of this genus can be discussed any further. See also the remarks under genus *Bicorona*.

Dicyclocoryne filamentata (Annandale, 1907) Fig. 44A-C

Syncoryne filamentata Annandale, 1907: 139, figs 1-2.
Dicyclocoryne filamentata – Annandale, 1915: 110, pl. 9 fig. 4a-c.
TYPE LOCALITY – Port Canning, Lower Bengal, in brackish water.

DESCRIPTION – (after Annandale, 1907 and 1915) Hydroid stolonal or occasionally branching. Hydrorhiza branching sparingly, not anastomosing, often not adhering and drawn into long filamentous processes with clubbed terminal endings. Pedicels of hydranths smooth or slightly corrugated. Hydranths about 1.5-2.5 mm high, spindle-shaped, with one oral whorl of 4 capitate tentacles and one whorl of up to 6 capitate in the middle of the hydranth. The gonophores develop at the bases or distinctly below the aboral whorl of tentacles, 6 or more per hydranth. Gonophores are released as free, immature medusae. Colour: white. Nematocysts unknown.

Newly released medusa bell-shaped, slightly deeper than broad, diameter 0.4 mm, exumbrella covered by minute tubercules (nematocysts ?). Manubrium shorter than bell cavity, cylindrical. Four radial canals and ring canal present. Radial canals end in prominent tentacle bulbs. Gastrodermal chamber ovoid, entrance of radial canal at top. Epidermal ring of bulb complete, studded with nematocysts, below this ring another ring with nematocysts. Four tentacles, short, shorter than bell height. With a large, globular, terminal nematocyst cluster.

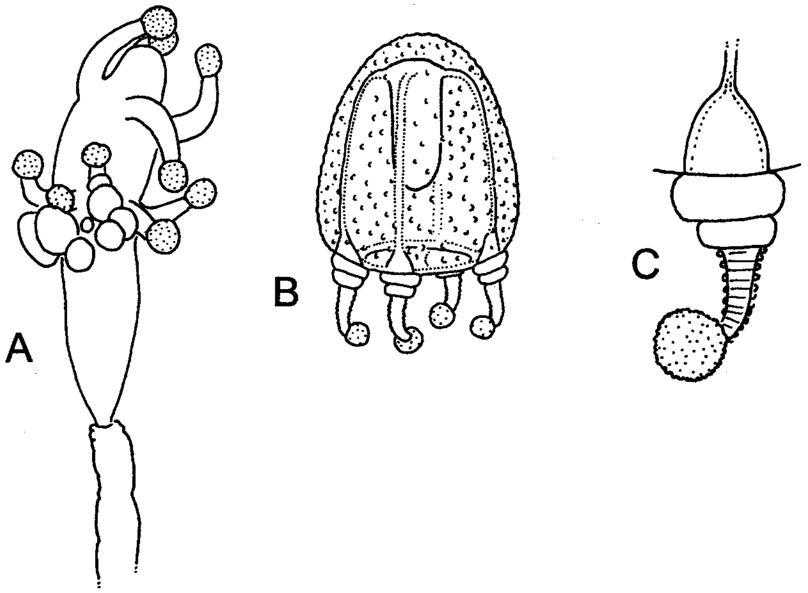

FIG. 44
Dicyclocoryne filamenata (Annandale, 1907), modified after Annandale (1915). A) Hydroid with medusae buds. B) Newly released medusa. C) Tentacle and bulb.

DISTRIBUTION – *Dicyclocoryne filamentata* has only been found in brackish waters of the Ganges delta.

REMARKS – Although the hydroid is distinctive and recognisable, *Dicyclocoryne filamentata* is insufficiently known as only the newly released medusa is known. Furthermore, we do not have any information on the cnidome of this species. The spherical terminal nematocyst clusters of the medusa tentacles suggest some relation to certain *Dipurena* or *Cladosarsia* species. The absence of ocelli in the newly released medusae does not mean that they are also absent in the adult. Other Corynidae, e. g. *Coryne nipponica*, are sometimes also released with underdeveloped ocelli.

5.8. **Problematic or indeterminable species**

REMARKS – This section lists Corynidae, or species once associated with this family, that are either unrecognisable or so imperfectly known that their systematic position remains disputable.

The following species could not be traced to the original source, but were already considered indeterminable or invalid by Allman (1871): *Coryne ramosa* Chamisso & Eysenhardt, 1821 (=*Syncoryne chamissonisi* Ehrenberg, 1832), *Coryne prolificata* (Bosc, 1797), *Coryne amphorata* (Bosc, 1797), *Coryne filifera* (Bosc, 1797).

Coryne angulata (Mayer, 1900)

Syndictyon angulatum Mayer, 1900a: 5, fig. 6-8, pl. 3.
Sarsia angulata – Mayer, 1910: 60, pl. 5 fig. 1, pl. 6 fig. 3; Kramp, 1959: 80, fig. 17; Kramp, 1961: 25.
TYPE LOCALITY – Bahamas.
MATERIAL EXAMINED – USNM 57718, USNM7712, USNM 57713, USNM 57965, all Carrie Bow Cay, Belize, collected R. J. Larson, March-April 1978, many mature medusae.

DIAGNOSIS – Medusa 3 mm high, half-egg-shaped, moderately thick walls. Manubrium spindle-shaped, without apical chamber, 2/3 as long as bell cavity, gonads from base almost to the mouth. Slender tentacles with fairly thick, spindle-shaped ends (Kramp, 1961). Polyp unknown.

DISTRIBUTION – Bahamas; Florida.

REMARKS –According to Kramp (1959a), the diagnostic traits of this medusa are the thickened distal ends of the tentacles. In the figure given, however, this thickening looks just like normal contracted tentacles and nothing distinguishes this medusa from *C. eximia.* Because life-cycle studies might nevertheless prove the existence of a distinct polyp phase at the type locality, the name is here retained. Additionally, its tropical occurrence argues in favour of it being different from *C. eximia,* which is clearly a species of temperate waters. Perhaps the hydroid depicted by Berrill (1953: 281, fig 3) is the polyp phase of this species. Berrill (1953) noted that it is common along the coast of Florida and perhaps also Deevey's (1950) *S. eximia* could belong to here.

