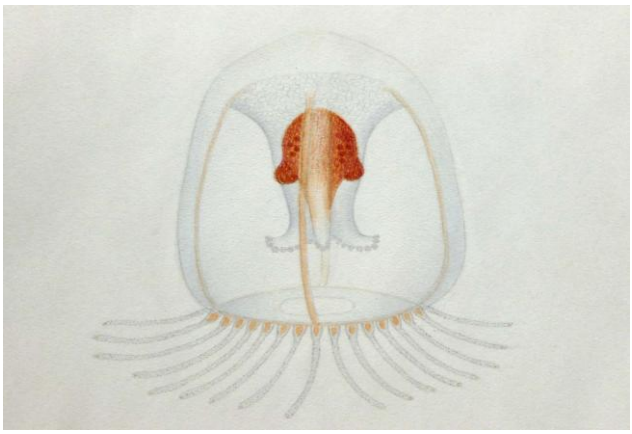
MARINE ZOOPLANKTON OF SOUTHERN BRITAIN

Part 1:
Radiolaria, Heliozoa, Foraminifera, Ciliophora, Cnidaria, Ctenophora, Platyhelminthes, Nemertea, Rotifera and Mollusca

David V.P. Conway



Edited by Anthony W.G. John

Marine Biological Association Occasional Publications No. 25

Front cover from top left to right: The Citadel Hill Laboratory, Plymouth; MBA plankton sampling off Plymouth circa 1900; National Marine Biological Library at the MBA, reception and expeditions gallery; The medusae *Turritopsis nutricula,* unpublished 1903 illustration by E.T. Browne (NMBL archive collection); WP3 net sampling at Station L4 on PML research vessel "Plymouth Quest", 2010 (Image: Matt Frost).

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Marine Biological Association, Plymouth, UK

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This publication has been prepared as accurately as possible, but any suggestions or corrections that could be included in any revisions would be appreciated.

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CONTENTS

Acknowledgements

In 1963 I applied for a position at the Marine Laboratory in Aberdeen, Scotland when several unspecified ones were being advertised, attracted by the requirement to spend time at sea on research vessels. I was offered a post in the Plankton Section and had to consult an encyclopaedia to find out exactly what I would be working on, as the general public at that time were less aware of the existence of plankton. I would like to acknowledge the initial training and advice on zooplankton identification, generously given by the late James Fraser, Duncan Seaton and Norman Nicol, and also by Jimmy Adams during my thirteen years in Aberdeen before moving to Plymouth to the Plymouth Marine Laboratory (PML) and subsequently the Marine Biological Association (MBA) Laboratory. My thanks to the many other colleagues, both in the UK and abroad, who have shared their expertise and enthusiasm over the years, including, in recent years, the analysts of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in Plymouth. Thanks also to Roger Harris who involved me in the L4 sampling programme. Compiling this series of three guides would have been impossible without the superb resources available at the National Marine Biological Library (NMBL) here at the MBA, and the support provided by the librarians, particularly Linda Noble and Sandra Robinson. I greatly appreciate the permissions granted by the many authors, publishers and journals to reproduce material. My thanks to Steve Hawkins and Colin Brownlee, past and present directors respectively of the MBA and David Sims, Deputy Director (Research) for their support. I greatly appreciate the offer by Tony John, who shares a similar number of years as myself working on plankton, to do the editing. These guides were part funded by the MBA's contribution to the NERC Oceans 2025 Strategic Research Programme (Theme 10, Sustainable Observations in a Changing marine Environment).

Purpose of this guide

Plymouth, in south-west Britain, is one of only a few centres in northern Europe where comprehensive long-term data are available and continues to be collected by the MBA and PML on the local marine plankton and marine fauna in general. It is also the base of SAHFOS, whose extensive long-term plankton survey in the north Atlantic includes routes from Plymouth and through the English Channel.

Surprisingly, while the zooplankton of the northern European region has probably been studied more than any other sea area in the world, currently there is no single, comprehensive, taxonomic identification guide to the range of species and larval stages found. Taxonomic information is largely spread through a wide range of monographs, papers and group-specific identification guides, many of which are out of print and only easily available to researchers with access to good library facilities. This series of three guides is being assembled to collate taxonomic identification information for the zooplankton groups recorded off south-west Britain, primarily for local identification and training purposes. However, because prevailing currents also bring oceanic zooplankton into the English Channel, the range of species sampled off Plymouth covers the majority found over the shallower parts of northern European continental shelf (excluding the Mediterranean Sea), so the guides should be more widely useful and hopefully make tackling zooplankton identification easier for a wider audience. The commonest truly planktonic species and the most widely studied groups are covered in most detail, but some information is also included on benthic, epibenthic and parasitic species that are sampled occasionally. For all groups there is at least information on their morphology, guidance on their identification and bibliographies giving identification resources.

The species list was mainly compiled from records from the Plymouth Marine Fauna (PMF; Marine Biological Association, 1957) publication, from various MBA sampling station records and from the current long-term sampling by the PML at Station L4 off Plymouth. Distributional information for some species has also been obtained from the Marine Life Information Network (MarLIN) website and sampling at Southampton (Muxagata & Williams, 2004). Some species have been included that have not been recorded off Plymouth, but have been found in adjacent sea areas. Details about whether the various species have been recorded in the PMF, at Station L4 or surrounding area, and a brief note of their general distribution in the northern European area (excluding Mediterranean Sea) are also included. Distributional information often relies on local observations from widely dispersed laboratories, so is only a very rough indication. Descriptions and terminology have, as far as possible, been deliberately kept reasonably basic.

Brief history of plankton sampling at Plymouth

Since the formation of the MBA in 1884, and the opening of its laboratory in Plymouth in 1888, much original zooplankton research has been carried out by many distinguished researchers, unravelling the biology of a wide range of organisms and gathering long-term data on their seasonal abundance in the Western English Channel, particularly at a series of stations off Plymouth. The PMF compiles a list of all the marine fauna that had been recorded off Plymouth, up until its last publication in 1957, including zooplankton, along with details of where they were sampled and some indication of their seasonal abundance. Subsequent to the publication of the PMF, long-term zooplankton data continued to be collected, but the emphasis was mainly on selected "indicator" species, rather than the complete range of organisms. In the early 1980s long-term data sets were losing their funding appeal and sampling became more targeted at specific stations, including mid-Channel station E1, from which zooplankton is still sampled by the MBA. In the 1960s and 70s, MBA scientists including the late Alan Southward demonstrated important links between climate fluctuations and biological changes in the sea. By the late 1980s and the emerging ideas about human-driven climate change, the necessity for long-term monitoring data sets, including those of zooplankton, was recognised.

Building on nearly a century of zooplankton sampling by the MBA, in 1988, Roger Harris of the PML Zooplankton Group began a programme of weekly observations that included zooplankton sampling at Station L4, located ten nautical miles south-west of Plymouth (50º15'N, 04º13'W, water depth ~55 m) and the previous detailed identification of species was reinstated. Routine zooplankton sampling at L4 continues to be carried out weekly as part of the Oceans 2025 Programme, following the founding of the Western Channel Observatory project. A complete guide to the L4 programme, sampling methods, the dataset and publications are given on the PML website (http://www.westernchannelobservatory.org.uk/L4/).

Classification system used in the guide

The classification of many groups is contentious and continuously evolving, so as a foundation, the online World Register of Marine Species (WORMS) scheme has generally been followed. The emphasis in these guides is on species identification and because classifications keep changing, for each group only a simple classification is given, usually missing out several taxonomic levels.

Taxonomic resources

For the European area, some basic zooplankton guides have been available (e.g. Johnstone *et al*., 1924; Newell & Newell 1963; Todd *et al*., 1991; Larink & Westheide, 2006), but these are mainly for students and cannot be used for accurate species level identification. Some, more detailed taxonomic guides have been produced for the Mediterranean, such as Trégouboff & Rose (1957) and Avancini *et al*., (2006). Resources available free online include the ICES zooplankton sheets (1939-2001), the photographic guide to the mesozooplankton of the Southampton area by Muxagata & Williams (2004), the Marine Species Identification Portal (http://species identification.org) and the ZIMNES guide (http://192.171.193.133/). Additional online resources are listed in Jouenne *et al*. (2008). A selection of general zooplankton texts is given below.

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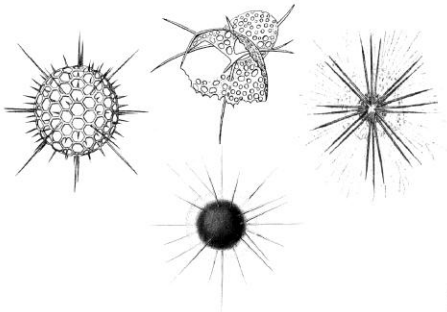
PICTORIAL KEY TO ZOOPLANKTON

(Not to scale; numbers in brackets are part numbers of the guide)

KINGDOM PROTOZOA

Phylum Sarcomastigophora (1)

Subphylum Radiolaria



KINGDOM CHROMISTA

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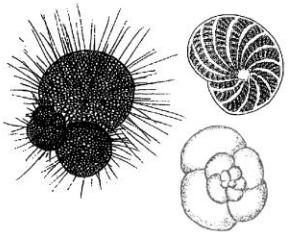

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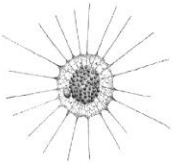
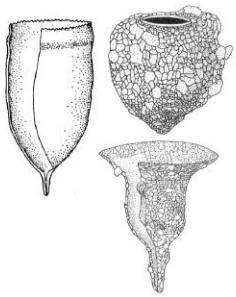


Phylum Ciliophora (1)

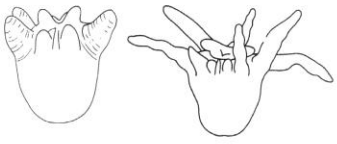
Order Tintinnida



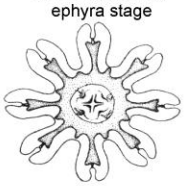
KINGDOM ANIMALIA
NON-CRUSTACEAN ZOOPLANKTON

Phylum Cnidaria (1)

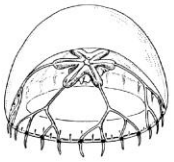
Class Anthozoa, anemone larva



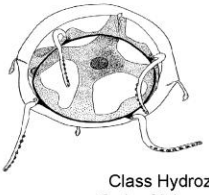
Class Scyphozoa, ephyra stage



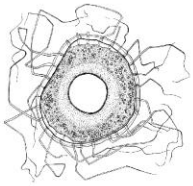
Class Hydrozoa, Order Limnomedusae



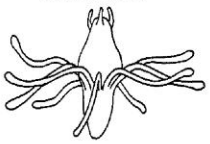
Class Hydrozoa, Order Trachymedusae



Class Hydrozoa, Order Narcomedusae



Class Hydrozoa, Order Anthothecata, actinula larva



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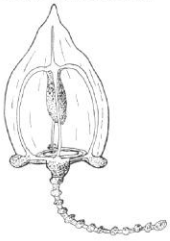
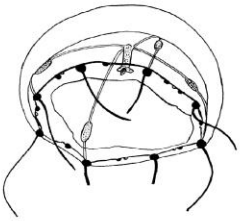
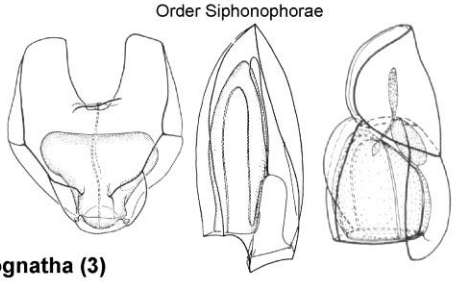


Class Hydrozoa, Order Leptothecata



Class Hydrozoa, Order Siphonophorae



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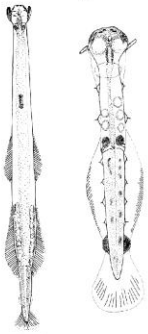

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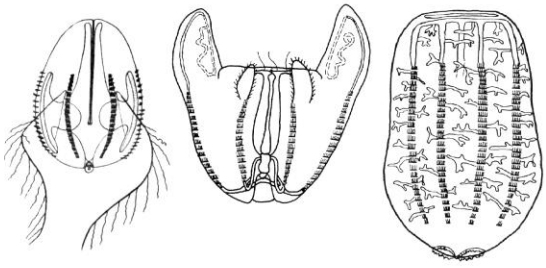


Phylum Brachiopoda (3)

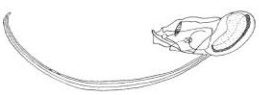
larva

Phylum Chordata (3)

Subphylum Tunicata

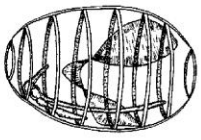
Class Ascidiacea

Class Larvacea

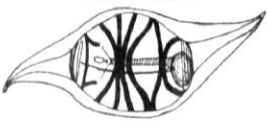


Class Thaliacea

Order Doliolida

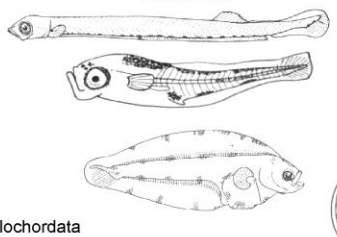


Order Salpida

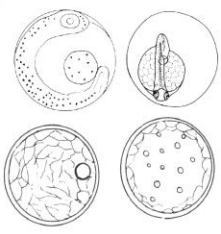


Subphylum Vertebrata

Fish larvae



Fish eggs



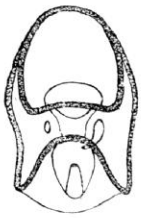
Subphylum Cephalochordata

NON-CRUSTACEAN ZOOPLANKTON AND LARVAE

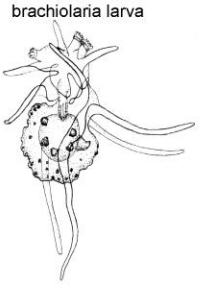
Phylum Echinodermata (3)

Subphylum Asterozoa

Class Asteroidea, bipinnaria larva



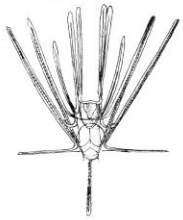
Class Asteroidea, brachiolaria larva



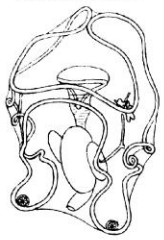
Class Ophiuroidea, ophiopluteus larva

Subphylum Echinozoa

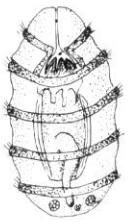
Class Echinoidea, echinopluteus larva



Class Holothuroidea, auricularia larva



Classes Holothuroidea and Crinoidea, doliolaria larva



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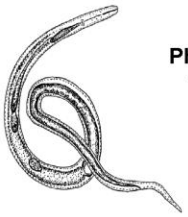
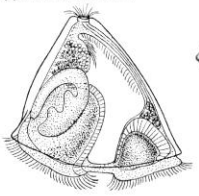


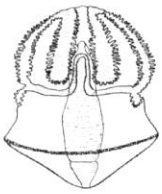
Phylum Bryozoa (3)

cyphonautes larva



Phylum Hemichordata (3)

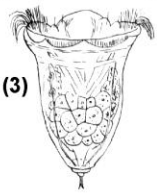
tornaria larva



Phylum Phoronida (3)

actinotroch larva

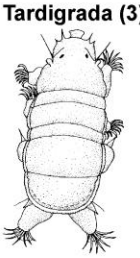
Phylum Rotifera (1)



Phylum Nemertea (1)

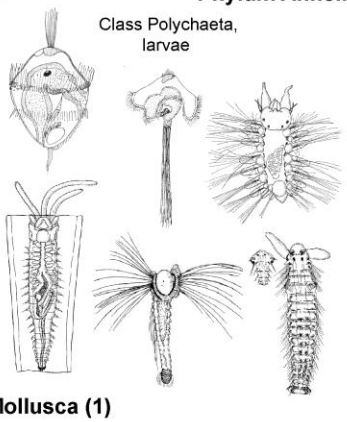
pilidium larva

Phylum Tardigrada (3)

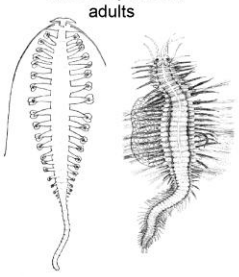


Phylum Annelida (3)

Class Polychaeta, larvae



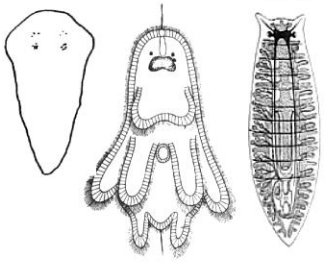
Class Polychaeta, adults



Phylum Platyhelminthes (1)

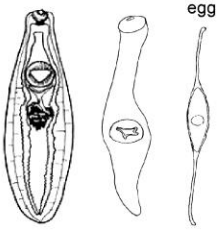
Class Turbellaria

Larva Müllers larva Adult



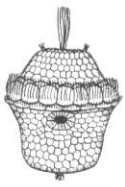
Class Trematoda

Adult Larva Parasite egg



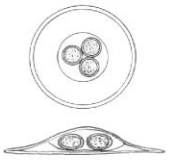
Phylum Mollusca (1)

Trochophore larva

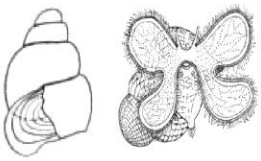


Class Bivalvia, veliger larva

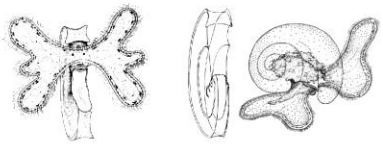
Subclass Prosobranchia, *Littorina* egg capsules



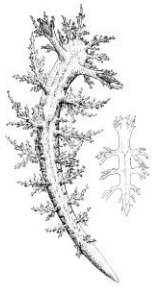
Subclass Prosobranchia, veliger larvae



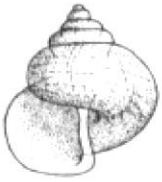
Subclass Prosobranchia, echinospira larvae



Subclass Opisthobranchia Order Nudibranchia

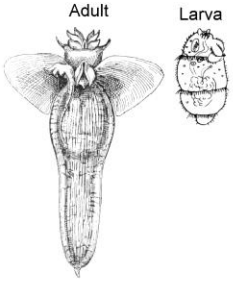


Subclass Opisthobranchia, Order Thecosomata



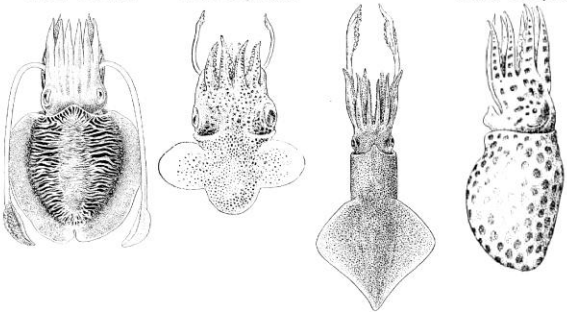
Subclass Opisthobranchia, Order Gymnosomata

Adult Larva



Class Cephalopoda

Order Sepiida Order Sepiolida Order Teuthida Order Octopoda

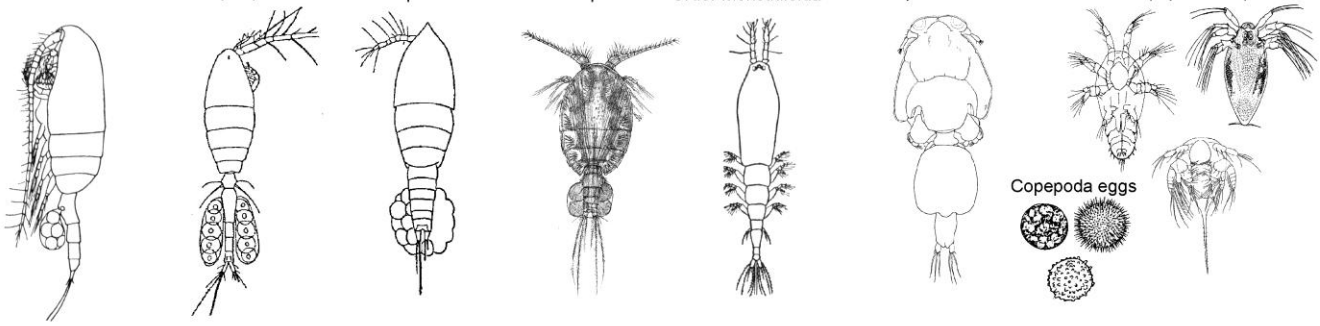


CRUSTACEAN ZOOPLANKTON

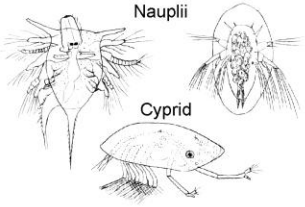
Phylum Arthropoda - Subphylum Crustacea

Subclass Copepoda (2)

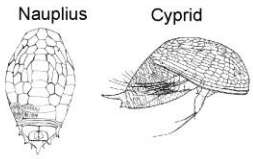
Order Calanoida Order Cyclopoida Order Harpacticoida Order Misophrioida Order Monstrilloida Order Siphonostomatoida Copepoda nauplii



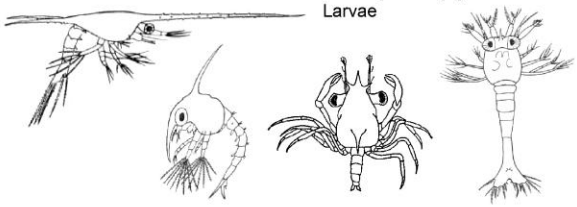
Infraclass Cirripedia (2)



Infraclass Facetotecta (2)

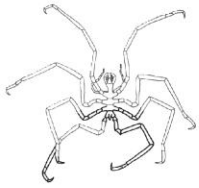


Order Decapoda (3)



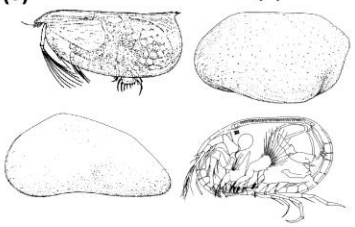
Class Arachnida (2)

Class Pycnogonida (2)

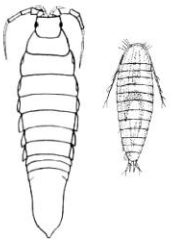


Order Stomatopoda (3)

Class Ostracoda (3)

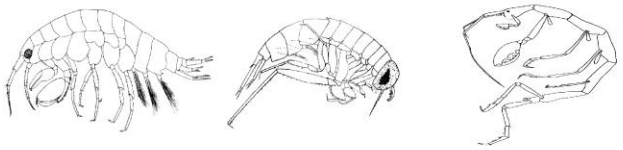


Order Isopoda (3)

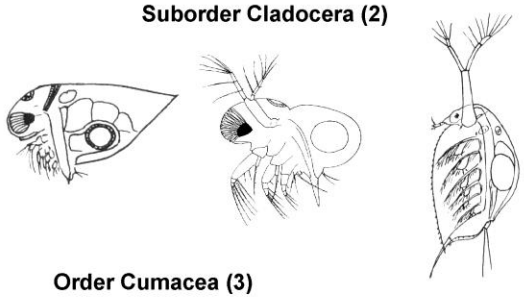


Order Amphipoda (3)

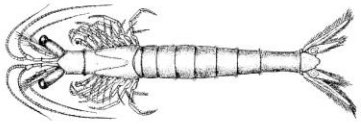
Suborder Gammaridea Suborder Hyperiidea Suborder Corophiidea



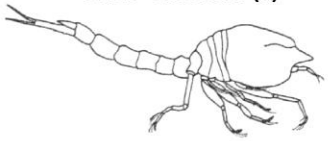
Suborder Cladocera (2)



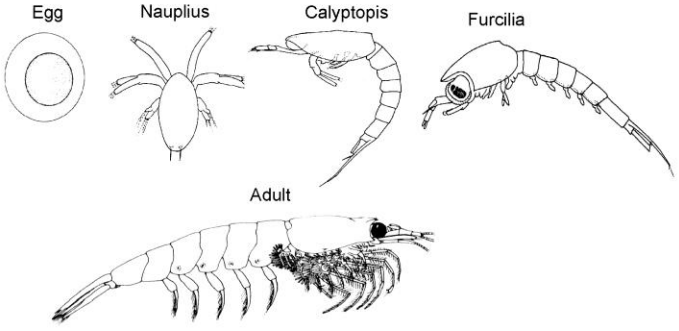
Order Mysida (3)



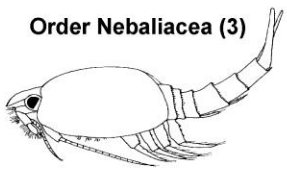
Order Cumacea (3)



Order Euphausiidae (3)



Order Nebaliacea (3)



KINGDOM PROTOZOA
PHYLUM SARCOMASTIGOPHORA

Sarcomastigophora is the largest protozoan phylum and includes the amoebas and related organisms that move and capture food by means of pseudopodia, flowing temporary extensions of the cell. The only members likely to be caught during zooplankton sampling, that will survive routine preservation techniques, are in Subphylum Radiolaria.

Subphylum Radiolaria:

There are some very large colonial species of Radiolaria, but most are single structures, generally less than two millimetres in diameter, but large for a single celled organism. They typically have stiffened radiating pseudopodia and a central endoplasm, separated from the outer web-like ectoplasm by a capsule membrane or wall (Fig. 1A). The ectoplasm usually contains a zone of frothy gelatinous bubbles. Many have radiating skeletal spines that are usually symmetrical. They have been provisionally divided into three classes, **Acantharea**, **Polycystinea** and **Phaeodarea**.

Class Acantharea:

This group differs from other radiolarians in that the skeleton is mainly composed of celestite (strontium sulphate). When they die the skeleton rapidly dissolves. The skeletal elements usually consist of 20 evenly spaced, radiating, solid spicules, not always of the same length, which characteristically meet at the centre (Fig. 1). Where they meet, the spicules may cross loosely or fuse. In some species the spicules produce lateral plates, forming a spherical perforated shell (Fig. 1A) and resemble members of Class Polycystinea, but in the latter the spicules do not extend to the centre. Acanthareans are generally spherical, but some have their greatest diameter around the equator, while others are flattened. Only *Acanthochiasma fusiforme* has been recorded at Plymouth (Fig. 1B).

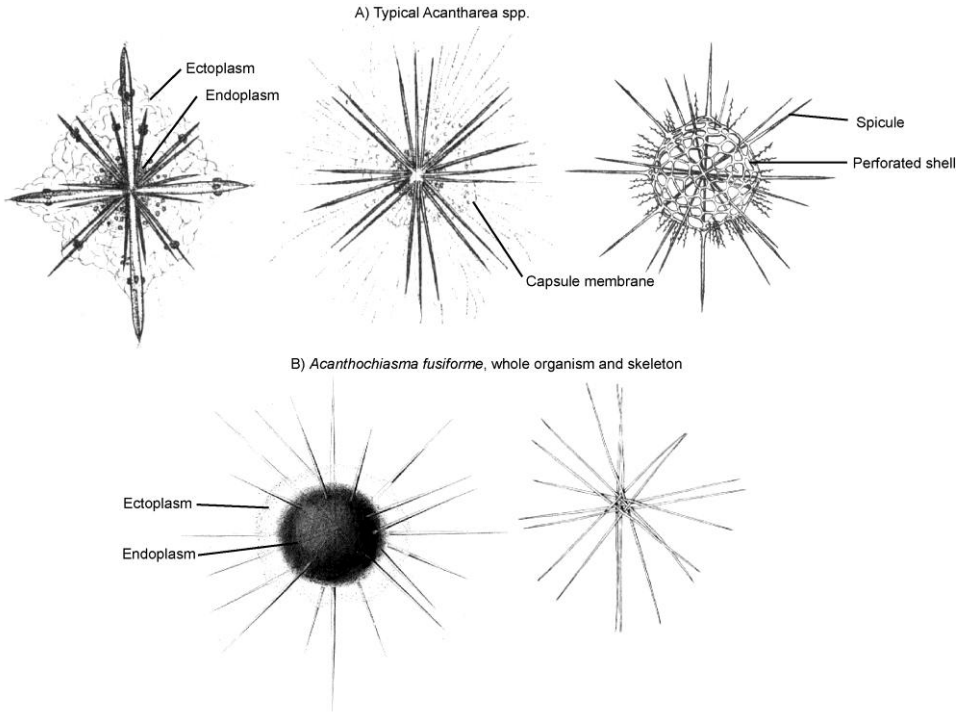


Fig. 1. Acanthareans (from Schewiakoff, 1926).

Recorded: PMF, only *Acanthochiasma fusiforme* Haeckel, 1861. L4, but not identified to species. European region, a range of species.
Size: Group in general ~0.05-0.5 mm
Further information: Schewiakoff, 1926; Bottazzi *et al*., 1969; Bernstein *et al*., 1999; Larink & Westheide, 2006.

PHYLUM SARCOMASTIGOPHORA: Subphylum Radiolaria:

Class Polycystinea:

This is the largest radiolarian group and there are both solitary and colonial species. Only three species are recorded locally (Fig. 2). The skeleton is usually a complex structure (Fig. 2A, B), composed of simple opaline silica, the skeletal elements of which do not meet at the centre of the organism, but some species lack a skeleton or have only simple spicules (Fig. 2C), Most have delicate latticed or spongy skeletons in a range of shapes, consisting of from one to five concentric spheres and lacking spines, or with numerous spines and other structures such as sequences of conical chambers. Often the skeleton cannot be seen because of the dense cytoplasm. The skeletons of this group do not easily dissolve and are a major contributor to the deep sea sediments and fossil record. Algal symbionts often live in the ectoplasm.

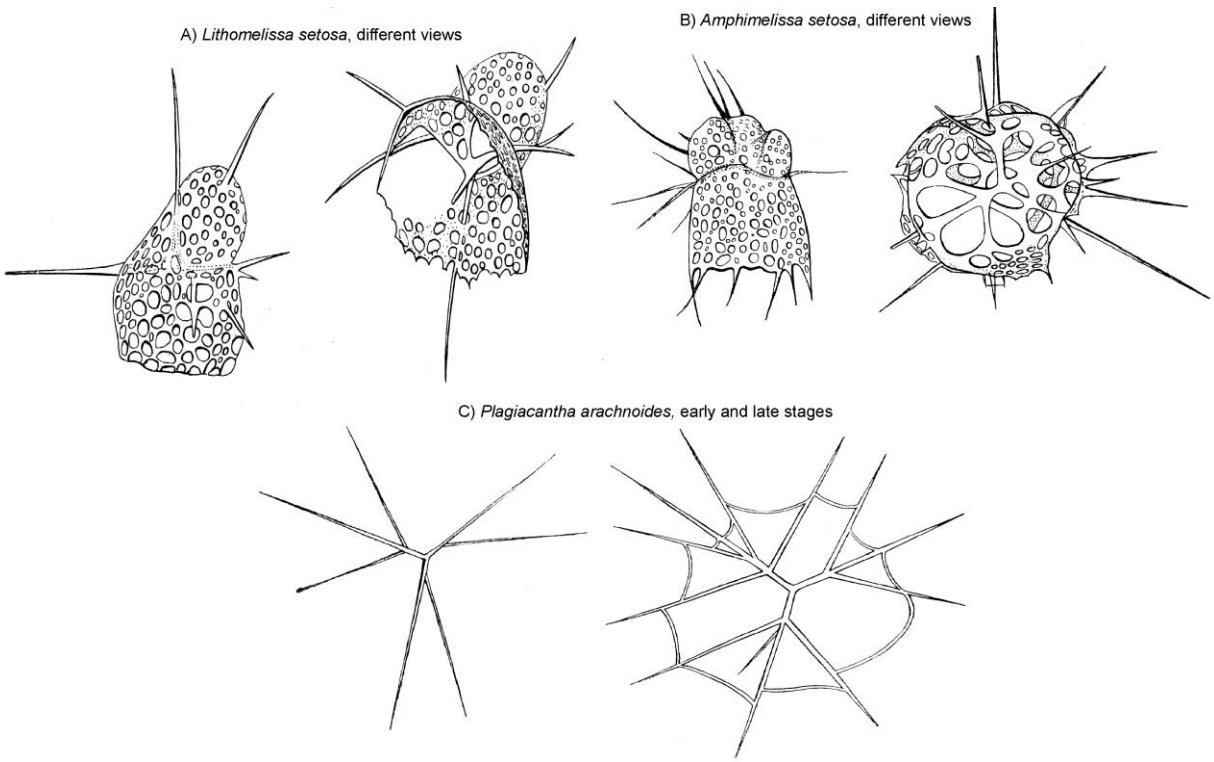


Fig. 2. Skeletons of Polycystinea species recorded at Plymouth (from Schröder, 1914).

Recorded: PMF, three species *Lithomelissa setosa* Joergensen, 1905; *Amphimelissa setosa* (Cleve) Bernstein, 1934; *Plagiacantha arachnoides* Claparède, 1856. L4, not recorded. European region, a range of species.
Size: ~0.03-2.0 mm.
Further information: Haeckel, 1862; Schröder, 1914; Trégouboff & Rose, 1957; Boltovskoy, 1999; Larink & Westheide, 2006.

PHYLUM SARCOMASTIGOPHORA: Subphylum Radiolaria:

Class Phaeodarea:

Phaeodarians are traditionally considered radiolarians, but recent molecular evidence suggests that they are not closely related to the other two classes. They differ from the Polycystinea by distinctive features of the central capsular membrane and by the presence of a phaeodium, an aggregate of waste particles within the cell (Fig. 3). Most are basically circular, but some are elaborate branched structures. They are generally solitary and have skeletal elements that are hollow rather than solid, composed of a poorly understood mixture of silica with some organic content that rapidly dissolves in seawater on death. Similar to Polycystinea, the skeletal elements do not meet at the centre of the organism. They lack algal symbionts, as they generally live below the photic zone. *Aulacantha scolymantha* Haeckel, 1862 is given as an example.

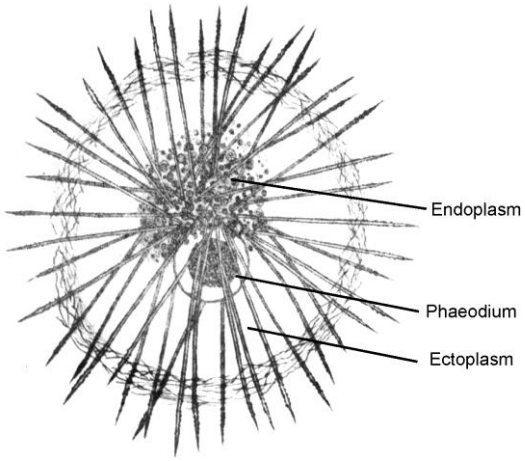


Fig. 3. Typical phaeodarian, *Aulacantha scolymantha* (from Haeckel, 1862).

Recorded: Not recorded from the Plymouth area, deeper water organisms.
Size: ~0.2-0.4 mm.
Further information: Haeckel, 1862; Trégouboff & Rose, 1957; Kling & Boltovskoy, 1999; Larink & Westheide, 2006.

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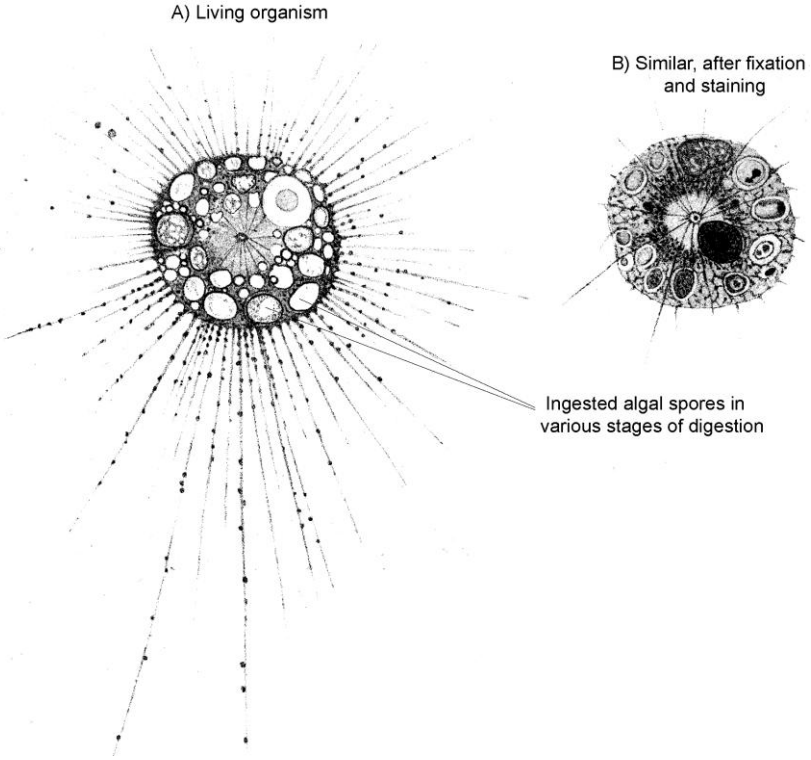
KINGDOM CHROMISTA
PHYLUM HELIOZOA

Heliozoa, or “sun animalcules”, are roughly spherical amoeboids with numerous stiff, thread-like pseudopodia that radiate outwards from a delicate silica endoskeleton, giving them the characteristic sun-like appearance. The pseudopodia are not very useful for locomotion, but are involved in food capture, sensory function and attachment. Heliozoa appear similar to radiolaria, but can be distinguished by the lack of a central capsule between the endo- and ectoplasm and other complex skeletal elements, although some produce simple scales and spines. There are only a few marine species. The only species recorded locally is *Oxnerella maritima*, but is not listed in the WORMS database.



Oxnerella maritima (from Dobell, 1917).

Recorded: PMF, only *Oxnerella maritima* (Dobell, 1917). L4, not recorded. European region, a limited range of species.
Size: ~0.1-0.8 mm.
Further information: Dobell, 1917; Doflein & Reichenow, 1953; Trégouboff & Rose, 1957; Larink & Westheide, 2006.

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PHYLUM FORAMINIFERA

Foraminifera is a diverse protozoan group, most of which have shells. The shell can be composed of calcium carbonate or sand grains and other particles such as sponge spicules cemented together. The shell is usually arranged in a series of chambers of increasing size, the last open to the outside. Some have the appearance of flattened gastropod shells, but there are a great variety of shapes (Figs. 1, 2) and some bear numerous spines. The simplest forms are open tubes or hollow spheres, while others form tree shapes. Some have protoplasm covering the shell.

The cell is divided into granular endoplasm and transparent ectoplasm from which a pseudopodial net may emerge through a single opening or through many perforations in the shell. The pseudopodia are used for locomotion, anchoring, and in capturing food that consists of small plankton, diatoms, bacteria or dissolved organic molecules. The majority are benthic (Fig. 1) but there are several planktonic forms in **Order Globigerinida** (Fig. 2). In shallow water, turbulent conditions often cause benthic individuals to be carried up into the water column.

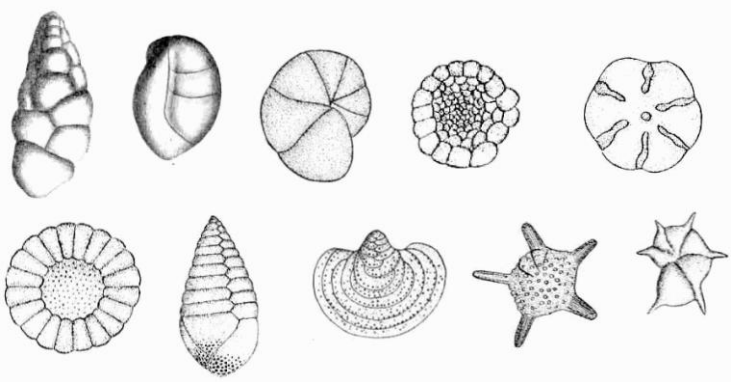

Fig. 1. Examples of benthic foraminiferans (from Cushman, 1928).

Order Globigerinida:

Order Globigerinida includes the exclusively planktonic families Globigerinidae, Globorotaliidae and Candeinidae and ten species from these families are recorded in the PMF.

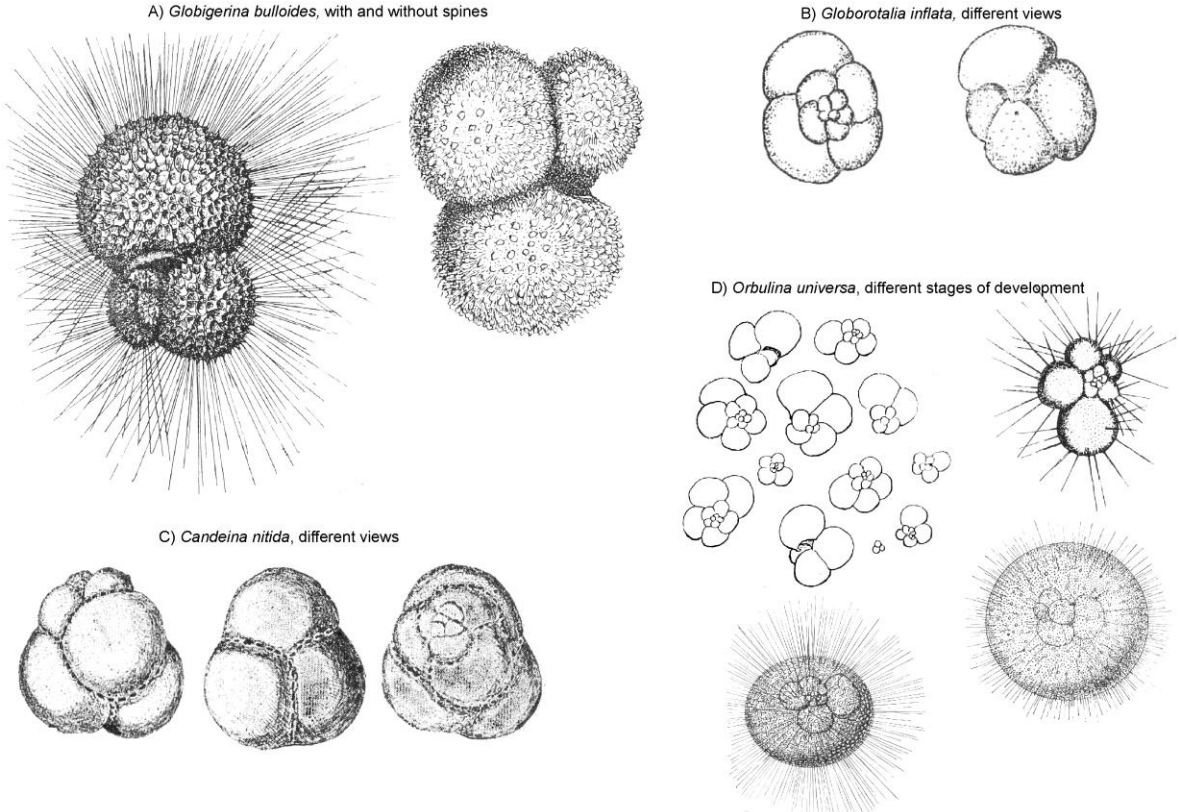

Fig. 2. Examples of pelagic foraminiferans recorded in the PMF (from Rhumbler, 1901).

Globigerinidae (Fig. 2A, D) have spines at some stage of their development, while Globorotaliidae (Fig. 2B) and Candeinidae (Fig. 2C) never have them. *Globigerina bulloides* (Fig. 2A) is a common species, usually found as a multichambered shell with spines like a sea urchin, but the spines can be lost during sampling and preservation and also at particular stages of the life-cycle. Bé (1967) gives a key for and descriptions of pelagic foraminiferans, but because development is progressive, identification of foraminiferans is a specialist task.

Recorded: PMF, a wide range of benthic species but also the following pelagic species: Family Globigerinidae - *Globigerina bulloides* d'Orbigny, 1826; *Globigerinoides ruber* (d'Orbigny, 1839) (as *Globigerinoides rubra*); *Orbulina universa* d'Orbigny, 1839; *Sphaeroidinella dehiscens* (Parker & Jones, 1865). Family Candeinidae - *Candeina nitida* d'Orbigny, 1839. Family Globorotaliidae - *Globorotalia inflata* (d'Orbigny, 1839) (as *Globigerina inflata); Globorotalia menardii* (d´Orbigny, 1826); *Globorotalia crassaformis* (Galloway & Wissler, 1927) (as *G. punctulata*); *Globorotalia scitula* (Brady, 1882); *Neogloboquadrina dutertrei* (d'Orbigny, 1839) (as *Globigerina dutertrei*). L4, benthic species recorded and also *Globigerina* spp. European region, a wide range of species.
Size: ~0.1-0.6 mm
Further information: Rhumbler, 1901; Trégouboff & Rose, 1957; Bé, 1967; Murray, 1979; Mücke & Hemblen, 1999; Larink & Westheide, 2006.

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Trégouboff, G. & Rose, M. 1957. Manuel de Planctonologie Méditerranéenne. Paris, Centre National de la Recherche Scientifique, Volume 1, 587pp.; Volume 2, 207 pls.

PHYLUM CILIOPHORA

Ciliophora are protozoa that use cilia for locomotion. The only members generally caught in mesozooplankton nets are in **Order Tintinnida**.

Order Tintinnida:

The main body of tintinnids is enclosed in a flask-shaped shell or lorica, composed of gelatinous proteinaceous material, usually smooth, sometimes spirally fluted or with a honeycomb of openings, but in some groups embedded with mineral fragments, giving a granular external appearance. In live animals a crown of cilia emerges from the lorica, sometimes interdispersed with small tentacles. On the body, cilia are reduced or absent. Because cilia do not survive routine preservation, characteristics of the lorica are used to distinguish between species. Like other members of the microzooplankton they are a vital link in aquatic food chains as they primarily feed on bacteria and phytoplankton (algae and cyanobacteria) and in turn act as food for larger organisms such as copepods and larval fish. Illustrations of the species that have been sampled at Plymouth are given in Figure 1.

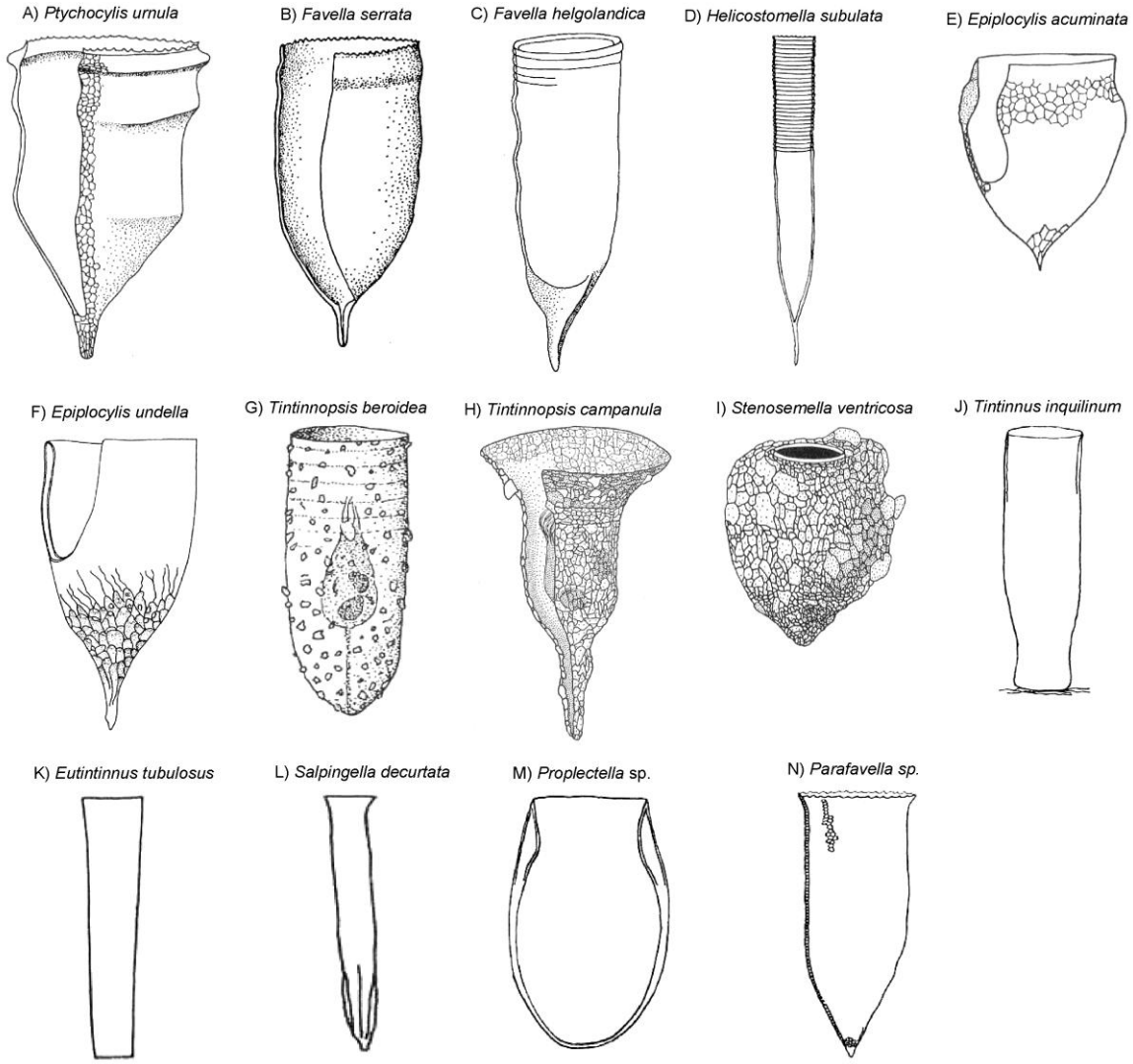

Fig. 1. Tintinnid species sampled at Plymouth (from Marshall, 1969; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF, eight species: Family Ptychocylidae - *Ptychocylis urnula* (Claparède & Lachmann, 1858); *Favella serrata* (Möbius, 1887) Jörgensen, 1924. Family Metacylididae - *Helicostomella subulata* (Ehrenberg, 1833) Jörgensen, 1924. Family Epiplocylididae - *Epiplocylis acuminata* (Daday, 1887) (as *Epiplacylis acuminata*). Family Codonellidae - *Tintinnopsis beroidea*

Stein, 1867; *Tintinnopsis campanula* Ehrenberg, 1840. Family Codonellopsidae - *Stenosemella ventricosa* (Claparède & Lachmann, 1858) Jörgensen, 1924. Family Tintinnidiidae - *Tintinnus inquilinum* (O.F. Müller, 1776) (as *Tintinnidium inquilinum*) (attaches to algae by the base of the lorica, Fig. 1J). WORMS lists both names, and also *Eutintinnus inguilinus,* but they may all be the same species. L4, during routine sampling, but only recorded as tintinnid spp. L4, a further six species from microzooplankton sampling: Family Ptychocylidae - *Favella helgolandica* (Brandt). Family Epiplocylididae - *Epiplocylis undella* (Ostenfeld & Schmidt) Jörgensen, 1927. Family Tintinnidae - *Eutintinnus tubulosus* (Ostenfeld, 1899) Kofoid & Campbell, 1939; *Salpingella decurtata* Jörgensen, 1924. Two tintinnids were only identified to genera, Family Undellidae - *Proplectella* sp. Kofoid & Campbell, 1929 and Family Xystonellidae - *Parafavella* sp. Kofoid & Campbell, 1929. Illustrations of examples from these latter two genera are given in Fig. 1. European region, a wide range of species.
Size: ~0.02-0.2 mm
Further information: Daday, 1886; Trégouboff & Rose, 1957; Marshall, 1969; Alder, 1999; Larink & Westheide, 2006.

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KINGDOM ANIMALIA
PHYLUM CNIDARIA

Phylum Cnidaria (formerly Coelenterata) gets its name from the presence of stinging cells called cnidoblasts or nematocysts that all members of this phylum possess. There are typically two adult forms, polypoid (or hydroid), which are tubular and usually permanently attached to a substrate (sessile), and medusoid forms that are in most cases free-swimming, flattened or bell-shaped. Some cnidarians have only one of the forms in their life cycle, others both. Most alternate between sexual and asexual stages and there are many variations in reproductive strategy. Because of turbulence inshore, a variety of stages, including those that are not planktonic, can be sampled.
In Phylum Cnidaria there are three classes that have representatives in the plankton of southern Britain, separated using distinctive features in their polypoid or medusoid phases:

Class Anthozoa - includes sea anemones and corals.
Class Scyphozoa - the large “jellyfish”.
Class Hydrozoa - includes the small “jellyfish” and siphonophores.

Typical early larval stages
Cnidarian life cycle strategies are very diverse, so it is difficult to generalise, but the typical early larval stage of cnidarians is the planula larvae, which may be released when the egg hatches, or sometimes brooded to a later stage. Newly hatched planulae are generally too delicate to survive routine samping and preservation. They are covered in cilia and there may be a terminal ciliary tuft. They can be flattened, spherical, cylindrical or pear-shaped and not all have a central cavity. Planulae feeding on plankton (planktotrophic) develop a mouth and spend longer in the plankton than those that subsist on nutriment from the egg until settlement (lecithotrophic). Anthozoa have the largest planulae and these are mostly planktotrophic. Cilia of planulae are difficult to discern after routine formaldehyde preservation and the body shape and colour may change. Small amorphous blobs often turn up in plankton samples, so it is sometimes difficult to know if they might be planulae, or a fragment or larva of another organism.

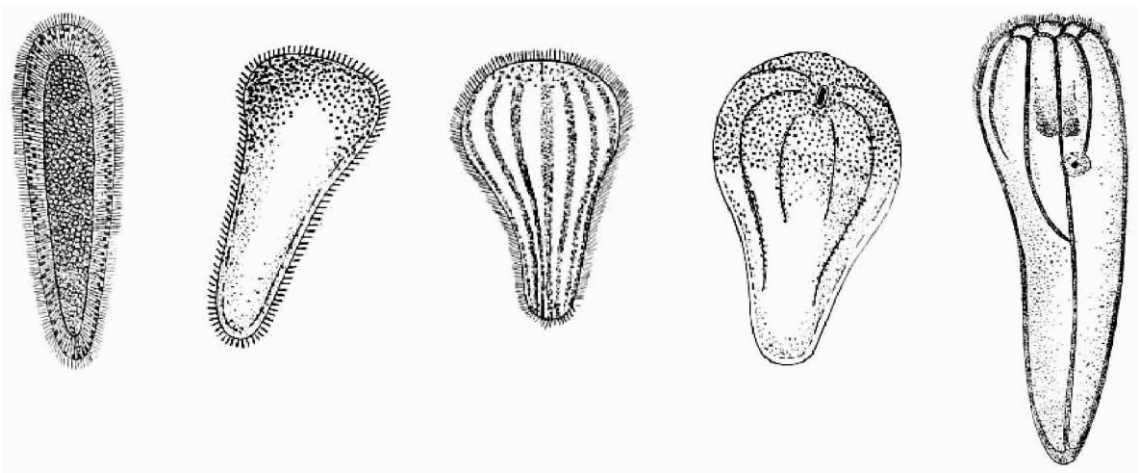


Fig. 1. Various early and late planula larvae (from Hyman 1940).

Recorded: PMF, not recorded. L4, recorded as planulae. European region, found throughout.
Size: ~0.1-5.0 mm
Further information: Hyman, 1940; Mianzan & Cornelius, 1999; Sadro, 2001; Larink & Westheide, 2006.

Class Anthozoa:

Anthozoa means the “flower animals” and included in this group are corals and sea anemones. Adult anthozoans have a polypoid shape and medusae are never produced.

Anthozoan planulae may remain for a time in the plankton and settle as late planulae before developing tentacles, or while still in the plankton they may develop tentacle buds and then tentacles, already resembling a small anemone (Fig. 2). Pelagic anemone larvae with tentacles are classified depending on the number and rows of tentacles and number of septae partitioning the gastrovascular cavity etc., so identification is for specialists. The terms “edwardsia” and “halcampoide” are sometimes used for developmental stages of these miniature anemones. The commonest tentaculate larvae sampled are of the bottom-burrowing, tube anemones (Ceriantharia) and these have their own recognised larval stages called antipathula and cerinula. The rather vague term “arachnactis larvae”, after the ceriantharian genus *Arachnactis,* has sometimes been used for larval cerianthids and also probably wrongly for floating anemone larvae in general. Corbin & Panikkar (1942) described the distribution of *Arachnactis albida* Sars, 1846 in the Celtic sea.

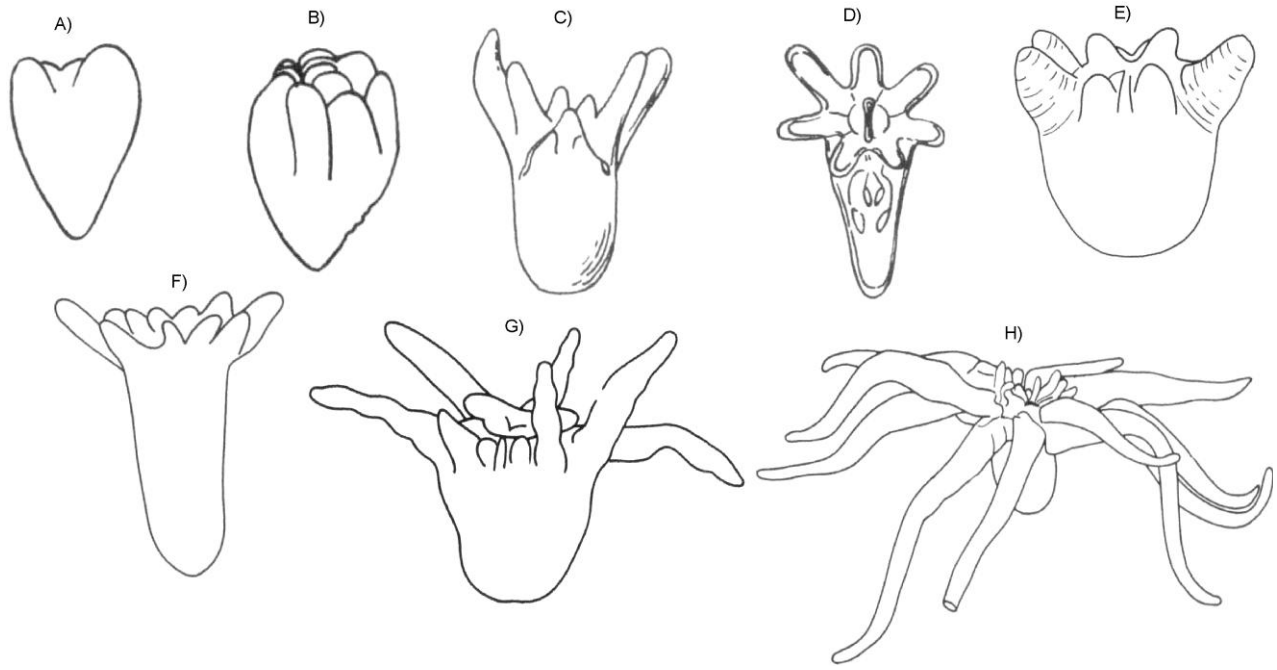


Fig. 2. Examples of developmental stages of anemone larvae (A, C from Carlgren, 1906; B, D, E, G from van Beneden, 1923; F from Nyholm, 1943; H from Leloup, 1962).

