THE HYDROID SPECIES OF *OBELIA* (COELENTERATA, HYDROZOA: CAMPANULARIIDAE), WITH NOTES ON THE MEDUSA STAGE

BY
PAUL FREDERICK SINEL CORNELIUS

Pp. 249–293 ; 5 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 28 No. 6
LONDON: 1975

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 28 *No.* 6 *of the Zoology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Zool.).

ISSN 0007-1498

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 5 *November,* 1975 *Price* £2·50

THE HYDROID SPECIES OF *OBELIA* (COELENTERATA, HYDROZOA: CAMPANULARIIDAE), WITH NOTES ON THE MEDUSA STAGE

By P. F. S. CORNELIUS

CONTENTS

SYNOPSIS

The genus *Obelia* Péron & Lesueur, 1810a, is redefined and nominal taxa already described from the hydroid stage are assessed. Three species are considered valid, *O. bidentata* Clarke, 1875, *O. dichotoma* (Linnaeus, 1758) and *O. geniculata* (Linnaeus, 1758). Each is diagnosed, redescribed and illustrated with notes on morphological variation, nematocysts, identification, nomenclature, synonymy, type specimens and distribution. Owing to the paucity of information the many species described from the medusa stage cannot yet be evaluated or related to the hydroids. The affinities of those species of hydroids no longer assigned to *Obelia* are discussed briefly. The genus *Laomedea* Lamouroux, 1812, is reduced to a synonym of *Obelia* but the genus *Campanularia* Lamarck, 1816, is regarded as valid.

INTRODUCTION

In many genera of hydromedusae there is specific diversity of the medusa generation while the hydroid stage appears uniform. However, in the genus *Obelia* Péron & Lesueur, 1810a, the reverse is the case and it is the medusae which cannot be distinguished. Thus, as summarized by Russell (1953), medusae liberated from the hydroid species *Obelia dichotoma* (Linnaeus, 1758) and *O. geniculata* (Linnaeus, 1758) and reared to maturity appear morphologically identical, both being referable to the medusa *O. lucifera* (Forbes, 1848) as known from the plankton. Further

confusion results from the large number of species that has been described from the hydroid, some seventy having been proposed between 1830 and 1948. It seemed timely to evaluate the systematic criteria on which these species were proposed, hopefully to provide a basis for evaluating taxa described from the medusa. Previously, the genus had been fully revised only in the publications of Bedot (1901, 1905, 1910, 1912, 1916, 1918, 1925) who recognized thirty-seven hydroid species described up to the end of 1910. In the present work, however, these and subsequently described species are referred to only three nominal species. Some species previously assigned to *Obelia* are removed to allied genera. Although an attempt has been made to consider all described hydroid species, only the more important usages of the name of each have been cited. Full reference lists are already available in the works of Bedot and in abstracting journals.

The taxonomic status of all of the numerous species described from the medusa generation remains problematical. The difficulties outlined by Russell (1953) and Kramp (1961) still remain, and further rearing work may be necessary before the hydroid and medusa species can be related. References to species described from the medusa before 1910 were provided by Mayer (1910) and Bedot, while those described between then and 1959 were listed by Kramp (1961).

The material examined during the present study was drawn mainly from the collections of the British Museum (Natural History). The figures were prepared with the aid of a camera lucida.

GENERIC DIAGNOSIS AND IDENTIFICATION OF THE HYDROID STAGE

Genus ***OBELIA*** Péron & Lesueur, 1810a[1]

Sertularia Linnaeus, 1758 : 807 (part).
Medusa : Slabber, 1769 : 67, pl. 9, figs 5–8 (part) ; Slabber, 1775 : 40, pl. 9, figs 5–8 (part) ; Modeer, 1791 : 25 (part).
Obelia Péron & Lesueur, 1810a[1] : 355 ; Oken, 1815 : 115, pl. 5, fig. 3 ; Deshayes & Edwards, 1840 : 170–171 ; McCrady, 1857 : 197–198, pl. 11, figs 5–7 ; Hincks, 1868 : 146 (part) ; Fraser, 1937 : 82 ; Fraser, 1944 : 151 ; Russell, 1953 : 296 ; Naumov, 1960 : 260 (part); Naumov, 1969 : 281 (part) ; [non *Obelia* : Lamouroux, 1821 : 81 ; Deshayes & Edwards, 1836 : 245–246 ; Michelin, 1847 : 321 ; = Bryozoa (d'Orbigny, 1853 : 751 ; Gregory, 1909 : 47 ; Buge, 1951 : 464)].
Laomedea Lamouroux, 1812 : 184 (part) ; Johnston, 1847 : 101 (part) ; Kramp, 1935 : 106 (part).
Slabberia Oken, 1815 : 828 (rejected work, Opinion 417, International Commission on Zoological Nomenclature ; Benthem Jutting, 1970 : 60).
Campanularia Lamarck, 1816 : 112–113 (part).
Thaumantias : Forbes, 1848 : 41 (part).
Eucope Gegenbauer, 1856 : 241 (part) ; [syn. nov.].
Schizocladium Allman, 1871 : 18.
Obelaria Haeckel, 1879 : 173 (nom. nov. pro hydroid stage of *Obelia*).
Obeletta Haeckel, 1879 : 173 ; [syn. nov.].
Obelissa Haeckel, 1879 : 175 ; [syn. nov.].
Monosklera von Lendenfeld, 1885b : 910.

[1] See footnote on facing page.

TYPE SPECIES. *Obelia sphaerulina* Péron & Lesueur, 1810a[1] (nom. nov. pro *Medusa marina* Slabber, 1769) ; by monotypy ; for nomenclatural purposes taken as conspecific with the hydroid *O. dichotoma* (Linnaeus, 1758) (van der Hoeven, 1862 : 280 ; Russell, 1953 : 297), not *O. geniculata* (Linnaeus, 1758) as proposed by Naumov (1960 : 260 ; 1969 : 281).

DIAGNOSIS. Colonial Campanulariidae (sensu Russell, 1953) with free medusae. Polyp generation forming upright colonies, branched or unbranched, variably flexuose ; internodes annulated proximally, supporting hydrothecal pedicel on distal lateral process. Hydrotheca bell-shaped, hydranth with prominent spherical hypostome. Gonotheca inverted cone-shaped, usually with raised tubular aperture, occasionally simply truncate. Medusa umbrella flat, eversible, mesogloea thin ; mouth of manubrium 4-sided, lacking tentacles ; marginal tentacles 16+ on release, numerous in adult ; gonads 4, spherical, on radial canals.

REMARKS. This restricted diagnosis agrees with that of Fraser (1937, 1944) in excluding from the genus species with no medusa generation (accommodated in the genera *Campanularia* Lamarck, 1816, and *Gonothyrea* Allman, 1864) and also those in which the medusa has only 4 tentacles on release and which, when sexually mature, has a hemispherical umbrella (referred to the genus *Clytia* Lamouroux, 1812). There seems little justification in synonymizing the first two genera plus *Laomedea* Lamouroux, 1812, with *Obelia* as has been proposed by Naumov (1960, 1969). The appearance of the adult medusa of *O. bidentata* Clarke, 1875, is as yet unrecorded, but the characters of its young stages and of the hydroid fall within the above diagnosis.

The polyphyletic genus *Medusa* Linnaeus (1758 : 659) was disbanded by Péron & Lesueur (1810a) who assigned the originally included species to other genera. No species of *Obelia* was included in the original scope of *Medusa*, however, and Péron & Lesueur were justified in forming the genus *Obelia* to accommodate *Medusa marina* Slabber (1769). They also provided a new trivial name for the species, calling it *Obelia sphaerulina*.

d'Orbigny (1853 : 684, 751) cited earlier uses of *Obelia* by Péron in 1803 and 1804, but gave no bibliographic information. Biographies about Péron (Alard, 1811a, b ; Audiat, 1855 ; Girard, 1857) do not list any publication by him in 1803, while Péron's 1804 papers (Péron, 1804a–f) contain no mention of *Obelia*. It seems that d'Orbigny was mistaken in giving these dates and that the name *Obelia* was not introduced until 1810, by Péron & Lesueur.

The genus *Laomedea* Lamouroux, 1812 : 184 was proposed to accommodate two species, *Sertularia dichotoma* Linnaeus, 1758, and *S. spinosa* Linnaeus, 1758. The first-named had, however, previously been removed from *Sertularia* under the name *Obelia sphaerulina* Péron & Lesueur, 1810a, while the second species is currently referred to the bryozoan genus *Vesicularia* Thompson, 1830 (Prenant & Bobin,

[1] Although dated 1809, Péron & Lesueur's paper was not published until January 1810 (Sherborn, 1929 : 4455). They later published a second designation of *Obelia*, dated May 1810, but this work was largely a reprint of part of the earlier paper (Péron & Lesueur, 1810b). A footnote in the first paper states that the plates did not appear with it, and although Lesueur (1811) later published some plates, those from the 1810a paper apparently remain unpublished.

1956 : 276). *S. dichotoma* Linnaeus, 1758, is here selected as type species of the genus *Laomedea* which can thus be considered a junior synonym of *Obelia*. The next available name in place of *Laomedea* auct. appears to be *Campanularia* Lamarck, 1816, which originally included the four species *Sertularia verticillata* Linnaeus, 1758, *S. volubilis* Linnaeus, 1758, *S. syringa* Linnaeus, 1767, and *S. dichotoma* Linnaeus, 1758. Although Nutting (1915 : 28) made *Sertularia verticillata* genotype of *Campanularia*, Naumov (1960 : 249) later nominated *S. volubilis* Linnaeus, 1758 (*not* sensu Ellis & Solander, 1786), as type-species of *Campanularia* and made *Sertularia verticillata* genotype of a new genus, *Verticillina* Naumov, 1960 : 269. Millard (1966 : 477) commented on this confusion and nominated *S. volubilis* sensu Ellis & Solander, 1786 : 51 as type-species of *Clytia* Lamouroux, 1812 : 184. She showed the correct identification of this type-species to be *Medusa hemisphaerica*[1] Linnaeus, 1767 : 1098. However, this species had previously been nominated type-species of the medusoid genus *Thaumantias* Eschscholtz, 1829 : 102, by Forbes (1848 : 41) and *Thaumantias* can be regarded a junior objective synonym of *Clytia*. The status of these genera and their genotypes will be elucidated further by reference to the International Commission on Zoological Nomenclature.

The availability of the generic name *Eucope* Gegenbauer (1856) was discussed by Rees (1939).

The genus *Schizocladium* Allman (1871) was regarded as a junior synonym of *Obelia* by Bedot (1910 : 470). The sole included species is reduced to a synonym of *Obelia dichotoma* in the present review (p. 272).

The genus *Obelaria* Haeckel (1879) was proposed as a nom. nov. for the hydroid stage of *Obelia*, of which it is a junior objective synonym, as recognized by Bedot (1912 : 326). The two subgenera *Obeletta* Haeckel (1879) and *Obelissa* Haeckel (1879) were introduced to accommodate taxa defined from the medusa stage. Although thus outside the scope of the present survey they nevertheless at present seem superfluous and can be regarded as junior synonyms of *Obelia*.

The genus *Monosklera* von Lendenfeld, 1885b : 910, was synonymized under *Obelia* by Bedot (1916 : 152). The sole included species is regarded as a synonym of *Obelia geniculata* in the present review (p. 273), following Vanhoffen (1910).

Three species are recognized from the hydroid stage, *O. bidentata* Clarke, 1875, *O. dichotoma* (Linnaeus, 1758) and *O. geniculata* (Linnaeus, 1758). They can usually be identified using the characters shown in Table 1, but occasional specimens occur with characters apparently intermediate between *O. dichotoma* and *O. geniculata*. Usually such specimens are examples of *O. dichotoma* with a slight thickening of the internodal perisarc, and can nevertheless be identified from the characters shown.

[1] Although this species name has been attributed to Gronovius (1760 : 38), his usage was not strictly binominal (Millard, 1966 : 477).

TABLE 1

Identification characters of the hydroid stage of *Obelia*

SPECIES	HYDROTHECAL RIM	ASYMMETRIC THICKENING OF INTERNODAL PERISARC	GROWTH HABIT	SUBSTRATE*
O. bidentata	Bimucronate or cusped (Fig. 2)	Absent (Fig. 2)	Mature colonies polysiphonic at base, numerous monosiphonic side-branches ; up to *c.* 350 mm	Probably usually on inert solid substrates and sand
O. dichotoma	Even, sinuous or castellated (Fig. 4)	Absent (Fig. 3)	Usually monosiphonic, much branched, up to *c.* 350 mm	Usually on animal or inert substrates, less often on algae
O. geniculata	Even (Fig. 5)	Present (Fig. 5)	Monosiphonic ; usually unbranched ; up to *c.* 40 mm	Usually on brown algae, rarely on animal or inert substrates

* See also the remarks on page 259.

MORPHOLOGICAL AND OTHER VARIATIONS

THE large number of species of *Obelia* described from the hydroid stage reflects the high degree of morphological variation present. Although between-colony variation is readily apparent and many characters are inconstant in expression, nevertheless such characters have been freely used in diagnosing new species. That much variation is phenotypic has long been suspected (Mayer, 1910; Hammett, 1943) but does not seem to have been given due attention in systematic accounts of the genus. All of the new synonymies proposed here result from the adopting of wider specific limits to take account of this variation. The characters used in defining the specific limits are now discussed.

COLONY SIZE. Crowell & Wyttenbach (1957) indicated that there are probably no endogenous factors operating to limit colony-size in *Campanularia flexuosa* (Hincks, in Alder, 1856), and it would seem likely that this also holds in *Obelia*. It follows that colony-size is probably of little or no systematic value. They suggested that colonies of *C. flexuosa* continue their apical growth until natural breakage occurs. It is relevant that the long colonies referred to *O. longissima* by some authors (pp. 256–266) are found in places of limited wave-action, such as broad estuaries [the late D. N. Huxtable (personal communication); personal observation], while shorter colonies hitherto regarded as more typical of *O. dichotoma* occur intertidally and sublittorally where wave-action is greater. Colonies of intermediate lengths occur and on present evidence it appears that colony-size in *O. dichotoma* s. lat. is related to wave-action. The status of *O. longissima* is discussed further below (p. 271).

O. geniculata colonies at a single locality in Massachusetts were usually shorter than 25 mm (Hammett, 1943). Ralph (1956), however, demonstrated a correlation between length and latitude in populations between 35° S and 41° S around New Zealand. Cold-water specimens were up to 40 mm long, while those from the warmest places measured only 5 mm. Later Ralph & Thomson (1968) showed that in Wellington harbour colonies formed in the austral winter were longer than those formed in the summer. Nevertheless, it appears that variationin colony-size in *O. geniculata* is less than in *O. dichotoma*. Information on *O. bidentata* is apparently lacking.

MONOSIPHONIC VERSUS POLYSIPHONIC STEMS. Old stems of *O. bidentata* are invariably polysiphonic, those of *O. dichotoma* are usually monosiphonic and those of *O. geniculata* always so.

BRANCHING OF COLONY. Several species of *Obelia* have been proposed on the basis of the pattern of branching of the colonies. However, this appears not to be correlated with other morphological features. Similarly the length of the branches seems unimportant. The influence of habitat on branching is poorly documented, but Ralph & Thomson (1968) reported that low temperatures induced branching in *O. geniculata*. Occasional dichotomously branched specimens occur in *O. dichotoma*, but it is questionable whether such specimens are truly dichotomous.

INTERNODES. Inter-colony variation occurs throughout the genus in internode length, breadth, length : breadth ratio, curvature, amount of asymmetric internal perisarc thickening, angle of flexure and number of annulations. Of these only the

amount of perisarc thickening seems to have systematic value, being pronounced and asymmetric (although variable) in *O. geniculata* and usually slight and symmetrical in the other two species. Occasional specimens of *O. dichotoma* occur in which the internodal perisarc is slightly thickened on one side, but such specimens can be identified by their hydrothecae. Asymmetric internodal thickening is further discussed below (pp. 271, 277).

Darkening of perisarc. In large colonies of *O. dichotoma* darkening of the internodal perisarc proceeds with age, older parts being dark brown, grading to brown, horn-coloured or transparent in younger parts of the colony. Colonies of *O. geniculata* do not become so dark, while the limited material of *O. bidentata* available suggests that no darkening occurs. Histochemical studies by Knight (1970) showed that in the normal perisarc tanning process of *Campanularia flexuosa* several of the biochemical precursors of melanin are formed and it is possible that this is the dark pigment in *O. dichotoma*.

Hydrotheca. Many hydrothecal characters appear to be systematically sound, and they are here regarded as important in defining specific limits within the genus. The hydrothecal rim may be bimucronate or mucronate as in *O. bidentata* (Fig. 2), even, sinuous or castellate as in *O. dichotoma* (Fig. 4) or invariably even as in *O. geniculata* (Fig. 5). The greater variability shown by *O. dichotoma* is not understood, but colonies otherwise similar may differ in having one type of rim or another. The factors involved in the rupture of the embryonic operculum and the consequent formation of the hydrothecal rim are only partly known (Knight, 1965) and it would seem unwise to attach systematic importance to rim-variation until more is known of the factors responsible.

The shape of the hydrotheca appears to be variable in length : breadth ratio, in the angle between the sides as seen in median vertical section and in the degree to which the basal region is curved inwards. Hydrothecae of *O. bidentata* are tubular with a curved basal region while those of *O. geniculata* usually have walls curved throughout their length (Figs 2, 5). Those of *O. dichotoma* are more variable, being tubular to conical (Fig. 4), with or without a curved basal region. A variable amount of thickening of the basal region of the hydrothecal wall occurs in *O. geniculata* but apparently not in the other two species.

The possession of an oblique hydrothecal diaphragm has been used to delimit species otherwise resembling *O. dichotoma*, but it appears to be a variable character and such species are not here regarded as valid (see p. 272). In *O. geniculata*, however, the diaphragm is always transverse while in *O. bidentata* it is always oblique. It has been noted that oblique diaphragms seen in optical section can, from certain angles, appear transverse (Mammen, 1965).

Hydrothecal pedicel. Although the number of annulations of the hydrothecal pedicel has been reported as constant at 4–6 in *O. geniculata* (Hammett, 1943), in *O. dichotoma* the number varies between the approximate limits 2–10 and in *O. bidentata* between 3–26 (Mammen, 1965). In both there is often a smooth central portion. There seems to be no indication at present whether this variation is phenotypic or genotypic.

