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Best wishes.
Paul Cornelius

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Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera

P. F. S. Cornelius

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Synopsis

Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic are revised. Of more than three hundred nominal species just twenty-three are regarded valid. Their taxonomy, nomenclature, morphology, ecology, reproduction, distribution and relationships are discussed and a key is provided for their identification. The genera occurring in the eastern North Atlantic are revised in detail. In addition the genera not represented in this area are briefly reviewed and notes are included to update a previous revision of the genus *Obelia*.

Type designations

Type material is designated of the nominal species *Campanularia laevis* Couch, 1844, to facilitate comparison with *Campanularia laevis* Hartlaub, 1905, for which a new name is proposed (p. 54). Lectotype material is designated of *Sertularia uniflora* Pallas, 1766 (p. 78), *Laomedea gracilis* Sars, 1850 (for which a new name is proposed, p. 78), and *Campanularia intertexta* Couch, 1844 (p. 122).

Type species are designated of two genera and a subgenus: *Cymodocea* Lamouroux, 1816, family Plumulariidae (p. 121); *Eucope* Gegenbaur, 1856 (p. 71); subgenus *Eucampanularia* Broch, 1910 (p. 52). The type genus of the subfamily Clytiinae nom. nov. is designated as *Clytia* Lamouroux, 1812 (p. 69), and that of the subfamily Phialiinae (Family Lovenellidae) as *Phialium* Haeckel, 1879 (p. 69).

Introduction

The family Campanulariidae is represented in all oceans. The species are found mainly within continental shelf depths, and some occur intertidally. Many of the genera and species are cosmopolitan. For example, many of the species recorded from New Zealand by Ralph (1957) occur also in British waters (see Geographical distribution, p. 44).

Several European authors have revised the species of Campanulariidae recorded from their home waters (e.g. Hincks, 1868; Linko, 1911; Broch, 1918; Nobre, 1931; Kramp, 1935; da Cunha, 1944; Vervoort, 1946*a*; Leloup, 1947; Russell, 1953; Naumov, 1960, 1969; Patriti, 1970; Rossi, 1971). But apart from the synoptic lists of Bedot (1901, 1905, 1910, 1912, 1916, 1918, 1925) and a review of the genus *Obelia* (by Cornelius, 1975*a*) there has been no previous attempt to compare the nominal species recorded from the whole of the eastern North Atlantic. As a result many straightforward taxonomic questions have been left unresolved. No doubt the wide range of phenotypic variation typical of this family has caused problems. But it is apparent also that the wide geographical ranges of many of the species has led to unwitting duplication of work between countries. The resulting literature is widely scattered, and this too has imposed problems since only a few libraries have all the relevant publications.

This report attempts to revise the species of the family Campanulariidae, excepting those in the genus *Obelia*, recorded from the eastern North Atlantic. *Obelia* is excluded since it was revised recently (Cornelius, 1975*a*) but notes are included to update that revision. The area extends southwards to the equator and west to the 30° meridian. It includes the Mediterranean, Black and Baltic Seas, and extends in one region beyond 30° W to include the coastal waters of Greenland. In general there have been few records of the family north of 80° N, but this must reflect collecting difficulties since several species have been reported from these high latitudes (Linko, 1911). One dubious tropical species, *Orthopyxis africana,* is not treated fully because it has been recorded only once, near the southern limit of the area.

Most genera of Campanulariidae are nearly cosmopolitan. It happens that the majority are represented in the eastern North Atlantic. Further, most were described first from European waters; so that a revision of the NE Atlantic genera comes close to a complete revision. A comprehensive generic synopsis is not intended here, however, since not all the nominal species are covered. But at least an interim generic list can be given (Table 1). Most of the nominal genera are discussed, whether or not they have been recorded in the NE Atlantic, and the relevant discussion sections can be found through the index. All are at least mentioned.

Table 1 The subfamilies and accepted genera of the Campanulariidae. Those not recorded from the NE Atlantic are treated only briefly in this paper, and are marked by an asterisk.

Subfamily/genus	Recent redefinition, if any	Notes
CAMPANULARIINAE	p. 50	
Campanularia Lamarck, 1816	p. 51	
**Eucalix* Stechow 1921*a*		p. 50
**Orthonia* Stechow, 1923*a*		p. 51
Orthopyxis Agassiz, 1862	p. 58	
Rhizocaulus Stechow, 1919*b*	p. 67	
**Silicularia* Meyen, 1834	Ralph, 1957; Stepanyants, 1979	p. 50
CLYTIINAE *nom. nov.*	p. 69	
Clytia Lamouroux, 1812	p. 71	
**Gastroblasta* Keller, 1883	Kramp, 1961	p. 72
**Tulpa* Stechow, 1921*a*	Ralph, 1957; Stepanyants, 1979	p. 70
OBELIINAE Haeckel, 1879	p. 91	
Gonothyraea Allman, 1864*a*	p. 92	
Hartlaubella Poche, 1914	p. 94	
Laomedea Lamouroux, 1812	p. 97	
Obelia Péron & Lesueur, 1810*a*	p. 112	

Taxonomy and the phenotype

The long synonymies and remarks sections in this paper and in that on *Obelia* (see Cornelius, 1975*a*) reflect the fact that wide phenotypic variation has led to nominal taxa being based on unimportant characters. Even the usually reliable Hincks (1868) was misled; but in fairness it should be remembered that Hincks, and his colleagues Alder and Allman, were breaking new ground when seriously considering the taxonomy of this family. Now, with a century of hindsight, the taxa they and others proposed can be better assessed. The early workers did not realize how much these hydroids vary, compared with the usually much less variable species of Haleciidae, Sertulariidae and Plumulariidae which they knew already.

Some of the literature on variation in the species of this and other thecate families has been reviewed recently (Cornelius, 1975*a*, *b*, 1979). The notes in the 1975*a* paper, on *Obelia*, are now summarized and this is followed by some new comments. Authorities for the species names are mostly omitted here since they are adequately indicated in the Taxonomic Section (p. 47).

Colony size in erect species probably increases till mechanical breakage occurs (Crowell & Wyttenbach, 1957, in *Laomedea flexuosa*; Cornelius, 1975*a*, in *Obelia dichotoma*) and is of little taxonomic value. *Obelia geniculata* growth was studied by Ralph (1956) and Ralph & Thomson (1968) in New Zealand. Growth was faster in cool conditions than warm.

Polysiphonic stems occur sometimes in *Obelia dichotoma* (*cf.* Millard, 1973) and *Laomedea neglecta*, and are usual in *Hartlaubella gelatinosa* and *Rhizocaulus verticillatus*. The species *Obelia plicata* Hincks, 1868, was based on *O. dichotoma* material of this kind (p. 119). Occasional overgrowth of one colony by another of the same species is a rather different phenomenon now called auto-epizoism (p. 119).

Branching was most frequent in low water temperatures in *Obelia geniculata* in New Zealand (Ralph & Thompson, 1968). Similar results were obtained from '*Clytia attenuata*' by West & Renshaw (1970) who discussed the taxonomic implications (see also notes on Growth, p. 42).

Internode length, extent of annulation, curvature, amount of asymmetric thickening and angle of flexure have all be used to define species limits in the Campanulariidae; but only asymmetric thickening (in *Obelia geniculata*) and sometimes curvature (in *Laomedea flexuosa*) seem good characters (Cornelius, 1975*a*; below, p. 113).

Perisarc tanning has been included in some species descriptions, for example in that of the now discredited *Obelia longissima* (discussion in Cornelius, 1975*a*), but has not been taken as a unique species character. The intensity of tanning increases with age in many species. In some the perisarc does not seem to darken appreciably, but this might be due simply to its thinness. Knight (1965, 1970, 1971) studied the tanning process in *Laomedea flexuosa*.

Hydranth characters are not useful at species level but the shape of the hypostome is consistent throughout some genera. Tentacle number is usually too variable to be useful, notably in *Clytia hemisphaerica* and *Obelia dichotoma*, but it has been used in defining *Orthopyxis crenata*.

Hydrothecal characters are useful in this family. But despite their confusing intraspecific variation (Broch, 1910, and later workers) we hardly know how the characters develop (e.g. Berrill, 1949, in *Obelia*; Berrill, 1950, in *Clytia hemisphaerica, Laomedea flexuosa* & *Orthopyxis integra*; Knight, 1965, in *Laomedea flexuosa*; Beloussov, 1973, in *Gonothyraea loveni*). Several authors have reported chitinous structures in the hydrothecae of *Gonothyraea loveni* and *Obelia bidentata* which, however, have proved merely to be regularly arranged folds in the delicate hydrothecal walls. Minor variations in the pattern of cusps on the hydrothecal rims of several of the species have been given undue weight by some authors (see Remarks under *O. bidentata*). Presence or absence of the hydrothecal diaphragm is a subfamily character but is not useful at genus or species level.

Mammen (1965) noted that an oblique hydrothecal diaphragm viewed from the 'front' appears transverse in optical section—a point not realized by some taxonomists. It follows that rotation of a sloping diaphragm produces a whole series of angles, from horizontal to the true maximum slope. Further, even when correctly viewed, a transverse diaphragm is not a consistent character (Cornelius, 1975*a*).

Naumov (1969 : 123) stated that many hydroids have larger hydrothecae in cool waters than warm, but offered data in only one species (*Orthopyxis integra*). Although the relation might well be valid in many species, detailed proof is needed. Possibly it has already caused taxonomic confusion since large, northern specimens of *Clytia hemisphaerica* have been referred to the invalid *C. gigantea* by several authors (p. 81)—but not all of the large specimens were from cool areas.

Hydrothecal pedicels are variable in length, in amount of annulation and in the presence or absence of a smooth central portion. Most species vary widely in these characters. Pedicels of reptant species are usually longer than those of upright colonies, perhaps in response to greater feeding opportunities away from the substrate than close to it. A peculiar case is the long hydrothecal pedicels of floating colonies of the usually reptant *Clytia hemisphaerica,* which have often been regarded a distinct species (*C. sarsi* nom. nov., p. 78). Implicitly, minor variations in pedicel length are phenotypic and overall length ranges are genotypic; but evidence is lacking.

A more useful pedicel character than length is the occurrence of spiral grooving in some species in place of the more usual annuli. Spiral grooving seems constant in those species having it, and has not been found even exceptionally in annulated species; but annulated pedicels have been recorded in the usually smooth to spiral *Rhizocaulus verticillatus* (p. 68). When present a spirally ornamented pedicel is a safe character.

Another reliable character is the formation in some species of a sub-hydrothecal 'spherule', first described by Ellis (1755) and noted by many subsequent authors. It is formed between two annuli just below the hydrotheca and spaced apart on the pedicel by a distance about equal to its width (Fig. 6). Some authors have regarded possession of spherules by distinct species as indicating affinity, and this seems usually justified. But spherules are simple modifications of existing structures and might have evolved more than once. Thus *Clytia hummelincki* is alone in its genus in having a spherule.

The spherule structure is otherwise found in the genera *Campanularia, Orthopyxis* and *Rhizocaulus.* It recalls the basic arthropod joint in having structures analogous to arthrodial membranes, but in other ways it resembles the vertebrate ball-and-socket joint. Considerable passive flexibility is achieved with little materials, enabling the hydrotheca to be rapidly orientated downstream in response to local water movement. It would seem that fewer materials are needed in this arrangement than would be needed to construct a rigid, unbending pedicel which could maintain the hydrotheca broadside on in strong currents. The spherule joints seem to be an evolutionary advance on the simple annulations seen in many species of Campanulariidae. Uniformly annulated pedicels bend a little at each annulation and have tissue-attachment problems associated with repeated asymmetric compression along their whole length. A hydrotheca supported by a spherule can simply flip-flop from side to side in response to local current surges, and bends just at one point. In addition, spherules would appear more resistant to vertical compression than annuli.

Murdock (1976) considered very briefly the role of annuli in *Obelia* sp. main stems. He observed that they help bending, an obvious conclusion not often repeated. Hughes (1980) studied *Laomedea flexuosa* and *Obelia dichotoma* at a few sites on British coasts and found higher numbers of pedicel annuli in sheltered situations than exposed.

Gonothecal shape provides good taxonomic characters in *Laomedea* but in *Clytia, Obelia* and *Orthopyxis* it does not. Some nominal species have been based on immature gonothecae, for example the invalid '*Laomedea conferta*' (p. 104).

Most species have monomorphic gonothecae but strongly marked sexual dimorphism does occur. It has caused taxonomic confusion in *Laomedea calceolifera*, which was formerly regarded as two species. The two kinds of gonothecae proved to be male and female of the same species. Gonothecae of *L. angulata, L. flexuosa* and *Gonothyraea loveni* tend towards sexual dimorphism, and the few *L. pseudodichotoma* specimens available indicate it occurs in that species too. In the other species described herein the gonothecae are monomorphic, so far as is known.

Nematocysts have not yet proved useful in delimiting species in *Obelia* (Cornelius, 1975*a*) but little is known of their potential value in the rest of the family (review in Östman, 1979). As in most hydroids, they are among the smallest of nematocysts and their study requires refined techniques. Although Östman reported slight differences in basal armature between the nematocyst threads of some pairs of species here regarded conspecific [*Clytia hemisphaerica* (Linnaeus, 1767) and *C. sarsi* nom. nov. (=*Laomedea gracilis* Sars, 1850); *Obelia dichotoma* (Linnaeus, 1758) and '*O. longissima* (Pallas, 1766)'], rather few populations have yet been studied. She commented that microbasic mastigophores have hitherto been separated on characters which are optical artefacts, a conclusion borne out by some unpublished electron micrographs she has kindly shown me (Östman, pers. comm.). If the populations having distinct, although very similar, nematocyst types can be distinguished on other characters also then Östman's conclusions will be corroborated. But the undischarged capsules are only 6 μm to 8 μm long, and the fine details of thread structures are unlikely to prove useful in routine identification. Some correlation with gross morphological characters would seem desirable. See also page 78 concerning '*Clytia gracilis* (Sars, 1850)'.

Habitat preferences and substrate associations are discussed under ecology. Few members of the family have a regular habitat association and most seem able to live on a wide variety of substrates. The prime exception is *Laomedea angulata*, living exclusively on eel grasses; but since other hydroids live there too this does not help in identification.

Medusa generation Russell (1953) showed best the extent to which intraspecific variation in hydromedusae has led to many invalid species being described; but the factors controlling this apparently phenotypic variation are almost unknown.

The problems surrounding the two nominal species of *Obelia* recognized from the medusa stage in British waters still remain (summarized in Cornelius, 1975*a*, but based largely on Russell, 1953 and pers. comm.). In addition there is no clue as to why *Obelia* medusae on release should not always be at the same stage of development. Some authors have based nominal species of *Obelia* partly on tentacle number at the time of release, and although this seems unwise the cause of the variation is still unexplained.

In contrast, four tentacles on release is characteristic of the medusae of most of the *Clytia* species (see generic diagnosis, p. 71). Adult medusae of *Clytia linearis, C. hummelincki, C. paulensis* and *Orthopyxis crenata* (but see p. 59) are undescribed, as are the hydroid stages of *C. discoida*, *C. pentata*, *C. islandica* and arguably *C. mccradyi.* When all stages in the life cycles of these species are known some of the nominal taxa may fall.

It is remarkable that only a little taxonomic confusion has resulted from the unusual habit in *Orthopyxis integra* of releasing medusae on some occasions and not on others (p. 63).

Growth is affected by many factors and has been widely studied in this family. Hammett (1943) is now thought to have studied growth in *Laomedea flexuosa,* not *Obelia geniculata* as he stated (Crowell, 1957; Cornelius, 1975*a*). Toth (1969) studied colony 'senescence' in *L. flexuosa.* Wyttenbach, Crowell & Suddith (1973) reviewed their own work on stolon elongation in thecate and athecate hydroids, treating *Laomedea calceolifera, L. flexuosa* and *Gonothyraea loveni* among the present family. They reported similar results in the two *Laomedea* species but found generic differences in the growth cycles of the stolon tips. Cyclic increases in length had been demonstrated earlier in *L. flexuosa* by Wyttenbach (1968, 1969) alone; and Beloussov (1961) and Hale (1964) had still earlier found the same peculiar phenomenon in stolons of *Laomedea flexuosa* and *Clytia hemisphaerica* respectively. Hale (1973*a, b*) later reported further morphogenetic work on *C. hemisphaerica* stolons and reviewed the literature. Beloussov's (1973) important paper described more work on the stolons of *G. loveni* but he did not take environmental factors into account. Nevertheless, phenotypic responses to changes in temperature and feeding opportunity are known to occur in the stolon of *L. flexuosa* (e.g. Crowell, 1957, 1961), mainly in 'alterations largely due to the sensitivity of zones of prospective growth'. These observations are interesting in themselves, but their experimental requirements make them unsuitable for regular taxonomic use.

Phenotypic response to temperatue change was noted in the hydroid stage of '*Clytia attenuata*' by West & Renshaw (1970) who incidentally regarded that species as valid (but see p. 40). In vitro colonies at 13°–15°C were unbranched and could not be distinguished from '*Clytia cylindrica* Agassiz'; but at 17°–19°C a kind of branching occurred which these authors considered characteristic of *C. attenuata*. Whatever the validity of the two nominal species involved, West & Renshaw drew attention to a taxonomic difficulty resulting from phenotypic response. Their extensive review and discussion mainly concerns western North Atlantic species of *Clytia* hydroids and medusae, and further comment would be out of place here.

Finally Stebbing (1976, 1979, 1981; see also p. 107) has studied the influence of toxic inorganic ions on the growth and death of *Laomedea flexuosa.* He found that growth was actually enhanced at sub-inhibitory concentrations of the toxic ions. It seems that care should be taken when assessing the morphological characters of material collected from slightly polluted places.

Ecology

Associations. Only one of the species included here has an apparently obligatory substrate association: *Laomedea angulata,* which has been reliably recorded growing only on eel grasses. *Obelia geniculata* tends to occur on brown algae whereas the very similar *O. dichotoma* grows usually on other substrates; but each occurs occasionally on the substrate more usual for the other. The other North Atlantic species of the family show no marked substrate associations. They repeat the general hydroid pattern of a few species having some substrate specificity with the majority having only loose associations or none at all; but the association of *L. angulata* with eel grasses is unusually close. Nishihira (1968) reported '*Clytia edwardsia*' to be 'characteristic of' *Zostera marina* in Japanese waters. However, both Nishihira and Picard (1955, in Algeria) reported many hydroid species growing on *Zostera* but not confined to it.

Brackish water and estuarine species. Many species of Campanulariidae are tolerant of reduced salinity. But while many of the species included here occur either occasionally or habitually in low salinity areas, none has been reported from fresh water. The species comprise more than a third of the present faunal list: *Laomedea angulata, L. calceolifera, L. neglecta, Clytia paulensis, Gonothyraea loveni, Hartlaubella gelatinosa, Obelia bidentata, O. dichotoma* and *O. geniculata.* All records refer to the hydroid stage and none to the medusa. Further details are given in the Habitat sections of these species.

A similar impression of the family was given by Calder (1976). He found as many as 40 brackish water hydroids in South Carolina, and of these no fewer than ten were from the Campanulariidae.

Interactions between species. Although the phenomenon of overgrowth has been studied in a variety of coelenterates and other colonial invertebrates (review in Larwood & Rosen, 1979), among hydroids it has been recorded infrequently. Sustained overgrowth of one hydroid colony by another is unusual, and in the present family there are a few instances only. For example, occasional colonies of *Obelia dichotoma* with erect stems comprising more than one hydrocaulus were once regarded a distinct species (*O. plicata,* p. 119); and the regularly polysiphonic stems of some other species treated here may be derived in the same way (*Rhizocaulus verticillatus,* p. 67; *Hartlaubella gelatinosa,* p. 95; *Obelia bidentata,* p. 113). Overgrowth has been recorded occasionally in *Laomedea neglecta* (p. 107) but the species is not well enough known for this to be assessed. Millard (1973) listed several species of thecates from other families showing growth of one colony on another, and introduced the descriptive term auto-epizoism.

Antagonism between colonies is widely known among other coelenterates and in many of the invertebrate phyla (Larwood & Rosen), but like overgrowth has seldom been reported among hydroids. Hughes (1975) reviewed work on a few species of Campanulariidae ('*Clytia volubis* Packard', *C. hemisphaerica, Obelia dichotoma*); while in another family Warburton (1953) recorded aggression between a colony of *Hydractinia echinata* (Fleming, 1828) and one of *Podocoryne ?carnea* Sars, 1846, on a gastropod shell inhabited by *Pagurus* sp.

Geographical distribution

Most species of Campanulariidae are widely distributed, some occurring nearly throughout the World in shallow waters. For example, of the 18 species recorded from New Zealand no fewer than seven occur also in British waters (Ralph, 1957). The corresponding figures for southern African seas are 21 species and 8 (after Millard, 1975; the immigrant *Gonothyraea loveni* would be additional), and for the antarctic area 13 and five (after Stepanyants, 1979, with some taxonomic revision). But few species of the family appear uniformly distributed, and many have a patchy local distribution. The local variations are best documented in European waters, towards which the following notes on the eastern North Atlantic species are unavoidably biased. Further details are given in the Taxonomic Section under each species.

Orthopyxis integra. Although one of the most nearly cosmopolitan of all shallow-water hydroids this species has not been found in the Kattegat, Skagerrak, Baltic Sea and Dutch waters; and has only occasionally been recorded from Belgium, western Scotland and the Irish Sea.

Clytia hummelincki. So far this species has been reported only from the West Indies, Florida, Massachusetts, South Africa and Ghana (p. 83).

Clytia paulensis. Known for some years from parts of NW France but only recently added to the British faunal list (p. 89). However, a specimen collected in S Devon in 1899 has now been correctly identified. In the 1970s the species was found in Devon and Suffolk.

Gonothyraea loveni. In South Africa this species is known from Cape Town docks only, and Millard (1975) considered it had spread from Europe to the Southern Hemisphere on ships.

Hartlaubella gelatinosa. The several nineteenth century Scottish records contrast with a single Scottish record this century, in 1932 (p. 95). But the species is still common at least as far north as NW England (J. Clare, pers. comm.) and the lack of recent Scottish records may be misleading.

Laomedea angulata. There are few reliable records from the British Isles this century, in contrast to an abundance of nineteenth century records (p. 100). Apparently the species has yet to regain its former distribution after the temporary decline of the *Zostera* beds in the 1930s (described by Tutin, 1942). Although *L. angulata* was recorded from the Scillies in 1967 (Robins, 1969) there is apparently no other reliable British record since those from S Devon before 1910 (Marine Biological Association, 1957). (But see Addendum.)

Laomedea calceolifera. Although widespread in North Atlantic waters, relatively conspicuous, and distinctive when fertile, this species has been reliably recorded only twice from British waters (S Devon, *c.* 1871, by Hincks, 1871; Norfolk, in 1951, by Hamond, 1957), with a third dubious record (Norfolk, in 1899, quoted by Hamond, 1957). Probably the species reaches its northern limit in southern England but the paucity of British records is still remarkable as the species is well known from NW France (p. 104).

Laomedea pseudodichotoma. This species has yet to be recorded away from the coastal waters of tropical W Africa but it would be remarkable if this indicated the true geographical range (p. 112).

Obelia bidentata. This species was first reported from British waters only some 25 years ago; and the first record from the south coast of England is reported here (p. 115). It seems unlikely that the nineteenth century British collectors would have overlooked so distinctive a species, and the absence of earlier records may be genuine. The species was not known in Europe until the 1900s. Indeed, it may have been an immigrant into E Atlantic waters from the American coast, but this is not certain and early confusion with *Hartlaubella gelatinosa* is not excluded as a reason for the absence of earlier records. See also the next species.

Obelia dichotoma & *O. geniculata*. There are records of these widespread species on many swimming vertebrates, including a turtle, a shark, the blueback herring and a sea-horse; and also on drifting kelp (pp. 117, 118, 120). Taken together the records suggest that these species might be transported over vast distances. The potential was realized long ago in other hydroid families (e.g. Alcock, 1892; Lloyd, 1907; Heath, 1910; review in Gudger, 1928, 1937). Transport might explain the appearance of the previous species in European waters around the 1900s, carried perhaps by ships rather than by vertebrates. However, turtles regularly cross the Atlantic (Parker, 1939; E. N. Arnold, pers. comm.) so that natural means are not excluded. *Clytia hemisphaerica*, another widespread species, has similarly been found on fish, attached to their crustacean ectoparasites (p. 77). It seems plausible that continuous transport across deep ocean basins will promote exchanges between the gene pools of these species on different continental shelves; and might explain why many hydroid species are virtually cosmopolitan at shelf depths. Paradoxically, it may be that the hydroid stages of such species sometimes travel further than their medusae which live for just a few weeks.

Key to species (hydroid stages)

Many of the species of Campanulariidae are so variable that overlap in characters occurs, and identification by a dichotomous key is not always possible. Young and infertile specimens are particularly difficult and even with the help of long Museum series some specimens cannot be identified. Close study of a single, undamaged hydrotheca is often useful and the outline of the unabraded rim can be diagnostic. Hydranth characters are seldom useful for identification in this family.

Provisional identification can frequently be made from the illustrations of the gonothecae. Characters based on reproductive structures are mostly omitted from the key, however, as many specimens are infertile. When identifying fertile material it can be helpful to determine whether the ova develop within the gonotheca or in an external acroyst, and if the gonotheca contains developing medusae; but these characters too are mostly avoided in the key.

1	Colony with erect stems each supporting several to many hydrothecae	2
–	Colony mainly stolonal, each stem or pedicel supporting one or just a few hydrothecae	18
2	Rim of hydrotheca even to sinuous	3
–	Rim of hydrotheca definitely cusped [Rims often abrade smooth in *Gonothyraea loveni, Hartlaubella gelatinosa* and *Laomedea neglecta*]	10
3	Terminal region of hydrotheca flared	4
–	Terminal region of hydrotheca not flared	5
4	Gonothecal aperture narrow; recurved in mature ♀	*Laomedea calceolifera* (p. 102; Fig. 18)
–	Gonothecal aperture broad, never recurved [tropical]	*Laomedea pseudodichotoma* (p. 111; Fig. 21)
5	Internodes curved	6
–	Internodes straight	8
6	Hydrotheca thickened, sometimes much so	*Obelia geniculata* (p. 119)
–	Hydrotheca with little or no thickening	7
7	Hydrotheca usually 1½ times long as broad, or longer; gonothecal aperature usually raised; releases medusa	*Obelia dichotoma* (p. 117)
–	Hydrotheca not much longer than broad; gonothecal aperture not raised; no medusa stage	*Laomedea flexuosa* (p. 105; Fig. 19)
8	With sub-hydrothecal spherule [a locally distributed species]	*Clytia hummelincki* (p. 82; Fig. 10)
–	Lacking sub-hydrothecal spherule	9
9	Internodes rigidly straight; terminal tendrils present in autumn; gonotheca borne on stolon; no medusa [on eel grass]	*Laomedea angulata* (p. 98; Fig. 17)

– Internodes slightly curved; terminal tendrils unusual; gonotheca nearly always axillary; medusa released [on many substrates, but including eel grass] . *Obelia dichotoma* (p. 117)

10 Hydrothecal cusps sharp 11
– Hydrothecal cusps blunt, square, notched or rounded 15

11 Hydrothecal cusps usually bimucronate (hard to see; four species difficult to separate when immature) 12
– Hydrothecal cusps all same length *Clytia hemisphaerica* (p. 73; Fig. 9; see also *C. mccradyi* p. 87, Fig. 13)

12 Mature colony tall and bushy, with polysiphonic stem and second-order branching; gonothecal aperture usually raised, slightly narrower than gonotheca *Obelia bidentata* (p. 113)
– Mature colony small, with up to *c.* 20 hydranths; stem monosiphonic (except occasionally in *L. neglecta*); gonothecal aperture not raised, as broad as gonotheca 13

13 Hydrothecal pedicels longer than hydrotheca . . . . *Clytia paulensis* (p. 88; Fig. 14)
– Hydrothecal pedicels roughly same length as hydrotheca or shorter 14

14 Each internode of constant diameter; hydrothecal cusps strengthened by substantial chitinous strip; medusa released [Mediterranean southwards] . . *Clytia linearis* (p. 84; Fig. 12)
– Internodes slightly bulging; hydrothecal cusps without strengthening strip (folds in hydrothecal wall can be confusing); no medusa [Mediterranean northwards] (see also young *Obelia bidentata*) . . . . *Laomedea neglecta* (p. 107; Fig. 20)

15 Hydrothecal margin with rounded cusps 16
– Hydrothecal margin with square cusps, often notched (abrade easily). 17

16 Mature colony large, polysiphonic; most hydrothecae with subhydrothecal spherule; no medusa stage . . . . *Rhizocaulus verticillatus* (p. 67; Fig. 7)
– Mature colony not usually large, always monosiphonic; no spherule; medusa released *Clytia hemisphaerica* (p. 73; Fig. 9) (also *C. mccradyi*, ?S France only; p. 87; Fig. 13)

17 Small slender colony, stem monosiphonic; primary branching only; medusa retained as gonomedusa external to gonotheca . . . . *Gonothyraea loveni* (p. 92; Fig. 15)
– Large bushy colony, stem polysiphonic; with secondary branching; large ova, developing into planulae within gonotheca; no medusa. . *Hartlaubella gelatinosa* (p. 95; Fig. 16)

18 Sub-hydrothecal spherule present 19
– Sub-hydrothecal spherule absent 24

19 Rim of hydrotheca even 20
– Rim of hydrotheca cusped or undulating 21

20 Hydrotheca usually much thickenend [common] *Orthopyxis integra* (p. 60; Fig. 6) (also *O. crenata* with even hydrothecal rims; see text)
– Hydrotheca unthickened [scarce] . . . . *Clytia hummelincki* (p. 82; Fig. 10)

21 Hydrotheca > 0·5 mm long, with lines running downwards from rim (sometimes absent in one species) 22
– Hydrotheca < 0·5 mm long, without lines 23

22 Lines meeting tips of cusps, which are roundly pointed, not notched; hydrotheca 2+ times long as broad [probably not south of Newfoundland and Spitzbergen] *Campanularia crenata* (p. 52; Fig. 2)
– Lines meeting bottoms of embayments; cusps flat-topped with notch; hydrotheca up to 1·5 × long as broad [widespread] . . . . . *Campanularia hincksii* (p. 53; Fig. 3)

23 Hydrotheca usually much thickened [probably Mediterranean southwards] *Orthopyxis crenata* (p. 58; Fig. 5)
– Hydrotheca unthickened [Mediterranean northwards] . *Campanularia volubilis* (p. 55; Fig. 4)

24 Hydrothecal cusps bimucronate [S England southwards] . *Clytia paulensis* (p. 88; Fig. 14)
– Hydrothecal cusps simple [widespread] *Clytia hemisphaerica* (p. 73; Fig. 9; also *C. mccradyi*, ?S France only; p. 87; Fig. 13)

Taxonomic section

Family CAMPANULARIIDAE Johnston, 1836

DIAGNOSIS. Colonial Thecata (sens. Millard, 1975); hydroid stage stoloniferous or erect, stolon when present may be branched or unbranched; hydrotheca bell-shaped, radially symmetrical, pedicellate, with diaphragm and an associated annular thickening, or with annulus alone and without diaphragm; no operculum; hydranths radially symmetrical, usually with prominent hypostome; no caecum; one ring of tentacles; nematophores absent; ♂ & ♀ gonothecae usually externally identical. Medusa generation when present variable; reduced in *Obelia* and (?) facultatively retained in *Orthopyxis*; typical leptomedusan in *Clytia* and *Gastroblasta*; always retained as gonomedusa in *Gonothyraea*; identifiable in more reduced form in at least some other genera and species.

REMARKS. The family was first proposed by Johnston (1836, 1847, but not 1838). Originally *Lafoea dumosa* (Fleming, 1820) was included in its scope but was removed to the Lafoeidae by Hincks (1868). The limits of the family have remained unchanged ever since and the redefinition by Millard (1975) seems sound. Ralph (1957) also provided a detailed appraisal.

Much has been written about generic limits within the family but it is convenient to go no further back in the literature than the works of Broch (1905, 1910) and Goette (1907). Broch recognized two broad genera. These he called *Campanularia* Lamarck, 1816, which had no hydrothecal diaphragm, and *Laomedea* Lamouroux, 1812, which had one. He divided his concept of *Campanularia* into the subgenera *Eucampanularia* Broch, 1910, having sessile gonophores, and *Clytia* Lamouroux, 1812, with free medusae. Broch split his other broad genus concept, *Laomedea*, into the three subgenera *Eulaomedea* Broch, 1910, with sessile gonophores and no medusoid structures; *Gonothyraea* Allman, 1864*a*, with retained 'eumedusoids' (now called gonomedusoids, p. 93); and *Obelia* Péron & Lesueur, 1810*a*, with free medusae. Thus Broch's basic division within the family was on a hydrothecal character; while within each of the two main divisions his classification was on the state of reduction of the medusa generation (following and elaborating on the interpretation of these structures by Goette, 1907).

Splettstösser (1924 : 424–425) followed Broch's system but further split Broch's subgenus *Eulaomedea* into one group with intracapsular gonophores ('*Laomedea gelatinosa*', *L. flexuosa* and *L. calceolifera*) and a second, in which the mature gonophores were extracapsular (*L. neglecta*). Splettstösser acknowledged that the classification might be criticized since just a small number of species was considered. But Broch (1928) gave it support when he later introduced the subgeneric name *Paralaomedea* for the '*L. neglecta* group', comprising that species alone, in the combination '*Laomedea* (*Paralaomedea*) *brochi* Splettstösser (= *Laomedea neglecta* Alder)'. [Splettstösser's restriction of the subgenus concept was thus cited as indication by Broch; but the authority for the associated subgenus name *Paralaomedea* was Broch (1928).] Finally Hummelinck (1936) redefined the subgenus rather tightly, again to include only *L. neglecta*.

As Splettstösser had commented, very few species were considered in his classification and it is questionable whether so many infra-generic divisions were justified. (Some additional sub-divisions of '*Eulaomedea*' proposed by Splettstösser were not given names, and are not mentioned here.) His own work on *L. neglecta* and other species, and that for example of Goette (1907) and Miller (1973), emphasized that the gonophore 'types' identified by Splettstösser form part of a series in which the medusa is progressively reduced. The gonophore of *L. neglecta* seems simply to fit into this series. Further, Broch's (1910) primary division of the family into two was on the basis of a single hydrothecal character, and this division too might be challenged.

The extent to which the medusa-medusoid-gonomedusoid-gonophore series should be classified into genera will perhaps be debated for as long as the series is regarded valid. But today as in Broch's time, most is known about the life-cycles of the western European species. Until more information is available on species from other parts of the World it seems unwise to split *Laomedea* into subgenera.

Aside from the taxonomic debate, there are some nomenclatural problems which need solution. These I have considered in a submission to the International Commission on Zoological Nomenclature (Cornelius, 1981). The aims of the proposals are provisionally included in the present paper.

The subgenera proposed by Broch, Splettstösser and others need not be recognized. But the evolutionary fate of the medusa generation is still reflected in the classification adopted here. In *Orthopyxis* the medusa is reduced and lacks several normal adult characters, functioning simply as an ephemeral gamete carrier. It is thought to be facultatively released in some or all of the *Orthopyxis* species (see p. 63); while in the closely related *Orthonia* it is still further reduced, to a retained acrocyst. In *Campanularia, Rhizocaulus* and *Silicularia* the gonosome has become intracapsular, with no obvious indications of a medusoid ancestry.

A parallel series showing progressive retention of the medusa can be demonstrated within the genera *Obelia, Gonothyraea, Laomedea* and *Hartlaubella.* In *Obelia* the medusa is released. The extra-capsular gonomedusoids of *Gonothyraea* are easily identified as retained and vestigial medusae; and in *Laomedea* it has been shown that the gonosomes of several species represent reduced medusae. Indeed, so reduced has the medusa generation of *Laomedea* become that until the work of Miller (1973; see also Goette, 1907) the medusoid nature of the gonophore was not appreciated. The same confusion prevailed also in interpretations of the reproductive structures in *Orthopyxis integra*, in which the medusa is sometimes retained. It was thought until quite recently that the retained examples had 'sporosacs' in place of medusae, and that they might therefore be a different species (*O. caliculata*; p. 65–66)!

The genera *Clytia, Gastroblasta* and *Tulpa,* which have a true hydrothecal diaphragm and sub-hydrothecal spherules, apparently form another group but their relation to the rest of the family is not clear.

The three series recognized are shown in Figure 1. The groupings seem natural and are here given subfamily status: Campanulariinae (p. 50), Clytiinae nom. nov. (p. 69) and Obeliinae Haeckel, 1879 (p. 91). See also page 49.

The generic limits suggested by Millard (1975) are slightly modified, as is her nomenclature. *Orthopyxis* is here separated from *Campanularia* sens. Millard. *Eulaomedea* sens. Millard is here called *Laomedea. Sertularia gelatinosa* Pallas, 1766, not in Millard's faunal area, is referred to the monotypic genus *Hartlaubella*; and another species not in her list, *S. verticillata* Linnaeus, 1758, is here referred to the nearly monotypic *Rhizocaulus.*

To promote stability of nomenclature I have attempted to include all extra-limital generic synonyms. The valid genera found outside the NE Atlantic are treated briefly. They are *Eucalix, Orthonia* and *Silicularia* from the Campanulariinae (p. 50); and *Gastroblasta* and *Tulpa* from the Clytiinae (p. 70). The problem genus *Hypanthea* is discussed along with *Silicularia* (p. 50).

From the medusa stage, Kramp (1961) recognized only five genera World-wide: *Agastra, Eucopella*, *Gastroblasta*, *Obelia* and *Phialidium*; but of these only *Gastroblasta* and *Obelia* can now be recognized. Reference to discussions of these genera can be made using the index.

I have previously commented (Cornelius, 1975*a*) on the genera *Medusa* Linnaeus, 1758 (part); *Schizocladium* Allman, 1871; *Obelaria, Obeletta* & *Obelissa*, all Haeckel, 1879 (*Obelaria* Hartlaub, 1897, is a junior homonym and is discussed here under *Hautlaubella*); and *Monosklera* von Lendenfeld, 1885; all except the first of which fall into the synonymy of *Obelia* Péron & Lesueur, 1810*a*. I then mentioned also *Thaumantias* Eschscholtz, 1829, a junior subjective synonym of *Clytia* Lamouroux, 1812 (see below, p. 71). I overlooked (p. 254) that Mayer (1910: 262) had designated *Sertularia volubilis* sens. Ellis & Solander, 1786 (non Linnaeus, 1758) type species of *Clytia* (see p. 70 below). Lastly, I have reversed my opinion on the use of the genus name *Laomedea.*

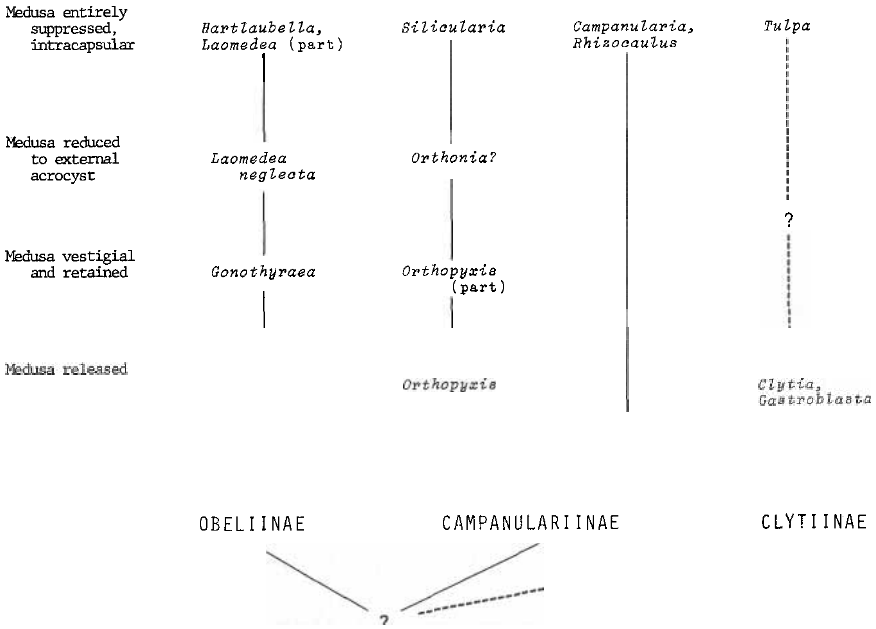


Fig. 1 Affinities within the Campanulariidae. The genus *Eucalix* is not included since its method of reproduction is unknown, but vegetative characters suggest it is close to *Orthopyxis* (discussion on pp. 50–51). The diagram shows present-day similarities, not phylogenies, but the general direction of evolutionary advance is up the page and towards the right. Knowledge of the group is incomplete and the chart should be regarded as provisional.

Some of the species described herein are known only from either hydroid or medusa stages, and others were formerly so. Most species in which the two stages have been reconciled are now known by appropriate combinations, based on application of the International Code of Zoological Nomenclature; but those with incompletely known life-cycles cannot yet have their names confidently derived. Current knowledge in this family seems adequate for the Code to be applied to the two stages simultaneously, but this is arguably not so in all hydromedusan families and in some there may still be a case for retaining the dual system.

The subfamily divisions and their nomenclature

Although the limits of the family Campanulariidae have been agreed for nearly a century and a half (p. 47) only three authors (Haeckel, 1879; Mayer, 1910; Russell, 1953) have sought to group the genera into formal subfamilies. Indeed, until some quite recent studies of the range of reproductive structures found within the family had appeared (Miller, 1973; but also Splettstösser, 1924) interpretation and grouping had been difficult. Miller's important work showed that the structures which had once been called fixed gonophores in for example *Laomedea* spp. were vestigial, retained medusae; and that the curious externally-held 'meconidium' of *Gonothyraea loveni* is similarly to be regarded as a retained medusa.

Happily, this new interpretation of the dispersive generations (planulae and medusae) corroborates the broad divisions of the family based long ago solely on the vegetative characters of the hydroid stage (Broch, 1905, 1910; Goette, 1907; see p. 47, above). Hence the subfamily divisions adopted here, which draw on both groups of characters, might seem soundly based. But some problems remain and further refinement will no doubt be achieved when more is known of the non-European members of the family.

Subfamily **CAMPANULARIINAE**

Campanulariadae Johnston, 1836 : 107 (part).
Obelidae Haeckel, 1879 : 163 (part).
Obelinae: Mayer, 1910 : 231 (part).
Orthopyxinae Russell, 1953 : 303.
non Campanularinae: Russell, 1953 : 284 (=Clytiinae *nom. nov.*; see p. 69).

NOMENCLATURE. The spelling Campanulariinae takes as its root the genus name *Campanularia*, and Campanularinae is wrong.

DIAGNOSIS. Campanulariidae with colony usually reptant, secondarily erect and polysiphonic in *Rhizocaulus*; no true hydrothecal diaphragm; medusa absent except in *Orthopyxis*, where reduced.

TYPE GENUS. *Campanularia* Lamarck, 1816, the nominate genus.

SCOPE. The genera *Campanularia* Lamarck, 1816; *Silicularia* Meyen, 1834; *Orthopyxis* Agassiz, 1862; *Rhizocaulus* Stechow, 1919*b*; *Orthonia* Stechow, 1923*a*; and probably *Eucalix* Stechow, 1921*a*.

REMARKS. Of the included genera only *Campanularia, Orthopyxis* and *Rhizocaulus* are fully treated in this paper. The others have not been recorded from the eastern North Atlantic and are discussed only in this section.

Millard (1975 : 201) united *Campanularia* and *Orthopyxis* because she had seen *Orthopyxis* colonies having some unthickened hydrothecae; but I feel the remaining characters justify a separation.