Recorded: PMF, *Cerianthus lloydii* Gosse 1859 (as *C. lloydi*) adults are recorded, with a note that arachnactis larvae can be common inside and outside Plymouth Sound in spring and summer. L4, as anemone larvae, can be common. European region, found throughout.
Size: ~2-10 mm.
Further information: Corbin & Panikkar, 1942; Trégouboff & Rose, 1957; Leloup, 1962; Larink & Westheide, 2006; Martin & Koss, 2002.

PHYLUM CNIDARIA:

Class Scyphozoa:

Scyphozoans are the organisms generally associated with the word “jellyfish”. They can be distinguished from the smaller hydrozoan “jellyfish” by their larger adult size, absence of a velum, the circular flap of tissue partially closing off the aperture of the subumbrellar cavity in hydrozoan medusae (Fig. 11A) and presence of clefts in the umbrella margin forming marginal lappets (Fig. 3). The British Scyphozoa, developmental stages and adults, have been extensively described in a monograph by Russell (1970), downloadable free from the “Full text books” section on the National Marine Biological Library (NMBL) website (see bibliography). Illustrations from Russell (1970) included here are reproduced by permission of the Cambridge University Press.

There are seven scyphozoan species in two orders, **Semaeostomeae** and **Rhizostomeae** that have been recorded off Plymouth, only four of which are common. One species, *Discomedusae lobata* Claus, 1877 (Order Semaeostomeae: Family Ulmaridae) is a southern, warm water species that was recorded off the Eddystone lighthouse in 1936 and 1937 (Russell, 1937, 1938a). Because of its rarity Russell did not consider *D. lobata* as a British species, or include it in his scyphozoan monograph (Russell, 1970), nor is it included here.

Adult scyphozoans are generally commonest during summer, tending to disappear in the autumn after spawning, when many dead individuals can be washed ashore. However, some can survive over the winter in deeper water or sheltered areas. Only small individuals are usually sampled in plankton nets, so only the earliest and some juvenile stages are described here.

Development and structure of ephyrae

Most semaeostome and rhizostome medusae produce gametes that develop into the typical cnidarian planula larvae (Fig. 1). Planulae attach to some suitable substrate, such as a rock, and develop into a polyp stage called a scyphistoma, which resembles a sea anemone. The scyphistoma may increase their numbers by budding new polypoid individuals, but they eventually produce and release, by a budding process known as strobilation, from few to many flattened immature medusoid stages called ephyrae (Fig. 3). Food availability and temperature appear to be the main factors regulating strobilation. *Pelagia noctiluca* differs in that there is direct development from gametes produced by the adult medusae, through a planula stage to an ephyra that gradually develops into an adult medusa, so the life cycle is completely pelagic, hence its generic name. A pictorial key to the ephyrae of the main British species is given in Figure 3. The early ephyrae of *Aurelia aurita, Cyanea lamarckii, C. capillata, Chrysaora hysoscella* and *Rhizostoma pulmo* (*as R. octopus*) are described in Straehler-Pohl & Jarms (2010) from living individuals.

Adult scyphozoans are thankfully rarely caught in plankton samples. Numbers of ephyrae and juveniles usually peak around March/April, but they can be taken even during winter. Newly liberated ephyrae of the two orders are very similar. They are typically flattened and thin with a circular central disk, inside which the stomach cavity is located (Fig. 3). In all British species there are initially eight radiating lobes, each with paired terminal lappets. The stomach cavity connects to the extremities of the ephyra through a series of gastrovascular canals that radiate out from the centre, inside the lobes and also to the base of the cleft between them. The canals that extend into the lobes are termed rhopalial canals, as at their distal ends in the clefts between the lappets are marginal sense organs called rhopalia. The rhopalia are hollow club-like structures into which a small channel from the canal connects. They bear a solid terminal statocyst that has associated nervous tissue and sometimes ocelli, so are considered to be involved in orientation and light sensitivity. For descriptive purposes the rhopalial canals are termed interradial or perradial, depending on their axis of orientation (see Fig. 13). The eight shorter canals between the lobes do not have rhopalia and are termed adradial or tentacular canals, as marginal tentacles will eventually develop in the region beside their distal ends. The eight tentacles do not always appear at the same time and emerge either just on the margin of the umbrella or on the subumbrella, and the tentacular canals then expand to form gastric pouches. However, *Rhizostoma pulmo* does not develop tentacles, adult *Chrysaora hysoscella* have 24 tentacles and *Aurelia aurita* has a completely different tentacle arrangement. In later stages the gastrovascular canal system can becomes very complex, forming a network.

The central stomach leads to the exterior through a mouth in the centre of the manubrium (Fig. 3), which has lips developed to different extents. Small tentacles called gastric filaments are

visible inside the stomach, arranged in four interradial groups. These may be involved in stinging prey in the stomach and in digestion. They may initially be missing in some species, but increasing numbers develop as the ephyrae grow. The exumbrella surface may be smooth, but some ephyrae develop raised warts with nematocysts (Fig. 4A). Coronal (circular; Fig. 4C) muscle bands gradually develop.

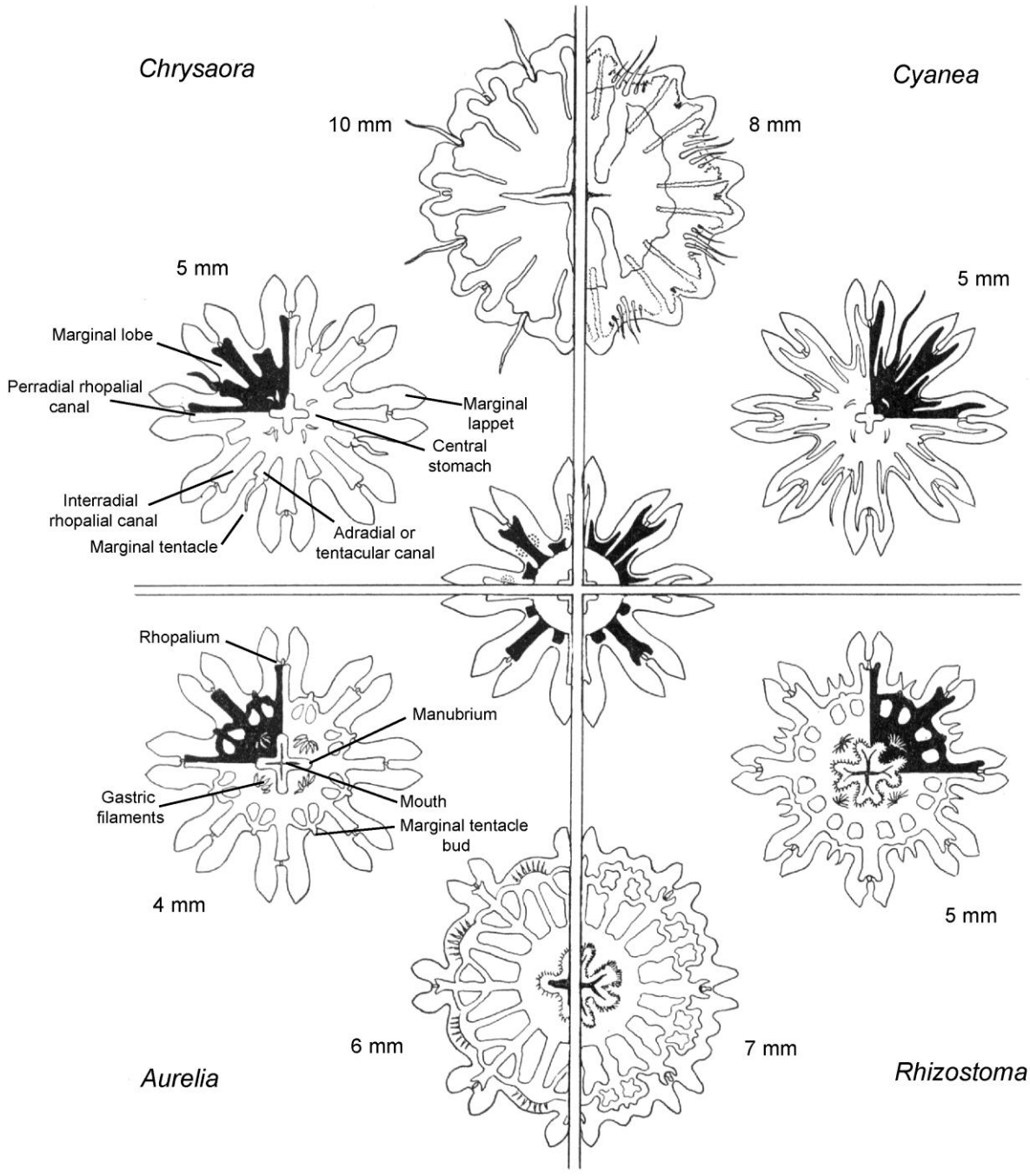


Fig. 3. Pictorial key for the identification of ephyrae (after Russell, 1970). *Pelagia* not included.

Size:

Size ranges from published data (Russell, 1970; Straehler-Pohl & Jarms, 2010) are included in the descriptions for newly liberated ephyrae of each species, along with information on morphological changes with development. The developmental information is mainly based on sparse observations from individual ephyrae of specific sizes. Size on liberation is very variable and will depend on temperature (Straehler-Pohl & Jarms, 2010) and nutrition, so appearance at a particular size is not predictable. Additionally, some descriptions are based on fresh specimens and features may differ in preserved material.

PHYLUM CNIDARIA: Class Scyphozoa:

Order Semaeostomeae:
Family Pelagiidae:

Genus *Pelagia*:

Pelagia noctiluca (Forsskål, 1775)

Pelagia has direct development with no sessile scyphistoma stage. They develop up to eight marginal tentacles, alternating with eight marginal sense organs. Their sting can be quite painful, hence their common name “mauve stinger”.

On liberation the ephyra is ~1 mm in diameter. At ~2 mm a specimen had pointed marginal lappets, narrow rhopalial canals and conspicuous nematocyst warts sparsely distributed over the whole exumbrellar surface. These warts are arranged in a distinctive pattern (Fig. 4A-D), differing from the irregular patterns and generally less prominent clusters of nematocysts found in all the other species. The warts run in two rows on each marginal lobe, diverging from the base of each rhopalial canal and running along either side of a canal to the ends of the marginal lappets. Warts are also distributed over the centre of the exumbrella, but mainly concentrated around the periphery of the central disk.

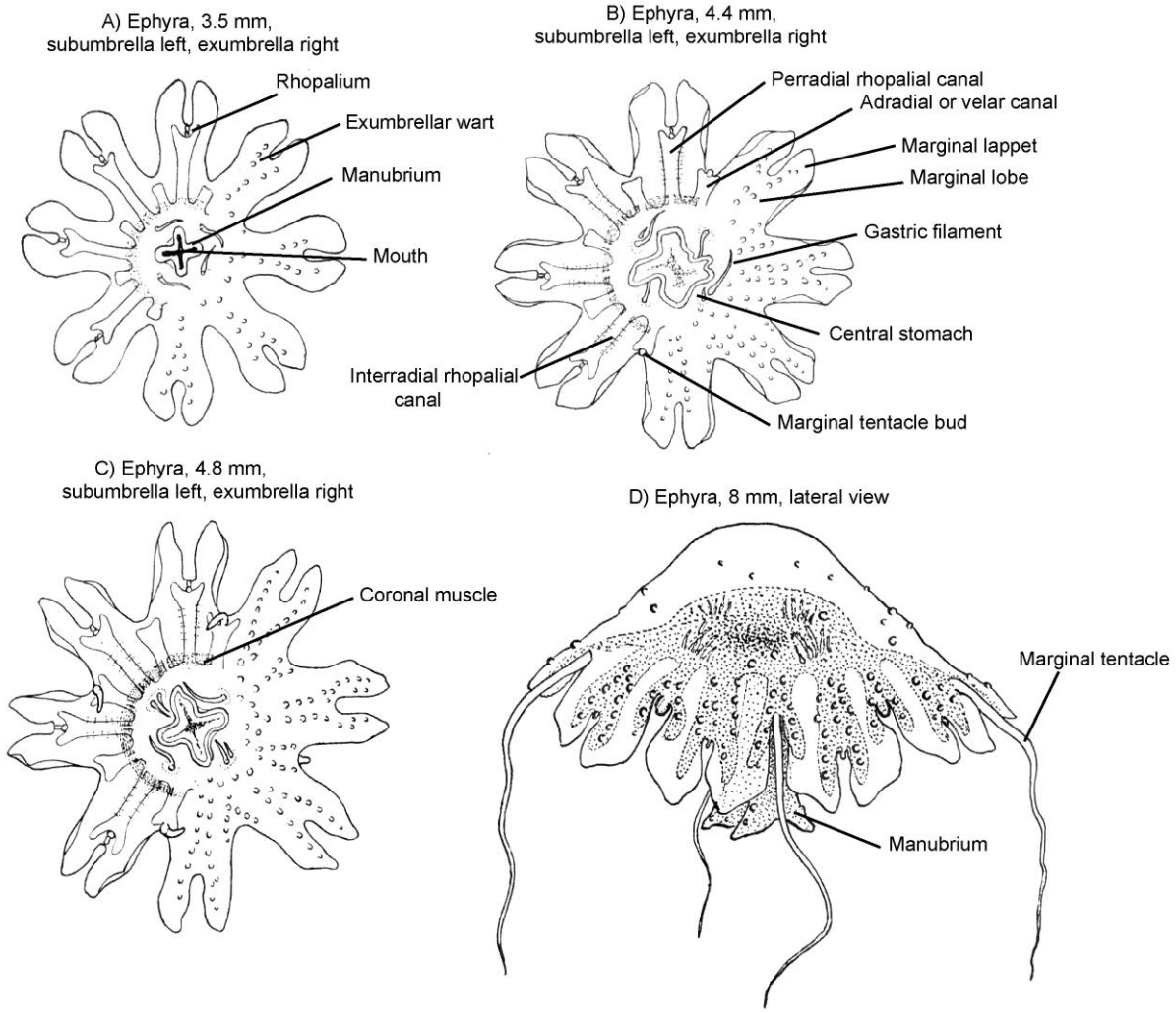


Fig. 4. *Pelagia noctiluca* ephyrae (from Russell, 1970).

Pelagia differs from the ephyrae of *Chrysaora*, *Cyanea* and *Aurelia* in the shortness of the marginal lappets in relation to the diameter of the disk, and the ends are more rounded. However, the shape of the marginal lappets is probably variable. In a specimen of ~3 mm diameter there was a wide stomach cavity with a gastric filament internally in each interradius (Fig. 4A), but no marginal tentacles. The coronal muscle was apparent, but weakly developed and the manubrium cruciform. Usually up to ~4.5 mm there is only one gastric filament and marginal tentacles may be absent or just starting to appear as two opposite, or four alternate small rudiments. By the time the ephyra is ~5.5 mm, the jelly at the centre of the disk is thickening and there may be groups of

two to three gastric filaments (Fig. 4C). The first four marginal tentacles are usually fully formed and a second series of four are starting to develop. The rhopalial canals are clearly forked distally and the adradial canals have lengthened and started to fork. In younger specimens the shape of the forking is intermediate between that found in *Aurelia* and *Cyanea* (Figs. 3; 4A-C).
In a specimen of diameter ~8 mm, the four primary marginal tentacles were well developed, four small secondary tentacles had appeared and there were four or five gastric filaments in each quadrant (Fig. 4D). The four mouth lips were well developed and pointed. However, the number of gastric filaments and marginal tentacles at any particular size is variable. Colouration in later stages is usually pale purple.

Recorded: PMF, only gives two records of adults, but they have probably not been well recorded. L4, ephyrae recorded but not identified. MarLIN notes it as an occasional oceanic visitor. Station E1 in mid-Channel, some juveniles sampled in January 2010. Western English Channel. West and north coasts of Scotland and Ireland, quite common. Irish Sea. Northern North Sea. Southern North Sea, rare.

Genus *Chrysaora:*

Chrysaora hysoscella (Linnaeus, 1767)

Chrysaora develop up to 24 marginal tentacles in the adult, arranged in eight groups of three, alternating with the eight marginal sense organs.

The ephyrae are ~1.6-3.4 mm in diameter on liberation and their colour has been noted as pinkish, changing to a translucent white. Initially there are no marginal tentacles or tentacle bulbs. The marginal lappets may be more elongated and rounded than illustrated below (Straehler-Pohl & Jarms, 2010), becoming broader with development, but shape is variable. The ends of the rhopalial canals are quite sharply forked distally, intermediate in shape between those of *Aurelia* and *Cyanea* (Figs. 3; 5A, B), the ends of the forks extending level with the rhopalia. The adradial canals are much longer than in *Aurelia* and the distal forks more conspicuous. The gastric filaments (zero to four) are either not developed, or much shorter, and the rhopalium much narrower. There are characteristic pairs of nematocyst clusters on the exumbrella, at the base of the marginal lobes and scattered single clusters nearer the centre of the disc (Fig. 5A), but not as prominent as the raised warts on *Pelagia*. At around 6 mm the first four marginal tentacles develop simultaneously (Fig. 5C) and the ephyrae in general appearance resemble *Pelagia* of the same size. By around 12 mm there can be four or even eight marginal tentacles and the mouth has four oral arms. The adradial canals in *Pelagia* remain simple and only eight marginal tentacles develop, but in *Chrysaora* protrusions develop from the corners of each of the adradial canals forming an additional gastric pouch each side (Fig. 5E), from which further marginal tentacles will arise to form eight groups of three tentacles in the adult (Fig. 5F).

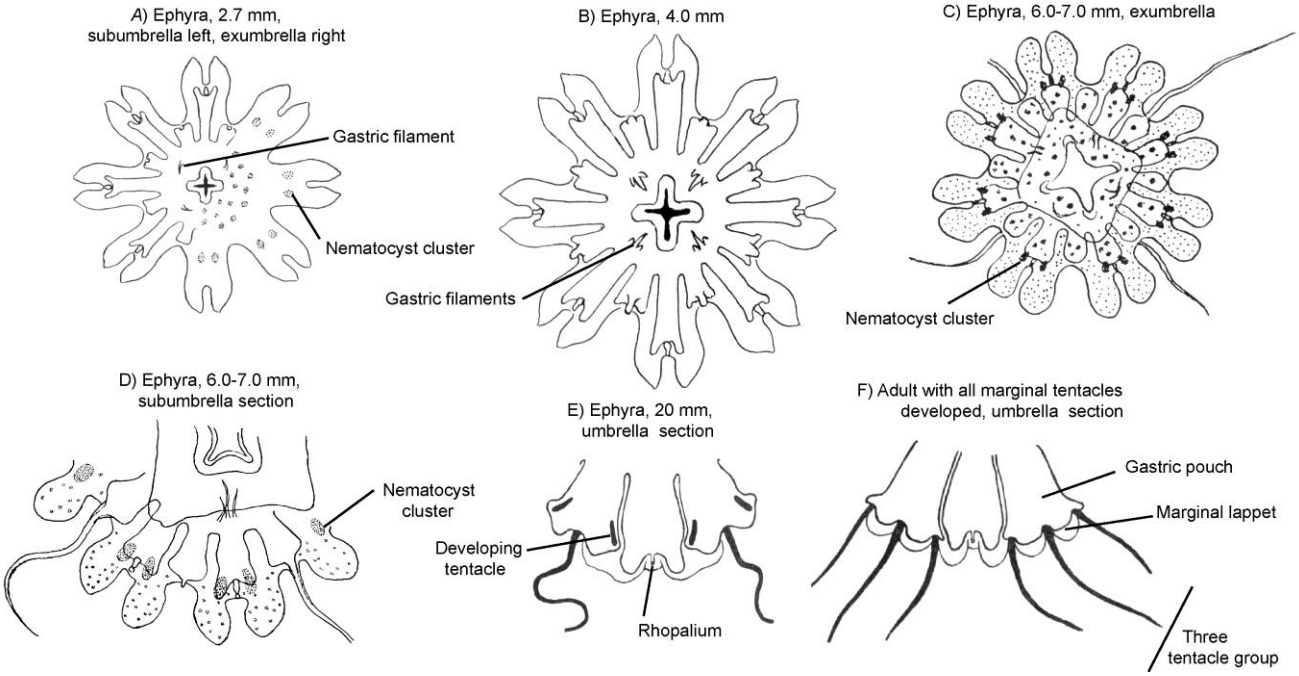


Fig. 5. *Chrysaora hysoscella* ephyrae and adult (from Russell, 1970).

Recorded: PMF, adults regularly recorded. L4, ephyrae recorded but not identified. All around Britain and Ireland. North Sea. Quite common.

PHYLUM CNIDARIA: Class Scyphozoa: Order Semaeostomeae:

Family Cyaneidae:

Genus *Cyanea*:

Cyanea capillata (Linnaeus, 1758)

Adults are brownish in colour and have eight adradial groups of marginal tentacles, situated well in from the umbrella margin, and eight marginal sense organs.

Ephyrae are noted as being reddish brown to yellow ochre. On liberation they are around 1.5-9.5 mm in diameter, depending on temperature, with the tips of the marginal lappets quite slender and pointed. They are immediately distinguishable as *Cyanea* by the very long pointed forks at the ends of all the rhopalial canals (Fig. 6A-C). They have a long manubrium and zero to one gastric filaments in each quadrant, approximately eight in specimens 5-9 mm. Soon after liberation, a marginal tentacle bud appears at the base of the cleft between two marginal lobes (Fig. 6A), then another in the opposite position, these gradually extending into tentacles. Other opposing tentacle buds and tentacles similarly develop (Fig. 6B). Other tentacle buds and shorter tentacles develop beside the initial tentacles to form groups (Fig. 6C). The timing of tentacle development appears to be quite variable in relation to size, but individuals of 4.0 mm can have two tentacles in a group. These marginal tentacles are located further back from the umbrella margin than in the other genera. There are no prominent exumbrellar nematocyst warts as found in *Pelagia*.

They are very similar to *C. lamarckii* in appearance and development, and are probably indistinguishable with any certainty until from ~30 mm in diameter, when small pit-like intrusions develop in the radial folds of the circular muscles (Fig. 6D), not found in *C. lamarckii*.

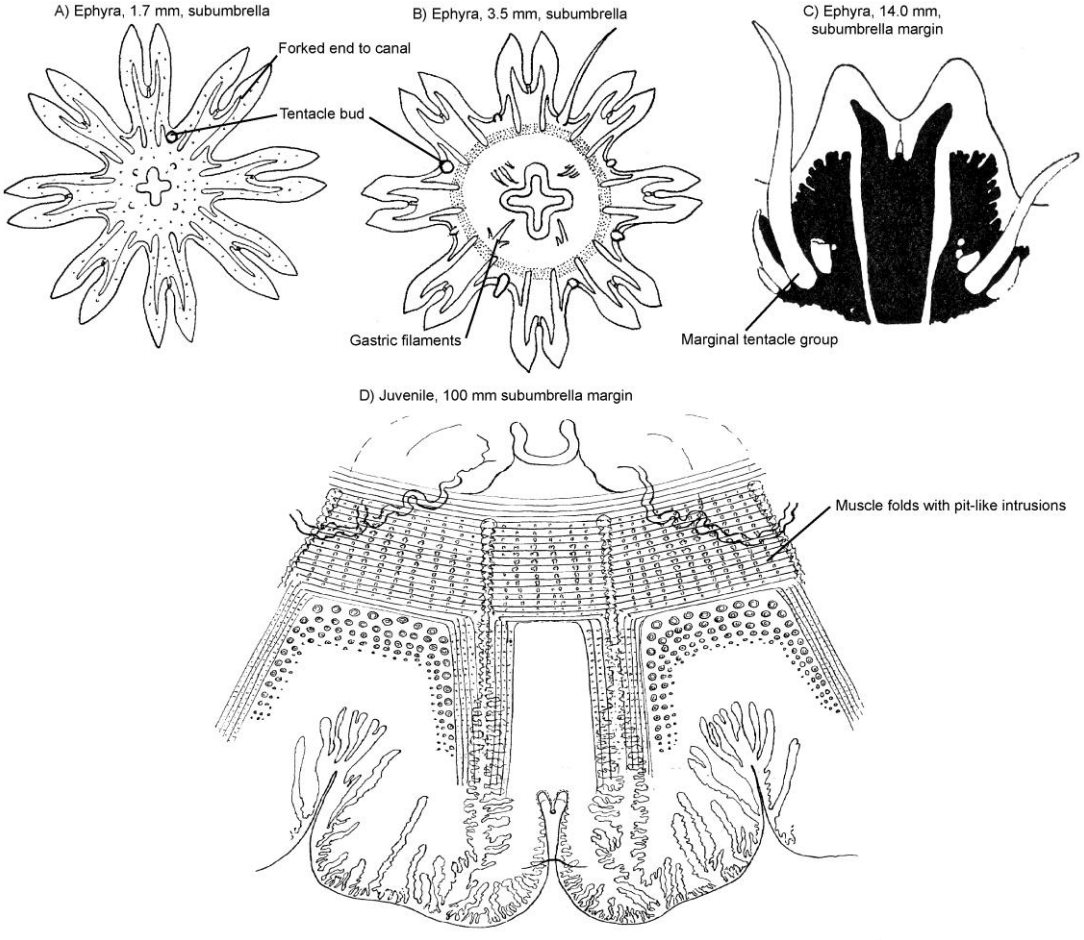


Fig. 6. *Cyanea capillata* ephyrae and juvenile (A-B, D from Russell, 1970; C from Kramp, 1937).

Recorded: PMF, not recorded. L4, ephyrae recorded but not identified. Russell (1970) noted this species as northern boreal, with no records from the western or central English Channel, but there are recent records from the Plymouth area (MarLIN). Irish Sea. North Sea. Common species.

Cyanea lamarckii Péron & Lesueur, 1810
Adult morphology is similar to *C. capillata*, but they are smaller and coloured pale yellow to deep blue.
On liberation the ephyrae are ~2.1-4.0 mm in diameter. Colouration has been noted as white or blue-grey. The ends of all the rhopalial canals have the distinctive forked *Cyanea* shape (Figs. 3, 7A). The rhopalial lappets are shaped like a sword tip. As in *C. capillata*, in early ephyrae there are zero to one gastric filaments in each quadrant. Initially, no marginal tentacles or bulbs are present. One marginal tentacle develops first, in the cleft at the base of a marginal lobe (Fig. 7A), then another in the opposite position. The two tentacles in the remaining similar positions develop next, then finally the four other tentacles. Similar to *C. capillata* the size at which tentacles are developed is variable, but a specimen of 20 mm had all eight tentacles completely developed as well as extended oral lips. At 30 mm the same medusa had additional tentacles of varying lengths beside the original tentacle, forming eight groups. Marginal tentacles are grouped further back from the umbrella margin than in the other genera. There are no prominent exumbrellar nematocyst warts as found in *Pelagia*.
The ephyrae are probably difficult to separate from those of *C. capillata* until around a size of 30 mm when small pit-like intrusions develop in the radial folds of the circular muscles in *C. capillata* (Fig. 6C), not found in *C. lamarckii* (Fig. 7B)

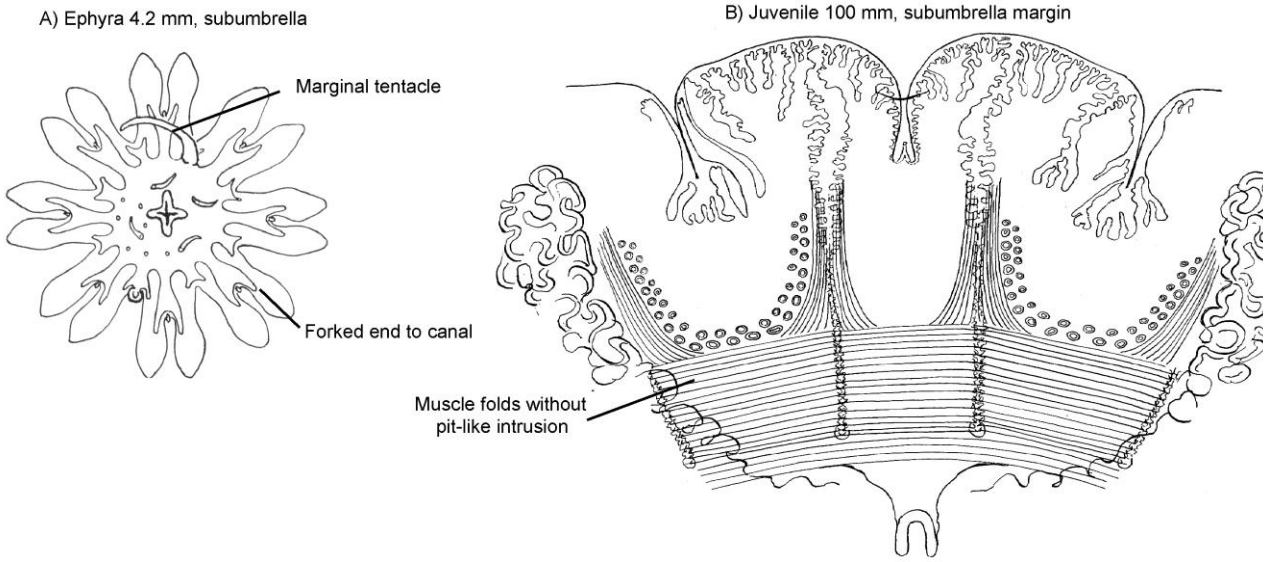


Fig. 7. *Cyanea lamarckii* ephyra and juvenile (from Russell, 1970).

Recorded: PMF (as *Cyanea capillata* var. *Lamarckii*). L4, ephyrae recorded but not identified. All around Britain and Ireland. North Sea. Common species.

PHYLUM CNIDARIA: Class Scyphozoa: Order Semaeostomeae:

Family Ulmaridae:

Genus *Aurelia*:

Aurelia aurita (Linnaeus, 1758)

The adult has eight simple marginal lobes, eight sense organs and long oral arms.

Ephyrae are liberated at ~1.5-4.5 mm in diameter. The tips of the marginal lappets are quite slender and pointed, but this is variable, and there are from zero to two gastric filaments in each interradius. Initially, the perradial and interradial rhopalial canals have squared ends (Figs. 3, 8A-E), sometimes slightly lobed, and the adradial canals are just short bulges with square ends. Coronal and radial muscles are already visible (not drawn). There are no marginal tentacles or tentacle buds. In a specimen of 2.0-2.5 mm there were three gastric filaments in each quadrant and the rudiments of the marginal lappet-like structures were appearing. When the ephyra is ~4.0 mm, outgrowths of the perradial and interradial canals develop at their bases and on the sides of the adradial canals (Fig. 8B, D). At this stage there are around six to eight gastric filaments in each group and the first rudiments of the eight adradial marginal tentacles develop more or less simultaneously. At a diameter of ~5-6 mm, canals develop laterally from each side of an adradial canal and join the straight rhopalial canals (Fig. 8E-F) to form the primary ring canal. *Pelagia*, *Chrysaora* and *Cyanea* do not develop these peripheral connecting canals. This is the first appearance of the quite complex branching gastrovascular system found in adult *Aurelia*. Small tentacles appear on the margins of the oral lips, but the lips do not divide as in *Rhizostoma*. Number of marginal tentacles between each lobe increases and by ~8 mm there are five to six tentacles each side of a primary marginal tentacle (Fig. 8G, H), making 10-12 in a group. With increase in size the canal system becomes increasingly complex (Fig. 8I, J).

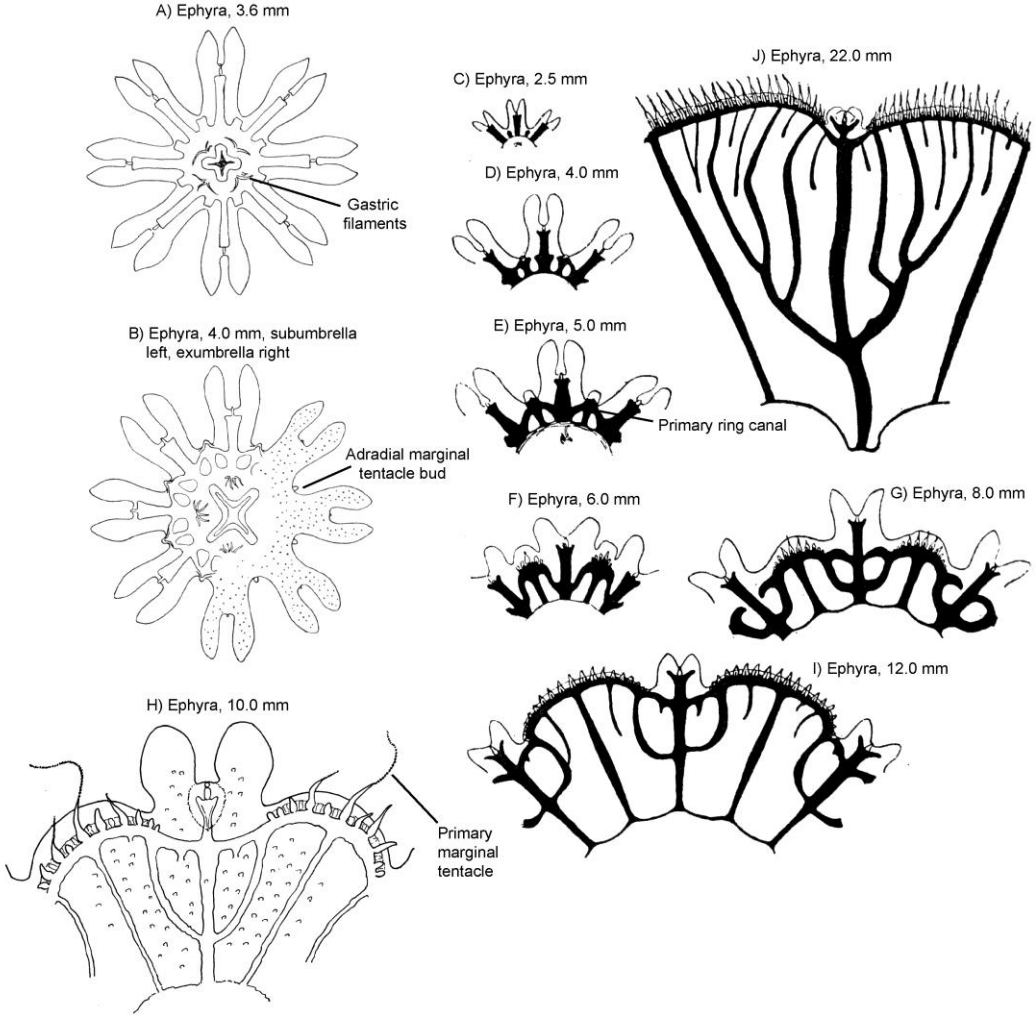


Fig. 8. *Aurelia aurita* ephyrae (A, B, H from Russell, 1970; C-G, I, J from Kramp, 1937).

Recorded: PMF. L4, ephyrae recorded but not identified. All around Europe. Extremely common.

PHYLUM CNIDARIA: Class Scyphozoa:

Order Rhizostomeae:
Family Rhizostomatidae:

Genus *Rhizostoma*:

Rhizostoma pulmo (Macri, 1778)

Until recently called *R. octopus*. Adults lack marginal tentacles and have a manubrium that branches distally to form eight characteristically shaped oral arms. There are ten marginal lappets, called velar lappets, in each octant, the octants separated by pairs of rhopalial lappets

The newly liberated ephyrae are ~2.7-6.0 mm in diameter. In a specimen of 2.7 mm, small tentacles were starting to appear on the margins of the oral lips (Fig. 9C). The paired marginal lappets are more rounded externally than internally (Fig. 9A, B), but shape is variable. There are two to three gastric filaments in each quadrant and quite a long manubrium (Fig. 9G). The rhopalial canals are slightly forked with rounded ends, intermediate between those of *Aurelia* and *Cyanea* (Fig. 3). The adradial canals are short with blunt pointed ends, reminiscent of *Aurelia*. The primary ring canal can form from ~3 mm (Fig. 9F), from outgrowth of the adradial canals joining up with the rhopalial canals (*Pelagia*, *Chrysaora* and *Cyanea* do not develop these peripheral connecting canals). However, in one specimen of 3.5 mm the primary ring canal had still not formed, there were around five gastric filaments in each quadrant and prominent exumbrellar nematocysts warts were present. However, these warts were not in a regular pattern as found in *Pelagia*. At around 4.5 mm the oral lips start to divide to form the eight oral arms (Fig. 9E). In a specimen of 5 mm the primary ring-canal was fully formed, the manubrium was quite long and divided and 11-12 gastric filaments were present in each quadrant (Fig. 9B). The first pair of velar lappets had already formed on the umbrella margin in the cleft between the rhopalial lobes and the exumbrella was covered in nematocyst warts. Marginal tentacles never develop. In a specimen of 7 mm (Fig. 9I) the marginal velar lappets were clearly separated and the first marginal ring of canals had already developed. In a specimen of 18 mm (Fig. 9H) there were four rounded velar lappets in each quadrant and the network of canals was quite complex.

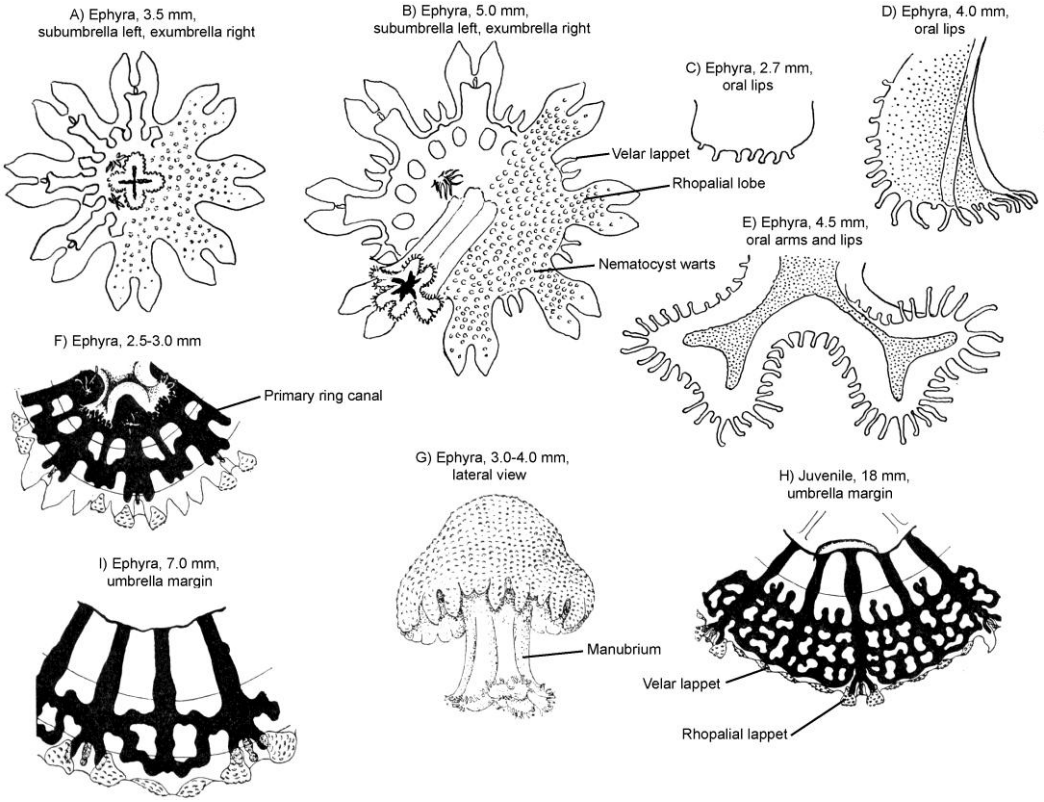


Fig. 9. *Rhizostoma pulmo* ephyrae and juvenile (A, B from Russell, 1970; C-G, I from Stiasny, 1928; H from Stiasny, 1927. All as *R. octopus*).

Recorded: PMF, a fewl adults recorded each year (as *R. octopus*). L4, ephyrae recorded but not identified. MarLIN, regular records (as *R. octopus*). Southern warmer water species. Mainly southern Britain and Ireland. Southern North Sea. Can be common.

PHYLUM CNIDARIA:

Class Hydrozoa:

The Hydrozoa (excluding Order Siphonophorae) are extensively described by Bouillon (1999) and specifically for the Britis Isles, in a monograph by Russell (1953), the latter available for free download from the “Full text books” section on the National Marine Biological Library (NMBL) website (see bibliography). The following section is largely an updated condensation with additions, of Russell’s monograph, specifically for southern British species. The many illustrations from Russell (1953) included here are reproduced by permission of the Cambridge University Press.

There are over 100 species of Hydrozoa with planktonic stages recorded in British waters, many of which are oceanic, deep-sea species, unlikely to be sampled in inshore waters. Almost all the Hydrozoa described here, some 66 species (including Siphonophorae), were recorded from the Plymouth area (Marine Biological Association, 1957), but actually represent the majority of European, neritic species.

As noted by Bouillon & Boero (2000),”the systematics of the Hydrozoa is complicated and confused”, but is separated here into two subclasses, **Trachylinae** (orders Limnomedusae, Trachymedusae and Narcomedusae) and **Hydroidolina** (orders Anthothecata, Leptothecata and Siphonophorae). There is a further Order called Actinulida in Subclass Trachylinae, but these live in bottom sediments. The morphology of Order Siphonophorae is rather distinctive, so the Hydrozoa section has been arranged so that they come last and their features are described separately.

Development and morphology (excluding Siphonophorae)

Hydrozoa are either single (solitary), or form colonies and may have a life cycle that is exclusively polypoid, exclusively medusoid, or with both phases. Typically, medusae are budded off asexually from polyps (Fig.10) that are found attached to rocks, shells, seaweed etc. The free-swimming medusoid stages (Fig. 11A) generally have separate sexes and release gametes into the sea when mature. A free swimming planula larva (Fig. 1) develops from the fertilised egg, which settles and grows into a new polyp. However, some members do not have a sessile bottom living stage, but a completely planktonic life cycle, while others lack a medusoid stage. Only the medusoid stage will normally be collected in plankton samples, but polyps that have been detached by turbulence etc. are frequently taken.

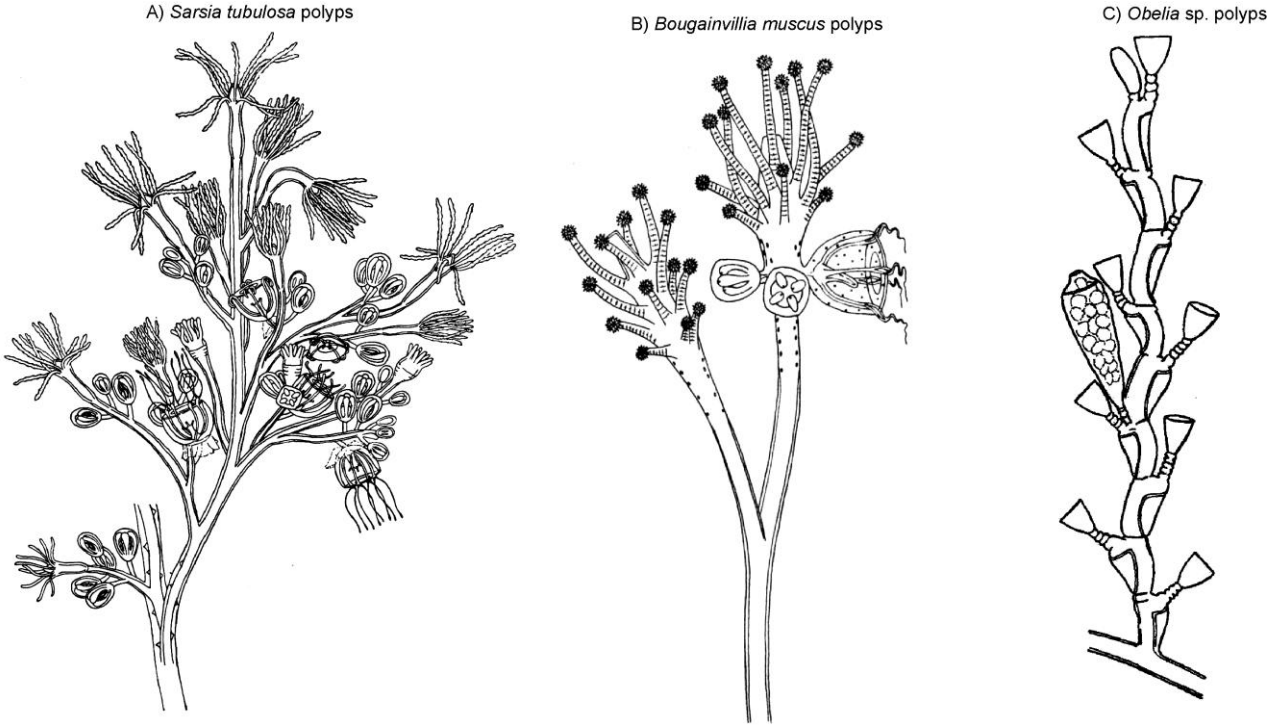


Fig. 10. Examples of polyps (A, B after Allman, 1871; C after Hincks, 1868).

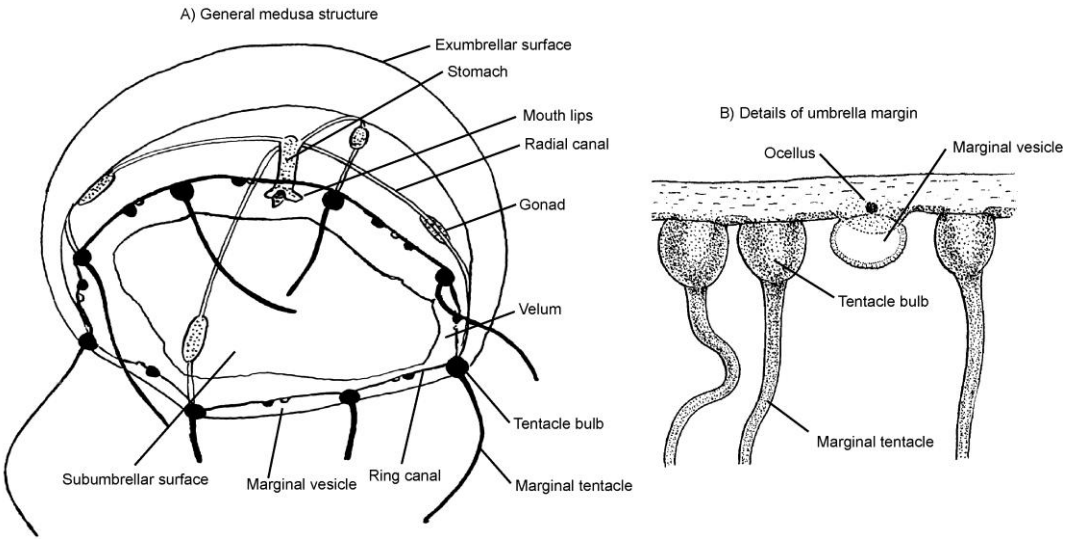


Fig. 11. General structure of a medusa (from Russell, 1953).

General structure of a medusa is given in Fig. 11. The stomach and gonads are located on the subumbrellar (lower internal) surface. Radial canals radiate out from the stomach and join a ring canal that runs around the umbrella margin. Also on the umbrella margin are varying numbers of marginal tentacles, number and type depending on species. Sense organs may also be present. Around the aperture of the subumbrellar cavity is a shelf-like velum, varying in width with species, which partially closes the cavity, determining the type of swimming jet produced.
Medusae occur in a variety of different shapes of umbrella and thicknesses of jelly, from completely flat to bell-shaped, sometimes with apical projections (Fig. 12).

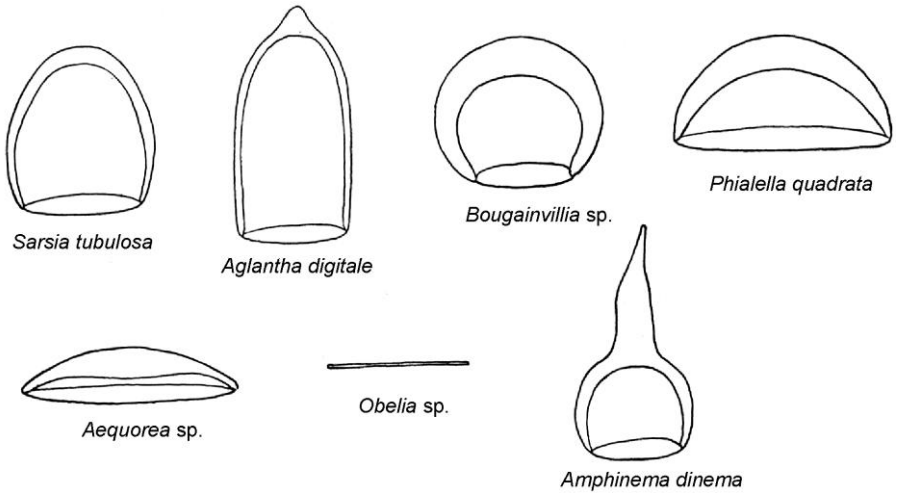


Fig. 12. Examples of hydrozoan umbrella shapes (from Russell, 1953).

Number of radial canals is usually four or eight, but *Aequorea* can have up to 100. The canals are named as in Fig. 13. The perradial canals are the four primary radial canals.

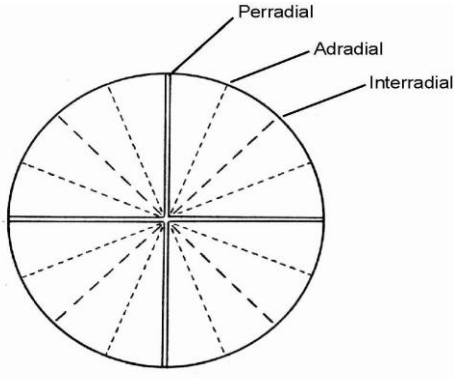


Fig. 13. Radial canal nomenclature (from Russell, 1953).

Medusoids have a central stomach that may be short, or on a peduncle (stalk) terminating in a mouth with lips of various types; simple, crenulated, stalked, branching, bearing nematocyst clusters etc. (Fig. 14)

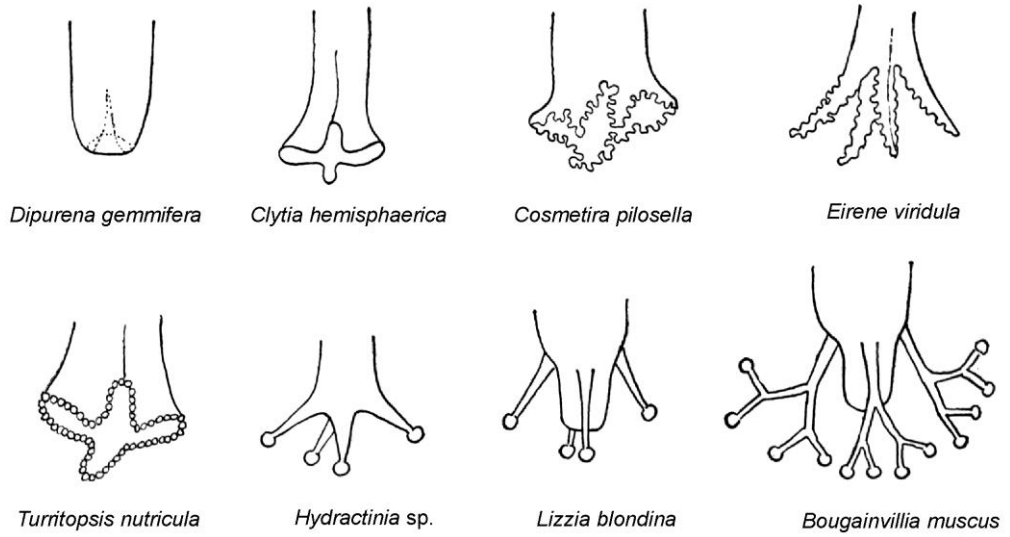


Fig 14. Examples of different types of medusoid mouths (from Russell, 1953).

The gonads are usually situated on the stomach, or on the radial canals that run between the stomach and circumference of the medusa (Fig. 15). They can surround the stomach or be arranged linearly along it. On the radial canals the gonads may be simple or folded, or may even hang into the subumbrellar cavity.

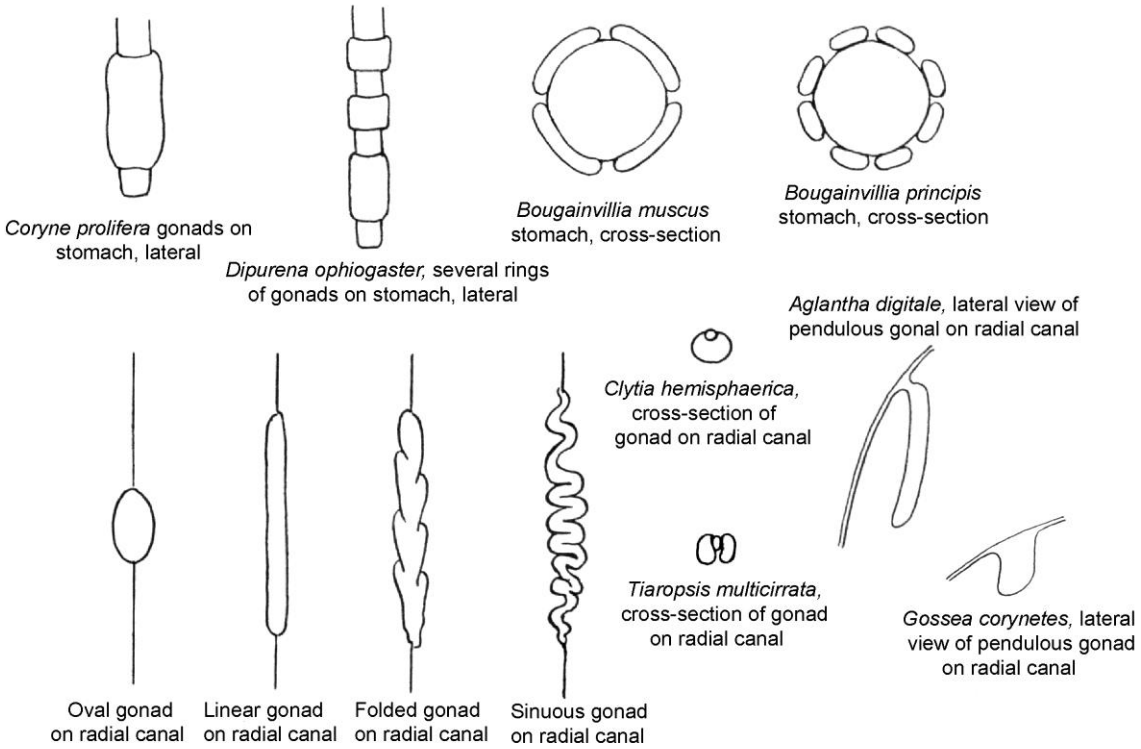


Fig. 15. Examples of different types of medusoid gonad types (from Russell, 1953).

Marginal tentacles are located around the umbrella margin, arranged singly or in groups, at or close to the umbrella margin in different combinations of numbers, sizes and shapes, depending on species (Fig. 16). Light sensitive ocelli are sometimes found on the base of the marginal tentacles. Genera such as *Lovenella* have additional small tentacles called marginal cirri (Fig. 61).

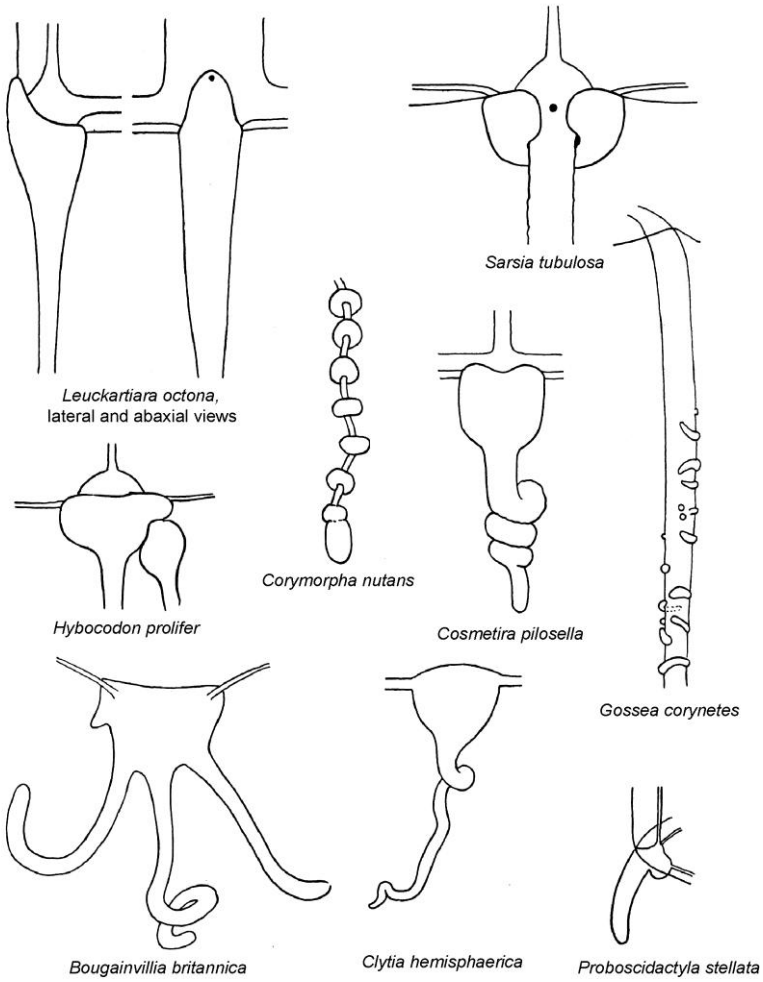


Fig. 16. Examples of different types of medusoid marginal tentacles (from Russell, 1953).

Sensory organs called statocysts, probably used in orientation, may be present around the umbrella margin. They are ectodermal in origin in the Leptothecata, endodermal in Limnomedusae, Trachymedusae and Narcomedusae, and completely missing in the Anthothecata.

