MARINE ZOOPLANKTON OF SOUTHERN BRITAIN

Part 3:
Ostracoda, Stomatopoda, Nebaliacea, Mysida, Amphipoda, Isopoda, Cumacea, Euphausiacea, Decapoda, Annelida, Tardigrada, Nematoda, Phoronida, Bryozoa, Entoprocta, Brachiopoda, Echinodermata, Chaetognatha, Hemichordata and Chordata

David V.P. Conway






Edited by Anthony W.G. John

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Front cover from top left clockwise and centre: Krill caught in small mesh trawl in central northern North Sea; Parasitic isopod, microniscus stage, attached to the copepod *Paracalanus parvus*; Phoronida actinotroch larva, *Actinotrocha branchiata*; Brachiolaria larva of the sea star *Asterias rubens* (Image, R. Kirby); School group in the resource centre at the MBA learning about plankton during National Science Week; Loxostomatidae entoproct larva (Image, R. Foster, Scottish Environment Protection Agency (SEPA)).

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

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Preface

This is the final in a series of three identification guides to the zooplankton found around southern Britain. The list of species included and described is primarily based on those that have been recorded in the Plymouth Marine Fauna (PMF; Marine Biological Association. 1957. Plymouth Marine Fauna, Third edition. Plymouth, Marine Biological Association, 457 pp.). The PMF lists the wide range of marine organisms, both pelagic and benthic, collected in the Plymouth area between the opening of the Marine Biological Association (MBA) laboratory in 1888 until 1957, when the PMF was last published. Also described are additional zooplankton species that have been recorded at Station L4, a sampling station 10 nautical miles off Plymouth, where plankton collections have been made weekly by the Plymouth Marine Laboratory (PML) since 1988, and some other species recorded from the more general area. An unplanned addition phylum has been included in this part, Entoprocta, as the larvae have been turning up in plankton samples from different UK areas.

The guides were originally planned solely for local training and identification purposes. However, as the southwest of the UK is also exposed to influences from oceanic currents, it became evident that they would contain, in one source, enough information to identify most of the holoplanktonic species from the northern European shelf area (excluding the Mediterranean), so they have been made more widely available. Information is also given on identification of some of the vast range of meroplanktonic larvae that are produced by the rich and diverse European benthos. Taxonomy is mainly based on the World Register of Marine Species (WoRMS) scheme, which is constantly being modified, so at least lower level classifications unfortunately soon become outdated. To avoid copyright issues, cost and the effort of redrawing organisms, many of the illustrations included are from old publications, but are still of high quality and accuracy.

Full details about the guides are given in Part 1 of the series (Conway, D.V.P. 2012. Marine zooplankton of southern Britain. Part 1: Radiolaria, Heliozoa, Foraminifera, Ciliophora, Cnidaria, Ctenophora, Platyhelminthes, Nemertea, Rotifera and Mollusca. A.W.G. John (ed.). Occasional Publications. Marine Biological Association of the United Kingdom, No. 25, Plymouth, United Kingdom, 138 pp.), available for free download at - http://plymsea.ac.uk/id/eprint/5631

Part 2: Arachnida, Pycnogonida, Cladocera, Facetotecta, Cirripedia and Copepoda. A.W.G. John (ed.). Occasional Publications. Marine Biological Association of the United Kingdom, No. 26, Plymouth, United Kingdom, 163 pp. is also available free at - http://plymsea.ac.uk/id/eprint/5633

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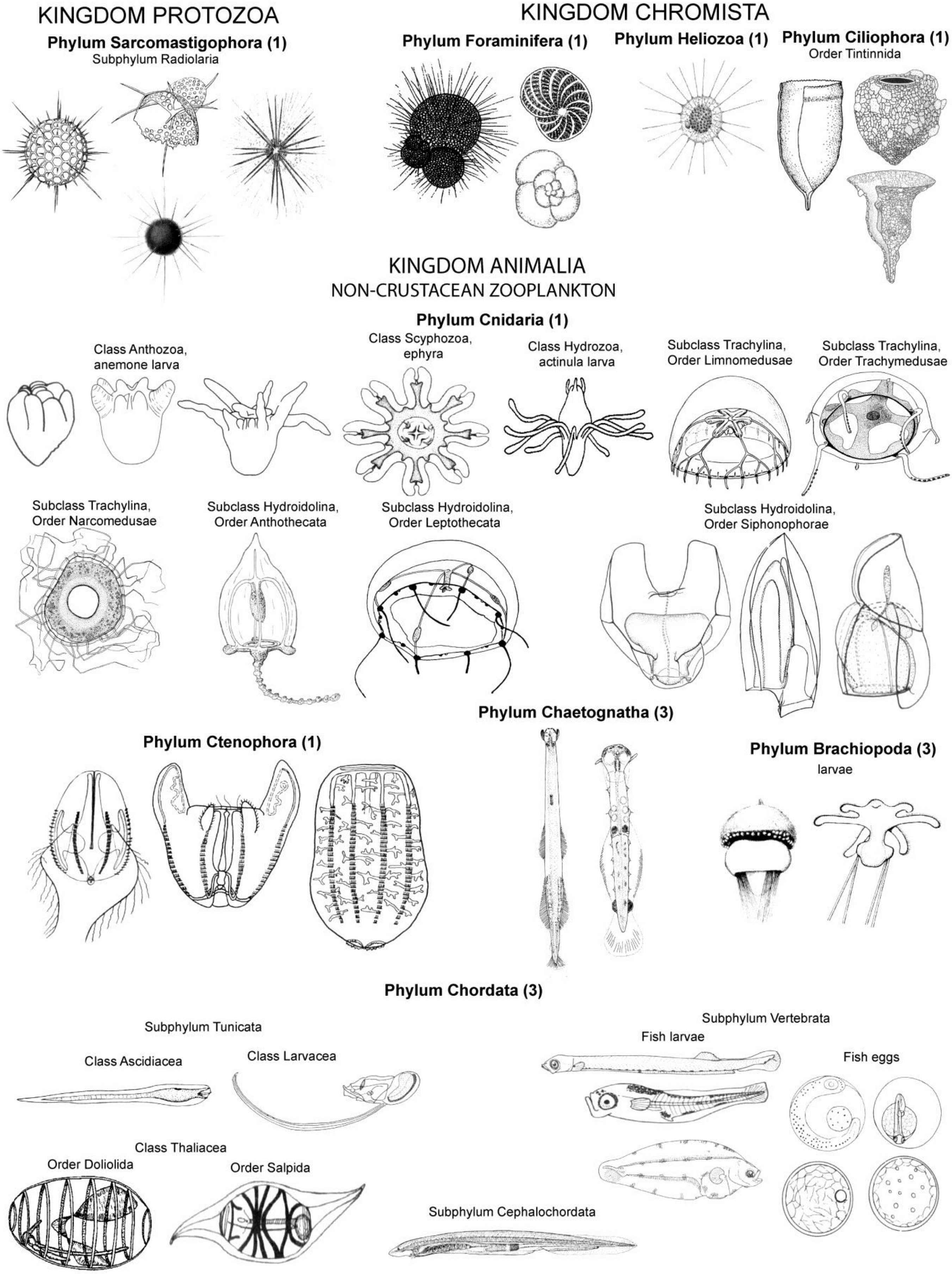
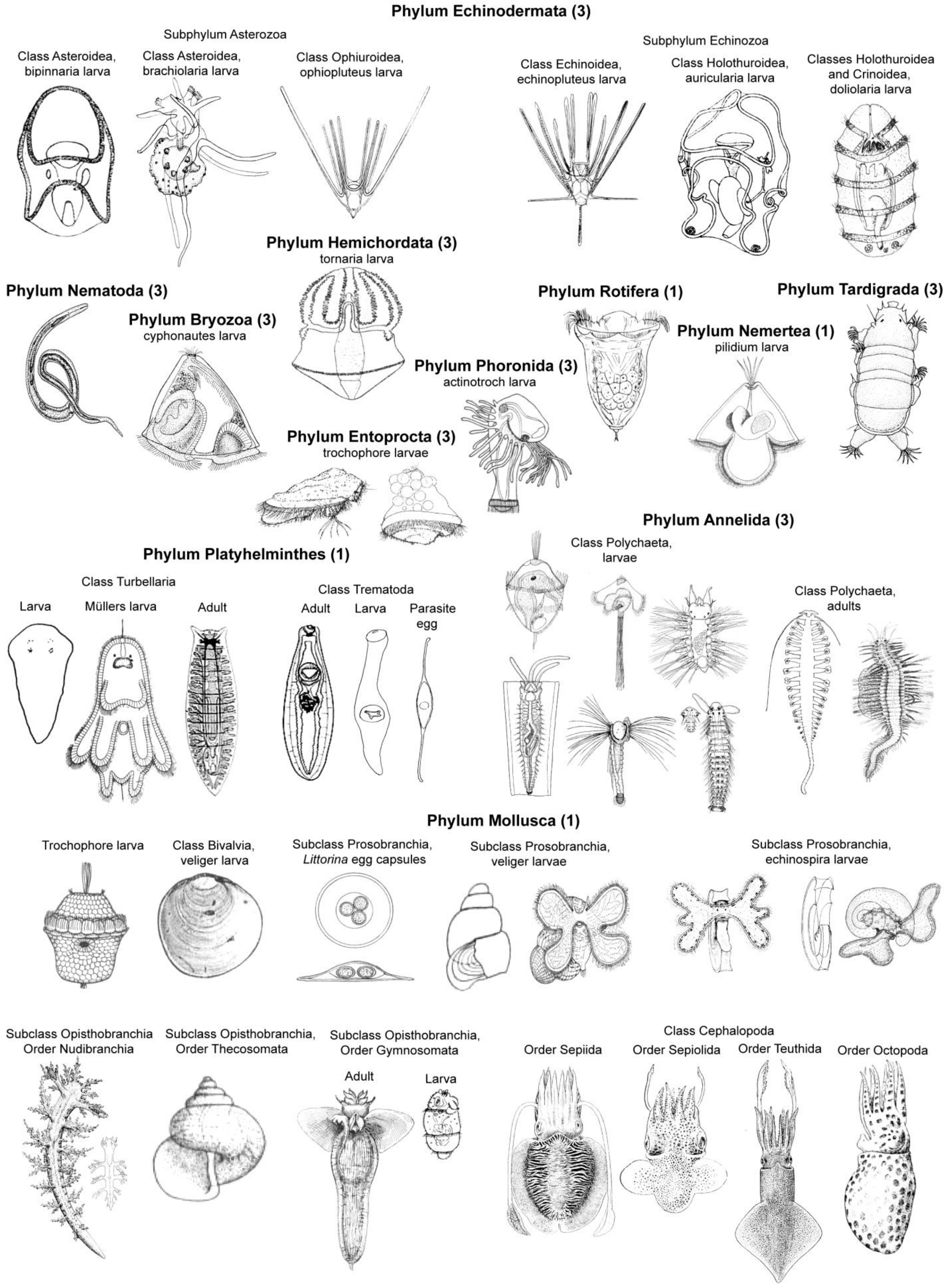
PICTORIAL KEY TO PLANKTON

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

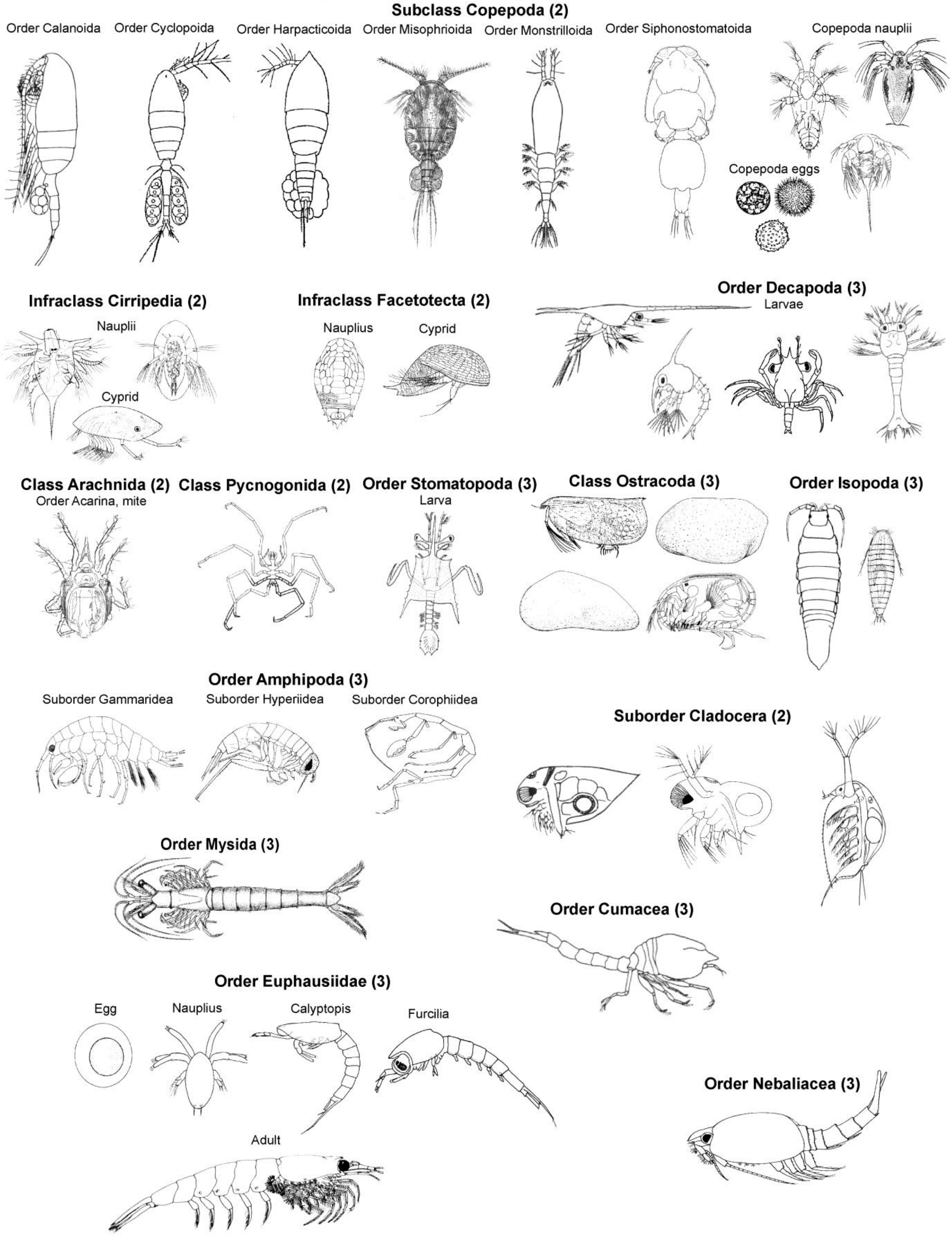


NON-CRUSTACEAN ZOOPLANKTON AND LARVAE



CRUSTACEAN ZOOPLANKTON

Phylum Arthropoda - Subphylum Crustacea



PHYLUM ARTHROPODA

Subphylum Crustacea:

Class Ostracoda:

The body of ostracods is largely enclosed within a shell-like carapace which, depending on species, is impregnated with varying amounts of calcareous material. The carapace is formed of two valves (bivalve) hinged longitudinally along the top (Fig. 2A) and because of their bean-like appearance their common name is "seed shrimp". Various limbs, used in feeding, locomotion and mating, partially protrude from the carapace. Ostracods are found in almost all aquatic habitats, and in the sea there are both planktonic, epibenthic and benthic species. In northern European waters, benthic and epibenthic ostracods are often sampled, especially close inshore or in turbulent conditions, but the majority of the truly planktonic species are only found in more oceanic areas, so are rarely sampled coastally unless there is deep water nearby. Ostracods have a wide range of diets and the class includes carnivores, herbivores, scavengers and filter feeders, and also a few commensal and parasitic species. They are sometimes misidentified as the cyprid stage of barnacles, or even as cladocerans, both of which groups they superficially resemble.

Classification

According to the WoRMS classification there are only two subclasses of living ostracods, **Podocopa** and **Myodocopa**. Numbers in brackets below are numbers in each main taxonomic group recorded in the PMF, as an indication of their typical biodiversity and relative abundance in shallow coastal European waters.

Subclass Podocopa

- **Order Podocopida** - freshwater, marine and brackish, mainly bottom-living coastal (60).
- **Order Platycopida** - marine, a few brackish, mainly bottom-living in deeper waters (0).

Subclass Myodocopa

- **Order Myodocopida**
  - **Suborder Myodocopina** - marine, mainly neritic bottom-living, a few planktonic (2).
- **Order Halocyprida**
  - **Suborder Halocypridina** - marine, neritic to oceanic, mainly planktonic (0).
  - **Suborder Cladocopina** - marine, bottom-living, some cave-dwelling (3).

Morphology

Ostracoda is a very large class and members show considerable variability in their morphology, related to their niche. They are mainly small, particularly the benthic and epibenthic species. Their bivalve carapace is typically elliptical, rectangular, or almost circular in outline (Figs. 3, 8) and usually laterally, but sometimes also quite dorsoventrally compressed. The appearance of the carapace can vary between individuals of the same species, but is usually still constant enough to be used for taxonomic purposes. In some species there are projections at one or both posterior corners of the carapace (Figs. 5H, 6A). The two valves differ slightly, one fitting inside the other, to varying extents in different groups. The carapace surface may be covered in hairs or spines, smooth, or with a variety of surface ornamentation (Fig. 3) and calcified to varying degrees. It tends to be smooth, thin and transparent in planktonic species, more robust and often sculptured and heavily calcified in bottom living species. In the species of suborders Myodocopina and Halocypridina of Subclass Myodocopa, each valve is produced into an anterodorsal rostrum (Figs. 5A, B, E, H, 6A), a beak-like projection, below which is an antennal notch, through which the exopods of the antennae project laterally during swimming.

The carapace valves are closed by a transverse adductor muscle (Fig. 4A), resembling a similar mechanism found in bivalve molluscs. The carapace hinge varies from simple, where the valves are connected by ligaments, to a complex structure of teeth and sockets. The body is mainly enclosed within the carapace and is unsegmented, or the segmentation is difficult to discern (Fig. 2). It consists of a cephalon (head) and thorax, often with a slight constriction between them ventrally. The abdomen is fused with the thorax, or is absent. Depending on group, there are between five and seven paired limbs, much fewer than found in most crustaceans. In Crustacea, the paired limbs from the anterior backwards would typically be called antennules, antennae, mandibles, maxillules, maxillae and maxillipeds, but in Ostracoda several nomenclature variations have been used, making literature comparisons a nightmare. Maxillae are usually considered cephalic limbs and maxillipeds the first limbs of the thorax, but because of some ostracod developmental and structural anomalies there is debate whether their maxillae are actually on the cephalon or thorax (Schram, 1986; Athersuch *et al*., 1989). Because of this, the limbs are sometimes just named by sequential numbers (one up to seven), or alternatively the maxillae are named the fifth limbs and any further limbs numbered sequentially. This latter scheme is followed here.

The antennules are uniramous, usually with short setae if a crawling or burrowing species (Fig. 4). They can serve a variety of functions, including sensory, locomotory and assisting in copulation. The antennae are the main limbs used in locomotion, whether swimming or crawling. They are biramous, but there are considerably differences between orders and sexes in comparative development of the exopod and endopod (Figs. 2C, 4B). The remaining limbs are involved in locomotion, feeding, respiration, mating and cleaning. On the posterior body is a paired appendage, fused at the base, called the caudal furca. The furca generally projects from the carapace, usually pointing downwards and slightly forwards (Fig. 4A), but is greatly reduced in some species (Fig. 2A). Some authors believe the furca are homologous with the telson of other crustaceans, others interpreting them as a uropod and thus should be considered a true limb. Ostracods generally have a naupliar eye (Fig. 2A) and in Order Myodocopida, usually a large pair of lateral, compound eyes (Fig. 5A).

Males and females

Some ostracod species appear to be partially or wholly parthogenetic and in some cased males have never been found. The carapaces of the sexes of the same species range in appearance from similar (Fig. 5B, E) to quite different, and are often of different sizes. Sexual dimorphism is sometimes slight, but is usually obvious in the presence and structure of particular limbs and other appendages. Between the last limbs and the furca, male ostracods possess relatively large copulatory appendages (Figs. 2B, 6F) that are paired except in Suborder Halocypridina. They are variable in appearance and correspond to genital openings on the female. In suborders Myodocopina and Halocypridina the endopod of the antenna is generally modified into a conspicuous hook, used for clasping the female (Figs. 5G, 6E). The fifth or sixth limbs in some ostracods can function for walking or feeding, but may be strongly sexually dimorphic (Figs. 2A, B, 4D), used for clasping the female.

Reproduction and development

Mating typically occurs when the sexes swarm together. Eggs, which are sometimes brightly coloured, may be spawned directly into the water column, or attached to some substrate, but many species brood their eggs inside the carapace in a brood chamber (Fig. 4A, 5B, 7A) and release late development, miniature adult, stages.

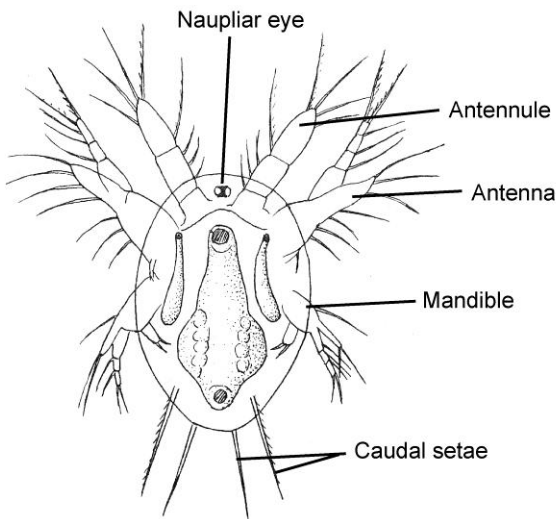


Fig. 1. Typical ostracod nauplius (from Trégouboff & Rose, 1957).

Eggs hatch into a nauplius larva (Fig. 1) resembling a copepod first nauplius, but apparently with an extra pair of caudal setae. Nauplii, if released, are short-lived and small, so are unlikely to be taken in plankton nets and would probably only be seen in laboratory cultures. There is only one nauplius stage and this moults into a miniature ostracod. There are generally between five and eight moults before they are adults, and number of limbs and carapace features change at each moult. Typical of crustaceans, the carapace is lost and replaced between moults, and moulting stops when they are adults. In juveniles, any carapace ornamentation is usually similar, but more subdued than in the adults, but in some species marked changes in ornamentation and shape occur at the final moult.

Key to the suborders and orders of Ostracoda

1. Carapace with antennal notch (Figs. 5, 6) --- **2**
- Carapace without antennal notch (Figs. 2-4, 8) --- **3**

2. Seventh limb elongate, worm-like, sometimes reduced; compound eye present in almost all genera --- Suborder Myodocopina (Fig. 5)
- Seventh limb thin and quite short ; no compound eye -------- Suborder Halocypridina (Fig. 6)

3. Body with only five pairs of limbs; carapace valves almost circular; caudal furca with short conical projections between setae ---------------------------- Suborder Cladocopina (Figs. 7, 8)
- Body with more than five pairs of limbs; carapace valves not circular; caudal furca without conical projections between setae --- **4**

4. Carapace valves variously shaped, right valve partially overlaps left; seven pairs of limbs; antenna with one basal segment, exopod usually greatly reduced, endopod with stout terminal setae --- Order Podocopida (Figs. 2, 3)
- Carapace valves ovate, usually strongly calcified, right valve overlaps left around entire margin; six pairs of limbs; antenna with two basal segments, exopod and endopod well developed, broad and flattened, bearing stout setae --------------- Order Platycopida (Fig. 4)

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Ostracoda:

Subclass Podocopa:

Order Podocopida:

In coastal waters these, typically bottom-living ostracods, are the main group found. Carapace without antennal notch, often heavily calcified, oval with rounded corners or sometimes more angular (Figs. 1, 2), often rather flat along ventral edge, right valve overlapping the left at least along the anterior margin when closed; seven pairs of limbs; antenna with one basal segment in both sexes, exopod usually greatly reduced (Fig. 2C; often more reduced than one illustrated), endopod with stout terminal setae; fifth limb sexually dimorphic, in the male may be modified for clasping the female (Fig. 2B, D); furca narrow bearing a few setae, reduced (Fig. 2A, B), or absent; naupliar eye present (Fig. 2A); no compound eye.

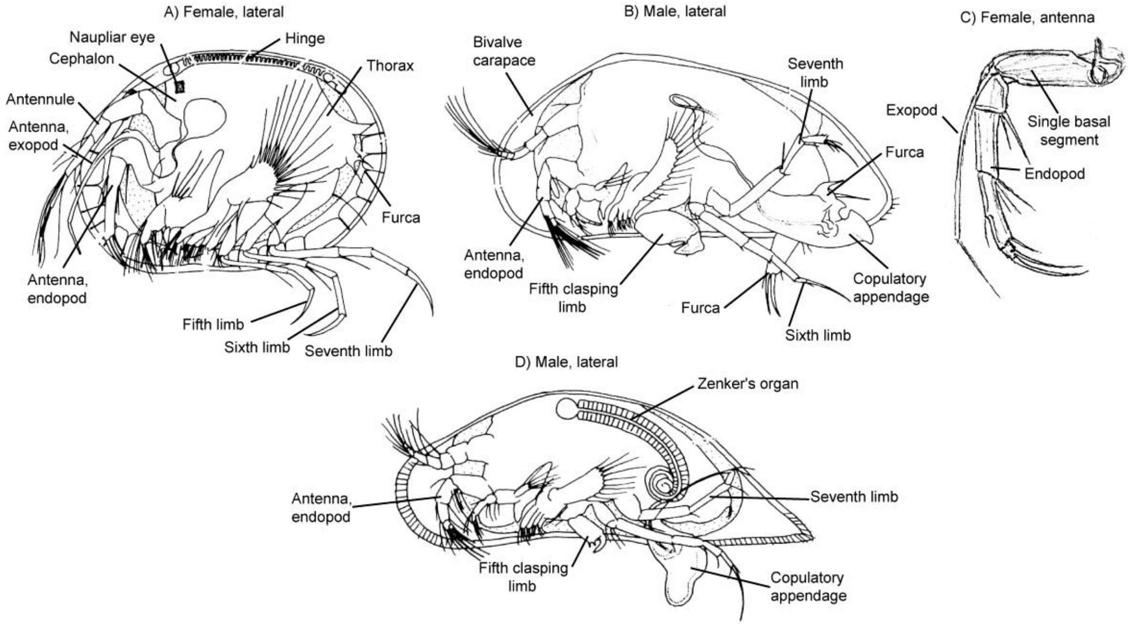


Fig. 2. Order Podocopida, examples of general morphology (A, B, D from Athersuch *et al.*, 1989; C from Sars, 1928).

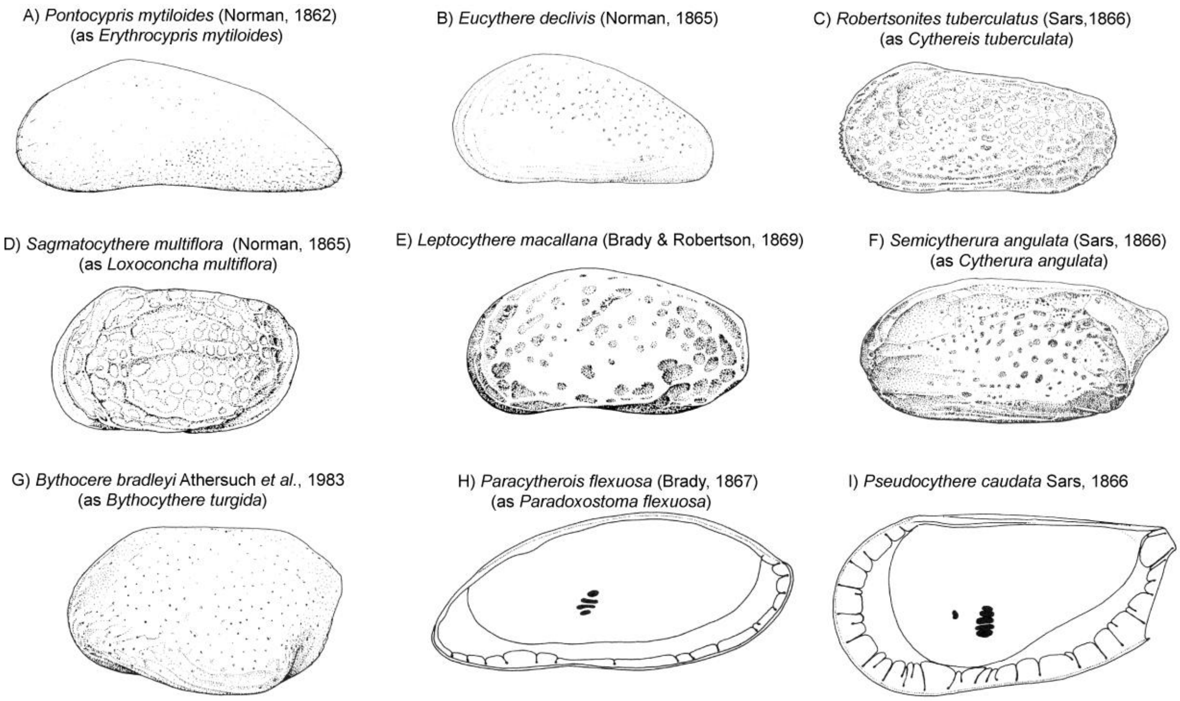


Fig. 3. Order Podocopida, some of the 60 species recorded in the PMF (from Athersuch *et al.*, 1989).

In some males of Order Podocopida (Suborder Cypridocopina), the testes lead by way of a tubular structure, called a Zenker's organ (Fig. 2D), to the copulatory appendage. The Zenker's organ is wreathed by rings of chitinous spines and acts to pump sperm during copulation. It should not be confused with the seventh worm-like limb found in Suborder Myodocopina (Fig. 5A).

Recorded: PMF, 60 benthic/epibenthic species. L4, unidentified species. All European waters.
Size: Most ~0.3-1.0 mm, but some up to 8 mm.
Further information: Sars, 1928; Howe *et al*., 1961; McGregor & Kesling, 1969; Neale, 1969; Poulsen, 1969; Schram, 1986; Angel, 1993, 1999; Athersuch *et al*., 1989.

Order Platycopida:

Order Platycopida is a small order of mainly bottom-living ostracods, containing only one family (Cytherellidae). Carapace ovate (Fig. 4A), strongly calcified, smooth or ornamented, without antennal notch, right valve usually overlaps the left around the complete margin; six limbs; both the antennal exopod and endopod are strong (Fig. 4B), almost equally developed, short and flattened; sixth limb in males modified for clasping the female (Fig. 4D), reduced in females to a small plate (Fig. 4C); male copulatory appendage conspicuous (Fig. 4E); furca well developed in both sexes (Figs. 4A, E).

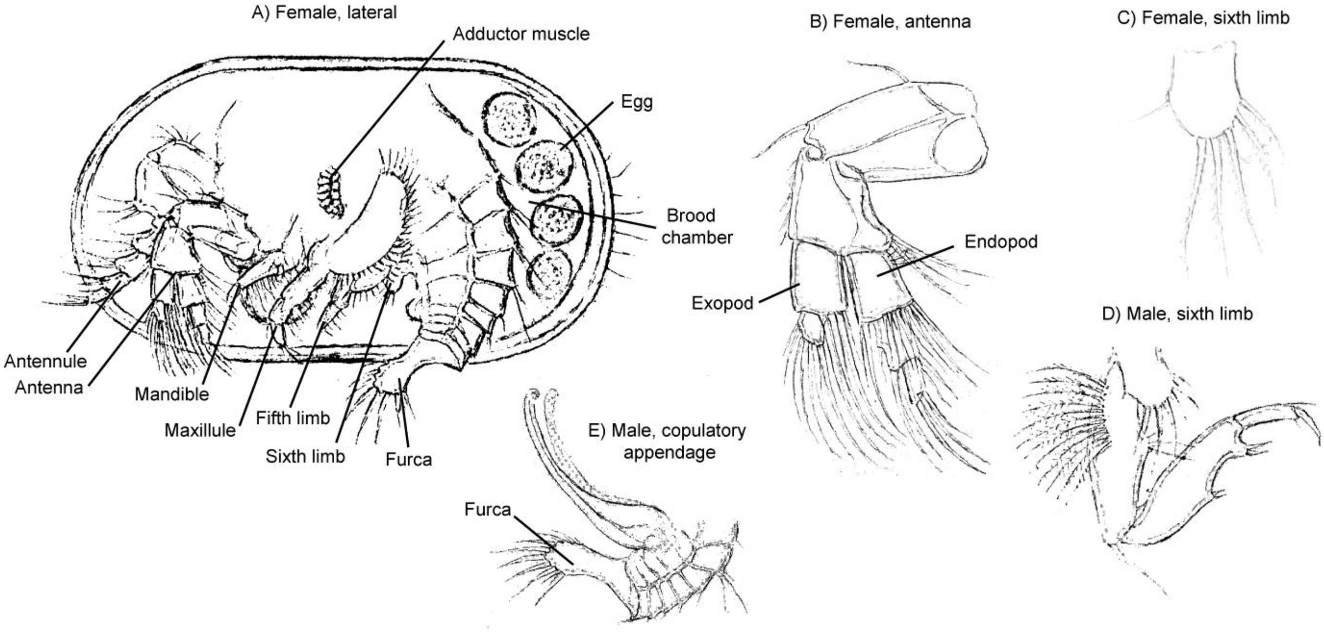


Fig. 4. General morphology of Order Platycopida, *Cytherella abyssorum*, G.O. Sars, 1866 (from Sars, 1928).

Recorded: PMF and L4, not recorded, (*Cytherella abyssorum* found around at least British and western Norwegian coasts).
Size: Most <1.0 mm.
Further information: Sars, 1928; Howe *et al*., 1961; McGregor & Kesling, 1969; Neale, 1969; Schram, 1986; Angel, 1993, 1999; Athersuch *et al*., 1989.

Subclass Myodocopa:

Apart from Suborder Cladocopina, each valve is produced anteriorly into a rostrum (Fig. 5A, B, E, H), a beak-like projection, below which is an antennal notch through which the exopods of the antennae project laterally during swimming. Five or seven pairs of limbs; terminal segment of the endopod of the antennule in males usually developed as a hook appendage (Fig. 5G), the shape of which is useful in identification.

Order Myodocopida:

Suborder Myodocopina:

Carapace with rostrum and antennal notch (Fig. 5A, B), ovoid, elongate, sometimes deep-bodied (Fig. 5H); antenna a powerful locomotory limb, exopod well developed (Fig. 5D) bearing long setae, endopod reduced, in male the endopod may be developed into a clasping hook (Fig. 5G); seven pairs of limbs, seventh worm-like with bristles and teeth (Fig. 5A), used for cleaning; male copulatory organ paired; furca well developed, with strong marginal setae; lateral compound eyes usually present.

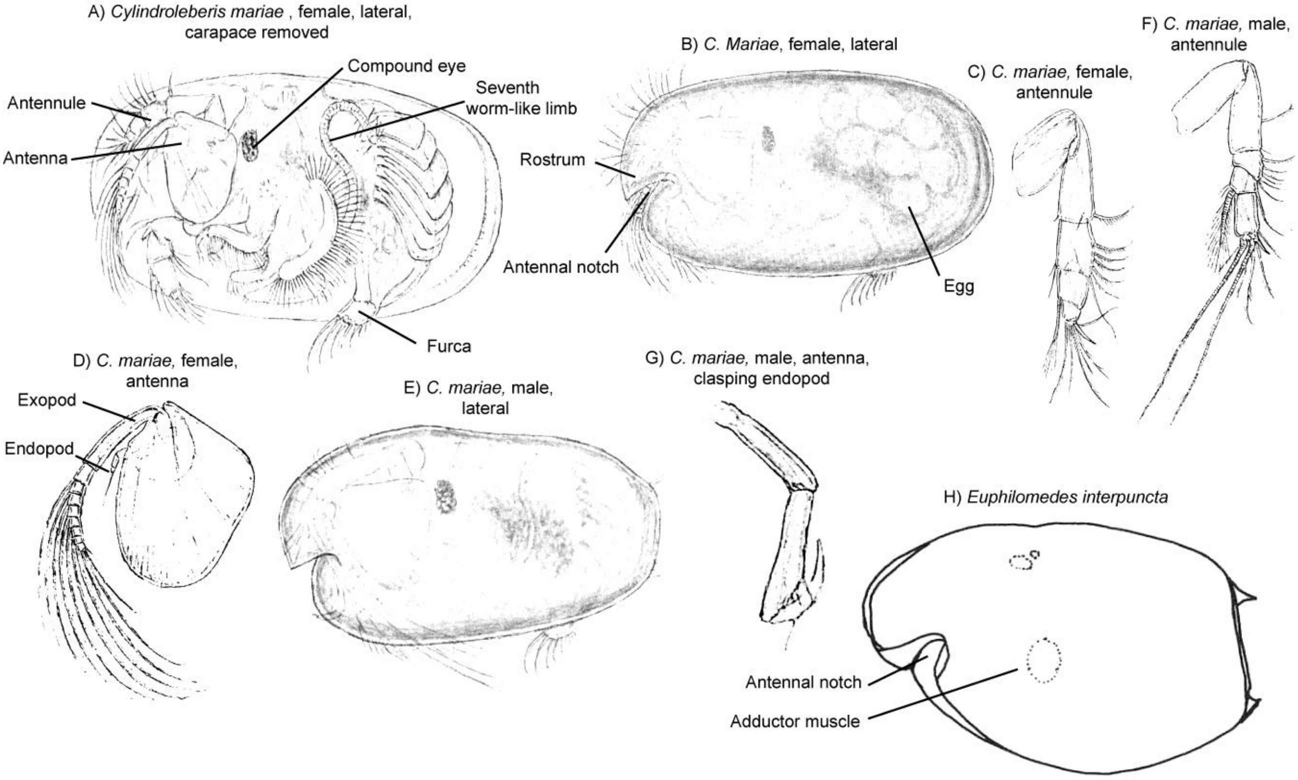


Fig. 5. Suborder Myodocopina, general morphology using the two species recorded in the PMF, *Cylindroleberis mariae* (Baird, 1850)(as *Asterope mariae*) and *Euphilomedes interpuncta* (Baird, 1850)(as *Philomedes interpuncta*). (A-G from Sars, 1928; H from Angel, 1993).

Recorded: PMF, two epibenthic species. L4, not recorded. European coasts.
Size: Most ~0.3-2.0 mm.
Further information: Sars, 1928; Trégouboff & Rose, 1957; Howe *et al*., 1961; McGregor & Kesling, 1969; Neale, 1969; Poulsen, 1969; Schram, 1986; Kornicker, 1987; Angel, 1993, 1999; Athersuch *et al*., 1989; Blachowiak-Samolyk & Angel, 2008.

Order Halocyprida:
Suborder Halocypridina:

Pelagic ostracods. Carapace with rostrum and antennal notch (Fig. 6A, B), usually ovoid, dorsal margin straight or slightly concave, ventral margin usually curved; antenna a powerful swimming limb, exopod and endopod both quite well developed (Fig. 6C), terminal segment of the male endopod usually developed as a hook (Fig. 6E), the shape of which is useful in identification. Seven limbs (Fig. 6B), the seventh usually small, finger-shaped with terminal setae; male copulatory appendage (Fig. 6F) not paired; no lateral compound eyes.

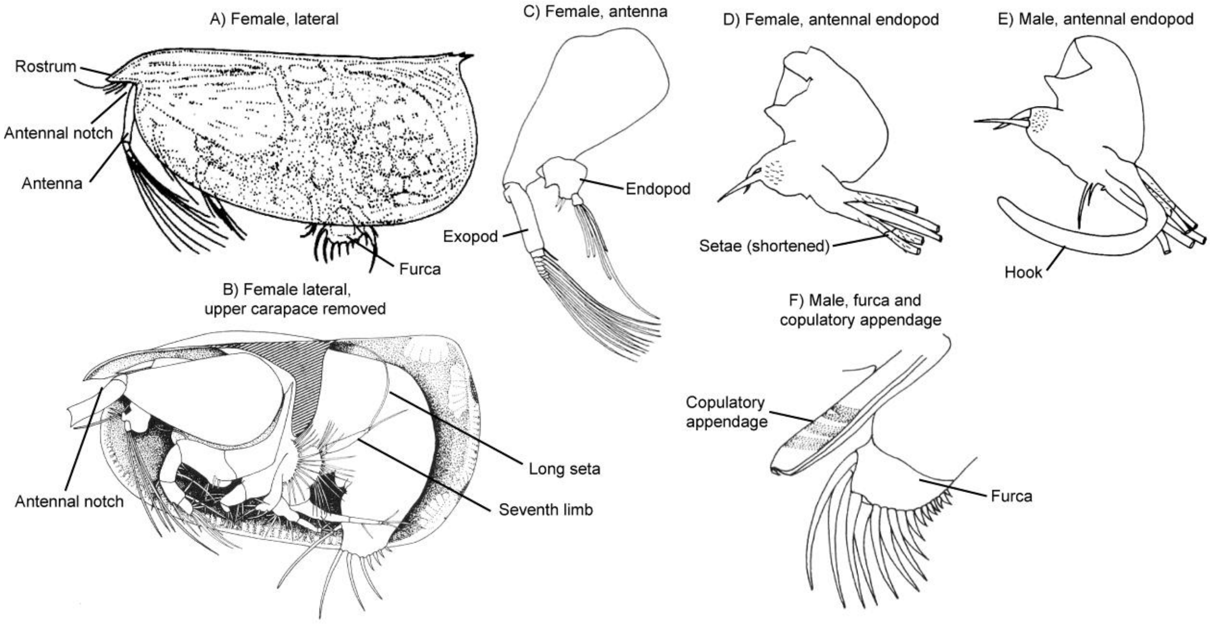


Fig. 6. Suborder Halocypridina, general morphology (A from Trégouboff & Rose, 1957; B-F from Angel, 1993).

Recorded: PMF and L4 not recorded. European areas with oceanic or deep water influences.
Size: Most ~0.3-2.0 mm.
Further information: Sars, 1928; Trégouboff & Rose, 1957; Howe *et al*., 1961; McGregor & Kesling, 1969; Neale, 1969; Poulsen, 1969; Schram, 1986; Kornicker, 1987; Angel, 1993, 1999; Athersuch *et al*., 1989; Blachowiak-Samolyk & Angel, 2008.

Suborder Cladocopina:

Carapace without antennal notch, usually almost circular (Figs. 7A, 8); antennal exopod and endopod both well developed (Fig. 7C); only five pairs of limbs (Fig. 7A); furca well developed with strong conical projections between setae (Fig. 7B).

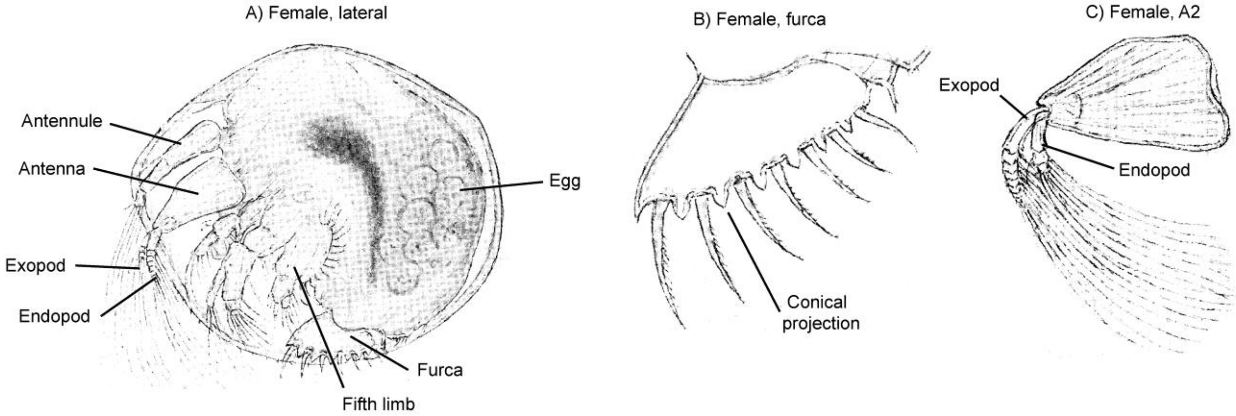


Fig. 7. Suborder Cladocopina, general morphology (from Sars, 1928).

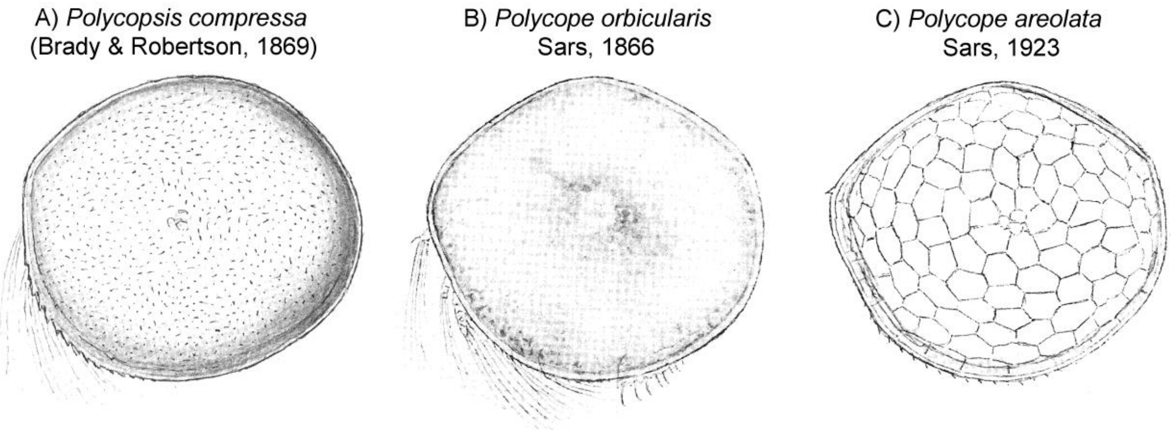


Fig. 8. Suborder Cladocopina, the three species recorded in the PMF (from Sars 1928).

Recorded: PMF, three epibenthic species. L4, not recorded. European coasts.
Size: Most ~0.3-2.0 mm.
Further information: Sars, 1928; Trégouboff & Rose, 1957; Howe *et al*., 1961; McGregor & Kesling, 1969; Neale, 1969; Poulsen, 1969; Schram, 1986; Kornicker, 1987; Angel, 1993, 1999; Athersuch *et al*., 1989; Blachowiak-Samolyk & Angel, 2008.

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PHYLUM ARTHROPODA: Subphylum Crustacea:

Class Malacostraca:

Malacostraca is the largest of the six classes of Subphylum Crustacea and comprises 16 orders, united by a common body plan. They are generally composed of 19 body somites, rarely 20, divided, into three morphologically distinct regions (tagmata) that have traditionally been called head (cephalon), thorax, and abdomen (pleon). The head theoretically comprises five somites, the thorax eight and the pleon six, except in Subclass Phyllocarida, Superorder Leptocostraca that retain the ancestral condition of seven abdominal somites. Each body somite bears a pair of jointed appendages, but these may be lost secondarily. However, there is considerable variation between malacostracan orders and species in the way that the body somites fuse together, particularly between the head and thorax regions. There are also variations between orders and species in the structure and function of the appendages on different body regions. Accommodating this variability has led to rather disparate terminology in the scientific literature, not aided by variations in the spelling of some terms. The terminology used here for the morphology of individual malacostracan orders has been kept quite basic to try and maintain some uniformity. However, because the current terminology for some groups is quite well established there is still variation in the terminology used, but this is explained in the introduction to each group.

Subclass Hoplocarida:

Order Stomatopoda:

Stomatopods are commonly known as ‘mantis shrimps’, because of their physical resemblance to shrimps (to which they are not closely related) and the terrestrial insect, the praying mantis. Adults (Fig. 1I) are benthic and live in burrows or rock crevices. The eyes are stalked and large. The small carapace covers the cephalon and is fused to the first two thorax somites. The third and fourth thoracic somites are reduced and hidden under the rear margin of the carapace, but not fused to it, leaving the fifth to eighth somites visible. In Crustacea, the paired limbs from the anterior backwards would typically be called antennules, antennae, mandibles, maxillules, maxillae and maxillipeds, the maxillipeds being the first of the eight thoracic limbs (thoracopods or pereiopods). In stomatopods the mandibles and the following four limb pairs, because of their structure and function, are all termed maxillipeds and are numbered sequentially. The first pair are long and project in front of the carapace. They are covered in setae and used in cleaning. The second maxillipeds (or raptorial claws) project anterolaterally and are characteristically very large and powerful for smashing their live prey, hard-shelled bivalves, shelled gastropods, crabs etc., or for spearing fish and other soft-bodied organisms. The third to fifth maxillipeds project anteriorly under the body and are not visible dorsally. These are all similar, with a simple claw (subchelate) and quite setose. The sixth to eighth thoracic somites bear the remaining thoracopods, which project laterally and are used for walking, the last in the male bearing a long papilla that acts as a penis.
The first five abdominal (pleon) somites bear pairs of pleopods used for swimming and respiration. The sixth somite bears modified pleopods termed uropods, which together with the terminal telson form a tail fan. There are only two species recorded in northern European waters *Rissoides desmaresti* and *Platysquilla eusebia*, only the former recorded as adults in the PMF, but the larvae of both have been collected in low numbers off Plymouth (A. Lindley, pers. comm.).

Reproduction and development

Adult females lay a loose egg mass that they tend until the eggs hatch. The typical crustacean nauplius stage is passed in the egg and the first larval stage emerges on hatching. The two species found moult through nine stages, remaining in the plankton for up to three months, but some other species have been shown to have only seven larval stages. The larvae of many species spend their early lives deep in the burrow, protected by the female and subsisting on stored lipid. They usually do not emerge and take up a planktonic existence until they develop into larval stage four. However, all larval stages of the two species recorded in northern European waters have been collected in plankton samples, which may relate to the adults of these species not living permanently in burrows. Larvae are almost transparent and generally only sampled during the warmest months.
Length of the larval carapace in relation to total length varies depending on species (Figs. 2, 3). The carapace typically has an anterior rostrum, a posterior, mediodorsal spine and two characteristic, long posterolateral spines as well as some other less prominent spination. From

stage one the antennules, antennae and first and second maxillipeds are quite well developed, particularly the second maxillipeds, which are characteristically extremely large, as they are in the adult. However, some of the feeding limbs may be absent or poorly developed, as the first three larval stages may not feed. The stage at which the other limbs appear varies with species. For example, pleopods are present from stage one in the two European species, but this is not the case in some other species. Uropods appear either side of the characteristically broad telson in later stages. A recognisable metamorphosis takes place at the end of the larval series into a postlarval stage, which is a miniature adult. The carapace becomes reduced, carapace spines are lost, the rostrum is reduced, the tail fan develops and the postlarva settles to the bottom and takes up an adult existence.
Stage development has only been described for a few species. There is very little information available for the two species described here, so only a brief account can be given.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Hoplocarida: Order Stomatopoda:

Superfamily Squilloidea:

Rissoides desmaresti (Risso, 1816)

Adults are very characteristic in appearance, having the typical, dorsoventrally flattened stomatopod body, with conspicuously large second maxillipeds (Fig. 2I). They are small, reaching a length of ~70 mm and live in burrows from the subtidal down to depths of around 40 metres.

Giesbrecht (1910) illustrated limbs etc. from nine larval stages, but only included illustrations of the complete bodies of four stages (Fig. 2A-D). In all larval stages the eyes are stalked and there are distinctive, broadly spaced, long posterolateral spines on the carapace; a mediodorsal spine is also usually present, in addition to a few other more minor spines. The carapace is around half the length of the body in all stages. There are posteroventral spines on the abdominal somites (Fig. 2D) from stage one, not obvious in Fig. 2A-C, due to poor tracing of the original figures. The shape and spination of the telson can be used to separate the larvae from those of *Platysquilla eusebia*. The posterior telson margin is broad, with a shallow V-shaped central indentation (Fig. 2E-H), the posterior margin lined with fine teeth of similar size and terminating in two larger spines. There are two large spines on the lateral edges of the telson, with fine spines between the distal of these spines and the telson terminal spines. By stage nine the telson lateral spines are very prominent and the telson shape is reminiscent of the shape of the adult telson (Fig. 2H).

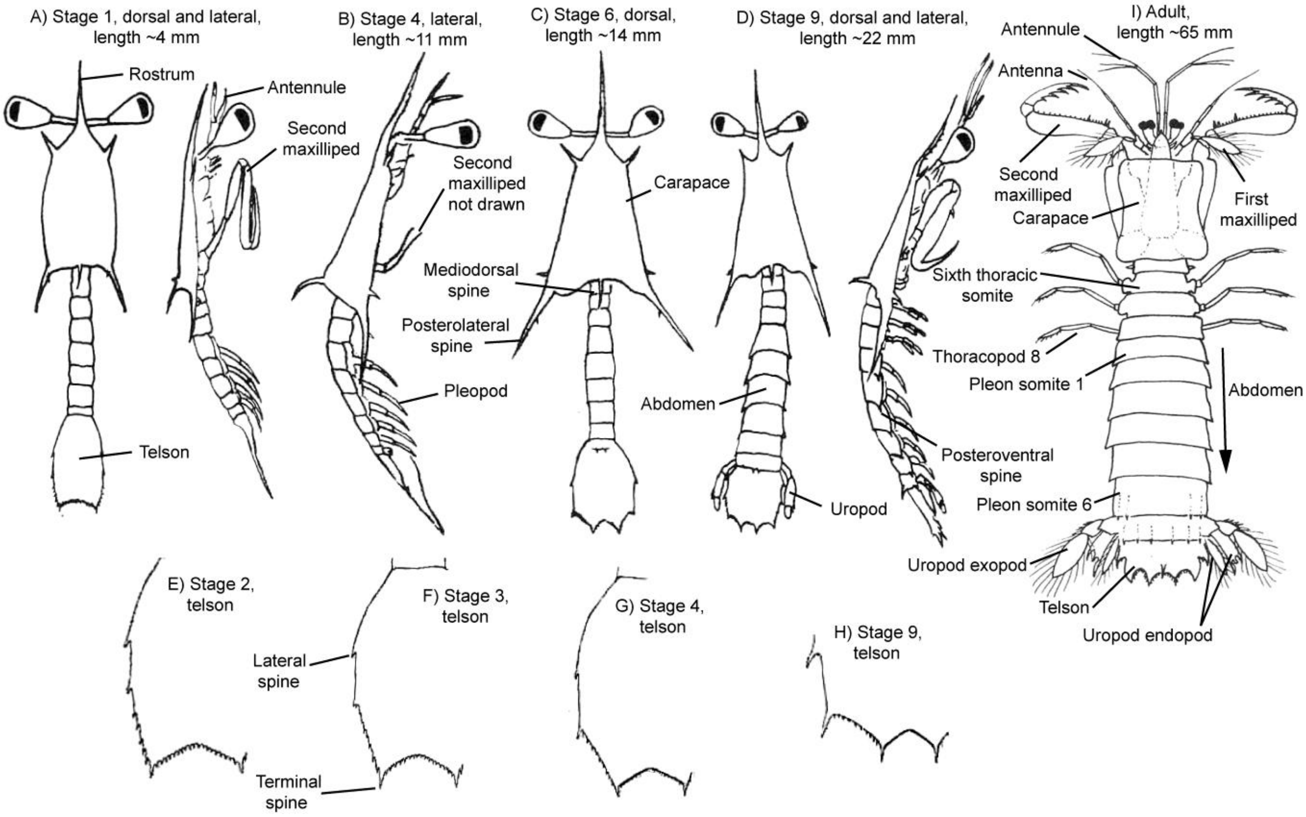

Fig. 1. *Rissoides desmaresti* larval stages and adult (A-D, I from Mauchline, 1984, as *Meiosquilla desmaresti*, after Giesbrecht, 1910, as *Squilla desmaresti*; E-H from Giesbrecht, 1910, as *S. desmaresti*).

Recorded: PMF, adults and larvae (as *Squilla desmaresti*). L4, but not from routine sampling. Southern North Sea. English Channel. Western Ireland.

Size: Larvae ~4-22 mm.

Further information: Giesbrecht, 1910 (as *Squilla desmaresti*); Mauchline, 1984 (as *Meiosquilla desmaresti*); Schram, 1986; Diaz, 1998; Vansteenbrugge, 2012.

Superfamily Lysiosquiloidea:

Platysquilla eusebia (Risso, 1816)

Adults are similar in appearance to adults of *Rissoides desmaresti*, separable by comparing telson shape (Figs. 2I, 3G). They are small, reaching a length of ~70 mm and found in depths of 10-25 m. Giesbrecht (1910) illustrated limbs etc. from nine larval stages, but only included illustrations of the complete bodies of stages one and five (Fig. 3A, B). Larvae share basic similarities with larvae of *R. desmaresti*, but in the first larval stage (Fig. 3A) the eyes are not stalked (sessile), stalked in subsequent stages (Fig. 3B). The carapace also differs in the earliest stages, exceeding half the body length, the pleon lengthening in later stages (Fig. 3A, B). The posterolateral spines on the carapace are also not as broadly spaced as in *R. desmaresti.* A mediodorsal spine is usually present on the posterior carapace, in addition to a few other more minor spines. Posteroventral spines on the abdominal somites do not appear to be as well developed, at least in the early stages, compared to *R. desmaresti.*

The shape and spination of the telson can be used to separate larvae from those of *R. desmaresti*. There are three larger spines on the lateral edges of the telson (Fig. 3C-F), compared to two in *R. desmaresti.* Initially, the posterior telson margin is almost straight (Fig. 3C, D), but protruding slightly in the centre. The margin is furnished with small spines, with a slightly larger single spine in the centre and a large terminal spine at either end. From stage three the margin becomes slightly indented in the centre (Fig. 3E) and by stage nine is broadly U-shaped with a slight central indentation (Fig. 3F).

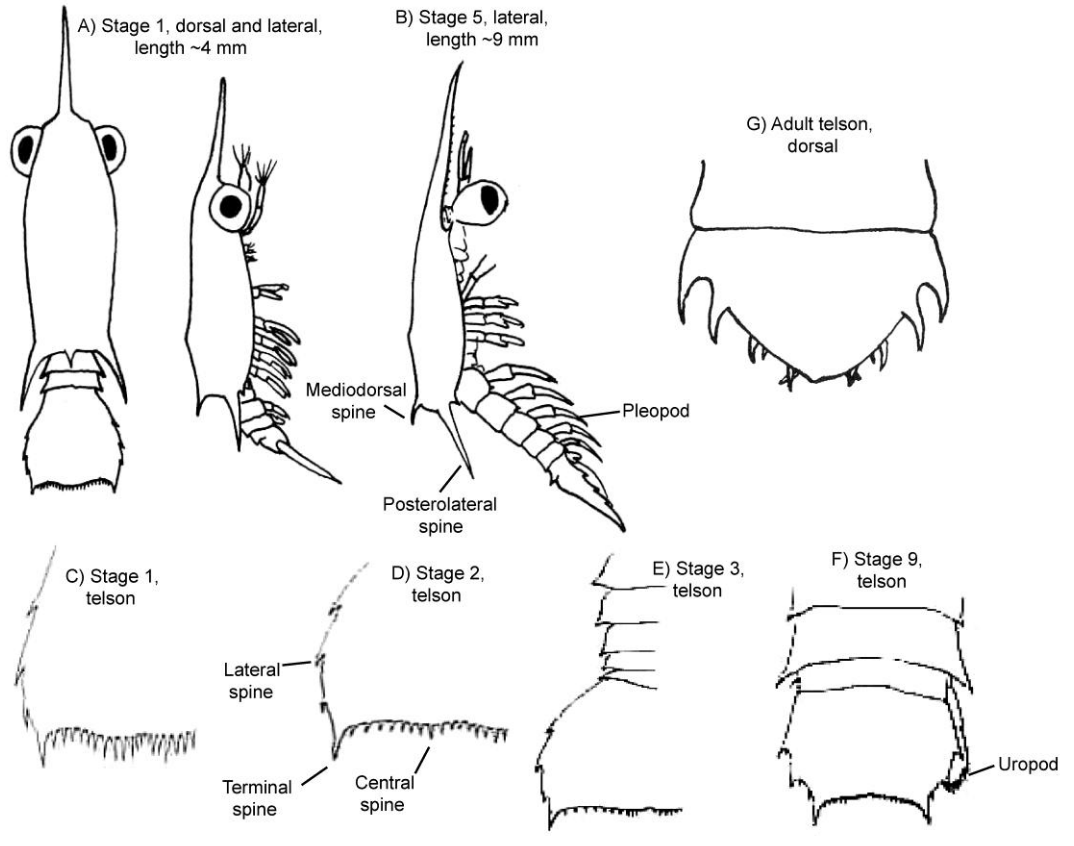

Fig. 2. *Platysquilla eusebia*, second maxillipeds not drawn (A, B from Mauchline, 1984 after Giesbrecht, 1910 (as *Lysiosquilla eusebia)*; C-F from Giesbrecht, 1910, as *L. eusebia*); G after Manning, 1977).

Recorded: PMF and L4, not recorded. Off Plymouth from non-routine sampling. Western Ireland. Southern North Sea.

Size: Larvae ~4-20 mm.

Further information: Giesbrecht, 1910 (as *Lysiosquilla eusebia*); Manning, 1977; Mauchline, 1984; Schram, 1986; Morgan & Goy, 1987; Diaz, 1998.

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PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca:

Subclass Phyllocarida: Superorder Leptostraca: Order Nebaliacea:

These are small, marine crustaceans distinguished from all other members of Malacostraca by having seven pleon (abdominal) somites rather than six (Fig. 1). They have anterior stalked compound eyes. The carapace is large, consisting of two valves without a definite hinge line, and covers the head (cephalon), thorax and several of the pleon somites. The carapace can be closed by an adductor muscle. There is an anterior extension of the carapace, the rostral plate. Only the first six of the seven pleon somites bear pleopods, the first four pairs biramous, the fifth and six pairs uniramous and rudimentary. Beyond the seventh pleon somite is the telson, which bears the setous caudal furca. There are no uropods. They have gills on the thoracic limbs (thoracopods), but also breathe through a respiratory membrane on the inside of the carapace. Eggs are laid in the space between the two sides of the carapace. The eggs hatch as a postlarval stage that lacks a fully developed carapace, but otherwise resembles the adult. The embryos are brooded, so there are no planktonic larval stages. The adults may be taken in plankton samples, but generally only very close to the shore.

Nebalia bipes (Fabricius, 1780)
This species lives intertidally and in shallow coastal areas under stones, in burrows or amongst macroalgal debris. They are often found in rock pools or attracted to crab pot bait. Body slender, light brown, greenish or dark brown in colour; eyes large, red in living specimens; carapace bulky (Fig. 1A); rostral plate distinctly hinged to carapace (Fig. 1B), rounded anteriorly; biramous antennules (Fig. 1C) shorter than the uniramous antennae (Fig. 1D) in both sexes; antennae in males as long as entire body. Caudal furca (Fig. 1E) narrow, longer in males than in females.

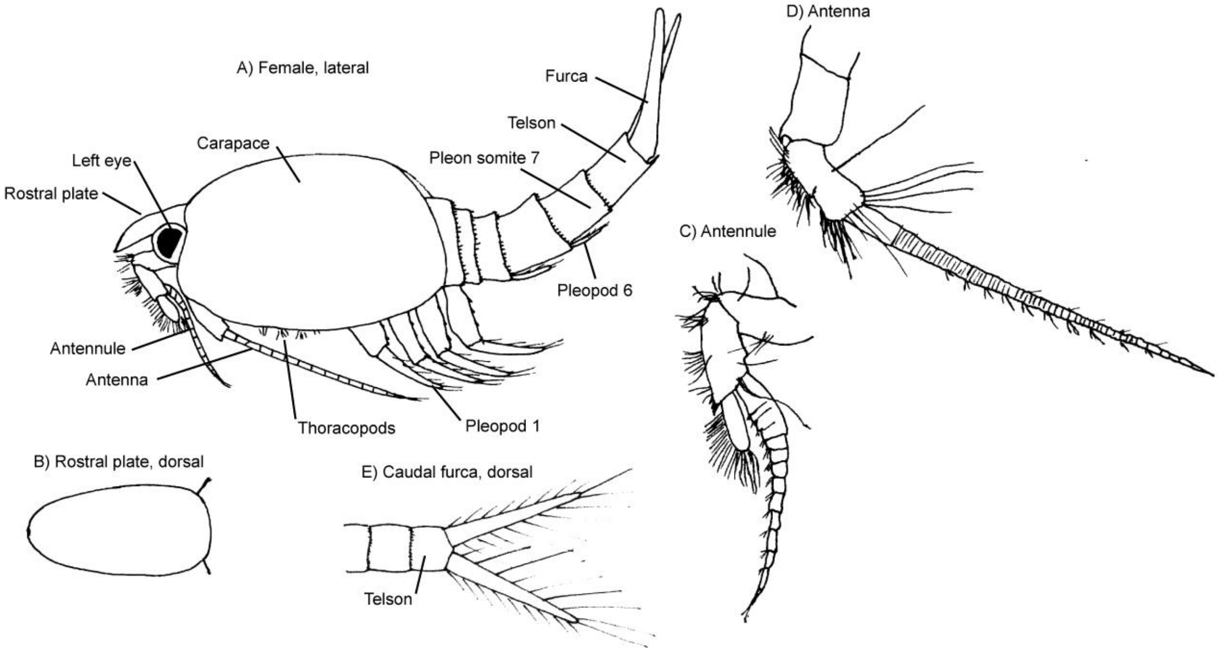

Fig. 1. *Nebalia bipes* female (from Mauchline, 1984).

Recorded: PMF. L4, not recorded. North Sea coasts. English Channel coasts. All around UK and Ireland.
Size: Up to 12 mm.
Further information: Mauchline, 1984; Schram, 1986; Hayward & Ryland, 1995.

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PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca:

Subclass Eumalacostraca:

Superorder Peracarida:

Peracarida means “near to shrimps”, a large group of malacostracan crustaceans that includes the major orders Mysida, Amphipoda, Isopoda, Cumacea, and according to the current WoRMS classification eight other more obscure orders. They are mainly defined by the presence of a brood pouch or marsupium, where eggs and young are retained until released at a late stage of development. The marsupium is formed from thin flattened plates borne on the basal segments of some of the thoracic limbs. There may or may not be a cloak-like carapace, but it is never fused to the posterior thoracic somites as found in euphausiids and decapods etc.

Order Mysida:

Mysids are commonly known as “opossum shrimps” because of the presence of the marsupium in females, alluding to the pouch found in marsupial mammals. There are marine, brackish and freshwater species, both epibenthic and pelagic. They are especially common inshore, particularly in estuaries, where they are important in the diet of fish and birds. During the day many tend to remain closer to the bottom, so may be taken in larger numbers in plankton samples at night, possibly also due to reduced net avoidance at night. They are mainly free-living omnivores, feeding on algae, organic debris and zooplankton, but there are some commensal species associated with sea anemones and hermit crabs etc. Adults of most species fall within the length range 5-25 mm. Body length measurement does not include the rostrum, the anterodorsal extension of the carapace, as this is of variable length. Total length is generally measured from the anterior, curved margin of the carapace behind the eyes, to the tip of the telson (Fig. 1A).
The text and figures reproduced here have been mainly taken, with some modifications, from the very comprehensive Ray Society publication on British Mysidacea by Tattersall & Tattersall (1951). Some recent texts giving useful general information on mysids include Mauchline (1980), Schram (1986), Murano (1999) and Nouvel *et al*. (1999).

Classification

All peracaridans considered to be mysids were previously included in Order Mysidacea in two suborders, Mysida and Lophogastrida (e.g. Tattersall & Tattersall, 1951). However, on morphological and molecular grounds, Lophogastrida, which are mainly deep water species that do not occur off southern Britain, are now placed in a separate order and all “true” mysids are in Order Mysida. There are two families in Order Mysida, **Mysidae** and **Petalophthalmidae**. Family Petalophthalmidae are deep-water species so are not considered here. All the 29 typically coastal species of Family Mysidae recorded in the PMF are in subfamilies Siriellinae (4), Gastrosaccinae (5), Erythropinae (1), Leptomysinae (5), Mysinae (12) and Heteromysinae (2). All of these are described here, plus an additional three from Subfamily Erythropinae, one from Leptomysinae three from Mysinae and one from Heteromysinae, probably covering all the mysids that may be sampled on the shallow northern European shelf. Keys to most of the British coastal mysids are given by Nouvel (1950), Tattersall, 1949; Tattersall & Tattersall (1951), Makings (1977) and Hayward & Ryland (1995), and for the Baltic by Köhn (1992).

Morphology

Species now included in Family Mysidae, differ from all other peracaridans (including Family Petalophthalmidae) in having from the larval stage, in the distal end of each of the endouropods of the tail fan, a clear vesicle containing a single, circular, flattened statolith with sensory connections. These organs are called statocysts (Fig. 1A) and are considered to inform the mysid about orientation of the body and velocity through the water. The exoskeleton is usually thin and generally smooth and in most cases without processes or spines. Mysidae are usually translucent when alive and often have patches of dark pigment or are coloured. Pigmentation can be useful in identification, but can be bleached out by preservation.

Cephalon: The cephalon (head) and the first four anterior thoracic somites are fused to the carapace dorsally. The carapace projects rearwards, covering and hiding most of the other thoracic somites laterally, often exposing a few behind the carapace dorsally (Fig. 1A-C) where there is usually a broadly rounded concavity. There is sometimes a transverse, dorsal cervical groove on the carapace that probably marks the cephalon/thorax junction. The anterodorsal margin may come to a rounded or pointed rostrum, but if present this is typically small. A slender spine sometimes arises from between the bases of the antennules, visible from above, appearing like a sharp rostrum. The anteroventral carapace margins may come to a point, but are generally rounded.

Shallow water Mysidae typically have a pair of stalked, semi-globular, usually movable compound eyes that have a faceted cornea, situated distally on the stalk. However, in *Pseudomma affine* (Fig. 14) their plate-like eyes are fused together. Eyestalks are usually short, hardly protruding beyond the lateral margins of the carapace, but in a few species are long. In living mysids from shallow waters the eyes are usually black, in deeper-living species sometimes, golden, red or colourless.

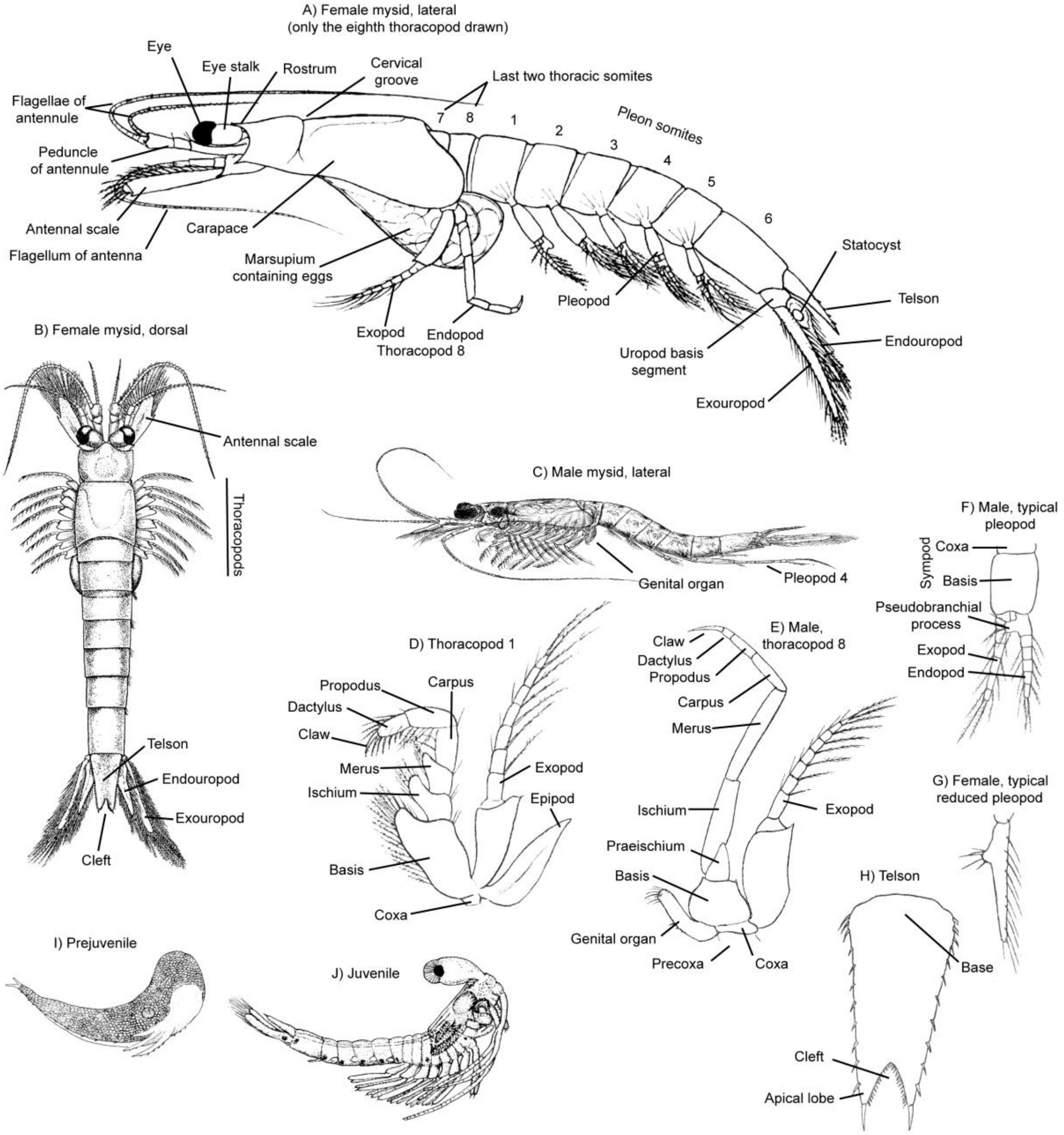

Fig. 1. Mysidae morphology (A, B, D-H after Tattersall & Tattersall, 1951; C from Sars, 1879; I from Nussbaum, 1887; J from Nair, 1939).