Medusae allocated to this species originating from Belize and held by the USNM could be examined for this study. The material is in no way distinguishable from *C. eximia.*

Coryne brachygaster (Grönberg, 1898)

Sarsia brachygaster Grönberg, 1898: 459, pl. 27, figs 3-4, (not material from Greenland); Hartlaub, 1907: 11, fig. 3; Kramp, 1926: 20; Kramp, 1959: 207, fig. 18; Kramp, 1961: 26.
TYPE LOCALITY – Danes Gat, Spitzbergen, North Atlantic.

DESCRIPTION – Medusa bell 15-18 mm high, 8-10 mm wide. Manubrium 2/3 as long as bell cavity, cylindrical, without apical chamber, completely encircled by gonad. Tentacle bulbs of medium size, ocelli very small. Polyp unknown.

DISTRIBUTION – Spitzbergen, West Greenland.

REMARKS – Kramp (1926) re-examined Grönberg's material from Greenland and found it was *Euphysea flammea.* The figures of *Sarsia brachygaster* as given by Grönberg (1898) resemble closely *Coryne eximia,* except for their size. Although Kramp regarded the species as doubtful, its size might well make it recognisable. The species should be re-described from new material collected at the type locality.

Coryne brevicornis Bonnevie, 1898

Coryne brevicornis Bonnevie, 1898b: 3-4, pl. 1 figs 2 & 2a; Rees, 1956: 111.
TYPE LOCALITY – Hammerfest, Norway, 100-200 m.

DESCRIPTION – (after Bonnevie, 1898b) Colonies reaching 10 mm in height, branched, perisarc without distinct annulation. Tentacles scattered, gonophores arise among tentacles, with very long pedicels, without radial canals.

REMARKS – Rees (1956) re-examined type material of this species and thought it to be conspecific with *C. hincksii.* Because he might have been wrong concerning the radial canals of the latter species (see above) this synonymy must be doubted. *Coryne brevicornis* is an inadequately known species, the only special character being the long pedicels of the gonophores. It has close affinities with *C. pusilla.*

Coryne brevis Stechow, 1923

Corynidae species A Hickson & Gravely, 1907: 15.
Clavatella juv. Ritchie, 1913: 13, fig. 1.
Coryne brevis Stechow, 1923a: 1; Stechow, 1923b: 42.
TYPE LOCALITY – McMurdo Bay, Antarctica, 36 m.

REMARKS – The single corynid hydranth of Hickson & Gravely (1907) was clearly insufficient to be identified and they wisely enough did not name it. However, Stechow (1923a) did so and included also another corynid described by Ritchie (1913) in it. Ritchie considered his single, juvenile hydranth so ill defined that he also refrained from naming it.

Coryne caespes Allman, 1871

Coryne caespes Allman, 1871: 270; Brinckmann-Voss, 1970: 47.
TYPE LOCALITY – La Spezia, Italy, Mediterranean.

DESCRIPTION – (after Allman, 1871) Colonies mostly stolonal or occasionally sparingly branched, reaching a height of 6 mm. Stolons a creeping, entangled mass of tortuous tubes. Cauli and stems densely aggregated. Perisarc irregularly annulated. Hydranth elongated and with about 25 tentacles. Gonophores globular, scattered on the lower portion of the hydranth body, where they spring by short peduncles from the axils of the tentacles. Gonophores develop in March.

DISTRIBUTION – Type locality only.

BIOLOGY – Grows on rocks among *Cystoseira*, 0.6 m.

REMARKS – Allman (1871) regarded this species as distinct on account of its dense, crowded, moss-like growth. He states that the colonies "spread like a turf for many square miles (sic!) over the submerged rocks". This seems quite unrealistic to me and may be a typographic error. *Coryne caespes* has never been found again and could belong to *Coryne pintneri* or *C. muscoides.*

Coryne coccometra (Bigelow, 1909)

Sarsia coccometra Bigelow, 1909: 179, pl. 7 fig. 8, pl. 40 fig. 1, pl. 43 fig. 8-9; Mayer, 1910: 488; Kramp, 1968: 7, fig. 5; Kramp, 1961: 26.
TYPE LOCALITY – Pacific Ocean, near Coiba Island, Panama.
MATERIAL EXAMINED – USNM 59195, 00°17.5'S 081°53'W, 202 m, 8.02.1967; one damaged, contracted, mature medusa – USNM 59216, 03°52'N 085°57W, 180 m, 19.03.1967, one very damaged medusa without manubrium.

DESCRIPTION – Medusa 5 mm high, 4 mm wide; thin walls, with apical projection of variable size; with apical canal. Manubrium as long as bell cavity, (?) entirely encircled by gonad, gonad fills subumbrella, eggs very large. Tentacles ringed with prominent nematocyst rings, distal end swollen, knob-like; bulbs large, with ocelli (Kramp, 1961).

REMARKS – This is certainly a valid species, but with its apical projection *Sarsia coccometra* is unlike any other *Sarsia* species. Bigelow (1909: pl. 40 fig. 9) depicts the manubrium with deep perradial clefts, although he insists that the gonads are not interrupted perradially which he confirmed by horizontal sections. He interpreted the clefts as folds due to contractions. Despite this, it is very likely that *S. coccometra* is actually referable to the family *Sphaerocorynidae*, as postulated by Petersen (1990: 213). However, until this assertion can be proved by life observations or life-cycle information, it is here kept provisionally in the Corynidae.

The material available for this study clearly agreed with the given description and figures of this species. However, its state of preservation did not allow an examination to determine whether the gonads are partitioned, which would be clear sign that they belong to the Sphaerocorynidae. The nematocysts found were stenoteles and desmonemes.

DISTRIBUTION – Pacific Coast of Central America (Bigelow, 1909), Ecuador (this study).

Coryne conferta Allman, 1876

Coryne conferta Allman, 1876: 115; Allman, 1879: 285, pl. 18 fig. 1-3; Vanhöffen, 1910: 274, fig. 1; Millard, 1971: 401.

TYPE LOCALITY – Observatory Bay, Kerguelen Island, at lower intertidal level.

DISTRIBUTION – Kerguelen Island, Marion Island, Tierra del Fuego.

BIOLOGY – Occurs on mussels and stones.

REMARKS – No gonophores have ever been described for this species. It is therefore not sufficiently well described and is at present not distinguishable from *Coryne pusilla* or *Coryne eximia*. Vanhöffen (1910) described infertile *Coryne conferta* colonies from close to the type locality and also fertile colonies of *Coryne pusilla* on floating *Fucus*. However, his concept of both species was based on characters today seen as unreliable (annulation, colony size). Only new investigations at the type locality can bring us more clarity.