The genus *Silicularia* Meyen, 1834, was proposed to include two species, *S. rosea* and *S. gracilis*, both being described as new. The early date of *Silicularia* and inadequacies in the descriptions of the two species make detailed comments necessary. The type species of *Silicularia* is *S. rosea*, designated by Stepanyants (1979 : 33). The species was based on Ethiopian and South African material. It was redescribed by Nutting (1915) and Stepanyants (1979), and Blanco (1967*a*) provided useful notes. The second species, *S. gracilis*, was based on infertile hydroid material from the Sargasso Sea and the Azores. It was probably a *Clytia* species. However, the figures and description do not include details of the hydrothecal rim or reproductive structures and I agree with Bedot (1905 : 171) that the species cannot be confidently assigned (see also p. 118). Nutting (1915 : 66) referred '*S. gracilis*' to the rather dubious species *Orthopyxis clytioides* (Lamouroux, in Freycinet, 1824, as *Tubularia*). He wrongly quoted Meyen as using the combination *Silicularia clytioides*. Meyen actually used *S. gracilis*. Rees & White (1966) made the same error when citing Meyen's Azores record. There seem no other reports of '*S. gracilis*' from the eastern North Atlantic. I provisionally refer *T. clytioides* Lamouroux to *Obelia dichotoma*, under which it is discussed further (p. 118). *S. gracilis* was mentioned recently by Stepanyants (1979), as *Campanularia*.

Nutting (1915), Bedot (1925), Broch (1929) and Stepanyants (1979) all regarded as congeneric with *Silicularia* the later genus *Hypanthea* Allman, 1876*a* (type species *H. repens* Allman, 1876*a*, by monotypy; type locality of the type species, Kerguelen I.), and I agree. *Hypanthia* Nutting, 1915 : 22, was a lapsus. Both Allman's (1876*a*, 1888) concept of *Hypanthea* and Nutting's and Stepanyants' of *Silicularia* included thick, asymmetrical hydrothecae, pedicels and stolons reminiscent of *Orthopyxis* Agassiz, 1862, to which the original concepts of the two genera come close. I have not located the type material of *H. repens*, but later material referred to *Hypanthea* species by Allman (1888) had an anastomosing stolon and other orthopyxine features.

So far as I can determine no *Silicularia* species has been recorded from the eastern North Atlantic. *S. atlantica* (Marktanner-Turneretscher, 1890, as *Hypanthea*), was based on material said to have come from 6° S, 38° W, but this position is on the mainland of South America!

The genus *Eucalix* Stechow, 1921*a* : 254, was proposed to accommodate the sole species

Campanularia retroflexa Allman, 1888, type locality Honolulu. Stechow maintained that the unusual hydrotheca of *E. retroflexus* justified generic separation. Both the type series (BMNH reg. no. 1888.11.13.14) and the original illustration (Allman, 1888 : pl. 11, figs 1, 1a) show the hydrothecal characters regarded important by Stechow. These characters, together with the anastomosing stolon of the type material, suggest that Stechow was justified in proposing the new genus. Millard (1957 : 196; 1975 : 212, as *Campanularia morgansi*) listed relevant literature. (I am grateful to Professor W. Vervoort for discussing the characters of this species; and to Dr D. M. Devaney for identifying the substrate of the type material. The substrate is a coralline alga, *Halimeda* sp., not a millepore as Allman stated. Dr Devaney informs me millepores have not been recorded from Hawaii.)

The genus *Orthonia* Stechow, 1923*a* : 94, 107, was proposed to accommodate a single orthopyxine species, *Campanularia everta* Clarke, 1876 : 253–254, pl. 39, fig. 4, type locality San Diego. Nutting had subsequently assigned to this species material having acrocysts and it was this character on which Stechow distinguished the genus from *Orthopyxis*. An element of subjectivity was thereby introduced since Stechow assumed that Nutting had material of the same species as had Clarke; and Stechow had no proof. Further revision of the orthopyxine species seems necessary before *Orthonia* is evaluated further.

Genus **CAMPANULARIA** Lamarck, 1816

Campanularia Lamarck, 1816 : 112 (part); Hincks, 1868 : 160 (part); Nutting, 1915 : 27 (part).
Campanula Westendorp, 1843 : 23 (lapsus pro *Campanularia*).
Campanulata Agassiz, 1862 : 354 (lapsus pro *Campanularia*).
Campanularia (*Eucampanularia*) Broch, 1910 : 184 (part).
Paracalix Stechow, 1923*c* : 3.

TYPE SPECIES. Provisionally to be taken as *Sertularia volubilis* Linnaeus, 1758 : 811 (*non* Ellis & Solander, 1786, see p. 70) as designated by Naumov (1960 : 249). Nutting (1915 : 28) earlier designated *S. verticillata* Linnaeus, 1758 : 811, as type species but application has been made to the International Commission on Zoological Nomenclature for this designation to be set aside (Cornelius, 1981; see Remarks). Broch (1905 : 10) proposed that '*Campanularia calyculata* Hincks, 1853' should be type species, but '*calyculata*' was not among the species originally included in the genus and so is not eligible. The correct spelling is of course *caliculata* (p. 65).

DIAGNOSIS. Stoloniferous and colonial Campanulariidae, stolon not anastomosing; hydrothecae borne on pedicels inserted on the stolon at irregular intervals; true diaphragm absent; sub-hydrothecal spherule present; no medusa stage.

REMARKS. The species *Sertularia verticillata* Linnaeus, 1758, was designated type species of *Campanularia* by Nutting (1915). But some authors, with whom I agree, have sought to remove *verticillata* to a distinct genus (Stechow, 1919*b*, *c*; Naumov, 1960, 1969). This would leave the name *Paracalix* Stechow, 1923*c*, available for the present genus; so that *Paracalix* would become applied for example to the common hydroids widely known as *Campanularia hincksii* (p. 53) and *C. volubilis* (auct.; p. 55). The genus *Paracalix* Stechow, 1923*c*, was proposed to accommodate only *Campanularia pulcratheca* Mulder & Trebilcock, 1914 : 11, pl. 2, figs 1–2, a species based on sterile material from Torquay, Victoria, Australia. (The generic name was actually misprinted *Cmpanularia* in Mulder & Trebilcock's heading.) The hydrotheca was sigmoid in lateral view and Stechow was impressed by the resulting bilateral symmetry. This was the main character on which the species, and subsequently Stechow's proposed genus, were based; but the specimen seems simply to have been a deformed specimen of *C. volubilis* or a closely related species. On this interpretation the species *pulcratheca* and the genus *Paracalix* are referred to *Campanularia*.

I have applied to the International Commission on Zoological Nomenclature for Nutting's designation of *S. verticillata* as type species of *Campanularia* to be set aside (Cornelius, 1981). If approved, this will validate Naumov's (1960) designation of *S. volubilis* Linnaeus, 1758, as type species of *Campanularia*. As a consequence the genus name *Rhizocaulus* Stechow, 1919*b*, can then be applied to the species *verticillata* (in the combination *R. verticillatus*, p. 67). See also the notes under *Rhizocaulus* (p. 67).

The subgenus *Eucampanularia* Broch, 1910, was introduced to embrace the five species *Sertularia volubilis* Linnaeus, 1758, *Campanularia integra* Macgillivray, 1842, *C. groenlandica* Levinsen, 1893, *C. speciosa* Clarke, 1877 and *S. verticillata* Linnaeus, 1758. The subgenus name has hardly been used in the literature. I designate *S. volubilis* Linnaeus, 1758, as its type species; so that *Eucampanularia* can be regarded a junior objective synonym of *Campanularia* (subject to my proposals to the ICZN being accepted; see also Cornelius, 1981).

Campanularia crenata Allman, 1876*b*

(Fig. 2)

Campanularia crenata Allman, 1876*b* : 258–259, pl. 11, figs 1–2.
Campanularia speciosus Clarke, 1877 : 210 (lapsus pro *speciosa*).
Campanularia speciosa (Clarke, 1877 : 214–215, pl. 9, fig. 11; Linko, 1911 : 185–187, fig. 34 (syn. *C. crenata* Allman); Broch, 1912*a* : 17–18, fig. 3; Nutting, 1915 : 48, pl. 8, fig. 5 (syn. *C. crenata* Allman); Broch, 1918 : 158–159 (syn. *C. magnifica* Fraser); Calder, 1970 : 1519, pl. 4, fig. 3.
Campanularia magnifica Fraser, 1913 : 164, pl. 11, figs 1–3.

NOMENCLATURE. The widely used trivial name *speciosa* was introduced in a paper published on 2 January, 1877, and not in 1876 as usually assumed. Hence *crenata*, genuinely introduced in 1876, has priority (see note on page 129 under Clarke, 1877).

The combination *Campanularia crenata* has been applied also to the species here called *Orthopyxis crenata*; but in that species the original binominal was *Eucopella crenata*, and primary homonymy has not occurred. There is secondary homonymy, however, and this is discussed under *O. crenata* (p. 60).

TYPE LOCALITY AND MATERIAL. Infertile colony on '*Thuiaria crassicaulis*' (Sertulariidae), ?Tsuger Straits, Japan, 183 m (100 fms); 1877.4.12.8 (previously unpublished data with specimen).

OTHER MATERIAL EXAMINED. All BMNH material is listed. 45 m, Store Hellefiskebanke, Greenland, fertile colony on *Sertularia mirabilis* (Verrill, 1873), coll. G. M. R. Levinsen, exch. Copenhagen Mus.; 1896.8.15.2 (Fig. 2; ?mentioned, Broch, 1918). 'Greenland', infertile colony on *Sertularia mirabilis*, ex D'Arcy Thompson colln, pres. Univ. Dundee; 1957.1.1.12. Infertile colony on *Sertularella* sp., Norman St, Labrador, Canada, ex D'Arcy Thompson colln, pres. Univ. Dundee; 1956.10.23.69. Infertile colony on *Symplectoscyphus* sp., Bell I, Newfoundland, Canada, 17 Apr 1892, ex D'Arcy Thompson colln, pres. Univ. Dundee; 1957.1.3.24. Infertile fragment, Bel Sund, Spitzbergen, 14 Jul 1898, 20 m, coll. Spetsberg Expedn, exch. Stockholm Mus.; 1960.8.29.33. No locality, fertile colony on sertulariid hydroid, exch. Copenhagen Mus.; 1912.12.21.44.

DESCRIPTION. Colony reptant. Stolon tortuous, branched, rugose. Hydrothecae on usually long pedicels, at irregular intervals; large, narrowest *c.* $\frac{1}{3}$ from rim, bulging out basally; rim much flared, with *c.* 10 rounded cusps, usually with striations running proximally from apex of each cusp; sub-hydrothecal spherule present; pedicel usually longer than hydrotheca, up to *c.* 3x length, spirally grooved throughout. Gonotheca ?♂ = ♀, elongate-ovoid, with or without long neck, borne on stolon.
Variation. The short necked gonotheca illustrated was apparently mature, indicating that the long necks usually regarded distinctive are not invariably present.

DISPERSIVE STAGE. Planulae, which develop within the gonotheca. Present material (1896.8.15.2) has just one in each gonotheca but there may have been more in life.

REPRODUCTIVE SEASON. No information.

DISTRIBUTION. A circumpolar Arctic Ocean and cold water species recorded in the Atlantic as far south as Newfoundland (present material), W Greenland and Spitzbergen (Broch, 1912*a*; Calder, 1970).

HABITAT. Usually reported epizoic on other hydroids. Naumov (1960, 1969) found an extreme depth range of 3 m to 600 m in Russian seas, most of his records being between 20 m and 200 m.

REMARKS. This species has been widely known by the combination *Campanularia speciosa*.

The long gonothecal neck often thought characteristic of the species is not present in all the material listed here, and is evidently variable in length.

Broch's (1918) attack on the validity of *Campanularia magnifica* Fraser, 1913, left no doubt that it is conspecific.

Campanularia hincksii Alder, 1856*a*

(Fig. 3)

Campanularia hincksii Alder, 1856*a* : 360, pl. 13, fig. 9; Hincks, 1868 : 162–163, pl. 24, fig. 3; Goette, 1907 : 189–193, pl. 15, figs 307–312; Broch, 1933 : 87–93 (syn. *C. alta* Stechow); Vervoort, 1946*a* : 276–277, fig. 122 (syn. *C. alta* Stechow); Patriti, 1970 : 33–34, fig. 41 (syn. *C. brachycaulis* Stechow, 1919*a*, here referred to *Clytia hemisphaerica*, see p. 82; *C. macrotheca* Leloup); Millard, 1975 : 208, fig. 67b–e.

Campanularia alta Stechow, 1919*a* : 54–57, fig. P.

Campanularia rara Stechow, 1919*a* : 60–61, fig. R.

Campanularia macrotheca Leloup, 1930*a* : 101–102, figs 1–3.

TYPE LOCALITY AND MATERIAL. Coast of Northumberland, England (Alder, 1856*a*; Millard, 1975). The syntype series is preserved jointly in the Hancock Museum, Newcastle upon Tyne, Northumberland (several colonies in spirit, epizoic on sertulariid hydroids) and the BMNH [small dry colony, 1857.8.3.58, epizoic on *Lafoea dumosa* (Fleming, 1820)]. It has been catalogued by Cornelius & Garfath (1980).

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia alta* Stechow, 1919*a*, infertile fragment of syntype on microslide, Naples; Munich Zoological Museum.

C. rara Stechow, 1919*a*, infertile fragment on microslide, Marseille; MZM.

OTHER MATERIAL EXAMINED. BMNH collection, *c*. 50 specimens. The following, collected by W. J. Rees, had fertile ♂ gonothecae: Hjeltefjord, nr Bergen, Norway, 40–90 m, 9 Apr 1962, 1962.10.7.20; I of Cumbrae, W Scotland, 90 m, 11 Jul 1966; 1967.12.1.10–12.

DESCRIPTION. Colony a tortuous stolon bearing unbranched hydrothecal pedicels at irregular intervals. Hydrotheca large, campanulate, truncate basally; length : breadth ratio variable (1·3–2·25 : 1, Millard, 1975); rim castellate, 8–15 blunt cusps each usually notched, occasionally deeply; main embayments deep, curved, often conspicuous, with characteristic folds trailing down from centres. Hydrothecal pedicel long, with spherule distally; shaft smooth to sinuous, usually with several annuli basally, sometimes also 1 – several annuli along length (Vervoort, 1946*a*). Hydranth ?undescribed, 18–24 tentacles visible in contracted BMNH material. Gonothecae ♂ = ♀, borne on stolon; sub-cylindrical, sometimes asymmetrical; broadest near base, truncate below, tapering gradually above; sides smooth to irregularly sinuous in a loose succession of rings; truncated and sometimes slightly flared distally; aperture wide, terminal; planula development probably internal; gonothecal pedicel short, ringed; colonies dioecious.

Variation. The BMNH series shows variation in the following features: size and length : breadth ratio of hydrotheca, height and number of cusps, depth of notch in cusps, presence or absence of longitudinal folds in hydrothecal wall; sinuosity of perisarc of hydrothecal pedicel, length of pedicel, number of basal annulations (may be absent), shape of proximal cavity in hydrotheca; sinuosity of gonothecal wall, amount of flaring below gonothecal aperture. Billard (1934) reported that the notch in the tips of the hydrothecal cusps may be absent, when the hydrothecae sometimes resemble those of *Campanularia volubilis* (p. 55).

DISPERSIVE STAGE. Planulae, which probably develop within the female gonotheca. Development of the male gonomedusoid was described by Goette (1907).

REPRODUCTIVE SEASON. Jun–Oct in NW France (Teissier, 1965). BMNH fertile material has collection dates within these limits except a male specimen from near Bergen, dated 9 Apr 1962.

DISTRIBUTION. Nearly cosmopolitan in shallow waters. Although not the most abundant hydroid *C. hincksii* can be expected almost throughout the eastern North Atlantic, local conditions permitting. Notable records include: N & S Iceland, Lofoten Is & Norway (Kramp, 1938); Mediterranean (Picard, 1958*b*); Italy (Rossi, 1971); Portugal (Da Cunha, 1950); Cap Spartel, Tangier & Cap Blanc, Morocco (Billard, 1907); Azores (Rees & White, 1966); Mauritania (Billard, 1931*a*); South Africa ('rare', Millard, 1975). The species is widespread in parts of temperate western Europe, including the British Isles (Hincks, 1868), but is scarce in Dutch and Belgian waters (Vervoort, 1946*a*; Leloup, 1952). There are several records from the Skagerrak and Kattegat (Kramp, 1935) and W Sweden (Jägerskiöld, 1971), but no records from the Baltic Sea (Stechow, 1927; Broch, 1928; Naumov, 1960, 1969) or Black Sea (Naumov).

HABITAT. Usually recorded between 20 m and 200 m but occasionally deeper: 'a few metres down to 800 m' (Kramp, 1938); 20–100 m, SW England (Marine Biological Association, 1957); *c*. 20 m, SW Wales (Crothers, 1966); 25–50 m, Scilly Is (Robins, 1969); below 20 m, NW France (Teissier, 1965); 112–120 m, Strait of Gibraltar & Morocco (Billard, 1907); 27–98 m, Azores (Rees & White, 1966); 86–210 m, southern Africa (Millard, 1975). Shallow records include: 15 m, NW Wales (Knight-Jones & Jones, 1956); 10–112 m, Faeroes (Kramp, 1929); 9·5–80 m, W Sweden (Jägerskiöld, 1971). Apparently no intertidal records.

The species seems unrecorded from brackish waters and may be stenohaline.

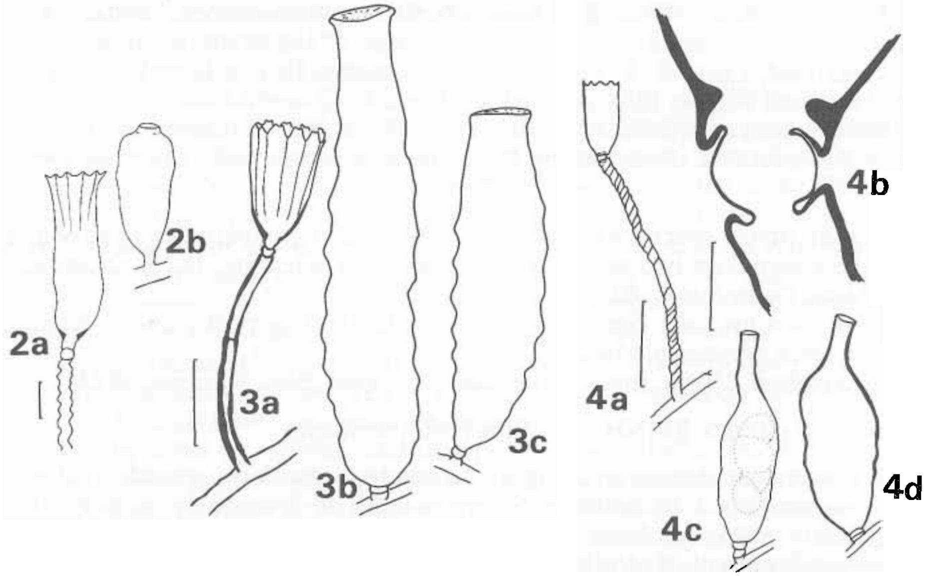
REMARKS. Millard (1975) summarized the doubts concerning the shape of the ♂ gonotheca, which it seems has not been reported before now. The BMNH series includes several colonies in which the gonothecal contents are preserved. The ♂ and ♀ gonothecae are identical, and are borne on separate colonies. The *contents* of the ♂ were described by Goette (1907) and are clearly gonomedusoid in Miller's (1973) terminology.

The name applied to the distinct but closely related nominal species *Campanularia laevis* Hartlaub (1905 : 565–567, pl. 1, based on Chile material) is a junior homonym of *Campanularia laevis* Couch, 1844 (see p. 65). I propose the name *Campanularia agas* nom. nov. for the Hartlaub species. *C. agas* was recently redescribed by Vervoort (1972 : 85–87, as *Campanularia laevis*). Both Hartlaub and Vervoort discussed similarities between *C. agas* (= *C. laevis* Hartlaub) and *C. hincksii*.

Hickson & Gravely (1907) referred additional material to '*C. laevis* Hartlaub', but Totton (1930) considered their material distinct. He referred it to a third nominal species, *Campanularia hicksoni* Totton, 1930. This was a species proposed to accommodate the material described by Hickson & Gravely, and also some collected by the 'Terra Nova'. It was discussed briefly by Rees & Thursfield (1965 : 90, as *Campanularia laevis* sensu Hickson & Gravely) and in detail by Stepanyants (1979 : 29).

Campanularia alta Stechow, 1919*a*, was based partly on new material from Villefranche and partly on some accounts of earlier authors. Stechow's material had young male gonothecae characteristic of *C. hincksii*, but he illustrated a hydrotheca more typical of *Clytia hemisphaerica*. However, the earlier descriptions included (i.e. those of Billard, 1907; Goette, 1907; Broch, 1912*b*) seem undisputedly of *C. hincksii*. Hence I concur with Broch (1933) and Vervoort (1946*a*) in regarding *C. alta* conspecific, and not with Picard (1951*a*, 1955) who maintained it distinct.

Campanularia macrotheca Leloup, 1930*a*, based on material from Monaco, was justifiably referred to the present species by Patriti (1970).



Figs 2–4 **Fig. 2** *Campanularia crenata.* (a) hydrotheca and (b) ♀ gonotheca, Greenland, 1896.8.15.2. Scale 500 μm. **Fig. 3** *Campanularia hincksii.* (a) hydrothecal pedicel and part of stolon. The pedicel is unusually short for the species. Note the irregular thickening. W Norway, 30–40 m. (b) ♀ and (c) ♂ gonothecae, sexes identified from contents. W Scotland, 90 m, July 1966; 1967.12.1.16 and .10 respectively. The ♀ gonotheca is unusually long. Scale (a–c) 500 μm. **Fig. 4** *Campanularia volubilis.* (a) hydrotheca and pedicel, 30–40 m, nr Bergen, 15 August 1962; 1962.11.7.6. Scale 500 μm. (b) vertical optical section through (a), showing flexible region. Scale 50 μm. (c–d) two gonothecae, one with ova, from a single colony, Shetland; 1912.12.21.55. Scale as (a).

Campanularia volubilis (Linnaeus, 1758)
(Fig. 4)

Corallina minima scandens, vesiculas campaniformes in summo caule lineari contorto gerens. Ellis, 1755 : 24–25, pl. 14, figs A, a.

Sertularia volubilis Linnaeus, 1758 : 811; Linnaeus, 1767 : 1311; (*non* Pallas, 1766 : 122, junior homonym, = *Calycella syringa* (Linnaeus, 1767), see also Cornelius, 1978; *non* Ellis & Solander, 1786 : 51, pl. 4, figs E, e, F, f, = *Clytia hemisphaerica*, see p. 70).

Sertularia uniflora Pallas, 1766 : 121–122 (nom. nov. pro *S. volubilis* Linnaeus, 1758; see pp. 77–78); (non Ellis, 1768 : 434, pl. 19, fig. 9, = *Clytia hemisphaerica*, see p. 78).

Campanularia volubilis: Alder, 1857 : 125–126, pl. 4, fig. 7; Hincks, 1868 : 160–162, pl. 24, fig. 2 (non Hincks, 1852, nec Du Plessis, 1871, = *Clytia hemisphaerica,* see p. 70).

Campanularia groenlandica Levinsen, 1893 : 168, pl. 5, figs 10–12; Naumov, 1960 : 252–253, fig. 139; Naumov, 1969 : 273–274, fig. 139; see Remarks.

non *Clytia volubilis:* Hargitt, 1909 : 373–374 (= *C. hemisphaerica*, see p. 78).

Clytia mollis Stechow, 1919*a* : 44–45, fig. L (?syn. *Clytia laevis* Weismann, 1883).

Campanularia brachycaulis Stechow, 1919*a* : 62–63, fig. T.

NOMENCLATURE. Further synonymies were given by Bedot (1901–1925), Vervoort (1946*a*) and Naumov (1960, 1969) among others.

TYPE MATERIAL AND LOCALITY. Linnaeus (1758) gave only Ellis' (1755) illustration as indication. As with some other hydroids (Cornelius, 1979 : 309, notes 11–14) Linnaeus apparently based the designation on Ellis' plate and not on specimens. Almost certainly the material now in the Linnaeus collection in the Linnean Society of London (Savage, 1945 : 206) reached Linnaeus after the original description was published and cannot be regarded as type (Cornelius, 1975*a* : 273, footnote). The material collected and described by Ellis [infertile colony on *Hydrallmania falcata* (Linnaeus, 1758); Brighton, Sussex, England, June, 1754; illustrated, Ellis, 1755 : pl. 14, figs A, a] can thus be considered type. Although some hydroid material of John Ellis survived until recently it seems that only a single specimen (of *Nemertesia* sp.) escaped destruction during World War II (Cornelius, 1975*a* : 267, footnote) and the specimen illustrated by Ellis can be assumed lost. The type locality is Brighton.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia groenlandica* Levinsen, 1893, infertile syntype material on two pieces of *Lafoea dumosa* (Fleming, 1820), in spirit, exch. Copenhagen Mus., Davis Strait, '80 fms'; 1896.8.15.1.

Campanularia brachycaulis Stechow, 1919*a*, infertile fragments on 2 microslides, Villefranche; Munich Zoological Mus.

Clytia mollis Stechow, 1919*a*, small fertile colony on weed, Sète, S France; MZM.

OTHER MATERIAL EXAMINED. BMNH collection, *c.* 60 specimens.

DESCRIPTION. Colony comprising creeping stolon bearing irregularly spaced, erect, straight pedicels each supporting a hydrotheca. Stolon smooth to irregularly spirally grooved. Pedicels apparently always unbranched, smooth to spirally grooved throughout; subhydrothecal spherule present. Hydrotheca tubular, tapering abruptly basally; rim with 10–12 shallow blunt cusps; sometimes with fine longitudinal striae associated with the cusps. Gonothecae scarce, ♂ = ♀, on short pedicels; flask-shaped, smooth, aperture at end of neck of indefinite length; neck forms after body of gonotheca; on stolon or (Hincks, 1868) on hydrothecal pedicels.

DISPERSIVE STAGE. Planulae, brooded in the ♀ gonotheca. There is no medusa stage.

REPRODUCTIVE SEASON. Apparently the only published information is of a fertile specimen off Norfolk, 16 June, 1951 (Hamond, 1957). None of the dated specimens in the BMNH is fertile. Possibly reproduction in this species is usually vegetative. Hamond found fertile material just once, and only a few of the BMNH specimens have gonothecae.

DISTRIBUTION. Common from southern England northwards, but probably present in scattered localities further south. Not recorded from NW France or Belgium, nor reliably from the Netherlands (Teissier, 1965; Leloup, 1952; Vervoort, 1946*a*). However, the species is well known from the south coast of England (Ellis, 1755; Marine Biological Association, 1957). Vervoort (1949) recorded a single specimen from the Channel Isles but was 'unable to trace records along the NW coast of France'. There are some records from the Mediterranean Sea (Stechow, 1923*a*; Riedl, 1959; Naumov, 1969) but Picard (1958*b*) excluded the species from his faunal list. There is a record from N Spain (Santander; Rioja y Martín, 1906) and another from Mauritania (Billard, 1931*a*); but in general there are few records further south than the British Isles.

Northerly records include: Iceland, numerous examples (Kramp, 1938); Greenland, widespread up to 72° N (Kramp, 1943); N Norway and N coast of Russia (Mathiesen, 1928; and Naumov, 1969, as *C. groenlandica*).

HABITAT. Both Mathiesen (1928, N Norway) and Naumov (1969, Russian seas) reported a usual depth range of 25–100 m, Naumov giving extreme limits of 5–250 m. Kramp (1943, Greenland) gave a range of 25–650 m.

Hincks (1868) stated the substrate to be other hydroids. All the BMNH material is on hydroids, especially *Tubularia larynx* (sens. auct., e.g. Hincks, 1868), *Hydrallmania falcata* (Linnaeus, 1758) and *Abietinaria abietina* (Linnaeus, 1758), and other sertulariids. Although Couch (1844) reported material on the antennae of crabs and on a bivalve (*Pinna fragilis,* as '*P. ingens*'), his description of the gonotheca suggests his material was *Clytia hemisphaerica*. He evidently confused the two species.

REMARKS. Some nomenclatural confusion between the present species and *Sertularia uniflora* Pallas, 1766, is discussed below (pp. 77–78).

Rees & Thursfield (1965) suggested that *C. volubilis* might prove conspecific with *Rhizocaulus verticillatus* (p. 67). Their evidence was some similarity in the hydrothecae and gonothecae of the two species. However, the long BMNH series confirms the several constant differences. The linear dimensions of hydrothecae, hydrothecal pedicels, gonothecae and stolon diameters in *C. volubilis* are about half the same dimensions in *R. verticillatus*. And while none of the *C. volubilis* specimens has polysiphonic, erect stems these are present in all the *R. verticillatus* specimens. There is no intermediate material. Further, the perisarc tubes in *R. verticillatus* are nearly all parallel. Had the two forms been conspecific, colonies of *C. volubilis* s. str. with some aggregation of the perisarc tubes might have been found; but there are no such specimens in the BMNH series.

As noted by Hincks (1868) the distinction between *C. volubilis* and the hydroid stage of *Clytia hemisphaerica* was overlooked by Johnston (1847), but recognized soon afterwards by Alder (1857). Couch (1844) also confused the two.

Confusion between *C. volubilis* and the species now called *Calycella syringa* (Linnaeus, 1767) occurred in the mid-eighteenth century but was resolved by Linnaeus (1767) himself. Essential details are given in the above synonymy, and further discussion in Cornelius (1978). The species is currently referred to the family Campanulinidae.

Campanularia groenlandica Levinsen, 1893, although widely recognized, was apparently founded on *C. volubilis* material from the Davis Strait. Syntype material in the BMNH shows features present in the original illustrations of *groenlandica*, for example spirally sculptured hydrothecal pedicels and blunt cusps on the hydrothecal rim; and the gonotheca shown in the original illustration is identical with that normal in *C. volubilis*. Thus the two taxa appear conspecific. Material has been recorded as *C. groenlandica* from Trondheim Fjord (Mathiesen, 1928) north to 68° 20′ N (Kramp, 1943; 50–525 m depth); and Naumov (1969) recorded '*C. groenlandica*' from the N coast of Russia.

The type material of *Clytia mollis* Stechow, 1919*a*, examined here, comprises immature colonies of *C. volubilis*. Stechow's original illustration incorrectly shows a truncate, wide mouthed gonotheca. It is simply a young one in which the long neck has yet to form. The hydrothecal pedicels illustrated are topped by sub-hydrothecal spherules not present in *Clytia*. Stechow tentatively included in the synonymy of '*C. mollis*' the nominal species *Clytia laevis* Weismann, 1883, based on Naples material. However it is clear from Weismann's description that *C. laevis* was founded on normal *Clytia hemisphaerica* material, and it is here referred to that species.

Genus ***ORTHOPYXIS*** Agassiz, 1862

Clytia: Westendorp, 1843 : 23 (part; see Remarks under *Orthopyxis integra*).
?*Silicularia* Meyen, 1834 : 206 (?part; see Remarks and p. 50).
Campanularia: Macgillivray, 1842 : 465 (part); Couch, 1844 : 40 (part); Hincks, 1868 : 160 (part); Millard, 1975 : 203 (part); (see Remarks below, and under *O. integra*).
Clytia (*Orthopyxis*) Agassiz, 1862 : 297.
Clythia Agassiz, 1862 : pl. 28 (lapsus for *Clytia*).
Orthopyxis Agassiz, 1862 : 355; Ralph, 1957 : 834; Arai & Brinckmann-Voss, 1980 : 101.
Hincksia Agassiz, 1862 : 355 (sic).
Eucopella von Lendenfeld, 1883*a* : 188.
Agastra Hartlaub, 1897 : 452 (nom. nud.), 504; Kramp, 1961 : 160.
Leptomedusa Browne, 1900 : 714 (see notes on Nomenclature under *O. integra*).

TYPE SPECIES. *Clytia* (*Orthopyxis*) *poterium* Agassiz, 1862; by monotypy; may be conspecific with *O. integra*. *Orthopyxis* was introduced by Agassiz as a subgenus of *Clytia* on page 297 of his work, comprising the 'new' species *poterium* alone; but on page 355 he upgraded it to genus. On that page he implicitly used the combinations '*Orthopyxis* (*Orthopyxis*) *poterium*', '*Orthopyxis* (*Campanularia*) *volubiliformis*' and '*Orthopyxis* (*Laomedea*) *integra*' (of various authors). Thus *poterium* should rightly be taken as type species by monotypy of the subgenus *Orthopyxis* Agassiz, 1862. Nutting's (1915 : 63) designation of *Campanularia caliculata* Hincks, 1853, as type species must be disregarded since *caliculata* was not originally included. It was unfortunately repeated by Arai & Brinckmann-Voss (1980).

DIAGNOSIS. Campanulariidae forming stoloniferous or short unbranched upright colonies; stolon anastomosing; true diaphragm absent; hydrotheca fundamentally radially symmetrical but often asymmetrically thickened; medusa reduced, lacking manubrium and tentacles, not feeding, believed facultatively retained in at least one species.

REMARKS. The genera *Silicularia* Meyen, 1834, and *Hypanthea* Allman, 1876*a*, are discussed on page 50.

Ralph (1957) listed some works in which *Orthopyxis* was discussed in relation to *Eucopella* von Lendenfeld, 1883*a* (based partly on *Campanularia bilabiata* Coughtrey, 1875); and other discussion was provided for example by Bale (1914), Nutting (1915) and Fraser (1918). The species *Eucopella campanularia* was described in greater detail in another paper (von Lendenfeld, 1883*b*). Bale, Ralph and others referred *Eucopella* to *Orthopyxis*; but Hirohito (1969) held the two genera distinct on the presence or absence respectively of marginal vesicles in the (retained) 'eumedusoid'. He referred *caliculata* Hincks, 1853, to *Eucopella*, stating an intention to discuss the generic question later. However, *caliculata* is here referred to *O. integra*; and generic separation seems unjustified. I provisionally follow several previous authors in regarding *Eucopella* congeneric. However, Kramp (1961) accepted the genus and included in it the two species *bilabiata* Coughtrey, 1875, and *crenata* Hartlaub, 1901. He designated *bilabiata* type species. The two species Kramp included may not be distinct: they are treated here under *O. crenata* (p. 60). Kramp's generic separation, from the 'medusa' genus *Agastra*, was based on minor differences in the medusa and is not upheld here.

The genus *Hincksia* Agassiz, 1862, was proposed to accommodate solely the well described species *Campanularia tincta* Hincks, 1861*a*; but Bedot (1910 : 311), Stechow (1923*a* : 94) and Rees & Thursfield (1965 : 93) referred the genus to *Campanularia* auct. In proposing the genus Agassiz stated merely 'The genus *Hincksia* is characterized by its one-sided, ringled, fertile hydra', hardly an acceptable diagnosis. Nevertheless, type material of *C. tincta* is available (BMNH reg. no. 1899.5.1.219–220), as noted by Rees & Thursfield. Although dry the material shows the characters of the genus *Orthopyxis* Agassiz, 1862, and *Hincksia* and *Orthopyxis* (not *Campanularia*) can be regarded congeneric. Under the first reviser principle I retain *Orthopyxis*, which has been widely used, and suppress *Hincksia*, which has not. *O. tincta* is an Australian species and so is outside the present scope, but it may be noted in passing that the type material has an anastomosing stolon like *Orthopyxis* s. str. and a highly distinctive, closely ringed gonotheca. Useful synonymies of the species were provided by Nutting (1915), Stechow (1923*a*) and Rees & Thursfield (1965), and a redescription by Stepanyants (1979). *Campanularia tincta* sensu Warren, 1908, is mentioned here under *C. africana* Stechow, 1923*d*, a junior synonym of *O. crenata* (p. 60).

The genus *Agastra* Hartlaub, 1897, was based on Helgoland material of the medusa stage of *Orthopyxis integra* (see also p. 67). Kramp (1961) resurrected the genus but there seems no doubt that its synonymy with *Orthopyxis* is justified.

Orthopyxis crenata (Hartlaub, 1901)
(Fig. 5)

?*Campanularia bilabiata* Coughtrey, 1875 : 291–292, pl. 20, figs 46–49.

?*Campanularia everta* Clarke, 1876 : 251, 253–254, pl. 39, fig. 4; Garcia Corrales *et al.*, 1978 : 24–25, fig. 9 (syn. *C. lennoxensis* Jaderholm).

Eucopella crenata Hartlaub, 1901 : 364–366, pl. 22, figs 27–31, 33–35; Hirohito, 1969 : 7, fig. 7.

?*Campanularia lennoxensis* Jaderholm, 1904*b* : 268–269, pl. 12, figs 4–5.

Campanularia ?intermedia Stechow, 1919*a* : 66–68, fig. V.

?*Orthopyxis delicata* Trebilcock, 1928 : 3, pl. 2, fig. 1; Garcia Corrales *et al.*, 1978 : 22–23, fig. 8.

Campanularia crenata forma *intermedia:* Picard, 1951*a* : 345.
Campanularia crenata: Picard, 1955 : 186; Millard & Bouillon, 1973 : 47–48, fig. 6B–F; Millard, 1975 : 204–206, fig. 68A–F (?syn. *Orthopyxis delicata* Trebilcock, 1928); Garcia Corrales *et al.*, 1978 : 19–22, fig. 7; (non Allman, 1876*b*).
Orthopyxis crenata: Trebilcock, 1928 : 3; Ralph, 1957 : 838–840, fig. 6g–v (syn. *O. formosa* Trebilcock, 1928); Rees & Thursfield, 1965 : 104.

TYPE MATERIAL AND LOCALITY. The species was based partly on material from French Pass, Bare Island, New Zealand, and partly on the original description of *Campanularia bilabiata* Coughtrey, 1875. I have located none of the type material. Ralph (1957) restricted the type locality to French Pass.

MATERIAL EXAMINED. I have seen no Atlantic material of this species.

DESCRIPTION AND IDENTIFICATION OF HYDROID STAGE. The lack of available material of this species and the taxonomic confusion surrounding the whole genus together make redescription difficult. The following identification notes are adapted from Ralph (1957), Millard & Bouillon (1973) and Millard (1975). Differing from *O. integra* as follows: hydrothecal rims smooth through gently wavy to crenate, with 8–12 short rounded cusps, commonly varying within a colony (always smooth in *O. integra*); hydranth with *c.* 14 tentacles (> 20 in *O. integra*: Ralph, 1957; but see p. 40). Other reported differences seem invalid (but see Dispersive stage).

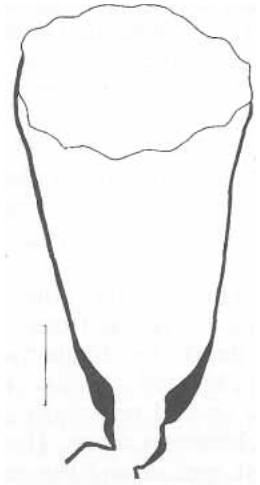


Fig. 5 *Orthopyxis crenata.* Hydrotheca, Port Phillip, Australia, intertidal; 1959.10.1.1. Scale 10 μm.

Variation. Ralph (1957) and Millard (1975) indicated that the variation in *O. crenata* parallels that in *O. integra* (p. 63).

DISPERSIVE STAGE. A medusa. By homology with *O. integra* it might be expected that the medusa is short lived and does not feed. Hirohito (1969) described newly released medusae. The umbrella was sub-spherical (0·5 mm high, 0·6 mm wide). There was a distinct velum, 4 broad radial canals and 8 statocysts; but no tentacles or stomach. Published descriptions suggest that the medusa of *O. integra* differs in being proportionately taller.

REPRODUCTIVE SEASON. Fertile material recorded early March near Marseille (Stechow, 1919*a*).

DISTRIBUTION. From N coast of Spain (Garcia Corrales *et al.*, 1978, as *Campanularia everta*) and Mediterranean Sea southwards (S France, Stechow, 1919*a* as *C. intermedia*; Picard, 1951*a*, 1958*b*; Millard, 1975; Algeria, Picard, 1955; S Spain, Garcia Corrales *et al.*). Widely distributed in warmer parts of all oceans (Millard). Cape Verde Islands (Rees & Thursfield, 1965).

HABITAT. On *Posidonia* (eel grass) and Bryozoa (Millard & Bouillon, 1973, Seychelles); intertidal to about 3 m (Millard, 1975, southern Africa); 1–20 m, Spain (Garcia Corrales *et al.*, 1978). *Campanularia africana* sens. Buchanan (1957), possibly conspecific, came from 14 m off Ghana (see Remarks).

REMARKS. Authors who have placed this species in the genus *Campanularia* have apparently overlooked the senior homonym *Campanularia crenata* Allman, 1876*b* (see p. 52). If the present species is again referred to *Campanularia* another specific name would be required, and one of the names discussed by Hartlaub (1901) might be available.

Hartlaub thought *O. crenata* (Hartlaub) close to *Eucopella campanularia* von Lendenfeld, 1883*a*, *b*, and 'identical with' *Campanularia bilabiata* Coughtrey, 1875. Ralph (1957), however, treated '*Orthopyxis crenata*' and '*Silicularia bilabiata*' under different genera. In this Ralph was unwise since *crenata* Hartlaub was, in part, a nom. nov. for *bilabiata*. The name *bilabiata* might prove to be available for the present species but to avoid further confusion *crenata* is retained pending a review of the whole genus. See also the notes on *Eucopella* (p. 58).

Picard (1958*b*) recorded the nominal species *Orthopyxis everta* (Clarke, 1876, as *Campanularia*, based on Californian material) from 'the Mediterranean'. The original description resembles the present species, and the two might prove conspecific; but I have seen type material of neither. Ralph (1957) separated them on the structure of the gonotheca. If a synonymy were propsed *everta* might take priority for the present species but *C. bilabiata* Coughtrey is still older. Vervoort (1972 : 87) redescribed '*O. everta*' recently and gave further synonymy.

The nominal species *Campanularia ?intermedia* Stechow, 1919*a*, was based on material from Marseille. I have not located type material but the vegetative characters given in the description seem identical with those of the present species as currently understood. As suggested by Stechow, and also by Garcia Corrales *et al.* (1978), *C. lennoxensis* Jaderholm, 1904*b*, is probably conspecific.

Campanularia africana Stechow (1923*d*: 104, nom. nov. pro *C. tincta* sensu Warren, 1908, from Natal; non *C. tincta* Hincks, 1861a, from 'Australia', see p. 58) was recorded from Takoradi, Ghana at 14 m depth by Buchanan (1957). *O. africana* has been distinguished from *O. crenata* by Millard (1975), who redescribed both, mainly on gonothecal characters; and from the several reportedly endemic South African species she recognized on variations in these characters alone. However, the relatively poor original descriptions of most of the nominal species and the general taxonomic confusion in the genus make it unwise to accept Buchanan's record without further evidence. It is the only record of *O. africana* from north of the equator.

Discussion of the non-Atlantic nominal species of *Orthopyxis* having crenate hydrothecal margins was provided by Ralph (1957).

Millard (1975) provisionally referred *Orthopyxis delicata* Trebilcock, 1928, to the present species; and it seems likely that *O. delicata* sensu Garcia Corrales *et al.* (1978; N & S Spain) is similar.

Orthopyxis integra (Macgillivray, 1842)

(Fig. 6)

?*Clytia undulata* Lamouroux, in Freycinet, 1824 : 617–618, pl. 94, figs 4–5.

Campanularia integra Macgillivray, 1842 : 465; Johnston, 1847 : 109, pl. 28, fig. 2 (syn. *C. laevis*: Saunders, in Johnston, 1847); Hincks, 1868 : 163–164, pl. 31, fig. 1; Levinsen, 1893 : 168–169, pl. 5, figs 14–18 (syn. *C. caliculata* Hincks; *C. gracilis* Allman, 1876*b*); Broch, 1918 : 159–162 (syn. *C. compressa* Clarke; *C. ritteri* Nutting, 1901*a*); Vervoort, 1946*a* : 274–276, figs 120–121 (syn. *C. laevis* Couch; *C. caliculata* Hincks; *C. breviscyphia* Sars; *Clytia* (*Orthopyxis*) *poterium* Agassiz; *Laomedea repens* Allman); Millard, 1975 : 208–211, fig. 69 (syn. *C. caliculata* Hincks; *C.

compressa Clarke; *Agastra mira* Hartlaub; *Agastra rubra* Behner; ?*Campanularia gracilis:* Stechow, 1925).

Clytia ryckholtii Westendorp, 1843 : 23–24, pl. 1, figs e, f.