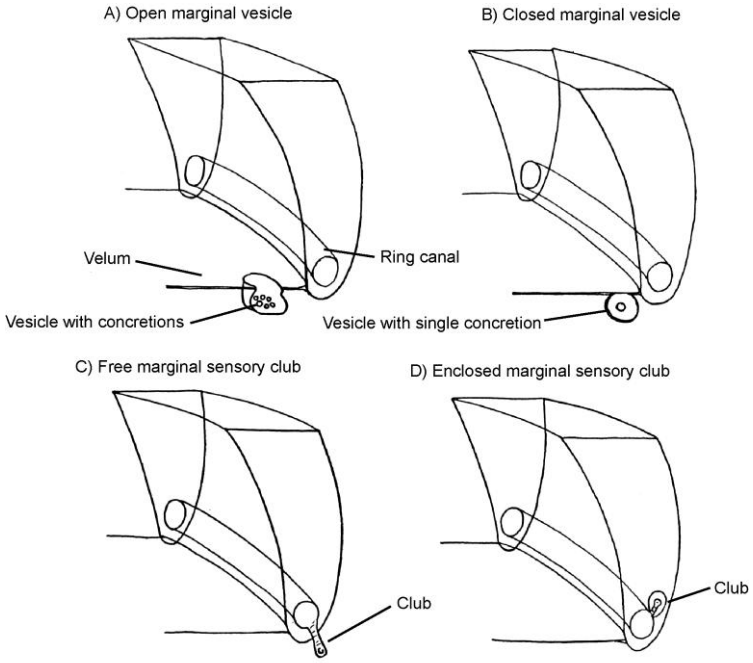


Fig. 17. Examples of different types of medusoid marginal sensory organs; upper ectodermal on velum, lower endodermal in umbrella margin (from Russell, 1953).

Ectodermal statocysts develop on the velum and are small hollows or pits that may remain open or be completely closed over, thus forming a cavity or vesicle and are known as marginal vesicles (Fig. 17). If they are open pits they are called open marginal vesicles. If the velar tissue seals off the upper cavity, so that complete spherical capsules are formed that hang on the underside of the velum, they are known as closed marginal vesicles. They contain from one to many small particles or concretions. Vesicles are easiest seen in unpreserved specimens.
Endodermal statocyst structure is different (Fig. 17). These are sensory clubs, small tentacle-like structures that grow out from inside the umbrella margin. Some have in their distal portion one or more large endoderm cells, each containing a solid concretion and are known as free marginal sensory clubs. In some medusae the endoderm surrounds the club, so that it is enclosed in a vesicle. This is called an enclosed marginal sensory club. Different marginal, club-like structures called cordyli, also thought to be sensory in function, are found in Family Laodiceidae (Fig. 56).

It is sometimes difficult to identify medusae in their early stages, before adult characteristics develop, as development is progressive. Additionally, size on liberation is very variable and will depend on temperature and nutrition, so appearance at a particular size is not entirely predictable. Some of the most useful publications on Hydrozoa (apart from siphonophores) are by Mayer (1910a, b), Kramp (1959, 1961), Pagès *et al.* (1992), Russell (1953), Cornelius (1995), Bouillon & Boero (2000); for siphonophores, Totton (1965), Kirkpatrick & Pugh (1984).
For initial rapid identification, a pictorial guide to all the hydrozoan species (excluding Siphonophorae) that have been recorded off south-west Britain is given below (Figs. 18, 19).

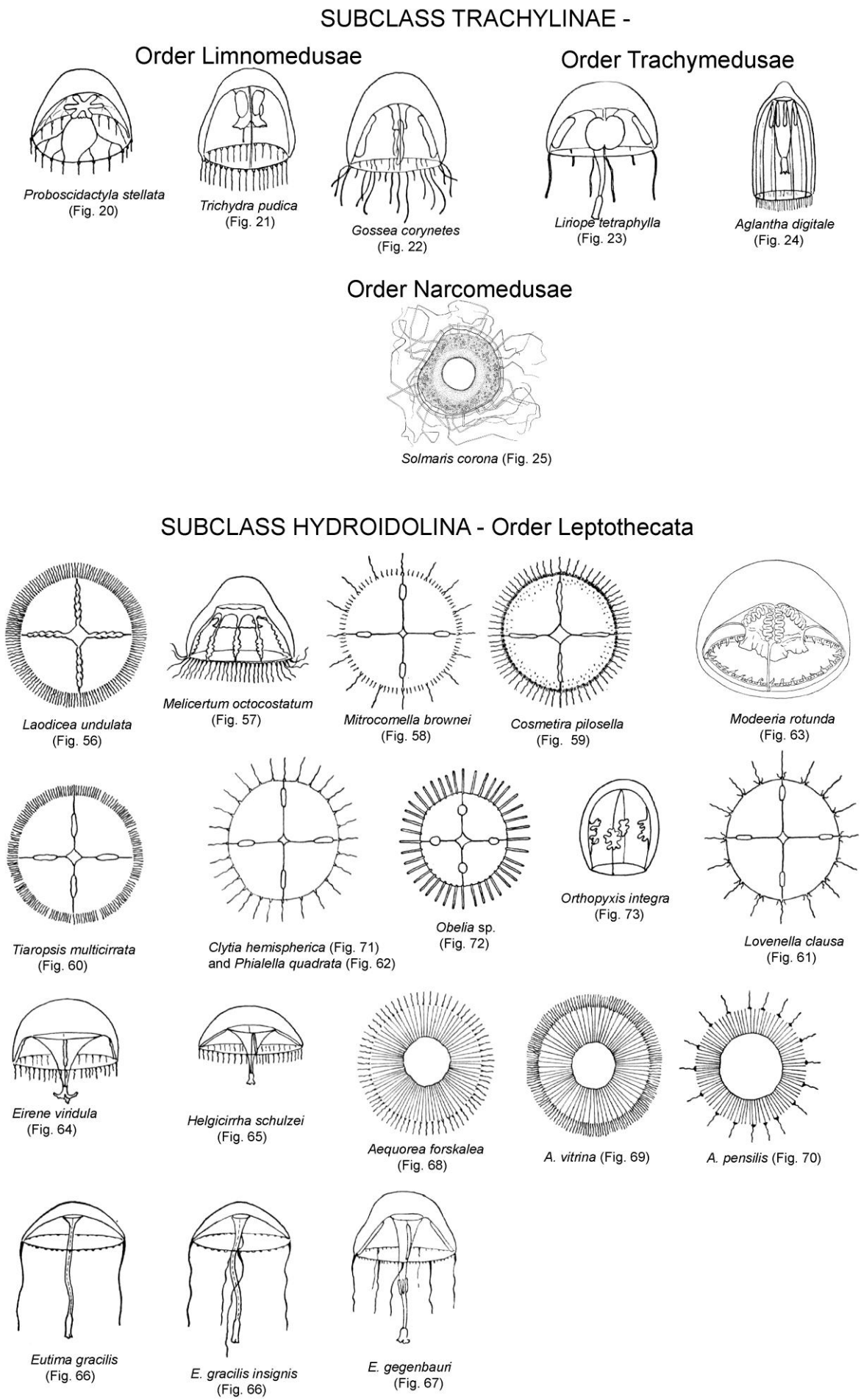
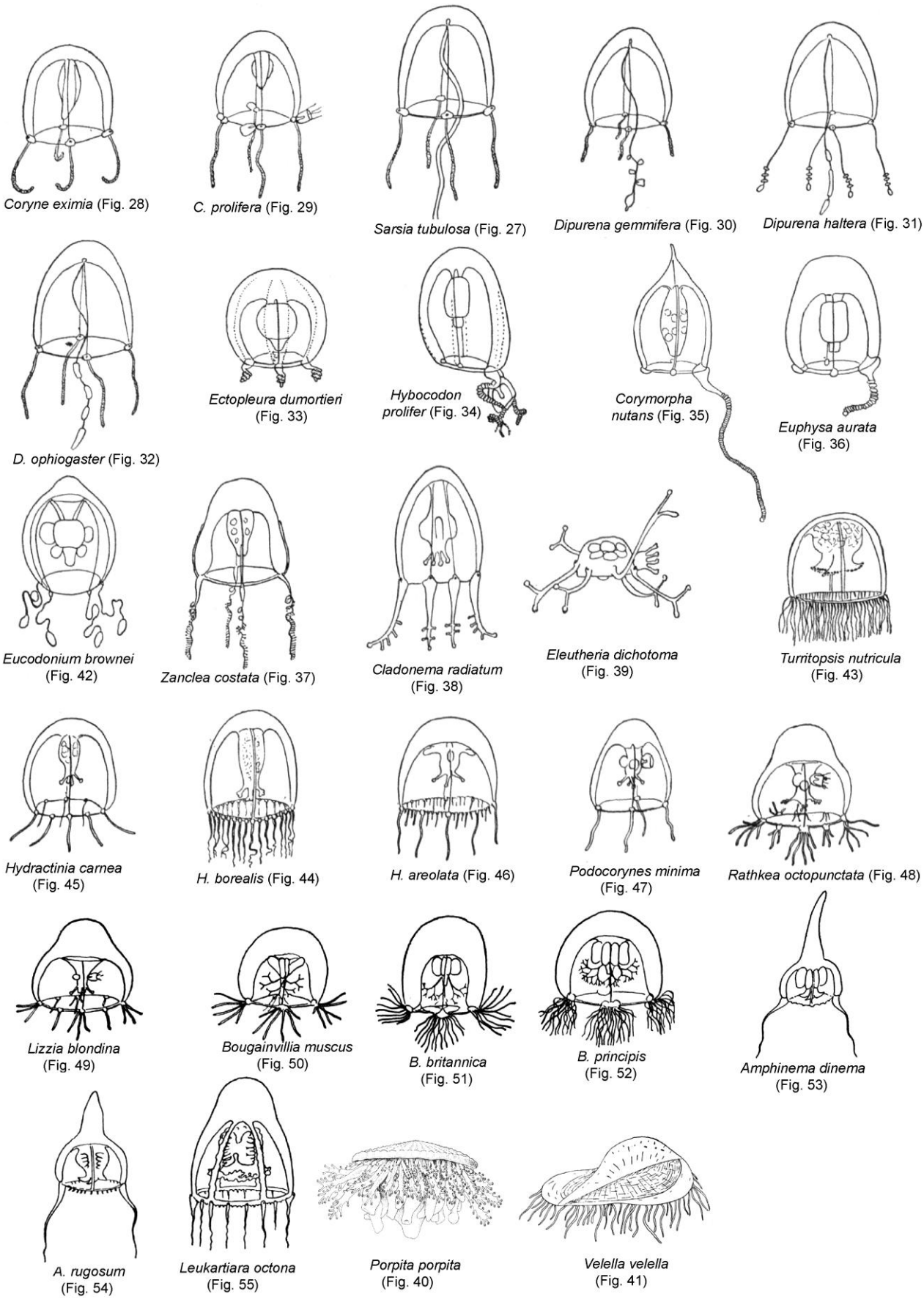


Fig. 18. Pictorial key and figure index to Limnomedusae, Trachymedusae, Narcomedusae and Leptothecata, recorded off south-west Britain (from Russell, 1953).



Fig, 19. Pictorial key and figure index to Anthothecata recorded off south-west Britain (from Russell, 1953; *Porpita* from Pagès *et al*., 1992; *Velella* from Hyman, 1940).

Subclass Trachylinae

The polypoid stage is reduced or absent; development is usually directly from planula to adult. There are three orders, **Limnomedusae**, **Trachymedusae** and **Narcomedusae**.

Order Limnomedusae:

In Limnomedusae with a polyp stage, the polyp is tiny and simple. Most of the medusae have thick bell-shaped umbrellas with thin sides; with gonads either only on stomach, on stomach extending for a short distance along the radial canals, or only on the radial canals. Marginal tentacles without a true basal bulb, usually with an endodermal core at the base, embedded in the umbrella near the ring canal, or in the velum. With or without enclosed marginal sense organs; without ocelli. Mainly open sea species.

Family Proboscidactylidae:

Genus *Proboscidactyla*:

Proboscidactyla stellata (Forbes, 1846)

Umbrella dome-shaped, thick at apex; six primary radial canals (Fig. 20A), unusual for a medusa, but canals often faint and very difficult to see. Initially six marginal tentacles, but as additional ones appear the radial canals branch and a branch goes to each tentacle bulb; 24 tentacles develop, so each canal divides twice until ~24 canals reach the umbrella margin (but branching is variable and irregular). A cushion of nematocysts on inner side of each tentacle (Fig. 20F); stomach short with hexagonal base and six lobes that extend a short distance along radial canals. Mouth with six folded lips (Fig. 20D, E); short peduncle; gonads located at base of stomach wall and extend over the six stomach lobes (Fig. 20B, C). Nematocyst clusters around umbrella margin, connected to margin by narrow canals (Fig. 20G). These faint clusters, often difficult to see, are produced at the umbrella margin at different stages of development, so end up at varying distances from margin.

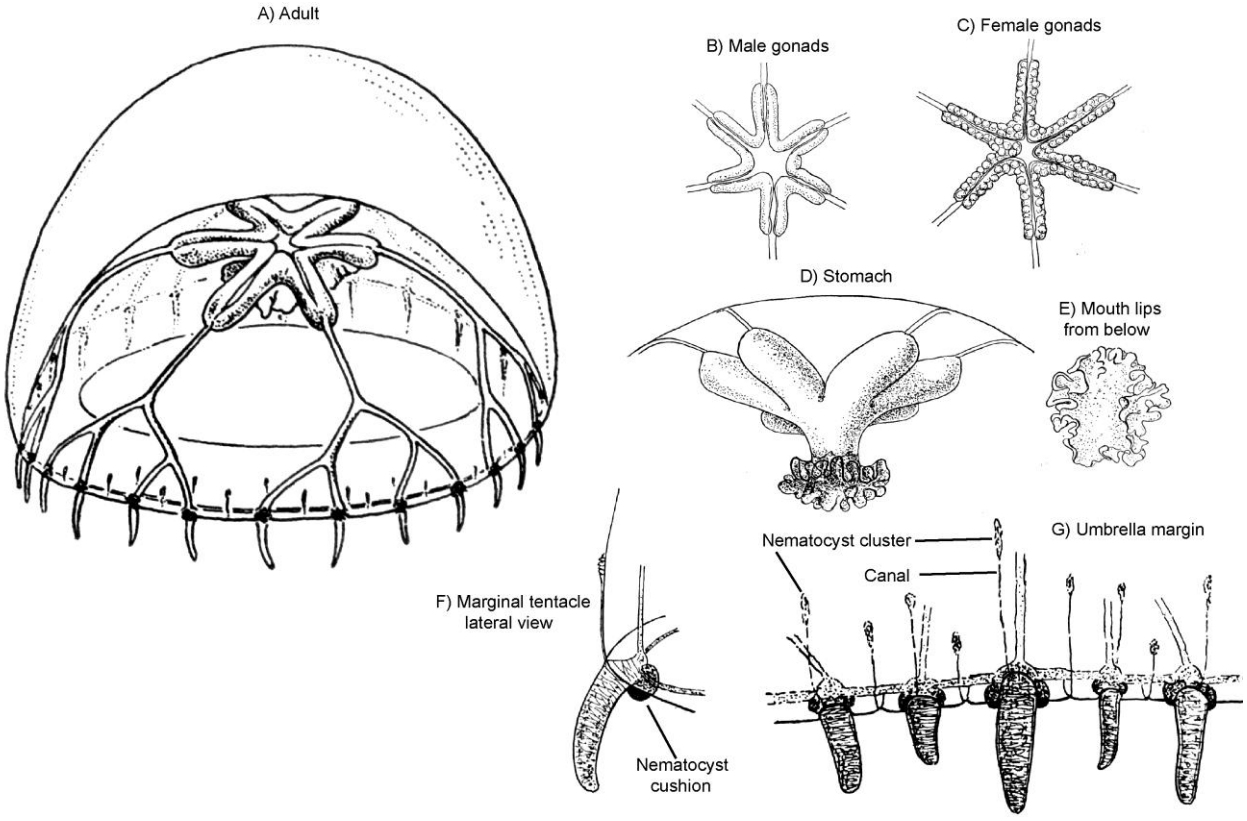


Fig. 20. *Proboscidactyla stellata* (A from Kramp, 1959; B-G from Russell, 1953).

Recorded: PMF. L4, rare. Around Britain and Ireland. North Sea. French coast.
Size: Umbrella height ~8 mm and diameter ~9 mm when fully grown.
Further information: Russell, 1953; Kramp, 1959, 1961; Pagès *et al*., 1992; Bouillon & Boero, 2000.

Family Trichydridae:

Genus *Trichydra*:

Trichydra pudica Wright, 1858

Umbrella bell-shaped, jelly thick, velum broad (Fig. 21A-C); stomach large, four-sided, around two-thirds height of sub-umbrellar cavity; mouth with four slightly folded lips; four straight, quite broad radial canals, often with very fine lateral branches (Fig. 21F); four interradial gonads on stomach wall, each covering most of the interradial wall (Fig. 21D); 30-40 or more marginal tentacles with large round bases (Fig. 21E); no ocelli.

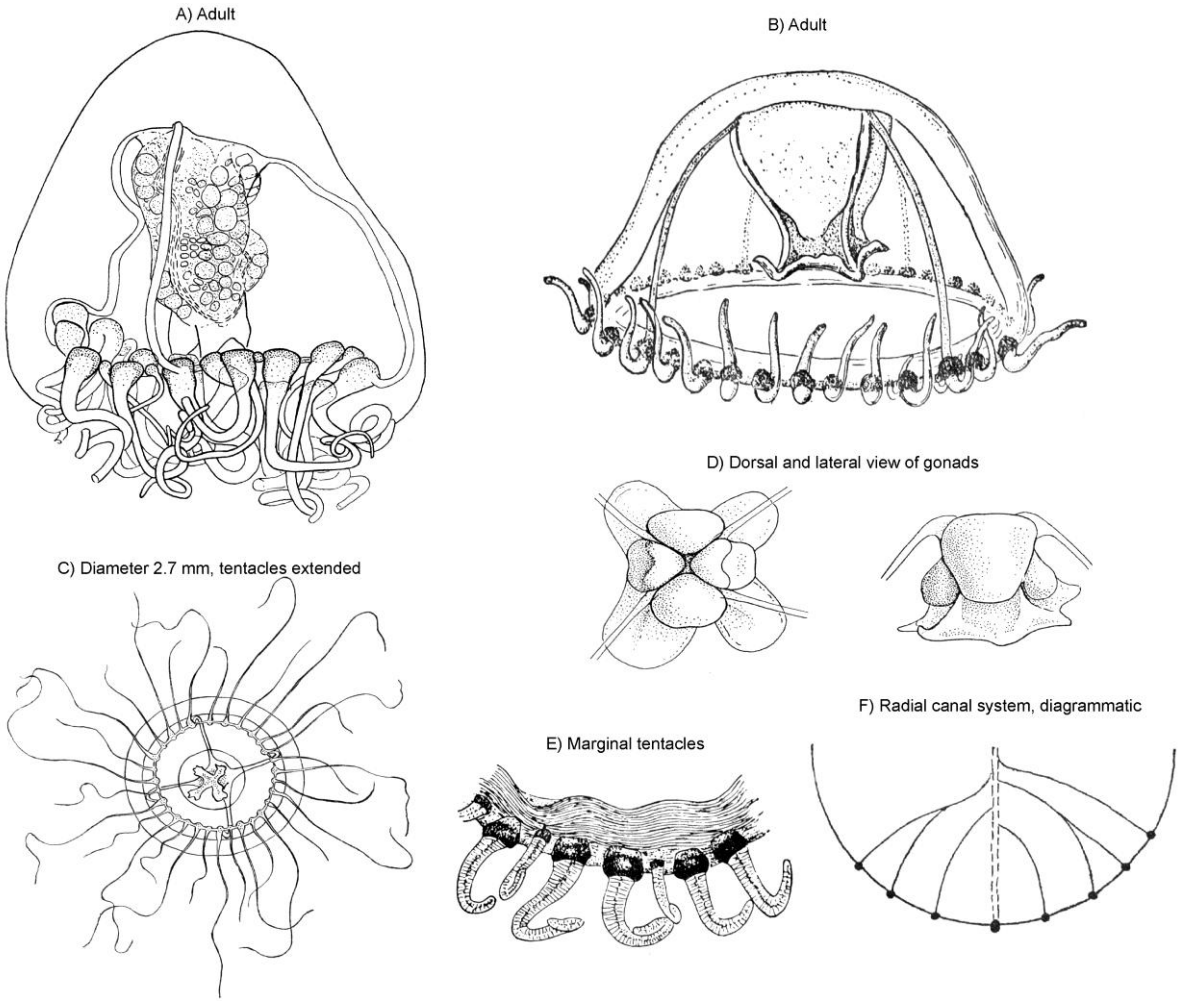


Fig. 21. *Trichydra pudica* (from Russell, 1953).

Recorded: PMF (as *Pochella polynema*). L4, not recorded. Northern North Sea. West Scotland. Rare species.

Size: Umbrella diameter 2-3 mm.

Further information: Russell, 1953; Kramp, 1961; (both as *P. polynema*); Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Trachylinae: Order Limnomedusae:

Family Oliniidae:

Genus *Gossea:*

Gossea corynetes (Gosse, 1853)

Umbrella bell-shaped or hemispherical, generally wider than high (Fig. 22A, C); jelly thick, especially in apical region; velum broad. Stomach small, quadratic, one-third to one-half height of subumbrellar cavity, square base, no peduncle. Mouth with four simple or slightly folded lips; four straight radial canals; four gonads, initially small hanging pouches (Fig. 22A), later forming deep linear hanging pouches along two-thirds of each radial canal (Fig. 22C), not attached at the ends, leaving distal ends of canals free. Eight groups of three large marginal tentacles, four perradial and four interradial; 8-16 small or rudimentary marginal tentacles, situated singly, one or two between adjacent large tentacle groups, typically pointing inwards (Fig. 22B); all marginal tentacles with nematocyst rings (Fig. 22D); usually 24 or more closed marginal vesicles, three between adjacent triple groups of marginal tentacles (Fig. 22C).

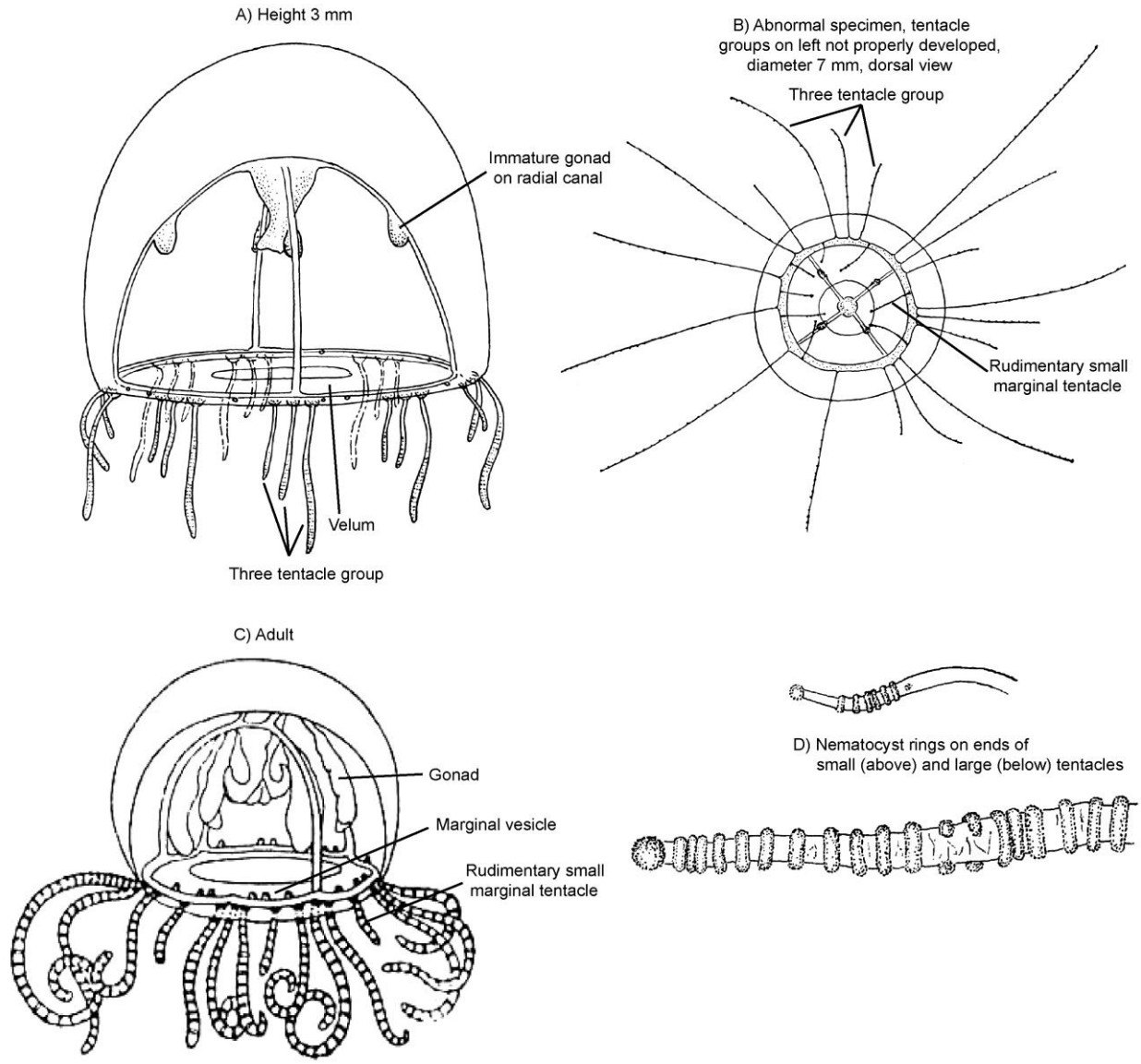


Fig. 22. *Gossea corynetes* (from Russell, 1953).

Recorded: PMF. L4, not recorded. Southern North Sea. English Channel. Bristol Channel. Southern Ireland.

Size: Umbrella height 8-10 mm and diameter 12-16 mm when fully grown.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Order Trachymedusae:

Without a polypoid stage. Hemispherical or bell-shaped umbrella; usually with eight radial canals; gonads only on radial canals, or at junction of radial canals and manubrium; numerous solid marginal tentacles without bulbs, evenly distributed around umbrella margin or arranged in groups; free, rarely enclosed, marginal sensory clubs, usually growing out of umbrella margin; without ocelli. A characteristic feature of most Trachymedusae is the conspicuous musculature of the subumbrella and the wide velum. Predominantly open sea group.

Family Geryonidae:

Genus *Liriope*:

Liriope tetraphylla (Chamisso & Eysenhardt, 1821)

Umbrella hemispherical, jelly thick, especially at apex; velum well developed. Small stomach on elongated peduncle (Fig. 23C, D), variable in length, from one to three times umbrella height; mouth with four simple or slightly folded lips, with nematocyst clusters on margin (Fig. 23E). Four straight radial canals; in each quadrant, one to three or more short, faint blind canals directed inwards, termed centripetal canals (Fig. 23F). Large flattened, broad gonads of varying shape, on subumbrella portion of radial canals (Fig. 23C, D), sometimes almost covering whole under surface. Four hollow perradial marginal tentacles with nematocyst rings and four solid interradial marginal tentacles with nematocyst clusters (Fig. 23B, G). Eight closed marginal vesicles embedded in umbrella jelly, four interradial beside interradial marginal tentacles and four perradial beneath bases of perradial marginal tentacles (Fig. 23F, G).

In young medusae ~1.0-2.0 mm in diameter (Fig. 23A. B), umbrella nearly hemispherical, jelly thick; no peduncle, stomach short, mouth with four simple lips, stomach area often just a clear lens; radial canals broad, widest at distal ends; no gonads developed; four small perradial primary marginal tentacles on exumbrella, short distance above margin; four short interradial tentacles on umbrella margin with characteristic, obvious clusters of nematocysts on adaxial side (Fig. 23G). Peduncle does not develop until medusae are ~3 mm in diameter, when mouth still does not extend below umbrella margin. Gonads appear at diameter of ~4.0 mm.

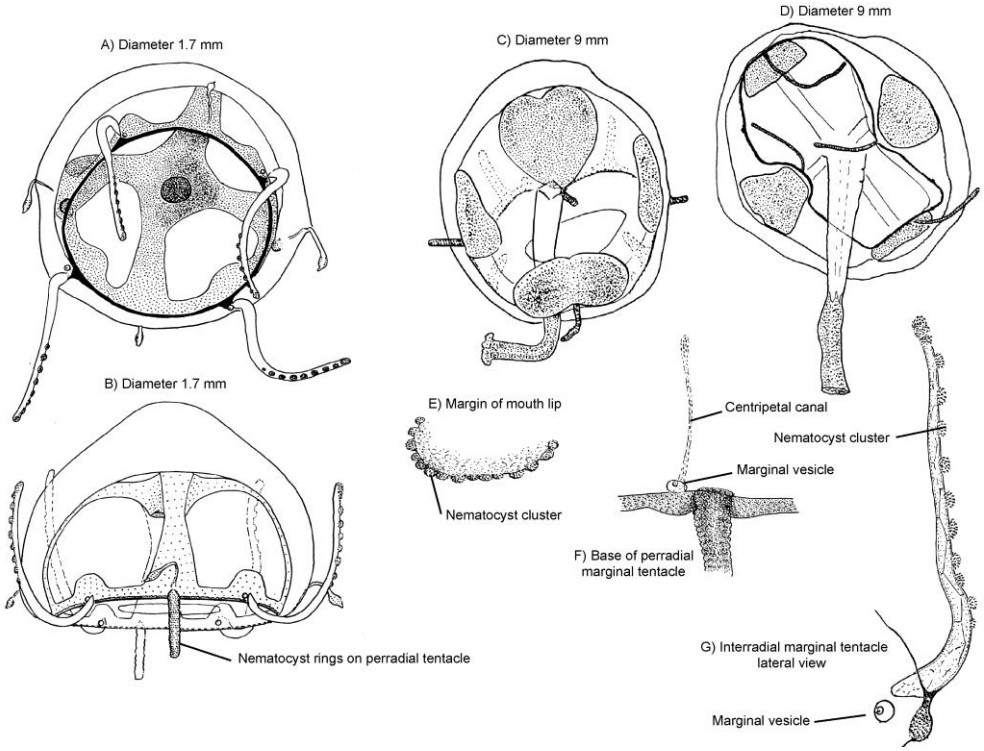


Fig. 23. *Liriope tetraphylla* (from Russell 1953).

Recorded: PMF. L4, seasonally very common. South-western coasts of Britain and Ireland.
Size: Umbrella diameter up to 30 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Pagès *et al*., 1992; Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Trachylinae: Order Trachymedusae:

Family Rhopalonematidae:

Genus *Aglantha*:

Aglantha digitale (O.F. Müller, 1766)

Umbrella deep, cylindrical bell-shaped (Fig. 24A), twice as long as wide, with small apical projection; jelly thin; very broad velum. Stomach small, situated on end of long peduncle that reaches nearly to umbrella margin; mouth with simple lips. Eight straight radial canals; eight sausage-shaped gonads hanging freely in subumbrellar cavity, situated close to base of peduncle. Eighty or more solid, smooth marginal tentacles that are usually destroyed during sampling and preservation (Fig. 24B). Eight sensory clubs situated singly between adjacent radial canals (Fig. 24C). Muscle bands in the umbrella are characteristically silvery with transverse striations.

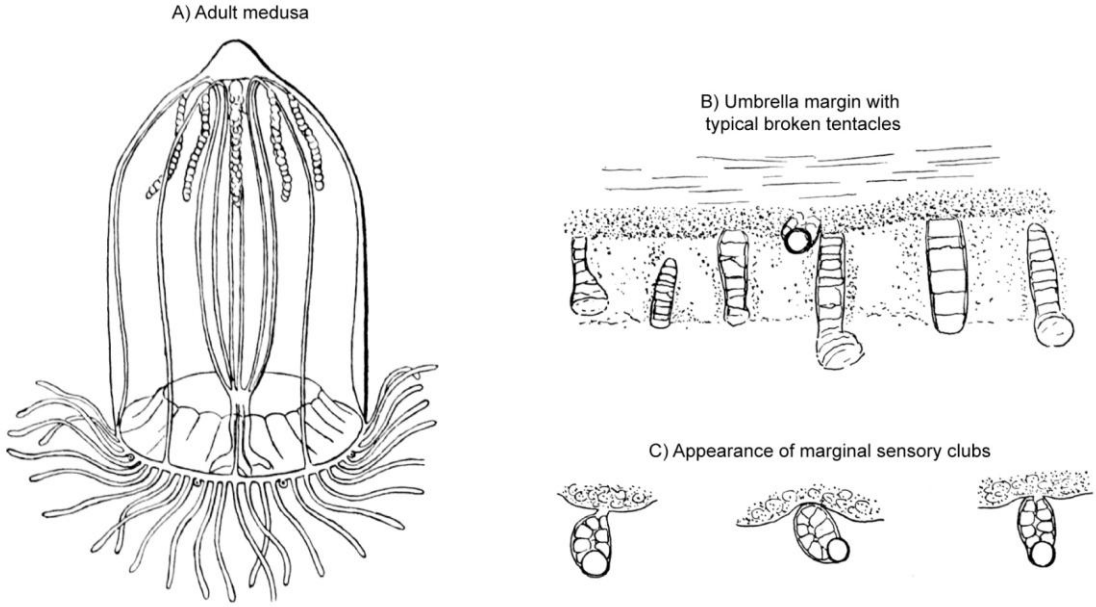


Fig. 24. *Aglantha digitale* (A from Kramp, 1959; B-C from Russell, 1953).

Recorded: PMF. L4, seasonally can be common. Western coasts of Britain and Ireland. Northern North Sea. Sometimes carried through English Channel into southern North Sea.
Size: Umbrella height 5-8 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Order Narcomedusae:

Without a polypoid stage, or an extremely reduced one. Flattened exumbrella divided by grooves, so that umbrella margin may be lobed; with broad stomach, with or without peripheral pouches; thick upper umbrella; no radial canals and with the gonads only on the stomach walls; with sense organs in form of free sensory clubs growing out of umbrella margin; without ocelli. The solid marginal tentacles lack bulbs and do not emerge on the edge of the umbrella, but some distance above. Predominantly open sea, oceanic species.

Family Solmarisidae:

Genus *Solmaris*:

Solmaris corona (Keferstein & Ehlers, 1861)

Upper portion of umbrella with thick, flat, lens-shaped jelly (Fig. 25A, B); marginal portion of umbrella thin, with up to 35 or more rectangular marginal lappets. Stomach circular, covering large area of umbrella; simple circular mouth aperture; gonads forming broad ring on upper part of subumbrellar stomach wall; up to 35 or more long stiff marginal tentacles (Fig. 25C) embedded in exumbrella between the marginal lappets; tentacles with transverse divisions; one to three rarely four marginal sensory clubs on each marginal lappet, each club on a swollen cushion surrounded by long bristles (Fig. 25D).

These medusae are quite delicate and easily damaged; often found as small, flattened transparent discs with just a few intact tentacles that on cursory examination could be confused with *Obelia* sp. (Fig. 72).

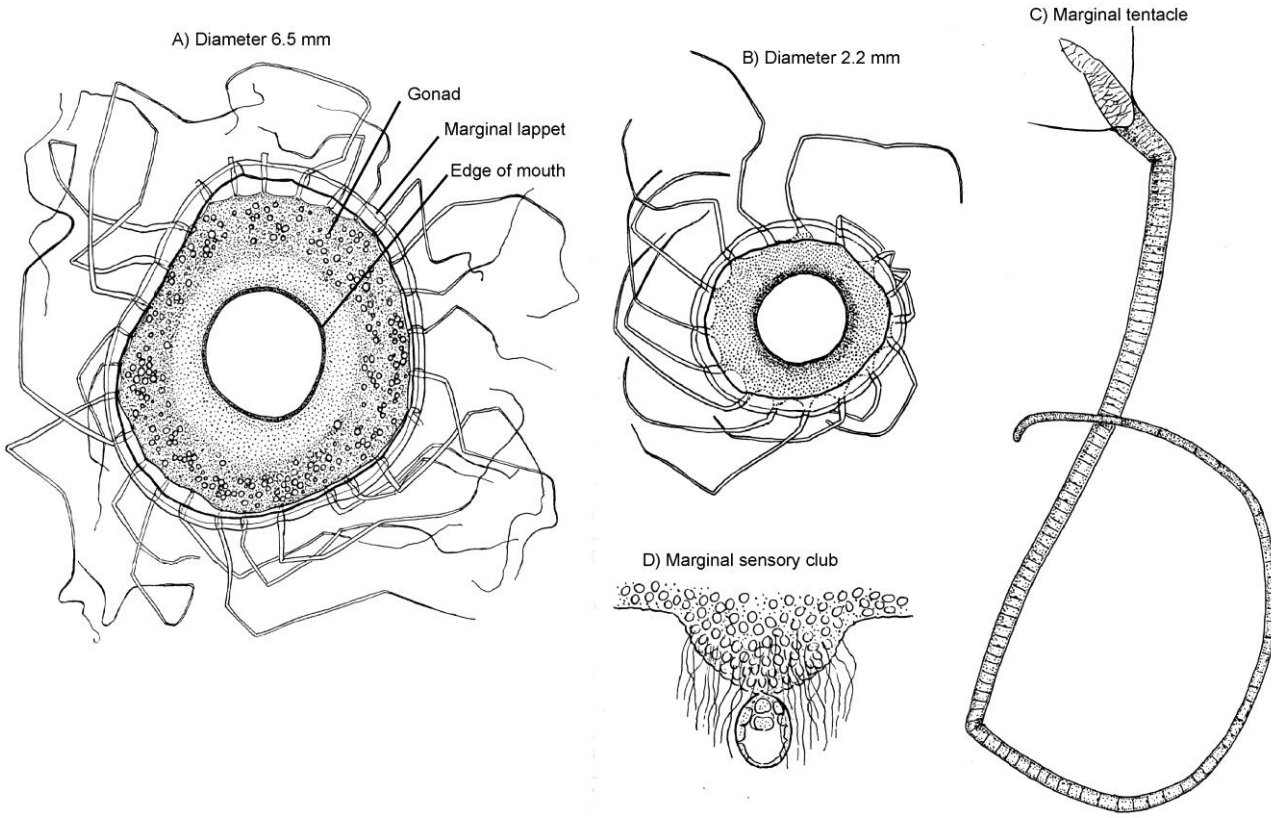


Fig. 25. *Solmaris corona* (from Russell, 1953).

Recorded: PMF. L4, occasionally common. Western coasts of Britain and Ireland. Northern North Sea.

Size: Umbrella diameter up to 15 mm when fully grown

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Subclass Hydroidolina

Subclass Hydroidolina typically have both a polypoid and medusoid stage during their life-cycle. There are three orders - **Anthothecata**, **Leptothecata** and **Siphonophorae**. The Anthothecata and Leptothecata are separated based on the structure of the benthic polyp. The polyp in Leptothecata is always colonial, while in Anthothecata it is sometimes solitary. Additionally Anthothecata medusae lack statocysts. Siphonophorae do not have an alternation of generation between an attached, asexual polyp stage and a free-swimming sexual medusa, but modifications of both stages are found, attached to the free-swimming colonial organism.

Order Anthothecata:

There are many species in this order. The medusae usually have a deep, bell-shaped umbrella, but are variable in shape. The gonads are usually situated on the stomach or occasionally both on the stomach and extending a short distance along the radial canals. Tentacles of most species have bulbs. They have no statocysts, the only marginal sense organs, if present, are ocelli. Some Leptothecata liberate bell-shaped medusae that appear like Anthothecata, e.g. *Clytia* (Fig. 71A), but can be identified as Leptothecata by the presence of statocysts.

Some Tubulariidae Anthothecata have no medusoid phase, the polyps releasing an actinula larva (Fig. 26) that are occasionally taken in plankton samples. The actinula resembles a short, stalk-less polyp and has two whorls of tentacles, one mid-way down the body. It creeps along the substrate, attaches and develops directly into a polyp.

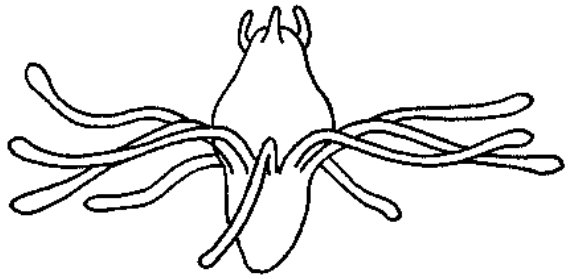


Fig. 26. Actinula larvae (from Wickstead, 1965).

Recorded: PMF. L4, occasional. All European regions.
Size: Height ~4 mm.
Further information: Wickstead, 1965; Larink & Westheide, 2006.

Suborder Capitata: Family Corynidae:

The three genera of Family Corynidae sampled off Plymouth, *Sarsia, Coryne* and *Dipurena* are superficially similar and difficult to separate when immature.

Genus *Sarsia*:

Sarsia tubulosa (M. Sars, 1835)

Umbrella higher than wide (Fig. 27A-C); jelly moderately thick; velum broad; stomach cylindrical, length when contracted around half the height of umbrella, when extended reaching far beyond umbrella margin. An apical knob or chamber usually present in the exumbrella above the stomach; mouth simple; gonads forming a continuous cylinder around stomach, leaving a short proximal region and mouth free. Four simple radial canals join four marginal tentacles that bear many clusters of nematocysts; large tentacle bulbs with large circular dark ocellus (Fig. 27D); can be bleached out by preservative). Appearance of stomach very variable, related to preservation. From liberation has an interradial furrow or crease running down the exumbrella between each radial canal (difficult to see), lacking in the closely related *Coryne eximia*. There is no asexual budding from the base of the tentacles as in *Coryne prolifera*, or from the stomach as can occur in *Dipurena gemmifera.* Both of these latter species are smaller than *S. tubulosa* and *C. eximia* when mature. In early stages stomach cylindrical, short, extending to only half the height of the subumbrellar cavity. As the medusa grows there is little change in appearance, except the lengthening of the stomach.

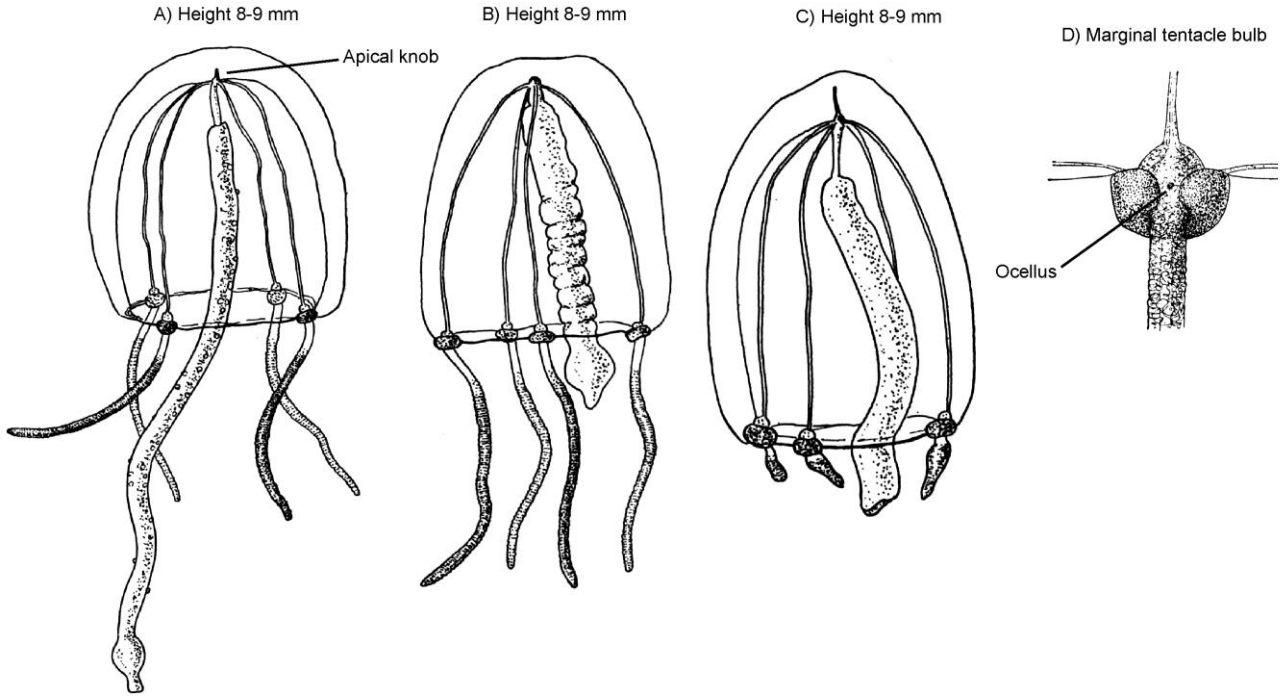


Fig. 27. *Sarsia tubulosa* (from Russell, 1953).

Recorded: PMF. L4, occasional. All around Britain and Ireland. North Sea.
Size: Umbrella height ~1.3 mm on liberation; ~10 mm when fully grown in British waters, reaching up to 18 mm in northern waters.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

Genus *Coryne*:

Coryne eximia Allman, 1859

Umbrella bell-shaped (Fig. 28), slightly higher than wide; jelly moderately thick; velum broad; stomach cylindrical, in full extension about as long as subumbrellar cavity, but not extending beyond margin. Mouth simple; gonads surround stomach, extending from its base nearly to mouth; females with few and large eggs. Four perradial marginal tentacles with many clusters of nematocysts and usually a large terminal cluster. Marginal tentacle bulbs large and oval, each with large ocellus.

When newly liberated there are no interradial furrows on the umbrella as found in newly liberated *S. tubulosa*. There is little change in appearance during development and the stomach only lengthens slightly.

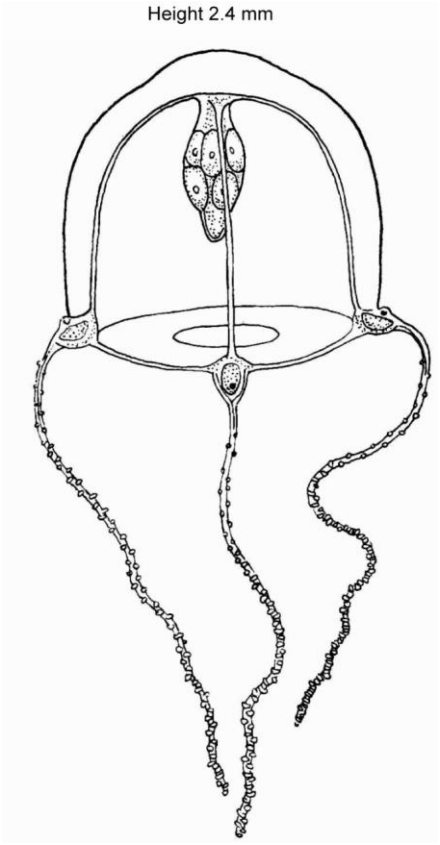


Fig. 28. *Coryne eximia* female (from Russell, 1953).

Recorded: PMF (as *Sarsia eximia*). L4, not recorded. All around Britain and Ireland. North Sea. Rare.

Size: Umbrella height on liberation ~1.3 mm; 3-4 mm when fully grown.

Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000 (all as *S. eximia*).

Coryne prolifera (Forbes, 1848)
Bell-shaped umbrella (Fig. 29), higher than wide, jelly moderately thick. Stomach small, cylindrical, around one- to two-thirds the subumbrellar cavity height, does not extend beyond umbrella margin; apical knob may be present; gonads surround stomach leaving proximal and distal ends free. Mouth simple, tube-like; four radial canals and four extensile marginal tentacles with irregularly scattered clusters of nematocysts; tentacle bulbs large and tapering, each with an ocellus.
From liberation the first signs of asexual budding from the marginal tentacle bulbs are already apparent, with as many as three buds on each bulb. Medusae do not change much in appearance during development.

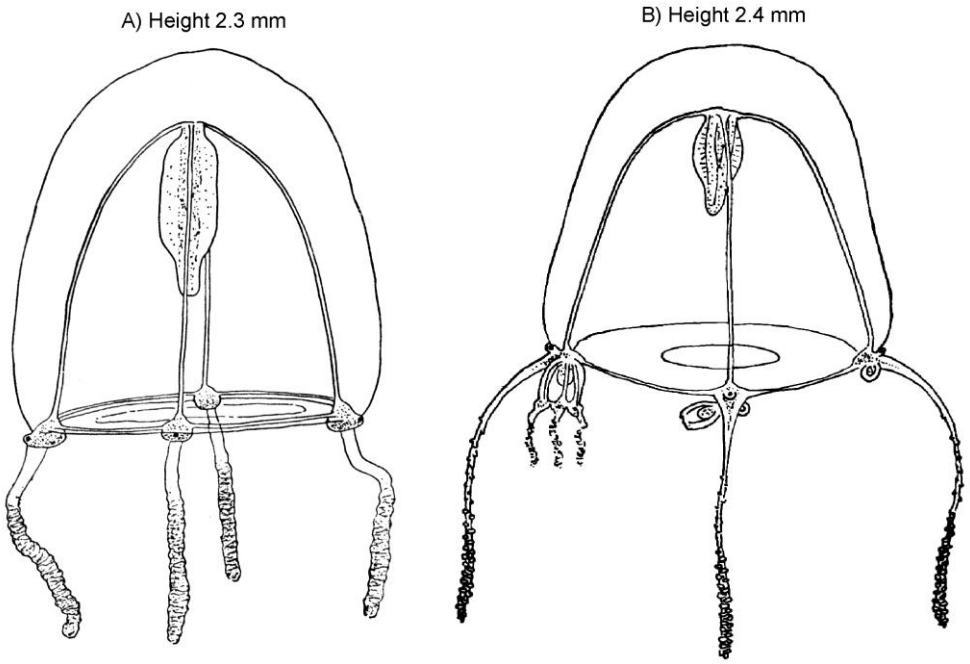


Fig. 29. *Coryne prolifera* (A from Russell, 1953; B from Kramp, 1959).

Recorded: PMF (as *Sarsia prolifera*). L4, occasional. All around Britain. Southern Ireland. France.
Size: Umbrella height on liberation ~1 mm; usually less than 2 mm when full grown, but can be up to 3 mm.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000 (all as *S. prolifera*).

Genus *Dipurena:*

Dipurena gemmifera (Forbes, 1848*)*

Umbrella bell-shaped (Fig. 30), higher than wide, jelly moderately thick, velum narrow; radial canals extremely narrow; apical knob always present; sometimes a short umbilical canal extending upwards above the stomach (Fig. 30B); stomach characteristically widens at oral end, gonad completely surrounding widened portion. Stomach when fully extended reaches far beyond umbrella margin. Four short marginal tentacles, each with moderate sized bulb and ocellus, with irregularly scattered clusters of nematocysts and large terminal knob of nematocysts. Widening of stomach and short marginal tentacles readily distinguishes it from *S. tubulosa*. There can be asexual reproduction by budding from the stomach region (Fig. 30B) from a height of 1.0 mm. The medusa does not change much in appearance during development.

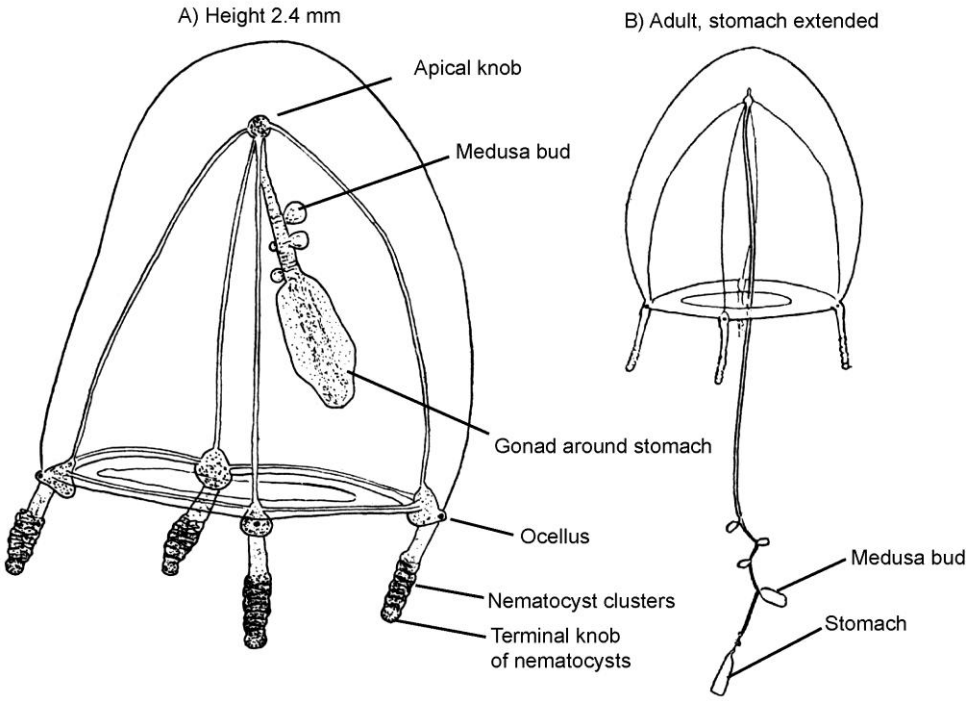


Fig. 30. *Dipurena gemmifera* (A from Russell, 1953; B from Kramp, 1959).

Recorded: PMF (as *Sarsia gemmifera*). L4, not recorded. All around Britain. Southern North Sea. Rare.

Size: Umbrella height 2-3 mm when fully grown, sometimes up to 5 mm.

Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000 (all as *S. gemmifera*).

Dipurena haltera (Forbes, 1846)
Umbrella bell-shaped, higher than wide (Fig. 31), jelly thick; velum quite broad. Stomach cylindrical, swollen at oral end, two to three times the length of umbrella when fully extended; apical knob present (Fig. 31B). Similar to *Sarsia* sp., but gonads surround the stomach in two or more separate rings, leaving upper half free (Fig. 31B, C); four narrow radial canals, often with linear swellings; four marginal tentacles, each with large terminal knob of nematocysts, with three to six nematocyst rings immediately above. Marginal tentacle bulbs quite large, each with a large ocellus.
Newly liberated medusae bell-shaped (Fig. 31A) with thin jelly and broad velum; stomach cylindrical, in length around two-thirds the height of the umbrella; slight apical knob, but no linear swellings on the radial canals, which do not develop until the umbrella height is around 2.8 mm.

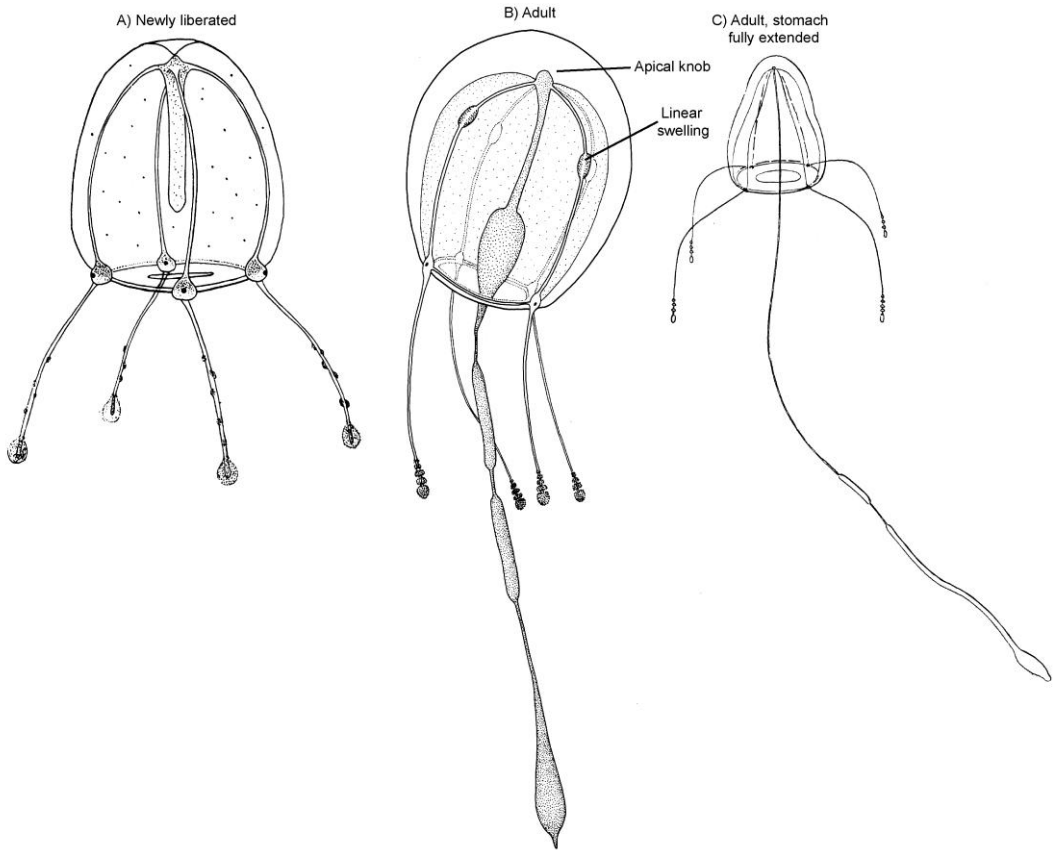


Fig. 31. *Dipurena haltera* (A, C from Russell 1953; B from Pagès et al, 1992, drawing by J. Corbera).

Recorded: PMF. L4, not recorded. English Channel. Southern Ireland. Irish Sea. Western Scotland. Eastern England. Rare.
Size: Umbrella height ~1.5 mm on liberation; ~8 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Pagès et al, 1992; Bouillon & Boero, 2000.

Dipurena ophiogaster (Haeckel, 1877)
Umbrella bell-shaped, higher than wide (Fig. 32), velum moderately broad. Similar in appearance to *Sarsia* spp., but gonads surround stomach in three to six rings with upper part free (Fig. 32C, D). Stomach cylindrical, enlarging into bulbous mass at oral end, in full extension reaching up to several times the length of umbrella; apical knob present; four marginal tentacles with irregularly distributed nematocyst clusters and no distinct rings, unlike *D. haltera*
At umbrella height of ~1.0 mm (Fig. 32A) the stomach is half the length of subumbrellar cavity, but increases in length rapidly; small apical knob present. By ~2.2 mm the stomach extends beyond umbrella margin.