Coryne conica (Haeckel, 1880)

Codonium conicum Haeckel, 1880: 634.
Sarsia conica – Kramp, 1961: 27.
TYPE LOCALITY – Indian Ocean.

REMARKS – This species was described by Haeckel (1880) from its medusa phase only and no pictures are available. It might be difficult to recognize this species. The mature medusa is 12 mm high, 4 mm wide, manubrium half as long as bell cavity, with long apical canal.

Coryne corrugata Fraser, 1925

Coryne corrugata Fraser, 1925: 167, fig. 1; Fraser, 1937: 27, pl. 2 fig. 9.
Coryne corrigata – Berrill, 1953: 297, fig. 12 [misspelling].
TYPE LOCALITY – near jetty, San Diego, California, USA.

DESCRIPTION – (after Fraser, 1937) 3.5 cm high colonies, much branched, branches coming off with a definite knee-joint at a very acute angle with stem, secondary branches arise in the same manner from the primary branches; many of these secondary branches, while terminating in a hydranth, give off numerous branchlets that have no hydranths; perisarc thick, with deep annulations or corrugations throughout the whole stem and branches; hydranths capable of great extension and usually appearing long and slender, 20-30 scattered tentacles.

DISTRIBUTION – Type locality only.

REMARKS – The gonophores of *Coryne corrugata* are unknown and the species is therefore not recognisable. The branchlets mentioned by Fraser (1937) recall the brachioles of *C. brachiata*. The syntype material in the Royal British Columbia Museum (Victoria, Canada) has dried out (M. Arai, pers. com.).

Berrill (1953) in a paper describing growth and form of corynid hydroids mentions two *Coryne* species. At least one of them (Berrill, 1953, fig. 12) was from the Pacific coast and he identified it with *C. corrugata* Fraser. The outgrowths on the upper end of the hydranth pedicels clearly match Fraser's (1937) description and Berrill's identification appears correct. Berrill also shows fertile *Coryne* hydranths (figure 13) which are in no way distinguishable from *C. pusilla*. Because Berrill (1953) speaks of two *Coryne* species and because he repeatedly lumped species in this paper, it is highly probable that the fertile hydranths shown in his figure 12 are not identical with the material shown in his figure 13.

Coryne cylindrica (Kirkpatrick, 1890)

Coryne vel *Syncoryne Cylindrica* Kirkpatrick, 1890: 605, pl. 14 fig. 1
TYPE LOCALITY – Albany Pass, Sommerset, North Queensland, 15 m.

DESCRIPTION – (after Kirkpatrick, 1890) Stolons and hydranths partially embedded in bryozoan host, hydranths in the angles between bryozoan zooids, hydranths sessile, about 4 mm in height, about 15 tentacles, clustered in the upper half of the hydranth, sub-sessile.

DISTRIBUTION – Type locality only.

BIOLOGY – Occurs on *Celleporaria granulosa* (Haswell) (Bryozoa).

REMARKS – The gonophores of this species are unknown. The intimate association of this hydroid with its bryozoan host suggests that it is actually a member of the family Zancleidae. There are numerous species of this family tightly associated with bryozoans, while this so far unknown for the Corynidae (see Boero, Bouillon, and Gravili, 2000).

Coryne dubia Ritchie, 1907

Coryne (?) *dubium* Ritchie, 1907: 491, pl. 23, fig. 1-2.
TYPE LOCALITY – on seaweed taken from piles of pier, Porto Praya, Santiago, Cape Verde Islands.

DESCRIPTION – (after Ritchie, 1907) Small irregularly ramified colonies, 7 mm, ramification to fourth order, transparent brown perisarc, branches arise at narrow angles, nearly parallel to sister branches. Perisarc wrinkled or annulated throughout, no funnel-shaped dilation at end of branch. Hydranth 0.5 mm, 12-15 scattered tentacles.

DISTRIBUTION – Type locality only.

SUBSTRATES – Red algae.

REMARKS – As the gonophores are unknown for this species it remains unrecognisable. It could well belong to *Coryne pusilla* or *Coryne eximia*, as both species can be expected to occur at the Cape Verde Islands.

Coryne ferox Wright, 1867

Coryne ferox – Hincks, 1868: 319; Allman, 1871: 283.
TYPE LOCALITY – Firth of Forth.

BIOLOGY – Occurs on shells inhabited by hermit crabs and under stones (Hincks, 1868).

REMARKS – *Coryne ferox* is insufficiently described and not recognisable. Perhaps it belongs to *Sarsia tubulosa*.

Coryne fucicola (de Filippi, 1866)

Halobotrys fucicola de Filippi, 1866: 383, pl. 2.
Coryne fucicola – Brinckmann-Voss, 1970: 53, fig. 58.

DISTRIBUTION – Mediterranean.

REMARKS – *Coryne fucicola* was described from an aquarium culture. De Filippi's (1866) account is quite precise, especially his figures. The gonophores are clearly sessile sporosacs and they could be in the upper axils of the tentacles. The hydranths of *C. fucicola* are very large and reach 5-6 mm in length. This size, however, seems to be unrealistic. Picard (1960) thought that it might correspond to *C. filiformis*, although no filiform tentacles are present in Filippi's figure.

Coryne graeffei Jickeli, 1883

Coryne graeffei Jickeli, 1883: 607, pl. 26 figs 11-22, pl. 28 fig. 4.

REMARKS – *Coryne graeffei* is an inadequately described species that is not identifiable. It was postulated as a new species by Jickeli (1883) in a paper studying the microscopic structure of hydroids. Jickeli stated that it differs from *C. pusilla* by the presence of only one medusa bud [sic!] and by the absence of a perisarc on the caulus. If Jickeli's hydroid really produced medusae, then it could belong to one of several species and the species is here regarded as doubtful.

Coryne longicornis Bonnevie, 1898

Coryne longicornis Bonnevie, 1898a: 492, pl. 27 figs 50-50a.
TYPE LOCALITY – Husø, Oslofjord.

DESCRIPTION – (after Bonnevie, 1898a) Colony on sponge, stolonal, 1-2 mm high, perisarc not annulated. About 10-12 long capitae tentacles. Gonophores develop below capitate tentacles, most probably released as medusae.

DISTRIBUTION – Type locality.

REMARKS – *Coryne longicornis* is insufficiently described and not recognisable. The association with a sponge and the gonophore production below the tentacles compare favourably with *Dipurena simulans*.

Coryne heroni Pennycuik, 1959

Staurocoryne heroni Pennycuik, 1959: 158, pl. 1 fig. 1.
TYPE LOCALITIES – Heron Island and Low Island, Queensland, Australia.