The cephalon bears five pairs of appendages: antennule, antenna, mandible, maxillule and maxilla. The antennules have a three-segmented base (peduncle) and in most cases two well developed flagella, the outer usually larger and longer than the inner. The antennules are sexually dimorphic, in males often much more robust and setose than in the female and in addition most have a cylindrical process at the distal end of the third segment of the peduncle, densely covered with long coiling sensory bristles. This male lobe (Fig. 2B) is usually well developed, but reduced in *Heteromysis* spp. to a small ridge with setae. The antennae also have a peduncle composed of three basal segments, individual segments sometimes difficult to discern, and a long flattened segment called the antennal scale (Fig. 1A, B), a modification of the exopod. The shape of the scale varies between species and it may be triangular, oval, elongate etc. The inner margin usually bears setae, while the outer margin may be naked, setose, spiny etc., often with a single, larger marginal spine. The scale is usually divided distally by a suture into two segments. Each antenna also bears a single flagellum that probably has a sensory function.

Thorax: There are eight thoracic somites, of which the last four are not fused to the carapace. Each bears a pair of biramous thoracopods (Fig. 1A, B, D, E), usually just named by sequential number. In all except the first pair there is at the base of each limb a flat plate, attached to the body wall, but with its distal margin protruding freely, considered to be the first segment, the precoxa, of a three-segmented sympod (Fig. 1E). The thoracopod distal segment normally bears an exopod and an endopod. The exopods are usually well developed, at least on the third to eighth thoracopods and curve up beside the body. They are fringed with setae and used for swimming (natatory). On the outer edge of the coxa of the exopod of the first thoracopod there are typically large, lamellar epipods (Fig. 1D), reduced or absent on other thoracopods. The epipod may be involved in enhancing respiratory currents over the body. The endopods typically end in carpus, propodus and dactylus segments and a spine-like claw or nail (Fig. 1D, E). The carpus and propodus may be fused into a single carpopropodus, but sometimes are then divided into a carpopropodus of multiple segments. The endopods of the thoracopods are mainly used for walking or clinging, although the first one or two pairs (sometimes termed gnathopods) often have the terminal claw modified to different extents into pincers (chelae) that can function as accessory mouthparts. At the base of the eighth thoracopods, males have a pair of short, conical genital organ or papillae (Fig. 1C, E), long in some genera. In all the species described here, mature females bear flattened, plates called brood lamellae (oostegites) on the last two or three of the thoracopods. The lamellae typically overlap, or are interlocked by means of the setae that fringe their edges, to form the marsupium (Fig. 1A) in which the eggs are carried. Mysidae do not have gills, respiratory exchange being through the body surface.

Pleon: In the females of *Gastrosaccus* spp. and to a lesser extent in *Anchialina* spp., there are lateral expansions of the first pleon (abdominal) somite to form epimeral plates (Fig. 9A), which are involved in the formation of the marsupium.
The first five of the six pleon somites bear pairs of pleopods (Fig. 1A, C) that are sexually dimorphic. Pleopods of males of most species are typically well developed and many-segmented, consisting of a two-segmented sympod, comprising a small coxa and large basis segments (Fig. 1F), apart from the first pair where the endopod is reduced to a single segment, while the exopod is normal. However, in some genera one or more of the male pleopods may be completely rudimentary. The pleopods of females are usually reduced to simple unjointed, setose plates (Fig.1G) that generally become progressively longer towards the rear. Near the base of the endopod of the male pleopod is an outgrowth of varying form called a pseudobranchial process (Fig. 1F), thought to be involved in respiration. One or two pairs of the male pleopods, usually the third or fourth, may be elongated (Fig. 1C) and armed with specially modified setae. These limbs may be used for clasping the female during copulation.
The sixth pleon somite is usually the longest and bears well developed, biramous, flattened uropods (Fig. 1A), the endouropod usually shorter than the exouropod. In many mysids the margins of both exouropod and endouropod are fringed with close-set, regular, plumose setae, but in some the exouropod is totally or in part devoid of setae and armed along its whole length or at the distal end only, with a series of spines. The inner margin of the endouropod is thick and typically armed with setae and sometimes also spines. The setae are on the dorsal edge and spines, if present, on the ventral edge. The position and number of spines is a useful guide to identification, but it should be noted that in some of the figures, for clarity, the endouropod setae are not drawn, only the spines. Proximally, each endouropod has a conspicuous statocyst.
Projecting from the sixth pleon somite is the telson (Fig. 1B, H), which is not a true somite, but along with the uropods form the tail fan act as a powerful swimming organ. The telson can have a variety of shapes, ranging from rounded to triangular and the apex may be cleft to different degrees, or entire. It is armed with spines and setae of different sizes and arrangement. The shape and structure of the uropods, telson and antennal scale are the main features used in identification.

Development and reproduction

The length of time until mysids reach sexual maturity depends on water temperature and food availability. Most species continue to grow after maturity and the proportions of the rostrum antennal scale and other appendages, structure of the uropods and telson, and the number and arrangement of spines arming the antennal scale and telson etc. may show progressive changes. Because of these factors, a young individual of either sex that has just become sexually mature may differ from an older individual.

Copulation typically takes place ventral surface to ventral surface. The male introduces sperm into the marsupium and leaves the female before she lays eggs into the marsupium from the paired oviducts that open at the bases of the sixth thoracopods. There is no larval stage, the young hatch in the marsupium to a postlarval, prejuvenile stage that lacks uropods (Fig. 1I), but has a complete limb set by the time they are released as juveniles (Fig. 1J). At this stage they are around two to three millimeters in length and show some characteristics of the adult. Number of eggs produced and juveniles released tends to be quite low. However, depending on species, water temperature and also size of female, a new brood can typically be produced every 3-30 days, but sometimes only after several months. Young are often dislodged prematurely from the marsupium during sampling and can be recognized by their characteristic, comma-shaped appearance (Fig. 1I).

Key to the genera of the species of Family Mysidae described

Characters should be taken in combination. As there is no larval stage, the key may also be used for young specimens, but experience is needed, especially with the earlier individuals, as some changes take place during development and even after they become sexually mature. Abnormal features are sometimes found, in some cases resulting from regeneration of damaged limbs.

Appendages often bear arrays of setae, <u>but for clarity these are not always drawn in the figures</u>, omitted particularly on the antennal scale and uropods. Setae on the inner endouropod are typically on the dorsal edge and spines (if present), on the ventral edge, so spines are easiest to observe from the ventral aspect.

1. Exouropod with short spines on outer margin ---**2**
- Exouropod with long setae on outer margin -- **3**

2. Exouropod with distinct distal suture; telson without distal cleft ------------- *Siriella* (Figs. 2-5)
- Exouropod without distal suture; telson with obvious distal cleft; dorsoposterior margin of carapace concave; epimeral plates of first pleon somite of female very enlarged, forming part of marsupium; male third pleopod exopod very long; spines on outer margin of exouropod large -- *Haplostylus*, *Gastrosaccus* (Figs. 6-9)
- Exouropod without distal suture; telson with obvious distal cleft; dorsoposterior margin of carapace straight; epimeral plates of first pleon somite of female only slightly produced; male third pleopod exopod not particularly elongated; spines on outer margin of exouropod small --- *Anchialina* (Fig. 10)

3. Telson entire, or with small unarmed cleft -- **4**
- Telson cleft --- **10**

4. Antennal scale setose all around, distal outer margin not ending in spine --------------------- **5**
- Antennal scale without setae on outer margin, sometimes strongly serrated and ending in spine distally --- **9**

5. Telson lateral margins armed with many spines, sometimes large and small ------------------ **6**
- Telson lateral margins with few (<18) usually large, or no spines -------------------------------- **8**

6. Strong spines along whole inner margin of endouropod; pleopods of male well developed -- *Leptomysis* (Figs. 15-17)
- Few or no strong spines on inner margin of endouropod; pleopods of male rudimentary, fourth with very long exopod -- **7**

7. Antennal scale very long, three times as long as peduncle, apex acutely pointed --- *Neomysis* (Fig. 34)
- Antennal scale short and narrow, apex rounded -------------------------- *Acanthomysis* (Fig. 35)

8. Telson lateral margins unarmed except for one large spine marking the distal end; apex produced, rounded, armed with a comb-like row of spines ------------ *Mesopodopsis* (Fig. 33)
- Telson lateral margins with a few small spines, apex entire, or with small unarmed cleft -- *Mysidopsis* (Figs. 18-20)

9. Eyes kidney-shaped, flattened dorsoventrally; telson shorter than broad, no lateral spines, two pairs of strong distal spines with pair of fine setae between ------ *Erythrops* (Figs. 11-13)
- Eyes fused to form a plate with median cleft and serrated margins; telson longer than broad with a few lateral spines towards distal end, apex armed with a pair of plumose setae and usually four pairs of spines -- *Pseudomma* (Fig. 14)

10. Antennal scale setose all around -- **11**
- Antennal scale with at least part of outer margin naked --- **12**

11. Antennal scale oval, rounded distally; endopods of third thoracopods enlarged, carpus and propodus fused, swollen, with strong subchelae ---------------------- *Heteromysis* (Figs. 36-38)
- Antennal scale long, sharply pointed distally; endopods of thoracopods normal, carpopropodus divided into 6-7 sub-segments --------------------------------------- *Mysis* (Fig. 22)

12. Naked outer margin of antennal scale with no distal spine ----------------- *Hemimysis* (Fig. 21)
- Naked outer margin of antennal scale with a distal spine -- **13**

13. Antennal scale generally long and narrow, apex either not extending beyond tip of distal spine or extending only short distance, spine articulated at base; fourth pleopod of male very long, armed with long distal spine ending in knob ------------------- *Praunus* (Figs. 30-32)
- Antennal scale generally more oval, apex produced well beyond distal spine, spine not articulated at base; fourth pleopod of male very long, armed distally with two pincer-like setae -- **14**

14. Proximal subsegment of carpopropodus of thoracopods 3-7 short - *Paramysis* (Figs. 23-25)
- Proximal subsegment of carpopropodus of thoracopods 3-7 longer than the succeeding subsegments -- *Schistomysis* (Figs. 26-29)

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Peracarida: Order Mysida: Family Mysidae:

Subfamily Siriellinae:

Genus *Siriella*:

Siriella armata (Milne-Edwards, 1837)

Body long and slender (Fig. 2A), not tapering markedly posteriorly; carapace small, concave dorsoposteriorly; rostrum long and acutely pointed, reaching almost to distal end of second antennule peduncle segment (Fig. 2B); antennule peduncle long, slender, more than half the length of carapace, male with large setose male lobe at distal end of third segment, in female the inner margin of third segment usually bears around four long, plumose setae in addition to a group of two or three at the distal inner corner (Fig. 2C). Antennal scale quite long and narrow with sides almost parallel (Fig. 2B), a small distal suture present, outer margin naked and slightly concave, terminating in a strong tooth beyond which the apex clearly extends, inner margin setose and slightly convex. Eyes with long cylindrical stalks, projecting laterally well beyond the sides of the carapace, cornea broader than stalk, pigment very black. First thoracopods small with inconspicuous distal claw on endopod, second thoracopods longer than first, third to eighth very slender with long, slender distal claw on endopod (Fig. 2D), surrounded by a dense brush of stiff, spinous setae that emerge from distal end of propodus. Pleopods of female reduced to small, simple linear plates with a few plumose setae. Uropods long and slender (Fig. 2E), with distal suture, exouropod outer margin armed with continuous row of about 30 spines, from near the proximal end back to the suture, spines increase regularly in size; endouropod shorter than, and about half as broad as exouropod, tapering distally, armed along inner margin with row of spines that increase in size distally. Telson long, entire, slightly tapering (Fig. 2E), narrowly rounded distally, marginal spines without naked space as found in the other *Siriella* spp. described here, proximal spines large but of varying lengths, large spines distally with small ones between in groups of six to ten and very close together, terminating in two large spines with three to five small spinules between them of similar size, and also two small setae (Fig. 2G).

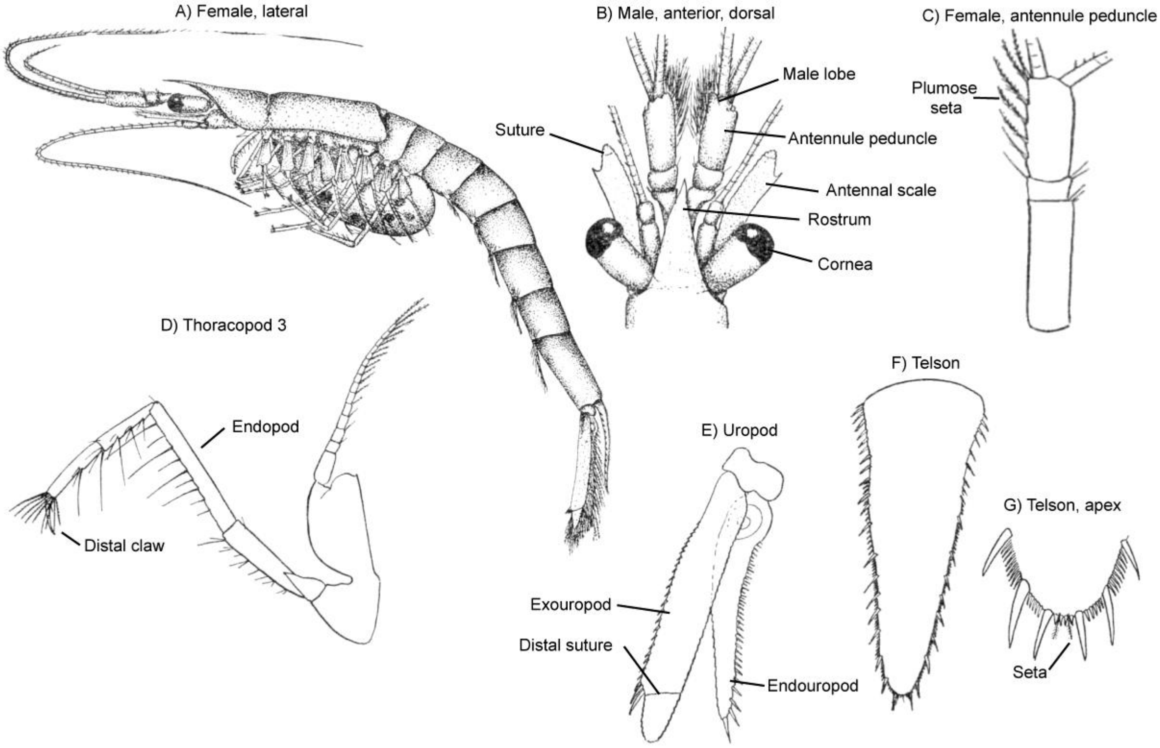

Fig. 2. *Siriella armata* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. Around the British Isles. North coast of France. All North Sea. Found in shallow waters 0-30 m, rarely sampled deeper than 20 m.

Size: Up to 21 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Siriella clausii G.O. Sars, 1877
Body long and slender (Fig. 3A), carapace very short, concave dorsoposteriorly; closely resembles *S. armata* but rostrum shorter and less acute, reaching only half-way along the first joint of the antennule peduncle (Fig. 3B); antennule peduncle third segment in female armed with only one plumose seta on inner margin in addition to a group at inner distal corner (Fig. 3B, C), outer flagellum much longer and stronger than inner; antennal scale extending nearly to distal end of antennule peduncle, about three times as long as broad, with straight, naked outer margin with strong lateral spine (Fig. 3B, D). Eyes large, dense black, stalks much shorter and thicker than in *S*. *armata*. Thoracopods slightly shorter and more robust than in *S*. *armata*, endopods of at least third to eighth pairs with slender distal claw surrounded by a dense brush of stiff, spinous setae (Fig. 3E). Pleopods of female reduced to small, simple linear plates with a few plumose setae. Uropods shorter and broader than in *S*. *armata*, exouropod only slightly longer than telson, less than five times as long as broad (Fig. 3F), with distinct distal suture, outer margin armed with eight to ten spines that increase in size distally; endouropod shorter and narrower than exouropod, inner margin armed with a continuous row of spines, mostly with groups of smaller spines between, the distal three or four spines very large without intermediates. Telson slightly shorter and broader than in *S*. *armata*, entire and rounded distally, margins armed proximally with around three or four strong spines (Fig. 3G) separated from those more distally by a short naked space, distally a series of large spines with three to five small spines between each, apex with two large terminal spines, between them three spinules of similar size and two setae (Fig. 3H).

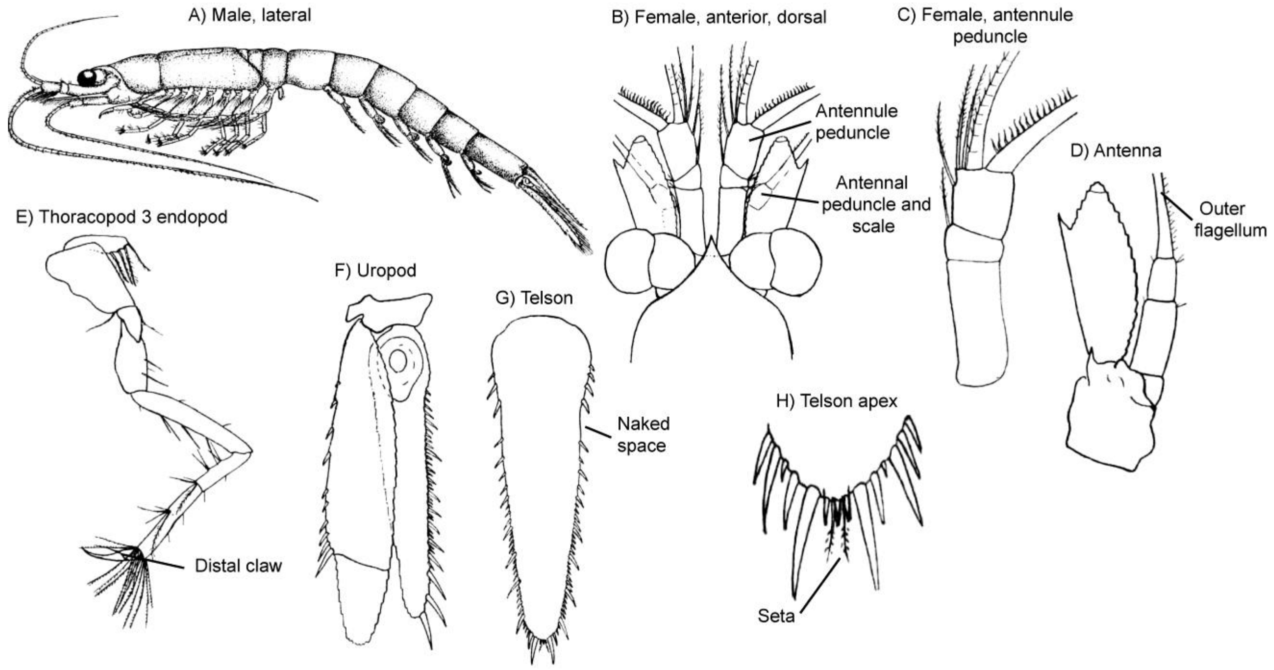

Fig. 3. *Siriella clausii* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. All coastal North Sea.
Size: Female ~10 mm, male ~11 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Siriella jaltensis Czerniavsky, 1868

General form very similar to that of *S. clausi*, but slightly more robust (Fig. 4A), especially in the pleon region; carapace short, concave dorsoposteriorly; cornea occupying about one-third of the whole eye; antennal scale outer margin naked, with strong spine (Fig. 4B, C), similar to that of *S. clausii*, except that outer margin is slightly concave; antennal peduncle in female with the inner margin of the third segment armed with three long, plumose setae in addition to a group of three or four at inner distal corner (Fig. 4D). Endopods of at least thoracopods three to eight with slender distal claw surrounded by a dense brush of stiff, spinous setae (Fig. 4E, F). Pleopods of female reduced to small, simple linear plates with a few plumose setae (Fig. 4G). Uropods much slenderer than in *S. clausi*, exouropod with 10 to 15 spines on outer margin, tapering markedly distally, with distinct distal suture (Fig. 4H); endouropod with the spines arming the inner margin more regular spaced than in *S. clausi*, increasing in size towards apex and only at the proximal end showing an arrangement of smaller spines between larger. Telson entire, rounded distally (Fig. 4I, J), very similar to that of *S. clausi* with proximal area naked of spines, but the spines arming the lateral margins appear more crowded, from two to six small spines in the intervals between large spines; two large spines at apex with three spinules between, the central largest, with two plumose setae arising from base.

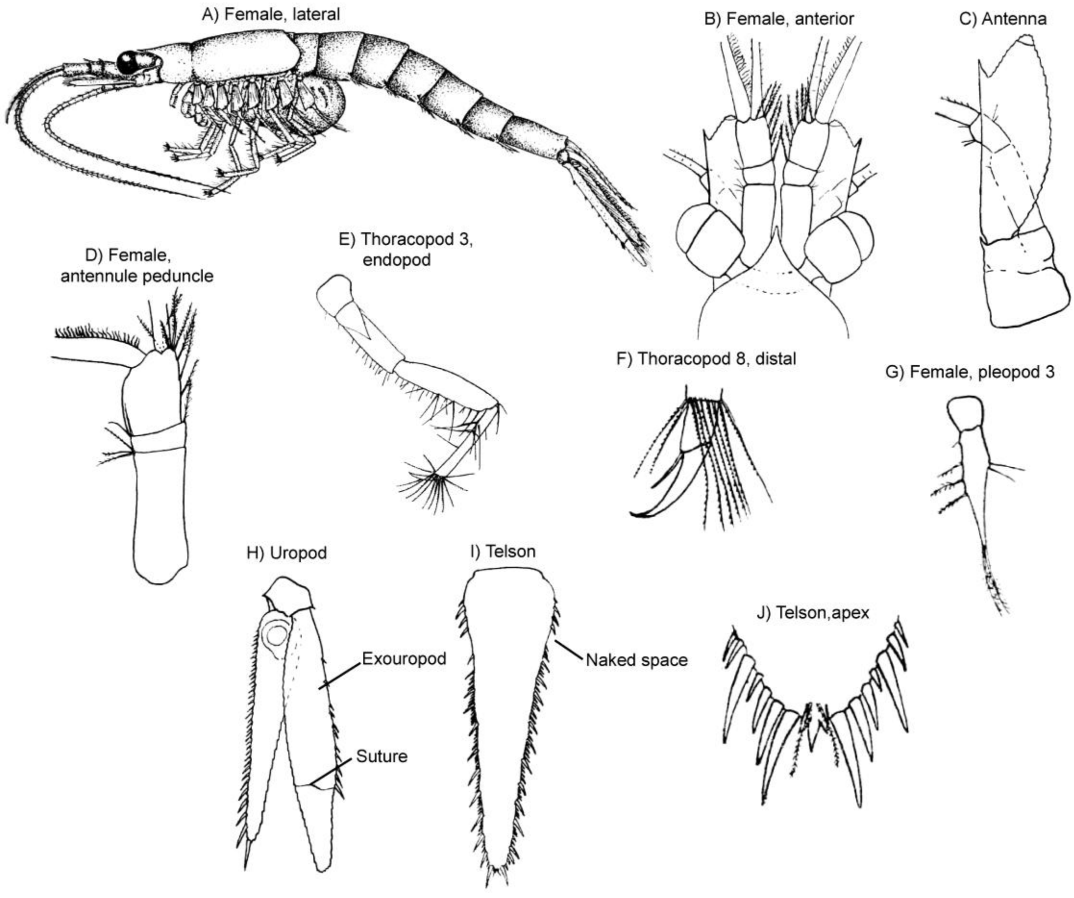

Fig. 4. *Siriella jaltensis* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. Western North Sea. English Channel.
Size: Up to ~15 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Siriella norvegica G.O. Sars, 1869

Very like *S. clausii* in general form, but has larger maximum size and tends to be more northerly in distribution than other *Siriella* spp. Body very slender (Fig. 5A), carapace short, concave dorsoventrally as in *S. armata*. Antennal peduncle with inner margin of third segment in female with three plumose setae as well as group at inner distal corner (Fig. 5B); antennal scale longer than antennule peduncle, two and a half times as long as broad (Fig. 5C), outer margin naked, straight, with strong distal spine, inner margin convex. Endopods of thoracopods three to eight at least with slender distal claw surrounded by a dense brush of stiff, spinous setae (Fig. 5D, E). Pleopods of female reduced to small, simple linear plates with a few plumose setae. Exouropod nearly twice as wide as endouropod (Fig. 5F), outer margin armed with 15 to 23 spines, distal suture; endouropod slightly longer than telson, inner margin armed with row of spines that increase regularly in size distally and have small spines in groups of two or three between. Telson entire, rounded distally, constricted near proximal end (Fig. 5G), margins armed, proximal to the constriction, with five or six subequal spines followed by a naked space, the distal three-quarters of margin armed with large spines with three to six smaller spines between. Two large spines at telson apex with three spinules between (Fig. 5H), the central of the three spinules longest, with two plumose setae arising from base.

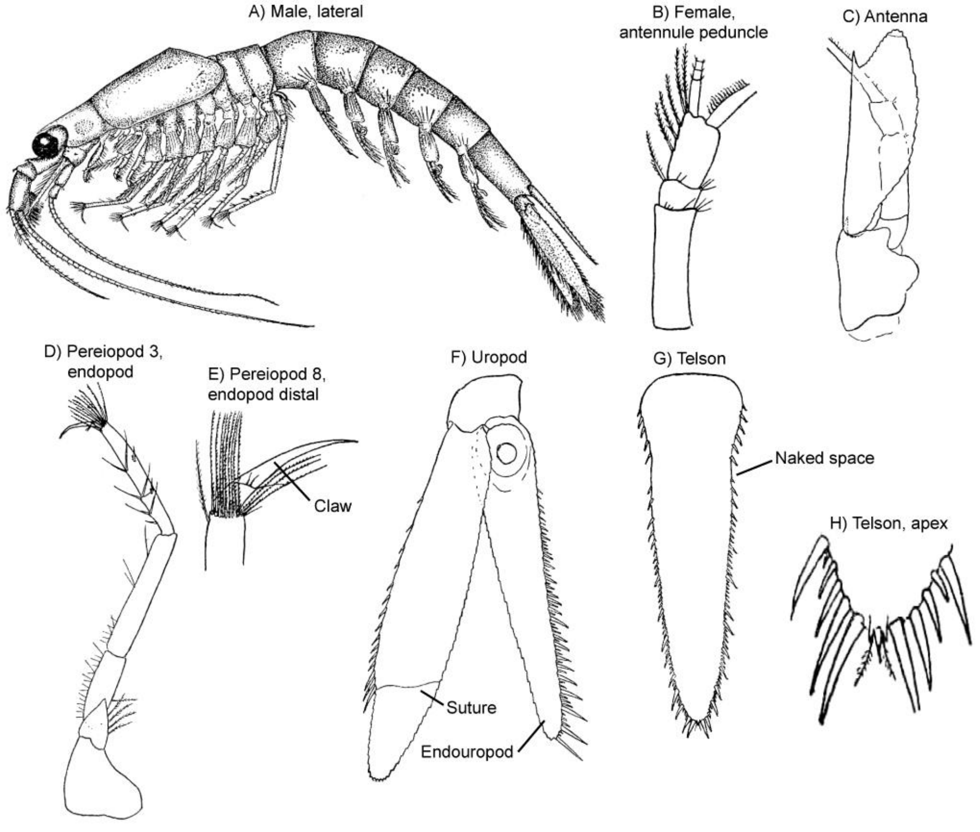

Fig. 5. *Siriella norvegica* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. All North Sea.
Size: Up to ~21 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Peracarida: Order Mysida: Family Mysidae:

Subfamily Gastrosaccinae:

Genus *Haplostylus*:

Haplostylus normani (G.O. Sars, 1877)

This species (as *Gastrosaccus normani* G.O. Sars, 1877) was originally thought to show considerable morphological variability in the same population, but Nouvel (1951) recognised that one of the variants was a different species and named it *Gastrosaccus lobatus*. Some of the descriptions and drawings for *G. normani* given by Tattersall & Tattersall (1951) were from a mixture of the two species, so only the original drawings from Sars (1877) and later drawings from Nouvel (1951) are included here.

Similar to *G. sanctus*, but slightly smaller and slenderer (Fig. 6A, B); carapace small, narrowing anteriorly, sides covering basal segments of the thoracopods, posterodorsal margin deeply concave and without lobes as found in *G. sanctus* and *G. lobatus*; rostrum short, blunt (Fig. 6C). Antennal scale small, shorter than peduncle (Fig. 6A, D), slightly longer and narrower in male (Fig. 6E), outer margin naked, terminating in a sharp spine, rounded apex with small distal suture; peduncle with single seta on inner margins of second and third segments (Fig. 6D). Thoracopods three to eight similar to *G. sanctus*. Second pleopod of male rudimentary (Fig. 6F), endopod characteristically sigmoid. Third pleopod of male long (Fig. 6B, G), axe-shaped process on outer side of distal margin of sympod; endopod rudimentary; exopod typically with two short spines near base, distal end of penultimate segment swollen Fig. 6H), two distal segments around same length, distal segment with median triangular expansion. Pleopods four (Fig. 6I) and five of male very small, endopod reduced to single segment, distal end bearing a long plumose seta at each side. Uropods slightly longer than telson (Fig. 6A), endouropod tapering distally (Fig. 6J), similar length to exouropod, inner margin with eight or nine slender spines set irregularly among setae (not drawn); exouropod with proximal quarter of outer margin bare, remainder armed with a close set row of spines to the tip. Telson longer and slenderer than in *G. sanctus*, lateral margins armed with nine or ten spines (Fig. 6K), the distal ones longest, narrow cleft lined with fine spinules.

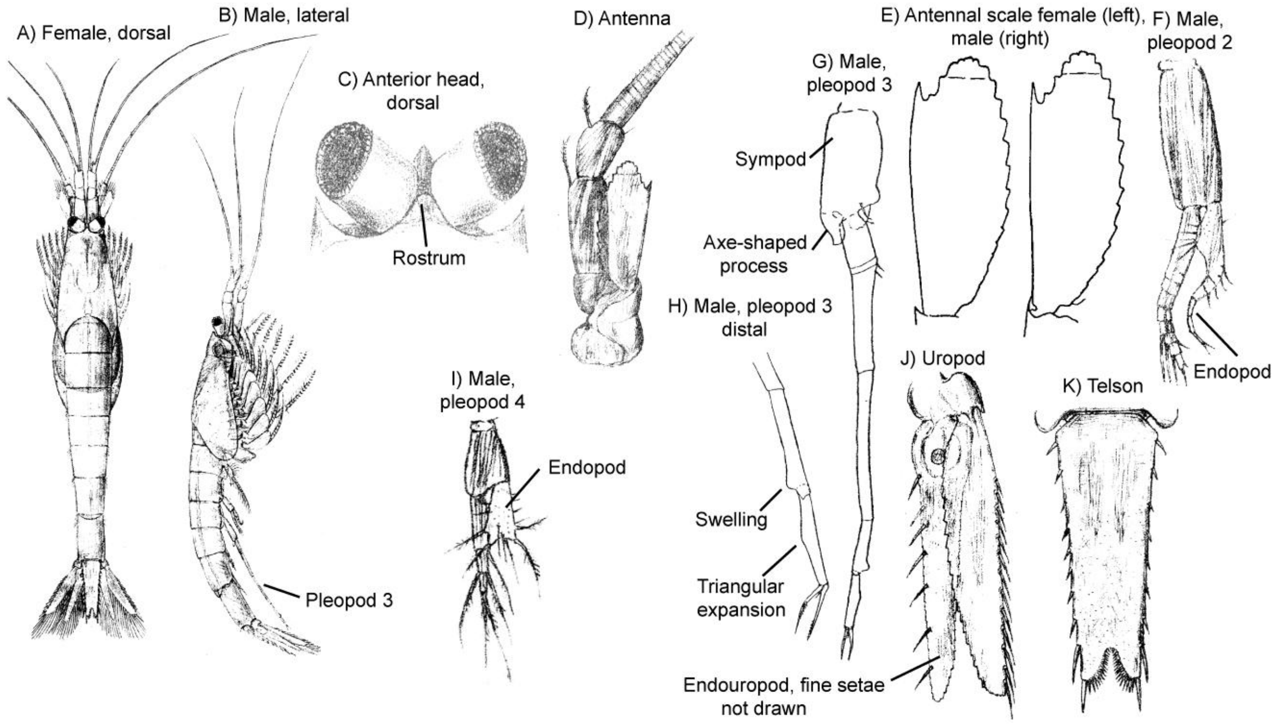

Fig. 6. *Haplostylus normani* (A-E, G, J-L after Sars, 1877; F, H, I after Nouvel, 1951, both as *Gastrosaccus normani*)

Recorded: PMF (as *G. normani*). L4, not recorded. Southern North Sea. English Channel.
Size: Up to ~11 mm.
Further information: Sars, 1877; Nouvel, 1951; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995 (all as *G. normani*).

Genus *Gastrosaccus*:

Gastrosaccus lobatus Nouvel 1951

This species and *Haplostylus normani* (as *Gastrosaccus normani* G.O. Sars, 1877) were thought to be just variations of *G. normani*, but were separated by Nouvel (1951). Nouvel (1951) described the major differences between the two species, but did not provide detailed morphological information for *G. lobatus*.

Body slender, somewhat laterally compressed (Fig. 7A); carapace strongly concave dorsoposteriorly where, in adults, there are prominent dorsal lobes (Fig. 7A, B) that distinguish it from *H*. *normani*, although lobes are usually also found in *G. sanctus*; antennal scale similar in both sexes, three times as long as wide (Fig. 7C), apex slightly more elongate than in *H. normani* and external border slightly straighter; carpus and propodus segments of the endopod of the third to the eighth thoracopods fused, the fused segment divided into many small subsegments. Epimeral plates of first pleon somite of female very enlarged, forming part of the marsupium. Male pleopods biramous, natatory, not as rudimentary as in *H. normani*; pleopod three exopod very large (Fig. 7A, D), resembles that of *H. normani* with the penultimate segment swollen distally, but distal segment much shorter than penultimate segment (Fig. 7E) and quite parallel-sided, typically has three fine, long spines near base (Fig. 7F); uropod armature similar to *H. normani*. Telson long with nine or ten lateral spines, apical cleft armed with small spinules.

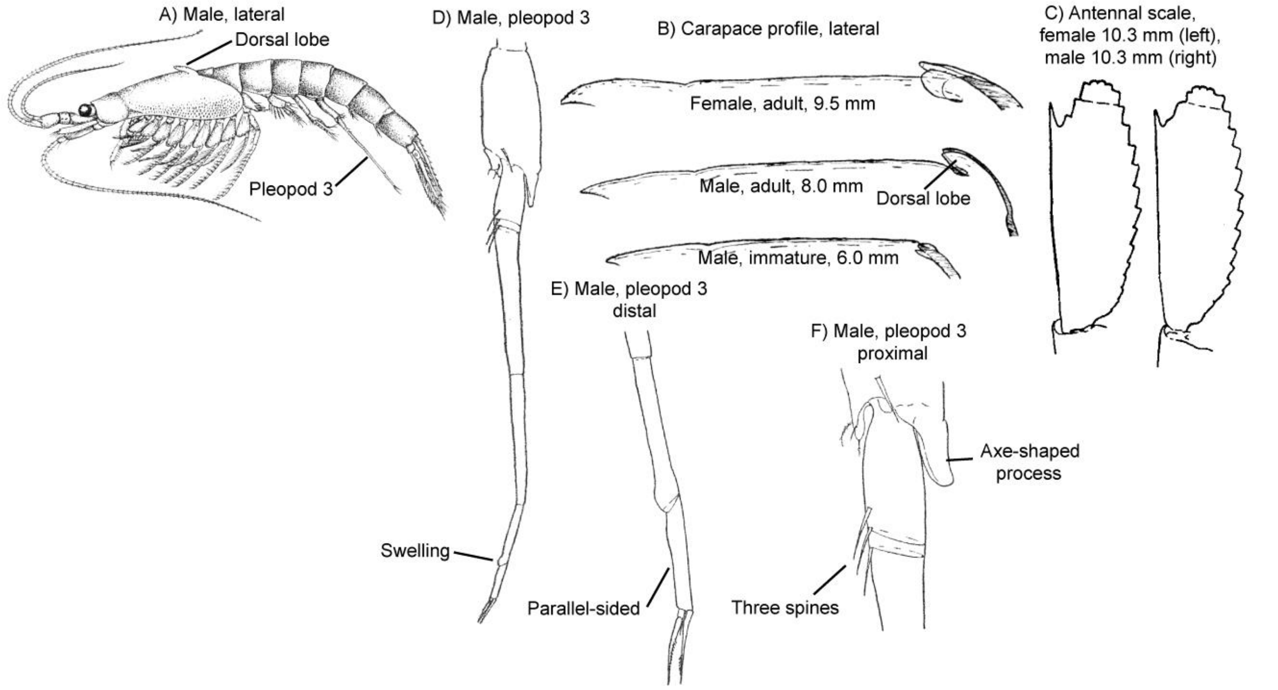

Fig. 7. *Gastrosaccus lobatus* (A after Tattersall & Tattersall, 1951; B-F after Nouvel, 1951).

Recorded: PMF (Addenda). L4, not recorded. South west North Sea. English Channel. Coast of Brittany

Size: 11 mm.

Further information: Nouvel, 1951; Makings, 1977; Hayward & Ryland, 1995.

Gastrosaccus sanctus (van Beneden, 1861)

Body slender; carapace completely covering sides of body (Fig. 8A), anterior margin produced into short blunt rostrum, a deep depression dorsally, posterior to cervical groove in the mid-dorsal line, posterior carapace margin deeply concave exposing last two thoracic somites, in adults rear of concavity usually with projecting flap-like lobes. Antennule peduncle long and stout (Fig. 8B), second segment short and armed on outer margin with three blunt spines, third segment nearly as long as first, bearing a curved, finger-shaped process, in males the usual hairy lobe present. Antennal peduncle second segment three times as long as the third (Fig. 8C), three to five long setae on inner margin of second segment and two to three on the third segment, scale shorter than peduncle, outer margin straight, naked, terminating in a strong spine that extends well beyond the apex with its small distal suture. Thoracopods three to eight becoming progressively stronger and longer posteriorly; large genital appendage at the base of the eighth thoracopod in male (Fig. 8F). Pleopods in female very reduced (Fig. 8D, E), first pair with long sympod bearing one group of very long plumose setae at the proximal end and another at the distal end, exopod unsegmented, oblong with a few plumose setae, endopod triangular, tapering to a sharp point that bears a single long plumose seta. Remaining female pleopods reduced to small simple plates with a few setae. Sympod of first pair of pleopods in male swollen, armed with 10-12 long plumose setae on inner margin (Fig. 8G), exopod small, unjointed, pleopod three exopod long and slender, three small segments close to the proximal end followed by four long segments, apex armed with two unequal, strong, barbed setae and a small bristle, fourth and fifth pleopods small. Uropods slightly longer than telson (Fig. 8H), endouropod slenderer than exouropod, tapering distally, armed with six long irregularly-spaced spines among the setae (not drawn) of the inner margin, outer margin of exouropod bearing a close-set row of large spines on the distal two-thirds of its length. Telson narrowing slightly distally, lateral margins armed on each side with six large, irregularly spaced spines, of which the one at the apex is the longest, apex cleft to about one-ninth of the length of the telson, cleft armed with about twelve spinules on each side.

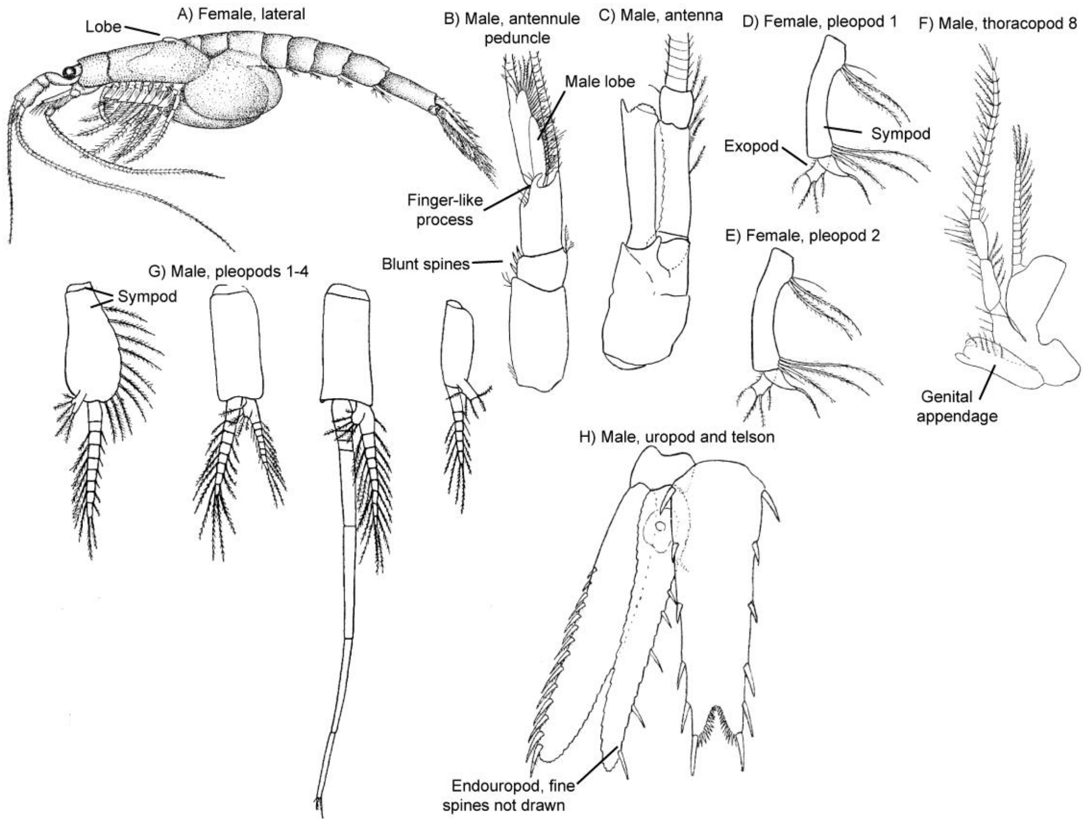

Fig. 8. *Gastrosaccus sanctus* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. All North Sea.
Size: Female ~13 mm, male ~15 mm
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Gastrosaccus spinifer (Goës, 1864)
Body slender (Fig. 9A, B) similar to *G. sanctus*, eyes small, carapace with deeply concave posterior margin bearing eight or nine delicate, fringing spines (Fig. 9C), on either side of which the margin is cut into a small split of which the posterior edge overlaps the anterior forming a tiny raised lobe. Antennule (Fig. 9D) similar to that of *G. sanctus*, scale short (Fig. 9E), outer margin naked, terminating in a strong spine around same length as apex, peduncle setation similar to *G. sanctus*. First three pleon somites almost cylindrical, fourth laterally compressed, with a distinct ridge running along the mid-dorsal line (Fig. 9B), in the fifth somite lateral compression much more marked and the dorsal ridge forms a sharp keel that ends posteriorly in an upturned spiny process that in dorsal view is broad at its base and tapers to a point, from which the species gets its name. The sixth somite is less compressed laterally, so that in dorsal view the pleon widens posteriorly before the start of the telson. Large epimeral plates on the first pleon somite in female (Fig. 9A, B) not as rounded as in *G. sanctus* and *Haplostylus normani*, attached to the anterior end of the somite, ventrally these plates bent under the body covering the marsupium, the anterior edge of the plates sometimes with tiny serrations. Endouropod upper surface, near statocyst, with strong, posteriorly directed spine (Fig. 9F), inner margin armed with about ten very long, slender spines set irregularly among other setae (not drawn), exouropod slightly shorter than endouropod, with about twelve strong spines arming the distal two-thirds of outer margin, tips of these spines less tapering than in *G. sanctus* and *H. normani*. Telson equal in length to last pleon somite (Fig. 9B), lateral margins armed with six to eight spines that increase in size distally (Fig. 9G), but the last two on each side are not markedly larger than the others as in *H. normani,* deeply cleft to more than one quarter of length, cleft armed with about 20 spinules each side.

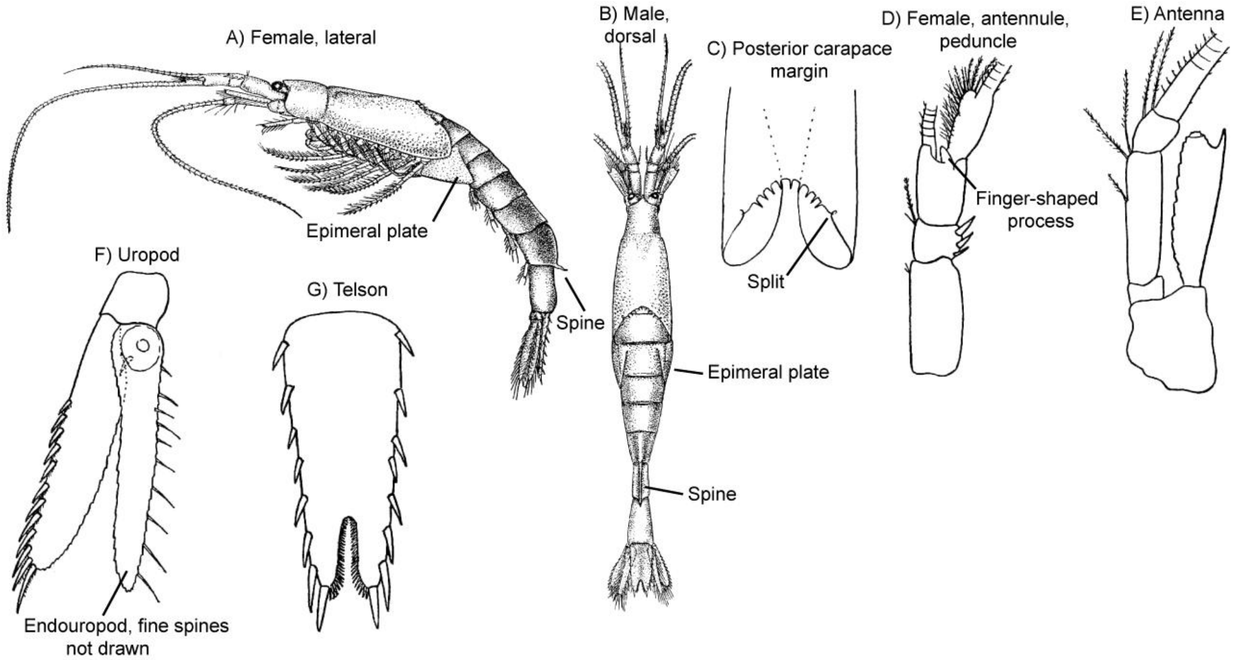

Fig. 9. Gastro*saccus spinifer* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. All North Sea, from coast to deep water. English Channel.
Size: Up to ~21 mm
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Genus *Anchialina*:

Anchialina agilis (G.O. Sars, 1877)

Body robust (Fig. 10A, B); carapace long, covering thorax and more than half of first pleon somite, in dorsal view, widening considerably posteriorly, posterodorsal margin straight; eyes thick, cornea occupying about a third of the whole eye. Rostrum large, triangular, anterior tip usually bent downward between the antennules so appearing short. Antennule more robust in male than in female, short and thick (Fig. 10C); antennal scale very small, not reaching end of antennal peduncle (Fig. 10D) and extending only slightly beyond first segment of antennule peduncle, outer margin naked, terminating in a small spine beyond which the apex extends considerably, small distal suture present. First thoracopods larger in male (Fig. 10E) than in female (Fig. 10G), with very large axe-shaped epipod in both sexes, dactylus small, bearing a long, strong, curved claw. Second thoracopods short, basal segment large, carpus in male swollen irregularly along inner and distal margins (Fig. 10F), less so in Female (Fig. 10H). First pleon somite in female with small, lateral epimeral plates on either side (Fig. 10B), covering a small part of the marsupium. Pleopods in male well developed, natatory, biramous (except the first pair in which the endopod is lacking), large oval pseudobranchial process borne at the base of endopod, third and fourth pairs with exopod much longer than endopod (Fig. 10J). First pair of pleopods in female small, reduced to a simple styliform segment (Fig. 10I), remaining pairs reduced to very delicate lamellae. Endouropods longer than exouropods (Fig. 10K), bowed inward at distal end, inner margin armed with row of large plumose spines with small spines closely set between them, the two strong spines arming the distal end very characteristic of the species, statocysts small, exouropod with outer margin naked proximally, then armed with a close regular row of spines of which the distal ones are larger and may be slightly plumose. Telson very long, nearly half as long as whole pleon (Fig. 10A, L), lateral margins straight, armed with 25-30 closely set, plumose spines, distal ones much longer, apex of each telson lobe armed with a strong spine; cleft narrow, armed with a close row of about 25 teeth on each side.

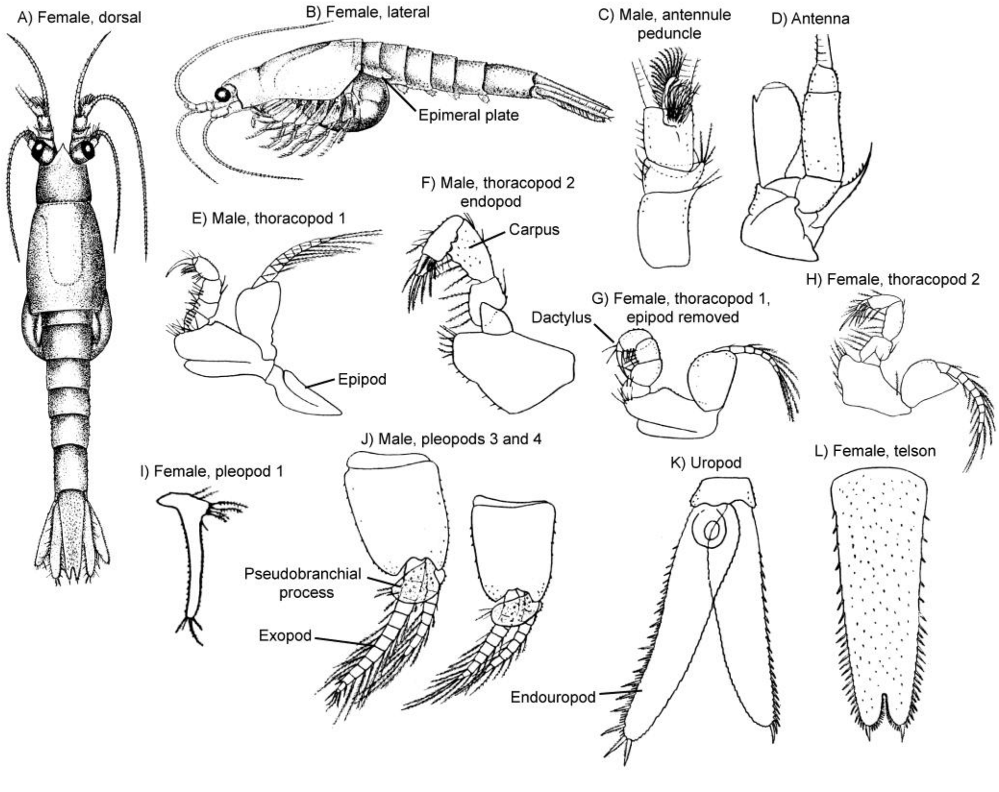

Fig. 10. *Anchialina agilis* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. Eastern and southwestern North Sea. English Channel. Coastal to deep water.

Size: Up to ~9 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Peracarida: Order Mysida: Family Mysidae:

Subfamily Erythropinae:

Genus *Erythrops*:

Erythrops elegans (G.O. Sars, 1863)

One of the smallest member of the genus; body robust, cephalon and thorax slightly broader than pleon (Fig. 11A); carapace produced anteriorly between the eyes into a short blunt rostrum; dorsoposteriorly slightly concave. Eyes greatly enlarged distally (Fig. 11B), stalks short and thick, less tapering proximally than in *E. erythrophthalma*, very flattened dorsoventrally, cornea kidney-shaped, red, conspicuous white line between the stalk and cornea, then a regular close row of red facets followed by another white line and another close row of facets, in living specimens these white lines very conspicuous. Antennal scale about four times as long as broad (Fig. 11C), outer margin naked, straight, terminating in a spine beyond which the apex projects, no distal suture; two to three small spines, below scale, on outer margin of second basal segment. First thoracopods small (Fig. 11D), inner margin of merus slightly expanded, dactylus conical, bearing a well developed claw. Second thoracopods (Fig. 11E), smaller than the first and more slender, dactylus tapering and armed with four peculiar, strong, ciliated bristles on one side and three on the other and terminating in a slender claw which is not surrounded by the usual dense brush of setae, endopod of eighth thoracopods only extending to posterior margin of fourth pleon somite (Fig. 11A). Exouropod and endouropod margins without spines, only regular setae (not drawn); female endouropods only slightly shorter than exouropods, but in male the endouropod is much shorter (Fig. 11F) and more slender than exouropod, statocyst particularly large. Telson entire, distal margin straight, terminal spines in female of varying lengths (Fig. 11G), in male the outer pair usually shorter than the inner (Fig. 11H), two fine setae in centre.

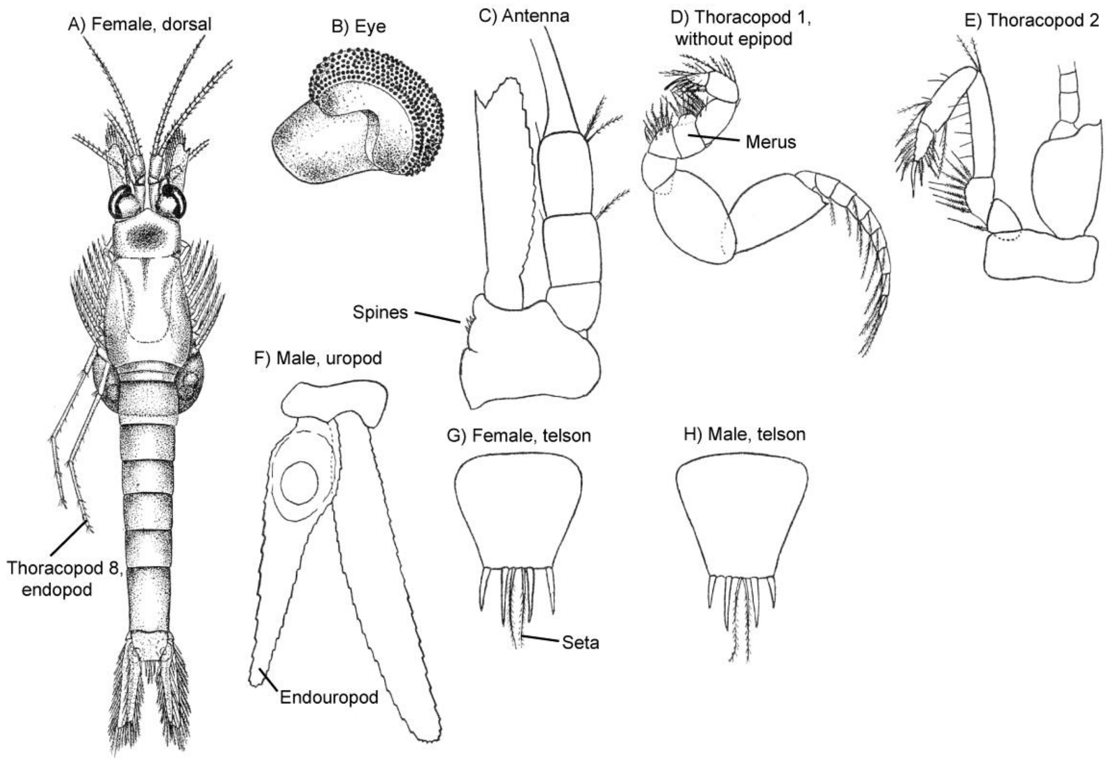

Fig. 11. *Erythrops elegans* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Skagerrak. Western Norway. Coastal.
Size: Up to ~6 mm
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Erythrops serrata (G.O. Sars, 1863)
Body slender and delicate, cephalon and thorax wider than pleon (Fig. 12A). On the mid-ventral surface of each thoracic somite there is in males and immature females a stalked, club-shaped process, rounded distally, thickly set with short strong spines, these processes smaller on the first and last somites. Eyes large, flattened dorsoventrally, cornea much wider than stalk, kidney-shaped in dorsal view, pigmented brilliant red. Carapace slightly extended between the eyes but not forming a distinct rostrum, dorsoposterior margin slightly concave, leaving the last two thoracic somites exposed in dorsal view. Antennal scale longer than both the antennal and antennule peduncle, outer margin without setae, but with eight to ten strong serrations (Fig. 12B) of which the most distal extends beyond the apex of the scale, no distal suture. Thoracopods three to eight with the endopods very long and fragile (Fig. 12C), becoming progressively longer posteriorly, the eighth extending, when stretched backwards, to the posterior margin of the last pleon somite (Fig. 12A), carpus nearly twice as long as propodus, from which it is divided by an oblique suture, propodus divided into two subsegments of which the proximal is the shorter, distal claw long and very delicate. Pleopods of male well developed, biramous, natatory except for the first pair (Fig. 12D) in which the endopod is reduced to a single segment bearing the usual setiferous pseudobranchial process. Pleopods of female reduced to simple linear unsegmented plates that are progressively longer towards the telson. Exouropod long and narrow (Fig. 12E), without spines, setose all around (not drawn), endouropod shorter than exouropod, tapering distally, outer margin setose with a few delicate plumose submarginal setae in addition to the usual marginal ones, inner margin finely serrated and setose throughout in females and immature males, serrations disappearing in males as they become mature, but retained in females. Telson short (Fig. 12F), about half as long as last pleon somite, tapering distally, width at base equal to length, lateral margins naked and slightly concave, posterior margin entire and straight, armed with two pairs of strong spines and two median plumose setae. In female the four spines are almost equal in length, but in the male the outer pair are shorter than the inner.

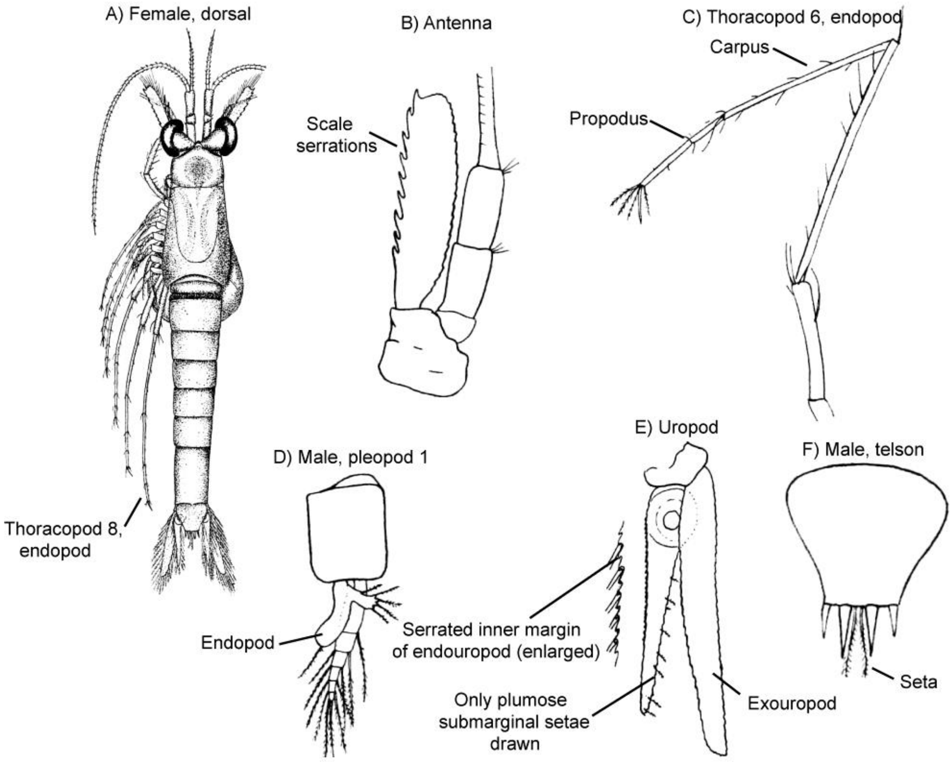

Fig. 12. *Erythrops serrata* (after Tattersall & Tattersall, 1951).

Recorded: PMF and L4 not recorded. Northern and eastern North Sea. Deeper water.
Size: Up to 11 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951.

Erythrops erythrophthalma (Goës, 1864)
Cephalon and thorax distinctly wider than pleon (Fig. 13A); carapace with anterior margin produced between the eyes into a short blunt rostrum, slightly concave dorsoposteriorly. Eyes very large and set close together, very flattened dorsoventrally, kidney-shaped, pigmented brilliant red, each facet in retina surrounded by a white margin, stalk tapering rapidly proximally. Antennal scale about four times as long as broad (Fig. 13B), considerably longer than antennal and antennule peduncle, outer margin naked, terminating in a strong spine, apex extending to about twice length of terminal spine, no distal suture. First thoracopods of normal type (Fig. 13C), with extremely delicate distal claw surrounded by fine setae, second thoracopods well developed (Fig. 13D), carpus markedly bowed, equal in length to the remainder of distal limb. Third to eighth thoracopods shorter than in *E*. *serrata*, eighth endopod (Fig. 13A, E) when stretched backwards only reaches the anterior margin of the sixth pleon somite. Exouropod with only setae around margin (not drawn), much longer than endouropod (Fig. 13F), the latter slender, tapering distally, with six to seven delicate plumose sub-marginal setae as well as usual marginal setae, inner margins not serrated as in *E. serrata*. Telson broader than long (Fig. 13G), lateral margins straight, posterior margin entire, slightly convex, with two pairs of spines and a pair of setae, middle pair of spines twice as long as the outer in both sexes.

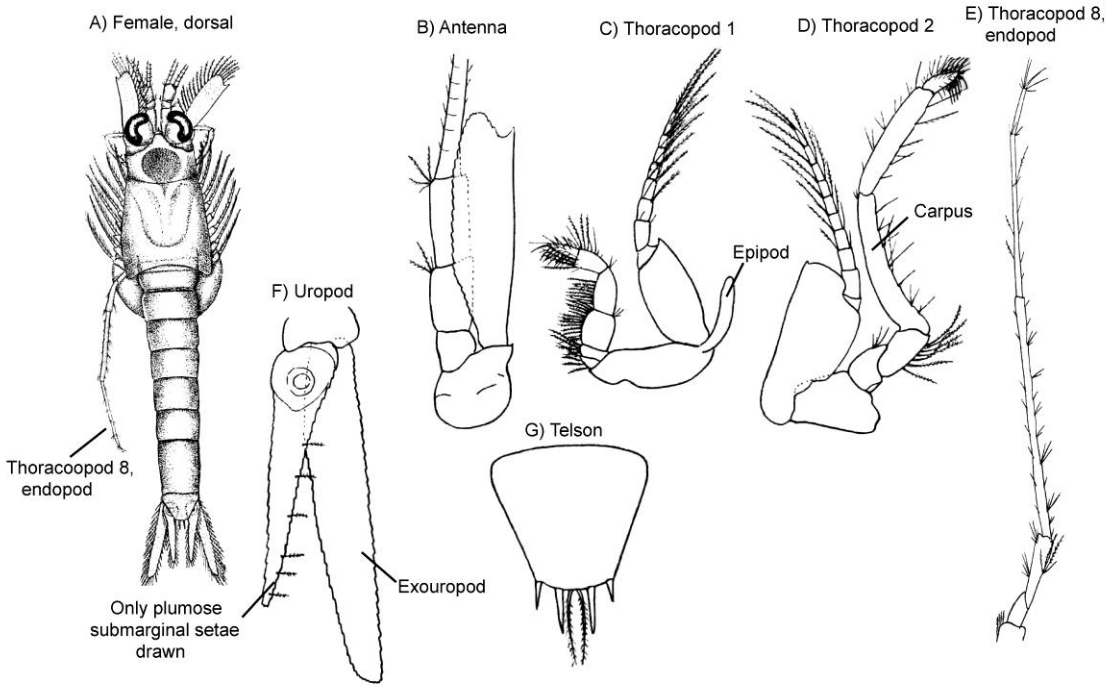

Fig. 13. *Erythrops erythrophthalma* (after Tattersall & Tattersall, 1951).

Recorded: PMF and L4 not recorded. Northern North Sea. Deeper water.
Size: Up to ~11 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951.

Genus *Pseudomma*:

Pseudomma affine G.O Sars 1870

Body compact, in dorsal view, almost parallel-sided (Fig. 14A), carapace only slightly wider than pleon, anterior margin evenly rounded, without rostrum, posterior carapace margin concave leaving last part of the seventh thoracic somite exposed in dorsal view. Eyes fused into a plate with serrations on the whole anterolateral and lateral margins (Fig. 14B), extending forwards barely to the distal end of the first segment of the antennule peduncle. Antennule peduncle with the first and third segments of similar lengths in the female (Fig. 14A) and second segment very short, in the male the third segment longer than first. Antennal scale outer margin naked, terminating in a strong spine (Fig. 14C), apex extending well beyond the spine, strong spine on the outer distal corner of the second basal segment. Endouropod shorter and slenderer than exouropod (Fig. 14G), both setose (not drawn), without spines. Telson entire, slightly shorter than last pleon somite (Fig. 6A, H), lateral margin on distal half armed with three to seven spines that are usually not symmetrically arranged, increasing in length towards the apex, apex broadly rounded, armed with a pair of median plumose setae and four, sometimes five or rarely six pairs of spines, of which the middle pair is the longest.

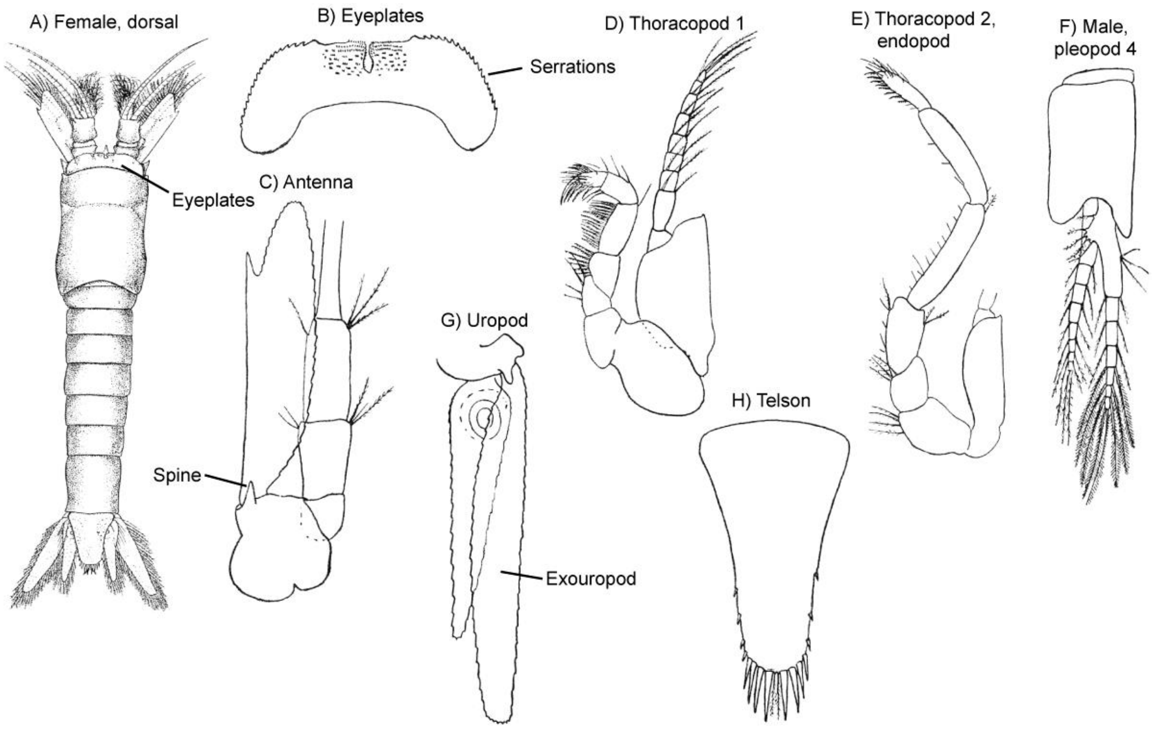

Fig. 14. *Pseudomma affine* (after Tattersall & Tattersall, 1951).

Recorded: PMF and L4 not recorded. Northern North Sea. Western Norway. Skagerrak. Deeper water.

Size: Females up to ~12 mm, males ~10 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Peracarida: Order Mysida: Family Mysidae:

Subfamily Leptomysinae:

Genus *Leptomysis*:

Leptomysis gracilis (G.O. Sars, 1864)

Body slender; carapace short, only slightly wider than pleon (Fig. 15A), concave dorsoposteriorly, anterior produced into pointed, triangular rostrum, (Fig. 15B) sides concave distally, with notch on each side at the base, anterolateral angles produced into short acute points. Surface of whole body, including appendages and eyestalks, covered with minute oblong scales (Fig. 15C) that tilt upward distally and appear in profile as small spinules. Eyes large, projecting well beyond lateral margins of the carapace, pigmented black. Antennule peduncle comparatively slender (Fig. 15D), first segment hollowed laterally, with the outer distal corner produced and armed with a brush of two to five plumose setae, second segment very short. Antennal scale long and slender (Fig. 15A, E), segment beyond suture about one-third of length of whole scale and armed with five setae on each side and a terminal seta (not drawn). First thoracopods with epipod well developed (Fig. 15F), bearing long seta proximally, endopod slender, terminal segment broader than long and armed with strong, barbed setae. Remaining thoracopods very slender, dactylus very small with long slender claw (Fig. 15G). Genital organ on the eighth thoracopods of the male small, conical and armed with a few curved bristles (Fig. 15H). Pleopods of female rudimentary, simple, unsegmented plates, those of male well developed, biramous, natatory, exopod of fourth pair longer than the endopod (Fig. 15I). Uropods very narrow (Fig. 15J), exouropod very long and slightly curved outward, endouropod about three-quarters of the length of exouropod, with large statocyst, armed along the inner margin with a row of irregularly arranged unequal spines. Telson long and narrow (Fig. 15A, K), equal in length to last pleon somite, constricted near the base, armed throughout with crowded spines which, distally, are arranged in series of large spines with between them one to six smaller spines, usually a constriction in the region of the insertion of the last large, distal marginal spines, apex narrowly rounded, terminating in two large spines with two smaller spines between.