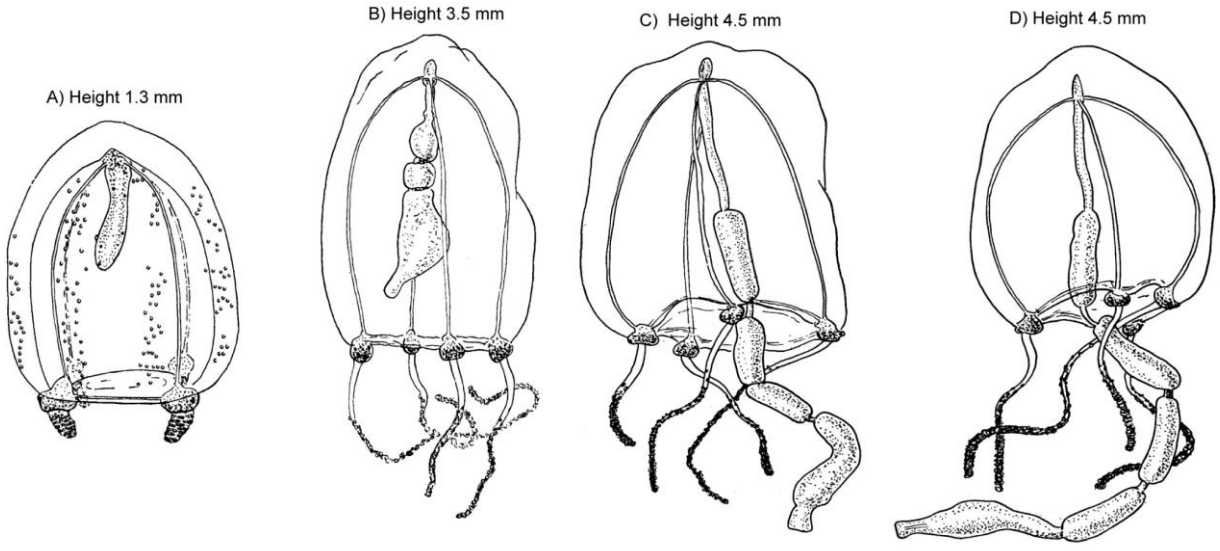


Fig. 32. *Dipurena ophiogaster* (from Russell, 1953).

Recorded: PMF. L4, not recorded. Southern Ireland. Rare.
Size: Umbrella height ~1.0 mm on liberation; up to 5.0 mm when fully grown.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

Family Tubulariidae:

Genus *Ectopleura*:

Ectopleura dumortieri (Van Beneden, 1844)

Umbrella almost spherical (Fig. 33); jelly thick, especially at apex; velum broad; four characteristic pairs of nematocyst tracts extend up umbrella (Fig. 33A). Stomach very large, spherical towards base, tapering towards mouth, extensile, reaching beyond umbrella margin in full extension; gonads surround stomach leaving mouth free; mouth simple tube, armed with nematocysts. Four narrow radial canals; four marginal tentacles with rounded nematocyst clusters on abaxial surface (Fig. 33C).

On liberation a fine umbilical canal is sometimes present, extending into the apex over the stomach; characteristic nematocyst tracts already on the exumbrella, arising either side of the tentacle bulbs, extending to top of the umbrella; stomach extends into the jelly of the umbrella as a dome-shaped structure, but in older specimens this appearance is reversed to give a slight peduncle. Appearance does not change much during development.

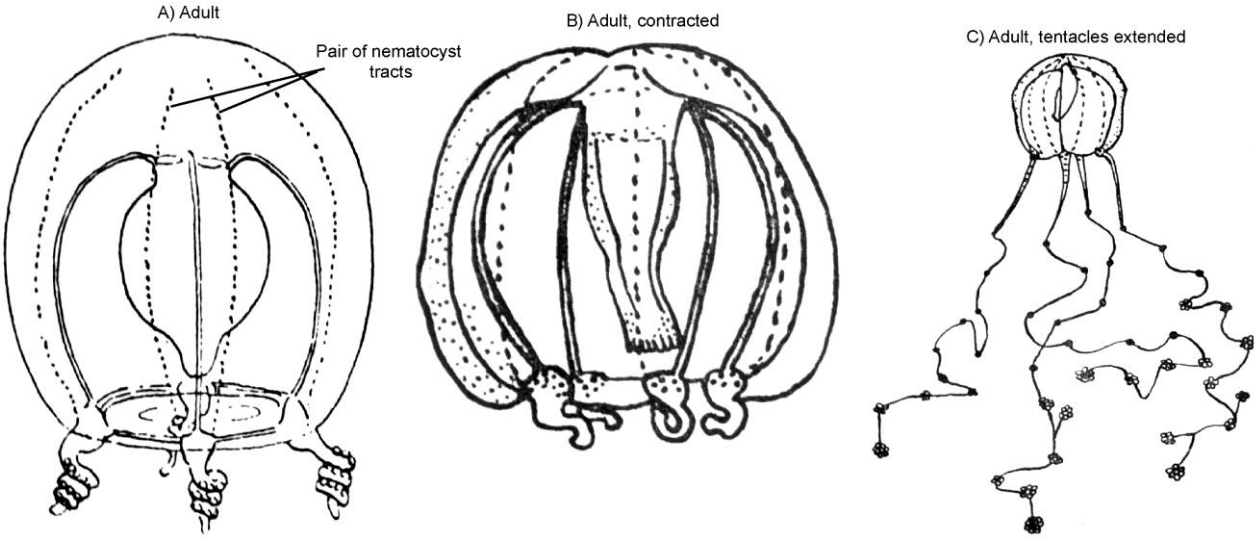


Fig. 33. *Ectopleura dumortieri* (A from Kramp, 1959; B-C from Russell, 1953).

Recorded: PMF. L4, not recorded. Southern Ireland. Eastern Scotland. Rare.
Size: Umbrella height ~1 mm on liberation; ~1.8 mm when adult, but up to 4 mm.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

Genus *Hybocodon*:

Hybocodon prolifer Agassiz, 1860

Umbrella bell-shaped, higher than wide (Fig. 34), conspicuously asymmetrical (so can easily be distinguished from *Euphysa aurata;* Fig. 36), sloping upwards from tentacular side, with rounded apex; jelly thick, especially on tentacular side. Exumbrella with five meridional nematocyst tracts extending towards apex (Fig. 34A); velum moderately broad; stomach large and cylindrical, around half to two-thirds the length of umbrella cavity, never reaching beyond umbrella margin; mouth simple and tube-like. Three small, poorly developed marginal bulbs without tentacles, which do not continue as spurs up the exumbrella surface as seen in *Euphysa aurata*; fourth larger bulb with one to four tentacles, the basal bulbs usually differing in size, the smaller bulbs appearing to develop from the sides of the larger; tentacles robust and ringed with nematocysts. Four radial canals and ring canals quite broad, radial canal on tentacular side longer than the one opposite; gonads surround stomach, leaving both ends of peduncle free. There can be asexual budding from the tentacular bulb (Fig. 34B).

In early stages an umbilical canal may extend into the apex above the stomach, occasionally persisting into the adult. Three perradial nematocyst tracts arise in the vicinity of the three non-tentacular bulbs and extend upwards over the exumbrella surface. Shows little change in structure during development.

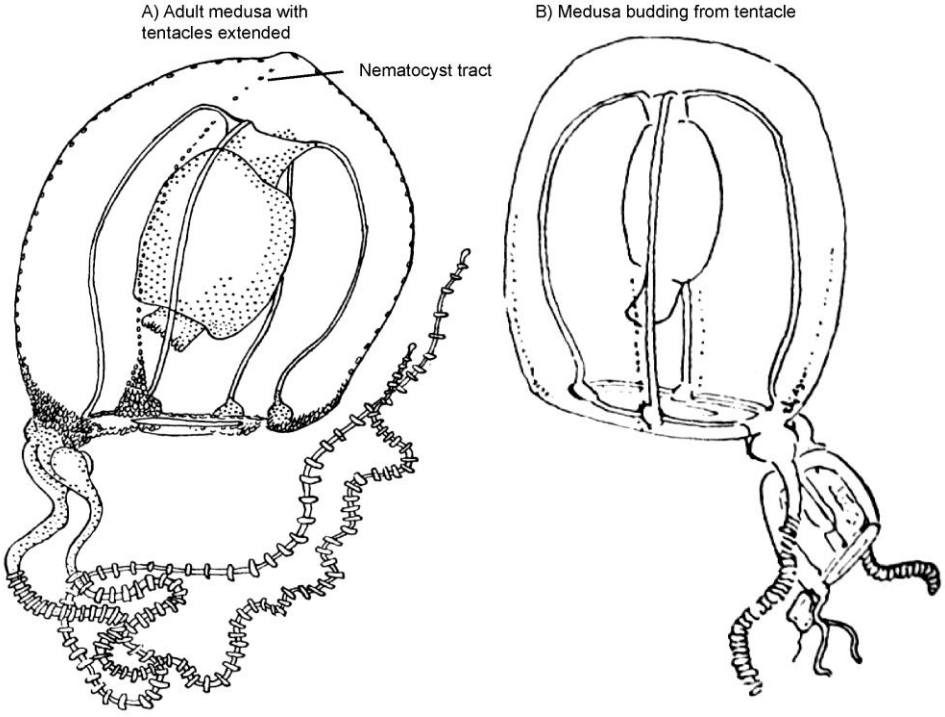


Fig. 34. *Hybocodon prolifer* (A from Russell, 1953; B from Kramp, 1959).

Recorded: PMF. L4, not recorded. All coasts of Britain and Ireland. North Sea. Can be common, particularly in north.

Size: Umbrella height ~1 mm on liberation; 2-4 mm when fully grown.

Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

Family Corymorphidae

Genus *Corymorpha*:

Corymorpha nutans M. Sars, 1835

Umbrella bell-shaped, jelly thick, nearly twice as high as broad (Fig. 35A), with pointed conical apical process that is often floppy and thin in preserved specimens (Fig. 35B), with a characteristic umbilical canal extending towards the apex of this process; velum fairly broad; four radial canals and ring canals fairly broad; one fully developed, strong marginal tentacle with nematocyst rings and terminal nematocyst cluster, bulb of this tentacle two to three times larger than the three other marginal bulbs, which lack tentacles; stomach large and cylindrical on short peduncle, about two-thirds the length of subumbrellar cavity, in full extension reaching slightly beyond umbrella margin; gonads surround stomach leaving mouth and peduncle free; mouth simple and tube-like. Shows few morphological changes during development.

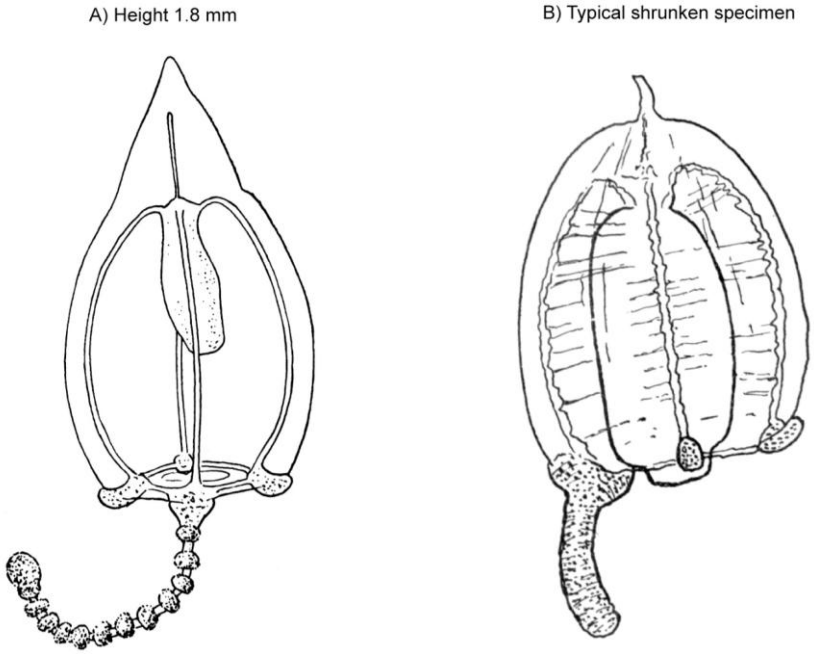


Fig. 35. *Corymorpha nutans* (from Russell, 1953).

Recorded: PMF (as *Steenstrupia nutans*). L4, occasionally common. All coasts of Britain and Ireland. North Sea.
Size: Umbrella height 1.1-1.4 mm on liberation; 5-6 mm when fully grown.
Further information: Russell, 1953 (as *S. nutans*); Kramp, 1959, 1961 (as *S. nutans*); Bouillon & Boero, 2000.

Genus *Euphysa*:

Euphysa aurata Forbes, 1848

Umbrella barrel-shaped with rounded apex (Fig. 36A); jelly thick especially at apex; velum fairly wide. Stomach large and cylindrical with rounded apex, two-thirds the length of the umbrella cavity, at full extension, never reaching beyond the umbrella margin; mouth simple and circular. Gonads surround stomach leaving mouth and upper end free. Four radial canals and ring canals narrow; one single short marginal tentacle with numerous nematocyst rings and three smaller marginal bulbs without tentacles, extending as spurs slightly up exumbrellar surface (Fig. 36B).

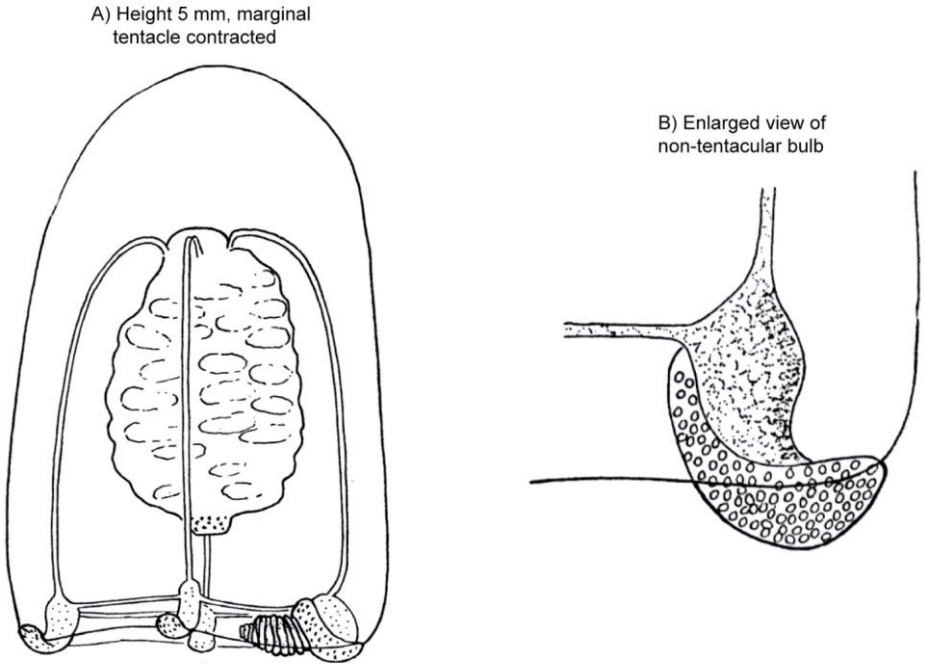


Fig. 36. *Euphysa aurata* (from Russell, 1953).

Recorded: PMF. L4, not recorded. Western, northern and north-eastern coasts of Britain. Southern Ireland.

Size: Umbrella height 0.6-1.0 mm on liberation; up to 6.0 mm when fully grown.

Further information: Russell, 1953; Kramp, 1959, 1961; Pagès *et al*., 1992; Bouillon & Boero, 2000.

Family Zancleidae:

Genus *Zanclea*:

Zanclea costata Gegenbaur, 1857

Umbrella bell-shaped, about as high as wide, with quite thick jelly, sometimes thicker in apical region and near umbrella margin (Fig. 37A, B); velum quite broad. Stomach cylindrical, when fully extended reaching near, but never beyond, the umbrella margin; mouth simple and circular; four straight radial canals and ring canal quite broad. Gonads covering most of the stomach, leaving the mouth end free. Can have two opposite marginal tentacles and two opposite non-tentacular marginal bulbs Fig. 37A), or four marginal tentacles; marginal tentacles with elongated conical bases (Fig. 37C). There may be nematocyst patches, narrow at the base and wider distally, arising from the outer, upper base of the marginal tentacles or non-tentacular marginal bulbs (Fig. 37B). These can extend around a third of the way up the exumbrella surface. On the tentacles there may be obvious stalked oval capsules or cnidophores (Fig. 37D), each containing two to five nematocysts.

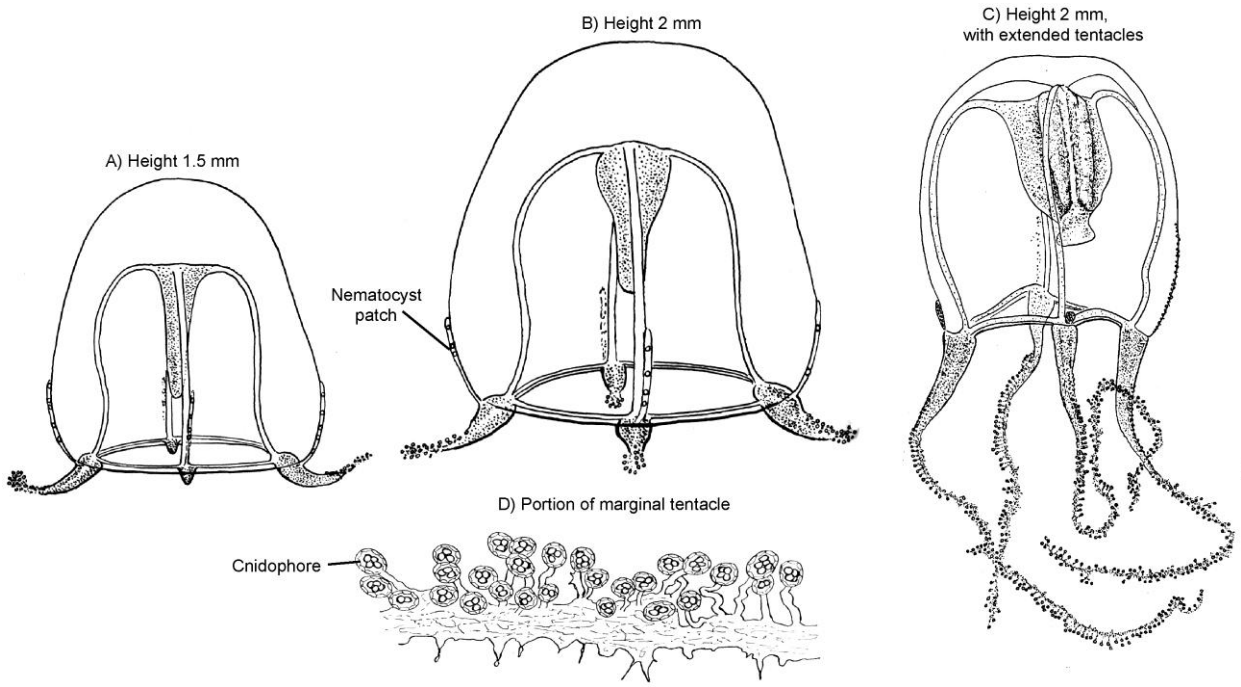


Fig. 37. *Zanclea costata* (from Russell, 1953).

Recorded: PMF. L4, not recorded. All coasts of Britain. Southern Ireland. North Sea. Sampled in low numbers.
Size: Umbrella height ~0.6-0.7 mm on liberation; 1.5-3.0 mm when fully grown.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Hydroidolina: Order Anthothecata: Suborder Capitata:

Family Cladonemidae:

Genus *Cladonema:*

Cladonema radiatum Dujardin, 1843

This is a creeping and sometimes swimming species. Umbrella bell-shaped, higher than wide (Fig. 38B, C); jelly quite thin, sometimes with small apical projection; velum broad. Stomach usually with five, sometimes four pouch-like outgrowths in the middle region; mouth with four or five short lobes with nematocyst clusters (Fig. 38B); stomach not reaching beyond umbrella margin. Gonads completely surround stomach on its upper half; eight or ten radial canals. Usually eight, sometimes ten marginal tentacles, the same number as radial canals, branched with elongated thickened bases, from the underside of which grow one to four, usually three adhesive organs; ocellus on the abaxial side of each marginal tentacle bulb.

On liberation, usually five, sometimes four thin primary radial canals; marginal tentacles unbranched and do not bear the adhesive organs that develop later. At this stage it resembles *Eleutheria dichotoma* (Fig. 39). As it develops, the marginal tentacles branch two to three times (Fig. 38A) and the adult characters gradually appear.

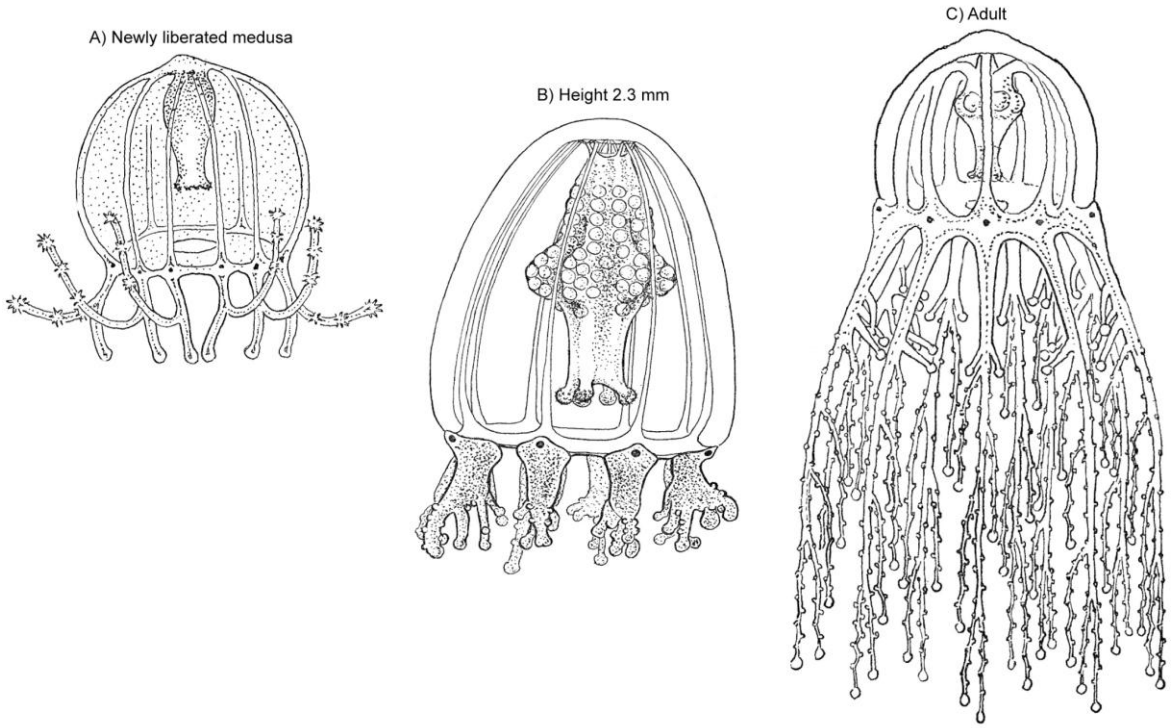


Fig. 38. *Cladonema radiatum* (from Russell, 1953).

Recorded: PMF. L4, not recorded. English Channel. Southern North Sea.
Size: Umbrella height ~1 mm on liberation; ~4 mm when fully grown.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

Genus *Eleutheria*:

Eleutheria dichotoma De Quatrefages, 1842

Umbrella a flattened hemisphere, with its ventral surface more or less six-sided (Fig. 39). Stomach cylindrical, extending slightly below umbrella margin; mouth simple and tubular. Radial canals short, usually six in number; gonads in specialised brood pouch situated above the stomach, in which the embryos develop to the planula stage. Asexual reproduction by medusae-bud formation from ring canal on exumbrella. Marginal tentacles four to 14 in number, usually five or six, twice the diameter of the umbrella in length, bifurcating into an upper branch with a single terminal nematocyst cluster and a lower unarmed branch terminating in an adhesive disc. One abaxial ocellus on base of each marginal tentacle.

Found among weeds in rock pools and inshore, creeping along the substrate using the adhesive discs on the tentacles, so will only be sampled by chance.

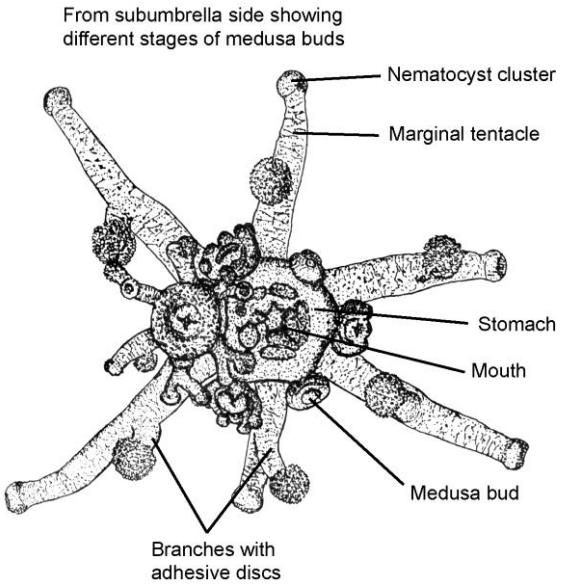


Fig. 39. *Eleutheria dichotoma* (from Russell, 1953).

Recorded: PMF. L4, not recorded. Western Scotland. Southern Ireland. Southern North Sea. Common if specifically searched for.

Size: Umbrella diameter 0.4-0.5 mm.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Family Porpitidae:

Genus *Porpita*:

Porpita porpita (Linnaeus, 1758)

Commonly known as 'blue button', the floating polypoid colony is covered by a chitinous float, surrounded by a membrane that lies on the water surface. The float is opaque, golden-tinged and the membrane and polyps vary from blue to yellow. Liberated medusae contain yellowish zooxanthellae; bell-shaped with eight radial canals and two opposing tentacles that terminate in nematocyst clusters.

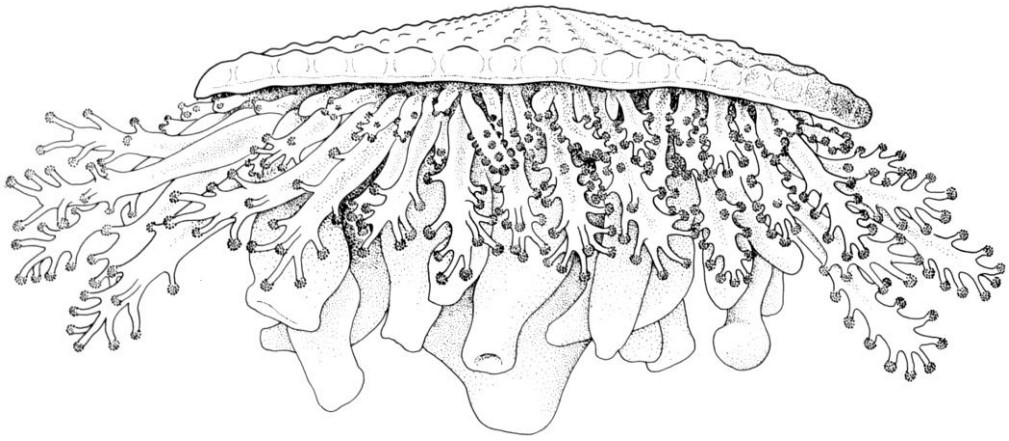


Fig. 40. *Porpita porpita* polypoid colony (from Pagès *et al*., 1992, drawn by J. Corbera).

Recorded: Sub-tropical species. Divers have reported seeing colonies off south-west Britain, but this has not been verified and it is possible that they were *Velella velella*.
Size: Medusae umbrella height 0.3-2.5 mm when liberated; colony ~30 mm in diameter.
Further information: Totton, 1954; Brinckmann-Voss, 1970; Wrobel & Mills, 1998.

Genus *Velella:*

Velella velella (Linnaeus, 1758)

Commonly known as “by-the-wind sailor”, the polypoid phase of *Velella* (Fig. 41A) can be found floating on the sea surface in great numbers at certain times of year, their arrival related to wind and current conditions. They are composed of a characteristic floating colony, with an upright triangular chitinous sail and an elliptical to rectangular float, surrounded by a membrane that lies on the sea surface, probably acting as a stabilizer. The sail and float are clear/opaque, while the membrane is deep blue. Beneath the float are attached various organs, the most conspicuous of which is a central siphon, surrounded by many smaller siphons. These smaller siphons may ingest food, but also bear the reproductive organs. The float is fringed below by a large number of tentacles. Some of the organs below are brown, as they contain zooxanthellae.

The umbrellas of the bell-shaped medusae that are liberated (Fig. 41B) are also brown from contained zooxanthellae. They have four radial canals, but only two opposing marginal tentacles with terminal nematocyst clusters.

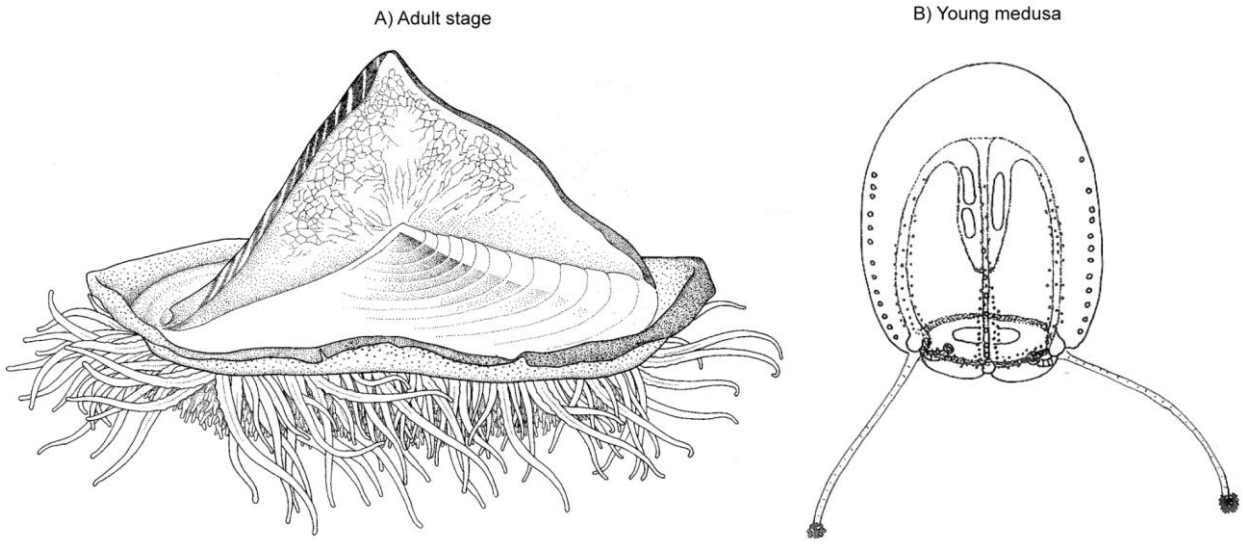


Fig. 41. *Velella velella* (A from Pagès *et al*., 1992, drawn by J. Corbera; B source unknown).

Recorded: PMF. L4, occasionally very common at the surface, but rarely taken in nets. Western Britain and Ireland. English Channel.

Size: Medusae umbrella height 1-3 mm; colony float/base 40-100 mm in length.

Further information: Kirkpatrick & Pugh, 1984; Pagès *et al*., 1992; Wrobel & Mills, 1998.

Suborder Filifera

Family Eucodoniidae

Genus *Eucodonium*:

Eucodonium brownei Hartlaub, 1907

Umbrella almost hemispherical, with slight apical bulge (Fig. 42), margin of umbrella slightly four-cornered; jelly thin; velum broad. Stomach short, cylindrical with short peduncle; mouth tube-like; asexual budding from stomach; four narrow radial canals; four thin marginal tentacles, extending to twice the height of umbrella, with irregularly distributed nematocysts and large terminal nematocyst knobs. Marginal tentacle bulbs small, without ocelli

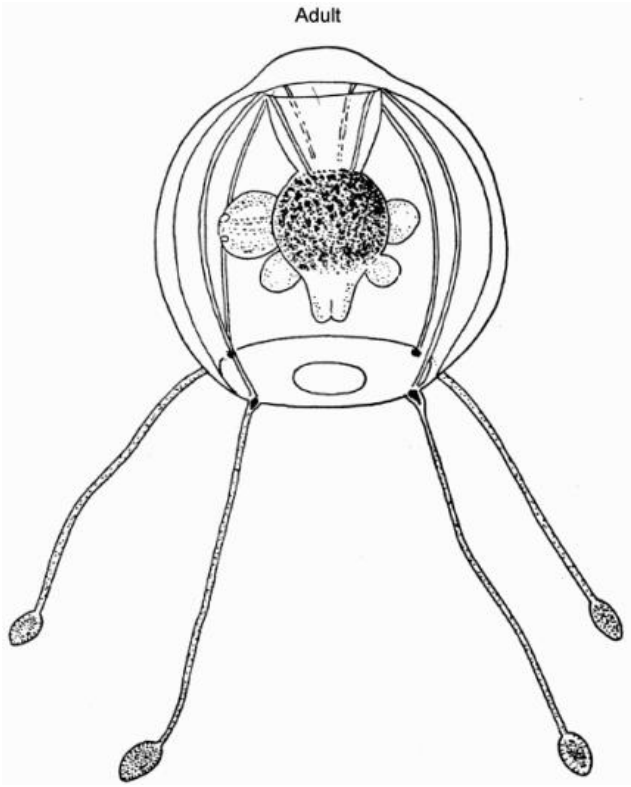


Fig. 42. *Eucodonium brownei* (from Russell, 1953).

Recorded: PMF. L4, not recorded. English Channel. Southern North Sea. Very rare.
Size: Umbrella height and width ~1mm.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Hydroidolina: Order Anthothecata: Suborder Filifera:

Family Oceaniidae:

Genus *Turritopsis*:

Turritopsis nutricula McCrady, 1857

Umbrella bell-shaped, slightly higher than wide, composed of quite thin jelly (Fig. 43A, B). Stomach cross-shaped in section, not reaching beyond umbrella margin. Four radial, compact masses of large vacuolated endodermal cells above the stomach. Mouth with four lips, with many circular masses of nematocysts along its edge (Fig. 43B, C). Four radial canals and ring canal quite broad; radial canals extend through endodermal masses to stomach. Gonads in four pairs, on interradial wall of stomach. Initially around eight marginal tentacles, increasing to 80-90, close together in a single row with nematocyst clusters on tip (Fig. 43D, E); small ocelli present on tentacle bulbs.

T. nutricula has a life cycle in which it reverts to the polyp stage after becoming sexually mature. It is the only known case of a metazoan capable of reverting completely to a sexually immature, colonial stage after having reached sexual maturity as a solitary stage. It does this through the cell development process called transdifferentiation. Theoretically, this cycle can repeat indefinitely, rendering it biologically immortal, hence its common name “Immortal jellyfish”, but in practice there is probably high mortality. Originally from the Caribbean, it has spread world-wide, probably through ballast water transfer. It is found in temperate to tropical regions in all of the world's oceans.

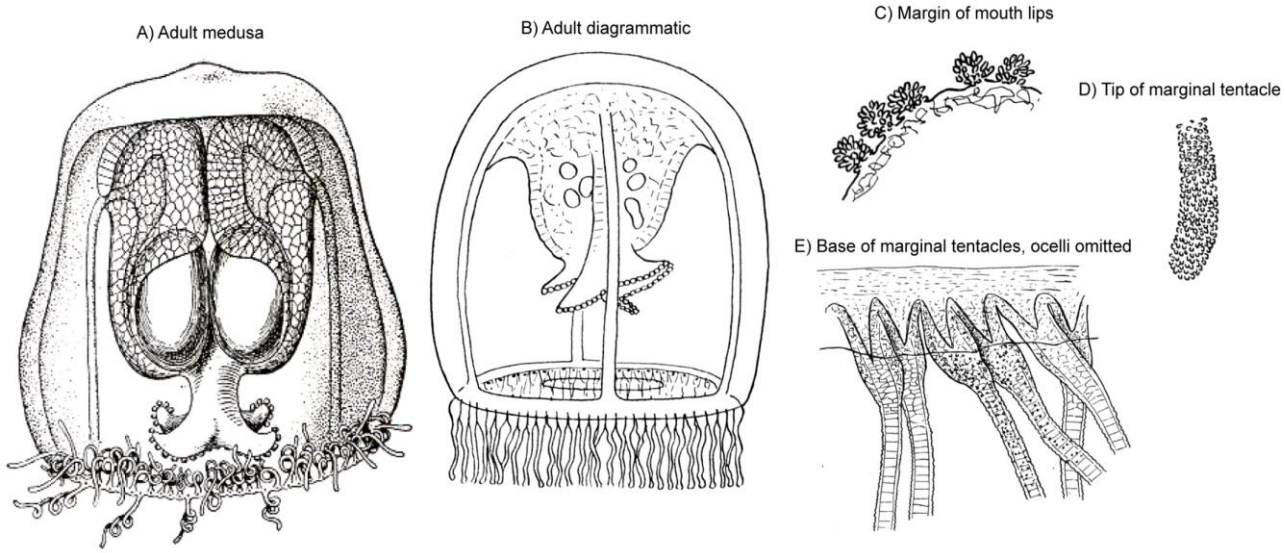


Fig. 43. *Turritopsis nutricula*. (A from Mayer, 1910a; B from Kramp, 1959; C-E from Russell, 1953).

Recorded: PMF. L4, rare. English Channel. Southern North Sea. Irish Sea. Eastern Scotland.
Size: Umbrella height ~0.8 mm on liberation; 4-5 mm when fully grown.
Further information: Mayer, 1910a; Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Family Hydractiniidae:

Genus *Hydractinia*:

Hydractinia borealis (Mayer, 1900)

Umbrella bell-shaped (Fig. 44); jelly thin, thicker in apical region; stomach four-sided, not extending beyond umbrella margin; mouth with four lips, extended to form tentacles that branch dichotomously one or two times, each branch with a terminal nematocyst cluster (Fig. 44F); no asexual budding from stomach. Gonads interradial on stomach (Fig. 44D), covering upper half and separated radially, but this can be difficult to see. Initially there are four large perradial and four smaller interradial tentacles, increasing to around 16-32, closely spaced around umbrella margin; reddish/yellow tinge to tentacle bulbs, no ocelli; four radial canals and ring canal narrow. Because development is progressive and number of tentacles gradually increases from four, certain young stages of *Hydractini*a can resemble young *Lizzia blondina*, but in *Lizzia* the stalks with nematocysts emerge from the side of the stomach wall instead of from the ends of the lips.

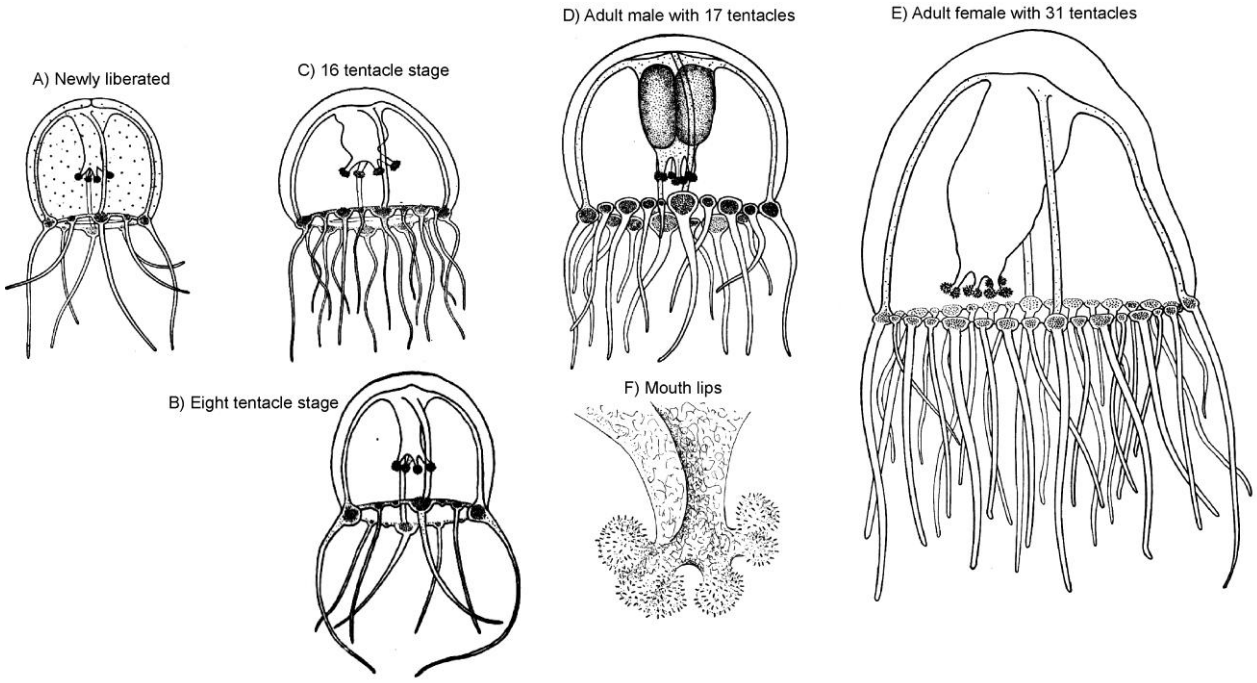


Fig. 44. *Hydractinia borealis* (A-E from Rees, 1941; F from Russell, 1953).

Recorded: PMF (as *Podocoryne borealis*). L4, rare. Western Scotland. Irish Sea. Southern Ireland. Southern North Sea.
Size: Umbrella height ~0.8 mm on liberation; ~5 mm when fully grown.
Further information: Rees, 1941; Russell, 1953; Kramp, 1961 (all as *P. borealis*); Bouillon & Boero, 2000.

Hydractinia carnea (M. Sars, 1846)
Umbrella bell-shaped, higher than wide, rounded apex, jelly quite thin (Fig. 45A). Stomach cylindrical, length around half the height of subumbrella; gonads on stomach. Russell (1953) states that the nematocyst clusters on the mouth margin are not on stalks as in other *Hydractinia* spp., but have four separate, characteristic cylindrical clusters of elongated nematocysts, as in the young specimen in Figure 45B, but included an illustration from Rees (1941; Fig. 45A) showing definite stalks? Four radial canals and ring canal narrow; four perradial marginal tentacles and one to four interradial tentacles, so can be a maximum of five to eight in total (at least in British waters); reddish/yellow tinge to tentacle bulbs; no ocelli.
When liberated does not show any great structural difference from the adult, apart from all the tentacles may not be developed.

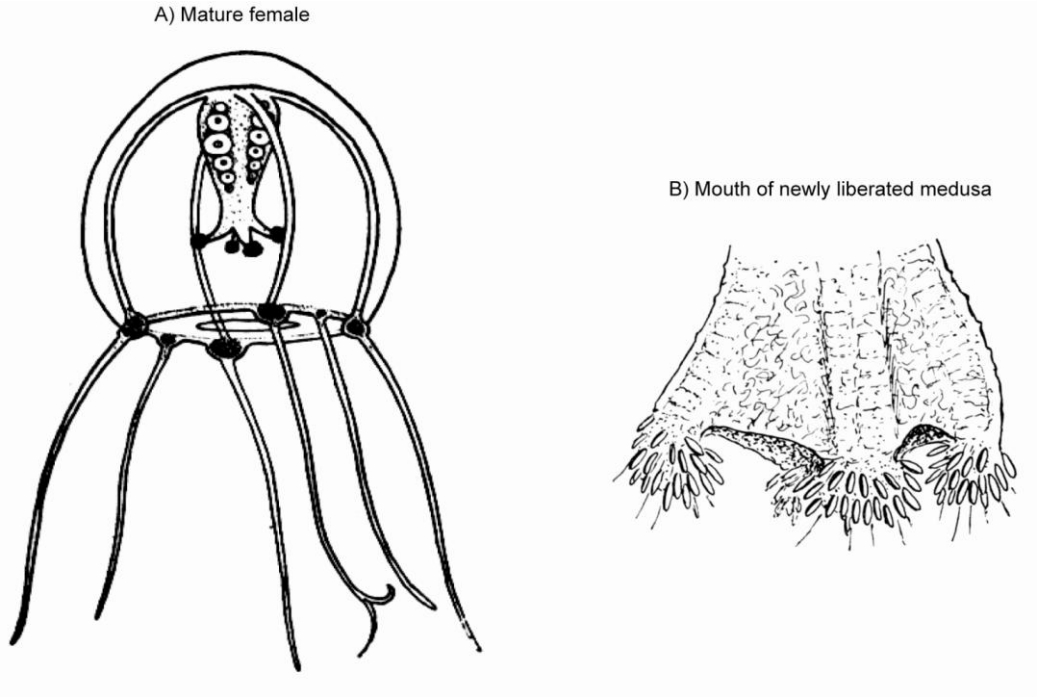


Fig. 45. *Hydractinia carnea* (A from Rees, 1941; B from Russell, 1953).

Recorded: PMF (as *Podocoryne carnea*). L4, not recorded. Eastern and western Scotland. Irish Sea. Southern Ireland. English Channel.
Size: Umbrella height ~0.8 mm on liberation; adults to ~1 mm in British waters.
Further information: Rees, 1941; Russell, 1953; Kramp, 1961 (all as *P. carnea*); Bouillon & Boero, 2000.

Hydractinia areolata Alder, 1862
Umbrella bell-shaped, about as high as wide, rounded apex, jelly thin, thicker in apical region. Stomach cylindrical, length around half the height of subumbrella cavity. Up to 57 marginal tentacles with swollen basal bulbs; four perradial and four interradial, larger tentacles of similar size, while remainder are smaller and variable in size (Fig. 46A, C); reddish/yellow tinge to tentacle bulbs; no ocelli. Mouth lips with four tentacles emerging from the lips, each terminating in a single, cylindrical nematocyst cluster (Fig. 46E). However, a specimen with obvious gonads was collected at L4 in January 2011 that showed the typical marginal tentacle arrangement for this species, but there appeared to be a slight division of the lip tentacle nematocyst clusters. Its identity was confirmed by genetical sequencing (R. Kirby, pers. comm.). Four radial canals and ring canal narrow; gonads on stomach wall and extending for a short distance along radial canals (Fig. 46D).
Immature individuals of this species could possibly be confused with early stages of *H. borealis* while it still has a single nematocyst cluster on the lip tentacles.

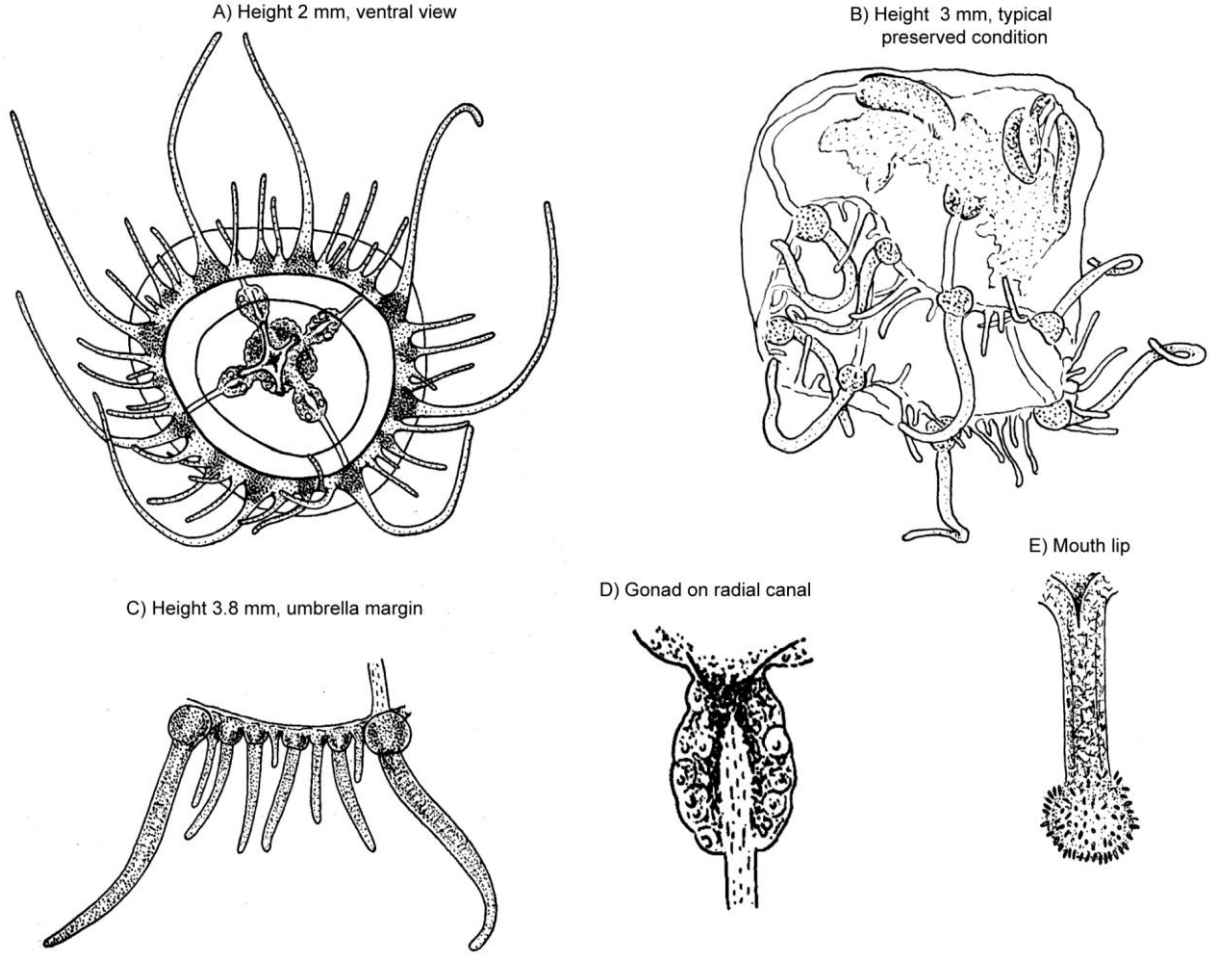


Fig. 46. *Hydractinia areolata* (from Russell, 1953, as *P. hartlaubi*).

Recorded: PMF (as *Podocoryne hartlaubi*). L4, rare. Western English Channel. Southern Ireland.
Size: Umbrella height ~4 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961 (both as *P. hartlaubi*); Bouillon & Boero, 2000.

Family Rathkeidae

Genus *Podocorynoides:*

Podocorynoides minima (Trinci, 1903)

Umbrella bell-shaped, slightly higher than wide (Fig. 47A), jelly moderately thick, slightly thicker at apex. Velum well developed; stomach short, cylindrical. Four mouth lips elongated to form four simple tentacles, each terminating in a single nematocyst cluster (Fig. 47C). Four radial canals; four interradial gonads; asexual reproduction by budding from stomach wall (Fig. 47A). Four marginal tentacles, each with large swollen basal bulbs; no ocelli.

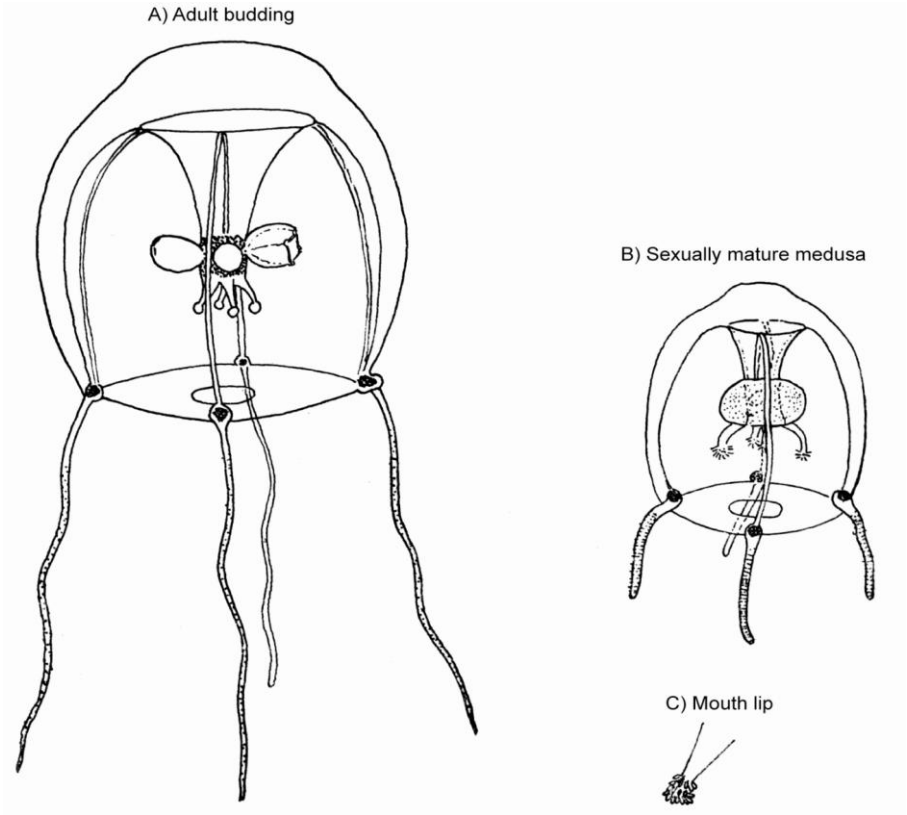


Fig. 47. *Podocorynoides minima* (from Russell, 1953).

Recorded: PMF (as *Podocoryne minima*). L4, not recorded. Western English Channel.
Size: Umbrella height up to 1 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961 (both as *Podocoryne minima*); Bouillon & Boero, 2000 (as *Hydractinia minima*).

Genus *Rathkea*:

Rathkea octopunctata (M. Sars, 1835)

Umbrella slightly higher than wide (Fig. 48B), apex thick with rounded apical process. Stomach short cylindrical with conical peduncle, not extending beyond umbrella margin. Mouth with four lips each extending at their tips into short arms dividing at their ends into pairs of short stalks with terminal nematocyst clusters (Fig. 48C). When fully grown there are also paired nematocyst clusters either side of the lip extensions (Fig. 48C, D). Four radial canals; gonads completely surround stomach; asexual reproduction by budding from stomach wall (Fig. 48A, B, D). Eight marginal tentacle bulbs, four perradial each with up to five tentacles and four interradial with up to three tentacles (Fig. 48A, E); no ocelli. Because tentacle number increases variably between bulbs during development, there are many possible tentacle number combinations.

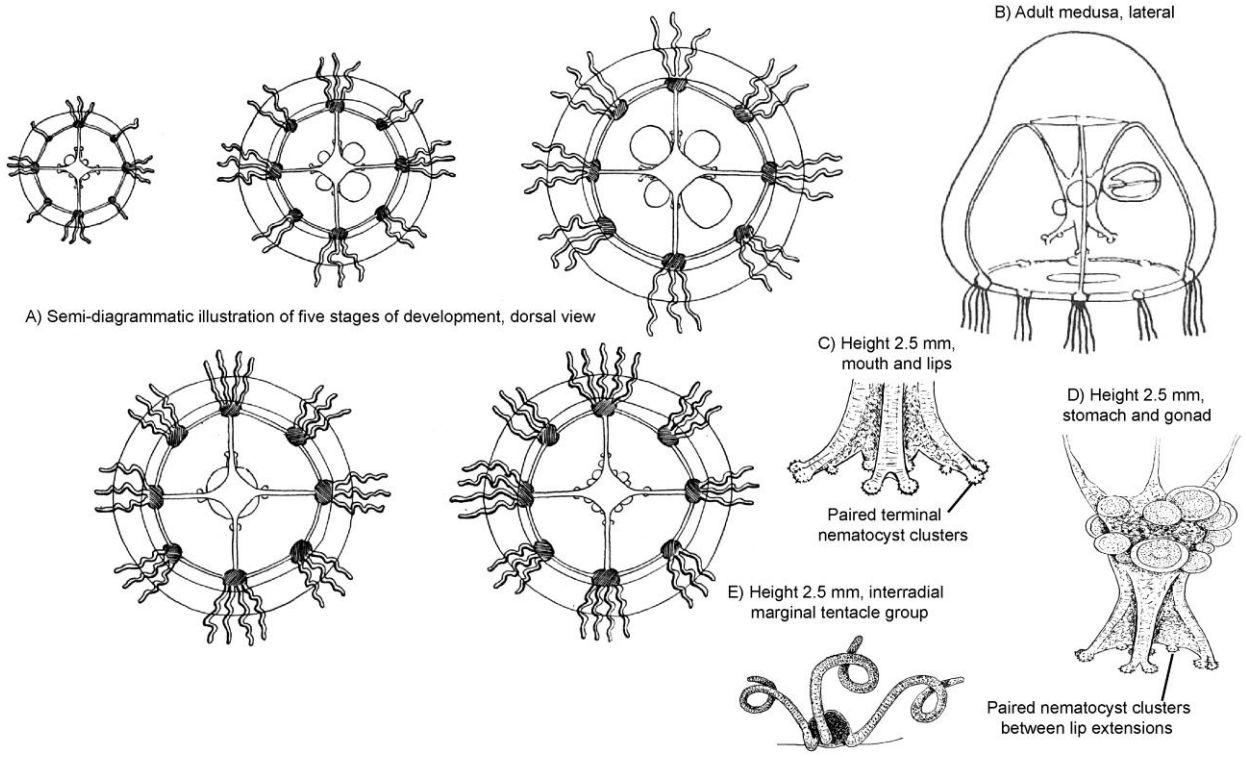


Fig. 48. *Rathkea octopunctata* (A-E from Russell, 1953; B from Kramp, 1959).

Recorded: PMF. L4, occasional. All European coasts.
Size: Umbrella height ~1 mm on liberation; 3-4 mm when fully grown.
Further information: Russell, 1953; Kramp, 1959, 1961; Bouillon & Boero, 2000.

Genus *Lizzia*:

Lizzia blondina Forbes, 1848

Rounded body with thick jelly, especially at apex (Fig. 49A); stomach short with broad base, attached to a conical peduncle, not reaching beyond umbrella margin; four unbranched oral tentacles arising from the wall above the mouth margin (Fig. 49C), each with one terminal nematocyst cluster. Four radial canals; gonads surround stomach in a ring-shaped cushion when fully mature (Fig. 49D). Eight marginal tentacle bulbs, four perradial, each with one to three tentacles, depending on stage of development (Fig. 49B, E), four interradial each with a single tentacle, rarely two; no ocelli. Asexual budding from stomach wall (Fig. 49A, B).