GONOTHECA. Gonotheca shape is similar in the three species and with the exception of the terminal region is approximately constant. In *O. bidentata* and to a lesser extent in *O. dichotoma* gonothecae with apparently truncate ends have been described, there being only a trace of a raised central aperture (Fig. 2 ; pp. 263–264).

NEMATOCYSTS. Previous work, and also that reported here, suggests that nematocysts do not provide useful specific criteria in *Obelia*.

a. *O. dichotoma* and *O. geniculata*. The lengths of fresh, undischarged microbasic mastigophores from living hydranth tentacle-tips of the two species are shown in Table 2. The sizes varied to the extent that the range of measurements obtained

TABLE 2

Measurements of undischarged nematocysts from the tips of hydranth tentacles of *Obelia* spp., ±0·2 μm

SPECIES	LOCALITY	LENGTH			WIDTH	REMARKS
		n	$\bar{x}$	S.E.		
O. geniculata	Cornwall (1973.9.24.2)	22	6·8	0·0826	All 2·0	Fresh
	Cornwall (1973.9.24.3)	20	6·9	0·0444	All 2·0	Fresh
O. dichotoma	Devon (1973.7.23.1)	20	7·3	0·0857	All 2·0	Fresh
	Devon (1973.9.24.4)	20	6·7	0·0466	All 2·0	Fresh, specimen resembled *O. longissima* sensu Alder
O. bidentata	Norfolk (1953.11.16.1)	10	5·6	0·0897	All 1·5	Formalin-preserved

n = number in sample, $\bar{x}$ = mean, S.E. = standard error. 'Fresh' nematocysts are those taken from living hydranths.

from one species fell within the range recorded from the other. Application of Student's *t*-test showed nematocyst-length to be similar in the two *O. geniculata* populations ($p < 0{\cdot}001$), but dissimilar in the two groups of *O. dichotoma* ($p > 0{\cdot}32$).

Two types of nematocyst have previously been recorded from *O. geniculata*. Ito & Inoue (1962) reported microbasic mastigophores (measuring 4·9–5·2 μm × 1·3–1·5 μm undischarged) from the hydranths, while Weill (1934b) identified basitrichous isorhizas (length 5 μm) from the tentacles of both hydranth and medusa. Only the latter type has been recorded from *O. dichotoma*, from the medusa (Westfall, 1966, as *O. longissima* ; measurements not stated). Thus the present recording of microbasic mastigophores in *O. dichotoma* is new. However, the identification of the two kinds of nematocyst depends on the presence or absence of a butt (Fig. 1), a feature which can be ascertained only in discharged capsules (Weill, 1934a). Maybe a butt is not always present. It is certainly so small in *Obelia* as to be difficult to observe with the light microscope. Possibly more extensive observations on *Obelia* from various localities will explain the reported occurrence of both types.

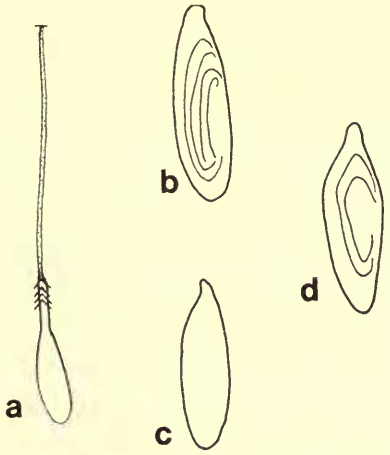

FIG. 1. *Obelia geniculata*. Microbasic mastigophores from live hydranths. SW. England (1973.9.24.2). (a) Discharged. Capsule, 7 μm ; butt, 6 μm ; barbs *c.* 1·5 μm ; thread, 63 μm (not all shown). Note distinct butt at base of thread. (b–d) Undischarged, different scales. Lengths, 6·8 μm ; breadths, 2 μm (see Table 2 for standard error). One side is slightly flatter than the other, and the tip of the capsule inclines to one side.

b. *O. bidentata*. Measurements of undischarged nematocysts from the tentacle-tips of formalin-preserved hydranths are shown in Table 2, living material being unobtainable. The preserved nematocysts at least were similar in size to those from live hydranths of the other two species. Identification was not attempted as no discharged nematocysts were seen, but the undischarged ones closely resembled those of the other species and may prove to be of the same kind.

BIOLUMINESCENCE. Although Hincks (1868) reported bioluminescence only in *O. geniculata*, it has now been reported in all three *Obelia* hydroids (Morin & Cooke, 1971).

SUBSTRATE. *O. geniculata* has been widely recorded on the blades of laminarian and fucoid algae, whereas *O. dichotoma* occurs usually on animal and inert substrates and less frequently on algae (Hincks, 1868 ; Hammett, 1943 ; Barrett & Yonge, 1958 ; Fey, 1969). Manton (1942) examined the attachment of the hydrorhiza of *Obelia* sp. to an unspecified substrate, and found that the coenosarc was not involved. Sections cut during the present study along the stolons of *O. geniculata* (1973.7.23.2–3) and into the algal substrate showed no tissue connections between hydroid and alga. It seems likely, therefore, that the growth-form of O. *geniculata* is not related to substrate. The occasional occurrence of each species on the substrate more usual for the other is additional evidence that substrate does not influence morphology. The substrate-preference of *O. bidentata* is less well known but is said to be for inert solid substrates and also sand (Vervoort, 1946a) to which neither of the other two species attaches directly.

MEDUSA GENERATION. The medusae of the three hydroid species, although variable, cannot at present be distinguished (see pp. 278–279).

Obelia bidentata Clarke, 1875

(Fig. 2)

Obelia bicuspidata Clarke, 1875 : 58, pl. 9, fig. 1 ; Bedot, 1912 : 326 ; Nutting, 1915 : 80, pl. 20, figs 5–6 (= *O. bidentata* Clarke) ; Bedot, 1916 : 160 ; Bedot, 1918 : 195 ; Bedot, 1925 : 298–299 (= *O. bidentata* Clarke) ; Fraser, 1944 : 153–154, pl. 27, fig. 125 (= *O. bidentata* Clarke ; *L. spinulosa* var. *minor* Leloup) ; Deevey, 1950 : 343 (= *O. oxydentata* Stechow ; *L. spinulosa* var. *minor* Leloup) ; Leloup, 1952 : 157, fig. 89 (= *C. spinulosa* Bale) ; Vannucci, 1954 : 108–110, pl. 2, figs 2–7, 9–10 (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *O. bifurca* Hincks ; *Obelia* sp. Clarke ; *O. oxydentata* Stechow) ; Millard, 1958 : 174 ; Mammen, 1965 : 11–13, figs 37–38 ; Millard & Bouillon, 1973 : 56 (= *G. longicyatha* : Jarvis).

Obelia bidentata Clarke, 1875 : 58–59, pl. 9, fig. 2 ; Pictet, 1893 : 25–26, pl. 1, figs 20–21 ; Jaderholm, 1904a : 270–271 (= *O. bicuspidata* Clarke) ; Jaderholm, 1904b : vii (= *O. bicuspidata* Clarke) ; Jaderholm, 1905b : 17 ; Mayer, 1910 : 254 [= *O. bicuspidata* Clarke ; ? = *O. austrogeorgiae* Jaderholm ; (see below, p. 280)] ; Bedot, 1912 : 326 ; Billard, 1912 : 463, fig. 2 (= *O. bicuspidata* Clarke) ; Bedot, 1916 : 160 ; Bedot, 1918 : 195 ; Kramp, 1961 : 162 ; Teissier, 1965 : 16 ; Fey, 1969 : 393.

? *Obelia longicyatha* Allman, 1877 : 10, pl. 7, figs 4–5 ; (see below, p. 264).

Campanularia spinulosa Bale, 1888 : 756–757, pl. 12, figs 5–7.

Obelia andersoni Hincks, 1889 : 132–133, pl. 12, figs 2–4 ; Thornely, 1904 : 113 ; Ritchie, 1910 : 810 ; [syn. nov.].

Obelia bifurca Hincks, 1889 : 133, pl. 12, fig. 1 ; Mayer, 1910 : 494 ; [syn. nov.].

Gonothyrea longicyatha Thornely, 1899 : 454–455, pl. 44, figs 4, 4a (non *O. longicyatha* Allman, 1877).

Obelia corona Torrey, 1904 : 14, figs 5–6 ; Nutting, 1915 : 79, pl. 20, figs 1–2 ; [syn. nov.].

Obelia sp. Clarke, 1907 : 10–12, pl. 5, figs 5–7.

Obelia bifurcata Thornely, 1908 : 81–82, pl. 9, fig. 2 (nom. nov. pro *O. bifurca* Hincks).

Laomedea bidentata : Babič, 1913 : 284–286, fig. 1 (= *O. bicuspidata* Clarke).

Obelia multidentata Fraser, 1914 : 154, pl. 17, fig. 56 ; Fraser, 1937 : 89–90, pl. 18, fig. 93 ; [syn. nov.].

Obelia oxydentata Stechow, 1914 : 131–132, fig. 7 (nom. nov. pro *Obelia* sp. Clarke) ; Stechow, 1919 : 50 ; Vannucci Mendes, 1946 : 555–556, pl. 2, fig. 22 ; Hirohito, 1969 : 9–10, fig. 8a–b.

Gonothyrea bicuspidata : Stechow, 1919 : 50–51 (= *O. bidentata* Clarke ; *G. longicyatha* Thornely) ; Vannucci Mendes, 1946 : 556–557, pl. 3, fig. 23 [= *O. bidentata* Clarke ; ? = *O. austrogeorgiae* : Nutting, 1915 ; (see below, p. 280)].

Obelia longa Stechow, 1921a : 221–223, fig. 1 ; Stechow, 1925 : 436–437, figs 12b, 13 ; [syn. nov.].

Gonotha longicyatha (sens. Thornely) : Jarvis, 1922 : 336.

Clytia longitheca Hargitt, 1924 : 484, pl. 3, fig. 9 ; [syn. nov.].

Obelia longitheca Hargitt, 1924 : 484–485, pl. 3, fig. 10 ; [syn. nov.].

Obelia attenuata Hargitt, 1924 : 486, pl. 3, fig. 11 ; [syn. nov.].

Obelia spinulosa : Billard, 1927 : 333–334, fig. 2.

Laomedea bicuspidata var. *picteti* Leloup, 1932 : 151–153, pl. 17, figs 4, 4d, text-fig. 19.

Laomedea spinulosa var. *minor* Leloup, 1932 : 155–158, pl. 17, figs 6, 6a, text-figs 24–25.

Laomedea bicuspidata : Hummelinck, 1936 : 53–57, fig. 8a-v (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *G. longicyatha* Thornely ; *Obelia* sp. Clarke ; *O. oxydentata* Stechow ; *L. bicuspidata* var. *picteti* Leloup ; *L. spinulosa* var. *minor* Leloup) ; Vervoort, 1946a : 298–300, fig. 132a-f (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *G. longicyatha* Thornely ; *O. oxydentata* Stechow) ; Vervoort, 1946b : 344–345, fig. 10a–b ; Hamond, 1957 : 312–313, figs 20–21 ; Vervoort, 1959 : 315 ; Vervoort, 1972a : 92–93, fig. 26d (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *L. spinulosa* var. *minor* Leloup ; *Obelia* sp. Clarke ; *O. oxydentata* Stechow).

? *Clytia longicyatha* (sens. Allman) : Fraser, 1944 : 142, pl. 25, fig. 114 ; (see below, p. 264).

Clytia longicyatha (sens. Allman) : Rees & White, 1966 : 276.

Laomedea bicuspidata var. *tenuis* Vervoort, 1946b : 345–346, fig. 10c (nom. nov. pro *L. spinulosa* var. *minor* Leloup).

? *Laomedea longicyatha* (sens. Allman) : Vervoort, 1946b : 343–344.

Laomedea (*Obelia*) *bicuspidata* : Vervoort, 1968 : 19–21, fig. 7 (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *Obelia* sp. Clarke ; *C. spinulosa* var. *minor* Leloup).

Laomedea (*Obelia*) *longicyatha* (sens. Allman) : Vervoort, 1968 : 21–22, fig. 8 ; Vervoort, 1972a : 93.

non *Clytia longicyatha* (sens. Allman) : Pictet, 1893 : 28–29, pl. 2, figs 22–23 (= *Clytia* sp., see below, p. 264).

TYPE LOCALITY. Greenport, Long Island, New York, U.S.A., on wharf piles (Clarke, 1875).

DIAGNOSIS. *Obelia* hydroid usually with branched, erect hydrocaulus ; polysiphonic basally, internodes straight, narrow, lacking internal thickening of perisarc and not usually strongly tanned ; rim of hydrotheca with a variable number of cusps, usually bimucronate.

DESCRIPTION. Mature colony comprising several erect, sometimes flexuose, polysiphonic stems up to 350 mm, alternate lateral hydrocauli bearing the hydrothecae ; basal hydrorhiza on sandy substrates a tangled mass of stolons. Lateral

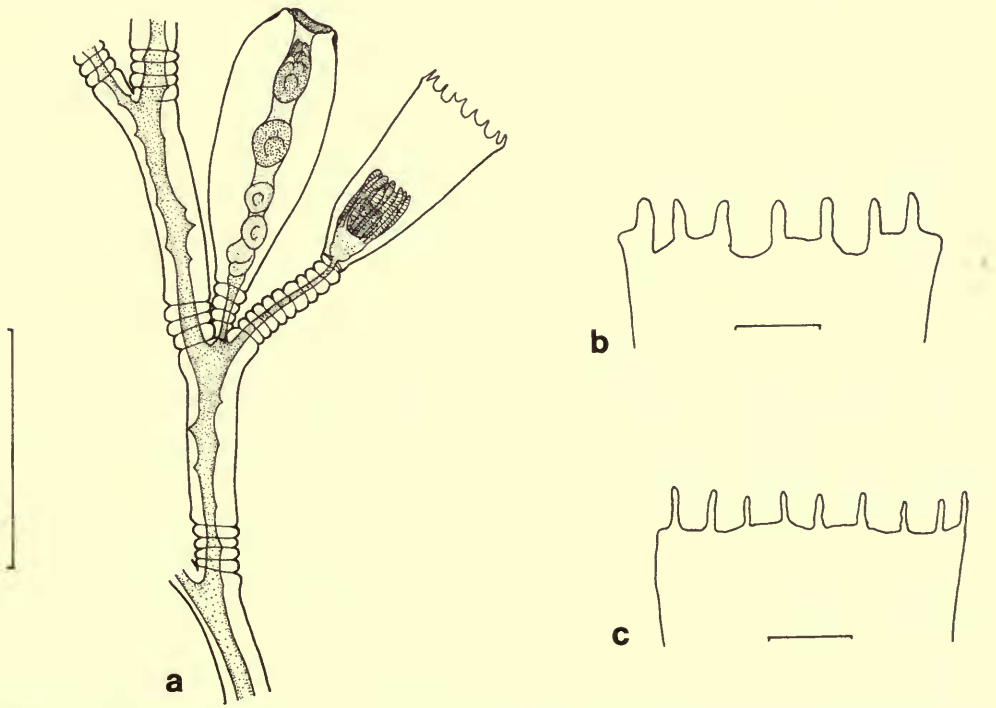

Fig. 2. *Obelia bidentata*. (a) Nigeria (1966.10.6.1). Part of hydrocaulus and ripe gonotheca with aperture only slightly raised. Scale = 500 μm. (b) Sierra Leone (1966.10.7.5). Bimucronate hydrothecal rim slightly irregular. Scale = 50 μm. (c) Nigeria (1966.10.8.117). Hydrothecal rim with indentations of similar depth (? atypical). Scale = 50 μm.

hydrocauli delicate, slightly flexuose; internodes long, annulated proximally, with lateral process distally to which hydrothecal pedicel is attached. Pedicel ringed throughout or with central smooth portion; hydrotheca 1–3 times long as broad, bell-shaped, slightly asymmetric, sometimes having folds in the hydrothecal wall between cusps running proximally from the rim; diaphragm oblique (can appear transverse in optical section); rim with 10–20 bimucronate cusps (rarely, simply cusped; Fig. 2a–c); hydranth undescribed. Gonotheca usually an inverted cone with raised aperture; occasionally truncated with broad aperture, lacking raised structure. Measurements – see Table 3.

TABLE 3

Measurements of the hydroid stage of *Obelia bidentata* in μm

	NIGERIA (1966.10.6.1; Fig. 2a)	SIERRA LEONE (1966.10.7.8)	SOUTH YEMEN (1966.11.15.2)	NORFOLK, ENGLAND (1953.11.16.1)
HYDROTHECA				
Length (diaphragm to tips of cusps)	400–470	340–490	320–430	380–430
Breadth at rim	210–270	120–230	180–280	200–220
HYDROTHECAL PEDICELS				
Length	070–240	070–580	060–410	070–240
INTERNODES				
Length	450–680	400–570	320–480	480–710
Maximum breadth	080–130	070–080	070–090	080–120
Length/breadth ratio	*c.* 6	5–6	5–6	5–6
GONOTHECA				
Length	550–600	—	—	—
Maximum breadth	220–260	—	—	—

MATERIAL EXAMINED. *Atlantic Ocean* – Greenport, Long Island, New York, U.S.A., 5 August 1874, several infertile hydrocauli in spirit, **syntypes**, Yale Peabody Museum of Natural History no. 3119. Thimble Island, Branford, Connecticut, U.S.A., 23 September 1874, three fragments in spirit, **syntypes** of *O. bicuspidata* Clarke, Yale Peabody Museum of Natural History no. 7265.

Hunstanton, Norfolk, England, 26 September 1953, several large colonies in spirit, coll. R. Hamond, 1953.11.16.1[1] (Table 2). Shellness, Isle of Sheppey, Kent, England, strandline, 23 September 1973, two abraded colonies in spirit, coll. P. F. S. Cornelius, 1973.9.24.1.

Zeeland Province, Netherlands, 20 August 1946, several colonies in spirit, Leiden Rijksmuseum van Natuurlijke Historie no. 3687.

Monte Brazil W., Terceira I., Azores, 29 m, 27 July 1959 and August 1959, several colonies in spirit, coll. Imperial College Azores Expedition, 1962.1.15.17, 21 (Rees & White, 1966, as *Clytia longicyatha*; see p. 264).

[1] Registered numbers of this format refer to British Museum (Natural History) collections, unless otherwise stated.

Trinidad, West Indies, August 1966, three microslides of fragments, coll. J. H. Wickstead, 1966.11.11.1.