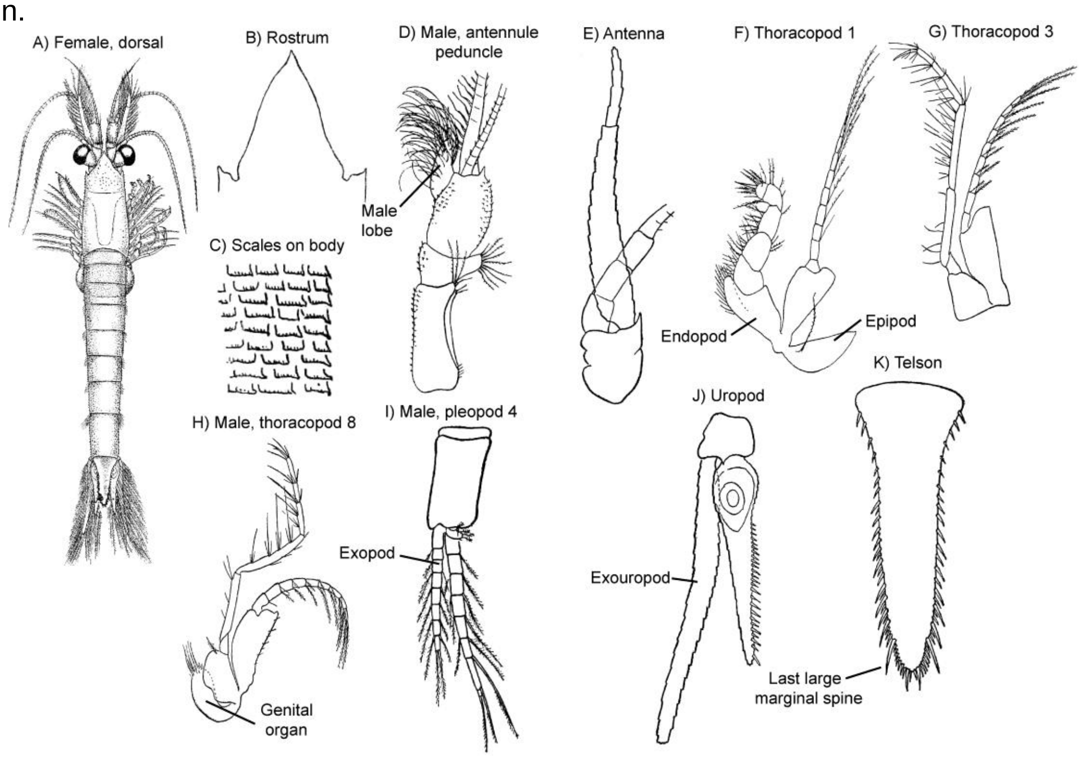

Fig. 15. *Leptomysis gracilis* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Western Norway. Skagerrak. English Channel. Coastal to deep water.
Size: Up to ~13 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Leptomysis mediterranea G.O. Sars, 1877
This species resembles *Leptomysis gracilis* so closely that only details that separate them are given here. Carapace posterior margin concave, produced anteriorly into a quite acutely pointed, triangular rostrum (Fig. 16A) about the same length as in *L*. *gracilis* but the sides are straight and not convex and there are no notches at the base. Eyestalks broader proximally than in *L*. *gracilis*. The body surface is smooth without any trace of the scales that are a marked feature of *L*. *gracilis*. Antennal scale longer and narrower in proportion to its length than in *L*. *gracilis*, the segment beyond the suture more than half as long as the proximal one (Fig. 16B) and has from 11-16 very short setae on each side (not drawn). Thoracopods and uropods (Fig. 16C) not as slender as in *L*. *gracilis* and statocyst not as large, spines arming inner margin of endouropod very crowded proximally, extending from the proximal region of the statocyst to the tip of the endouropod, more regular than in *L*. *gracilis* and increasing in length gradually to the large spine situated closest to the apex. Telson less constricted near the base than in *L. gracilis* and broader (Fig. 16D), especially towards the distal end, with no trace of a constriction marking the insertion of the last large, distal pair of marginal spines, these are separated from the large apical spines by a shorter interval than in *L*. *gracilis* and there are only two or three small spines in that interval.

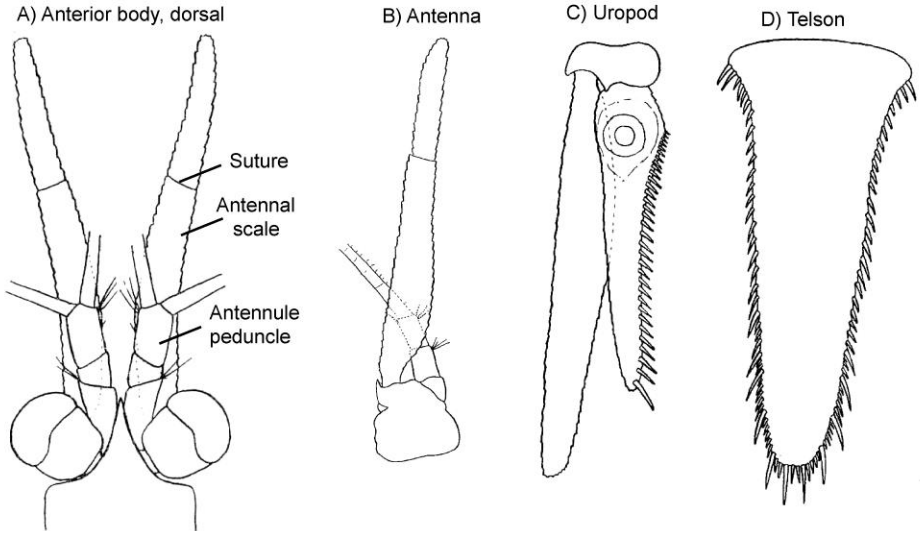

Fig. 16. *Leptomysis mediterranea* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Coastal.
Size: Up to 18 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Leptomysis lingvura (G.O. Sars, 1866)

Very similar to the other two *Leptomysis* species described here, but body much shorter, more compact and robust, surface smooth, carapace posterior margin concave, produced anteriorly into a more or less acutely pointed, short, triangular rostrum (Fig. 17A) that extends to less than half the length of the first segment of the antennular peduncle, no notches on margin. The form of the rostrum is the most reliable character by which this species may be recognised. Eyes more closely spaced than in the other two species, with only the cornea projecting beyond the lateral margins of the carapace, eyestalks less contracted at the base than in *L*. *gracilis*. Antennal scale shorter than in *L*. *mediterranea*, being less than twice the length of the antennular peduncle (Fig. 17B), segment beyond suture occupies one quarter to one third of the total length and has from four to five setae on each margin (not drawn). Thoracopods with basal segment of the exopod limbs much larger and stouter than in either of the other species (Fig. 16C). Uropods shorter and broader than in either of the other species (Fig. 17D), the spines arming the inner margin of the endouropod (Fig. 17D) are similarly graduated to those of *L*. *mediterranea* and extend over a similar distance, but are very much more crowded in the region of the statocyst. Telson shorter and considerably broader than in the other two species (Fig. 17E), shorter than the last pleon somite, apex broadly rounded, normally armed distally with two long spines and two much smaller spines between, no constrictions marking the insertion of the most distal large marginal spines, apical long spines usually separated from the most distal large, marginal spines by three or four small spines.

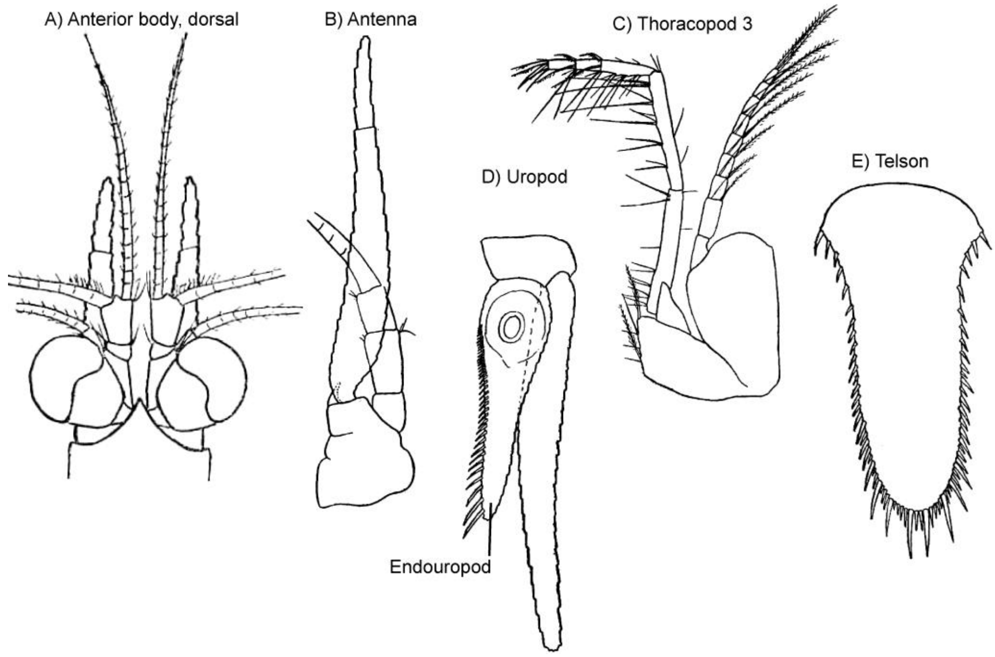

Fig. 17. *Leptomysis lingvura* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Coastal.
Size: Up to 17 mm.
Further information: Nouvel, 1950 (as *L. linguura*); Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Genus *Mysidopsis*:

Mysidopsis angusta G.O. Sars, 1864

Body slenderer than in the other two *Mysidopsis* species described here, very slender anteriorly but becoming wider in the region of the sixth to the eighth thoracic somites (Fig. 18A). Carapace long and narrow, without nodules on the dorsal surface as found in *M. gibbosa*, anterior margin produced forward into a very short, obtuse, triangular rostrum that usually extends only to the bases of the eyestalks (Fig. 18B), but may reach almost to the middle of the first segment of the antennule peduncle, anterolateral angles produced and rounded, posterior border concave. Eyes large, extending well beyond lateral margins of carapace, a finger-like papilla on the dorsal distal surface of the eyestalk. Antennule peduncle more robust in the male than in female (Fig. 18C), distal outer angle of first segment extended and tipped with a few plumose setae, second segment short, its distal margin extended dorsally into a male lobe armed at its base with a strong spine and tipped with setae. Antennal scale narrow, long, seven to eight times as long as broad (Fig. 18D), a small distal suture present, very large spine on the outer distal corner of the outer basal segment. Thoracopods three to eight endopods (Fig. 18E) shorter and less robust than in the other two species, merus longer and broader than the remainder of the limb and armed with a tuft of particularly long setae on the inner margin close to the distal end, propodus distal end and the small dactylus covered with a dense mass of very fine setae that completely covers and hides the long slender terminal claw. Pleopods of male well developed (Fig. 18F, G), biramous, natatory, exopod of fourth pair slightly longer than the endopod, terminating in a single long, strong, modified seta. Uropods short and robust (Fig. 18H), exouropod much wider and nearly half as long again as the endouropod, endouropod broad proximally with a very large statocyst, tapering rapidly, slender distally, armed on the inner distal end of the statocyst with a single, strong spine. Telson hollowed from above into a trowel shape (Fig. 18A), small, similar in shape to that of *M. didelphys,* but with deep, unarmed, wedge-shaped cleft (Fig. 18I) that is about as deep as the apex is wide, lateral margins almost straight, armed with 14-18 spines that increase in size distally, each lobe at the apex armed with two large spines, the outer shorter than the inner.

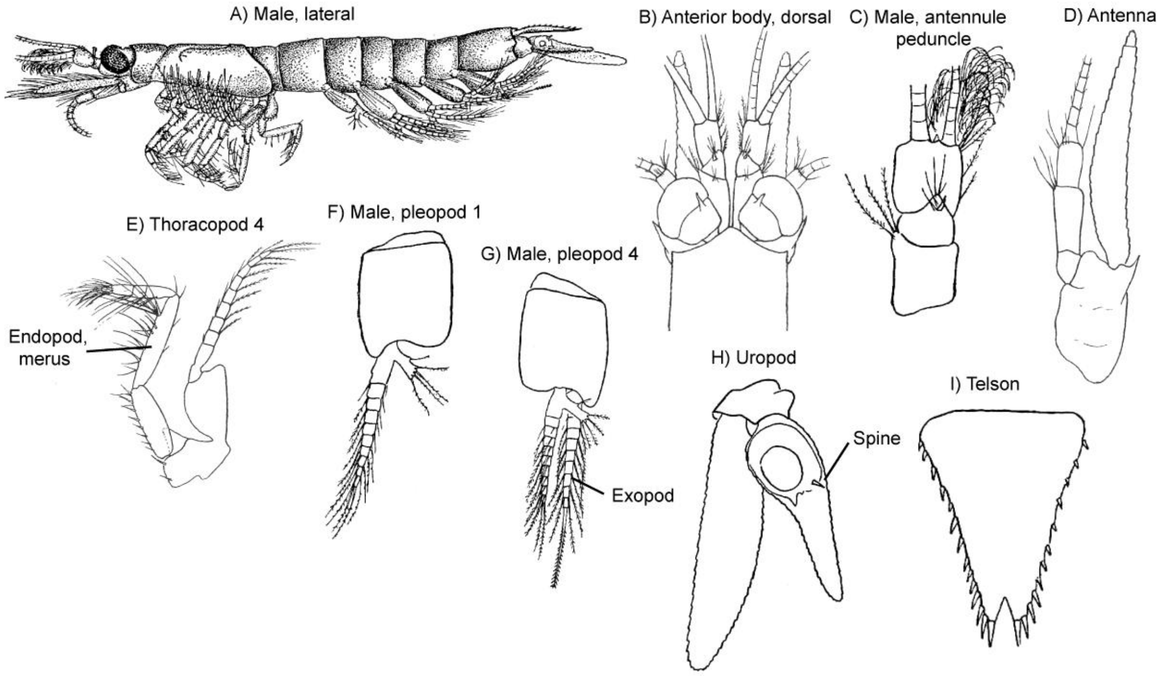

Fig. 18. *Mysidopsis angusta* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Skagerrak. Western Norway. English Channel. Deeper water.

Size: Up to ~9 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Mysidopsis didelphys (Norman, 1863)
Body robust (Fig. 19A), cephalon narrowing anteriorly, carapace with anterior margin produced into a broad triangular rostrum with an acute apex that extends more than half-way along the first segment of the antennule peduncle (Fig. 19B), anterolateral angles of carapace smoothly rounded, posterior border concave leaving the last two, and part of the sixth, thoracic somites exposed in dorsal view. Eyes large, set somewhat apart, globular but slightly flattened dorsoventrally, extending well beyond the lateral margins of the carapace, a small finger-like papilla present on the inner dorsal side of the eyestalk. Antennule peduncle much more robust in male than in female. Antennal scale narrowing distally (Fig. 19C), oval, setose all around (setae not drawn), about one-third longer than peduncle of antennule, a small distal suture present. First thoracopods robust (Fig. 19D), epipod with two strong setae at base, endopod claw well developed. Second thoracopods not much longer than first (Fig. 19E), merus long and stouter than the carpus, claw strong and curved. Genital appendages at the base of eighth thoracopods of male short and cylindrical, armed distally with seven to eight curved bristles (Fig. 19F). Pleopods of female broader than in *Leptomysis,* but of the same general form, those of the male well developed. Exouropod particularly broad (Fig. 19G), outer margin straight, inner convex, endouropod less than half as broad as the exouropod and about two-thirds as long, armed on the inner margin near the statocyst with a single long spine. Telson longer than last pleon somite (Fig. 19A, H), lateral margins rounded near base, concave at about one-third of their length from the base and then converging to a very narrow apex without cleft, armed with eight to twelve unevenly spaced spines, more crowded proximally, armed distally with two strong spines. The whole telson is hollowed from above as in *Leptomysis*.

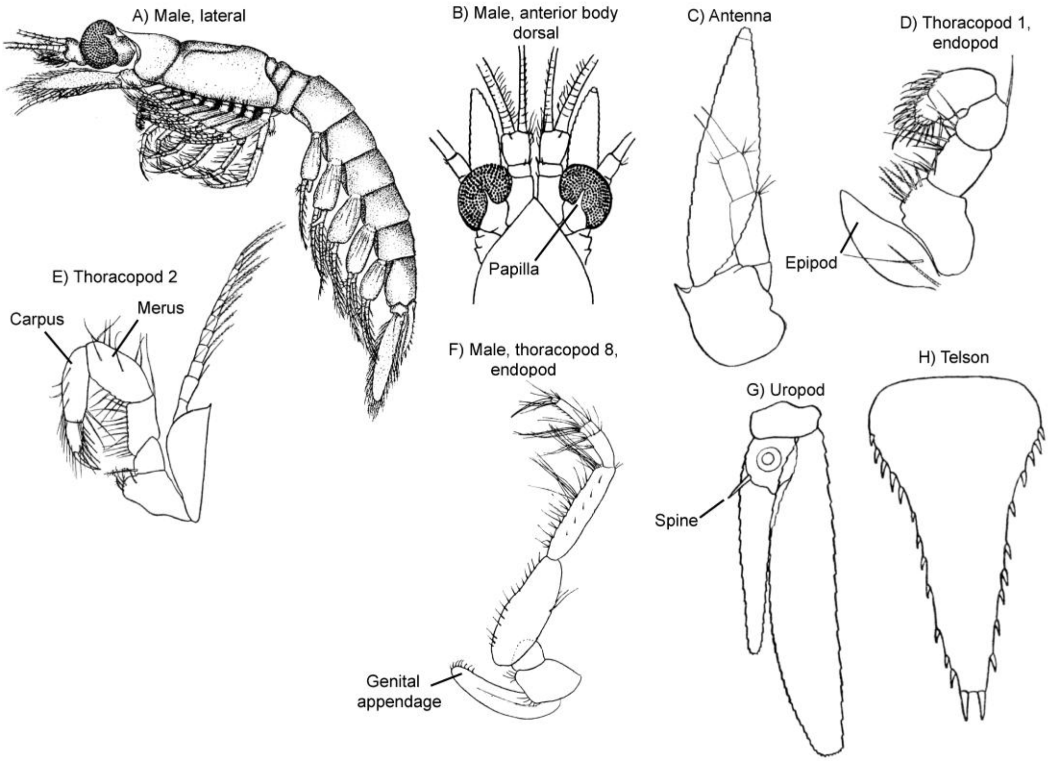

Fig. 19. *Mysidopsis didelphys* (after Tattersall & Tattersall, 1951).

Recorded: PMF and L4 not recorded. Northern North Sea. Western Norway. Skagerrak. Usually deeper water.
Size: Up to 16 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951.

Mysidopsis gibbosa G.O. Sars 1864
Robust, compact body (Fig. 20A, B), much smaller than *M. didelphys*; carapace short, anterior margin produced into a very short, pointed rostrum (Fig. 20C), anterolateral angles rounded, in dorsal view posterior border concave, leaving the last two, and part of the sixth, thoracic somites exposed. On the dorsal surface of the carapace, there are two nodules, very noticeable in lateral view, one just behind the cervical groove and the other distally. Eyes large, set widely apart and extending well beyond the lateral margins of the carapace, distal dorsal margin of eyestalk produced in the median line into a finger-like papilla. Antennal scale oval (Fig. 20C, D), setose all round (setae not drawn), outer margin straight, inner margin convex, extending about one-third of its length beyond the antennule peduncle, three times as long as broad at its widest, a small distal suture present. First and second thoracopods and pleopods (Fig. 20E-G) as in the others of the genus. Uropods short and broad (Fig. 20H), exouropod four times as long as broad, outer margin straight, inner margin convex, endouropod shorter, tapering distally, inner margin armed near the statocyst with a row of five small spines. Telson without distal cleft, shorter and broader than in *M. didelphys*, especially at the apex (Fig. 20I), hollowed from above with lateral margins upturned, lateral margins armed, according to age, with eight to eighteen evenly spaced spines, apex with outer corners rounded and without spines at the angles, two, rarely three, small spines at the tip. The form of the telson varies to some extent with age. In young specimens there are fewer spines on the lateral margins and the apex is more evenly rounded.

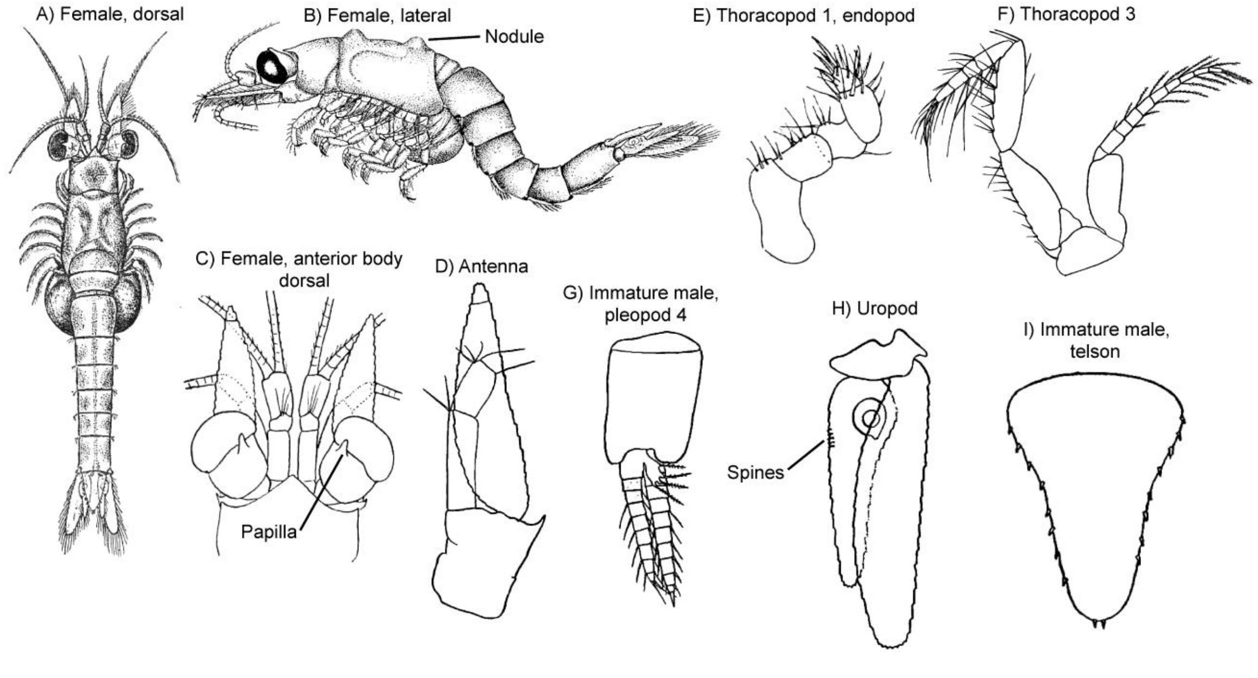

Fig. 20. *Mysidopsis gibbosa* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. Northeastern North Sea. Skagerrak. Western Norway. English Channel. Coastal to deep water.
Size: U to ~7 mm.
Further information: Nouvel, 1950; Makings, 1977; Köhn, 1992; Tattersall & Tattersall, 1951.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Peracarida: Order Mysida: Family Mysidae:

Subfamily Mysinae:

***Genus** Hemimysis*:

Hemimysis lamornae (Couch, 1856)

Body short, robust (Fig. 21A), carapace with very short triangular rostrum, dorsoposterior margin in dorsal view concave, leaving last two thoracic somites exposed. Eyes very large, rounded extending well beyond the lateral margins of carapace. Antennal scale small, extending only slightly beyond the eyes, about three times as long as the broadest part (Fig. 21B) and about the same length as antennule peduncle, proximal half of the outer margin naked and straight, not ending in a spine. First thoracopods with well developed lobes from the second and third segments of the endopod, but the lobe from fourth segment only slightly produced. Endopods of third to eighth thoracopods with four or five subsegments in the carpopropodus (Fig. 21C), the first longest, outer distal angles of the subsegments armed with stiff setae that are spiny on one side only. Pleopods of female rudimentary, first two pairs of male similar to those of female, but stronger and larger, third pair with exopod extremely small, reduced to a small knob (Fig. 21D), fourth pair with small two-segmented endopod (Fig. 21E), exopod six-segmented, penultimate segment bearing on its outer distal angle an extremely long setae that is armed with small spines along one side. Exouropod slender, about half as long again as the telson (Fig. 21A, F), endouropod shorter, armed on the inner margin with a row of 10-12 spines that extend from the statocyst for about three quarters of the length of the endouropod, increasing in length distally. Telson short, about equal in length to the last pleon somite (Fig. 21A, G), lateral margins armed on distal half with seven to ten small spines, cleft to about one quarter of its length, the cleft armed along its margins with a close-set row of teeth, apical lobes very convex on inner margins and each armed distally with a long strong spine.

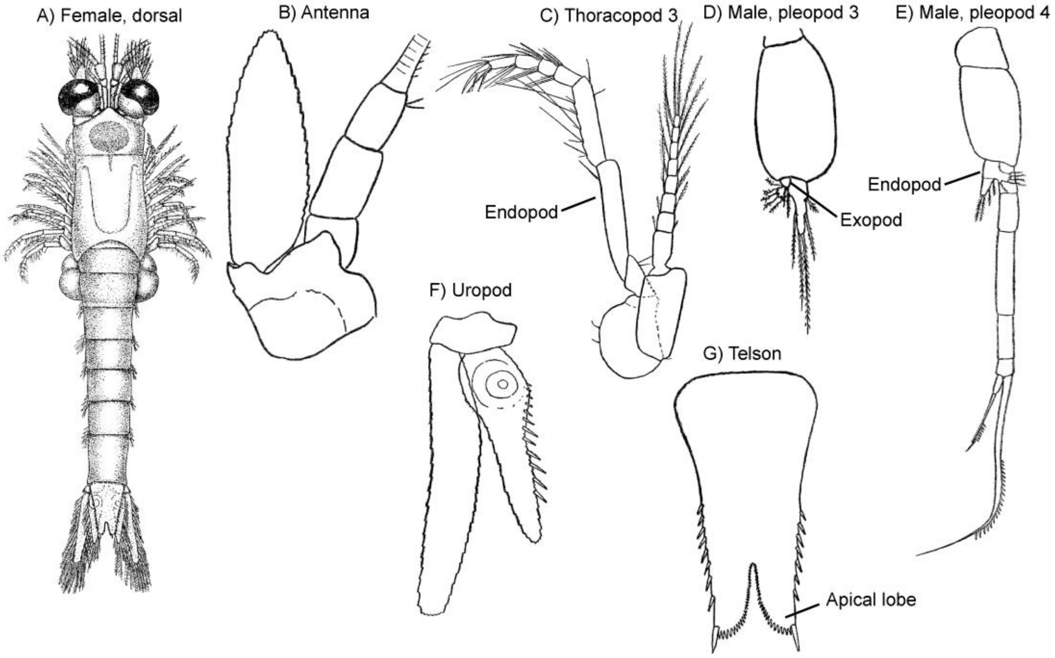

Fig. 21. *Hemimysis lamornae* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Western Norway. Skagerrak. Shallow water.
Size: Up to 10 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Genus *Mysis*:

Mysis mixta Lilljeborg, 1852

Carapace short, in dorsal view concave dorsoposteriorly (Fig. 22A); antennal scale nine times as long as broad, sharply pointed distally (Fig. 22C), distally rounded in juveniles, no spine on outer margin, setose all around; carpopropodus of endopod of third to eighth thoracopods divided into eight to nine sub-segments; sixth pleon somite one and a half times longer than the fifth (Fig. 22A, B); third and fourth pleopods of males biramous (Fig. 22D, E), both long, especially the fourth (Fig. 22B), fifth rudimentary (Fig. 22F); uropods longer than telson (Fig. 22A, G), inner margin of endouropods armed with an irregular row of 14 spines; telson as long as the sixth pleon somite, narrowly cleft (Fig. 22A, H), the cleft quarter of total telson length, lined with small spinules, lateral margins of telson with about 30 spines, distal lobes ending in single spine.

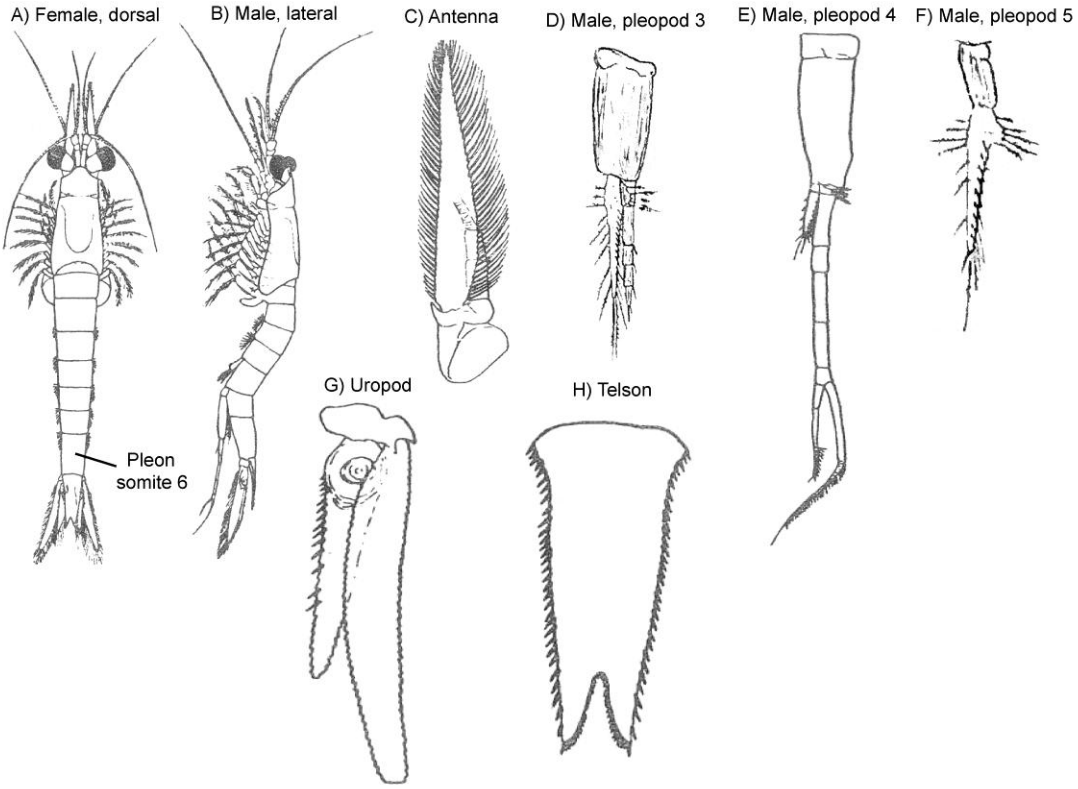

Fig. 22. *Mysis mixta* (A-C, E, G, H after Nouvel, 1950; D, F after Sars, 1879).

Recorded: PMF and L4 not recorded. Western Norway. Skagerrak. Baltic. Shallow water, euryhaline.

Size: Up to ~25 mm.

Further information: Sars, 1879; Nouvel, 1950; Köhn, 1992.

Genus *Paramysis*:

Paramysis arenosa (G.O. Sars, 1877)

Carapace with very short, rounded rostrum with small pointed tip (Fig. 23A), anterolateral angles rounded, carapace concave dorsoposteriorly, cervical groove well defined. Eyes short and thick, slightly flattened dorsoventrally, extending just beyond the lateral carapace margins. Antennal scale about twice as long as broad (Fig. 23B), outer proximal margin naked, ending in a strong spine, beyond which the apex extends considerably, apex rounded, a tiny distal suture present. Thoracopods three to seven endopods with the total length of the four segments of the carpopropodus shorter than the merus (Fig. 23C), the first segment very short and swollen, armed with long setae, terminal claw small and thin. Endopod of eighth thoracopods smaller and shorter than the preceding ones, with the merus equal in length to the remaining limb, without terminal claw. First and second pleopods of male rudimentary as in the female, third pair biramous (Fig. 23D), exopod slender and tapering to a rounded point, armed with a single seta, endopod longer than exopod, unsegmented, with obvious, setose pseudobranchial process and armed distally with a row of six to eight setae, pleopod four endopod small, two-segmented, with the convex outer margin armed with a row of plumose setae (Fig. 23E), very small, setose pseudobranchial process on first segment, two distal segments of exopod each armed with a long barbed seta, together forming a weak form of pincer, fifth pleopods rudimentary, uniramous, unsegmented (Fig. 23F). Uropods short, endouropod only slightly longer than the telson (Fig. 23A, G), statocyst small, inner margin armed along the whole of its length with 28-30 spines arranged in an irregular row of large spines with small spines between them, exouropod oval, about one-fifth as long again as endouropod. Telson longer and narrower than the last pleon somite (Fig. 23A, H), tapering distally, lateral margins armed with 19-22 small spines, largest on terminal lobes, apex deeply cleft for about one quarter of total length, armed with even, close-set teeth. May be distinguished from the other species of the genus, except *P. helleri*, by the very long apex of the antennal scale. From *P. helleri* it may be distinguished by its shorter and more robust form, narrower telson and by the armature of the endouropods.

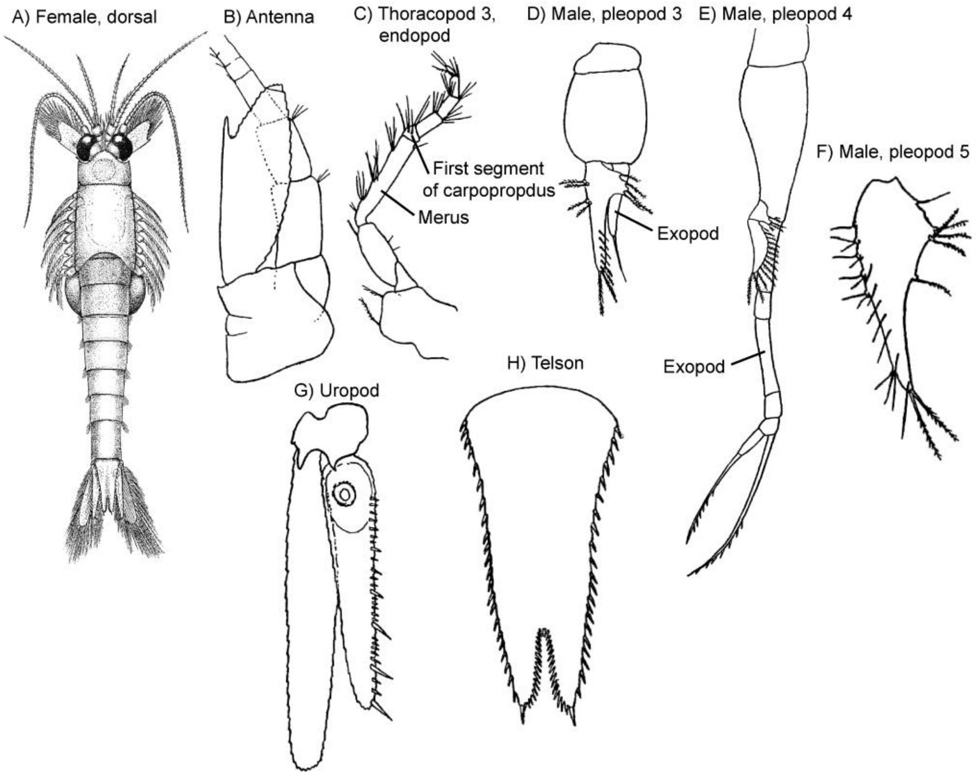

Fig. 23. *Paramysis arenosa (*after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. English Channel. Shallow water.
Size: Up to ~7 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Paramysis (*Longidentia*) *helleri* (G.O. Sars, 1877)
P. *helleri* is morphologically very similar to *Paramysis arenosa*, so only a brief summary of the main differences is given. Body longer and slightly less robust (Fig. 24A), eyes not as broad and thick, yet extending rather more beyond the lateral margin of the carapace. According to Tattersall & Tattersall (1951) the antennule peduncle is proportionately longer than in *P. arenosa* (*cf.* Figs 23A and 24A); antennal scale longer and narrower (Fig. 24A, B), with the apex relatively less produced, but these latter differences are not particularly obvious from the figures. Thoracopods with merus of the endopods broader but equal in length to remainder of limb (Fig. 24C). Endouropod armed with an irregular row of nine to ten spines of similar length and a group of around three spines, two of which are situated internal to the margin (Fig. 24D), the spines extending from the statocyst for about three-quarters of the endouropod length. This differs from *P. arenosa*, in which the spines extend right to the apex and are much more numerous. Telson broader than in *P. arenosa*, with the cleft more open distally (Fig. 24E). Some abnormal specimens can have two spines distally on the apical lobes. (Fig. 24F).

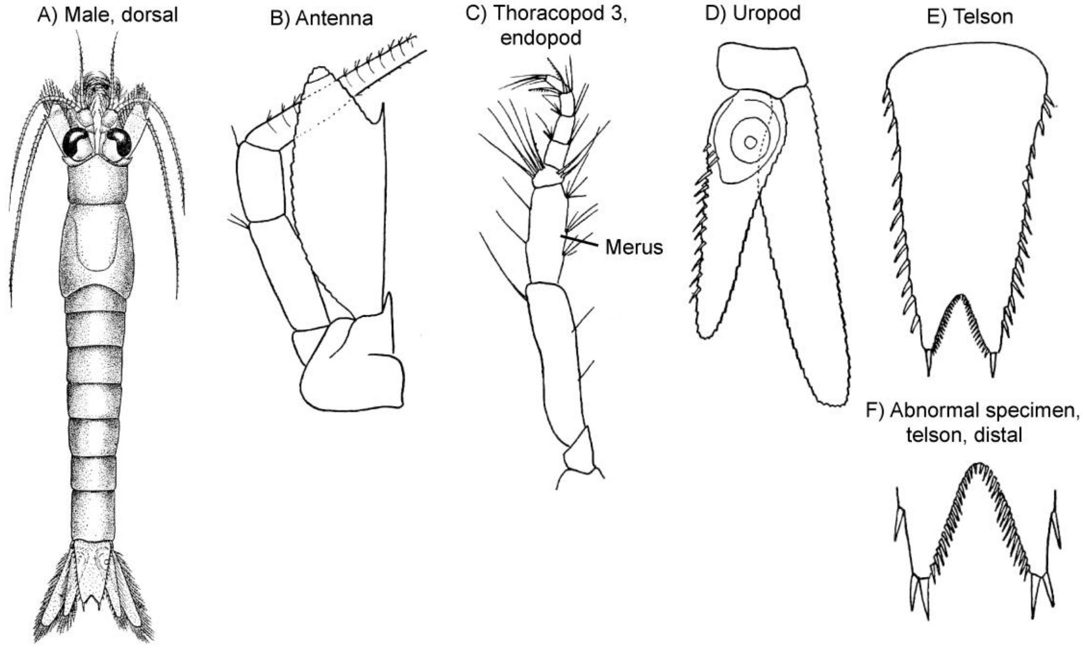

Fig. 24. *Paramysis* (*Longidentia*) *helleri* (after Tattersall & Tattersall, 1951, as *Paramysis helleri*).

Recorded: PMF. L4, not recorded. English Channel. Coastal, euryhaline.
Size: Up to ~11 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951 (both as *Paramysis helleri*).

Paramysis (*Longidentia*) *nouveli* Labat, 1953.
Also very similar to *P. arenosa*. Body robust; carapace anterior produced into a broadly rounded rostrum with tiny spine at apex (Fig. 25A, B), cervical groove well developed; eyes on short stalks, barely extending beyond the carapace margins. Antennule peduncle in female with many setae (Fig. 25A, C), proximal segment twice as long as wide, much shorter in male (Fig. 25D), in both sexes peduncle hardly reaches the external spine on the antennal scale margin; antennal scale broad, tip extending quite far beyond spine (Fig. 25E), with small distal suture. Thoracopods three to eight robust (Fig. 25F-H), their length progressively reducing towards the posterior, the eighth pair half the length of the third. Female with two pairs of brood lamellae on the bases of the seventh and eighth thoracopods (Fig. 25G). In male the endopod of pleopod four is of two segments and very short (Fig. 25I), not reaching the mid length of the second segment of the exopod. Exouropod longer than the endouropod by around a quarter of its length (Fig. 25J), endouropod internal border armed with 13-18 strong spines, starting from level with the statocyst, but not reaching right to the distal end. In the region of the proximal seven spines, a row of around six smaller spines run parallel, the number and disposition of these spines a useful diagnostic character for this species. Telson quite elongated (Fig. 25K), armed with 13-18 marginal spines, cleft around a quarter of the total length of the telson, narrower in the male than in the female, armed with 20-30 spinules each side.

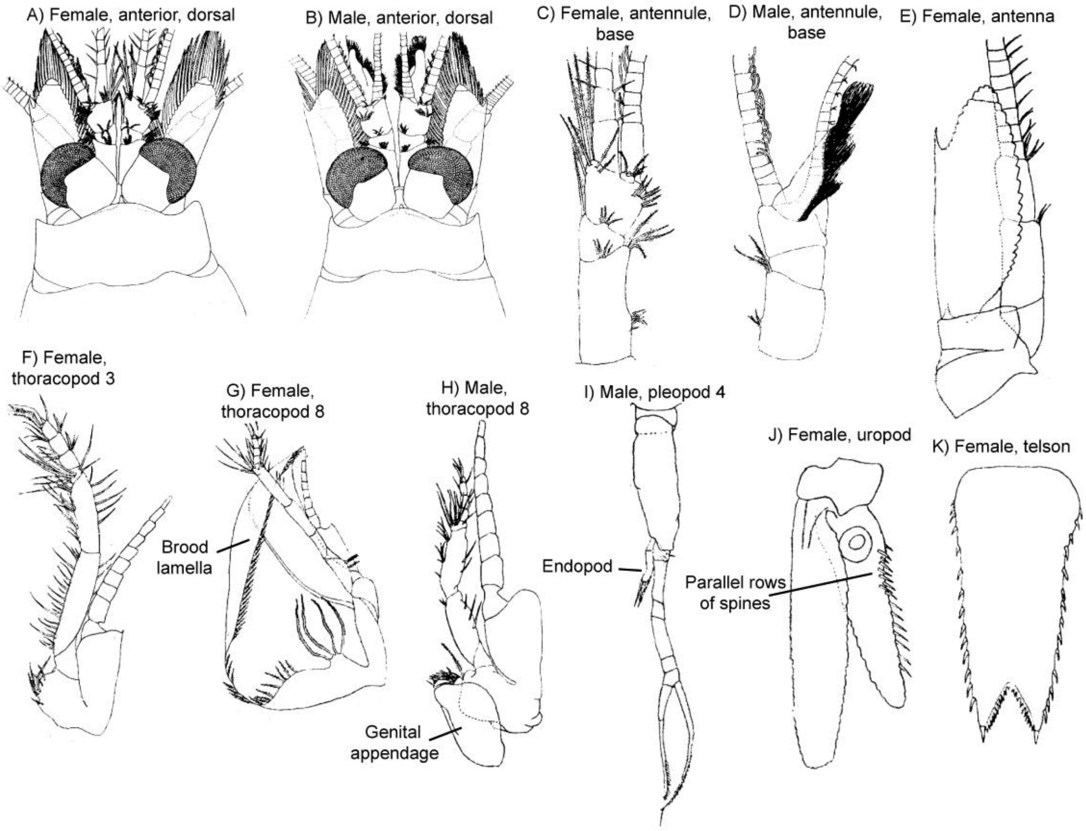

Fig. 25. *Paramysis* (*Longidentia*) nouveli (after Labat, 1953).

Recorded: PMF, L4, not recorded. Western English Channel. Brittany and northern coasts of France.
Size: Female 7.0-11.5 mm; male 5.5-9.0 mm.
Further information: Labat, 1953; Makings, 1977; Hayward & Ryland, 1995 (all as *Paramysis nouveli*).

Genus *Schistomysis*:

Very similar to *Paramysis*, but may be distinguished by the form of the carpopropodus of the third to seventh thoracopods. The proximal subsegment in *Paramysis* is short and swollen (Fig. 23C) and in *Schistomysis* longer and no more swollen than the more distal subsegments, and always considerably longer than broad (Fig. 26E).

Schistomysis spiritus (Norman, 1860)

Carapace unusually narrow, cervical groove prominent (Fig. 26A), anterodorsal margin broadly rounded without obvious rostrum, anterolateral angles rounded, posterodorsal border concave. Eyes narrow, long and cylindrical, extending well beyond lateral margins of carapace. Antennule peduncle long and slender, the first segment longer than the third and fourth together, flagella, especially the inner, short. Antennal scale long and narrow, extending slightly beyond the antennule peduncle, outer proximal margin naked and terminating in a strong spine (Fig. 26B), apex extending well beyond the spine, a small distal suture present. Endopod of first thoracopods with well developed lobes from the second, third and fourth segments (Fig. 26C), second thoracopods slender, endopod short (Fig. 26D), endopods of third to seventh thoracopods very slender and short (Fig. 26E), carpopropodus longer than the merus and divided into nine subsegments of which the first is the largest, endopod of the eighth limb smaller than the other endopods (Fig. 26F), with only six or seven subsegments to the carpopropodus and no distal claw. First and second pairs of male pleopods rudimentary as in female, third pair biramous with the unsegmented exopod shorter than the endopod and armed with one terminal plumose seta (Fig. 26G), fourth pair with extremely small two-segmented endopod (Fig. 26H), exopod long, extending to the distal end of the telson, penultimate and last segments each armed with a very long barbed seta, forming a weak pincer. Exouropod long and slender, more than half as long again as the telson (Fig. 26A, I), endouropod shorter than telson, tapering and slightly curving inward, inner margin armed with a dense row of spines roughly arranged in series of larger spines with smaller spines between. Telson long and slender with an obvious constriction near the base (Fig. 26J) and a weaker constriction distally, lateral margins armed with a row of 24-30 small spines of similar length, somewhat inset from the margin around the proximal constriction, spines missing from a short region near the distal end, cleft broad and triangular, with slightly convex margins, armed with 24-28 spinules each side.

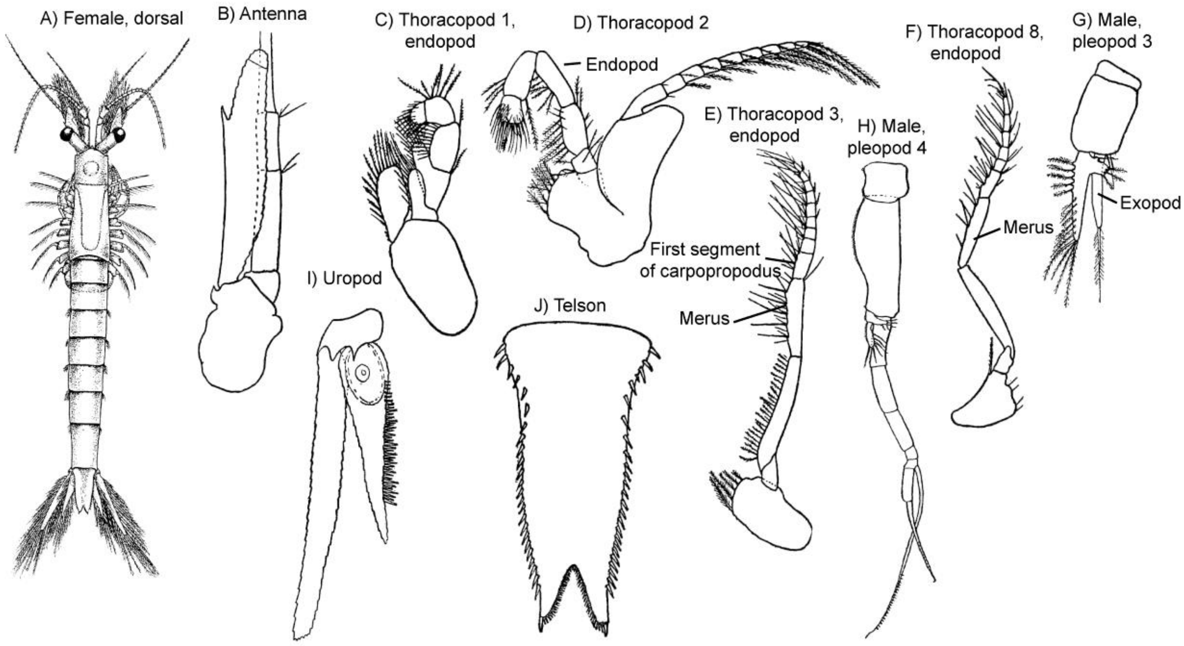

Fig. 26. *Schistomysis spiritus* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Western Norway. Mainly coastal, also deep water.
Size: ~18 mm.
Further information: Nouvel, 1950 (as *Paramysis* (*Schistomysis*) *spiritus*); Köhn, 1992; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Schistomysis ornata (G.O. Sars, 1864)

Body larger and much more robust than in *S. spiritus*, carapace short (Fig. 27A), anterior margin somewhat convex on either side of the very short, rounded rostrum, cervical groove obvious. Eyes large and short, only slightly longer than broad, extending slightly beyond lateral margins of the carapace. Antennal peduncle moderately long, the second segment the longest (Fig. 27B), outer flagellum more than twice as long as the inner, scale with outer proximal margin short and naked, terminating in a strong spine beyond which the apex extends for nearly half the total length of the scale. Endopods of third to eighth thoracopods slender (Fig. 27C, D), carpopropodus longer than the merus, divided into five to six subsegments, of which the first is the longest, dactylus extremely small, claw thin, seta-like. Third pair of pleopods of male biramous (Fig. 27E), rather larger than in the genus *Paramysis*, exopod very slender and shorter than endopod, fourth pair with very small two-segmented endopod (Fig. 27F), sympod two-segmented, long and slender, fifth pair rudimentary (Fig. 27G) as in the female. Uropods long and slender (Fig. 27A, H), endouropod tapering, about two-thirds as long as the exouropod, inner margin armed with a row of about sixteen spines that extend from the statocyst irregularly to the tip of the endouropod. Telson longer than last pleon somite (Fig. 27A, I), very similar to that of *S. spiritus*, but with the cleft deeper and much na

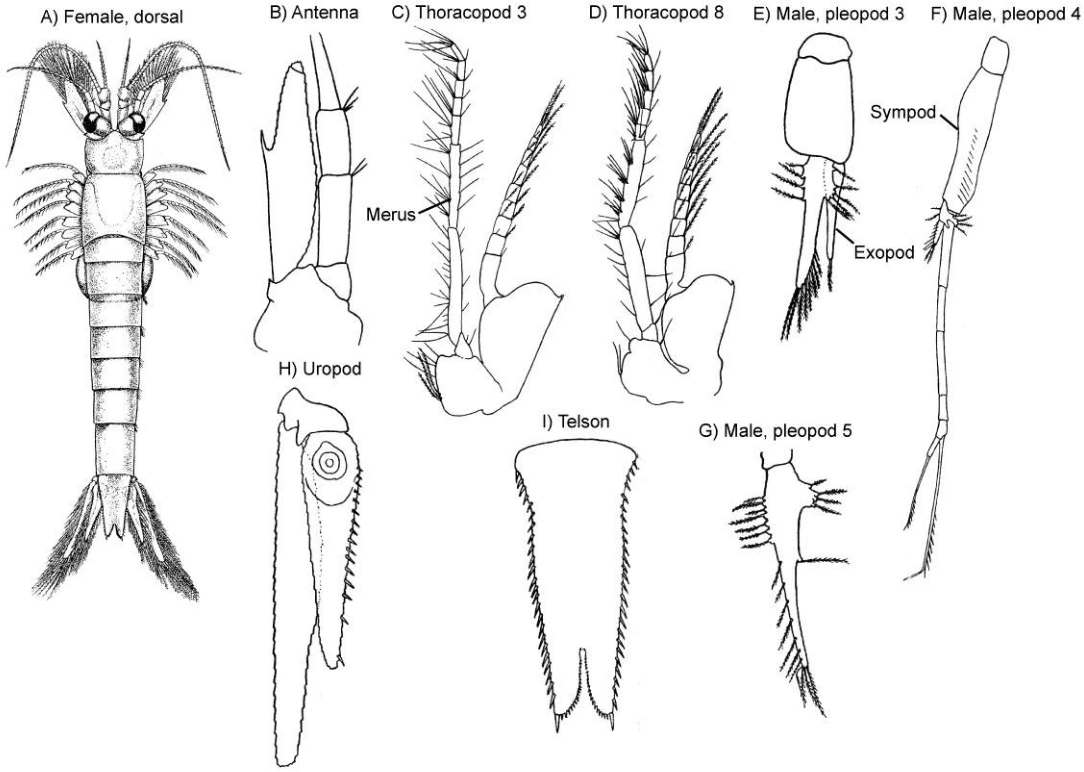

Fig. 27. *Schistomysis ornata* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Skagerrak. Western Norway. Usually shallow, but also deep water.

Size: Up to ~19 mm.

Further information: Nouvel, 1950 (as *Paramysis* (*Schistomysis*) *ornata*); Köhn, 1992; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Schistomysis parkeri Norman, 1892

Drawings and detailed descriptions of the body appear to be lacking. Body shorter and more robust than *S. spiritus*. Eyes nearly globular, only extending slightly beyond the lateral margins of the carapace. Antennule peduncle short, distal segment broader than long, male lobe on distal segment unusually long, arched backwards and inwards distally. Antennal scale ovate and broad (Fig. 28A), outer proximal margin naked, straight, terminating in a strong spine, apex produced beyond this spine for about one-fifth of the total length of the scale, small distal suture. Thoracopods with short endopods and carpopropodus divided into five or six subsegments (Fig. 28B, C), endopod of eighth thoracopods not smaller than those of the preceding limbs. Third pleopod of male biramous (Fig. 28D), exopod slender and shorter than endopod, fourth pair with very small endopod (Fig. 28E), sympod long and slender, two-segmented, fifth pair rudimentary (Fig. 28F) as in female. Uropods distinctive, with the endouropod curved strongly inwards for the distal third of its length (Fig. 28G), armed on the inner margin with a row of irregular spines that are extremely small at the proximal end of the row and extend from the statocyst to about two-thirds the length of the margin. The spines increase in size distally and tend to be arranged in series of large spines with smaller ones between, the three spines at the distal end of the row, twice as long as any other spines in the row, a single, long, strong spine at the apex. Telson cleft to about one-quarter of its length (Fig. 28H), cleft narrower and the spines arming its margins larger and fewer than in *S. spiritus*. This species may be recognised by the shape and peculiar armature of the endouropods. There is only slight incurving at the distal end of the endouropod in *S. spiritus*. The form of the spines arming the inner margin of the endouropod, with the long spine at the distal end, is unlike that of any other species of the genus.

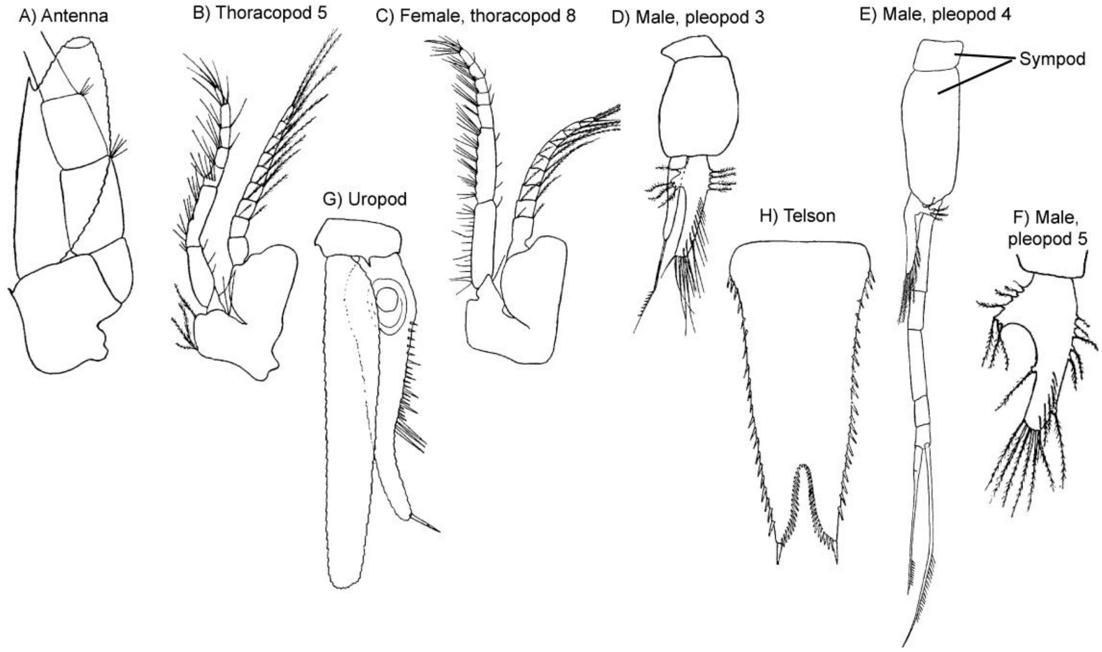

Fig. 28. *Schistomysis parkeri* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. English Channel. Shallow water.
Size: Up to ~10 mm.
Further information: Nouvel, 1950 (as *Paramysis* (*Schistomysis*) *parkeri*); Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Schistomysis kervillei (G.O. Sars, 1885)
S. *kervillei* is so similar in general form to *S*. *ornata* (Fig. 27) that it is difficult to separate them unless both species are compared together. It is a smaller species with large eyes and rostrum very slightly more produced. Antennal scale is longer (Fig. 29A), apex less produced, unarmed portion of the outer margin of the antennal scale longer. The carpopropodus of the endopods of the thoracopods is usually composed of six subsegments, in addition to the very small dactylus (Fig. 29B, C), whereas in *S*. *ornata* there are usually only five. Proximal subsegment of carpopropodus longer than the succeeding subsegments; fourth pleopod of male very long, armed distally with two "pincer" setae. Spines arming the inner margin of the endouropod are less regular in size than in *S*. *ornata* and tend to be grouped in series of large and small (Fig. 29D). While the distal end of the endouropod is illustrated without a spine, as is found in *S. ornata*, this difference is not commented on by Tattersall and Tattersall (1951). Telson somewhat broader and the deep cleft proportionally narrower (Fig. 29E).

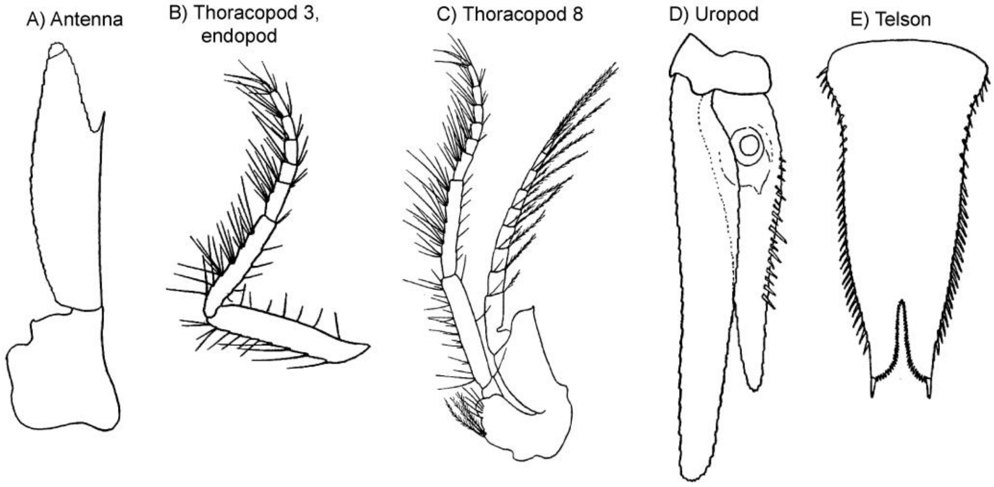

Fig. 29. *Schistomysis kervillei* (after Tattersall & Tattersall, 1951).

Recorded: PMF and L4, not recorded. Southern North Sea. Irish Sea. Shallow waters.
Size: 16 mm.
Further information: Nouvel, 1950 (as *Paramysis (Schistomysis) kervillei*); Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

Genus *Praunus*:

Praunus flexuosus (Müller, 1776);

Closely resembles *P. neglectus* and some of the differences between them are not apparent in specimens that have not reached full size. Body slender, carapace short and narrow (Fig. 30A), especially anterior to the well defined cervical groove, anterodorsal margin rounded, without distinct rostrum, anterolateral margins acutely pointed. A slender spine arises from between the bases of the antennules, and can be seen from above, appearing like a sharp rostrum. Eyes large, eyestalks long, extending laterally well beyond carapace. Antennal scale distinct from all other British mysids except *P. neglectus,* very long and narrow (Fig. 30A, B), seven to eight times as long as broad, parallel-sided, more than three times as long as antennule peduncle, outer margin naked, apex with tiny suture, rounded and shorter than the spine terminating the outer margin. Thoracopods three to seven with six segments after merus (Fig. 30C), eighth thoracopod shorter with five segments after merus. Pleopods of female rudimentary unsegmented plates, fourth pleopod of male very long, armed distally with a long setae ending in a knob (Fig. 30D). Exouropod long, linear, about half as long again as telson (Fig. 30A, E), endouropod three-quarters as long as exouropod, inner margins of with 11-14 spines, crowded proximally, more spaced distally, not extending right to apex. Telson cleft to one sixth of its length (Fig. 30F), lateral margins armed with 21-28 small spines on each side.

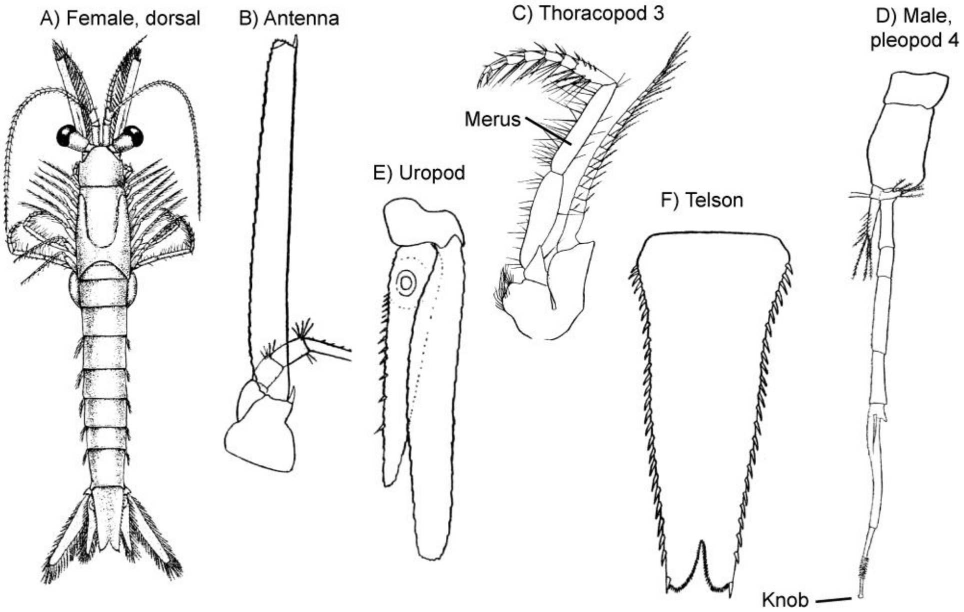

Fig. 30. *Praunus flexuosus* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Skagerrak. Baltic Sea. Shallow water.

Size: Up to ~26 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Praunus neglectus (G.O. Sars, 1869)
Very similar to *P. flexuosus*. Body slender (Fig. 31A); antennal scale five times as long as broad (Fig. 31B), less than three times as long as antennule peduncle, apex slightly longer than the spine terminating its outer margin. Thoracopods three to seven with five segments after merus (Fig. 31C), eighth thoracopod with four segments after merus (Fig. 31D), and terminal claw more defined than in *P. flexuosus*. Fourth pleopod of male very long, armed distally with a long setae ending in a knob. Exouropod long, linear, about half as long again as telson (Fig. 31A, E), endouropod three-quarters as long as exouropod, inner margins of with 11-14 spines, crowded proximally and set in from margin, more spaced distally, not extending to apex. Telson cleft to one fifth of its length (Fig. 31F), cleft very narrow proximally, lateral margins armed with 18-20 spines each side, that are slightly larger than in *P. flexuosus*.

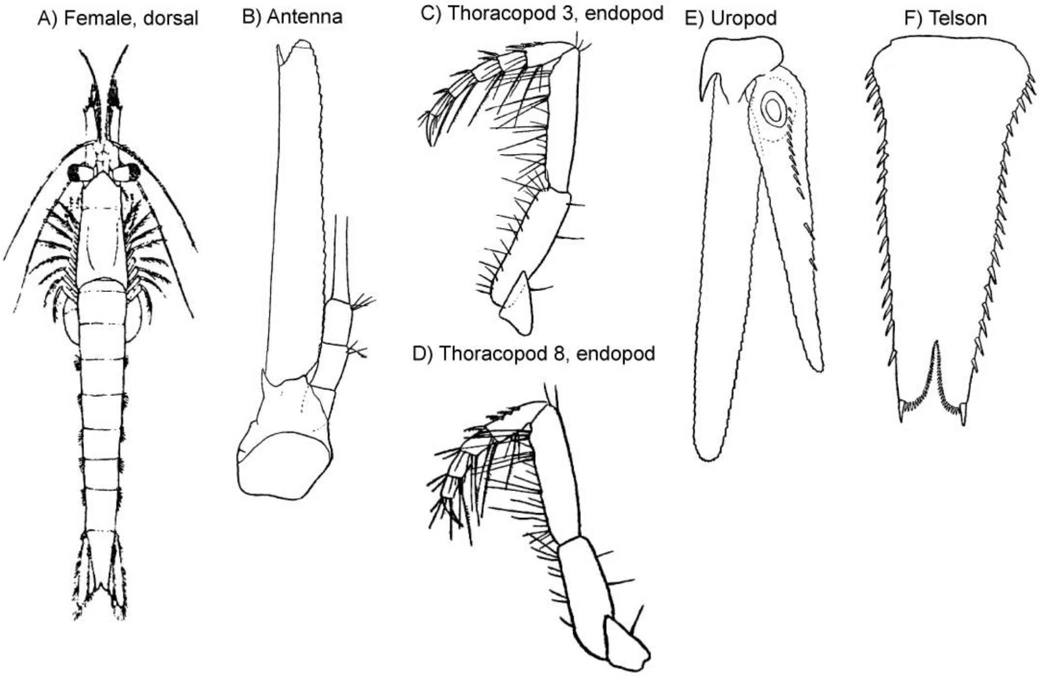

Fig. 31. *Praunus neglectus* (A after Nouvel, 1950; B-F after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Skagerrak. Western Norway. Shallow water.
Size: Up to ~20 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Praunus inermis (Rathke, 1843)
Carapace with anterodorsal margin broadly rounded (Fig. 32A) and less produced than in *P. flexuosus* and *P. neglectus,* only just covering the bases of the eyestalks. A long slender spine arises from between the bases of the antennules, and can be seen from above, looking like a sharp rostrum. Eyes shorter and more robust than in either of the other two species, protruding well beyond edges of carapace. Antennule peduncle only a little longer than the eyes, antennal scale half as long again as antennule peduncle, about four times as long as broad (Fig. 32A, B), apex produced well beyond the articulated spine terminating the outer margin, distal suture present. Thoracopods three to eight with four segments after merus (Fig. 32C, D), distal claw large, eighth thoracopods shorter and more slender than the preceding limbs. Fourth pleopod of male very long, armed distally with a long setae ending in a knob (Fig. 32E). Uropods shorter than in either of the other two species with the endouropod shorter than the telson (Fig. 32A, F) armed along the proximal portion of the inner margin with five to six spines that increase in size distally. Telson cleft to nearly one-third of its length (Fig. 32G), cleft very narrow, lateral margins armed with 15-17 spines each side.

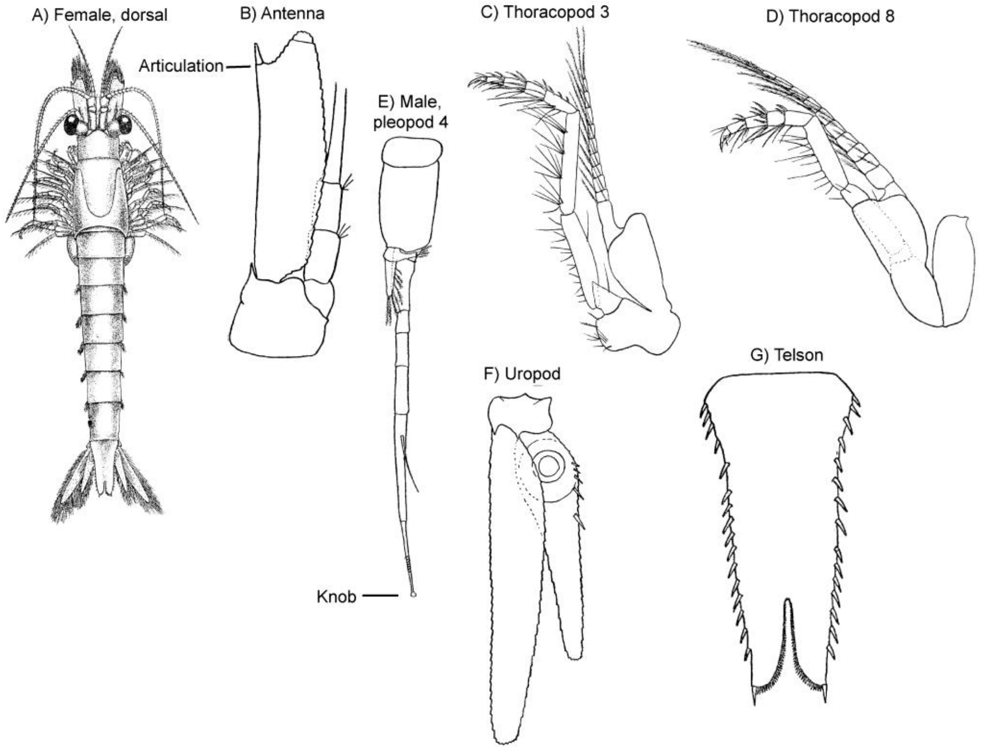

Fig. 32. *Praunus inermis* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Skagerrak. Western Norway. Shallow to deep water.
Size: Up to ~15 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Genus *Mesopodopsis*:

Mesopodopsis slabberi (van Beneden, 1861)

Body long and slender (Fig. 33A), carapace relatively short, anterodorsal margin rounded and slightly produced into a rostrum, anteriolateral angles each produced into a spine, posterodorsal margin slightly concave. Eyes on extremely long eyestalks over three times as long as broad. Antennule peduncle very long and slender, first segment almost as long as the other two combined, an extra flagellum present in the male (Fig. 33B). Antennal scale long and tapering (Fig. 33A, C), shorter than antennule peduncle, setose all around, small distal suture, no external spine. Thoracopods three to eight with endopods long and slender (Fig. 33D), seven to eight subsegments after merus, no distal claw. Third pleopod of male with long sympod (Fig. 33E), endopod slender, unsegmented, armed with around six long plumose setae on inner margin and a further one at apex, exopod only about half as long as endopod, two-segmented. Fourth pleopod of male with second segment of sympod very long (Fig. 33E), endopod minute, three-segmented, exopod very long, extending beyond the posterior margin of the last pleon somite, three-segmented, third very short, armed with two very long setae, of which the inner is shorter and is furnished with a fine comb-like row of minute spinules, outer seta about three times as long as inner. Exouropod long, narrow, slightly bowed outward distally (Fig. 33A, G), more than three times as long as telson, setose all around, endouropod about two-thirds as long as exouropod, tapering distally, armed with a single small spine on the inner margin, level with the distal end of the statocyst. Telson short, less than half as long as the last pleon somite (Fig. 33A, H), lateral margins terminating in a strong spine each side, the apex produced between the spines into a rounded plate densely armed with spines.

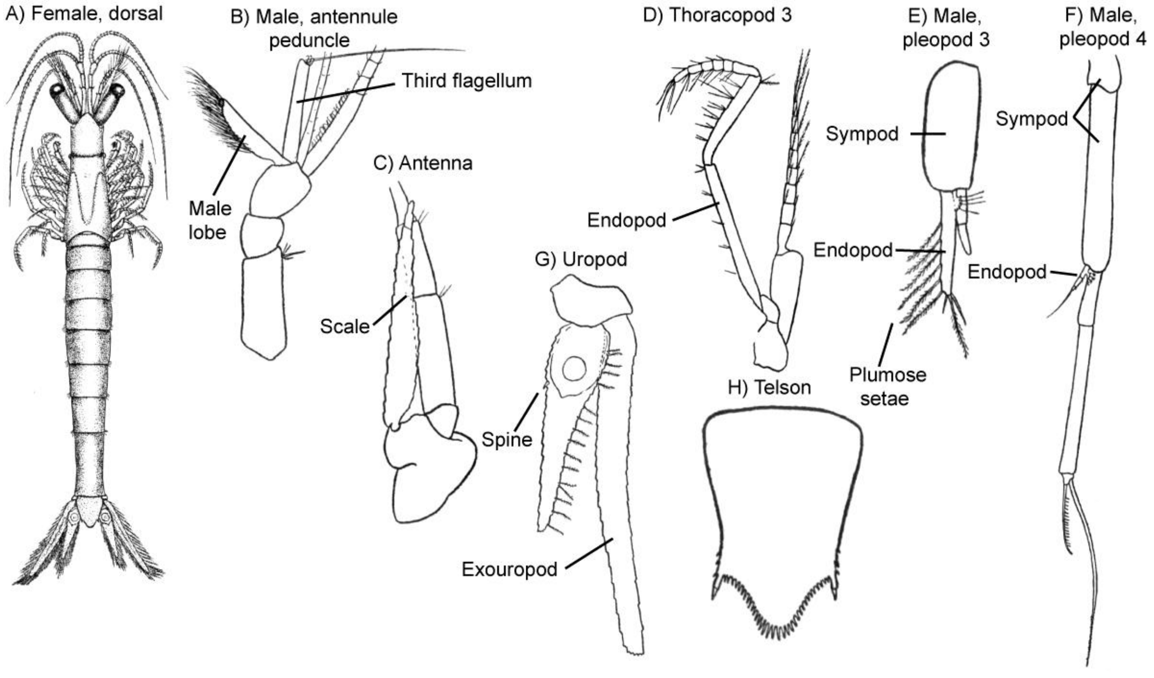

Fig. 33. *Mesopodopsis slabberi* (after Tattersall and Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. Irish Sea. English Channel. Shallow and estuarine waters.