Campanularia laevis Couch, 1844 : 42; Gosse, 1855 : 25; (non *C. laevis* Hartlaub, 1905 = junior homonym).

Capsularia integra: Gray, 1848 : 86 (?syn. *Campanularia laevis* Couch).

Capsularia laevis: Gray, 1848 : 87.

Campanularia caliculata Hincks, 1853 : 178–179, pl. 5, fig. B; Hincks, 1868 : 164–167, pl. 31, fig. 2 (syn. *C. breviscyphia* Sars; *Clytia* (*Orthopyxis*) *poterium* Agassiz.

Campanularia breviscyphia Sars, 1857 : 158–159, pl. 1, figs 12–13.

Clytia (Orthopyxis) poterium Agassiz, 1862 : 297–304.

Clythia poterium Agassiz, 1862 : pl. 28, figs 1–20, pl. 29, figs 1–5.

Orthopyxis poterium Agassiz, 1862 : 355.

Clytia posterior Wright, 1862 : 308 (lapsus pro *poterium* Agassiz).

Laomedea repens Allman, 1871 : 49, fig. 20.

?*Eucopella campanularia* von Lendenfeld, 1883*a* : 186–189.

Campanularia compressa Clarke, 1877 : 214, pl. 8, figs 5–6; Patriti, 1970 : 34–35, fig. 43 (syn. *C. platycarpa* Bale).

Campanularia borealis Marktanner-Turneretscher, 1890 : 206.

Campanularia integriformis Marktanner-Turneretscher, 1890 : 207, pl. 3, fig. 2.

'A leptomedusan' Browne, 1897 : 832, pl. 49, figs 3, 3a.

Agastra mira Hartlaub, 1897 : 452, 504–506, pl. 22, figs 5, 8–10; Mayer, 1910 : 234 (syn. *Campanularia caliculata* Hincks); Russell, 1953 : 303–306, pl. 19, fig. 1, text-figs 186–188 (syn. '*Leptomedusa* sp.' Browne; *Campanularia caliculata* Hincks).

Agastra caliculata: Browne, 1900 : 714–715 (syn. *A. mira* Hartlaub; *Leptomedusa* Browne).

Leptomedusa gen.? sp.? Browne, 1900 : 714.

Campanularia calyculata: Goette, 1907 : 193–204, pl. 15, figs 313–325 (syn. *Clytia poterium* Agassiz).

?*Agastra rubra* Behner, 1914 : 393–398, pl. 7, fig. 6, text-figs 8–10.

Orthopyxis compressa: Stechow, 1919*a* : 69, fig. Wa–b; Picard, 1951*b* : 110; Picard, 1958*a* : 2.

Orthopyxis asymmetrica Stechow, 1919*a* : 71–72, fig. Xa–e.

Clytia rijckholtii Leloup, 1947 : 22 (unjust. emend. pro *C. ryckholtii* Westendorp).

Orthopyxis caliculata: Ralph, 1957 : 838, text-figs 6a–f (syn. *O. macrogona* von Lendenfeld); Picard, 1958*b* : 191 (syn. *Campanularia integriformis* auct.; see Remarks).

Orthopyxis integra: Rees & Thursfield, 1965 : 103–104.

Eucopella caliculata: Hirohito, 1969 : 6–7, fig. 6.

NOMENCLATURE. An unjustified emendation of the nominal species name *caliculata*, to *calyculata*, was followed by several authors (listed in Bedot, 1918, 1925).

Browne (1897) described the medusa of the present species but did not identify it, calling it simply 'A Leptomedusa gen.? sp.?'. Evidently Browne did not then regard Leptomedusa a generic name; but he later (Browne, 1900) used it thus: '*Leptomedusa* gen.? sp.?', in a formal synonymy under '*Agastra caliculata* (Hincks, 1853)'. Nevertheless it seems in keeping with Browne's intentions not to regard *Leptomedusa* as part of nomenclature.

The widely used species name *integra* may prove to be threatened by an older but obscure name, *undulata*.

TYPE LOCALITY AND MATERIAL. Mouth of River Don, Aberdeen, Scotland; on *Tubularia indivisa* Linnaeus, 1758; material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia laevis* Couch, 1844, neotype, proposed herein.

Campanularia caliculata Hincks, 1853, colony on *Laminaria* sp. and the red alga *Phycodrys rubens* (L.) Batt. (det. J. H. Price), in spirit, nr Old Head of Kinsale, Co Cork, Eire, coll. R. Allman, syntype; 1853.4.7.16. Remainder of type series, from Pegwell Bay, E. Kent, England, coll. R. S. Boswell, not located. The type locality of *C. caliculata* was restricted to Pegwell Bay by Ralph (1957) but the Co Cork material remains part of the syntype series.

Orthopyxis asymmetrica Stechow, 1919*a*, infertile material on 2 microslides, Marseille; Munich Zoological Museum.

OTHER MATERIAL EXAMINED. BMNH collection, *c.* 50 specimens, mostly from the British Isles.

DESCRIPTION OF HYDROID STAGE. Colony a creeping hydrorhiza with single, irregularly spaced hydranths and hydrothecae on long pedicels and, separately, subsessile gonophores and gonothecae. Hydrorhiza smooth but sinuous, walls almost unthickened but often (Ralph, 1957; Millard, 1975) with a flat lateral flange of perisarc; branched frequently and (e.g. BMNH 1922.3.6.170, 1962.11.7.9) occasionally anastomosing. Hydrothecal pedicels usually narrower than hydrorhiza; walls usually much thickened; typically grooved with a smooth spiral; often 2–3 widely spaced shallow annuli near top; sub-hydrothecal spherule present; hydrotheca cup-shaped, length : breadth ratio variable; base wide to narrow, walls almost straight and diverging in narrower-based specimens; often flared near rim; walls thin to very thick, but rim region almost always unthickened; amount of thickening varying between adjacent hydrothecae and within a single hydrotheca (Fig. 6); rim even; small spherical chamber formed basally within hydrotheca by internal ring of perisarc. Hydranth with 20–30 tentacles (histological details in Agassiz, 1862; Stefani, 1956, 1959; Kawaguti, 1966; anatomical details of a possibly conspecific form in von Lendenfeld, 1883*b*). Gonotheca ♂ = ♀; broad, roughly parallel sided; truncated and slightly narrowing above, tapering more or less abruptly below; length usually $1\frac{1}{2}$–2x breadth, occasionally 5–6x (e.g. Allman, 1871 : fig. 20, as *Laomedea repens*; Vervoort, 1946*a* : fig. 120); usually laterally flattened but sometimes circular in transverse section; walls of gonotheca often thickened, sometimes much so; smooth through sinuous to deeply grooved spirally; aperture distal,

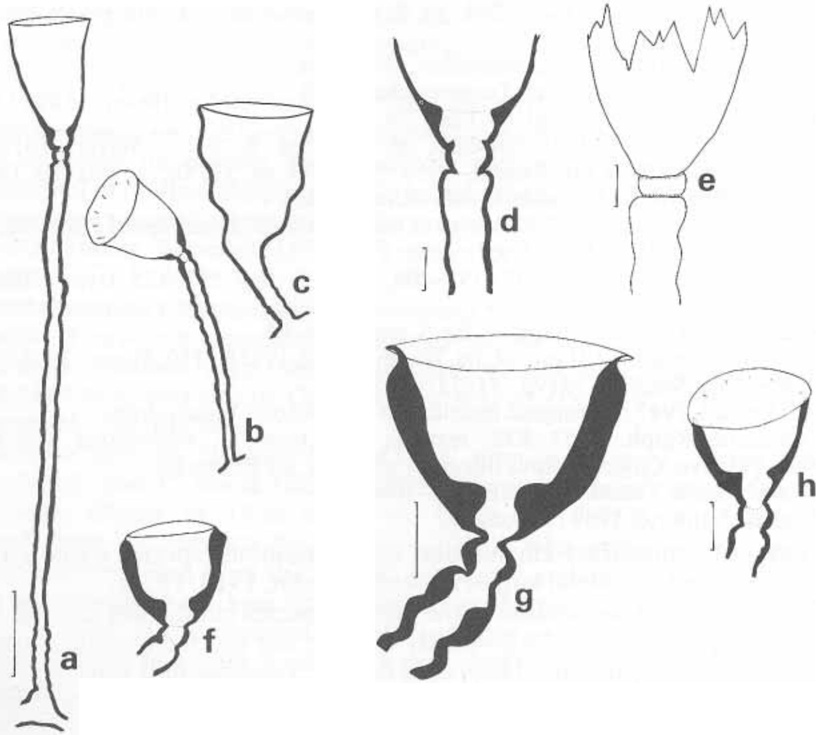


Fig. 6 *Orthopyxis integra.* (a–e) 15–25 m, Espegrend, W Norway, 13 April 1962; 1962.10.7.11. (a–b) adjacent hydrothecae with differing pedicel lengths. (c) gonotheca, sex unknown. (d–e) sub-hydrothecal spherule. (f–h) Knysna, Cape Province, Republic of South Africa, 1922.3.6.170. Scales: (a–c, f) 500 μm; (d–e) 10 μm; (g) 10 μm; (h) 10 μm.

nearly as wide as maximum diameter of gonotheca. Pedicel short to absent, usually unringed and grading into base of gonotheca (but see Fig. 6). Blastostyle with one well developed medusa, whether retained or released, and a second basal bud the fate of which seems unrecorded (see Dispersive stage). Present evidence suggets that medusae of either sex are sometimes retained. Nematocysts described by Östman (1979).

Variation in hydroid stage. See also the comments of Ralph (1957 : 838) and Millard (1975 : 209). Even among the Campanulariidae *O. integra* is unusually variable in morphology, and is unusual also in its habit of sometimes releasing and at other times retaining the medusa. Some of the variation may be genotypic, but the controlling factors are hardly known. Naumov (1969) referred colonies with thick walled hydrothecae to a variety, *caliculata* Hincks, 1853, which he considered grew only in strong currents; but although this relation seems logical he offered no proof. In his introductory sections (p. 123) he reported that hydrothecae of this species grow larger in cool water than in warm.

DISPERSIVE STAGE. Basically a short lived medusa. But this is often retained (as a gonomedusa), when the planula is the only motile stage. The free medusa was perhaps first described by Hartlaub (1897) from Helgoland, and shortly after by Browne (1897) working independently in SW Ireland. But von Lendenfeld (1883*a, b*) had earlier described a closely similar nominal species which may prove identical, from Australia ('*Eucopella campanularia*'; see Remarks); and Agassiz (1862, as *Clytia poterium*) had still earlier described planula release from retained medusae.

The medusa, when released, is degenerate and ephemeral. It lacks organs of feeding and survives only a few days. Umbrella height *c.* 1 mm, width *c.* 0·65 mm; jelly thick, velum broad; stomach, manubrium and mouth absent; four narrow radial canals each with lobed gonad midway along; no tentacles or marginal cirri (after Russell, 1953). Apparently only one medusa at a time is produced from each blastostyle. The medusae swim actively (Hartlaub, 1897) but are probably short lived since they are presumed not to feed. They are sexually mature on release and do not develop further (Russell, 1953).

Giard (1898) has often been thought the first to have linked the medusa to its hydroid but von Lendenfeld's (1883*b*) earlier work might have been on this species (see Remarks). Giard was certainly the first to record that the medusa is not always released. He has been misquoted but his paper was quite explicit. Giard thought that time of year influenced medusa release, and so did Behner (1914) who worked on the probably conspecific Mediterranean medusa *Agastra rubra* Behner, 1914. But Stefani (1959) recorded liberation in turbulent water and retention under calmer conditions. Millard (1975; pers. comm.), however, stated that medusa release had not yet been recorded in southern African populations (see also Remarks). The factors influencing release are still unclear.

The female gonophore was recorded by several of the earlier workers but the male was not described until the work of Stefani (1956) and Hamond (1963), again excepting the much earlier and largely overlooked work of von Lendenfeld (1883*b*) on the possibly identical Australian populations.

Some authors (Russell, 1953, quoted in Rees & Thursfield, 1965; Hamond, 1963) have interpreted the retained medusae as sporosacs, but current knowledge of the life cycle confirms that they are medusoid. Following Miller (1973) they can be called gonomedusae. The often reported 'second medusa bud' near the base of the blastostyle [e.g. von Lendenfeld, 1883*b*; Giard, 1898; Hamond, 1963 (♂); Hirohito, 1969 (♀); Millard, 1975 (♀); BMNH 1915.3.6.12 (♂); also in congeneric species, Ralph, 1957] corroborates Miller's theory of descent from a gonophore producing medusae. Evidently the ancestral form produced several medusae on each blastostyle but today only one is produced at a time.

REPRODUCTIVE SEASON. Free medusae recorded May–November in British waters (Russell, 1953); June–September in NW France (Teissier, 1965); December–February & July at Naples (Lo Bianco, 1909). Some authors, from Giard (1898) onwards, have considered that medusa release occurs only towards the end of the reproductive season and that gamete release from sessile medusae occurs earlier in the year; but precise dates are unrecorded.

Teissier (1965) found reproductive structures on the hydroid stage from May to October in NW France.

Distribution. Nearly cosmopolitan, occurring in all oceans from the intertidal to a little below Continental Shelf depths (at least in cold seas); and from the tropics to latitudes as high as 76° 40′ N (Greenland). The species is one of the most widely distributed of all hydroids. Noteworthy records from the eastern North Atlantic include: E & W Greenland (Kramp, 1929, 1943), N Norway (Mathiesen, 1928), Greece (Yamada, 1965), Black Sea (Manea, 1972; possibly also Naumov, 1960, 1969, as *Campanularia integriformis*, see Remarks), Morocco (Patriti, 1970, as *Campanularia compressa*), Ghana (Buchanan, 1957), Senegal (Leloup, 1939), Cape Verde Is (Ritchie, 1907); and the range of the species extends at least to the southernmost tip of Africa (Millard, 1975).

However, there are gaps in this wide distribution. Broch (1928) thought the species to be absent from the Kattegat, Skagerrak and Baltic, and Stechow (1927) from the Baltic alone; but Kramp (1935) and Jägerskiöld (1971) recorded it from W Sweden. Apparently there are still no records from the Baltic Sea. The species evidently did not occur in the Zuider Zee (Hummelinck, 1936) and has probably never been reliably recorded from Dutch waters (Vervoort, 1946*a*). However, it is sometimes washed ashore on the Belgian coast (Leloup, 1952).

Similarly, Irish Sea and W Scottish records are few: Bardsey I, Wales (Knight-Jones & Jones, 1956), Isle of Man (Bruce, Colman & Jones, 1963), Isle of Cumbrae, Clyde Sea (Chopin, 1894; Rankin, 1901), 10 m depth in Cregan Narrows, Loch Creran, Argyll (C. Edwards colln, pers. comm.). Chumley (1918) recorded no Clyde Sea material; and Stephens (1905) gave only a few Irish localities: Belfast, Dublin and Co Cork, the last including some of the syntypes of *Campanularia caliculata*. Possibly the only record from the west coast of Ireland is from Valencia I, Co Kerry (Browne, 1900), incidentally one of the earliest descriptions of the medusa. Hincks (1868) and Russell (1953) similarly listed no records from the western coasts of Eire and Scotland but the species is small and may have been overlooked. Broch (1918) included the NW Irish and W Scottish coasts in the North Atlantic distribution but did not cite material and may have been guessing.

Lastly, Arai & Brinckmann-Voss (1980 : 103) thought the species might not occur in British Columbia and Puget Sound.

Habitat. World depth data range from intertidal (e.g. Hincks, 1853, British Isles) through 300 m (Broch, 1918, Davis Strait) exceptionally to 470 m (Kramp, 1929, W Greenland). The deepest records are from cold waters. The species has been recorded on a wide variety of algae, hydroids, other animals and inorganic substrates, and there is no regular association. Mathiesen (1928) recorded *O. integra* on *Laminaria* sp. to depths of *c.* 100 m off Norway. Broch (1918) regarded the species as stenohaline, a view supported by the lack of records from the Baltic Sea and Zuider Zee.

Remarks. Several species closely related to *O. integra* were recognized by Ralph (1957), Millard (1975) and Gow & Millard (1975), and a world revision of the genus would be timely. Much discussion was provided by Arai & Brinckmann-Voss (1980).

O. integra itself is both variable and nearly cosmopolitan, and has consequently been described under many species names (*cf. Clytia hemisphaerica*, p. 73). The above synonymy includes only North Atlantic synonyms and main ones from other areas when they enter the discussion. The following notes on them are arranged in date order where possible.

Baster (1762 : pl. 2, fig, 7A, a) published some unidentified illustrations which Maitland (1876) referred to the present species. Vervoort (1946*a* : 276) regarded them as indeterminate, however, and I concur. They are discussed further under *Clytia hemisphaerica* (p. 78). Although Pallas (1766) arguably applied an earlier species name partly to Baster's illustrations, the later name *integra* is not threatened (but see the paragraph after next).

Clytia urnigera Lamouroux (1816 : 203, pl. 5, fig. 6), based on 'Australasian' material, was discussed by Couch (1844) when proposing *Campanularia laevis* Couch, a nominal species considered below. Couch noted a resemblance between the hydrothecae of *urnigera* and those of *laevis* but rightly pointed out that the narrow gonothecal aperture of *urnigera* contrasted with the wide aperture in *laevis*, and held them distinct. *C. urnigera* is here referred to *Clytia hemisphaerica* (p. 78); and *C. laevis* to *O. integra* (see below).

Clytia undulata Lamouroux, in Freycinet, 1824, was based on a fertile colony growing on 'marine plants' at Port Jackson, New South Wales. The species was regarded by Lamouroux as close to '*Clytia urnigera* Lamouroux', here referred to *C. hemisphaerica*. It was mentioned again only twice in the literature according to Bedot (1905), in 1824 and 1836, but no further taxonomic features were mentioned. *C. undulata* seems to be closer to the present species than to '*C. urnigera*' and *C. hemisphaerica*. It is mentioned here as it predates other *Orthopyxis* species and might prove conspecific with *O. integra*; but before it can be fully assessed more information is needed about the Australian populations of *Orthopyxis*.

Clytia ryckholtii Westendorp, 1843, was based on material from Ostend, Belgium. It was referred to *O. integra* by Billard (1914); and also by Leloup (1947) as '*C. Rijckholtii Slab.*'. Both Leloup's spelling and his reference to Slabber are wrong: Slabber (1769–1778) did not treat *O. integra* or anything similar. I have not located the type material; but Westendorp's illustrations show a reptant colony with long hydrothecal pedicels spirally grooved top and bottom each with an intervening smooth portion, and an even rimmed hydrotheca. They are the earliest illustrations of *O. integra* yet identified—but those of *Clytia undulata* Lamouroux, in Freycinet, 1824, which might prove conspecific, are earlier. The description of '*ryckholtii*' states the pedicels to be 3 mm long and mentions an even rimmed hydrotheca, confirming the identification. A rare and later work by Westendorp (1853) on Belgian zoophytes was illustrated by actual specimens. Had *C. ryckholtii* been included the specimens might have been types; but it was not (see note 1, p. 123), and I agree with Billard (1914) that the type material is probably lost.

Campanularia intertexta Couch, 1844, was based on a mixed type series comprising *Lafoea dumosa* (Fleming, 1820) and an unidentified campanulariid which might have been *O. integra*. *C. intertexta* is now referred to *L. dumosa* (see p. 122) but the original illustration, which included the campanulariid, was one of the earliest of *O. integra*.

Campanularia laevis Couch, 1844, type locality Polperro, Cornwall, was implicitly referred to the present species by Johnston (1847). The type material may be have been preserved for a long time in the Royal Institution of Cornwall, Truro, but if present would have been destroyed by a flood in 1953 (Curator, Roy. Inst. Cornwall, pers. comm.). Johnston (1847) mentioned material sent to him by W. W. Saunders (BMNH reg. no. 1847.9.24.65, on a herbarium sheet). The material is labelled in Johnston's hand '*Campanularia laevis!* W. Wilson Saunders, Hastings, 1840' and a label has been glued on later, also in Johnston's hand, on which is written '*Campanularia integra*'. I concur with Johnston's later identification as *O. integra*. In the absence of the original type material I designate the specimen 1847.9.24.65 neotype of *C. laevis* Couch, 1844; and extend the type locality to comprise coastal waters of the south of England. I agree also with Johnston's suggestion that the original description of *C. laevis* Couch should be referred to *O. integra*; and with the tentative but similar opinion of Bedot (1905 : 157) that the two are conspecific. Gray (1848 : 86) too referred both the species *C. laevis* and the material just mentioned to *O. integra*; but, inconsistently, on the next page gave *C. laevis* Couch full specific rank. He did this under the genus name *Capsularia* Cuvier, 1797, now regarded a junior objective synonym of *Coryne* Gaertner, in Pallas, 1774 (see Cornelius, 1975*b* : 378). Turning to a later work, it seems that Hincks' (1868 : 164) Hastings record of Saunders' material refers to the same specimen. Since Johnston (1847) did not publish the locality it seem likely Hincks deduced if from Gray (1848), who did. The junior homonym *Campanularia laevis*, Hartlaub, 1905, is discussed under *Campanularia hincksii*, which that nominal species most resembles (p. 54).

Campanularia caliculata Hincks, 1853, is the main European synonym to have been applied to the hydroid stage. When proposing the nominal taxon Hincks in fact provided the first good description of the present species. Bedot (1918) recorded that Levinsen (1893) was the first to refer *caliculata* to *integra*. Several senior authors have accepted this synonymy (e.g. Broch, 1918; Kramp, 1935; Vervoort, 1946*a*; Millard, 1975) and examination of type and non-type BMNH material supports their view. Hincks (1853) stated clearly the differences from *integra* as he saw them. They were simply: a 'double' hydrotheca and pedicel (inaccurate observation of thick walled material) and a more gradual tapering of the hydrotheca in *caliculata* than in *integra* (a variable feature). Neither character is reliable (see the above description and the discussion by Millard, 1975 : 209–210). Russell (1953) drew attention to the gonothecal contents later illustrated by Hincks (1868 : pl. 31, figs. 1a, b) as *integra*. They seemed to be sporosacs, and Russell was not entirely ready to accept the synonymy. It then seemed plausible that there were two species, one with sporosacs and the other with facultatively released medusae. The question was resolved when Millard (1975) illustrated structures similar to those shown by Hincks and described release of gametes from them. Millard had not recorded medusa release in her area (southern Africa). Still, she commented 'In partly spent gonophores the medusoid structure can sometimes be seen and is best observed by dissecting the gonophore out of the gonotheca' (op. cit., p. 209). Evidently the sessile eumedusoids (called gonomedusae by Miller, 1973) resemble sporosacs closely and their medusoid nature is not easy to see. Hence Russell's point is answered, and synonymy seems in order.

Campanularia breviscyphia Sars, 1857, was referred to *C. caliculata* Hincks, 1853, by Hincks (1868), and to the present species by Vervoort (1946*a*).

Clytia (Orthopyxis) poterium Agassiz, 1862, was a nominal species apparently based on North American material. Agassiz' description was exceptionally detailed and beautifully illustrated, but he failed to consider the several related species already described from European waters (*integra, ryckholtii, laevis, caliculata, breviscyphia*). His account suggests strongly that his material was merely *O. integra*. Hincks (1868) and Bale (1914) summarily dismissed *poterium* as conspecific; but Agassiz' account remained the most detailed of the species for many years. It was the earliest of the medusa, albeit of retained specimens. The caption to the plates included the spelling '*Clythia*', an unjustified emendation of *Clytia*.

Laomedea repens Allman, 1871, was referred to the present species by Bedot (1910) and Vervoort (1946*a*), and I concur. The originally illustrated material was said to have come from Scotland (Allman, op. cit., p. 48) and comprised only a female gonophore of *O. integra*. The nominal species was apparently never described again. Allman later applied the same specific name to another taxon, *Hypanthea repens* Allman, 1876*a*, type locality Kerguelen Island (see also p. 50).

Campanularia gracilis Allman (1876*b* : 260, pl. 12, figs 5–6), from Japan, was referred to the present species by Levinsen (1893) but this was quite unjustified. The type material (BMHN reg. no. 1877.4.12.5) is clearly distinct and not closely related to *O. integra*. Stechow (1925 : 423, fig. 6) described new material of *C. gracilis* Allman but Millard (1975 : 208) provisionally referred it to *O. integra*. However, Stechow's illustration closely resembles the type material and Millard, like Levinsen, was apparently mistaken in uniting the two taxa. Yamada (1959 : 35) evidently regarded *C. gracilis* as valid but recorded no material apart from the type.

Campanularia compressa Clarke, 1877, based on the hydroid stage, was referred to the present species by Broch (1910, 1918) and Millard (1975), although Arai & Brinckmann-Voss (1980) regarded it distinct. Other material of *O. integra* was recorded under the species name *compressa* by Stechow (1919*a*, Villefranche), Picard (1951*b*, Senegal), Picard (1958*a*, Israel) and Patriti (1970, Morocco). See also the comments on *Agastra rubra* Behner, 1914, the corresponding nominal species based on the medusa, below.

Eucopella campanularia von Lendenfeld, 1883*a*, is discussed above (p. 60).

Campanularia borealis Marktanner-Turneretscher, 1890, was based on hydroid material from Spitzbergen. No illustration was provided. Linko (1911 : 164) referred the species to *O. integra* and I concur.

Campanularia integriformis Marktanner-Turneretscher, 1890, based on hydroid material from Trieste, seems the same as *O. integra.* Naumov (1960, 1969) briefly described specimens from the Black and Adriatic Seas as *C. integriformis* but this too was probably *O. integra.* If so, Naumov's report of *O. integra* in the Black Sea predates that of Manea (1972), who had claimed the first record. Picard (1958*b*) referred *integriformis* to *caliculata* Hincks, 1853, without comment but *caliculata,* too, is now referred to *integra.*

Agastra mira Hartlaub, 1897, based on Helgoland material, has been widely regarded as the first description of the *free* medusa of *O. integra.* Browne (1897) described the medusa from SW Eire in the same year, as an unidentified leptomedusan; but a footnote in Browne's paper comments on Hartlaub's account, which had presumably already appeared. Both accounts of the medusa might be predated, however, if the closely similar Australian nominal species *Eucopella campanularia* von Lendenfeld, 1883*a*, *b*, proves conspecific.

Several authors listed by Bedot (1918, 1925) applied the combination *Agastra caliculata* to the medusa stage.

Agastra rubra Behner, 1914, a medusa from the Mediterranean, was referred to *O. integra* by Stefani (1959) and Millard (1975) among others. Its nominal hydroid, *Campanularia compressa* Clarke, 1877 (see above), was referred to *O. integra* by Broch (1910, 1918); and both stages were so treated by Millard (1975). Kramp (1961), however, considering the medusa stage alone, held *A. rubra* distinct on the shape of the gonads. Further work seems necessary to resolve these different views, but the majority opinion is that *A. rubra* is invalid.

Finally, the type material of *Orthopyxis asymmetrica* Stechow, 1919*a*, from Marseille, was examimed and found merely to be *O. integra.* Philbert (1935*a*) described growth forms under this name.

Genus ***RHIZOCAULUS*** Stechow, 1919*b*

Sertularia Linnaeus, 1758 : 811 (part).
Campanularia Lamarck, 1816 : 112 (part); Hincks, 1868 : 160 (part).
Rhizocaulus Stechow, 1919*b* : 852; Stechow, 1919*c* : 16.
Verticillina Naumov, 1960 : 9, 115, 122, 269; Naumov, 1969 : 6, 115, 123, 291.

TYPE SPECIES. *Sertularia verticillata* Linnaeus, 1758; by original designation.

DIAGNOSIS. Campanulariidae forming erect, polysiphonic colonies; hydrothecae in whorls; no true hydrothecal diaphragm; sub-hydrothecal spherule present; no medusa stage.

REMARKS. Nutting (1915 : 28) designated *Sertularia verticillata* Linnaeus, 1758, type species of the genus *Campanularia* Lamarck, 1816, but for the reasons given under that genus (p. 51) I have applied to the International Commission on Zoological Nomenclature for that designation to be set aside (Cornelius, 1981).

Rees & Thursfield (1965) opposed the erection of a distinct genus to accommodate *verticillata* on the grounds that in *Lafoea* Lamouroux, 1821, family Lafoeidae, there are both stolonal and erect colonies; but colony habit does not have the same taxonomic value in all families, and the separation is upheld here.

Stechow (1919*b*) listed several nominal species in the genus but they may prove conspecific with *R. verticillatus.*

Rhizocaulus verticillatus (Linnaeus, 1758)
(Fig. 7)

Corallina ramosa, ramis singulis equisitiformibus in summis capillamentis contortis et verticillatim dispositis . . . Ellis, 1755 : 23–24, pl. 13, figs A, a.
Sertularia verticillata Linnaeus, 1758 : 811.
Campanularia verticillata: Lamarck, 1816 : 113; Hincks, 1868 : 167–168, pl. 32, fig. 1, 1a; Goette, 1907 : 179–189, pl. 14, figs 294–304, pl. 15, figs 305–306; Linko, 1911 : 188–200, fig. 35 (syn. *Clytia olivacea* Lamouroux, 1821).
Clytia olivacea Lamouroux, 1821 : 13, pl. 67, figs 1–2.
Campanularia verticellata Couch, 1842 : 49 (lapsus).

Campanulata verticillata: Agassiz, 1862 : 354, footnote (unjustified emendation of *Campanularia*).
Rhizocaulus verticillatus: Stechow, 1919*b* : 852; Stechow, 1919*c* : 16; Stechow, 1923*a* : 105–106.
Verticillina verticillata: Naumov, 1960 : 269–270, fig. 159; Naumov, 1969 : fig. 159.

TYPE MATERIAL AND LOCALITY. Linnaeus (1758) provided only a diagnosis of this species, implying that he did not see material (*cf.* Cornelius, 1979 : 309). Indeed, there is none in the Linnaeus collection held by the Linnean Society of London (Savage, 1945). Linnaeus (1758) cited only the illustration of Ellis (1755 : pl. 13, fig. A, but not fig. a), and the colony Ellis illustrated can be regarded as holotype. It was collected from the coast of Cumberland, NW England, to which the type locality can be restricted. The specimen is almost certainly now lost (Cornelius, 1975*a* : 267, footnote).

MATERIAL EXAMINED. BMNH collections, about 40 specimens. Some northerly material deserves mention: Barents Sea, 74° 8′ 50″ N, 30° 31′ 28″ E, 375 m, 1882, ex D'Arcy Thompson collection; 1956.10.23.180.

DESCRIPTION. Colony large, erect, occasionally and irregularly branched; stems polysiphonic with pedicels roughly in whorls, recalling the terrestrial horse-tail plants (*Equisetum* L.). Component perisarc tubes straight, parallel, each bearing straight, smooth or spirally grooved hydrothecal pedicels (sometimes annulated, e.g. Fig. 7) at approximately regular intervals. Hydrotheca bell shaped, sub-hydrothecal spherule present; rim with *c.* 12 blunt cusps. Gonotheca ?♂ = ♀, flask shaped, with neck of varied length; on short pedicel.

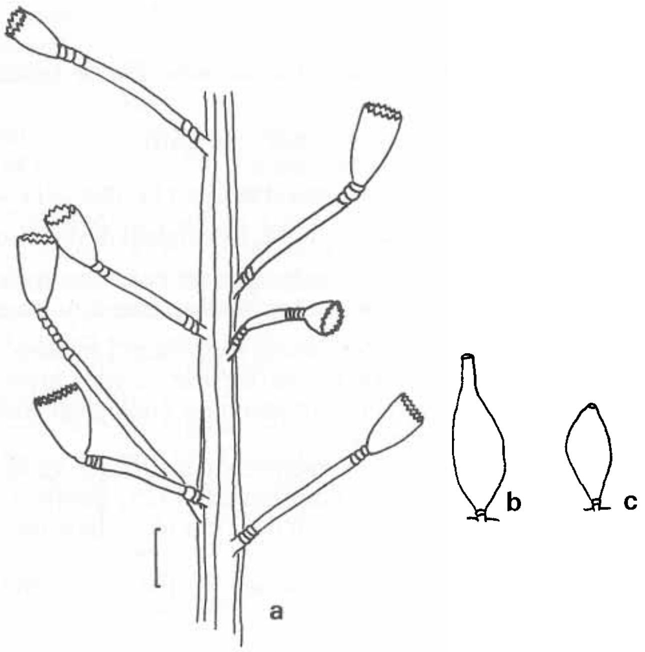


Fig. 7 *Rhizocaulus verticillatus.* (a) part of colony, Isle of Man, 25 March 1894; 1948.10.1.21. (b) gonotheca with long neck, 30–40 m depth, nr Bergen, 15 August 1962; 1962.11.7.8. (c) gonotheca with short neck, 45 m depth, W Scotland; 1888.4.2.39. Scale (a–c) 500 μm.

DISPERSIVE STAGE. Planulae, probably developing within the gonotheca. Early gonophore development was described by Goette (1907). No medusa.

REPRODUCTIVE SEASON. Fertile material recorded May, 1934, off NE England (H. O. Bull, in Evans, 1978); July, NW France (Teissier, 1965); 15 August, 1962, nr Bergen, Norway (BMNH reg. no. 1962.11.7.8).

DISTRIBUTION. Widespread in sublittoral and coastal waters from Tromso, Norway (Mathiesen, 1928) and Danmarks Havn, Greenland (Kramp, 1943) at least to Roscoff, NW France (Teissier, 1965). The species is well known from offshore areas of Britain, the Netherlands, Belgium, Denmark and Sweden. See also Material examined.

The status of *R. verticillatus* along the W coast of France and the Bay of Biscay is unclear. Vervoort (1946*a*) and Naumov (1969) recorded it but the species was not listed in several local faunal surveys (Billard, 1927; Nobre, 1931; Da Cunha, 1944, 1950; Fey, 1969) and there is no BMNH material from south of the English Channel. Picard (1958*b*) did not record the species from the Mediterranean Sea; but Manea (1972) provided an acceptable record from the Black Sea, possibly the farthest south the species has been found on European coasts.

HABITAT. Naumov (1969) gave a usual depth range of 50–200 m, with extremes of 15 m and 680 m. Mathiesen (1928) gave a range of 20 m to 600 m in S Norway.

Hamond (1957) associated the species with 'sandy grounds' off the Norfolk coast, but Teissier (1965) recorded it on algae in NW France. Hincks (1868) and Leloup (1952) found the species on pebbles and shells. *R. verticillatus* seems to occur typically on occasional solid substrates in otherwise sandy areas.

REMARKS. There seems no need for revision of this distinctive species. Rees & Thursfield (1965) drew attention to the superficial similarities between it and *Campanularia volubilis* (but see p. 57).

The development and structure of the compound stem of *R. verticillatus* was studied by Schach (1935).

The combination *Campanularia verticillata* var. *grandis* Hickson & Gravely, 1907, related to an antarctic species now known as *Stegella grandis* (Hickson and Gravely) and assigned to the Campanulinidae (e.g. Totton, 1930; Stepanyants, 1979). The similarity in colony form is striking but *S. grandis* lacks a sub-hydrothecal spherule and the hydrothecal rim is quite different.

Subfamily **CLYTIINAE** nom. nov.

Phialidae Haeckel, 1879 : 163 (part).
Phialinae: Mayer, 1910 : 232 (part).
Campanularinae: Russell, 1953 : 284.

DIAGNOSIS. Campanulariidae with a usually reptant, branched but not anastomosing stolon; with true hydrothecal diaphragm; usually without subhydrothecal spherule (but present in *Clytia hummelincki*); medusa present in some genera, a typical leptomedusa with prominent velum.

SCOPE. The genera *Clytia* Lamouroux, 1812; *Gastroblasta* Keller, 1883; and *Tulpa* Stechow, 1921*a*. *Gastroblasta* and *Tulpa* have not been recorded in the eastern North Atlantic and are discussed only under Remarks, but *Clytia* is treated below.

TYPE GENUS. *Clytia* Lamouroux, 1812.

REMARKS. Previous subfamily names applied in part to this group (Phialidae Haeckel, 1879; Phialinae Mayer, 1910) have been derived from *Phialium* Haeckel, 1897, the name of a genus now referred to the Lovenellidae (Mayer, 1910; Kramp, 1961). *Phialium* can be taken as type genus of the nominal subfamily Phialiinae; and there seems no available name for the present group.

There has no doubt been confusion between *Phialium* Haeckel and *Phialidium* Leuckart, 1856. *Phialidium* is today referred to *Clytia* Lamouroux, 1812, and basing a new subfamily name on *Phialidium* might be confusing. Haeckel (1879 : 186) indicated that he understood the relation between *Phialidium* and *Clytia* by including *Clytia johnstoni* sensu Böhm in the synonymy of *P. variable.* This relationship had only just been understood (p. 76) and Haeckel might have been reticent to consider all the nomenclatural implications.

The subfamily name Clytiinae is to be considered a nom. nov. applied to the present subfamily as restricted by Russell (1953) under the preoccupied name Campanulariinae. It should not be confused with family group names derived from *Clytus*, a coleopteran genus name. These are spelt Clytinae, Clytini and so on (C. R. Smith, pers. comm.), being derived from the root Clyt. The root from which Clytiinae is derived is Clyti.

The genus *Gastroblasta* Keller, 1883 : 622, is now restricted to a single, distinctive medusa species based on Red Sea material (Kramp, 1961). The name was once applied to species now referred to one or other of the *Clytia* species treated below (discussion on p. 72).

The genus *Tulpa* Stechow, 1921*a* : 254, was proposed to embrace three species none of which has been recorded from the eastern North Atlantic. The type species is *Campanularia tulipifera* Allman, 1888, by original designation (= *C. tulpifera* lapsus auct.). The genus was accepted by Totton (1930) who described another species. *Tulpa* was reviewed by Ralph (1957) and redefined by Stepanyants (1979); and discussed also by Vervoort (1972) and Gravier-Bonnet (1979) who gave systematic notes.

Genus *CLYTIA* Lamouroux, 1812

Medusa: Linnaeus, 1767 : 1096 (part).
Sertularia Ellis & Solander, 1786 : 51 (part).
Oceania Péron & Lesueur, 1810*a* : 343 (part).
Clytia Lamouroux, 1812 : 184.
Campanularia auct., part (see Remarks under *Clytia hemisphaerica*, p. 77).
Thaumantias Eschscholtz, 1829 : 102; Forbes, 1848 : 52 (part).
Silicularia Meyen, 1834 : 206 (part; see p. 50).
Eucope Gegenbaur, 1856 : 241 (part).
Phialidium Leuckart, 1856 : 18; Kramp, 1961 : 164.
Epenthesis McCrady, 1857 : 191; Haeckel, 1879 : 182.
Clytia (Trochopyxis) Agassiz, 1862 : 304.
Clytia (Platypyxis) Agassiz, 1862 : 306.
Clytea Wright, 1862 : 308 (lapsus pro *Clytia).*
Clythia van Beneden, 1866 : 166 (lapsus pro *Clytia*).
Gastroblasta auct., part (*non* Keller, 1883, s. str.).
Pseudoclytia Mayer, 1900 : 53.
Multioralis Mayer, 1900 : 54.
non *Clythia* Agassiz, 1862 : pl. 28 (lapsus pro *Clytia,* but referred to *Orthopyxis*, p. 57).

TYPE SPECIES. There were three species originally included in the genus, listed thus: '*Sertularia volubilis* Ellis, *S. syringa* Ellis, *S. verticillata* Ellis'. The descriptions cited are presumably those of Ellis & Solander (1786), in which book binominals were employed, and not those of Ellis (1755) which lacked them. The point is important since '*S. volubilis* sens. Lamouroux, 1812' was subsequently designated type species (see next paragraph). Confusion was caused when Lamouroux himself (in Lamouroux, Bory de Saint-Vincent & Deslongchamps, 1824 : 202) later applied the name *S. volubilis* to another species, citing therein the Ellis, 1755, illustration which in fact shows the species here called *Campanularia volubilis* (p. 55). Lamouroux' (1812) earlier citation, then, refers to *Sertularia volubilis* Ellis & Solander, 1786 [=the nominal hydroid species *Clytia johnstoni* (Alder, 1856*a*), usually regarded the same as the medusa *Clytia hemisphaerica* Linnaeus, 1767; see p. 77]; and the later citation (Lamouroux *et al.*, 1824), employing the same combination, refers to *Campanularia volubilis* (Linnaeus, 1758) (see p. 77 for further discussion).

The type species of *Clytia* might appear to be *Sertularia volubilis* Ellis & Solander, 1786 (non Linnaeus, 1758, see above), as designated by Mayer, 1910 : 262; but as just explained the combination is a junior homonym. This would be unimportant to current nomenclature if the hydroid *Sertularia volubilis* Ellis & Solander, 1786, were definitely known to be the same species as *Medusa hemisphaerica* Linnaeus, 1767. A relation is usually assumed (see notes under *Clytia hemisphaerica*, p. 79), and Linnaeus indicated Gronovius' (1760 : pl. 4, fig. 7) illustrated specimen, collected from Belgian waters (the type locality of *hemisphaerica*). The illustration shows a strongly convex exumbrella surface, suggesting *C. hemisphaerica* sens. auct. (e.g. p. 73); but the lingering doubts over the identity of the hydroid *C. gracilis* (Sars, 1850; see p. 78) make the relation of the two nominal species uncertain. Therefore, it is useful to establish a soundly based name for the type species of the genus *Clytia*. The earliest available name which can be unequivocally linked with *S. volubilis* sens. Ellis & Solander, 1786, is *Campanularia johnstoni* Alder, 1856*a*. Hence the correct name for the type species of *Clytia* is *C. johnstoni*. The often quoted synonymy with *C. hemisphaerica*, repeated below, is subjective. See also Cornelius (1981), and page 78 concerning the very similar '*Laomedea gracilis*' Sars, 1850.

DIAGNOSIS. Colonial Campanulariidae with free medusa stage; hydroid generation forming umbranched stoloniferous or branched upright colonies; hydrotheca with true diaphragm, rim sinuous to deeply indented with round to sharp clefts and cusps; diaphragm transverse; no sub-hydrothecal spherule; medusa hemisphaerical to flat, with hollow marginal tentacles, velum well developed; manubrium short; 4–8 marginal tentacles on release (in species so far studied), many tentacles in adult.

REMARKS. A summary of the species of *Clytia* in which the life cycles have been worked out was given by West & Renshaw (1970); and Roosen-Runge (1970) and Arai & Brinckmann-Voss (1980) gave detailed appraisals of several North American species.

Early generic names applied to the type species were broad in concept (*Sertularia volubilis* = *Medusa hemisphaerica* = *Campanularia johnstoni*) and the diagnosis of them by successive workers often overlapped. Hence it is not unexpected that species now included in *Clytia* s. str. should at one time or another have been included in one or more other genera. There is little value in discussing past uses of generic names such as *Medusa, Sertularia, Oceania* and *Campanularia* for species now referred to *Clytia*.

The name *Thaumantias* Eschscholtz, 1829, was also once widely used. It is a junior subjective synonym of *Clytia*, since Forbes (1848 : 41) nominated *Medusa hemisphaerica* Linnaeus, 1767, its type species. This medusa is, of course, widely held to come from the hydroid which is type species of *Clytia*; but the link is neverthless subjective and is likely to remain so as the original description of the medusa was brief.

The genus *Silicularia* Meyen, 1834, is discussed on page 50.

Availability of the generic name *Eucope* Gegenbaur, 1856, was discussed by Haeckel (1879), Mayer (1910), Rees (1939) and Russell (1953) among others. The four originally included species were referred to *Obelia* and *Clytia* (or *Phialidium*) by Mayer and subsequent authors; but so far as I can determine no type species has been designated. Russell (1953) referred three of the originally included species (*E. thaumantoides, E. campanulata* & *E. affinis*) to *Clytia hemisphaerica* (as *Phialidium*); and the remaining one (*E. polystyla*) is *Obelia* (e.g. following Cornelius, 1975*a*). I designate *E. affinis* Gegenbaur, 1856, type species of *Eucope*, which falls in the subjective synonymy of *Clytia* (see also Bedot, 1910 : 414 and Hincks, 1868 : 143).