Port Harcourt, Nigeria, 11 July – 14 November 1957, 26 microslides of fragments, coll. H. G. Stubbings, 1966.10.8.14, 31, 44, 55, 56, 58, 70, 74, 92, 93, 95, 112, 117, 119, 120, 124 (Fig. 2c). Lagos, Nigeria, 1957, four microslides of fragments, coll. M. B. Hill, 1958.3.1.1–4. Lagos Harbour, Nigeria, January 1959, 1 m, one microslide of fragments, coll. M. B. Hill, 1966.10.6.1 (Fig. 2a).

Bunce Island, Sierra Leone, 19 February 1955, seven microslides of fragments, coll. A. Longhurst, 1966.10.7.5–11 (Fig. 2b).

Indo-Pacific Ocean – Sapper Bay, Aden, South Yemen, 17 August 1966, coll. K. W. England, one microslide of fragments, 1966.11.15.2.

Amoy, China, December 1925, one colony in spirit, coll. C. Ping, 1926.3.17.36.

On Hong Kong to Manilla cable, 20°57′ N, 115°23′ E, *c.* 200 m, 21 February 1929, one microslide of fragments, coll. British East India Company, 1929.4.18.20.

Other material recorded. *North Atlantic* – West European waters from Helgoland (Kramp, 1961), Netherlands, Belgium, northern France (Vervoort, 1946a ; Leloup, 1952 ; Teissier, 1965 ; Fey, 1969); Mediterranean Sea (Vervoort, 1946b), Algeria (Picard, 1955), Azores (Rees & White, 1966), Ghana (Buchanan, 1957), tropical W. Africa (Vervoort, 1959). North American coast from Casco Bay, Maine, south to Caribbean and Panama (Fraser, 1946 ; Vervoort, 1946b, 1968).

South Atlantic – South American coast from Brazil (Fraser, 1946 ; Vannucci Mendes, 1946) and near Tierra del Fuego (Vervoort, 1972a).

Pacific – San Francisco Bay (Fraser, 1937, 1946), Hawaii (Vervoort, 1946b), Japan (Hirohito, 1969, as *O. oxydentata*), New Britain Island (Vervoort, 1946b), Port Jackson, New South Wales, Australia (Bale, 1888, as *Campanularia spinulosa*).

Indian Ocean – Several localities off India and Malaya (Vervoort, 1946b ; Mammen, 1965), Kerguelen Island (Stechow, 1925, as *O. longa*), Natal (Millard, 1958), Mozambique and Seychelles (Millard & Bouillon, 1973, 1974).

Distribution. Continental shelf depths in tropical, sub-tropical and some temperate seas in both northern and southern hemispheres. Records furthest from the equator are Helgoland (54° N), South Georgia and Tierra del Fuego (both 54° S). Reported unrecorded from Argentina (Vervoort, 1972a), New Caledonia (Redier, 1966), Tasmania (Hodgson, 1950), South Australia (Blackburn, 1942), New Zealand and the Chatham Islands (Ralph, 1957, 1961), south and west coasts of the Republic of South Africa (Millard, 1957).

Remarks. The number of bimucronate cusps on the hydrothecal rim may vary between 10 and 20 (Nutting, 1915 ; Mammen, 1965), although at any one locality the range of variation is less. Most specimens have alternating deep and shallow notches around the hydrothecal rim but in some the gaps are of almost equal depth and the bimucronate condition is obscured (Fig. 2b–c).

Two kinds of gonothecae have been recorded. The more usual kind is typical of *Obelia*, with a tubular aperture (Nutting, 1915 ; Hamond, 1957 ; Hirohito, 1969) while the other is truncated distally and opens directly (Babič, 1913 ; Fraser, 1937 ; Mammen, 1965). Possibly a reduced tubular aperture was overlooked by

authors describing a truncate gonotheca. Medusa release was recorded from normal gonothecae by Hamond, while a BM(NH) specimen shows medusae developing within an apparently truncate gonotheca (Fig. 2a).

The two nominal species *O. bicuspidata* and *O. bidentata* were first described on the same page by Clarke (1875). They were synonymized under *O. bidentata* by Jaderholm (1904a, b, 1905a), whose usage as first reviser was followed by Mayer (1910), Billard (1912) and Babić (1913). Nutting (1915), however, used *O. bicuspidata* as the senior synonym, although including Jaderholm's 1904a paper in his synonymy. Since then *bicuspidata* has been used more frequently than *bidentata* but Jaderholm's usage gives *bidentata* priority.

Two varieties of the species have been described. *Laomedea spinulosa* var. *minor* Leloup, 1932, was erected to accommodate forms differing only in the height of the colony. Vervoort (1972a), however, placed var. *minor* Leloup together with *L. bicuspidata* var. *tenuis* Vervoort, 1946b (a new name for Leloup's variety), in the synonymy of *O. bicuspidata*. The second variety, *O. bicuspidata* var *picteti* Leloup, 1932, was distinguished on specimens with long gonothecae. As such variation is common and has no apparent taxonomic value, the separation is not upheld here.

There is some confusion concerning *Obelia longicyatha* Allman, 1877, and another nominal species of the same name, *O. longicyatha* (Thornely, 1899). The type specimens of neither species could be located. Allman's species, described from infertile material, was said to have long pointed cusps on the hydrothecal rim reminiscent of *Clytia*, to which genus the species has been referred by several authors (references in Fraser, 1944). Nevertheless, the form of the colony as illustrated by Allman equally suggests *O. bidentata*, and the affinities of the species remain unclear. Pictet (1893) referred to Allman's species material with developing medusae clearly not of *Obelia* type and referred his material to *Clytia*. Vervoort (1946b) described under Allman's species material identical with *O. bidentata* except that the hydrothecae were unusually long (900–950 μm). The gonothecae were typical for the species. Vervoort (1968) later described other, infertile, material with hydrothecae nearer in size (580–620 μm) to the measurements given here (320–490 μm) and illustrated an oblique hydrothecal diaphragm characteristic of *O. bidentata*. Vervoort (1972a) subsequently referred another infertile specimen to Allman's species, distinguishing it from *O. bidentata* on the basis of hydrothecal length. However, it seems unclear at present whether or not specimens of such dimensions fall within the range of variation of *O. bidentata*, and the identity of Vervoort's material is problematical. In contrast the material identified with Allman's species by Rees & White (1966) and re-examined here seems identical with *O. bidentata*, having characteristic bimucronate hydrothecal rims and falling within the normal size-range. The other species, *O. longicyatha* (Thornely, 1899), was stated in the original description to have such hydrothecal rims and Stechow (1919) and Hummelinck (1936) justifiably referred it to *O. bidentata*. Jarvis (1922) referred to *Gonotha longicyatha* specimens with bimucronate hydrothecal cusps and truncate gonothecae which seem also to have been typical *O. bidentata*.

Obelia andersoni Hincks, 1889, from the Mergui Archipelago, can be referred to *O. bidentata*. It was originally distinguished on the basis of a sharp demarcation

between the cylindrical side of the hydrotheca and its inward-sloping base. Thornely (1904) found similar material in which there was no sharp demarcation, and the species appears invalid.

The affinities of *O. austrogeorgiae* Jaderholm, 1904b, are discussed on page 280.

MEDUSAE. It has often been established that *O. bidentata* releases a medusa (Hincks, 1889, as *O. andersoni*; Pictet, 1893, as *O. bidentata*; Thornely, 1899, as *Gonothyrea longicyatha*; Billard, 1927, as *O. spinulosa*; Fraser, 1944, as *Clytia longicyatha* sensu Allman; the following, as *O. bicuspidata*: Vervoort, 1946a, b; Vannucci, 1954; Hamond, 1957; Mammen, 1965; and Fey, 1969, as *O. bidentata*). However, the medusae were apparently not recorded as resembling those of the other *Obelia* species until Billard (1927) identified them in the gonotheca. Subsequently Hamond (1957) and Mammen (1965) confirmed the resemblance by observing newly liberated medusae. Adult specimens have not been described and the best available description, of the young stage, is that by Mammen. The young stage at least is very similar to that in the other two species.

Obelia dichotoma (Linnaeus, 1758)

(Figs 3 & 4)

Sertularia dichotoma Linnaeus, 1758 : 812 ; Linnaeus, 1767 : 1312 (= *S. longissima* Pallas) ; Maratti, 1776 : 34 ; Rees, 1819 : unpaginated ; Dalyell, 1836a : 91–92, 94, fig. 1 ; Dalyell, 1836b : 84–85, 87, fig. 1.

Sertularia longissima Pallas, 1766 : 119–121 (nom. nov. pro *S. dichotoma* Linnaeus).

Sertolare genicolata Cavolini, 1785 : 205, pl. 8, figs 1–4 (lapsus pro *Sertularia geniculata* Linnaeus).

Laomedea dichotoma : Lamouroux, 1812 : 184 ; Johnston, 1838 : 150–151, pl. 22, figs 1–2 (= *Sertularia longissima* Pallas) ; Johnston, 1847 : 102–103, 119, pl. 26, figs 1–2 (= *S. longissima* Pallas) ; Alder, 1857 : 121 (= *Campanularia gelatinosa* : van Beneden) ; Hincks, 1861 : 258.

Sertularia geniculata : Sprengel, 1813 : 95–97, pl. 8, figs 3–4.

Campanularia dichotoma : Meyen, 1834 : 193–195, pl. 30, figs 1–4, pl. 31, fig. 1 ; [non *C. dichotoma* : Grant, 1826 : 150–156 (= *Laomedea flexuosa* Hincks, in Alder, 1856)].

Campanularia maior Meyen, 1834 : 196–197, pl. 32, figs 1–4 ; Bedot, 1905 : 53 ; [syn. nov.].

Campanularia brasiliensis Meyen, 1834 : 198, pl. 32 ; Nutting, 1915 : 77, pl. 18, figs 8–9 ; [syn. nov.].

Campanularia cavolinii Deshayes & Edwards, 1836 : 133 (nom. nov. pro *Sertularia geniculata* : Cavolini) ; [syn. nov.].

Campanularia caulini Chiaje, 1841 : 143 (unjustified emendation of *C. cavolinii* Deshayes & Edwards).

Sertularia cavolinii : Kölliker, 1843 : 81 ; [syn. nov.].

Campanularia gelatinosa : van Beneden, 1844 : 33–34, pls 1–2 ; Maitland, 1876 : 13 (= *Obelia sphaerulina* Péron & Lesueur, 1810a) ; (see p. 279).

Laomedea longissima : Alder, 1857 : 121–122 ; Hincks, 1861 : 259.

Obelia commissuralis McCrady, 1857 : 197–198, pl. 11, figs 5–7 ; Agassiz, 1862 : 315–321, pls 33–34, figs 10–21 ; Agassiz, 1865 : 91–92, figs 134–135 (= *Laomedea dichotoma* : Leidy ; *L. gelatinosa* : Gould, Stimpson) ; Norton, 1896 : 291–296, figs 1–12 ; Nutting, 1915 : 83, pl. 21, figs 1–5 ; Berrill, 1949 : 235–264 ; Vannucci, 1951 : 80–81, pl. 2, figs 8–9 ; Mammen, 1965 : 14–15, fig. 41 (? = *O. hyalina* Clarke) ; [syn. nov.].

Laomedea divaricata McCrady, 1857 : 195–196 ; Agassiz, 1865 : 91.

Eucope parasitica Agassiz, 1865 : 87 ; [syn. nov.].

Eucope pyriformis Agassiz, 1865 : 88–89 ; Mayer, 1910 : 247 (? = *Laomedea divaricata* McCrady) ; [syn. nov.].
Eucope articulata Agassiz, 1865 : 89–90, figs 130–131.
Campanularia flabellata Hincks, 1866 : 297 (nom. nov. pro *C. gelatinosa* : van Beneden).
Obelia longissima : Hincks, 1868 : 154–155, pl. 27 (= *Campanularia gelatinosa* : van Beneden) ; Russell, 1953 : 303, fig. 185c ; Naumov, 1960 : 263–264, figs 149–151 ; Naumov, 1969 : 284, figs 149–151.
Obelia dichotoma : Hincks, 1868 : 156–157, pl. 28, fig. 1, 1a–b ; Mayer, 1910 : 245–246, 248, pl. 30, figs 1–2 ; text-figs 125–127 (= *Eucope articulata* Agassiz ; *O. sphaerulina* : Haeckel ; ? *O. australis* von Lendenfeld ; *O. rhunicola* Billard) ; Bedot, 1925 : 301 (= *O. rhunicola* Billard) ; Russell, 1953 : 303, fig. 185b ; Millard, 1966 : 483 (= *O. dubia* : Vanhoffen ; *Campanularia obtusidens* Jaderholm).
Obelia flabellata : Hincks, 1868 : 157–158, pl. 29 ; Nutting, 1915 : 84–85, pl. 22, figs 3–4 (= *O. plana* : Mayer ; see footnote, p. 271).
Obelia plicata Hincks, 1868 : 159, pl. 30, figs 1, 1a ; Nutting, 1915 : 78, pl. 19, figs 5–6 ; [syn. nov.].
Schizocladium ramosum Allman, 1871 : 18–21, pl. 2, figs 1–8 ; [syn. nov.].
Obelia pygmaea Coughtrey, 1876 : 25, pl. 3, fig. 3 ; Ralph, 1957 : 832 [? = *O. longissima* (Pallas)] ; [syn. nov.].
Obelia hyalina Clarke, 1879 : 239, 241–242, pl. 4, fig. 21 (non *Gonothyrea hyalina* Hincks, 1866).
Obelia adelungi Hartlaub, 1884 : 164–165, text-fig. 1 ; [syn. nov.].
Obelia helgolandica Hartlaub : 1884 : 165–167, text-fig. 2 ; [syn. nov.].
Obelia australis von Lendenfeld, 1885a : 604, 630 ; Bale, 1888 : 753–754, pl. 12, figs 1–2 ; Ralph, 1957 : 830, fig. 4a–h ; Mammen, 1965 : 11.
Obelia angulosa Bale, 1888 : 752–753, pl. 12, fig. 3 ; Mayer, 1910 : 257 ; [syn. nov.].
Obelia chinensis Marktanner-Turneretscher, 1890 : 209–210, pl. 3, figs 6–7 ; Mayer, 1910 : 242 (? = *O. plana* : Haeckel) ; [syn. nov.].
Obelia arruensis Marktanner-Turneretscher, 1890 : 210, pl. 3, fig. 8 ; [syn. nov.].
Obelia nigrocaulus Hilgendorf, 1898 : 203–204, pl. 17, figs 1, 1a ; Bale, 1924 : 230.
Obelia gracilis Calkins, 1899 : 353–354, pl. 3, figs 13, 13a–c, pl. 6, fig. 13d [non *Laomedea gracilis* Sars, 1850 = *Campanularia pelagica* van Breemen, 1905 (Vervoort, 1946a : 285)] ; Nutting, 1915 : 78, pl. 19, figs 2–4 ; Hargitt, 1927 : 504–505 ; Ling, 1938 : 183 ; Blanco, 1967 : 130–134, figs 1–16 ; [syn. nov.].
Obelia surcularis Calkins, 1899 : 355, pl. 3, figs 14, 14a–b, pl. 6, fig. 14c ; Nutting, 1915 : 84, pl. 22, figs 1–2 ; [syn. nov.].
Obelia fragilis Calkins, 1899 : 355–356, pl. 3, figs 15, 15a–b, pl. 6, fig. 15c ; Nutting, 1915 : 87, pl. 33, fig. 6 ; [syn. nov.].
Obelia griffini Calkins, 1899 : 357, pl. 4, figs 18, 18a–c, pl. 6, fig. 18d ; Nutting, 1915 : 87, pl. 23, figs 4–5 ; Vannucci Mendes, 1946 : 552–553, pl. 2, figs 16–17 ; [syn. nov.].
Obelia rhunicola Billard, 1901b : 522–523.
Obelia borealis Nutting, 1901 : 174, pl. 19, figs 4–6 ; Nutting, 1915 : 85, pl. 22, figs 5–7 ; [syn. nov.].
Obelia dubia Nutting, 1901 : 174, pl. 20, fig. 1 ; Nutting, 1915 : 77, pl. 19, fig. 1 ; Mayer, 1910 : 248 (? = *O. dichotoma* : Hincks) ; Vanhoffen, 1910 : 307–308, fig. 27 ; Bedot, 1925 : 302 (= *Campanularia obtusidens* Jaderholm).
Obelia solowetzkiana Schydlowsky, 1902 : 123–125, pl. 3, figs 20–22 (nom. nov. pro *O. flabellata* : Schlater) ; Jaderholm, 1909 : 63 ; [syn. nov.].
Campanularia obtusidens Jaderholm, 1905a : 2, pl. 1, fig. 1.
Obelia congdoni Hargitt, 1909 : 375–376 (nom. nov. pro *O. hyalina* Congdon) ; [syn. nov.].
Obelia articulata : Mayer, 1910 : fig. 126.
Obelia pyriformis : Mayer, 1910 : 240, 247, fig. 128 (= *Laomedea divaricata* McCrady).
Obelia piriformis Bedot, 1910 : 342 (lapsus pro *pyriformis*).
Obelia undotheca Stechow, 1923a : 4 ; Stechow, 1923b : 115–117, fig. O ; [syn. nov.].
Obelia nodosa Bale, 1924 : 230, fig. 1 ; Ralph, 1957 : 832, fig. 5i–k ; [syn. nov.].

Obelia coughtreyi Bale, 1924 : 230–231, fig. 2 ; [syn. nov.].
Obelia obtusidentata Bedot, 1925 : 302 (lapsus pro *obtusidens*).
Obelia everta Hargitt, 1927 : 505, fig. 4 ; [syn. nov.].
Obelia alternata Fraser, 1938 : 35–36, pl. 8, fig. 38 ; [syn. nov.].
Obelia equilateralis Fraser, 1938 : 36–37, pl. 9, fig. 39 ; Fraser, 1944 : 157, pl. 28, fig. 128 ; [syn. nov.].
Obelia microtheca Fraser, 1938 : 37, pl. 9, fig. 40 ; [syn. nov.].
Obelia tenuis Fraser, 1938 : 38–39, pl. 9, fig. 42 ; [syn. nov.].
Obelia racemosa Fraser, 1941 : 82, pl. 15, fig. 7 ; [syn. nov.].
Obelia irregularis Fraser, 1943 : 77 ; Fraser, 1944 : 162, pl. 29, fig. 132 ; [syn. nov.].
? *Obelia obtusidens* : Fraser, 1944 : 163–164, pl. 29, fig. 134 ; (see p. 272).
Obelia braziliensis Vannucci Mendes, 1946 : 553–555, pl. 2, figs 20–21 (lapsus pro *brasiliensis*).
Obelia biserialis Fraser, 1948 : 213, pl. 24, fig. 6 ; [syn. nov.].
Laomedea (*Obelia*) *dichotoma* : Vervoort, 1959 : 315–316.
Laomedea (*Obelia*) *congdoni* : Vervoort, 1968 : 23 (= *O. hyalina* Clarke ; *L. sargassi* Leloup).