Size: Up to ~15 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Genus *Neomysis*:

Neomysis integer (Leach, 1814)

Carapace only slightly concave dorsoposteriorly (Fig. 34A, B), produced anteriorly into a short, triangular rostrum, anterolateral angles with acute points. Antennule peduncle with the third segment about the same length as the first but much stouter, setose male lobe as long as the last two segments, long and finger-shaped (Fig. 34B). Antennal peduncle about one third of the length of the scale (Fig. 34C), a prominent spine on the outer, distal angle of the sympod and a similar spine centrally, scale long and narrow, around ten times as long as broad, setose all around, terminating in an acutely pointed apex with distinct distal suture. Thoracopods three to eight with carpopropodus of the endopods divided into six to eight subsegments (Fig. 34D), claw distinct, basal plate of the exopods with an acute spine on outer distal corner. Genital organ on eighth thoracopods of male short and barrel-shaped. Pleopods of female all simple, unsegmented, short setose plates, male, first, second, third and fifth pairs rudimentary as in female, fourth pair greatly elongated (Fig. 34B, E), extending backward half-way along the telson, endopod a simple setose plate, exopod two-segmented, first segment four and a half times as long as second, armed with a single, short, distal seta, second segment terminating in two equal, strong, barbed setae. Endouropod as long as the telson (Fig. 34A, F), armed with a dense row of around 25 comb-like spines, on the ventral surface near the inner margin, extending from the distal end of the statocyst to about half the length of the endouropod, exouropod one and a half times as long as the telson. Telson long and narrow (Fig. 34A, G), longer than the last pleon somite, triangular in shape, apex narrow and armed with two pairs of spines of which the outer are more than twice as long as the inner, lateral margins armed throughout their length by a continuous series of 20-24 spines, crowded near the base and becoming gradually more spaced distally.

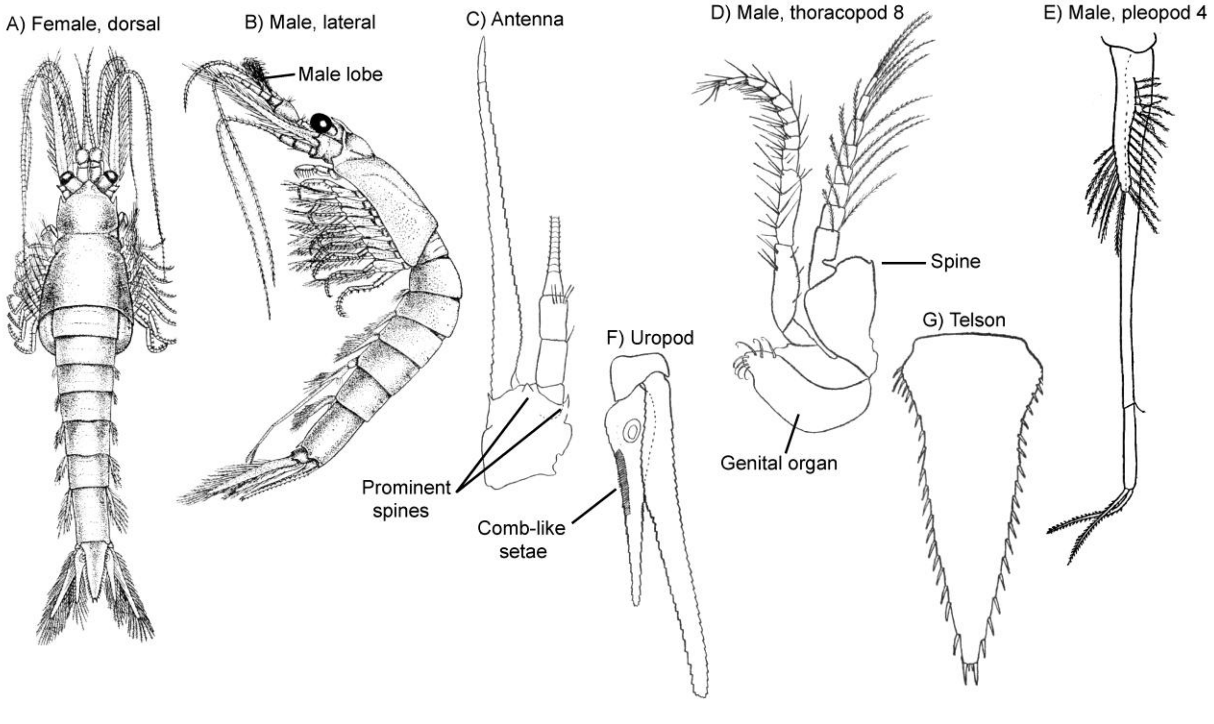

Fig. 34. *Neomysis integer.* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Skagerrak. Wadden Sea. Shallow water

Size: Up to ~17 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Köhn, 1992; Hayward & Ryland, 1995.

Genus *Acanthomysis*:

Acanthomysis longicornis (Milne-Edwards, 1837)

Body long and slender (Fig. 35A), dorsoposterior carapace concave, produced into short pointed rostrum anteriorly, anterolateral margins rounded, distinct cervical groove. Eyes large, somewhat widely separated, projecting well beyond lateral margins of carapace, eyestalk broad. Antennule with very long peduncle (Fig. 35B), second segment small, distal segment swollen and almost equal in length to the first. Antennal scale extending only slightly beyond the antennule peduncle, narrow with rounded apex, about eight times as long as broad (Fig. 35C), with distal suture. Thoracopod endopod claws distinct, long and very slender (Fig. 35D). Pleopods similar to those in the genus *Neomysis*, fourth pleopod of male (Fig. 35A, E) reaching the middle of the last pleon somite, exopod two-segmented, with the first segment about seven times as long as the second, which terminates in two long, unequal, spinous setae, the longest twice as long as the segment. Endouropod nearly equal in length to the telson, broad at the base and narrowing sharply distally (Fig. 35F), inner margin armed in the region of the statocyst with a row of small spines, of which the distal two or three are much larger, exouropod long and narrow, half as long again as the endouropod. Telson elongate, without cleft (Fig. 35G), wide at the base and then strongly constricted, with the distal portion tongue-like, apex rounded, proximal margin armed with two spines on each side, posterior two-thirds of margin and apex densely armed with numerous, unequal spines arranged with larger spines separated by series of three, four or five smaller ones. Apex with two small central spines flanked by two larger.

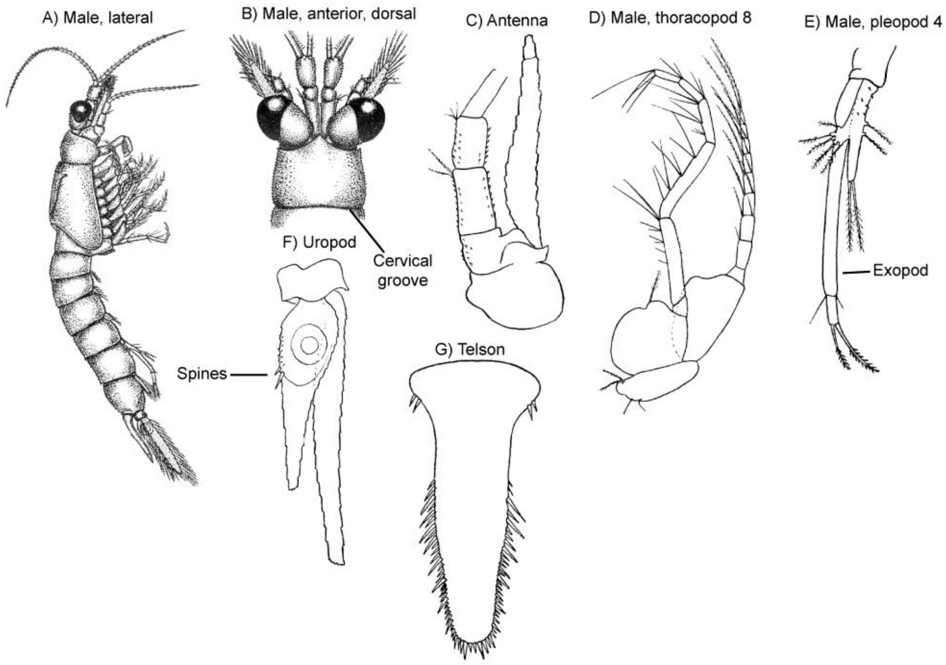

Fig. 35. *Acanthomysis longicornis* (after Tattersall & Tattersall, 1951).

Recorded: PMF. L4, not recorded. Southwestern North Sea. English Channel. Shallow to deep water.

Size: Up to ~9 mm.

Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Makings, 1977; Hayward & Ryland, 1995.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Peracarida: Order Mysida: Family Mysidae:

Subfamily Heteromysinae:

Genus *Heteromysis*:

Heteromysis (*Heteromysis*) *norvegica* Sars, 1882

This species, when sampled in European waters, was widely misidentified as *H. formosa* Smith, 1873, which is now known to be restricted to the western Atlantic, and all previous European records are considered to be *Heteromysis norvegica,* described by Sars (1882). The original description and drawings are very limited, so the drawings and descriptions of *Heteromysis* (*Heteromysis*) *norvegica* (as *H. formosa*) from Tattersall & Tattersall (1951) are included here.

Body robust, carapace short and broad in dorsal view (Fig. 36A), anterodorsal margin not produced into a pronounced rostrum, dorsoposterior margin very deeply cleft. Antennule peduncle strong and extending forward to the distal end of the antennal scale, inner flagellum short, outer flagellum much thicker and longer. Unusual among mysids the male lobe on distal end of third segment of peduncle reduced to setose ridge. Antennal peduncle well developed, equal in length to the scale (Fig. 36B), scale short, setose all around, without lateral spine, small distal suture, prominent spine on the outer distal corner of the sympod. First thoracopods moderately long with well developed lobe on the second segment (Fig. 36C), epipod long and narrow. Second thoracopods slender, second segment produced on the inner margin (Fig. 36D), endopod terminal segment swollen, armed with nine or ten strong spines and many long slender setae, of which a long straight row runs obliquely across the segment, no claw. Third thoracopods with the endopod very strong and stout (Fig. 36E), carpus and propodus fused, nearly equal in length to the merus, dactylus small, almost square in lateral view, bearing a large strong nail which bends down to form a prehensile claw. Fourth to eighth thoracopods (Fig. 36F) slightly longer, but much slenderer than the third, carpopropodus six- to eight-segmented, nail small and bristle-like. Pleopods reduced to small plates in both sexes. Exouropod (Fig. 36G) slightly longer than endouropod, endouropod with around 17-20 spines along inner margin between statocyst and tip and around five on inner distal margin. Telson cleft, without spines on proximal third to half of lateral margins (Fig. 36H), around 12-16 spines each side distally, with a further two longer pairs on apex, teeth lining inner margin of cleft missing on distal portion.

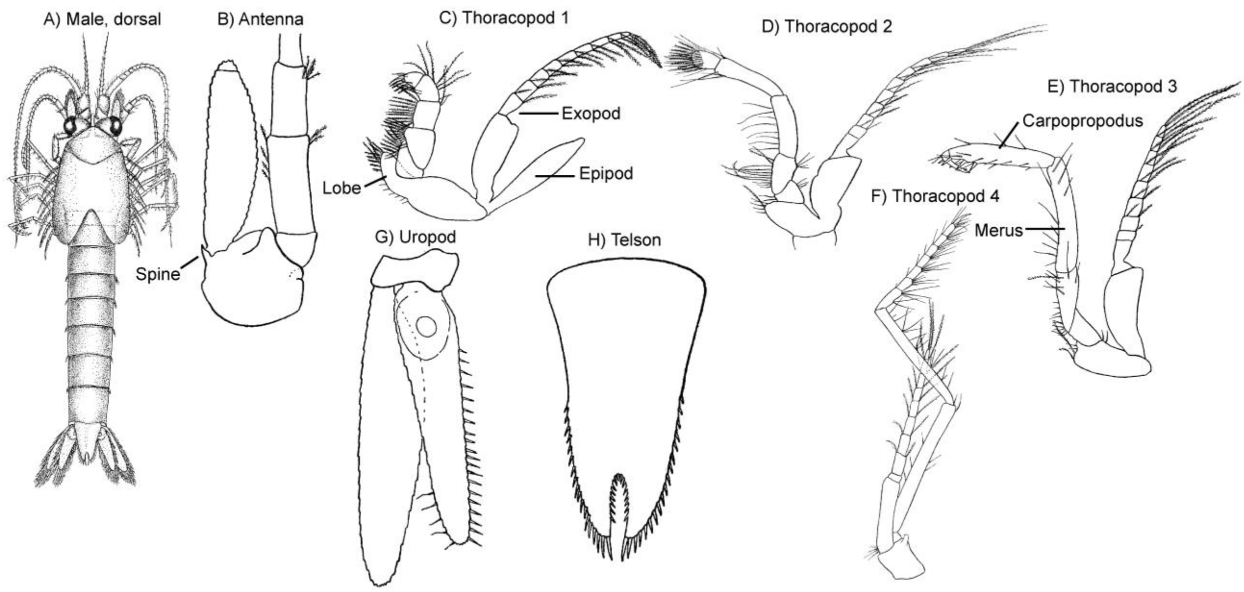

Fig. 36. *Heteromysis* (*Heteromysis*) *norvegica* (after Tattersall & Tattersall, 1951 as *H. formosa*).

Recorded: PMF (as *Heteromysis formosa*). L4, not recorded. Northwest North Sea. Western Norway. English Channel. Shallow to deep water.

Size: 8.0-9.4 mm.

Further information: Sars, 1882; Băcescu, 1941(as *H. formosa*); Nouvel, 1950 (as *H. formosa*); Tattersall & Tattersall, 1951 (as *H. formosa*); Makings, 1977 (as *H. formosa*); Hayward & Ryland, 1995 (as *H. formosa*); Wittmann, 2000.

Heteromysis (*Heteromysis*) *microps* (G.O. Sars, 1877)
Body short and robust, carapace larger than in *H. norvegica*, completely covering the bases of the thoracopods (Fig. 37A), anterior margin produced into a short acute rostrum, anterolateral angles broadly rounded, dorsoposterior margin deeply concave. Eyes small, not extending laterally to outer margin of carapace, stalks slenderer than in *H. norvegica*. Antennule peduncle long and strong, especially in male. Unusual among mysids the male lobe on distal end of third segment of peduncle reduced to setose ridge. Antennal peduncle slender, almost as long as scale, scale small, shorter than antennular peduncle, oval, a small distal suture present. Endopod of third thoracopods very robust (Fig. 37B), merus swollen, armed along the inner margin with ten setae with a thickened base bearing a long barbed seta set in a socket (Fig. 37C), carpopropodus large and swollen, equal in length to merus, but less robust, armed at the distal end of the inner margin with two pairs of small spines, distal margin of the segment produced on its inner side into two long, strong, non-articulated, finger-like projections, between which the dactylus, with its very strong claw bends down to form a powerful sub-chelae. Fourth to eighth thoracopods very slender. Pleopods rudimentary in both sexes. Uropods short and broad (Fig. 37A, D), endouropod slightly longer than telson, armed with a single slender spine on the inner margin near the statocyst, exouropod only slightly longer than endouropod. Telson equal in length to last pleon somite (Fig. 37A, E), but much narrower, lateral margins converging evenly and not convex distally, armed with 12-14 spines on each side, one spine proximally, separated by a long unarmed interval from the rest, spines increase in size and spacing distally. A pair of spines distally on each lobe, the inner much smaller, apex cleft to nearly one-third of the telson length, cleft widely open distally, with almost straight margins, armed throughout length with 16-20 small teeth each side.

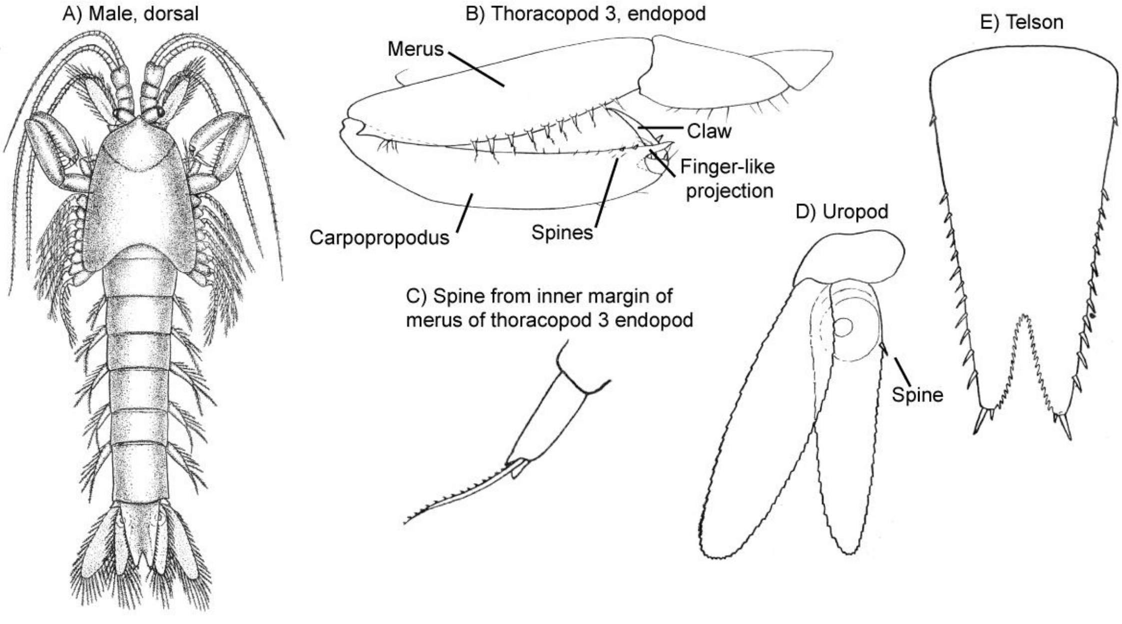

Fig. 37. *Heteromysis* (*Heteromysis*) *microps* (after Tattersall & Tattersall, 1951, *as Heteromysis microps*).

Recorded: PMF. L4, not recorded. Western English Channel.
Size: 8-10 mm.
Further information: Nouvel, 1950; Tattersall & Tattersall, 1951; Hayward & Ryland, 1995 (all as *Heteromysis microps*).

Heteromysis (*Heteromysis) armoricana* Nouvel, 1940

Unusual among mysids, in *Heteromysis* spp. males, the male lobe on distal end of third segment of peduncle of antennule reduced to setose ridge. Antennal scale quite short, oval, apex rounded, without marginal spine, setose all around. Endopod of third thoracopods large (Fig. 38B), slender, carpus and propodus fused, not strongly armed, but with powerful terminal claw. Female with two pairs of brood lamellae arising from the last two pairs of thoracopods. Male with the pleopods rudimentary and a characteristic long, tubular genital organ. Inner margin of endouropod armed throughout with close-set regular spines (Fig. 38C). Lateral margins of telson armed throughout their length with about 18 spines, which are more crowded and somewhat larger distally, two spines on apex, the inner one much longer; inner margin of convex-sided cleft lined with teeth, absent on distal portion.

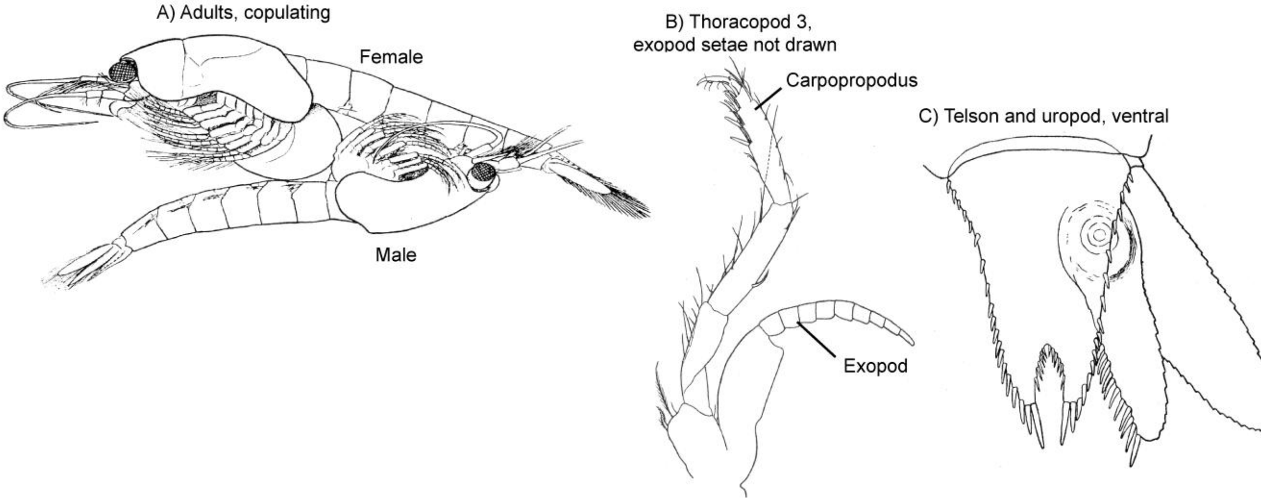

Fig. 38. *Heteromysis* (*Heteromysis) armoricana* (After Nouvel, 1940).

Recorded: PMF and L4, not recorded. South and west British coasts. English Channel.
Size: 8-9 mm.
Further information: Nouvel, 1940, 1950; Tattersall & Tattersall, 1951.

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PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida:

Order Amphipoda:

Few amphipod species are truly pelagic, most living on or close to the sea bottom, but sometimes venturing higher into the water column, so are often caught in plankton nets, especially in inshore areas. Pelagic species, in open sea areas, can often be sampled in high numbers. Amphipods are generally detritivores or scavengers, but some are predatory, commensal or parasitic. They live in almost all aquatic environments and the most familiar are the terrestrial “sand hoppers” found under damp, decaying seaweed at the strand line on beaches.

Classification

The taxonomy of Amphipoda is in a state of considerable flux. Classification has not been based on evolutionary relationships, so requires some revision. Historically there have been four suborders: Caprellidea, Gammaridea, Hyperiidea and Ingolfiellidea. The latter two suborders each have very recognisable characteristics and remain unchanged, while Gammaridea, which has been used as a dumping ground, has been revised (Lowry & Myers, 2013). 95 families formerly in Gammaridea have been reassigned, along with all of Caprellidea into a new suborder, Senticaudata, defined by a character trait not previously used, presence of robust setae on the distal tip of the rami of the first and second uropods (Fig. 12H). However, several other genera and families still remain classified *incertae sedis*, so more changes will follow. Current information is also available on the World Amphipod Database (Horton *et al*., 2013 onwards). Because of the absence of texts and keys that incorporates these recent changes, it is easier to identify specimens using older keys such as those in e.g. Lincoln (1977) and Hayward & Ryland (1995) and then, if precise classification is required, checking where they are currently classified using the WoRMS website.
Gammaridea and Senticaudata are by far the largest suborders, but few are pelagic, while Hyperiidea are mainly pelagic, although often associated with gelatinous organisms. Ingolfiellidea are a tiny suborder, typically living in sediments and only recorded from a few locations around the world (Vonk & Schram, 2003). The current WoRMS classification scheme is listed below, with the numbers of each group recorded in the PMF and southwest UK area noted in brackets as an example of typical coastal/estuarine amphipod species diversity.

Suborder Hyperiidea: (3)
Suborder Gammaridea: (75)
Suborder Senticaudata:
- **Infraorder Corophiida**
  - **Parvorder Corophiidira** (25)
  - **Parvorder Caprellidira** (28)
- **Infraorder Gammarida** (18)
- **Infraorder Hadziida** (21)
- **Infraorder Talitrida** (9)
- **Infraorder Bogidiellida** (0)
- **Infraorder Carangoliopsida** (0)

Suborder Ingolfiellidea: (1)

Because of their considerable species diversity, amphipod identification is a specialist task. While 180 species of amphipods are recorded in the PMF from the Plymouth area, only detailed descriptions are given here for six Hyperiidea species that are pelagic and could occur in shallow European waters. Individual information is given for the single Ingolfiellidea species recorded locally, as an example of the suborder, but it is a benthic species. It is outside the scope of this guide to give a key to the remaining non-pelagic local species, so only a key to distinguish the suborders, some general descriptions and examples are given.

Morphology

Few of the above taxonomic groups have a unique set of characters to distinguish them, rather a combination of characters, although a few groups have very strong morphological features that make them instantly recognisible, such as the large eyes in Suborder Hyperiidea, or the skeletal bodies in some members of Parvorder Caprellidira (Family Caprellidae).

It is difficult to give a general description of amphipods, as in all groups particular features can vary from being well developed to completely missing. The body is divided into a maximum of 14 visible somites (Fig. 1A-C), sometimes less due to fusion. It is sometimes elongate, but often curled up, usually laterally compressed but sometimes quite globular, and there are often differences between the sexes in shape, morphology and dimensions. There is no carapace, and similar to other Peracarida, the head is short and fused with the first thoracic somite, so seven thoracic somites are visible. The exoskeleton sometimes bears sharp or blunt outgrowths, either as isolated spines, or as ridges. These outgrowths are usually situated dorsally, sometimes only on the posterior somites. Terminology currently used for different regions of the body are head (cephalon fused with first thoracic somite, equivalent to cephalothorax), pereion (or pereon; the remaining seven thoracic somites) and pleon (abdomen). The pleon is further subdivided into pleosome and urosome.

Head: The head is relatively short (Fig. 1A-C) and an anterodorsal rostrum may be present, but more typically is reduced or absent. Eyes are generally present laterally and these do not have facets. They are typically paired, unstalked (sessile) and well developed, but may be fused dorsally, reduced or missing. They may be round, oval, elongate or irregular in shape and vary from being very large and brightly pigmented to just a simple pigmented spot, or completely unpigmented. Their presence/absence and characteristics are an important diagnostic character.
The head outwardly appears as one somite and as it is fused to the first thoracic somite it bears six paired appendages: antennules, antennae, mandibles, maxillules, maxillae and maxillipeds. The antennules have a peduncle of one to three segments, the outer segment bearing a flagellum, and sometimes also a much smaller accessory flagellum. In some groups an organ called a callynophore (Lowry, 1986) is found at the base of the flagellum in both sexes, or only in the male. It is formed from complete or partial fusion of the proximal segments of the flagellum and comprises rows of sensory setae that are usually grouped together to form a brush, but may be enclosed in a cap. Structure of the callynophore is used in detailed taxonomic studies. The uniramous antennae have a peduncle with between one and five segments and a single flagellum. The antennae are sometimes enlarged and used in locomotion, or can be greatly reduced. The remaining four limb pairs are largely hidden beneath the body. The mouth is situated between the mandibles (Fig. 1D). The labrum (Fig. 1E), which is attached anterior to the mouth and covers it, may be a simple lobe or have an apical notch. The labium, the hind lips of the mouth (Fig. 1F) can vary from simple narrow lobes to a more complex arrangement with accessory inner lobes, the shape of the whole structure sometimes used in identification. The mandibles (Fig. 1D) can range from being large to vestigial and in most amphipods there is a three-articulated palp attached distally. The maxillules are typically small, usually with inner and outer lobes, the inner lobe sometimes reduced or absent (Fig. 1G). The lobes may bear setae and spines, the outer lobe sometimes bearing a palp with one or two segments, often reduced or absent. The maxillae in amphipods are typically reduced to two setose lobes arising from the base (Fig. 1H) and lack a palp. The maxillipeds (theoretically the first thoracic appendages) are typically formed of an inner and an outer lobe, the outer lobe with a palp, reduced or missing in some groups, the entire limb sometimes reduced (Fig. 1I).

Pereion: The term pereion is widely used for the second to seventh group of thoracic somites. These are usually all visible (Fig. 1A) and only in some rather bizarre members of Parvorder Caprellidira in Family Caprellidae, is one of these somites fused to the head (Fig. 10). Each pereion somite bears a pair of uniramous limbs termed pereiopods (or pereopods) or sometimes thoracopods, but two pairs may be missing in some Caprellidira. The first segment of the pereiopod is termed the coxa (or coxal plate) and is an immovable flat plate inserted into the lateral surface of the pereion somite (Fig. 1A) and sometimes fused to it. Coxae are usually well developed and large in most groups, but generally small in most Caprellidira and Ingolfiellidea. The subsequent pereiopod segments are called basis, ischium, merus, carpus, propodus and the seventh the dactylus (Fig. 1J, K). These segments may broaden in different ways or be elongate. The basis in particular may be broad and plate-like. The pereiopods are typically arranged in two groups, the first four pairs directed forward, with the terminal dactylus pointing backwards and the last three directed backwards with the dactylus directed forward (Fig. 1A). The first two pairs of pereiopods are also sometimes called gnathopods and at least the first pair are sometimes shorter

and more delicate than the other pereiopods. The first two pereiopod pairs are sometimes developed distally to varying extents into a simple claw (chela or subchelae) and used as accessory mouthparts, or sometimes used by males to grasp the females during copulation. The second pair in particular may be sexually dimorphic in mature males. Other pereiopods sometimes also have chelae and the more posterior ones can display a great variety of forms depending whether used for locomotion or prey capture, but in many amphipods all the pereiopods are quite simple.
Inserted into the internal surface of some of the coxae are gills (Fig. 1A, K), which may be simple, elaborate, or reduced. There are varying numbers of pairs of gills in the different sub-orders and they are always absent on the first pereiopods. Mature females are recognised by the presence of a ventral marsupium that encloses the eggs, formed from a variable number of paired plates called brood lamellae (or oostegites) that are usually broad and fringed with setae, at least in later stages of development, but may be narrow with few setae, or in Hyperiidea completely lacking in setae. The brood lamellae originate from between pereiopods two to five proximally and overlap to form the marsupium. In young females the brood lamellae are simple buds, which progressively develop through the moults. In at least one genus the brood lamellae are greatly reduced and their function replaced by the gills. Males have a pair of, often small and inconspicuous, copulatory appendages (penes) ventrally, on the seventh pereion somite. The female reproductive organs are on the fifth somite.

Pleon: The pleon usually comprises six somites, five in Hyperiidea as the last two somites are fused (Fig. 1A), but is completely vestigial in some Caprellidira (Fig. 10). The first three somites are termed the pleosome and each bear a pair of biramous, multi-segmented, generally setose pleopods (Fig. 1A), used for swimming when away from the bottom and also for producing respiratory currents. There may be ventrolateral, plate-like extensions of the pleosome segments called epimeral plates or epimera, the shape of which is important in at least gammarid identification. The last three somites of the pleon, the last two in Hyperiidea, form the urosome and these are usually smaller than other somites. They typically bear three pairs of biramous uropods (Fig. 1L, M), directed backwards, the last pair vestigial in Ingolfiellidea. The uropods usually consist of a basal peduncle and one or two distal rami. The last urosome somite (urosomite) usually has a small extension called the telson that is not generally fused to the somite, apart from in some Hyperiidea. Depending on species, the telson may bear spines or setae, be pointed, rounded, divided (cleft), indented, undivided (entire) etc. Amphipod pleon characteristics are unique, all other similar groups of crustaceans, e.g. stomatopods, mysids and euphausiids, have five pairs of pleopods and a single pair of uropods that form a tail fan with the telson.
Some useful information on amphipod morphology is given in e.g. Bowman & Gruner (1973), Schram (1986), Barnard & Karaman (1991), Hayward & Ryland (1995), Vinogradov *et al*. (1996), Bellan-Santini (1999), Vinogradov (1999); Johnson *et al*., (2001), Lowry & Springthorpe (2001) and Chapman (2007).

Reproduction and development
In some benthic species the male clasps the female until she moults and then fertilises the eggs as they are laid into the marsupium. In other species there is no precopulatory mounting period and mating occurs in the water column, some species using "jellyfish" as a platform for moulting and copulation (Sheader, 1977). Eggs are retained in the marsupium and pass through a nauplius stage within the egg. There are no larval stages, the eggs hatching directly into a juvenile form resembling the adult. Plankton samples often contain large numbers of these juveniles, dislodged from the marsupium of females during the sampling process. Sexual maturity is generally reached after six moults.

Key to main groups of Order Amphipoda:

It should be noted that certain features in the key, such as presence or absence of apical spines on the first and second pleopods, used to separate Suborder Senticaudata from Suborder Gammaridea, and the thickness of the telson used to separate some of the Senticaudata group, are sometimes not very obvious.

1. Head typically fused to first pereion somite; body long and slender; some pereiopods reduced or absent; pleon usually vestigial with no pleopods or uropods; two or three pairs of gills ---------- Suborder Senticaudata (Part), Infraorder Corophiida, Parvorder Caprellidira -- Family Caprellidae (Fig. 10)
- Head not fused to first pereion somite; pleon and pereion distinct, pleopods and uropods usually present, sometimes vestigial; three or more pairs of gills ------------------------------- **2**

2. Eyes usually very large; pereiopod coxae generally small, sometimes absent; maxillipeds without palp; only two somites in urosome; telson never cleft --------------------------------------- -- Suborder Hyperiidea (Figs. 1-6; see separate key)
- Eyes usually small, sometimes absent; pereiopod coxae present, usually large but sometimes small or absent; maxillipeds with palp; three somites in urosome ----------------- **3**

3. Pleopods vestigial; last pair of uropods reduced or absent; three pairs of gills; eye a tiny separate lobe or missing -- Suborder Ingolfiellidea (Fig. 15)
- Pleopods, uropods and eyes usually well developed -- **4**

4. No robust setae on apex of uropods one and two --------- Suborder Gammaridea (Figs. 7, 8)
- Robust setae on apex of uropods one and two -- **5**

5. Telson generally dorsoventrally thickened; pereiopods three and four with glands inside basis -------------------- Suborder Senticaudata (part), Infraorder Corophiida (remainder) --- **6**
- Telson generally dorsoventrally flattened; pereiopods three and four without glands inside basis --- Suborder Senticaudata (remainder) --- **7**

6. Antennule third peduncular segment always short, half or less length of second segment; pereiopod one coxa enlarged in both sexes, generally larger than coxa on pereiopod two --- -- Parvorder Corophiidira (Fig. 9)
- Antennule third peduncular segment long, more than half, or usually much more than half length of second segment; pereiopod one coxa when present small, almost always smaller than coxa of pereiopod two ------------------------ Parvorder Caprellidira (remainder) (Fig. 11)

7. First antennal peduncular segment bulbous; hind lips of mouth without inner lobes ----------- -- Infraorder Gammarida (Fig. 12)
- Pereiopod two stouter than first; pair of small, robust setae dorsally on urosomite two; uropod one peduncle with robust lateral seta proximally -------- Infraorder Hadziida (Fig. 13)
- Antennule accessory flagellum absent; mandibular palp vestigial or absent; maxillule palp vestigial or absent; no oblique setal row on basal endopod of maxilla; curl-tipped setae on brood lamellae --- Infraorder Talitrida (Fig. 14)

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Amphipoda:

Suborder Hyperiidea:

Hyperiids are marine and mainly planktonic, although some associate with or are parasites of gelatinous organisms such as scyphomedusae and salps (e.g. Bowman *et al*., 1963; Harbison *et al*., 1977; Laval, 1980; Gasca *et al*., 2007). In some, more open sea areas, they can be very numerous in plankton samples.

Body usually laterally compressed (Fig. 1), but sometimes quite rounded. Head globular; rostrum may be present; paired eyes, usually very large, often brightly coloured, occupying most of each side of head and may fuse dorsally; no accessory flagellum on antennule so antennules and antennae both uniramous, inserted in the anterior or ventral head, both short or vestigial in females, typically both long in male; mouthparts reduced, mandibles and maxillules usually with palp, but may be reduced or absent, maxillae often reduced or absent, maxillipeds with one to four segments usually without palp; head not fused to first pereion somite; pereiopods well developed, but number of segments may be reduced; chelae of pereiopods one and two usually small; pereiopods five to seven often long and slender, fifth sometimes adapted for prey capture, coxae usually small and sometimes fused to the pereion somite; usually five pairs of gills on pereiopods two to six; four pairs of brood lamellae on pereiopods two to five, without marginal setae in the later stages of development; pleon slender, laterally compressed; pleosome with well developed epimeral plates; urosomites two and three fused, pleopods well developed, often elongate; uropods present, biramous well developed, lacking spines; telson triangular or semicircular, never cleft.

Only three hyperiid amphipods are recorded in the PMF, but descriptions of six of the seven northern European shelf species are included here. The one species excluded is *Tryphana malmii* Boeck, 1871, a deep water species (Sars 1890, as *Tryphaena Malmi*).

Key to Hyperiidea described (after Dunbar, 1963)

1. Pereiopods 5 and 6 longer than pereiopods 3 and 4; pereiopod 7 much shorter than pereiopods 5 and 6 -- *Hyperioides longipes* (Fig. 5)
- Pereiopods 5-7 considerably longer than pereiopods 3 and 4 ------------------------------------- **2**
- Pereiopods 5-7 not longer than pereiopods 3 and 4 -- **3**

2. Pereiopods 5-7 approximately equal in length; margins of carpus segment of pereiopods 3 and 4 almost parallel; no obvious dorsal spination ---------------- *Themisto abyssorum* (Fig. 3)
- Pereiopod 5 distinctly longer than pereiopods 6 and 7; carpus segment of pereiopods 3 and 4 expanded, margins not parallel; dorsal spination well developed in mature specimens >10 mm in length -- *Themisto gaudichaudii* (Fig. 4)

3. The fixed process on carpus of pereiopods 1 and 2 slightly longer than movable propodus joint -- *Hyperoche medusarum* (Fig. 6)
- The fixed process on carpus of pereiopods 1 (if present) and 2 shorter than movable propodus joint --- **4**

4. Pereiopods 1 and 2 with a few strong setae and distinctly shorter than pereiopods 3-7; carpus of pereiopod 1 with short fixed process, pereiopod 2 with distinct process -- *Hyperia galba* (Fig. 1)
- Pereiopods 1 and 2 densely setose, not distinctly shorter than pereiopods 3-7; carpus of pereiopod 1 without distinct fixed process, pereiopod 2 with short process -- *Hyperia medusarum* (Fig. 2)

Genus *Hyperia*:

Hyperia galba (Montagu, 1815)

Head shorter than high, shorter than first two somites of pereion together; eyes reddish brown, occupying the entire lateral sides; female body short and compact with very broad pereion (Fig. 1A, B); male body slender, with much longer pleon than female (Fig. 1C). Female with very short antennules and antennae, of slightly different lengths, in male both long, antenna longest. Outer plate of maxilliped broad lancet-shaped, the inner margin with bundles of tiny setae (Fig. 1I). First two pereiopods (gnathopods) rather small (Fig. 1A), bearing a few strong setae (Fig. 1J, K), basis about twice as long as wide, posteroventral margin of carpus elongated and pointed, forming a fixed process, shorter on first pereiopod, both limbs with propodus distally narrowed and minutely serrated on hind margin, dactylus slender, with serrated hind margin. Pereiopods three to seven quite short and of similar shape. Pleon with distally pointed epimeral plates; pleopods well developed; uropods broad, especially in male (Fig. 1L, M), laminar, rami lanceolate, with finely denticulate margins; telson large, triangular.

Associated with: Medusae - *Rhizostoma pulmo*, *Aurelia aurita*, *Cyanea capillata*, *Chrysaora hysoscella*, *Pelagia noctiluca*, *Tima bairdii*, *Melicertum* spp., *Leuckartiara* spp.; Salps - *Salpa fusiformis*.

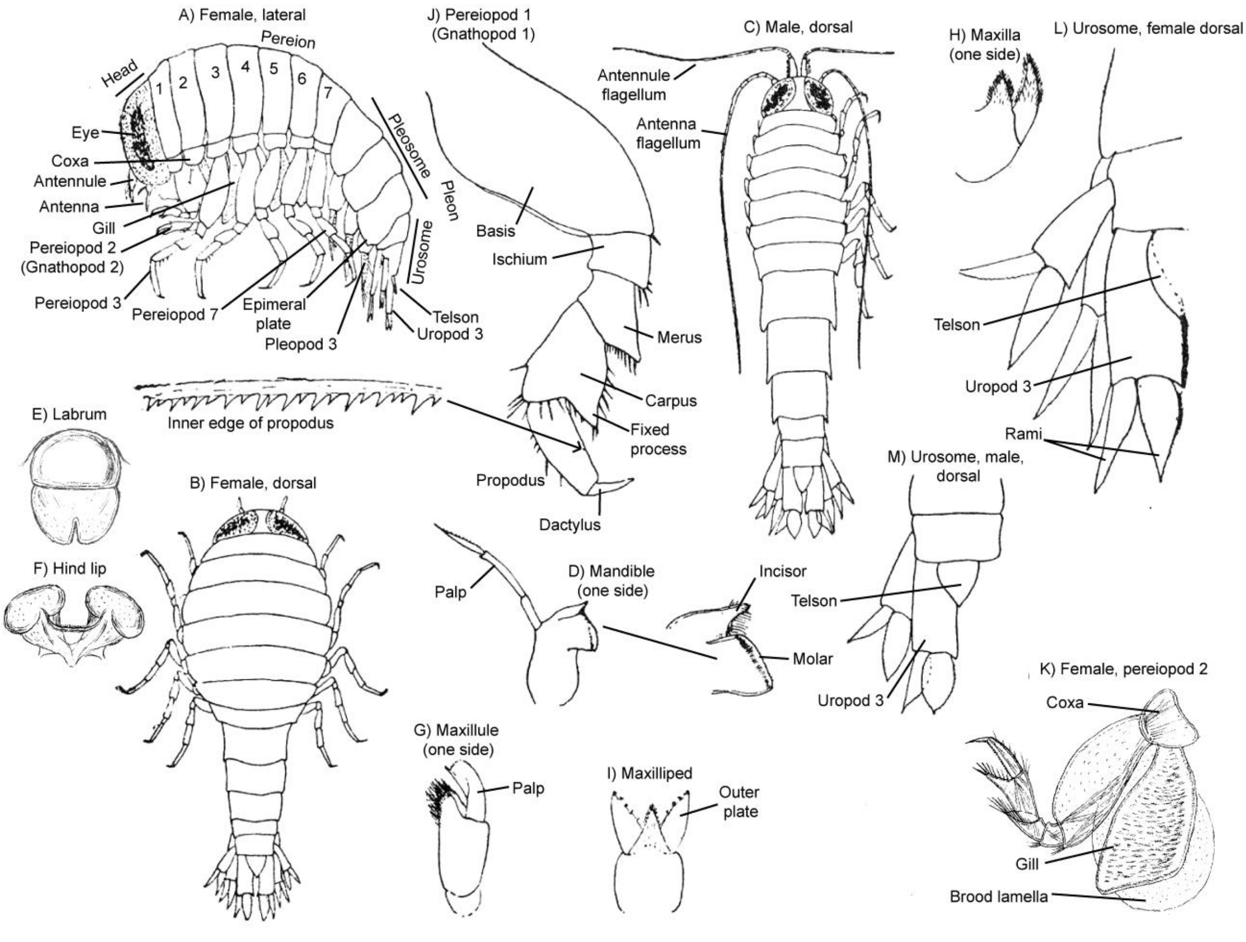

Fig. 1. *Hyperia galba* (A-D, G-J, L from Chevreux & Fage, 1924, after Sars, 1890; E, F, K from Sars, 1890).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Irish Sea. West of Ireland.

Size: Female ~14 mm, male ~12 mm, larger in colder water areas.

Further information: Sars, 1890; Chevreux & Fage, 1924; Dunbar, 1963; Dittrich, 1988; Hayward & Ryland, 1995; Vinogradov *et al*., 1996.

Hyperia medusarum (Müller, 1776)
Generally resembling *Hyperia galba*, but first two pereiopods much longer (Fig. 2A). Very little information appears to be available for the male. Head equal in length to the first two somites of the pereion together; eyes reddish brown, occupying the entire lateral sides; female with small antennules and antennae, the antennae very thin, in male both appendages long, antenna longest; pereiopods one and two similar in length to pereiopods three to seven, with densely setose distal segments (Figs. 2B, C), carpus of first pereiopod without a distinct fixed process, carpus of second pereiopod with a short process, propodus of both these pereiopods long and oval, dactylus very small and short; pereiopods five to seven approximately equal in length in females, but in males pereiopods five are somewhat longer. Epimeral plates of pleon with pointed posteroventral margins, especially well developed in the third somite (Fig. 2A); urosome (Fig. 2E) very similar to that of *H. galba*, that of male broader than in female.
As its name suggests this hyperiid parasitises cnidarians, but also ctenophores, laying eggs on the host, on which juveniles and adults feed, primarily on tentacles and gonads (Laval, 1980).
Associated with: Medusae - *Rhizostoma pulmo*, *Cyanea capillata*, *Aurelia aurita*; Ctenophores – *Pleurobrachia pileus*, *Beroe cucumis.*

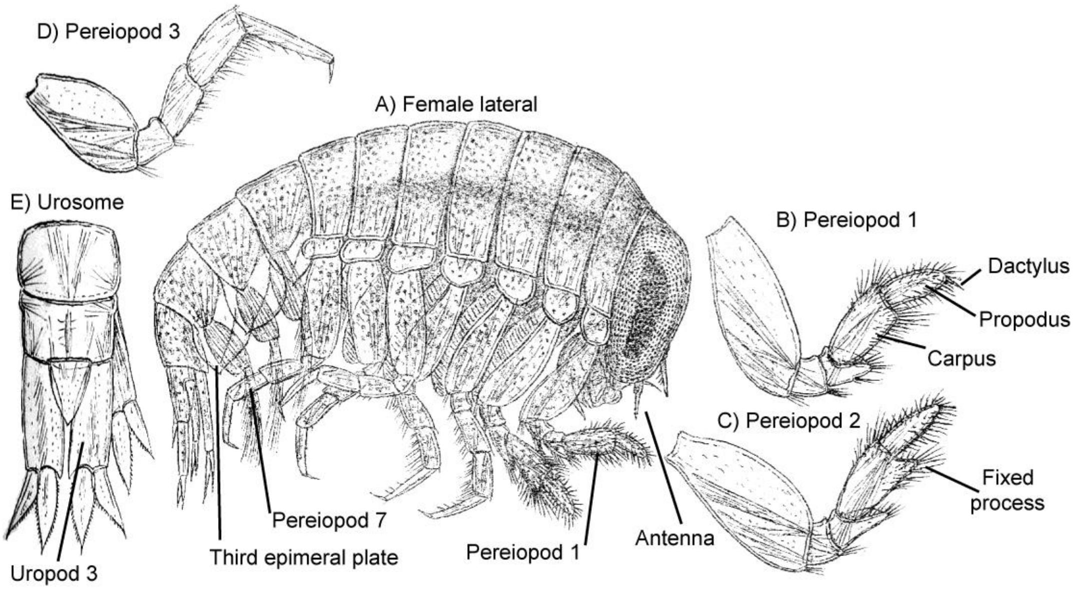

Fig. 2. *Hyperia medusarum* (From Sars, 1890).

Recorded: PMF. L4, not recorded. Northern North Sea. West of Ireland. English Channel.
Size: 8-15 mm, larger in colder water areas.
Further information: Sars, 1890; Dunbar, 1963; Bowman & Gruner, 1973; Laval, 1980; Vinogradov *et al*., 1996.

Genus *Themisto*:

Themisto abyssorum Boeck, 1870

Body laterally compressed (Fig. 3A, B), head shorter than high; eyes reddish brown, occupying the entire lateral sides; antennule in female quite short, slightly curved and as long as antenna, antennule in male long, around half as long as antenna (Fig. 3C). Carpus and propodus of pereiopods one and two strongly setose (Fig 3D, E), carpus of pereiopod one without any fixed process, but pereiopod two carpus with process that forms a chela with propodus. Pereiopods three to four with carpus hardly enlarged (Fig. 3F), hind margin with few thin setae, pereiopods five to seven of similar length in both sexes (Fig. 3A), with very slender propodus, about as long as segments three to five. Even young stages only 2 mm in length can be distinguished from *T. gaudichaudi* by the lack of elongation of pereiopod five. Uropods relatively slender; telson small, oval-triangular, with an acute apex (Fig. 3G).

May be associated with: Medusa - *Aurelia* aurita.

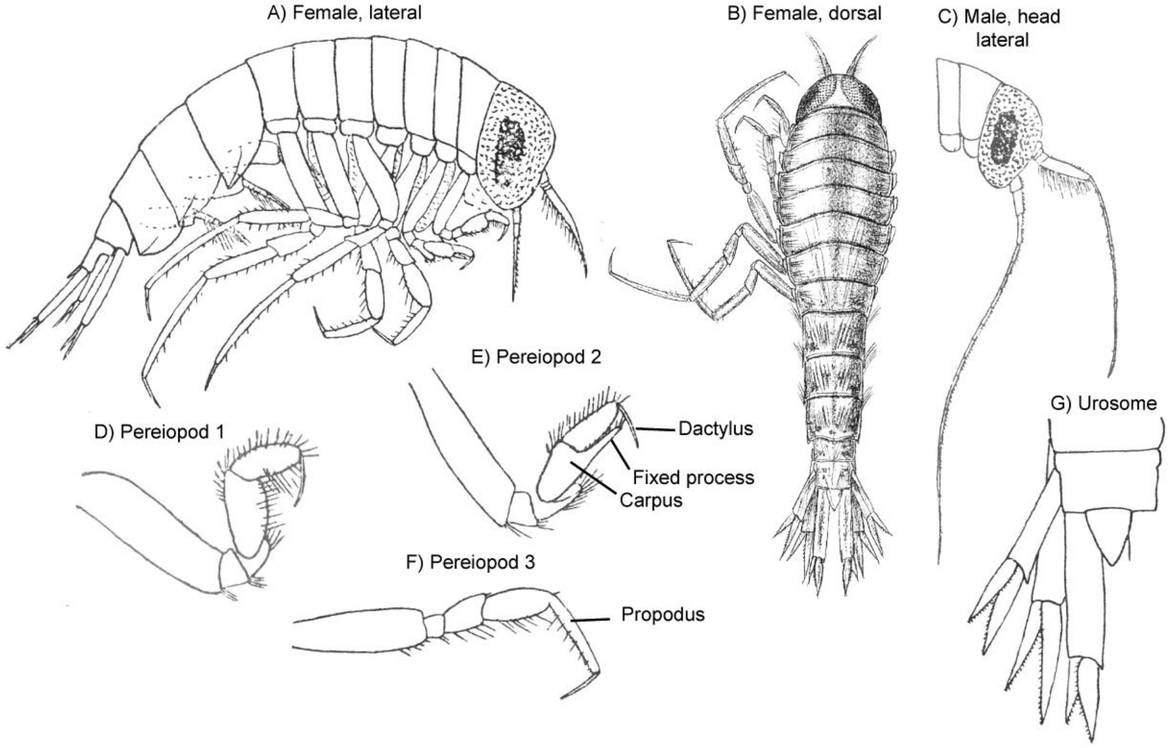

Fig. 3. *Themisto abyssorum* (A, C-G from Chevreux & Fage, 1924, after Sars, 1890; B from Sars, 1890; both as *Parathemisto oblivia)*.

Recorded: PMF and L4, not recorded. North Sea. West of Ireland.

Size: ~9 mm, larger in colder water areas.

Further information: Sars, 1890; Chevreux & Fage, 1924 (both as *Parathemisto oblivia*); Dunbar, 1963; Bowman & Gruner, 1973 (both as *Parathemisto abyssorum*).

Themisto gaudichaudii Guérin, 1825

Compared with other members of the genus *T. gaudichaudii* is very variable in form (Sheader & Evans, 1974) to the extent it was originally separated into two species. Very little descriptive information is available for males.

Body laterally compressed (Fig. 4A); eyes reddish brown, occupying the entire lateral sides; in adult females antenna longer than antennule, in male both long. Carpus and propodus of pereiopods one and two setose (Fig 4B, C), carpus of pereiopod one without process, carpus of pereiopod two with fixed process that almost reaches to end of propodus, forming a chela; pereiopod five with long, lanceolate carpus (Fig. 4A), straight, narrow propodus (Fig. 4D), whole limb much longer than pereiopods six and seven. In individuals over nine millimetres in length, pereion somites six and seven and pleon somites one and two have more or less developed dorsal spines (Fig. 4A). Pleon epimeral plates with sharp posterodorsal corners; uropods relatively slender (Fig. 4E), last pair nearly twice the length of urosome; in this species at least, the inner proximal end of each ramus of the first uropod concave (Fig. 4F), used in sperm bundle transfer (Sheader, 1977); telson small, triangular.

May be associated with: Scyphomedusae, siphonophores, ctenophores and salps. Uses jellyfish as a platform for moulting and copulation (Sheader, 1977).

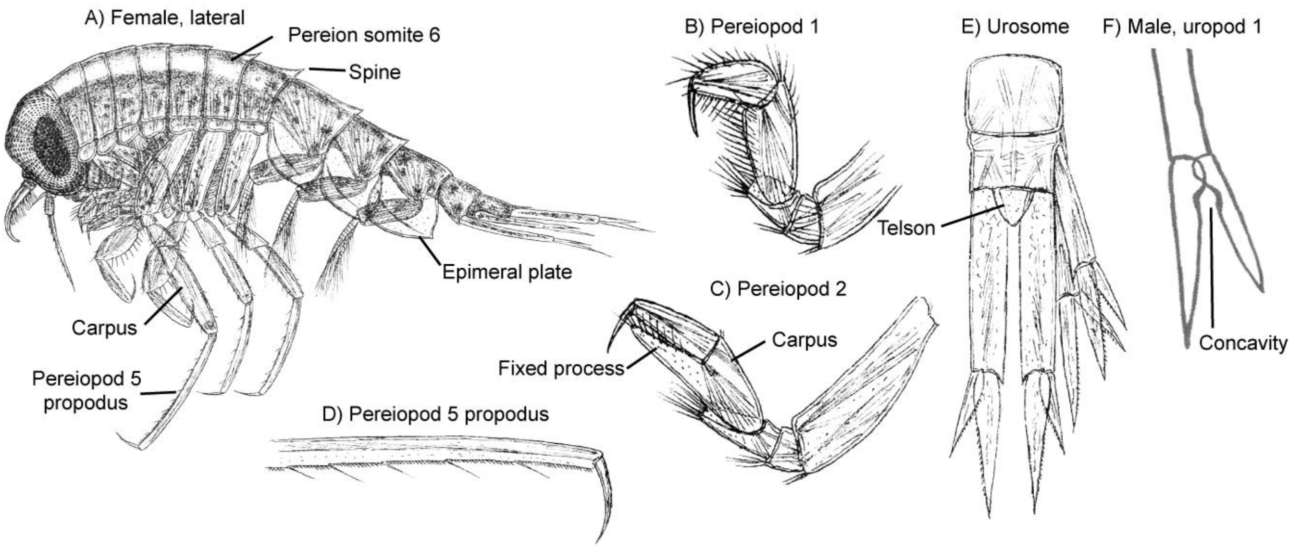

Fig. 4. *Themisto gaudichaudii* (A-E from Sars, 1890, as *Euthemisto compressa;* F from Sheader, 1977 as *Parathemisto gaudichaudi*).

Recorded: PMF (as *Themisto gracilipes*). L4 not recorded. North Sea. West of Ireland. English Channel.

Size: ~7-12 mm but up to 30 mm in colder water areas.

Further information: Sars, 1890 (as *Euthemisto compressa*); Dunbar, 1963 (as *Parathemisto gaudichaudi* and *P. gracilipes*); Evans, 1968 (as *P. gracilipes*); McHardy, 1970 (as *P. gaudichaudi* and *P. gracilipes*); Sheader & Evans, 1974; Sheader, 1977; Williams & Robins, 1981 (all as *P. gaudichaudi*).

Genus *Hyperioides*:

Hyperioides longipes Chevreux, 1900

Body more laterally compressed than in Genus *Hyperia*. Eyes only occupy the upper part of the head (Fig. 5A); head long, as long as first five pereion somites, projecting forwards anteriorly above the insertion of the antennules; in female, antennule and antennae both short and of similar length (Fig. 5B), in male antennule around half length of body (Fig. 5A), antenna around two thirds length of body, remaining limbs similar in both sexes. Basis of maxilliped elongated (Fig. 5C), internal lobe poorly developed; carpus of pereiopod one equal in length and width (Fig. 5D) and the posterior distal angle is produced into a narrow, fixed process extending to half the length of the broadly oval propodus, pereiopod two is somewhat longer than pereiopod one (Fig. 5E), the fixed process on the carpus extending to two-thirds the length of the propodus; pereiopods three and four longer than pereiopod two (Fig. 5A); pereiopods five and six (Fig. 5A, F, G) much longer than pereiopods three and four. The basis segment of pereiopod seven (Fig. 5H) approximately the same length as in pereiopods five and six but the other segments are shorter, so pereiopod seven is significantly shorter (Fig. 5A). Rami of uropods narrowly lanceolate and the exopods coarsely denticulate along the external margin (Fig. 5I, J); telson semicircular, its length less than the width of the base.

May be associated with: Siphonophores.

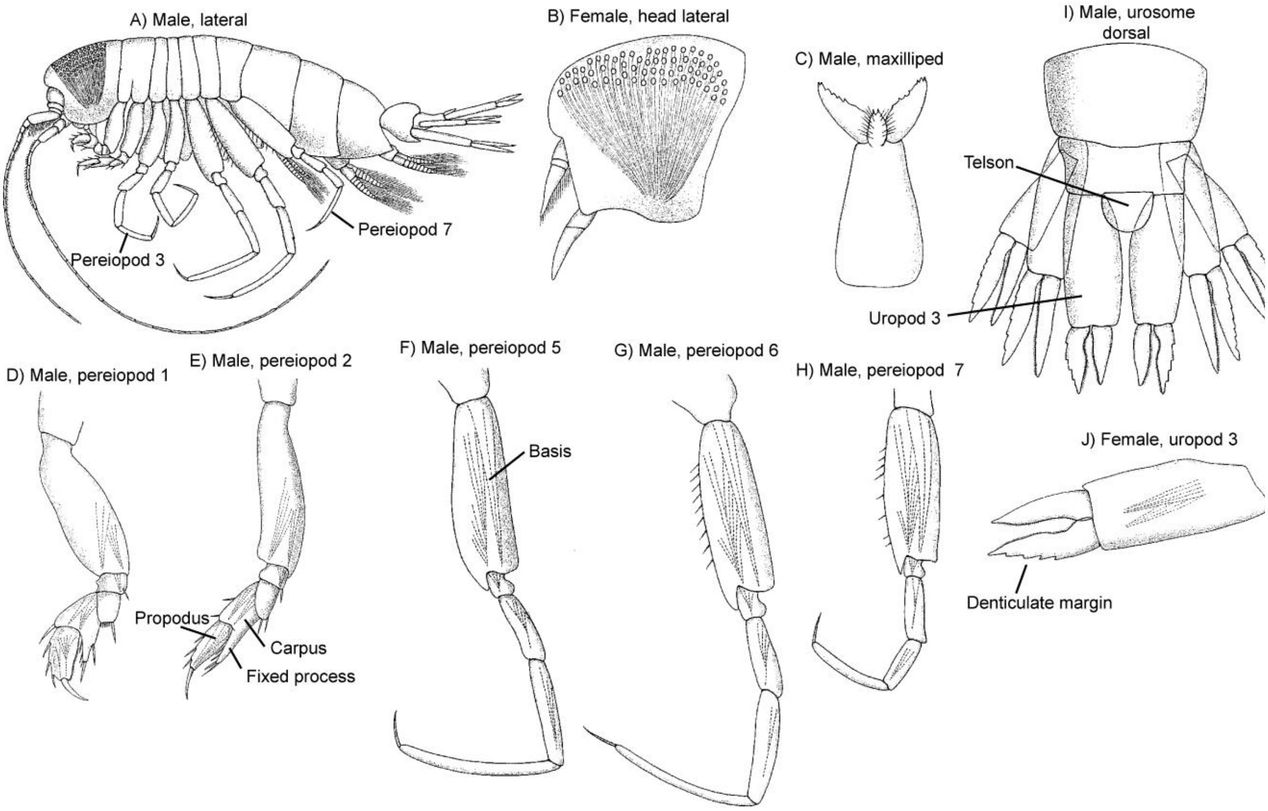

Fig. 5. *Hyperioides longipes* (from Chevreux, 1900).

Recorded: PMF and L4, not recorded. West of Ireland

Size: 5.0-7.5 mm.

Further information: Chevreux, 1900; Dunbar, 1963; Bowman & Gruner, 1973; Vinogradov *et al*., 1996.

Genus *Hyperoche*:

Hyperoche medusarum (Kröyer, 1838)

As its name suggests this hyperiid closely associates with "jellyfish". Female body short, male slenderer, laterally compressed (Fig. 6A-C), both similar in shape to *Hyperia* species. Head semi-globular, frontally rounded, almost as long as first two pereion somites combined; eyes reddish brown, occupying the entire lateral sides. Female antennule longer than antenna, both short, male antennule around half as long as body, antenna almost as long as body. Pereiopods one and two similar, almost without setae (Fig. 6D, E), carpus of both with fixed process that extends slightly beyond movable propodus segment, forming a chela, propodus narrow, with serrated inner margin, dactylus small, short. Pereiopods three to four with slightly widened carpus (Fig. 6F), with minutely serrated hind margin and ending in short triangular extension (Fig. 6G), pereiopods five to seven similar in shape, not longer than pereiopods three to four (Fig. 6A, C), completely smooth, basis rather narrow. Pleon relatively slender, with larger epimeral plates on pleosome in male than in female, plates with sharp posterodorsal corners; uropod three basal segment broader in male than in female (Fig. 6H, I); telson triangular, with rounded or pointed apex.

May be associated with: Medusae - *Cyanea capillata*, *Aurelia aurita*; Ctenophores - *Pleurobrachia pileus*, *Beroe cucumis.*

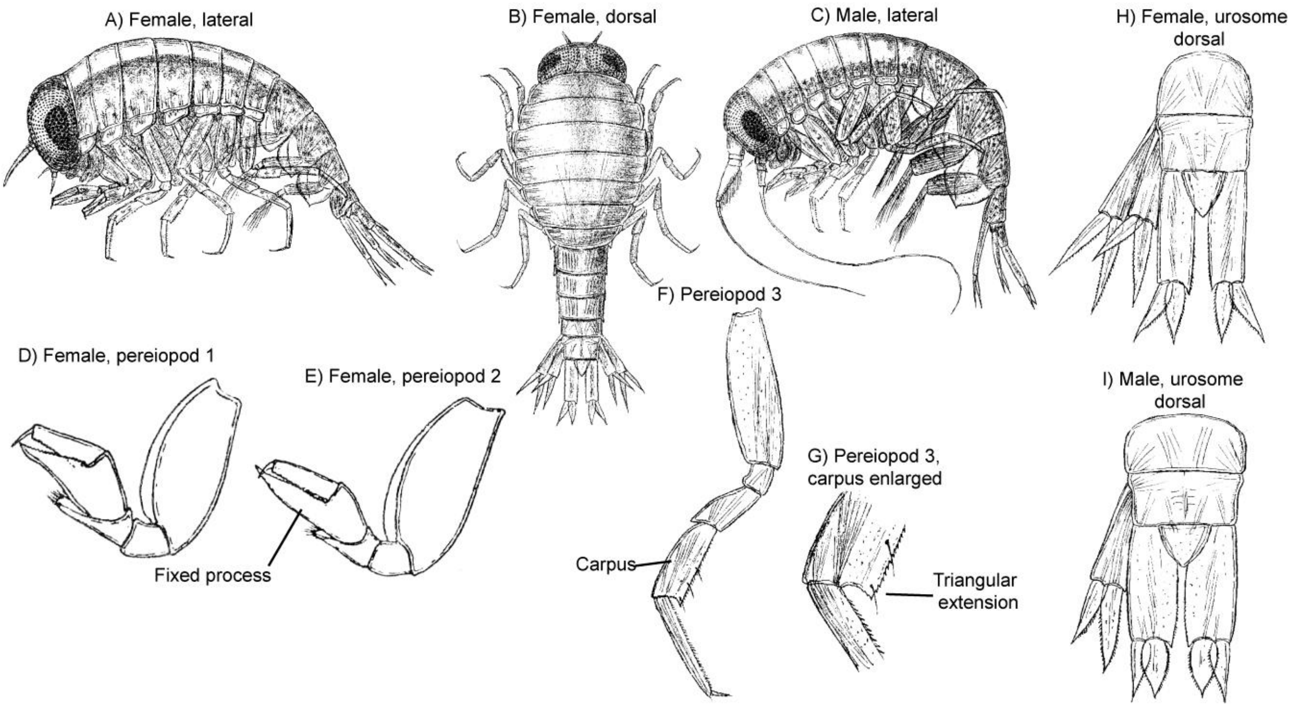

Fig. 6. *Hyperoche medusarum* (A-C, F-H from Sars, 1890; D, E from Chevreux & Fage, 1924 after Sars 1890; both as *Hyperoche Kröyeri*).

Recorded: Not recorded at Plymouth. Northern North Sea. West of Ireland.

Size: 5-6 mm, larger in colder water areas.

Further information: Sars, 1890; Chevreux & Fage, 1924 (both as *Hyperoche Kröyeri*); Dunbar, 1963.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Amphipoda:

Suborder Gammaridea:

A large and diverse suborder of mainly benthic and epibenthic, and only a few pelagic species. Body usually laterally compressed (Figs. 7, 8), but some species more rounded or dorsoventrally compressed. Head not fused to first pereion somite; anterodorsal rostrum sometimes present (Fig. 7B); eyes usually lateral, small, but of variable size, round or kidney-shaped, sometimes indistinct or missing, one or two additional eye pairs sometimes present. Antennules and antennae always well developed, often differing in size between sexes; antennule with basal peduncle of three segments and a slender flagellum of a few or many segments, sometimes with a small or well developed accessory flagellum at the distal tip of the third peduncle segment; antenna with peduncle of five segments and a flagellum; maxilliped with palp (Fig. 7C). First two pairs of pereiopods modified, usually one or both with distal pincers (chelae; Fig. 7A, B, F) of different types, usually larger than other pereiopods and often sexually dimorphic, larger or more complex in the male; coxae usually well developed and large, plate-like, rarely vestigial. Four pairs of brood lamellae on pereiopods two to five in adult females, with marginal setae in the later stages of development. Six pairs of gills on pereiopods two to seven. Pleon somites may bear dorsal teeth; epimeral plates project ventrally overhanging the pleopods (Fig. 7B); pleopods usually biramous, strongly setose, multisegmented endopod and exopod. The three urosomites free, but the last two may be partially fused, all generally of similar length, but one may be elongate, may have spines, setae or teeth dorsally, each somite usually with biramous uropods, the third sometimes modified or reduced; serrations, spines or setae may be present on the uropods (Fig. 7G-I), but not at the distal tip of the rami as in Suborder Senticaudata. Telson of various shapes, rounded, pointed (Fig. 7J), cleft etc. and may bear spines, hooks or setae.

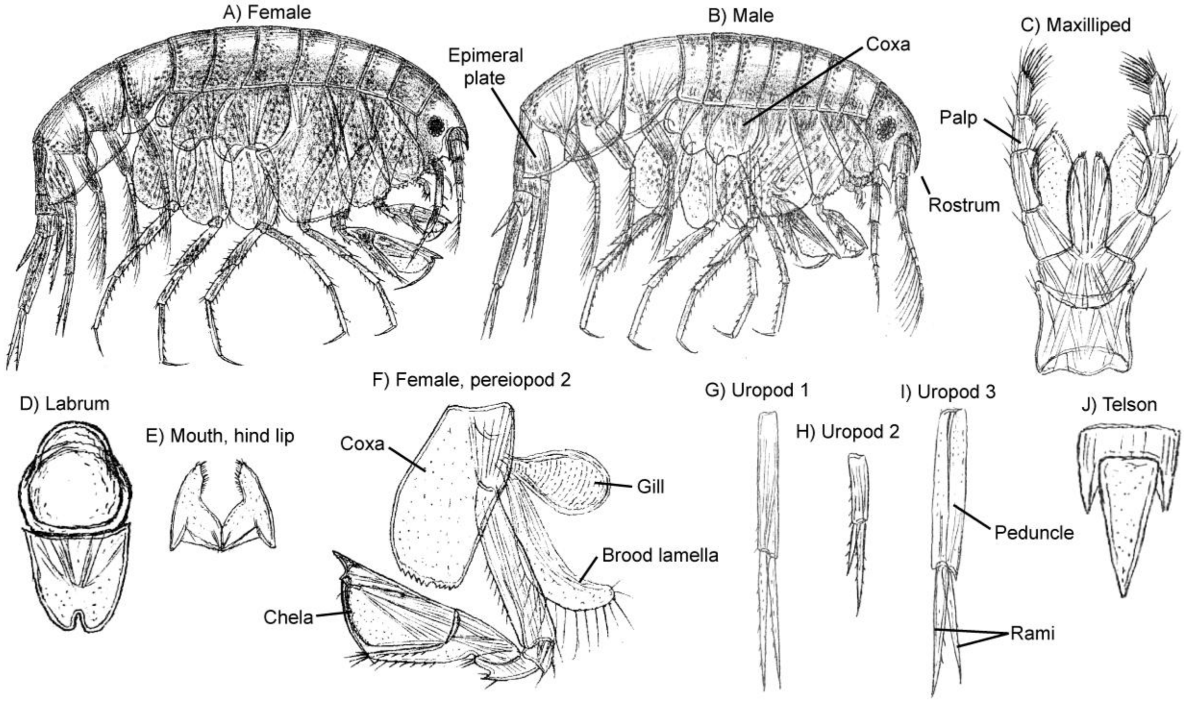

Fig. 7. Example of an amphipod of Suborder Gammaridea recorded in the PMF, *Amphilochus manudens* Bate, 1862 (from Sars, 1892).

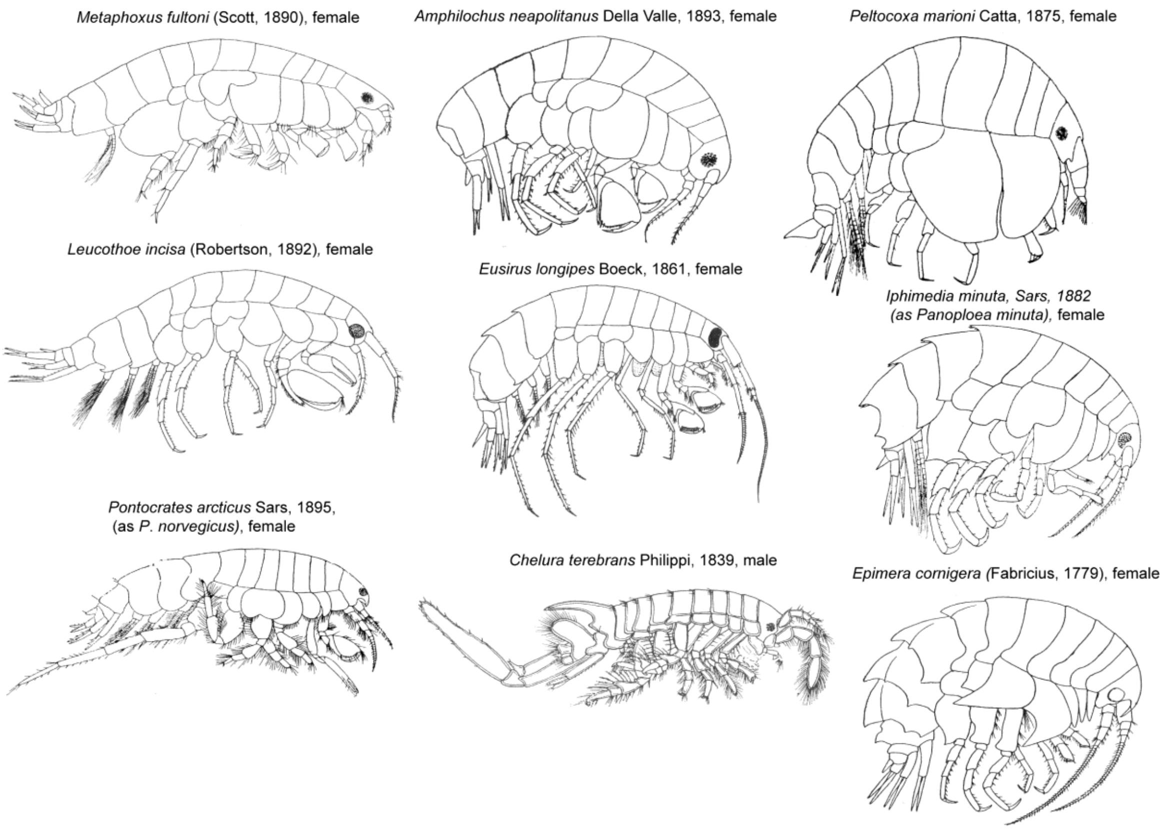

Fig. 8. Examples of the range of amphipods of Suborder Gammaridea recorded in the PMF (from Chevreux & Fage, 1924).

Suborder Senticaudata:

This is large and diverse suborder that includes some very characteristic looking members. They are identified (Lowry & Myers, 2013) by the presence of robust setae on the distal tips of uropods one and two (Figs. 9G, 12H); the antennule lacks a complex callynophore (a sensory organ located at the proximal end of the outer flagellum of the antennule (Lowry 1986) and the antenna lacks tufts of setae (brush setae) or an elongate flagellum in the male, as found in male Hyperiidea. According to the current WoRMS classification there are six Infraorders: Corophiida, Gammarida, Hadziida, Talitrida, Carangoliopsida and Bogidiellida, but no species of the latter two small infraorders are listed in the PMF, so are not included here (Bogidiellida are freshwater).

Infraorder Corophiida:

Suborder Corophiida is divided into parvorders Corophiidira and Caprellidira and are described in detail in Myers & Lowry (2003), using a slightly different classification. Pereiopods one and two of different sizes (Fig. 9A, B); pereiopods three and four with glands inside basis (Fig. 9E); telson dorsoventrally thickened; uropod three outer ramus usually with robust, slender or recurved setae, often a mixture of robust and slender (Fig. 9G).