The genus *Phialidium* Leuckart, 1856, was based on a single species, *P. viridicans* Leuckart (1856 : 18–19, pl. II, figs 12, 14) which is therefore type by monotypy. Mayer (1910) confirmed its type status, and Kramp's (1961) designation of '*P. hemisphaericum* L.' is incorrect. Russell (1953) drew attention to the close similarity between *P. viridicans* and *Clytia hemisphaerica*, including them in the same species synonymy. Thus the case for regarding *Clytia* and *Phialidium* congeneric is strong and *Phialidium*, being the later name, need no longer be used.

The genus *Epenthesis* McCrady, 1857, was referred to *Clytia* by Mayer (1910 : 261) and Nutting (1915 : 1) among others. The name is clearly a junior synonym of *Clytia*.

The subgenus *Platypyxis* Agassiz, 1962, was referred to *Clytia* by Bedot (1910), and I concur (see Remarks under *C. hemisphaerica*).

The genus *Gastroblasta* Keller, 1883, now includes just one species, from the Red Sea. All other uses of the generic name have related to abnormal medusae of *Clytia* species (Kramp, 1961; also Mayer, 1910, Kramp, 1957, 1965).

The genera *Multioralis* Mayer, 1900, and *Pseudoclytia* Mayer, 1900, were referred by Kramp (1957, 1961) to *Phialidium* Leuckart, 1856, and hence fall into *Clytia.*

Luminescence has long been known in the genus (e.g. Darwin, 1860 : ch. 2, hydroid stage; other references in Forbes, 1848, medusa stage). Light emission was probably first recorded in *Clytia* by Macartney (1810). In October, 1804, he demonstrated to an invited audience at Herne Bay, Kent, that flashing in the medusa of *C. hemisphaerica* (which he called *Medusa lucida*) was induced by raised temperature, electric shock and alcohol. His published illustration of the medusa is among the earliest of the genus.

Clytia discoida (Mayer, 1900)
(Fig. 8)

Oceania discoida Mayer, 1900 : 51, pl. 20, figs 53–55.
Phialidium discoidum Mayer, 1910 : 272, pl. 33, figs 9–11; Kramp, 1959 : 148, fig. 187; Kramp, 1961 : 165–166; Schmidt & Benovič, 1977 : 637.

TYPE LOCALITY. Tortugas, Florida; in plankton.

MATERIAL EXAMINED. None.

DESCRIPTION (after Mayer, 1910; Kramp, 1959; Schmidt & Benovič, 1977). Adult medusa 'quite flat' (Mayer), about 4 mm diameter; 16 short marginal tentacles with large basal bulbs; usually 3 statocysts between tentacle bases; velum well developed; 4 straight radial canals; gonads along almost whole length, eggs in ♀ unusually large and prominent; manubrium 'urn-shaped' (Mayer) with 4 recurved lips. Hydroid stage not recorded.

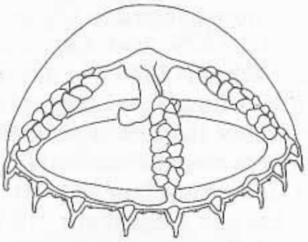


Fig. 8 *Clytia discoida.* Adult medusa. Diameter *c.* 4 mm. Redrawn after Mayer (1910 : pl. 33, fig. 10).

DISPERSIVE STAGE. The species is known from the medusa alone. See also notes under Dispersive stage of *C. linearis.*

REPRODUCTIVE SEASON. Summer; June–August (Mayer, 1900; Schmidt & Benovič, 1977).

DISTRIBUTION. Recorded from: Florida, Mexico, Brazil and W. Indies (references in Kramp, 1961); southern Adriatic Trough (once only, Schmidt & Benovič, 1977). Several records from the Pacific Ocean were discredited by Kramp (1961).

HABITAT. Coastal plankton.

REMARKS. The species is distinguished by its small size at maturity and by the extension of the gonads along almost the entire length of the radial canals. Kramp (1959, 1961) seems mistaken in stating the umbrella to be 'almost hemispherical'. Others have reported it nearly flat in the adult (Mayer, 1900, 1910; Schmidt & Benovič, 1977). However, younger stages are reportedly less flat (Mayer), but Schmidt & Benovič reported a young specimen only

1·5 mm in diameter which was already 'more flat than hemispherical'. The adult diameter is 4 mm.

The species is known in the NE Atlantic from a single Adriatic specimen (Schmidt & Benovič, 1977). Kramp (1961) provided a literature synopsis.

Clytia hemisphaerica (Linnaeus, 1767)

(Fig. 9)

Medusa hemisphaerica Linnaeus, 1767 : 1098; Müller, 1776 : 233.

Sertularia uniflora: Ellis, 1768 : 434, pl. 19, fig. 9.

Sertularia volubilis: Ellis & Solander, 1786 : 51, pl. 4, figs E, e, F, f (non *S. volubilis* Linnaeus, 1758; see p. 76 and Remarks).

Oceania flavidula Péron & Lesueur, 1810*a* : 345; Péron & Lesueur, ?1810*b* : 33.

Oceania hemisphaerica: Péron & Lesueur, 1810*a* : 347; Péron & Lesueur, 1810*b* : 35.

Clytia urnigera Lamouroux, 1816 : 203, pl. 5, fig. 6 (see Remarks under *Orthopyxis integra*).

Thaumantias inconspicua Forbes, 1848 : 52, pl. 8, fig. 3 a–d; Ritchie, 1911 : 31.

?*Laomedea gracilis* Sars, 1850 : 138; Sars, 1857 : 160, pl. 2, figs 1–3, 5 (but not fig. 4, = *Gonothyraea loveni*; see Stechow, 1923*a* : 111); (*non* Dana, 1846 = *Obelia dichotoma*).

Campanularia volubilis: (sens. Ellis & Solander) Hincks, 1852 : 84–85, pl. 3, fig. 5 (see Dispersive stage and Remarks).

Campanularia sp. Gegenbaur, 1854 : 154, 189, pl. 1, figs 8, 8a, 9.

Campanularia johnstoni Alder, 1856*a* : 359–360, pl. 8, fig. 8 (nom. nov. pro *Sertularia volubilis* Ellis & Solander, 1786).

?*Phialidium viridicans* Leuckart, 1856 : 18–19, pl. 1, figs 12, 14 (see pp. 71, 86).

?*Clytia noliformis* McCrady, 1857 : 194–195, pl. 11, fig 4; Fraser, 1944 : 144–145, pl. 26, fig 117 (syn. *C. simplex* Congdon).

Campanularia gegenbauri Sars, 1857 : 48–49.

Campanularia volubiliformis Sars, 1857 : 156 (nom. nov. pro *Campanularia* sp. Gegenbaur, 1854).

Campanularia raridentata Alder, in Hincks, 1861*b* : 292; Hincks, 1868 : 176–177, fig. 2.

Clytia (Trochopyxis) bicophora Agassiz, 1862 : 304–305, pl. 29, figs 6–9.

?*Clytia (Platypyxis) cylindrica* Agassiz, 1862 : 306–307, 354, text-figs 41–44, pl. 27, figs 8–9.

Clytea vicophora Wright, 1862 : 308 (unjustified emendation of *Clytia bicophora*).

Campanularia ?gigantea Hincks, 1866 : 297; Hincks, 1868 : 174–175, pl. 35, fig. 1; Jaderholm, 1909 : 19, 33, 69, pl. 7, figs 1–3.

Clytia johnstoni: Hincks, 1868 : 143–146, pl. 24, figs 1, 1a (syn. *Sertularia volubilis* Ellis & Solander; *Eucope campanulata* Gegenbaur; *E. thaumantoides* Gegenbaur; *E. affinis* Gegenbaur; *Campanularia gegenbauri* Sars; *Clytia bicophora* Agassiz; see Remarks); Böhm, 1878 : 167–171, pl. 2, figs 1–9 (syn. *Platypyxis cylindrica* Agassiz; *Eucope picta* Keferstein & Ehlers, 1861; *E. exigua* Keferstein & Ehlers, 1861; *E. variabilis* Claus; *E. gemmifera* Keferstein; *Thaumantias dubia* Kölliker; *T. thompsoni* Forbes; *T. convexa* Forbes); Billard, 1928 : 456–457 (syn. *C. raridentata* Hincks); Russell, 1953 : 293, fig. 179; Ralph, 1957 : 823–824, figs 1h–u, 3a–f (syn. *C. compressa* Totton, 1930).

Clytia volubilis: Du Plessis, 1871 : 167–170, pl. 2; Hargitt, 1909 : 373–374.

Clytia laevis Weismann, 1883 : 158–159 (see Remarks under *Campanularia volubilis*, p. 57).

Clytia flavidula: Metschnikoff, 1886*a* : 241–243, 257, 260, pl. 22, figs 9–10, 15.

Campanularia? serrulata Bale, 1888 : 757, pl. 12, fig. 4.

Campanularia raridentata var. Marktanner-Turneretscher, 1890 : 205, pl. 3, figs 3a–b.

Thaumantias hemisphaerica: Browne, 1896 : 480–482 (syn. *Medusa cymbaloidea* Slabber, 1775; *M. campanella* Shaw & Nodder, 1795; *M. lucida* Macartney, 1810; *Thaumantias lucida:* Lesson, 1843; *Epenthesis cymbaloidea* Haeckel, 1879).

Campanularia inconspicua: Calkins, 1899 : 349.

?*Campanularia attenuata* Calkins, 1899 : 350, pl. 2, figs 9, 9a–c, pl. 6, fig. 9d.

?*Campanularia edwardsi* Nutting, 1901*b* : 346, fig. 28.

?*Campanularia pelagica* Van Breemen, 1905 : 205–209, fig. 18.

Clytia simplex Congdon, 1907 : 471–472, figs 14–15.

Clytia obeliformis Stechow, 1914 : 128–129, fig. 6.

?*Clytia pelagica:* Billard, 1917 : 539–542, fig. 1.

?*Clytia serrulata:* Stechow, 1919*a* : 46–47, fig. M.

Campanularia acuta Stechow, 1919*a*: 54 (nom. nov. pro *C. raridentata* var. Marktanner-Turneretscher).
Campanularia ?attenuata Stechow, 1919*a* : 61–62, fig. S (non Calkins, 1899).
Campanularia brachycaulis Stechow, 1919*a* : 62–63, fig. T.
Orthopyxis volubiliformis: Stechow, 1919*a* : 70.
Campanularia villafrancensis Stechow, 1919*a* : 157 (nom. nov. pro *C. attenuata* Stechow, 1919*a* (sic) : 61, preoccupied).
Clytia uniflora: Stechow, 1923*a* : 111 (non *Sertularia uniflora* Pallas).
Thaumantias raridentata: Stechow, 1923*a* : 107–108, fig. 17.
Clytia villafrancensis: Stechow, 1923*a* : 109–110.
Clytia compressa Totton, 1930 : 146–148, text-fig. 6.
?*Phialidium bicophorum:* Thiel, 1935 : 172; Kramp, 1959 : 149; Kramp, 1961 : 164–165.
?*Laomedea pelagica:* Vervoort, 1946*a* : 285–288; Vervoort, 1959 : 313–315, fig. 55b–c; Vervoort, 1968 : 15–17, fig. 5; Vervoort, 1972 : 91–92, fig. 26c.
Laomedea gigantea: Leloup, 1952 : 161, fig. 93.
Phialidium hemisphaericum: Billard, 1928 : 457 (syn. *Thaumantias inconspicua* Forbes); Kramp, 1919 : figs 16–17 (syn. *P. temporarium* Browne, 1896; *Thaumantias buskiana* Gosse, 1853); Russell, 1953 : 285–294, pl. 16, fig. 1, pl. 17, fig. 6, text-figs 172–179 (syn. *Thaumantias pileata* Forbes, 1841; *T. sarnica* Forbes, 1841; *T. thompsoni* Forbes, 1841; *T. punctata* Forbes, 1841; *T. lineata* Forbes, 1848; *T. hemisphaerica*: Forbes, 1848; *T. inconspicua* Forbes, 1848, Hincks, 1868; *T. buskiana* Gosse, 1853; *Eucope affinis* Gegenbaur, 1856; *E. campanulata* Gegenbaur, 1856; *E. thaumantias* Gegenbaur, 1856; *Phialidium viridicans* Leuckart, 1856; ?*T. typica* Green, 1857; *Clytia johnstoni:* Hincks, 1868; *T. leucostyla* Spagnolini, 1876; *Campanulina acuminata* Böhm, 1878; *Epenthesis cymbaloidea* Haeckel, 1879; *P. variabile* Claus, 1881; *Clytia flavidula* Metschnikoff, 1886; *C. viridicans* Metschnikoff, 1886; *P. buskianum* Browne, 1896; *P. temporarium* Browne, 1896; *T. forbesi* Johansen & Levinsen, 1903; *Clytia volubilis:* Sverdrup, 1921; for these references see Russell, 1953); Kramp, 1955 : 256–257 (syn. *P. variabile* Haeckel, 1879; ?*Oceania languida* Agassiz, 1862).
Clytia hemisphaerica: Rees & Thursfield, 1965 : 95–96; Millard, 1966 : 478–480, fig. 14a–f; Vervoort, 1968 : 16–17; Calder, 1975 : 300–302, fig. 4a–b; Millard, 1975 : 217–218, fig. 72a–d.
Clytia gigantea: Rees & Thursfield, 1965 : 96–97.
Thaumantias raridentata: Teissier, 1965 : 17.
?*Laomedea (Clytia) pelagica* Garcia Corrales *et al.*, 1978 : 28–29, fig. 11.
?*Campanularia gracilis:* (sensu Sars, 1850) Stepanyants, 1979 : 32, pl. 5, fig. 3 (syn. *Clytia serrulata:* Vanhöffen, 1910).
?*Clytia sarsi* Present paper, p. 78 (nom. nov. pro *Laomedea gracilis* Sars, 1850, preocc; see p. 78).

For further synonmy see Bedot (1901–1925), Russell (1953) and Kramp (1961). Kramp cited just the following combinations from the World literature not included in Russell's British list: *Gastroblasta raffaelei, Clythia johnstoni,* ?*Phialidium languidum* (provisionally retained distinct by Kramp), *Pseudoclytia pentata* f. *hexaradiata.* See also *Clytia* incertae sedis (p. 91).

NOMENCLATURE. Millard (1966) has shown that the apparent use of the species name *hemisphaerica* by Gronovius (1760) was not strictly binominal. Neither also was that by Houttuyn (1770 : 423), cited by Bedot (1901 : 486) as *Medusa hemisphaerica,* despite the implication of Bedot's entry. Bedot dated Houttuyn's work as 1761–1773; but the volume in which the *hemisphaerica* reference appeared was published in 1770, three years after Linnaeus' (1767) introduction of the genuine binominal *Medusa hemisphaerica.* Linnaeus cited Gronovius' illustration as indication.

The combination *Clytia hemisphaerica* results from the subjective linking of hydroid and medusa, and was probably first used by Rees & Thursfield (1965). The next year, Millard (1966) too discussed the combination.

Many authors have placed *hemisphaerica* in the 'medusa' genus *Phialidium* Leuckart, 1856; but *Clytia* Lamouroux, 1812, is older and now the life cycle is known should be used instead. The reason why *Phialidium* need not be used for any species is given above (p. 71).

Browne (1896) incorrectly ascribed the combination *Medusa hemisphaerica* to Müller, whose work Browne dated as 1766. The correct date of Müller's work was 1776, and Linnaeus (1767) has clear priority.

TYPE LOCALITY AND MATERIAL. The type material of *C. hemisphaerica* Linnaeus, 1767, was the medusa described and illustrated by Gronovius (1760 : 38, pl. 4, fig. 7). I have not tried to find it. Linnaeus gave the type locality as 'Belgian seas', from whence Gronovius' material came.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. I have examined the type series of the hydroids *Campanularia johnstoni* Alder, 1856*a*, and *C. raridentata* Alder, in Hincks 1861*b*, and consider them to be *C. hemisphaerica* (see Cornelius & Garfath, 1980; see also Remarks). The holotype colonies of the hydroids *C. ?gigantea* Hincks, 1866 (BMNH reg. no. 1899.5.1.106, Lamlash, Arran, W Scotland) and *Clytia obeliformis* Stechow, 1914 (Munich Zoological Museum, fertile colony on microslide, Bergen) are also *Clytia hemisphaerica.*

OTHER MATERIAL EXAMINED. This species is well represented in the BMNH collections. The following material, from other Museums, deserves mention: 53° 01′ N, 4° 22′ E, numerous colonies in spirit, coll. Lightship 'Texel', 1961, *cf.* '*Laomedea pelagica*' (sensu Van Breemen), det. W. Vervoort; Rijksmuseum van Natuurlijke Historie, Leiden. 10° 40′ N,

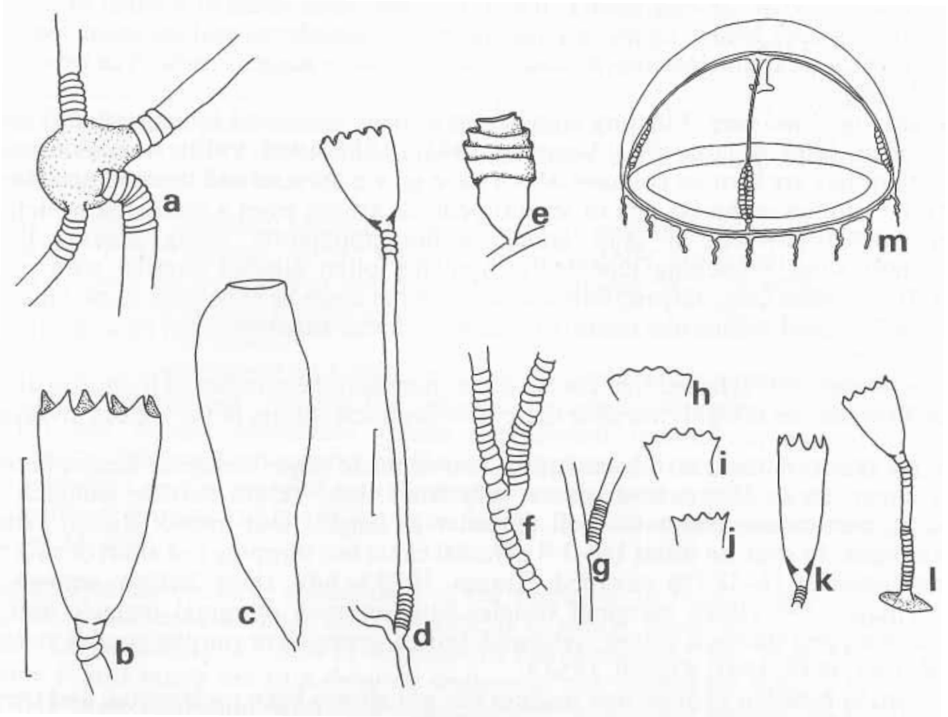


Fig. 9 *Clytia hemisphaerica.* (a–b) 'pelagic' form, from microslide preparation in Institut Royal des Sciences Naturelles de Belgique, det. '*Laomedea gracilis*' by A. Billard (mentioned, Billard, 1917; 'probably off Ostend'). (a) 'primary attachment disc' with four hydrothecal pedicels. Note absence of stolon. (b) hydrotheca. (c) 'pelagic form', gonotheca, 53° 01′ N, 4° 22′ E, det. '*Clytia pelagica*' by W. Vervoort; colln Rijksmuseum van Natuurlijke Historie, Leiden. (d–e) 'benthic form'; (d) hydrotheca and (e) gonotheca, S England; 1934.8.17.19. (f) 'benthic form', base of pedicel branch from extremely sheltered locality, Caol Scotnish, Loch Sween, Argyll, W Scotland, 1 m, 30 May 1962; 1962.6.19.21. (g) 'benthic form', base of pedicel branch, nr Bergen, 40–90 m, 9 April 1962; 1962.10.7.19. (h–j) three hydrothecal rims from same colony, Scotland; 1964.8.7.72. (k) hydrotheca, W Sweden, 20–30 m; 1962.11.8.10. (l) primary hydrotheca and attachment disc, reared from medusa ('*Phialidium hemisphaericum*' sens. Russell, 1953) by W. J. Rees, 2–17 March 1936; 1969.12.2.2. (m) medusa, Naples, redrawn after Mayer (1910 : text-fig. 144). Scales: (a–c, d–l) 500 μm; (m) unknown. See also Fig. 14(a).

6° 44′ W, 65 m, many colonies in spirit, coll. 'Atlantide' expedition, sta. 151, 16 Apr 1946, *cf.* '*L. pelagica*', det. W. Vervoort; RMNH, Leiden. Sète, S France, infertile material on three microslides, det. *Clytia serrulata* by Stechow, 1919*a* : 46; Munich Zoological Museum.

DESCRIPTION OF HYDROID STAGE. Among the most variable of all Atlantic hydroids. Detached colonies can continue growing in the plankton and form one extreme of variation, while benthic colonies are more typical of the species and form the other.

1. *Benthic colonies.* Colony comprising a creeping stolon from which short to long hydrothecal pedicels arise at irregular intervals. Hydrotheca thin walled, campanulate, length : breadth ratio 1–3, rim with 7–16 pointed to rounded or (?rarely) flat topped cusps, embayments typically pointed but sometimes rounded; hydrotheca usually round in cross-section but sometimes (Vervoort, 1968) sinuous near the top. Hydranth with the wide range of 20–30 tentacles (Hincks, 1868; *cf. Obelia geniculata*, p. 120). Pedicel straight, erect; annulated, usually with smooth central region and 2–10 annuli each end, rarely annulated throughout; sometimes branched, each branch having characteristic upward-curved basal region (similar to that in *C. paulensis*), branches often parallel with main pedicel; branch annulated basally and distally, central portion smooth. Gonotheca ♂ = ♀, broad, tubular, sometimes asymmetric, walls smooth to deeply concertinered, often with slight sub-terminal constriction; tapered below; aperture large, terminal; gonothecal pedicel short, on hydrothecal pedicel or on stolon. Medusa released at four-tentacle stage. Nematocysts described by Östman (1979).

2. '*Planktonic*' *colonies.* Floating colonies have been described by several authors (e.g. Van Breemen, 1905; Billard, 1907; Vervoort, 1946*a*, 1959, 1968, 1972). Available evidence suggests that they are benthic colonies which have grown on sand and become detached (see Remarks). Colonies comprise one to several pedicels arising from a basal disc which often (Leloup, 1933) envelops a sand grain, stolons apparently being absent. Pedicels exceptionally long, branching repeatedly, branches often aligned parallel with primary pedicel. Hydrotheca long, narrow, thin walled, terminal cusps as in benthic form. Gonotheca long, smooth walled; rugose and concertinered gonothecae apparently not recorded from free floating material.

Variation. Ralph (1957) found that cooler water increased the number of hydrothecal cusps. Although the species is highly variable there have been few studies of the factors involved.

DISPERSIVE STAGE. A medusa, released at the four-tentacle stage. Umbrella hemispherical or slightly flatter; up to 25 mm in diameter; jelly fairly thin. Velum narrow; stomach short, four-sided; manubrium about 1/6 bell diameter in length, four-lipped. Radial canals 4; gonads elongate to oval, on distal 1/4–3/4 of radial canal but stopping just short of ring canal. Marginal tentacles 16–32 [58 recorded, Kramp, 1919 (= 64)], short, hollow, smooth, with spherical bases. 1–3 closed marginal vesicles between each marginal tentacle and next. Tentacle bases and stomach yellow, yellowish brown, greenish or purple; gonads yellowish. (After Kramp, 1919, 1961; Russell, 1953.)

The relation between hydroid and medusa has not always been understood, and there are still some unsolved problems relating to the nominal species described from the hydroid stage as '*Laomedea gracilis* Sars'.

Böhm (1878), working at Helgoland, worked out the life cycle of *C. hemisphaerica* and his account was quoted by Haeckel (1879 : 187) in his World synopsis; but many years later Mayer (1910 : 267) wrote 'the mature hydroid is not known with certainty, but is probably a *Campanulina* (see Hincks, 1868 : 179)'. Mayer should have quoted Hincks as indicating '*Campanularia raridentata*', now regarded as conspecific with *hemisphaerica.* Hincks' citation in fact referred back to Wright's (1862) description of the hydroid stage under the name *Thaumantias inconspicua*; but Hincks (1852) himself had still earlier seen medusae released (identifying his material as '*Campanularia volubilis* Ellis & Solander'). Hincks thus seems to have been the first to record medusa release in the present species. Du Plessis (1871) also saw medusa release at an early date, but used the combination *Clytia volubilis.* (Notes on the widespread confusion between the species names *volubilis* and *hemisphaerica* are given below.) Mayer's oversight is the more surprising since he quoted Metschnikoff's (1886*b*) description of a polyp reared from the Mediterranean medusa *Clytia flavidula* (Péron & Lesueur, 1810a), which Mayer thought conspecific. The identity of *C. flavidula* is discussed under Remarks.

The later but independent suggestions of Browne (1896 : 488; 1900 : 725–726; Browne & Vallentin, 1904 : 125, 127) that the hydroid of '*Phialidium hemisphaericum*' was '*Campanularia johnstoni*' were supported by Kramp in 1914 (Kramp, 1919 : 93, footnote), some forty years after Böhm and Haeckel wrote and even longer after the suggestions of Du Plessis, Hincks and Wright. The delay parallels that which occurred in the working out of the *Obelia* life cycle (Cornelius, 1977*a*, *b*).

REPRODUCTIVE SEASON. Medusae occur all through the year in British waters but are most numerous from spring to autumn [Hincks, 1852, as *C. volubilis* (in February); Russell, 1953; J. H. Robson, in Evans, 1978, as *C. gracilis*)]. Lo Bianco (1909, as *Clytia flavidula* and *C. johnstoni*) recorded medusae off Naples from August to October and from January to March.

DISTRIBUTION. Nearly cosmopolitan in coastal waters (Ralph, 1957; Kramp, 1961), occurring in most of the present area. In European waters the medusa is one of the commonest (Russell, 1953). However, the species was said to be scarce in N Norway by Mathiesen (1928) who cited only two certain records, from Bergen and Hammerfest. It has been reported absent from Greenland (Kramp, 1943; Calder, 1970) although present in Iceland, Spitzbergen, the Faeroes and the Bering Sea (Calder, 1970). 'Planktonic' hydroid colonies have been reported as common in the southern North Sea and off much of the coast of W Africa (Vervoot, 1946*a*, 1959).

HABITAT. Usually benthic; intertidal to 150+ m (Crawshay, 1912; Marine Biological Association, 1957; Kramp, 1959; Millard, 1975; BMNH collections). Naumov (1969) reported a lower limit of 300 m but did not cite material. Rees & White (1966) listed a record from 1250 m off the Azores as *C. gigantea*, a species here regarded conspecific; but I have not checked this report.

The species has been found on a wide variety of invertebrate and algal substrates, and there is no regular association. Among the unusual recorded substrates are sand grains (see Remarks) and pelagic cirripedes. There are several records on parasitic copepods themselves on fish (on *Lernaeocera* on *Gadus* by Leloup, 1930*b*; on *Peniculus* on *Mullus*, on *Lernaeenicus* on *Clupea*, and on *Dinematura* on *Cetorhinus* (the Basking Shark), all by Debouteville & Nunes, 1951, 1952). As in *Obelia*, long distance transport would seem to result (pp. 45, 120).

REMARKS. Two factors have contributed to the profusion of redescriptions of this species and to the consequent number of synonyms: it is nearly cosmopolitan, and it is highly variable. The combination *Clytia hemisphaerica* was introduced only some fifteen years ago and there is still much use in a detailed analysis of the taxonomic history of the species. There has been confusion with other species and with other genera, and some of the problems have yet to be solved. The nominal species described from the NE Atlantic are considered below, so far as possible in chronological order.

The notes by Stechow (1921*a*, 1923*a*) and Rees & Thursfield (1965) on the nominal species *Sertularia uniflora* Pallas, 1766, were partly misleading. Pallas included in his synonymy Ellis' (1755) plate 14, figure A, Linnaeus' (1758) citing of that plate under the name *Sertularia volubilis*, and Baster's (1762) plate 2, figures 2a, b, d, 3, 4c, e, 7a–c. Ellis' illustration shows a campanulariid hydroid growing on *Hydrallmania falcata* (Linnaeus, 1758). The pedicels were spirally grooved throughout, not annulated top and bottom as in the present species, and had a spherule at the upper end. These two characters indicate that Ellis' material was the species here called *Campanularia volubilis*. Hargitt (1909), Stechow and Rees & Thursfield wrongly supposed Ellis' material to be *C. hemisphaerica*. The name *Sertularia uniflora* Pallas, 1766, was in fact a nom. nov. for *Sertularia volubilis* Linnaeus, 1758, and since both were based on Ellis' illustration *uniflora* is a junior objective synonym of *volubilis*.

The other illustrations cited by Pallas under *S. uniflora*, those of Baster, show in one place (fig. 2A, b) a sharply cusped hydrothecal rim, but nowhere show details of the pedicel. Hence it cannot be determined whether Baster's material was *volubilis* or *hemisphaerica*. Gonothecae were not shown. Maitland (1876, quoted in Vervoort, 1946*a* : 276) referred part of Baster's illustrations (pl. 2, fig. 7A, a) to *Orthopyxis integra* (Macgillivray, 1842), an opinion disagreed with by both Vervoort (1946*a*) and myself as the hydrotheca of *integra* does not have a cusped margin. Nevertheless, I here designate the material shown by Ellis (1755 : pl. 14, fig. A) lectotype of *S. uniflora* Pallas, 1766, to provide formal protection for the name *integra* from possible threat from *uniflora* should Maitland's opinion ever be upheld.

Rees & Thursfield (1965) were further confusing in stating that 'earlier references by Ellis (1755*a*, *b*) [sic] do not distinguish' between *hemisphaerica* and *volubilis*. They omitted the Ellis references from their paper: indeed, I cannot trace relevant papers by Ellis in that year. His only 1755 publication mentioning campanulariids was his book. In this Ellis (1755 : 25) stated clearly that there were two species and illustrated both on his plate 14. Linnaeus and Pallas (op. cit.) were each careful to cite only one of the species when referring Ellis' illustration respectively to their synonymies of *volubilis* and *uniflora*. The other illustrated species (Ellis, 1755 : pl. 14, B) was named *Sertularia syringa* by Linnaeus (1767 : 1311) and is now known as *Calycella syringa*, family Calycellidae (e.g. Cornelius, 1978).

Thus there is little confusion in the early literature; but Rees & Thursfield (1965) were probably correct in stating that the 'hydroid [stage of *C. hemisphaerica*] is recognisable for the first time under the name *Sertularia uniflora:* Ellis, 1768 : pl. 19, fig. 9'. And in this paper Ellis clearly did confuse the two species he had previously illustrated separately. His use of the name *uniflora* in that paper can be regarded as misidentification, not as homonymy. Ellis' (1768) illustrations show clearly the annulated, not spiralled, pedicels of *hemisphaerica*—incidentally slightly unusual in lacking a smooth central portion—and a characteristic 'concertinered' gonotheca. Further confusion might have resulted from Ellis & Solander's (1786) application of the name *Sertularia volubilis* to illustrations clearly of the present species, but the slightly earlier literature just discussed prevents it. However, Hargitt (1909) was not alone among later authors in applying the combination *Clytia volubilis* to the present species.

C. hemisphaerica was placed in the genus *Oceania* Péron & Lesueur, 1810*a* (as *O. flavidula*), by those authors.

Clytia urnigera Lamouroux, 1816, is referred to *C. hemisphaerica* but is discussed here under *Orthopyxis integra* (pp. 64–65).

The combination *Laomedea gracilis* Sars, 1850, has plagued the literature (see also Remarks under *Gonothyraea loveni*); but as noted by Vervoort (1946*a* : 285) the species name should not be used as it is preoccupied by '*Lomedea gracilis*' C. Pickering, in Dana, 1846 : 689 (lapsus pro *Laomedea gracilis*), which I refer to *Obelia dichotoma* (p. 117). I propose the name *Clytia sarsi* nom. nov. in place of *L. gracilis* Sars, 1850 (preocc.). Lectotype material of *L. gracilis* Sars is designated here on page 94. Nevertheless, the name *gracilis* has been widely applied to colonies having long, narrow hydrothecae and smooth gonothecae. But following Ralph's (1957) account of variation in New Zealand populations most authors have regarded '*sarsi*-type' colonies as an extreme variation of *hemisphaerica*. Further evidence was provided by W. J. Rees (in Rees & Thursfield, 1965) who reared a medusa from a *sarsi* ('*gracilis*') colony and found it the same as the medusa *hemisphaerica* s. str. Kühl (1967) regarded '*sarsi*-type' colonies conspecific with those of *hemisphaerica* on more subjective grounds. But Östman (1979) separated the species on the fine structure of the nematocysts (see also p. 42) and the problem is not yet resolved.

There has been some further debate over the degree of affinity between *C. sarsi* (= *L. gracilis* Sars, 1850), and *Campanularia pelagica* Van Breemen, 1905. Some authors have regarded them identical (e.g. Leloup, 1933, 1952; Vervoort, 1946*a*; Naumov, 1960, 1969;

Garcia Corrales *et al.*, 1978); but the validity of *C. pelagica* s. str. has been difficult to assess. (*Campanularia attenuata* Calkins, 1899, from Puget Sound, seems similar.) Among recent authors Vervoort's (1946*a*, 1959, 1968, 1972) descriptions of the *pelagica* 'form' have been important but the possibility has remained open that *pelagica* was simply based on *sarsi* or *hemisphaerica* material which had detached and grown in the plankton. Billard (1917) also had failed to resolve the question but E. T. Browne, A. Kemna and E. Leloup (in Leloup, 1933) thought *sarsi* (*gracilis*) just to be detached, floating colonies of *hemisphaerica*.

Vervoort (1959, as *Laomedea pelagica*) reported that 'floating' colonies occurred in the North Sea and along much of the west coast of Africa, but Millard (1966) referred Vervoort's African coast material to *C. hemisphaerica* without comment. Subsequently Vervoort (1968) reaffirmed his view that *pelagica* was distinct. He had not seen 'intermediate material'; but presumably there is no intermediate environment. Vervoort separated *pelagica* on its slender, gradually narrowing hydrothecae, an undulating cross-section just below the hydrothecal rim and a smooth walled gonotheca. He cautiously noted that two species of *Clytia* medusae had been recorded from the North Sea by Russell (1953) and that these might relate to the two hydroids, *pelagica* and *hemisphaerica*. He subsequently (Vervoort, 1972) retained specific status for *pelagica* but Millard (1975) again referred Vervoort's African coast material to *hemisphaerica*. So the experts were divided. Naumov (1960, 1969) meanwhile had considered *pelagica* distinct but extended its limits slightly further than Vervoort to include *sarsi*-type material with smooth walled gonotheca. Garcia Corrales *et al.* (1978) similarly regarded *sarsi* + *pelagica* distinct from *hemisphaerica*, based on sharper and longer hydrothecal cusps and longer hydrotheca in the former; and like Vervoort (1968) had seen no intermediate material. Other features on which *pelagica* has been distinguished are the frequency of branching and the tendency of the branches to run parallel with the primary stem, noted by Vervoort (1959) but not apparent in all planktonic material; and a smooth, asymmetric gonotheca (e.g. Billard, 1917).

Vervoort (1972 : 91, footnote) drew attention to the report by Sars (1850, 1857; ?repeated in Leloup, 1952) that '*pelagica*' had sessile gonophores. Vervoort cited observations that '*pelagica*-type' material released its medusae and (pers. comm.) now considers that the contrary observations of Sars might have been made on *Gonothyraea loveni* material.

Old and new evidence for uniting *pelagica* with *hemisphaerica* runs as follows. Ralph (1957) showed that smooth gonothecae are not unusual in *hemisphaerica*, and that the length of the hydrotheca and shape of the cusps on the rim vary widely, to an extent which encompasses the three nominal taxa. The *basal discs* (= *Haftplatte* of Kuhn, 1913, and *disque de fixation* of Houvenaghel-Crèvecoeur, 1973; there seems no English equivalent already) of attached *C. hemisphaerica* examined by me seem identical with the 'partie basale' or '*pied . . . globuleuse*' described in planktonic colonies by Billard (1917) and Leloup (1933) under the name *pelagica* (Fig. 9). Also, Leloup showed that the basal discs of these free-floating colonies often contain a sand grain, indicating a benthic origin. Next, the distinctive upward-swept pedicel bases in *hemisphaerica* s. str. seem identical with those described as *pelagica*. Finally, it might have been expected that a hydroid which was habitually planktonic would have some obvious modification to that end; but there seems none.

The relation between the three nominal forms *hemisphaerica*, *sarsi* and *pelagica* is certainly close, and the relation to *johnstoni* is still uncertain (see below). Whether the differences are phenotypic or genotypic cannot yet be decided; but on skeletal and medusa characters it seems best now to interpret the variation as representing a single 'morphological species'. More detailed studies, such as that of Östman (1979) on the nematocysts, might shed further light.

Campanularia volubilis (Ellis & Solander, 1786) sens. Hincks (1852) was the present species. Hincks' account was probably the earliest record of medusa release in *C. hemisphaerica*.

Campanularia johnstoni Alder, 1856*a*, is apparently the earliest available name for the hydroid stage most usually (but subjectively) connected with the medusa on which the present species is based (see Nomenclature, above). It is also the correct species name for the type species of the genus *Clytia* (p. 71). The type series of *Campanularia johnstoni* is mentioned under Material, above, and by Cornelius & Garfath (1980). See also Cornelius (1981).

Phialidium viridicans Leuckart, 1856, is discussed above (p. 71) and on page 86.

Clytia noliformis (McCrady, 1857, as *Campanularia*) was founded on a hydroid which released a *Clytia* medusa lacking gonads when liberated. Kramp (1959, 1961) regarded the lack of gonads on release an important character; and the species has been widely recognized from both hydroid and medusa stages in warm waters throughout the World (references in Fraser, 1944; Kramp, 1961; comment in Rees & Thursfield, 1965). Mammen (1965) gave this name to a medusa he reared but it closely resembled Russell's (1953 : pl. 17, fig. 6) illustration of *C. hemisphaerica*. Mammen's medusa differed only in not showing gonads till 48 hrs old. *C. noliformis* has not otherwise been redescribed since Kramp (1961) wrote and may prove conspecific. Picard (1949) referred medusa and hydroid material from Villefranche to *noliformis* but his specimens, like Mammen's, seemed to differ from *hemisphaerica* only in the short delay in acquiring gonads. Later he included the species in a Mediterranean faunal list, regarding *C. flavidula* Metschnikoff, 1886*a*, and *C. mollis* Stechow, 1919*a*, as conspecific (Picard, 1958*b*). These two species have both been referred to *hemisphaerica* by at least some senior authors; and are discussed in their chronological place below. Rees & Thursfield (1965) referred some Cape Verde material from James Ritchie's collection to *C. noliformis*. They regarded *Campanularia ptychocyathus* Allman, 1888, from the Azores, as conspecific; but Stechow (1925 : 521) treated *ptychocyathus* as dubious.

Campanularia gegenbauri Sars, 1857, was based on a fertile hydroid colony illustrated by Gegenbaur (1854 : pl. 1, figs 1, 1a, as *Campanularia* n. sp.). I concur with Hincks (1868 : 145), Böhm (1878 : 168) and Bedot (1910 : 254) that the species should be referred to *Clytia hemisphaerica*.

Campanularia volubiliformis Sars, 1857, was a name applied to material described as *Campanularia* sp. by Gegenbaur (1854). The shape of the hydrotheca, pedicel and gonotheca illustrated indicate the present species and not *Campanularia hincksii* as suggested by Carus (1844) and Broch (1912*b*). Heller (1868) and Picard (1951*a*) reported further material without description; while Stechow 1919*a* : 70) referred the species to *Orthopyxis*!

Campanularia raridentata Alder, in Hincks, 1861*b*, was referred to *Clytia hemisphaerica* by Billard (1928) and Rees & Thursfield (1965), and provisionally by Vervoort (1968). The synonymy was agreed by Cornelius & Garfath (1980), who alone saw the holotype. The specimen was simply a young colony of *C. hemisphaerica*. Rees & Thursfield wrongly ascribed the original description to 'Alder, 1857'.

Clytia bicophora Agassiz, 1862, originally based on hydroid material from New England, was recorded as a medusa in the Gulf of Trieste by Thiel (1935 : 172, as *Phialidium bicophorum*). But Agassiz' detailed description and clear illustrations appear to represent *C. hemisphaerica*, and *bicophora* can be regarded conspecific. Kramp (1959 : 149) listed other records of *bicophora* as 'uncertain', and indeed Böhm (1878) referred *bicophora* to *C. johnstoni*, which is also regarded conspecific. Kramp (1959, 1961) nevertheless described a medusa under the name *bicophora* and listed references to that species; but the supposed differences from *hemisphaerica* seem unimportant.

Clytia (Platypyxis) cylindrica Agassiz, 1862, was based on both hydroid and medusa material from Massachusetts Bay and Buzzards Bay, North America. The species was referred to *C. hemisphaerica* by Böhm (1878), but to *C. noliformis* (McCrady, 1857) by Bedot (1910 : 348) and Kramp (1961 : 170). (Bedot clearly regarded *Platypyxis* a synonym of *Clytia*, and I concur; see p. 71.) Agassiz' description of *cylindrica* includes no important differences from *hemisphaerica* and like Böhm I regard them conspecific. Vervoort (1968) described new material, and commented on the similarity of *C. elsaeoswaldae* Stechow, 1914. I agree with Vervoort in regarding the Stechow species conspecific.

The combination *Phialidium languidum* (Agassiz, 1862) has been applied to medusae caught off Senegal, but Kramp (1955) referred both the material involved and the nominal species itself to *C. hemisphaerica* (see Kramp, 1933, 1955, 1961, for discussion).

Campanularia ?gigantea Hincks, 1866, was probably based on large *hemisphaerica* hydroid material. The eleven hydrothecae of the holotype well enough preserved for study measured, in mm from diaphragm to tips of hydrothecal cusps, 1·18, 1·26, 1·29 (3), 1·53, 1·62 (2), 1·78, 1·88, 1·91. The wide range is striking, as is the sheer size of the largest; but Hincks was rightly cautious to introduce the name as *?gigantea*. Several authors have referred large material to *gigantea* solely on the basis of size. The pedicels too are long, but the upward curve of the pedicel bases recalls *hemisphaerica* s. str. and continued separation seems uncalled for. Gonothecae have never been reported in this large material. Hincks' (1868) later illustration of the holotype is accurate; and that of Jäderholm (1909), of non-type material, is similar. The material fron N Scotland listed by Rees & Thursfield (1965; BMNH 1964.8.7.75) is *C. hemisphaerica* and is smaller than the holotype of *?gigantea*. The material from Belgium cited by Leloup (1952) seems to have been the same, as does the North Sea material listed by Billard (1928, as *Clytia johnstoni*).

Gastroblasta raffaelei Lang, 1886, was based on a medusa from Naples. The species was provisionally referred to *C. hemisphaerica* by Kramp (1959 : 148).

Clytia flavidula: Metschnikoff, 1886*a*, was a comb. nov. for *Oceania flavidula* Péron & Lesueur, 1810*a*, originally described from medusae collected from Nice. Mayer (1910) referred the species to *C. hemisphaerica* and Russell (1953) concurred. Lo Bianco (1909 : 540) also used the combination *Clytia flavidula.* Kramp (1961 : 65) listed another use of the binominal *O. flavidula*, for *O. armata*, a clavid medusa.

The Mediterranean material referred by Stechow (1919*a*) to *Campanularia serrulata* Bale, 1888 (first described from Sydney), was examined here and found to be simply *Clytia hemisphaerica*; as indeed seems Bale's species, which was described from infertile material. In general agreement, Stepanyants (1979) referred *C. serrulata* to '*Campanularia gracilis*' Sars, 1850, itself regarded conspecific (see above). Picard (1958*b*) recorded the species as Mediterranean without comment.