TYPE SPECIMEN AND TYPE LOCALITY. Ellis, 1755 : 21–22, pl. 12, fig. A, but not fig. a ; coast of SW. England.[1] Location of specimen unknown.

DIAGNOSIS. *Obelia* hydroid usually with branched, flexuose, monosiphonic hydrocauli ; internodes long, straight or slightly curved, without asymmetric perisarc thickening. Perisarc colourless in small specimens ; tanned to a horn-colour, brown or black in large colonies. Hydrothecal pedicels long, ringed, sometimes with smooth central portion. Hydrothecae straight-sided, curving basally, often slightly flared at rim, which may be even, castellate or sinuous, frequently with minute longitudinal folds in the hydrothecal wall.

DESCRIPTION. Main stems of colonies usually monosiphonic, flexuose, 10–350 mm ; racemose hydrocauli with shorter lateral branches ; occasional specimens apparently dichotomous (see p. 256). Main hydrocauli frequently tanned to a horn-colour, often brown or black, darker basally ; internodes long, nodes usually annulated, process supporting hydrothecal pedicel distal (Fig. 3). Hydrothecal pedicel long, annulated throughout or with smooth central portion ; hydrotheca bell-shaped, occasionally flared distally ; length 1–2 times greatest breadth ; rim usually even but often sinuous or castellate (Fig. 4), frequently with minute longitudinal folds extending proximally from centre of each indentation ; ornamented rims easily abraded even ; diaphragm usually transverse but sometimes

[1] In the absence of Linnaean material, type selection depends on the sole work cited by Linnaeus (1758), i.e. Ellis (1755). The woodcut figure is a good representation of part of an *Obelia* colony. It shows four internodes with three attached gonothecae but no hydrothecae. The figure is thus compatible with Linnaeus' diagnosis, which similarly does not mention hydrothecae ('Sertularia denticulis obsoletis, calycibus [= gonotheca] obovatis axillaribus, pedunculis intortis, caule dichotomo geniculato'). Some of Ellis' hydroid material was eventually incorporated in Sir Hans Sloane's herbarium which formed the basis of the biological collections of the British Museum; but there are no specimens of *O. dichotoma* in that herbarium. Other Ellis hydroid material, some of it probably figured and hence eligible for typification, was until recently preserved in the Hunterian Museum of the Royal College of Surgeons of England (Royal College of Surgeons of England, 1830, 1860; Harmer, 1931). Fragments of *O. dichotoma* were evidently included (Royal College of Surgeons of England, 1860 : 137, as *Laomedea*) although it is not certain that they originated from Ellis. However, the bulk of the Ellis material was destroyed during the Second World War, and it is virtually certain that only a single specimen, of *Nemertesia* Lamouroux, 1812, survived (Dobson, 1971; Miss E. Allen, personal communication). The exquisite drawings listed by Harmer from which most of the plates of Ellis (1755) and Ellis and Solander (1786) were prepared still survive, however. Linnaeus gave no locality for the species, but Ellis recorded it as common on the coast of SW England.

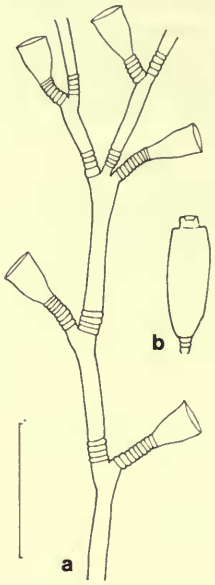

FIG. 3. *Obelia dichotoma*. (a) SW. England (1959.9.17.43). Part of hydrocaulus. (b) Ireland (1959.9.17.35). Detached gonotheca. Scale = 1000 μm for both diagrams.

oblique. Gonothecal pedicel annulated, situated in axil of hydrothecal pedicel; gonotheca inverted cone-shaped, apex domed with central tubular aperture. Measurements – see Table 4.

TABLE 4

Measurements of the hydroid stage of *Obelia dichotoma* in μm

	MASSACHUSETTS, U.S.A. (1915.3.6.37; Fig. 4d)	SW FRANCE (1959.11.17.4)	IRELAND (1959.9.17.35)	ISLE OF MAN, U.K. (1959.9.17.37)
HYDROTHECA				
Length (diaphragm to rim)	270–360	320–350	250–340	200–250
Breadth at rim	290–340	220–310	250–330	210–230
HYDROTHECAL PEDICELS				
Length	280–790	200–730	210–790	120–450
INTERNODES				
Length	750–1200	930–1150	830–930	430–500
Maximum breadth	080–150	070–110	120–190	080–110
Length/breadth ratio	*c.* 10	*c.* 10	*c.* 7	*c.* 4
GONOTHECA				
Length	—	750–800	870–1000	500–590
Maximum breadth	—	(obscure)	260–320	210–270

MATERIAL EXAMINED. *Atlantic Ocean* – Oban, Argyll, Scotland, 1877, several colonies in spirit, coll. A. M. Norman, 1912.12.21.276. North end of Loch Sween, Argyll, Scotland, 1 m, on *Halidrys siliquosa* (L.) Lyngbye, 1819,[1] 31 May 1962, numerous colonies in spirit and microslide, coll. W. J. Rees, 1962.6.19.13. Caol Scotnish, Loch Sween, Argyll, Scotland, 1 m, on *Halidrys siliquosa*, 30 May 1962, numerous colonies in spirit and two microslides, coll. W. J. Rees, 1962.6.19.23. Cuan Sound, Argyll, Scotland, LWST, on *Halidrys siliquosa*, 2 June 1962, numerous colonies in spirit and microslide, coll. W. J. Rees, 1962.6.19.11 (Fig. 4f). Millport, Isle of Cumbrae, Bute, Scotland, 17 September 1902, several colonies in spirit and microslide, coll. E. T. Browne, 1959.10.17.1–2. Clyde Sea, Scotland, 35 m, on stem of *Thecocarpus myriophyllum* (Linnaeus, 1758), 27 August 1920, several hydrocauli in spirit and microslide, coll. L. P. W. Renouf, 1920.9.10.1. Isle of Man,

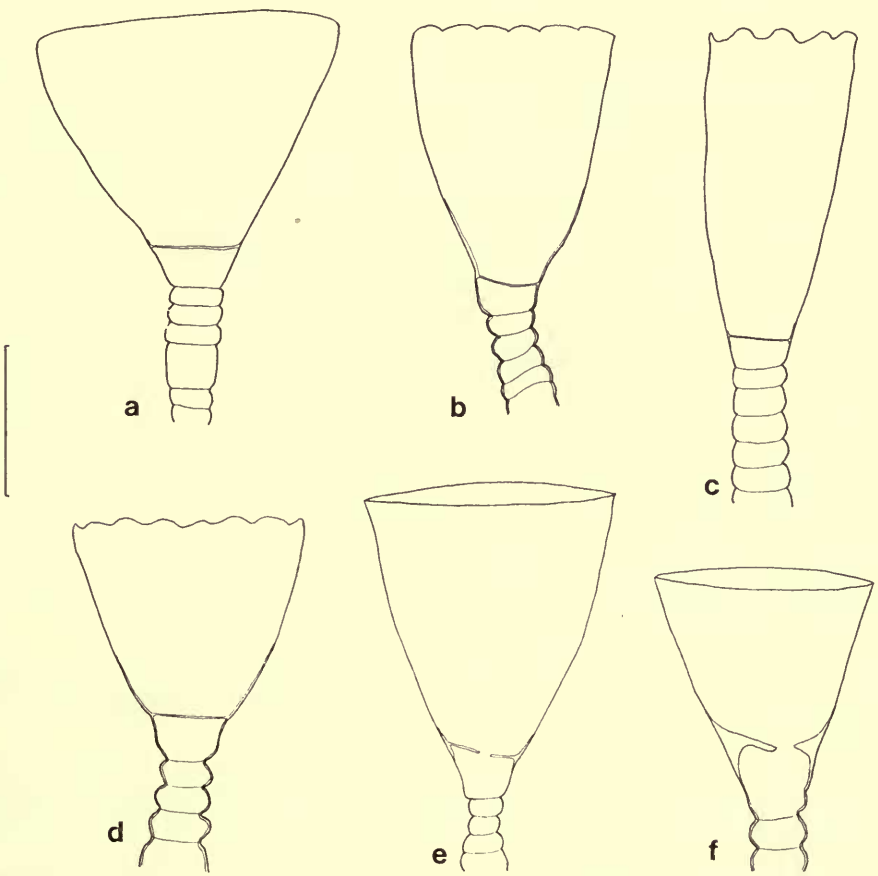

FIG. 4. *Obelia dichotoma*. Several hydrothecae showing variation in shape of rim and angle of diaphragm. (a) England (1973.7.23.1). (b) England (1929.1.1.1). (c) Probably British Isles (1920.3.1.1). (d) Massachusetts (1915.3.6.37) (Table 4). (e) Ireland (1967.6.15.106). (f) Scotland (1962.6.19.11). Scale = 250 μm.

[1] The scientific names of algae follow Parke & Dixon (1968).

British Isles, 10 September 1894, colony on microslide, coll. E. T. Browne, 1959.9.17.47. Port Erin, Isle of Man, British Isles, 6 October 1892, colony on microslide, coll. E. T. Browne, 1959.9.17.37. Martin's Beach, Marloes Peninsula, Pembrokeshire, Wales, colony on microslide, coll. P. Dick, 1959.9.23.2. Ireland, 24 July 1902, colony on microslide, coll. E. T. Browne, 1967.6.15.106 (Fig. 4e). Ireland, 2 May 1922, five colonies on microslide, coll. E. T. Browne, 1959.9.17.35 (Fig. 3b). Plymouth, England, 14 September 1897, several colonies on piece of wood, in spirit, coll. E. T. Browne, 1954.8.3.71. Plymouth, England, 14 March 1898, colonies on two microslides, coll. E. T. Browne, 1959.9.17.32, 43 (Fig. 3a). Millbay Dock, Plymouth, England, 2 November 1906, several hydrocauli in spirit, coll. E. T. Browne, 1954.8.3.77. Mewstone Ledge, Plymouth, England, colony on microslide, coll. R. Davis, 1962.8.8.1. Tinside, Plymouth, England, intertidal, on *Fucus vesiculosus* L., 22 September 1972, several colonies in spirit and microslide, coll. P. F. S. Cornelius, 1973.7.23.1 (Fig. 4a). River Tamar, Devon, England, 0·8 km upstream of Cargreen, sublittoral, 4 October 1972, several colonies in spirit, coll. P. F. S. Cornelius, 1973.9.24.4. Weymouth Bay, Portland, Dorset, England, on test of *Ascidiella* sp. Roule (Tunicata), 20 m, several hydrocauli in spirit, coll. R. Kirkpatrick, 1897.8.9.12. Hastings, Sussex, England, several colonies in spirit, coll. & det. T. Hincks (as *Obelia flabellata*), 1899.5.1.148 (non-type). Southend Pier, Essex, England, hydrocauli in spirit, coll. R. Kirkpatrick, 1897.8.9.12. Southend Pier, Essex, England, 24 July 1927, two microslides, coll. F. J. Lambert, 1927.9.7.3. Havengore Creek, Rushey I., near Foulness I., Essex, England, microslide with three colonies, coll. F. J. Lambert, 1929.1.1.1 (Fig. 4b). 'Probably British', two colonies on microslide, 1920.3.1.1 (Fig. 4c). Banyuls, S. France, intertidal, 19 October 1959, several colonies on alga, in spirit and microslide, coll. W. J. Rees, 1959.11.17.4.

Froggy Pond, station CP16, University of Cape Town Ecological Survey, Republic of South Africa, three fragments of colony on microslide, 1962.10.2.3 (mentioned, Millard, 1957 : 198).

Casco Bay, Maine, U.S.A., on unidentified plant, several hydrocauli in spirit and microslide, pres. Smithsonian Institution, Washington, D.C., 1880.9.27.93. Woods Hole, Massachusetts, U.S.A., on alga sp., 23 July 1911, several hydrocauli in spirit, coll. C. M. Fraser, 1915.3.6.37 (Fig. 4d).

Mediterranean/Red Seas – Suez Canal, 13 December 1924, several hydrocauli on wood in spirit and microslide, coll. Cambridge University Expedition to the Suez Canal, 1928.5.31.47, 49.

Pacific Ocean – Port Jackson, New South Wales, Australia, several colonies on algal stipe, in spirit, coll. R. von Lendenfeld, 1886.6.8.102.

No locality – Pseudo-dichotomous colony on microslide, prep. H. J. Waddington, ex A. M. Norman coll., 1919.5.26.12.

OTHER MATERIAL RECORDED. *North polar region* – Entire north coast of Russia (Linko, 1911 ; Naumov, 1969), Greenland, Bering Sea, Northern Canada and Alaska (Calder, 1970).

Atlantic – coasts of western Europe (Hincks, 1868), Mediterranean Sea and Suez Canal (Deevey, 1950), Azores (Rees & White, 1966), Ghana (Buchanan, 1957),

Tropical W. Africa (Vervoort, 1959), coast of North America from arctic to Caribbean (Fraser, 1944 ; Vervoort, 1967 ; Calder, 1970), Republic of South Africa (Millard, 1958).

Pacific – Coast of North America from arctic regions to southern U.S.A. (Fraser, 1937), Japan (Hirohito, 1969), China Sea, Galapagos Islands and coast of Ecuador (Deevey, 1950), Tasmania (Briggs, 1939, as *O. australis*), New Zealand (Ralph, 1957), Mozambique (Millard & Bouillon, 1974).

Distribution. Widespread in the northern hemisphere, but less frequently recorded south of the equator. Most northerly record probably 77° N, 138° E, north of New Siberian Islands (Linko, 1911, as *O. longissima*) ; most southerly record probably 61° S, 45° E, South Orkneys (Ritchie, 1909, as *O. longissima*).

Occurs intertidally and common at depths down to 100 m, seldom below 300 m, deepest record probably 510 m (Broch, 1918 ; Naumov, 1969). A world distribution map was given by Deevey (1950).

Remarks. Specimens having exceptionally thickened internodal perisarc consequently appear intermediate between this species and *O. geniculata*. Constant differences between the hydroid stages are given in Table 1.

Colonies of *O. dichotoma* showing variations in the length and nature of branching of the hydrocaulus and in the shape of the hydrothecal rim have been given specific status by some authors (see also p. 256). Alder (1857), Hincks (1868) and some subsequent authors assigned specimens with long, strongly tanned, dark main hydrocauli to *O. longissima* (Pallas, 1766), retaining only specimens with shorter, less tanned main hydrocauli in *O. dichotoma*. However, although specimens resembling *O. longissima* sensu Alder are distinctive, *Obelia* specimens in the B.M. (N.H.) collection form a continuous series between the two taxa. In addition, isolated second-order hydrocauli of '*longissima*' specimens cannot be distinguished from hydrocauli of *O. dichotoma*, and the two taxa appear inseparable. Thus specimens hitherto assigned to *longissima* are probably simply older colonies of *dichotoma* s. str. Originally Pallas (1766) introduced *longissima* as an alternative, perhaps more appropriate, name for Linnaeus' species but Linnaeus (1767) gave his own name priority. Johnston (1838, 1847) also regarded *longissima* as the junior synonym. *Obelia flabellata* (Hincks, 1866) represents an intermediate point in this series and can be regarded as conspecific with *O. dichotoma*.[1]

Obelia commissuralis McCrady, 1857, was founded on a medusa of which the hydroid was imperfectly known. Agassiz (1862) provided detailed descriptions of both stages and subsequent descriptions of the hydroid alone were given by Nutting (1915) and Fraser (1944). Berrill (1949), although describing the development of stolons, hydranths and medusae, did not describe systematic characters of his material. The species has been distinguished from *O. dichotoma* only once, by

[1] Certain species of medusae have been assigned to one or other hydroid species but owing to the confusion surrounding the validity of the medusa species it is probably best to regard these synonymies with caution. Thus, Sars (1835) described the medusa *Thaumantias plana* which Nutting (1915) and Stechow (1921b) referred to the hydroid *Obelia flabellata* (Hincks, 1866) (= *O. dichotoma*); Gegenbauer (1856) described the medusa *Eucope polystyla* which Mayer (1910) provisionally referred to *O. longissima* hydroid (= *O. dichotoma*); and Agassiz (1865) described the medusa *Eucope fusiformis* which Bedot (1910) synonymized under *O. fusiformis* (= *O. dichotoma*).

Nutting (1915) in a key to the genus, on the basis of the number of annuli per internode and the arrangement of the side-branches. These characters are variable in *O. dichotoma* and on present evidence *O. commissuralis* appears invalid.

The original description of *O. australis* von Lendenfeld, 1885a, is inadequate for identification, but the subsequent restriction by Bale (1888) is clearly referable to *O. dichotoma*, as also is the non-type material identified as *O. australis* by von Lendenfeld (1886.6.8.102). Recently the species was distinguished by Ralph (1957) solely on the presence of an oblique hydrothecal diaphragm, a character noted by Bale and present in von Lendenfeld's material. However, this is a common variation in specimens of *O. dichotoma* from British localities (Fig. 4e–f) and its occurrence in southern populations cannot be considered grounds for maintaining *O. australis* distinct.

Schizocladium ramosum Allman, 1871, was referred to *Obelia* sp. by Billard (1901a, 1904a) and to *O. geniculata* by Bedot (1918, 1925). However, Allman originally likened the species to *O. dichotoma* and his illustration, showing a much-branched campanularian hydroid with unthickened internodal perisarc, has greater resemblance to *O. dichotoma* to which the species is here referred.

Following Millard (1966 : 483) *Campanularia obtusidens* Jaderholm, 1905a, is assigned to *O. dichotoma*. Bedot (1925 : 302) had previously placed it in *O. dubia* Nutting, 1901, which Millard also assigned to *O. dichotoma*. The original description did not mention gonothecae, and those described by Fraser (1944) differed from those of *O. dichotoma* only in being stolonal. It seems probable that Fraser's material was simply a growth-form of *O. dichotoma*.