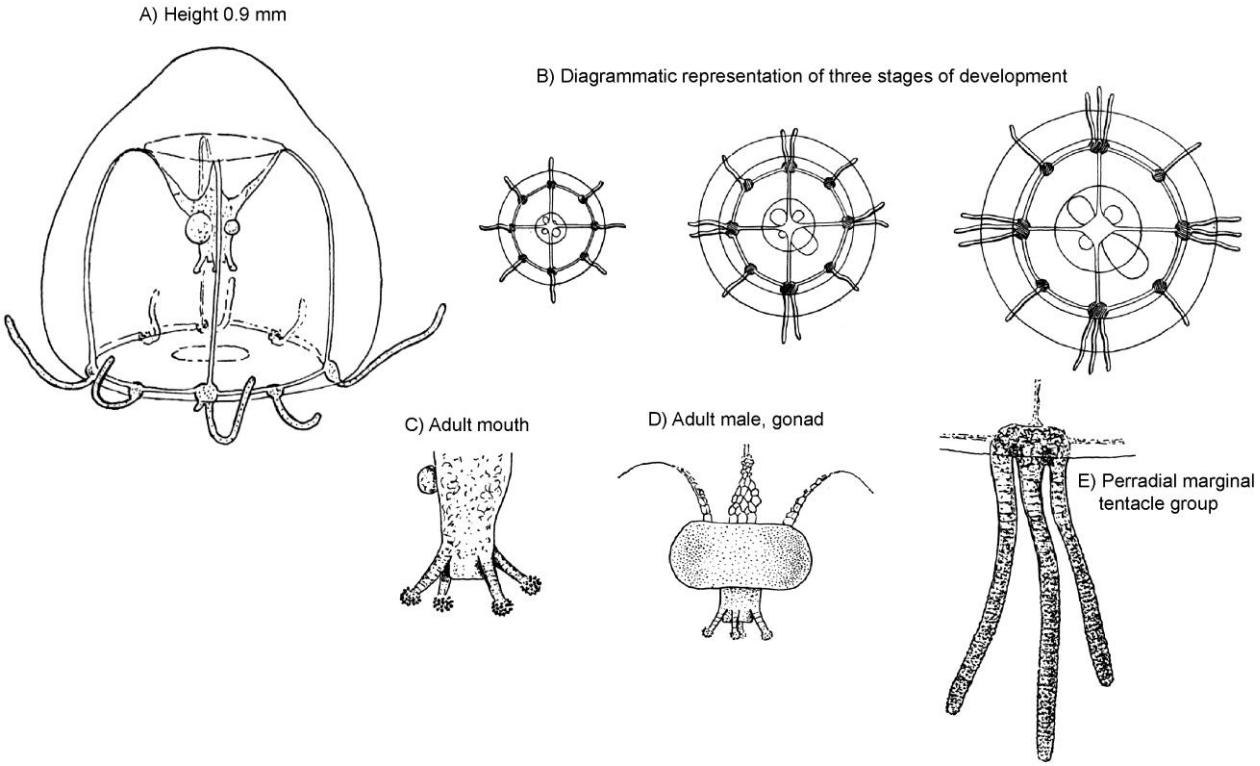


Fig. 49. *Lizzia blondina* (from Russell, 1953).

Recorded: PMF. L4, occasionally common. All around Britain and Ireland. North Sea.
Size: Umbrella height ~0.7 mm on liberation; up to 2 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Family Bougainvilliidae

Genus *Bougainvillia:*

Bougainvillia muscus (Allman, 1863)

Rounded umbrella with thick jelly, especially at the apex (Fig. 50); four narrow radial canals. Stomach short, sometimes with short peduncle. Four short oral tentacles, branching dichotomously twice, rarely three or four times, terminating in nematocyst clusters; four marginal tentacle bulbs, small and oval, four to nine tentacles on each, with ocelli on the bulbs at the base of each tentacle. Gonads on stomach, interradial, forming simple pad-like cushions, extending slightly along radial canals.

On liberation the jelly is uniformly thin; no peduncle; four small round tentacle bulbs, two tentacles (one usually less developed) and two ocelli on each bulb; four unbranched oral tentacles, usually turned upwards.

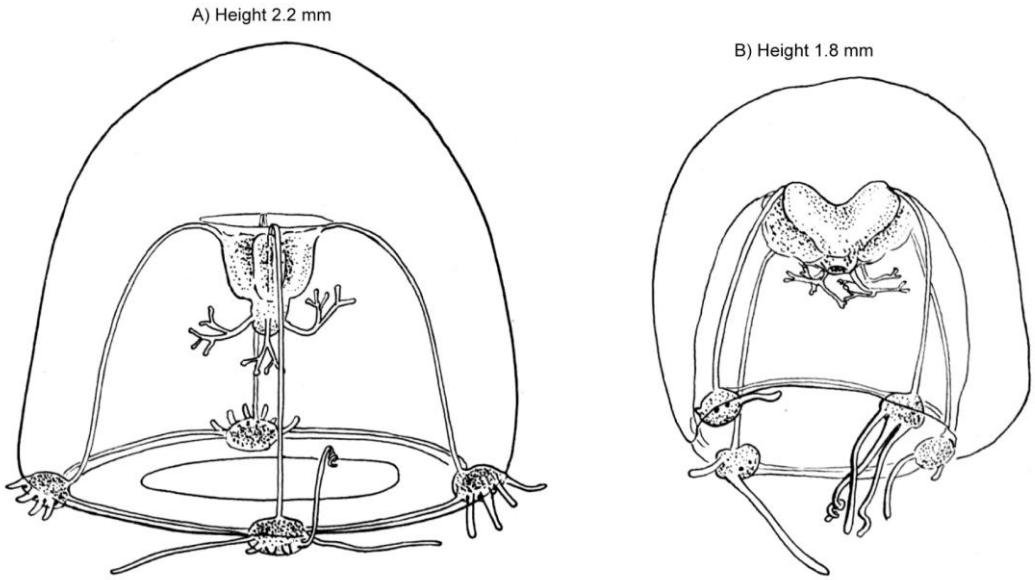


Fig. 50. *Bougainvillia muscus* (from Russell, 1953).

Recorded: PMF (as *Bougainvillia ramosa*). L4, occasional. All around Britain. Southern Ireland. North Sea.

Size: Umbrella height ~0.75 mm on liberation; 2.5-4.0 mm when fully grown

Further information: Russell, 1953; Kramp, 1961; Edwards, 1966 (all as *B. ramosa*); Bouillon & Boero, 2000.

Bougainvillia britannica (Forbes, 1841)
Jelly very thick (Fig. 51A, B), no peduncle; radial canals quite broad; tentacle bulbs triangular to kidney-shaped (Fig. 51C, F) depending on age, with up to 30 tentacles on each bulb; ocelli on bases of tentacles, not on bulbs, crescentic or oval bulbs, sometimes appearing almost linear; oral tentacles quite long (Fig. 51E), dichotomously branching five to six times, with long basal trunk; stomach broad-based, in form of perradial cross (Fig. 51D).
On release, jelly very thick; four marginal tentacle bulbs, one tentacle and no ocelli on each bulb; four unbranched oral tentacles; stomach small and tubular with quadrate base; four, quite wide radial canals.

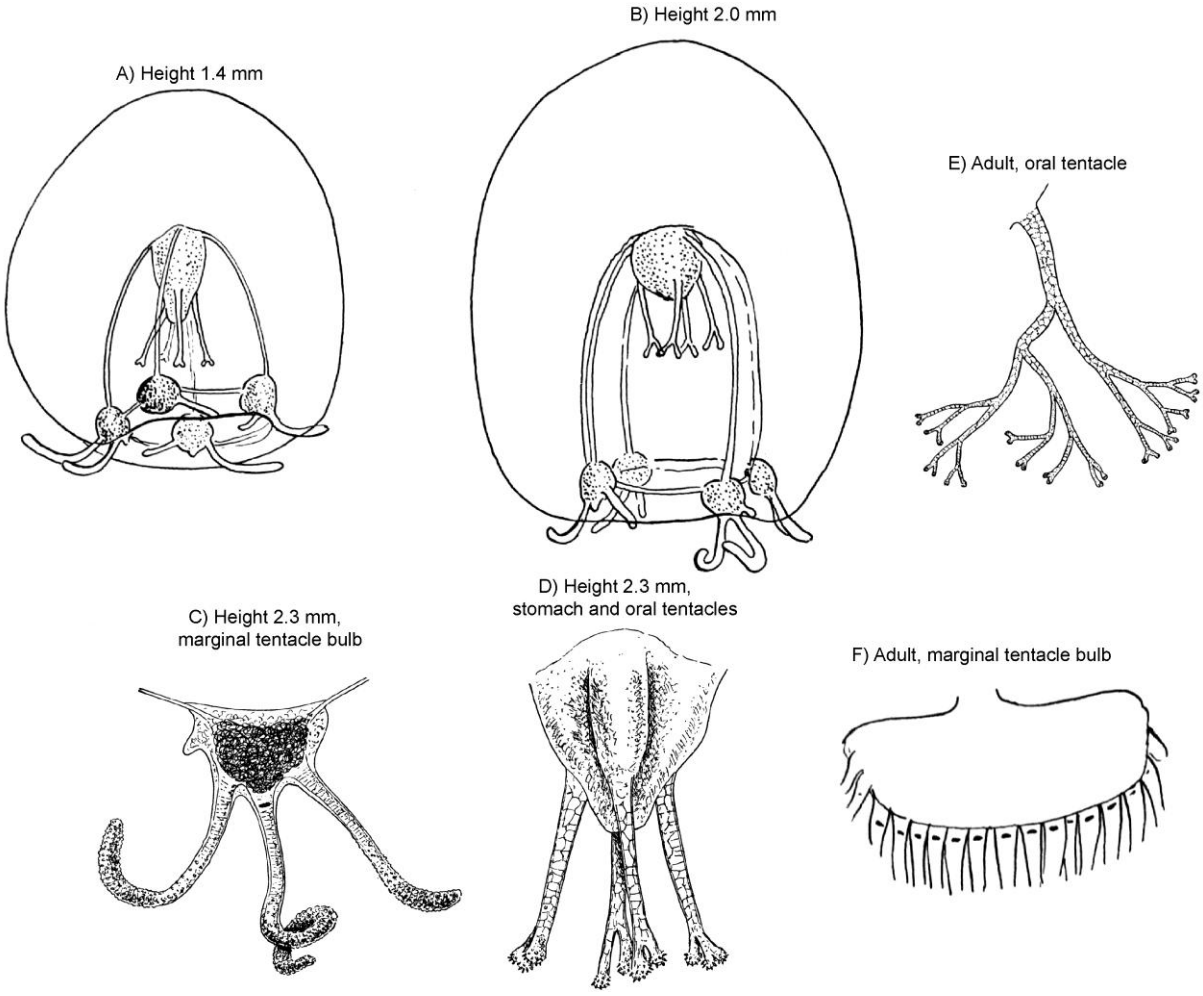


Fig. 51. *Bougainvillia britannica* (from Russell, 1953).

Recorded: PMF. L4, not recorded. All around Britain. North Sea.
Size: Umbrella diameter ~0.9 mm on liberation; up to 12 mm in height and 10 mm diameter when fully grown.
Further information: Russell, 1953, 1970; Kramp, 1961; Edwards, 1966; Bouillon & Boero, 2000.

Bougainvillia principis (Steenstrup, 1850)
Umbrella wider than high, jelly moderately thick (Fig. 52C, D), especially at apex; shallow peduncle; radial canals moderately wide; tentacle bulbs wide and epaulette-shaped (Fig. 52E), often wider than space between neighbouring bulbs, 30-40 tentacles per bulb; round ocelli on bulb at base of tentacles; oral tentacles quite short, dichotomously branching six to eight times (Fig. 52F), basal trunk very short; stomach short, broad-based, in form of cross; gonads on stomach, forming eight pad-like cushions (Fig. 15).
On release, jelly fairly thick (Fig. 52A, B); three tentacles with ocelli on each bulb; four oral tentacles, branching one or two times

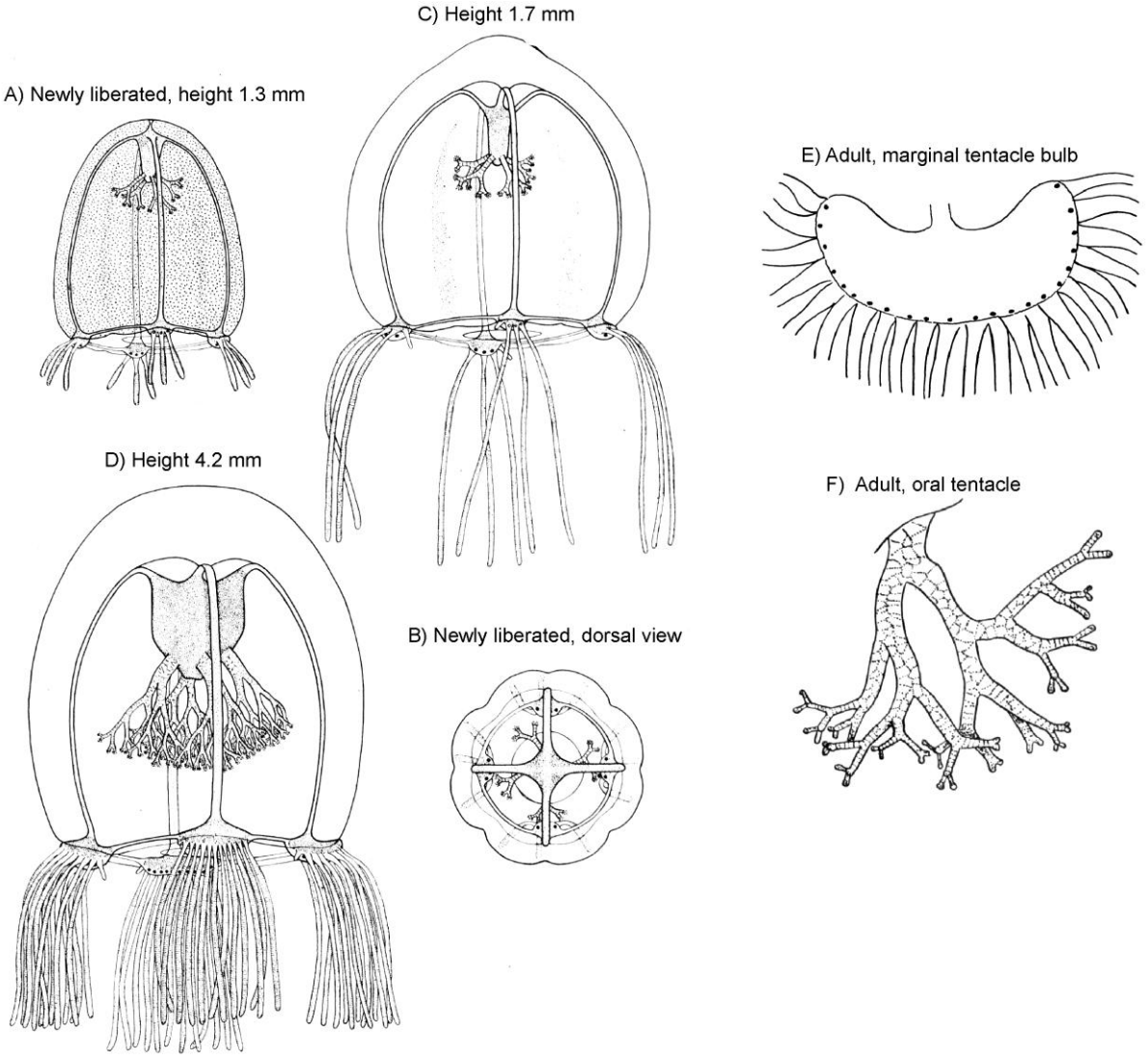


Fig. 52. *Bougainvillia principis* (from Edwards, 1966).

Recorded: PMF. L4, not recorded. All around Britain. Southern Ireland. Irish Sea. North Sea.
Size: Umbrella 1.3 mm in height and ~1.1 mm in diameter at liberation; 7-8 mm in height when fully grown, sometimes up to 10-11 mm.
Further information: Russell, 1953, 1970; Kramp, 1961; Edwards, 1966; Bouillon & Boero, 2000.

Family Pandeidae:

Genus *Amphinema*:

Amphinema dinema (Péron & Lesueur, 1810)

Umbrella bell-shaped, with a large, conical and often much elongated apical process (Fig. 53). Jelly moderately thick; stomach cross-shaped in section, coloured brownish, in full extension reaching around umbrella margin. Gonads not folded, simple pads, a pair between each radial canal; mouth with four prominent crenulated lips; four broad radial canals and ring canal with smooth or jagged outlines; two opposing, perradial marginal tentacles, very extensile, with large hollow, elongated basal bulbs; 14-24 tiny marginal warts; no ocelli.

On liberation no apical process, appearing around a height of 1.2 mm; umbrella bell-shaped, higher than wide, widest in the upper half; mouth simple.

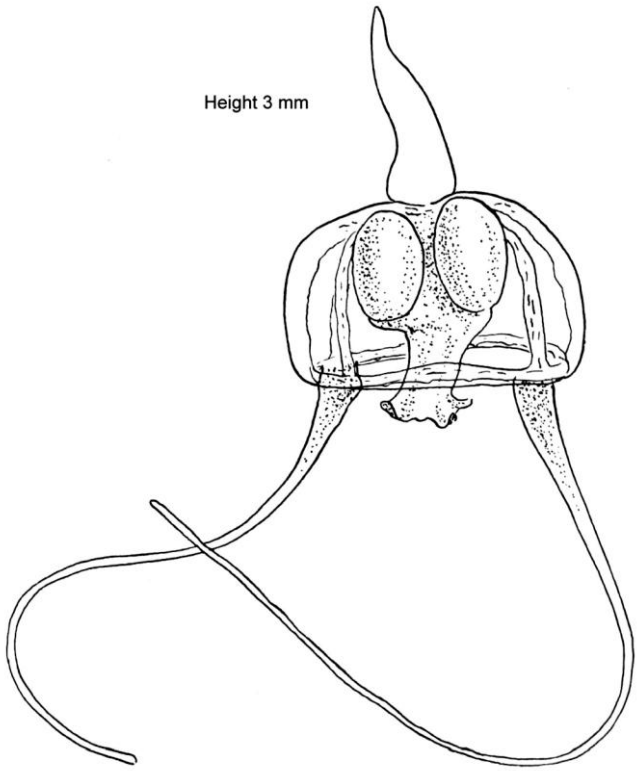


Fig. 53. *Amphinema dinema* (from Russell, 1953).

Recorded: PMF. L4, occasional. English Channel. Southern Ireland.
Size: Umbrella height ~0.7 mm on liberation; 6 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Amphinema rugosum (Mayer, 1900)
Umbrella bell-shaped with elongated rounded apical process (Fig. 54B); jelly moderately thick; stomach when fully extended almost reaching umbrella margin, coloured brownish; mouth cross-shaped with four crenulated lips; ring canal and four radial canals broad, with smooth or slightly jagged edges. Gonads between the radial canal formed into three to four opposing folds that slope slightly downwards; two opposing marginal tentacles, very extensile, with large hollow, elongated conical bulbs, red/blue when unpreserved; 16-24 small marginal tentacles; no ocelli. Umbrella typically turned inside out in preserved samples (Fig. 54A).
When newly liberated quite similar to the adult, but with simple mouth lips.

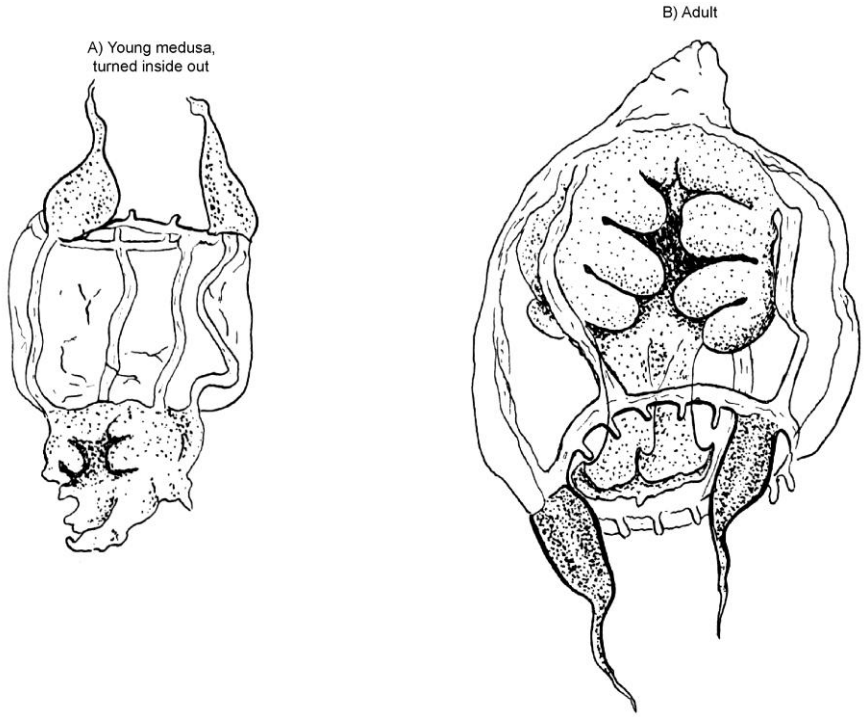


Fig. 54. *Amphinema rugosum* (from Russell, 1953).

Recorded: PMF. L4, not recorded. All around Britain. Southern Ireland. North Sea.
Size: Umbrella ~0.4-0.7 mm in height on liberation; 5-6 mm when fully grown
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Genus *Leuckartiara:*

Leuckartiara octona (Fleming, 1823)

Umbrella bell-shaped with thick apical process, very variable in size and shape (Fig. 55A-C); jelly thin; stomach large, not extending beyond umbrella margin in full extension, occupying up to half of the subumbrellar area; mouth with very crenulated lips; four broad radial canals and ring canal with smooth or jagged outlines; radial canals joined to stomach by mesenteries. Gonads typically brown/orange in colour with transverse folds pointing outwards towards radial canals; 16-23 long, hollow marginal tentacles with laterally compressed elongated basal bulbs, each with a spur extending onto exumbrellar surface (Fig. 55C, D), one to three small rudimentary marginal bulbs between each tentacle; one abaxial ocellus on all bulbs.

On liberation the mouth is initially simple; two opposing perradial marginal tentacles and two opposing perradial rudimentary marginal bulbs, but soon increase in number (Fig. 55A); no ocelli.

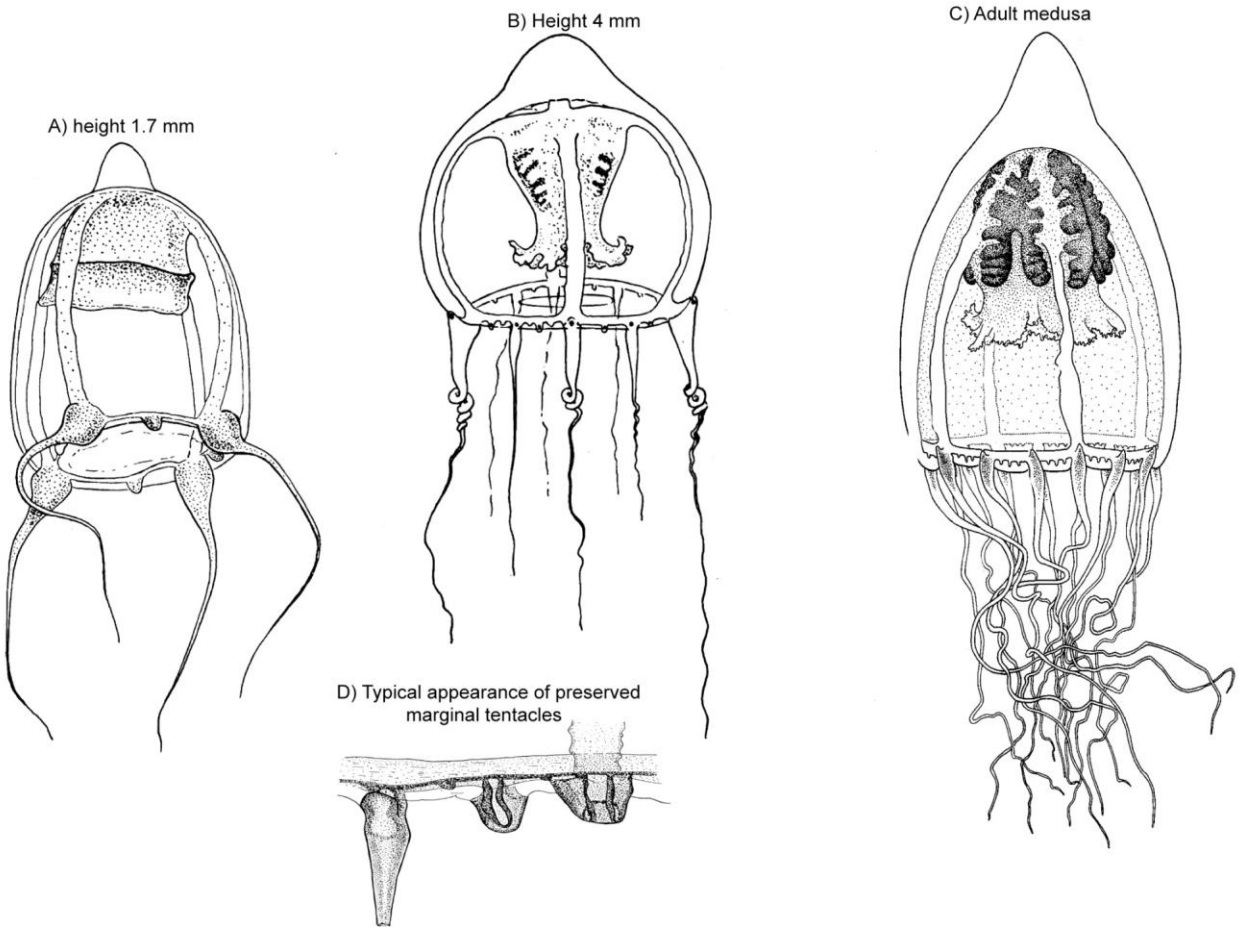


Fig. 55. *Leuckartiara octona* (A, B and D From Russell, 1953; C from Pagès *et al*., 1992, drawn by J. Corbera).

Recorded: PMF. L4, occasionally common. Over the whole European area.
Size: Umbrella height ~1.1 mm on liberation; up to at least 15 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Pagès *et al*., 1992; Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Hydroidolina:

Order Leptothecata

Medusae more flattened than bell-shaped. Gonads only found on the radial canals, although sometimes connecting onto stomach. Marginal sense organs when present are ectodermal statocysts on the velum, rarely cordyli, occasionally adaxial ocelli; marginal tentacles with bulbs; life cycle with polyp stage.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Hydroidolina: Order Leptothecata:

Suborder Conica: Family Laodiceidae:

Genus *Laodicea*:

Laodicea undulata (Forbes & Goodsir, 1853)

Umbrella variable in shape, usually flattened, jelly fairly thin; stomach quadratic, short, extending as long thin pouches on the radial canals to within a short distance of the umbrella margin (Fig. 56B, C); mouth with four lips with folded margins; four straight narrow radial canals. Gonads on upper parts of each side of the stomach pouches, extending to within short distance of umbrella margin, with five to eight pairs of lateral folds (Fig. 56C). Marginal tentacles 200-300 or more in number, with slightly swollen basal bulbs (Fig. 56D, F); small ocelli on some tentacle bases, variable in number; one to two small spiral cirri between adjacent marginal tentacles, but sometimes missing; usually one club-shaped marginal cordylus between adjacent marginal tentacles (Fig. 56D-F), but numbers variable. Over a white background the tentacles and gonads can appear greyish in preserved specimens.

On liberation the medusae is bell-shaped, higher than wide. Marginal cordyli do not appear until the medusae are ~2 mm in diameter and have 16 or more marginal tentacles (Fig. 56A).

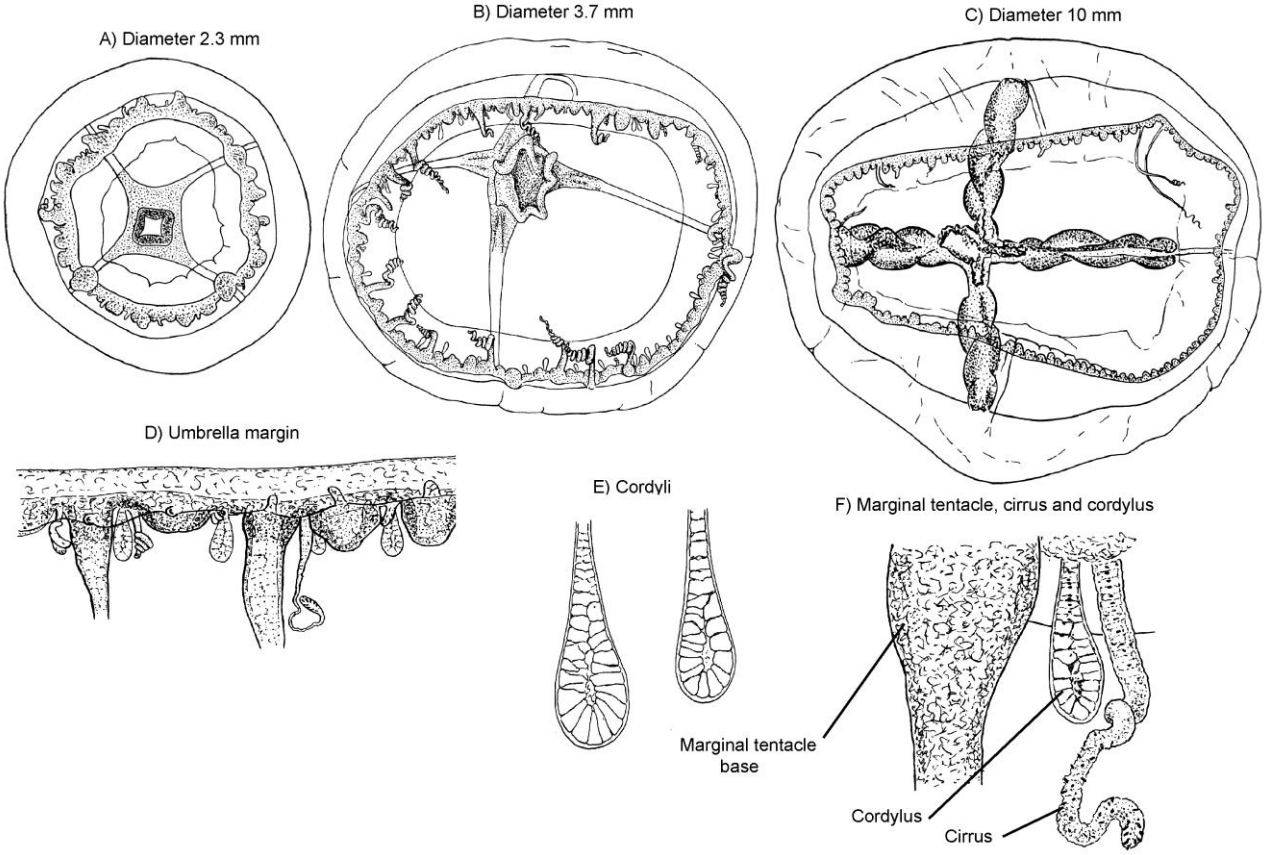


Fig. 56. *Laodicea undulata* (from Russell, 1953).

Recorded: PMF. L4, rare. Over most of the European region. Commonest on the northern and western coasts of Britain.

Size: Umbrella height ~0.7 mm on liberation; up to 26 mm in diameter when fully grown.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Family Melicertidae:

Genus *Melicertum*:

Melicertum octocostatum (Sars, 1835)

Umbrella bell-shaped; jelly quite thin, thicker in apex (Fig. 57A, B), velum narrow; stomach short, octagonal with a wide base. Mouth with eight simple or folded lips; eight broad radial canals, opening into stomach through vertical slits. Sinuous gonads in centre of radial canals, reaching almost to umbrella margin (Fig. 57A, B). Around 64-72 large marginal tentacle with laterally compressed bases and about 64-72 smaller marginal tentacles alternating approximately with the larger ones (Fig. 57C); no marginal cirri or marginal sense organs.

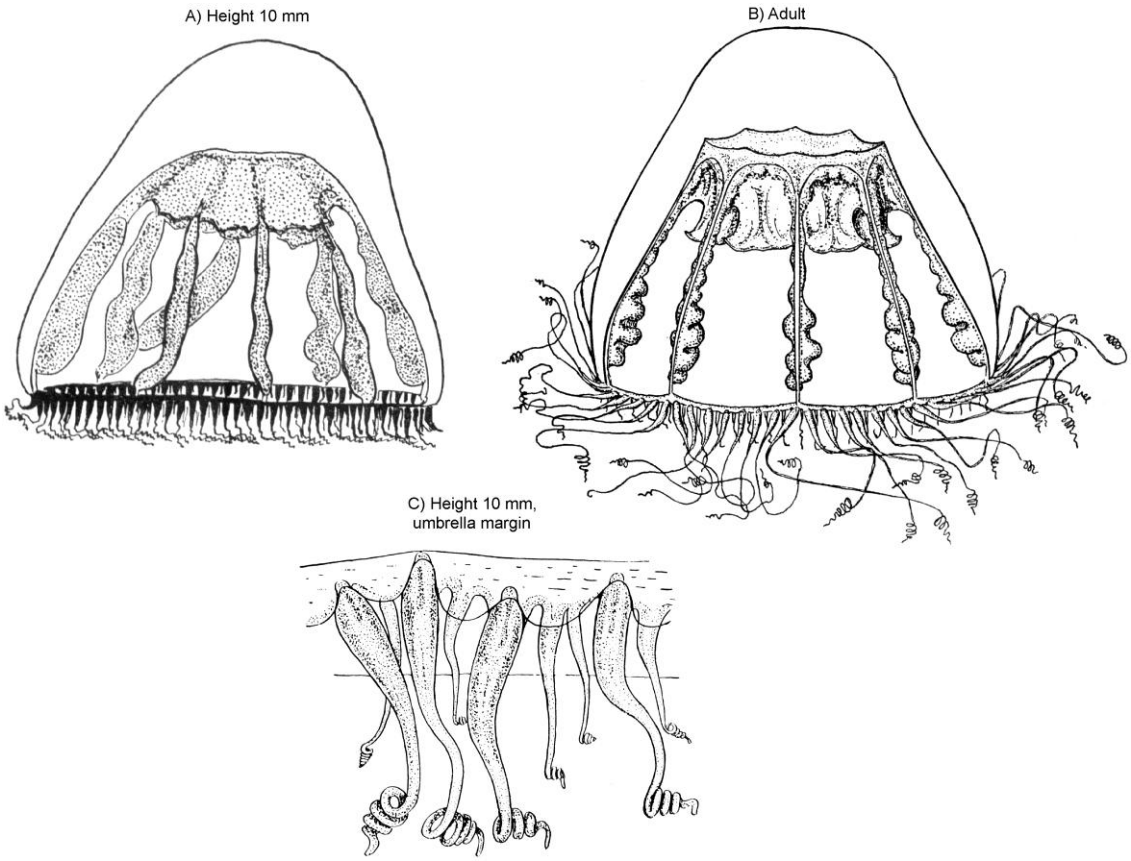


Fig. 57. *Melicertum octocostatum* (A, C from Russell, 1953; B from Kramp, 1933).

Recorded: Not recorded off Plymouth, but Russell (1953) gives records from nearby Falmouth harbour. Eastern and western Scotland. North-west and south-west Ireland. Irish Sea.
Size: Umbrella height when fully grown 11-13 mm, 10-14 mm in diameter.
Further information: Kramp, 1933, 1961; Russell, 1953; Bouillon & Boero, 2000.

Family Mitrocomidae:

Genus *Mitrocomella*:

*Mitrocomella brownei (*Kramp, 1930)

Umbrella usually flat, jelly thin; stomach quadratic, short with small base (Fig 58A, B); mouth with four simple lips. Gonads oval in male, sausage-shaped in female, situated near outer ends of the four radial canals. Marginal tentacles 11-24 but normally 16, with broad rounded bases (Fig. 58F); six to eight coiled marginal cirri between adjacent marginal tentacles (Fig. 58D-F); eight to 11, typically eight, open marginal vesicles around umbrella margin (Fig. 58E).

When newly liberated has four perradial and four interradial tentacles (Fig. 58A); gonads distinct though small, situated midway along the radial canals.

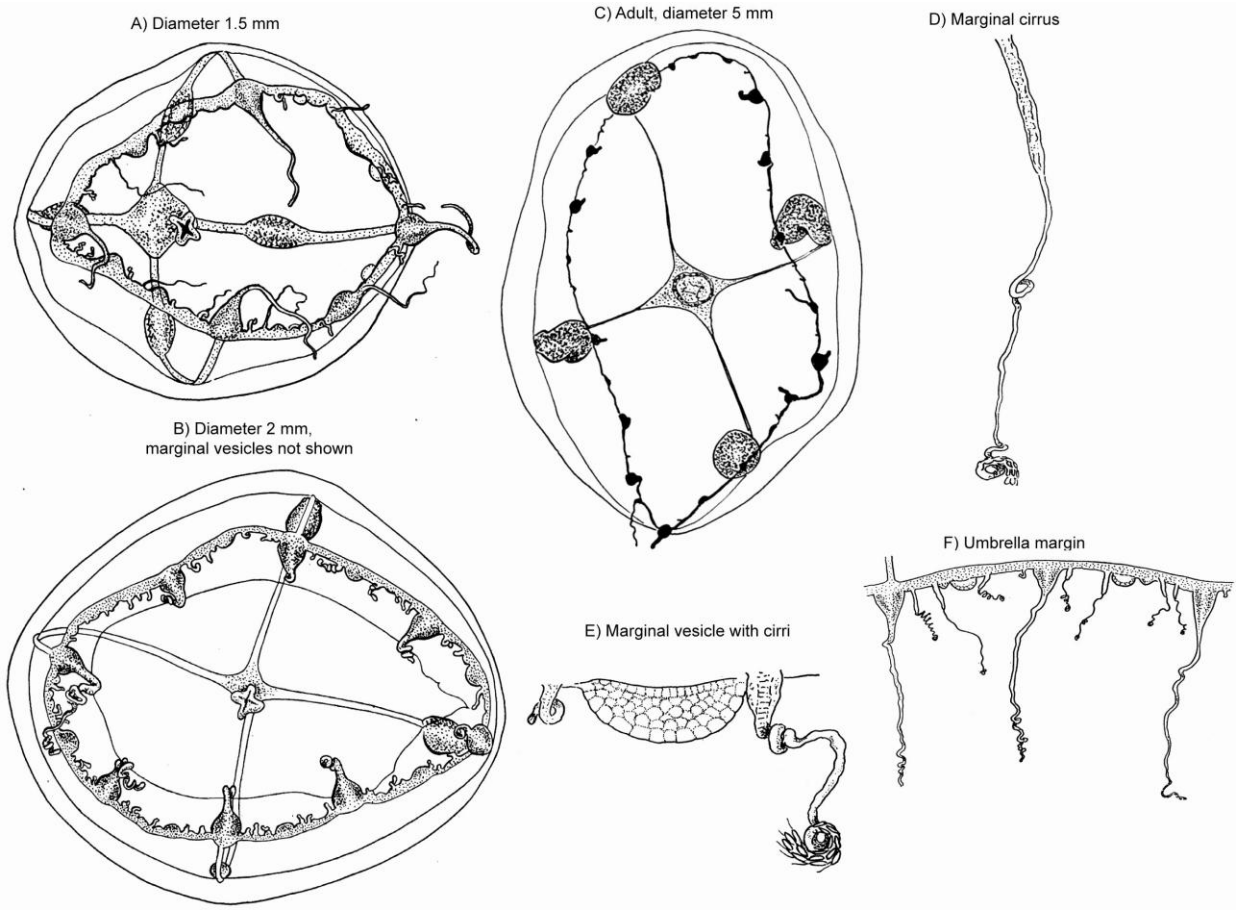


Fig. 58. *Mitrocomella brownei* (from Russell, 1953).

Recorded: PMF. L4, rare. Western English Channel. Southern Ireland. Irish Sea.
Size: Umbrella ~1.5 mm in diameter on liberation; 4-7 mm when fully grown.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Genus *Cosmetira*:

Cosmetira pilosella Forbes, 1848

Umbrella hemispherical or flattened; jelly thickened in apex; stomach short quadratic with very broad base (Fig. 59B), attached to sub-umbrella along arms of perradial cross, leaving four triangular pouches (Fig. 59C); mouth lips crenulated; four straight narrow radial canals; linear gonads on canals, slightly sinuous, half to three-quarters length of canals, slightly nearer umbrella margin than stomach, with median division. Marginal tentacles 65-100 with large rounded bases (Fig. 59D), conspicuously deep purple/black in colour; no ocelli; six to ten marginal cirri between adjacent marginal tentacles, older cirri extending up exumbrella surface; eight open marginal vesicles.

Bell-shaped when liberated, with a slightly conical apex; stomach short without lips, no signs of gonads; two opposing perradial marginal tentacles and two bulbs without tentacles; eight spirally coiled marginal cirri. By ~1 mm in height marginal vesicles started to appear. By ~1.7 mm high and 1.8 mm wide there were still only four marginal tentacles and four bulbs, and around four marginal cirri in each octant; gonads were starting to appear. At a diameter of ~5 mm the medusae had the adult characters.

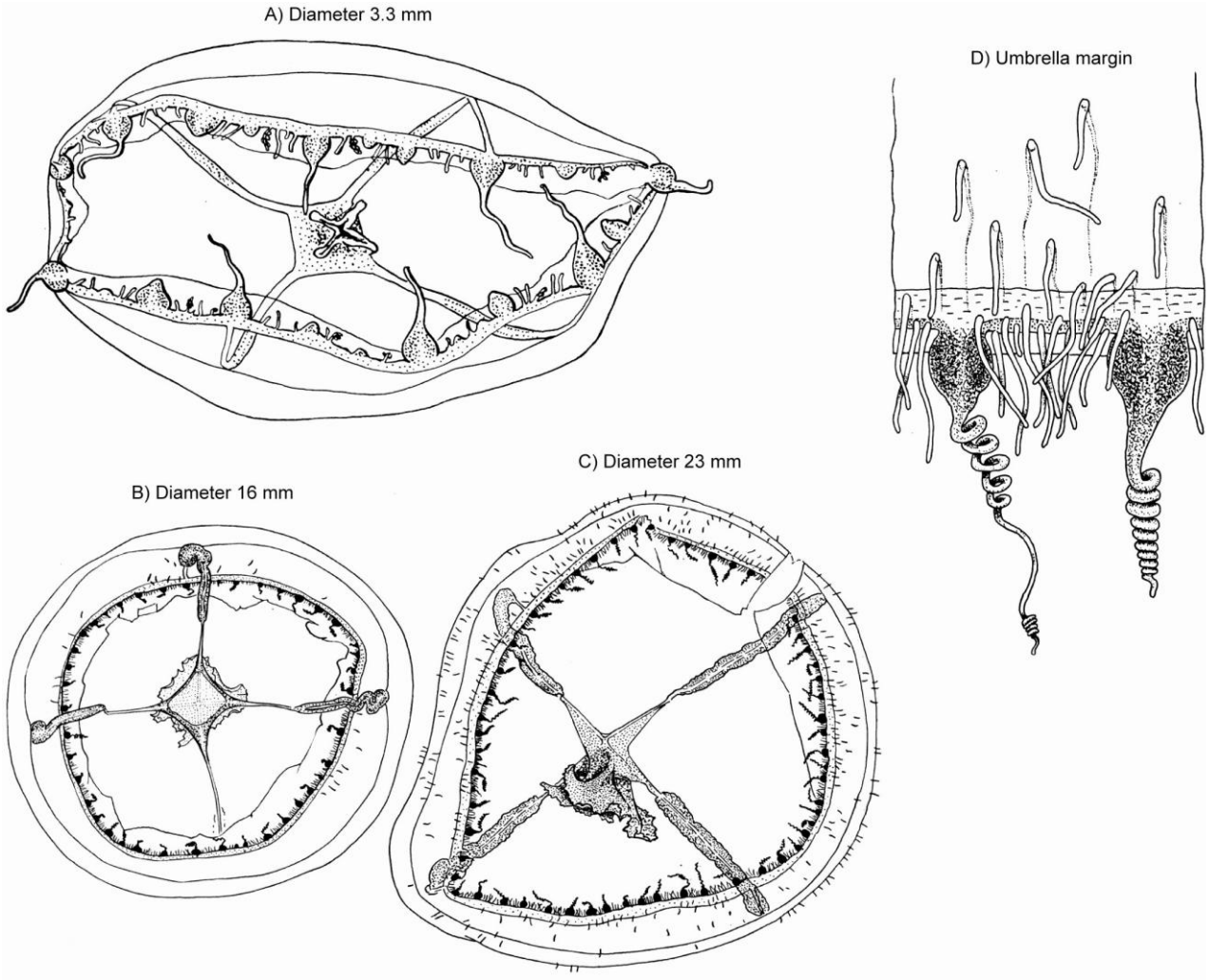


Fig. 59. *Cosmetira pilosella* (from Russell, 1953).

Recorded: PMF. L4, rare. All around Britain. North Sea. Irish Sea. Particularly where there is influence of Atlantic water.

Size: Umbrella ~0.75 mm in height on liberation; 20-48 mm in diameter when fully grown.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Family Tiaropsidae:

Genus *Tiaropsis*:

Tiaropsis multicirrata (Sars, 1835)

Umbrella slightly flatter than a hemisphere (Fig. 60A); jelly quite thick at apex; velum well developed; stomach short, on a short broad peduncle, attached to subumbrella along arms of radial canals, leaving small, flat triangular pouches. Mouth with four, quite long and broad lips, with folded margins; four straight radial canals (Fig. 60A, B); gonads on middle of radial canals, not reaching umbrella margin, linear and sometimes sinuous, with median divisions in both sexes. Marginal tentacles 200-300 in number, with swollen bases and no ocelli or marginal cirri (Fig. 60C). Eight open marginal vesicles with an ocellus at the base (Fig. 60C, D).

Bell-shaped when newly liberated; jelly thin; velum narrow; stomach short with a quadrangular base; mouth with four simple lips; no gonads apparent; ~24 marginal tentacles, the bases of the four perradial and interradial tentacles well developed compared to the other tentacles; eight open marginal vesicles with an ocellus.

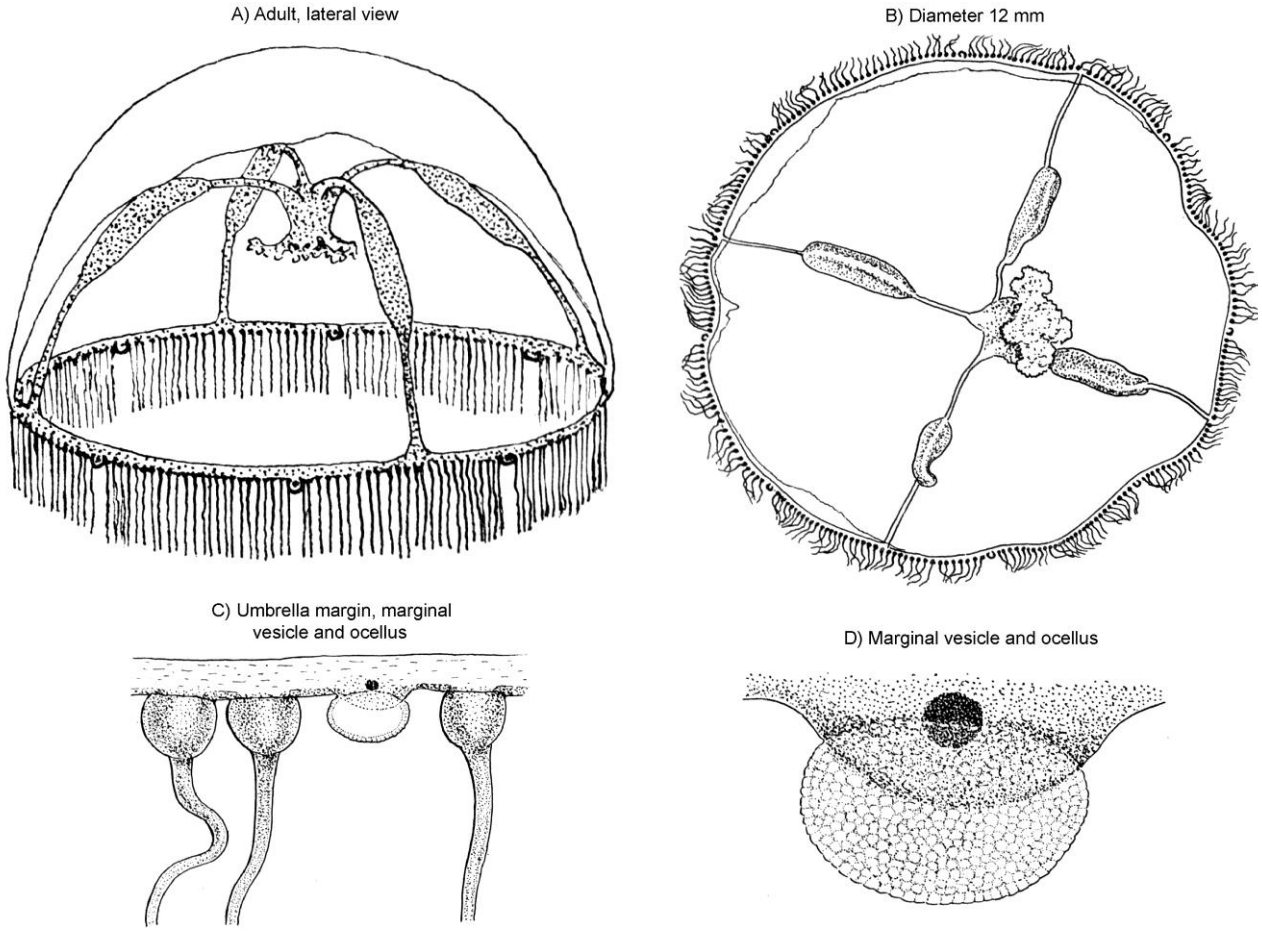


Fig. 60. *Tiaropsis multicirrata* (from Russell, 1953).

Recorded: PMF. L4, not recorded. All around Britain. Southern Ireland. Irish Sea. North Sea. Commoner in northern waters.

Size: Umbrella height ~1 mm on liberation; ~20 mm in diameter when fully grown.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Hydroidolina: Order Leptothecata: Suborder Conica:

Family Lovenellidae:

Genus *Lovenella:*

Lovenella clausa (Lovén, 1836)

Similar to *Clytia hemisphaerica*, distinguishable by presence of one to three spiral lateral cirri at base of tentacle bulbs and generally larger tentacle bulbs (Fig. 61A, D). Umbrella hemispherical, jelly moderately thick; stomach short, without peduncle (Fig. 61A); mouth with four simple lips. Four straight radial canals; gonads on canals, semicircular, divided longitudinally (Fig 61B, C), situated close to umbrella margin. From 16-24 marginal tentacles; 16-23 closed marginal vesicles, alternating approximately with tentacles (Fig. 61D).

When liberated bell-shaped and jelly thin (Fig. 61E); velum well developed; stomach short; mouth simple without lips; no traces of gonads; two opposing perradial marginal tentacles with one small or rudimentary cirrus on either side; two opposing marginal bulbs without tentacles or cirri; four interradial marginal cirri on the bell margin, one in each quadrant; four closed marginal vesicles. Tentacles, cirri, gonads and further marginal vesicles progressively develop (Fig. 61F-J).

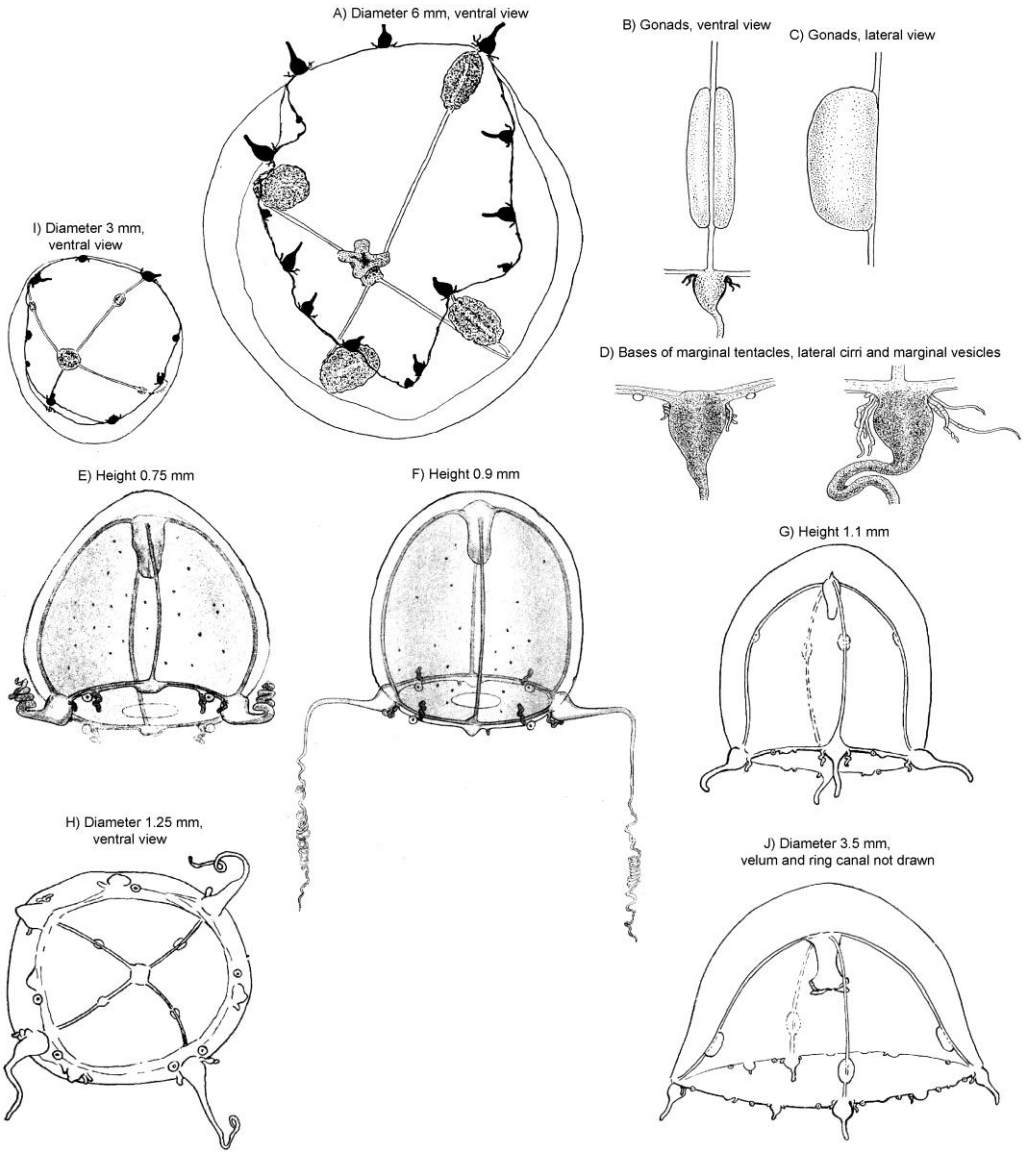


Fig. 61. *Lovenella clausa* (A-F, I from Russell, 1953; G, H, J from Russell, 1936, as *Eucheilota hartlaubi*).

Recorded: PMF. L4, rare. Southern Ireland. Irish Sea. English Channel. Southern North Sea.
Size: Umbrella ~0.75 mm in height and diameter when newly liberated; 5-9 mm when fully grown.
Further information: Russell, 1936 (as *Eucheilota hartlaubi*), 1953; Kramp, 1961; Bouillon & Boero, 2000.

PHYLUM CNIDARIA: Class Hydrozoa: Subclass Hydroidolina: Order Leptothecata: Suborder Conica:

Family Phialellidae:

Genus *Phialella*:

Phialella quadrata (Forbes, 1848)

Superficially resembles *Clytia hemisphaerica*, but has a fixed number of eight closed marginal vesicles (Fig. 62A-C, F) rather than one to three (or more) between each marginal tentacle. Jelly very thick, especially in apical region (Fig. 62B), compared to thin in *C. hemisphaerica*. Umbrella nearly hemispherical; velum well developed; stomach short with no peduncle, mouth with four short lips, with slightly folded margins. Some specimens have four black spots at the base of the stomach, visible from above, one in each interradius. Elongated gonads on outer third of the four radial canals (Fig. 62C, D), but not reaching the umbrella margin, gonads with median furrows; 16-32 marginal tentacles with globular bases (Fig. 62E), no ocelli; no marginal or lateral cirri.

When newly liberated bell-shaped, jelly quite thick (Fig. 62A); velum broad; stomach short, mouth with four small lips; the four gonads visible as swellings in the middle of the radial canals; four perradial marginal tentacles and rudiments of four interradial bulbs; eight adradial marginal vesicles.

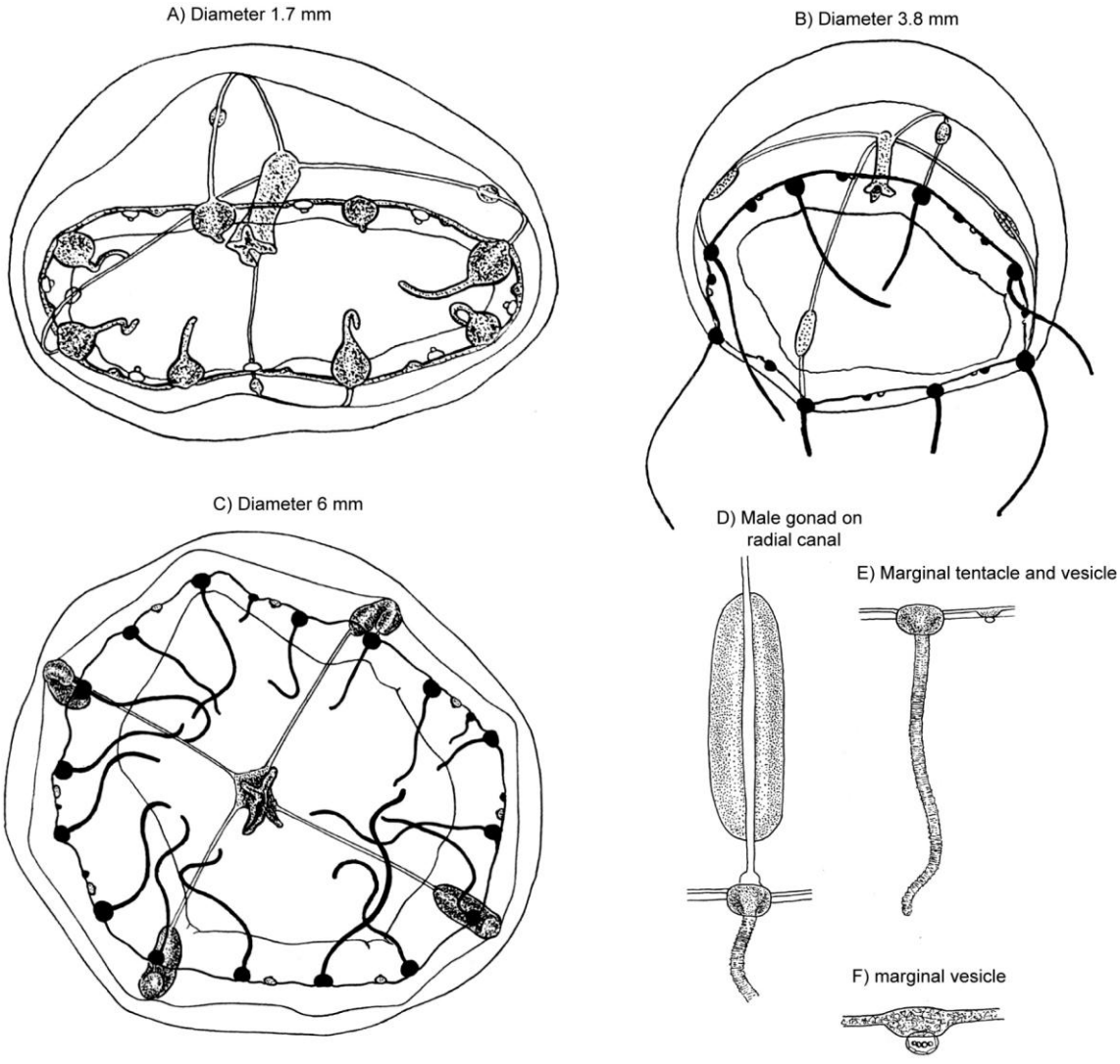


Fig. 62. *Phialella quadrata* (from Russell, 1953).