Campanularia attenuata Calkins, 1899, originally described from Puget Sound, resembles '*Laomedea pelagica* Van Breemen, 1905', and like it should probably be regarded conspecific with *Clytia hemisphaerica.* Material was recorded from Ghana by Buchanan (1957) and it is well known that '*pelagica*-type' colonies occur along the African coast (see above). Although West & Renshaw (1970) recognized the species on the basis of its branched colonies as grown *in vitro* at certain temperatures (see p. 40) further proof of validity seems necessary. *C. attenuata* Stechow, 1919*a*, from Villefranche, is a junior homonym and later in the same paper Stechow (1919*a*: 157) introduced the nom. nov. *Campanularia villafrancensis* instead. However, *villafrancensis* too seems conspecific with *hemisphaerica.*

Campanularia edwardsi Nutting, 1901*b*, based on material from Massachusetts, was redescribed at length by Kubota (1978, as *Clytia*). He provisionally referred *C. edwardsi* to the present species, and I concur.

Clytia simplex Congdon, 1907 : 471–472, figs 14–15, based on material taken off *Sargassum* weed near Bermuda, was reported south of the Azores by Vanhöffen (1910). Fraser (1944), however, referred the species to *C. noliformis* McCrady, 1857, here regarded conspecific with *C. hemisphaerica*; and it seems probable that *C. simplex* too is conspecific.

Clytia obeliformis Stechow, 1914, was based on material from Bergen, Norway. The original illustration shows both hydrotheca and gonotheca typical of *C. hemisphaerica* and the type material, examined here, comprises simply a rather elongate colony of the present species. There is no reason to maintain a separation.

Campanularia acuta Stechow, 1919*a*, was a nom. nov. applied to *C. raridentata:* var. Marktanner-Turneretscher, 1890, based on material from NW France. The variety was originally held to differ from *C. raridentata* s. str. in lacking annulations around the base of the gonotheca; and like that species seems to have been based on *Clytia hemisphaerica* material.

Campanularia brachycaulis Stechow, 1919*a*, was based on a small, infertile colony from Villefranche. The illustrated hydrotheca does not seem to differ from that of *Clytia hemisphaerica*; and I must disagree with Patriti (1970) who referred the species to *Campanularia hincksii*.

Clytia compressa Totton, 1930, was proposed on the basis of the shape of the hydrothecal cusps and of the gonotheca. Ralph (1957) and Vervoort (1968) regarded it conspecific, and I concur.

Stolon growth in the hydroid stage was described by Hale (1964, 1973*a*, *b*).

Clytia hummelincki (Leloup, 1935)

(Fig. 10)

Laomeda hummelincki Leloup, 1935 : 19, fig. 7; Buchanan, 1957 : 360, fig. 11 a–b.
Campanularia hummelincki: Fraser, 1944 : 122, pl. 21, fig. 93; Vervoort, 1966 : 96.
Clytia hummelincki: Deevey, 1954 : 270; Millard, 1966 : 480–481, fig. 14 g–l; Millard, 1975 : 218–220, fig. 72 f–h.

Type locality and material. Isle de Bonaire, West Indies, 0·7 m depth, on dead coral, infertile material on microslide (Fig. 10); Mus. Roy. Hist. Nat. Belg. collection.

Other material examined. Fragments of fertile colonies on two microslides, Aghulas Bank, off South Africa (34° 43′ S, 25° 40′ E); South African Museum reg. no. H 2967 (mentioned, Millard, 1966, 1975).

Description of hydroid stage (partly after Leloup, 1935; Buchanan, 1957; Millard, 1975). Colony a tortuous stolon bearing long hydrothecal pedicels at irregular intervals;

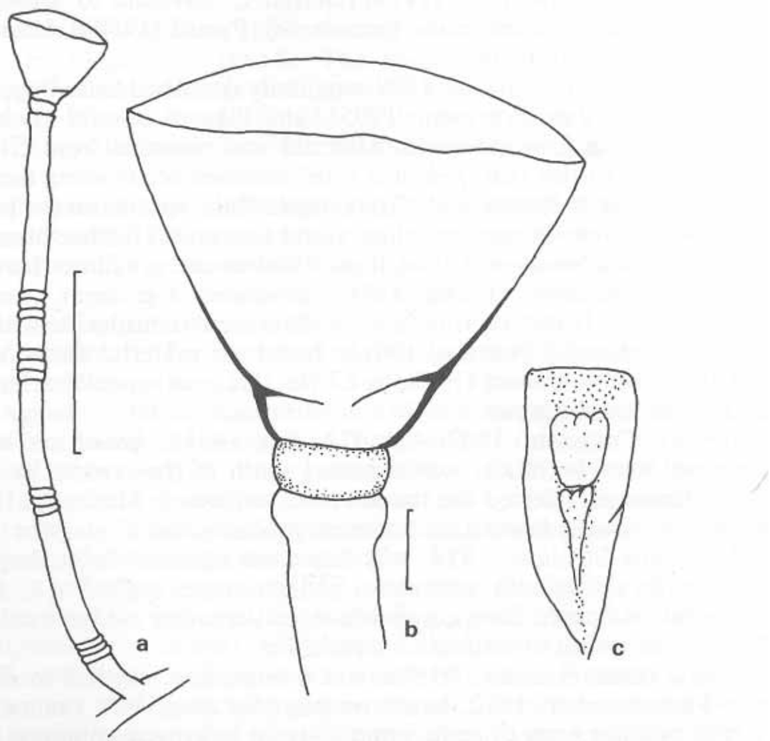


Fig. 10 *Clytia hummelincki.* (a–b) hydrotheca from syntype series, two magnifications. (c) ♀ gonotheca (after Millard, 1975 : fig. 72H). Scales: (a) 50 μm; (b–c) 500 μm.

gonothecae subsessile on stolon. Hydrothecae short, wide, unthickened, length = maximum breadth, tapering sharply towards base which is usually slightly constricted; rim often sloping, even to slightly and irregularly sinuous; diaphragm delicate, oblique in lateral view, either parallel with hydrothecal aperture or sloping in opposite direction; basal chamber small. Hydrothecal pedicel long, smooth or with several basal annulations and up to *c.* five groups of 3–5 annuli along length; sub-hydrothecal spherule present, below which often a slight constriction (see Fig. 10). Hydranth with spherical hypostome and *c.* 20 tentacles. Gonotheca (?♂ = ♀) sessile to shortly stalked, truncate; widest above, tapering below; sometimes asymmetric; aperture probably broad as end; with 1–2 medusa buds, development successive; buds with 4 radial canals and 4 tentacle rudiments (South African material); mature gonotheca and medusa undescribed.

MEASUREMENTS. See Table 2.

Table 2 *Clytia hummelincki* Measurements in μm.

	Caribbean (Leloup, 1935)	Ghana (Buchanan, 1957)	South Africa (Millard, 1966, 1975)
Hydrotheca			
Length	200–240	250	250–400
Breadth (max)	250	240–250	200–420
Length/breadth	*0·8–0·96*	*1·00–1·04*	*0·7–1·36*
Pedicel			
Length	1500–2000	2000	1920–4730
Breadth (max)	40–60		90–150
Gonotheca			
Length			730–1260
Breadth (max)			280–450

DISPERSIVE STAGE. Probably a medusa. Millard (1966, 1975) noted medusa buds with 4 marginal bulbs and so referred the species to *Clytia*. See also Description, Remarks under *C. hemisphaerica* and Dispersive stage under *C. gravieri*.

REPRODUCTIVE SEASON. The only recorded fertile material was collected from Aghulas Bank, South Africa, on 10 February, 1962 (Millard, 1966). The gonothecae contained well developed medusae.

DISTRIBUTION. A little known species, recorded in the NE Atlantic only from Ghana (Buchanan, 1957). Other Atlantic records indicate a wide distribution: West Indies (Leloup, 1935; Vervoort, 1966), Florida Keys and Woods Hole (Deevey, 1954, possibly northernmost record of species) and South Africa (Millard, 1966, 1975).

HABITAT. The few collected colonies have been on *Lepas* (Cirripedia) attached to a buoy, on sublittoral coral debris and on intertidal *Sargassum* weed (Leloup, 1935; Buchanan, 1957; Millard, 1966), indicating a wide substrate range. Recorded depths have so far ranged only from intertidal (Buchanan) to less than 1 m (Millard).

REMARKS. This rarely reported species is clearly widespread in the warmer parts of the Atlantic Ocean. It is retained in *Clytia* following Millard's notes on the developing medusa. Although the species has a sub-hydrothecal spherule it is not transferred to *Campanularia* since that character might be due to convergence (see p. 41). But the affinities of the species remain uncertain and the identity of the medusa might provide better indication.

Clytia islandica (Kramp, 1919)
(Fig. 11)

Phialidium islandicum Kramp, 1919 : 95, pl. 4, figs 11–13, pl. 5, figs 1–2; Russell, 1953 : 294–296, text-figs 180–181; Kramp, 1959 : 149, 215, 218, 221, 222, fig. 190; Kramp, 1961 : 169 (?syn. *Staurostoma laciniatum* var. *hybridum* Le Danois).

TYPE LOCALITY. Coastal waters of Iceland.

DESCRIPTION OF MEDUSA STAGE (Hydroid unknown). Diameter of adult 35–40 mm, umbrellar saucer-shaped, jelly thin; stomach small, cruciform; manubrium reduced, mouth square surrounded by crenulated lips; gonads narrow, along almost whole length of radial canals; tentacles *c.* 200, alternating with statocysts.
Variation. See Russell (1953) and Kramp (1959).

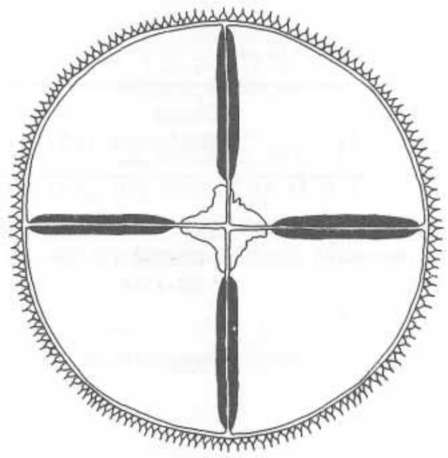


Fig. 11 *Clytia islandica.* Redrawn after Kramp (1959 : fig. 190). Diameter 35–40 mm.

DISTRIBUTION. Reported at least as far south as SW Ireland but records generally more northerly (Russell, 1953). Kramp (1961) cited unconfirmed records from the Bay of Biscay.

REMARKS. Distinguished from the medusa stage of *Clytia hemisphaerica* by: larger diameter (up to 40 mm, not up to 20 mm), flat (not hemispherical) shape, more numerous tentacles [up to *c.* 200, not up to (rarely) 58], usually rather larger gonads and one (not 1–3, usually 2) statocysts between tentacles. The hydroid is not known.

Disuse of the genus name *Phialidium* is discussed above (p. 74). Kramp (1961) referred the genus *Staurostoma* Haeckel, 1879 : 130, to *Staurophora* Brandt, in the family Laodiceidae.

Clytia linearis (Thornely, 1899)
(Fig. 12)

Obelia linearis Thornely, 1899 : 453, pl. 44, fig. 6.
Campanularia gravieri Billard, 1904*a* : 482, fig. 1; Billard, 1907 : 171–172.
?*Clytia geniculata* Thornely, 1904 : 112–113, pl. 3, figs 4, 4a.
Campanularia ?obliqua Clarke, 1907 : 9, pl. 5, figs 1–4.
Clytia linearis: Stechow, 1913 : 66–69, figs 23–25; Hirohito, 1977 : 14–20, fig. 4a–j (syn. *Campanularia gravieri* Billard; *Clytia hendersonae* Torrey, 1904; *C. alternata* Hargitt; *Laomedea bistriata* Leloup).
Clytia alternata Hargitt, 1924 : 483, pl. 2, fig. 7.
?*Clytia (?)foxi* Billard, 1926 : 93–94, fig. 9A–B.

Laomedea (Obelia) bistriata Leloup, 1931*a* : 4, figs 8–11.
Clytia gravieri: Billard, 1938 : 429–432, figs 1–3, ?fig. 4 (syn. *C. alternata* Hargitt, *Laomedea bistriata* Leloup); Picard, 1955 : 185–186; Millard & Bouillon, 1973 : 51–54, fig. 7e–g (syn. *Obelia striata* Clarke, 1907; *C. serrata* Millard, 1958); Millard, 1975 : 215–217, fig. 71 F–H (syn. *Obelia striata* Clarke, 1907); Garcia Corrales, Inchaurbe & Mora, 1978 : 29–30, fig. 12.
Clytia obliqua: Picard, 1950 : 51–52.
Campanularia (Clytia) gravieri: Vervoort, 1967 : 50–52, fig. 16 (syn. *Clytia alternata* Hargitt; *Laomedea bistriata* Leloup).

TYPE LOCALITY. Blanche Bay, New Britain, Bismarck Archipelago. Material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia obliqua* Clarke, 1907, infertile colonies on sertularian hydroid, in spirit, 'Perico Island', Gulf of Panamar, coll. r.v. 'Albatross'; Smithsonian Institution cat. no. 29616.

Clytia alternata Hargitt, 1924, fertile colonies preserved on microslide, Port Galero, Mindoro, Philippines; Smithsonian Institution cat. no. 42644 (Fig. 12).

OTHER MATERIAL EXAMINED. None.

DESCRIPTION OF HYDROID STAGE (partly after Thornely, 1899; Billard, 1904*a*, 1938; Stechow, 1925; Picard, 1951*a*; Vervoort, 1967; Millard & Bouillon, 1973; Millard, 1975; Hirohito, 1977). Colonies both stolonal and erect. When erect branching sympodially, up to *c.* 10 hydrothecae in extent, to 20 mm. Hydrothecal pedicels finely ringed throughout (6–37, usually *c.* 20) or with smooth central portions; distal pedicels shorter than proximal. Internodes of erect stems arcuate, narrowly ringed basally. Hydrothecae long, sides parallel to slightly divergent, often with slight asymmetric bulge; with 8–16 long narrow marginal cusps recalling those of *Clytia paulensis* and *Obelia bidentata* but each with internal

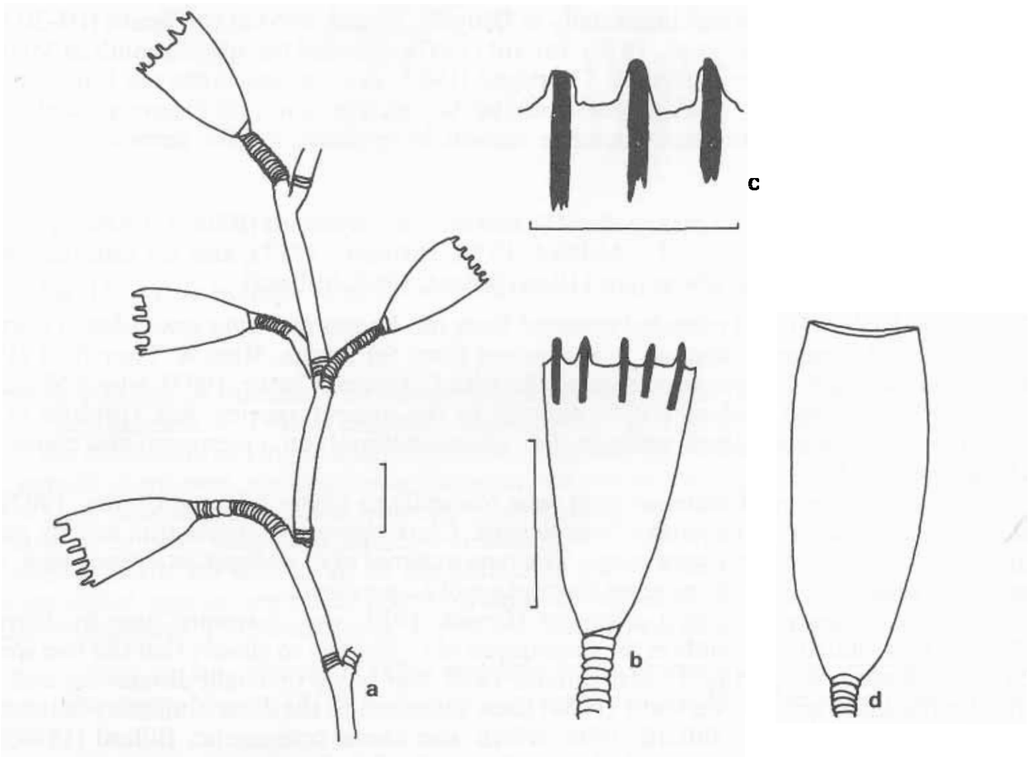


Fig. 12 *Clytia linearis.* The specimen illustrated is a syntype of *C. alternata* Hargitt, 1924, here regarded conspecific. (a) part of colony. (b–c) hydrotheca and part of rim. (d) ♀ gonotheca. Scales: (a) 500 μm; (b) 250 μm; (c–d) 500 μm.

stiffening strip reaching to tip and extending downwards sometimes to middle of hydrotheca; intervening bays rather wide and square, bulging out; diaphragm usually oblique but sometimes transverse. Hydranth with 12–15 tentacles (in holotype specimen of *C. alternata* Hargitt). Mature gonotheca (?♂ = ♀) elongate, on 2–3 ringed pedicel, either on stolon or on erect shoot in axil; widest in centre, tapering below and usually above; one-flapped circular deciduous operculum; young gonotheca shorter, more sharply truncated. Gonophore with one or more rows of developing medusae; pre-release medusae with hemispherical umbrella and four marginal tentacles.

Variation Hydrothecal length varies greatly, at least from 400 μm to 1100 μm (Millard, 1975). Internodes and pedicels are shorter in upper parts of the colony (Hirohito, 1977). Hirohito found little difference between Red Sea and Japanese specimens, indicating a rather constant phenotype. Hydrothecal pedicels were on the whole shorter in the Japanese specimens, but gonothecae were similar in size. Billard (1938) reported that the embayments between the hydrothecal cusps are often distorted in preserved material due to lateral folding.

DISPERSIVE STAGE. A medusa, with hemispherical umbrella and four marginal tentacles on release; earliest stage identical with newly liberated *Clytia hemisphaerica* medusa, even in cnidom according to Picard (1951*a*). Adult medusa not described (Millard, 1975). Russell (1953) noted that the Mediterranean medusa *Phialidium viridicans* Leuckart, 1856, might prove valid. It might follow that *Clytia linearis* is its hydroid, but evidence is only circumstantial and the hydroid stages of *C. hummelincki* and *C. paulensis* must also be considered. '*P. viridicans*' is here provisionally referred to *C. hemisphaerica.*

DISTRIBUTION. Circumglobal in tropical to warm shallow seas (Millard & Bouillon, 1973; Hirohito, 1977) extending northwards in the Atlantic Ocean at least to the south coasts of France ('extremely common' intertidally at Banyuls, Picard, 1951*a*) and Spain (10–20 m off Alicante, Garcia Corrales *et al.*, 1978). Billard (1907) recorded the species south of Madeira; Picard (1955) from Algeria; Rees & Thursfield (1965, as *C. striata*) from the Cape Verde Is and Rees & White (1966, as *C. striata*) from the Azores. Vervoort (1967) gave a list of known Indo-Pacific localities; and some possible records under other specific names are discussed below.

HABITAT. On cirripede and pteropod shells and on other hydroids (Billard, 1904*a*; Vervoort, 1967; Millard & Bouillon, 1973; Millard, 1975; Hirohito, 1977); also on intertidal rocks (Picard, 1951*a*). Intertidal (Picard) to 110 m (Billard, 1907; Millard).

REMARKS. Ritchie (1907) recorded material from the Azores as *Clytia geniculata* Thornely, 1904, a name originally applied to specimens from Sri Lanka. Rees & Thursfield (1965) tentatively thought *C. geniculata* conspecific with *C. striata* (Clarke, 1907), which Millard & Bouillon (1973) and Millard (1975) referred to the present species. But Hirohito (1977) described what he considered undoubted *C. striata* material (on a pteropod) and considered the species valid.

Picard (1950) assigned material from near Marseille to *Clytia ?obliqua* Clarke, 1907) but that species seems identical with *Clytia linearis.* Clarke based the distinction merely on the angle of slope of the hydrothecal cusps. The type material of *C. obliqua*, examined here, does not otherwise differ from the original description of *C. gravieri.*

The type material of *Clytia alternata* Hargitt, 1924, was examined also by Hirohito (1977). As he stated, it resembles the description of *C. linearis* so closely that the two species can be regarded conspecific. *C. foxi* Billard, 1926, was based on slight differences and may also be the same species. Vervoort (1967) drew attention to the close similarity between *C. alternata* and *C. gravieri* Billard, 1904, which also seems conspecific. Billard (1938) had earlier thought them conspecific along with *Laomedea bistriata* Leloup, 1931*a*. He saw four marginal tentacle bulbs in the pre-release medusa and hence assigned the species to *Clytia.* Detailed discussion of several Pacific forms was provided by Hirohito.

Clytia mccradyi (Brooks, 1888*b*)
(Fig. 13)

Oceania sp. Brooks, 1888*a* : 29–30.
Epenthesis mccradyi Brooks, 1888*b* : 147–162, pls 13–15; Sigerfoos, 1893 : 106.
Oceania mccradyi: Mayer, 1900 : 50, pl. 21, figs 56–59.
Phialidium mccradyi: Mayer, 1910 : 271–272, pl. 34, figs 2–3, pl. 35, figs 1–3; Kramp, 1959 : 149; Kramp, 1961 : 170; Bougis, 1963 : 2,2–2,3, pl. 9, fig. 2.
Further references were given by Mayer (1910) and Kramp (1961).

TYPE MATERIAL AND LOCALITY. Green Turtle, 1886, and Nassau, 1887, Bahamas (medusa stage only); material not located.

MATERIAL EXAMINED. None available.

DESCRIPTION OF HYDROID STAGE. The identity of the hydroid stage is unclear. The species was originally based on mature medusae collected from the plankton. Brooks (1888*b*) later saw young medusae released from a hydroid colony and, identifying the young medusae as the same species as the adults earlier described, concluded he had found the hydroid. Mayer (1910) was sceptical. Brooks' description of the hydroid did not differ from the hydroid of *C. hemisphaerica.* The description included stolonal gonothecae with lateral constrictions characteristic of the better known *hemisphaerica.* Only Brooks has reported a conventional hydroid stage. Others (Sigerfoos, 1893; Mayer, 1910; Bougis, 1963) have described a much reduced hydroid stage comprising only hydroid blastostyles within gonothecae, attached to the gonad of the medusa.

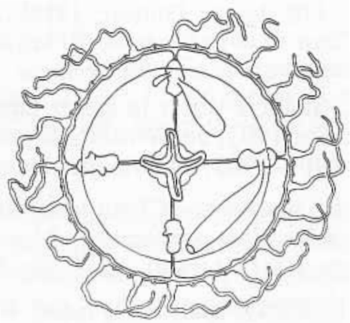


Fig. 13 *Clytia mccradyi.* Redrawn after Mayer (1910 : pl. 35, fig. 1). Diameter *c.* 15 mm.

DISPERSIVE STAGE. A medusa. The following description is after Brooks (1888*b*) and Mayer (1910). Bell shallow, *c.* 15 mm diameter, less than half as high as broad, flexible; stomach short, less than 1/8th as long as diameter of bell, quadrate, with four simple, slightly recurved lips; gonads short, oval, about mid-way between axis and bell margin; velum well developed; 16–24 long, contractile marginal tentacles (type material had 16 only), 'many times as long as diameter of bell', each with statocyst at base; 8–16 other marginal statocysts; 1–4 (?4+) gonothecae borne on one to all of the gonads in many individuals. Gonads of medusa develop either eggs or sperm, or into hydroid blastostyles which produce medusae direct (details in Sigerfoos, 1893 and Mayer, 1910). 4–8 tentacles on release (Brooks, 1888*b*).

REPRODUCTIVE SEASON. Brooks (1888*b*) recorded fertile hydroid material in June, 1887, at Nassau, Bahamas; Mayer (1910) in July at Tortugas, Florida. Medusae from April to July (Mayer).

DISTRIBUTION. In the eastern North Atlantic I know of only one record: Villefranche, S France, found 'from time to time' (Bougis, 1963). Reported elsewhere in the World from the Bahamas and Florida (Kramp, 1959, 1961).

HABITAT. Brooks (1888*b*) reported the 'free' hydroid stage on algae in the harbours of Nassau and Green Turtle, Bahamas.

The hydroid stage is at least sometimes partially suppressed and attaches to or grows on the medusa. Thus the species seems adapted to an oceanic existence and might be found away from coastal waters. Possibly the isolated record from the Mediterranean is evidence of a natural trans-atlantic dispersal.

REMARKS. The unusual life cycle of this species has been checked by at least three independent workers (Sigerfoos, 1893; Mayer, 1910; Bougis, 1963) since the original description by Brooks (1888*b*). Brooks alone claimed to have found a benthic hydroid stage, but Mayer evidently doubted his observation. Although Mayer studied live medusae of the species closely, Brooks' account is explicit and suggests strongly that the benthic hydroids he described were of this species. At the time Mayer wrote such plasticity in the life cycle of a single hydromedusa species would have been regarded unusual and requiring more rigorous proof than today, when several such examples are known (summary in Naumov, 1969).

Brooks stated that the medusa has either 4 or 8 tentacles on release, a departure from the unvarying four usually considered normal in this genus (see p. 42).

Clytia paulensis (Vanhöffen, 1910)
(Fig. 14)

Campanularia paulensis Vanhöffen, 1910 : 298, fig. 19.
Clytia ulvae Stechow, 1919*a* : 47–48, fig. N.
Clytia paulensis: Stechow, 1923*a* : 110, fig. N; Philbert, 1935*b* : 25–26, fig. 4; Picard, 1955 : 186; Millard, 1966 : 481–483, fig. 15 (?syn. *C. ulvae* Stechow, 1919*a*); Millard, 1975 : 221, fig. 73a–d.
Obelia paulensis: Naumov & Stepanyants, 1972 : 37, fig. 2a–b.

TYPE LOCALITY AND MATERIAL. Shallow water in crater lagoon of St Paul Island, S Indian Ocean (38° 40′ S, 77° 34′ E), 26 Apr 1903, on *Sertularella polyzonias* (Linneaus, 1758), coll. Deutsche Südpolar-Expedition 1901–1903; material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Clytia ulvae* Stechow, 1919*a*, infertile colony on *Ulva* (green alga), Marseille, microslide preparation; Munich Zoological Museum. Also 1 non-type specimen, 'Valdivia' sta. 100 (S Africa), det. E. Stechow as *C. ulvae*; MZM.

OTHER MATERIAL EXAMINED (All BMNH material is listed. None is fertile.). Breakwater at S end of Landguard Pt, Felixstowe, Suffolk, SE England, ELWS, Sep–Oct 1976, infertile colony on *Crisia* sp. (Bryozoa) itself on *Tubularia indivisa* Linnaeus, spirit + 1 microslide preparation, coll. & det. R. G. Hughes; 1977.5.7.2. Off Berry Head, Tor Bay, Devon, SW England, *c.* 15 m, Mar–Jun 1973, infertile colony on *Nemertesia* sp., spirit + 1 microslide preparation, coll. R. G. Hughes; 1973.8.13.1 (see Remarks; mentioned, Hughes, 1975 : 291). Off Berry Head, *c.* 15 m, summer 1974, infertile colony on *Nemertesia* sp., co-epizoic with *C. hemisphaerica*, spirit + 1 microslide preparation, coll. & det. R. G. Hughes; 1977.5.7.1 (Fig. 14). Mewstone Ground, near Plymouth, Devon, Oct 1899, infertile colony on *Laomedea flexuosa*, 1 microslide preparation, coll. Marine Biological Association of U.K., ex E. T. Browne colln; 1961.11.14.16 (see Remarks). R. Rance, nr St Malo, NW France, infertile colony on *Hydrallmania falcata* (Linnaeus, 1758), spirit + 2 microslide preparations, coll. M. Philbert; 1935.7.10.1 (?mentioned, Philbert, 1935*b*). Sta. SCD 258 W, Univ. Cape Town Ecol. Survey, 14 Jul 1961, infertile colonies on *Obelia dichotoma*, spirit + 1 microslide preparation, pres. N. A. H. Millard; 1962.6.18.9.

DESCRIPTION OF HYDROID STAGE. Colony stoloniferous, comprising a tortuous, branched, mostly unringed stolon from which usually unbranched pedicels arise at intervals. Pedicels long, occasionally branching as in *C. hemisphaerica* with similar upward-curved bases bringing branches approximately parallel with main pedicel; annulated basally, below hydrotheca and sometimes centrally, forming 1–2 smooth central portions. Hydrotheca

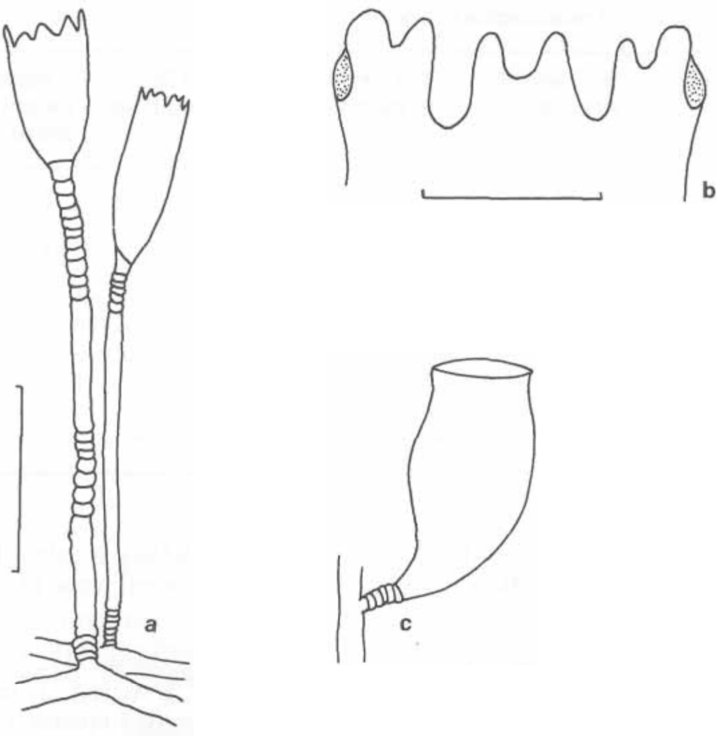


Fig. 14 *Clytia paulensis.* (a) single hydrotheca on pedicel (right) adjacent to same of *C. hemisphaerica* (left), SW England; 1977.5.7.1. (b) part of (a), right hand specimen, enlarged. (c) gonotheca (after Millard, 1975 : fig. 73D). Scales: (a, c) 500 μm; (b) 100 μm.

rather longer than in *C. hemisphaerica*, length : breadth ratio usually 3–4, exceptionally 1½; 7–11 rounded bimucronate cusps; flared appearance immediately below rim resulting from outward bulging of larger embayments; diaphragm oblique; longitudinal folds in hydrothecal wall in microslide preparations can look like striations (Millard, 1975) but are artefacts. Hydranths in present material with 16–22 tentacles. Gonotheca (not seen) ?♂ = ♀, cylindrical, tapering gradually below and slightly above, smooth (after Stechow, 1923*a*; Philbert, 1935*b*; Millard, 1975); borne on stolon on short annulated pedicel. 1–3 medusa buds per blastostyle, pre-release medusa with 4 tentacle buds (Millard, 1975); free medusa not yet described.

Variation. Cusps on hydrothecal rim variable in both length and breadth; always rounded in present material. Embayments between cusps irregular in depth so that adjacent ones are sometimes similar, obscuring bimucronate condition. Hydrotheca length : breadth ratio usually 3–4 but Millard (1966) gave 1¾–3¼, once 1½ (BMNH 1935.7.10.1). Angle of slope of diaphragm variable.

MEASUREMENTS. See Table 3.

DISPERSIVE STAGE. A medusa. Advanced embryos still in the gonotheca have been widely reported as having 4 tentacle buds, as they have in other *Clytia* species, but the free medusa has yet to be described. See also Dispersive Stage under *Clytia linearis.*

REPRODUCTIVE SEASON. No information.

DISTRIBUTION. A widespread, warm water species recorded in the N Atlantic north to Suffolk, SE England. However, *C. paulensis* has been found at only three English localities (present material). Fertile material was reported as 'very common' near St Malo, NW France (Philbert, 1935*b*) but all the English material has been infertile.

Table 3 *Clytia paulensis* Measurements in μm.

	NW France (1937.7.10.1)	NW France (Philbert, 1935*b*)	South Africa (Millard, 1966, 1975)	S Indian Ocean (holotype; Vanhöffen, 1910)
Hydrotheca				
Length	220–350		300–720	360–400
Breadth (max)	130–150		130–330	200
Pedicel length	550–900		500–1800	
Gonotheca (?♂ = ♀)				
Length		900–950		
Breadth (max)		330–410		
Aperture diameter		290		
Pedicel length		50–90		

Other European records are 'the Mediterranean' (Picard, 1958*b*), Naples (Riedl, 1959) and the Glénan Isles, NW France (Fey, 1969); but not the Roscoff area (Teissier, 1965; L. Cabioch, pers. comm.).

HABITAT. Lower shore (present material) to 200 m (Stechow, 1923*a*; Riedl, 1959; Mediterranean); 0–138 m, once 384 m (Millard, 1975, 1977; S Africa). Tolerant of reduced salinity at least as low as 17‰ (Calder, 1976). Usually recorded epizoic on hydroids and other inert animal substrates. The following have been reported: *Laomedea* sp., *Clytia hemisphaerica* (as *C. gracilis*), *Dynamena* sp., *Halecium beanii* Johnston, 1838, *Nemertesia antennina* (Linnaeus, 1758), *Pennaria disticha* sensu Brinckmann-Voss, 1970, *Sertularella* sp. and spines of an echinoid, *Cidaris* sp. (as *Dorocidaris* sp.) (all by Stechow, 1923*a*); *Sertularia cupressina* Linnaeus, 1758, and *Halecium beanii* (by Philbert, 1935*b*); *Hydrallmania falcata* (Linnaeus, 1758), *Obelia dichotoma* and a bryozoan, *Crisia* sp. (present material); and *Nemertesia* sp., *Tubularia* sp. and *Scrupocellaria scruposa* (Bryozoa) in Suffolk and Essex, SE England (by R. G. Hughes, pers. comm.).

REMARKS. The four tentacle buds of the pre-release medusa and the close similarity to *C. hemisphaerica* indicate that *paulensis* is correctly referred to *Clytia*. *C. paulensis* was placed in *Obelia* by Naumov & Stepanyants (1972) because the material they saw was 'strongly branched' but this seems slim reason. Stepanyants (1979) later referred *C. paulensis* to '*Obelia bicuspidata*' Clarke, 1875, a conclusion with which I cannot agree (see notes under *O. bidentata*, p. 117).

The earlier Torbay material listed above, collected in 1973, was the first to be recorded from the British Isles. E. T. Browne's Plymouth material had been collected in 1899 but was overlooked. Browne first identified it as *Campanularia raridentata* Alder, here referred to *Clytia hemisphaerica*; but in 1927 added a note doubting his determination (E. T. Browne ms notebooks **13** : 148–149; Zoology Library, BMNH). The material came to the BMNH as part of the E. T. Browne bequest and was re-identified by the then curator as '*Clytia gracilis* Sars'. The hydrothecal rims, with their rounded bimucronate cusps, clearly differ from those of *C. gracilis* s. str. auct. and the specimen resembles *C. paulensis* in all respects. Although Browne regarded the material as something unusual in 1899 *C. paulensis* was not described until 1910, and he may well have been the first in the World to collect this species.

The type material of *Clytia ulvae* Stechow, 1919*a*, from Marseille, has a bimucronate hydrothecal rim and is undoubtedly *C. paulensis*. Nevertheless, Stechow was among the first to collect *C. paulensis* from Europe and to recognize it as different from *C. hemisphaerica*.

Clytia paulensis is perhaps difficult to identify. It differs from *C. hemisphaerica* in its bimucronate hydrothecal rim, its slender hydrotheca and pedicel and, so far as is known, its consistently smooth gonotheca. Both species are widespread in the World. But in European waters *C. paulensis* has yet to be found north of Suffolk, SE England, whereas *C. hemisphaerica* ranges much further north. Other west European Campanulariidae having bimucronate hydrothecal rims are *Obelia bidentata* and *Laomedea neglecta* which produce taller colonies and branch differently.

Clytia incertae sedis

Two *Clytia* medusae, with 5 and 6 radial canals and diameters of 8 mm and 13 mm respectively, were taken in the southern Adriatic Trough on 9 August, 1969. They were referred to *Phialidium pentata* Mayer, 1900, by Schmidt & Benovič (1977), making the first NE Atlantic record of that species. Kramp (1961) had referred '*P. pentata*' to *Phialidium folleatum* McCrady, 1857 (= *Clytia folleata*) but there remains a possibility that both are abnormal variants of *C. hemisphaerica*. Indeed, Schmidt & Benovič considered: 'It might be possible that all [recorded] specimens [of *pentata, folleata* and also *P. gardineri* Browne, 1904] are abnormal forms of *C. hemisphaerica*'. I concur with their conclusion that more material is needed to resolve these problems.

Leloup (1940 : 21, as *Laomedea*) recorded *Campanularia kincaidi* Nutting, 1899, from the Azores, at 1187 m depth, without description or comment. The record was repeated by Rees & White (1966 : 277, as *Obelia*). The only previous record from the Atlantic was of two colonies from the Caribbean, also by Leloup (1935 : 20). In the absence of more definite indication it seems best to omit the species from the present survey. The nominal species was provisionally referred to *Clytia* by Cornelius (1975*a* : 280).

Subfamily **OBELIINAE** Haeckel, 1879

Obelidae Haeckel, 1879 : 163 (part).
Obelinae: Mayer, 1910 : 231 (part); Russell, 1953 : 296.

NOMENCLATURE. The root of the subfamily name is *Obelia*, and the spelling Obelinae is incorrect.

DIAGNOSIS. Campanulariidae with erect hydrocaulus and true hydrothecal diaphragm; no sub-hydrothecal spherule; stolon not anastomosing; medusa liberated but reduced (*Obelia*), or vestigial and retained (the rest).

TYPE GENUS. *Obelia* Péron & Lesueur, 1810*a* (by present designation).

SCOPE. The genera *Gonothyraea* Allman, 1864*a*, *Hartlaubella* Poche, 1914, *Laomedea* Lamouroux, 1812 and *Obelia* Péron & Lesueur, 1810*a*.

REMARKS. The subfamily name is the oldest available. The Obeliinae was recognized also by Mayer (1910) and Russell (1953), who like Haeckel based their classifications on the medusa stage alone. All the included genera occur in the eastern North Atlantic and are defined below.

Genus ***GONOTHYRAEA*** Allman, 1864*a*

Gonothyraea Allman, 1864*a* : 374.
Gonothyrea auct. (laspus pro *Gonothyraea*).
Campanularia, Laomedea and *Obelia* part, auct. (see Remarks).

TYPE SPECIES. *Laomedea loveni* Allman, 1859*a*; designated by Millard (1975). The originally included species were *L. loveni*, *Campanularia geniculata* sensu Lister (= *G. loveni*; see Cornelius, 1977*a* : 47) and *L. gracilis* Sars. The last named was based on a mixed series comprising what was probably *Clytia hemisphaerica* (hydroid) and *G. loveni*, but following designation of lectotype material (p. 94) it is now subjectively referred solely to *C. hemisphaerica*.

DIAGNOSIS. Campanulariidae forming upright, branched colonies; stem flexuose; hydrothecae tubular, pedicellate, alternate; diaphragm present; no sub-hydrothecal spherule; gonophore a gonomedusa.

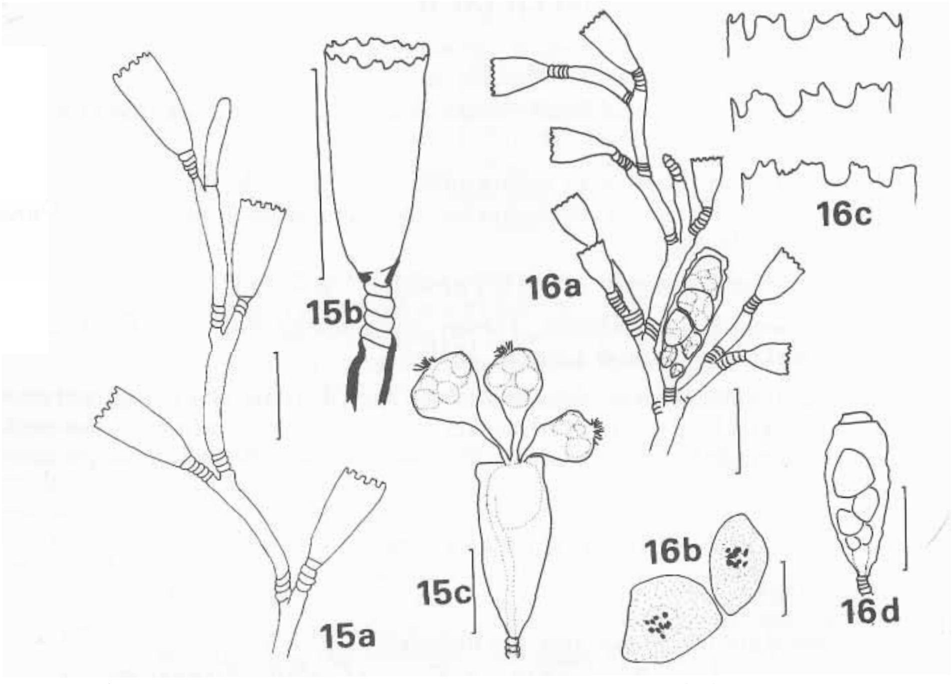
REMARKS. I have discussed elsewhere the past confusion between *G. loveni* and nominal species of *Campanularia, Laomedea* and *Obelia* (in Cornelius, 1977*a*). This confusion probably delayed by some decades the discovery of the alternation of generations in medusoid coelenterates; and, it can be claimed, in other animal groups.

Gonothyraea loveni (Allman, 1859*a*)

(Fig. 15)

Laomedea gracilis Sars, 1857 : pl. 2, fig. 4 only (not pp. 51–54, nor figs 1–3, 5, = *Clytia hemisphaerica*, q.v.).
Laomedea loveni Allman, 1859*a* : 138–140.
Gonothyraea (Laomedea) loveni: Allman, 1864*b* : 376.
Gonothyraea hyalina Hincks, 1866 : 297–298; Hincks, 1868 : 184–185, pl. 35, fig. 2.
Gonothyraea loveni: Hincks, 1868 : 181–183, pl. 25, fig. 2.
Obelia loveni: Naumov, 1960 : 264–265, fig. 152 (syn. *G. hyalina* Hincks); Naumov, 1969 : 285–287, fig. 152 (syn. *G. hyalina* Hincks).

NOMENCLATURE. Bedot (1912 : 294; 1916 : 107) listed but two uses of the combination *Obelia hyalina*, and none of *O. loveni*, in his synoptic works (1901–1925). *Obelia hyalina* Clarke, 1879, and *O. hyaliana* Vannucci, 1955, are different nominal species.



Figs 15–16 **Fig. 15** *Gonothyraea loveni.* (a) tip of colony, Bay of Biscay; 1959.9.17.59. (b) same, hydrotheca. (c) ♀ gonotheca and gonomedusa, Vadso, E Finmark, Norway, intertidal; 1912.12.21.184. Scales (a–c) 500 μm. **Fig. 16** *Hartlaubella gelatinosa.* (a) part of ♀ colony. Note large embryos. SW England; 1959.9.17.57 (microslide preparation). (b) same, two blastomeres. Note conspicuous chromosomes (see Remarks). (c) hydrothecal rims. Israel; 1932.8.13.1. (d) unopened ♂ gonotheca, NE England; 1969.11.28.2. Scales: (a, d) 500 μm; (b–c) 50 μm.

TYPE LOCALITY AND MATERIAL. Firth of Forth, Scotland (Allman, 1859*a* : 137); material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Gonothyraea hyalina* Hincks, 1866, syntypes, Shetland Is, Scotland, several colonies in spirit, coll. J. G. Jeffreys, on '*Tubularia, Halecium*, etc.', ex Hincks colln; 1899.5.1.157.

OTHER MATERIAL EXAMINED. BMNH collection, about 80 specimens.