DESCRIPTION – (after Pennycuik, 1959) Stolonal colonies, creeping stolons, hydranth on short caulus, covered with perisarc that widens or not towards distal. Young hydranths with one whorl of 4 longer oral tentacles, 3 whorls with each 3 shorter tentacles, 4-6 aboral filiform tentacles. Older hydranths with 4 more tentacles in indistinct whorls, filiform tentacles lost. Gonophores unknown.

SUBSTRATES – On rock and sea-weeds.

DISTRIBUTION – Type localities.

REMARKS – This species is not recognisable as it matches several other species. New material from the type locality and the life cycle of this species must be examined.

Coryne minima (von Lendenfeld, 1884)

Sarsia minima von Lendenfeld, 1884a: 584, pl. 21 figs 34-35; Kramp, 1953: 309; Kramp, 1961: 29.
TYPE LOCALITY – Port Jackson, New South Wales, Australia.

REMARKS – Only the polyp stage and the young medusa are known from this species. The medusa is different from *C. radiata* by having a manubrium that protrudes from the bell opening. Kramp (1953) re-examined the type material and found the species indeterminable. At the moment, *C. minima* is not recognisable and a re-examination of material from the type locality is needed.

Coryne nutans Allman, 1869

Coryne nutans – Allman, 1871: 271.
TYPE LOCALITY – Burraforth Caves, Shetland.

REMARKS – An unrecognisable species, perhaps *C. pusilla*. The gonophores are unknown. Even Allman (1871) himself considered it provisional and indeterminable.

Coryne occidentalis (Fewkes, 1889)

Syncoryne occidentalis Fewkes, 1889a: 99, pl. 3 figs 2-3.
? *Coryne rosaria* – Fewkes, 1889a: 100, pl. 4 figs 1 & 4.
Sarsia rosaria – Fewkes, 1889b: 597, pl. 25 fig 7, text figs 8-9.
TYPE LOCALITIES – Monterey Bay, San Francisco, and Santa Barbara; California.

REMARKS – Fewkes (1889a) based his new species on a medusa and considered it to be quite common in California. He apparently had mature medusae and his figures show a medusa with an apical canal. *Coryne occidentalis* is likely a valid species that can be recognised again. The medusa much resembles *Coryne cliffordi* (Brinckmann-Voss, 1989).

Fewkes (1889a) also found an abundant hydroid on wharf piles of California which he formally allocated to *Coryne rosaria* sensu A. Agassiz. Fewkes made no rearing experiments, but nevertheless thought that this hydroid produced the medusa he described as *Sarsia occidentalis*. Later, Fraser (1937: 28, fig. 12, as *S. mirabilis*) again described hydroid material that certainly belonged to same population. Fewkes' hydroids developed their medusae buds independent from the tentacles and may thus also belong to *C. cliffordi*. New life-cycle investigations on Californian corynid polyps and medusae have to clarify the status of Fewkes' hydroid and medusa.

Coryne radiata (von Lendenfeld, 1884)

Sarsia radiata von Lendenfeld, 1884b: 584; von Lendenfeld, 1884a: 583, pl. 20 figs 31-32, pl. 30 figs 1-4; von Lendenfeld, 1885: 637, pl. 30; Kramp, 1961: 30; Watson, 1978: 305, fig. 2A-D.

TYPE LOCALITY – Port Jackson, Australia.

MATERIAL EXAMINED – Museum of Victoria Melbourne, slide 1184, *Sarsia radiata*, coll J. Watson, Halibut oil station, Bass Strait, Mid littoral, June 1975 (described in Watson, 1978), contains branched corynid without gonophores, perisarc annulated.

DISTRIBUTION – southern Australia.

REMARKS – The adult medusa of *S. radiata* remains unknown. After Watson (1978), the polyp stage of *S. radiata* is identifiable without problems due to the microbasic euryteles. However, in the figure of Watson (1978), these microbasic euryteles appear atypical. Janette Watson told me recently, that these capsules had been misidentified due to unsuitable microscopic equipment. Most probably, *Coryne radiata* is conspecific with *C. eximia*.

Coryne repens Fraser, 1938

Coryne repens Fraser, 1938: 13, pl. 1 fig. 6.

TYPE LOCALITY – Black Beach, Charles Island, Galapagos Archipelago.

MATERIAL EXAMINED – RBCM 976-131-1, Fraser's original material from Charles Island, this material must be considered type material (see Arai, 1976), one slide with rather poorly preserved material, female gonophores present.

DESCRIPTION – Colonies stolonal or sparingly branched up to second order. Perisarc annulated over some stretches, otherwise smooth, without funnel-shaped dilation at end of cauli. Hydranths 1-1.5 mm, fusiform, with an oral whorl of 4 tentacles and below them additional 10-12 tentacles scattered over whole length of the hydranth. Mouth without button of high gland cells. Spherical gonophores arise in the upper axils of the lowest tentacles, sessile sporosacs without canal system. Largest gonophores seen were 0.13 mm in diameter, probably not fully mature. Nematocysts: probably only stenoteles.

BIOLOGY – Grows on coralline algae at low-water mark.

DISTRIBUTION – Known from first description only.

REMARKS – Fraser (1938) distinguished this species from *C. crassa* on account of its lesser degree of branching, the stouter hydranth and the more numerous and more slender tentacles. The first two characters are certainly of little value for distinguishing corynids and the tentacle number is well within the range of other similar species. The species differs little from *C. pusilla*, with perhaps the exception of the gonophore size. However, it is likely that the gonophores in the type material are not fully grown yet. For biogeographic reasons *C. repens* can be regarded as separate from *C. pusilla*. However, a re-description based on new material from the type locality is needed to consolidate its validity.

Coryne rosaria L. Agassiz, 1862

Coryne rosaria L. Agassiz, 1862: 340.
Sarsia rosaria – Haeckel, 1879: 18; Hartlaub, 1907: 50, fig. 45; Mayer, 1910: 59; Kramp, 1961: 31; Kramp, 1968: 7, fig. 4; Arai & Brinckmann-Voss, 1980: 18.
not *Coryne rosaria* – Fewkes, 1889a: 100, pl. 4 figs 1 & 4.
not *Sarsia rosaria* – Fewkes, 1889b: 597, pl. 25 fig 7, text figs 8-9.
TYPE LOCALITY – Strait of Rosario, North-eastern Pacific.