Campanularia obtusidentata is a name ascribed to Vanhoffen (1910 : 272) by Bedot (1925 : 302) in the latter's synonymy of *O. dubia* Nutting. However, the name does not occur in Vanhoffen's paper and seems to have been used by Bedot alone. It is clearly a *lapsus* for *obtusidens*.

Medusae. Those reared from both this species and from *O. geniculata* have been found to resemble *O. lucifera* (Forbes, 1848) (summary in Russell, 1953). Their relation with the hydroid is discussed below (p. 278). They were first recorded by Baster (1762) who saw their release on 3 June 1757. The subsequent history of the elucidation of the life-cycle was reviewed by van Beneden (1844) and briefly by Hincks (1868).

Obelia geniculata (Linnaeus, 1758)
(Figs 1, 5)

Sertularia geniculata Linnaeus, 1758 : 812 ; Pallas, 1766 : 117–119 ; Linnaeus, 1767 : 1312 (= *S. flexuosa* Linnaeus) ; Maratti, 1776 : 34.

Laomedea lairii Lamouroux, 1816 : 207 ; Lamouroux, 1821 : 14, pl. 67, fig. 3.

Campanularia geniculata : Meyen, 1834 : 195–196, pl. 31, figs 3–5 ; Bedot, 1905 : 51–52 (= *C. prolifera* Meyen ; *C. cavolinii* Deshayes & Edwards[1] ; *C. caulini* Chiaje[1]).

Campanularia prolifera Meyen, 1834 : 198–201, pl. 33, figs 1–5.

Sertularia prolifera : Deshayes & Edwards, 1836 : 139.

Laomedea geniculata : Johnston, 1838 : 151–152, pl. 21, figs 1–2 ; Johnston, 1847 : 103–104, pl. 25, figs 1–2 ; Gosse, 1853 : 84–90, pl. 4 ; Vervoort, 1946a : 294–298, figs 129–131 (= *L.*

[1] *C. cavolinii* and *C. caulini* are here assigned to *O. dichotoma*.

lairii Lamouroux ; *Sertularia prolifera* : Deshayes & Edwards ; *Campanularia cavolinii* Deshayes & Edwards[1] ; *Schizocladium ramosum* Allman[1]).

Eucope diaphana L. Agassiz, 1862 : 322–325, pl. 34, figs 1–9 ; (*non* A. Agassiz, 1865 : 83–85, figs 115–125 ; indeterminate).

Obelia geniculata : Allman, 1864 : 372 ; Hincks, 1868 : 149–151, pl. 25, fig. 1, 1a (= *Eucope diaphana* L. Agassiz ; *E. alternata* A. Agassiz) ; Bedot, 1910 : 338–340 (= *Laomedea lairii* Lamouroux ; *Schizocladium ramosum* Allman[1] ; *O. gymnopthalma* Spagnolini) ; Mayer, 1910 : 249–252, figs 132–133 (= *E. diaphana* L. Agassiz ; *E. alternata* A. Agassiz ; ? *E. polygena* A. Agassiz ; *E. fusiformis* A. Agassiz) ; Vanhoffen, 1910 : 304–306, fig. 25 (= *Monosklera pusilla* von Lendenfeld) ; Bedot, 1916 : 162–164 (= *E. diaphana* L. Agassiz) ; Bedot, 1925 : 304–307 (= *E. polygena* A. Agassiz) ; Vannucci Mendes, 1946 : 551–552, pl. 2, figs 14–15 ; Russell, 1953 : 302, fig. 185a ; Naumov, 1960 : 261–263, figs 147–148 ; Naumov, 1969 : 282–283, figs 147–148.

Eucope alternata A. Agassiz, 1865 : 86 (nom. nov. pro *E. diaphana* L. Agassiz, non *Thaumantias diaphana* A. Agassiz).

Eucope polygena A. Agassiz, 1865 : 86–87, fig. 126 ; Bedot, 1912 : 332.

Eucope fusiformis A. Agassiz, 1865 : 90, figs 132–133.

Obelia gymnopthalma Spagnolini, 1871 : 186 [nom. nov. pro medusa stage of *O. geniculata* (Linnaeus)].

Monosklera pusilla von Lendenfeld, 1885b : 911–912, pl. 40, figs 1–3.

Obelia geniculata var. *I* Marktanner-Turneretscher, 1890 : 207–208.

Obelia geniculata var. *II* Marktanner-Turneretscher, 1890 : 208.

Obelia geniculata var. *III* Marktanner-Turneretscher, 1890 : 208.

Campanularia coruscans Schneider, 1897 : 482 ; [syn. nov.].

Obelia geniculata f. *subsessilis* Jaderholm, 1905a : 2, pl. 1, fig. 2.

Obelia geniculata f. *gaussi* Vanhoffen, 1910 : 305, fig. 25d.

Obelia geniculata f. *subtropica* Ralph, 1956 : 285.

Obelia geniculata f. *intermedia* Ralph, 1956 : 285.

Obelia geniculata f. *subantarctica* Ralph, 1956 : 285.

TYPE SPECIMEN AND TYPE LOCALITY. Ellis, 1755 : 22, pl. 12, fig. B, but not fig. b[2] ; Dover, Kent, England ; intertidal, on fucoid alga. Present location of specimen unknown.

[1] *C. cavolinii*, and *S. ramosum* are here assigned to *O. dichotoma*.

[2] Linnaeus (1758) gave no type locality and cited only Ellis' description and figure. The illustration shows a specimen having typical *Obelia* gonothecae but lacking hydrothecae. Linnaeus' designation 'Sertularia denticulis obsoletis, calycibus [= gonotheca] obovatis subrostratis, caule geniculato flexuoso simplici' similarly describes the gonotheca, but omits reference to the hydrotheca. It is likely that the specimens in the Linnean herbarium of the Linnean Society of London (Savage, 1945) were not before Linnaeus when he wrote his designation since they possess both hydrothecae and gonothecae (see footnote, p. 267). It seems probable, therefore, that Linnaeus based his designation solely on Ellis' figure. The locality from which the figured specimen was obtained was not given precisely, although Ellis stated: 'This coralline was found at Dover; and I have lately received some specimens from Harwich; so that I believe it is not uncommon on our coasts.' The figured specimen is perhaps more likely to have come from the earlier locality, Dover, as the Harwich material possibly came to Ellis too late for an illustration to be prepared. He recorded it on 'podded *Fucus*', which could refer either to *Fucus vesiculosus* or *Ascophyllum nodosum* (L.) Le Jol (J. M. Price, personal communication).

As with *O. dichotoma*, it is virtually certain that the figured specimen no longer survives (see footnote, p. 267). However, it remains possible that some other hydroid specimens in the Linnaean herbarium are Ellis' figured material and hence type, since as late as 1 January, 1767, Linnaeus had received hydroid material from no source but Ellis (Smith, 1821 : 196). The type-series of *Sertularia echinata* Linnaeus, 1761, to be described in a later paper (Cornelius, 1975: *in press*), indicates that it at least had reached Linnaeus by or during 1761. This is evident since the original designation of *S. echinata* includes characters of both species represented in the type-series, which was mixed. Thus Harmer (1930 : 84) was apparently wrong in suggesting that Linnaeus received his first batch of Ellis' hydroid material at the end of 1766. Unfortunately the correspondence between Linnaeus and Ellis during 1763 and 1764 is missing (Smith, 1821 : 164 (footnote); Ahrling, 1885 : 55, 77; Savage, 1948 : 23–25; T. O'Grady, personal communication) so it is not at present clear which if any specimens were sent to Linnaeus during those two years.

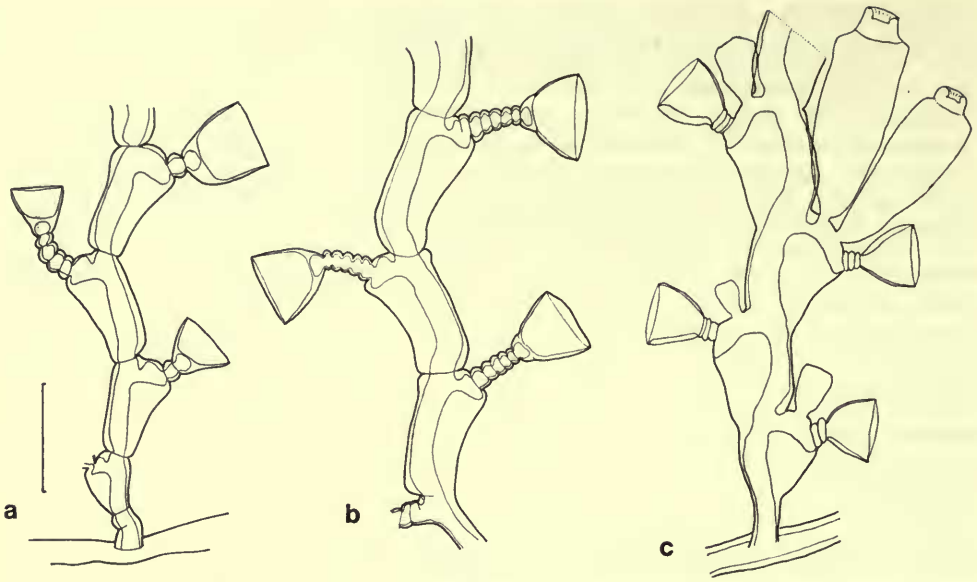

FIG. 5. *Obelia geniculata*. Parts of three hydrocauli to show differing extents of internodal thickening. (a) Republic of South Africa (1964.8.7.80). (b) SW. England (1966.10.28.7). (c) Republic of South Africa (1936.2.4.13), probably the extreme of shortening and thickening. Scale = 500 μm throughout.

DIAGNOSIS OF SPECIES. *Obelia* hydroid usually with unbranched, erect, flexuose, monosiphonic hydrocauli; internodes short, curved, with prominent internal thickening of perisarc below origin of pedicel; hydrotheca even-rimmed.

DESCRIPTION. Colony comprises attached stolons from which arise vertical monosiphonic hydrocauli, usually unbranched, up to 40 mm (Fig. 5). Hydrocaulus flexuose; internodes short, curved, internally thickened below origin of each pedicel, usually with one to five proximal annulations. Pedicel variable in length, attached to short lateral process near distal end of internode, annulated throughout or with smooth central portion. Hydrotheca broad, even-rimmed, bell-shaped, length about equal to width at rim. Gonotheca situated on short annulated pedicel in axil of hydrotheca; conical, wider distally, apex domed with narrow tubular aperture. Measurements – see Table 5.

MATERIAL EXAMINED. *Atlantic Ocean* – No locality (? Baltic), probably after 1758, coll. Linnaeus, two herbarium sheets, Linnean Society of London cat. no. 1298.19–20 (Savage, 1945).[1] Balta Sound, Shetland, on *Laminaria* sp., 1867,

[1] Sheet 1298.19 bears a specimen of a fucoid alga with an attached colony of *O. geniculata* comprising about 20 erect hydrocauli. All the hydrothecae are missing, and only two gonothecae remain. Sheet 1298.20 bears four specimens, one at the top of the sheet, two side by side in the centre and one at the bottom. The top specimen is a piece of *Laminaria* sp. Lamour. to which a colony of *O. geniculata* is attached. It has many hydrothecae but no gonothecae. Of the two centre specimens that on the left is a piece of alga with no hydroids attached, and that on the right is another piece of alga, probably *Fucus* sp. L. or *Laminaria* sp. with colonies of *O. geniculata* attached. A few hydrothecae are present, but no gonothecae. The specimen at the bottom of the sheet is not *Obelia*, and is not readily identified as it is decayed. It appears from an attached label to have been added later. These specimens are probably not type material (see footnote, p. 273).

TABLE 5

Measurements of the hydroid stage of *Obelia geniculata* in μm

	SW ENGLAND (1973.9.26.1)	REPUBLIC OF SOUTH AFRICA (1936.2.4.13 ; Fig. 5c)*	W SCOTLAND (1962.6.19.5)†
HYDROTHECA			
Length (diaphragm to rim)	240–290	220–270	210–300
Breadth at rim	270–390	250–310	230–320
Maximum thickness of hydrothecal perisarc	20	50	20
HYDROTHECAL PEDICELS			
Length	070–170	070–140	240–370
INTERNODES			
Length	600–700	470–590	600–820
Maximum breadth	160–250	290–440	210–270
Length/breadth ratio	*c.* 3	*c.* 1–1·5	*c.* 3
Maximum diameter of asymmetric thickening	050–100	270	100
GONOTHECA			
Length	700–800	820–940	1030–1070
Maximum breadth	240–300	290–340	270–320
GONOTHECAL PEDICELS			
Length	030–080	020–030	090–100

* Specimen resembles *O. geniculata* 'var. *subsessilis*' Jaderholm.
† Specimen has long internodes in distal parts.

several colonies in spirit and microslide, coll. A. M. Norman, 1912.12.21.262. Clachan Bridge, Seil, Argyll, Scotland, 1 June 1962, two hydrocladia on microslide, coll. W. J. Rees, 1962.6.19.5. Creagan Narrows, Argyll, Scotland, MLWST, on *Fucus vesiculosus*, 10 September 1970, several hydrocladia, spirit, coll. P. F. S. Cornelius, 1971.5.11.18. Port Erin, Isle of Man, British Isles, 26 September 1892, two hydrocauli on microslide, coll. E. T. Browne, 1959.9.17.29. Port St Mary, Isle of Man, British Isles, on *Laminaria* sp., 30 m, several hydrocladia in spirit, coll. J. Lomas, 1886.1.9.2. St Ives, Cornwall, England, hydrocaulus on microslide, coll. R. E. W. Vallentin, 1935.8.12.24. Looe, Cornwall, England, LWM, on *Cystoseira* sp. Agardh, 21 September 1972, several hydrocauli in spirit, coll. P. F. S. Cornelius, 1973.9.24.2 (Fig. 1). Looe, Cornwall, England, LWM, on *Laminaria saccharina* (L.) Lamour., 21 September 1972, several hydrocauli, coll. P. F. S. Cornelius, 1973.9.24.3. Drake's Island, Plymouth, Devon, England, June 1965, three hydrocauli on microslide, coll. R. C. Vernon, 1969.12.1.20. Torpoint pontoon, Plymouth, Devon, England, 13 August 1963, four hydrocauli on microslide, coll. R. C. Vernon, 1973.9.26.1. Plymouth, Devon, England, 29 September 1947, coll. E. White, two hydrocauli on microslide, 1947.10.8.1. Plymouth, Devon, England, 29 August 1947, coll. E. White, hydrocaulus on microslide, 1947.10.8.3. R. Yealm, Devon, England, MLWST, on *Fucus serratus* L., 4 July 1973, several

colonies in spirit and six microslides, coll. P. F. S. Cornelius, 1973.7.23.2. R. Yealm, Devon, England, MLWST, on *Laminaria* sp., 4 July 1973, several colonies in spirit and six microslides, coll. P. F. S. Cornelius, 1973.7.23.3. Start Bay, Devon, England, on *Laminaria* sp., 10 m, spirit material and microslide, coll. R. Kirkpatrick, 1893.8.7.7. Eddystone grounds, western English Channel, 2 September 1898, several hydrocauli on microslide, coll. E. T. Browne, 1959.9.17.30. Great Britain Rock, St Mary's, Scilly Isles, on *Laminaria* sp., 10 m, 22 July 1964, several colonies in spirit and two microslides, coll. Queen Mary College expedition, 1966.10.28.2. Great Britain Rock, St Mary's, Scilly Isles, 15 m, 23 July 1964, three hydrocauli on microslide, coll. Queen Mary College expedition, 1966.10.28.7 (Fig. 5b).

South of Fugloy, Espegrend, Norway, 40 m, on bryozoan, 7 August 1962, spirit material and microslide, coll. W. J. Rees, 1962.11.7.47.

Nez de Joburg, NW. of Cherbourg Peninsula, France, on *Laminaria* sp., 3 May 1965, several colonies in spirit, coll. A. M. Clark, det. W. J. Rees, 1965.5.14.2.

Newport, Rhode Island, U.S.A., on wood, 25 m, several colonies in spirit and microslide, pres. Smithsonian Institution, 1890.8.23.14. Potts Point, South Harspowell, Maine, U.S.A., on *Fucus* sp., seven hydrocauli on microslide, coll. C. M. Fraser, 1915.3.6.38. Vineyard Sound, Massachusetts, U.S.A., on *Laminaria* sp. spirit material and microslide, pres. Smithsonian Institution, 1880.9.27.94.

Gough Island, Tristan da Cunha, 22 April 1904, hydrocaulus on microslide, coll. Scottish National Antarctic Expedition, det. J. Ritchie, 1964.8.7.79.

Oudekraal, Republic of South Africa, two microslides, University of Cape Town Ecological Survey, 1936.2.4.13 (Fig. 5c). Entrance to Saldanha Bay, Cape Colony, Republic of South Africa, 50 m, 21 May 1904, two hydrocauli on microslide, coll. Scottish National Antarctic Expedition, det. J. Ritchie, 1964.8.7.80 (Fig. 5a).

Pacific Ocean – New Zealand, 20 hydrocauli on algal thallus in spirit, coll. R. von Lendenfeld, 1886.6.8.107, ('*Monosklera pusilla*', det. von Lendenfeld, not type). Off Port Ross, Auckland Islands, New Zealand, on *Laminaria* sp., 28 March 1904, several colonies in spirit, coll. 'Discovery' Antarctic Expedition, 1907.8.20.44.

Other material recorded. *North Atlantic* – White Sea (Linko, 1911), Jan Mayen Island, Iceland, coast of Norway at least to 68° N (Broch, 1918); Barents Sea, European coast and Mediterranean Sea (Naumov, 1969); fjords of West Greenland (Calder, 1970); whole Atlantic coast of North America (Fraser, 1944); Coats Island, Hudson Bay (63° N) (Calder, 1970); parts of Caribbean (Vervoort, 1968).

South Atlantic – Zaire (Leloup, 1939), Ghana (Buchanan, 1957), Luderitz Bay (26° S) and other localities in Republic of South Africa (Broch, 1914; Millard, 1957, 1966); Kerguelen Island (Vanhoffen, 1910); Falkland Islands (M. W. Robins, personal communication); South Georgia (Deevey, 1950) and Brazil (Vannucci Mendes, 1946).

North Pacific – Japan (Yamada, 1958); British Columbia and whole of U.S.A. coast except Alaska (Fraser, 1937).