DESCRIPTION. Colony erect, stem monosiphonic, delicate, variably flexuose, internodes usually slightly curved, irregularly branched, up to *c.* 100 mm. Annuli above origins of branches. Hydrothecal pedicels usually annulated throughout but smooth central portion frequent; usually tapering distally to roughly half proximal diameter. Hydrotheca cylindrical, campanulate, length 1½–3 times maximum breadth; rim delicate, slightly outturned, castellate, raised portions often notched (Fig. 15); often longitudinal folds in hydrotheca. Hydranth with 20–25 tentacles; branched tentacles recorded but rare (Hamond, 1957); hypostome spherical. Gonotheca (♂ narrower than ♀, otherwise similar; Miller, 1973) cylindrical, truncated above, tapering below. Conspicuous sporosacs or ova develop internally and later extrude up to four together as tentaculate, sub-spherical reduced medusae termed gonomedusae (formerly called meconidia; see Dispersive stage).
Variation. Internode length and curvature, length of hydrotheca and the degree of tanning and translucency of the perisarc are all variable.

DISPERSIVE STAGE. A planula larva. The reduced medusa is retained until after the planulae have escaped. It does not swim but simply drops off. Ellis (1756*a*, *b*, *c*, 1767, but not 1755; see Cornelius, 1977*a*) recorded that the 'released' gonomedusae exhibited strong tentacle movements and adopted a 'worm-like' shape, but his observations seem not to have been repeated.

The gonomedusae were interpreted as highly developed sporosacs by Allman (1859*a*) who coined for them the long standing term meconidia. But Goette (1907) and more recently Miller (1973) have shown that they are actually reduced medusae. Miller introduced the preferable term gonomedusae. Wulfert (1902) provided a summary of early reproductive studies on this species.

REPRODUCTIVE SEASON. Published records suggest that in the English Channel and southern North Sea the species breeds almost throughout the year (Mar–Sep, Hamond, 1957; Jan–Apr & Sep–Nov, Marine Biological Association, 1957; May–Aug & Oct–Nov, Teissier, 1965); but an intertidal population which I studied in 1974 in Sussex, SE England, bore gonomedusae only during the first two weeks of April. Some of the published records might refer to colonies with developing gonothecae, or with empty ones.

Fertile gonothecae were reported at Naples from January to May and in September by Lo Bianco (1909).

DISTRIBUTION. Widespread in suitable habitats and often common. Occurs throughout western Europe north to W Greenland (but not E), Iceland, Faeroes, Spitzbergen, Barents Sea, Murman coast and White Sea (Mathiesen, 1928; Kramp, 1929, 1938; Calder, 1970). In the Baltic *G. loveni* is said to penetrate as far as Helsinki in the Gulf of Finland and the Aland Isles in the Gulf of Bothnia (Linko, 1911; Stechow, 1927; Naumov, 1969). It has been recorded from the Mediterranean Sea (Picard, 1958*b*; Riedl, 1959) and Black Sea (Naumov, 1969); and on the Atlantic coast from W France and Morocco (Billard, 1927; Patriti, 1970).

Millard (1975) recorded the species in South Africa only from Cape Town docks and considered this and other Southern Hemisphere records to result from transport by ships. Hence *G. loveni* might be found further south than Morocco. Rees & White (1966) listed a dubious old Azores record from the unusual depth of 845 m.

HABITAT. Intertidal, usually in pools, and offshore. Naumov (1960, 1969) gave a normal depth range of 0–30 m, with an extreme lower limit of 200 m; and Mathiesen (1928) similarly gave 6–200 m. The BMNH material falls within these limits. The record at 845 m off the Azores listed by Rees & White (1966) is much deeper, and needs confirmation. *G. loveni* is tolerant of reduced salinity at least to 12‰ (Calder, 1976). It has been recorded on a variety of animal, plant and inorganic substrates (Hincks, 1868; Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965), and there is no regular association.

REMARKS. Hummelinck (1936), Naumov (1960, 1969) and others listed by Calder (1970) regarded *Gonothyraea loveni* and *G. hyalina* as conspecific and I concur.

The distinctive method of reproduction has been described in part by many authors from Ellis onwards. Nevertheless *G. loveni* was widely confused with *Obelia* spp. and with *Laomedea flexuosa* until Wright (1858, 1859) realized it was distinct (Cornelius, 1977*a*; Cornelius & Garfath, 1980). But Wright did not provide a name. The species was soon named by Allman (1859*a*) who took Joshua Alder's suggestion (in litt.) that the species was valid. Alder was perhaps unaware of Wright's publications. From the literature it would appear that Wright and Alder worked independently; but since both communicated freely with Hincks (e.g. 1868 : preface) they could have been in touch directly. It may be difficult to find out who among these British workers really was first to recognize *G. loveni.*

Most of the life cycle is well understood and has been redescribed in detail by Miller (1973; see also Bergh, 1879, Wulfert, 1902, and Goette, 1907). Aspects of stolon growth were described by Wyttenbach, Crowell & Suddith (1973).

Laomedea gracilis Sars, 1850, 1857, was based on a mixed type series and this has caused confusion. The material illustrated in 1857 was partly *G. loveni* (see synonmy) but predominantly *Clytia hemisphaerica* (see Stechow, 1923*a* : 111). The material resembling *C. hemisphaerica* in this series is here designated lectotype. Hence the species name *loveni* Allman, 1859*a*, remains available. In any case, the name *gracilis* is preoccupied. This and other problems relating to '*L. gracilis*' are considered under *C. hemisphaerica*, where a new name is introduced in place of *L. gracilis* (p. 78).

Obelia hyalina Clarke, 1879, has been referred to *Obelia dichotoma* (by Cornelius, 1975*a* : 266) and is not *G. hyalina* Hincks. Hence Billard's (1931*a*) record of '*Obelia hyalina* Clarke' from Mauritania refers to *O. dichotoma* and not *G. loveni.* This homonymy is discussed further under *O. dichotoma* (p. 119).

The affinities of *G. loveni* are discussed above (pp. 47–49).

Genus *HARTLAUBELLA* Poche, 1914

Sertularia, Campanularia, Obelia and *Laomedea* auct., part.
Obelaria Haeckel, 1879 : 172 (part).
Obelaria Hartlaub, 1897 : 488 (homonym).
Hartlaubella Poche, 1914 : 76.

TYPE SPECIES. *Sertularia gelatinosa* Pallas, 1766; by monotypy.

DIAGNOSIS. Erect, colonial Campanulariidae with polysiphonic stems and second order branching; hydrotheca pedicellate, with diaphragm and castellated rim, without spehrule; no medusa stage (see Remarks under *H. gelatinosa*).

REMARKS. The genus name *Obelaria* Haeckel, 1879, was proposed as a nom. gen. nov. for the hydroid stage of *Obelia*, of which name it is a junior synonym (Cornelius, 1975*a* : 254). Haeckel included *Sertularia gelatinosa* Pallas, 1766, in its scope. Confusion was caused later when Hartlaub (1897) independently coined the generic name *Obelaria* to apply to a gen. nov. comprising *Sertularia gelatinosa* alone. Although Hartlaub's name is a homonym of Haeckel's and cannot be used, Hartlaub's generic concept is accepted here. The next available name for the genus is *Hartlaubella* Poche, 1914, of which *gelatinosa* has always been the only member.

Hartlaubella gelatinosa (Pallas, 1766)
(Fig. 16)

Sertularia gelatinosa Pallas, 1766 : 116–117.
Campanularia flemingii Deshayes & Edwards, in Lamarck, 1836 : 133–134.
Laomedea gelatinosa: Couch, 1884 : 4–5, 39–40; Hincks, 1852 : 85–86; Da Cunha, 1944 : 65–66; Vervoort, 1946*a* : 300–303, fig. 133 (syn. *Campanularia flemingii* Deshayes & Edwards).
Obelia gelatinosa: Hincks, 1868 : 151–154, pl. 26, fig. 1; Naumov, 1960 : 268–269, figs 157–158; Naumov, 1969 : 290–291, figs 157–158.
Obelaria gelatinosa: Haeckel, 1879 : 172, 173, 176; Hartlaub, 1897 : 488–495 (non Haeckel); Nutting, 1915 : 88–90, pl. 24, figs 1–5.
Hartlaubella gelatinosa: Poche, 1914 : 76; Stechow, 1925 : 522; Stechow, 1927 : 309; Teissier, 1965 : 17; Calder, 1970 : 1543; Cornelius & Garfath, 1980 : 283.
Campanularia gelatinosa: Ralph, 1957 : 820, fig. 1b–f.

TYPE LOCALITY AND MATERIAL. Belgian coast (Pallas, 1766; Ralph, 1957); specimen not located.

MATERIAL EXAMINED. BMNH collection, about 50 specimens.

DESCRIPTION. Colony elongate; small colonies loosely conical, large colonies bushy, up to *c.* 200 mm; main stems straight or branched, polysiphonic. Final branches monosiphonic, arranged irregularly all round stem, ± dichotomous, flexuose; internodes usually curved but sometimes straight, length varied, 5–9 rings basally. Hydrothecae on ringed, slightly tapering pedicels, long-campanulate to cylindrical; rim often abraded even but initially castellate with notch of varied depth in centre of each blunt cusp; embayments rounded; diaphragm transverse. Hydranth with 22–28 tentacles, hypostome spherical. Propagation by stolons in spring. Gonotheca ♂ = ♀, axillary, inverted-conical, sides smooth to sinuous; aperture wide, distal, on short collar; ova (4–6) and embryos larger than usual in family; nuclei of blastomeres large, with unusually conspicuous chromosomes.
Variation. Internode length and curvature, angle of flexure of stem and length : breadth ratio of hydrotheca are all variable. The hydrothecal rim often abrades smooth.

DISPERSIVE STAGE. Planulae, developing within the gonotheca. Some authors have mistakenly reported a medusa stage.

REPRODUCTIVE SEASON. May–August in NW France (Teissier, 1965); July, 1934, Northumbria (H. O. Bull, in Evans, 1978).

DISTRIBUTION. Recorded from southern Scotland, Oslo Fjord, Danish waters and part of the Baltic south to the Mediterranean and Black Seas. The species is common in Dutch, Belgian, Irish, Welsh, English and N & W French waters (Vervoort, 1946*a*; Leloup, 1952; BMNH collection; Billard, 1927; Teissier, 1965).

Trustworthy Scottish records are few and there seems only one this century, although the species is still common in NW England: Tay Estuary (Fleming, 1820; Alexander, 1932); Shetlands, Berwick Bay and Solway Firth (Johnston, 1847); ?Dundee (BMNH 1851.7.25.227, specimen not located). Hincks (1868) repeated several of these records and Norman (1869) gave another Shetlands locality. Recent English records are numerous, northerly ones including Northumberland (Alexander, 1932) and Morecambe Bay (J. Clare, pers. comm. & BMNH 1970.8.28.6–10).

The species was recorded from 13 localities in Oslo Fjord by Christiansen (1972) but his statement that the species occurs north to Finmark is questionable, and Linko (1911) and Broch (1918) listed no records so far north. Neither also did Kramp (1929, 1938), who likewise considered the species absent from Iceland and the Faeroes. Naumov (1969) gave an Iceland record without further detail; but with greater precision stated the northern limit in the Baltic to be 'Port Liepaja = Libava', Latvia. Kramp (1935) listed several Danish records north to Frederikshavn, NE Denmark, and repeated Stechow's (1927) record from Travemünde, near the southern limit of the Baltic Sea. Rasmussen (1973) reported the species from Siaelland Island, southern Denmark.

Mediterranean records are few. Naumov (1969) gave 'Black Sea, Mediterranean and Gibraltar'. Although Picard (1958*b* : 197) expressly excluded the species from the Mediterranean list Rossi (1950 : 205) had earlier recorded it from NW Italy, the Adriatic and Strait of Gibraltar. Linko (1911) listed Black Sea material.

The species is known from Portugal (Nobre, 1931; Da Cunha, 1944) but has yet to be recorded so far south as Morocco (Patriti, 1970).

HABITAT. Intertidal, particularly in pools and run-off from saltings, and shallow depths offshore. Often in estuaries and tolerant of reduced salinity at least to 6·2‰ (Vervoort, 1946*a*). Also tolerant of silt.

The lower depth limit is probably *c.* 15 m. A record from 30 m off the Scilly Isles was based on *Obelia bidentata* material (BMNH 1969.9.9.6; mentioned, Robins, 1969). Couch (1844) recorded material from beneath intertidal stones and on algae, but that under stones might have been *Laomedea neglecta* (*cf.* p. 107).

REMARKS. The nomenclatural history of this species is involved. The name *Sertularia gelatinosa* was first applied by Pallas (1766) to the 'Corallina confervoides, gelatinosa alba, geniculis crassiusculis, pellucidis' of Ray (1724 : 34, para. 7). However, Ellis (1755 : 20, p. 11, figs B, b) assigned bryozoan material to Ray's species, providing clear illustrations. Linnaeus (1758 : 812) included the descriptions of both Ray and Ellis in a single species to which he gave the new name *Sertularia spinosa.* This name is currently applied to a bryozoan species in the combination *Vesicularia spinosa* (Linnaeus, 1758), for example by Prenant & Bobin (1956). The bryozoan name *Sertularia sericea* Pallas, 1776 : 114, was a nom. nov. for *S. spinsoa* and is its junior objective synonym. Pallas elsewhere (1766 : 116–117) adequately described *gelatinosa.*

Fleming (1820) noted that Ray and Ellis each described a different species but referred Ray's description to *Obelia geniculata*, not to the present species. However, Pallas' account is clear and he contrasted *gelatinosa* with both *O. geniculata* and *O. dichotoma.* Also he noted the polysiphonic stem and cusped hydrothecal rim—both unusual in *Obelia.* Even so, it could be argued that Pallas had material of *Obelia bidentata* before him since that species superficially resembles *H. gelatinosa.* There is some evidence that *O. bidentata* did not then occur in European waters. Even if it did, Pallas might have overlooked the fine cusps on the hydrothecal rim which are a main distinction. But despite these small doubts it seems highly likely that Pallas' description indeed refers to the present species. Hincks (1868 : 152) himself commented that Pallas' description was 'admirable, and is the only one we possess which is not positively incorrect'; so the case is strong. Hincks summarized some of the additional taxonomic confusion surrounding the species between 1820 and 1868.

Campanularia flemingii Deshayes & Edwards, in Lamarck, 1836, was based on material of the present species described by Fleming (1820) from Scotland—although Deshayes & Edwards gave the type locality as coasts of England! Fleming had referred his material to *gelatinosa* but noted that it disagreed with Pallas' description in having even hydrothecal rims. Fleming thought Pallas might have mistaken tentacle tips for castellations on the rim, and assumed that *gelatinosa* always had an even rim. Deshayes & Edwards thought Pallas too careful to make this mistake and concluded that two species were involved, one with castellations and one without. Probably Fleming's material simply had hydrothecae in which the rims were worn smooth! Johnston (1838, 1847) realized the confusion and referred *flemingii* back to *gelatinosa.* He was followed by Bedot (1905) and Vervoort (1946*a*), and I concur. Gray (1848), however, gave *C. flemingii* specific rank, but did not cite material. Gray seems usually to have relied heavily on Johnston's work but on this occasion clearly did not. Possibly Edwards, who sometimes worked on the British Museum collections, persuaded him to accept the species.

Thaumantias leucostyla Will, 1844 : 73, pl. 2, figs 16–17, based on an *Obelia* medusa, was referred to the present species by Bedot (1912 : 328) without comment; but as *gelatinosa* has no medusa stage this must be wrong (see next paragraph). It would be difficult to identify the medusa beyond *Obelia* sp. from Will's description.

Several authors, including Hincks (1852, 1868), have stated that *H. gelatinosa* releases a medusa, which it does not (Cornelius, 1975*a* : 279). It could be that Hincks and the others saw medusa release from *Obelia bidentata*. But the first European records of that species date from the early 1900s; and it seems improbable that Hincks would have made such a mistake when identifying a hydroid. His comment that the branches of *gelatinosa* 'droop slightly' fits *bidentata*, but this is not conclusive. Another possible explanation of his apparent mistake is that he took the unusually large ova of *H. gelatinosa* for developing medusae.

Couch (1844) had much earlier given a correct (and posthumous) description of the life cycle, reporting planula development and release, and early development of the young colony. In addition he noted that the planulae were propelled by cilia. But his contemporaries were still muddled, and had Couch lived a little longer he might have corrected some of the ensuing confusion. Van Beneden (1843, 1844) reported medusa release in *H. gelatinosa* but his material was actually *Obelia dichotoma* (see Cornelius, 1975*a*; and 1977*a* for other references). Hincks (1852) also attributed a medusa to *gelatinosa*. Van Beneden's error of identification was later appreciated by Hincks, who referred Van Beneden's material to a synonym of *O. dichotoma*, namely *O. longissima* (Pallas, 1766). Similarly, the much later report by Godeaux (1941) that *gelatinosa* had a medusa was also based on *O. dichotoma* material. It might be relevant that Godeaux worked at the Van Beneden Institute! Then Leloup (1947), paralleling Hincks, referred Godeaux' material to *O. longissima*.

A convenient distinction between *O. bidentata* and *H. gelatinosa* is that in side view the branches of *bidentata* show a graceful sigmoid curvature lacking in *gelatinosa*.

The large chromosomes illustrated here recall in shape and size those of *Obelia* medusae, shown by Faulkner (1929).

Genus *LAOMEDEA* Lamouroux, 1812

Laomedea Lamouroux, 1812 : 184.
Campanularia Lamarck, 1816 : 112 (part).
Lomedea Pickering, in Dana, 1846 : 689 (lapsus pro *Laomedea*, see p. 78).
Campalaria Hartlaub, 1897 : 449.
Eucampanularia Broch, 1910 : 184 (part; see p. 52).
Eulaomedea Broch, 1910 : 189; Millard, 1975 : 223.
Cmpanularia Mulder & Trebilcock, 1914 : 11 (part; lapsus pro *Campanularia*).
Laomedea (*Paralaomedea*) Hummelinck, 1936 : 57; Vervoort, 1946*a* : 285.
Eulaomeda Rees & Thursfield, 1965 : 102 (lapsus pro *Eulaomedea*).

TYPE SPECIES. *Laomedea flexuosa* Alder, 1857 (proposed designation by Cornelius, 1981). Broch (1905 : 10) proposed '*Laomedea loveni* Allman, 1859*a*' as type species but *loveni* was not among the species originally included in the genus and is not eligible.

DIAGNOSIS. Colonial Campanulariidae with: polyp generation forming upright colonies; stolon branching but not anastomosing; hydrotheca pedicellate, lacking spherule; true diaphragm present; annular perisarc thickening inside base of hydrotheca; gonotheca stolonal or axillary, aperture typically circular, wide; gonophores sessile, interpreted as vestigial medusae in many species.

REMARKS. I have previously pointed out (Cornelius, 1975*a*) that *Laomedea* Lamouroux, 1812, is a junior synonym of *Obelia* Péron & Lesueur, 1810*a*. But the name *Laomedea* is so well known that I have submitted a case to the International Commission on Zoological Nomenclature recommending that it be conserved by application of the Plenary Powers. I have proposed that *Laomedea flexuosa* Alder, 1857, be designated type species although it was not originally included. The alternative, of applying the Rules of Nomenclature, would result in the virtually unused name *Campalaria* Hartlaub, 1897, being employed for the present genus. Further details of the case, and another concerning the genus name *Campanularia* (p. 51), have been presented elsewhere (Cornelius, 1981).

The subgenus name *Eulaomedea* Broch, 1910, type species *Laomedea flexuosa* Alder, 1857, by monotypy, is a junior synonym. Stechow (1923*a* : 95) referred *Eulaomedea* to *Laomedea* Lamouroux, 1812, and apart from subgeneric use by Splettstösser (1924), Hummelinck (1936) and Vervoort (1959) there seems to have been no further appearance of *Eulaomedea* in the literature until Rees & Thursfield (1965). These authors upgraded *Eulaomedea* to genus status, including within its scope '*E. angulata*', '*E. flexuosa*' and '*E. calceolifera*'. Finally Millard (1975) employed *Eulaomedea* to embrace *flexuosa* and *calceolifera* alone. Thus the name has not been widely used and Broch (e.g. 1918) himself came to drop it, without comment. For further details see Cornelius (1981).

The subgenus *Paralaomedea* was apparently introduced by Hummelinck (1936). The type species is *Laomedea neglecta* (Alder, 1856*b*; by monotypy). Vervoort (1946*a*) followed Hummelinck's usage. But the unusual acrocyst of *neglecta* was shown by Splettstösser (1924) to be medusoid in origin, so there seems inadequate reason for subgeneric separation.

Laomedea angulata Hincks, 1861*b*
(Fig. 17)

Laomedea angulata Hincks, 1861*b* : 261, pl. 8; Hummelinck, 1936 : 51–52, fig. 5; Picard, 1958*b* : 191 (syn. *L. sphaeroidea* Stechow); (*non* Da Cunha, 1944 : 63, fig. 36; = *Laomedea calceolifera*).
Campanularia angulata: Hincks, 1868 : 170–171, pl. 34, fig. 1, woodcut 14 (p. 136); Fraipont, 1880 : 433–466, pls 32–34; Billard, 1904*b* : 46, 47, 53, 55, 57, 65, 67, 72–82, 97, 144, 173, pl. 3, figs 1–7, pl. 5, figs 1–2, 7, 10; Faure, 1965 : 419–426, figs 1b, d, 2a, b, 3a, b.
Laomedea sphaeroidea Stechow, 1932 : 85–86.
Eulaomedea angulata: Rees & Thursfield, 1965 : 101–102.

TYPE LOCALITY AND MATERIAL. Hincks (1861*b*) based the original description on specimens from South Devon and the Isle of Man. Some of this material is preserved as follows: (i) Hancock Museum, Newcastle upon Tyne, infertile colony on single blade of *Zostera* L. (eel grass), in spirit, labelled '*Laomedea angulata*, Ramsey, Isle of Man. Revd T. Hincks' and, on a second label, '*Campanularia angulata* Hincks' (mentioned, Cornelius & Garfath, 1980); (ii) BMNH, several colonies on blades of *Zostera*, in spirit, in two tubes. One contains a single, wide blade of *Zostera* supporting an infertile colony of *C. angulata*; the other tube five *Zostera* blades, all much narrower than that in the first, each supporting one or more fertile colonies of *C. angulata*. The two tubes, in one jar, jointly bear the registered number 1899.5.1.149. In the bottom of the jar, detached from the tubes, were two faded labels written by Hincks: '*Campanularia angulata* Hincks, Isle of Man', and '*Campanularia angulata* Hincks, Britain'. There seems no indication which label originally belonged to which tube. Although the narrow leaved *Zostera* resembles that in the Hancock Museum specimen, labelled Isle of Man, there is no further indication that the BMNH thin leaved specimen came from there too.

Probably all this material was identified by Hincks at some time, but whether he saw it before or after the date of publication of the first description is not clear. Hence, it is not possible to decide whether the specimens should be treated as syntypes or neotypes.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Laomedea sphaeroidea* Stechow, 1932, fertile colonies taken from *Zostera*, Sète, S France, microslide preparations; Munich Zoological Museum.

OTHER MATERIAL EXAMINED. BMNH collection, *c.* 30 specimens from Britain and the Channel Islands and 13 microslide preparations from the Lagoon of Venice. Amsterdam Zoological Museum and Leiden Natural History Museum, Netherlands, *c.* 20 specimens.

DESCRIPTION. Mature colony comprising several erect, monosiphonic stems inserted at approximately regular intervals on an almost straight, little branched or unbranched, smooth hydrorhiza; recorded reliably only on eel grasses; stolons usually (Fraipont, 1880; Billard, 1904*b*) growing parallel with the leaf margins. Stems flexuose, internodes markedly straight (rarely, faintly curved), angle between them 90°–120°, length : breadth ratio variable; 1–*c.* 10 annuli basally in BMNH material. Late in season stems terminate in long, often curling

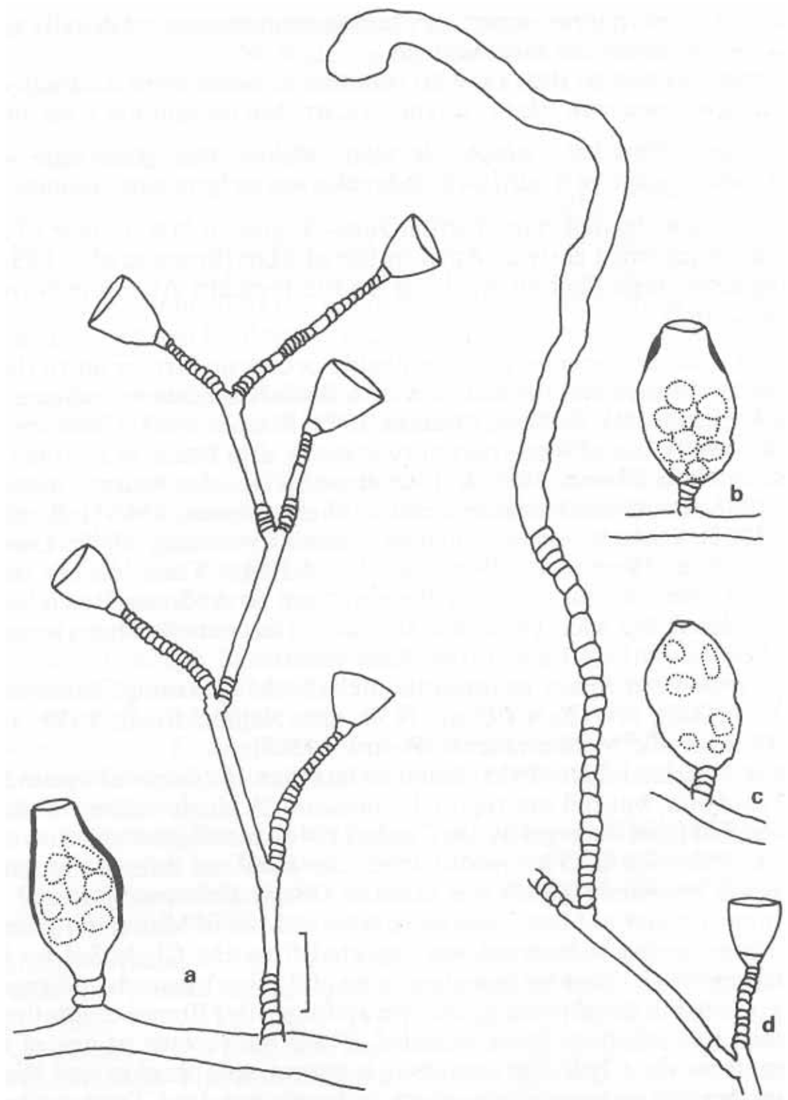


Fig. 17 *Laomedea angulata.* (a) part of colony, including hydrocaulus and stolonal ♀ gonotheca with embryos at different stages of development, Jersey; 1959.9.17.11. (b–c) ♂ gonothecae, Plymouth, SW England; 1959.9.17.3, 12. (d) vegetative terminal stolon; as (c). Scale (a–d) 500 μm.

tendrils approximately same width as internodes except at often recurved tip region which is wider. Tendrils probably represent modified hydranths: those of *Obelia dichotoma* differ (see Remarks). Hydrothecae campanulate, delicate, usually slightly flared distally, length *c.* 1½ times maximum breadth, thin walled and not thickened; diaphragm usually transverse but occasionally slightly oblique; pedicels 3–15 ringed, slightly tapering distally, sometimes with smooth central portion (e.g. BMNH 1959.9.17.11). Hydranth with 24–30 long tentacles alternately elevated and depressed; hypostome large, spherical when dead but (Fraipont, 1880) when alive constantly changing in shape; tissues colourless. Gonothecae apparently always borne on stolon. ♀ elongate-ovate, aperture distal, wide, on slightly demarcated neck, usually with sub-terminal internal strengthening ring; on short, 3–6 ringed pedicel; containing several eggs (see Remarks); planulae brooded internally. ♂ similar, aperture narrower;

containing several ♂ gonophores; sometimes said to be more tapered distally than ♀, but this not evident in BMNH series. No medusa stage.
Variation. Apparently minor. Broch (1933) regarded *L. calceolifera* a variety of the present species, proposing a forma *typica* for *L. angulata* s. str., but his opinion is no longer followed.

DISPERSIVE STAGE. Planulae, which develop within the gonotheca (e.g. BMNH 1959.9.17.11). Also vegetative tendrils which break away to form new colonies.

REPRODUCTIVE SEASON. Sexual reproduction June–August in NW France (Teissier, 1965), but fertile material recorded early as April in Isle of Man (Bruce *et al.*, 1963, material not examined). Vegetative reproduction involving tendrils typically August to November in NW France (Teissier, 1965).

DISTRIBUTION. A southerly species which probably occurs no further north than the British Isles. Unchecked published records and data with BMNH specimens indicate the following localities in NW Europe: SW Scotland (Rankin, 1901; Ritchie, 1911; Chumley, 1918); N & S Ireland (Hincks, 1868); Isle of Man (part of type series; also Bruce *et al.*, 1963); Scilly Isles, 1967 (Robins, 1969); S Devon, 1898 & 1906 (type series; also Marine Biological Association, 1957; a 1936 record on a barnacle seems unlikely); Dorset, BMNH; Roscoff (Fraipont, 1880; Faure, 1965; Teissier, 1965); Channel Islands (Vervoort, 1949; Leiden NHM & BMNH); Netherlands (Vervoort, 1946*a*; Leiden NHM). There seems only a single, unchecked record from the east coast of Britain, from St Andrews Bay (Crawford, 1895, repeated in Laverack & Blackler, 1974); and the species has not often been recorded from the many *Zostera* beds of southern England (see Addendum).

Published records from Spain southwards include the following: Santander, N Spain, (Rioja y Martín, 1906); NW Italy (Rossi, 1950; also Naples, Riedl, 1959, and lagoon of Venice, BMNH material); 'Mediterranean' (Picard, 1958*b*).

At Castiglione, Algeria, Picard (1955) found no less than 18 species of hydroids growing on the eel grass *Posidonia*, but did not report *L. angulata.* A single colony of the species was erroneously reported from Portugal by Da Cunha (1944), his illustration showing a mature ♀ gonotheca of *L. calceolifera.* The record from the Falkland Islands by James Ritchie, repeated by Rees & Thursfield (1965), was based on *Obelia dichotoma* material.

The northernmost material I have seen came from the Isle of Man (type series; also Bruce *et al.*, 1963). More northerly material was reported from the Clyde Sea by both Rankin (1901) and Ritchie (1911), the latter repeating some of Rankin's records and giving some new ones. However, the depth range given by the two authors, 30–130 m, exceeds the depths from which the species has otherwise been recorded. There are records of one of the substrate plants, *Zostera*, from the Clyde Sea area so it is conceivable Rankin and Ritchie at their deeper localities dredged up loose plants which had sunk; but dead *Zostera* often floats! Den Hartog (1970) gave 7 m as the deepest British record of *Zostera marina* L. (in the Scilly Isles) but cited Danish and Mediterranean records down to 11 m and one from the Pacific coast of the U.S.A. at 30 m, adding credibility to at least some of the Clyde Sea records. He gave the NE Atlantic distribution of *Z. marina* as Algeria (Castiglione), S France (rare) and N Mediterranean north to the arctic coast of the U.S.S.R., so it can be assumed that the northern limit of *L. angulata* is not determined by availability of eel grass.

However, the close association of this species with the eel grasses certainly affects its distribution. Thus *Zostera* almost died out in England in the 1930s (Tutin, 1942), and there is a virtual lack of *L. angulata* records since the 1900s. See also Addendum.

L. angulata was *not* recorded in several surveys of North Sea coasts, as follows: Northumberland and Durham (Robson, 1914), Norfolk (Hamond, 1957; Hamond & Williams, 1977), Belguim (Leloup, 1952), Denmark (Kramp, 1935; Rasmussen 1973) and W Sweden (Rees & Rowe, 1969). The record from Danish waters by Vervoort (1946*a*) probably referred to Broch's (1928) record as *Campanularia conferta* and should be rejected (W. Vervoort, pers. comm.). The species has still to be recorded from Denmark (K. W. Petersen, pers. comm.); but a record from the Great Belt, Kattegat, by Winther (1879, repeated in Stechow, 1927) if confirmed would be the most northerly of the species. A record dated 1960 from 20 m depth off SW Wales, quoted by Crothers (1966), seems dubious since both depth and area would be unusual. However, *Zostera* does occur there (K. Hiscock, pers. comm.).

HABITAT. Intertidal and shallow sublittoral, the deepest reliable record being 6–8 m (Studland Bay, Dorset, during or before 1890, coll. R. Kirkpatrick, pres. F. Beckford; BMNH 1899.7.22.1). Deeper records, from the Clyde Sea and off SW Wales, cannot be substantiated. Faure (1965) reported that *L. angulata* grew in a zone on the shore at Roscoff above that occupied by *L. calceolifera*; but the numerous records from shallow offshore localities show that *L. angulata* is not confined to the intertidal zone. A record from 64 fathoms (130 m) near the Falkland Is repeated by Rees & Thursfield (1965) was based on *Obelia dichotoma* material.

L. angulata has been widely recorded on the eel grasses, *Posidonia* and *Zostera* (Hincks, 1861*b*; Fraipont, 1880; Philbert, 1935*b*; Hummelinck, 1936; Vervoort, 1946*a*; Rossi, 1950; Riedl, 1959; Faure, 1965) and only seldom on other substances (sertularian hydroids by Bétencourt, 1888; *Laminaria* by R. Oppenheim, in Vervoort, 1949; *Dictyota dichotoma* by Philbert, 1935*b*; *Balanus improvisus* by W. J. Rees, in Marine Biological Association, 1957; *Fucus* by several recorders listed in Teissier, 1965). The overwhelming majority of published reports, and all the BMNH, Amsterdam Zoological Museum and Leiden Natural History Museum material are from *Zostera*, however, and it is likely that records on other substrates are wrong. Possibly some at least refer to *L. calceolifera*, since the two species were confused for several decades. Although Bétencourt noted terminal tendrils on his material it might have been *Obelia dichotoma* which also has tendrils and can look remarkably similar.

Nishihira (1968) made a detailed study of the hydroids epizoic on *Zostera* in northern Japan, but did not report *L. angulata* which seems (Stechow, 1923*b*) not to occur there. Picard (1955) made a similar study in Algeria, where he found *L. angulata* absent from the *Posidonia* beds of Castiglione.

The species is tolerant of brackish conditions. Hummelinck (1936) noted a tolerance of 9·8‰ Cl, a figure repeated by Vervoort 1946*a*) and, incorrectly as salinity, by Naumov (1960, 1969). The corresponding salinity figure is 17·7‰. Morri (1979*a*) found *L. angulata* in a range of salinities down to 27‰ in Tuscany, Italy.

REMARKS. Athough Hincks (1868, 1871) and several subsequent authors distinguished correctly between the present species and *L. calceolifera* some later authors (e.g. Babič, 1912; Broch, 1928, 1933; Vervoort, 1946*a*; Naumov, 1960, 1969) regarded them conspecific. A summary of this confusion and a taxonomic assessment of the two species was provided by Faure (1965). The main differences are as follows, in approximate order from most to least useful. The gonothecae differ both in structure and position (hydrorhizal in *L. angulata*, on the stem and axillary in *L. calceolifera*). The internodes in *angulata* are usually straight, and curve slightly in most *calceolifera* specimens. Terminal tendrils are often present, particularly in autumn, in *angulata* but are unrecorded in *calceolifera* (*Obelia dichotoma* sometimes has them also). Eel grasses are probably the only substrate for *angulata* but *calceolifera* occurs on a variety of inert, solid substrates. Faure reported *angulata* growth at its peak in summer, and that of *calceolifera* in spring, at the same place. He reported erect stems spaced at 2–5 mm intervals in *angulata* and often clustered in *calceolifera*; but the extent to which this character in *angulata* is phenotypic, induced by the elongate shape of the eel grass leaves, is not known. Finally, Faure reported that colony height was 5–10 mm in *angulata*, 13–16 mm in *calceolifera*, each stem bearing respectively at maturity 4–6 and 10–15 hydrothecae. Despite this list of differences it remains difficult to identify some infertile material, even with the aid of long reference series; and some young colonies are probably impossible to identify.

A straight hydrorhiza occurs in *Obelia geniculata* also, in which it can be interpreted as a genotypic character adapted to keeping neighbouring, parallel-running hydrohizae adequately spaced along their whole lengths. *O. geniculata* occurs on broad thalloid algae, and spacing is probably an advantage. *L. angulata* is unusual among thecate hydroids in being closely adapted to its substrate in a number of obvious ways, and may have taken to living on eel grasses in relatively recent geological time. It seems likely that since eel grasses are themselves quite recent, being derived from more conventional terrestrial angiospermes, other campanularian and laomedean hydroids were living on algal substrates long before *L. angulata* or its ancestors took to eel grasses. Maybe hydroids of this group, having straight hydrorhizae, were pre-adapted to growing on the long narrow leaves of eel grasses.

However, at least some orientation of stolon growth occurs in *L. angulata* in a direction parallel with the eel grass leaf since diagonal or transverse stolons do not occur. *O. geniculata* stolons, although straight, are not orientated along the lamina and it may be that *angulata* stolon tips have a geotropic response which keeps them growing vertically (upwards or downwards) along the leaf, which floats upright when the tide is in. The fact that stolons of *angulata* grow sometimes along the narrow edges of the substrate leaves suggests that the planula does not seek a central position; or that once a tendril attaches and forms a new colony the hydrorhizal tip cannot locate the centre of the leaf; but there is no experimental evidence.

The terminal tendrils of *L. angulata* were found to be most common from August to November at Roscoff by Faure (1965). Billard (1904*b*) suggested that their function was to attach to adjacent eel grass leaves and hence enable the species to colonize fresh plants vegetatively. The tendrils of BMNH specimens differ from those of occasional *Obelia dichotoma* colonies in having dilated recurved end regions, the ends of *O. dichotoma* tendrils being uniform in width and approximately straight. Study of the BMNH material suggests that tendrils in *L. angulata* are modified hydranth/hydrotheca complexes.

The most detailed histological and general biological account of *L. angulata* is that of Fraipont (1880). However, he stated that the female gonophore contains a single egg; but one of his illustrations (pl. 34, fig. 3) showed a female gonotheca containing several planulae, as illustrated also here, and more than one egg seems normal.

The nominal species *Laomedea sphaeroidea* Stechow, 1932, was based on material from near Sète (Cette), S France, which Stechow (1919*a*) had earlier referred to *L. angulata*. The type material is referrable to *L. angulata* as defined here and it seems unnecessary to recognize the second species. Picard (1958*b* : 191) also suggested this synonymy, without comment.

Laomedea calceolifera (Hinckes, 1871)
(Fig. 18)

?*Laomedea exigua* Sars, 1857 : 50–51.
Campanularia calceolifera Hincks, 1871 : 78–79, pl. 6; Faure, 1965 : 419–426, figs 1a, c, 2c, d, 3c, d; Miller, 1973 : 377–386, figs 6c, d, 10 a–d.
Campalaria conferta Hartlaub, 1897 : 495–496, pl. 19, figs 2–12.
Laomedea angulata: Babič, 1912 : 457–460, figs 1–5; Da Cunha, 1944 : 63, fig. 36.
Laomedea conferta: Splettstösser, 1924 : 403–420, figs X¹–Z¹, A²–T²; Da Cunha, 1944 : 63–64.
Laomedea calceolifera: Billard, 1931*b* : 390; Picard, 1955 : 187.
Obelia calceolifera: Picard, 1955 : 187.
Laomedea (*Campalaria*) *conferta:* Hamond, 1957 : 315, fig. 23.
Eulaomedea calceolifera: Rees & Thursfield, 1965 : 102; Millard, 1975 : 223–224, fig. 73g–k.

TYPE LOCALITY AND MATERIAL. Salcombe, Devon, England, 'on stones &c', offshore (Hincks, 1871 : 73–74, 79), several colonies in spirit and one microslide preparation; BMNH 1899.5.1.155. Some of the spirit material is attached to a worm tube, possibly a sabellariid (det. J. D. George).

TYPE MATERIAL OF OTHER SPECIES. Prof. Dr M. Dzwillo tells me that there is no material labelled '*Campalaria conferta* Hartlaub' in the Zoologisches Institut und Zoologisches Museum, University of Hamburg, where Hartlaub worked; and the type material is probably therefore lost. The original illustrations were detailed, however, and some appraisal of *Laomedea conferta* is possible.

I could not locate type material of *Laomedea exigua* Sars.

OTHER MATERIAL EXAMINED. All BMNH non-type material is listed. Camara do Lobos, Madeira, 146 m ('80 fms'), coll. & pres. R. Kirkpatrick, ♀ colonies in spirit; 1922.3.4.6. 'Probably Woods Hole', Massachusetts, U.S.A., ex James Ritchie collection, parts of two colonies on microslide; 1964.8.7.83 (mentioned, Rees & Thursfield, 1965 : 102). Cape Town, Republic of South Africa, on moored raft, 15 Dec 1949, ♂ & ♀ colonies on two microslides; South African Museum coll. SH 423 (Fig. 18).

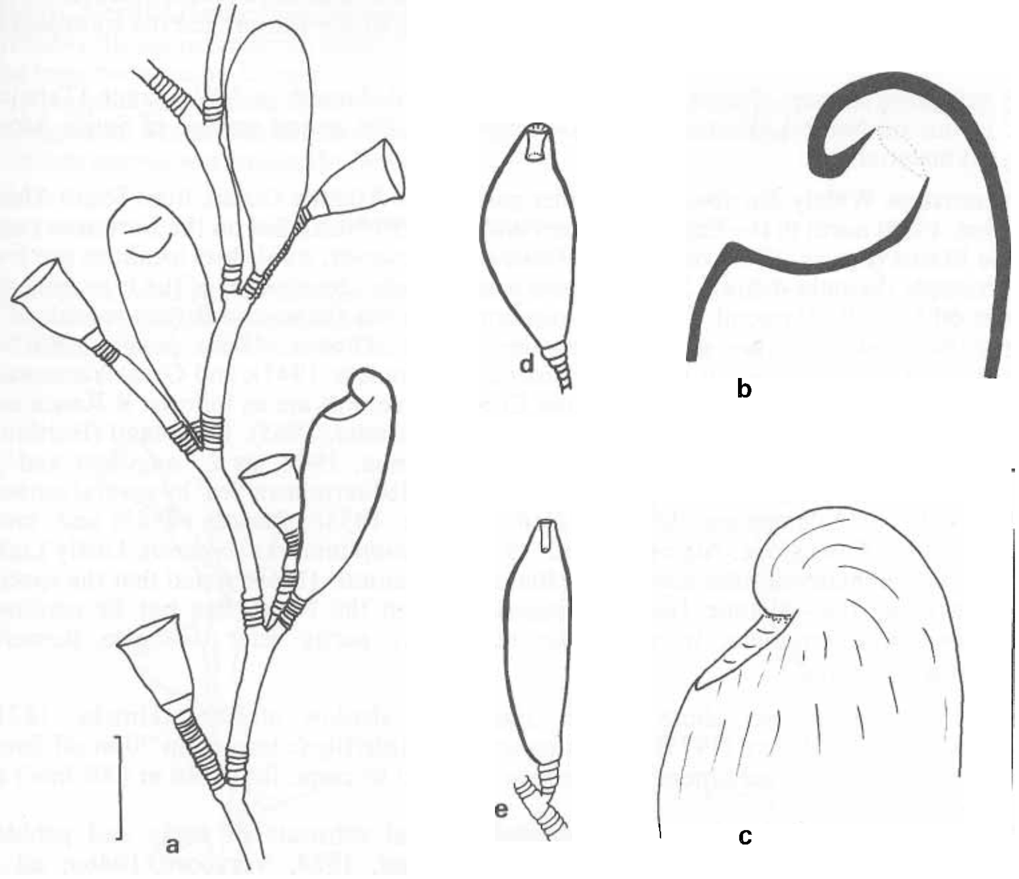


Fig. 18 *Laomedea calceolifera*. (a) part of ♀ colony, showing two mature gonothecae and, uppermost, an immature one. 'Probably Woods Hole', ex James Ritchie colln (mentioned, Rees & Thursfield, 1965 : 102); 1964.8.7.83. (b–c) optical sagittal section and sketch of part of lowermost gonotheca in (a). (d) ♂ gonotheca, Gulf of Pago, NW Yugoslavia; after Babič (1912). (e) ♂, Cape Town docks, ex South African Museum, microslide preparation SH423. Scale (a–c, e, and probably d) 500 μm.