REMARKS – Agassiz' (1862) description refers to a corynid medusa with a manubrium longer than the bell. Agassiz (1862) states that his species resembles *Coryne pusilla* (sic!) from the English Channel. There is nothing in Agassiz's description that renders this species distinguishable from other species of the *Sarsia tubulosa*-like medusae occurring in the region. Later, his son (A. Agassiz, 1865) allocated a hydroid from the same region to this species. This was not based on rearing experiments and thus this identification is highly unreliable.

Coryne vanbenedenii Hincks, 1868

Syncoryne pusilla – van Beneden, 1844: 52, pl. 3 figs 1-10.
Coryne VanBenedenii Hincks, 1868: 45, pl. 9 fig. 1.
Actinogonium pusillum– Allman, 1871: 273.
TYPE LOCALITY – Belgium.

DESCRIPTION – (after van Beneden, 1844 and Hincks, 1868) Polyp colony small and very delicate (13-19 mm); stem flexuous, irregularly branched, bearing many short, non-polypiferous ramules; perisarc transparent, paper-like, pale-yellow, with few obscure wrinkles. Polyps small, subclavate, with slight membranous cup round the base. Tentacles from 12-16, sometimes more. Gonophores few in number (2-3), very large, pedunculate, situated below or among the lowest tentacles. Gonophores remain fixed as sporosacs. Radial canals present, tentacles rudimentary. Gonophores produce 1-4 larva that leave the gonophore as a juvenile polyp with four filiform tentacles.

BIOLOGY – Grows on crabs.

REMARKS – A little known species, but perhaps valid. It is mainly characterised by its vivipary. Hincks (1868) described material he obtained from van Beneden and which the latter had previously identified as *Syncoryne pusilla*. Hincks realised that it could not be this species and proposed the new name *vanbenedenii*. Although coming from a well investigated area, the species has not been found ever since. However, it should be recognisable, if it is not based on a misinterpretation.

Coryne wortleyi (Rotch, 1872)

Staurocoryne wortley Rotch, 1872: 126.
Coryne wortleyi – Rees, 1936: 140, table 1.

REMARKS – An altogether unrecognisable species known from an aquarium culture only.

Dicodonium cornutum Haeckel, 1879

Dicodonium cornutum Haeckel, 1879: 27, pl. 1 fig. 6; Mayer, 1910: 46, fig. 12; Kramp, 1961: 20

TYPE LOCALITY – Tur, Sinai, Red Sea (Haeckel, 1879).

REMARKS – *Dicodonium cornutum* has no ocelli and has its tentacular nematocysts concentrated into abaxial clusters. Haeckel described no exumbrellar nematocyst tracks, but even without them it seems clear that *Dicodonium cornutum* is more likely referable to the Tubulariidae. The resemblance to other medusae of the genus *Ectopleura* is obvious and it probably belongs to this genus. *Dicodonium cornutum* is the type species for the genus *Dicodonium*. Because *D. cornutum* is most probably an *Ectopleura* species, the genus *Dicodonium* can thus no longer be placed among the Corynidae, a family it was traditionally placed in (see Kramp, 1961). New investigations at the type locality, however, could probably identify this medusa again. Further knowledge of the species is thus crucial for the validity of genus *Dicodonium*. Kramp (1959a: 83), Brinckmann-Voss & Arai (1998) and others considered *Dicodonium* a doubtful genus, characterised by the presence of only two well developed tentacles. The species usually placed into this genus, where recognisable at all, obviously belong to different families. Only *Dicodonium floridana* is reasonably well described. However, it differs very much from others of the genus. Arai & Brinckmann-Voss (1998) moved *Dicodonium punctatum* to a new genus, *Paulinium*. *Paulinium* is at present not allocated to a family (Capitata *incerta sedis*).

Dicodonium adriaticum Graeffe, 1884

Dicodonium adriaticum Graeffe, 1884: 351; Mayer, 1910: 47; Neppi & Stiasny, 1913: 31, pl. 1 fig. 1; Kramp, 1959: 84, fig. 28; Kramp, 1961: 20.

TYPE LOCALITY – Trieste, Adriatic Sea.

REMARKS – The original description of Graeffe indicates that *Dicodonium adriaticum* was probably a member of the Pandeidae, perhaps an *Amphinema* species. Graeffe's species had stiff sensory cilia around the ocelli and might thus be recognisable again. Although it is not clear whether Neppi & Stiasny's (1913) *Dicodonium adriaticum* was really that species, their medusa is obviously also a juvenile pandeid.

Dicodonium dissonema Haeckel, 1879

Dicodonium dissonema Haeckel, 1879: 27; Mayer, 1910: 46; Kramp, 1968: 9.

TYPE LOCALITY – Australia.

REMARKS – There exist no figures of this species and its original description is not sufficient enough to recognise it, even more so as Haeckel gives no exact type locality. It has not been recorded again. The species could belong to several different families.

Dicodonium floridana Mayer, 1910

Dicodonium floridana Mayer, 1910: 46, pl. 2 fig. 5; Kramp, 1959: 83, fig. 27.
TYPE LOCALITY – Tortugas, Florida, USA.

DESCRIPTION – (after Mayer, 1910) bell about 4 mm high, 3 mm wide, with thin, uniform walls and a slight apical projection. With two equally-developed, diametrically opposed tentacles, each about 3/4 as long as bell-height. Near the distal end of the tentacles a knob-like swollen region, hollow, with a thin terminal process. Marginal bulbs small, without ocelli. In addition to the large tentacles there are 2 small, tapering, rudimentary tentacles placed at 90° to the large tentacles. Four narrow, straight radial canals and circular canal present. Manubrium flask-shaped, thickened in middle region. The gonads develop around the manubrium. The rudimentary tentacles may occasionally develop so as to be nearly as long as the pair of large tentacles.

REMARKS – The very peculiar shape of the tentacles make this species easily recognisable. Although Mayer observed several specimens, the species has not been found again. The absence of ocelli is a good argument for not allocating this species in the Corynidae. New life cycle observations and information on the nematocysts are needed to allow a correct placement of this species. It is presently best classified as Anthoathecata *incerta sedis*.

Dicodonium punctatum Vanhöffen, 1911

Dicodonium punctatum Vanhöffen, 1911: 196, fig. 1.
Paulinium punctatum – Brinckmann-Voss & Arai , 1998: 56, fig. 8.
TYPE LOCALITY – Valdivia station 168, north New Amsterdam, southern Indian Ocean, depth 200 m.