Parvorder Corophiidira:

Typically benthic tube or burrow-dwelling amphipods. Head in lateral view extended anteriorly into weakly projecting cephalic lobe (Fig. 9B), anteroventral margin slightly shortened, rarely not shortened and moderately excavated inwards or strongly excavated for insertion of a large antenna; eye if present situated at base of cephalic lobe; antennule distal peduncular segment always short, half or less length of second segment (Fig. 9C); pereiopod one coxa enlarged in both sexes (Fig. 9D), generally larger than coxa on pereiopod two (Fig. 9E); uropod three usually with a mixture of robust and slender setae (Fig. 9G), or with one to two recurved, robust apical setae; telson sometimes with hooks or denticles.

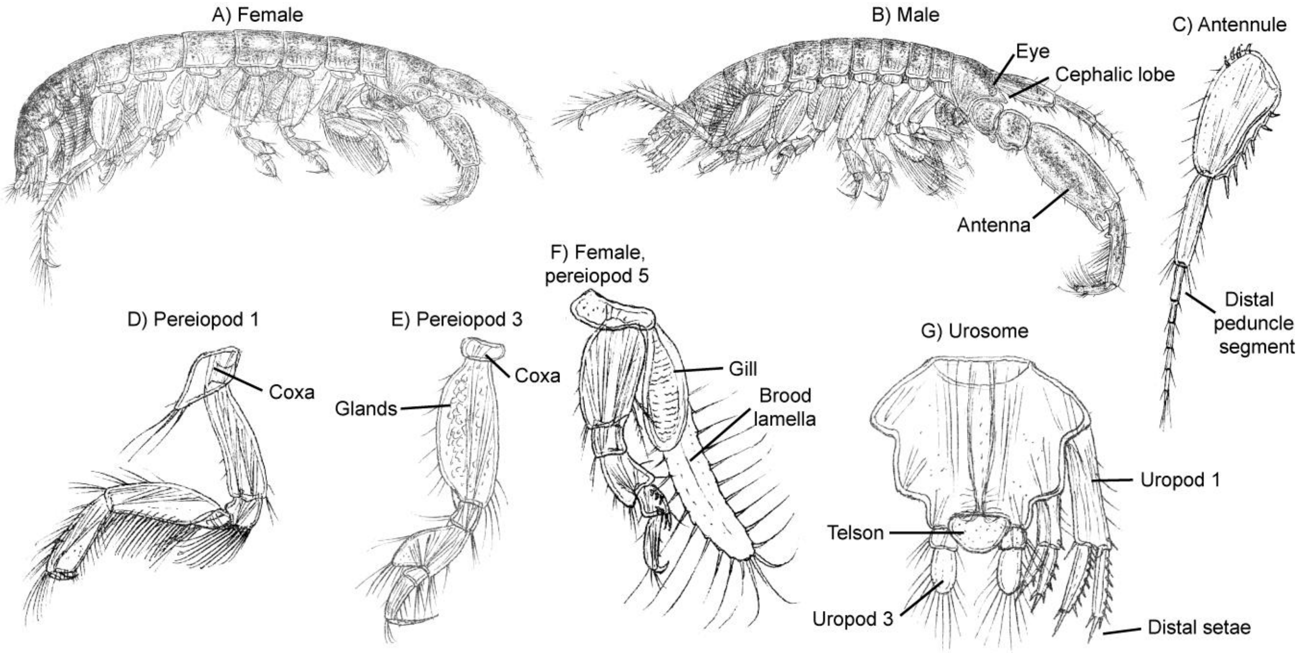

Fig. 9. Example of an amphipod of Parvorder Corophiidira recorded from the PMF, *Crassicorophium crassicorne* (Bruzelius, 1859)(as *Corophium crassicorne*), (from Sars 1894; as *Corophium crassicorne*).

Parvorder Caprellidira:

Head region rectangular, rounded or triangular in lateral view (Figs. 10, 11), anterior margin may be recessed at insertion of antennule, anteroventral margin slightly to very shortened, moderately excavated inwards or strongly excavated for insertion of a large antenna; antennule third segment long, more than half, or usually much more than half length of second segment; pereiopod one coxa when present small, almost always smaller than coxa of pereiopod two; uropod three with combination of slender and robust setae, with or without recurved spines; telson with or without hooks, denticles or recurved spines. Included in this disparate amphipod parvorder are the flattened whale “lice”, Family Cyamidae.

Family Caprellidae (Fig. 10) is a rather bizarre and instantly recognisable group within Parvorder Caprellidira (Guerra-García, 2012), usually found clinging to seagrass, hydroids and bryozoans. They are sometimes called “skeleton shrimps” because of their skeletal, elongate, cylindrical appearance. Head may be round with a distinct neck; typically have the first pereion somite partially or completely fused to the head; pereiopods three to four may be reduced and three, or both three and four missing, coxae vestigial or absent; usually with a pair of round or club-shaped gills on the ventrolateral edges of pereion somites three and four, sometimes also on somite two; females with brood lamellae on the ventral borders of pereion somites three and four. Pleon extremely reduced, almost invisible, urosomites one and two usually fused, pleopods and uropods vestigial or absent.

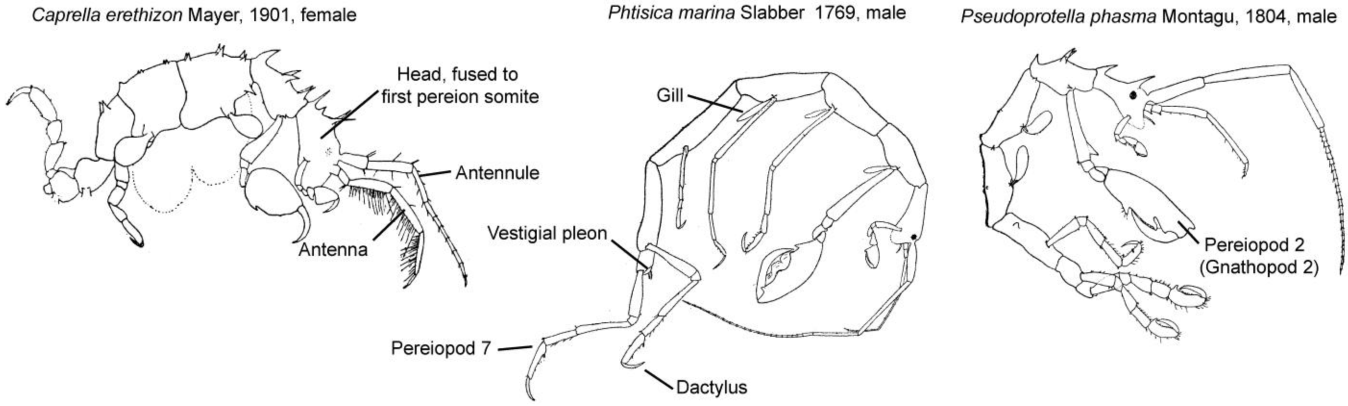

Fig. 10. Examples of Parvorder Caprellidira, Family Caprellidae recorded in the PMF (from Chevreux & Fage, 1924).

Examples of other members of Parvorder Caprellidira, non Family Caprellidae, so with more conventional body form, recorded in the PMF are given in Figure 11.

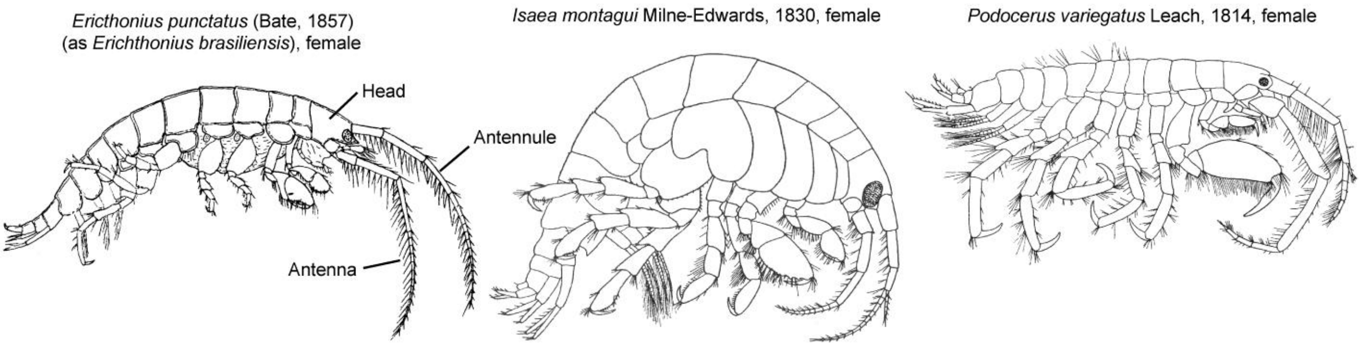

Fig. 11. Examples of other amphipods of Parvorder Caprellidira recorded in the PMF (from Chevreux & Fage, 1924).

Infraorder Gammarida:

Antennule and antenna often of similar length (Fig. 12A, B); first segment of antenna bulbous; mouth hind lips without inner lobes (Fig. 12D); pereiopod two stouter than pereiopod one.

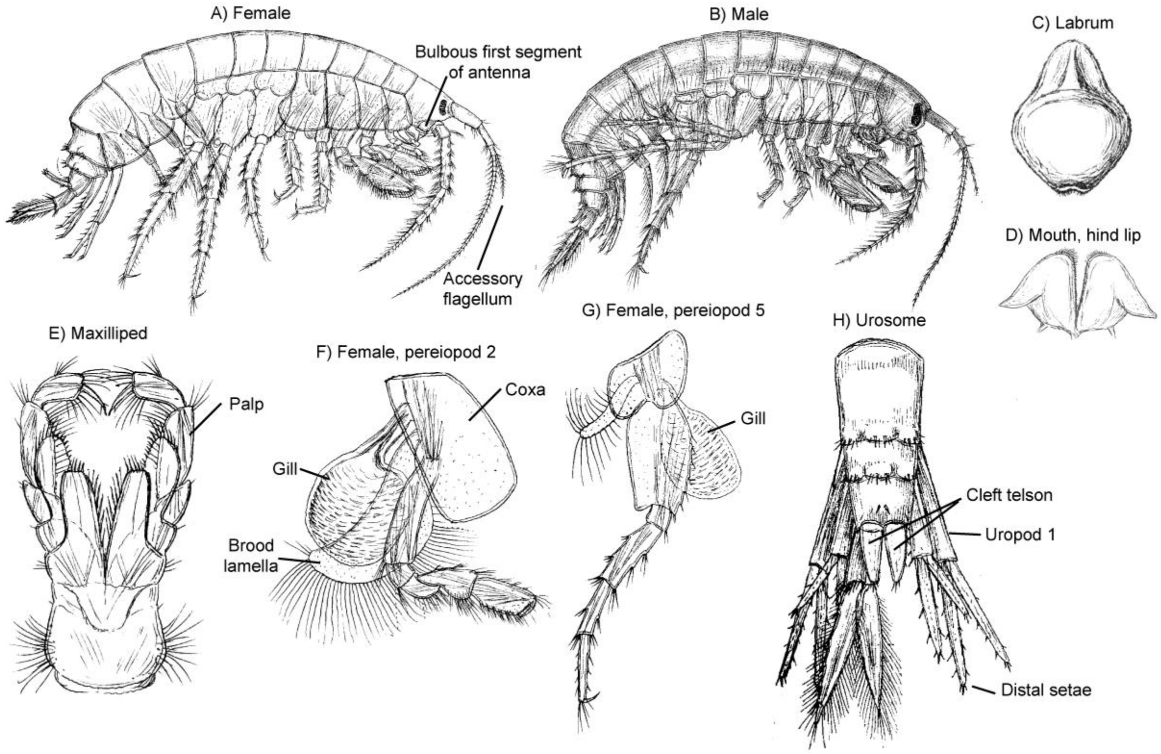

Fig. 12. Example of an amphipod of Infraorder Gammarida recorded in the PMF, *Gammarus locusta* Linnaeus, 1758 (from Sars, 1894).

Infraorder Hadziida:

Antennule longer than antenna in most families (Fig. 13A, B); pereiopod two stouter than pereiopod one; pair of small robust setae dorsally on urosomite two (Fig. 13G); uropod one peduncle sometimes with a robust, external seta proximally.

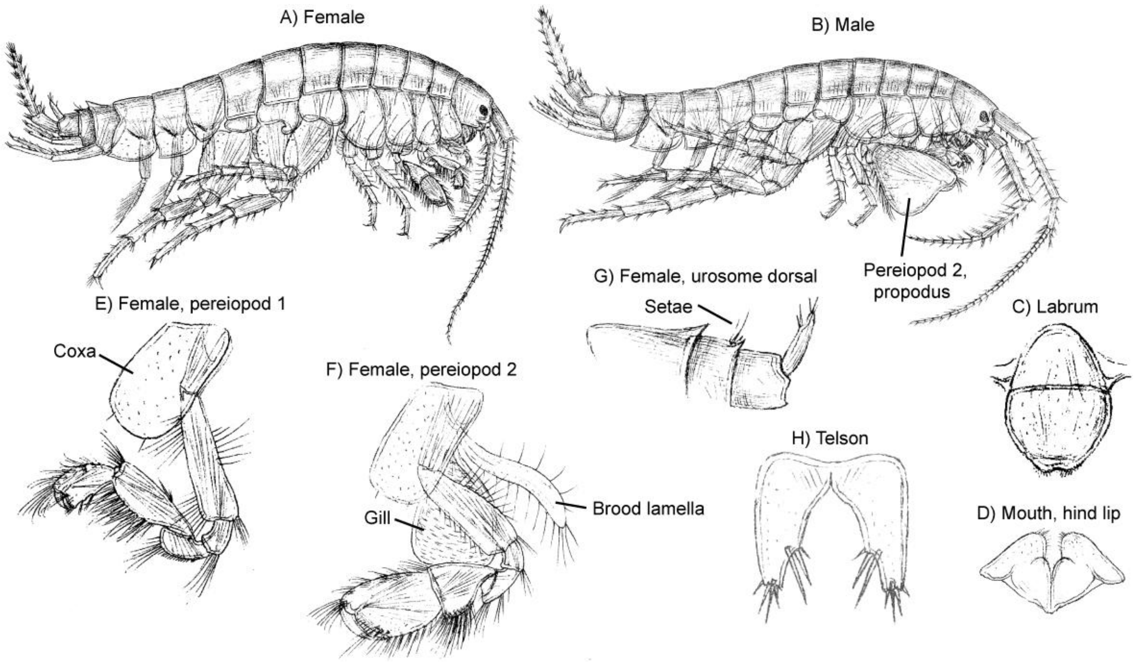

Fig. 13. Example of an amphipod of Infraorder Hadziida recorded in the PMF, *Melita palmata* (Montagu, 1804)(from Sars 1894).

Infraorder Talitrida:

No accessory flagellum on antennule (Fig. 14A, B); mandibular palp vestigial or absent; maxillule palp vestigial or absent; no oblique setal row on the basal endopod of maxilla; mouth hind lips lack inner lobes; setae on the brood lamellae sometimes curl-tipped; most with third uropod internal ramus vestigial or absent (Fig. 14D), or both absent.

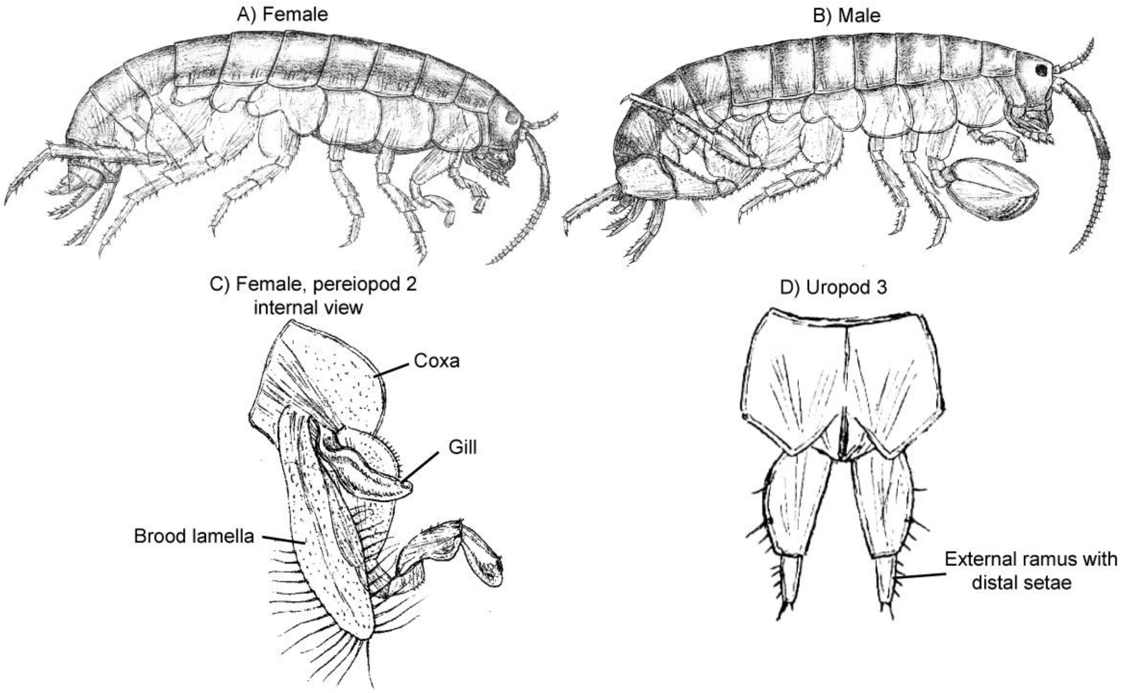

Fig. 14. Example of an amphipod of Infraorder Talitrida recorded in the PMF, *Orchestia gammarellus* (Pallas, 1776), as *Orchestia gammarella* (from Sars, 1890, as *Orchestia littorea*).

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Amphipoda:

Suborder Ingolfiellidea:

A small suborder of benthic species found in a remarkable range of habitats, from mountain rivers to deep ocean sediments, typically living interstitially. Most are small and none are pelagic. Only one species is recorded from Plymouth.

Body worm-like, cylindrical, cuticle smooth (Fig. 15A); head not fused, or partially fused, to first pereion somite, short rostrum may be present; each body somite typically with a seta on either side of the median line and also on the posterior, lateral margin. Eyes absent, but paired, unpigmented ocular lobes usually present, lacking lenses and nerve supply (Fig. 15B); antennule with flagellum of four segments (Fig. 15C) and small accessory flagellum of two to four segments; antenna uniramous, flagellum typically of five segments; mandible without palp; maxilliped reduced, with palp (Fig. 15D); second pereiopod larger than first, each with well developed chelae (Fig. 15A), pereiopods three to seven without chelae, coxae rudimentary; simple oval gills on pereion somites three to five or four to six; all pleon somites free, pleopods vestigial, generally reduced to uniramous plates and some may be missing; pleosome without epimeral plates; three pairs of small brood lamellae on the bases of pereiopods three to five; generally first two pairs of uropods biramous (Fig. 15F, G), third pair uniramous and reduced or absent; telson (Fig. 15H) reduced or absent.

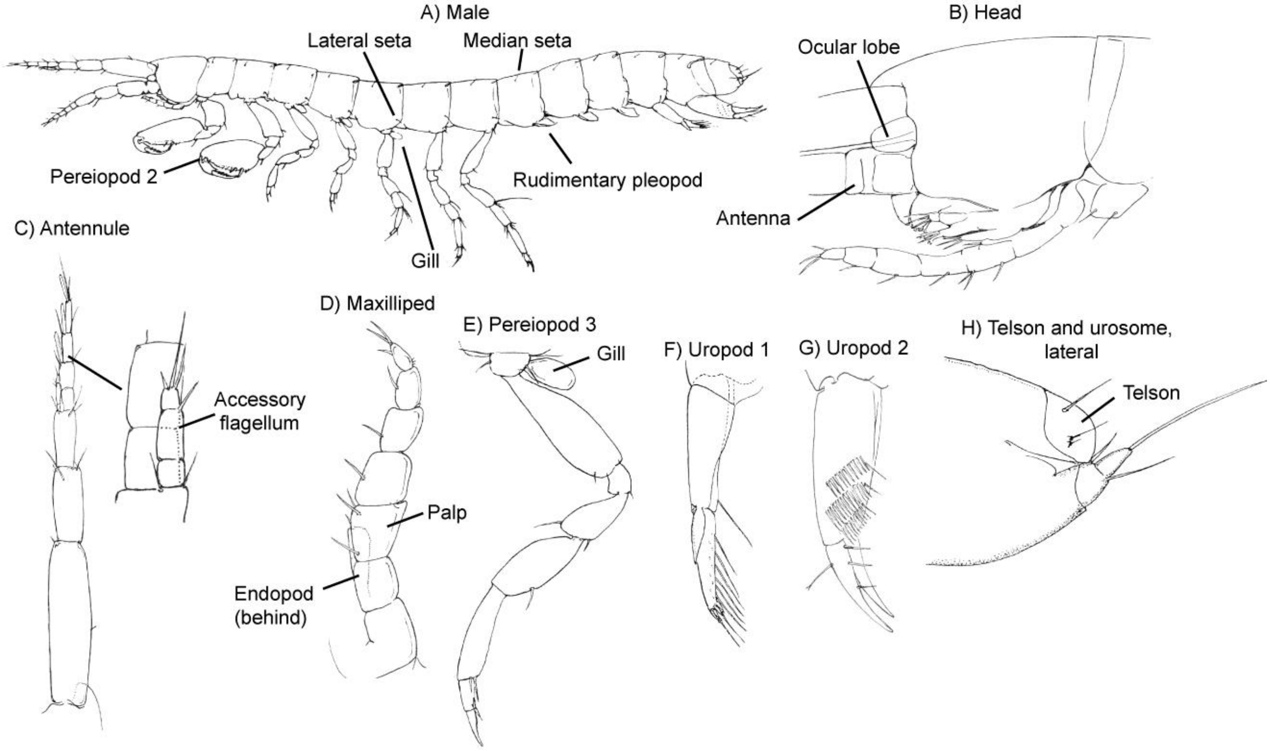

Fig. 15. Example of an amphipod of Suborder Ingolfiellidea, *Ingolfiella britannica* Spooner, 1960, (from Spooner, 1960).

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PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida:

Order Isopoda:

Around 4500 marine isopod species have been described, but relatively few are truly pelagic and the majority are restricted to inshore areas. They exhibit a great variety of body form and while most are benthic grazers/detritivores or predators, some are wood-borers such as the Limnoriidea, or are parasites (mainly of fish and crustaceans). Some species will attack wounded fish and fish in traps (Naylor, 1972; Stepien & Brusca, 1985), and even bathers sometimes report getting nips. Inshore, particular juvenile stages of some parasitic species are probably the most regularly sampled in plankton nets, although offshore, certain species (e.g. *Eurydice*) can occasionally be taken in high numbers. In the PMF some 75 isopod species are recorded and at least examples of each group are included here.

Classification

Isopod classification, especially at some of the higher levels, is currently in considerable turmoil and several genera are still assigned *incertae sedis.* According to WoRMS, Suborder Flabellifera has been replaced by Suborder Cymothoida and various groups reassigned within it as shown below. The basic classification given covers the majority of marine isopods that potentially could be sampled in plankton nets in the northern European area. The number of species in each group recorded in the PMF is given in brackets as an indication of typical inshore biodiversity.

Suborder Asellota
- **Superfamily Janiroidea**
  - **Family Janiridae** (2)
  - **Family Munnidae** (1)

Suborder Cymothoida
- **Superfamily Anthuroidea**
  - **Family Anthuridae** (2)

Superfamily Cymothooidea
  - **Family Gnathiidae** (5)
  - **Family Cirolanidae** (7)
  - **Family Cymothoidae** (2)
  - **Family Aegidae** (4)
- **Infraorder Epicaridea**
  - **Superfamily Bopyroidea**
    - **Family Bopyridae** (19)
  - **Superfamily Cryptoniscoidea**
    - **Family Cryptoniscidae** (2)

Suborder Limnoriidea
- **Superfamily Limnorioidea**
  - **Family Limnoriidae** (2)

Suborder Oniscidea (7 - really terrestrial, so excluded)

Suborder Sphaeromatidea
  - **Family Sphaeromatidae** (7)

Suborder Valvifera
  - **Family Idoteidae** (11)
  - **Family Arcturidae** (4)

Morphology

Isopods are typically dorsoventrally flattened, although some species are quite cylindrical, or laterally compressed, while some females of the parasitic forms are little more than reproductive bags, bearing scant resemblance to a typical isopod. Terminology typically used for different regions of the body (Fig. 1) are head (cephalon, fused to first thoracic somite), pereion (or peraeon; thorax) and pleon (abdomen). As with other Peracarida, females develop a brood chamber (marsupium) in which the young are brooded, formed from flattened plates on the limbs of the pereion. Additionally, the head is fused with only the first and sometimes the second pereion somites and not several somites as found in euphausiids and decapods etc. An excellent description of morphology is given in Roman & Dalens (1999; in French).

Head: Head relatively short (Fig. 1), fused to the first theoretical thoracic somite that bears the maxillipeds. It outwardly appears as one somite and typically bears six paired appendages: antennules, antennae, mandibles, maxillules, maxillae and maxillipeds. In one parasitic group (Family Gnathiidae), because the second thoracic somite is fused to the head, they have seven pairs of appendages on the head. A pair of well developed, compound, unstalked (sessile) eyes are generally present, but may be reduced or absent. While unstalked, the eyes may be on short, immovable peduncles. Antennules are usually uniramous, the peduncle typically of three segments, but may have two or four. The flagellum is short, reduced in some groups. Antennae are typically uniramous and longer than the antennules, the peduncle composed of between four and six segments, some groups with a small accessory flagellum on the fourth segment. In some cases the antennae are modified for walking, or can be greatly reduced. Mouthparts are small, usually hidden beneath the maxillipeds, the mouth bordered anteriorly by the labrum, posteriorly by the bilobed labium (or paragnath) and laterally by the asymmetric mandibles. The labrum and labium are generally rounded lobes, but in some parasitic species they form an oral cone that encloses styliform mandibles. The structure of the mandibles reflects the feeding method.

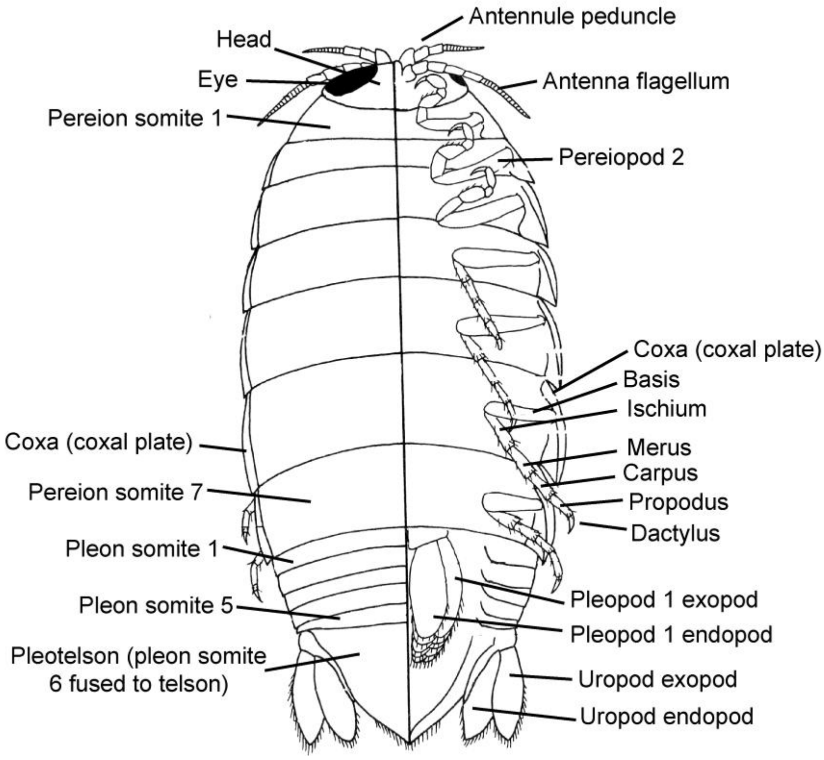

Fig. 1. Schematic illustration of an isopod (mouthparts not drawn) of Superfamily Cymothooidea, Family Cirolanidae: left half, dorsal surface, right half, ventral surface (after Naylor, 1972).

Pereion: The pereion usually has seven visible somites (Fig. 1), apart from (Family Gnathiidae) that have six or four visible somites, due to fusion of the first somite with the head and fusion between other somites. Each of the pereion somites bear a pair of uniramous pereiopods (the exopod is lost), apart from Family Gnathiidae where there are none on the last somite. The pereiopods are quite similar in most groups and generally used for walking (ambulatory), modified in a few groups for swimming. They each consist of seven segments. The first segment is a coxa followed by an elongated basis, an ischium, merus, carpus, propodus and dactylus. The coxae may be small, or developed into large backwardly developed plates (coxal plates). These coxal plates, when large, are visible laterally in dorsal view. The coxae may be fused to varying degrees into the body wall. The first pereiopod pair (gnathopods) are occasionally developed distally to different degrees, into chelae. Late development females may have brood lamellae (oostegites) at the inner bases of some of the anterior pereiopods, generally the first five or six. These enclose the embryos in a marsupium, but are reduced or absent in some species. In males, paired penes project backwards from near the ventral midline of pereion somite seven.

Pleon: This comprises six somites, the most posterior fused with the telson to form a pleotelson, although additional, or even all somites may be fused. The first five somites bear paired, biramous, swimming/respiratory pleopod appendages, sometimes reduced or absent. In most isopod families the second pleopod pair in the male bears a long, often grooved appendix masculina on the inner edge of each side (Fig. 2D). In some females of Suborder Asellota, the first pleopods are fused to form a large plate-like operculum (Fig. 2C) that covers the remaining pleopods. In the corresponding males the first pleopods are modified as a praeoperculum (Fig. 2D) that combines with the second pleopods to form a structure used in copulation. The sixth somite usually bears a pair of uropods that are typically biramous, uniramous in only a few species, sometimes uniramous only in males of particular species. Depending on suborder, the uropods may be terminal or subterminal, with segments that are cylindrical, lateral and flattened, ventral and hinged laterally, or completely missing as in some parasitic species. The anus is terminal or subterminal.

Reproduction and development

In free living isopods the sexes come together for breeding, the male generally carrying the female for a short period until she moults. Isopods differ from other crustaceans in that they typically moult in two phases (biphasic moulting), the posterior body moulting first to facilitate copulation, followed after an interval by the anterior, then a brood pouch is produced. As far as is known, sperm are transferred in spermatophores that emerge from the paired penes on pereion somite seven of the male and are presumably transferred to the female genital ducts on pereion somite five by the appendix masculina or praeoperculum (when these latter appendages are present). As with all Peracarida there is no pelagic egg or larval stage. Eggs are typically laid into the marsupium and the embryos undergo direct development there, emerging as a post-larval juvenile. This is known as a manca (or praniza in Family Gnathiidae). The manca is essentially a replica of the adult but lacks the last (seventh) pair of pereiopods. Dispersal appears to be limited to the crawling ability of the manca, and this has resulted in many species having very limited distributions. In some parasitic species females have no marsupium and the eggs are incubated internally in pouches.

For some species it is possible to identify the development stages (instars) following each moult. The first stage acquires the seventh pair of pereiopods when it moults to the second stage and other stages can sometimes be determined on the basis of size, number of flagellum segments on the antenna etc. In species that are strongly sexually dimorphic it may also be possible to separate the stages into males and females.

Approximately eight percent of described isopods are parasitic and exhibit some fascinating life cycles. Suborder Cymothoida contains many parasitic species and the reproduction of these is described separately.

Key to the main isopod groups (after Naylor, 1972)

1. First two thoracic somites fused to head, so pereion a maximum of six somites, sixth somite reduced, without pereiopods, so only five pereiopod pairs in both juveniles and adults; late juveniles and adult females with pereion somites 3-5 fused and inflated; adult males with massive projecting mandibles, adult females without mandibles -- Superfamily Cymothooidea, Family Gnathiidae (Figs. 4, 5)

\- Only first thoracic somite fused to head; pereion of seven somites, each with pereiopods in adult --- **2**

2. Tiny juvenile planktonic forms, free or attached to copepods; broad or more elongate, often curled up; with or without eye pigment; antennules reduced, usually flattened, often toothed; pereiopods typically with little segmentation, terminating in simple hooks --- Suborder Cymothoida, Infraorder Epicaridea (Figs. 15-17)

\- Not tiny; antennules small but elongate; pereiopods clearly segmented ----------------------- **3**

3. Uropods ventral or lateral --- **4**

\- Uropods terminal --- **9**

4. Uropods ventral, hinged ventrolaterally with pleotelson to form opercular plate covering pleopods -- Suborder Valvifera --------- **5**

- Uropods lateral, flattened, forming a tail fan with pleotelson -- **6**

5. Pereiopods all quite similar, pereion somites all of similar length ----------------------------------- -- Family Idoteidae (Figs. 20-30; see separate key)
- Pereiopods 1-4 plumose, pereiopods 5-7 hooked; pereion somite 4 long, cylindrical ---------- --- Family Arcturidae (Fig. 31)

6. Body long, narrow, subcylindrical; uropod bases extending above pleotelson dorsally; caudal fan arching ------------------- Suborder Cymothoida, Superfamily Anthuroidea (Fig. 3)
- Body robust, broad; uropod bases not extending above pleotelson ------------------------------ **7**

7. Pleon first 5 somites fused, the last 2 incompletely ------ Suborder Sphaeromatidea (Fig. 19)
- Pleon with first 5 somites distinct -- 8

8. Uropod rami flattened, fan-like -- ----------------- Superfamily Cymothooidea, Family Cirolanidae (Figs. 6-14; see separate key)
- Uropods tubular, outer ramus claw-like --------------------------- Suborder Limnoriidea (Fig. 18)

9. Aquatic; antennules well developed; antennal peduncle usually with a scale; most pleon somites fused to pleotelson; uropods tubular ------------------------- Suborder Asellota (Fig. 2)
- Terrestrial, coastal margins; antennules vestigial, minute; pleon always of 5 free somites plus the pleotelson --- Suborder Oniscidea (not figured)

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Isopoda:

Suborder Asellota:

Asellota comprises around a quarter of marine species, most successful and diverse in deeper water. There are four superfamilies, but only superfamilies Janiroidea and Munnidae are recorded in the PMF. Three species are recorded and one is included here as an example. As they are benthic they are unlikely to be taken in plankton samples. One of the most characteristic features of Suborder Asellota is that the uropods are terminal and tubular.

Superfamily Janiroidea:

Family Janiridae:

Genus *Janira*:

Janira maculosa Leach, 1814

This is the only British species in the genus. Body oblong (Fig. 2A, B); eyes dorsal; antennules well developed; antennae longer than body, with a scale on the outside of the third peduncular segment. Anterior pereion somites concave on lateral edge, particularly somites two and three, with coxal plates tiny and bilobed. Pleon of one small, inconspicuous somite, others all fused to form a large, shield-shaped pleotelson; posterolateral borders of pleotelson serrated (Fig. 2C); first pair of pleopods in female transformed into a broad opercular plate ventrally, that covers the remaining pleopods, in male the first pleopods form the middle of the copulatory structure, the praeoperculum (Fig. 2D), the lateral parts of which are formed from the second pleopods, each of which bear an appendix masculina. Uropods biramous, terminal, tubular (Fig. 2E), longer than, or more or less equal in length to the pleotelson, covered in bristles.

In fresh specimens colour typically yellowish, densely mottled with red or brown specks, sometimes with an unpigmented band across the head, anterior to the eyes.

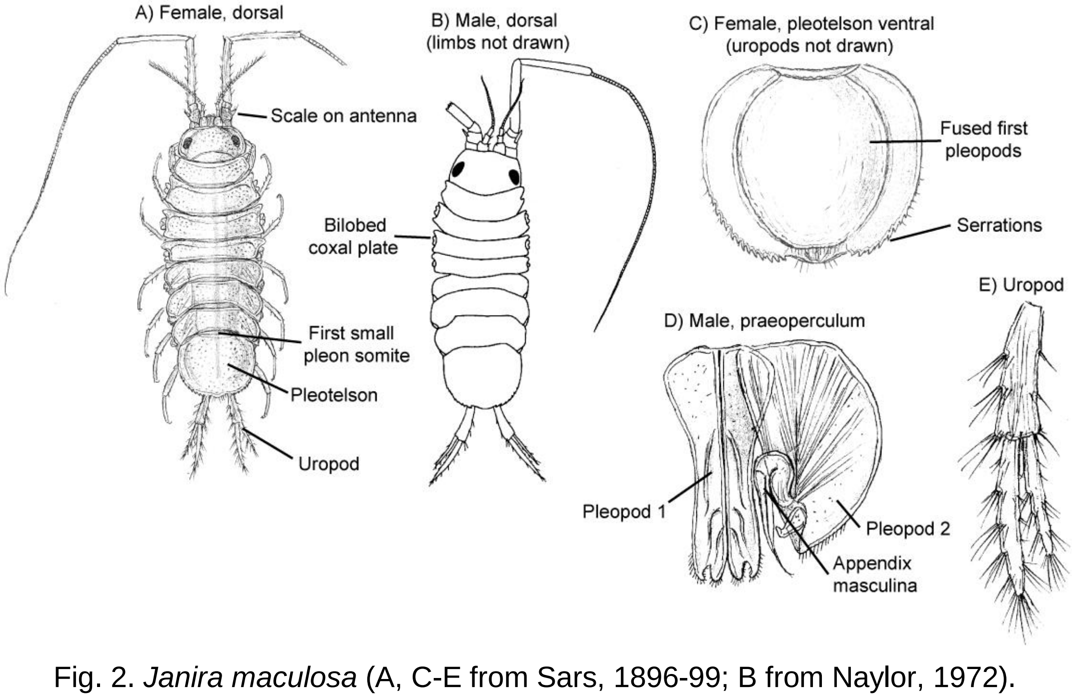

Fig. 2. *Janira maculosa* (A, C-E from Sars, 1896-99; B from Naylor, 1972).

Recorded: PMF. L4, not recorded. Northern Norway to Atlantic coast of France. Britain and Ireland, most coasts.

Size: Females up to 7 mm; males up to 10 mm.

Further information: Sars, 1896-99 (as *Ianira maculosa*); Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1972; Hayward *et al*., 1995.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Isopoda:

Suborder Cymothoida:

In this very diverse suborder there are four superfamilies, **Anthuroidea, Cymothooidea, Bopyroidea** and **Cryptoniscoidea**, the latter two separately placed in Infraorder Epicaridea. The suborder are united on mandible and maxilliped structure (Brandt & Poore, 2003). Superfamily Anthuroidea and Family Cirolanidae of Superfamily Cymothooidea are carnivores, the remainder mainly parasitic (reviewed by Williams & Boyko, 2012). Some members of Superfamily Cymothooidea are recorded in the PMF. Families Cymothoidae (as Family Anilocridae) and Aegidae have been found attached to sea anemones and polychaetes, but are typically fish ectoparasites, feeding on the blood and tissue of hosts both as juveniles and adults. Resembling conventional isopods, they are unlikely to be sampled in plankton nets, so are not included here. Family Gnathiidae are unique in that they parasitise a single fish host only during their juvenile phase. Superfamilies Bopyroidea and Cryptoniscoidea are parasites of crustaceans. Only members of families Gnathiidae, Cirolanidae and the juvenile stages of Infraorder Epicaridea are likely to be sampled in plankton nets.

Superfamily Anthuroidea:

Characterised by an elongate cylindrical body, the pereion somites longer than wide and with the uropod exopods arching over the pleotelson. These are benthic and unlikely to be taken in plankton samples, but one is included here as an example.

Family Anthuridae:

Genus *Anthura*:

Anthura gracilis (Montagu, 1808)

Benthic carnivore; body long and narrow (Fig. 3A, B), subcylindrical; eyes large, particularly in males. Antennae of female small, those of male elongate, with the flagellum densely covered in fine setae. Pleon somites of females difficult to discern, those of males more distinct; uropods lateral, forming an arching tail fan, exopods arching over the pleotelson; pleotelson rectangular (Fig. 3C), widest distally, with small statocysts near base.

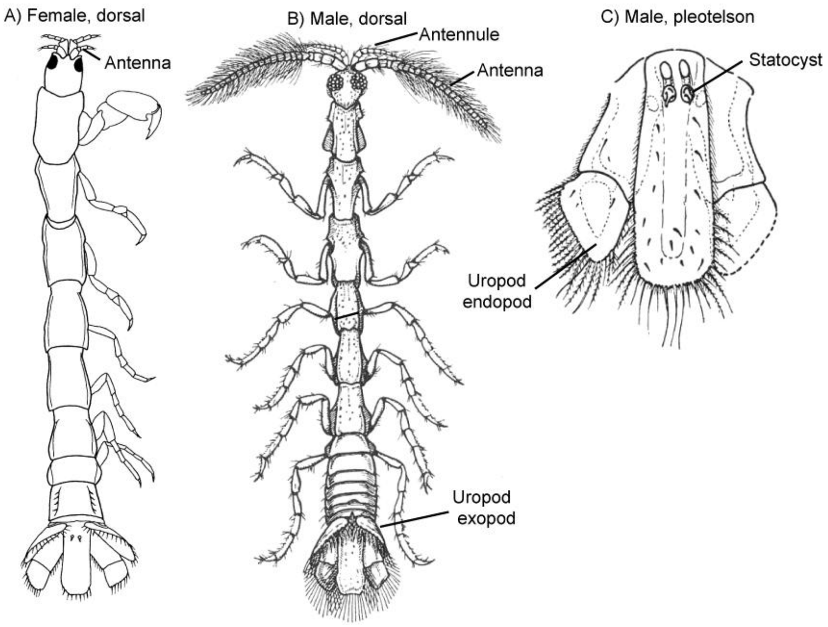

Fig. 3. *Anthura gracilis* (A from Naylor, 1972; B, C from Sexton, 1914).

Recorded: PMF. L4, not recorded. Irish Sea. English Channel. Southern species.
Size: Females up to 11 mm; males up to 4 mm.
Further information: Sexton, 1914; Naylor, 1972; Hayward *et al*., 1995.

Superfamily Cymothooidea:
Family Gnathiidae:

Apart from the juveniles of epicarideans, the only parasitic isopods regularly taken in plankton samples are the juvenile and occasional adult stages of Family Gnathiidae. These bizarre looking isopods (Fig. 4), found from the littoral zone to the deep sea, are the commonest parasite of coral reef fish (Grutter, 2003) and one of the main parasites removed by cleaner fish. Adults are benthic, probably do not feed and are often found in crevices on the sea bed or associated with barnacle aggregations, sponges, polychaete tubes etc.

Most females incubate the eggs and embryos internally, causing distension of the entire body cavity and displacing the internal organs. The life cycles of only a few species have been described, but in a detailed study of one species *Gnathia africana* Barnard, 1914 (Smit *et al*., 2003) the zuphea 1 stage juveniles that are released start the parasitic cycle, finding then feeding on a fish for minutes to several hours. They are initially quite slender, but on completion of feeding are bloated. These leave the fish and are called the praniza 1 stage. They moult, probably on the sea bottom in the shelter of sponges or barnacle aggregations etc. to become the slender zuphea 2 stage. This finds another host fish for a similar period as the previous zuphea stage and leaves as a praniza 2 stage for the bottom, where it moults. The same cycle continues through a zuphea 3 stage until the praniza 3 stage, at which point they migrate to the bottom to moult to the adult stage. Males and females can be recognised from the praniza 3 stage by the mandibles, which are greatly enlarged in the male. Pranizas are good swimmers, so are the stage usually taken in plankton nets.

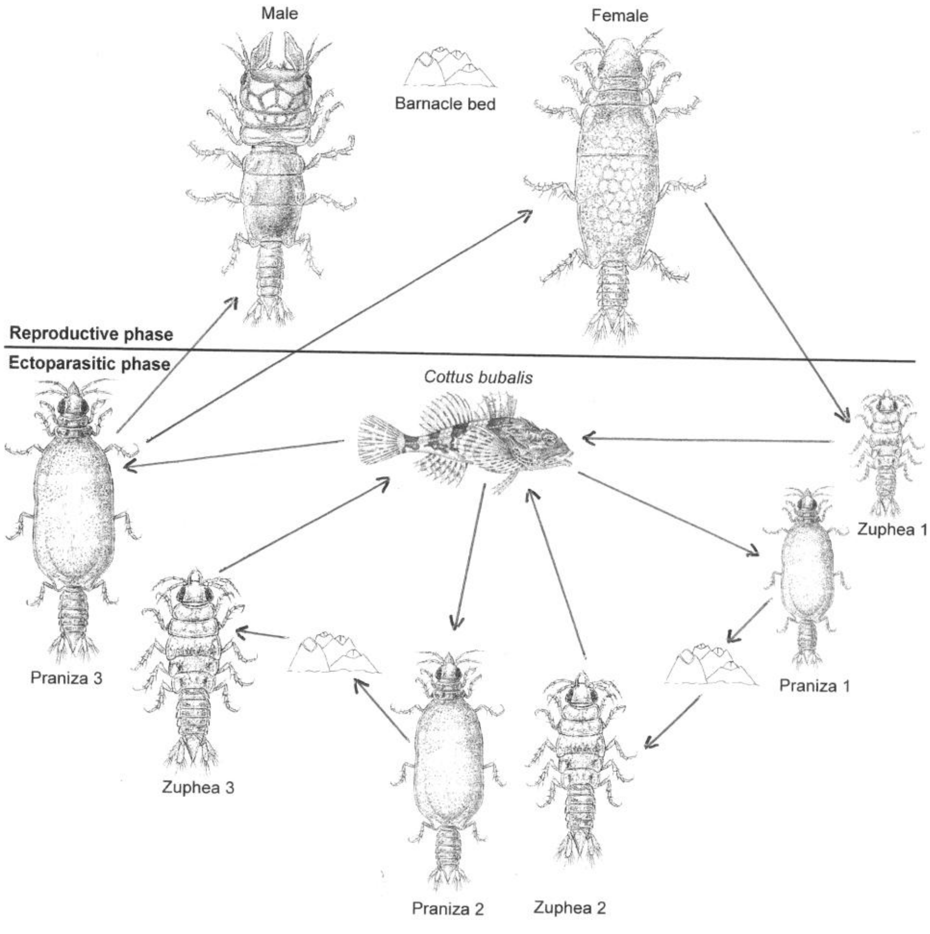

Fig. 4. Example of the life cycle of a Gnathiidae isopod (after Smit *et al*., 2003; isopod figures from Sars, 1896-99).

In adult Gnathiidae the eyes are well developed and sometimes on short processes (ocular lobes). Adult males have broad flattened heads with massive forcep-like mandibles that project anteriorly (Fig. 5), while females have small narrow heads and lack mandibles. There are only six pereion somites, as an additional thoracic somite is fused to the head, not just the first as is typical in most

isopods. The limbs on the additional fused somite are flattened and not visible dorsally. They function as a second pair of maxillipeds and are termed pylopods. Females also have pereion somites three to five fused and inflated, particularly inflated in females that incubate eggs internally. The sixth pereion somite is greatly reduced and without pereiopods, so there are only five pairs. This sixth somite is difficult to discern in the female, more obvious in the male. The pleon is much narrower than the pereion and always has five free somites, plus the pleotelson.
Females and juveniles cannot easily be identified to species and the taxonomy of this family is based entirely on males. *Gnathia oxyuraea* is given as an example of Family Gnathiidae (Fig. 5).

Genus *Gnathia*:

Gnathia oxyuraea (Lilljeborg, 1855)

Only six pereion somites, as an additional thoracic somite is fused to the head. In pranizas and females, pereion somites three to five fused and inflated (Fig. 5A, B, D); head triangular, with convex lateral margins. In juveniles and adults of both sexes, pleotelson similar, pointed with two slender terminal bristles; large eyes; sixth pereion somite reduced and without limbs, so only five pairs of pereiopods on pereion; pleon narrower than pereion.

Male anterior head with a median tooth bordered by a shallow concavity on each side (Fig. 5E), lateral corners square, head broader than long, with a pronounced ridge over each eye; large mandibles that project anteriorly, forceps-like, indistinct depression on outer edge, inner edge bulging in the middle with crenulated distal edge. Anterior pereion divided from posterior by deep constriction; pleon narrow with well developed pleopods

Juveniles were recorded in the PMF on the gills of conger eel and among worm tubes.

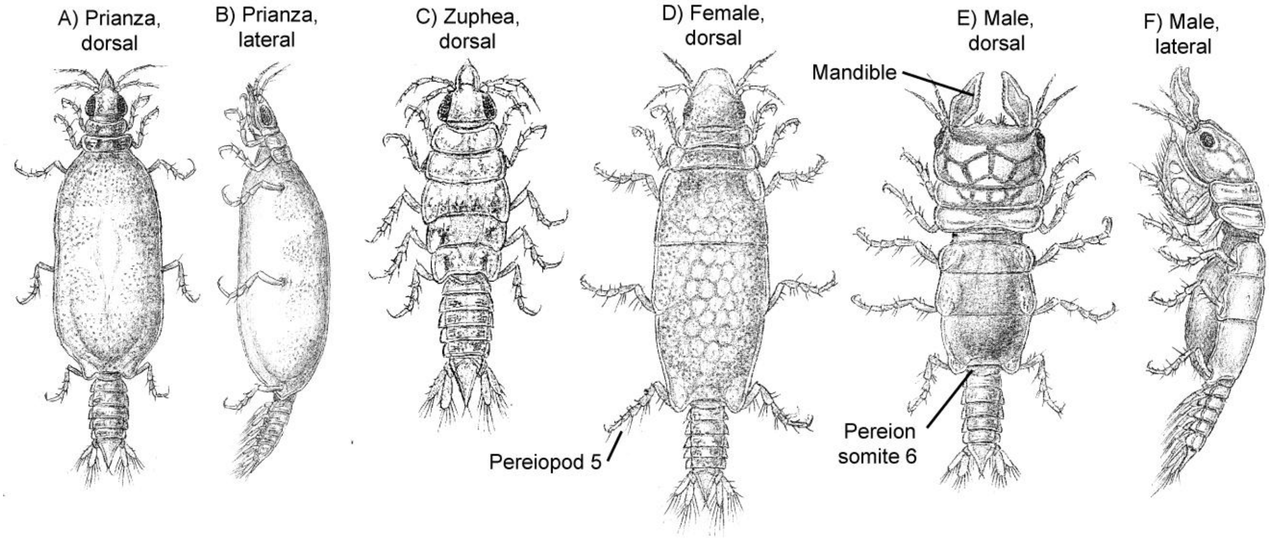

Fig. 5. *Gnathia oxyuraea* (from Sars, 1896-99, as *G. maxillaris*).

Recorded: PMF. L4, not recorded. British and Irish coasts. Norwegian coast.

Size: Praniza, lengths not recorded; female ~4.0 mm; male 2.4-5.4 mm.

Further information: Sars, 1896-99 (as *G. maxillaris*); Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957b, 1972; Hayward *et al*., 1995.

Family Cirolanidae

Most members of this family will mainly be sampled inshore, only a few are typical of more open sea areas.

Key to Family Cirolanidae (after Hansen, 1905)

1 Peduncle of antenna with 5 distinct segments; peduncle of uropod with acute internal process extending back to middle of endopod --- **2**
- Peduncle of antenna with 4 distinct segments; peduncle of uropod without acute internal process -- *Eurydice* spp. ----- **4**

2 Pleopod 1 endopod with both rami heavily chitinised and forming an operculum, peduncle longer than broad; body obviously elongated ---------------------- *Conilera cylindracea* (Fig. 8)
- Pleopod 1 with endopod normal, not heavily chitinised, peduncle broader than long; body not obviously elongated --- **3**

3 Pleotelson narrowing distally, tip rounded, with 8-12 marginal spines each side; uropod endopod extending beyond pleotelson ------------------------------------ *Cirolana cranchi* (Fig. 7)
- Pleotelson broad, bluntly pointed, with 3-4 small marginal spines each side; uropod endopod slightly longer than pleotelson ------------------------------ *Natotolana borealis* (Fig. 6)

4 Posterior margin of pleotelson concave, with 2 conspicuous spines close to each other at each end; second to sixth pereion somites with coxal plate produced into long processes -- *Eurydice spinigera* (Fig. 11)
- Posterior margin of pleotelson never concave, either convex or nearly straight, spines if present rather small; second to fourth pereion somites with coxal plate either not produced, or with short processes -- **5**

5 Posterior margin of pleotelson at least half as wide as the anterior margin, prominent tooth at each end, but no spines between; coxal plate of pereion somite 6 with short processes, similar to somite seven --- *Eurydice grimaldii* (Fig. 14)
- Posterior margin of pleotelson considerably less than half as wide as anterior margin; coxal plate of pereion somite 6 with moderate or large process -- **6**
- Posterior margin of pleotelson considerably less than half as wide as anterior margin; coxal plate of pereion somite 6 with very small or no process --- **7**

6 Coxal plate of somite 5 with small process, 6 with quite long process; posterior pleotelson margin without spines, but a conspicuous tooth at each end and just outside this (in larger specimens) a minute tooth -- *Eurydice truncata* (Fig. 13)
- Coxal plate of somite 5 without process, of 6 with quite long process; posterior pleotelson margin with 4 spines but no conspicuous tooth at each end --------- *Eurydice pulchra* (Fig. 9)

7 Pleotelson posterior margin width around one third of the anterior margin, with tooth either end and 2 spines at each side -- *Eurydice affinis* (Fig. 10)
- Pleotelson posterior margin width less than a quarter of the anterior margin, with no teeth or spines -- *Eurydice inermis* (Fig. 12)

Genus *Natotolana*:

Natotolana borealis (Lilljeborg, 1851)

Benthic, but also free-swimming, voracious carnivore on e.g. dead fish on bottom, in crab pots or on long-lines. Body oval, broadest in middle (Fig. 6A), gradually tapering both in front and behind; coxal plates quite large and perfectly smooth; pleon much narrower than pereion. Antennule short; antenna almost half length of body, peduncle with five distinct segments, flagellum with about 30 segments. Pereiopod seven with basal joint very broad, densely fringed with fine setae (Fig. 6C). Uropods with the peduncle segment produced inwards to a short acute process (Fig. 6D), endopod slightly longer than pleotelson, both endopod and exopod bearing spines between fringe of setae. Pleotelson generally broader than in *Cirolana cranchi*, tip bluntly pointed, fringed with long setae, with three to four small marginal spines on each side (Fig. 6E).

In fresh specimens, body coloured light brown, mottled with darker brown.

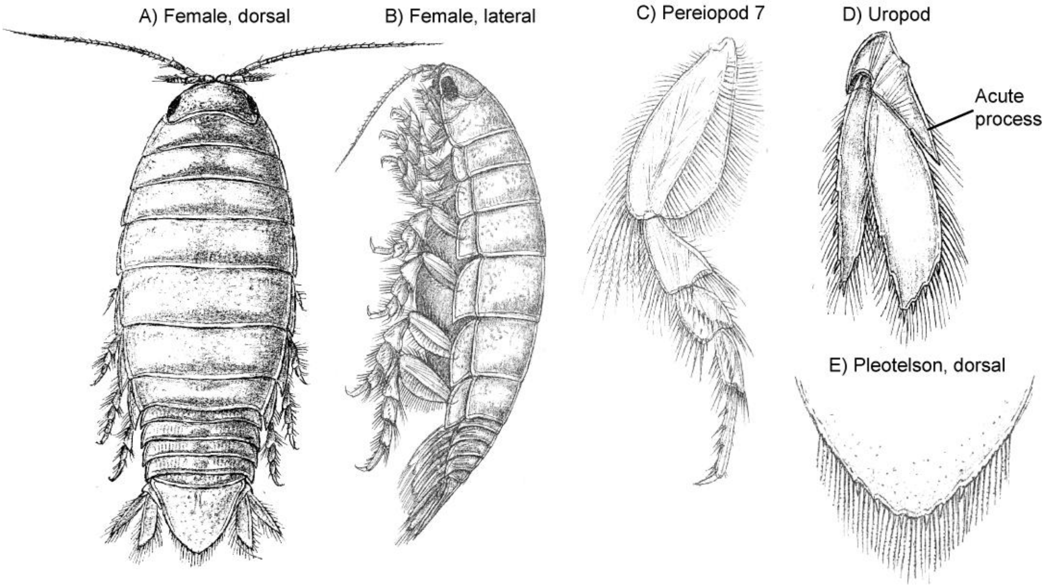

Fig. 6. *Natotolana borealis* (from Sars, 1896-99).

Recorded: PMF (as *Cirolana borealis*). L4, not recorded. British, Norwegian and French coasts.

Size: 27-33 mm.

Further information: Sars, 1896-99; Hansen, 1890, 1905; Nierstrasz & Schuurmans Stekhoven, 1930 (all as *Cirolana borealis*).

Genus *Cirolana*:

Cirolana cranchi Leach, 1818

Benthic, sometimes pelagic, carnivorous, pest for eating lobster-pot fish bait. Body oval (Fig. 7A), eyes black, moderately large, from the side longer than deep (Fig. 7A-C); frontal lamina, between the bases of the antennae and antennules ventrally, is small, pentagonal and less than twice as long as broad; antennules about as long as peduncle of antennae; antennae long, reaching around middle of body, peduncle of five distinct segments; coxal plates increase gradually in size rearwards, each with a deep oblique furrow. Few if any plumose swimming setae on the last three pereiopods, pereiopod seven without swimming setae, but with numerous simple sharp spines and some short setae (Fig. 6G). Pleotelson subtriangular, narrowing distally, with rounded apex, with around eight to 12 marginal spines each side among the setae (Fig. 7F); uropods quite broad, endopod extending beyond pleotelson, around twice as long as broad, exopod about three times as long as broad, slightly shorter than endopod, peduncle segment produced inwards to a short acute process (Fig. 7E).

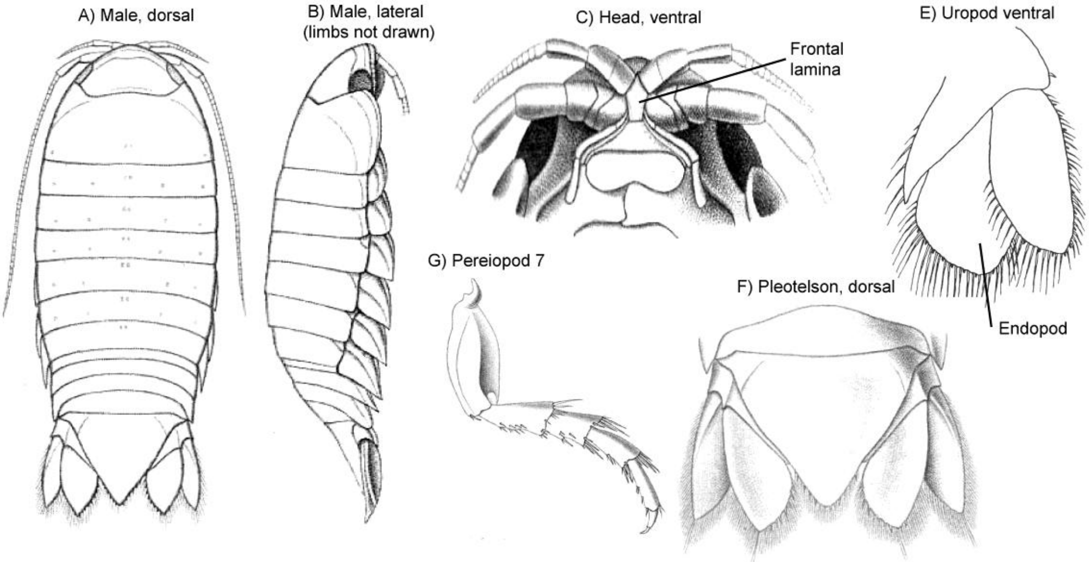

Fig. 7. *Cirolana cranchi* (A-C, F, G from Hansen, 1890; E from Naylor, 1972, both as *Cirolana cranchii*).

Recorded: PMF. L4, not recorded. Southern and western British coasts. Western Ireland. French coast.

Size: Up to 18 mm.

Further information: Hansen, 1890, 1905; Naylor, 1972; Hayward *et al*., 1995 (all as *Cirolana cranchii*).

Genus *Conilera*:

Conilera cylindracea (Montagu, 1804)

Benthic carnivorous, mainly inshore species, often found eating lobster-pot bait. Characteristic slender, elongated, cylindrical body (Fig. 8A, B); elongated frontal lamina on ventral surface (Fig. 8C); antennule short, peduncle of five segments. First pleopods in female heavily chitinised, forming an operculum. Pleotelson subtriangular, narrowing distally, with blunt apex (Fig. 8D), around eight marginal spines each side among the setae; uropod with the peduncle segment produced inwards to a short acute process, endopods outer distal edge slightly concave, with spines among the setae.

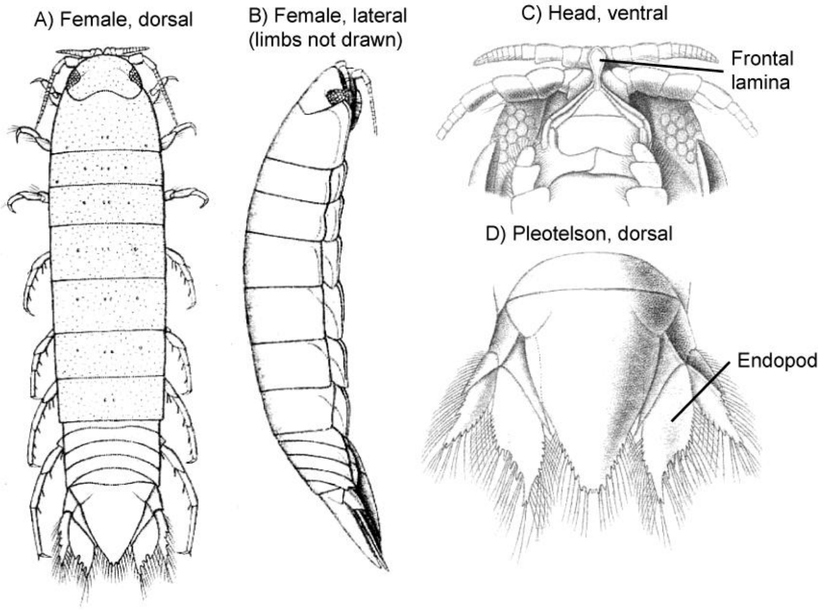

Fig. 8. *Conilera cylindracea* (from Hansen, 1890).

Recorded: PMF. L4 not recorded. English Channel. Irish Sea. Western Ireland.
Size: Up to ~28 mm.
Further information: Hansen, 1890, 1905; Naylor, 1972; Hayward *et al*., 1995.

Genus *Eurydice*:

Eurydice pulchra Leach, 1815

Mainly intertidal, benthic species. Body short and stout (Fig. 9A); antennules similar in both sexes, short, at right angles to first segment of peduncle; antennae long, reaching to around the last somite of pereion in female, two thirds of body length in male, peduncle of four distinct somites, last segment, about the length of the preceding ones combined. Coxal plates of pereion somite five not produced into processes, sixth with the posterior angles produced into fairly long, sharp processes (Fig. 9B), which separates it from the similar but smaller *E. affinis* with which it has been previously confused (Jones & Naylor, 1967) and which lacks this long process; coxal plates of pereion somite seven with shorter processes at posterior angle. Pleotelson with posterior border broadly rounded (Fig. 9C), with fairly long plumose setae emerging from between small serrations, with two tiny spines near each corner.

In fresh specimens, colour darker than *E. affinis*, numerous black chromatophores on dorsal, lateral and ventral surfaces.

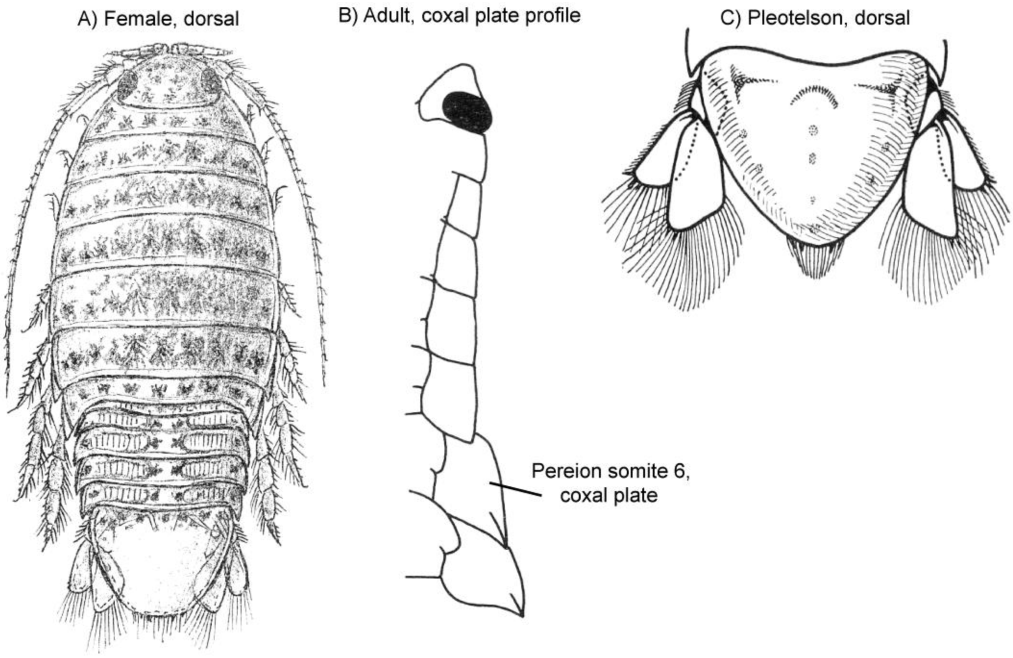

Fig. 9. *Eurydice pulchra* (A from Sars, 1896-99; B from Naylor, 1972; C from Nierstrasz & Schuurmans Stekhoven, 1930, after Hansen, 1890).

Recorded: PMF. L4, not recorded. North Sea coasts. English Channel. Irish Sea. Western Ireland.
Size: Female 4-8 mm; male 4-7 mm.
Further information: Hansen, 1890; Sars, 1896-99; Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957b, 1972; Jones & Naylor, 1967; Hayward *et al*., 1995.

Eurydice affinis Hansen, 1905

Intertidal, benthic species. Antennule short, slightly more robust in male than in female, at right angles to first segment of peduncle; antennal peduncle of four distinct segments. Coxal plates of pereion somites six to seven with sharp posterior angles but no extended processes (Fig. 10A). This separates it from *E. pulchra* with which it has been previously confused (Jones & Naylor, 1967) because the pleotelson is similar. *E. inermis* (Fig. 12B) also lacks processes, but the distal pleotelson margin differs in length, shape and armature. Pleotelson hind margin fairly broadly rounded (Fig. 10B, C), somewhat convex, slightly serrated, limited at each end with a distinct but short tooth, with two small spines towards each corner and a series of fairly long plumose setae.

In fresh specimens, colour lighter than *E. truncata*, pale, with black chromatophores restricted to the dorsal body surface and yellowish abdomen.

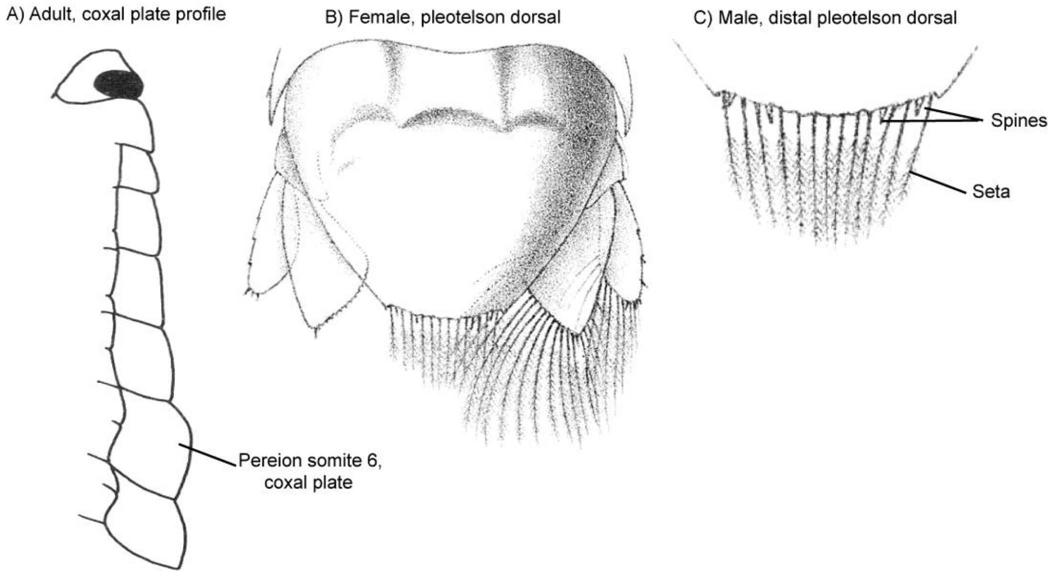

Fig. 10. *Eurydice affinis* (A from Naylor, 1972; B, C from Hansen, 1905).

Recorded: PMF, not recorded, as misidentified among *E. pulchra* specimens (Jones & Naylor, 1967), but actually common. L4, not recorded. North Sea Coasts. English Channel. Irish Sea. Western Ireland. French and Dutch coasts.

Size: Female 2-6 mm; male 2-5 mm

Further information: Hansen, 1905; Wolff, 1966; Naylor, 1957b, 1972; Jones & Naylor, 1967; Hayward *et al*., 1995.

Eurydice spinigera Hansen, 1890
Sublittoral and mainly coastal, benthic species, but ranges into the water column. Antennules short, at right angles to first segment of peduncle, flagellum robust in both sexes; antennae long, reaching to around the last somite of pereion in female, slightly longer in male (Fig. 11A), peduncle with four distinct segments. Pereion somites two to six with the coxal plates produced into fairly long processes, those on somite six especially, this process longer than in any other species. Pleotelson sharply narrowing posteriorly (Fig. 11B), posterior border concave and slightly serrated, with plumose setae and two conspicuous spines at each corner.

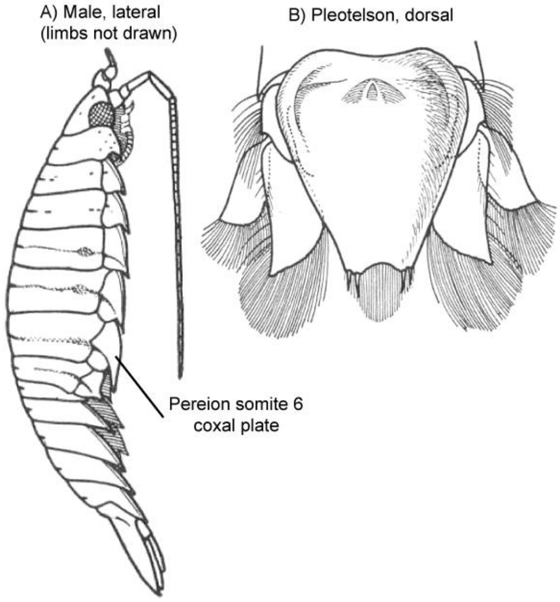

Fig. 11. *Eurydice spinigera* (from Nierstrasz & Schuurmans Stekhoven, 1930, after Hansen, 1890).

Recorded: PMF. L4, not recorded. All North Sea. Irish Sea. English Channel. West Ireland.
Size: Up to ~9 mm.
Further information: Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957b, 1972; Jones & Naylor, 1967; Hayward *et al*., 1995.

Eurydice inermis Hansen, 1890

Found offshore as well as inshore, benthic, but ranges into the water column. Body about three times longer than wide. Antennules short, at right angles to first segment of peduncle; antennae long reaching the posterior pereion somite in females, around two thirds body length in male, peduncle of four distinct segments. Pereion coxal plates without sharp processes posteriorly (Fig. 12A); pleotelson with broad transverse depression, posterior margin narrow, around a quarter width of anterior margin (Fig. 12B), broadly rounded and slightly concave, with around nine small serrations with a few plumose setae between, no large teeth or spines. Uropods very short, the endopod not reaching the posterior border of the pleotelson.

In fresh specimens, colour, brown or grey, with black spots.

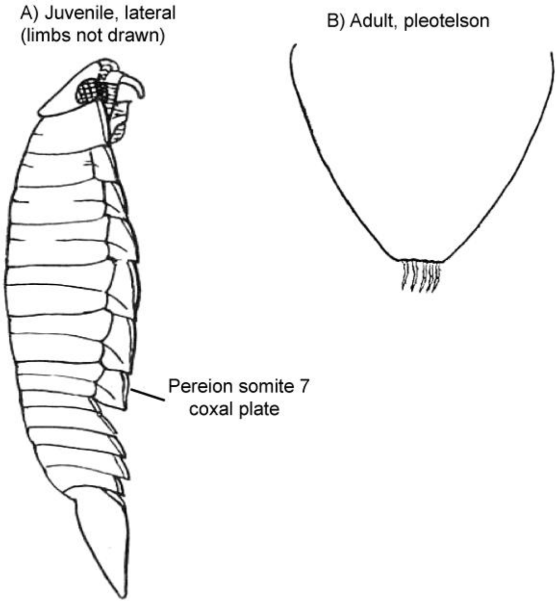

Fig. 12. *Eurydice inermis* (A from Nierstrasz & Schuurmans Stekhoven, 1930, after Hansen, 1890; B from Naylor, 1957b).