Recorded: PMF. L4, occasional. Western Britain. Northern North Sea.

Size: Umbrella ~1.5 mm in height when newly liberated and ~1 mm in diameter; up to 13 mm in diameter when fully developed.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Family Tiarannidae:

Genus *Modeeria*:

Modeeria rotunda (Quoy & Gaimard, 1827)

This medusa was previously included in Order Anthothecata. Umbrella hemispherical, about as wide as high or wider (Fig. 63A); jelly very thick; stomach short and broad, mouth with slightly crenulated lips. Four straight radial canals emerging from lower corners of stomach, at junction with mouth; gonads transversely folded, on interradial walls of stomach. Marginal tentacles usually 16, but may be up to 28, with conical bulbs. One to three, rarely five spindle-shaped marginal cordylus-like structures between adjacent marginal tentacles (Fig. 63C); no ocelli.

At 1.5 mm the stomach is relatively large (Fig. 63B), attached to umbrella along perradii only; mouth large, quadrate, with four simple lips; four radial canals, narrow and smooth; four perradial marginal tentacles with large conical basal bulbs; four interradial bulbs without tentacles and eight adradial marginal swellings. The cordylus structures develop when the medusa is slightly larger.

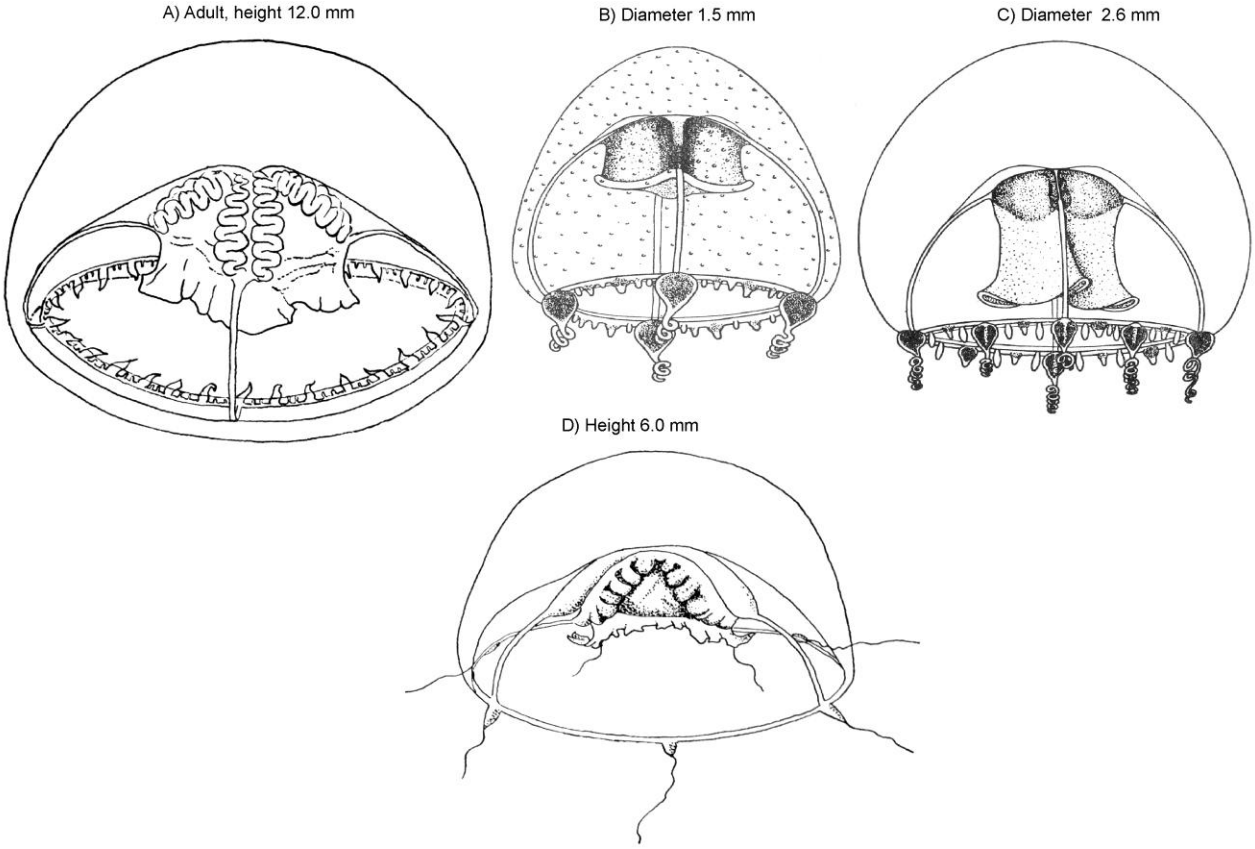


Fig. 63. *Modeeria rotunda* (A from Russell, 1953; B, C from Edwards, 1963; D from Kramp, 1959 (all as *Tiaranna rotunda*).

Recorded: PMF, medusae not sampled off Plymouth, but polyps (as *Stegopoma fastigiata*) have been recorded near the Eddystone lighthouse. L4, not recorded. Western Scotland. Northern North Sea.

Size: Up to 22 mm in diameter when fully grown.

Further information: Russell, 1953, 1970; Kramp, 1959, 1961; Edwards, 1963 (all as *T. rotunda*); Bouillon & Boero, 2000.

Family Eirenidae:

Genus *Eirene*:

Eirene viridula (Péron & Lesueur, 1809)

Umbrella hemispherical, thick in upper portion; stomach short, on elongated conical peduncle extended a short distance along radial canals (Fig. 64), peduncle extending beyond umbrella margin; mouth with four long perradial lips with crenulated margins; velum narrow; four straight radial canals. Gonads do not extend onto peduncle, reaching almost to umbrella margin, straight or slightly sinuous (Fig. 64C), completely surrounding lower wall of radial canal. Up to 70 or more marginal tentacles of rather unequal size, with conical bases; no marginal or lateral cirri; 50 or more closed marginal vesicles.

In young stages, at a diameter of 1.5 mm the umbrella is bell-shaped and the jelly thick; stomach short with no peduncle; mouth with four distinct short lips; gonads not visible, four perradial marginal tentacles with rounded bases; eight marginal vesicles, one each side of the marginal tentacles. It resembles a newly liberated *Clytia hemisphaerica*, but has no gonads or interradial tentacular marginal bulbs. By 2.0-2.5 mm the peduncle is indicated as a lens-shaped thickening at the stomach base; small gonads may be present; rudiments of four further tentacular bulbs may be present. The gonads if present are more elongated than in *C. hemisphaerica*.

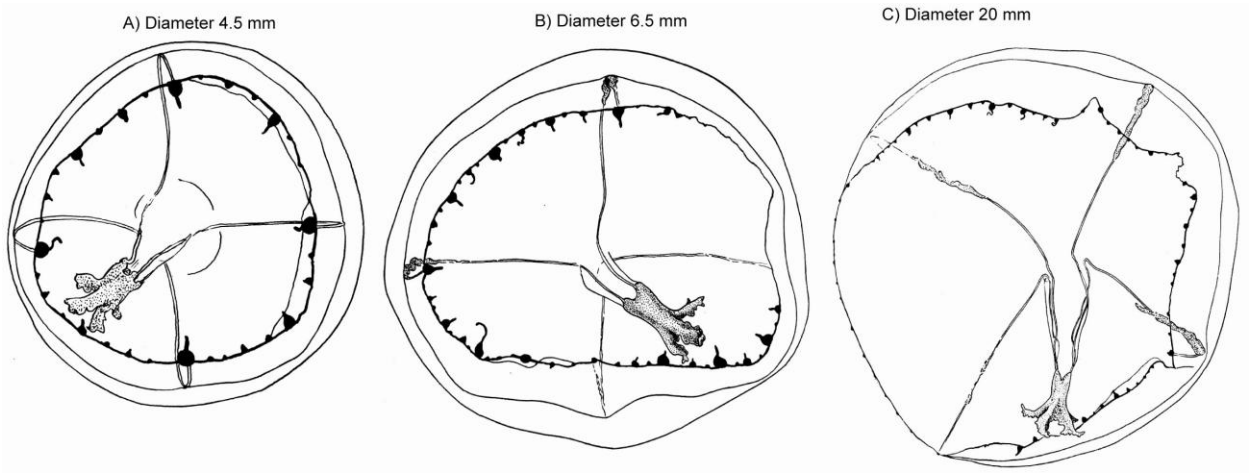


Fig. 64. *Eirene viridula* (from Russell, 1953).

Recorded: PMF. L4, not recorded. English Channel. Southern North Sea. Western Scotland.
Size: 20-30 mm or more in diameter when fully grown.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Genus *Helgicirrha*:

Helgicirrha schulzei Hartlaub, 1909

Umbrella flatter than a hemisphere (Fig. 65C); jelly quite thick; velum narrow; stomach short, on a narrow elongated conical peduncle that extends just beyond umbrella margin; mouth with four short slightly upturned lips with folded margins (Fig. 65D). Four straight or slightly sinuous narrow radial canals; gonads on radial canal, usually limited to the outer umbrella, but may extend to near base of peduncle (Fig. 65A-C). Up to 30-40 large marginal tentacles with elongated bases, with or without spiral lateral cirri (Fig. 65E). Up to 100 or more small marginal tentacles or rudimentary marginal tentacle bulbs, each with one or a pair of lateral cirri. Up to 50 or more closed marginal vesicles.

There is little information on the earliest stages. When 3 mm in diameter they were hemispherical with quite thick jelly and well developed peduncle (Fig. 65F); four well developed perradial marginal tentacles, each with a lateral cirrus; four developing interradial marginal bulbs with lateral cirri developing; eight adradial marginal vesicles; gonads just starting to develop about halfway along the radial canals. By 4.5 mm in diameter there were four fully developed perradial marginal tentacles; four well developed interradial marginal bulbs, still without tentacles; rudiments of eight adradial marginal bulbs; gonads starting to elongate.

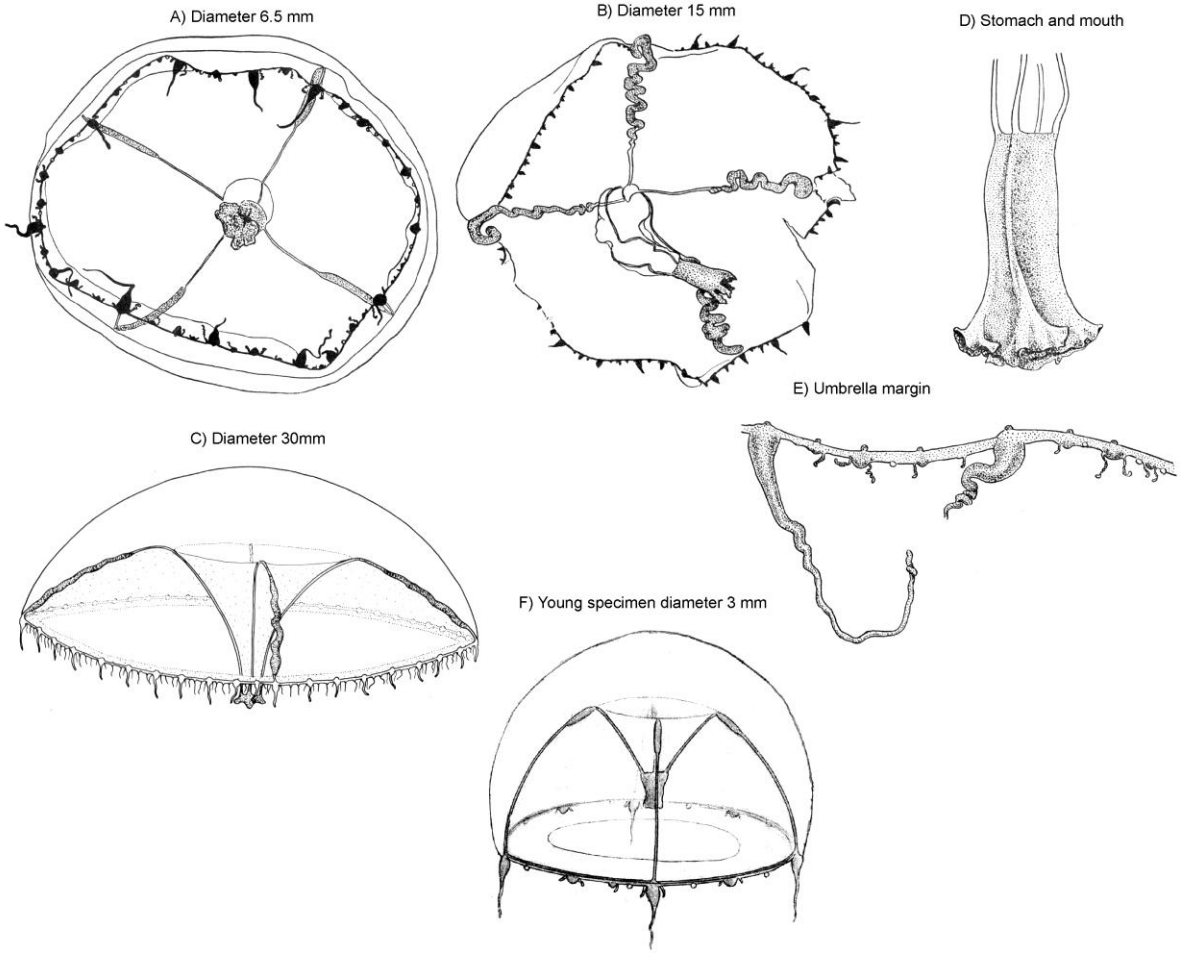


Fig. 65. *Helgicirrha schulzei* (from Russell, 1953).

Recorded: PMF. L4, not recorded. Western English Channel. Southern Ireland. Southern North Sea.

Size: 30-40 mm in diameter when fully grown.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Genus *Eutima*:

Eutima gracilis (Forbes & Goodsir, 1853)

Jelly thick, especially on apex (Fig. 66A-C); velum narrow; stomach short (Fig. 66D), cross-shaped in section, situated on long, narrow peduncle that extends far beyond umbrella margin; mouth with four simple lips; four straight radial canals; gonads not on subumbrella, restricted to peduncle, extending almost from base of peduncle to stomach. Two long opposing marginal tentacles, but there is a variety (*insignis*) that has four tentacles (Fig. 66C). Tentacle bases not swollen (Fig. 66E), with spiral lateral cirri on either side and usually one either side of most of the 50-80 or more marginal swellings; eight closed marginal vesicles.

Russell (1953) reproduced illustrations from Browne (1896; Fig. 66H) of a newly liberated medusa sampled at Plymouth that he considered could be this species, which differs slightly from an unpublished illustration of a similarly newly liberated medusae of this species by Werner (Fig. 66G, I; in Russell, 1970).

When newly liberated the umbrella is bell-shaped; stomach short with no peduncle; no sign of gonads; two opposing marginal tentacles and two opposing marginal bulbs without tentacles; lateral cirri on both sides or only one side of each marginal tentacle and bulb; cirri also present where interradial marginal bulbs will develop; eight closed marginal vesicles.

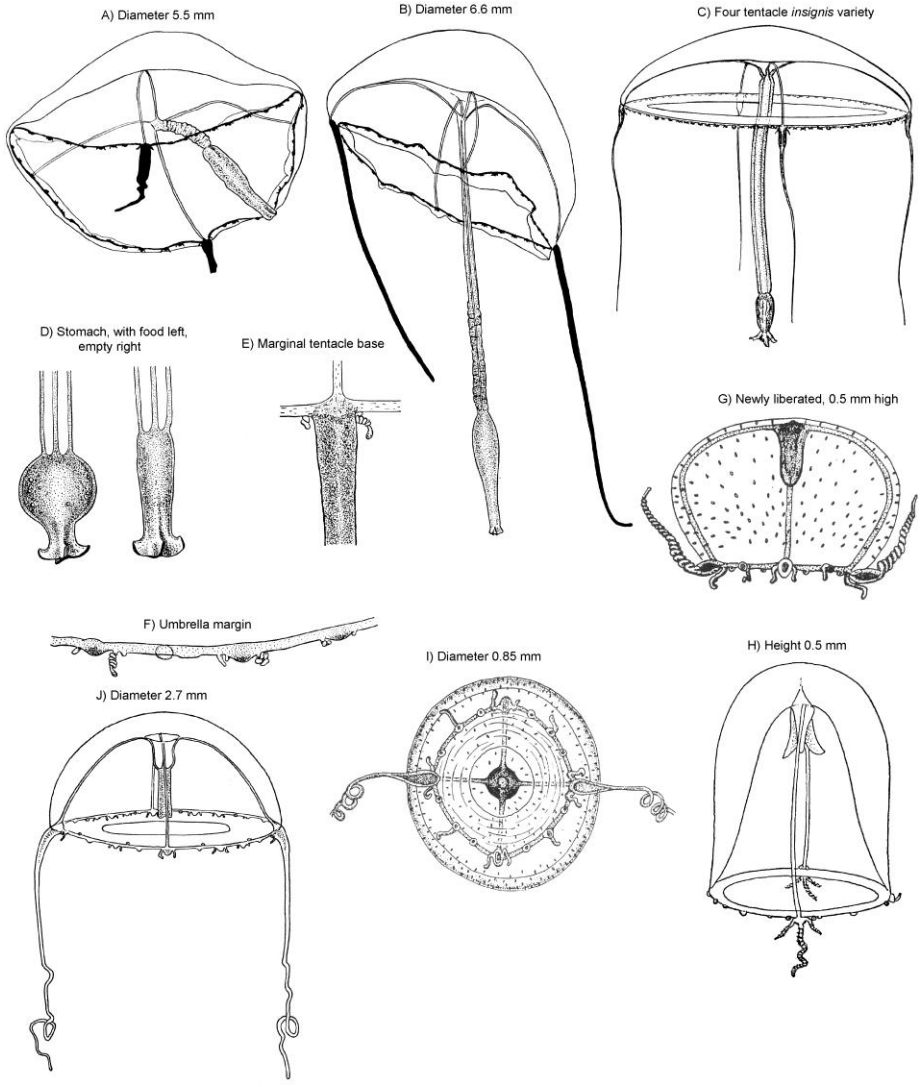


Fig. 66. *Eutima gracilis* (A-F, H, J from Russell, 1953; G, I from Werner unpublished, in Russell, 1970).

Recorded: PMF. L4, occasional. British coast, except south-east. Southern North Sea.

Size: Umbrella height when newly liberated ~0.5 mm and 0.85 mm in diameter; up to 13 mm in diameter when fully grown

Further information: Russell, 1953, 1970; Kramp, 1961; Bouillon & Boero, 2000.

Eutima gegenbauri (Haeckel, 1864)
Umbrella nearly hemispherical, jelly thick, especially in the apical region; stomach short, cross-shaped in section, on a long narrow peduncle with a wide base (Fig. 67B-D); mouth with four lips and crenulated margins; four straight radial canals; eight gonads, four on radial canals on subumbrella, each extending from base of peduncle nearly to ring canal, and four on radial canals on middle third of peduncle (Fig. 67D). Eight to 16, sometimes more, thick marginal tentacles, without distinct swelling at base (Fig. 67E); 60-80 or more marginal swellings with one, rarely two, spiral lateral cirri either side; eight closed marginal vesicles.
When newly liberated umbrella bell-shaped, higher than wide with a broad velum (Fig. 67F, G); jelly thin; stomach short and mouth simple; four radial canals and no signs of gonads; two opposing marginal tentacles and two opposing marginal bulbs without tentacles. Lateral cirri on both sides, or only one side of each marginal bulb; rudiments of four interradial marginal bulbs appearing, indicated by cirri; eight closed marginal vesicles.

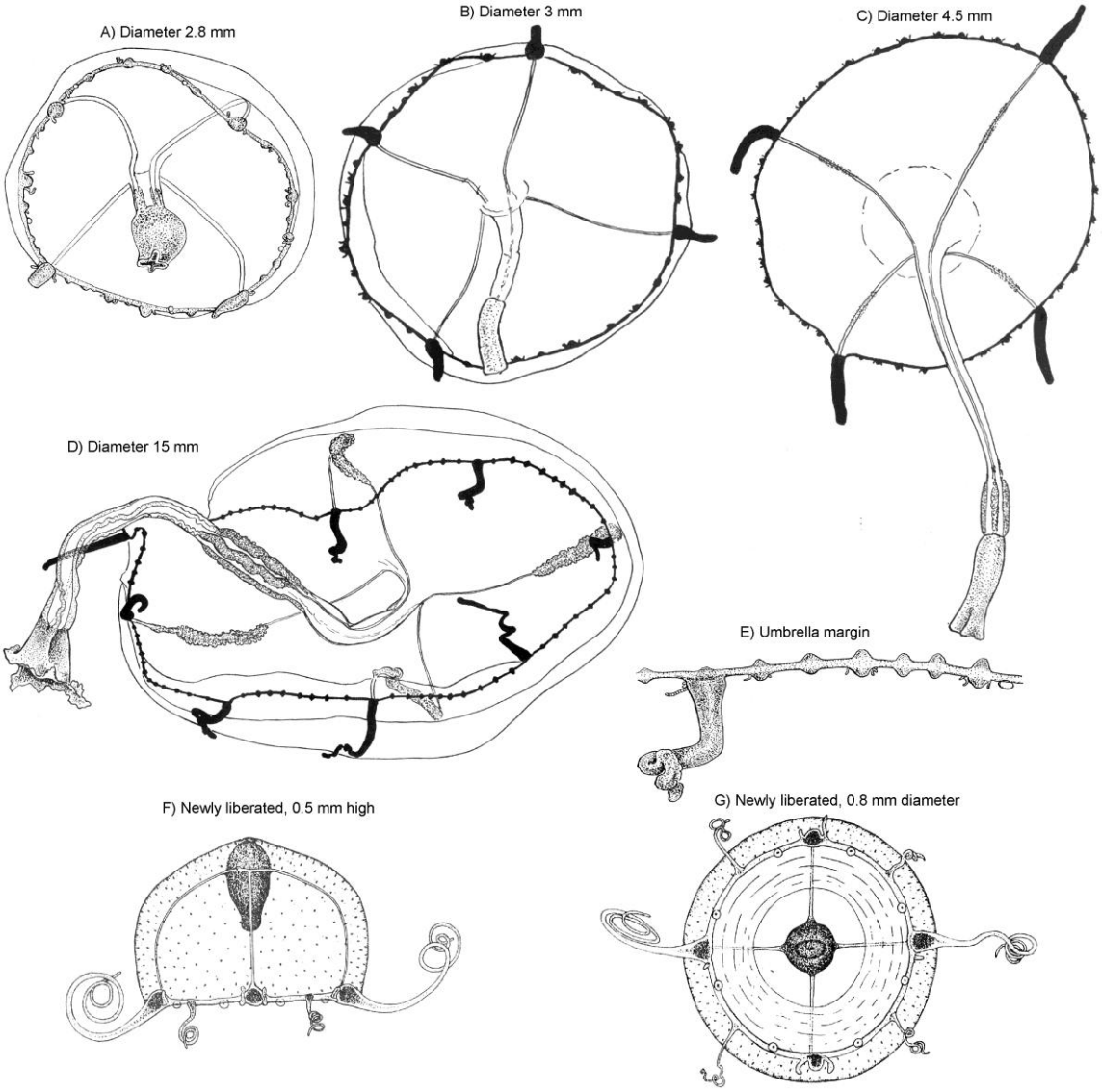


Fig. 67. *Eutima gegenbauri* (A-E from Russell, 1953, as *Octorchis gegenbauri*; F, G from Werner unpublished, in Russell, 1970).

Recorded: PMF (as *Octorchis gegenbauri*). L4, not recorded. English Channel. Southern Ireland. Western Scotland. Southern North Sea.
Size: Umbrella height when newly liberated ~0.5 mm, ~0.8 mm in diameter; up to ~20 mm in diameter when fully grown
Further information: Russell, 1953; Kramp, 1959 (both as *O. gegenbauri*); Russell, 1970; Bouillon & Boero, 2000.

Family Aequoreidae:

Genus *Aequorea:*

Aequorea forskalea (Forsskål, 1775)

Umbrella flat, with solid jelly, thick in centre, thinning towards outer umbrella; velum narrow. Stomach large, diameter of base variable, usually around half the diameter of the umbrella (Fig. 68B); mouth lips elongated with crenulated margins; radial canals straight and narrow, number variable but usually around 60-80. Gonads linear, on both sides of each radial canal, leaving short sections at distal and proximal ends free; marginal tentacles approximately the same number as radial canals, but varying from half to twice their number, irregularly distributed, with elongated conical bases, narrowing distally (Fig. 68C); partially developed tentacle bulbs often present; closed marginal vesicles numerous, about five to ten between adjacent radial canals.

When newly liberated, bell-shaped with two opposite marginal tentacles and two opposite tentacle bulbs without tentacles (Fig. 68A); eight closed marginal vesicles.

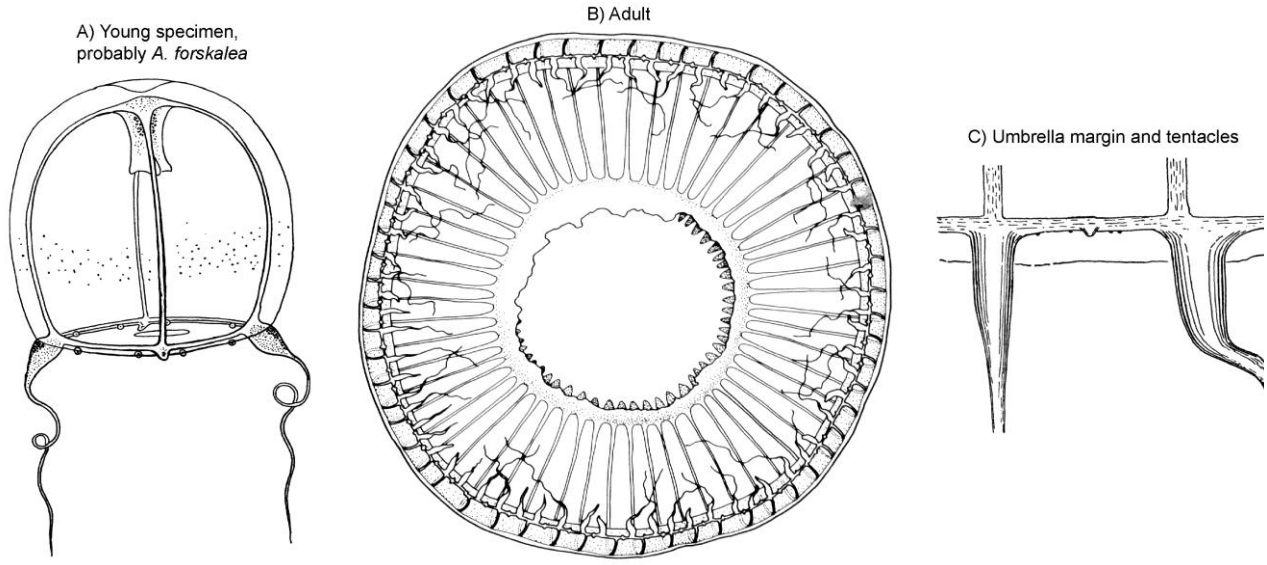


Fig. 68. *Aequorea forskalea* (A, C from Russell, 1953; B from Pagès et al., 1992, drawn by J. Corbera).

Recorded: PMF. L4, not recorded. Western English Channel. Southern Ireland. Eastern Scotland. North Sea.

Size: Umbrella up to 175 mm in diameter when fully grown.

Further information: Russell, 1953; Kramp, 1961; Pagès *et al*., 1992 (as *A. aequorea*); Bouillon & Boero, 2000.

Aequorea vitrina Gosse, 1853
Umbrella saucer-shaped with solid transparent jelly, thickest in centre; velum narrow; stomach large, base diameter usually around half the diameter of umbrella (Fig. 69A), lateral walls very extensile with translucent lines radiating from approximately every alternate radial canal to mouth lips that are elongated with crenulated margins. Radial canals straight and narrow, usually ~60-90; gonads linear, on both sides of each radial canal, leaving short areas free of gonad at either end; marginal tentacles very numerous, always more than three times as many as radial canals, probably reaching 600 or more, packed closely around umbrella margin (Fig. 69B). One to two closed marginal vesicles between adjacent radial canals.

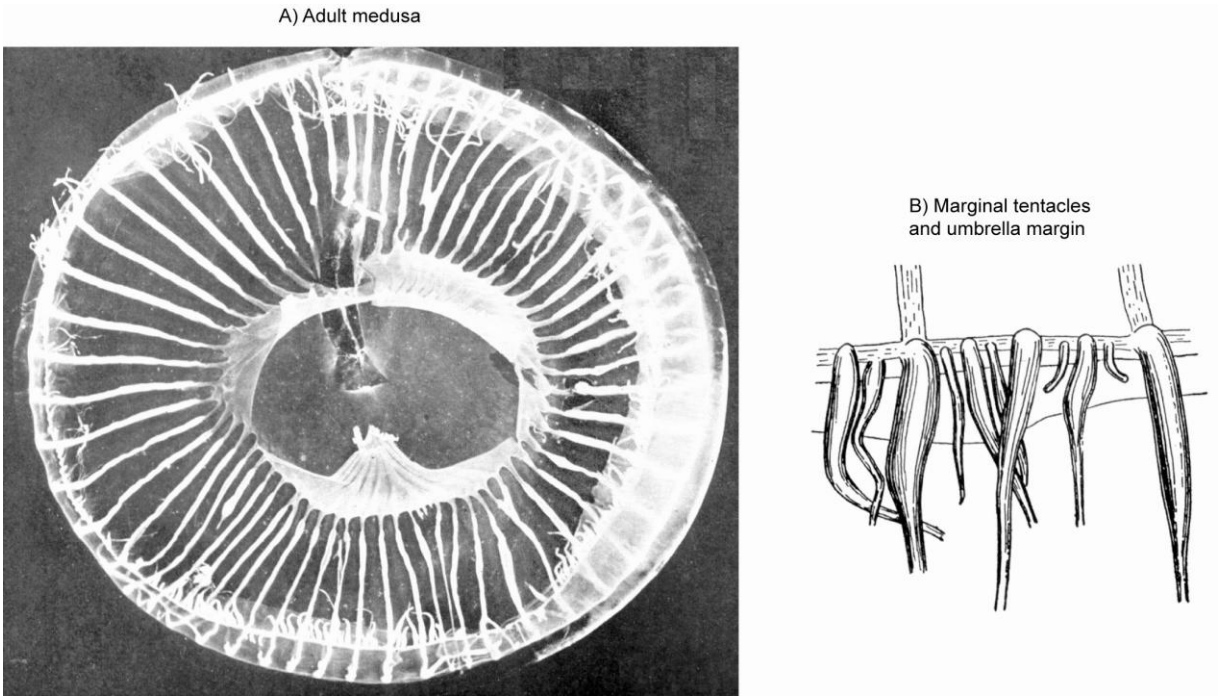


Fig. 69. *Aequorea vitrina* (from Russell, 1953).

Recorded: PMF. L4, not recorded. Western English Channel. Southern Ireland. Irish Sea. Eastern Scotland. Southern North Sea.
Size: Umbrella up to 170 mm in diameter.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Aequorea pensilis (Haeckel, 1879)
Umbrella saucer-shaped with solid transparent jelly, thickest in centre; velum narrow; stomach large, base diameter variable, usually around half the diameter of umbrella (Fig. 70A). Usually 120-180 straight and narrow radial canals, but may be half this number; gonads linear, on both sides of each radial canal, leaving short areas free of gonad at either end; marginal tentacles usually fewer than the radial canals (Fig. 70B), about 16, increasing to 40 or more in old specimens; hollow with short, laterally expanded conical bases, with median abaxial spur and ridge (Fig. 70C). Marginal bulbs and swellings numerous, up to nine between adjacent marginal tentacles (Fig. 70B); closed marginal vesicles extremely numerous, up to seven or eight between adjacent marginal bulbs, often closely crowded on umbrella margin (Fig. 70C).

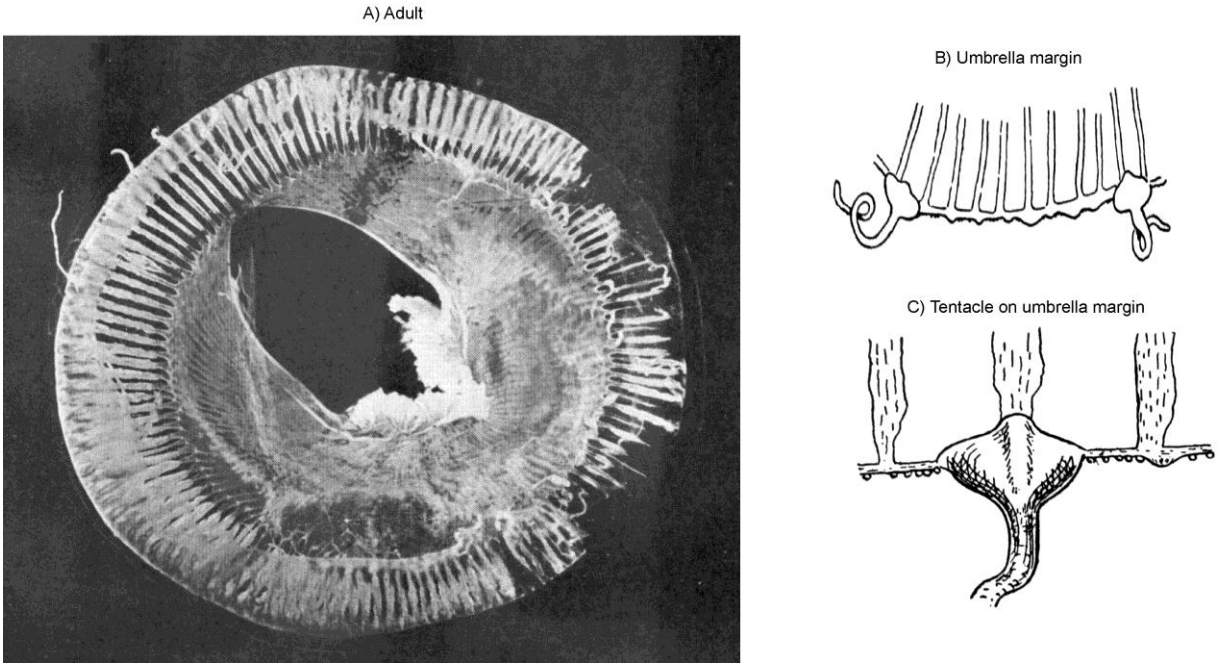


Fig. 70. *Aequorea pensilis* (A-C from Russell, 1953).

Recorded: PMF. L4, not recorded. Western English Channel. Southern Ireland.
Size: Umbrella up to 100 mm or more in diameter, but usually around 60 mm.
Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Suborder Proboscoida: Family Campanulariidae:

Genus *Clytia*:

Clytia hemisphaerica (Linnaeus, 1767)

Umbrella hemispherical or slightly flattened; jelly thin; stomach short, quadrate, without peduncle, mouth with four simple or folded lips (Fig. 71B-E). Four oval or straight gonads, on distal region of radial canals, extending over half to three-quarters of the canals, not quite reaching ring canal, continuous over lower wall of radial canal, so without median furrow; 16-32 marginal tentacles with prominent spherical bases (Fig. 63F, G); a few partially developed marginal bulbs; no ocelli, or marginal or lateral cirri. One to three, usually two, closed marginal vesicles between each pair of tentacles (Fig. 71F, H).

When newly liberated umbrella bell-shaped, jelly thin; the four gonads already visible on radial canals; four marginal tentacles, four marginal swellings and eight marginal vesicles. By ~2-3 mm the umbrella is more flattened and eight or more tentacles are fully developed (Fig. 71A).

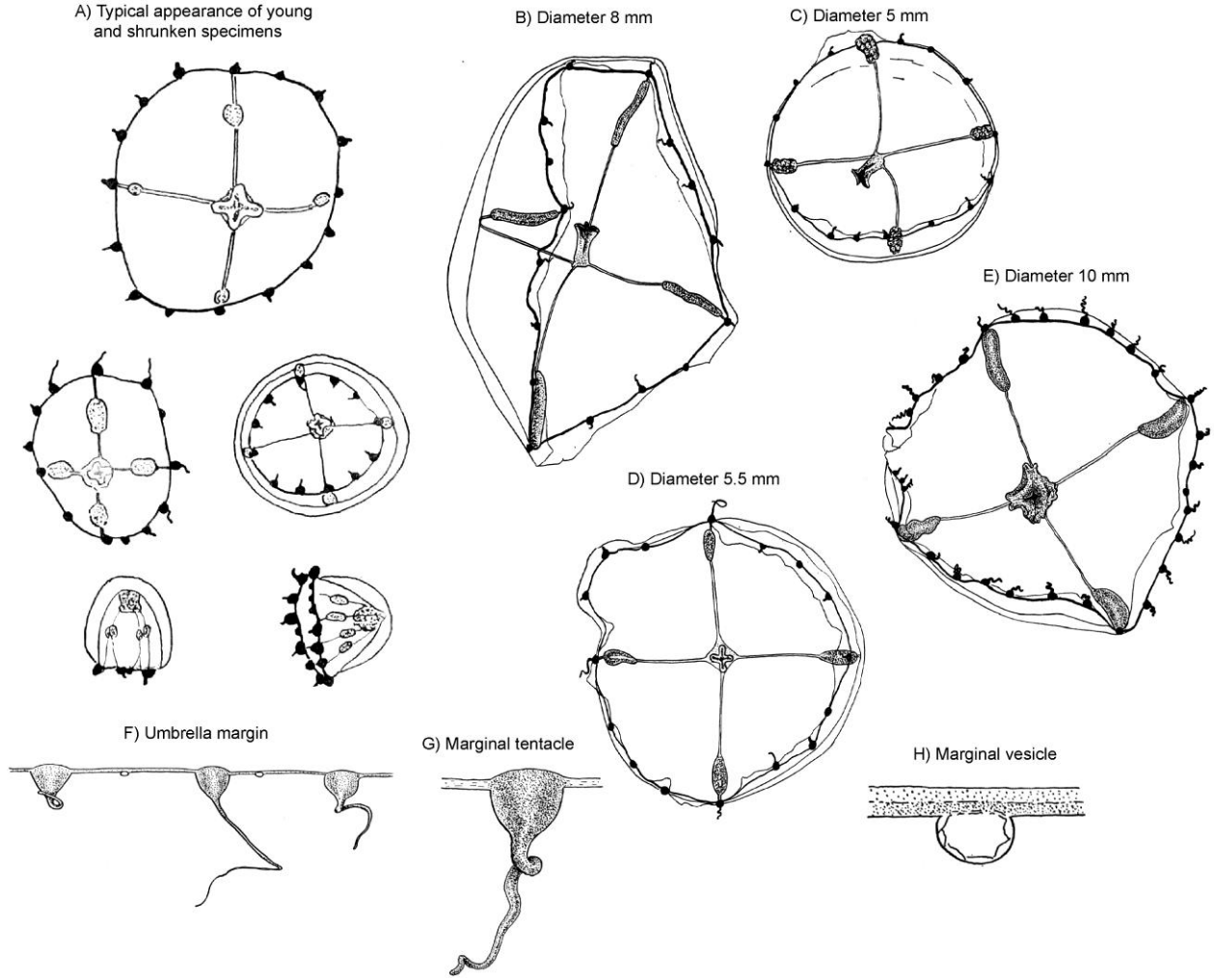


Fig. 71. *Clytia hemisphaerica* (from Russell, 1953).

Recorded: PMF (as *Phialidium hemisphaericum*). L4, common. All European area.

Size: Umbrella height ~0.75 mm when newly liberated; up to 20 mm in diameter when fully grown.

Further information: Russell, 1953; Kramp, 1961 (both as *P. hemisphaericum*); Bouillon & Boero, 2000.

Genus *Obelia:*

Obelia spp. Péron & Lesueur, 1810

There are several *Obelia* spp. and while the polyps can be identified, the medusae are very similar and cannot be identified with certainty unless cultured, so are generally recorded as *Obelia* spp.

Umbrella, flat and thin; velum rudimentary; stomach short without peduncle, with four simple lips (Fig. 72A); four straight radial canals with oval or circular gonads, situated around middle of canals. Many short marginal tentacles with basal bulbs that are usually dark brown/black, with endodermal roots (Fig. 72C); no ocelli. Eight adradial closed marginal vesicles on umbrella margin, situated on underside of a basal bulb (Fig. 72D).

On liberation 16-24 marginal tentacles; gonads absent, or visible as traces.

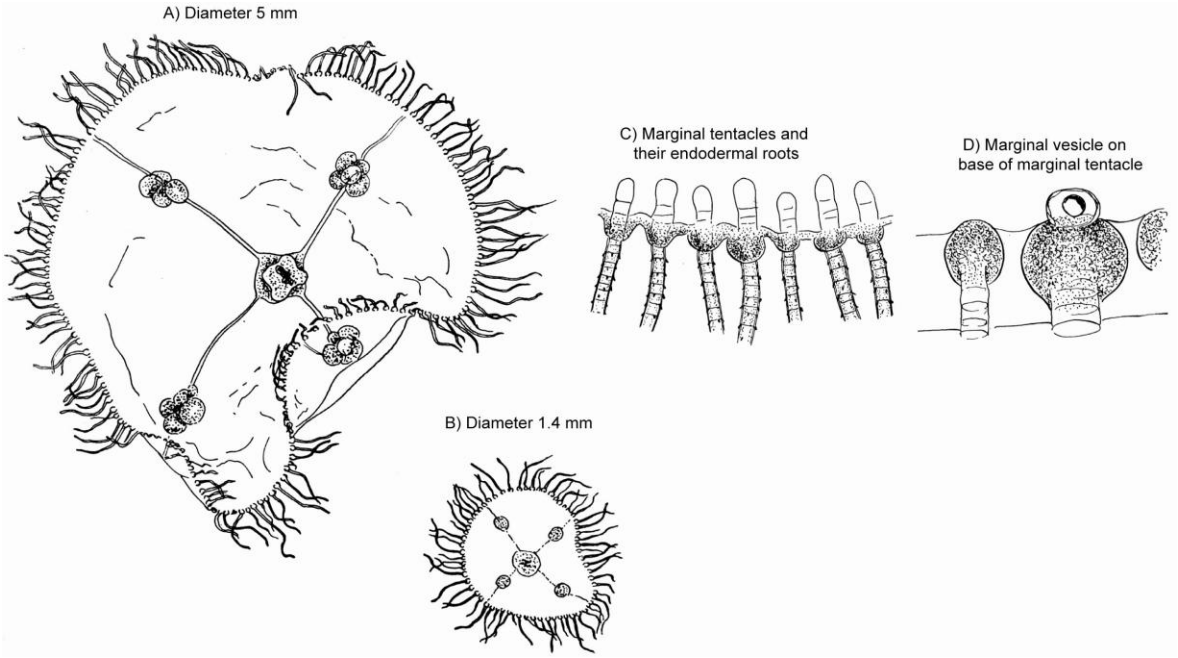


Fig. 72. *Obelia* sp. (from Russell, 1953).

Recorded: PMF. L4, very common. All European area.

Size: Umbrella ~1 mm in diameter on liberation; ~2.5-6.0 mm when fully grown.

Further information: Russell, 1953; Kramp, 1961; Bouillon & Boero, 2000.

Genus *Orthopyxis:*

Orthopyxis integra (MacGillivray, 1842)

Umbrella bell-shaped, higher than wide (Fig. 73); jelly thick; velum broad; no stomach, Four radial canals, either meeting at, or terminating before the apex; irregularly lobed outgrowths on middle portions of the radial canals, with gonads on lobes. No marginal tentacles, four small tentacle bulbs; no marginal or lateral cirri; eight closed marginal vesicles.

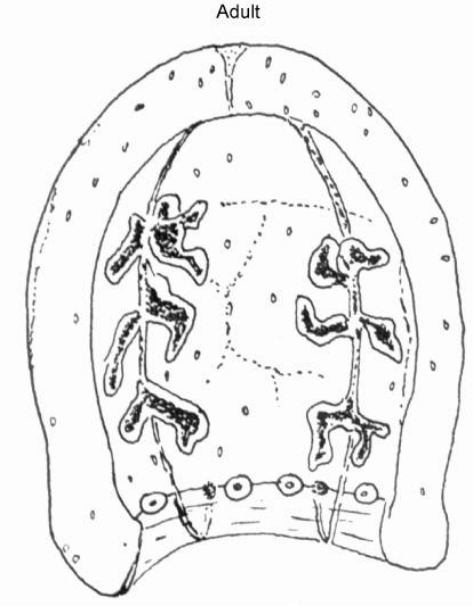


Fig. 73. *Orthopyxis integra* (from Russell, 1953).

Recorded: PMF (as *Agastra mira*). L4, not recorded. English Channel. Southern North Sea.
Size: Umbrella height ~1 mm.
Further information: Russell, 1953; Kramp, 1959, 1961 (all as *Agastra mira*); Bouillon & Boero, 2000.

Order Siphonophorae

The Order Siphonophorae is divided into three Suborders, **Cystonectae**, **Physonectae** and **Calycophorae**, on the basis of whether or not they have a gas-filled float called a pneumatophore, or swimming bells called nectophores.

Siphonophores differ in structure from the free-swimming stage of the other hydrozoa. They do not have an alternation of generation between an attached, asexual polyp stage and a free-swimming sexual medusa. They are colonial, composed of medusoid and polypoid zooids that are morphologically and functionally specialized. Medusoids may be released, but in many cases they remain as part of the colony. Siphonophores usually break up when caught in plankton nets, so it is often difficult to estimate the number of complete individuals in a sample. Because many of the structures found in siphonophores are only found in these organisms, a unique terminology has been developed.

The most useful siphonophore texts are Totton (1954, 1965), Kirkpatrick and Pugh (1984), Mackie *et al*. (1987), Pagès and Gili (1992) and Pugh (1999).

Suborder Cystonectae:

Siphonophores in Sub-order Cystonectae have no nectophores, only a large gas-filled pneumatophore.

Family Physaliidae:

Genus *Physalia:*

Physalia physalis (Linnaeus, 1758)

Commonly known as the Portuguese Man of War, this colonial species is the only member of this family found in the region. Because of its size it is familiar to many people who have seen it floating on the sea surface, stranded on a beach or have received a painful sting.

There is an apical gas-filled float or pneumatophore and nectophores are absent. Locomotion is by using the float as a sail and by water currents. Below the pneumatophore the stem region, or siphostome, bears polypoid and medusoid structures associated with feeding and reproduction. Parts attached to the organism cannot function on their own, but only as part of the colony.

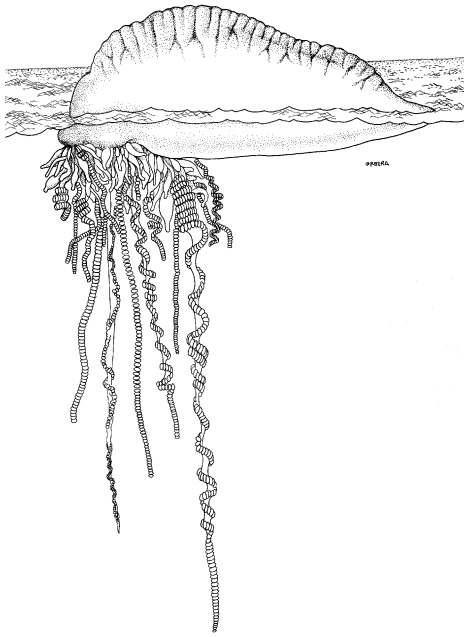


Fig. 74. *Physalia physalis* (from Pagès *et al*., 1992, drawn by J. Corbera).

Recorded: PMF. L4, not recorded. Western European coasts.

Size: Float up to 300 mm long and 150 mm above the water surface. Tentacles usually ~10 m in length, but up to 50 m.

Further information: Pagès *et al*., 1992; Wrobel & Mills, 1998.

Suborder Physonectae:

There are only a few species in Suborder Physonectae. They have a small terminal pneumatophore and a long central stalk or stem that forms a tube through which nutrition and body fluids pass (Fig. 75A). Different body parts are attached to the stalk in two regions. The nectosome region is situated just below the pneumatophore and usually only bears asexual (non-reproductive), medusoid nectophores (Fig. 75B), which are swimming bells used in jet propulsion. The morphology of the nectophores is an important characteristic used in identification. Physonectid colonies typically disintegrate in plankton nets, but their nectophores all have the same basic design, so are easily recognised. Below the nectosome lies the siphosome, which is usually the longest part of the organism. Here both polypoid and medusoid structures are attached to the stem. These have different functions and are arranged in a succession of groups called cormidia (Fig. 77B). Each cormidium bears a single gastrozooid, which is involved in feeding and digestion and usually has a tentacle and several small tentacles called tentilla (Fig. 75A), which are armed with nematocysts for capturing prey. Palpons, which are modified gastrozooids, are also usually present on the cormidia and may have a sensory or excretory function. These may also have a tentacle attached. The cormidia can also bear asexual nectophores and bracts composed of thick jelly (Fig. 75C). The bracts are probably for buoyancy, or protection of the other structures. In most physonectids the cormidia remains attached to the stem, although a part called the gonophore, which produces eggs and sperm can become detached and are equivalent to the eudoxid stage of other siphonophores. Only one egg is produced in each gonophore and fertilisation is external. A planuloid larva is produced which eventually develops a float, then progressively the other features.

Family Agalmatidae:

Genus *Agalma:*

Agalma elegans (Sars, 1846)

The pneumatophore is ovoid or elongated (Fig. 75A), usually with a spash of red pigment on top. There are no tentacles in the nectosomal region. The nectophores (Fig. 75B) can vary in shape depending on their age, their size and also their position on the siphosomal stalk. There are generally two lateral ridges either side, one of them an apico-lateral that sweeps down towards the ostium, the aperture where water is drawn in and expelled during locomotion, but these ridges can be missing or difficult to discern in smaller nectophores. The apical wings are generally long with square ends, but can be smaller with rounded ends. The nectosac is T-shaped and the radial canal at its apex is quite straight, extending outwards almost to each end, before looping ventrally behind and into two distinct undulations before coiling back laterally towards the ostium.

The bracts (Fig. 75C) are thin and leaf-like, ending in three projections that are missing in some of the smaller bracts. The convex dorsal side has three ridges on the distal half, often indistinct in smaller bracts. A bracteal canal extends to about four-fifths the length of the bract, occasionally continuing as a very fine canal to the distal tip.

The early post-larvae, termed ‘athorybia’ larvae (Fig. 75D, E) have four to six small, thick triangular bracts with serrated edges, below which develops a single gastrozooid.

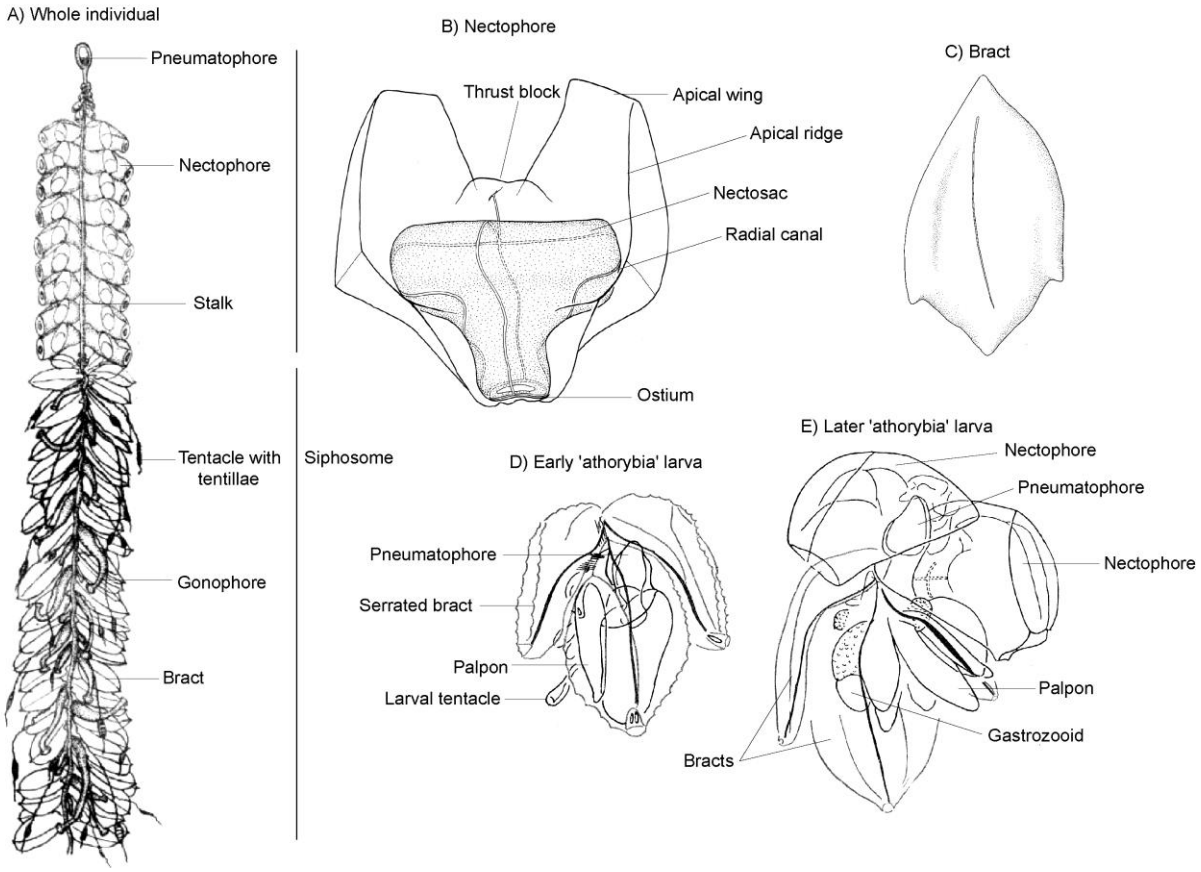


Fig. 75. *Agalma elegans (*A from Trégouboff & Rose, 1957; B-C from Pagès *et al*., 1992, D-E from Totton, 1956).

Recorded: PMF. L4, quite common. Northern North Sea. Exceptionally southern North Sea. Irish Sea. Southern Ireland. Western English Channel.

Size: Adult nectophore ~7 mm in length.

Further information: Vanhöffen, 1906; Totton & Fraser, 1955a; Totton, 1965; Kirkpatrick & Pugh, 1984; Pagès & Gili, 1992; Pugh, 1999.

Genus *Nanomia*:

Nanomia cara Agassiz, 1865

The complete colony (Fig. 76A) is similar in structure to an *Agalma elegans* colony.

The pneumatophore is small and ovoid with a red pigmented cap. There are no tentacles in the nectosomal region. The nectophores (Fig. 76B) can vary in shape depending on their age and position on the siphosomal stem. There is generally one lateral ridge either side but these can be missing or difficult to discern in smaller nectophores. The apical wings are generally shorter than in *A. elegans* with oblique rather than square ends, but can be variable in shape. The nectosac is Y-shaped. The tract of the radial canal differs from, and is more complex than that of *A. elegans*. It extends laterally, halfway along either side at the apex, before coiling onto the dorsal surface then back over onto the ventral surface and into a single undulation. It then coils back onto the dorsal surface and then laterally towards the ostium. The bracts are thin and leaf-like, of the general agalmid form.

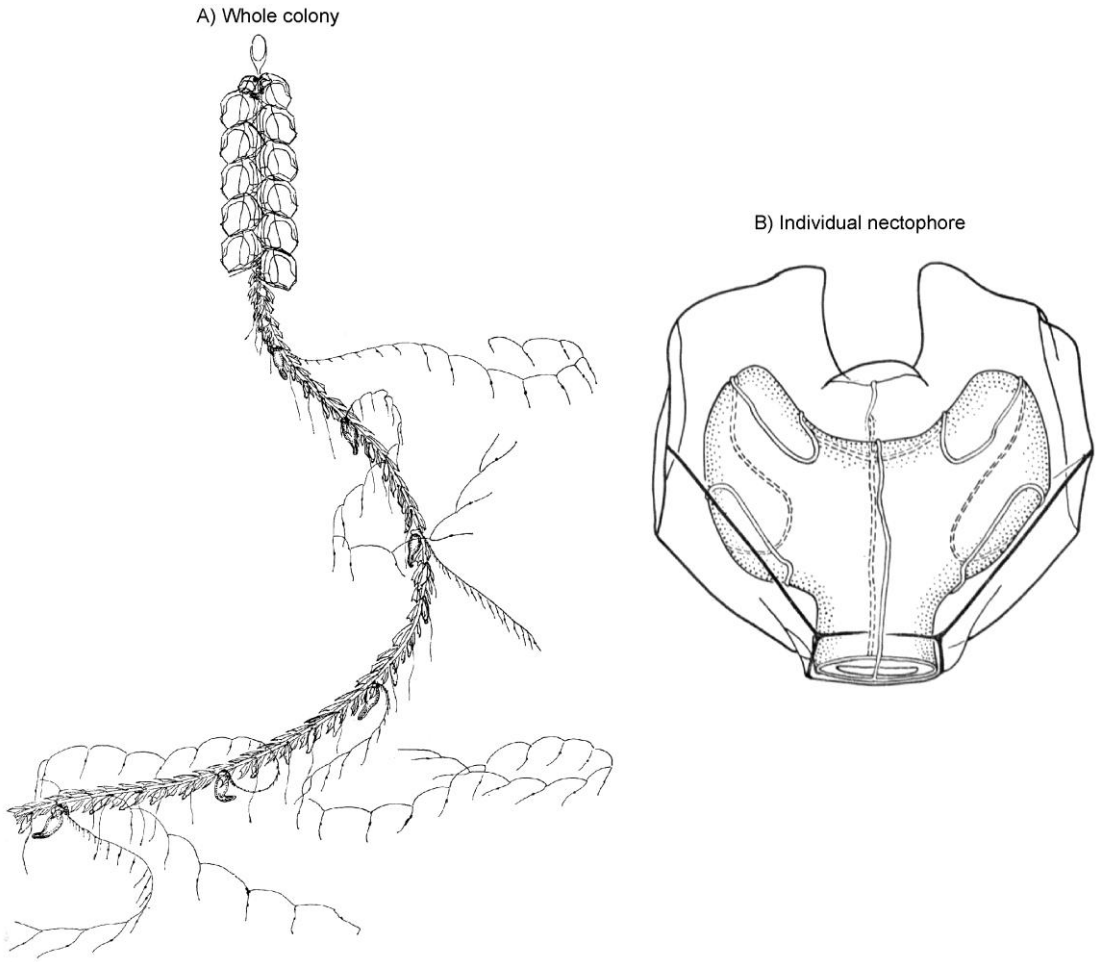


Fig. 76. *Nanomia cara.* (A from Mackie, 1964; B from Totton & Fraser, 1955a).