DESCRIPTION – Medusa bell 1 mm, higher than wide, jelly evenly thick, provided with coloured inclusion along radial canals that are most probably zooxanthellae. Manubrium short, broad. With four broad radial canals and circular canal. Four marginal bulbs, one opposite pair larger than the other, without ocelli. One pair of tentacles larger, relatively short, ending in a spherical nematocyst cluster. The other pair of tentacles very small, without capitation. Gonads not observed.

REMARKS – Vanhöffen based his description of *Dicodonium punctatum* on only one preserved medusa taken at 200 m depth. On account of its capitate tentacles, Brinckmann-Voss & Arai (1998) removed it from the Corynidae and placed it into the new genus *Paulinium*, together with another newly described species that has perhaps four tentacles. The higher systematic position of *Paulinium* is not clear and Brinckmann-Voss & Arai (1998) classified it as Capitata *incertae sedis*.

Dinema jeffersoni Mayer, 1900

Dinema jeffersoni Mayer, 1900b: 30, pl. 37 fig. 126.
Dicodonium jeffersoni – Mayer, 1910: 46, pl. 2 fig. 4, pl. 3 fig. 1; Vanhöffen, 1913a: 415; Kramp, 1959: 83, fig. 25.
TYPE LOCALITY – Tortugas, Florida, USA.

REMARKS – A simple, small, *Sarsia*-like medusa with unequally developed tentacles. Life-cycle observations must be made before this species can reliably be allocated to a higher taxon, but it could belong to the Corynidae. If so, it can easily be placed in the genus *Coryne*. Mayer (1910) mentioned it to be quite common at the Tortugas in May and early June.

Dipurena dolichogaster Haeckel, 1864

Dipurena dolichogaster Haeckel, 1864: 337; Haeckel, 1879: 25, pl. 2 figs 1-7; Russell, 1953: 75; Kramp, 1961: 22.
TYPE LOCALITY – Nice, Mediterranean.

REMARKS – A doubtful species, possibly conspecific with *Dipurena ophiogaster*.

Dipurena pyramis (Haeckel, 1879)

Bathycodon pyramis Haeckel, 1879: 26.
Dipurena pyramis – Kramp, 1961: 23.
TYPE LOCALITY – Corfu, Mediterranean, 40 m, on ascidian.

REMARKS – According to Haeckel (1979), this *Dipurena*-like medusa has four stiff tentacles ending in suckers, four meridional exumbrellar ridges with nematocysts, and gland cells along the radial canals. Haeckel found only one specimen and the species has not been found since. If it is not a hoax, it might be recognised again due to these peculiarities and I would not consider it a doubtful species as Kramp (1961) did.

Sarsia erythrops Romanes, 1876

Sarsia erythrops Romanes, 1876: 274, note.

REMARKS – In his experimental studies on the nervous system of medusae, Romanes (1876) mentions *Sarsia erythrops*. It was not supplemented by any description nor figure and is therefore not a validly described species. Bedot (1912: 465) thinks Romanes' medusa was *Coryne eximia*.

Sarsia frutescens (Allman, 1871)

Syncoryne frutescens Allman, 1871: 281, pl. 6 fig. 4-6; Hartlaub, 1907: 37, fig. 29; Mayer, 1910: 54, fig. 17.
TYPE LOCALITY – Kingstown, Dublin, Ireland.

BIOLOGY – Occurs on floating timber.

REMARKS – Only the hydroid stage and juvenile medusae are known of this species. Its hydranths correspond to the ones of *S. tubulosa*. It differs from typical *S. tubulosa* in having much larger colonies 2.5 to 5 cm that are branched up to the third order, thus resembling *Sarsia densa*. Hartlaub (1907) kept it separate from this species on account of Allman's (1871) figure of the medusa which shows no terminal nematocyst cluster. This is, however, most probably erroneous.

Sarsia hargitti (Mayer, 1910)

Sarsia producta Hargitt, 1902: 550, fig. 3.
Sarsia hargitti Mayer, 1910: 63 fig. 26, new name; Kramp, 1959: 78 fig. 11; Kramp, 1961: 28.
TYPE LOCALITY – Woods Hole Massachusetts, USA.

DESCRIPTION – Medusa 1.5 mm high, 1 mm wide, apex dome-like, very thick. Manubrium may project far beyond velar opening, its terminal end bulb-like, in its proximal part a whorl of medusae buds (or medusiform gonads). Small, round apical chamber. Tentacles with large bulbs.

REMARKS – Hargitt (1902) described this species from a single medusa and it has never been found again, despite coming from a well investigated area. Mayer (1910) gave it a new name because the former name was preoccupied by *Sarsia producta* (Wright, 1858). Hargitt was somewhat unclear in his description as he mentions "medusiform gonads". Most probably he was not referring to gonads in the usual sense, but to medusae buds. Later Kramp (1959a) interpreted them as sac-shaped gonads. With this interpretation, the species becomes difficult to integrate into the Corynidae. Considering his comparisons with *S. gemmifera,* it is thus much more probable that Hargitt (1902) observed normal medusae buds. The only difference of Hargitt's species to *Dipurena gemmifera* is that the medusae buds are in a whorl at the very base of the manubrium and not spread over it. If it was based on a healthy specimen, Hargitt's medusa could be recognised again. However, I suspect that it was *D. gemmifera.*

Sarsia marii Schierwater & Ender, 2000

Sarsia marii Schierwater & Ender, 2000: 119, fig. 1.
TYPE LOCALITY – Banyuls-sur-Mer, France, Mediterranean.

DIAGNOSIS – Hydroid growing on *Ulva lactuca,* with one whorl of 4 oral capitate tentacles and one aboral whorl of filiform tentacles. Gonophores develop in zone between filiform and capitate tentacles, liberated as free medusae. Newly released medusa similar to other corynid medusae, tentacles with one spherical terminal nematocyst cluster. Development, adult medusa, and cnidome are unknown.

REMARKS – This is an insufficiently described species, but its growth on *Ulva* as well as the known 16S ribosomal DNA sequence should render it recognisable. Because the adult medusa is not known it cannot be allocated to a genus unambiguously. Because there are no *Coryne* species known with only one whorl of capitate tentacles, and because its molecular phylogeny placed it closer to *Sarsia tubulosa* than to *Dipurena reesi,* it is here left in the genus *Sarsia.* The capitate tentacles of the medusa, however, suggest more affinities with *Dipurena.* Formally, *Sarsia marii* is not distinguishable from *Dipurena strangulata,* except for the different substrates of the hydroid (*Ulva* versus sponge).