Recorded: PMF. L4, not recorded. English Channel. Irish Sea. South and western Ireland.

Size: Up to 7 mm.

Further information: Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957b; Jones & Naylor, 1967.

Eurydice truncata (Norman, 1868)
Mainly pelagic species, although can also be taken on the bottom, found both inshore and in open sea. Antennule at right angles to first segment of peduncle; antennae of male long, reaching beyond the middle of the pleotelson (Fig. 13A), much shorter in female, peduncle of four distinct segments. Pereion coxal plates of somites two to four scarcely or not produced behind (Fig. 13B), somite five with small process, somite six with moderate or large process, larger than on somite seven. Uropods almost reaching the posterior margin of the pleotelson (Fig. 13A); pleotelson with a dorsomedian transverse depression, posterior margin narrow (Fig. 13C), about one third as wide as anterior margin, slightly convex, with around seven tiny serrations in middle, with plumose setae between, a conspicuous tooth at either end and a small tooth, or projecting angle, outside these (at least in older individuals).

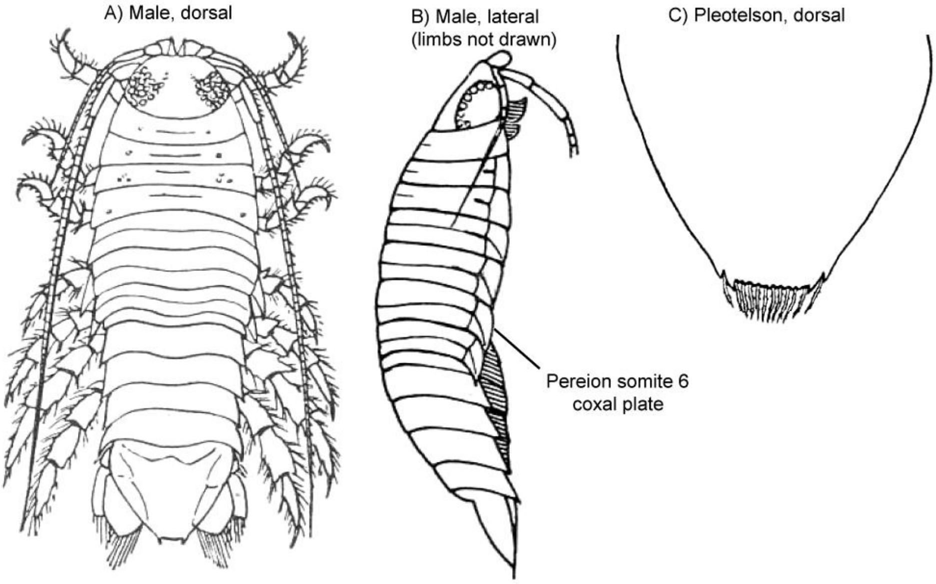

Fig. 13. *Eurydice truncata* (A, B from Nierstrasz & Schuurmans Stekhoven, 1930 after Hansen, 1895; C from Naylor, 1957b).

Recorded: PMF. L4, not recorded. North Sea. Irish Sea. Northern Scotland. English Channel.
Size: Female ~7 mm; male ~ 5mm.
Further information: Hansen, 1895, 1905; Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957b; Jones & Naylor, 1967.

Eurydice grimaldii Dollfus, 1888

Pelagic, mainly open sea species, but also taken in coastal area. Antennule at right angles to first segment of peduncle, thicker in male (Fig. 14A) than in female; antennae very long in male, almost reaching pleotelson, shorter in female. Coxal plates of pereion somites two to four produced into short processes (Fig. 14B) the fifth to seventh with slightly longer processes. Uropods slightly longer than the pleotelson (Fig. 14A); pleotelson with a dorsomedian oval depression, posterior margin at least half as wide as anterior margin (Fig. 14C), margin almost straight, or slightly convex, without spines but a conspicuous triangular tooth at each end, small serrations between teeth and plumose setae.

In fresh specimens, body with dark spots.

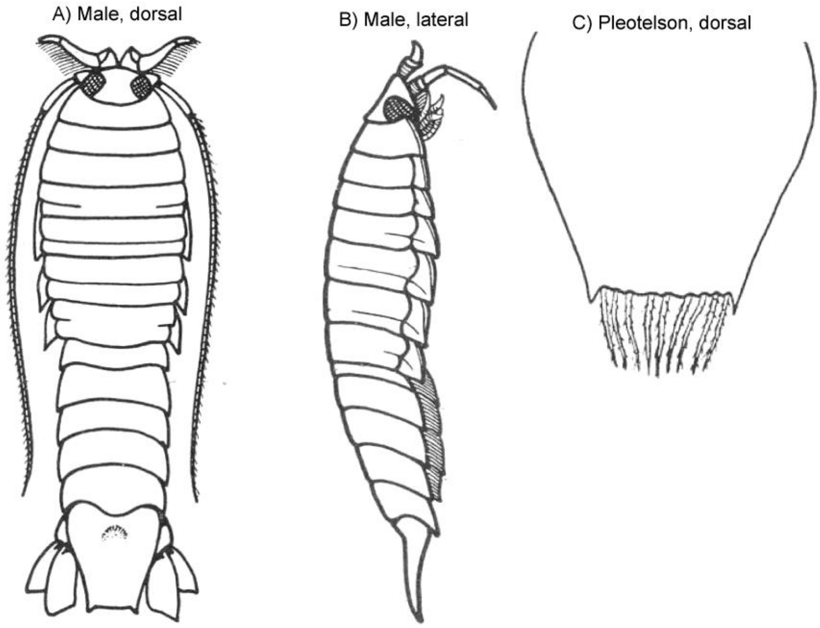

Fig. 14. *Eurydice grimaldii* (A, B from Nierstrasz & Schuurmans Stekhoven, 1930; C from Naylor, 1957b).

Recorded: PMF and L4 not recorded. English Channel. North Sea. Northern Scotland. Western Ireland.

Size: Female 7-9 mm; male 5-7 mm.

Further information: Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957b; Jones & Naylor, 1967.

Infraorder Epicaridea:

The following two parasitic superfamilies, **Bopyroidea** and **Cryptoniscoidea** are collectively referred to as epicarideans, as one of their juvenile stages is called an epicaridium (Fig. 15A, B). Epicarideans represent ~8% of all described isopods and are unique in that they typically parasitise two different crustacean hosts during their life cycle, intermediate and definitive hosts, and include both endo- and ectoparasites. Some are also hyperparasitic (parasites of other parasites), including other parasitic isopods (Fig. 17F). The adult female releases the pelagic epicaridium juvenile that searches out, attaches to and feeds on the intermediate host. For all species investigated a pelagic copepod is the intermediate host (Fig. 15G), typically a calanoid, but sometimes a cyclopoid (Owens & Rothlisberg, 1995). The tiny epicaridium (~0.1-0.67 mm) has well defined segmentation and develops on the copepod through an initially more rudimentary microniscus stages (Fig. 15C, D; ~0.63-0.90 mm) to the cryptoniscus stage (~0.83-1.35 mm) that has well defined segmentation (Fig. 15E, F). The cryptoniscus leaves the intermediate host and is pelagic until it finds and attaches to the definitive host, on which it develops into an adult. Definitive hosts include barnacles, isopods, ostracods and malacostracans, but the life cycles of many species have not been studied. Resultant from their feeding on host ovarian and other body fluids, epicarideans can cause partial or complete parasitic castration in both their intermediate (e.g. Uye & Murase, 1997) and definitive hosts. Parasitisation may also affect the appearance, morphology and behavior of hosts and may have an economic impact by reducing productivity of a variety of commercially important species (or of their prey) and negatively affecting saleability. While the various pelagic stages of epicarideans are regularly collected in at least fine mesh plankton samples, they appear quite similar, and for many species have not been described, so their specific identification is a specialist task. Bopyroidea and Cryptoniscoidea have slightly different life cycles, which are described below. An excellent account of epicaridean morphology and biology is given by Trilles (1999; in French).

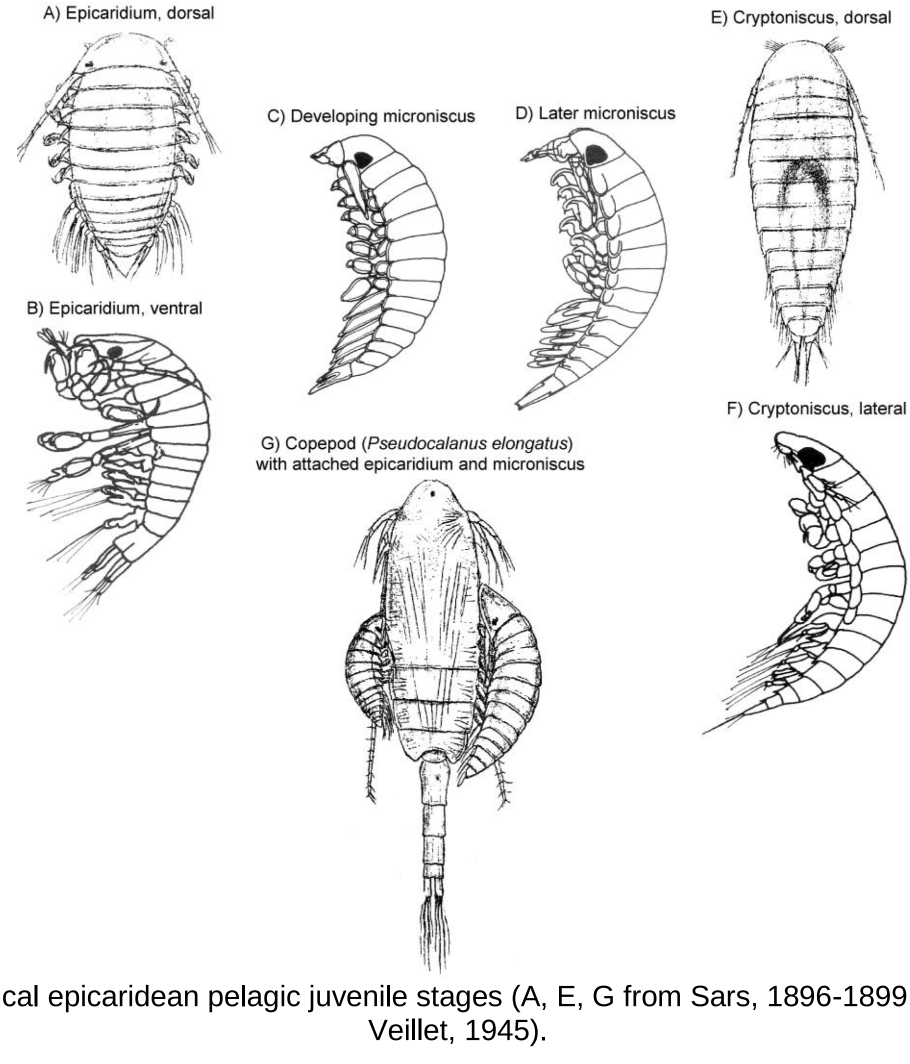

Fig. 15. Typical epicaridean pelagic juvenile stages (A, E, G from Sars, 1896-1899; B-D, F from Veillet, 1945).

Superfamily Bopyroidea:

Bopyroidea are all parasites, typically attached to large decapod crustaceans and only their pelagic, juvenile stages (Fig. 15) are likely to be collected in plankton samples. Very few are endoparasitic, almost all ectoparasitic on the carapace of hosts, some found in the branchial chambers, or under the abdomen. Adult females typically have a much modified body, often asymmetrical and with brood lamellae (Fig. 16H), while males are more like a generalized isopod, (Fig. 16I).

Bopyroidea reach sexual maturity on the definitive host and the tiny male lives on the female, and fertilises the eggs within the female marsupium. Eggs hatch within the marsupium to a broad, short, often curled up epicaridium juvenile (Fig. 15A, B) with well defined segmentation, and these are released into the water column. Their head curves ventrally and bears styliform, suctorial mouthparts, reduced antennules with two or three segments and longer antennae with four to seven segments. Anterolateral eyespots may be present. The pereion comprises seven somites, the first six bearing paired pereiopods of varying structure, or all similar, at least some with distal hooks. The pleon is of six somites, most bearing uniramous or biramous appendages.

The epicaridium attaches to a copepod intermediate host (Fig. 15G), piercing the body of the copepod, feeding on its body fluids. This juvenile then goes through a series of moults, four having been observed in some species. During the first moult the epicaridium regresses morphologically into a rudimentary microniscus (or microniscid) stage (Fig. 15C, D), without any setae or segmentation on the limbs. The pereiopods typically bear terminal hooks, apart from the seventh pair, which are rudimentary. During further moults, the body becomes more elongated and progressively less rudimentary, acquiring limb segmentation and setae until it becomes a cryptoniscus (or cryptoniscid) stage (Fig. 15E, F; front cover) and detaches to find the definitive crustacean host. From descriptions given in Sars (1896-99), the Bopyroidea cryptoniscus stage may or may not have eyes, the basal segment of the antennule is not expanded or toothed (Fig. 16D), the antennae have a flagellum of four segments, the seven pairs of pereiopods are of uniform appearance and the endopod of the uropod is much shorter than the exopod. This latter feature separates it from the cryptoniscus stage of Superfamily Cryptoniscoidea. The cryptoniscus settles on the host and moults to become a bopyridium stage (Fig. 16F) that lacks, or has reduced pleopods, but retains pereiopods. The first bopyridium becomes a female and subsequent settlers become male. The female moves to the final attachment site on the host, where it pierces the cuticle, feed on body fluids and develops into a mature individual with a massive ovary (Fig. 16H). The tiny males (Fig. 16I) effectively remains as a bopyridium, live on the females (Fig. 16H) and are not known to feed on the host. It is not clear whether they are hyperparasites on the female or do not feed at all.

There are six families in Bopyroidea and one species, *Hemiarthrus abdominalis* (Krøyer, 1840) from Family Bopyridae is given as an example (Fig. 16).

Family Bopyridae:

Genus *Hemiarthrus*:

Hemiarthrus abdominalis (Krøyer, 1840)

The epicaridium (Fig. 16A, B), microniscus and cryptoniscus (Fig. 16C) juveniles are typical of the epicaridean group. The cryptoniscus stage superficially resembles those of Superfamily Cryptoniscoidea, but the basal segment of the antennule is not greatly expanded (Fig. 16D) and the endopod of the uropod is much shorter than the exopod (Fig. 16E). The bopyridium juveniles, developing from the cryptoniscus stage, are slender and worm-like with a semi-circular head and the lateral ends of the somites bluntly pointed (Fig. 16F). The limbs are rudimentary, especially the pleopods. During development, the female still retains at least some indications of somites and limbs (Fig. 16G). The body of the fully grown female forms an irregular, globular mass (Fig. 16H), varying in form depending on the degree of distension of the marsupial pouch. One side may be more swollen than the other, so the axis of the body may be twisted to one side. The tiny adult males more or less retain their bopyridium morphology and are oblong, with the somites of the pereion widely separated (Fig. 16I). They are found clinging to the ventral face of the pereion of the female (Fig. 16H), usually partially concealed by the protruding marsupium. In immature females the attached male is sometimes still in the cryptoniscus stage (Fig. 16G).

H. abdominalis is usually recorded as a parasite on caridean shrimps of the genera *Spirontocaris* and *Pandalus*, typically attached to the basal part of one of the anterior pleopods (Fig. 16J).

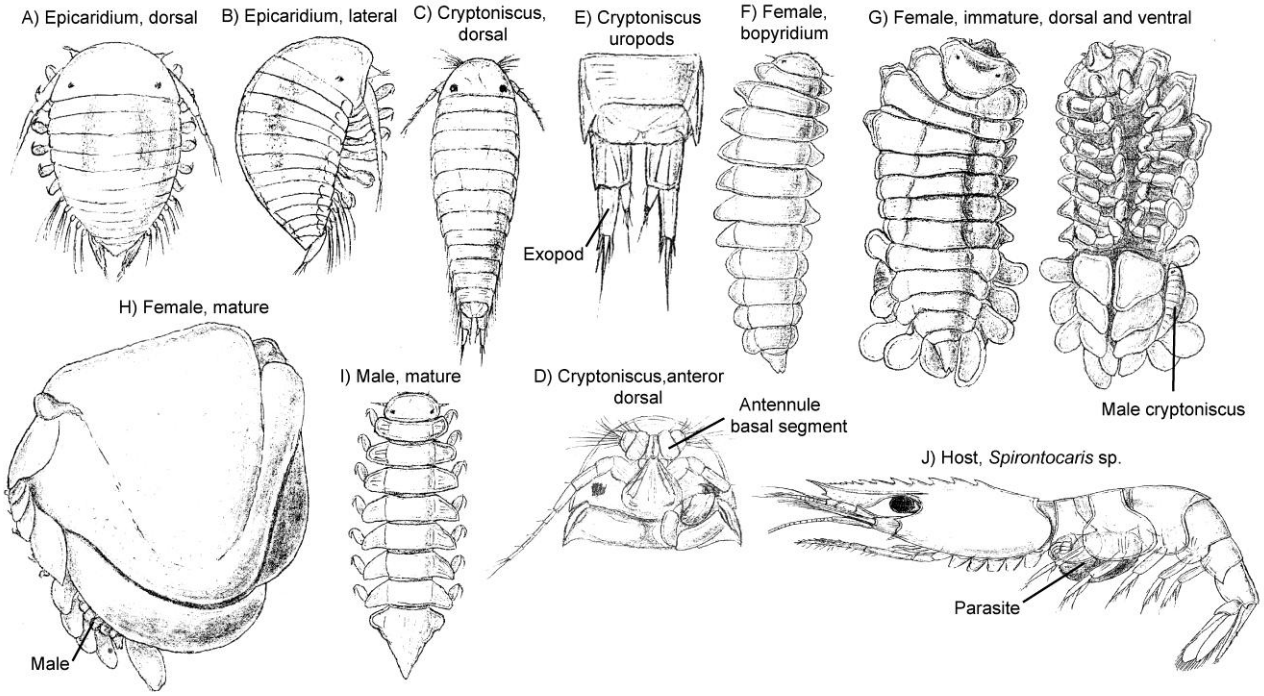

Fig. 16. *Hemiarthrus abdominalis* (from Sars, 1896-99, as *Phryxus abdominalis*).

Recorded: PMF, adults on decapods (as *Phryxus abdominalis*). L4, possibly sampled as unidentified juveniles. British coasts. Norway.

Size: Females up to ~11 mm; male ~3 mm.

Further information: Sars 1896-99; Nierstrasz & Brender á Brandis, 1926 (both as *Phryxus abdominalis*).

Superfamily Cryptoniscoidea:

Cryptoniscoidea contains eight families comprising endoparasitic adults associated with a broad range of crustacean hosts (mysids, isopods, ostracods, barnacles, amphipods and decapods) and include some species that are parasitic on other parasites (hyperparasitic). The intermediate hosts, as in Superfamily Bopyroidea, are pelagic copepods.

Cryptoniscoidea have the same pelagic stages as Bopyroidea (Fig. 15), but from descriptions given by Sars (1896-99) there are morphological differences. The basal segment of the antennule is greatly expanded behind and may be toothed, there are five segments in the flagellum of the antennae, the pereiopods vary in length and morphology and the uropod endopods are usually much longer than the exopods (Fig. 17). However, in some Cryptoniscoidea, at least in some of Family Dajidae, the uropod endopods are only slightly longer than the exopods, almost of equal length. A major difference in life cycle is that when the Cryptoniscoidea cryptoniscus settles on the definitive host they develop into hermaphrodite adults, rather than into separate sexes. Adult Cryptoniscoidea are the most highly modified parasitic isopods, often bearing little resemblance to typical isopods. They are usually sac-like forms, lacking pereiopods, brood lamellae and, in some families, all indication of somites. *Liriopsis pygmae*, (Rathke, 1843) is given as an example of this superfamily (Fig. 17).

Family Cryptoniscidae:

Genus *Liriopsis*:

Liriopsis pygmae (Rathke, 1843)

In the PMF this hyperparasitic species is recorded on the rhizocephalan cirripede parasite *Peltogaster paguri* Rathke, 1842 (Fig. 17F) while it is parasitising the hermit crab *Pagurus cuanensis* Bell, 1846 (as *Eupagurus cuanensis*). It draws resources away from the parasitic barnacle, using them for its own reproduction, so, the castrator, becomes the castrated.

The epicaridium, microniscus and cryptoniscus juveniles (Fig. 17A, B) are typical of the epicaridean group. The endopod of the uropod in the cryptoniscus differs from Bopyroidea cryptoniscus stages in being much longer than the exopod (Fig. 17D); eyes well developed; basal segment of the antennule projecting in front to a strong denticle, with a large tongue-like expansion behind, without any setae or teeth (Fig. 17C); antenna well developed, extending to end of fourth pereion somite; poor development of the last two pairs of pereiopods.

The adults are protandric hermaphrodites, being first male then female. Female looses segmentation; body of two sharply defined sections connected by a narrow neck (Fig. 17E), the anterior section of four poorly defined somites buried in the host (Fig. 17F), the posterior section exposed and without trace of somites.

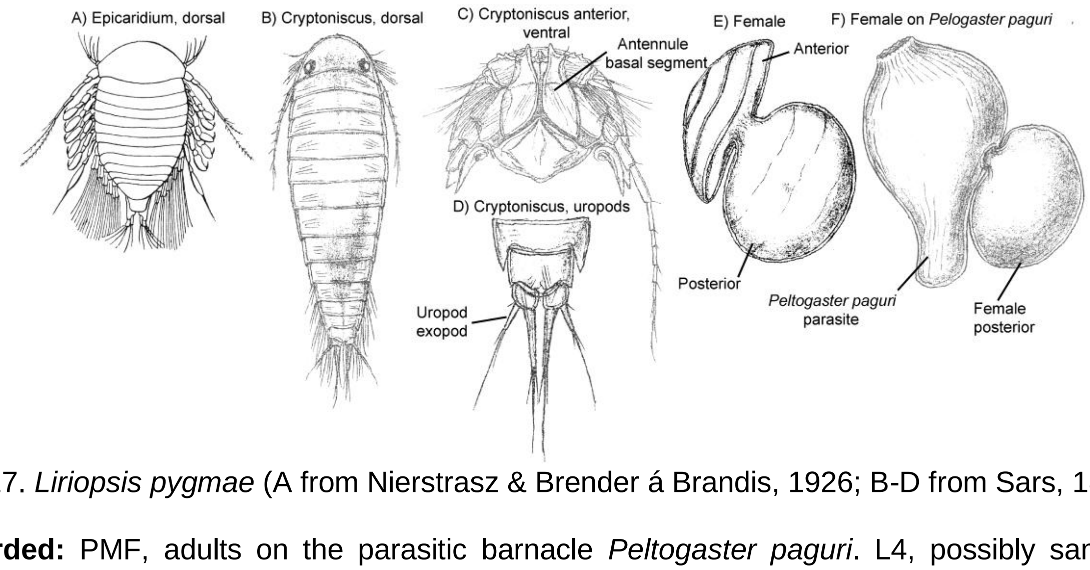

Fig. 17. *Liriopsis pygmae* (A from Nierstrasz & Brender á Brandis, 1926; B-D from Sars, 1896-99).

Recorded: PMF, adults on the parasitic barnacle *Peltogaster paguri*. L4, possibly sampled as unidentified juveniles. North Sea. English Channel. Irish Sea.

Size: Adults ~5 mm; cryptoniscus ~1.35 mm.

Further information: Sars, 1896-99; Nierstrasz & Brender á Brandis, 1926; Naylor, 1972; Hayward *et al*., 1995.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Isopoda:

Suborder Limnoriidea

Superfamily Limnorioidea

There are three families in this superfamily, but only Family Limnoriidae is recorded in the PMF.

Family Limnoriidae:

They are wood-boring isopods, so unlikely to be sampled in plankton nets, but one species, *Limnoria lignorum* (Rathke, 1799), is given as an example (Fig. 18).

Genus *Limnoria*:

Limnoria lignorum (Rathke, 1799)

Body about three times as long as broad (Fig. 18A, B); head nearly globular and partially covered dorsally by first pereion somite (Fig. 18C), which is longer than the others. Antennule and antenna flagellae with four segments. Pereion coxal plates fringed with ciliated bristles (Fig. 18C, D), the two anterior pairs oval quadrangular, the four posterior ones considerably larger and posteriorly produced to acute corners. Pleon of five free somites, fifth with a mid-dorsal, longitudinal ridge (carina; Fig. 18B); pleotelson with an anteriorly situated mid-dorsal longitudinal carina that bifurcates posteriorly and lacks tubercles, posterior margin broadly rounded with a fringe of small, dorsally directed strong setae (Fig. 18D); pleopods with marginal setae, except fifth; uropods tubular, exopod short, claw-like.

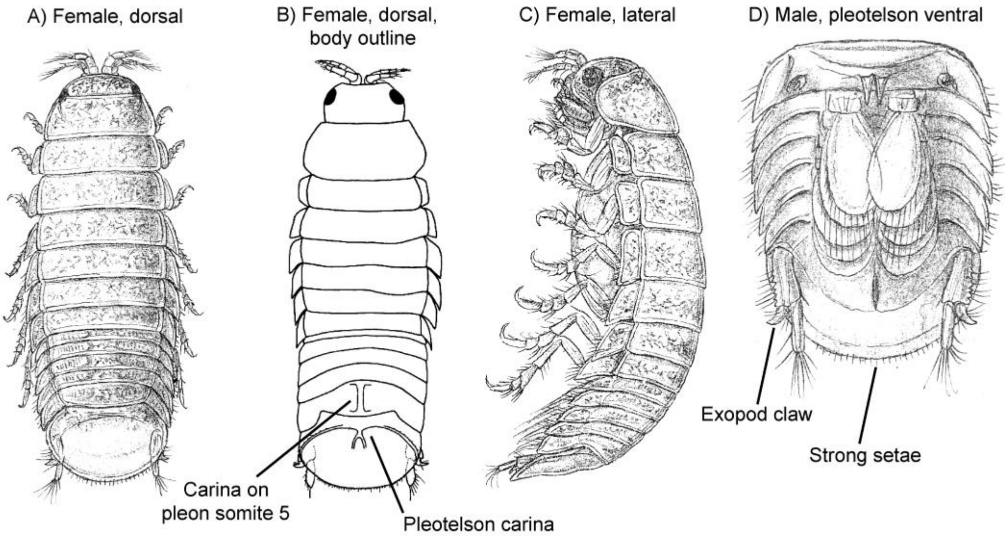

Fig. 18. *Limnoria lignorum* (from Sars, 1896-99).

Recorded: PMF. L4, not recorded. All northern European coasts.

Size: Up to 5 mm.

Further information: Sars, 1896-99; Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1972; Hayward *et al*., 1995.

Suborder Sphaeromatidea

One species from Family Sphaeromatidae, *Sphaeroma serratum* (Fabricius, 1787), is included as an example (Fig. 19).

Family Sphaeromatidae:

Genus *Sphaeroma*:

Sphaeroma serratum (Fabricius, 1787)

Body oval in outline (Fig. 19A, B), readily rolling into a ball. Coxal plates of pereion somites two to seven fused with the somites. Pereiopod one ischium with up to about 60 plumose setae in two rows (Fig. 19C), propodus with a distal row of 15 to 20 setae. Pleon with first five somites fused, the last two incompletely; pleotelson with a smooth dorsal surface and not extending beyond uropods (Fig. 19A, B), posterior border smoothly rounded or slightly acute; uropods lateral, with the exopod and endopod subequal in length, endopod rounded distally, exopod with four to seven well defined serrations on outer edge. Sexes separable when between 5 mm and 7 mm.

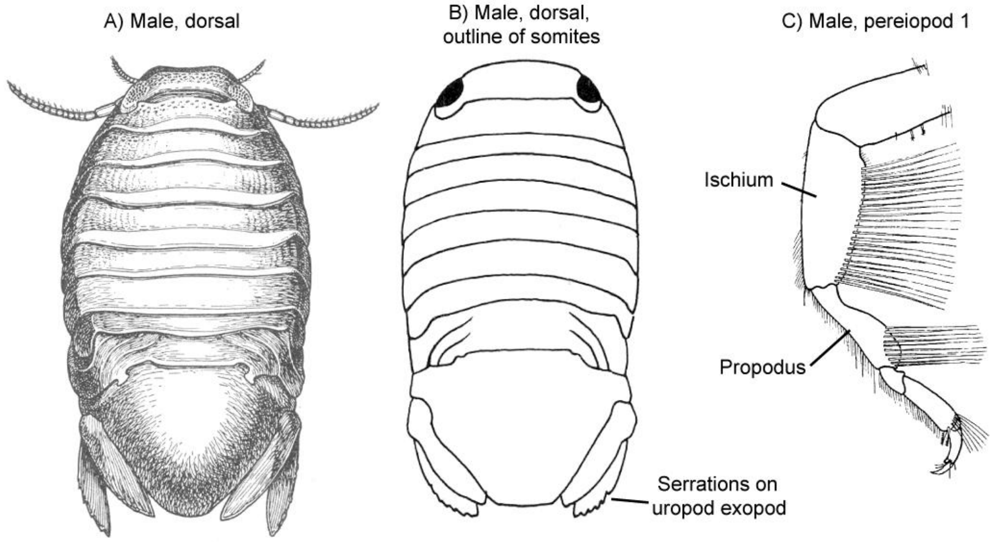

Fig. 19. *Sphaeroma serratum* (A from Torelli, 1930; B, C from Naylor, 1972).

Recorded: PMF. L4, not recorded. Southern Britain and Ireland. Northern French coast.
Size: Females up to 10 mm; males up to 11.5 mm.
Further information: Nierstrasz & Schuurmans Stekhoven, 1930; Torelli, 1930; Naylor, 1972; Hayward *et al*., 1995.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca; Superorder Peracarida: Order Isopoda:

Suborder Valvifera

There are 11 families in Suborder Valvifera, but only two are recorded in the PMF, **Idoteidae** and **Arcturidae**. All the 11 British species of Family Idoteidae are recorded in the PMF, and all are described here, as they are often sampled in low numbers in plankton nets, particularly in very shallow water. There are four species of Family Arcturidae recorded in the PMF, but are unlikely to be taken in plankton nets, so only one species is included as an example.

Key to Family Idoteidae (after Naylor, 1972)

1. Pleon with no distinct somites, partial sutures (not visible from above) indicate almost complete pleon/telson fusion -- **2**
- Pleon of 2 or 3 distinct somites, remainder fused or partially fused ------------------------------ **3**

2. Pereion lateral borders with serrated profile; pleotelson concave anteriorly, expanded posteriorly then narrowing to elongate tip -------------------------- *Stenosoma lancifer* (Fig. 29)
- Pereion lateral borders straight, parallel profile; pleotelson narrowing evenly to an acute tooth -- *Stenosoma acuminatum* (Fig. 30)

3. Pleotelson of 3 free somites and one partial suture; isopod typically found inside a case of organic material -- *Cleantis prismatica* (Fig. 28)
- Pleotelson of 2 free somites and one partial suture --------------------------- Genus *Idotea* --- **4**

4. Pleotelson apical border reasonably straight, or concave -- **5**
- Pleotelson apical border obviously produced centrally --- **7**

5. Body obviously narrow, pereion somites rounded laterally, coxal plates very small, not reaching posterior margin of any pereion somites ---------------------- *Idotea linearis* (Fig. 27)
- Body broad, coxal plates 3 to 7 reaching posterior margin of pereion somites ---------------- **6**

6. Pleotelson in adult with apical border concave, lateral borders slightly convex; head lacking complete suture behind the eyes ------------------------------------- *Idotea emarginata* (Fig. 21)
- Pleotelson in adult with apical border and lateral borders straight; head with distinct sinuous suture behind conspicuous eyes -- *Idotea metallica* (Fig. 26)

7. Pleotelson hind border with, or nearly with three blunt teeth --------- *Idotea balthica* (Fig. 20)
- Pleotelson hind border with single blunt tooth, lateral hind borders rounded ------------------- **8**

8. Pleotelson lateral borders in adult slightly concave, hind border with pronounced, acute central tooth --- *Idotea granulosa* (Fig. 23)
- Pleotelson sides in adult straight or slightly convex, hind border with at most an indistinct, blunt central tooth --- **9**

9. Antenna with flagellum much shorter than peduncle; flagellum densely covered with fine setae in males --- *Idotea pelagica* (Fig 25)
- Antenna with flagellum longer than peduncle; flagellum not densely covered with fine setae in males --- **10**

10. Body quite slender, length usually 4-5 times width; antennule reaching segment 4 of peduncle of antenna -- *Idotea chelipes* (Fig. 24)
- Body more robust, length around 3 times width; antennule only reaching segment 3 of peduncle of antenna -- *Idotea neglecta* (Fig. 22)

Genus *Idotea*:

Idotea balthica (Pallas, 1772)

Body oblong oval (Fig. 20A); antennule extending to or just beyond segment three of the peduncle of antenna; antennal flagellum longer than peduncle and about a quarter of body length. Coxal plates of pereion somites large in adults, extending from the anterior to the posterior borders of somites two or three to seven; pereiopods all similar. Pleon of two free somites, pleotelson with one partial suture, dorsally keeled, with more or less straight sides, terminating in a central blunt tooth and two shorter lateral ones (Fig. 20A-C) that are generally well defined, though lacking in juveniles (Fig. 20C); uropods typical of the genus, covering the pleopods, uniramous, shield-shaped (Fig. 20B).

Colour when fresh sometimes uniformly green or brown, but often with white spots or longitudinal lines and female often darker than male. Colour can vary geographically and seasonally (Salemaa, 1979).

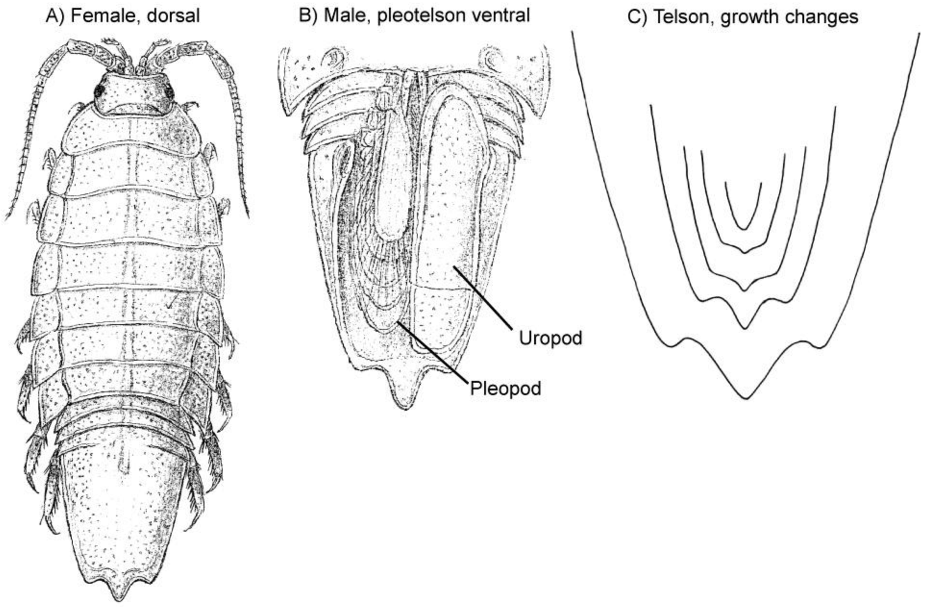

Fig. 20. *Idotea balthica* (A, B from Sars, 1896-99, as *Idothea baltica*; C from Naylor, 1972, as *Idotea baltica*).

Recorded: PMF (as *Idotea baltica*). L4, not recorded. North Sea.
Size: Females 10-18 mm; males 10-30 mm
Further information: Sars, 1896-99 (as *Idothea baltica*); Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a, 1972; Hayward *et al*., 1995 (latter three as *Idotea baltica*).

Idotea emarginata (Fabricius, 1793)
Body oblong oval (Fig. 21A, B); head subquadrate, partial or no suture behind the eyes; eyes prominent; antennule extending beyond segment three of the peduncle of antenna; antennal flagellum longer than peduncle and around one fifth body length. Pereion coxal plates broad, extending over the whole length of somites two to seven, larger in males; pereiopods all similar. Pleon of two free somites, pleotelson with one partial suture, lateral borders slightly convex, posterior border concave, but varies during growth (Fig. 21C); uropods uniramous, shield-shaped.
When fresh, colour of males often uniformly brown, though sometimes with white markings, females generally darker in background colour, often with longitudinal lateral white bands, or alternating white and darker transverse bands.

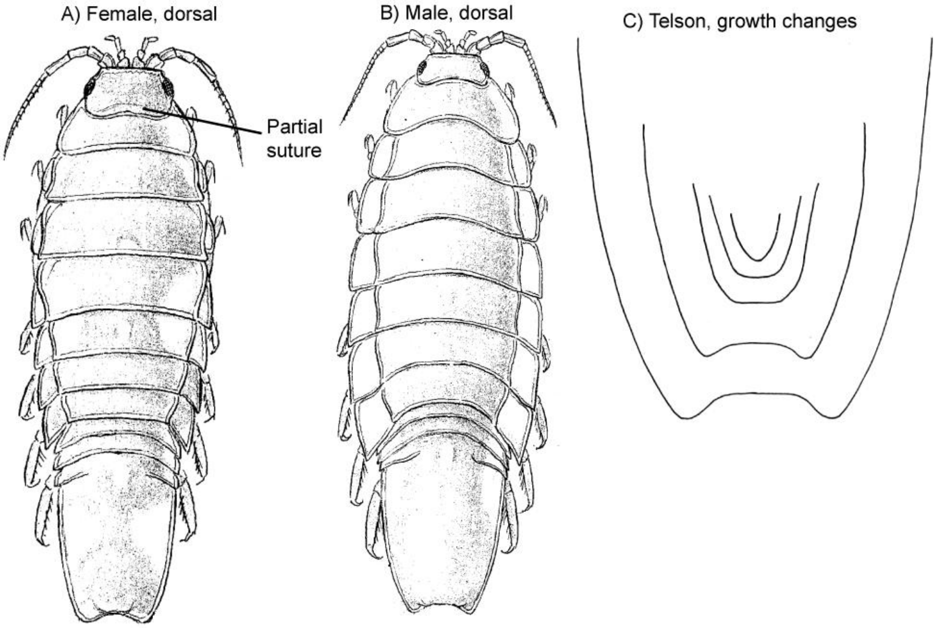

Fig. 21. *Idotea emarginata* (A, B from Sars, 1896-99, as *Idothea emarginata*; C from Naylor, 1972).

Recorded: PMF. L4, not recorded. North Sea.
Size: Females 9-18 mm; males recognisible from 7-9 mm and ranging to ~30 mm.
Further information: Sars, 1896-99 (as *Idothea emarginata*); Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a, 1972; Hayward *et al*., 1995.

Idotea neglecta Sars, 1897
Body oblong oval (Fig. 22A, B), length around 3 times width, female slightly shorter and stouter; head subquadrate; eyes prominent; antennule more or less reaching the distal end of segment three of peduncle of antenna; antennal flagellum longer than peduncle and around quarter of body length. Pereion coxal plates wide extending the whole length of pereion somites two or three to seven, larger in male; pereiopods all similar. Pleon of two free somites, pleotelson with one partial suture, the lateral borders fairly straight and converging posteriorly, posterior border with a median blunt tooth and rounded lateral shoulders, keeled; uropods uniramous, shield-shaped.
Colour when fresh, often uniformly brownish or almost black, sometimes with white longitudinal lateral markings, and occasionally with white marbling over the whole dorsal surface. Adult females usually darker than males.

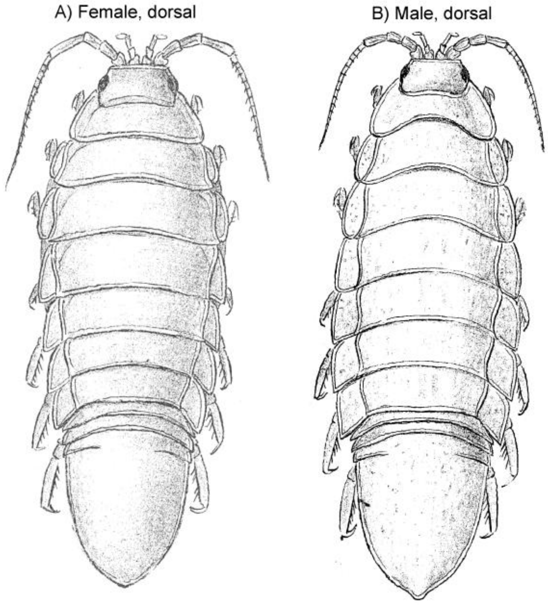

Fig. 22. *Idotea neglecta* (from Sars, 1896-99, as *Idothea neglecta*).

Recorded: PMF. L4, not recorded. North Sea.
Size: Adult females ~10-16 mm; males recognisable from ~8 mm, ranging to ~30 mm.
Further information: Sars, 1896-99, as *Idothea neglecta*; Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a, 1972; Hayward *et al*., 1995.

Idotea granulosa Rathke, 1843

Benthic, but sometimes pelagic. Body oval, narrowing rather sharply posteriorly (Fig. 23A, B); head subquadrate, eyes prominent. Antennule extending beyond segment two but not segment three of the peduncle of the antenna; antennal flagellum not as long as the peduncle and usually less than one fifth of the total body length. Coxal plates of pereion fairly narrow, only in somites five to seven reaching the posterior somite borders; pereiopods all more or less similar. Pleon of two free somites, pleotelson with one partial suture, narrowing sharply, with slightly concave lateral margins anteriorly, distally with a long, acute, central tooth and very rounded lateral shoulders, not keeled; uropods shield-shaped, uniramous.

Colour when fresh, mostly uniformly brown, red or green, depending on the nature of the weed inhabited, occasionally with longitudinal white markings.

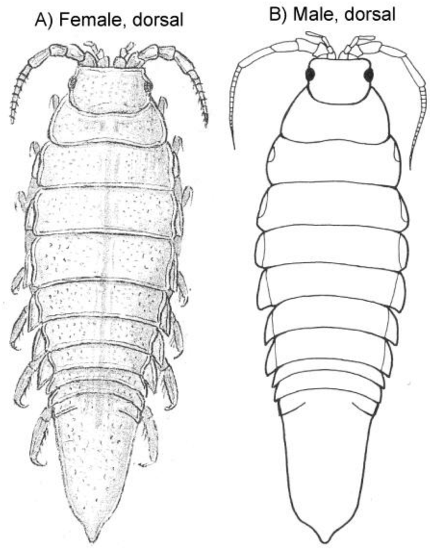

Fig. 23. *Idotea granulosa* (A from Sars, 1896-99, as *Idothea granulosa*; B from Naylor, 1957a).

Recorded: PMF. L4, not recorded. North Sea. Irish Sea.

Size: Females 6-13 mm; males up to ~20 mm.

Further information: Sars, 1896-99 (as *Idothea granulosa*); Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a, 1972; Hayward *et al*., 1995.

Idotea chelipes (Pallas, 1776)
Benthic, brackish water species. Body slender (Fig. 24), length four to five times width (except in ovigerous females, which are wider; antennule extending well beyond segment three of the peduncle of antenna similar to *I. linearis* (Fig. 27), but unlike other *Idotea* species, where they only extend beyond segment two. Antennal flagellum slightly longer than peduncle and about a quarter of body length; head subquadrate, eyes prominent; coxal plates narrow, only those of pereion somites five to seven reaching the posterior somite borders; pereiopods all quite similar. Pleon of two free somites, pleotelson with one partial suture, sides subparallel, slightly keeled posteriorly in the mid-dorsal line, distal border with a blunt, median tooth, with rounded lateral corners; uropods uniramous, shield-shaped.
Colour when fresh mostly uniformly green or brown sometimes with white markings; females often darker than males. Males recognisable from about 5 mm body length,

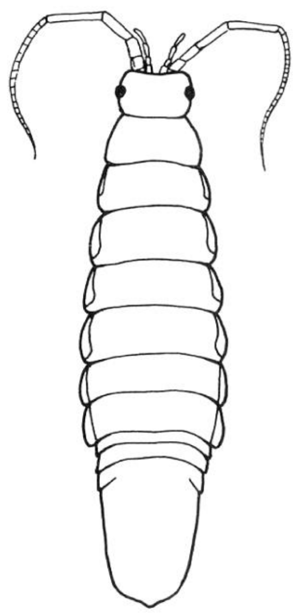

Fig. 24. *Idotea chelipes* (A from Naylor 1957a).

Recorded: PMF. L4, not recorded. North Sea. Irish Sea.
Size: Females ~6-10 mm; males up to 15 mm.
Further information: Sars, 1886-89 (as *Idothea viridis*, in plate as *I. angusta*); Nierstrasz & Schuurmans Stekhoven, 1930 (as *Idotea viridis*); Naylor, 1957a, 1972; Hayward *et al*., 1995.

Idotea pelagica Leach, 1815

Body short and stout (Fig. 25A, B); antennule extending well beyond segment two, but hardly beyond segment three of the peduncle of antenna. Antenna very robust (Fig. 25C), flagellum shorter than the peduncle and less than one sixth of the body length and with areas of fine setae in adult males. Head subquadrate, eyes prominent. Pereion coxal plates fairly broad, widening posteriorly, reaching the posterior border of somites four to seven. Pereiopods all very robust, the terminal claw being relatively larger than that of other *Idotea* spp. Pleon of two free somites, pleotelson with one partial suture, not keeled, distal border broadly rounded with slight, blunt tooth; uropods uniramous, shield-shaped.

Colour when fresh generally dark purple-brown, with white diamond-shaped patches or elongated stripes down the mid-dorsal line, and with white markings along the edges of the dorsal side; females often darker than males.

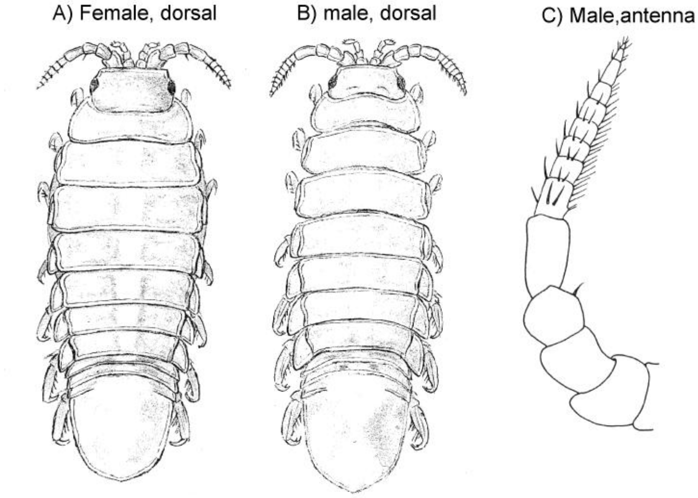

Fig. 25. *Idotea pelagica* (A, B from Sars, 1896-99, as *Idothea pelagica*; C from Naylor, 1972).

Recorded: PMF. L4, not recorded. North Sea. Irish Sea.
Size: Females 7-10 mm; males up to 11 mm.
Further information: Sars, 1896-99 (as *Idothea pelagica*); Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a, 1972; Hayward *et al*., 1995.

Idotea metallica Bosc, 1802
Body oblong (Fig. 26), head subquadrate, with a marked transverse sinuous suture behind the eyes thatb is not found in any other British species; eyes large and bulbous. Antennule hardly extending beyond segment three of the peduncle of antenna; antenna robust, flagellum shorter than peduncle and about one sixth body length. Coxal plates triangular, extending over the whole length of pereion somites two or three to seven; coxal plates five to seven sharply produced posteriorly; pereiopods all quite similar. Pleon of two free somites, pleotelson with one partial suture, lateral and posterior borders straight; uropods uniramous, shield-shaped.
Colour when fresh, uniformly greyish or brown.

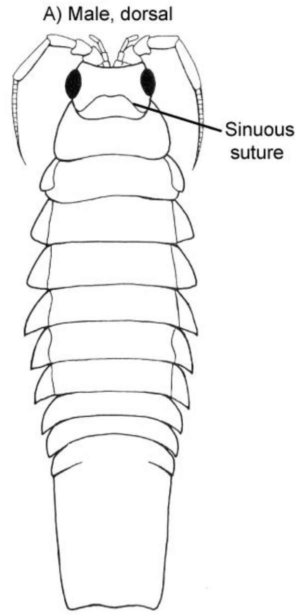

Fig. 26. *Idotea metallica* (from Naylor, 1957a).

Recorded: PMF. L4, not recorded. English Channel. Irish Sea. Western Ireland.
Size: Females ~9-18 mm; males recognisable from about 8 mm, ranging to about 30 mm
Further information: Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a, 1972; Hayward *et al*., 1995.

Idotea linearis (Linnaeus, 1766)
Body very narrow (Fig. 27), length four to seven times width; head subquadrate, eyes prominent. Antennule extending beyond segment three of the antennal peduncle as in *I. chelipes* (Fig. 24), but unlike other *Idotea* species where they only extend beyond segment two; antenna very long and slender, peduncle longer than the flagellum, which is about a third of the body length. Pereion somites rounded laterally, giving 'beaded' appearance to body; coxal plates very small, not extending to the posterior border of any pereion somite, pereiopods long and slender. Pleon of two free somites, pleotelson with one partial suture, lateral borders slightly concave anteriorly, posterior border concave, with a small median spine in young specimens; uropods uniramous.
Colour when fresh, green or brown, with darker or lighter longitudinal stripes; adult female often darker than male, frequently with paler markings around the edges.

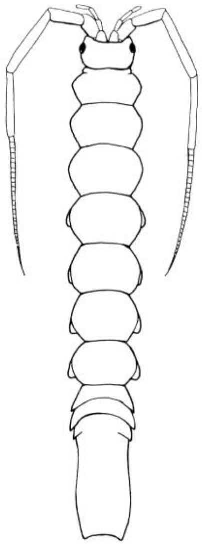

Fig. 27. *Idotea linearis* (from Naylor, 1972).

Recorded: PMF. L4, not recorded. English Channel. Irish Sea. North Sea.
Size: Female, smaller than male; male recognisable from about 15 mm, ranging to over 40 mm
Further information: Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1957a; Naylor, 1972; Hayward *et al*., 1995.

Genus *Cleantis*:

Cleantis prismatica (Risso, 1826)

Body long, slender and parallel sided (Fig. 28), head subquadrate, with small lateral eyes; antennules reaching end of segment three of the very short antennae. Coxal plates small and narrow, but distinct on at least pereion somites four to seven. Pleon of three free somites, pleotelson with one partial suture, pleon and proximal pleotelson lateral borders fringed with setae, pleotelson posterior border rounded.

Typically found inside a case fabricated from plant material, or old worm tubes.

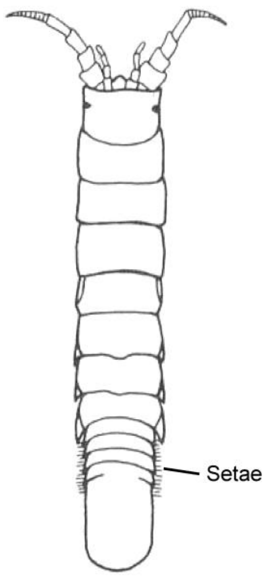

Fig. 28. *Cleantis prismatica* (from Naylor, 1957a, as *Zenobiana prismatica*).

Recorded: PMF (as *Zenobiana prismatica*). L4, not recorded. Irish Sea. English Channel.
Size: Up to 13.5 mm.
Further information: Naylor, 1957a, 1972; Hayward *et al*., 1995 (all as *Zenobiana prismatica*).

Genus *Stenosoma*:

Stenosoma lancifer Miers, 1881

Body elongate (Fig. 29), head projecting forwards laterally, eyes lateral, quite small. Pereion coxal plates small, triangular, giving symmetrical serrated profile to body. Pleon with no distinct somites, all fused, pleotelson lateral borders concave anteriorly, widening towards rear, then narrowing sharply to an elongate, median tooth.

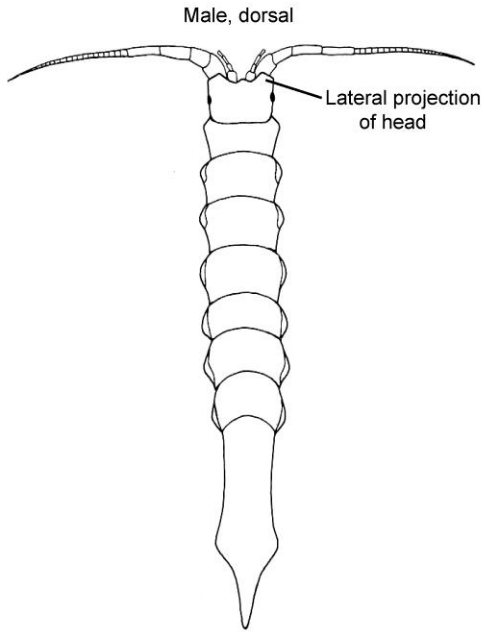

Fig. 29. *Stenosoma lancifer* (from Naylor, 1957a, as *Synisoma lancifer*).

Recorded: PMF (as *Synisoma lancifer*). L4, not recorded. English Channel.
Size: Females smaller than males; males up to 22.5 mm.
Further information: Naylor, 1957a, 1972; Hayward *et al*., 1995 (all as *Synisoma lancifer*).

Stenosoma acuminatum Leach, 1814

Body elongate, subcylindrical (Fig. 30), lateral borders straight and parallel; head projecting forwards laterally, eyes lateral, quite small. Pereion coxal plates very small, hardly visible from above. Pleon with no distinct somites, all fused, pleotelson without lateral shoulders, narrowing fairly evenly to an acute terminal tooth.

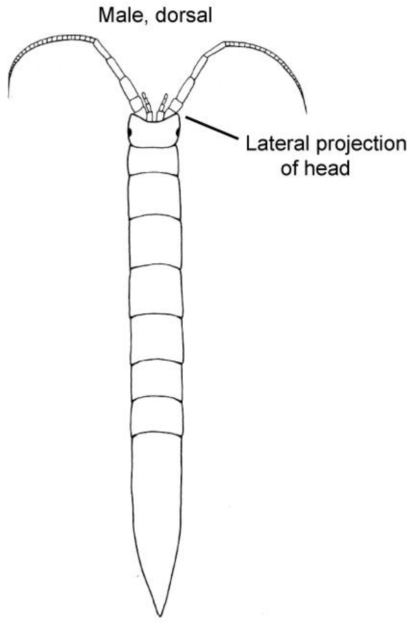

Fig. 30. *Stenosoma acuminatum* (from Naylor, 1957a, as *Synisoma acuminatum*).

Recorded: PMF (as *Synisoma acuminatum*). L4, not recorded. English Channel. Irish Sea. Western Ireland.

Size: Up to 25 mm

Further information: Naylor, 1957a, 1972; Hayward *et al*., 1995 (all as *Synisoma acuminatum*).

Family Arcturidae:

These curious benthic isopods are very unlikely to be sampled in plankton nets, but one, *Astacilla longicornis* (Sowerby, 1806), is included as an example (Fig. 31).

Genus *Astacilla*:

Astacilla longicornis (Sowerby, 1806)

Body extremely slender and subcylindrical (Fig. 31), anterior head produced dorsolaterally into a projection each side, the central portion deeply concave, eyes large, antennae very long. Pereion somite four around twice the length of anterior body, the surface covered with small tubercles in female (Fig. 31A, B), in male cylindrical with smooth surface (Fig. 31C); coxal plates of second to fourth somite very small, those of the three posterior somites well developed, triangular, extending laterally; pereiopods one to four directed forwards, elongate with long plumose setae (Fig. 31B, C), pereiopods five to seven short, strong and hooked for clinging; pleotelson cylindrical, pointed; uropods long, triangular.

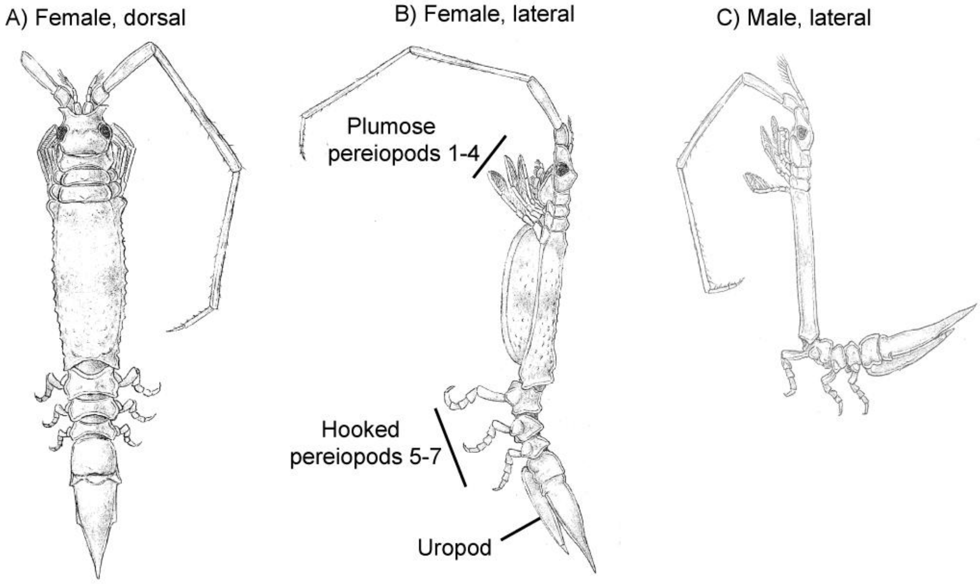

Fig. 31. *Astacilla longicornis* (from Sars 1896-1899).

Recorded: PMF. L4, not recorded. North Sea. English Channel. Irish Sea.
Size: Female, up to 30 mm; male up to 10 mm.
Further information: Sars 1896-1899; Nierstrasz & Schuurmans Stekhoven, 1930; Naylor, 1972; Hayward *et al*., 1995.

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Order Cumacea:

Cumaceans are almost entirely marine and brackish water crustaceans, abundant in shallow coastal areas, but also found at depth, where there is greater species diversity. There are no known planktonic species, most spending their lives on the sea bottom, burrowing in the sediments, but they are frequently collected in plankton nets, particularly during turbulent conditions in shallow waters. Additionally, many coastal species show a diurnal cycle, with males especially emerging from the sediments at night and swarming at the surface. Cumaceans mainly feed on microorganisms and organic material. In a few species the mandibles are transformed into piercing appendages that may be used for predation on small organisms.

Classification

According to the current WoRMS classification, Order Cumacea is subdivided into nine families, but is in process of reorganisation. Members of six of these nine families (see below) are known to occur in European shelf waters (Jones, 1976), with at least 41 species recorded from within 30 kilometers of the UK coast. Jones (1976) provides a key to these six families and species, updated by Shalla (2011), but as these benthic organisms are really outside the scope of this guide, only a brief description, to enable identification to at least Order Cumacea, is given here. Some 15 species are recorded in the PMF from the Plymouth region and numbers recorded in each family is given in brackets below as an example of typical coastal biodiversity.

Family Bodotriidae (5)
Family Diastylidae (6)
Family Lampropidae (0)
Family Leuconidae (1)
Family Nannastacidae (2)
Family Pseudocumatidae (1)

Morphology

Cumacea are a very distinctive and quite uniform order, easily recognisable by their strongly enlarged anterior body region (Fig. 1), slender pleon terminating in forked, styliform uropods and their lack of conspicuous eyes, giving them a tadpole-like appearance. As with other Peracarida, females develop a marsupium (brood pouch) in which the young are brooded. Terminology currently used for sections of the body is carapace for the anterior, fused with the first three thoracic somites (Fig. 1A-E), pereion for the remaining five unfused thoracic somites and pleon for the abdominal region.

Carapace: The carapace is latterly developed into overhanging folds that cover the feeding and branchial appendages. The anterior carapace is produced into a lappet on each side to form pseudorostral lobes (Fig. 1A) that project forwards and come together, but are not fused, forming a pseudorostrum. Behind the pseudorostrum is a triangular or rounded frontal lobe, typically bearing anteriorly a tiny, simple, single eye composed of a globular ocular lobe studded with minute visual elements (Fig. 1A, F, G), although one genus has paired eyes. The visual elements are usually not all paired and one central element is often larger than the others. From the illustrations given in Sars (1900) number of elements appears to vary between three and eight, depending on species. In some species the visual elements may be absent, but the ocular lobe may persist. The eye in males is typically more developed than in females. In developing juveniles there are paired, close-set eyes (Fig. 1J, K) that fuse, probably before the juveniles leave the marsupium. The antennule usually has two flagellae, the outer typically longer than the inner one. The antenna has one flagellum, the whole appendage rudimentary and tiny in females. In males the flagellum is well developed and typically very long (Fig. 1C, D), sometimes modified for clasping the female.

Pereion: The pereion is composed of five unfused thoracic somites (Fig. 1C), but in some species some of these may also be fused with the carapace, or some at least partially fused with each other. Each pereion somite bears pereiopods (Fig. 1B) that are similar in form, but vary in orientation. In adult females a marsupium is present, formed from brood lamellae (oostegites) on the third to sixth pereiopods (Fig. 1H).

Pleon: The pleon (abdomen) consists of six cylindrical somites (Fig. 1C), the fifth typically the longest. Pleopods are almost always missing in females (Fig. 1B), while in males one to five pairs may be present (Fig. 1D), or there may be none. The sixth pleon somite bears paired styliform, biramous uropods (Fig. 1A), each with an exopod of two segments and an endopod with anywhere from one to three segments. This somite also bears a telson that can be short (Fig. 1I) or long (Fig. 1A), is usually free and can articulate, but in some families is fused with the sixth pleon somite as a pleotelson and only projects backwards slightly (Fig. 1E).

The sexes have different ornamentation (setation, knobs, and ridges) on the exoskeleton, the surface often sculptured with grooves, ridges, spines, tubercles, setae and may have a fine reticulated, pitted or scaled appearance, sometimes even covered in sand grains.

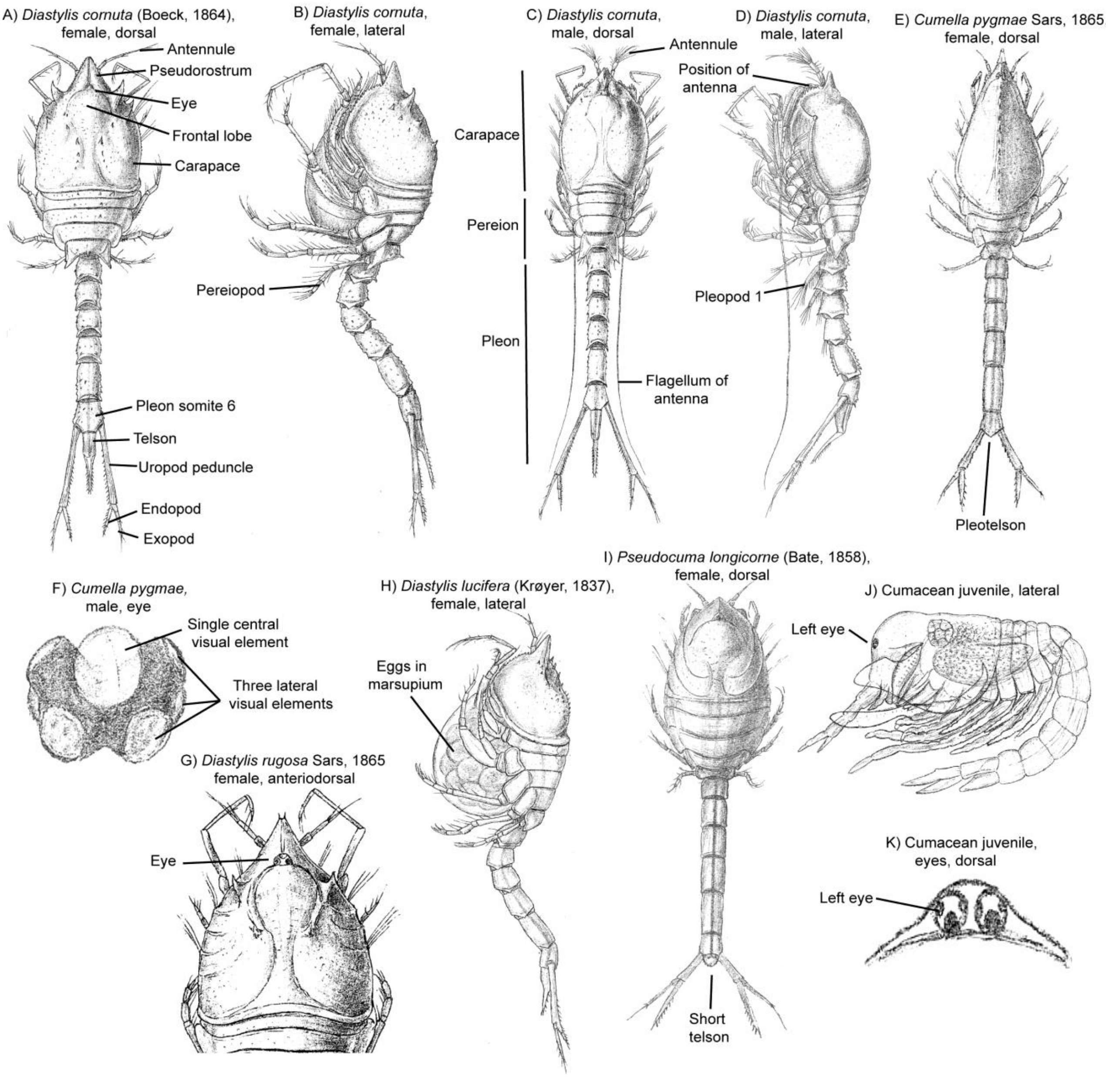

Fig. 1. Cumacean morphology (from Sars, 1900; *Pseudocuma longicorne* as *P. cercaria*).

Reproduction and development

Most shallow water species live for one year or less, and reproduce twice in their lifetime. After fertilisation the eggs are released into the marsupium, where they may be brooded for between one and three months depending on species and water temperature. The juveniles leave the marsupium as miniature adults, almost fully developed, only their last pair of pereiopods missing. They moult several times until they reach the pre-adult stage, when the gonads mature. On moulting to the adult stage the marsupium is fully developed in the female and the second antennal flagellum and pleopods in the male (when present). In large species the female may moult at least two more times, leading to a second or third reproductive period. There are generally more females than males in samples and females are also larger than males. Cumaceans are unusual in that the number of body segments does not change during development (epimorphic).

Recorded: PMF. L4, but not identified to species. All European areas.
Size: Mainly ~1-10 mm, but some up to 35 mm.
Further information: Sars, 1900; Fage, 1951; Jones, 1957, 1976; Schram, 1986; Hayward *et al*., 1995; Băcescu & Petrescu, 1999; Larink & Westheide, 2011; Shalla, 2011.

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Superorder Eucarida:
Order Euphausiacea:

Euphausiids, or krill, are relatively large, pelagic shrimp-like organisms, of which there are around 86 valid species. There are two families, **Bentheuphausiidae** and **Euphausiidae**, of which only genera from the latter should be sampled on the shallow, northern European shelf, so Bentheuphausiidae have not been included here. Family Euphausiidae are unique among crustaceans in having light organs (photophores) distributed over specific parts of their bodies and also conspicuous external gills. While popularly associated with Antarctic waters, where they are fished commercially, they can also comprise a considerable proportion of the total zooplankton biomass in the northern European area (see front cover), especially in winter. They often swarm in large numbers and are notable for their vigorous diurnal vertical migratory behaviour. Only three euphausiid species are recorded in the PMF, of the five that are likely to be sampled on the northern European shelf. These five are described here, plus another four rarer species that could potentially be sampled in deeper water areas.

Morphology

Cephalothorax: The anterior body is covered by the carapace, which extends posteriorly and is fused to all the thoracic somites, unlike in Peracarida, where only some of the anterior thoracic somites are incorporated. Because of this fusion, the whole cephalic/thoracic region is termed the cephalothorax (Fig. 1). The frontal plate of the anterior carapace is extended anteriorly into a rostrum of varying length, depending on species. The rostrum is never spiny, as found in some decapods. A dorsal keel (or carina) may also be present behind the frontal plate. In some species postocular spines may be located anteriorly on the carapace (Fig. 5) and sometimes there are one or two small denticles on the lower, lateral carapace margins. The paired antennules each consist of a three-segmented peduncle bearing two multi-segmented flagellae. The peduncle segments sometimes bear projections such as recurved lappets (or leaflets; Fig. 5) and comb-like processes (Fig. 6) etc. The paired antennae have a basal segment bearing a flattened antennal scale and also a three-segmented peduncle ending in a single, long flagellum. The generally large and black compound eyes vary from being circular in shape (Fig. 1) to sub-circular (Fig. 7A) or bilobed (Fig. 10A) and are borne on short stalks. Emerging from below the carapace are various small feeding appendages, that are relatively hidden, and up to eight generally large, paired thoracic limbs termed pereiopods (or thoracopods), the last pair usually reduced, sometimes the last two pairs (Fig. 1). The pereiopods are typically biramous, the endopod usually long and used to filter food, while the short exopods produce water currents over the feathery gills that they bear laterally. The gills are simple flaps on the first pair of limbs, more elaborate on the others, especially the last. In some species the second or third pereiopods are particularly elongated (Figs. 9, 10A, 13A) and distally may bear tufts of spines or simple chelae.

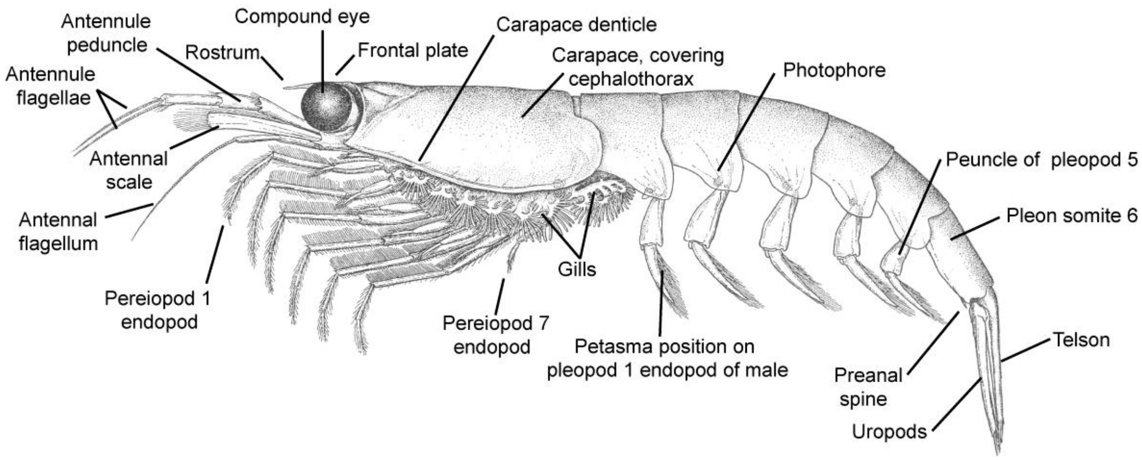

Fig. 1. Generalised adult euphausiid morphology (basic figure from Einarsson, 1945).

Pleon: The posterior body (abdomen) is termed the pleon and is always composed of six somites. The dorsal surface of somites three to five may be raised to form a longitudinal keel. Ventrally the first five somites bear paired, biramous pleopods used in swimming. In males the endopods of the first and second pairs of pleopods are modified as copulatory organs. The first pleopod endopod is modified as a petasma (Fig. 2A), the rami developed as lobes, some with secondary lobes, hooks or spines, all folded on each other, the morphology species specific. The second pleopod bears an appendix masculina. The last (sixth) pleon somite in both sexes usually bears a small, dorsoposterior preanal spine. Laterally there are biramous uropods and centrally an elongate subtriangular telson, armed distally with a pair of lateral spines (Fig. 4F).
The external opening to the female reproductive tract is termed the thelycum (Fig. 2B) and is found on the ventral surface of the cephalothorax at the base of the sixth pereiopod. It generally consists of various outgrowths from the ventral body wall and the coxal plates, but is difficult to observe in detail. A pair of spermatophores are often attached and these are typically light brown in colour.

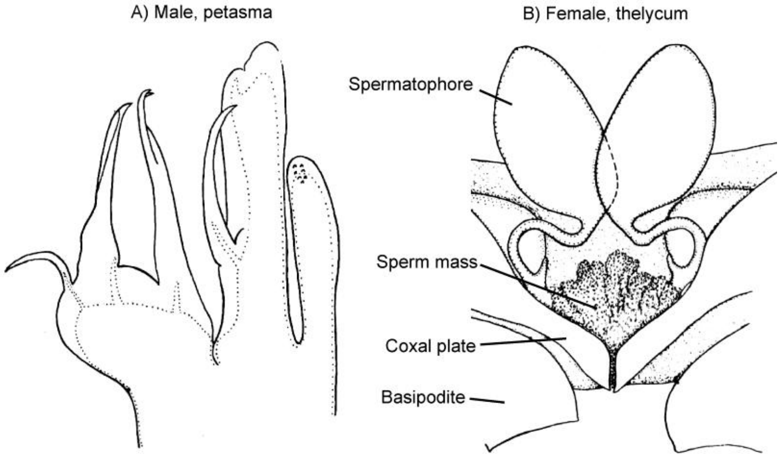

Fig. 2. Examples of typical euphausiid reproductive organs, *Thysanoessa longicaudata* (from Einarsson, 1945).