Recorded: PMF (as *N. bijuga*). L4, quite common. Northern North Sea. Irish Sea. Southern Ireland. Western English Channel.

Size: Adult nectophore ~10 mm in length.

Further information: Vanhöffen, 1906; Totton & Fraser, 1955a; Mackie, 1964; Totton, 1965; Kirkpatrick & Pugh, 1984; Pugh, 1999.

Family Apolemiidae:

Genus *Apolemia:*

Apolemia uvaria (Lesueur, 1815)

Commonly known as string jellies, the colonies can reach a remarkable length and can give a powerful sting. Live and freshly preserved they are pale orange in colour and in a sample present a confusing tangle of different components. The pneumatophore is bulb-shaped (Fig. 77A), widening near the apex and often with red tinges. There are five to six tentacles between each pair of nectophores in the nectosome region. The nectosome can have up to 12 nectophores in two parallel rows on the stem. The nectophores have pointed apical wings with a narrow, deep cleft between them (Fig. 77C). The nectosac is Y-shaped and has slightly sinuous lateral radial canals which may have numerous, short, blind-ending diverticulae near the axial wings. For some reason nectophores have not been sampled at Plymouth. The siphosome can be several metres in length, composed of many cormidia (Fig. 77A, B). Each cormidium consists of bracts, a gastrozooid (Fig. 77E) and many palpons of different types that are long and delicate. The bracts (Fig. 77D) are flimsy, semi-circular when young, and often covered in opaque patches of nematocysts.

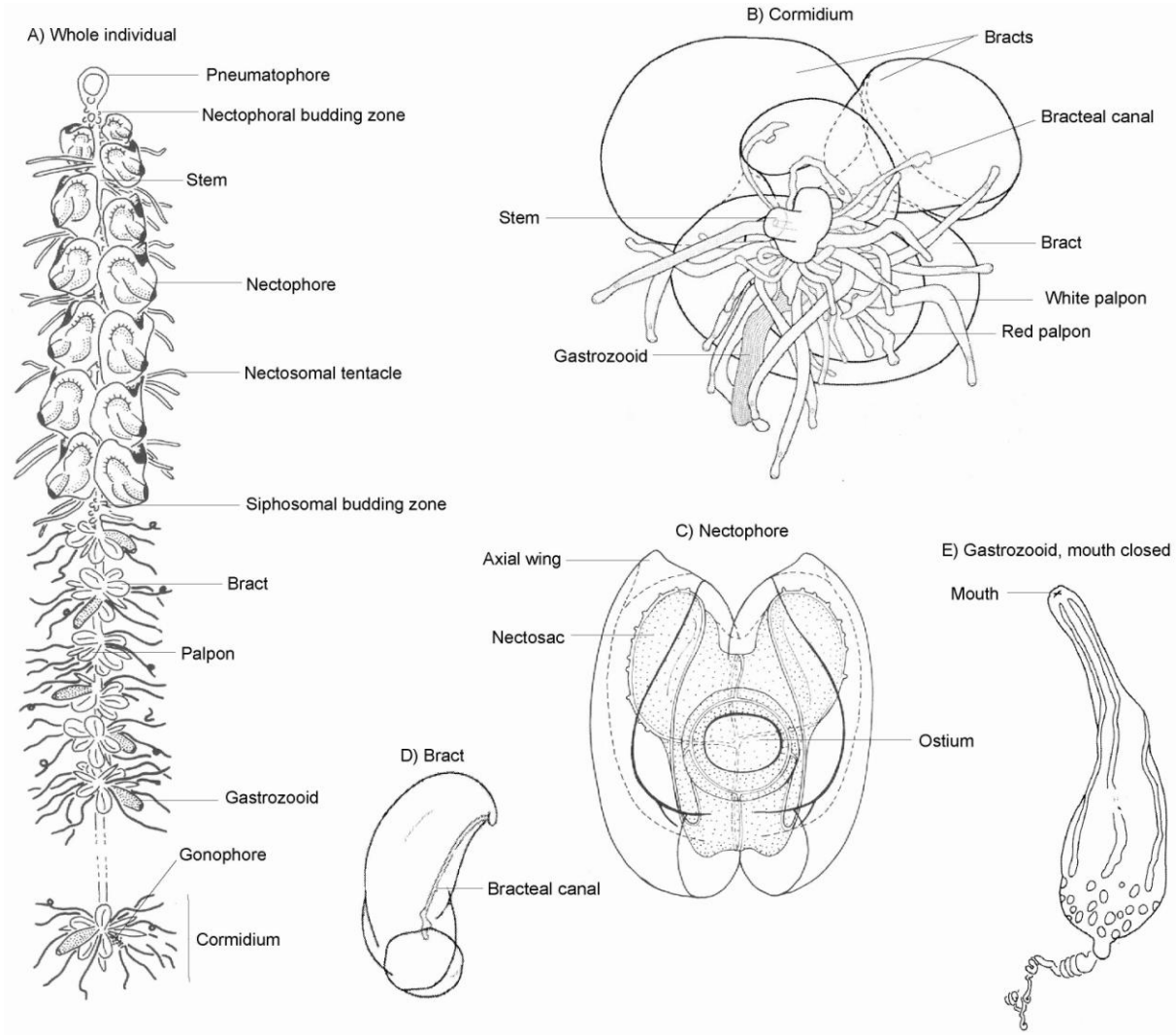


Fig. 77. *Apolemia uvaria*. (A from Mapstone, 2003; B, D-E from Hiscock *et al*., 2010; C from Totton & Fraser, 1955a).

Recorded: PMF, not recorded. L4, rare. In October/November 2007 and September to December 2008 seen by divers all around south-west Britain. Oceanic species. Western Britain and Ireland.
Size: Nectophore 15-20 mm in length; Colonies recorded up to 30 m in length.
Further information: Totton & Fraser, 1955a; Totton, 1965; Kirkpatrick & Pugh, 1984; Pugh, 1999; Hiscock *et al*., 2010.

Suborder Calycophorae:

Calycophoran siphonophores are the siphonophore group with the most members. They do not have a pneumatophore and the nectophores are often very specialised, their structure varying between species. The number of nectophores present can be from one to 15, depending on species, all appearing quite similar. Usually the cormidia of the asexual polygastric phase break off successively to form the free swimming sexual eudoxid stage. They have a somatocyst, an extension of the gastrovascular system associated with digestion.

Family Sphaeronectidae:

Genus *Sphaeronectes:*

Sphaeronectes gracilis (Claus, 1873)

The asexual polygastric stage (Fig. 78A) is almost spherical, composed of a single nectophore, with a large nectosac reaching to almost half its height. Four straight radial canals arise at the apex of the nectosac, over which bends the long narrow hydroecium. The somatocyst is short and curved with a slight swelling at the tip. The sexual eudoxid stage (Fig. 76B) has two nectophores. The anterior nectophore is small and spherical with a long phyllocyst, which is the reduced gastrovascular canal system.

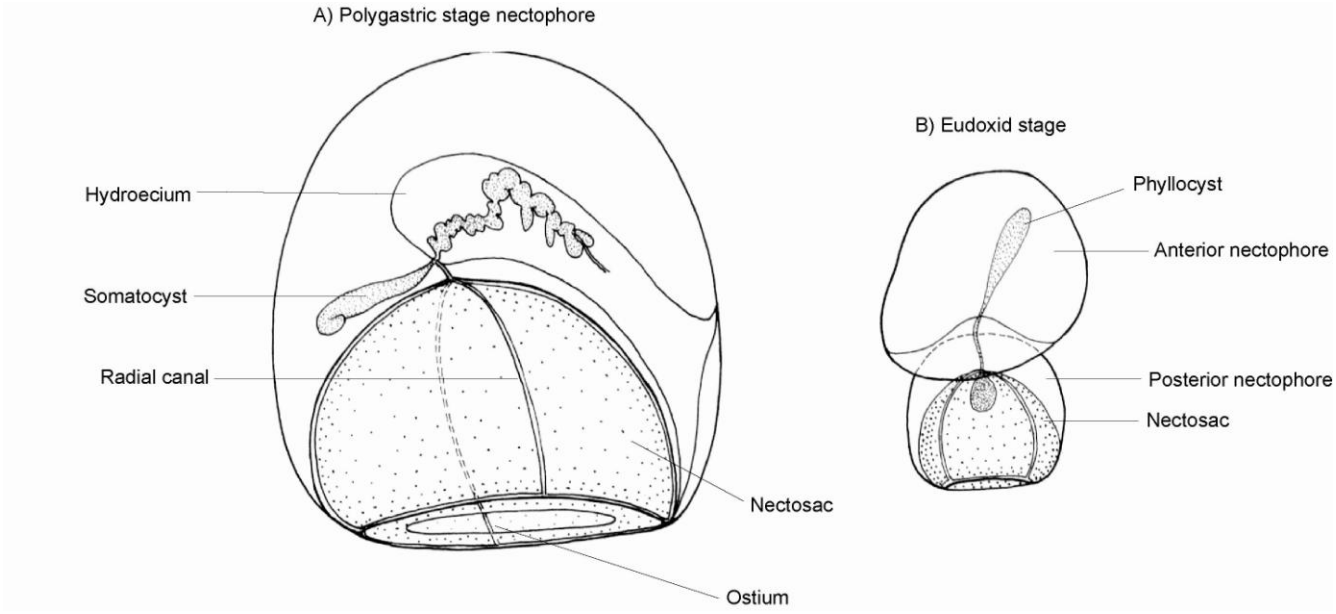


Fig. 78. *Sphaeronectes gracilis* (from Kirkpatrick & Pugh, 1984).

Recorded: PMF, rare (sampled mid-channel). L4, not recorded. Western Britain and Ireland.
Size: Polygastric stage up to 8 mm in height.
Further information: Kirkpatrick & Pugh, 1984

Family Diphyidae:
Subfamily Diphyinae:
Genus *Muggiaea:*

Muggiaea atlantica Cunningham, 1892

Diphyidae have streamlined bodies with a large nectosac, features related to their relatively fast swimming speed. They typically have two nectophores in both the asexual polygastric and sexual eudoxid stages. The upper nectophore is called the anterior nectophore and the lower has a different structure and is called the posterior nectophore. However, *Muggiaea* spp. in the early polygastric stage discard a nectophore and only the anterior nectophore (Fig. 79A, B) remains to adulthood. The anterior nectophore of the polygastric stage is the most useful part to identify Diphyidae spp., recognised by its long triangular shape and presence of the lateral sac-like somatocyst.

In *M. atlantica* there are five complete but relatively straight longitudinal ridges on the polygastric nectophore (Fig. 79A, B) and the thin somatocyst extends to around the top of nectosac. The hydroecium is deep, extending to about one third of the height of the nectophore.

The eudoxid stage (Fig. 79C, D) is composed of two nectophores, the anterior, or bract, is roughly conical, with a flattened face, an asymmetric base with shallow depression in which the somatocyst is situated. The phyllocyst is club-shaped. The posterior nectophore or gonophore has four longitudinal ridges, usually with a spiral twist to the right. The two ventral ridges are extended below to form a short curved mouth plate; the right ventral ridge is particularly strongly developed, bulging out to the side.

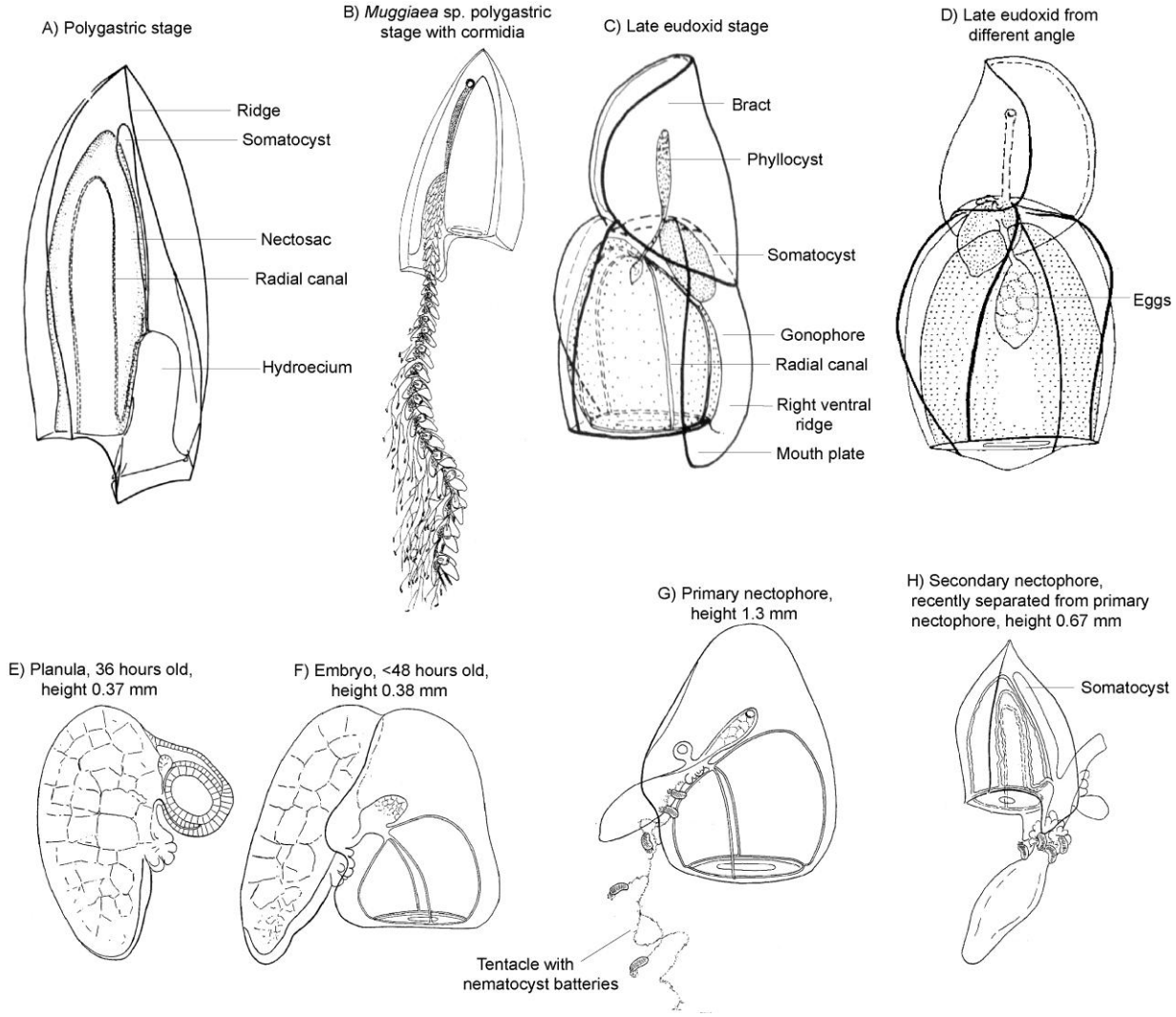


Fig. 79. *Muggiaea atlantica.* (A from Totton & Fraser, 1955b; B from Hyman, 1940; C-H from Russell, 1938b).

Eggs produced by the eudoxid stage develop into a small planula and then an embryo with the primary nectophore attached (Fig. 79E, F). The remains of the planula disappears and the primary nectophore develops a somatocyst, a tentacle with seven to eight nematocyst batteries and the rudiments of the secondary nectophore (Fig. 79G). Russell (1938b) did not find specimens in the plankton in which the primary and fully developed secondary nectophores were present together, but only very small secondary nectophores (Fig. 79H) with the remains of their attachment to the primary nectophore still present, and many loose, discarded primary nectophores. The secondary nectophore develops into the adult polygastric stage.

Recorded: PMF. L4, very common. Western Britain and Ireland. Irish Sea. Northern North Sea.
Size: Polygastric stage ~7 mm in height; eudoxid stage 2.0-2.5 mm.
Further information: Russell, 1938b; Totton & Fraser, 1955b; Totton, 1965; Kirkpatrick & Pugh, 1984.

Muggiaea kochi (Will, 1844)
The general description of *M. atlantica* can also be applied to *M. kochi*. The only obvious difference is that the somatocyst in the polygastric stage extends only half way up the side of nectosac. Although they are very similar and can often be sampled together off Plymouth, genetical analysis confirms they are different species (R. Kirby, pers. comm.)

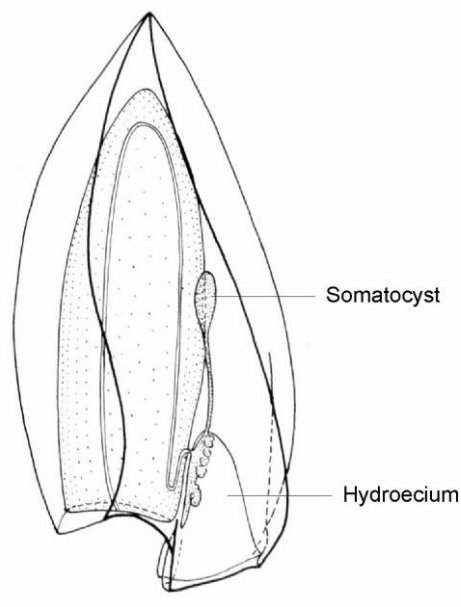


Fig. 80*. Muggiaea kochi.* Polygastric stage (from Totton & Fraser, 1955b).

Recorded: PMF. L4, seasonally common. Western Britain and Ireland.
Size: Polygastric stage ~7 mm in height; eudoxid stage 2.0-2.5 mm.
Further information: Totton & Fraser, 1955b; Totton, 1965; Kirkpatrick & Pugh, 1984.

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PHYLUM CTENOPHORA

Ctenophores, like cnidarians, are gelatinous organisms, but are morphologically quite different and do not possess nematocysts. Most are at least partially transparent and many are bioluminescent, producing blue or green light. Some species are very fragile, breaking up when caught in plankton nets and can only be observed intact by divers. All species found around Britain are holoplanktonic, but parasitic and bottom-creeping species exist.

Morphology

Ctenophores are mainly spherical/ovoid or bell-shaped. The spherical species, often seen stranded and rolling around at the sea edge, are commonly called "sea gooseberries". Ctenophores are the largest non-colonial organisms to use cilia for locomotion. The characteristic of this phylum is that the cilia are joined together in rows like a comb, called comb-plates or ctenes (Fig. 1A), apart from in young stages where the cilia are longer and separate. The presence of these comb-plates gives them their other common name of "comb-jellies". On the outer surface of all European species there are eight rows of ctenes, oriented to run from near the mouth or oral pole, towards the opposite end or aboral pole. In adults, these rows are spaced more or less evenly around the body and generally extend only part of the distance from the aboral pole towards the mouth. They beat in metachronal waves (sequentially as in "Mexican waves") and the propulsion stroke is normally away from the mouth, so unlike cnidarians, ctenophores usually swim in the direction in which the mouth is pointing. However, some can also reverse direction. Light is diffracted as the ctenes beat, giving beautiful rainbow-coloured iridescence.

Digested food and food remains are transported in the various gastrovascular canals (Fig. 1A) and wastes are removed via both the mouth and the anus. There are no special organs of gaseous exchange, this occurs across the whole body surface. Ctenophores have no brain but a network of nerves run beneath the outer skin. The main sense organ is the statocyst, situated apically (near the anus), which detects the animal's orientation, stimulating it to make modifications.

Reproduction

Almost all species are hermaphroditic, but most probably cannot self-fertilise. A very few species can reproduce asexually. In at least some species, juveniles are capable of reproduction, the combination of hermaphroditism and early reproduction enabling populations to grow at an explosive rate. As they are all carnivores (Fraser, 1970) they can have a considerable impact on the abundance of other zooplankton. There are approximately 100 species of ctenophores described worldwide and three are recorded in the PMF. There are only two classes, **Tentaculata** and **Nuda**.

Phylum Ctenophora:

Class Tentaculata:

Order Cydippida:

Genus *Pleurobrachia*:

Pleurobrachia pileus (O.F. Müller, 1776)

The body is simple, ovoid to spherical in shape (Fig. 1A) with a long contractile tentacle either side that can be retracted into sheaths. The tentacles can be 15-20 times the length of the body and have sub-tentacles called tentillae along one side (Fig. 1C). Each tentilla is armed with special adhesive cells called colloblasts to which prey stick and the tentacles are then drawn across the mouth so that the prey can be eaten. The mouth and anus are at opposite poles, the gut running in a straight line between them. The mouth opens into a narrow, flattened pharynx where food is rapidly digested. The partly digested food then enters the stomach and is circulated through gastrovascular canals that extend out to the ctene rows and other active parts of the body. Material is moved around these canals by cilia. There are eight rows of ctenes (Fig. 1B), all the same length, extending from near the aboral pole to three-quarters of the distance to the mouth. Most of the body is transparent, but the ctene rows are milky white and the tentacles, tentacle sheaths and pharynx are usually either milky or dull orange in colour.

Eggs and sperm are shed into the water and after fertilisation a free-swimming, cydippid larva (Fig. 1D-E) develops. When newly hatched these have four paired parallel rows of long, free cilia. The body is pear-shaped and tentacles develop at the surface. During development the cilia fuse into rows of ctenes which broaden and separate from each other until they are more or less equidistant, the tentacle base invaginates and the body becomes more spherical (Fig. 1F).

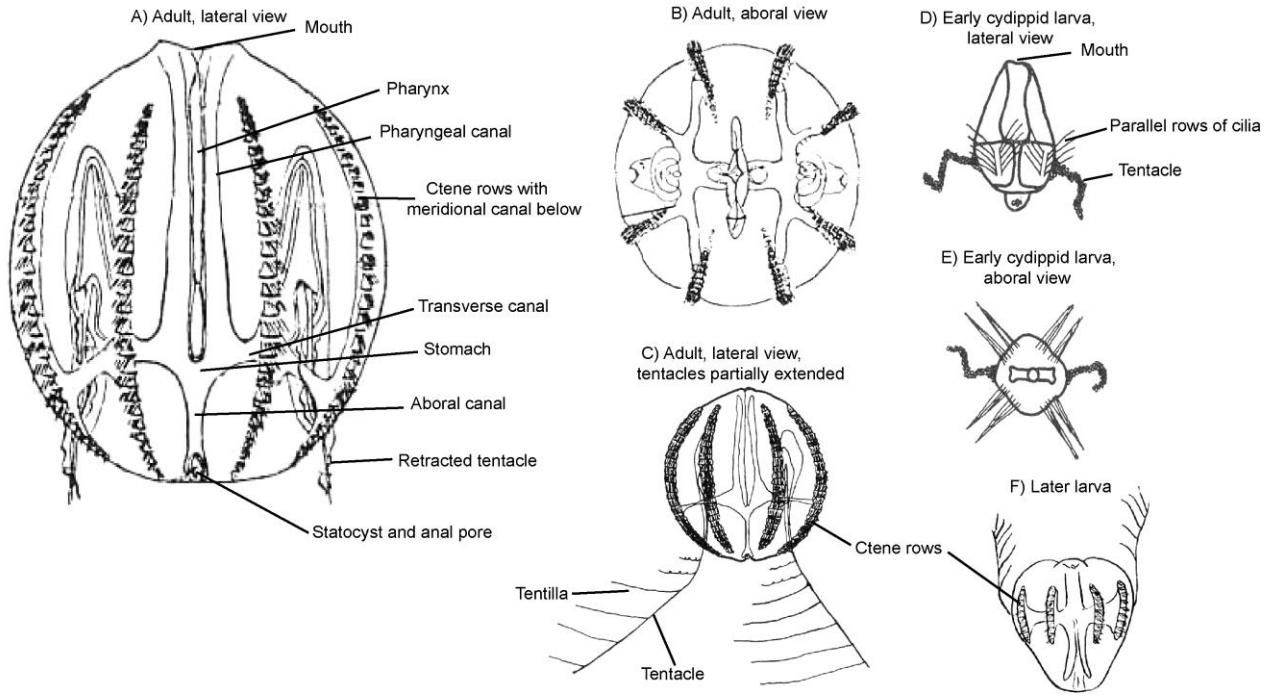

Fig. 1. *Pleurobrachia pileus* (A-B, F from Liley, 1958; C-E from Greve, 1975; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF. L4, common. All European waters.
Size: Larva ~1.5 mm in height; adult 10-25 mm.
Further information: Liley, 1958; Greve, 1975; Mianzan, 1999; Martindale, 2002; Larink & Westheide, 2006.

Order Lobata:

Genus *Bolinopsis*:

Bolinopsis infundibulum (O.F. Müller, 1776)

Bolinopsis is very fragile and disintegrates during sampling and preservation, so the sparse records do not reflect its true abundance.

The body is translucent, pear-shaped and laterally flattened to around half the width (Fig. 1A-B). It has two large oral lobes, one third of the body length, that form an enclosure into which prey are driven by cilia and by the forward swimming momentum. There are four slender, smaller lobes called auricles near the base of the oral lobes, close to the mouth. The gastrovascular system is complicated and loops around the active parts of the body and into the oral lobes. Two adjacent, opposite pairs of the eight ctene rows reach the auricles and carry on around them as ciliary fringes, the other two opposite, adjacent pairs reach and terminate at the base of the oral lobes. There are two short tentacles situated at opposing sides of the mouth. These do not have sheaths and may not be used in the adult (Greve, 1970). A few tiny accessory tentacles may also be present along the edge of the mouth.

An ovoid cydippid larva emerges from the egg (Fig. 2C-D) that can be distinguished from *Pleurobrachia* larvae by the V-shape between the paired ctene rows, caused by the rows being closer to each other at the aboral end (Fig. 2C). The tentacles are functional, used in food capture, and are longer than in the adult. They are also inserted into the body of the larva, rather than being on the surface. During development the tentacle bulbs migrate orally and the oral lobes start to appear (Fig. 2E).

An alien Lobata species from the USA called *Mnemiopsis leidyi* Agassiz, 1865 has been recorded in the southern North Sea, Baltic and parts of the Norwegian coast. It resembles *Bolinopsis*, but the origins of the oral lobes are much deeper in the body, almost level with the statocyst. It is likely that *Mnemiopsis* will become more widespread.

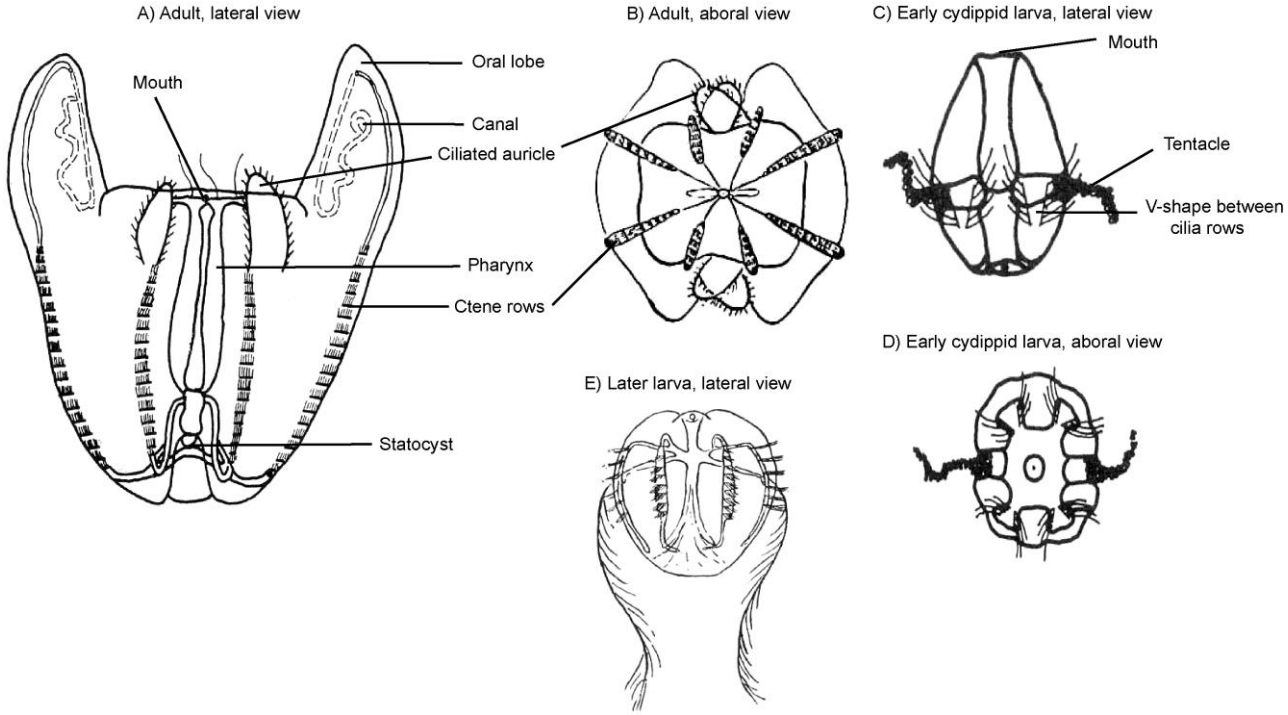

Fig. 2. *Bolinopsis infundibulum* (A, C-D from Greve, 1975; B-E from Liley 1958; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF. L4, not recorded. Probably widespread in European region, but poorly recorded because of fragility.

Size: Larva ~ 1.5 mm in height; adult up to 150 mm

Further information: Liley, 1958; Greve, 1975; Mianzan, 1999; Martindale, 2002; Larink & Westheide, 2006.

Class Nuda:
Order Beroida:
Genus *Beroe*:

Beroe cucumis Fabricius, 1780

Ctenophores in Class Nuda have no tentacles. The body is sac- or vase-shaped (Fig. 3A), often quite flattened, with a very large slit-like mouth. They feeding exclusively on other ctenophores and can ingest prey larger than themselves, which is then digested in their broad pharynx. They have stiffened cilia internally, to allow them to hold their prey and glands that secrete a paralysing poison. The eight ctene rows are equal in length, extending from the aboral pole to about three-quarters of the distance towards the mouth. There is a row of branched papillae in the form of a figure eight at the aboral pole. Eight broad, longitudinal (meridional) canals connect to the pharangeal canals and a network of blind canals branch through the body walls. The adult is usually milky pink when living.

Eggs and sperm are shed into the water and after fertilisation the young that develop are miniature adults (Fig. 3B, C). The individual cilia are arranged in eight longitudinal rows that gradually develop into ctenes. They cannot be distinguished from the larvae of *Beroe gracilis*, but can be distinguished from those of *Pleurobrachia* and *Bolinopsis* by the lack of tentacles.

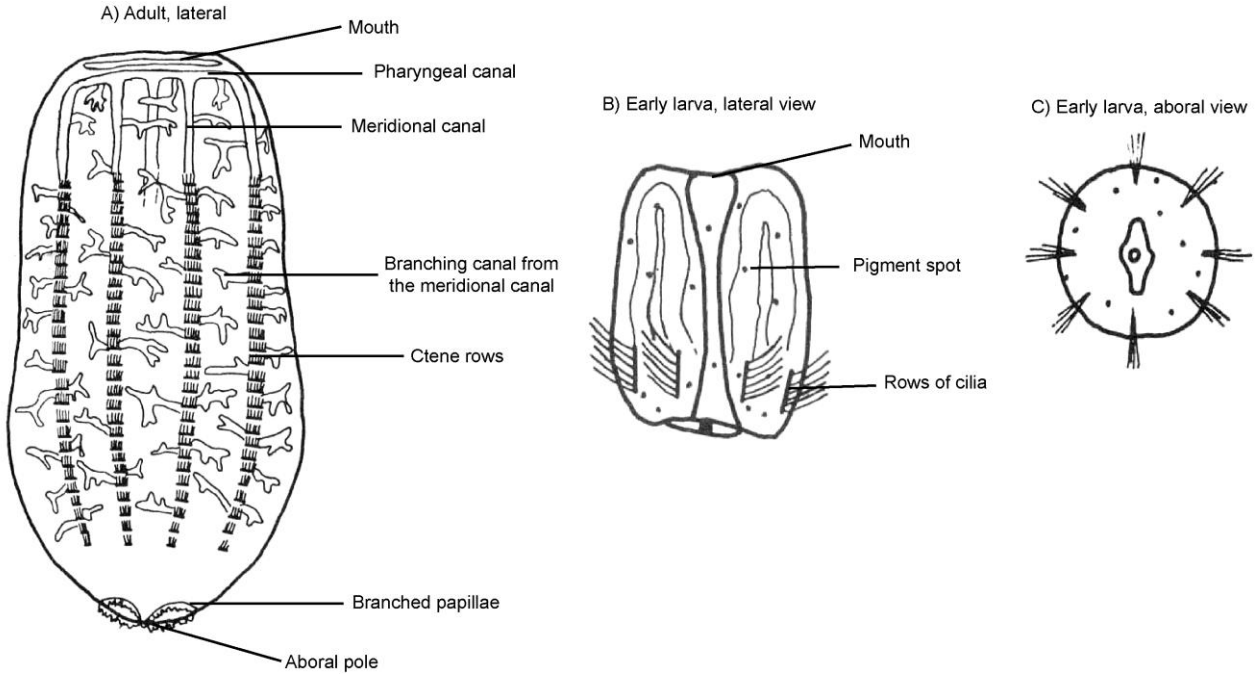

Fig. 3. *Beroe cucumis* (A-C from Greve, 1975; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF. L4, rare. Widespread in European region.
Size: Larvae ~1.5 mm in height; adult up to 150 mm.
Further information: Liley, 1958; Greve, 1975; Mianzan, 1999; Martindale, 2002; Larink & Westheide, 2006.

Beroe gracilis Künne, 1939
As with *B. cucumis*, there are no tentacles. The body is slender, cylindrical and slightly flattened. The eight ctene rows extend from the aboral pore to three-quarters of the distance towards the mouth. There is a row of branched papillae in the form of a figure eight at the aboral pole. The meridional canals are connected to the pharyngeal canal, but do not have the side branches as found in *Beroe cucumis*. They superficially resemble stretched *Pleurobrachia*. The adult is milky-coloured and some specimens can be tinged pink.
The young are miniature adults and cannot be distinguished from young of *B. cucumis*, but can be distinguished from *Pleurobrachia* and *Bolinopsis* larvae by the lack of tentacles. They may have pink pigment spots.

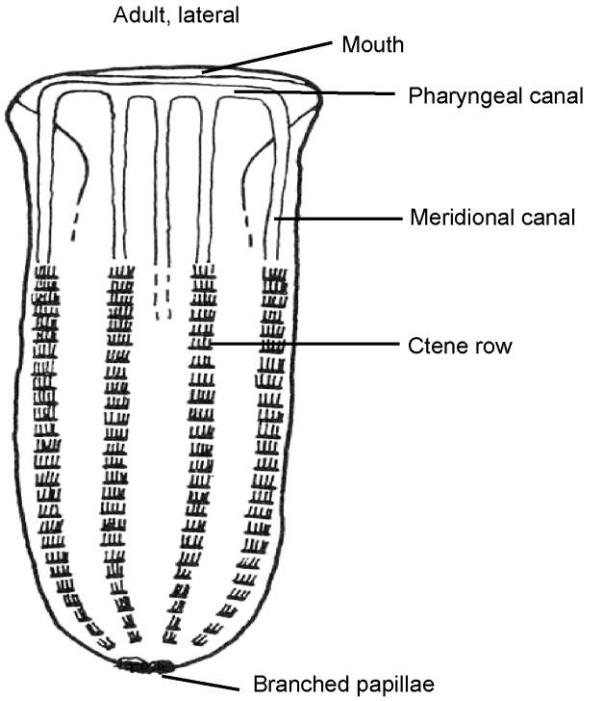

Fig. 4. *Beroe gracilis* (From Greve, 1975; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF, not recorded. L4, not recorded. Southern North Sea. Irish Sea. Western Britain.
Size: Larva ~1.5 mm in height; adult up to 30 mm.
Further information: Liley, 1958; Greve, 1975; Mianzan, 1999; Martindale, 2002; Larink & Westheide, 2006.

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PHYLUM PLATYHELMINTHES

Because of their compressed shape, platyhelminths are commonly known as ‘flatworms’. Most marine classes of this phylum contain only parasitic species; the only class that is mainly free-living is Class **Turbellaria**. However, developmental stages of the parasitic Class **Trematoda** can sometimes be observed inside a range of transparent, planktonic organisms such as medusae and chaetognaths, which are usually only intermediate hosts. They are sometimes dislodged and found in plankton samples. The distinctive eggs of one species are also sometimes sampled.

Class Turbellaria

In the PMF 78 species of adult turbellarians are recorded. They are usually found on or close to the sea bottom, but can be carried higher in the water column under turbulent conditions.

Morphology

Food and also waste pass through the same pharyngeal opening, which is generally located on the dorsal mid-body (Fig. 1A). In some species the pharynx can be extended as a dangling tube with the mouth on the end. In larger flatworms the gut is often very highly branched. The body surface is usually covered in cilia, used in locomotion, but some species can swim in an undulating pattern by rhythmic muscle contractions. Usually only juveniles are sampled in plankton nets and these can only be classified by a specialist. Their bodies are usually distorted, opaque or cream coloured and somewhat featureless when preserved. They are generally flattened, leaf-shaped with rounded corners (Fig. 1B) and with two faint clusters of black, light-sensitive organs (ocelli) on their upper surface. The internal organs are usually not visible.

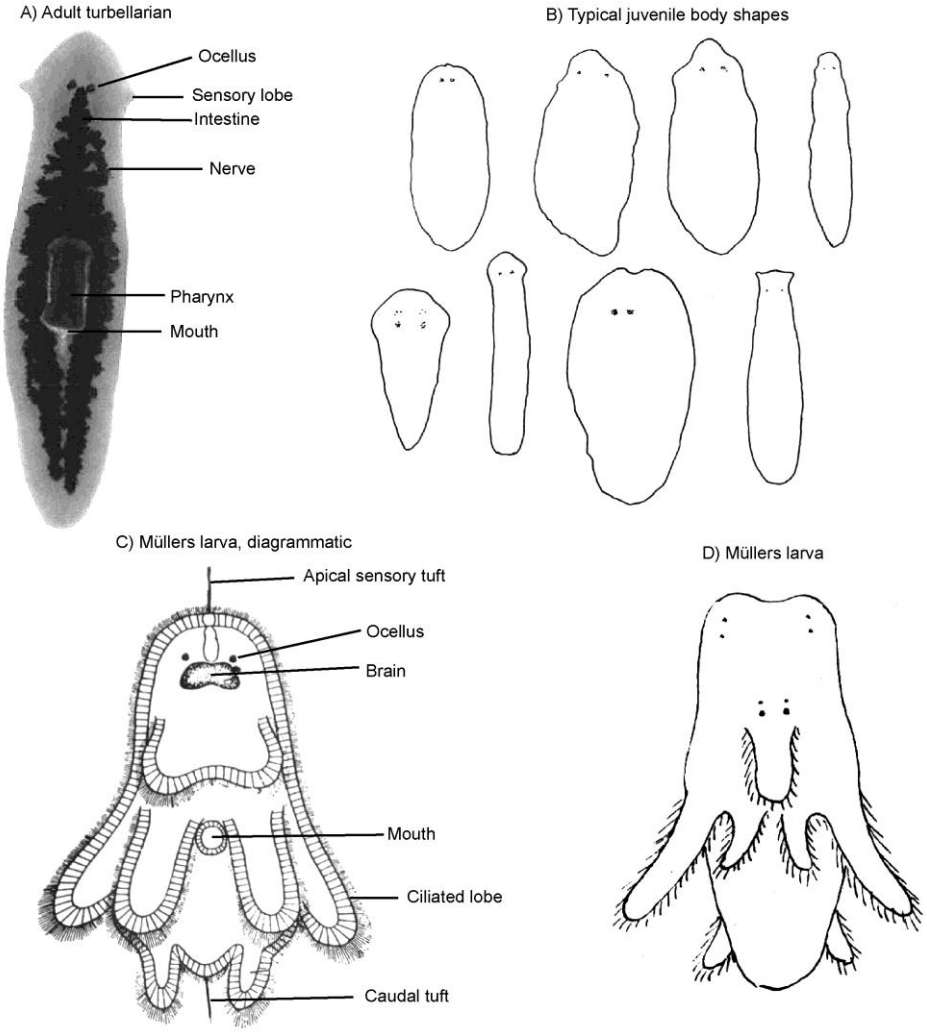

Fig. 1. Turbellarian adult, juveniles and larvae. (A source unknown; C after Hyman, 1951; D from Trégouboff & Rose 1957).

Reproduction and development
Eggs are deposited in capsules on the sea bottom and usually hatch into tiny individuals that resemble the adults. However, some species in Order Polycladida have indirect development via ciliated larvae that resemble an annelid trochophore. The commonest larval type is known as a Müller's larva (Fig. 1C, D), characterised by a variable number of posteriorly projecting lobes. Prior to metamorphosis there may be seven to ten lobes arranged over the body. Most larvae have pigmented ocelli, three in early larvae, sometimes more later. The other rarer larval type is known as a Götte larva that only develops four lobes on the body. Both larval types are completely ciliated, the cilia longer in particular regions, usually with longer tufts on the anterior and posterior ends. When alive they may be pigmented, mainly brown to orange. Metamorphosis transforms the swimming, particulate feeding larva into a creeping, generally predatory adult. During this process the body flattens, the larval lobes are gradually absorbed and ocelli number increases.

Recorded: PMF. L4. Throughout the European region.
Size: Müller's larvae ~0.15-1.8 mm in length; juveniles 5-50 mm.
Further information: Trégouboff & Rose, 1957; Ball & Reynoldson, 1981; Hyman, 1951; Larink & Westheide, 2006; Prudhoe, 1982; Shanks, 2001; Smith et al., 2002.

Class Trematoda

There are around 100 trematode adults recorded in the PMF, mainly found in fish and molluscs. These are unlikely to be found in plankton samples, but trematode larvae (Fig. 2) are occasionally found, usually present because they have been dislodged from their host or intermediate host, such as a medusa, ctenophore or chaetognath. They are typically elongated, slightly opaque and sometimes tinged brown. Their most distinctive feature is the presence of two suckers, one close to the mouth and the other on the underside, in the central region, where the body is usually wider.

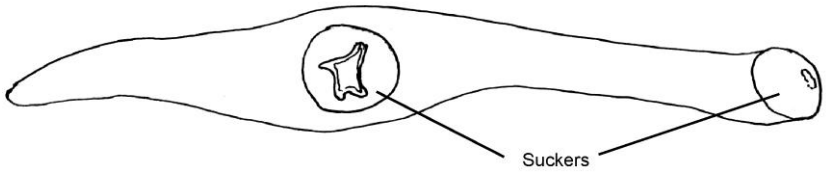

Fig. 2. Typical larval trematode.

Recorded: PMF, not recorded. L4. Widespread.
Size: ~0.4 mm.
Further information: Shanks, 2001; Smith *et al*., 2002; Larink & Westheide 2006

Kuhnia scombri (Kuhn, 1829) Sproston, 1945, eggs
Kuhnia scombri is a common, trematode gill parasite of mackerel (*Scomber scombrus* Linnaeus) and the characteristic, dark brown, spindle-shaped eggs (Fig. 3) are occasionally taken in plankton samples. They have an ovoid centre and filaments each end. There is a region in the egg where the case fractures to allow the ciliated larva to emerge. Before they were recognised as *K. scombri* eggs they were called “spindelei” (Lohmann, 1910).

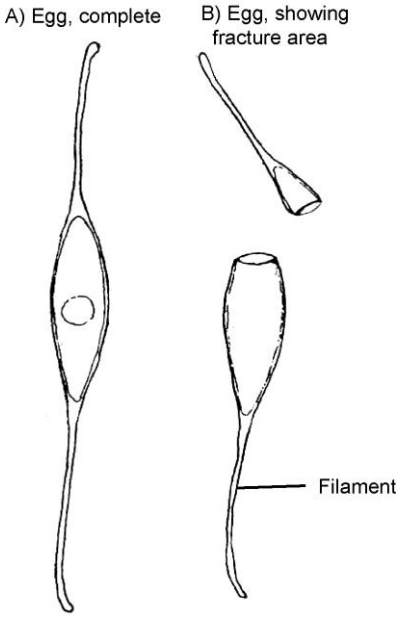

Fig. 3. *Kuhnia scombri* eggs (from Gallien & Le Calvez, 1947; as *Octobothrium scombri*).

Recorded: PMF, as adults on gills of mackerel; L4, as eggs, rare. Probably anywhere that mackerel occur.
Size: Eggs 0.85 mm in length; length central section 0.30 mm; width central section 0.08 mm.
Further information: Lohmann, 1910 (as “spindelei”); Gallien & Le Calvez, 1947 (as *Octobothrium scombri*)

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PHYLUM NEMERTEA

Nemertines are a poorly known group of unsegmented, worm-like organisms with approximately 100 marine species found in European waters. They are commonly called 'ribbon-worms', as some are very long and capable of extreme contraction and elongation, although most are less than 300 mm in length. They are also called 'proboscis worms', because they can evert a proboscis to capture their food. Adult marine nemertines are most abundant in coastal areas, generally found on the sea bottom, beneath rocks and thick algal growth, or burrowing into soft mud or sand. Some species live commensally, while others are parasitic. They are mainly carnivores and can be key predators, but some also scavenge on animal remains.

Reproduction and development

Some species breed throughout the year, while others have particular breeding seasons. The reproductive process is extremely variable between groups, but fertilisation is most commonly external and gametes are shed freely into the sea. In species with direct development the eggs hatch and, depending on species, a miniature adult at different stages of development emerges. The appearance and shape of these larvae is very variable, but they can resemble a cnidarian planula or a flatworm larva. They are flattened, usually elongated and can have a single, or one or two pairs of ocelli on the anterior body. These larvae could probably only be identified with certainty from unpreserved material, so are not figured.

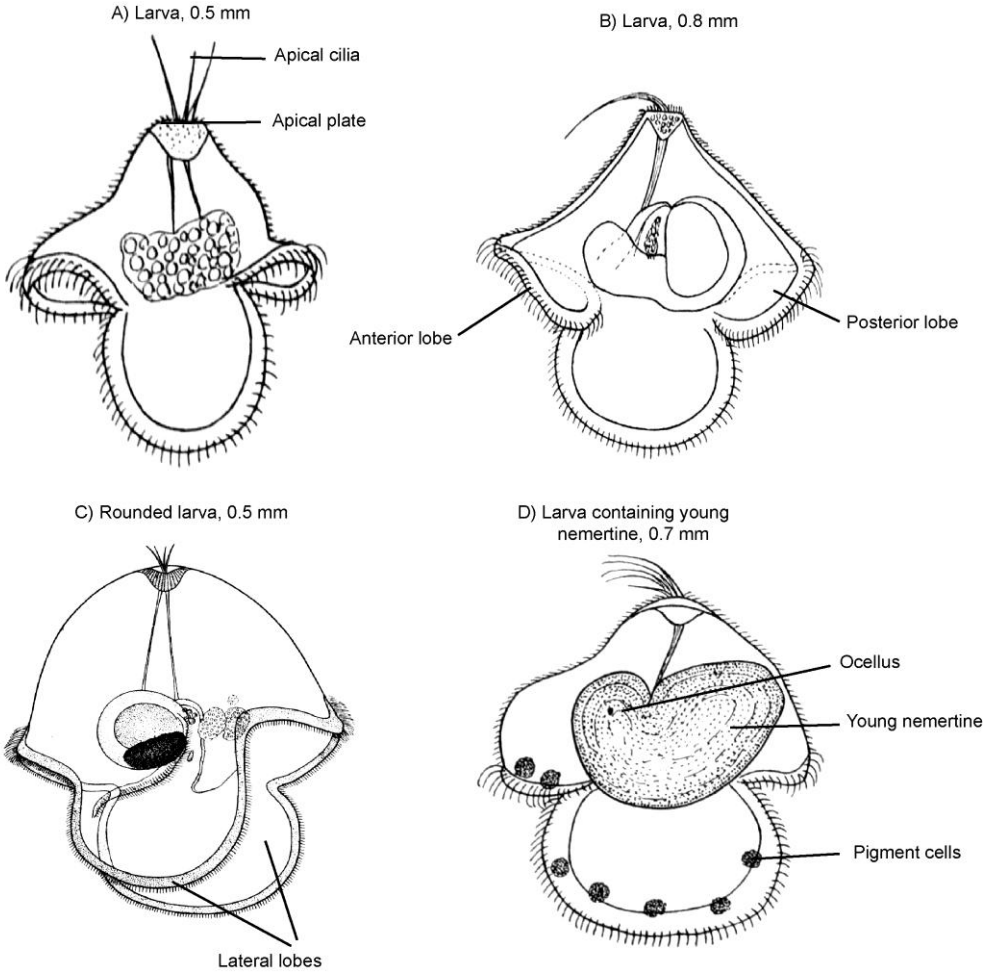

Fig. 1. Nemertean pilidium larvae. (A-D from Thorson, 1946).

Indirect development also occurs, when a distinct, intermediate larva emerges from the egg and subsequently undergoes a metamorphosis to the adult form. There are different types of indirect larvae, but the only pelagic one occurring in European waters is the pilidium (Fig. 1), which often occur, usually in small numbers, in finer mesh, shallow water plankton samples. Pilidium larvae hatch from the egg at a very early stage of development. They develop from an initial simple ciliated larva that has a domed body with a tuft of sensory cilia sprouting from the top of the apical

plate (Fig. 1A), variable in shape depending on species. The lower body is formed from a series of four lobes, single anterior and posterior lobes (Fig. 1B) that can differ in shape, and a lateral pair that are identical (Fig. 1C). The edges of the lobes are ciliated for locomotion and to generate a current of water carrying small phytoplankton food towards the mouth, which is situated internal to the lobes. The epidermis may contain groups of pigmented cells (Fig. 1D). Ocelli may be present, but only develop in species that have them as adults. After a short feeding period the pilidium commences metamorphosis. The young worm develops within the pilidium (Fig. 1D) and metamorphosis is completed when it breaks out, often feeding initially on the remnants of the pilidium.

Recorded: PMF, 55 adult species. L4, larvae occasionally taken. All around European region.
Size: Direct larvae ~0.2-1.0 mm total length; pilidium larvae ~0.5-0.8 mm from apical tuft to distal edge of lateral lobe.
Further information: Thorson, 1946; Todd et al., 1991; Gibson, 1994, 1999; Johnson, 2001; Norenburg & Stricker, 2002; Larink & Westheide 2006.

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PHYLUM ROTIFERA

Rotifers are tiny organisms with very variable appearance, that are usually only caught in fine mesh plankton nets. Some are truly planktonic while others crawl over or attach to the substrate. They feed primarily on phytoplankton, bacteria and detritus. Most are single individuals, but there are some colonial species, both sessile and planktonic.

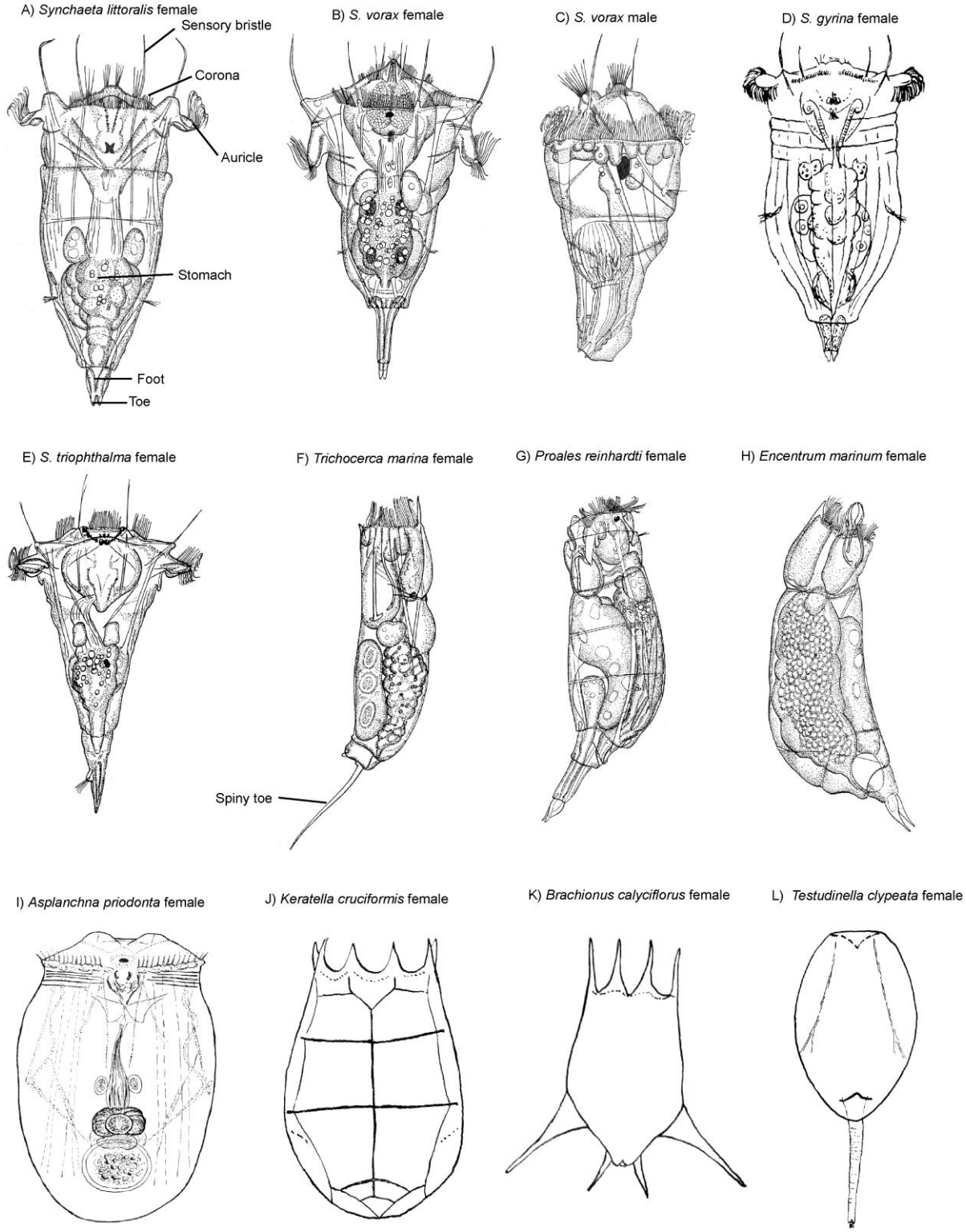

Fig. 1. Examples of rotifers, some of which are recorded in the PMF (A-C, E-H from Hollowday, 1949; D from Berzins, 1960a; I from Berzins, 1960e; J from Berzins, 1960c; K from Berzins, 1969d; L from Berzins, 1960f; Berzins diagrams used with the kind permission of the International Council for the Exploration of the Sea).

Morphology

Rotifers usually have a characteristic crown or corona of fine cilia on two lobes surrounding the mouth area (Fig. 1A). This corona gives them their common name “wheel animals” although the corona does not actually rotate. The commonest genus sampled at Plymouth, *Synchaeta* spp., also have characteristic, ciliated auricles laterally (Fig. 1A). In some rotifers, cilia are modified into bristles (Fig. 1A-D) or tufts, or lost altogether. The cilia beat in waves to draw water currents and thus food towards the mouth. The cilia can only be observed in unpreserved or specially preserved samples.
The body is divided into a head, trunk, and foot, and is typically flask-shaped. There is a well-developed cuticle that may be thick and rigid, or flexible, giving the animal a worm-like appearance. Rigid cuticles are often composed of multiple plates and may bear spines and other ornamentation (Fig. 1J, K). The trunk forms the major part of the body, and encloses most of the internal organs. The foot projects from the rear of the trunk, and is usually much narrower (Fig. 1A). The cuticle over the foot often has rings, making it appear segmented. The foot ends in from one to four toes, which, in sessile and crawling species contain adhesive glands to attach the animal to the substratum. In many planktonic species, the foot may be reduced in size, or absent (Fig. 1I). In one species sampled at Plymouth (*Trichocerca marina;* Fig. 1F), the toes are spine-like. The gut consists of a pharynx, stomach, and intestine. The pharynx of rotifers is called the mastax and is lined with cuticle, modified into hard masticatory elements called trophi. The structure of the trophi depends on the feeding habits of the rotifers and is an important diagnostic feature.

Reproduction and development
In rotifers the sexes are separate and some can reproduce both sexually or parthenogenetically (without fertilisation). Females are usually completely different in appearance from the males (Fig.1B, C) and may be up to ten times larger. Males are short-lived, but for many of the species that reproduce parthenogenetically, males have never been discovered. Fertilisation is internal and the male either inserts his penis into the female's cloaca or uses it to penetrate her skin, injecting the sperm into the body cavity. The egg has a shell and when laid is attached either to the substratum or to the female's own body. A few species retain the eggs inside their body until they hatch. Most young emerge as miniature versions of the adult. Under unfavourable conditions resting eggs may be produced that are able to survive extreme conditions, such as may occur during winter, or when the pool they are in dries up. These eggs resume development when conditions improve. Resting eggs can be produced commercially and are commonly used in fish farms to generate food, when required, to feed to larval fish as their first feed. Some rotifers are unable to produce resting eggs, while others can survive adverse conditions by losing almost all body water, then rehydrating when conditions improve.

A wide range of rotifers are illustrated in Berzins (1960a-f). Eight species are recorded in the PMF, but identification is a specialised task, requiring fresh or specially preserved material. For these reasons, only illustrations of seven of the eight local species, without detailed descriptions are given here (Fig. 1). Illustrations of some other rotifers are also given to show the variety in shape.