Sarsia nana Stechow, 1923

Sarsia nana Stechow, 1923b: 40, fig. B,
TYPE LOCALITY – European coasts.
MATERIAL EXAMINED – ZSM, slide, *Coryne nana,* locality: Europäische Küsten, is most probably type material.

REMARKS – The description of this species was based on infertile polyp material. As a distinguishing character Stechow (1923b) gave the pronounced annulation of the stem. This is of course no valid trait and the species is definitely not recognisable anymore. It may belong to any of several species. Re-examination of the type material also did not give any further cues to the identity of this species.

Sarsia ocellata Busch, 1851

Sarsia ocellata Busch, 1851: 16, pl. 2 figs 1-3; Hartlaub, 1907: 68, fig. 63.
Dicodonium ocellatum – Kramp, 1961: 21.
TYPE LOCALITY – Trieste, Adriatic Sea, Mediterranean.

REMARKS – Mayer (1910) thought this to be an abnormally developed *Sarsia* medusa, while Kramp (1959a) qualifies it as an "altogether doubtful species". It is likely that Busch based his description on mutilated specimens as he noted (cited in Hartlaub, 1907) that the medusa has normally four tentacles and that in the two tentacled specimen the missing ones seemed to have fallen off. Somewhat unique are the black tufts of nematocysts on the exumbrella, but this could have been due to deterioration. Hartlaub (1907) thought it to be conspecific with the equally doubtful *Sarsiella dinema*. I favour Mayer's view that *D. ocellatum* was based on mutilated or abnormally developed specimens of a *Sarsia* spec.

Sarsia pattersoni Haddon, 1886

Sarsia pattersoni Haddon, 1886: 525; Kramp, 1961: 29.
TYPE LOCALITY – Ireland.

REMARKS – Could be *S. tubulosa,* doubtful species.

Sarsia polyocellata Uchida, 1927

Sarsia polyocellata Uchida, 1927: 182, fig. 25; Kramp, 1961: 29; Kramp, 1968: 8, fig. 9.
TYPE LOCALITY – Misaki, Japan.

DIAGNOSIS – Medusa 2 mm high, 2.2 mm wide, without apical projection, jelly soft, equally thick throughout. Manubrium short and wide, mouth small. Gonads dispersed on manubrium. Tentacle bulbs triangular, each with five ocelli, ocelli arranged in triangle. Tentacle bulbs apparently without gastrodermal chamber. Tentacles with patches of nematocyst clusters on whole length. Gonads vermilion, ocelli black.

DISTRIBUTION – Known from the type locality only.

REMARKS – This species is almost certainly not a member of the Corynidae. Uchida (1927) speaks of "separate gonads" and his figure shows a number of patches on the manubrium which must be interpreted as gonads. All Corynidae have gonads that encircle the manubrium without interruption. Furthermore, his figure quite clearly shows that the tentacle bulbs have no gastrodermal chambers. These traits, combined with the five ocelli per bulb exclude this species from the Corynidae. *Sarsia polyocellata* is perhaps a member of the Sphaerocorynidae, although no presently known genus is suitable to place it in. Most likely, a new genus will have to be created for it. Because no type material could be found and its nematocysts, and more importantly its life-cycle, remain unknown, I refrained from doing so in this publication. We have to wait for new findings of this species.

Sarsia pulchella Forbes, 1848

Sarsia pulchella Forbes, 1848: 57, pl. 6 fig. 3; Hartlaub, 1907: 36, fig. 28.
TYPE LOCALITY – Great Britain.

REMARKS – This is probably *S. tubulosa.* Forbes distinguished it from *S. tubulosa* on account of its size (25 mm for *S. tubulosa* and 6 mm for *S. pulchella*).

Sarsia turricula McCrady, 1859

Sarsia turricula McCrady, 1859: 36, pl. 8 figs 6-8; Kramp, 1961: 32.
TYPE LOCALITY – Charleston Harbor, USA.

REMARKS – Not identifiable medusa known only from immature specimen, may be *S. tubulosa.*

Sarsiella dinema Hartlaub, 1907

Dinema slabberi – Haeckel, 1879: 28.
[not *Dinema slabberi* van Beneden, 1866 = ? *Leuckartiara octona* (Fleming, 1823)]
Sarsiella dinema Hartlaub, 1907: 67, new name; Kramp, 1961: 33.
TYPE LOCALITY – Coast of Normandy.

REMARKS – Hartlaub (1907) thought that Haeckel (1879) misidentified a corynid medusa from the Channel coast with *Dinema slabberi* van Beneden, 1866. *Dinema slabberi* van Beneden, 1866 clearly belongs to the Pandeidae, and it probably is a synonym of *Leuckartiara octona.* Although there is no reason to assume that Haeckel had a corynid medusa, Hartlaub (1907) proposed the new name *Sarsiella dinema* for Haeckel's medusa. Hartlaub even created a new genus based on the assumption that it has only two marginal bulbs. He thought that *Dicodonium* differed from *Sarsiella* by having four marginal bulbs. There exists no figure of Haeckel's medusa and it must be considered unrecognisable. I tend to follow the opinion of Mayer (1910: 47) that it was based on an abnormal or mutilated specimen.

Syncoryne loveni van Beneden, 1867

Syncoryne loveni van Beneden, 1867: 121, pl. 5 figs 6-8; Allman, 1871: 285.

REMARKS – An indeterminable, dubious species, not to be confounded with *Sarsia lovenii* (M. Sars, 1846).

Syncoryne johnstoni van Beneden, 1867

Syncoryne johnstoni van Beneden, 1867: 120, pl. 5 figs 1-3.

REMARKS – An indeterminable, dubious species.

Syncoryne listerii van Beneden, 1844

Syncoryne listerii van Beneden, 1844: 54, pl. 3 figs 11-12.

REMARKS – An indeterminable, dubious species. See also comments by Hincks (1868: 40). Bedot (1910) referred it to *C. pusilla.*

5.9. Unnamed Corynidae

Many findings of Corynidae cannot be identified due to lack of life cycle information. Some authors therefore correctly avoided naming new species when there is clearly not enough information available. Some morphotypes will nevertheless be recognisable and in the following some of these species are listed, although the list is incomplete.