Photophores: A characteristic, unique among crustaceans to euphausiids, is the presence of light emitting photophores on specific parts of the body (Fig. 1). In almost all species there is a photophore in each eye stalk, lateral pairs at the bases of the second and seventh pereiopods, and single ones ventrally between each of the first to fourth pleopods, but in Genus *Stylocheiron* there are none beside the second pereiopods, or between the second to fourth pleopods. The function of the photophores may relate to mating, social interaction or orientation and as a form of counter-illumination camouflage to compensate their shadow against overhead ambient light. Euphausiids can also have anterior tinges of red pigment.

An excellent key and descriptions for the euphausiids of the world are given in Baker *et al*. (1990) and European shelf species in Einarsson (1945) and Mauchline (1971a, b, 1984). Further general information on euphausiids is given in Mauchline & Fisher (1969); Mauchline, (1980), Schram (1986); Gibbons *et al.*, (1999) and Spiridonov & Casanova (2010).

Reproduction and development
Euphausiid species that carry their eggs have no dedicated brooding structures as found in Peracarida. Females attach the eggs below the cephalothorax inside a simple membranous sac or pair of sacs (Fig. 6A). Eggs are large, typically 0.3-0.9 mm in diameter, with, at least in free spawned eggs, a perivitelline space of varying diameter between the embryo and the outer membrane (Fig. 3A). The larva that emerges from free spawned eggs is the typical crustacean unsegmented nauplius larva. They are oval, pale golden coloured and have only three pairs of limbs, antennules, antennae and mandibles. They moult through a second nauplius stage (Fig. 3B) and then a metanauplius stage (Fig. 3C), which is similar in form to the nauplius, but the rudimentary pleon protrudes from the carapace and it has only the two anterior limb pairs (although mandibles, maxillae and maxillipeds are present as buds). In species that retain the eggs in a sac, the larva that emerges is more advanced than a nauplius, but less advanced than a metanauplius, as the pleon barely protrudes from below the carapace. This is termed a pseudometanauplius (Fig.

3D). This moults immediately into a metanauplius stage. In both cases, following the metanauplius are three calyptopis stages (Fig. 3E). Only when the calyptopis stage is reached does feeding commence. The calyptopis body is formed of two principal divisions. The carapace is distinct, forming a hood-like expansion anteriorly, covering the unpigmented and imperfectly developed eyes. The pleon gradually becomes segmented between moults and while mouth parts and uropods sequentially appear, there are no pereiopods or pleopods. The third calyptopis stages moults into the first of several furcilia stages (Fig. 3F-K), the number varying with species and also determined by environmental conditions, and may be as many as 19. During the furcilia stages photophores develop, which are usually red, the compound eyes emerge from beneath the carapace and become increasingly pigmented and mobile. The antennae are initially simple and used in swimming (natatory) but gradually loose this function as other limbs develop. Pereiopods and gills, then pleopods successively develop towards the posterior, each new pair of limbs becoming setose and functional only at the next moult. Depending on environmental conditions, the number of somites added during any one of the furcilia stages may vary, even within the same species.

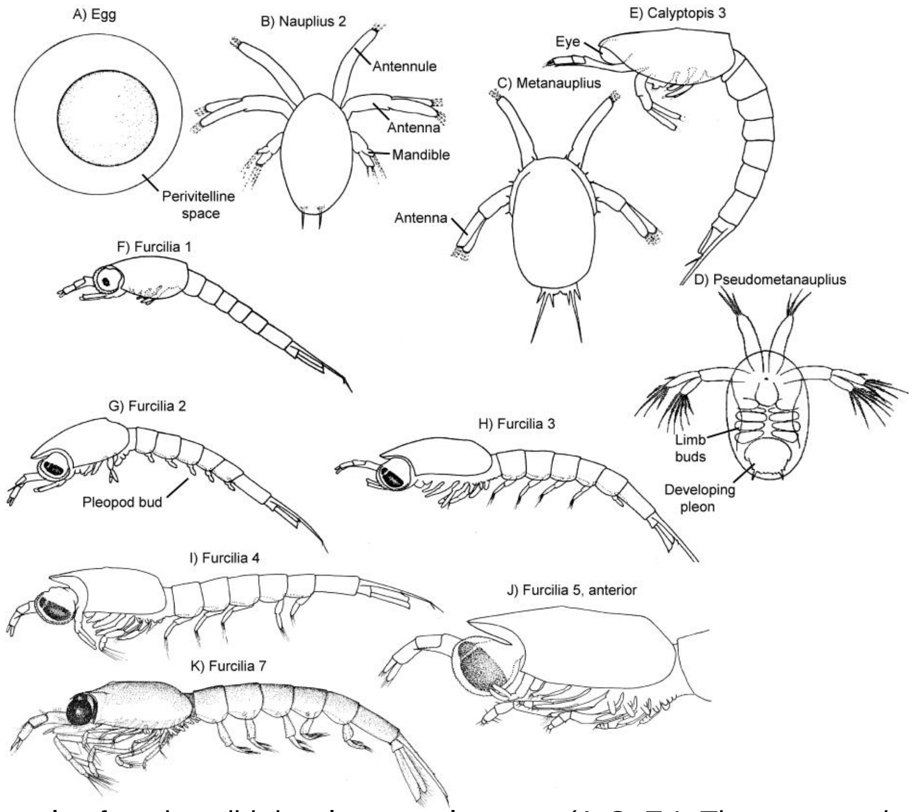

Fig. 3. Example of euphausiid developmental stages. (A-C, E-L *Thysanoessa inermis* from Einarsson, 1945; D from Lebour, 1924).

The furcilial telson is never cleft distally (Fig. 4), as is seen in many decapods. There is a reduction in the number of distal telson spines as the last furcilial stage is approached, until there are only two spines, one each side of the central telson (Fig. 4F) and extending beyond it. The juvenile that emerges from the final moult is morphologically similar to an adult, however, it cannot be considered adult until capable of reproduction, and until this time are termed postlarvae.

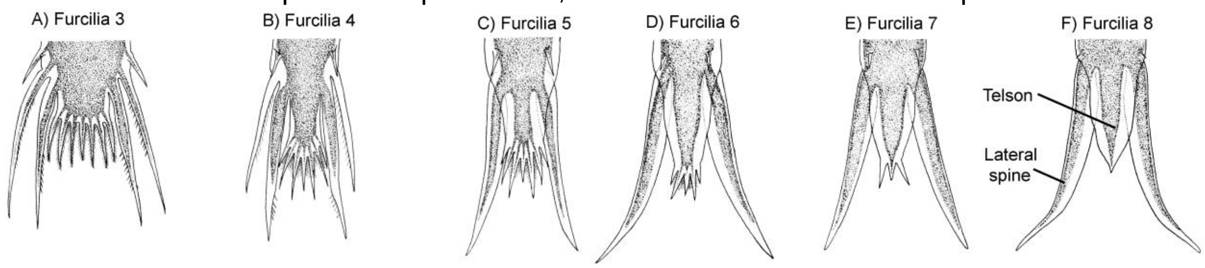

Fig. 4. Changes in the spination of the telson of *Thysanopoda acutifrons* furcilia stages during development (from Einarsson, 1945).

Being able to identify early euphausiid stages to the level of just egg, nauplius, metanauplius and furcilia is probably adequate for most people analysing zooplankton samples, but detailed information on the identification of the developmental stages of some species is given in Einarsson (1945) and excellent information and keys in Mauchline (1971b).

Key to postlarval northern European shelf euphausiids (after Einarsson, 1945)

1. Lateral denticles on the carapace -- **2**
- No lateral denticles on the carapace --- **4**

2. Two pairs of lateral denticles on the carapace ---------------------- *Euphausia krohnii* (Fig. 11)
- One pair of lateral denticles on the carapace -- **3**

3. Anterior margin of carapace with postocular spines; recurved lappets on first peduncular segments of antennules; no long rostrum ---------------- *Meganyctiphanes norvegica* (Fig. 5)
- No postocular spines on carapace or recurved lappets on antennules; long rostrum -- *Thysanoessa raschii* (Fig. 8)

4. Dorsoposterior spine on last pleon somite -- **5**
- No dorsoposterior spine on last pleon somite --- **6**

5. Recurved lappets on first peduncular segments of antennules and comb-like processes on second segments; no long rostrum ---------------------------------- *Nyctiphanes couchii* (Fig. 6)
- No recurved lappets on first peduncular segments of antennules; long rostrum -- *Thysanoessa inermis* (Fig. 7)

6. Eyes quite small, circular -- *Thysanopoda acutifrons* (Fig. 12)
- Eyes large, bilobed --- **7**

7. Photophore only on first pleon somite; pereiopod 3 elongated --- *Stylocheiron longicorne* (Fig. 13)
- Photophores on first four pleon somites; pereiopod 2 elongated --------------------------------- **8**

8. Upper part of bilobed eye narrower and smaller than lower part; last pleon somite approximately equal in length to two preceding ones together -- *Thysanoessa longicaudata* (Fig. 9)
- Both parts of bilobed eye almost the same size and width --- *Nematoscelis megalops* (Fig. 10)

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Subclass Eumalacostraca: Superorder Eucarida: Order Euphausiacea:

Family Euphausiidae:

Eyes well developed; lower posterior margin of carapace not serrated, but smooth, or bearing one or two small denticles each side; photophores present; last or last two pairs of pereiopods rudimentary; exopods of uropods without transverse suture; endopods of first two pairs of pleopods in male transformed into copulatory organs.

Genus *Meganyctiphanes:*

Meganyctiphanes norvegica (Sars, 1857)

One of the largest of the Euphausiidae. Eyes round and large (Fig. 5); first peduncular segments of the antennules have a prominent, recurved lappet in both sexes. The triangular frontal plate of the carapace curves slightly downward, with a short, blunt central projection, but no prominent rostrum; a well developed, sharp postocular spine either side of frontal plate; a single lateral denticle on each side of the carapace, around the middle, close to the edge, easiest observed from ventral view; anterior six pereiopods of similar size and structure, endopods of the seventh pair shorter, consisting of only two elongated segments, exopod of normal size; eighth pair of pereiopods rudimentary. No dorsoposterior spine on last pleon somite. Eggs free-spawned 0.65-0.67 mm (own measurements).

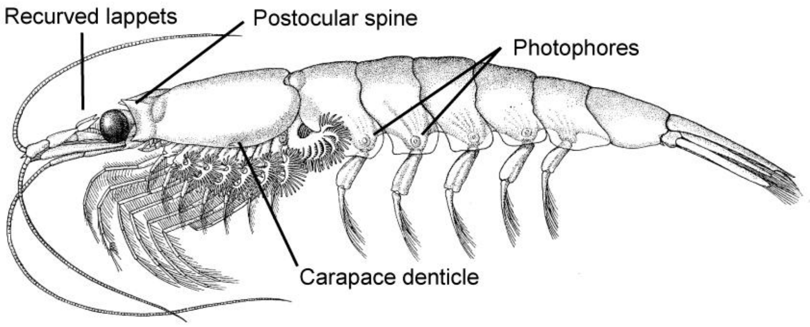

Fig. 5. *Meganyctiphanes norvegica* female (from Einarsson, 1945).

Recorded: PMF. L4. North Sea. Central and western English Channel. Western Britain and Ireland.

Size: ~22-50 mm.

Further information: Lebour, 1924, 1925; Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990; Tarling, 2010.

Genus *Nyctiphanes:*

Nyctiphanes couchii (Bell, 1853)

Eyes circular, large (Fig. 6); dorsal surface of first peduncular segments of antennules bearing a small, pointed recurved lappet on upper distal margin; in the male the lappet angles more horizontally than in the female. Second antennular segments bear a multi-toothed "comb", arising from the anterior upper margin, variable in shape, the teeth sometimes reduced in larger specimens. On anterior carapace, frontal plate short, forming an obtuse triangle with raised margins and without a pronounced central rostrum; no lateral carapace denticles. Endopods of pereiopods one to six similar, the seventh shorter, of only two segments; sixth and seventh pereiopods in female without exopods; eighth pereiopod rudimentary**.** Last pleon somite bears small, dorsoposterior spine (Fig. 6A). Einarsson (1945) was unable to observe a thelycum in females. Females carry eggs in paired eggs sacs. Egg diameter 0.37-0.39 mm (own measurement).

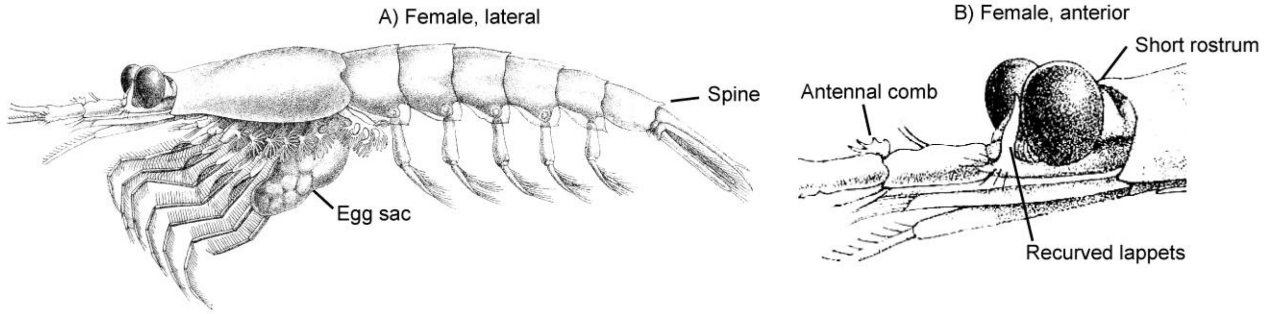

Fig. 6. *Nyctiphanes couchii* (from Einarsson, 1945).

Recorded: PMF. L4. North Sea. English Channel. Western Britain.
Size: Up to ~17 mm.
Further information: Lebour, 1924, 1925; Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Genus *Thysanoessa:*

Thysanoessa inermis (Krøyer, 1846)

Eyes sub-circular with inconspicuous transverse constriction in upper half (Fig. 7A); rostrum narrow, pointed, reaching beyond eyes, pointing somewhat downwards, so that tip is lower than frontal plate. In male, first antennular segments have on inner edge, a rounded lobe directed forward and upward, bearing two rows of slightly curved setae (Fig. 7B); second segments have outer, anterior margin produced dorsally as a finger-like process, the inner margin produced as an upward-pointing lobe, the upper margin armed with hook-shaped setae; third segments with high dorsal keel, all these features lacking in female. No denticles on carapace lateral margin. First six pairs of pereiopods usually similar in length, uniformly setose, the second pair sometimes slightly elongate and thickened; seventh pereiopods with exopods fully developed, endopods missing in males, short, unsegmented or two-jointed in females; eighth pereiopods rudimentary with styliform exopod, endopod missing. Strong dorsoposterior spine on last pleon somite, but in some specimens there may also be a spine on fifth somite (two-spined form), and rarely a spine on somites four to six (three-spined form). Because of apparent distributional differences of these three different spine types, it is useful to record the number of spines observed. Eggs free-spawned and ~0.41 mm in diameter (Lebour, 1924; as *T. neglecta*).

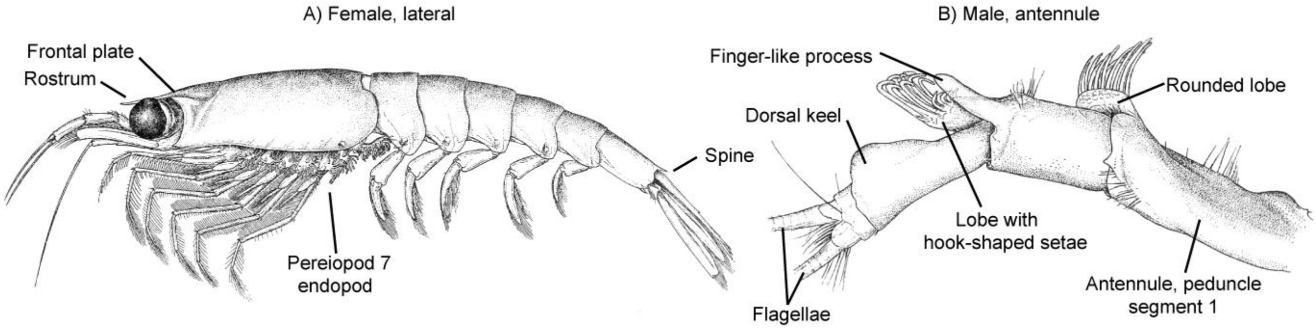

Fig. 7. *Thysanoessa inermis* (from Einarsson, 1945).

Recorded: PMF. L4, not recorded. Northern North Sea. Western English Channel. Western Britain and Ireland.

Size: Up to ~32 mm.

Further information: Lebour, 1924, 1926; Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Thysanoessa raschii (Sars, 1864)
Eyes large, nearly round (Fig. 8A); rostrum in males in dorsal view broad with blunt tip (Fig. 8B), in females narrower and tapers more gradually to a point. One small carapace denticle situated either side on lateral margin, anterior to the middle (Fig. 8A, B). First six pereiopods usually similar in length, uniformly setose, the second sometimes slightly elongate; pereiopods of seventh exopods fully developed, endopod missing in males, short and unsegmented or two-jointed in females; eighth pereiopods rudimentary, endopods missing, exopods styliform. Last pleon somite shorter than preceding two together, without spine on dorsoposterior border. Eggs free-spawned. Neritic coastal species.

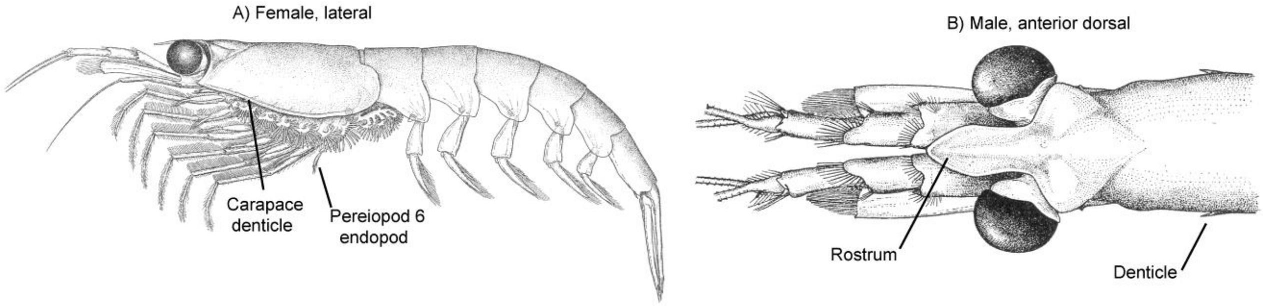

Fig. 8. *Thysanoessa raschii* (from Einarsson, 1945).

Recorded: Not recorded in the PMF or at L4. Northern, mainly coastal species.
Size: Up to ~30 mm.
Further information: Macdonald, 1928; Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Thysanoessa longicaudata (Krøyer, 1846)
Small, slender species (Fig. 9); eyes bilobed with marked, transverse constriction, upper lobe much narrower than lower lobe. Rostrum acute, extending beyond middle of first antennular segments; no denticles on lateral carapace margin; second pair of pereiopods always elongate and thickened, with setae present on both margins of last two segments; remainder of first six pereiopods usually similar in length and uniformly setose; seventh pereiopod pair with exopods fully developed, endopods missing in males, short, unsegmented or two-jointed in females; eighth pereiopods rudimentary, endopods missing, exopods styliform. No spine on last pleon somite, the somite approximately equal in length to two preceding somites together. Eggs free-spawned. Deeper water species.

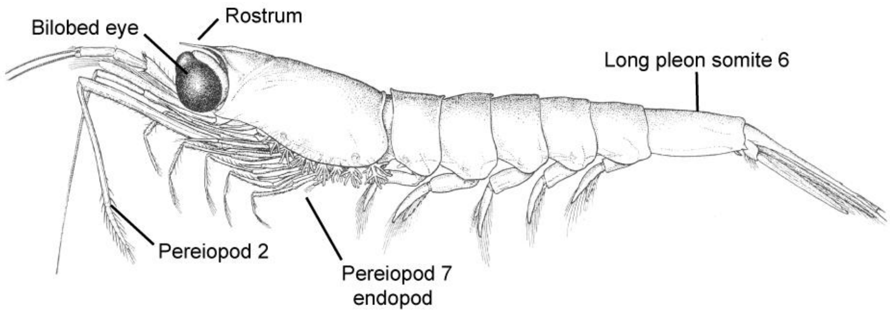

Fig. 9. *Thysanoessa longicaudata* female (from Einarsson, 1945).

Recorded: Not recorded in the PMF or at L4. Northern North Sea. Western Britain.
Size: Up to ~16 mm.
Further information: Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Genus *Nematoscelis:*

Nematoscelis megalops Sars 1883

Eye bilobed, large (Fig. 10A, B), upper lobe almost as wide as lower lobe. No lappets on peduncle segments of the antennules; rostrum variable in length, in females usually long, slender, and down curving, in males often short or missing. No lateral carapace denticles in adults, but one may be present either side in immature specimens. Second pereiopod very long, with a distal tuft of long, straight, spines (Fig. 10C). No dorsoposterior spine on last pleon somite; toothed ventral, preanal spine present (Fig. 10D). Eggs carried by female, ~0.44 mm in diameter (own measurement). Rare, deeper water species.

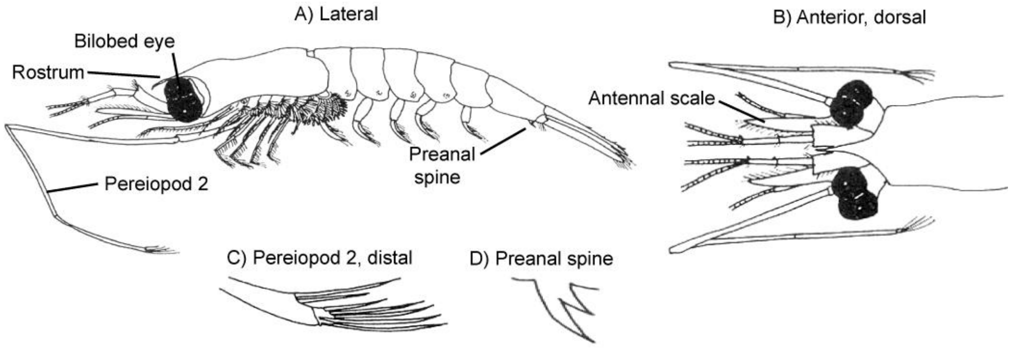

Fig. 10. *Nematoscelis megalops* (from Mauchline, 1971a).

Recorded: Not recorded in the PMF or at L4. Northern North Sea. Norwegian coast. West of Britain.

Size: ~20-26 mm.

Further information: Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Genus *Euphausia:*

Euphausia krohnii (Brandt, 1851)

Eyes round, quite large (Fig. 11A); first segment of antennular peduncle with lappet, bearing nine teeth, projecting anteriorly over second segments, outer tooth of lappet produced into an oblique, thin process that is distally trifurcate; dorsal margin of second peduncle segments with two short, prominent, forward-projecting spine-like tubercles, one on outer edge and other on inner edge, these hardly extend beyond distal limit of the segments; third segments keeled. Rostrum long, sharply pointed, reaching anterior edge of eyes; anterior carapace domed dorsally, with small high keel at its apex; two lateral denticles on each side of carapace. Both seventh and eighth pereiopod pairs rudimentary; no posterodorsal spines on last pleon somite; toothed preanal spine, variable in shape (Fig. 10B). Eggs free-spawned. Rare, deeper water species.

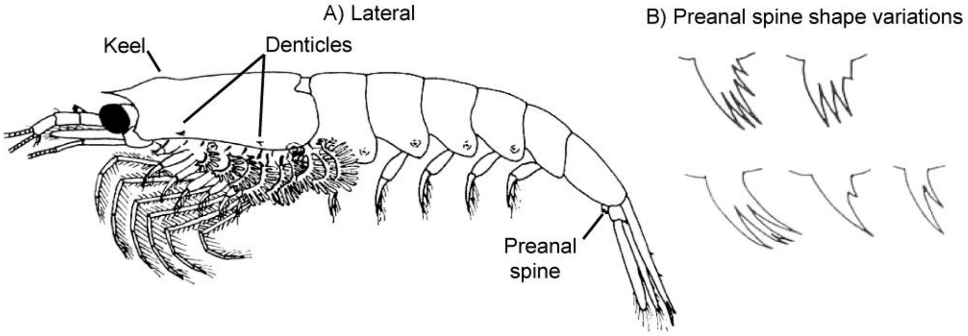

Fig. 11. *Euphausia krohnii* (from Mauchline, 1971a).

Recorded: Not recorded in the PMF or at L4. Northern North Sea. West of Britain.
Size: 12-19 mm
Further information: Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Thysanopoda acutifrons Holt & Tattersall, 1905
Eyes small, circular (Fig. 12); distal, dorsal margin of first peduncular segments of antennules extend forward about one-third of the way along the second segment as roughly triangular extensions (Fig. 12B). Carapace frontal plate triangular, rostrum short, pointing forwards and slightly upwards, extending to, or beyond the eyes, depending on the eye stalk orientation, apical angle greater than a right angle. No carapace lateral denticles in adults, but a pair may be present in immature specimens; no spines on pleon somites, the median posterior margins of all segments smoothly curved. Eggs free-spawned. Rare deeper water species.

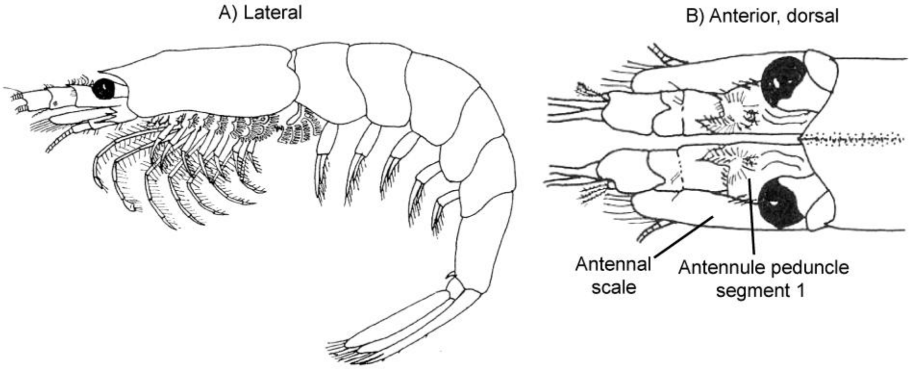

Fig. 12. *Thysanopoda acutifrons* (from Mauchline, 1971a).

Recorded: Not recorded in the PMF or at L4. Northern North Sea. Norwegian coast. West of Ireland.
Size: 35-50 mm.
Further information: Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

Genus *Stylocheiron:*

Stylocheiron longicorne Sars, 1883

Eyes usually coloured light brown, narrow, bilobed, lower lobe slightly wider than upper lobe (Fig. 13), but sometimes smaller, upper lobe with 7-19 enlarged crystalline cones in distal transverse row, fewest in smaller specimens. Antennule peduncles with long, slender second and third segments in female, shorter and thicker in male; upper flagellum shorter than lower. Carapace frontal plate produced into short acute rostrum that extends almost to anterior edge of eye, when eye is vertical. Anterior carapace domed dorsally, with an indistinct short, low, median keel; no lateral denticles on carapace. Third pereiopods elongated, bearing false chelae (Fig. 13B) formed of bristles from the propodal and dactyl segments; last pleon somite variable in length. Photophores only in eye stalks, a pair at base of seventh pereiopods and a single one ventrally on first pleon somite. Female carries eggs, normally 4-16. Rare deeper water species.

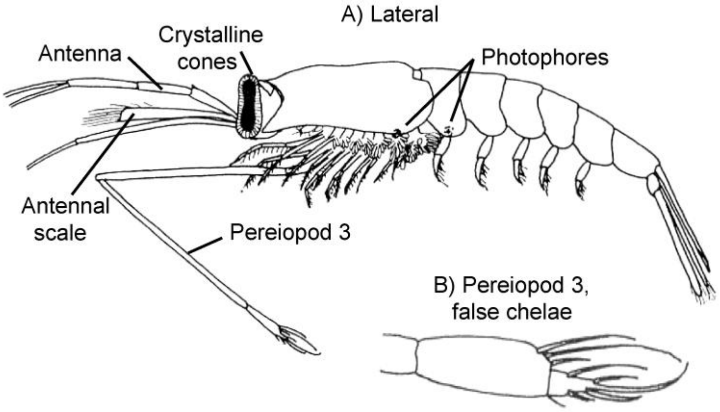

Fig. 13. *Stylocheiron longicorne* female (from Mauchline, 1971a).

Recorded: Not recorded in the PMF or at L4. Northern North Sea. West of Britain

Size: ~6-13 mm.

Further information: Einarsson, 1945; Mauchline, 1971a, b; Baker *et al*., 1990.

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Order Decapoda:

Decapoda is the largest order in Subphylum Crustacea and contains the familiar crab, lobster, prawn and shrimp groups, the order name originating from the five pairs of "walking legs" on the last five somites of the thorax region. These legs are found in at least later stages and adults, although not all decapods use them for walking. Current classification is in a state of flux, but is based on the structure of the gills, exoskeleton and limbs, and the way in which the early stages develop, giving rise, according to the WoRMS classification, to three suborders: **Pleocyemata, Macrura Reptantia** and **Dendrobranchiata**. The gills of adult Pleocyemata and Macrura Reptantia are plate-like (phyllobranchiate), while those of Dendrobranchiata are feather-like (dendrobranchiate). Dendrobranchiata are oceanic or sub-tropical/tropical species, unlikely to be sampled on the shallow shelf, so are not included here.

Decapoda developmental stages can superficially resemble those of some other groups of crustaceans, such as euphausiids, mysids, cumaceans or stomatopods. However, they can be separated from these groups relatively easily, as they do not have the luminescent photophores or external gills as found in euphausiids, the conspicuous circular statocysts in the endopods of the uropods as found in most mysids, the characteristic three-pronged tail and inconspicuous eyes of cumaceans, or the characteristic large raptorial claws, wide carapace and gill-bearing pleopods of stomatopods.

Suborders Pleocyemata and Macrura Reptantia:

Classification:

Suborders Pleocyemata and Macrura Reptantia include the shrimps, prawns, crabs and lobsters, but these common names, some of which are given below, are very loosely used, often spanning quite separate taxonomic groups. The current WoRMS scheme lists eleven infraorders in these two suborders, only seven of which appear to occur in the northern European area. There are 90 species of adult decapods recorded in the PMF, the number occurring in each of the seven infraorders given in brackets below, illustrating how the various developmental stages of a very wide range of different species could potentially be collected in coastal temperate plankton samples.

The keys and description included here will only identify most specimens to their infraorders or families. To identify them further will require using more comprehensive keys (e.g. Williamson, 1957a; Ingle, 1992; Barinch, 1996; Pohle *et al*., 1999; Martin, 2001; Puls, 2001; dos Santos & González-Gordillo, 2004; Pan & Hay, 2010). Because of the great diversity of decapod species, the numerous developmental stages, the variation in developmental pattern between species and stages, the similarities between some groups, the lack of descriptions of some species and the sometimes conflicting published descriptions, specific identification is a specialist task.

Suborder Macrura Reptantia

- **Infraorder Astacidea** – (1) Clawed lobster and Norway lobster.
- **Infraorder Achelata –** (2) Spiny and slipper "lobsters".

Suborder Pleocyemata

- **Infraorder Caridea –** (25) Includes the "true" shrimps.
- **Infraorder Axiidea** – (2) Burrowing "lobsters".
- **Infraorder Gebiidea** – (3) Mud "shrimps".
- **Infraorder Anomura –** (15) Hermit and porcelain "crabs", squat "lobsters" etc.
- **Infraorder Brachyura –** (42) The "true" crabs - brown, shore, swimming etc.

General body plan:

Early stages of different decapod infraorders can sometimes appear quite similar, but some have quite unique morphology, so a variety of names have been given to the developmental stages, some group specific. The basic stage names used are zoea, which have limited setation on the appendages, and megalopa, which resemble more closely the adults and have more extensive setation and also reduction in some of the limbs (see below). The zoea is sometimes referred to as a larva, the megalopa as a postlarva and the settled stage resembling the adult as a juvenile.

Decapod developmental stages all have the same basic body plan (Figs. 1-3), but as development is progressive, the full limb complement etc. will not be present until the later stages. Using current terminology, the body is separated into cephalothorax and pleon (abdominal) regions (Fig. 1).

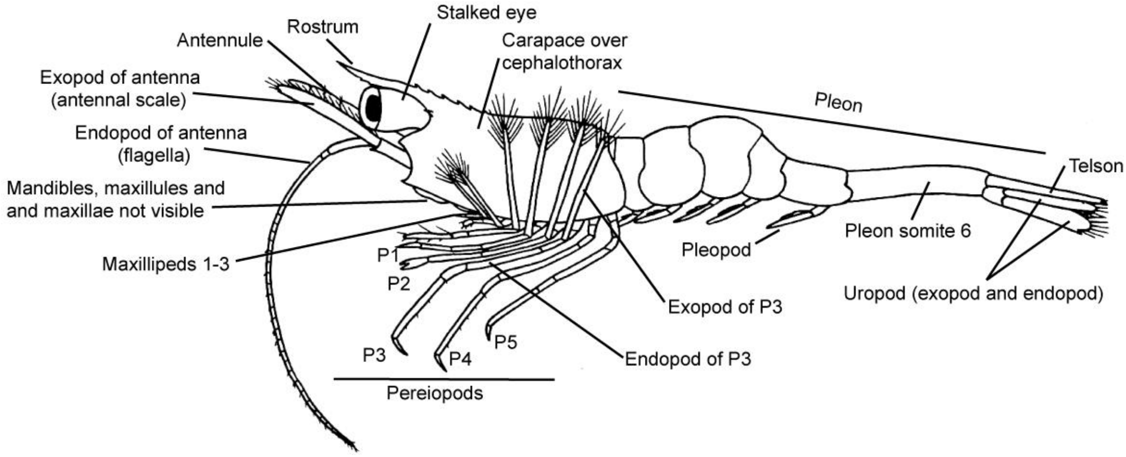

Fig. 1. Pleocyemata (Caridea) zoea general morphology (*Pandalus montagui* Leach, 1814), sixth (last) zoeal stage (after Williamson, 1967).

Cephalothorax: The somites of the cephalon and thorax are fused together to varying extents and typically covered by a cloak-like carapace, so this whole region is termed the cephalothorax. In members of Infraorder Achelata the carapace does not cover the posterior thoracic region. The anterior carapace usually has a projecting rostrum, sometimes serrated. Other spines and teeth of various sizes may be present on the carapace or extending from the edges, and these are named according to location. Typical of crustaceans, the cephalon comprises five somites, each bearing paired, usually biramous appendages. From the anterior they are termed antennules, antennae, mandibles, maxillules and maxillae, the latter three functioning as mouthparts. In early stages the antennules are usually uniramous. The thoracic region is composed of eight somites with corresponding paired appendages that gradually develop. Some of the appendages are biramous, while some, particularly the posterior ones, may have only rudimentary exopods, or none. The first three pairs of appendages are termed maxillipeds, are used in feeding and are tucked under the carapace. The remaining five pairs are termed pereiopods (P1-P5), which in benthic species typically lose their exopods at a late stage of development and become uniramous walking legs. Some of the pereiopods, especially the first, may have claws (chelae) for holding and processing food.

Pleon: The maximum number of somites in the pleon is six and these sometimes bear dorsal or lateral spines. The pleon ends in a somite termed the telson, which in some species is fused or partially fused to the last pleon somite. The shape of the telson varies widely between species, so is useful in identification. The distal margin may bear several processes and often a single median process. These processes may be setae, articulated spines, fused spines or extensions of the telson. In early stages the pleon may lack appendages, but later, all or most of the somites carry a pair of biramous pleopods, the last of which form, together with the telson, the tail fan and are called uropods. Uropods are missing in Infraorder Brachyura.

Development:

The commonest pattern of decapod development is indirect, where the larva that hatches from the egg must moult through one or more zoeal stages to reach the first postlarval (usually megalopa) stage. In the less common direct development, initial development is within the egg and the development stage that can be released is reported to be as late as a first instar juvenile, which can immediately settle. Because of the great interspecific variability in morphology of decapod stages, it is difficult to give a generalised description of development.

Egg, prezoea and zoea stages: The females typically carry the eggs until they hatch and the nauplius stage is passed in the egg, a zoea stage emerging on hatching. In some species and under particular conditions the emerging stage is a prezoea stage (Fig. 2A), a transition stage to the first zoea, but this stage typically moults within minutes and is rarely found in the plankton. It is very rudimentary, usually lacking projecting spines and setae.

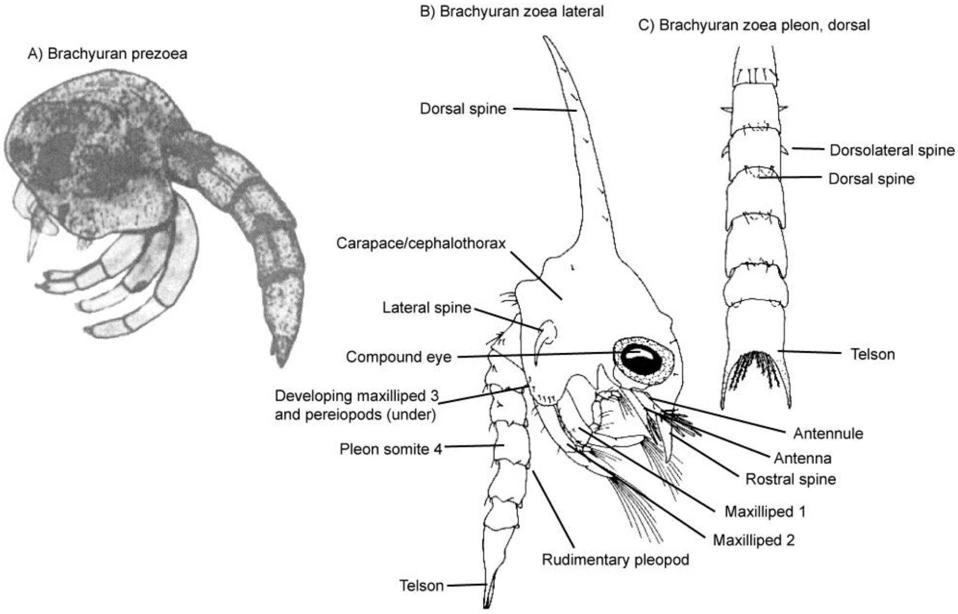

Fig. 2. Pleocyemata (Brachyura) zoea general morphology. (A from Robertson, 1938; B, C after Gore & Scotto, 1982).

The zoea usually has an anterior spiny rostrum from the first or second stage (Figs. 1, 2B, 3A, C). The eyes do not have stalks so cannot move (sessile) until the second zoea stage. There are plumose setae on the thoracic appendages, particularly the first and second maxillipeds, which are initially used in locomotion. The pleon in the first stage is typically composed of five somites, although fewer somites or the full complement of six may be present. When there are five somites, the last somite divides in two at the next moult to give the full complement. Rudimentary, non-setose pleopods may or may not be present on the pleon somites (Figs. 1, 2B, 3A, C), or very rarely these are setose but non-functional. In species with uropods (Figs. 1, 3A), these usually do not develop until the third zoeal stage. Zoeae can moult through from one to more than ten stages before becoming megalopae, the number usually similar in the same family, but can vary between families.

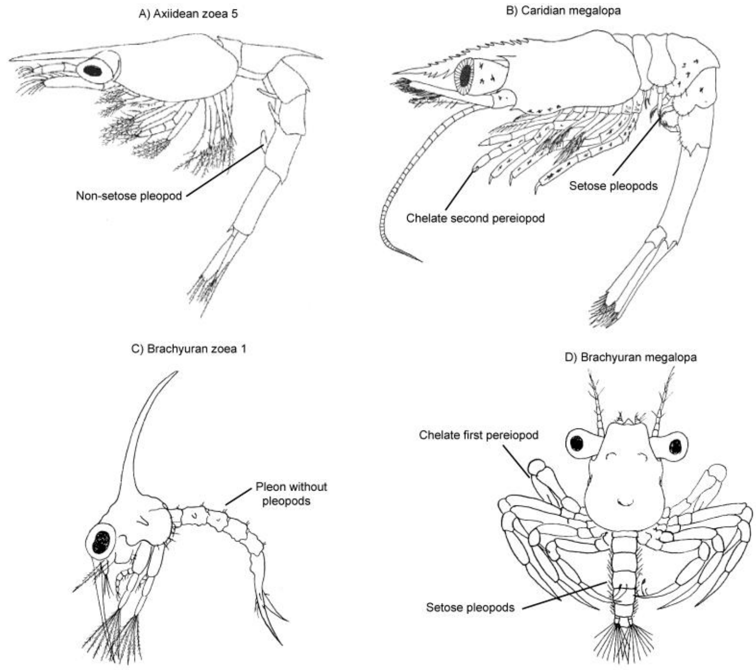

Fig. 3. Pleocyemata zoea and megalopae (A from Gurney, 1942; B from Price & Chew, 1972; C, D from Lebour, 1928).

Megalopa stages: The megalopa is defined by the appearance of setae on the pleopods (Fig. 3B, D). They superficially resemble the adults, but usually with proportionately larger eyes and smaller pereiopods, and the carapace is commonly narrower and smoother. The change in appearance from zoea to megalopa is not great in most groups, but dramatic in some e.g. Brachyura (Fig. 3C, D). There is generally only one megalopa stage, but in certain species there may be more. In benthic species megalopae settle on the bottom and moult to the first instar juvenile.

Keys to separate developmental stages to infraorders

Setae on some or all thoracic appendages, but usually none on pleopods (if present) ---------- **Zoea**
Pleopods setose; exopods of maxillipeds and pereiopods reduced or absent; morphologically resemble adults -- **Megalopa**

Zoea Key – Based on Williamson (1957a), Martin (2001), and dos Santos & González-Gordillo (2004).

1. Carapace strongly dorsoventrally flattened -- **Achelata** (Fig. 5)
- Carapace almost spherical, usually with spines, 4 or fewer but up to 20; rostrum pointing ventrally or absent, telson forked; no uropods ------- **Brachyura** (except Dromiidae)(Fig. 10)
- Carapace much longer than wide or deep; rostrum pointing forwards (or absent in stage 1 only) ---**2**

2. With a long "neck" between antenna and mouth ----------- *Jaxea nocturna* (**Gebiidea**)(Fig. 8)
- Without a long neck --- **3**

3. Telson with median spine (except in zoea 1); lateroposterior carapace border usually rounded and smooth --- **4**
- Telson without median spine; lateroposterior carapace border smooth, serrated or produced into spines -- **6**

4. P3 with chelae; P1-5 with setose exopods in all stages; zoea not shrimp-like --- **Astacidea** (Fig. 4)
- P3 without chelae; setose exopods on pereiopods in late stages only, probably never on P5; second telson spine reduced to a fine hair-like seta in early stages of some species; zoea shrimp-like -- **5**

5. Pleon somites without dorsal or lateral spines ------------------------------------ **Gebiidea** (Fig. 8)
- At least one pleon somite with spine or spines ------------------------------------ **Axiidea** (Fig. 7)

6. Posterolateral margins of carapace with spines, denticles or both; carapace surface without spines --- **7**
- Posterolateral margins of carapace without spines or denticles ----------------------------------- **8**

7. Antennal scales with very fine setae on outer edge in zoea 1, coarser setae in subsequent stages; setose exopod on P1, exopods rudimentary on P2 and P3 in later stages --- Dromiidae (**Brachyura**)(Fig. 11)
- Antennal scales without setae on outer edge; no exopods on the pereiopods -- (**Anomura** part)(Fig. 9)

8. Second telson spine not fine, hair-like; in zoeae 1 and 2 antennal endopod ends in a single spine or a spine and a setae, or is unarmed --------------------- **Caridea** (separate key; Fig. 6**)**
- Second telson spine not "hair-like"; antennal endopod ends in 3 prominent setae; rostrum shorter than antennules or antennal scale. --------- *Upogebia* zoea 1 only (**Gebiidea**)(Fig. 8)
- Second telson spine hair-like; rostrum longer than the antennules or antennal scale -------- --- (**Anomura** part)(Fig. 9)

Stage identification of zoea

Characters used in the Identification of the stages of Pleocyemata and Macrura Reptantia zoea are detailed in dos Santos & González-Gordillo (2004) and Puls (2001), but as they point out, it is difficult to give a generalised description, as there is a wide variety of forms and differences in number of stages between species. Brachyuran zoea are simplest to stage, as in stage 1 there are four distal setae on the maxillipeds and an additional pair appears in each subsequent stage. The other zoeae are more complex to stage, as limb development etc. varies between families.

Megalopa Key – Based on Williamson (1957a) and Martin (2001).

1. Uropods ventral, resembling pleopods; few body spines -- **Brachyura** (except Dromiidae)(Fig. 10
- Uropods lateral forming fan with telson; P4 and P5 not rudimentary ---------------------------- **2**

2. No claws on P1-P3 -- **Achelata** (Fig. 5)
- Claws on at least one pair of the first 3 pereiopods -- **3**

3. Claws on P1-P3, first pair largest-- **Astacidea** (Fig. 4)
- No claws on P3 -- **4**

4. Antennal scale large with bristles; 5 pairs of pleopods ---------------------------- **Caridea** (Fig. 6
- Antennal scale reduced or absent; 2-4 pairs of pleopods --- **5**

5. Exoskeleton covered in tiny spines; rostrum bent downwards -- Dromiidae (**Brachyura**)(Fig. 11)
- Exoskeleton with few spines, or smooth -- **6**

6. P5, or P4 and P5 much smaller than P2 and P3; P1 with claws, pleon slightly reduced and bent under cephalothorax -- **Anomura** (Fig. 9)
- P2 to P5 of similar size; pleon not reduced -- **7**

7. Three pairs of pleopods; claws on P1 and P2 ---- **(Axiidea** part, e.g., *Callianassa* sp.)(Fig. 7)
- Four pairs of pleopods --- **8**

8. Claws on P1 and P2 -- (**Axiidea** part e.g. *Axius* sp.)(Fig. 7)
- Well developed claws on P1, developing pair on P2 ----- (**Gebiidea**) *Jaxea nocturna* (Fig. 8)
- Claws only on P1, sometimes with a very small immovable digit -- (**Gebiidea** e.g. *Upogebia* sp.)(Fig. 8)

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda:

Sub-order Macrura Reptantia:
Infraorder Astacidea:
Family Nephropidae:

The only members of Infraorder Astacidea found on the northern European shelf are two species from **Family Nephropidae**, the true or “clawed” lobsters. These have full claws on the first three pereiopods. Although other groups of decapods are commonly known as "lobsters," the clawed lobsters are most often associated with the name. They are not closely related to spiny lobsters and slipper lobsters (Infraorder Achelata), or squat lobsters (Infraorder Anomura).
The two species found are the common lobster *Homarus gammarus* (Linnaeus 1758), which is found all over the region and the Norway lobster or Dublin Bay prawn *Nephrops norvegicus* (Linnaeus, 1758), which is found in highest numbers in the north of the European region, but is found sporadically over a wide area, distribution determined by the availability of suitable substrate in which the adults can burrow.
There are normally three zoeal stages. The carapace is laterally flattened and the telson is flat. All zoeae have five pairs of segmented pereiopods with setose exopods and there are chelae on pereiopods one to three. The carapace has relatively few spines and is approximately the same length as the pleon. *H. gammarus* usually has seven (zoea 1; Fig. 4B) or eight setae (later zoea) in each half margin of the telson, but sometimes more. *N. norvegicus* has a very distinctive zoea with a very deeply cleft telson (Fig. 4D-F), the lateral spines as long as the pleon. Both species have a median telson spine (Fig. 4B, D), more prominent in *H. gammarus*. The pleon somites in *H. gammarus* bear short spines, longer in *N. norvegicus*. The megalopae (Fig. 4C, G) are miniatures of the adults. Early stages of *H. gammarus* are rarely collected in plankton sample, but *N. norvegicus* can be taken in moderate numbers close to the spawning grounds.

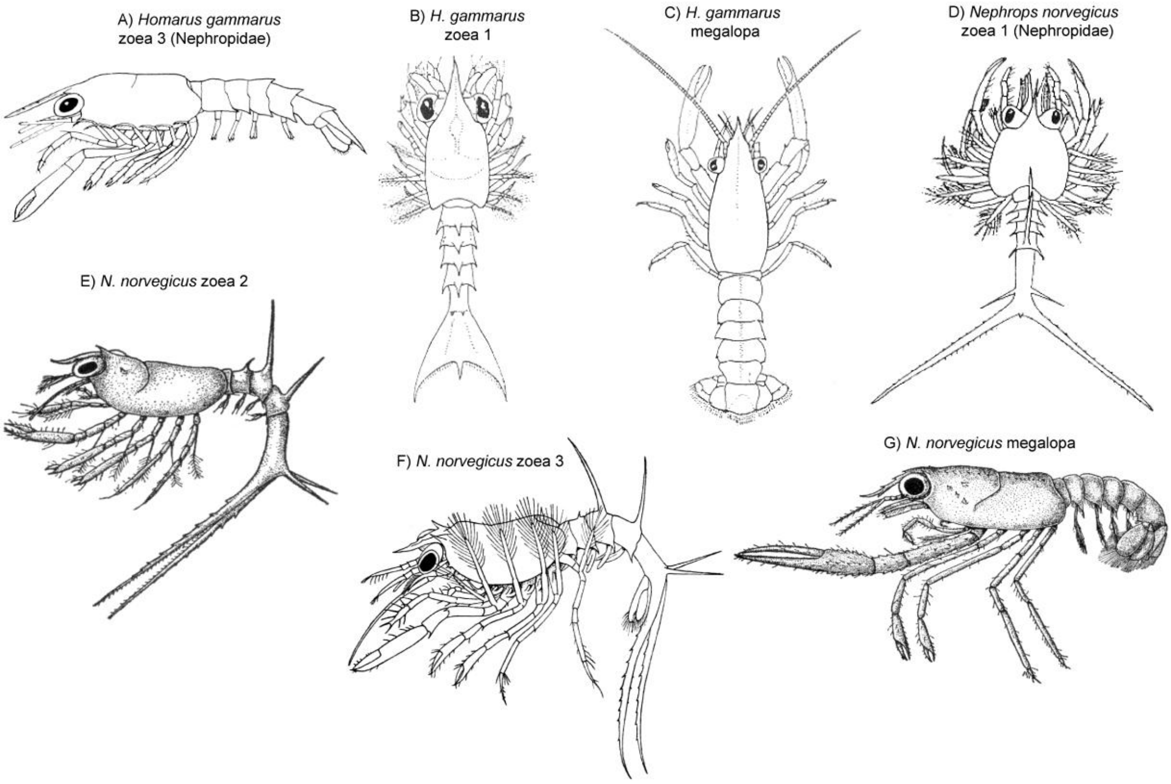

Fig. 4. Examples of Family Nephropidae developmental stages. (A from Williamson, 1983; B-D from Ingle, 1997; E, G from Figueiredo & Thomas, 1967; F from Gurney, 1942).

Further information: Gurney, 1942; Newell & Newell, 1963; Figueiredo & Thomas, 1967; Williamson, 1983; Ingle, 1997; Martin, 2001; Puls, 2001; Harvey *et al*., 2002; dos Santos & González-Gordillo, 2004; Pan & Hay, 2010; Larink & Westheide, 2011.

Infraorder Achelata:

There are only two families of this small infraorder likely to be found on the northern European shelf and only one species from each family. **Family Palinuridae**: *Palinurus elephas* (Fabricius, 1787) commonly known as the spiny lobster or crawfish. **Family Scyllaridae**: *Scyllarus arctus* (Linnaeus, 1758), commonly known as the slipper lobster. Both species are recorded in the PMF (*P. elephas* as *P. vulgaris*).

Developmental stages are particularly distinctive and the typical larval form is termed a phyllosoma (Fig. 5A, C). They are rarely collected in plankton nets, generally only if a large volume of water has been filtered. Females carry the eggs until hatching and the emerging larva passes through a short-lived (minutes to a few hours) naupliosoma stage that moults to the first phyllosoma stage. This is transparent, very broad and extremely dorsoventrally flattened. Other unusual features include the eyes, which are stalked from the first stage. The cephalon and the thoracic somites are fused, but the thin, oval carapace does not cover all of the disc-shaped thoracic region.

There are at least eight phyllosoma stages. The third maxilliped has an exopod in all stages and the pleon is small, especially in the early stages. Pleopods and uropods appear from stage five. Pereiopods four and five are rudimentary until the later stages and are smaller than the other pereiopods, the fifth with no exopod. The last stage moults into an unusual form of megalopa termed a puerulus (Fig. 5B, D) that resembles the adult. This has large setose pleopods and may remain in the plankton for several weeks before settling and metamorphosing.

Sufficient information is given below to identify the phyllosoma and puerulus stages of the two northern species. Sources of information on individual stages is given in Williamson (1983).

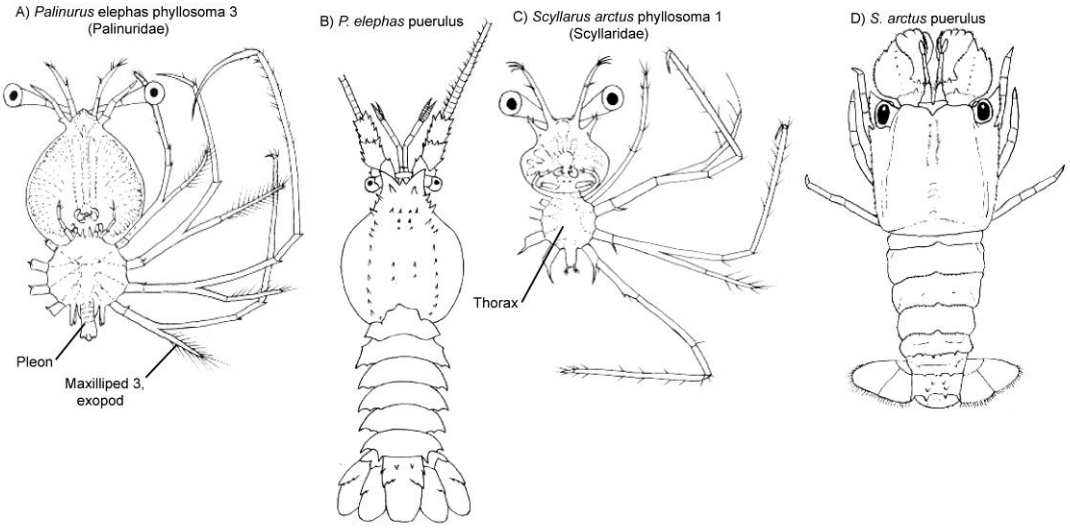

Fig. 5. Examples of Infraorder Achelata developmental stages. (A, C from Gurney, 1942; B from Bouvier, 1914; D from Fedele, 1926).

Palinurus elephas: The antenna projects beyond the eye in phyllosoma stage four and subsequent stages and is around the same length as the body in the puerulus (Fig. 5A, B). Maxilliped three has an exopod in all phyllosoma stages and the carapace is longer than broad in late stages.

Distribution: From southwest Norway south.

Length: 2.9-3.9 mm in phyllosoma one, 20-22 mm in last phyllosoma.

Further information: Cunningham, 1892; Bouvier, 1914; Gurney, 1942 (all as *P. vulgaris*); Williamson, 1983; Baisre, 1994; Harvey *et al*., 2002.

Scyllarus arctus: The antenna does not extend as far as the eye in all phyllosoma stages and is flattened, broad and shorter than the carapace in the puerulus (Fig. 5C, D). In all phyllosoma stages maxilliped three lacks a setose exopod and the carapace is broader than long.

Distribution: From the southern UK southwards.

Length: 1.1-1.5 mm in phyllosoma one, 20-28 mm in last phyllosoma.

Further information: Santucci, 1925; Fedele, 1926; Thomas, 1963; Williamson, 1983; Baisre, 1994; Harvey *et al*., 2002.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda:

Sub-order Pleocyemata:

Infraorder Caridea:

Caridea are the "true" shrimps and is a large group containing several important commercial species such as *Pandalus borealis* Krøyer, 1838 the pink shrimp and *Crangon crangon* (Linnaeus, 1758) the brown shrimp.

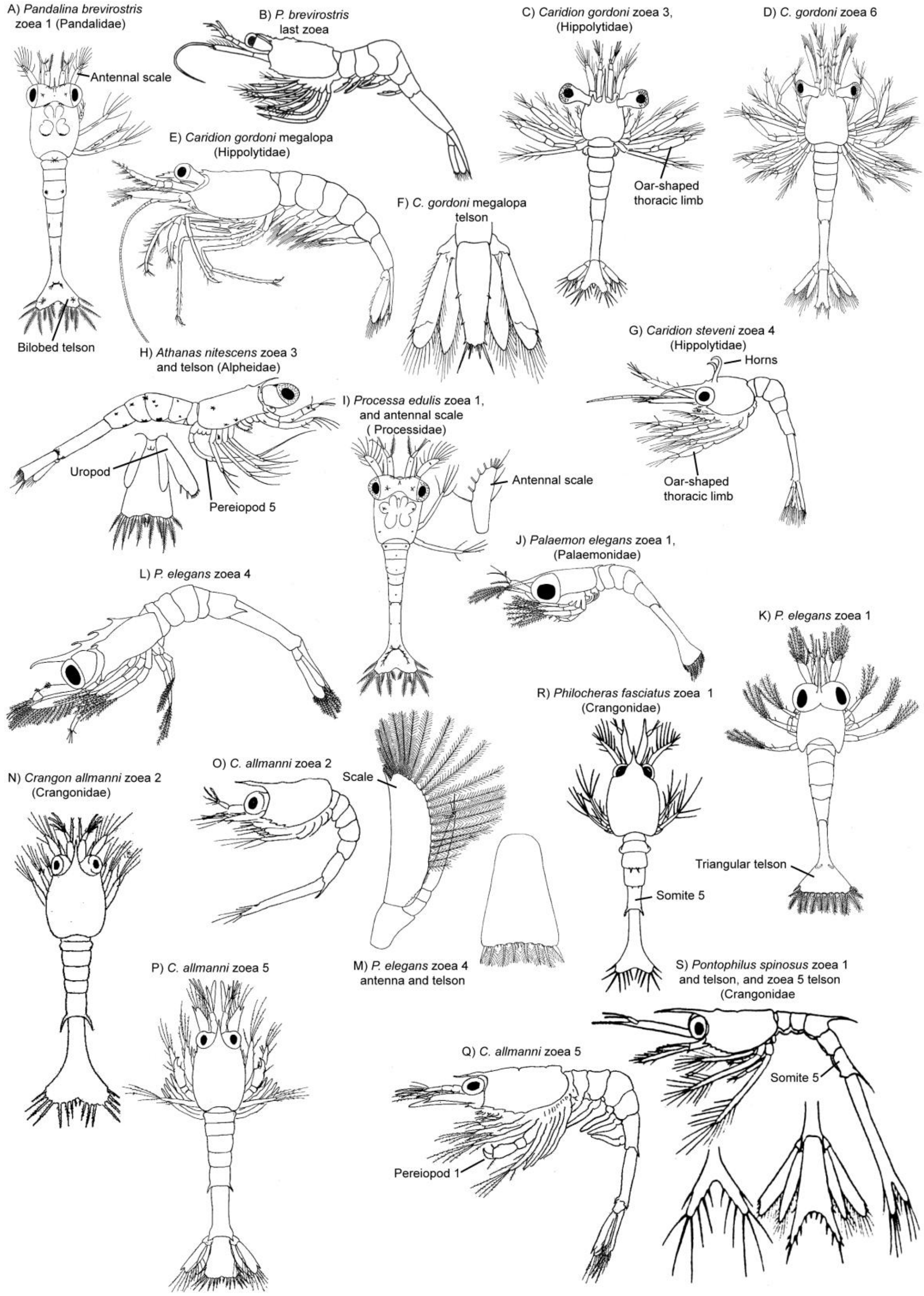

Fig. 6. Examples of Infraorder Caridea developmental stages. (A, H, I from Gurney, 1942; B from Williamson, 1967; C-G from Lebour, 1930a; L, M from Fincham & Williamson, 1978; N-Q from Lebour, 1931; R from González-Gordillo & Rodríguez, 2000; S from Williamson, 1960).

In all carideans the posterior border of the carapace is rounded. There may be up to nine zoeal stages. The rostrum is cylindrical or laterally compressed, never horizontally flattened throughout its length, and often quite small. In later zoeae of some groups the rostrum is serrated (Fig. 1). At least in the early stages the antennal scale may be unsegmented as in *Processa edulis* (Risso, 1916 (Fig. 6I), or segmented as in *Pandalina brevirostris* (Rathke, 1843)(Fig. 6A). The first two pereiopods are chelate in later stages, the second usually larger. In the early zoea stages the telson is usually bilobed as in *Caridion gordoni* (Spence Bate, 1858)(Fig. 6C), triangular as in *Palaemon elegans* Rathke, 1837 (Fig. 6K), or parallel sided, tapering distally (Fig. 6F). There is no median spine on the telson and the second telson spine is not fine, hair-like. The telson usually has seven spines (zoea 1) or eight (later zoeae) in each half margin. Uropods do not appear until the third zoea as in *Athanas nitescens* (Leach, 1813)(Fig. 6H), in common with most species that have uropods. Pleon somite three sometimes has a dorsal spine or spines as in *Philocheras fasciatus* (Risso, 1816)(Fig. 6R) and *Pontophilus spinosus* (Leach, 1816)(Fig. 6S) and somite five often has lateral spines as in *Crangon allmanni* Kinahan, 1869 (Fig. 6N). In some species there are also small spines on somite four (Fig. 6R). In late stages claws (chelae) or sub-chelae (the last segment of the appendage closes against a short projection on the penultimate one) may start to develop on pereiopods one and two (Fig. 2, 6Q). One species, *Caridion steveni* Lebour, 1930, has a characteristic pair of carapace horns from zoea 2 (Fig. 6G), disappearing in the megalopa.

Key to the zoeal stages of the six main families in Infraorder Caridea:

1. One or more thoracic endopods thickened, oar-shaped (dorsal horns in one species (*Caridion steveni* Lebour, 1930; Fig. 6G)) ---------------------------- Hippolytidae (part)(Fig. 6C-G)
- None of thoracic endopods oar-shaped, no dorsal horns -- **2**

2. P5 much longer than P4; endopod of maxilliped 1 very small and unsegmented --- Alpheidae (Fig. 6H)
- P5 around equal in length to P4 or shorter; endopod of maxilliped 1 well developed or only slightly reduced --- **3**

3. Carapace with 1-3 large mediodorsal spines (except in zoea 1 of some species); rostrum without spines; telson posterior margin straight ---------------- Palaemonidae (Fig. 6J-L)
- Carapace without mediodorsal spines or small spines near rostrum base; rostrum may be spiny in late stages; telson posterior margin with median cleft in zoeae 1 and 2 ----------------- **4**

4. Eye-stalks hemispherical, almost touching in mid line; antennules touching at base; no supraorbital spine; often with broad rostrum or broad telson ----------- Crangonidae (Fig. 6N-S)
- Eye-stalks (except in zoea 1) tapering or cylindrical, well separated; antennules separated at base; supraorbital spine present except in zoea 1; rostrum tapering from base or absent; telson not very broad --- **5**

5. Bases of antennules separated by not more than width of one of them, peduncles stout and almost straight; eye-stalks cylindrical ----------------------------- Hippolytidae (part)(Fig. 6C-G)
- Bases of antennules separated by more than width of one of them, peduncles often slender and curved; eye-stalks usually tapering --- **6**

6. Rostrum usually long and toothed in later zoeal stages; antennal scale usually segmented at tip in early zoeae; exopods present on P1-3 in late zoeae --------------------- Pandalidae (Fig. 6A, B)
- Rostrum small (absent in zoea 1), never toothed; antennal scale never segmented; exopods on P1-4 in late zoeal stages --- Processidae (Fig. 6I)

Further information: Sars, 1911; Webb, 1921; Lebour, 1930a, 1931,1932a, b, 1936a, b; 1940a, b; Gurney, 1942; Williamson, 1957a, b, 1960, 1967; Pike & Williamson, 1961, 1964; Newell & Newell, 1963; Fincham & Williamson, 1978; Williamson & Rochanaburanon, 1979; Gurney, 1982; Pessani & Godino, 1991; Martin, 2001; Puls, 2001; Harvey *et al*., 2002; dos Santos & González-Gordillo, 2004; Bartilotti, *et al*., 2005; Pan & Hay, 2010.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda: Sub-order Pleocyemata:

Infraorder Axiidea:

Adults burrow in muddy bottoms so their common name is "burrowing lobster". There appears to be only four Axiidea species recorded from the northern European area (Fig. 7): *Calocaris macandreae* Bell, 1853 and *Axius stirynchus* Leach, 1815 in Family Axiidae and *Pestarella tyrrhena* (Petagna, 1792) and *Callianassa subterranea* (Montagu, 1808) in Family Callianassidae. Only *A. stirynchus* and *C. subterranea* are recorded in the PMF (*A. stirynchus* as *A. stirhynchus*). *A. stirynchus* has two zoeal stages, *P. tyrrhena* and *C. macandreae* have three, although Thessalou-Legaki (1990) noted that *P. tyrrhena* only had two. *C. subterranea* has five zoeal stages. The zoeae typically have a long, flattened, pointed rostrum with small serrations on the edges, at least from zoea two. Uropods appear during the zoeal stages, apart from in *A. stirynchus* where they only appear in the megalopa. The endopods of pereiopods four and five may be chelate in later stages. There is a large median telson spine in both *C. subterranea* and *A. stirynchus* from zoea one (Fig. 7B, F), but does not appear until zoea three in *C. macandreae* (Fig. 7K) and from zoea two in *P. tyrrhena* (Fig. 7L). In some early stages, the second telson spine from the outside is reduced to a tiny, fine hair-like seta (Fig. 7C, K). Telson shape in *A. stirynchus* is very characteristic (Fig. 7F, H) and there are a pair of dorsolateral spines on pleon somite five. In the other species there are single dorsal spines on at least the second pleon somite (Fig. 7A, F) and at least from the second zoea, apart from *C. macandreae*, which only has a small spine on pleon somite six (Fig. 7J). The megalopae (Fig. 7I) resemble the adults.

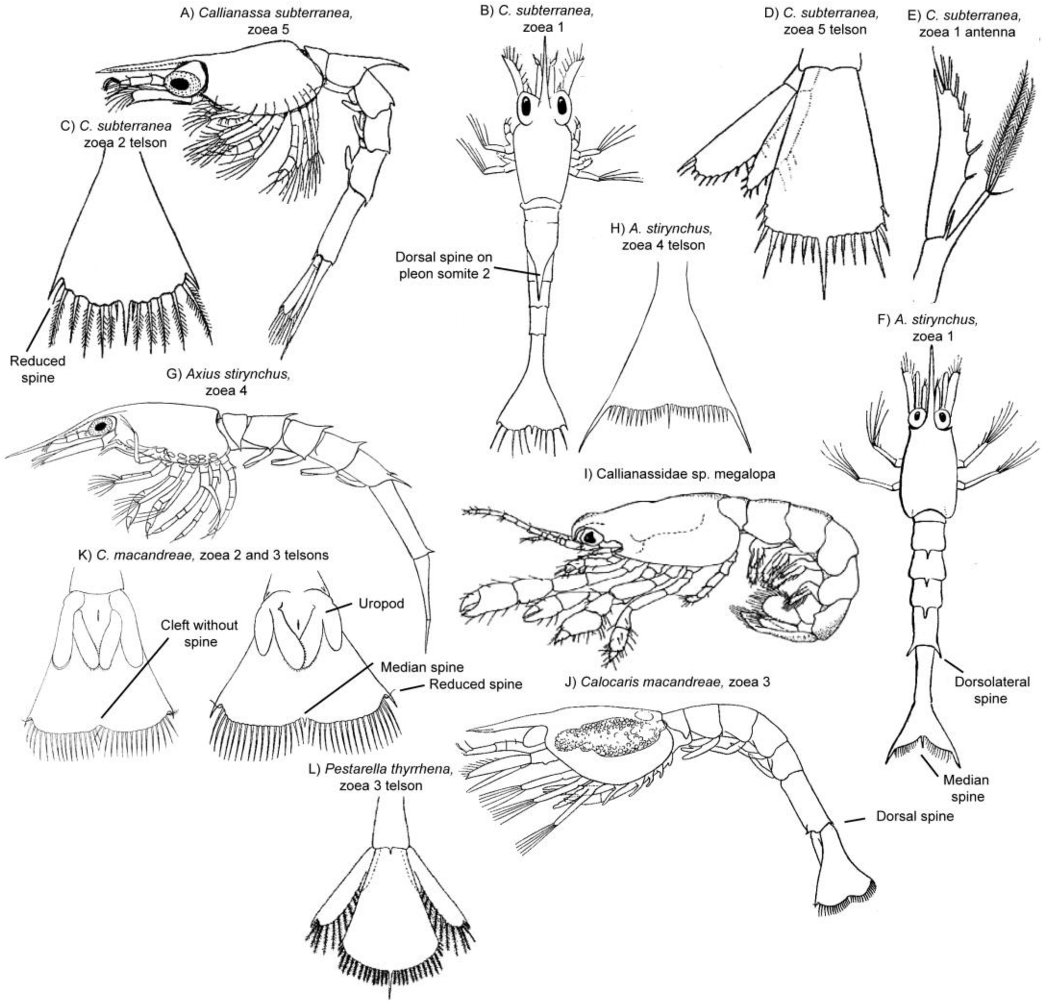

Fig. 7. Examples of Infraorder Axiidea developmental stages (A, D, E, G, J, K from Gurney 1942; B, C, F, H from Webb, 1921; I from Abrunhosa *et al*., 2005; L from dos Santos & González-Gordillo, 2004).

Further information: Webb, 1921; Gurney, 1942; Thessalou-Legaki, 1990; Martin, 2001; Puls, 2001; Harvey *et al*., 2002; dos Santos & González-Gordillo, 2004; Pan & Hay, 2010; Larink & Westheide, 2011.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda: Sub-order Pleocyemata:

Infraorder Gebiidea:

Adults burrow in muddy bottoms and have the common name of "mud shrimps". There are only three Gebiidea species recorded in the PMF, probably the only Gebiidea species found in the northern European area: *Jaxea nocturna* Nardo, 1847, *Upogebia deltaura* (Leach, 1815) and *U. stellata* (Montagu, 1808). Gebiidea have no dorsal spines on the pleon somites. The zoea of *J. nocturna* is easy to recognise with its very elongated "neck" between the antenna and feeding limbs (Fig. 8A) and small, triangular, smooth rostrum, while *Upogebia* spp. have an intermediate length of rostrum (Fig. 8D, F). In *Upogebia* spp. the antennal endopod has three prominent setae at the tip in zoea stages 1 (Fig. 8E) and 2, reducing to a single spine by the third stage. There is usually a small median telson spine, but this does not appear until the second zoea. (Fig. 8M) and is absent in *J. nocturna* until zoea four, in which it is not prominent. The second telson spine from the outside is described as sometimes being reduced to a tiny, fine hair-like seta, at least in early stages. However, *Upogebia* spp. do not appear to show this characteristic until at least zoea three (Fig. 8H, N). Caroli (1924) does not illustrate any of the stages of *J. nocturna* with a reduced spine, but Gurney (1942) shows a reduced spine in at least zoea two (Fig. 8B), so this does not appear to be a consistent character to be able to use in identification. There are usually 8+1+8 telson spines in late stages, but there can be more. The two *Upogebia* species are quite similar, but zoeae one and two of *U. stellata* have a plumose seta on the second joint of the endopod of maxilliped one (Fig. 8L) that does not appear in *U. deltaura* until the third zoea, and in zoea three and four a plumose seta on the same joint of maxilliped two, that is not found in *U. deltaura*. By zoea two In *U. deltaura*, the telson median notch has almost gone (Fig. 8F), while it is still present in *U. stellata* (Fig. 8M). In zoea three the telson in *U. deltaura* is weakly concave (Fig. 8H), strongly concave in *U. stellata* (Fig. 8N), although by zoea four, the final zoeal stage, there is less of a distinction in shape (Fig. 8I, J, O).
The megalopae of Gebiidea (Fig. 8C, K) resemble the adults. The rostrum in *U. deltaura* may reach the eye (Fig. 8K), but extends beyond the eye in *U. stellata*.