South Pacific – Chile (Jaderholm, 1905b), Indonesia and Galapagos Islands (Deevey, 1950), West Australia, South Australian Bight, Victoria, New South

Wales and Tasmania (Hodgson, 1950), Macquarie Island (Briggs, 1939), New Zealand, adjacent seas between 35° S and 49° S and the Chatham Isles (Ralph, 1956, 1961).

Indian Ocean – Two localities in southern India (Mammen, 1965), Mozambique (Millard & Bouillon, 1974).

Distribution. Almost cosmopolitan in continental shelf seas. Deevey (1950) stated that *O. geniculata* is the most widely distributed of all hydroids, being absent only from the northern Indian Ocean and the tropical West Atlantic (although subsequently recorded from the Caribbean). Apart from South Georgia and Macquarie Island there appear to be no records also from the Southern Ocean, and the species appears unrecorded from much of the Pacific, including northern parts of the Australian mainland, Brisbane and the Great Barrier Reef (Ralph, 1956).

In the northern hemisphere the species extends almost as far north as *O. dichotoma*, being known from the White Sea. Although it was reported absent from Greenland by Broch (1918) and was not found by Kramp (1932) in some west Greenland collections, Calder (1970) nevertheless recorded the species from both east and west Greenland, but did not cite material.

Remarks. Variation in the hydroid stage of this species occurs mainly in the angle of flexure between internodes, the asymmetric thickening of the internodal perisarc, the length to breadth ratio of the internodes and the shape of the hydrotheca. Apart from the form of the hydrotheca, these characters can be placed in a series ranging from specimens with shallow angles between internodes, little internodal thickening and proportionately long internodes to more flexuous specimens with greater internodal thickening and shorter internodes (Fig. 4a–c).

The occurrence of these variations has prompted authors to recognize several varieties and formae. Vanhoffen (1910), however, was of the opinion that the following of these taxa fall within the limits of normal variation : Varieties *I*, *II* and *III* of Marktanner-Turneretscher, 1890 ; forma *gaussi* Vanhoffen, 1910 (nom. nov. pro var. *I* of Marktanner-Turneretscher) and forma *subsessilis* Jaderholm, 1905b. Further varieties (*subtropica*, *intermedia* and *subantarctica*) were described by Ralph (1956) based on variations in length of hydrocaulus, number of annulations of the internodes, amount of branching and linear dimensions of all structures. These characters are known to be variable (p. 256) and it is perhaps best at present not to regard them as systematically valid.

The species appears to be variable within the above limits over the whole of its range. Thus, specimens showing the extreme of shortening and internodal thickening have been reported from Chile, Kerguelen Island and the Republic of South Africa (Jaderholm, 1905b ; Vanhoffen, 1910 ; Fig. 5c), while specimens with both minimal and maximal thickening are known from the English Channel (1959.9.17.30). Almost the full range of variation is represented in British specimens in the BM(NH) collection, and the naming of distinct varieties seems unnecessary.

Hammett & Hammett (1945) followed the seasonal morphological changes in colonies of *O. geniculata* during several summers in Massachusetts but variations in features of accepted systematic importance were not reported. More recently detailed accounts of variation in New Zealand populations by Ralph (1956) and Ralph & Thomson (1968) demonstrated that over a wide geographical range and

from season to season at a single locality certain morphological characters varied with temperature. Low temperatures induced longer colonies with longer internodes, and colonies from warmer localities showed a reduction in branching.

Laomedea lairii Lamouroux, 1816, was placed in the present species by Bedot (1901) and also by Billard (1909) who examined the type specimen. The specimen was subsequently destroyed in the Second World War (Redier, 1967).

Campanularia coruscans Schneider, 1897, was originally stated to release a medusa and was subsequently assigned to *Obelia* by Stechow (1921b, 1923b). The wide distal shelf in each internode supporting the hydrotheca, as described by Schneider, suggests that *C. coruscans* is referable to *O. geniculata*.

MEDUSAE. Those reared from both this species and *O. dichotoma* have been found to resemble *O. lucifera* (Forbes, 1848) (summary in Russell, 1953). Their relation with the hydroid is discussed below. The earliest record of medusa release in *O. geniculata* seems to be that of F. W. L. Thomas (*in* Johnston, 1847 : 467), who commented on the similarity between the medusa of this species and that of *O. dichotoma*. Medusae of *O. geniculata* were apparently first illustrated by Gosse (1853).

THE MEDUSA PROBLEM

Many nominal species of *Obelia* are based solely on the medusa stage, most having been described in the past 100 years (references in Mayer, 1910 ; Bedot, 1901–25 ; Kramp, 1961). However, they are very similar and it is likely that many are conspecific (Kramp, 1961). As noted by Russell (1953), it is at present impossible to relate them to the hydroid species, and it may remain so until further rearing work has been done and the characters of the medusae reassessed.

Although all three species recognized from the hydroid stage occur in British seas, only two nominal species of medusae are known. The five taxa recorded are as follows (modified from Russell, 1953) :

HYDROIDS	
O. bidentata	Mature medusa not described
O. dichotoma	Mature medusa resembles *O. lucifera*
O. geniculata	Mature medusa resembles *O. lucifera*
MEDUSAE	
O. lucifera	Reared to maturity from both *O. dichotoma* and *O. geniculata*, and known from the plankton
O. nigra Browne, 1900	Known only from the plankton

It has been suggested by elimination (Browne, in Kramp, 1927 ; Russell, 1953) that *O. longissima* might prove to be the hydroid of *O. nigra*. However, this cannot be the whole answer if, as is shown above, *O. longissima* is conspecific with *O. dichotoma* from which *O. lucifera* has been reared. The occurrence of the hydroid *O. bidentata* in the North Sea and English Channel, and the fact that the appearance of its medusa when adult is unrecorded, add further complications.

The possibility that *O. nigra* alone is released from *O. bidentata* is unlikely as the two species have different distributions in western Europe. Thus, the hydroid occurs no further north than the coasts of France, Belgium and Holland and the southern North Sea (Vervoort, 1946a ; Leloup, 1952 ; Hamond, 1957 ; Kramp, 1961 ; Teissier, 1965), while the medusa is known from as far north as western Scotland, Iceland and Bergen, Norway (Browne, 1905 ; Thiel, 1932 ; Kramp, 1939 ; Rees, 1953).

Sir Frederick Russell (personal communication) is of the opinion that in the seas around the British Isles *O. nigra* is associated with mixed oceanic and coastal water typified by the presence of *Sagitta elegans* (Chaetognatha), while *O. lucifera* occurs in coastal water of which *S. setosa* is characteristic (Meek, 1928). *O. nigra* is said to be larger than *O. lucifera* and to have darker pigmentation around the tentacle bases (Russell, 1953). It has long been suspected that the mixed water is more productive than British coastal water (Russell, 1939), and as suggested by Browne (in Kramp, 1927) the larger size characteristic of *O. nigra* might simply reflect better feeding opportunities. Thus it is possible that medusae from all three hydroid species develop *O. lucifera* characters in coastal water and those of *O. nigra* in more productive areas. It is noteworthy that although Browne recorded both species of medusae off Plymouth between 1897 and 1899, published records suggest that he never obtained them together (Marine Biological Association, 1957). This perhaps indicates that the furthest extent of mixed water into the English Channel then varied in position around Plymouth. Although mixed oceanic and coastal water frequently reached Plymouth in the 1920's, it did not do so for some decades after the early 1930's (Russell *et al.*, 1971). During that time *O. lucifera* was the prevalent species (Russell, personal communication), further suggesting a correlation with water mass and, possibly, feeding opportunity.

Although it might be inferred from the available evidence that the two medusa species are conspecific, the possibility that they are genetically distinct nevertheless remains open, while another possibility is that the hydroid of *O. nigra* is as yet undescribed.

SPECIES TRANSFERRED TO OTHER GENERA

Although *Campanularia gelatinosa* (Pallas, 1766) was reported to release a medusa by van Beneden (1844), his illustrations identify his material as *Obelia dichotoma*. Hincks (1868) was aware of this misidentification, but independently described a medusa stage in *C. gelatinosa* and placed the species in *Obelia*. Later Maitland (1876 : 13) identified the medusa *Obelia marina* (Slabber, 1769) with *Campanularia gelatinosa* auct. (? sensu Hincks). A medusa has not been reported since in the species, and recent opinion (Vervoort, 1946a ; Naumov, 1969 ; J. Clare, personal communication) is that one is not released. It is possible that Hincks mistook the large ova characteristic of *C. gelatinosa* for developing medusae.

Campanularia denticulata Clarke (1876 : 9, pl. i, fig. 4) has usually been referred to *Obelia* (references in Bedot, 1912–25) although Pictet (1893) assigned it to *Clytia noliformis* McCrady, 1857. Mammen (1965) did not agree with Pictet's synonymy

and Clarke's nominal species still stands as *Campanularia denticulata*. However, the acutely cusped hydrothecal rim originally described suggests that the species should nevertheless be referred to *Clytia*.

Obelia marginata Allman (1877 : 9–10, pl. 6, figs 1–2) is now accepted as a species of *Cnidoscypus* Splettstösser, 1929 (Vervoort, 1968).

The two nominal species *Obelia longicyatha* Allman, 1877, and *O. longicyatha* Thornely, 1899, are discussed above under *O. bidentata* (p. 264).

Eucope annulata von Lendenfeld (1885a : 602–603, pl. 28, figs 53–57) was placed in *Obelia* by Bedot (1925 : 298), but von Lendenfeld's illustration shows an approximately hemispherical medusa quite unlike *Obelia* and Kramp (1961) referred the species to *Phialella* Browne, 1902.

Campanularia serrulata Bale (1888 : 757, pl. 12, fig. 4) was referred to *Obelia* by Thornely (1899) and Mayer (1910, mis-spelt as *O. serratula*) but later transferred to *Clytia* by Bedot (1918, 1925). Although the triangular cusps on the hydrothecal rim shown by both Bale and Mayer are typical of *Clytia*, the gonotheca described by Thornely was unlike that of *Clytia* in having a rounded, truncate top. However, as the gonotheca may have been immature, it is still possible that the three authors were describing the same species. Nutting (1927), however, provided the new name *Obelia thornelyi* for Thornely's material. Nevertheless, the nature of the hydrothecal rim described by both Bale and Mayer suggests that their material at least should be referred to *Clytia*.

Campanularia castellata Clarke (1894 : 71–72) (= *Obelia castellata* Clarke, 1894 : 73, pl. 1, fig. 3–8, pl. 2, fig. 9) is referable to *Campanularia gelatinosa* (Pallas, 1766) as it had a castellated hydrothecal rim. Bedot (1918 : 196 ; 1925 : 300) mis-spelt the name as *castellana*.

Campanularia kincaidi Nutting (1899 : 743–744, pl. 62, figs 2a–c) was referred to *Laomedea* by Leloup (1940 : 21) and to *Obelia* by Rees & White (1966 : 277). Its creeping habit and singly cusped hydrothecal rim are reminiscent more of *Clytia*, however ; and in the absence of information on the life-history the species is probably best excluded from *Obelia*.

Obelia linearis Thornely (1899 : 453, pl. 44, fig. 6), although retained in *Obelia* by Mayer (1910 : 257), was transferred to *Clytia* sp. by Mammen (1965 : 21). The presence of a deeply cleft hydrothecal rim and a reflexed gonothecal aperture support Mammen's opinion.

Obelia delicatula Thornely (1899 : 453, pl. 44, fig. 7) was assigned to *Clytia* by Stechow (1923b) and Blackburn (1942). Although the medusa is unknown, its stolonal gonotheca and sharply-cusped hydrothecal rim are features typical of *Clytia* and the species is for the present probably best assigned to that genus.

Obelia austrogeorgiae Jaderholm (1904b : 7 ; 1905b : 17, pl. 17, figs 1–2) has not been shown to produce a medusa and is here provisionally referred to the genus *Campanularia*. The species has also been recorded by Nutting (1915) and Vervoort (1972b, as *Laomedea* (*Obelia*) *austrogeorgiae*). As reported by Jaderholm, gonothecae are absent from the schizoholotype material (1960.8.29.34) which was examined during the present work, and have not yet been recorded for the species. At present, therefore, its generic affinity is obscure, but the bimucronate hydrothecal rim

originally described suggests that Mayer (1910) may have been correct in assigning the species to *O. bidentata*.

Obelia striata Clarke (1907 : 9–10, pls 6–7) is a distinctive hydroid known since the first description to release a medusa with four tentacles. It was, therefore, referred to *Clytia* sp. by Rees & Thursfield (1965) and to *Clytia gravieri* (Billard, 1904b) by Millard & Bouillon (1973), while Vervoort (1966) assigned it to *Laomedea* (*Phialidium*). As adult medusae are unrecorded it is difficult to assign the species to a particular genus with confidence, but the four tentacles of the young medusa suggest that it is not an *Obelia* species. Vervoort (1968 : 19) considered that *Laomedea tottoni* Leloup, 1935, was very similar to *O. striata* Clarke.

Laomedea (*Obelia*) *bistriata* Leloup (1931 : 4–6, figs 8–11) was referred to *Clytia hendersonae* Torrey, 1904, by Mammen (1965) and to *C. gravieri* (Billard, 1904b) by Vervoort (1967), Schmidt (1972) and Millard & Bouillon (1973). The spines associated with the cusps on the hydrothecal rim were illustrated by Leloup (1931, 1932) and Vervoort, and resemble closely those of *O. bidentata*. Although such spines are otherwise unreported from *Clytia*, Vervoort's observation that the developing medusa has a 'strongly convex umbrella', and Millard & Bouillon's that it has four tentacles, are evidence that the species should be assigned to the genus *Clytia*.

As stated in the generic diagnosis, several of the species admitted to the genus *Obelia* by Naumov (1960, 1969) are here referred to the genera *Campanularia* and *Gonothyrea*. The species involved are *Campanularia gelatinosa* (Pallas, 1766), *C. gracilis*[1] Sars, 1850 (non *O. gracilis* Calkins, 1899, = *O. dichotoma*), *C. flexuosa* (Hincks, in Alder, 1856) and *G. loveni* (Allman, 1859), none of which releases a medusa.

ACKNOWLEDGEMENTS

I am grateful to R. W. Sims and Dr W. Vervoort for detailed criticism of the manuscript, and to Dr Elaine Robson and Sir Frederick Russell, F.R.S., for commenting on parts of it. The last-named kindly allowed me to quote unpublished observations on the distribution of *Obelia* medusae in the British Isles, and Dr M. W. Robins provided an unpublished locality record of *O. geniculata*, in the Falkland Islands. I am grateful also to the following for helpful conversation and correspondence : Miss P. L. Cook, J. Clare, Dr C. Edwards, Dr R. Hamond, the late D. N. Huxtable, J. M. Price and Dr M. W. Robins.

D. W. Cooper kindly prepared serial sections of *Obelia geniculata*, and A. Varley, Librarian at the Marine Biological Association's Plymouth Laboratory, helped with literature. I was fortunate in being permitted to work at that Laboratory and to make use of its research vessels, and similarly fortunate in being able to work for a short time at the Laboratory of the Scottish Marine Biological Association, Oban, and to collect from its vessel. T. O'Grady of the Linnean Society of London kindly allowed me to study Linnaeus' hydroid material and correspondence with John Ellis, and Miss Elizabeth Allen of the Hunterian Museum of the Royal College of Surgeons of England provided information about the Ellis material held there.

[1] Vervoort (1946a : 285) had previously suggested that the correct name for Sars' species is *C. pelagica* van Breemen, 1905.

Specimens were lent by Dr W. D. Hartman of the Peabody Museum of Natural History, Yale, and Dr W. Vervoort of the Rijksmuseum van Natuurlijke Historie, Leiden. Fig. 3a was drawn by Miss J. B. Garfath and Figs 2a, 5a and 5b by Miss J. M. Paul.

REFERENCES

Agassiz, A. 1865. *Illustrated catalogue of the Museum of Comparative Zoology, at Harvard College. No. II. North American Acalephae.* Cambridge, Massachusetts.

Agassiz, L. 1862. Hydroidae. *Contributions to the natural history of the United States of America. Second monograph,* **4** : 181–380. Boston.

Ahrling, E. 1885. *Carl von Linnés brefvexling.* Stockholm.

Alard, M. 1811a. *Éloge historique de François Péron.* Paris.

—— 1811b. *Éloge historique de François Péron.* 2nd edition. Paris.

Alder, J. 1856. Descriptions of three new British zoophytes. *Ann. Mag. nat. Hist.* (2), **18** : 439–441.

—— 1857. A catalogue of the zoophytes of Northumberland and Durham. *Trans. Tyneside Nat. Fld Cl.* **3** : 93–162.

Allman, G. J. 1859. Notes on the hydroid zoophytes. *Ann. Mag. nat. Hist.* (3), **4** : 137–144.

—— 1864. On the construction and limitation of genera among the Hydroida. *Ann. Mag. nat. Hist.* (3), **13** : 345–380.

—— 1871. On a mode of reproduction by spontaneous fission in the Hydroida. *Q. Jl microsc. Sci.* (n.s.) **11** : 18–21.

—— 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, assistant United States Coast Survey. *Mem. Mus. comp. Zool. Harv.* **5** (2) : 1–66.

Audiat, L. 1855. *F. Péron (de Cérilly). Sa vie, ses voyages et ses ouvrages.* Moulins.

Babič, K. 1913. Bemerkungen zu den zwei in der Adria vorkommenden thecaphoren Hydroiden. *Zool. Anz.* **43** : 284–288.

Bale, W. M. 1888. On some new and rare Hydroida in the Australian Museum collection. *Proc. Linn. Soc. N.S.W.* (2), **3** : 745–799.

—— 1924. Reports on some hydroids from the New Zealand coast, with notes on New Zealand Hydroida generally, supplementing Farquhar's list. *Trans. Proc. N.Z. Inst.* **55** : 225–268.

Barrett, J. H. & Yonge, C. M. 1958. *Collins pocket guide to the sea shore.* London.

Baster, J. 1762. *Opuscula subseciva, observationes miscellaneas de animalculis et plantis.* Volume 1. Haarlem, Holland.

Bedot, M. 1901. Matériaux pour servir à l'histoire des hydroïdes. 1er période. *Revue suisse Zool.* **9** : 379–515.

—— 1905. Matériaux pour servir à l'histoire des hydroïdes. 2me période (1821 à 1850). *Revue suisse Zool.* **13** : 1–183.