Sarsia spec. of Uchida (1927: 187, fig. 26) could not be sufficiently examined by the author as the material was lost in an earthquake, it resembles *C. eximia* and *C. japonica.*

Sarsia spec, II of Menon (1932: 5, pl 1 fig. 8) is probably an *Euphysora* species (Kramp, 1961).

Syncoryne spec. from Florida described by Berrill (1953) develops its medusae buds below the capitate tentacles at a very early stage. Later, the capitate tentacles also start to grow in the zone occupied by the medusae buds. This course of development is quite unusual and Berrill's *Syncoryne* species might belong to an undescribed species or perhaps *C. angulata.* See also discussion under *C. eximia* and *C. angulata.*

Sarsia sp. of Brinckmann-Voss (1970: 69, fig. 79) from a Cave at Nisida (Naples, Mediterranean), has four oral tentacles and filiform aboral tentacles. Its gonophores had the typical corynid marginal bulbs provided with black ocelli. There were no gonads around the manubrium.

Sarsia sp. of Arai & Brinckmann-Voss (1980: 29, fig. 14), from British Columbia and Pudget Sound (Canada, Pacific Ocean), is similar to *Sarsia tubulosa* but with thicker nematocyst pads of the marginal bulbs.

Coryne spec. 1 of Schuchert (1996) from Wellington, New Zealand, is perhaps not a corynid due to the presence of desmonemes in the polyp. Its stout appearance and the characteristic cnidome render this hydroid recognisable. Schuchert (1996) speculated that it might be the polyp of *Tiaricodon coeruleus,* a species with some superficial resemblance to corynids. In view of the currently known life cycle of *Tiaricodon coeruleus* and related species (see Xu & Chen, 1998; Mills, 2000), this seems now less likely.

Coryne spec. 2 of Schuchert (1996) from Wellington, New Zealand, is certainly a corynid, but it cannot be allocated to the correct genus because no information on the gonophores is available. Its nematocysts will probably allow a future identification of material from New Zealand. The presence of a basitrichous isorhiza and the close approximation of the tentacles indicates that this species more probably belongs to the genus *Dipurena* or *Sarsia.*

Coryne spec. in Gibbons & Ryland (1989: 385, fig 4), lack of information on the sporosacs precludes an identification at the moment.

5.10. **Species not referable to Corynidae**

Syncoryne flexibilis Fraser, 1938 must be transferred to the genus *Sphaerocoryne.* Part of the syntype material of *Syncoryne flexibilis* Fraser, 1938 was examined for this study (BCPM 976-138-1 and BCPM 976-138-2, Secas Island). It was compared with type material of *Sphaerocoryne bedoti* Pictet, 1893 (MHNG INVE 27134). The material from Secas Island has no gonophores, but Fraser (1938: 15, fig. 8) described them as medusae buds originating distal to the tentacle whorls. *Syncoryne flexibilis* is indistinguishable from *Sphaerocoryne bedoti* (see Millard, 1975;

Calder, 1988; Petersen, 1990 for descriptions). Because there are also *Sphaerocoryne* medusae for which we do not know the polyp phase, *Sphaerocoryne flexibili* cannot a priori synonymised with *S. bedoti*. The full life cycle of *Sphaerocoryne flexibilis* from the type localities must be examined before a valid comparison is possible. Perhaps there is a relationship to *Sarsia* (*Sphaerocoryne*?) *coccometra* Bigelow, 1909 (see discussion under this species).

The type material of *Syncoryne crassa* Pictet, 1893 (MHNG INVE 25777) was re-examined for this study. Although the polyps are rather poorly preserved, it is evident that they have moniliform tentacles and conform rather well to the genus *Pteroclava* as described by Boero, Bouillon & Gravier-Bonnet (1995). Also the few gonophores revealed that they consist of a liberable medusae with two tentacle bulbs only. The material closely resembles *Pteroclava krempfi* (Billard, 1919) that they might indeed be conspecific. However, as *Pteroclava krempfi* is only known to occur on Octocorallia while *Pteroclava crassa* was found on the hydrorhiza of hydroid *Macrorhynchia philippina*. Boero, Bouillon & Gravier-Bonnet (1995) regarded them therefore as separate species. This seems to be a preferable solution until perhaps further records will widen the host range of *P. krempfi*.

Sarsia nodosa Busch, 1851 is perhaps an aberrant *Hydractinia carnea* (M. Sars, 1846), see also Russell (1953: 481).

Coryne sessilis Gosse, 1853 is *Zanclea sessilis* (Gosse, 1853), see Boero, Bouillon & Gravili (2000).

Coryne pelagica Alder, 1857 was referred to *Zanclea costata* by Russell (1953), see also Cornelius & Garfath (1980).

Gymnocoryne coronata Hincks, 1871 is probably a *Zanclea* species.

Coryne gigantea Bonnevie, 1898 is a synonym of *Monocoryne gigantea* (Bonnevie, 1898) (family Candelabridae).

Dipurella clavata Hargitt, 1902 is probably a young *Sphaerocoryne agassizii* (McCrady, 1859) (Calder, 1970).

Sarsia flammea Linko, 1905 is a synonym of *Euphysa flammea* (Linko, 1905).

Sarsia japonica Maas, 1909 and *Sarsia flammea* Foerster, 1923 are synonyms of *Euphysa japonica* (Maas, 1909).

Sarsia resplendens Bigelow, 1909 is a synonym of *Hydrocoryne miurensis* Stechow, 1907 (family Hydrocorynidae).

Sarsia brevia Uchida, 1947 is a synonym of *Euphysomma brevia* (Uchida, 1947) (see Kramp, 1962).

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8. INDEX

Survey of the family Corynidae (Cnidaria, Hydrozoa)

Abstract

All genera and species of the family Corynidae are reviewed and the validity of some species discussed. Descriptions and figures for most valid species are given. The classification based on cladistic principles established by Petersen (1990) is discussed and modified. The family Corynidae encompasses the genera *Coryne*, *Sarsia*, *Dipurena*, *Nannocoryne*, *Cladosarsia*, *Bicorona*, and *Dicyclocoryne*. The family Dicyclocorynidae is not recognised and its members returned to the Corynidae. The genus *Bicorona* is emended to accommodate *Coryne tricycla* Schuchert, 1996 as *Bicorona tricycla*. The genus *Dicodonium* is excluded from the Corynidae because its type species is most probably an *Ectopleura* species and thus belongs to the Tubulariidae.

Keywords: Marine invertebrates, Cnidaria, Hydrozoa, Anthoathecata, Corynidae, worldwide survey, revision, descriptions, taxonomy.