Recorded: PMF, *Synchaeta littoralis* Rousselet, 1902; *S. vorax* Rousselet, 1902; *S. gyrina* Hood, 1887*; S. triophthalma* Lauterborn, 1894*; Trichocerca marinum* (Daday, 1890); *Proales reinhardti* (Ehrenberg, 1834); *Encentrum marinum* (Dujardin, 1841); *Zelinkiella synaptae* (Zelinka, 1887). L4, only recorded as rotifers unidentified. All around European region.
Size: Mainly 0.1-0.5 mm, but up to 2.0 mm.
Further information: Hollowday, 1949; Berzins, 1960a-f; Larink & Westheide, 2006.

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PHYLUM MOLLUSCA

Marine molluscs are a diverse range of unsegmented soft-bodied organisms, partially or wholly covered by a mantle, a sheet of tissue exclusive to this phylum. The body is often divided into a head, with eyes or tentacles, a muscular foot used for locomotion that is modified in some species for swimming and a visceral mass housing the organs. Most have a protective shell, usually external, that is excreted by the mantle, but in a few species the shell is internal, or absent altogether. Many have a feeding structure, the radula, largely composed of chitin, while cephalopods (squid, octopus and cuttlefish) have a chitinous beak.

Classification

Molluscs have adaptated to a wide range of habitats, leading to a vast variety of forms and species. Following the WORMS classification there are eight classes:

Class Monoplacophora – rare deep-sea molluscs, with cap-like shells.
Class Caudofoveata – worm-like deep-sea molluscs without shells.
Class Solenogastres – worm-like molluscs, lacking a shell, covered by calcareous spicules.
Class Polyplacophora – shells made out of eight plates – the chitons.
Class Scaphopoda – tusk shells, or "elephant's tusks".
Class Bivalvia – oysters, mussels, clams etc.
Class Gastropoda
- **Subclass Prosobranchia** – whelks, periwinkles, janthinids etc.
- **Subclass Opisthobranchia**
  - **Order Nudibranchia** – nudibranchs.
  - **Order Thecosomata** – "sea butterflies" (*Limacina*).
  - **Order Gymnosomata** – "sea angels" (*Clione*, *Pneumodermopsis*).

Class Cephalopoda – squid, octopus, cuttlefish.

Classes Monoplacophora and Caudofoveata are not found off Plymouth, but recorded in the PMF are adults of three species of Class Solenogastres, six Polyplacophora, two Scaphopoda, 225 Gastropoda, 125 Bivalvia and 14 Cephalopoda. There are only three adult holoplanktonic molluscan species recorded in the PMF or from L4 and these are all in Class Gastropoda. However, the larvae of molluscs are routinely taken in plankton samples, mainly from the two most abundant classes, Bivalvia and Gastropoda.

Molluscan development

General development

Molluscs typically develop from eggs that are retained in the mantle cavity, deposited on some surface, or shed into the water column, but there are many developmental variations. In some species a planktonic larval stage called a trochophore (Fig. 1A) emerges from the egg. This is typically small, top-shaped, with a mouth opening just below an equatorial ring of cilia and with an apical tuft of cilia. Beating of the cilia spins them and propels them through the water.

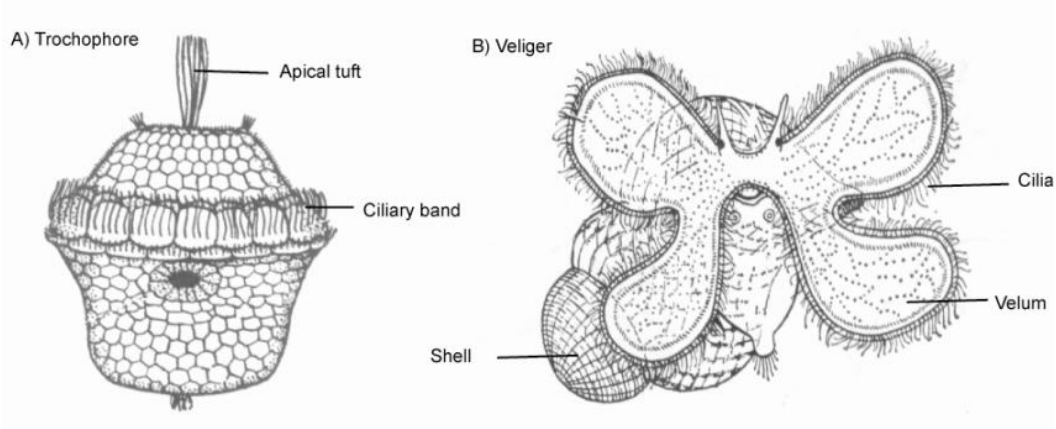

Fig. 1. Typical molluscan larvae. (From Fretter & Graham, 1962).

The trochophore develops into the veliger stage (Fig. 1B), or veligers are liberated directly. The majority of molluscan larvae caught will be veligers, as trochophores generally only spend a short time in the plankton before developing further. They are generally also small and delicate, so may be destroyed, or not retained, by coarser plankton nets. The veliger characteristically has a shell, the shape depending on the group it belongs to, and a densely ciliated velum composed of a variable number of lobes. The lobes function in locomotion, feeding and respiration and can be withdrawn into the protective shell, but the lobes, cilia and fine details can usually only be observed in unpreserved or specially preserved specimens. The time the veliger spends in the plankton varies with species, but can be anything from a few hours, to over a year.
Identifying early molluscan larvae is a specialist task and many have still not been described, but it is possible to roughly classify some veligers on shell shape and other features. Excellent diagrams and photographs of a wide selection of mollusc larvae are given by Buckland-Nicks *et al*. (2002a, b), Shanks (2001) and Zardus & Martel (2002).

Class Bivalvia: Development
There are no planktonic adult bivalves, but their larvae can be very abundant in plankton samples, including some surprisingly large ones. Reproduction is usually by release of gametes into the water column. A trochophore (Fig. 1A) emerges from the eggs, although some species retain their larvae in the mantle cavity until they are veligers. Bivalve veligers have typically flattened bivalve shells (Fig. 2B, C). It is difficult to identify species in the early stages, but some later larvae can be identified using their shape and hinge structure (Rees, 1950; Brink, 2001). Length is generally measured as the greatest distance in a line parallel to the hinge.

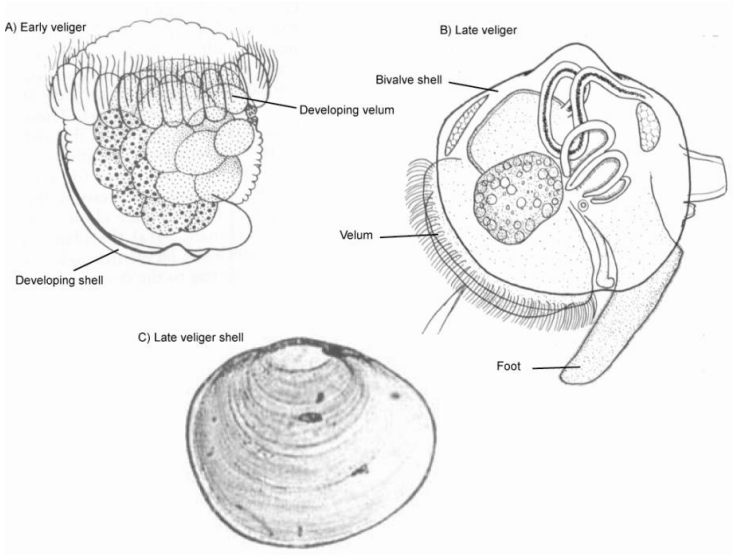

Fig. 2. Bivalve developmental stages. (A from Fretter & Graham, 1962; B from Thorson, 1946; C from Rees, 1950).

Recorded: PMF, only adults recorded. L4, larvae found all year round. Throughout the European region.
Size: Trochophores ~0.05-0.2 mm in length; veligers ~0.07-0.4 mm in width.
Further information: Jørgensen, 1946; Rees, 1950; Fretter & Graham, 1962; Brink, 2001; Zardus & Martel, 2002.

Class Gastropoda: Eggs
The majority of benthic gastropods lay their eggs in gelatinous masses attached to the substratum. Some exceptions include two common periwinkle species *Littorina littorea* (Linnaeus, 1758) and *Melarhaphe neritoides* (Linnaeus, 1758)(formerly *Littorina neritoides*). Easily identifiable egg capsules of these species are dispersed in the plankton and are often abundant in inshore waters. In both species the capsules appear circular from above, but in lateral view those of *L. littorea* are flattened with a domed centre (Fig. 3A), while *M. neritoides* are deeper, but also slightly domed (Fig. 3B). In *L. littorea*, there may be up to nine eggs in one capsule. In these species the trochophore stage is passed in the egg, a veliger emerging.

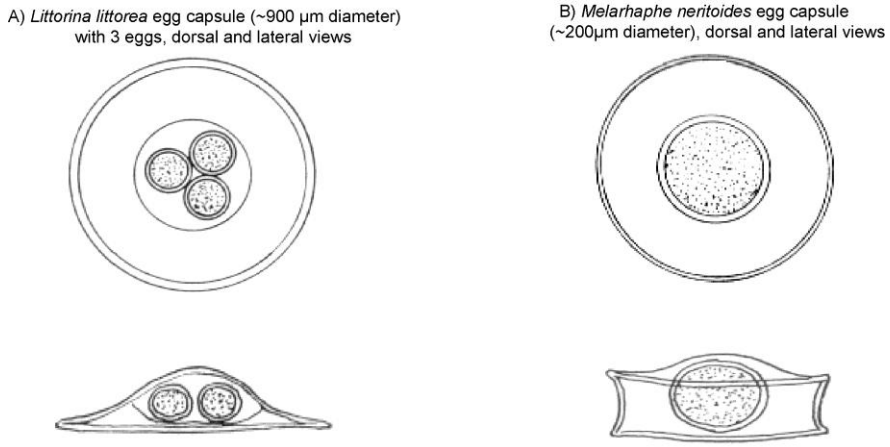

Fig. 3. *Littorina* spp*.* egg capsules. (from Lebour, 1935a).

Class Gastropoda: Veligers
Subclasses: Prosobranchia and Opisthobranchia

Gastropod veligers typically have a bilobed velum (Fig. 4A), some multilobed (Fig. 4E) others single (Fig. 4H), the number of lobes sometimes increasing during development. Most, but not all species have coiled shells, number of whorls increasing during development, and an operculum that closes the shell mouth. Their shells may have a plain surface, while others have striae or sculpturing, but the shells do not necessarily closely resemble the adult shell. The veliger body may also be pigmented to varying degrees.

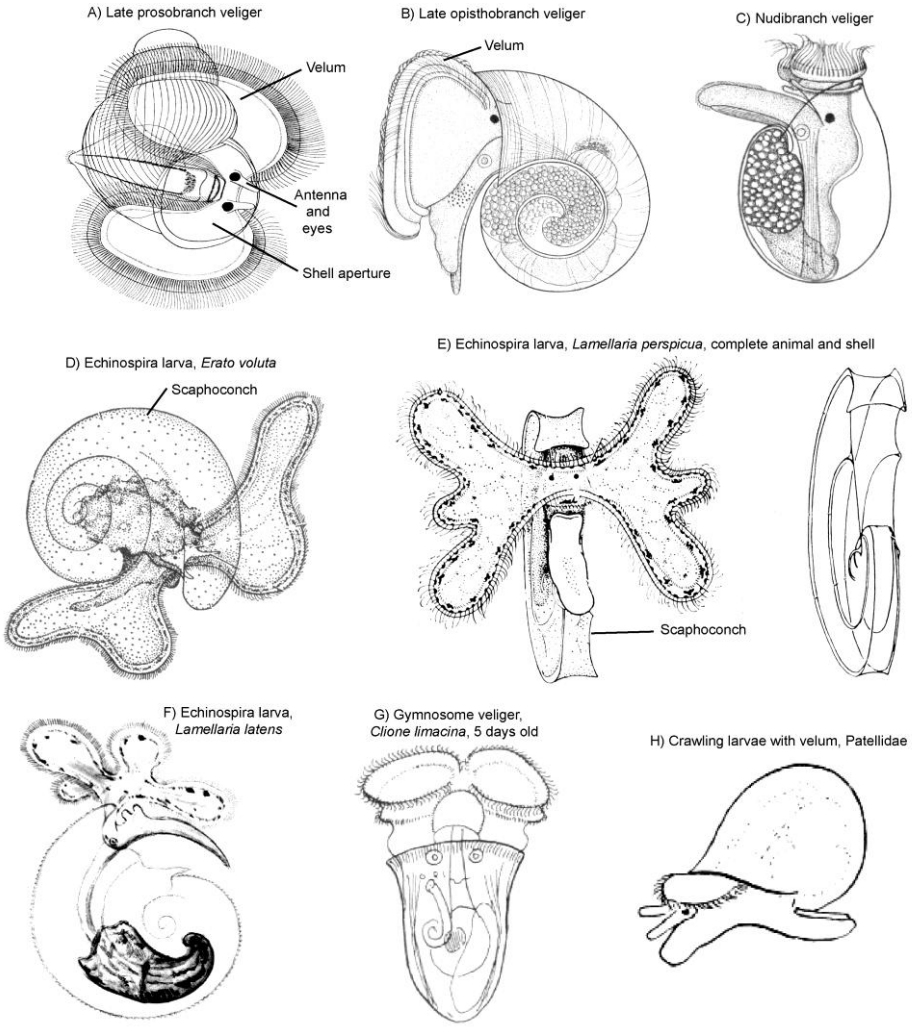

Fig. 4. Gastropod veligers. (A-C from Thorson, 1946; D, E from Fretter & Graham, 1962; F from Lebour, 1935b; G from Lebour, 1931; H from Lebour, 1937).

Prosobranch gastropod larvae typically have a dextrally coiled shell (coiled clockwise), such that when the shell is positioned with the spire pointing upwards, the aperture opens on the right (Fig. 4A, D). In opisthobranchs with a coiled shell, the coiling is typically sinistral (coiled anticlockwise; Fig. 4B). Some opisthobranch nudibranch veligers have a shell that is not coiled, but egg-shaped (Fig. 4C). The direction of coiling in both prosobranchs and opisthobranchs is determined from the veliger stage. A small number of prosobranch species do not follow these coiling rules and open on the left, but the coiling direction usually reverses to opening on the right during settlement, in a process known as heterostrophy.
There is an additional unusual prosobranch veliger larval type called an echinospira, typical of a few gastropod groups (e.g. families Lamellariidae, Eratoidae and Capulidae). These veligers can either have a large transparent spiral shell called the scaphoconch, surrounding the true shell or protoconch e.g. *Erato voluta* (Montagu, 1803)(Fig. 4D). In other species the echinospira is flattened, the edge of the scaphoconch usually ornately toothed; fine teeth in *Lamellaria perspicua* (Linnaeus, 1758)(Fig. 4E), coarse in *L. latens* (Müller, 1776)(Fig. 4F).
Identifying veligers is a specialised task and many of the features can only be seen when they are unpreserved and alive, or at an advanced stage of development. The earliest veligers are particularly difficult to identify, as shell spiralling may not have started, or it can be difficult to discern the direction of coiling. They often lack pigment and thus can all appear very similar. Keys to gastropod veligers are given by Hadfield (1964) and Fretter & Pilkington (1970).

Recorded: PMF, only adults recorded. L4, can be found all year round. Throughout the European region.
Size: Very variable because of the different shapes, but the shells are ~0.16-0.8 mm wide by ~0.16-1.0 mm high.
Further information: Lebour, 1931, 1935a, b, 1937; Thorson, 1946; Fretter & Graham, 1962; Newell & Newell, 1963; Hadfield, 1964; Fretter & Pilkington, 1970; Goddard, 2001; Buckland-Nicks *et al*., 2002a, b.

Phylum Mollusca:

Class Gastropoda:

This is the largest marine molluscan class and comprises two subclasses, **Prosobranchia** and **Opisthobranchia**. Most gastropods only have planktonic stages during larval development, but there are several species that are also planktonic as adults. The name gastropod means stomach foot, as the typical gastropod consists of a head and the visceral mass (the internal organs), sitting on top of a muscular foot. The visceral mass is usually protected by a typically coiled shell, although in some groups the shell is not coiled and in others is missing. As noted in the larval development section, prosobranch gastropods typically have a dextrally coiled shell (coiled clockwise) and in opisthobranchs with a coiled shell, the coiling is typically sinistral (coiled anticlockwise).

Phylum Mollusca: Class Gastropoda:

Subclass Prosobranchia:

Prosobranchia is divided into three orders Mesogastropoda, Archaeogastropoda and Neogastropoda, but while larvae of non-planktonic species of all of these orders can be taken in inshore samples, the only planktonic adults that could possibly be sampled off southern Britain are all in Order Mesogastropoda. Mesogastropods usually have planktonic dispersal phases, sometimes initially as a trochophore, but the majority are released as veligers. The only adults that could be sampled in plankton nets are in superfamilies Heteropoda and Epitonioidea.
Superfamily Heteropoda are the atlantids and "sea elephants", but these are oceanic species in the North Atlantic, unlikely to be sampled inshore, so are not included here. In Superfamily Epitonioidea the janthinids (Fig. 5) are not strictly planktonic, but surface dwelling oceanic snails.

Phylum Mollusca: Class Gastropoda: Subclass Prosobranchia: Order Mesogastropoda: Superfamily Epitonoidea:

Family Janthinidae:

These are oceanic snails, living suspended at the sea surface by a raft of air bubbles of hardened mucous, below which the animal hangs (Fig. 5A). They can be sampled in plankton nets, but are most frequently found washed ashore. Their dextrally coiled shell (Fig. 5B) is quite fragile and the animal and shell are a vivid blue or violet colour, hence their common names, "purple shell" or "violet sea snail". Preferred prey is the drifting, colonial hydrozoan *Velella velella* (by-the-wind-sailor). An operculum is present only in the veliger stage. Some species are viviparous, releasing veligers, while others produce pear-shaped egg capsules, typically with distal spines and containing many eggs (Fig. 5C), suspended below the bubble raft (Fig. 5A).

Genus *Janthina:*

Janthina janthina (Linnaeus, 1758)

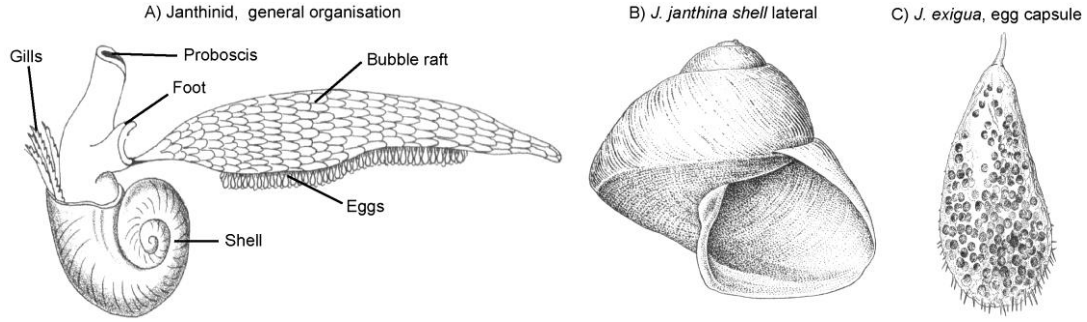

Fig. 5. *Janthina* spp. (A from Meglitsch, 1967; B-C from Laursen, 1953).

Janthina janthina (Fig. 5B) is the most frequently recorded janthinid in the European area. There are ~4 whorls in the shell, which has surface striations, with most regular striations on the first 1.5 whorls. The shell is blue to violet in colour, the spire tip fairly flat, although shape is variable. The profile is triangular to roundish-triangular. It is viviparous, releasing veligers.

Recorded: PMF, not recorded. L4, not recorded. Frequently washed ashore on western beaches of Britain and Ireland.
Size: Shell up to 31 mm high; aperture up to 22 x 20 mm.
Further information: Laursen, 1953.

Subclass Opisthobranchia:

There are nine orders of opisthobranchs, but only orders **Nudibranchia**, **Thecosomata** and **Gymnosomata** have planktonic adults. Nudibranchia and Gymnosomata have shells reduced to varying extents to minimise sinking, but all adult Thecosomata have a substantial shell. Thecosomes and gymnosomes, although not particularly closely related, are often grouped under the common name of "pteropods", meaning wing-foot, as part of the foot and body wall is developed into wing-like flaps used for swimming.

Opisthobranch larvae hatch as veligers, or less commonly as juveniles, having passed through the trochophore stage within a gelatinous egg mass. Veliger larvae initially have a sinistrally coiled shell, although nudibranch shells can be cup- or egg-shaped with little obvious spiralling. The shell is lost during metamorphosis in nudibranchs and also in gymnosome species without an external shell in the adult. For further information see Lalli & Gilmer (1989) and Thompson (1976).

Order Nudibranchia:

Around 90 British nudibranch species have been recorded (Thompson & Brown, 1976). They superficially resemble some of the pelagic polychaetes, but are not segmented. All British species are benthic as adults, living either in sand, or on rocks and seaweed. A few can swim weakly when required to perform an escape reaction, but juveniles and adults are rarely taken in plankton samples. Their spawn is usually jelly-like and deposited on the substrate, and eggs hatch as swimming veligers with simple shells that only have a short planktonic existence before settling.

Family Tritoniidae:

Genus *Dendronotus:*

Dendronotus frondosus (Ascanius, 1774)

This species is given as an example of an adult and juvenile nudibranch (Fig. 6). The whole body is laterally compressed and can be lashed from side to side in a feeble escape reaction.

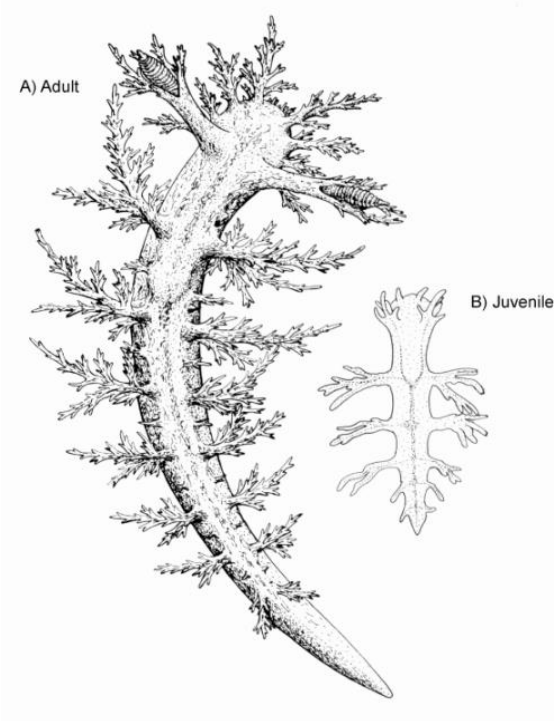

Fig. 6. Example of a nudibranch, *Dendronotus frondosus* (from Thompson & Brown, 1976).

Recorded: PMF, 66 adult nudibranch species recorded. L4, not recorded. Throughout the European region.

Size: Juveniles ~4 mm, adults up to 100 mm.

Further information: Thompson & Brown, 1976; Picton & Morrow, 1994.

Order Thecosomata:

All thecosomes have shells, but they are very fragile, so are often damaged to varying degrees in samples. Additionally, if the preservative is not buffered to neutralise acidity, the shells can dissolve and only the internal bodies remain. In response to this problem, van der Spoel (1972) provided a separate identification key for specimens lacking their shells. In species with coiled shells, the spiralling is sinistral. Thecosomes feed using a mucous net to trap microzooplankton. Some of the species are described as having several sub-species or formae, these formae often showing distinct morphological differences in separate parts of their geographic range.

Family Limacinidae:

Genus *Limacina*:

Shell spiralling is sinistral, as in other thecosomes with spiralled shells, and an operculum is present. The spire in different species can be high or flattened. The lower edge of the aperture is rounded and not produced into a point as in some other genera. The shell is usually translucent brown, typical of most thecosomes with shells. The large, winged foot sometimes protrudes from the shell aperture, but preservation usually causes it to retract. They are hermaphroditic and most produce floating egg masses. Veligers hatch out from the eggs and do not have pigment spots on the shell, which can be found on the shells some benthic gastropod veligers.

Limacina retroversa (Fleming, 1823)

This is the main thecosome species sampled around Britain. There are two formae, forma *retroversa* (Fig. 7A) and forma *balea. Balea* is larger with more coils and is distributed in northern colder waters. *Limacina* can be consumed in high numbers by pelagic fish such as herring, to the extent that when the fish is opened the gut appears black due to the contained dark shells, a phenomenon that was recognised by herring fishermen, who referred to it as “black-gut”.

Eggs are laid in gelatinous strips around 2.0 mm long by 0.5 mm wide. Veligers that emerge, initially have no shell. The shell appears, coils sinistrally, then two lappets form on the sides of the foot that develop into the swimming “wings” (Fig. 7B). Number of whorls in the shell increases until there are five in the adult, the last whorl very large in comparison to those at the apex (Fig. 7A). The shell has fine spiral striations and the aperture is irregularly rounded.

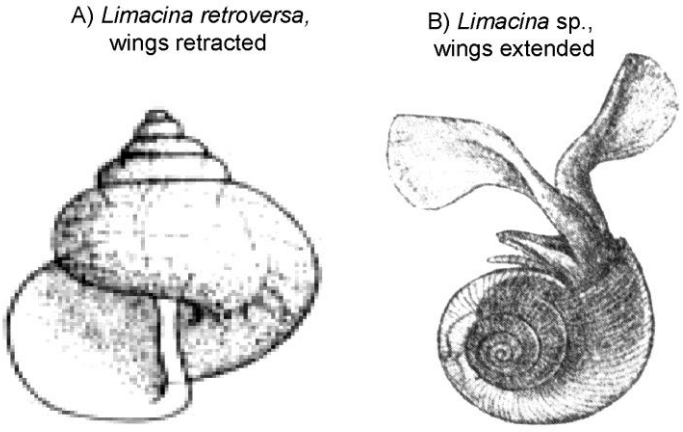

Fig. 7. *Limacina retroversa*. (A from van der Spoel, 1972; B from Lenz, 1906).

Recorded: PMF (as *Spiratella retroversa*). L4, regularly taken. Widely **t**hroughout the European area.

Size: Up to 2.5 mm in height, 3 mm in diameter.

Further information: Morton, 1954a; Tesch, 1947; van der Spoel, 1967, 1972; van der Spoel *et al*., 1997; Newell & Newell, 1963.

Limacina lesueurii (d'Orbigny, 1836)
Adult shell with 4.5 whorls (Fig. 8), translucent, flatly coiled, broader than high with straight inner aperture border. This species can probably only be accurately distinguished from *L. retroversa* when fully grown.

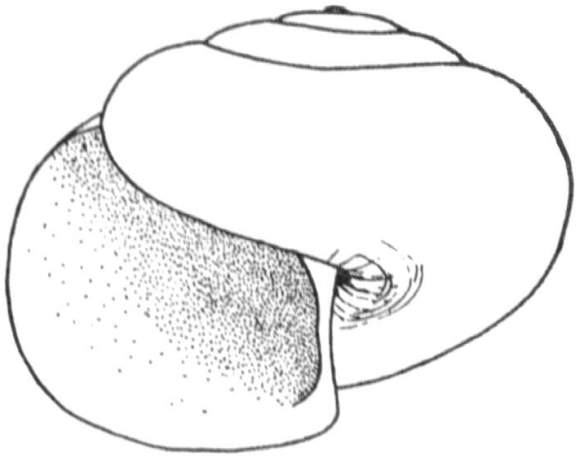

Fig. 8. *Limacina lesueurii* (from van der Spoel, 1972).

Recorded: PMF (as *Spiratella lesueuri*), occasionally found. L4, not recorded, but may have been overlooked. Oceanic species, to the south-west of Britain.
Size: Up to ~0.8 mm in height, width up to 1.3 mm.
Further information: van der Spoel, 1967, 1972; van der Spoel *et al*., 1997.

Order Gymnosomata:

These opisthobranchs lack a shell in the adult. Most of the foot is transformed into a pair of swimming “wings” or parapodia. However, the wings and remnants of the foot are often difficult to see in preserved specimens, disappearing into a roll of skin surrounding the mid-body. The feeding apparatus is important for species identification, but is usually retracted. Lack of a shell means they can also suffer much distortion during preservation. See van der Spoel (1976; p. 65) and Morton (1957a) for suggestions on identification techniques.

Family Clionidae:

Genus *Clione*:

Clione limacina (Phipps, 1774)

There are at least two forms of *Clione limacina* found in the European area (van der Spoel, 1976). Forma *limacina* (Figs. 9, 10A-D) is large (>5 mm), light coloured, matures around 12 mm and is distributed in more northern waters. The “wings” are short, the body ends bluntly and there is a central cusp on the median plate of the radula (Fig. 10D). Forma *minuta* (Fig. 10E, F) is smaller (<5 mm), dark coloured, matures around 3 mm and is distributed in more southern areas. The “wings” are long, the body has a sharper end and the median plate of the radula lacks cusps (Fig. 10F).

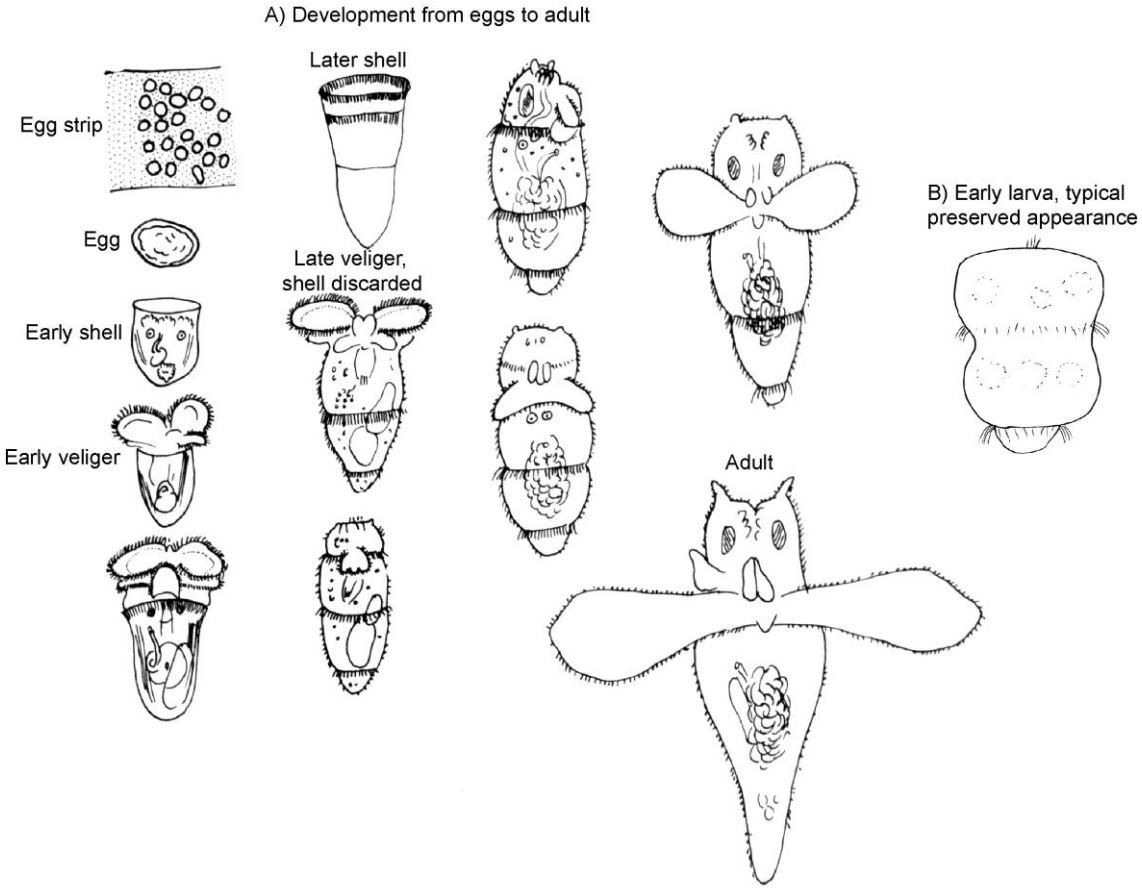

Fig. 9. *Clione limacina* forma *limacina* development. Egg to adult, including individual shells. Arranged from top to bottom, left to right (A from van der Spoel, 1976; B from preserved L4 specimen).

Stages in the development of *C. limacina* forma *limacina* are given in Figure 9. The colourless eggs are laid in a gelatinous ribbon (Fig. 9A). The veliger that emerges has a thimble-shaped, uncoiled shell that it discards after a few days. In the larvae, three rows of cilia encircle the body and these are gradually lost, but the posterior row may sometimes persist, even into the adult.

In adults there is a small tentacle either side of the head (Fig. 10A-C). Adults are extremely voracious and commonly occur with the thecosome *Limacina*, on which they feed (Fig. 10C). This association develops from an early age, as immediately the *Clione* veliger loses its shell, it starts

feeding on *Limacina* veligers, capturing them with six specialised oral appendages called buccal cones or cephalocones that are hydraulically everted, elongated very rapidly and act like tentacles. These appendages, which are reported to be adhesive, hold prey during the feeding process. On the inside wall of the buccal cavity are a pair of lateral sheaves of hooks, curved at the ends and carried in eversible sacs from which they protrude. A radula is situated between the hook sacs (Fig. 10B, D, F) and in adults is strong and has two rows of teeth, 6-15 teeth wide, depending on the size of the animal, either side of central single row of curved and weakly serrated teeth. There is no multi-hooked jaw associated with the radula, or suckers or long proboscis in the feeding apparatus as found in Family Pneumodermatidae.
The viscera extend about halfway down the abdomen, so the posterior part of the tapered body is empty and is where the eggs develop. The large parapodia project well beyond the sides of the body. Other remnants of the foot are represented by three lobes situated centrally behind the head, two lateral and one median (Fig. 10A). There are no lateral gills, unlike in Family Pneumodermatidae.

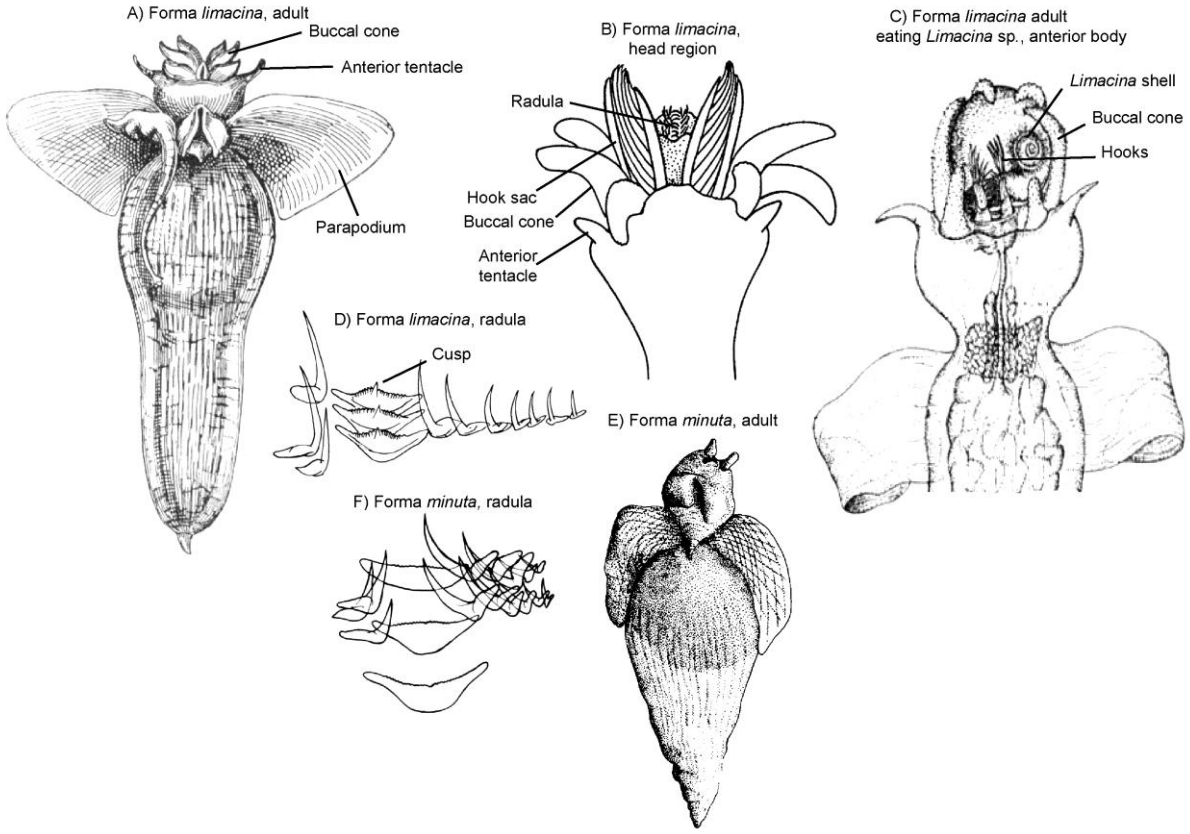

Fig. 10. *Clione limacina* forma *limacina* and forma *minuta* adults. (A from Lenz, 1906; B from Morton, 1958; C from Thompson & Brown, 1976; D-F from van der Spoel, 1976).

Recorded: PMF. L4 (both probably forma *minuta*). Northern North Sea. Western Britain and Ireland.
Size: Forma *limacina* up to 21 mm in length, forma *minuta* up to 5 mm in length.
Further information: Lenz, 1906; Pruvot-Fol, 1926; Lebour, 1931; Morton, 1957b; Morton, 1958; Conover & Lalli, 1972; van der Spoel, 1976; Thompson & Brown, 1976; Norekian & Satterlie, 1993; van der Spoel *et al*., 1997.

Family Pneumodermatidae:

Specific differences compared to Family Clionidae are mainly based on the presence of suckers in the buccal cavity and features of the teeth and radula. The arrangement of hook sacs and radula are similar to Clionidae, but in addition they have a multi-hooked jaw, situated on the proboscis, associated with the radula. The muscular parapodia are smaller than in *Clione*. Posterior or lateral external gills are usually present.

Genus *Pneumodermopsis:*

Only the early veliger has a simple shell. In adults the body narrows posteriorly, but is not sharply tapered as in *Clione*. On either side of the head is a small tentacle (Fig. 11A). The mouth opens into a proboscis (Fig. 11B) that can be evaginated along with the complicated buccal organs (Fig. 11A-D). When not evaginated the buccal organs are covered by a head cap (Fig. 11A). The buccal organs are composed of a median arm with a terminal sucker and lateral suckers on stalks. On either side of the median arm is a row of suckers that can be on a pair of arms, or emerging directly from the wall of the buccal cavity, on stalks or sessile. Two hook sacs are also present, with short hooked teeth. The radula is composed of two lateral rows of tiny multiple teeth and in the centre a single row. Jaws are present, close to the radula. The lateral gill is a simple triangular flap on the right and there is no posterior gill. A circle of cilia, a remnant from the larval stage, is usually present towards the anterior (Fig. 11B), often persisting long into adult life. To observe the teeth and hooks of the mouthparts microscopically, small specimens can be digested for a short time in a weak caustic solution on a slide, and then squashed under a cover slip.

Pneumodermopsis ciliata (Gegenbaur, 1855)

Body with a pale purple tinge, barrel-shaped with a large lateral gill hanging free (Fig. 11A, B). On the median arm are five suckers (Fig. 11D), the two uppermost lateral suckers are very large (Fig. 11B-D), typical of this species. There are two lateral sucker-bearing arms, short but distinct, each with seven to eight suckers. The radula has three to eight rows of teeth each side depending on age, and a single row in the centre that has three cusps (Fig. 11E), the central one tiny. There are around 8-40 teeth in the hook sacs (Fig. 11A, F). The jaws are well developed and are formed of multiple rows of long teeth (Fig. 11A). Behind the head are three foot-lobes, two lateral and a longer median one (Fig. 11A-C).

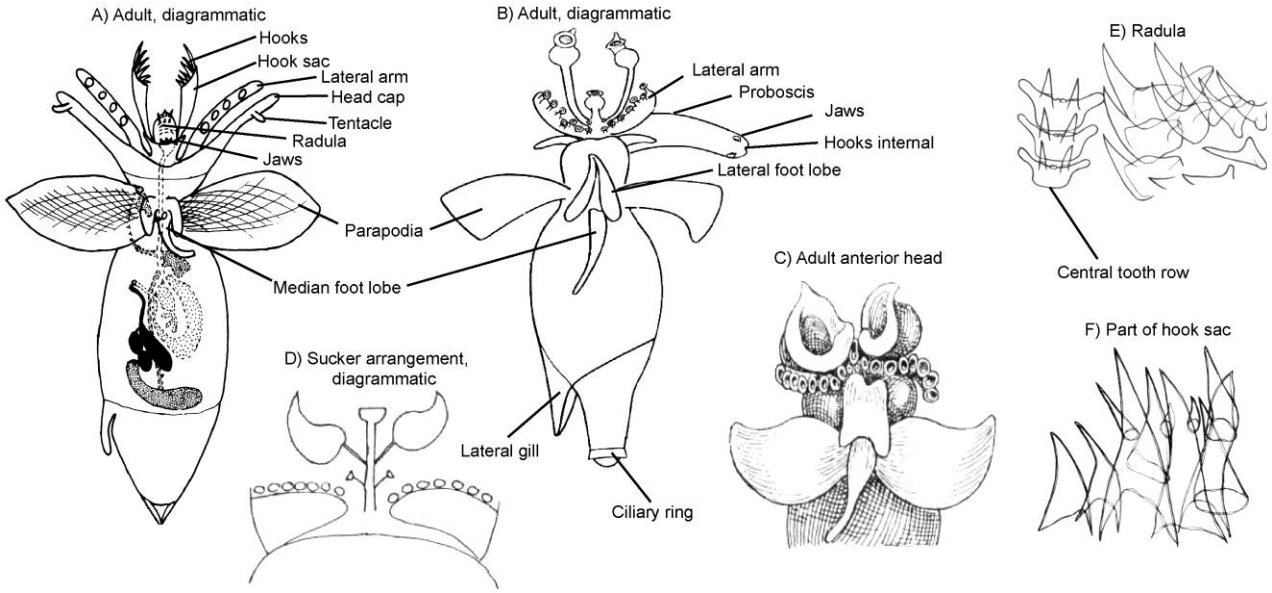

Fig. 11. *Pneumodermopsis ciliata.* (A, E, F from van der Spoel, 1976; B from Morton, 1957a; C from Lenz, 1906; D from Tesch, 1950).

Recorded: PMF, not recorded. L4, not recorded. Northern North Sea. South and west Ireland
Size: Up to 15 mm in length.
Further information: Pruvot-Fol, 1926, 1932; Morton, 1957a; van der Spoel, 1976; van der Spoel *et al*., 1997.

Pneumodermopsis paucidens (Boas, 1886)
Two formae are reported, *paucidens* (Fig 12A) and *pulex* (Fig. 12B), the main difference being the absence of lateral gills in forma *pulex*. Appearance of preserved specimens is very variable (Fig. 12C). Lateral suckers on the median arm are usually smaller than the terminal one. There are no lateral arms on the buccal tentacle apparatus, but instead an indistinct transverse row of 10-12 suckers on very short stalks on the inside wall of the buccal cavity, five to six either side of the median arm (Fig. 12D). The radula has two to three rows of teeth each side of a single median row that has two central cusps (Fig. 12E). The jaws, associated with the radula, are well developed. The teeth in the hook sacs are short and number five to six, fewer than in *P. ciliata*. Behind the head are three foot lobes (Fig. 12A-C), two lateral and one median, of similar length in young specimens, the median lengthening with age.

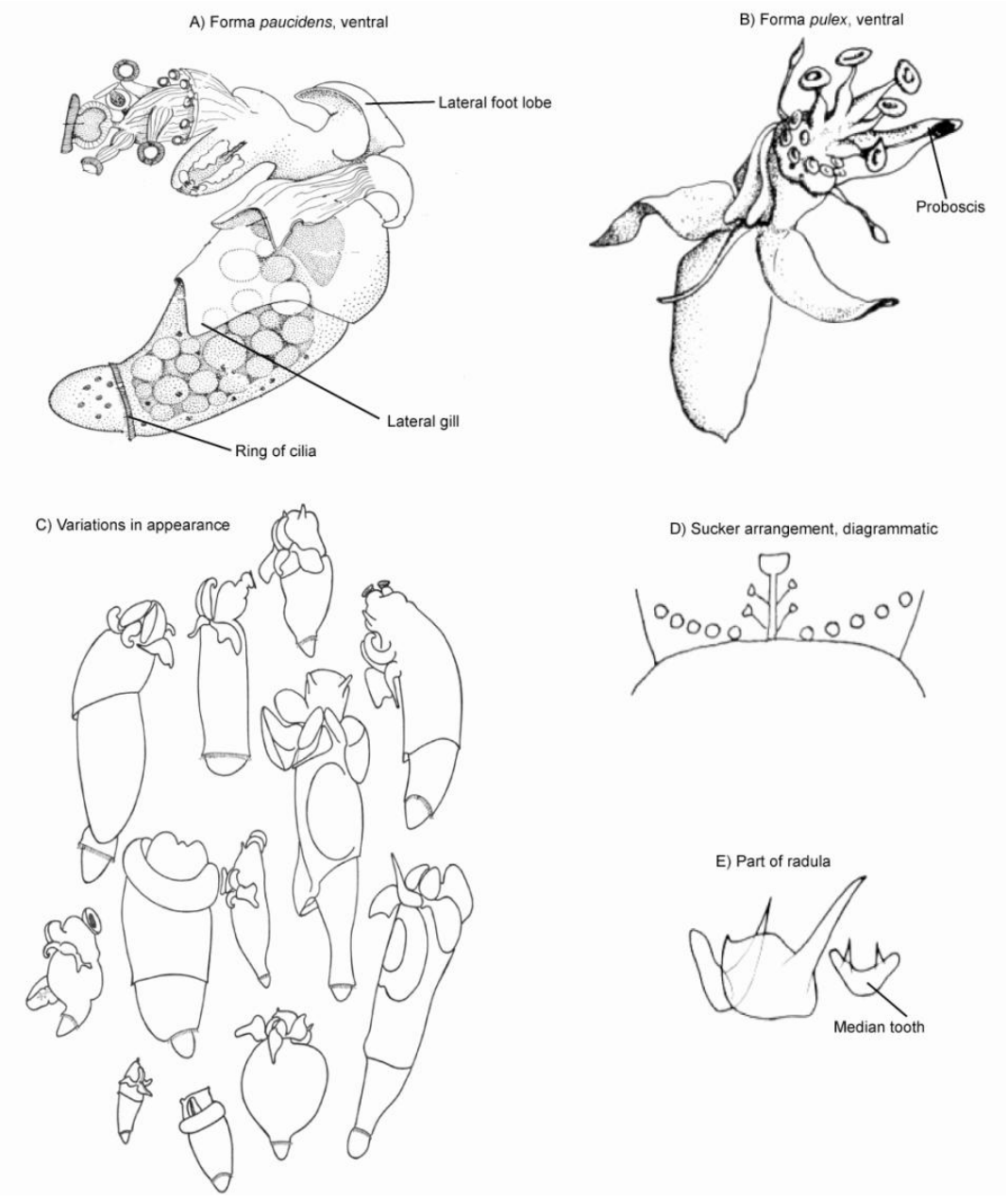

Fig. 12. *Pneumodermopsis paucidens.* (A, C from Morton, 1954b; B, E from Boas, 1886, 1976; D from Tesch, 1950).

Recorded: PMF, not recorded. L4, not recorded. South and west Ireland. A more oceanic species.
Size: Up to 5 mm in length.
Further information: Boas, 1886; Morton, 1954b, 1957a; Pruvot-Fol, 1926; van der Spoel, 1976; van der Spoel & Dadon, 1999; van der Spoel *et al*., 1997.

Phylum Mollusca:

Class Cephalopoda:

Class Cephalopoda is divided into Subclasses **Nautiloidea** and **Coleoidea.** Nautiloidea have an external shell and are only found in the tropics, so are not included here. Coleoidea are the soft-bodied cephalopods, most of which have an internal structure that is used for support or buoyancy.

Subclass Coleoidea:

Coleoidea comprises two infraclasses, **Decapodiformes** that have ten limbs and includes cuttlefish and squid, and **Octopodiformes** that have eight limbs and includes octopus. Further separation is based on type and shape of the lateral fins on the posterior sac or mantle that encloses the organs. A distinct larval stage is lacking, the juveniles being miniature adults. There are few juvenile illustrations, so mainly only adult illustrations are given. There are 14 species recorded in the PMF and some examples only are included here. For further information see Nesis (1999) and Sweeny *et al*. (1992).

Key to Subclass Coleoidea

1. Eight tentacles around mouth, all same length ---------- Order Octopoda (Fig. 16)
   Ten tentacles around mouth, two usually obviously longer than others ---------- 2

2. Mantle sac-like; fins extend right around the mantle ---------- Order Sepiida (Fig. 13)
   Mantle rounded; circular fins on opposing sides of mantle ---------- Order Sepiolida (Fig. 14)
   Mantle torpedo-shaped; fin terminal, single, triangular ---------- Order Teuthida (Fig. 15)

Phylum Mollusca: Class Cephalopoda: Subclass Coleoidea: Infraclass Decapodiformes:

Order Sepiida: Family Sepiidae:

Genus *Sepia*:

Sepia officinalis Linnaeus, 1758

Cuttlefish larvae have ten tentacles around the mouth, one pair longer than the others and a sac-like body with long narrow lateral fins extending longitudinally around the mantle, apart from a short cleavage at the lower end (Fig. 13). The shell is a large internal calcified structure commonly called the cuttle bone. There is a low, forward projection of the mantle behind the head in *S. officinalis* that is much more pronounced in the closely related *S. elegans* Blainville, 1827.

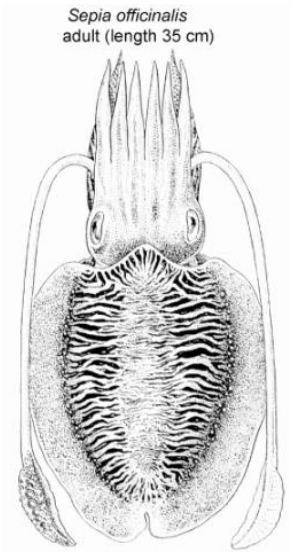

Fig. 13. *Sepia officinalis* (length excludes tentacles; from Muus 1963a; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF, adults of *Sepia officinalis* and *S. elegans.* L4, not recorded. Southern North Sea. English Channel. Irish Sea. Southern Ireland.
Size: Adult, mantle length in *S. officinalis* ~400 mm, in *S. elegans* ~80 mm.
Further information: Muus, 1963a.

Order Sepiolida: Family Sepiolidae:

These are a group of tiny cephalopods, closely related to cuttlefish, also having eight suckered arms and two longer tentacles (Fig. 14). They are commonly known as 'bobtail squid' and lack a cuttlebone, the inner shell being chitinous and rudimentary. They tend to have a rounder mantle than cuttlefish, on either side of which is a pair of lateral, well separated, circular fins.

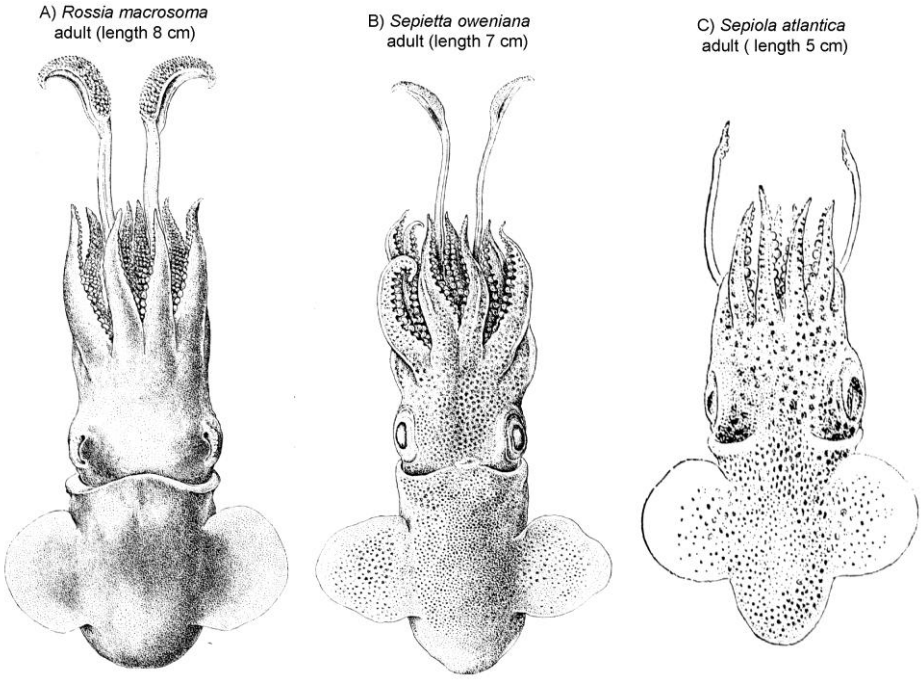

Fig. 14. Sepiolidae species found off southern Britain (lengths exclude tentacles; from Muus, 1963a; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF, adults of *Rossia macrosoma* (Delle Chiaje, 1828); *Sepietta oweniana* (d'Orbigny, 1839); *Sepiola atlantica* d'Orbigny, 1839. L4, not recorded. Northern North Sea. Southern North Sea. English Channel. Irish Sea. South and west Ireland.
Size: *R. macrosoma* maximum mantle length 60 mm; *S. oweniana* 50 mm; *S. atlantica* 21 mm.
Further information: Muus, 1963a.

Order Teuthida:

This order includes the more familiar larger squid, the larvae of which, as in orders Sepiida and Sepiolida, have ten tentacles around the mouth, one pair longer than the others. Bodies of species found off south-west Britain are torpedo-shaped with a single terminal fin. In *Loligo* and *Alloteuthis* spp. (Fig. 15A, B) the anterior mantle has a blunt, forwardly directed projection, behind the head, absent in *Todaropsis* (Fig. 15C). Most species have a pair of blunt triangular fins, but in *Alloteuthis* the posterior body is greatly extended and the fins are more heart-shaped.

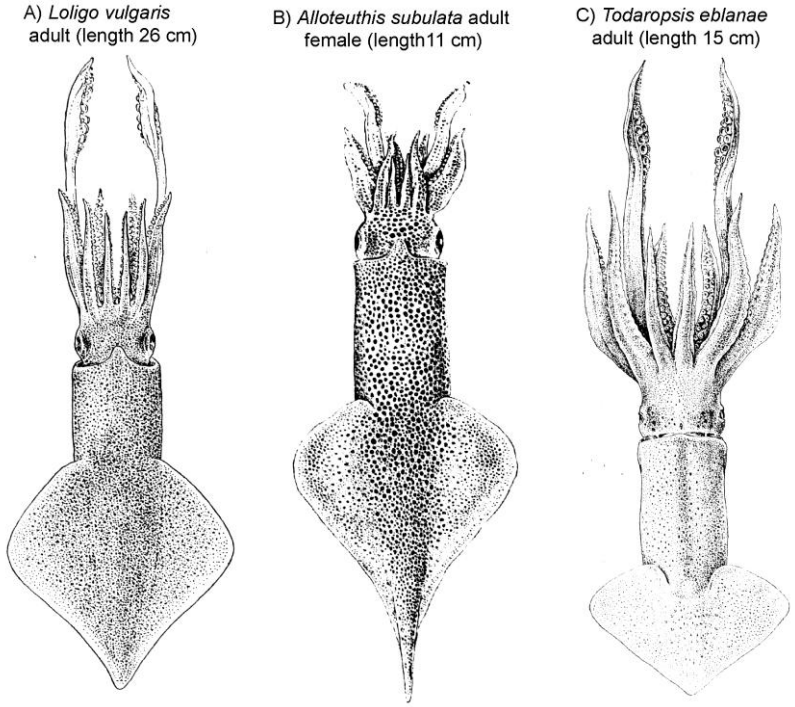

Fig. 15. Examples of Order Teuthida found off southern Britain (lengths exclude tentacles; from Muus, 1963b, c; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF, adults of *Loligo vulgaris* Lamarck, 1798; *L. forbesi* Steenstrup, 1856; *Alloteuthis subulata* (Lamarck, 1798); *Illex coindeti* Vérany, 1839; *Todaropsis eblanae* (Ball, 1841); *Sthenoteuthis pteropus* (Steenstrup, 1855) (as *Ommastrephes pteropus*); *Ommastrephes bartramii* (Lesueur, 1821) (as *O. caroli*). L4, not recorded. North Sea. English Channel. Irish Sea. South and west Ireland.
Size: *Loligo* spp. mantle length to ~300 mm, *Alloteuthis* ~50 mm.
Further information: Muus, 1963b, c.

Order Octopoda: Family Octopodidae:

The two Octopoda species found off southern Britain have eight tentacles around the mouth, approximately all the same length. There are no fins on the body. In *Eledone cirrhosa* (Fig. 16A) the tentacle suckers are in one row, two rows in *Octopus vulgaris* (Fig. 16B).

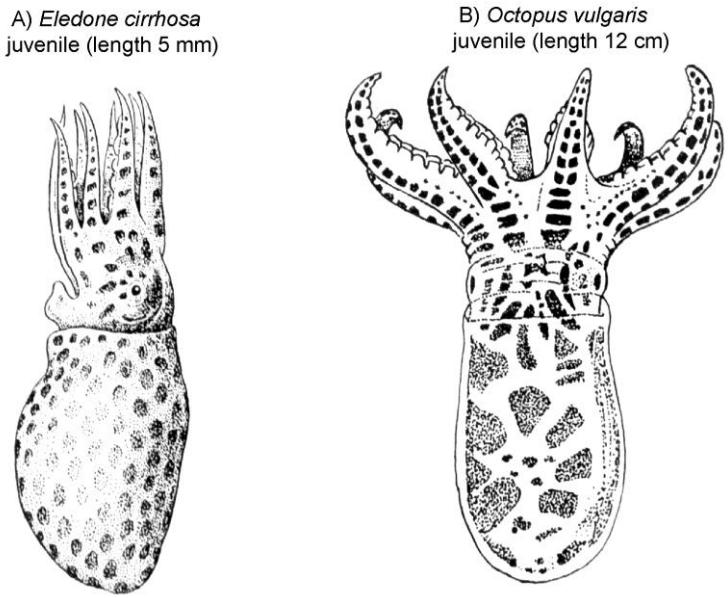

Fig. 16. Examples of the Family Octopodidae (from Muus, 1963d; Used with the kind permission of the International Council for the Exploration of the Sea).

Recorded: PMF, adults of *Eledone cirrhosa* (Lamarck, 1798); *Octopus vulgaris* Cuvier, 1797. L4, not recorded. North Sea. English Channel. Western Britain. Irish Sea. South and west Ireland.
Size: No information.
Further information: Muus, 1963d.

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