DESCRIPTION. Mature colony comprising one to several erect, monosiphonic stems inserted at short, irregular intervals on a smooth, tortuous hydrorhiza. Stems probably usually unbranched, flexuose; internodes slightly curved to almost straight, long, 3–10 annulations basally. Terminal tendrils not recorded. Hydrothecae campanulate, delicate, flared distally, length *c.* 1½ × breadth, thin walled, rim even; diaphragm transverse to oblique; pedicels 3–20 ringed, sometimes with smooth central portion (Fig. 18). Hydranth (BMNH 1964.8.7.83)

with 15–20 tentacles; hypostome large, probably sub-spherical in life. Gonothecae in axils, single or in clusters of up to 3; ♀ club-shaped with sub-terminal introverted curving tubular aperture on one side, several embryos developing internally; ♂ roughly cylindrical, elongate, tapering gradually below, more sharply above, aperture terminal, central, at end of introverted tube (as ♀ but straight). Young ♀ gonotheca truncate (Miller, 1973), lacking distinctive aperture until late in development (? young ♂ similar). Reproduction described in detail by Miller. No medusa stage.
Variation. Little information. Male gonothecae vary in width (Fig. 18).

DISPERSIVE STAGE. Planulae, which develop within the gonotheca. Splettstösser (1924, as *C. conferta*) described the early stages in sporasac development and more recently Miller (1973) gave a detailed account of the whole reproductive cycle. Miller interpreted the sporosacs as retained medusae ('gonomedusae').

REPRODUCTIVE SEASON. Fertile material recorded April–August in NW France (Teissier, 1965), June off Norfolk (Hamond, 1957), December in the austral seasons of South Africa (present material).

DISTRIBUTION. Widely distributed in warmer parts of the Atlantic Ocean, from South Africa (Millard, 1975) north to the English Channel and southern North Sea on the European coast and to Maine (Fraser, 1946) on the American side. However, published localities are few. For example the only definite British record since Hincks' description of the type material is from off Norfolk (Hamond, 1957, as *L. conferta*). Possibly the several British records of *L. exigua* Sars refer to this species: Swanage, Dorset (Hincks, 1868; possibly BMNH 1899.5.1.153 is this material); Kilve, N Somerset (Bassindale, 1941); and Great Yarmouth, Norfolk (Harmer, in Hamond, 1957). Other European records are as follows: R Rance and Roscoff, NW France (Philbert, 1935*b*; Faure, 1965; Teissier, 1965), Helgoland (Hartlaub, 1897, as *Campalaria conferta* and Portugal (Da Cunha, 1944, as *L. angulata* and *L. calceolifera*). The species has been recorded from the 'Mediterranean Sea' by several authors (Babič, 1912, as *L. angulata*; Billard, 1931*b*; Philbert, 1935*b*; Picard, 1958*b*) and, more precisely, from Castiglione, Algeria (Picard, 1955, as *Campanularia conferta*). Lastly Linko (1911) reported material from Sebastapol, Black Sea. Naumov (1969) stated that the species occurred along the 'Atlantic coast of England' and in the North Sea but he confused *calceolifera* with *angulata*, to which his notes may partly refer (see also Remarks concerning '*C. exigua*').

HABITAT. Extreme lower shore (Faure, 1965) and shallow offshore (Hincks, 1871), sometimes deeper. Millard (1975) listed a record of an infertile colony from 70 m off South Africa; and one of the specimens listed above was said to come from 146 m ('80 fms') off Madeira.

Faure (1965) and Teissier (1965) recorded a usual substrate of rocks and pebbles. However, some authors (Hartlaub, 1897; Splettstösser, 1924; Vervoort, 1946*a*; all as '*conferta*') have noted an affinity for *Sabellaria* tubes (see also notes under Type material) while other 'living' substrates recorded include a spider crab (*Hyas araneus*) carapace and an ascidian (*Styela coriacea*) (both by Hamond, 1957, as *Laomedea conferta*), and intertidal *Lithothamnion* pools (Teissier, 1965). Morri (1979*a*, *b*) recorded *L. calceolifera* in a range of salinities down to 27‰ in brackish lagoons in Italy.

REMARKS. For distinguishing features from *Laomedea angulata* see that species. Infertile specimens can be difficult to distinguish from some young, infertile *L. angulata* and *Obelia dichotoma* colonies.

Type material of the nominal species *Campalaria conferta* Hartlaub, 1897, could not be located but the original description and detailed illustrations agree with the type material of the present species in vegetative features. A difference, however, is that the material described by Hartlaub had gonothecae with truncated ends. Miller (1973) has shown that the peculiar asymmetric terminal region with its introverted tubular aperture forms late in ♀

gonotheca development, indicating that Hartlaub's account was probably of immature *L. calceolifera* material. Splettstösser (1924) and Hamond (1957) probably also had immature material which, following Hartlaub, they assigned to *C. conferta.*

The identity of *Laomedea exigua* Sars, 1857, remains obscure. The species was based on Gegenbaur's (1854) material from Sicily briefly described as *Campanularia* sp. nov. It might prove conspecific with *calceolifera*, which it predates. Van Beneden (1866), Hincks (1868) and Leloup (1947, 1952) assigned English Channel material to *exigua* but it seems likely their material was male *calceolifera.* Naumov (1960, 1969) provided a redescription of *L. exigua*, copying Hincks' figure of a colony and a gonotheca, already copied from Gegenbaur. He recorded the nominal species from the Black, Adriatic and Mediterranean Seas and the eastern North Atlantic from 'Gibraltar to the North Sea inclusive', but did not cite material. Probably his records refer to *calceolifera.* Bassindale's (1941) record from SW England might also have been young *L. calceolifera.*

Dimorphic gonothecae were probably first recognized in *L. calceolifera* by Babič (1912, as *L. angulata*), whose illustration of the male gonotheca is redrawn here.

Stolon growth was studied by Wyttenbach *et al.* (1973).

Laomedea flexuosa Alder, 1857
(Fig. 19)

Laomedea flexuosa Hincks, in Alder, 1856*b* : 440 (nom. nud.); Alder, 1857 : 122–123.
Campanularia flexuosa: Hincks, 1868 : 168–170, pl. 33.
non *Eulaomeda flexuosa:* Rees & Thursfield, 1965 : 102–103 (lapsus pro *Eulaomedea*; redet. *Obelia dichotoma*).

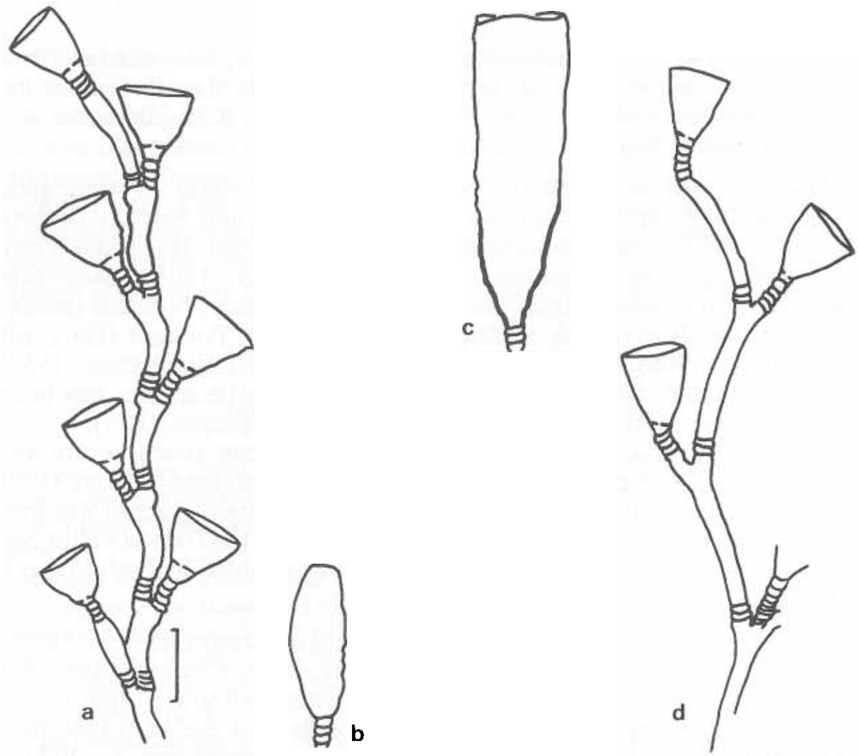


Fig. 19 *Laomedea flexuosa.* (a) New England, USA; 1915.3.6.7. (b) same, ♂ gonotheca. (c) ♀ gonotheca, ?British Isles: 1912.12.21.290a. (d) part of colony with internodes longer than normal, S Greenland; 1938.3.1.297. Scale (a–d) 500 μm.

NOMENCLATURE. The original publication of the name *flexuosa* (Hincks, in Alder, 1856*b*) lacked description, figures or other definitive indication but a description was published a year later (Alder, 1857). The species has been widely recognized and a lengthy synonymy is unnecessary.

TYPE MATERIAL AND LOCALITY. The type locality has been restricted to the British Isles by Cornelius & Garfath (1980). We listed the syntype material, which is preserved in the Hancock Museum, Newcastle upon Tyne.

OTHER MATERIAL EXAMINED. BMNH series, about 50 microslide preparations.

DESCRIPTION. Colony comprising often branched, erect stems up to *c.* 30 mm arising at irregular intervals from a straight, branching stolon. Stems and branches flexuose; internodes characteristically curved, length varied between colonies but constant within, each having 1–10 annuli basally. Hydrothecae campanulate, robust, sometimes asymmetrically thickened, length equal to or slightly longer than greatest width; rim even, diaphragm transverse; pedicels 3–20 ringed, slightly tapering distally, occasionally with smooth central portion. Hydranth with 17–23 tentacles, hypostome spherical. ♀ gonotheca subcylindrical, tapering basally, truncate distally; sides smooth to slightly sinuous; opening wide, terminal; pedicel short, ringed. ♂ shorter, tapering distally to narrower aperture than in ♀. Nematocysts described by Östman (1979). No medusa stage.
Variation. The following features are variable in the BMNH series: length : breadth ratio and radius of curvature of internodes (between, not within, colonies); length of hydrothecal pedicel and number of annuli; and gonothecal shape.

DISPERSIVE STAGE. Planulae, which develop within the gonotheca. Miller (1973) interpreted the gonophores as retained medusae ('gonomedusae'). Another description of their development was given by Goette (1907).

REPRODUCTIVE SEASON. Fertile material recorded April–July, Isle of Man (Bruce, 1948); June–July, 1934, Northumbria (H. O. Bull, in Evans, 1978); May–December, NW France (Teissier, 1965); February–March, May, September, S Spain (Chas Brinquez & Rodriguez Babio, 1977); November, Naples (Lo Bianco, 1909).

DISTRIBUTION. Recorded widely in the North Atlantic but status in some areas unclear. There are records from the Murman and White Sea coasts and Norway (intertidal pools, Mathiesen, 1928), the Faeroes and Iceland (Kramp, 1929, 1938), Hardanger Fjord, Norway (Brattegard, 1966) and the Shetlands southwards (Hincks, 1868; many other British authors). Records from warmer areas are numerous: Santander, N Spain (Rioja y Martín, 1906), S Spain (Chas Brinquez & Rodriguez Babio, 1977), Portugal (Da Cunha, 1950), Mauritania (Billard, 1906), Morocco (Patriti, 1970), Ghana (Buchanan, 1957); but not southern Africa (Millard, 1975). In the Mediterranean Sea the species has been recorded from Naples (Lo Bianco, 1909; Riedl, 1959) and 'E Adriatic' (Pieper, 1884).

The northern and southern limits on the North American coastline are also unclear. Although Kramp (1938) reported the species from W Greenland, Calder (1970) did not record it from Canadian waters and Fraser's (1944) most northerly record was from the Gulf of St Lawrence. The species has been reported along most of the United States coast, but the status in the Caribbean is just a single record which was doubted by both Fraser (1944) and Vervoort (1967).

HABITAT. Recorded on a wide variety of inert and living substrates (Hincks, 1868; Vervoort, 1946*a*; Marine Biological Association, 1957; Teissier, 1975; Chas Brinquez & Rodriguez Babio, 1977), probably lacking a strong substrate preference although often found on fucoid algae. Occurs intertidally, and probably not often deeper than the 37 m recorded by Miller (1961) and the 40 m from which a BMNH specimen was collected (reg. no. 1971.5.11.24, W Scotland). However, a deep record from '12 positions 20–48 miles (32–77 km) SW of Eddystone', SW England, 73–92 m (Marine Biological Association, 1957), suggests the species is not unusual at such depths; and Crawshay (1912) reported the species from

80–100 m at several stations in the western English Channel. The four microslide preparations listed under this species by Rees & Thursfield (1965), from depths down to 160 m, are of *Obelia dichotoma* material.

REMARKS. *Laomedea flexuosa* is type species of the unacceptable genus *Eulaomedea* Broch, 1910, and of the genus *Laomedea* (discussion of both on pp. 97–98).

Alder (1856*b*) introduced the name *flexuosa* in passing when describing *Laomedea neglecta* in the phrase '*L. flexuosa* Hincks, MS'; but the introduction was invalid as it lacked an acceptable indication. It is clear that in or shortly before 1856 Alder and Thomas Hincks concurred that *flexuosa* was a valid species, and were the earliest to recognize it. When first mentioning the name Alder (1856*b*) cited as indication 'the young of Johnston's small variety of *L. gelatinosa*'; but Johnston (1847 : 472) said that he had not seen material. He stated simply: 'variety α—with even margins and simple stem (not seen by me)'. Johnston apparently referred to hints by earlier authors that there was a species awaiting recognition. But Johnston did not see *flexuosa* material himself, nor did he cite this earlier literature. Hence Alder's (1856*b*) indication of Johnston's brief account does not satisfy the requirements of nomenclature, and the name *flexuosa* must date from the later paper (Alder, 1857).

The earlier mentions of the species which Johnston (1847) apparently had in mind are not easily traced. He may have thought that Couch (1844 : 39–40) had seen some *flexuosa* material when, in describing *gelatinosa*, he stated that species often to be just one inch (25·4 mm) high compared with the greater height usual in *gelatinosa* s. str. It can be noted that Couch might have included *neglecta* also within *gelatinosa*, since he recorded that '*gelatinosa*' sometimes grew under stones. Following Couch's early death it was left to Alder and Hincks to define correctly the three species involved. Thus, Alder (1856*b* : 440) stated that 'if observed [by earlier workers—possibly Couch] *neglecta* has been passed over as . . . *L. flexuosa*'

L. flexuosa has been used by several experimental biologists. Stolon growth has been much studied and was mentioned above (p. 42). Phenotypic response to simple environmental changes was described by Crowell (1957; 1961; see p. 42). Embryonic rupture of the hydrothecal bud was studied by Knight (1965, 1970, 1971). Stebbing (1976, 1979) investigated the influence of inorganic toxins on growth, noting that sub-inhibitory doses actually enhanced growth rates. Factors such as straightness of stolon, growth rate and frequency of gonophore production were all affected by water quality. In a later paper (Stebbing, 1981) he studied several factors affecting growth.

The material assigned to this species by Rees & Thursfield (1965) I refer to *Obelia dichotoma*.

Laomedea neglecta Alder, 1856*b*
(Fig. 20)

Laomedea neglecta Alder, 1856*b* : 440, pl. 16, figs 1–2; Vervoort, 1946*a* : 308–310, fig. 316 (syn. *L. brochi* Splettstösser; *L. lauta* Hummelinck); (*non* Da Cunha, 1950 : 142–143, fig. 9).

Campanularia fragilis Hincks, 1863 : 46–47; Hincks, 1868 : 175–176, pl. 32, fig. 3 (syn. *C. elongata* Van Beneden).

Laomedea decipiens Wright, 1863 : 49, pl. 5, fig. 9.

Campanularia elongata Van Beneden, 1866 : 164–165, fig. 6 (p. 150); Leloup, 1947 : 24–25.

Campanularia neglecta: Hincks, 1868 : 171–172, pl. 30, fig. 2; Hincks, 1872 : 390–391, pl. 20, fig. 4.

Campanularia decipiens: Hincks, 1868 : 173–174.

Laomedea brochi Splettstösser, 1924 : 376–403, figs A–Z, A′–W′.

Laomedea ?lauta Hummelinck, 1930 : 35–37, fig. 5.

Laomedea (*Paralaomedea*) *neglecta:* Hummelinck, 1936 : 57 (syn. *?L. brochi* Splettstösser; *L. lauta* Hummelinck).

TYPE MATERIAL AND LOCALITY. Single infertile colony preserved as two microslide preparations, Hancock Museum, Newcastle upon Tyne, Northumberland; designated neotype by Cornelius & Garfath (1980). Although the neotype was once part of Alder's collections and was probably identified by him it almost certainly came from an Essex locality, whereas most of Alder's collections came from NE England. The type locality remains 'Cullercoats and Tynemouth, Northumberland, on undersides of stones' (designated by Nutting, 1915; repeated by Cornelius & Garfath).

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Laomedea lauta* Hummelinck, 1930, holotype; Rijksmuseum van Natuurlijke Historie, Leiden, reg. no. 259. Hummelinck's illustration of this material is very accurate.

OTHER MATERIAL EXAMINED (*L. neglecta* is only poorly represented in the BMNH collection). Porth Cressa, St Mary's, Isles of Scilly, on underside of block of granite, *c.* LWM, 17 Apr 1903, fertile colonies, 'ova in an external capsule' (ms note by E. T. Browne, Zoological Notebook **10** : 15, preserved in BMNH), spirit + 2 microslide preparations, coll. E. T. Browne; 1948.9.8.119 (Fig. 20). Mewstone Echinoderm Ground, near Plymouth, Devon, *c.* 50 m, October 1899, infertile colonies, coll. Marine Biological Association of the U.K., det. E. T. Browne (ms note in Zoological Notebook **13** : 149), spirit material (1948.10.1.126) + 1 microslide preparation (1959.9.17.19). Gåsö Ranna, Gullmarsfjord, Sweden, 20–30 m, 27 Aug 1962, infertile colonies, spirit material + 1 microslide preparation, coll. W. J. Rees; 1962.11.8.9. *Zooligisch Museum, Amsterdam:* Brehorn, Zuider Zee, Netherlands, 14 Jun 1927, infertile and ♂ fragments in spirit (Zuider Zee Onderzoek sta. 1; det. & mentioned Hummelinck, 1936 : 57, fig. 9 a–g) (Fig. 20). Dollard, NE Netherlands, fertile colony in spirit, coll. A. P. C. de Vos, 9 Aug 1954. Kornwenderland, NE Zuider Zee, 4–6 m, coll. Zoological Station, den Helder, 29 Sep 1938, several infertile fragments in spirit, det. W. Vervoort. *Rijksmuseum van Natuurlijke Historie, Leiden:* Aberystwyth Bay, Wales, 17 Jun 1939, intertidal, several infertile fragments, coll. P. W. Hummelinck; RMNH reg. no. 968. Strand Renesse, Schouwen, Netherlands, 20 Dec 1941, infertile fragments on *Tubularia ?indivisa* stems, coll. J. Viergever; RMNH reg. no. 702 (some of these specimens are polysiphonic, having two hydrocauli fused basally). Kornwenderland, 6 m, 29 Sep 1938, four small colonies on one microslide, coll. Zoological Station, den Helder, det. W. Vervoort; RMNH reg. no. 1012.

DESCRIPTION. A small species. Hydrorhiza smooth, tortuous, sometimes branched; short, delicate monosiphonic to bisiphonic stems arising at irregular intervals. Internodes long, narrow, often wider in middle than at ends, 3–10 rings basally, curved (recalling *L. flexuosa*) to almost straight (e.g. Hummelinck, 1936 : fig. 9a); each sharply inturned basally; hydrothecal pedicel on short distal process in line with axis of internode. Hydrotheca long, delicate, unthickened, cylindrical; length = 3 x width; diaphragm oblique to transverse; rim usually bimucronate but often abrades smooth; pedicel long, tapering distally, up to *c.* 20 annuli, sometimes with 1–3 smooth central portions. Hydranth with *c.* 20 tentacles (Van Beneden, 1866, as *C. elongata*; present material, 1971.5.11.11). Gonotheca (after Splettstösser, 1924, as *L. brochi*) ♂ = ♀, cylindrical to inverted-conical, truncated above. Acrocyst in ♀, eggs possibly extruded singly (Hincks, 1868; Splettstösser, 1924).

Variation. The delicate hydrothecal rim easily abrades smooth. Some published descriptions suggest that there are minute spines associated with the cusps on the hydrothecal rim but these seem simply to be folds. Splettstösser (1924 : fig. B, as *L. brochi*) illustrated a hydrotheca in which the bimucronate condition was obscure, and quite apart from damage by abrasion it seems that not all specimens are perfectly bimucronate. Other bimucronate species vary in the same way (*Obelia bidentata*, *Clytia paulensis*; see also p. 40).

DISPERSIVE STAGE. Planulae, brooded in ♀ acrocyst derived from vestigial retained medusa (Splettstösser, 1924). Developing eggs have been reported in the endoderm tissues of the stem (Splettstösser).

Hincks (1872) described what was apparently a vegetative spore developing in place of a hydranth, on a specimen collected from British waters in June.

REPRODUCTIVE SEASON. Probably April–October, but infertile colonies not unusual during this period. All available information is given: fertile material recorded Netherlands, 14 June, 1927 (Hummelinck, 1936; also present material) and 9 August, 1954 (present material); Isle of Man, August (Bruce *et al.*, 1963); Norfolk, England, 18 September, 1954 (Hamond, 1957); Northumbria, June (J. H. Robson, in Evans, 1978); SE Scotland, October (Laverack & Blackler, 1974); Scilly Isles, 27 April, 1903 (present material).

Infertile material recorded Netherlands, 27 August, 1929 (Hummelinck, 1936), 29 September, 1938 & 20 December, 1941 (present material); Aberystwyth, Wales, 17 June, 1939 (present material); Norfolk, 2 July, 1952 (Hamond, 1957); W Sweden, 27 August, 1962; SW England, October, 1899 (present material).

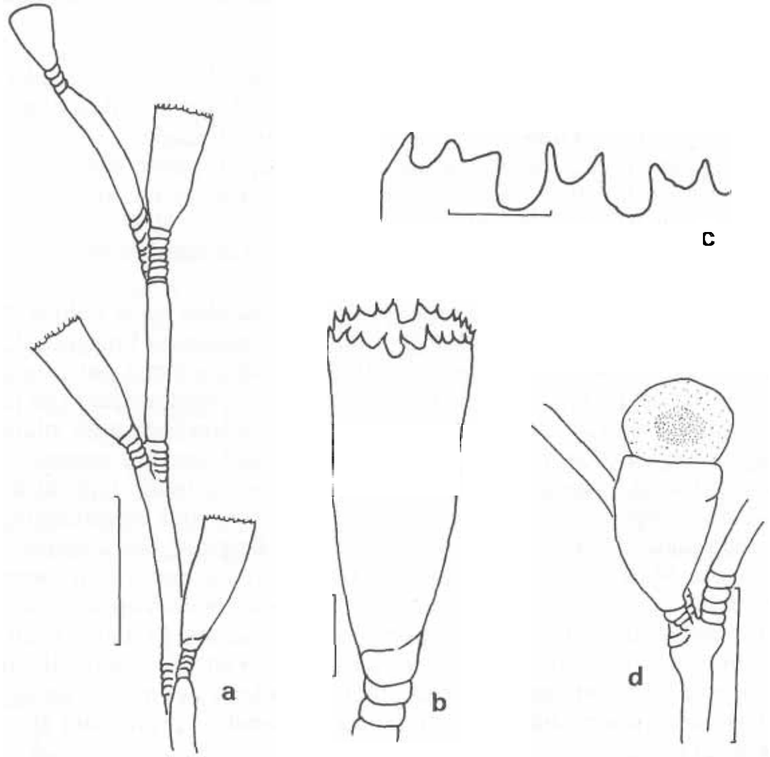


Fig. 20 *Laomedea neglecta.* (a) part of colony, Zuiderzee, Cl = 14·8‰; Amsterdam Zoological Museum collection. (b) same, one hydrotheca. (c) same, part of hydrothecal rim. (d) gonotheca with acrocyst, Is of Scilly, SW England; 1948.9.8.119. Scales: (a, c–d) 500 μm; (b) 100 μm.

DISTRIBUTION. Although infrequently reported *L. neglecta* seems widely distributed in the North Atlantic. The most northerly and southerly records are from Iceland (Kramp, 1938) and the Adriatic Sea (Vatova, 1928). All other published records are listed (see also Material list): England (Alder, 1856*b*; Hincks, 1868, 1872; Hamond, 1957); Isle of Man (Herdman, in Wood, 1901 : 20; Bruce *et al.*, 1963, as *Campanularia fragilis*); Scilly Isles (Vallentin, in Browne & Vallentin, 1904; repeated in Robins, 1969); SE Scotland (Wright, 1859, as *Laomedea decipiens*, see Remarks; Laverack & Blackler, 1974); Aberystwyth, Wales (present material); Netherlands (Vervoort, 1946*a*); Belguim (as *C. fragilis*, Van Beneden, 1866, repeated in Leloup, 1947, 1952); Kattegat (Jägerskiöld, 1971; Rasmussen, 1973); W France (Billard, 1927).

Picard (1958*b*) did not include the species in the mediterranean faunal list but Vatova's (1928) adriatic record seems soundly based. The records by Broch (1933), from the Adriatic, and Da Cunha (1950), from Portugal, were probably based on *Obelia bidentata* material.

L. neglecta has also been recorded from the eastern coast of North America (Fraser, 1944).

HABITAT. Intertidal to at least 50 m. All available information is given: intertidal, underneath stones and on other hydroids (in Britain, Alder, 1856*b*; Hincks, 1868); under stones, on *Tubularia* stems and at 50 m depth (present material); 15–50 m on sea-beds of mud, clay and shell gravel (Kattegat, Jägerskiöld, 1971); 'on stone embedded in meshes of whelk pot', offshore, and under rocks in tidal creek (SE England, Hamond, 1957); on pebbles & oysters (W France, Billard, 1927); LWM, underside of rock (Scilly Isles, present material, Browne & Vallentin, 1904; repeated in Robins, 1969).

Collected in salinity of 26·7‰ from Zuider Zee (Hummelinck, 1936 : 57; data with specimen in Zoologisch Museum, Amsterdam).

REMARKS (see also Remarks under *Laomedea flexuosa*). *Laomedea neglecta* is a small species and although widespread has been little recorded. It was first described from English waters but there are still only a few records from Britain and Europe.

Infertile colonies resemble *Obelia bidentata*, and there is some overlap in hydrothecal length. Although the stems of *L. neglecta* are probably always narrower than those of *O. bidentata*, identification of small specimens can still be difficult.

The spines associated with the hydrothecal rim by several authors are merely folds in the hydrothecal wall appearing as artefacts during preservation.

Campanularia fragilis Hincks, 1863, was probably founded on a colony of the present species. The original illustration was actually published, without a binominal, a year earlier than the species name and description, in vol. 10 of the same journal, forming plate 9, figure 3. The illustration seems to represent *L. neglecta.* Hincks distinguished the two species on the 'markedly flexuose character of the stem', the long hydrotheca with plain rim and the small size of the colony. Probably the hydrothecal rims had abraded smooth. The holotype (not found) was collected from under stones in a rock pool, a likely habitat for *L. neglecta.* Hincks later (1868) referred to the species as *C. ?fragilis*, and significantly regarded *C. elongata* Van Beneden, 1866, type locality Ostend, Belgium, as conspecific. Vervoort (1946*a* : 310) quoted Maitland's (1897) opinion that *elongata* and *fragilis* were conspecific; an opinion Vervoort considered to have been a *pers. comm.* from Van Beneden to Maitland. Leloup (1947) concurred with this synonymy. There seems to have been no material recorded as *elongata* since the original description. Van Beneden illustrated a long hydrotheca with even rim and described the (infertile) colony as small. The hydranth had *c.* 20 tentacles. His description, like that of Hincks, probably represents *L. neglecta* with abraded hydrothecal rims.

Laomedea decipiens Wright, 1863, although described with some precision, was illustrated only by a small woodcut of a hydrotheca. Wright likened the species to *L. neglecta* except that the hydrothecal rim was 'even, and had the appearance of being double for about half its length from the rim', arguably a misinterpretation; and that 'the reproduction' of *L. decipiens* resembled 'exactly' the process he had described (Wright, 1859) in *Opercularella lacerata* (Johnston, 1847). That is, there was an external acrocyst. But Wright said his '*decipiens*' material differed in that each acrocyst contained only three ova, while those of *O. lacerata* had seven or eight. *L. neglecta* is now well known to have an acrocyst containing rather few ova. Further, its hydrothecal rims often wear smooth. Hence it is plausible that *decipiens* was based on fertile material of *neglecta* in when the hydrothecal rims had worn. Hincks (1868) repeated Wright's description and indicated that Wright had obtained his material from the Firth of Forth—Wright had given no locality. Wright and Hincks were in close contact (Hincks, 1868 : preface) and Wright probably told Hincks the locality. Hincks did not know the gonosome of *neglecta* and was rightly cautious when treating *decipiens.* The record from the Firth of Forth was repeated uncritically by Leslie & Herdman (1881) and Pennington (1885), but the species seems not to have been recognized since.

Laomedea brochi Splettstösser, 1924, and *Laomedea lauta* Hummelinck, 1930, were referred to the present species by Hummelinck (1936) and Vervoort (1946*a*) with good reason. See also the notes under Variation.

Da Cunha (1950) recorded *L. neglecta* from Portugal growing on a species of *Sertularella*. However, his illustration shows a medusa developing within a gonotheca and his material was probably *Obelia bidentata*.

The affinities of *L. neglecta* are discussed above (p. 47–49).

Laomedea pseudodichotoma Vervoort, 1959
(Fig. 21)

Laomedea (*Eulaomedea*) *pseudodichotoma* Vervoort, 1959 : 316–318, figs 56–57; Vervoort, 1966 : 104.

TYPE MATERIAL AND LOCALITY. Lectotype designated from original syntype series by Vervoort (1966), 50 mm ♂ colony with developing and mature gonothecae, 13° 43′ N, 17° 23′ W (off Senegal); mostly preserved in University Zoological Museum, Copenhagen, with part on microslide in Rijksmuseum van Natuurlijke Historie, Leiden. 'Paralectotypes', ♀ colonies, from 5° 37′ N, 0° 38′ E (off Ghana); also preserved in Copenhagen.

OTHER MATERIAL EXAMINED. Off Abidjan, Ivory Coast, 35 m, 2 Mar 1966; Rijksmuseum van Natuurlijke Historie, Leiden, reg. no. 10410 (Fig. 21).

DESCRIPTION (partly after Vervoort, 1959, 1966). Colonies so far recorded up to 50 mm, polysiphonic basally; stem almost straight; roughly pinnate; some secondary branching; branches approximately alternate, in one plane, in the only available colony. Internodes slender, 2–3 ringed basally; some tanning. Hydrothecal pedicels short, 5–10 ringed; some axillary. Hydrothecae delicate, conical, some slightly swollen below; diaphragm oblique in side view, basal chamber large; rim even, circular. Gonothecae dimorphic. ♂ long, cylindrical to slightly tapering basally, widest about $\frac{1}{6}$ from aperture; truncate, aperture simple, not raised, as wide as gonotheca. Immature ♂ gonotheca much shorter. ♀ gonotheca long, widest in terminal $\frac{1}{4}$, tapering gradually below and abruptly above; truncate; aperture raised, half width of gonotheca; gonophores thought to be heteromedusoid, sessile.

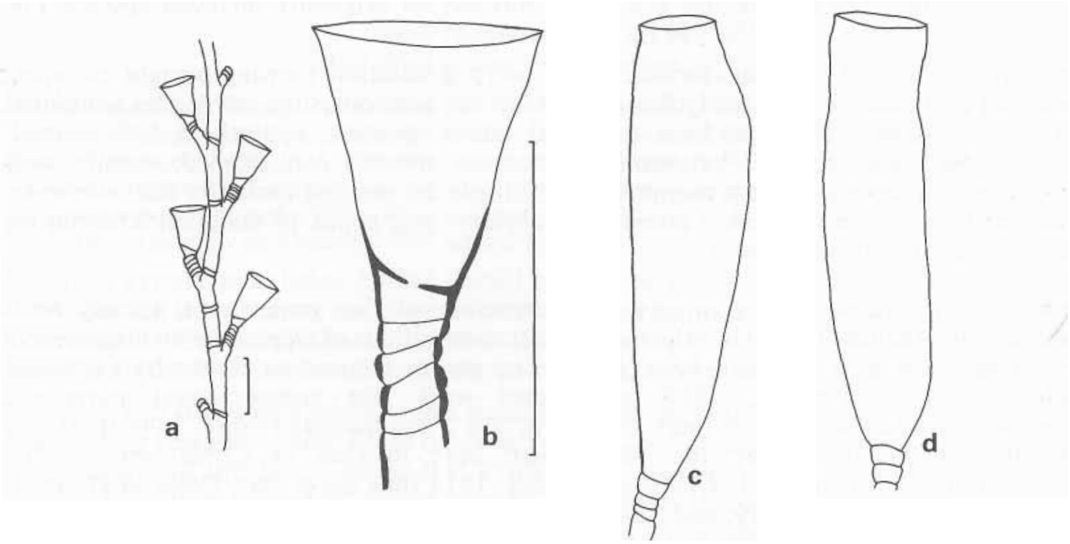


Fig. 21 *Laomedea pseudodichotoma.* (a–c) part of colony, single hydrotheca and ♀ gonotheca, Abidjan, Ivory Coast, 35 m. (d) ♂ gonotheca, off Senegal; syntype series. Scales: (a) 500 μm; (b–d) 500 μm.

DISPERSIVE STAGE. Almost certainly no medusa (Vervoort, 1959). Presumably planulae are released in the normal way.

REPRODUCTIVE SEASON. Fertile material recorded 30 January, 1946, 50 m, off Ghana, ♀; 2 March, 1966, 35 m, off Ivory Coast, ♀; 25 April, 1946, 65–89 m, off Senegal, ♂; (Vervoort, 1959; present material).

DISTRIBUTION. Recorded only from the coastal waters of Ghana, Ivory Coast and Senegal.

HABITAT. So far found only on *Sertularella cylindritheca* (Allman, 1888), at depths from 35 m to 89 m (Vervoort, 1959; present material).

REMARKS. This species is known only from tropical west Africa.

Genus ***OBELIA*** Péron & Lesueur, 1810*a*

Obelia Péron & Lesueur, 1810*a* : 355; Péron & Lesueur, ?1810*b* : 43.
Monopyxis Ehrenberg, 1834*a* : 297; Gray, 1848 : 84.
Obelomma Haeckel, 1879 : 176.
Obeliopsis Le Danois, 1913 : 110.
For other synonymy see Remarks, Cornelius (1975*a*) and page 114. See also note 3 (p. 124) concerning the date of introduction of the genus name *Obelia*.

TYPE SPECIES. *Obelia sphaerulina* Péron & Lesueur, 1810*a* (nom. nov. pro *Medusa marina* Slabber, 1769); by monotypy. For taxonomic purposes the type species was taken to be conspecific with hydroid *O. dichotoma* (Linnaeus, 1758) by van der Hoeven (1862 : 280) and Russell (1953 : 297), but this link is subjective. For the time being at least there is great difficulty in relating medusae collected from the plankton to their hydroids (e.g. Cornelius, 1975*a*). Péron & Lesueur cited as indication a specimen taken in Dutch waters, as illustrated in the German edition of Slabber's (1775–1781 : pl. 9, figs 5–8) work. But Goy (1980 : 72) links also to the published description an unpublished illustration by Lesueur. The specimen illustrated therein was taken near Le Havre, in the Museum of which town the illustration is preserved (see also note 3, p. 124).

Naumov (1960, 1969) and Stepanyants (1979) designated *Sertularia geniculata* Linnaeus, 1758, type species of *Obelia*; but *geniculata* was not an originally included species. For discussion see Cornelius (1975*a*, 1981).

DIAGNOSIS. Colonial Campanulariidae with: polyp generation forming upright colonies, branched or unbranched, variably flexuose; stolon not anastomosing; internodes annulated proximally, supporting hydrotheca on distal lateral process; hydrotheca bell shaped, hydranth with sub-spherical hypostome; gonotheca inverted cone-shaped, usually with raised terminal aperture but sometimes simply truncate; medusa umbrella flat, eversible, mesoglea thin; velum reduced to absent; manubrium long; about 16 marginal tentacles on release, numerous in adult, short.

REMARKS. An exhaustive synonymy and restriction of this genus have already been published (Cornelius, 1975*a*) but the most recent redefinitions of *Obelia* are by Stepányants (1979) and Arai & Brinkmann-Voss (1980). The genera referred to *Obelia* by Cornelius included: *Slabberia* Oken, 1815 (a 'rejected work' for nomenclatural purposes); *Campanularia* Lamarck, 1816 (part; but see p. 51); *Thaumantias* Forbes, 1848 (part; see also p. 71); *Eucope* Gegenbaur, 1856 (part; here referred to *Clytia*, see p. 71); *Schizocladium* Allman, 1871; *Obelaria* Haeckel, 1879 (but see p. 94); *Obeletta* Haeckel, 1879; *Obelissa* Haeckel, 1879; and *Monosklera* von Lendenfeld, 1885. The nomenclatural problems involving *Obelia* with *Laomedea* are discussed above (p. 97).

Three species of *Obelia* are recognized from the hydroid stage in the eastern North Atlantic but their medusae cannot be told apart (Russell, 1953; Cornelius, 1975*a*; Arai & Brinckmann-Voss, 1980). Two of the species were described from the hydroid stage before any of the medusae, and their 'hydroid names' can be regarded as having safe seniority. The description of the third valid hydroid stage, *O. bidentata* Clarke, 1875, post-dates several binominals applied to the medusa stage and this name cannot yet be regarded safe. But there are difficulties in identifying to species level the early descriptions of the medusa and linking them with the correct hydroid stages. Thus it seems probable that the name *O. bidentata* will be unchallenged for some time, and that a working stability has been reached.

The subgenus *Monopyxis* was introduced in the combination *Sertularia* (*Monopyxis*) *geniculata* Linnaeus, 1758, by Ehrenberg (1834*a* : 297). *S. geniculata* is type species of the subgenus, by monotypy. Since there are only 3–5 species of *Obelia* recognized or provisionally accepted from the hydroid stage (e.g. Cornelius, 1975*a*) it seems superfluous to subdivide the genus, and *Monopyxis* can be referred to *Obelia*. Ehrenberg's account was based on material from Norway, Denmark and Germany. Gray (1848 : 84) used *Monopyxis* as a supergenus, including in it the species *Obelia geniculata, Hartlaubella gelatinosa, Campanularia flemingii* (now referred to *H. gelatinosa*, p. 96) and *Monotheca obliqua* (e.g. Hincks, 1868, as *Plumularia*); but this supergenus name was not employed again. Finally Hincks (1868) included *Monopyxis* in his synonymy of *Obelia*.

The genus *Obelomma* Haeckel, 1879, was established to include *Obelia* medusae with 48 tentacles on release. It included three nominal species, each incorporating several others within the synonymies Haeckel presented. Most of those incorporated are now referred to *Obelia*, of which *Obelomma* should be regarded a synonym.

The generic names *Obelaria* Haeckel and *Obelaria* Hartlaub are considered under *Hartlaubella* (p. 94); and *Eucope* Gegenbaur is treated under *Clytia* (p. 71).

The genus *Obeliopsis* Le Danois, 1913, was erected to include material referred to a single species (see p. 120) and can be confidently referred to *Obelia*.

General notes on the medusa stage and indications to other literature are given under *O. dichotoma* (p. 118) and in Cornelius (1975*a*). Applications of the genus name *Obelia* to bryozoan species were also listed in that paper.

The three species of *Obelia* (hydroid) occurring in the NE Atlantic can usually be identified from the characters given by Cornelius (1975*a* : table 1); but occasional specimens of *O. dichotoma* approach *O. geniculata* in having a slight thickening of the internodal perisarc. Some of these specimens cannot be confidently identified to species.

Obelia bidentata Clarke, 1875
(For illustrations see Cornelius, 1975*a*)

Obelia bicuspidata Clarke, 1875 : 58, pl. 9, fig. 1; Stepanyants, 1979 : 37–38, pl. 7, fig. 1 (syn. *O. austrogeorgiae* Jaderholm, 1904*a*; *Clytia paulensis* Vanhöffen, 1910).
Obelia bidentata Clarke, 1875 : 58–59, pl. 9, fig. 2; Jaderholm, 1904*b* : 270–271 (syn. *O. bicuspidata* Clarke; first reviser); Cornelius, 1975*a* : 260–265, fig. 2 (syn. *O. bicuspidata* Clarke).
Clytia arborescens: Billard, 1907 : 167 (*non* Pictet, 1893).
For further synonymy see Cornelius (1975*a*) and Table 4.

NOMENCLATURE. Jaderholm (1904*b*) acted as first reviser when using the specific name *bidentata* for this species, and several contemporary authors followed him (references in Cornelius, 1975*a*). Although the superseded name *bicuspidata* has been widely used, *O. bidentata* is the available name under the current conventions of zoological nomenclature.

DISPERSIVE STAGE. The medusa of this species has probably still to be reared to maturity but when young resembles those of the other two *Obelia* species (Cornelius, 1975*a*, 1977*a*). I did not mention in the 1975*a* paper that Professor K. Ramunni 'reared the medusa of this species' from Bengal material (mentioned in Annandale, 1915, as *O. spinulosa*). The age to which he reared it was not recorded. Ramunni was by far the earliest to realize that the medusa resembled that of the other two *Obelia* species, and to see it released.

DISTRIBUTION. Recorded from the English Channel and southern North Sea southwards through most European and African coastal waters but not from the Black Sea or the Baltic.

Table 4 Synonymies among the nominal species of *Obelia* described from the hydroid stage (after Cornelius 1975*a*, with additions). Although the lists are World-wide most of the nominal species have been recorded from the eastern North Atlantic. Many were first described in genera other than *Obelia*. Discussion of species treated in the 1975*a* paper is not duplicated here. The references cited in the table are mainly as in that paper, only the few additional ones being included in the present reference list.