—— 1910. Matériaux pour servir à l'histoire des hydroïdes. 3me période (1851 à 1871). *Revue suisse Zool.* **18** : 189–490.

—— 1912. Matériaux pour servir à l'histoire des hydroïdes. 4me période (1872 à 1880). *Revue suisse Zool.* **20** : 213–469.

—— 1916. Matériaux pour servir à l'histoire des hydroïdes. 5me période (1881 à 1890). *Revue suisse Zool.* **24** : 1–349.

—— 1918. Matériaux pour servir à l'histoire des hydroïdes. 6me période (1891 à 1900). *Revue suisse Zool.* **26** (Suppl.) : 1–376.

—— 1925. Matériaux pour servir à l'histoire des hydroïdes. 7me période (1901 à 1910). *Revue suisse Zool.* **32** (Suppl.) : 1–657.

Beneden, P.-J. van 1844. Mémoire sur les campanulaires de la côte d'Ostende. *Nouv. Mém. Acad. R. Sci. Bruxelles,* **17** (5) : 1–42.

BENTHEM JUTTING, W. S. S. VAN 1970. Martinus Slabber (1740–1835). Amateur-zoölog in Zeeland. *Archf zeeuw. Genoot. Wet.* (1970) : 45–66.

BERRILL, N. J. 1949. The polymorphic transformations of *Obelia*. *Q. Jl microsc. Sci.* **90** : 235–264.

BILLARD, A. 1901a. De la scissiparité chez les hydroïdes. *C. r. hebd. Séanc. Acad. Sci., Paris,* **133** : 441–443.

—— 1901b. De la stolonisation chez les hydroïdes. *C. r. hebd. Séanc. Acad. Sci., Paris,* **133** : 521–524.

—— 1904a. Contribution à l'étude des hydroïdes. (Multiplication, régénération, greffes, variations.) *Annls Sci. nat., Zool.* (8) **20** : 1–251.

—— 1904b. Hydroïdes récoltés par M. Ch. Gravier dans le Golfe de Tadjourah. *Bull. Mus. Hist. nat. Paris,* **10** : 480–485.

—— 1909. Revision des espèces types d'hydroïdes de la collection Lamouroux conservée à l'Institut Botanique de Caen. *Annls Sci. nat., Zool.* (9), **9** : 307–336.

—— 1912. Hydroïdes de Roscoff. *Archs Zool. exp. gén.* **51** : 459–478.

—— 1927. Les hydroïdes de la côte Atlantique de France. *C. r. Congr. Socs sav. Paris, Sect. Sci.* (1926) : 326–346.

BLACKBURN, A. 1942. A systematic list of the Hydroida of South Australia with a summary of their distribution in other seas. *Trans. R. Soc. S. Aust.* **66** : 104–118.

BLANCO, O. M. 1967. Nueva distribución para 'Obelia gracilis' Calkins (un caso de epibiosis). *Revta Mus. La Plata,* N.S. (Zool.), **10** : 129–136.

BREEMEN, P. J. VAN 1905. Plankton van Noord- en Zuiderzee. *Tijdschr. ned. dierk. Vereen.* (2), **9** : 145–324.

BRIGGS, E. A. 1939. Hydroida. *Scient. Rep. Australas. antarct. Exped.* (C), **9** (4) : 1–46.

BROCH, H. 1914. Hydrozoa benthonica. *Beitr. Kennt. Meeresfauna Westafr.* **1** : 19–50.

—— 1918. Hydroida. (Part II). *Dan. Ingolf Exped.* **5** (7) : 1–206.

BROWNE, E. T. 1900. The fauna and flora of Valencia harbour on the west coast of Ireland. Part 1. The pelagic fauna. II. Report on the medusae. *Proc. R. Ir. Acad.* (3), **5** : 694–736.

—— 1902. A preliminary report on Hydromedusae from the Falkland Islands. *Ann. Mag. nat. Hist.* (7), **9** : 272–284.

—— 1905. A report on the medusae found in the Firth of Clyde (1901–1902). *Proc. R. Soc. Edinb.* **25** : 738–778.

BUCHANAN, J. B. 1957. The hydroid fauna of the Gold Coast. *Revue Zool. Bot. afr.* **56** : 349–372.

BUGE, E. 1951. Note sur la synonymie de trois anciennes espèces de Bryozaires : *Diastopora latomarginata* d'Orbigny, 1852, *Eschara andegavensis* Michelin, 1847 et *Obelia disticha Michelin,* 1847. *Bull. Soc. géol. Fr.* (5), **20** : 459–465.

CALDER, D. R. 1970. Thecate hydroids from the shelf waters of northern Canada. *J. Fish. Res. Bd Can.* **27** : 1501–1547.

CALKINS, G. N. 1899. Some hydroids from Puget Sound. *Proc. Boston Soc. nat. Hist.* **28** : 333–368.

CAVOLINI, F. 1785. *Memorie per servire alla storia de' polipi marini.* Naples.

CHIAJE, S. DELLE, 1841. Polipi sertolarici. *Animale senza vertebre del regno di Napoli* (5) : 1–165. Naples.

CLARKE, S. F. 1875. Descriptions of new and rare species of hydroids from the New England coast. *Trans. Conn. Acad. Arts Sci.* **3** : 58–66.

—— 1876. Report on the hydroids collected on the coast of Alaska and the Aleutian Islands, by W. H. Dall, U.S. Coast Survey, and party, from 1871 to 1874 inclusive. *In* W. H. Dall, ed., *Scientific results of the exploration of Alaska, by the parties under the charge of W. H. Dall, during the years 1865–1874,* **1** : 5–34. Washington.

—— 1879. Report on the Hydroida collected during the exploration of the Gulf Stream and Gulf of Mexico by Alexander Agassiz, 1877–78. *Bull. Mus. comp. Zool. Harv.* **5** : 239–252.

CLARKE, S. F. 1894. Reports on the dredging operations off the west coast of central America to the Galapagos, to the west of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer 'Albatross', during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XI. The hydroids. *Bull. Mus. comp. Zool. Harv.* **25** : 71–77.

—— 1907. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer 'Albatross', from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U.S.N., commanding. VIII. The hydroids. *Mem. Mus. comp. Zool. Harv.* **35** (1) : 1–18.

CORNELIUS, P. F. S. 1975. A revision of the species of Lafoeidae and Haleciidae (Coelenterata : Hydroida) recorded from Britain and nearby seas. *Bull. Br. Mus. nat. Hist.* (Zool.) **28** (*in press*).

COUGHTREY, M. 1876. Critical notes on the New-Zealand Hydroida, suborder Thecaphora. *Ann. Mag. nat. Hist.* (4) **17** : 22–32.

CROWELL, S. & WYTTENBACH, C. 1957. Factors affecting terminal growth in the hydroid *Campanularia*. *Biol. Bull. mar. biol. Lab., Woods Hole*, **113** : 233–244.

DALYELL, J. G. 1836a. Farther illustrations of the propagation of Scottish zoophytes. *Edinb. New phil. J.* **21** : 88–94.

—— 1836b. Fernere Beobachtungen über die Fortpflanzung der scottischen Zoophyten. *Froriep's Notizen* (1) **50** (6) : 81–90.

DEEVEY, E. S. 1950. Hydroids from Louisiana and Texas, with remarks on the Pleistocene biogeography of the western Gulf of Mexico. *Ecology*, **31** : 334–367.

DESHAYES, G. P. & EDWARDS, H. M. (Eds), 1836. *Histoire naturelle des animaux sans vertèbres par J. B. P. A. de Lamarck*. Volume 2. 2nd edition. Paris.

—— —— (Eds) 1840. *Histoire naturelle des animaux sans vertèbres par J. B. P. A. de Lamarck*, Volume 3. 2nd edition. Paris.

DOBSON, J. 1971. *Descriptive catalogue of the physiological series in the Hunterian Museum of the Royal College of Surgeons of England. Part II. Hunterian specimens demonstrating the products of generation together with surviving Hunterian specimens from other sections*. Edinburgh and London.

ELLIS, J. 1755. *An essay towards a natural history of the corallines, and other marine productions of the like kind, commonly found on the coasts of Great Britian and Ireland*. London.

—— & SOLANDER, D. 1786. *The natural history of many curious and uncommon zoophytes, collected from various parts of the globe*. Ed. M. Watt. London.

ESCHSCHOLTZ, F. 1829. *System der Acalephen*. Berlin.

FEY, A. 1969. Peuplements sessiles de l'archipel de Glénan. 1. Inventaire : Hydraires. *Vie Milieu* (B) **20** : 387–413.

FORBES, E. 1848. *A monograph of the British naked-eyed medusae: with figures of all the species*. London.

FRASER, C. M. 1914. Some hydroids of the Vancouver Island region. *Trans. R. Soc. Can.* (3) **8** (4) : 99–216.

—— 1937. *Hydroids of the Pacific coast of Canada and the United States*. Toronto.

—— 1938. Hydroids of the 1934 Allan Hancock Pacific Expedition. *Allan Hancock Pacif. Exped.* **4** : 1–105.

—— 1941. New species of hydroids, mostly from the Atlantic Ocean, in the United States National Museum. *Proc. U.S. natn. Mus.* **91** : 77–89.

—— 1943. Distribution records of some hydroids in the collection of the Museum of Comparative Zoology at Harvard College, with description of new genera and new species. *Proc. New Engl. zool. Club*, **22** : 75–98.

—— 1944. *Hydroids of the Atlantic coast of North America*. Toronto.

—— 1946. *Distribution and relationship in American hydroids*. Toronto.

—— 1948. Hydroids of the Allan Hancock Pacific Expeditions since March, 1938. *Allan Hancock Pacif. Exped.* **4** : 179–335.

GEGENBAUER, C. 1856. Versuch eines Systemes der Medusen, mit Beschreibung neuer oder wenig gekannter Formen ; zugleich ein Beitrag zur Kenntniss der Fauna des Mittelmeeres. *Z. wiss. Zool.* (1857) **8** : 202–273.

GIRARD, M. 1857. *F. Péron naturaliste, voyageur aux terres australes. Sa vie, appréciation de ses travaux.* Paris.

GOSSE, P. H. 1853. *A naturalist's rambles on the Devonshire coast.* London.

GRANT, R. E. 1826. Observations on the spontaneous motions of the ova of the *Campanularia dichotoma, Gorgonia verrucosa, Caryophyllea calycularis, Spongia panicea, Sp. papillaris, cristata, tomentosa,* and *Plumularia falcata. Edinb. New phil. J.* **1** : 150–156.

GREGORY, J. W. 1909. *Catalogue of the fossil Bryozoa in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa.* Volume II. London.

GRONOVIUS, L. T. 1760. Observationes de animalculis aliquot marinae aquae in-natantibus atque in littoribus belgicus obviis. *Acta helv.* **4** : 35–40.

HAECKEL, E. 1879. Das System der Medusen. Erster Theil einer Monographie der Medusen. *Denkschr. med.-naturw. Ges. Jena,* **1** : 1–360.

HAMMETT, F. S. 1943. The rôle of the amino acids and nucleic acid components in developmental growth. Part one. The growth of an *Obelia* hydranth. Chapter one. Description of *Obelia* and its growth. *Growth,* **7** : 331–399.

—— & HAMMETT, D. W. 1945. Seasonal changes in *Obelia* colony composition. *Growth,* **9** : 55–144.

HAMOND, R. 1957. Notes on the Hydrozoa of the Norfolk coast. *J. Linn. Soc.*, Zool. **43** : 294–324.

HARGITT, C. W. 1909. New and little known hydroids of Woods Hole. *Biol. Bull. mar. biol. Lab., Woods Hole,* **17** : 369–385.

—— 1924. Hydroids of the Philippine islands. *Philipp. J. Sci.* **24** : 467–505.

—— 1927. Some hydroids of south China. *Bull. Mus. comp. Zool. Harv.* **67** : 489–520.

HARMER, S. F. 1930. Presidential address, 24th May, 1929. *Proc. Linn. Soc. Lond.* (Nov. 1928–May 1929) **141** : 68–118.

—— 1931. Presidential address. Recent work on Polyzoa. *Proc. Linn. Soc. Lond.* (Oct. 1930–May 1931) **143** : 113–168.

HARTLAUB, C. 1884. Beobachtungen über die Entstehung der Sexualzellen bei *Obelia. Z. wiss. Zool.* **41** : 159–185.

HILGENDORF, F. W. 1898. On the hydroids of the neighbourhood of Dunedin. *Trans. Proc. N.Z. Inst.* (1897), **30** : 200–218.

HINCKS, T. 1861. A catalogue of the zoophytes of south Devon and south Cornwall. *Ann. Mag. nat. Hist.* (3) **8** : 251–262.

—— 1866. On new British Hydroida. *Ann. Mag. nat. Hist.* (3) **18** : 296–299.

—— 1868. *A history of the British hydroid zoophytes.* 2 volumes. London.

—— 1889. On the Polyzoa and Hydroida of the Mergui Archipelago collected for the Trustees of the Indian Museum, Calcutta, by Dr J. Anderson, Superintendent of the Museum. *J. Linn. Soc.* **21** : 121–135.

HIROHITO. 1969. Some hydroids of the Amakusa Islands. *Publ. Biol. Lab. Imp. Household, Tokyo* (1969), (9) : 1–32.

HODGSON, M. M. 1950. A revision of the Tasmanian Hydroida. *Pap. Proc. R. Soc. Tasm.* (1949) : 1–65.

HOEVEN, J. VAN DER 1862. Eenige aanteekeningen over Martinus Slabber's Natuurkundige Verlustigingen ; benevens opgave der systematische namen van de daarin afgebeelde diersoorten. *Versl. Meded. K. Akad. wet. Amst.* (Afd. Nat.) **14** : 270–285.

HUMMELINCK, P. W. 1936. Hydropoliepen. *Flora Fauna Zuiderzee* (Suppl.) : 41–64.

ITÔ, T. & INOUE, K. 1962. Systematic studies on the nematocysts of Cnidaria. 1. Nematocysts of Gymnoblastea and Calyptoblastea. *Mem. Ehime Univ.* (2, B) **4** : 445–460.

JADERHOLM, E. 1904a. Aussereuropäische Hydroiden im schwedischen Reichsmuseum. *Ark. Zool.* (1903) **1** : 259–312.

JADERHOLM, E. 1904b. Mitteilungen ueber einige von der schwedischen Antarctic-Expedition 1901–1903 eingesammelte Hydroiden. *Arch. Zool. exp. gén.* (4) **3**, Notes et Revue : I–XIV.

—— 1905a. Hydroiden aus den Küsten von Chile. *Ark. Zool.* (1) **2** (3) : 1–7.

—— 1905b. Hydroiden aus antarktischen und subantarktischen Meeren, gesammelt von der schwedischen Sudpolarexpedition. *Wiss. Ergebn. schwed. Südpolarexped.* **5** (8) : 1–41.

—— 1909. Northern and arctic invertebrates in the collection of the Swedish State Museum. IV. Hydroiden. *K. svenska VetenskAkad. Handl.* **45** (1) : 1–124.

JARVIS, F. E. 1922. The hydroids from the Chagos, Seychelles and other islands and from the coasts of British East Africa and Zanzibar. *Trans. Linn. Soc. Lond.* (Zool.) **18** : 331–360.

JOHNSTON, G. 1838. *A history of the British zoophytes.* London.

—— 1847. *A history of the British zoophytes.* 2nd edition, 2 volumes. London.

KNIGHT, D. P. 1965. Behavioural aspects of emergence in the hydranth of *Campanularia flexuosa* (Hincks). *Nature, Lond.* **206** : 1170–1171.

—— 1970. Sclerotization of the perisarc of the calyptoblastic hydroid, *Laomedea flexuosa*. 1. The identification and localization of dopamine in the hydroid. *Tissue Cell*, **2** : 467–477.

KÖLLIKER, A. 1843. Ueber die Randkorper der Squallen, Polypen und Strahlthiere. *Neue Notizen Geb. Nat. Heilk.* **25** : 81–84.

KRAMP, P. L. 1927. The hydromedusae of the Danish waters. *K. dansk. Vidensk. Selsk. Skr.* **8** : 1–291.

—— 1932. Hydroids collected in West-Greenland fjords in 1911 and 1912. *Meddr. Grønland*, **91** (3) : 1–35.

—— 1935. Polypdyr (Coelenterata). I. Ferskvandspolypper og goplepolypper. *Danm. Fauna*, **41** : 1–208.

—— 1939. Medusae, Siphonophora, and Ctenophora. *Zoology Iceland*, **2** (5b) : 1–37.

—— 1961. Synopsis of the medusae of the world. *J. mar. biol. Ass. U.K.* **40** : 1–469.

LAMARCK, J. B. P. A. DE 1816. *Histoire naturelle des animaux sans vertèbres.* Volume 2. Paris.

LAMOUROUX, J. V. F. 1812. Extrait d'une mémoire sur la classification des polypiers coralligènes non entièrement pierreux. *Nouv. Bull. Soc. philom. Paris*, **3** : 181–188.

—— 1816. *Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes.* Caen.

—— 1821. *Exposition méthodique des genres de l'ordre des polypiers.* Paris.

LELOUP, E. 1931. Trois nouvelles espèces d'hydropolypes. *Bull. Mus. r. Hist. nat. Belg.* **7**(25) : 1–6.

—— 1932. Une collection d'hydropolypes appartenant l'Indian Museum de Calcutta. *Rec. Indian Mus.* **34** : 131–170.

—— 1935. Hydraires calyptoblastiques des Indes Occidentales. *Mém. Mus. r. nat. Hist. Belg.* (2) **2** : 1–73.

—— 1939. Hydropolypes marins et dulcicoles du Congo Belge. *Revue Zool. Bot. afr.* **32** : 418–423.

—— 1940. Hydropolypes provenant des croisières du Prince Albert 1er de Monaco. *Résult. Camp. scient. Prince Albert I*, **104** : 1–38.

—— 1952. Coelentérés. *Faune Belg.* pp. 1–283.

LENDENFELD, R. VON 1885a. The Australian Hydromedusae. Part V. Conclusion. The Hydromedusinae, Hydrocorallinae and Trachymedusae. *Proc. Linn. Soc. N.S.W.* (1884) (1) **9** : 581–634.

—— 1885b. Addenda to the Australian Hydromedusae. *Proc. Linn. Soc. N.S.W.* (1884) (1) **9** : 908–924.

LESUEUR, C. A. 1811. *Voyage de découvertes aux terres australes. Histoire naturelle. Histoire générale et particulière de tous les animaux qui composent la famille des méduses, et de quelques autres radiares molasses.* Paris.