(a) Synonyms of *Obelia bidentata* Clarke, 1875
O. bicuspidata Clarke, 1875
Campanularia spinulosa Bale, 1888
O. andersoni Hincks, 1889
O. bifurca Hincks, 1889
Gonothyraea longicyatha Thornely, 1899 (non *O. longicyatha* Allman, 1877)
O. corona Torrey, 1904
Obelia sp. Clarke, 1907
O. bifurcata Thornely, 1908
O. multidentata Fraser, 1914
O. oxydentata Stechow, 1914
O. longa Stechow, 1921
Clytia longitheca Hargitt, 1924
O. longitheca Hargitt, 1924 (sic)
O. attenuata Hargitt, 1924
Laomedea bicuspidata var. *picteti* Leloup, 1932
L. spinulosa var. *minor* Leloup, 1932
L. bicuspidata var. *tenuis* Vervoort, 1946
?*Clytia arborescens:* Billard, 1893 (see present paper, p. 117)

(b) Synonyms of *Obelia dichotoma* (Linnaeus, 1758)
Sertularia longissima Pallas, 1766
Sertolare genicolata Cavolini, 1785 (lapsus pro *Sertularia geniculata*)
?*Cymodocea simplex* Lamouroux, 1816
?*Tubularia clytioides* Lamouroux, in Freycinet, 1824
Campanularia maior Meyen, 1834
C. brasiliensis Meyen, 1834
C. cavolinii Deshayes & Edwards, 1836
C. caulini Chiaje, 1841
Laomedea gracilis Dana, 1846
O. commissuralis McCrady, 1857
L. divaricata McCrady, 1857
Eucope parasitica Agassiz, 1865
E. pyriformis Agassiz, 1865
E. articulata Agassiz, 1865
Campanularia flabellata Hincks, 1866
O. plicata Hincks, 1868
Schizocladium ramosum Allman, 1871
O. pygmaea Coughtrey, 1876
O. hyalina Clarke, 1879
O. adelungi Hartlaub, 1884
O. helgolandica Hartlaub, 1884
O. australis von Lendenfeld, 1885
C. cheloniae Allman, 1888
O. angulosa Bale, 1888
O. chinensis Marktanner-Turneretscher, 1890
O. arruensis Marktanner-Turneretscher, 1890
O. nigrocaulus Hilgendorf, 1898
O. gracilis Calkins, 1899

(b) Synonyms of *Obelia dichotoma* (Linnaeus, 1758) (continued)
O. surcularis Calkins, 1899
O. fragilis Calkins, 1899
O. griffini Calkins, 1899
O. rhunicola Billard, 1901
O. borealis Nutting, 1901
O. dubia Nutting, 1901
O. solowetzkiana Schydlowsky, 1902
C. obtusidens Jaderholm, 1905*a*
L. congdoni Hargitt, 1909
O. piriformis Bedot, 1910
O. pyriformis: Mayer, 1910
L. sargassi Broch, 1913
O. undotheca Stechow, 1923
O. nodosa Bale, 1924
O. coughtreyi Bale, 1924
O. obtusidentata Bedot, 1925
O. dischotoma Billard, 1927 (lapsus pro *dichotoma*)
O. everta Hargitt, 1927
?*O. commensuralis* Gudger, 1937 (?lapsus pro *commissuralis*)
O. alternata Fraser, 1938
O. equilateralis Fraser, 1938
O. microtheca Fraser, 1938
O. tenuis Fraser, 1938
O. racemosa Fraser, 1941
O. irregularis Fraser, 1943
O. braziliensis Vannucci Mendes, 1946
O. biserialis Fraser, 1948
O. hyaliana Vannucci, 1955 (see present paper, p. 119)

(c) Synonyms of *Obelia geniculata* (Linnaeus, 1758)
Laomedea lairii Lamouroux, 1821
Campanularia prolifera Meyen, 1834
Eucope diaphana L. Agassiz, 1862
E. alternata A. Agassiz, 1865 (nom. nov. pro *E. diaphana* L. Agassiz; non *Thaumantias diaphana* A. Agassiz)
E. polygena A. Agassiz, 1865
E. fusiformis A. Agassiz, 1865
O. gymnopthalma Spagnolini, 1871
Monosklera pusilla von Lendenfeld, 1885
O. geniculata vars *I, II* & *III* Marktanner-Turneretscher, 1890
Campanularia coruscans Schneider, 1897
O. geniculata f. *subsessilis* Jaderholm, 1950*b*
O. geniculata f. *gaussi* Vanhöffen, 1910
O. geniculata ff. *intermedia, subantarctica* & *subtropica* Ralph, 1956

There are few English records but from the north coast of France southwards there are many: NW France, Belgium, Netherlands (earliest records in Table 5; also Vervoort, 1946*a*; Leloup, 1947; Teissier, 1965); Cadiz, Gibraltar, Morocco, Mauritania, S of Madeira (Stechow, 1925); Algeria, Senegal (Picard, 1951*b*, 1955); Ghana (Buchanan, 1957); Gambia (Vervoort, 1959); Morocco (Patriti, 1970); Azores, Nigeria, Sierra Leone (Cornelius, 1975*a*); South Africa (Millard, 1975). The recorded northern limits are north of the Wash (Table 5) and Schiermonnikoog in the Frisian Islands (53° 30′ N, 6° 15′ E; RMNH Leiden, W. Vervoort, pers. comm.). By coincidence the most southerly records, from South Georgia and Tierra del Fuego (Cornelius, 1975*a*), are from a similar latitude, 54° S. A record from Adelie Land, Antarctica, may be based on *Clytia paulensis* material (see Remarks).

My statement (Cornelius, 1975*a*) that Kramp (1961) recorded the species from Helgoland was incorrect and there are no records from that island (W. Werner, pers. comm.) or from any other German waters. The Kent material which I listed was wrongly identified.

The Dutch record of Leloup (1933 : 11) listed in Table 5 was referred by Hummelinck (1936 : 56) and Vervoort (1946*a* : 300) to *Hartlaubella gelatinosa*; but Leloup also recorded *gelatinosa* in his paper. I have not located Leloup's material but if *O. bidentata* it would be among the earliest Dutch records.

Some aspects of the European distribution deserve comment. Although the species is distinctive and occurs widely in warmer parts of the Atlantic and Indo-Pacific oceans, it was not recorded from the eastern side of the Atlantic until the 1900s. It might previously have been confused with *H. gelatinosa*, as suggested by both Billard and Leloup in various publications. Confusion certainly occurred in some of the published records of the species from Belgium and England (possibly Leloup, 1933; Robins, 1969; both as *H. gelatinosa*; see previous paragraph and Table 5). Further, the species was poorly documented before 1900 and the descriptions available then were in obscure literature. It is understandable that when Billard (1902) recorded the first French material he referred it to *Obelia bifurca* Hincks, 1889, described from the Indian Ocean. (*O. bifurca* is now regarded conspecific.) Much later Stechow (1925) too referred material to *O. bifurca*, 50 years after *O. bidentata* had first been described; and it is evident that news of *bidentata* had spread slowly.

Although the European records (Table 5) appear to show the arrival of the species in Cherbourg and Ostend in 1902, the Netherlands in 1926, Norfolk in 1951, the Scilly Isles in 1966 and Hampshire in 1975 (an unusually hot summer), there is no satisfactory proof of a gradual extension of range. Indeed, the apparent spread of the species along the coasts of France, Belgium and the Netherlands follows quite closely the coming of hydroid experts in those countries, by coincidence from west to east (Billard, Leloup, Hummelinck, Vervoort). South-east England has seldom been given close attention by hydroid workers. Hamond (1957) recorded *O. bidentata* off Norfolk in 1951 as 'rather common' over a wide area, suggesting that it was already long established—but for how long cannot be decided. Parallel evidence comes from another overlooked species, similarly told from its near relatives by a bimucronate hydrothecal rim: *Clytia paulensis.* Although some BMNH material of *paulensis* was collected from near Plymouth in 1899 (p. 90) it was not identified for 80 years; and the species was first recognized from British waters independently in 1973. It seems that for a long time it too was overlooked and thought to occur no further north than NW France; but now it has been found again in southern England and, like *O. bidentata*, in East Anglia.

It remains puzzling that the nineteenth century English and Belgian experts active around the English Channel (Couch, Van Beneden, Gosse, Hincks) did not find *O. bidentata*. Hincks (1889) in fact described the species from Indian Ocean material, as *O. bifurca*, and would surely have recognized British examples. So it might really have been absent at that time; and it may be relevant that in 1937–1938 Vervoort (1946*b*) did not record the species from the Waddenzee, N Netherlands, where it now occurs. Finally, although *O. bidentata* has been recorded from the well worked offshore region around Roscoff (Billard, 1912; Teissier, 1965) it is scarce and has been found only in deep water (L. Cabioch, pers. comm.). See also page 44.

Table 5 Records of *Obelia bidentata* from the English Channel and southern North Sea. All known English records are included.

Locality	Date	Collector	Material	Literature	Comments
England					
North coast of Norfolk and the Wash, several localities	1951 on	R Hamond	BMNH 1953.11.16.1	Hamond, 1957	Earliest British record; probably most northerly of species to date; 53° 15′ N, 0° 45′ E
Darrity's Hole, Scilly Isles; 22–30 m	11 Jul 1966	University of London Sub-Aqua Club	BMNH 1969.9.9.6	Robins, 1969 (as *Laomedea gelatinosa*)	Earliest record for south coast of England
Hunstanton & Wells, Norfolk	22–23 Sep 1975; 13 Aug 1979	P F S Cornelius	BMNH 1975.10.10.7.9; 1980.1.14.1	Unpublished	Live material from strandline
Langstone Harbour, Hampshire	Sep 1975	R G Withers	BMNH 1975.12.9.1	Unpublished	Small colony from moored raft
Netherlands					
Goes sluice, Zeeland	Aug 1926	?	RMNH, Leiden, 1174	Unpublished	Earliest Dutch record
Zuiderpier 'De Beer', nr Hoek van Holland	24 Aug 1928	?	RMNH, Leiden, 1172	Unpublished	
Kreupel, Zuiderzee; 52° 48′ N, 0° 20′ E; 3 m	19 Nov 1928	?		Hummelinck, 1936; Vervoort, 1946*a*	This locality since drained
Den Helder, North Holland	Jun 1933	E Leloup	?	Leloup, 1933	Doubted record; see Remarks
Renesse, Zeeland	pre-1946	P W Hummelinck	?	Vervoort, 1946*a*	Dead material from strandline
Renesse, Zeeland	20 Aug 1946	C J Verhey	BMNH 1976.11.12.1	Unpublished	
Belgium					
Blankenburge, nr Ostende	1902–1906, 1914	Various	?	Billard, 1922; Leloup, 1933	Earliest Belgian records
France					
St-Vaast-La-Hougue, Cherbourg	Probably 1902	A Billard	?	Billard, 1902	Earliest French record
Roscoff, 60–95 m	?1911 on	A Billard G Teissier	?	Billard, 1912; Teissier, 1965	Always scarce in Roscoff area (see text)

HABITAT. Substrates not recorded in my 1975*a* paper include an isopod, *Anilocra physodes* (Linnaeus), from Naples (Stechow, 1921*b*, 1925, as *Obelia bifurca*) and a commercial shrimp, *Pennaeus aztecus* Ives, from Florida (Kruse, 1959; via A. A. Fincham, pers. comm.); ships hulls, hermit crabs gastropod shells and algae (Millard, 1975). *O. bidentata* is highly tolerant of brackish water. It has been recorded at salinities of 18·6‰ (Netherlands; Vervoort, 1946*a*), 10–20‰ (Italy; Morri, 1979*b*) and even so low as 1‰ (S Carolina, U.S.A.; Calder, 1976). The species has often been recorded in shallow water and Millard (1978) listed it as intertidal.

REMARKS. A detailed, world-wide treatment has appeared recently (Cornelius, 1975*a*) and the notes given here are mainly intended to supplement that account. *O. bidentata* is a nearly cosmopolitan species, and a possible explanation is given above (pp. 44–45).

Differences from the superficially similar *Hartlaubella gelatinosa* are given under that species, and from the hydroid stages of other *Obelia* species by Cornelius (1975*a* : table 1).

Mayer (1910), Stechow (1925) and recently Stepanyants (1979) regarded *Obelia austrogeorgiae* Jaderholm, 1904*a*, as conspecific. I do not disagree (*cf.* Cornelius, 1975*a*) but have no fresh evidence. However, I cannot yet agree with Stepanyants that *Clytia paulensis* Vanhöffen, 1910, is identical with *O. bidentata.* The young medusae of both are sufficiently well described to indicate that two species are involved (see notes on Dispersive stage under the two species, pp. 89, 113). It could be argued that since Vanhöffen's material was infertile it was merely young *O. bidentata*: but this was not Stepanyants' argument. I believe neither Stepanyants nor I have seen the type material of *C. paulensis.* If it did prove to be young *O. bidentata* then a new name would have to be found for *C. paulensis* auct. (see synonymy in this paper). In that event it would be useful to apeal to the International Commission on Zoological Nomenclature to validate the widely used name *paulensis* sens. auct.

Clytia arborescens Pictet, 1893 : 34–35, pl. 2, figs 30–31, originally based on material from Indonesia, was reported south of Madeira at 100 m by Billard (1907); but Stechow (1925) included no further records in his synoptic list of warm water W Atlantic hydroids. Billard's material lacked gonothecae but, like the type material, had a compound stem and long hydrotheca (560–700 μm) with sharply pointed cusps. It is likely that his material was *O. bidentata*; and it is relevant that he had wrongly identified *O. bidentata* from the English Channel (see Distribution, above). *O. bidentata* was not well known at the time he published the *arborescens* record. The type material of *arborescens* was probably not *O. bidentata*, however, since Pictet reported hemispherical medusa buds in the gonotheca, indicating *Clytia* sp.

Obelia dichotoma (Linnaeus, 1758)
(For illustrations see Cornelius, 1975*a*)

Sertularia dichotoma Linnaeus, 1758 : 812.
?*Cymodocea simplex* Lamouroux, 1816 : 216, pl. 7, fig. 2 (see p. 121).
?*Tubularia clytioides* Lamouroux, in Freycinet, 1824 : 620, pl. 95, figs 6–8.
Lomedea gracilis C. Pickering, in Dana, 1846 : 689, pl. 61, figs 7, 7a–b (lapsus pro *Laomedea*; see p. 78).
Obelia dichotoma: Hincks, 1868 : 156–157, pl. 28; Cornelius, 1975*a* : 265–272, figs 3–4.
Obelia plicata Hincks, 1868 : 159, pl. 30, figs 1, 1a.
Campanularia cheloniae Allman, 1888 : 22, pl. 11, figs 2, 2a.
Obelia dischotoma Billard, 1927 : 332 (lapsus pro *dichotoma*).
?*Obelia commensuralis:* Gudger, 1937 : 1–6 (?lapsus pro *O. commissuralis* McCrady, 1857).
Obelia hyaliana Vannucci, 1955 : 56.
Laomedea plicata: Rasmussen, 1973 : 30, fig. 9.
Eulaomeda flexuosa: Rees & Thursfield, 1965 : 102–103 (lapsus pro *Eulaomedea*; redet.; see p. 105).
For further synonymy see Remarks, Table 4 and Cornelius (1975*a*).

DISPERSIVE STAGE. Medusae of *O. dichotoma* and *O. geniculata* reared from the hydroids in the laboratory still cannot be distinguished and some taxonomic confusion continues (Russell, 1953; Cornelius, 1975*a*; Arai & Brinckmann-Voss, 1980; see also Remarks). Russell's book includes the best account of the biology of *Obelia* spp. medusae.

The alternation of generations characteristic of medusoid coelenterates was actually first appreciated in scyphozoans, in 1829. It was reported in *Obelia* as early as 1836, first among the hydrozoans; but several still earlier workers had come close to its discovery in this genus. This and other historical aspects have been reviewed recently (Winsor, 1976; Cornelius, 1977*a, b*). A paper by Desor (1849) was missed by these reviewers. Desor provided an early confirmation of medusa release in *Obelia*, probably *O. dichotoma*. However, like several contemporary workers (see p. 97) he assigned his material to *Hartlaubella gelatinosa* which has no medusa. He probably identified his material using the well illustrated work of van Beneden (1844), who made the same error. Several other workers have assigned an *Obelia*-like medusa to *H. gelatinosa* and, despite the early clarification by Couch (1844), there was confusion for many years between *O. dichotoma, O. geniculata, H. gelatinosa* and *Gonothyraea loveni* (see notes under *H. gelatinosa* (p. 97), and Cornelius, 1977*a*).

Couch (1844) was in addition the first to note medusa release in *Obelia geniculata* (p. 120). Other early records in that species were contributed by F. W. L. Thomas (*in* Johnston, 1847 : 467), Hincks (1852 : 85) and Gosse (1853 : 84–90, pl. 4).

Illustrations of the medusae of *O. dichotoma* were first provided by Baster (1762, pl. 5, fig. 7), but the earliest of *O. geniculata* appeared nearly a century later, in Gosse's (1853) book.

Naumov (1969, as *O. longissima*, here referred to *O. dichotoma*) reported that 'the medusae were apparently not liberated from' Black Sea populations. But the species of *Obelia* are exceptionally well documented and since there is no other report of medusa retention in the genus a repeat of the observations would be desirable.

REPRODUCTIVE SEASON. Medusae of *Obelia* spp. have been reported around the British Isles in all months but are commonest from 'spring to late autumn' (Russell, 1953). Fertile colonies were recorded on the coast of Egypt between 6 Sep and 4 Oct, 1933 (Billard, 1936).

DISTRIBUTION. Found throughout European and African coastal waters with the exception of the Black Sea, from which there are no confirmed records (but see last paragraph of Dispersive stage). The species is remarkable in being nearly cosmopolitan in coastal waters and is one of the most widely distributed of hydroids. Aspects of this are discussed on page 45; and a detailed summary of locality records has appeared elsewhere (Cornelius, 1975*a*).

HABITAT. Tolerance of 12‰ salinity recorded by Calder (1976) in S Carolina. Unusual substrates noted in the literature included a sponge and the fins of a shark (Couch, 1844 : XV, as 'the sea thread of Ellis'), a turtle (Allman, 1888, as *Campanularia cheloniae*), a crab (Rasmussen, 1973: the colony was thought to be feeding on débris in the exhalent current); on the parasitic copepod *Lernaeocera* on the gills of a cod (*Gadus*); and on the back and claws of an anomuran 'crab', *Lithodes maia* (in Evans, 1978). Probably the record by Gudger (1937), of '*Obelia commensuralis*' on the blueback herring (*Alosa aestivalis*), referred to this species; but his account suggested that the hydrorhizae entered the muscles of the fish and the identification is not certain.

REMARKS. A revision of this species has appeared recently (Cornelius, 1975*a*) and only additional notes are given here. Identification of the hydroid stage is discussed above (p. 113). Nematocysts were described by Östman (1979) and by others whom she cited.

Tubularia clytioides Lamouroux, in Freycinet, 1824, was based on live material collected from algae in the Azores. Probably it was *Obelia dichotoma*. Rees & White (1966) evidently thought *Silicularia gracilis* Meyen, 1834, also described from Azores material, to be conspecific but while the *clytioides* type specimen was an erect colony that of *gracilis* was reptant. Rees & White presented a muddled synonymy, referring to the 'species' (*clytioides* + *gracilis*) as *Orthopyxis clytioides* (Lamouroux); and including in its synonymy the entry '*Silicularia clytioides* Meyen, 1834', evidently a lapsus for '*S. gracilis* Meyen'. Nutting (1915) had made the same error fifty years earlier (p. 50).

The once widely recognized nominal species *O. commissuralis* McCrady, 1857, based on the hydroid stage, was referred to *O. dichotoma* first by Böhm (1878), and again by me (1975*a*). Böhm's paper has been overlooked; and I know of no other works giving this synonymy.

Obelia plicata Hincks, 1868, described from infertile hydroid material, type locality 'Shetland', was recently referred to the present species without comment (Cornelius, 1975*a*). I have not been able to locate type material. The species deserves close evaluation as it has been recognized by several authors (Marktanner-Turneretscher, 1890; Nutting, 1915, as *?O. plicata*; Billard, 1927; Kramp, 1935, as *Laomedea plicata*; Fraser, 1944; Teissier, 1965; Rasmussen, 1973) although not by Broch (1912*b*). *O. plicata* was said by Hincks to resemble *H. gelatinosa* in having compound stems but the hydrothecal rims were even, not castellated. The hydrotheca was said by Hincks 'very much [to] resemble in form that of *O. dichotoma*'. Gonothecae were first assigned to *O. plicata* by Marktanner-Turneretscher (1890) who said they were the same as those of *O. dichotoma.* Indeed, the two species seem conspecific. Some older colonies of *O. dichotoma* (e.g. BMNH 1948.9.8.14, Plymouth, 21 Apr 1899, coll. E. T. Browne) exhibit compound stems resulting from overgrowth of up to 10 young, pale stems along the older, thicker and darker ones. The specimen mentioned resembles closely the colony illustrated by Hincks as *O. plicta*, and synonymy seems justified. Godeaux (1941, as *H. gelatinosa*) described similar *O. dichotoma* material, from the North Sea; while Billard (1927) maintained *O. plicata* distinct on the basis of the original characters. Broch (1912*b*) alone raised doubts, but was non-committal.

The factors causing overgrowth in occasional *O. dichotoma* specimens are not known, most colonies being solitary. However, such overgrowth has been described in other hydroids and called 'auto-epizoism' (Millard, 1973). If an overgrown specimen results from second and subsequent planulae settling on the original colony then the whole should be regarded as an aggregation of colonies, and not as a single colony. The phenomenon is discussed above (p. 40).

Campanularia cheloniae Allman, 1888, was based on infertile material collected during the '*Challenger*' expedition from the back of a turtle; but the locality of the turtle was not recorded. The original description and what remains of the type series (BMNH 1888.11.13.15, small colony in spirit + microslide preparation) are probably *O. dichotoma.*

Laomedea sargassi Broch, 1913, was recorded from Ghana by Buchanan (1957 : 360). The name *sargassi* was a nom. nov. for *O. hyalina* Clarke, 1879, introduced just to prevent confusion with *Gonothyraea hyalina* auct., and is therefore inadmissible under the current conventions of nomenclature. Congdon (1907 : 468) described material from Bermuda as *O. hyalina*, but Hargitt (1909) gave that material specific status, as *Laomedea congdoni*. I have previously (Cornelius, 1975*a*) referred *O. hyalina* Clarke and *O. congdoni* (Hargitt) to *O. dichotoma*, but overlooked the nom. nov. *sargassi*. Recent examination of the type material of *O. congdoni* (U.S. nat. mus. cat. no. 42647, microslide preparation of infertile fragments) confirms that it too is simply *O. dichotoma. Obelia hyaliana* Vannucci, ? in *ms*, was a name given to some '*O. hyalina*' material which Vannucci (1955) later considered conspecific.

Obelia geniculata (Linnaeus, 1758)
(For illustrations see Cornelius, 1975*a*)

Sertularia geniculata Linnaeus, 1758 : 812.
Obelia geniculata: Hincks, 1868 : 149–151, pl. 25, fig. 1, 1a; Cornelius, 1975*a* : 272–278, figs 1, 5.
For further synonymy see Cornelius (1975*a*), Remarks and Table 4.

DISPERSIVE STAGE. A medusa. See Remarks and notes under *Obelia dichotoma*.

REPRODUCTIVE SEASON. Russell (1953) recorded the following in British waters: *Obelia* sp. medusae found nearly throughout year, especially 'spring to late autumn' (Russell); medusae released at Plymouth, March–November (Orton, 1920); some evidence of lunar periodicity in release times (Elmhirst, 1925).

In the Mediterranean, Lo Bianco (1909) recorded medusa release at Naples March–June and October–January.

DISTRIBUTION. An almost cosmopolitan shallow water species found nearly throughout the eastern North Altantic.

The species was not recorded from the Black Sea by Naumov (1969). He listed the species as absent from the Baltic as well but Stechow (1927) reported it from Stockholm. It was recorded from Iceland and the Faeroes but not from Spitzbergen by Kramp (1929), although already known from Jan Meyen Island (Broch, 1918). Calder (1970) among others recorded the species from W Greenland; but I (Cornelius, 1975*a*) misquoted him as including E Greenland in its distribution. I know of no records from E Greenland.

HABITAT [see also Geographical distribution (p. 45), the habitat notes under *O. dichotoma* and Cornelius, 1975*a*]. The species was collected from the fins of a spur-dog (*Squalus acanthias*) by Couch (1844), who deduced that planula settlement must be rapid. Other actively swimming animals on which *O. geniculata* has been recorded include a sea-horse (*Hippocampus guttulatus*, by Zirpolo, 1939, 1940) and parasitic copepods themselves on fish (*Lernaeocera* spp. on *Gadus* (cod), by Leloup, 1931*b*; on *Lernaeocera* on *Clupea* (herring), by Debouteville & Nunes, 1951, 1952; on *Dinemoura* on *Cetorhinus* (basking shark) by Debouteville & Nunes). Long distance travel on floating algae has also been recorded (Arnaud, Arnaud, Intès & Le Loeuff, 1976). Recorded at 100 m depth by Naumov (1960). However, some of these records on fish might have been of *O. dichotoma*.

REMARKS. A revision of this species has appeared elsewhere (Cornelius, 1975*a*) and the present account simply adds to that.

Couch (1844) gave some interesting details. He stated the number of tentacles of the hydranth to vary widely (11–29 on p. 2, 14–28 on p. 38). He described medusa bud development but not medusa release, which was not known till 1847 in this species (Cornelius, 1975*a*, 1977*a, b*; see also p. 118). He recorded a range of tissue colour in the hydroid from 'white to deep red'.

The nematocysts were described by Östman (1979) and by others whom she cited.

Campanularia vermicularis Van Beneden, 1866, was described without illustrations and identification has been thought impossible (Vervoort, 1946*a*; Leloup, 1947). The species was based on Belgian material. Van Beneden kept live colonies for three weeks. He described the species as being more robust than *O. geniculata*, and as having larger hydrothecae and more numerous annulations. It was collected off the brown alga, *Fucus vesiculosus* L. The hydranth was said to have as many as 40–44 tentacles, a character which might one day help to identify his material (*cf.* Couch's observations, immediately above). Meanwhile I follow Vervoort in treating the species here but not including it in the synonymy.

Obelia **spp. indet.**

1. Hydroids. *Obelia longicyatha* Allman (1877 : 10, pl. 7, figs 4–5) was recorded from 35° 42′ N, 8° 40′ W (Cap Spartel, Tangier) and the Gulf of Cadiz by Billard (1907 : 168, as *Clytia longicyatha*), but the identity of the species remains unclear. I have discussed it elsewhere (Cornelius, 1975*a* : 264). See also the note on *Campanularia vermicularis* Van Beneden, 1866 (immediately above).

2. Medusae. Some species from the eastern North Atlantic cannot be assigned to a hydroid. *Obelia adriatica* Neppi (1912 : 726–727, pl. 3, fig. 8, 8a) was described from Adriatic material; and *Obeliopsis fabredomergui* Le Danois (1913 : 110) was based on material from the Little Minch, NW Scotland. It seems most unlikely that either is valid. *O. plana* Sars (1835 : 28, pl. 5, fig. 13, as *Thaumantias*) was referred to *O. flabellata* hydroid by Bedot (1910 : 484) and some later authors, and hence would fall in the synonymy of *O. dichotoma.*

But there seems slim reason for this identification (*cf.* Cornelius, 1975*a* : 271, footnote). Other pre-1910 medusa names in this genus were listed by Bedot (1901–1925) and Mayer (1910), and are not repeated here. As explained above (p. 118) most cannot be confidently assigned to a hydroid stage and a new list would serve little purpose.

Taxa now referred to other families

A few genera and species recorded from the eastern North Atlantic are no longer referred to the Campanulariidae. As several have been included in this family in some standard works notes on them are given here to summarize the current opinions. The taxa are treated in date order.

1. The genus *Capsularia* Cuvier, 1797, was used by Gray (1848 : 85–87) to embrace several British species of Campanulariidae but should be regarded a junior synonym of *Coryne* Gaertner, in Pallas, 1774 (discussion in Cornelius, 1975*b* : 378).

2. *Sertularia fruticosa* Esper, ?1810 [pl. 34, figs 1–2 (see note 2, p. 124); also Hammer, in Esper, 1829 : 162–163 (syn. *Sertularia laxa* Lamarck, 1816 : 116; *Laomedea sauvagii* Lamouroux, 1816 : 206; both nom. nov. pro *S. fruticosa*)] was recorded from the Adriatic Sea by Marktanner-Turneretscher (1890 : 205) as *Campanularia fruticosa*. The species is now referred to the genus *Thyroscyphus* in the family Sertulariidae (e.g. Vervoort, 1967; Millard, 1975). It is otherwise unrecorded from the eastern North Atlantic and Marktanner-Turneretscher's record may well be wrong. However, *T. fruticosus* occurs in the Red Sea as far north as the Gulf of Suez (Vervoort, 1967).

The exact date of publication of the species name is unusually difficult to determine and the necessary bibliographic work on Esper's important multi-part book has apparently not been done. Precise dating would be useful as the plates were issued several at a time around 1810, and they carry binominals. They thus predate the posthumous text, edited by Hammer (Esper, 1829), from which this part of the work is often thought to date. The plates predate also several important European works on zoophytes [e.g. those by Lamarck (1816) and Lamouroux (1812, 1816, 1821; Lamouroux *et al.*, 1824)]. Esper's work is rare, and few of the original wrappers survive; but the information on an incomplete set of wrappers in the BMNH library gives hope that dating would be simple if a complete copy were located. See also section 7, below.

3. The genus *Cymodocea* Lamouroux, 1816 : 214, originally included two species, *C. simplex* and *C. ramosa*, both described as new. *C. simplex* was based on material from Great Yarmouth and 'Ireland', *C. ramosa* on fragments from the Antilles. Johnston (1838) commented on the genus and on the identities of the two species; and Gray (1848) dismissed them as 'doubtful species' at the end of the Campanulariidae. Lamouroux (1821) and Lamouroux *et al.* (1824) included additional species in the genus but these do not enter the present discussion. Billard (1909), who saw some of Lamouroux' original material, referred the two species to *Nemertesia antennina* (Linnaeus, 1758), family Plumulariidae. I designate *C. ramosa* type species of the genus *Cymodocea*, the name of which hence becomes a junior subjective synonym of *Nemertesia* Lamouroux, 1812. Billard was confident that the *C. ramosa* material he saw was type, but had doubts about that of *C. simplex*. His doubts are significant since in J. Fleming's opinion, quoted by Johnston (1838), the original illustrations of *C. simplex* might be identified as an *Obelia dichotoma* colony lacking hydrothecae. I concur with Fleming's opinion; and disagree with Johnston who thought *simplex* was a plumularid. If the illustration is actually of *O. dichotoma* then Billard's caution was justified and the specimen he saw was not type. Almost all the Lamouroux collections were destroyed during the liberation of Caen on 7 July, 1944, so the *C. simplex* material is no longer available (Redier, 1967). However, *C. simplex* is here provisionally referred to *O. dichotoma* (p. 117).

The species *Cymodocea comata* Lamouroux, 1821, was recorded from the coast of Devon by W. E. Leach (in Johnston, 1838); but the species was referred to *Nemertesia ramosa* (Lamarck, 1816) by Billard (1909), who saw type material.

4. *Campanularia intertexta* Couch, 1844 : 41–42, pl. 11, fig. 3, was based on material then in the Museum of the Royal Institution of Cornwall, Truro. The material almost certainly no longer exists (Curator, Roy. Inst. Cornwall, pers. comm.). Johnston (1847 : 109–110) repeated Couch's description verbatim but regarded the species as unsoundly based. Gray (1848 : 88) listed it without comment, incidentally assigning to it Shetland material of *Lafoea dumosa* (Fleming, 1820), BMNH reg. no. 1847.9.24.66. At the same time Gray proposed the new genus *Conchella* (?lapsus pro *Couchella*), of which *Campanularia intertexta* is type species by monotypy. Hincks (1868 : 220) thought the species might be *L. dumosa*, stating that Couch's description was inadequate for identification. Later Bedot (1905 : 157) referred *intertexta* to '*Coppinia arcta*', an invalid species accepted by several nineteenth century authors but merely based on the coppinia or reproductive branch of *L. dumosa*. Couch's illustration shows an unidentifiable campanularid hydroid, possibly *Orthopyxis integra*, growing on a coppinia of *L. dumosa*. Thus the type 'series' was mixed. The name *intertexta* is here restricted solely to the illustrated coppinia, which becomes lectotype. Hence *Campanularia intertexta* is to be regarded a junior synoym of *L. dumosa*; and the genus name *Conchella* a junior synonym of *Lafoea* Lamouroux, 1821. See also page 65.

5. *Campanularia lacerata* Johnston, 1847 : 111, pl. 28, fig. 3, is now known as *Opercularella lacerata* and referred to the Campanulinidae (e.g. Millard, 1975). The species has been referred to a variety of genera in the literature, including *Capsularia, Laomedea, Wrightia* and *Calycella* (references in Hincks, 1868).

6. *Laomedea obliqua* Johnston, 1847 : 106–107, pl. 28, fig. 1, based on British material, is today known as *Monotheca obliqua* and *Plumularia obliqua* by different authors and referred to the Plumulariidae (e.g. Millard, 1975).

7. *Campanularia fruticosa* Sars, 1850 : 138–139, is today referred to *Lafoea dumosa* (Fleming, 1820), in the Lafoeidae (e.g. Cornelius, 1975*b*). It has often been given full specific status, as *L. fruticosa*. See also section 2, above.

8. *Campanularia abietina* Sars, 1850 : 139, based on Norwegian material, has long been known as *Grammaria abietina* and assigned to the family Lafoeidae (e.g. Cornelius, 1975*b*).

9. *Campanularia parvula* Hincks, 1853 : 178, pl. 5a, was probably based on material of *Calycella syringa* (Linnaeus, 1767) lacking operculae. Several authors have referred the species to *Lafoea* Lamouroux, 1821, but this seems wrong (references and discussion in Cornelius, 1975*b*).

10. *Campanularia gracillima* Alder, 1856*a* : 361, pl. 14, figs 5–6, based on hydroid material from NE England, has frequently been referred to *Lafoea*, family Lafoeidae; but lately to the species *Lafoea dumosa* (Fleming, 1820) (e.g. Cornelius, 1975*b*; Cornelius & Garfath, 1980).

11. *Laomedea acuminata* Alder, 1856*b* : 441, pl. 16, figs 5–8, based on hydroid material from NE England, is the hydroid of an *Aequorea* sp. medusa, family Aequoreidae. The two species recognized from British waters from the medusa stage were described earlier so the name *acuminata* should be regarded provisional. Although the medusa generation of the two can be separated the respective hydroids are morphologically identical, so far as is known. Hence at present it cannot be decided to which of the 'medusa species' *acuminata* should rightly be referred (Russell, 1953).

12. The nominal species *Laomedea tenuis* Allman, 1859 : 367–368, was once known as *Leptoscyphus tenuis* (e.g. Hincks, 1868). It is currently regarded as a campanulinid, having

been provisionally referred to *Phialella quadrata* (Forbes, 1848) by Stechow (1923*a* : 129) and Rees (1939 : 441). Browne (1896 : 479) summarized the mistaken observations by Allman who assigned the medusa of one species to the hydroid of another. *Campanulina tenuis* Van Beneden, 1886 : 174, 176, pl. 13, is a different nominal species, provisionally referred to *Aequorea vitrina* Gosse, 1853, by Russell (1953). Bedot (1910) listed an earlier homonym of *C. tenuis.*

13. *Campanularia fastigiata* Alder, 1860 : 73–74, pl. 5, fig. 1, based on Scottish material, was known for some decades as *Stegopoma fastigiatum.* Edwards (1973) showed that *fastigiatum* was the hydroid stage of the medusa *Modeeria rotunda* (Quoy & Gaimard, 1827), the binominal of which takes priority. The species is assigned to the family Laodiceidae (e.g. Rees & Rowe, 1969; Edwards, 1973; see also Cornelius & Garfath, 1980).

14. *Campanularia humilis* Hincks, 1866 : 298, is now known as *Cuspidella humilis.* Its affinities are unclear but it was removed from the Campanulariidae long ago (discussion in Cornelius & Garfath, 1980).

15. *Clytia eucophora* Haeckel, 1879 : 168, was a combination applied to the hydroid stage of *Eucopium primordiale* Haeckel, 1879 : 168 (sic), from Corsica. As Mayer (1910 : 236) pointed out, the two names are objective synonyms with the same date of publication. Mayer, as first reviser, suppressed *eucophora* in favour of *primodiale*; but at the same time referred Haeckel's species to *Eucope picta* Keferstein & Ehlers, 1861. Although Kramp (1961) omitted to treat *E. picta* there is no doubt that it and the Haeckel species should be referred to the Phialellidae. Weismann (1883 : 158) introduced the combination *Clytia eucopophora*, a lapsus of Haeckel's spelling.

16. *Campanularia mutabilis* Ritchie, 1907 : 504, pl. 23, figs 3–5, based on Azores material, is now known as *Scandia mutabilis* and referred to the Lafoeidae (e.g. Millard, 1975).

17. *Campanularia divisa* was attributed by Bassindale (1941 : 148) to Todd (1906 : 137) whom he supposed to have reported material from Ilfracombe. Bassindale misread Todd's list, which included *Campanularia* species and *Tubularia indivisa.* The word '*indivisa*' was split between the two lines (*in/divisa*) and evidently read wrongly by Bassindale.

18. The genus *Hincksella* Billard, 1918 : 22, was considered by Totton (1930) and Ralph (1957) to be closely related to the Campanulariidae, but is now referred to the Syntheciidae (e.g. by Millard, 1975).

19. The genus *Billardia* Totton, 1930 : 150 (type species *B. novaezealandiae*, by original designation) was based on southern hemisphere material. Totton assigned *Billardia* to the Campanulariidae but the genus is similar to *Hincksella* and like it comes within the scope of the Syntheciidae sensu Millard (1975), in my opinion. Blanco (1967*b*) and Stepanyants (1979), however, retained *Billardia* in the Campanulariidae. Possibly a greater understanding of the reproductive structures will help. Totton suspected that the blastostyles of *Billardia* were produced in place of hydranths, within the hydrothecae, but said his material was inadequately preserved for him to be certain. If his suspicion were confirmed the Syntheciidae would be the correct family for *Billardia.*

Notes

1 (See p. 65). G. D. Westendorp (1813–1868) apparently produced only two works involving coelenterates (Westendorp, 1843, 1853). Both were on the zoophytes of the Belgian coast. The first was a straightforward taxonomic account including some new genera and species, among them *Clytia ryckholtii* (here referred to *Orthopyxis integra*). Probably none is valid. His second work, published in 1853, was remarkable in being illustrated by dried specimens mounted on sheets. It is rare but still important since one of the included species was described as new in the 1843 work, and the specimens used in illustration might be considered types. The 1853 work comprised a printed title page, a printed page giving a list of species and localities, and 32 hebarium sheets each bearing one species. There were 16 hydroids, 14 bryozoans and 2 sponges. Examples of the work were seen by Neviani (1903), Bedot (1910 : 200–201) and Billard (1914; also seen by Leloup, 1947 : 5); and another, imperfect copy has recently been found in the British Museum (Natural History) (Cornelius, unpublished *ms* in BMNH). I have not seen an intact copy.

Neviani listed the 32 species but *C. ryckholtii* was not among them. The copy described by Billard (1914), in Brussels (Mus. roy. Hist. nat.; *inv. no.* 3440), similarly does not have *C. ryckholtii*. The BMNH example also does not include that species. The copy evidently came to the (then) British Museum library about 1867. Certainly a collection of specimens corresponding with Neviani's list was purchased from Westendorp at that time, and was given the 32 zoological accession numbers 1867.5.4.22–24 and 1867.5.7.1–29. The specimens were curated each under its own species, and the printed species list was cut up to provide labels which were in most cases glued to the herbarium sheets. Much, perhaps all, of this material survives and is still curated under the various species; but I have not found the title page of this copy.

Only one type specimen of any group is included in this collection, that of the hydroid, *Plumularia macleodi* Westendorp, 1843 (BMNH reg. no. 1867.5.7.7). It can be considered a syntype of *P. macleodi*; and is in fact a specimen of *Kirchenpaueria pinnata* (Linnaeus, 1758). *P. macleodi* is thus a junior synonym of *K. pinnata*. Billard (1914), working on the corresponding Brussels syntype specimen, reached the same conclusion.

2 (See p. 121). Some evidence was presented by Sherborn (1922 : 1, entry under Esper; Sherborn, 1926 : 2528, entries under *fruticosa, Laomedea* and *fruticosa, Sertularia*) that at least some of the plates of Esper's (1829) '*Die Pflanzen-Thiere*' appeared before 1816, possibly around 1810. Since the plates bear binominals, and might predate the synoptic works of Lamouroux (1812 onwards) and Lamarck (1816 onwards), correct dating is important. However, it seems that bibliographers have not yet dated the plates and Sherborn's (1926) provisional date of 1810 for the plate of *Sertularia fruticosa* Esper is the best compromise. Certainly the plate of *fruticosa* predated the works of Lamarck (1816) and Lamouroux (1816), which referred to Esper's plate as being already published. Indeed, they proposed new names in place of *fruticosa*. The three volume Esper work was issued in parts, some after Esper's death in 1810; and the few copies I have seen have been collated with the undoubtedly earlier *Sertularia* plates intermingled with the text. But the partial set of wrappers with the BMNH copy gives much detailed information, and a full set might enable all the plates of this scarce work to be dated accurately.

3 (See p. 112). Dating of the two works here listed as Péron & Lesueur, 1810*a*, ?1810*b*, has caused confusion. A clarification is desirable since in them many genus names of medusae were introduced which are still used. The works comprised the earliest serious systematic treatment of medusae, and these authors finally disbanded the genus *Medusa* Linnaeus, 1758. The first of the two works was one of a series of journal papers written by the two authors, and comprised their taxonomic treatment of medusae. Several other papers in the series also dealt with marine animals but are not important here. They have been listed by Goy (1980). The second work (Péron & Lesueur, ?1810*b*), a book entitled *Histoire générale des méduses*, brought the series of papers together each forming a chapter of the book. The book version was repaginated from 1 on, and was presumably published after the series of papers (although it might conceivably have been issued in parts as the papers appeared).

The publication date of the taxonomic paper (Péron & Lesueur, 1810*a*) has been taken as 1809 by most authors and this date might be inferred from the title page of the volume of the journal in which it appeared. But there is good evidence that it did not appear until January, 1810 (Sherborn, 1914; 1929 : 4455, entry under *Obelia*; Cornelius, 1975*a*; Goy, 1980). The book, the *Histoire générale des méduses*, has been almost entirely overlooked. It was dated

1809 in the *British museum catalogue of printed books.* But J. Goy (pers. comm.) and I concur that the book version almost certainly would have followed the series of papers, and so would have appeared at least as late as 1810 (unless the book version were issued in parts).

Hence the many names introduced by Péron & Lesueur almost certainly date from the 1810*a* paper, published January, 1810. Apart from minor heading changes the book version (?1810*b*) was apparently printed from the same 'blocks' as the series of papers. For taxonomic purposes the two versions differ only in date.

The numerous plates that were to have accompanied the account of the medusae (Péron & Lesueur, 1810*a*) were prepared but not published immediately (*cf.* Cornelius, 1975*a* : 253, footnote; 1977*a* : 49, footnote). But most of the illustrations showing Péron & Lesueur's 'new' species were brought together in an extremely rare work usually attributed to Lesueur alone (Péron & Lesueur, ?1815). This work was cited by Haeckel (1879, in several of his synonymies, as the *Planches inédités*) and Totton (1965 : p. 45, pl. 8) among others but almost all twentieth century medusa workers have overlooked it. Fewer than half a dozen copies are known (Totton, 1965; Goy, 1980). Goy (1980) cited evidence from the *P.-v. Seanc. Acad. Sci. Paris, 1795–1831* (issue covering 14 August 1815) **5** : 532, that 1815 is the correct date; and not ?1811 as given in the *British museum catalogue of printed books* (**187** : 111) under Péron alone. She concluded that the bulk of the illustrations, showing most of the nominal species newly described by Péron & Lesueur (1810*a*), were copied and published by a variety of contemporary compilers in their own works and so made public. They included such famous names as de Blainville, Cuvier, Milne Edwards, Lamarck and Lesson (references in Goy, 1980). The original Lesueur drawings are preserved in the Museum at Le Havre.

Although the bulk of the rare work (Péron & Lesueur, ?1815) comprised illustrations of medusae exquisitely drawn by Lesueur, the title page leaves no doubt that the authorship should be ascribed jointly to Péron & Lesueur (Mrs A. Datta, pers. comm.). Péron had died in 1810 and it can be inferred that Lesueur wished him still to be senior author, as he had been of the lengthy text (Péron & Lesueur, 1810*a*, ?1810*b*) of the work.

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Addendum

On 15 August 1981 I found *Laomedea angulata* (p. 98) common on the eel grass bed at Studland, Dorset. The previous record from the British mainland was dated 1906; and from Dorset was 1890, also at Studland. Whether or not the species had disappeared from that locality in the meantime might be hard to tell. On 15 September 1981 I found the same species abundant on eel grass near Misery Point, R Yealm, near Plymouth. At this locality too the status of the species during the last several decades was unclear.

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The Evolving Biosphere: 276×219 mm, approx. 320pp, 133 line illustrations

Published: May 1981

Co-published by the British Museum (Natural History), London and Cambridge University Press, Cambridge.

Titles to be published in Volume 42

The tick collection (Acarina: Ixodoidea) of the Hon. Nathaniel Charles Rothschild deposited in the Nuttall and general collections of the British Museum (Natural History).
By James E. Keirans

Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera.
By P. F. S. Cornelius

Miscellanea

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