LING, S. 1938. Studies on Chinese Hydrozoa. II. Report on some common hydroids from the East Saddle Island. *Lingnan Sci. J.* **17** : 175–184.

LINKO, A. K. 1911. Hydraires (Hydroidea). Volume I. Haleciidae, Lafoëidae, Bonneviellidae et Campanulariidae. *Fauna Rossii*, pp. 1–250.
LINNAEUS, C. 1758. *Systema naturae*. 10th edition. Holmiae.
—— 1761. *Fauna svecica, sistens animalia Sveciae regni*. 2nd edition. Stockholm.
—— 1767. *Systema naturae*. 12th edition. Tom I, Pars II. Holmiae.
MAITLAND, R. T. 1876. Determinatie der dieren, beschreven en afgebeeld in de werken van Job Baster en Martinus Slabber. *Tijdschr. ned. dierk. Vereen.* **2** : 7–15.
MAMMEN, T. A. 1965. On a collection of hydroids from south India. II. Suborder Thecata (excluding family Plumulariidae). *J. mar. biol. Ass. India*, **7** : 1–57.
MANTON, S. M. 1942. On the hydrorhiza and claspers of the hydroid *Myriothela cocksi* (Vigurs). *J. mar. biol. Ass. U.K.* **25** : 143–150.
MARATTI, J. F. 1776. *Plantis zoophytis et lithophytis in mari mediterraneo viventibus*. Rome.
MARINE BIOLOGICAL ASSOCIATION, 1957. *Plymouth marine fauna*. 3rd edition. Plymouth, England.
MARKTANNER-TURNERETSCHER, G. 1890. Die Hydroiden des k. k. naturhistorischen Hofmuseums. *Annln naturh. Mus. Wien*, **5** : 195–286.
MAYER, A. G. 1910. *Medusae of the world*. Volume II. *The Hydromedusae*. Washington.
MCCRADY, J. 1857. Gymnopthalmata of Charleston Harbor. *Proc. Elliott Soc. nat. Hist.* **1** : 103–221.
MEEK, A. 1928. On *Sagitta elegans* and *Sagitta setosa* from the Northumbrian plankton, with a note on a trematode parasite. *Proc. zool. Soc. Lond.* (1928) : 743–776.
MEYEN, F. J. F. 1834. Über das Leuchten des Meeres und Beschreibung einiger Polypen und anderer niederer Thiere. *Nova Acta Acad. Caesar. Leop. Carol.* **16** (Suppl. 1) : 125–216.
MICHELIN, J. L. H. 1847. *Iconographie zoophytologique, description par localités et terrains des polypiers fossiles de France et pays environnants*. Paris.
MILLARD, N. A. H. 1957. The Hydrozoa of False Bay, South Africa. *Ann. S. Afr. Mus.* **43** : 173–243.
—— 1958. Hydrozoa from the coasts of Natal and Portuguese East Africa. Part 1. Calyptoblastea. *Ann. S. Afr. Mus.* **44** : 165–226.
—— 1966. The Hydrozoa of the south and west coasts of South Africa. Part III. The Gymnoblastea and small families of Calyptoblastea. *Ann. S. Afr. Mus.* **48** : 427–487.
—— & BOUILLON, J. 1973. Hydroids from the Seychelles (Coelenterata). *Annls Mus. r. Afr. cent.* **206** : 1–106.
—— —— 1974. A collection of hydroids from Moçambique, east Africa. *Ann. S. Afr. Mus.* **65** : 1–40.
MODEER, A. 1791. Tentamen systematis medusarum stabiliendi. *Nova Acta physico-med.* **8** (Appendix) : 19–34.
MORIN, J. G. & COOKE, I. M. 1971. Behavioural physiology of the colonial hydroid *Obelia*. II. Stimulus-initiated electrical activity and bioluminescence. *J. exp. Biol.* **54** : 707–721.
NAUMOV, D. V. 1960. Gidroidy i gidromeduzy morskikh, solonovatovodnykh i presnovodnykh basseinov S.S.S.R. *Fauna S.S.S.R.* **70** : 1–626.
—— 1969. Hydroids and Hydromedusae of the U.S.S.R. *Fauna S.S.S.R.* **70**. Israel Program for Scientific Translation.
NORTON, G. W. 1896. The development of the free-swimming medusae of *Obelia commissuralis*. *Am. mon. microsc. J.* **18** : 291–296.
NUTTING, C. C. 1899. Hydroida from Alaska and Puget Sound. *Proc. U.S. natn. Mus.* **21** : 741–753.
—— 1901. Papers from the Harriman Alaska Expedition. XXI. The hydroids. *Proc. Wash. Acad. Sci.* **3** : 157–216.
—— 1915. American hydroids. Part III. The Campanulariidae and the Bonneviellidae. *Spec. Bull. U.S. natn. Mus.* pp. 1–126.
—— 1927. Report on the Hydroida collected by the United States Fisheries steamer 'Albatross' in the Philippine region, 1907–1910. *Bull. U.S. nat. Mus.* (100) **6** : 195–242.
OKEN, L. 1815. *Okens Lehrbuch der Naturgeschichte. Dritte Theil. Zoologie*. Jena.

Orbigny, A. d' 1853. *Paléontologie française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France. Terrains Crétacés.* **5**. *Bryozoa.* Paris.
Pallas, P. S. 1766. *Elenchus zoophytorum.* The Hague.
Parke, M. & Dixon, P. S. 1968. Check-list of British marine algae – second revision. *J. mar. biol. Ass. U.K.* **48** : 783–832.
Péron, F. 1804a. Mémoire sur le nouveau genre *Pyrosoma. Annls Mus. Hist. nat. Paris,* **4** : 437–446.
—— 1804b. Précis d'un mémoire lu à l'Institut National, sur la température de la mer soit à sa surface, soit à diverses profondeurs. *Annls Mus. Hist. nat. Paris,* **5** : 123–148.
—— 1804c. Mémoire sur le nouveau genre *Pyrosoma. J. Phys. Chim. Hist. nat.* **59** : 207–213.
—— 1804d. Observations sur la dyssenterie des pays chauds, et sur l'usage du bétel. *J. phys. Chim. Hist. nat.* **59** : 290–299.
—— 1804e. Extrait d'un mémoire sur la température des eaux de la mer, soit à sa surface, soit à diverses profondeurs, le long des rivages et en pleine mer. *J. Phys. Chim. Hist. nat.* **59** : 361–366.
—— 1804f. Mémoire sur quelques faits zoologiques applicables à la théorie du globe, lu à la classe des sciences physiques et mathématiques de l'Institut National. *J. Phys. Chim. Hist. nat.* **59** : 463–479.
—— & Lesueur, C. A. 1810a. Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. *Annls Mus. Hist. nat. Paris* (1809) **14** : 325–366.
—— —— 1810b. Suite de l'histoire générale et particulière de tous les animaux qui composent la famille des méduses. *J. Phys. Chim. Hist. nat.* **70** : 357–371.
Picard, J. 1955. Hydraires des environs de Castiglione (Algérie). *Bull. Stn Aquic. Pêche Castiglione* (n.s.), **7** : 177–199.
Pictet, C. 1893. Etude sur les hydraires de la Baie d'Amboine. *Revue suisse Zool.* **1** : 1–64.
Prenant, M. & Bobin, G. 1956. Bryozaires. Première partie. Entoproctes, phylactolèmes, cténostomes. *Faune Fr.* **60** : 1–398.
Ralph, P. M. 1956. Variation in *Obelia geniculata* (Linnaeus, 1758) and *Silicularia bilabiata* (Coughtrey, 1875) (Hydroida, F. Campanulariidae). *Trans. R. Soc. N.Z.* **84** : 279–296.
—— 1957. New Zealand thecate hydroids. Part I. Campanulariidae and Campanulinidae. *Trans. R. Soc. N.Z.* **84** : 811–854.
—— 1961. A checklist of the hydroid fauna of the Chatham Islands. *N.Z. Dept. Sci. Ind. Res. Bull.* **139** : 235–238.
—— & Thomson, H. G. 1968. Seasonal changes in growth in the erect stem of *Obelia geniculata* in Wellington Harbour, New Zealand. *Zool. Pub. Victoria Univ. Wellington,* **44** : 1–21.
Redier, L. 1966. Hydraires et bryozaires. *Cah. pacif.* **9** : 77–122.
—— 1967. Révision de la collection du Muséum des hydraires de Lamouroux. *Bull. Mus. natn. Hist. nat. Paris.* (2) **39** : 381–410.
Rees, A. 1819. Sertularia. *The Cyclopaedia: or, Universal Dictionary of Arts, Sciences and Literature.* Volume 32. (Unpaginated.) London.
Rees, W. J. 1939. A revision of the genus *Campanulina* van Beneden, 1847. *Ann. Mag. nat. Hist.* (11) **3** : 433–447.
—— 1953. Records of hydroids and medusae taken at Herdla, Bergen in 1937. *Univ. Bergen Arb.* (1952), (16) : 1–8.
—— & Thursfield, S. 1965. The hydroid collections of James Ritchie. *Proc. R. Soc. Edinb.* (B) **69** : 34–220.
—— & White, E. 1966. New records and fauna list of hydroids from the Azores. *Ann. Mag. nat. Hist.* (13) **9** : 271–284.
Ritchie, J. 1909. Supplementary report on the hydroids of the Scottish National Antarctic Expedition. *Trans. R. Soc. Edinb.* **47** : 65–101.
—— 1910. The marine fauna of the Mergui archipelago, lower Burma, collected by Jas. J. Simpson, M.A., B.Sc., and R. N. Rudmose-Brown, D.Sc., University of Aberdeen, February to May 1907. – The hydroids. *Proc. zool. Soc. Lond.* (1910) : 799–825.

ROYAL COLLEGE OF SURGEONS OF ENGLAND, 1830. *Catalogue of the contents of the Museum of the Royal College of Surgeons in London. Part 4, fasciculus 1, comprehending the first division of the preparation of natural history in spirit.* London. [Anonymous; compiled by Richard Owen.]

—— 1860. *Catalogue of the contents of the Museum of the Royal College of Surgeons of England. Part 1. Plants and invertebrate animals in the dried state.* London. [Anonymous.]

RUSSELL, F. S. 1939. Hydrographical and biological conditions in the North Sea as indicated by plankton organisms. *J. Cons. perm. int. Explor. Mer*, **14**: 171–192.

—— 1953. *The medusae of the British Isles. Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae and Narcomedusae.* Cambridge, England.

——, SOUTHWARD, A. J., BOALCH, G. T. & BUTLER, E. I. 1971. Changes in biological conditions in the English Channel off Plymouth during the last half century. *Nature, Lond.* **234**: 468–470.

SARS, M. 1835. *Beskrivelser og iagttagelser over nogle maerkelige eller nye i havet ved den Bergenske kyst levende dyr af polypernes, acalephernes, radiaternes, annelidernes og mollusk-ernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne arter og deres forekommen.* Bergen.

—— 1850. Beretning om en i Sommeren 1849 foretargen zoologisk Reise i Lofoten og Finmarken. *Nyt Mag. Naturvid.* **6**: 121–211.

SAVAGE, S. 1945. *A catalogue of the Linnaean herbarium.* London.

—— 1948. *Catalogue of the manuscripts in the library of the Linnean Society of London. Part IV. – Calendar of the Ellis manuscripts.* London.

SCHMIDT, H. 1972. Some new records of hydroids from the Gulf of Aqaba with zoogeographical remarks on the Red Sea area. *J. mar. biol. Ass. India* (1971) **13**: 27–51.

SCHNEIDER, K. C. 1897. Hydropolypen von Rovigno, nebst Uebersicht über das System der Hydropolypen im Allgemeinen. *Zool. Jb., Syst.* **10**: 472–555.

SCHYDLOWSKY, A. 1902. Matériaux relatifs à la faune des polypes hydraires des mers arctiques. I. Les hydraires de la Mer Blanche le long du littoral des Jsles Solowetzky. *Trudy khar'kov Obshch. Ispyt. Prir.* (1901) **36** (1): 1–276.

SHERBORN, C. D. 1929. *Index animalium sive index nominum quae ab A.D. MDCCLVIII generibus et speciebus animalium imposita sunt. Letters O, P.* London.

SLABBER, M. 1769–1778. *Natuurkundige verlustigingen, behelzende microscopise waarneem-ingen van in- en uitlandse water- en land-dieren.* Haarlem, Holland.[1]

—— 1775–1781. *Physicalische Belustigungen oder microscopische Wahrnehmungen in- und auslandischer Wasser- und Landthierchen.* Translated by P. L. St. Müller. Nürnberg.[1]

SMITH, J. E. 1821. *A selection of the correspondence of Linnaeus, and other naturalists, from the original manuscripts.* 2 volumes. London.

SPAGNOLINI, A. 1871. Catalogo degli acalefi discofori del golfo di Napoli. *Atti Soc. ital. Sci. nat.* **14**: 144–223.

SPLETTSTÖSSER, W. 1929. Beiträge zur Kenntnis der Sertulariiden. *Zool. Jb., Syst.* **58**: 1–134.

SPRENGEL, W. 1813. *Philip Cavolini's Abhandlungen über Pflanzen-Thiere des Mittelmeers.* Nurnberg.

STECHOW, E. 1914. Zur Kenntnis neuer oder seltener Hydroidpolypen, meist Campanulariden, aus Amerika und Norwegen. *Zool. Anz.* **45**: 120–136.

—— 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zool. Jb., Syst.* **42**: 1–172.

—— 1921a. Symbiosen zwischen Isopoden und Hydroiden. *Zool. Anz.* **53**: 221–223.

[1] Both editions of Slabber's work were issued in parts which were not dated individually (Benthem Jutting, 1970). Title-pages of the German version dated 1781 carried a slightly amended title, *Physikalische Belustigungen oder mikroskopische Wahrnehmungen von drey und vierzig in- und ausländchen Wasser- und Landthierchen*, while later title-pages of the Dutch version retained the original wording.

STECHOW, E. 1921b. Neue Genera und Species von Hydrozoen und anderen Evertebraten. *Arch. Naturgesch.* **87** (Abt. A, Heft 3) : 248–265.
—— 1923a. Neue Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andere Formen. *Zool. Anz.* **56** : 1–20.
—— 1923b. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II Tiel. *Zool. Jb., Syst.* **47** : 29–270.
—— 1925. Hydroiden der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*, **17** : 383–546.
TEISSIER, G. 1965. *Inventaire de la faune marine de Roscoff. Cnidaires – cténaires.* Roscoff, France.
THIEL, M. E. 1932. Die Hydromedusenfauna des Nordlichen Eismeeres in tiergeographischer Betrachtung. *Arch. Naturgesch.* (N.F.) **1** : 435–514.
THORNELY, L. R. 1899. The hydroid zoophytes collected by Dr Willey in the southern seas. *In* : Willey, A., 1898–1902, *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere. Collected during 1895, 1896 and 1897*, **4** : 451–457. Cambridge.
—— 1904. Report on the Hydroida collected by Professor Herdman, at Ceylon, in 1902. *Rep. Govt. Ceylon Pearl Oyster Fish. Gulf Manaar, Suppl. Rep.* **8** : 107–126.
—— 1908. Reports on the marine biology of the Sudanese Red Sea. X. Hydroida collected by Mr C. Crossland from October 1904 to May 1905. *J. Linn. Soc.* **31** : 80–85.
TORREY, H. B. 1904. The hydroids of the San Diego region. *Univ. Calif. Publs Zool.* **2** : 1–43.
VANHOFFEN, E. 1910. Die Hydroiden der Deutschen Südpolar-Expedition 1901–1903. *Dt. Südpol.-Exped. XI, Zoologie*, **3** : 269–340.
VANNUCCI MENDES, M. 1946. Hydroida Thecaphora do Brasil. *Archos Zool. Est. S. Paulo*, **4** : 535–597.
VANNUCCI, M. 1951. Hydrozoa e Scyphozoa existentes no Instituto Paulista de Oceanografia. *Bolm Inst. Oceanogr. S. Paulo* (1) **2** : 69–104.
—— 1954. Hydrozoa e Scyphozoa existentes no Instituto Oceanográfico, II. *Bolm Inst. Bolm Oceanogr. S. Paulo*, **5** : 95–149.
VERVOORT, W. 1946a. Hydrozoa (C 1). A. Hydropolypen. *Fauna Ned.* **14** : 1–336.
—— 1946b. Exotic hydroids in the collections of the Rijksmuseum van Natuurlijke Historie and the Zoological Museum at Amsterdam. *Zool. Meded. Leiden*, **26** : 287–351.
—— 1959. The Hydroida of the tropical west coast of Africa. *Atlantide Rep.* **5** : 211–325.
—— 1966. Bathyal and abyssal hydroids. *Galathea Rep.* **8** : 97–174.
—— 1967. The Hydroida and Chondrophora of the Israel South Red Sea Expedition, 1962. *Bull. Sea Fish. Res. Stn Israel*, **43** : 18–54.
—— 1968. Report on a collection of Hydroida from the Caribbean region, including an annotated checklist of Caribbean hydroids. *Zool. Verh. Leiden*, **92** : 1–124.
—— 1972a. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty Geological Observatory. *Zool. Verh. Leiden*, **120** : 1–247.
—— 1972b. Hydroids from submarine cliffs near Arthur Harbour, Palmer Archipelago, Antarctica. *Zool. Meded. Leiden*, **47** : 337–357.
WEILL, R. 1934a. Contribution à l'étude des cnidaires et de leurs nématocystes. I. Recherches sur les nématocystes. *Trav. Stn zool. Wimereux*, **10** : 1–347.
—— 1934b. Contribution à l'étude des cnidaires et de leurs nématocystes. II. Valeur taxonomique du cnidome. *Trav. Stn zool. Wimereux*, **11** : 347–701.
WESTFALL, J. A. 1966. The differentiation of nematocysts and associated structures in the Cnidaria. *Z. Zellforsch. mikrosk. Anat.* **75** : 381–403.
YAMADA, M. 1958. Hydroids from the Japanese Inland Sea, mostly from Matsuyama and its vicinity. *J. Fac. Sci. Hokkaido Univ.* (6) Zool. **14** : 51–63.

INDEX

Valid names are printed in Roman type and names regarded in this paper as synonyms are printed in *italic type*. Main page references also are in *italics*.

Dr P. F. S. Cornelius
Department of Zoology
British Museum (Natural History)
Cromwell Road
London SW7 5BD