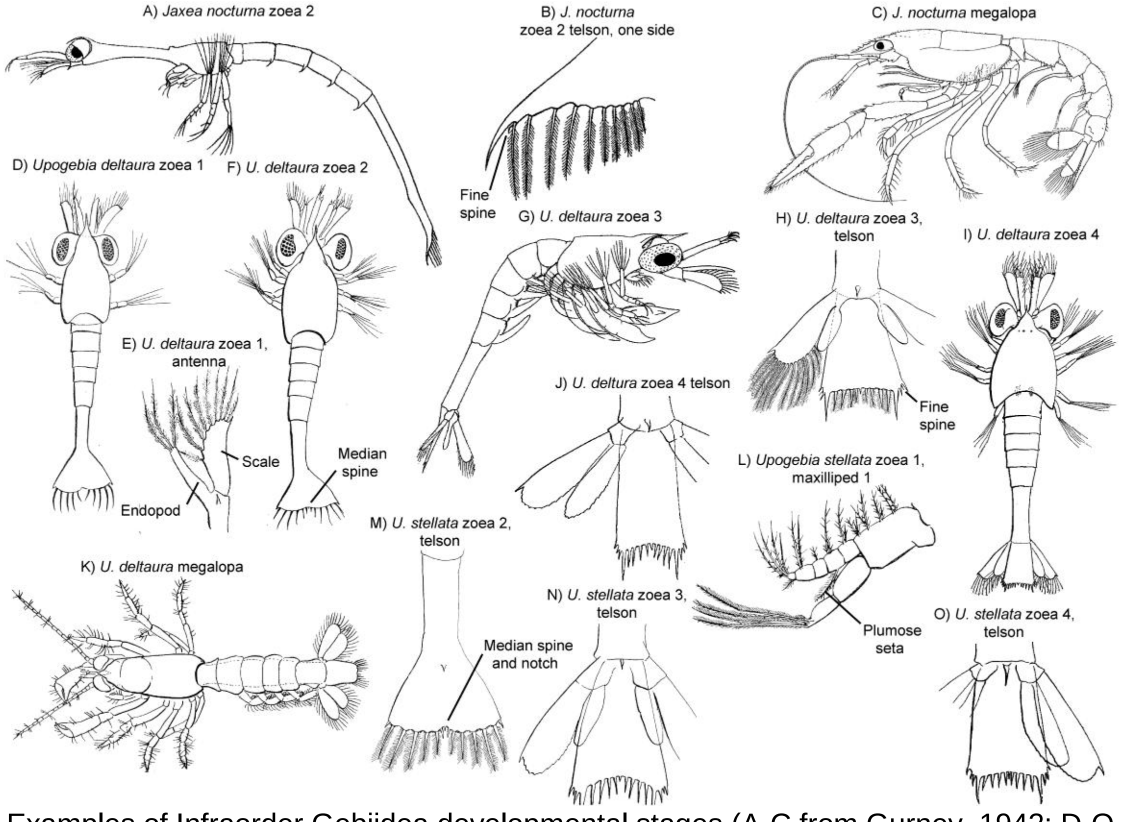

Fig. 8. Examples of Infraorder Gebiidea developmental stages (A-C from Gurney, 1942; D-O from Webb, 1919).

Further information: Webb, 1919; Caroli, 1924; Gurney, 1942; Newell & Newell, 1963; Martin, 2001; Puls, 2001; Harvey *et al*., 2002; dos Santos & González-Gordillo, 2004; Pan & Hay, 2010; Larink & Westheide, 2011.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda: Sub-order Pleocyemata:

Infraorder Anomura:

There are probably only three superfamilies of Infraorder Anomura with representatives in the northern European area: **Paguroidea, Galatheoidea** and **Lithodoidea**. There are 15 adult anomuran species recorded in the PMF, with representatives from only the former two superfamilies. In common with some other decapods, anomurans may hatch out as a short-duration prezoea (Fig. 9N). There are typically four or five zoeal stages, apart from Family Porcellanidae and Superfamily Lithodoidea, where there are only two. In the zoeal stages of most species the posterolateral margins of the carapace are extended in spines that are generally large (Fig. 9K). There may also be denticles on the carapace/spine margins and the rostrum is typically long. On the telson the second spine is often represented by a smaller spine, or a fine, hair-like seta (Fig. 9D, P). There is no median telson spine and there is usually a central cleft (Fig. 9K), but sometimes reducing during development (Fig. 9C, D). There are usually seven (zoea one) or eight spines/setae (later zoea) in each half margin of the telson (Fig. 9C). Uropods are generally present from stage three (Fig. 9G) and pleopods from stage four. In late zoeal stages the endopods of pereiopods one and two may be chelate.

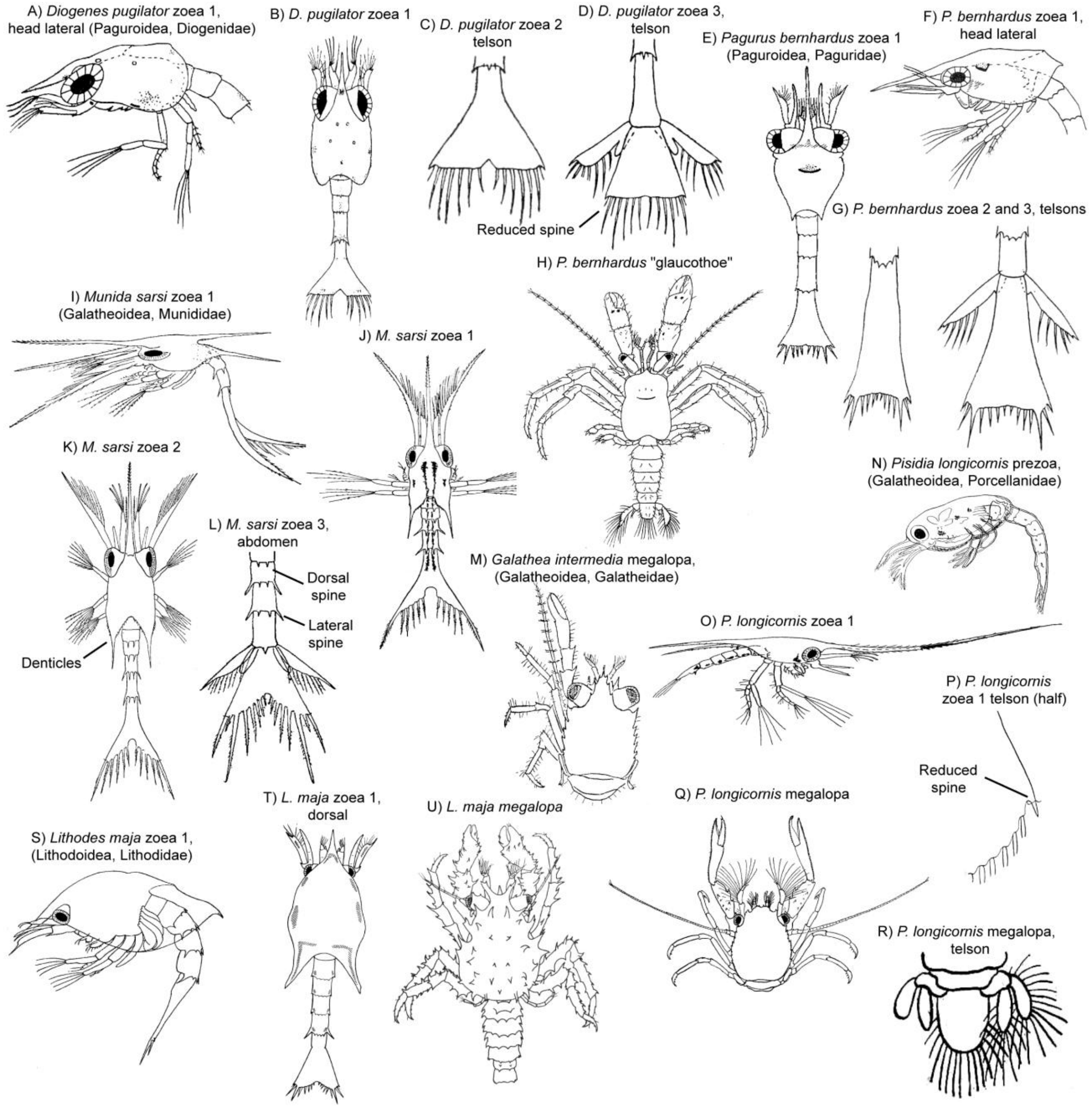

Fig. 9. Examples of Infraorder Anomura developmental stages. (A-H from Macdonald *et al*., 1957; I-L from Lebour, 1930b; M from Williamson, 1915; N-R from Lebour 1943; S from Gurney, 1942; T, U from Pike & Williamson, 1958).

The pleon of anomuran megalopae is narrow and in most, the last pair of pleopods form lateral uropods, making a fan with the tail (Fig. 9H, R), unlike most brachyuran megalopa where the pleopods are ventral.

Superfamily Paguroidea: There are four zoeal stages. The telson has little or no cleft, except in some early stages (Fig. 7E). In Family Diogenidae the posterior end of the carapace is rounded as in *Diogenes pugilator* (Roux, 1829)(Fig. 9A), but in Family Paguridae is typically produced into two short spines as in *Pagurus bernhardus* (Linnaeus, 1758)(Fig. 9F). The carapace margins are never denticulate.
The megalopae of *Pagurus* spp. were once thought to be a separate genus and were given the name "glaucothoe" (Fig. 9H), a term that is often still used; sometimes also for other anomuran megalopae. The exoskeletons of the megalopae are smooth.

Superfamily Galatheoidea: In families Galatheidae and Munididae the posterior carapace is produced into spines of intermediate length e.g. *Munida sarsi* Huus, 1935 (Fig. 9I-K) and there are typically denticles along the carapace/spine margins and dorsal and lateral spines on the pleon somites. The telson has a deep cleft. There are up to five zoeal stages (four in *Munida* spp., four or five in *Galathea* spp.). In Family Porcellanidae there are only two zoeal stages, the posterior carapace is produced into very long spines that extend beyond the telson (Fig. 9O) and the rostrum may be several times longer than the body. The telson border is convex (Fig. 9P). There are two common, easily identified European porcellanids, *Porcellana platycheles* (Pennant, 1777) and *Pisidia longicornis*. (Linnaeus, 1767). *P. longicornis* has a series of hooks on the tip of the second from outer telson spines in both zoeal stages. In the first zoea only, there are two obvious downward directed spines near the base of each of the posterior carapace spines. Neither of these features are found in *P. platycheles*.
In the megalopae of Galatheoidea the exoskeleton is spiny, as in *Galathea intermedia* Lilljeborg, 1851 (Fig. 9M) and *P. longicornis* (Fig. 9Q). The pleon curls under the carapace

Superfamily Lithodoidea: There is only one Lithodoidea species, found in the region, restricted to the north, the northern stone crab *Lithodes maja* (Linnaeus, 1758), which is in Family Lithodidae. There are only two zoeal stages (Fig. 9S, T). The smooth carapace has a pair of dorsolateral spines and there are both dorsal and lateral spines on the pleon somites. The telson has quite a deep cleft, with eight or nine spines each side. There are no uropods, but in zoea two, pleon somite six bears small pleopods.
In the megalopa the exoskeleton is very spiny (Fig. 9U). There are no uropods, but small pleopods on pleon somite six.

Further information: Williamson, 1915; Webb, 1921; Lebour, 1930b, c, 1943; Gurney, 1942; Macdonald *et al*., 1957; Pike & Williamson, 1958, 1972; Newell & Newell, 1963; Goldstein & Bookhout, 1972; Christiansen & Anger, 1990; González-Gordillo *et al*., 1996; Puls, 2001; Harvey *et al*., 2002; Pan & Hay, 2010; Larink & Westheide, 2011; Poore *et al*, 2011.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda: Sub-order Pleocyemata:

Infraorder Brachyura:

Brachyurans are the "true crabs" and the adults of 42 species are recorded in the PMF. The complete early development is not known for all species. The most comprehensive key to European, Atlantic coast brachyuran zoea is given in Paula (1996).

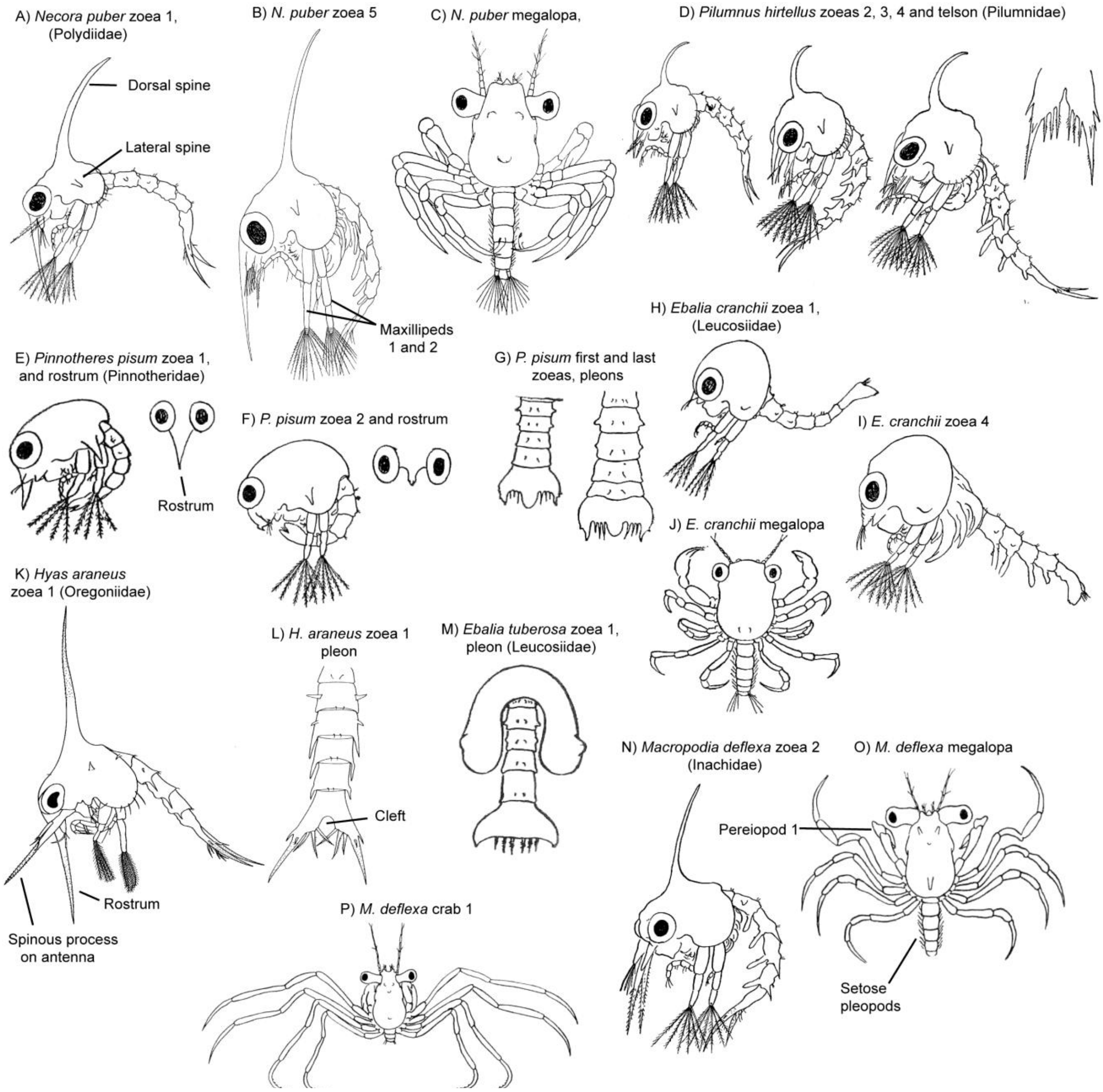

Fig. 10. Examples of Infraorder Brachyura development stages (A-J, M-P from Lebour, 1928; K, L from Christiansen, 1973).

Lebour (1928) found that all the British crabs she studied had a prezoea stage (Fig. 2A), but this is very short lived and unlikely to be caught in plankton nets. There can be from one to more than 10 zoeal stages in different species, but the majority have two to five. Within Family Inachidae there are just two zoeal stages, as in *Macropodia deflexa* Forest, 1968 (Fig. 10N). Brachyuran zoea, apart from *Dromia personata* (Linnaeus, 1758)(Fig. 11), which superficially resembles an anomuran zoea, are very characteristic in appearance, with a carapace that is typically almost spherical, usually with a pair of lateral spines and a single prominent dorsal spine as in *Necora puber* (Linnaeus, 1767)(Fig. 10A, B). However, these spines can sometimes be vestigial, or some missing e.g. zoeae of *Pinnotheres pisum* (Linnaeus, 1767)(Fig, 10E, F) and *Ebalia cranchii* Leach, 1817 (Fig. 10H, I). In a few cases there are additional spines, but always less than 20. In many species, such as *Hyas araneus* (Linnaeus, 1758)(Fig. 10K), there is a prominent spinous process on the antenna. The most prominent limbs protruding from the cephalothorax are the paired first and second maxillipeds (Fig. 1B) that are used in swimming. In older zoeae the eyes become movable, rudimentary claws and pereiopods develop under the carapace, limb buds develop on the pleon somites as in *Pilumnus hirtellus* (Linnaeus, 1761)(Fig. 10D) and locomotory limbs have an increasing number of setae. There are never any uropods on the pleon (Fig. 10G, L, M). The telson is usually deeply cleft and is typically armed with spines/setae (Fig. 10L), although in *Pinnotheres pisum* (Fig. 10G), *Ebalia cranchii* and *E. tuberosa* (Fig. 10M) the telson is completely different.

The megalopae are generally less well described than the zoea. They are strikingly different from the zoea and resemble small crabs (Fig. 10C, J, O). The carapace spines are either lost or reduced and the cephalothorax is somewhat dorsoventrally compressed, with strong chelae only on the first pereiopods. The narrow pleon, when it is unfolded from under the body, has setose pleopods for swimming (Fig. 10O). The last pair of pleopods do not form a lateral tail fan with the telson as in Anomuran megalopae (Fig. 9H, R), but remain ventrally as pleopods, apart from in *Dromia personata* (Fig. 11). The first crab stages do not differ greatly from the megalopa (Fig. 10P).

Further information: Lebour, 1928, 1944; Gurney, 1942; Newell & Newell, 1963; Christiansen, 1973; Rice & Ingle, 1975; Ingle, 1981, 1983, 1984, 1985, 1992; Paula, 1985, 1996; Barnich, 1996; Kim & Hong, 1999; Puls, 2001; Harvey *et al*., 2002.

PHYLUM ARTHROPODA: Subphylum Crustacea: Class Malacostraca: Order Decapoda: Sub-order Pleocyemata: Infraorder Brachyura:

Family Dromiidae:

Dromia personata (Linnaeus, 1758)

Dromia adults are commonly known as “sponge crabs” or “decorator crabs”, because of their habit of holding a piece of sponge or other material over their carapace as camouflage.

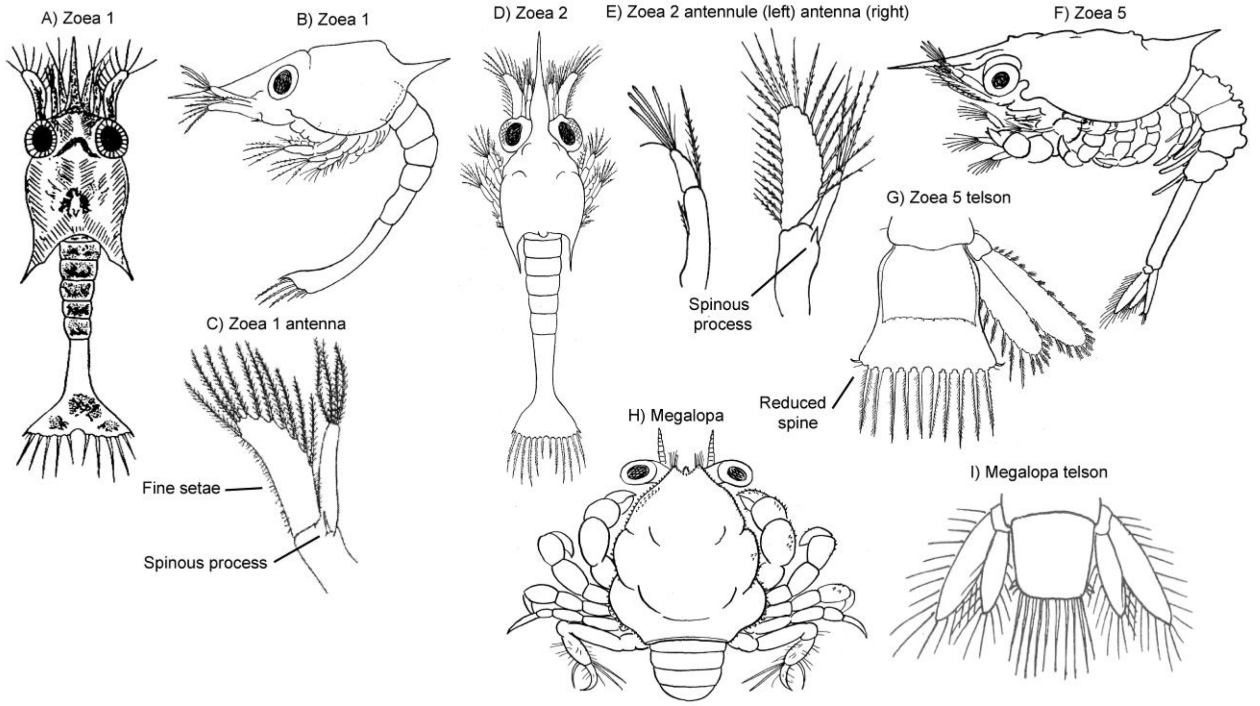

Fig. 11. *Dromia personata* (from Lebour, 1934).

This species has been included separately because the zoea differs from other brachyuran zoea, in that they do not have the typical rounded body, but a body more reminiscent of an anomuran larva (Fig. 11A, B). They have a long pointed rostrum and the posterolateral corners of the carapace are produced into spines that are not denticulate. The eyes are prominent, sessile only in zoea one, and the antenna has a large scale that in the first zoea bears long plumose setae on the inner margin and fine hairs on the outer margin (Fig. 11C). These fine hairs were not drawn by Lebour (1934). In later zoeal stages the long setae are spread all around the margin of the scale (Fig. 11E). The spinous process on the antenna (Fig. 11C, E) is vestigial compared to most brachyurans where this spine is well developed (Fig. 10K). The telson is only slightly indented on the central hind margin and bears seven spines each side in the first zoea (Fig. 11A), eight in the second (Fig. 11D) and seven in the third to fifth (last) stage (Fig. 11G). In all zoeal stages the second spine from the outside is reduced and hair-like (Fig. 11G). The first zoea and some of the subsequent stages of *D. personata* resemble *Upogebia* spp. (Gebiidea) in the telson, antennules, antennal exopods, mandibles, maxillae and first and second maxillipeds. They differ in the rostrum and carapace, which are similar in *D. personata* to those found in some anomurans, most of which also have “hair-like” second spines on the telson.

The megalopa (Fig. 11H) resembles other brachyuran megalopae, with the pleon curved under the body, but the arrangement of the last pair of uropods differs, as they form a tail fan with the telson (Fig. 11I) and do not remain ventrally as pleopods. The exoskeleton is covered in fine hairs.

Recorded: Adult recorded in the PMF (as *Dromia vulgaris*). L4, not recorded. Irish Sea. Southern North Sea. English Channel.

Further information: Lebour, 1934; Gurney, 1942 (both as *D. vulgaris*); Pike & Williamson, 1958 (as *D. personatus*); Ingle, 1992; Martin, 2001.

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PHYLUM ANNELIDA

Phylum Annelida is a large phylum of segmented worms. The current WoRMS scheme divides it into two classes, **Clitellata** and **Polychaeta**. Adult Clitellata are characterized by having a clitellum, a collar around their anterior body that secretes a cocoon that protects and nourishes fertilised eggs until they hatch. Polychaeta lack a clitellum and typically have paired, unjointed lateral outgrowths from their bodies called parapodia. Both classes usually have hair-like bristles known as chaetae (or setae) that are found along the body in various configurations and aid in locomotion, feeding and sometimes protection, but their number is few in Clitellata. Clitellata is divided into two sub-classes, Oligochaeta that includes the familiar earthworms and Hirudinea containing parasitic leeches, but there are relatively few marine representatives. Oligochaeta are found along the shoreline in brackish conditions and Hirudinea are all parasitic on fish, so neither are likely to be collected in plankton samples and are not considered here. Polychaeta are almost entirely marine. Adults of benthic species are occasionally taken in plankton samples, particular species quite regularly, mainly related to features of their reproductive behaviour. Few are completely planktonic as adults (Dales & Peter, 1972), only one out of the 268 species recorded in the PMF. However, a large proportion of benthic species produce planktonic larvae that can be very abundant in plankton samples, particularly in coastal areas.

Class Polychaeta:

Planktonic larval stages of polychaetes can be sampled throughout the year, certainly in inshore areas. Identification to species is a specialist task, as the larvae of many species have not been described, there are progressive changes in larvae morphology during development, particular developmental stages are not found in all species, there is often great similarity between at least related species and there is usually considerable biodiversity at any one site. Only examples of the larvae of some of the commoner European polychaete species have been included here and particular species with very characteristic larvae.
There are few comprehensive guides and keys available to identify polychaete larvae, but some of the most useful for the northern European area are: Thorson, 1946; Muus, 1953a, b; Hannerz, 1961; Hamond, 1967; Bhaud & Cazaux, 1952, 1987; Plate & Husemann, 1994 and Husemann, 1999. The Bhaud & Cazaux (1987) paper is particularly useful because of the large number of illustrations. For excellent colour images and information on a wide selection of polychaete larvae see Larink & Westheide (2011). A useful and well illustrated text on larval identification, but mainly for species that do not occur in the European area, is by Crumrine, 2001.

Classification:

For Polychaeta there is no widely recognised or consistent scheme of higher taxa. They have traditionally been divided, rather artificially by lifestyle, into two subclasses, Errantia that are typically free-moving and Sedentaria that live in burrows or tubes. WoRMS currently follows the basic scheme detailed below, with an additional subclass, incertae sedis, where exact classification of members is still controversial. Species from all of these groupings are recorded in the PMF, the number in each given in brackets as an example of typical coastal biodiversity.

Class Polychaeta:
- **Subclass Errantia**
  - **Order Phyllodocida (125)**
  - **Order Eunicida (20)**
  - **Order Amphinomida (2)**
- **Subclass Sedentaria**
  - **Family Chaetopteridae (2)**
  - **Infraclass Canalipalpata**
    - **Order Sabellida (32)**
    - **Order Spionida (18)**
    - **Order Terebellida (38)**
  - **Infraclass Scolecida (25)**
- **Subclass incertae sedis (6)**

Reproduction and Development

Most polychaetes have separate sexes, but some are hermaphrodite. A few species copulate, but most fertilise the eggs externally. Some eggs are laid on the bottom and the larvae remain on the bottom, but in species with planktonic larvae the gametes are typically expelled into the surrounding water. Additionally, some species retained the eggs in an external brood pouch. In a few species the egg hatches directly into a miniature postlarva, but in most cases they hatch into a trochophore larva (Fig. 1A-C; a term also used for the early larvae of five other phyla). In some species the egg case can have a honeycombed surface and can still be present in the early trochophore (Fig. 1B). Initially a large part of the trochophore body may be covered in fine cilia, and if this stage is present is termed a prototrochophore (Fig. 1A). Trochophores are generally circular, or broad and tapering posteriorly, ~100 µm in diameter and unsegmented. Some are lecithotrophic, surviving on yolk from the egg, others develop a mouth and gut and are planktotrophic (Fig. 1C). Exact morphology is variable between species, but in typical planktotrophic species a series of ciliary bands (trochs) are present. A narrow circular band of longer cilia develops anterior to the mouth, called the prototroch, used for locomotion and sometimes feeding. Parallel to the prototroch, posterior to the mouth region, there may be another band of cilia called the metatroch. Between the two bands is a ciliated region around the mouth called the food groove. Anteriorly there may be an apical sensory plate with a group of cilia called the apical tuft and posteriorly a group of cilia called the telotroch. Additional ciliary bands are sometimes present. Pigmented ocelli (eye spots) may be present, the number varying depending on species.

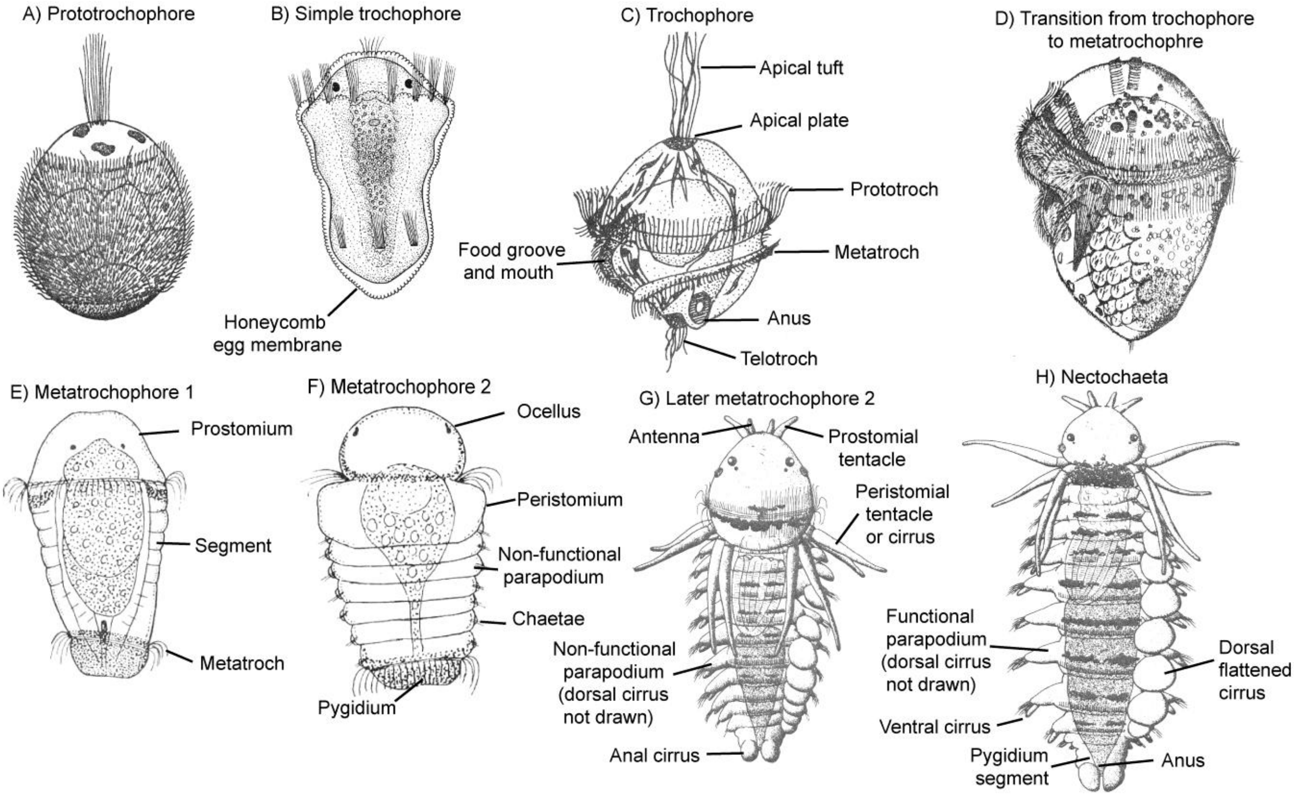

Fig. 1. Examples of polychaete larval stages (A, C, D, G, H from Bhaud & Cazaux, 1987; B from Day, 1934; E, F from Thorson, 1946).

The trochophore metamorphoses to the next stage, the metatrochophore (Fig. 1D-F) and marked segmentation becomes obvious, even while the trochophore shape is still present. There are two, not very precisely separable, metatrochophore stages. The first has few, sometimes indistinct segments and no parapodia developed (Fig. 1E), while the second has more segments and usually small non-functional parapodia (Fig. 1F, G). The anterior presegmental lobe of the metatrochophore is called the prostomium. This lacks chaetae but may bear ocelli, single or paired sensory antennae and sensory or feeding prostomial tentacles. These appendages vary in size and may be arranged proximally, laterally or dorsally. Posterior to the prostomium is the peristomium segment, fused to the prostomium to varying degrees, together composing the head.

The peristomium bears the mouth and may be fused to one or more subsequent segments. The peristomium and sometimes the most anterior segments may bear a variable number of tentacles or cirri, fleshy ones termed palps. **Nomenclature used for these anterior appendages is confusingly variable and sometimes conflicting, so has been kept deliberately simple here.** The distal segment from which the anus emerges is termed the pygidium and at least in later larvae may bear a pair of anal cirri. The metatrochophore is usually defined as becoming a nectochaeta stage (Fig. 1H) when at least three pairs of functional parapodia with chaetae have developed, but in some species parapodia, or prominent parapodia, do not develop. In at least later stages, a few or several parapodia may be fully developed, biramous and in a variety of shapes (Fig. 1H), composed of a neuropodia and a notopodia, each bearing an appendage (cirrus) and chaetae (Fig. 2D, F). The stage of development that nectochaetae settle to the bottom depends on the species. Chaetae may be long in early larvae, but they tend to be replaced by shorter chaetae prior to settlement. Trochophores are difficult to identify, even to the family level, sometimes even to the phylum, so most of the illustrations included here are for metatrochophores and nectochaetae.

LARVAL POLYCHAETES

PHYLUM ANNELIDA: Class Polychaeta:

Subclass Errantia:

Errantia adults comprise free-moving polychaetes with a large number of segments, capable of rapid locomotion and with a head bearing relatively few specialised appendages. They are generally predatory or scavengers, often with hard jaws and well developed eyes. They are characterized by having internal supporting chaetae (aciculae) in the parapodia and sensory appendages on the prostomium.

Order Phyllodocida

Phyllodocida is a very large order of a wide variety of typically free moving benthic species, ranging over the surface, burrowing in sediments or living in crevices. Nine of the largest families are, Polynoidae, Aphroditidae, Pholoidae, Sigalionidae, Nereididae, Hesionidae, Phyllodocidae, Glyceridae and Nephtyidae. There are a further three families, Tomopteridae, Alciopidae and Syllidae, the adults of which are pelagic or are frequently sampled in plankton nets. These are described separately.

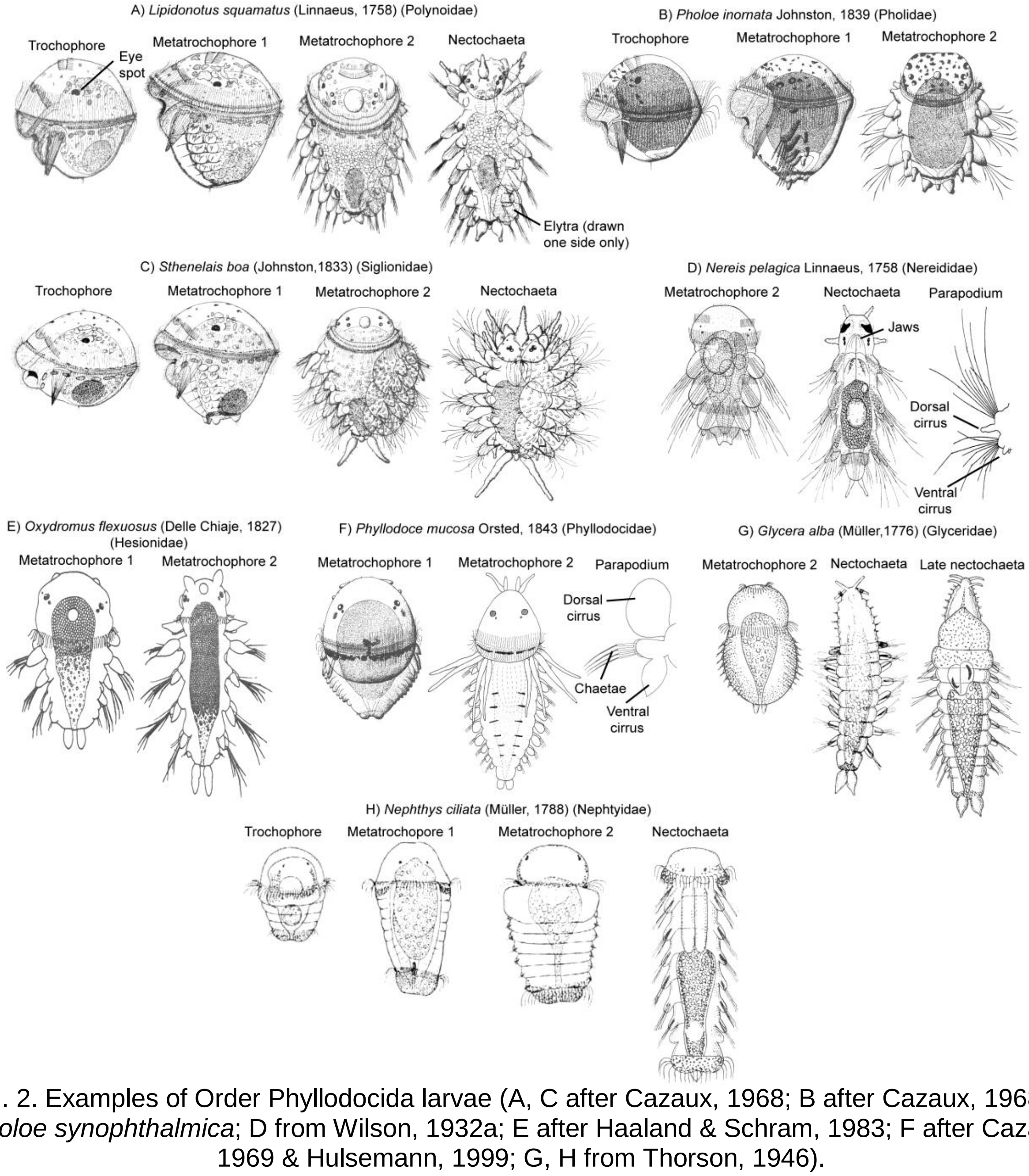

Fig. 2. Examples of Order Phyllodocida larvae (A, C after Cazaux, 1968; B after Cazaux, 1968 as *Pholoe synophthalmica*; D from Wilson, 1932a; E after Haaland & Schram, 1983; F after Cazaux, 1969 & Hulsemann, 1999; G, H from Thorson, 1946).

The trochophores of Order Phyllodocida are generally cone-shaped with paired eyespots (Fig. 2). From at least the second metatrochophore stage, larvae typically have well developed parapodia bearing flattened dorsal cirri and well developed antennae, prostomial and peristomial tentacles. The prototroch is often not lost until late in development. Even in the nectochaeta stage there are typically less than 10 segments.

Four of the families, Polynoidae, Aphroditidae, Pholoidae and Sigalionidae, are grouped in Suborder Aphroditiformea and are called “scale worms”, as the adults and usually also the larvae have, scale-like, dorsoventrally flattened appendages of the parapodia called elytra (Fig. 2A, C, D), probably modified dorsal cirri. In some larvae the elytra do not develop until the late nectochaeta stage, or are sometimes not present in the larvae, as in *Pholoe inornata* (Fig. 2B). Additionally, elytra often become detached from the larvae, especially following preservation. In Family Nereididae the metatrochophore is three-segmented (Fig. 2D) and develops into a nectochaeta with a pair of jaws in the pharynx and initially a single pair of prostomial antennae. The eyespots are typically red in fresh specimens.

In Family Hesionidae (Fig. 2E), metatrochophores usually have three pairs of red or brown eye spots, retain a prototroch and have prostomial antennae developing. Parapodia of the first chaetigerous segment lose their chaetae and develop into pairs of tentacles.

In Family Phyllodocidae (Fig. 2F; paddle worms), juveniles have obvious flattened dorsal parapodial cirri and a prototroch is retained until at least the stage when peristomial tentacles develop. Nectochaetes usually have a large number of chaetigerous segments, obvious proximal antennae, well developed peristomial tentacles and broad parapodia.

In Family Glyceridae (Fig. 2G; blood worms) the late metatrochophores have five to nine chaetigerous segments. The prototroch is retained and there are four small antennae on the conical prostomium, which is ringed in late stages. They have a proboscis with four jaws.

In Family Nephtyidae (Fig. 2H; cat worms), parapodia are not well developed until the nectochaeta stage. In the later stages there are often irregular bands of reddish brown pigment anteriorly and on the pygidium.

Order Eunicida:

Eunicida adults are usually carnivorous, burrowing or tube-living and have an elongated, segmented body and a distinct head, normally with a separate peristomium and prostomium. They have a prominent jaw system of several parts. While adult Eunicida can be quite abundant, many have larvae that are lecithotrophic, brooded and never pelagic, so larvae of a restricted number of species will be collected in samples.

Eunicida larvae tend to be very simple, with large yolk reserves, a well defined series of ciliary bands, sometimes very broad and short parapodia so are not well adapted for swimming (Fig. 3).

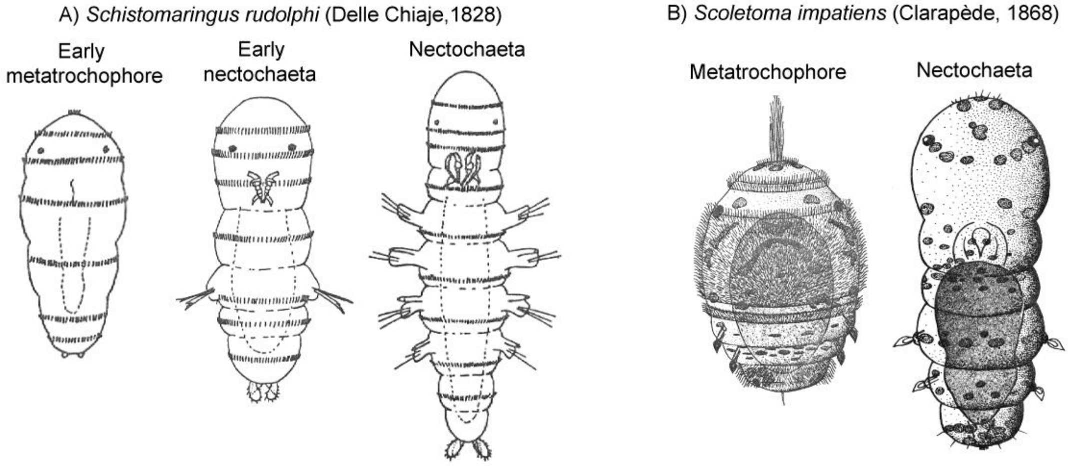

Fig. 3. Examples of Order Eunicida larvae (A after Richards, 1967 as *Stauronereis rudolphi*; B after Cazaux, 1972 as *Lumbrinereis impatiens*).

Order Amphinomida:

Amphinomida are free-living, their relationship with other polychaetes poorly resolved. Their best known members are the warm water "fireworms" that have venomous chaetae that can cause great pain to humans if they come in contact with skin. Although a small order and not usually very abundant, two species are recorded in the PMF.

Development includes a characteristic larva called a rostraria (Fig. 4). These have a pointed prostomium without appendages and thick, ciliated, extendable, backwardly directed peristomial tentacles that are used in swimming and feeding. The chaetae of the first segment are very long.

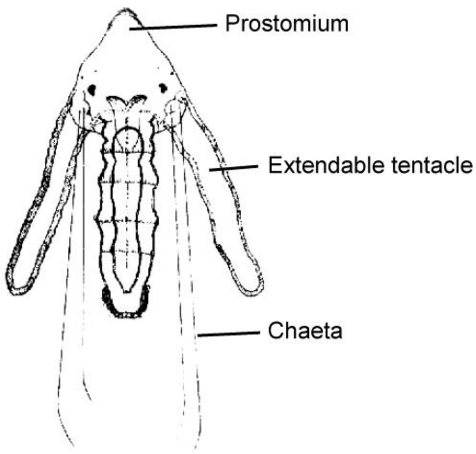

Fig. 4. Unidentified rostraria larvae (after Bhaud & Cazaux, 1987).

Subclass Sedentaria:

Adults typically have a limited number of segments and the body may be separated into different regions. Anterior appendages may be absent, or they may have a few to many similar appendages. Most live in tubes or burrow and they are usually filter or deposit feeders.

Family Chaetopteridae

Adults are filter feeders living in u-shaped tubes in tunnels buried in the sediment. They are highly adapted to living in the hard tube they secrete, as inside the tube the worm body is regionally specialized, with highly modified appendages on different segments for excavating the tunnel, feeding, or creating flow of water through the tube.

Chaetopteridae larvae are the largest among the polychaetes, ranging in size from 0.4-2.5 mm in length. Trochophores are barrel-shaped with a prostomium covered in cilia and no distinct prototroch. Metatrochophores have one to two (bitroch; Fig. 5A) ciliated bands on the hind-body, a large buccal funnel and a single contractile anal appendage. Lip-like pre- and post-oral lobes are present in later larvae (Fig. 5B). There are no setae on the simple parapodia. Larvae are often long lived, so can be widely dispersed. While most trochophores add segments sequentially from a posterior growth zone to produce a nectochaeta larva, these typically differ, as at no point in larval growth does the metatrochophore take on the clearly segmented form of the typical nectochaeta larva, the segments are formed by subdivision of existing segments.

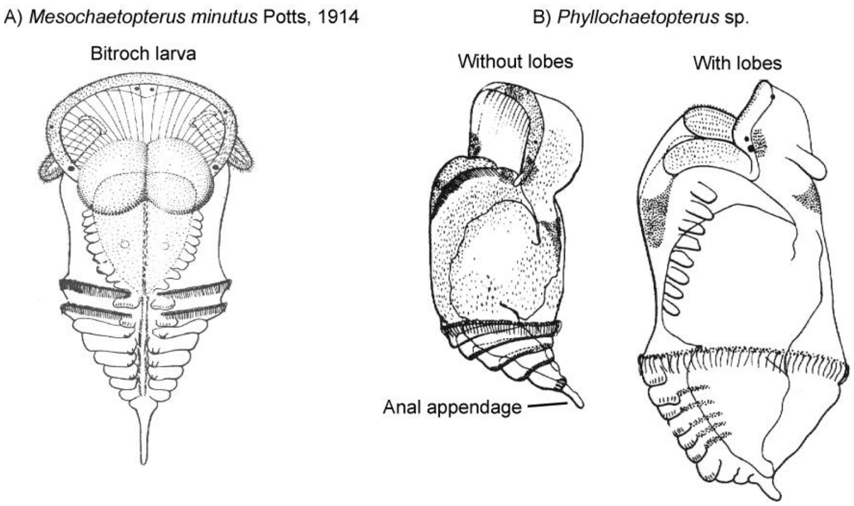

Fig. 5. Example of Family Chaetopteridae larvae (after Bhaud, 1971).

Infraclass Canalipalpata:

Adults are known as fan-head worms. They typically have no teeth or jaws as most are filter feeders, using an array of long grooved palps on the prostomium. They live in various types of tubes. Larvae can be very common in inshore plankton samples. Most species are in orders Sabellida, Spionida and Terebellida.

Order Sabellida:

Adults typically live in tubes formed from sand or shell fragments cemented together with mucous. In early larvae the body is no more than twice as long as wide, with a distinctly wide prostomium making them mushroom-shaped. From early stages they develop two bundles of chaetae that are held along the larval sides while swimming, but can be spread out in all directions when disturbed. The broad prostomium is surrounded by a prototroch. Later larvae resemble those of Order Spionida and also have bands of dark pigment on the segments, but Sabellida have much shorter larvae, with fewer segments and few chaetae on the segments.

Family Oweniidae have a very characteristic post-trochophore larva called a mitraria (Fig. 6A) with a helmet-shaped body that has an undulating posterior margin on which the well developed prototroch is situated, and very long chaetae. The mitraria is an endolarva, meaning that the body develops internally and frees and becomes extended during metamorphosis. The nectochaeta has a very wide head and there are two distinct anterolateral bundles of long, serrated chaetae that emerge from the lower face. There are no distinct parapodia.

Family Sabellariidae are mushroom-shaped anteriorly (Fig. 6B) and have two lateral bundles of setae that are slightly bent and armed with spiny collars. Later stages develop a pair of thick peristomial tentacles (palps).

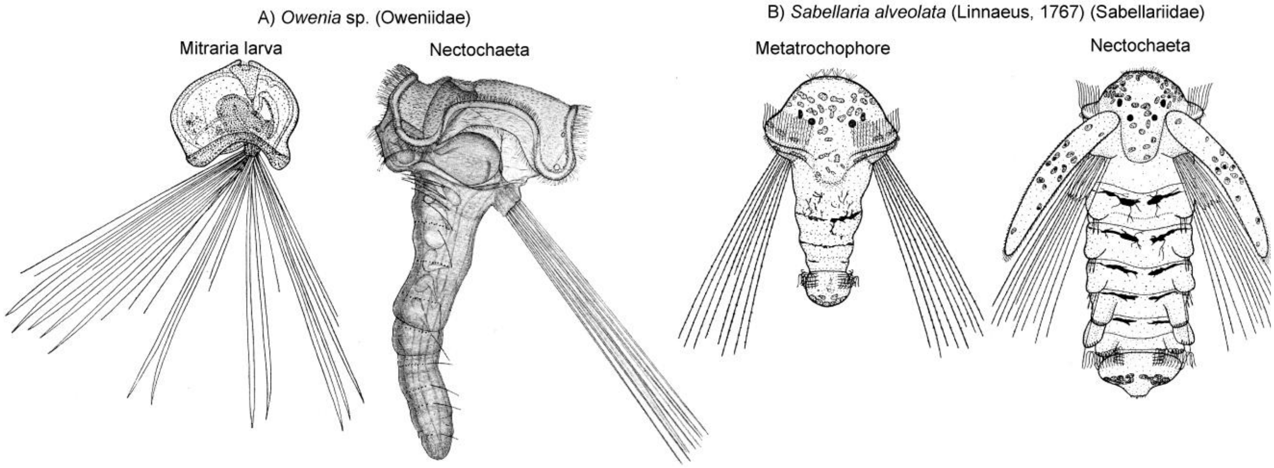

Fig. 6. Examples of Order Sabellida larvae (A from Wilson, 1932b; B from Wilson, 1929).

Order Spionida

Adults are generally tube-living and deposit feed using a pair of large tentacles. This group includes some of the commonest larvae taken in inshore plankton samples, but the earliest stages are difficult to identify. The three families with most members and some very characteristic larvae are Magelonidae, Spionidae and Poecilochaetidae. Early metatrochophores (Fig. 7A, B) are similar to those of Order Sabellida, but are longer in relation to width and typically have well developed chaetae on the parapodia that may be smooth or serrated. There is also sometimes a pair of anterolateral bundles of chaetae. There are typically rows and patches of pigment, particularly on the more posterior segments. In later stages the head usually bears very prominent swollen peristomial tentacles and the body develops a relatively large number of segments, often more than twenty.

In Family Magelonidae, the body is characteristically long and slim (Fig. 7A). The larval peristomial tentacles are asymmetrical in early stages of some species. These are replaced by very long adult tentacles, making later stages of this family easily recognisable. There is a pair of anterolateral bundles of long chaetae and also long chaetae on the posterior segments. There are no appendages on the small pygidium.

In Family Spionidae (Fig. 7B) there are chaetae on all segments from an early stage and prominent peristomial tentacles develop in the nectochaetae. Anterior bundles of chaetae are not well developed.

In *Poechilochaetus serpens* of Family Poecilochaetidae, larvae remain in the plankton as metatrochophores until around 30-38 segments are present. Locomotion is by trochs and long provisional setae, as the parapodia are weakly developed. The next stage has been termed the nectosoma stage (Fig. 7C), in which the trochs and setae are reduced and locomotion is by snake-like undulations of the body using the parapodia. The later stages are transparent, apart from a few yellow chromatophores close to the bases of the parapodia and brown pigment on head and pygidium.

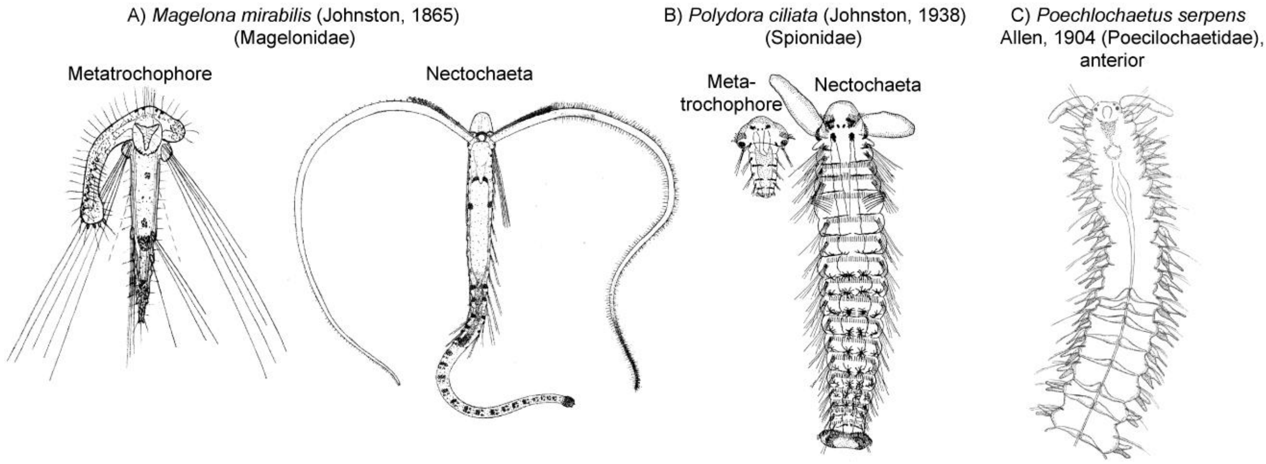

Fig. 7. Examples of Order Spionida larvae (A from Wilson, 1982; B, C from Thorson, 1946)

Order Terebellida

Adults are surface deposit feeders and have large numbers of contractile feeding tentacles that they spread out on the sea floor. Because of this they are known as spaghetti worms. Some are naked, living in burrows or under stones while others construct tubes, and these features are reflected in their larvae.

In Family Cirratulidae, *Cirriformia tentaculata* (Fig. 8A) the larva does not develop a tube and in early stages does not have clear segmentation. The whole body is enclosed in a two-layered egg membrane (not drawn) through which fine cilia pass. Chaetae do not appear until after metamorphosis to the nectochaeta, when most of the cilia are lost.

Family Pectinariidae are known as trumpet worms because of the shape of the conical tubes the adults construct out of sand grains. They live head down in the sediments. The metatrochophores have a retractable prototrochal lobe (Fig. 8B), which when extended makes the body asymmetrical. Nectochaetae secrete a transparent tube and develop forwardly directed, stout setae called palaea that surround the prostomium. The parapodia are narrow and short with short, sharp chaetae.

In Family Terebellidae *Lanice conchilega* is a very common European species. An odd number of characteristic, large prostomial tentacles are gradually added anteriorly as they develop (Fig. 8C). Later larval stages secrete a more or less parallel-sided, transparent tube that is often lost during sampling. Ciliary action pumps water out the open posterior end of the tube and propels the larvae along. The parapodia resemble those found in the larvae of Family Pectinariidae.

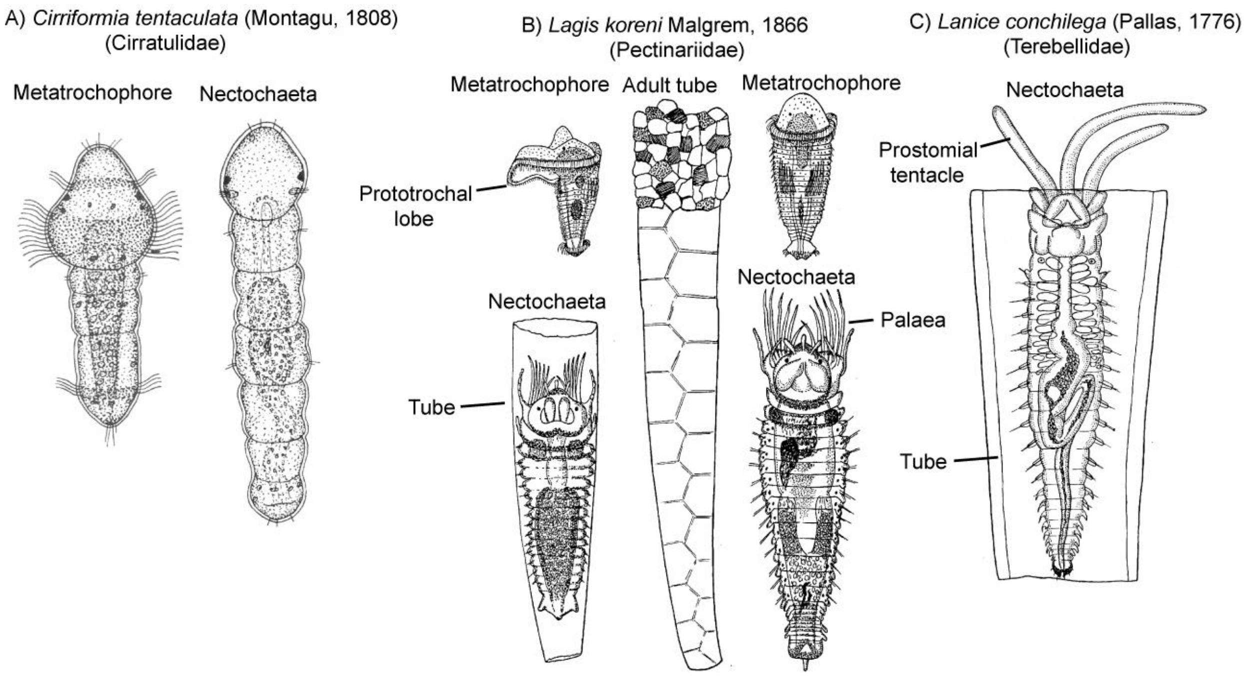

Fig. 8. Examples of Order Terebellida larvae (A from Wilson, 1936 as *Audouinia tentaculata*; B from Thorson, 1946 as *Pectinaria koreni*; C from Thorson, 1946).

Infraclass Scolecida

Adults are typically burrowing, unselective deposit feeders. The head is usually conical and bears no appendages. There are eight orders in Infraclass Scolecida, but those with most planktonic members are Capitellidae, Opheliidae and Arenicolidae.

In Order Capitellidae the early larvae are conical anteriorly (Fig. 9A, B) and the body bears a prototroch that may be narrow (Fig. 9A) or broad (Fig. 9B). Later larvae develop a sparse telotroch and a ventral ciliated band. The metatrochophore does not develop parapodia. The cylindrical body lengthens, creating a greater distance between the prototroch and telotroch. Short chaetae are found in later stages.

In Order Opheliidae larvae are roughly conical anteriorly (Fig. 9C). The body is transparent when unpreserved, with a ventral ciliated zone. Chaetae gradually appear on the segments, posterior to small parapodial lobes. Some of the chaetae are quite long. The telotroch is not well developed. Four anal papillae develop in the early metatrochophores. There may be slight pigmentation on the body with transverse spots.

Order Arenicolidae are also conical anteriorly and have a ventral ciliated band. Parapodia do not develop, but short, sparse chaetae gradually appear laterally with development. Both the prototroch and telotroch are quite broad.

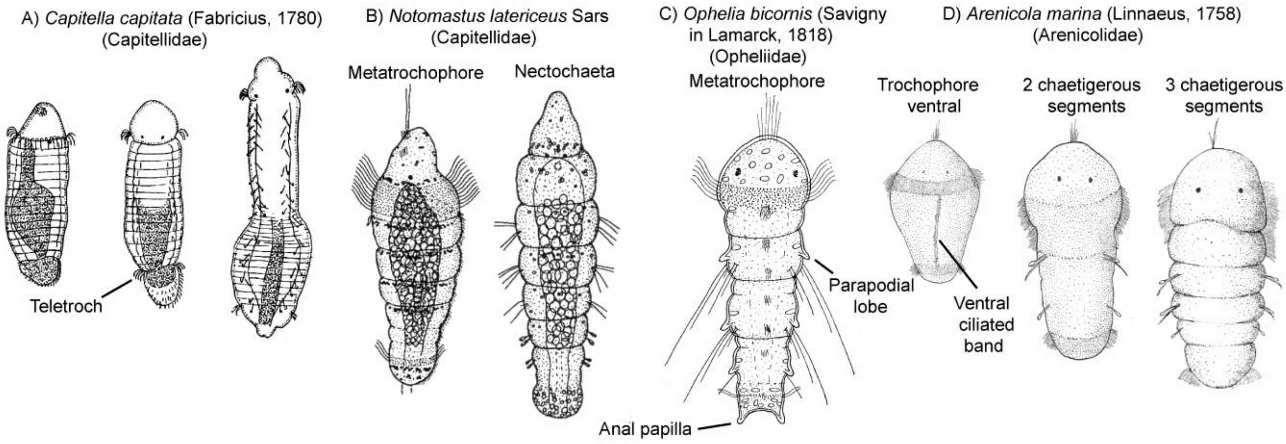

Fig. 9. Examples of Infraclass Scolecida larvae (A from Thorson, 1946; B from Wilson, 1933; C from Wilson, 1948; D from Newell, 1948, 1949).

Subclass incertae sedis:

Because classification is in a state of flux 12 disparate families are bundled in this subclass. Two of the families are Polygordiidae and Protodrilidae. The adults are interstitial species with a rather primitive organisation. They are sometimes taken in inshore samples and superficially resemble nematodes, thread-like without any external signs of segmentation, but with a pair of prostomial tentacles.

In Polygordiidae metatrochophores the prostomium is dome-shaped with a well developed prototroch (Fig. 10A). There are no larval chaetae, tentacles or anal appendages. A pair of red eyes are typically found, located in a hemispherical, anterior protrusion. Segmentation develops internally (an endolarva) and the body extends when it become free during metamorphosis.

In Protodrilidae the larvae are slender and elongated with four ciliary rings (Fig. 10B) and a ventral ciliary band. There are no parapodia or chaetae. The prostomium is round and a pair of red eyes may be present. In later larvae a pair of antennae may be present and two to three adhesive lobes on the pygidium.

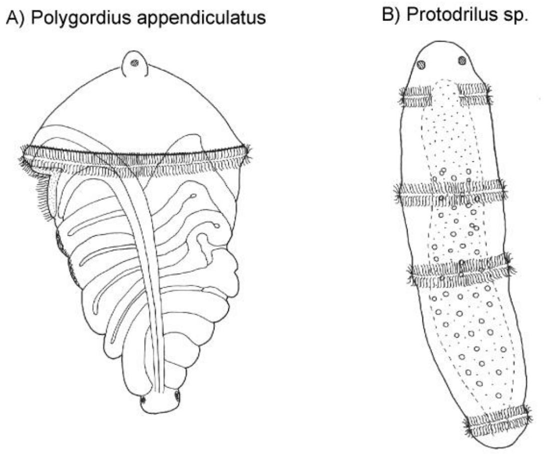

Fig. 10. Examples of Subclass Polychaeta incertae sedis (A, B after Plate & Hulsemann, 1994).

ADULT POLYCHAETES SAMPLED PELAGICALLY

The only adult polychaete species **regularly** sampled in plankton nets, either because they are pelagic, or emerge into the water column as part of their life cycle, are all in Order Phyllodocida in families Tomopteridae, Alciopidae and Syllidae.

Phylum Annelida: Class Polychaeta: Subclass Errantia: Order Phyllodocida: Suborder Phyllodocida incertae sedis:

Family Tomopteridae:

The Tomopteridae are wholly pelagic predators and there is only one genera and two species recorded from the European shelf area. The young and adults are regularly sampled, usually in small numbers. They are transparent when fresh, translucent when preserved and segmentation of the body is not obvious. The prostomium has two short, divergent, horn-shaped antennae and a pair of lensed eyes (Fig. 11A, B). A pair of ciliated nuchal organs (chemosensory) are also present, but not always obvious. The second pair of appendages in the adult are the cirriform appendages, which have internal aciculae (supporting chitinous rods) that are drawn out into long streamers and sweep backwards along the body. Latterly the body bears variable numbers of parapodia that are used in swimming and do not bear chaetae. The parapodial trunks are biramous distally with each conical ramus more or less surrounded by a paddle-like lobe called a pinna or pinnule. The parapodial rami contain the gonads, either in one or both, depending on species. There are usually various types of glands (hyaline, rosette and chromophil) in the pinnae, some of which require staining to see. Luminescence is produced by parapodial glands, but there is conflicting information whether the rosette or chromophil glands are the source.

Genus *Tomopteris*:

Tomopteris (Johnstonella) helgolandica (Greeff, 1879)

In adults the body is relatively short and broad with ~34 segments (Fig. 11A). The length of the cirriform appendages is around two thirds of body length. The anterior body bears 14-21 pairs of parapodia. The tail may be a third of the total length and bears 14-16 vestigial parapodia. All parapodia usually have distinct, rosette glands in both pinnae, close to the tips and inner edges of the rami (Fig. 11C). There are additional rosette glands on the trunks of the first two pairs of parapodia. The chromophil gland is large and situated below the ventral ramus, but is sometimes inconspicuous. Gonads are present inside each ramus. Juveniles (Fig. 11D), when alive, have delicate orange chromatophores scattered over the body. Their tail is absent, or vestigial, presence of which in older stages separates this species from the closely related *T. septentrionalis* (Fig. 12).

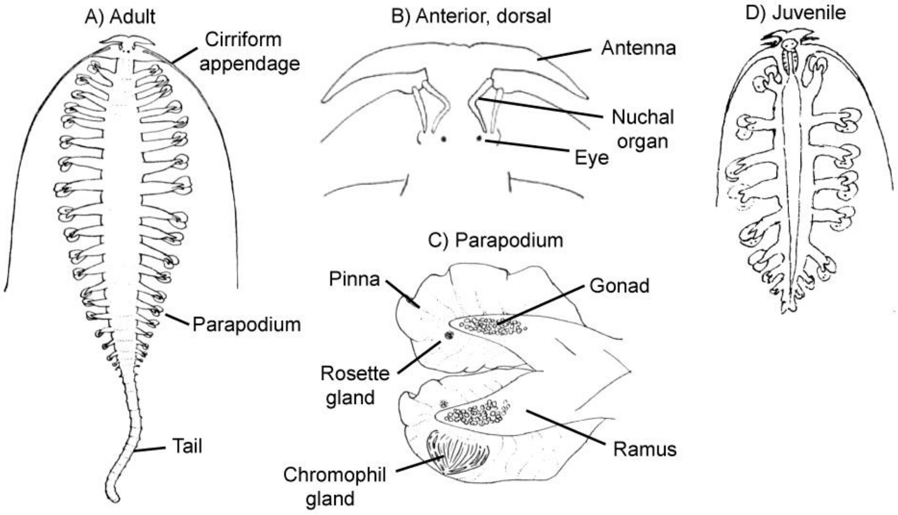

Fig. 11. *Tomopteris* (*Johnstonella*) *helgolandica* (A-C from Muus, 1953a; D from Trégouboff & Rose, 1957 (both as *Tomopteris helgolandica*)).

Recorded: PMF. L4. North Sea. English Channel. Irish Sea.
Size: Adult usually ~20-40 mm, but larger in colder water.
Further information: Muus, 1953a; Trégouboff & Rose, 1957; Todd *et al*., 1991; Pleijel & Dales, 1991; Gerber, 2000; Larink & Westheide, 2011 (all as *Tomopteris helgolandica*).

Tomopteris septentrionalis Steenstrup, 1849.
Adult body short with 17-24 long parapodia (Fig. 12A), tapering posteriorly, without a tail. Length of cirriform appendages at least half the body length. Nuchal organ V-shaped (Fig. 12B). Hyaline glands normally brown and usually visible in the dorsal part of the ventral pinna, but sometimes indistinct (Fig. 12C). No rosette glands. Chromophil gland not forming a compact mass and often poorly developed, but typically appearing as a series of parallel tubes below the hyaline gland. Gonads are found only in the dorsal ramus.

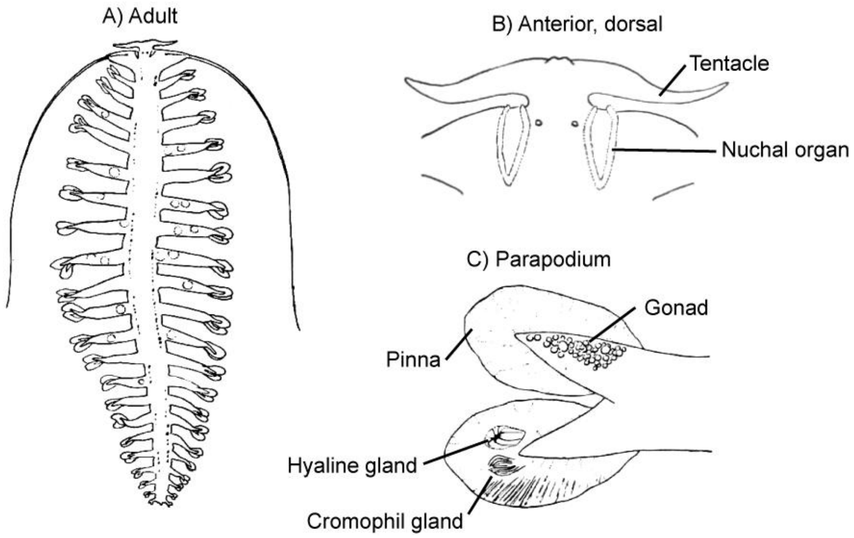

Fig. 12. *Tomopteris septentrionalis* (from Muus, 1953a).

Recorded: PMF and L4, not recorded. Generally a more northern species. Northern North Sea. Southern Ireland. Skagerrak.
Size: ~10-20 mm but up to 30 mm in colder waters.
Further information: Muus, 1953a; Todd *et al*., 1991; Pleijel & Dales, 1991; Larink & Westheide, 2011.

Phylum Annelida: Class Polychaeta: Subclass Errantia: Order Phyllodocida: Suborder Phyllodociformia:

Family Alciopidae:

Genus *Alciopa*:

Alciopa reynaudii Audouin & Milne-Edwards, 1833

Body delicate and transparent, segmentation obvious (Fig. 13A, B), with red eyes when fresh. Prostomium, small with five small antennae (two anteriorly, one dorsally and two ventrally). A single pair of very large, lensed eyes. Pharynx eversible, with two lateral horns (Fig. 13C), no jaws. First segment dorsally incomplete, with three pairs of short tentacles ventrally. The next segment with reduced parapodia, but later segments with well-developed parapodia with dorsal and ventral leaf-like cirri (Fig. 13D). Chaetae all slender and jointed. Parapodial glands dark, divided into dorsal and ventral parts in male. The distal body segment, the pygidium, has two cirri.

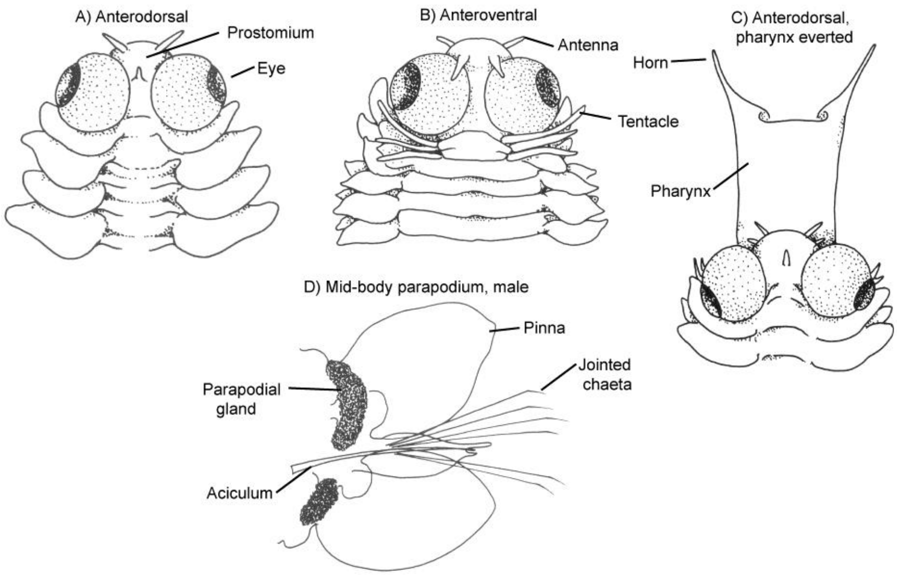

Fig. 13. *Alciopa reynaudii* (from Pleijel & Dales, 1991).

Recorded: PMF and L4, not recorded, but widely distributed.
Size: Usually 10-15 mm, but up to 60 mm.
Further information: Muus, 1953b (as *Greeffia celox*); Pleijel & Dales, 1991.

Phylum Annelida: Class Polychaeta: Subclass Errantia: Order Phyllodocida: Suborder Nereidiformia:

Family Syllidae:

Subfamily Autolytinae:

Adults of this benthic family typically live among hydroid colonies. Some species are occasionally taken in plankton samples, their presence in the water column relating to their extraordinary reproductive behaviour. On the bottom they resemble any other bottom-dwelling polychaete, cannot swim and are termed stock. However, as the breeding season approaches, at least some species can transform, through morphological, physiological and behavioural changes, into a male or female, non-feeding, reproductive body called an epitoke, allowing them to swim up from the bottom and release their gametes in the water column. The whole worm may becomes an epitoke and after release of gametes may die, or revert to the original form. However, most Syllidae reproduce by a second method. Asexual reproduction takes place in both male and female stocks. Typically a new head forms mid-body and this posterior section detaches as a free-swimming stolon, the anterior body remaining as a stock. Several stolons can form simultaneously, but break off singly. The female stolon has three anterior, unbranched antennae (Fig. 14A, C, E, G), the male an anterior bifurcating pair of antennae and three large tentacles behind (Fig. 14B, D, F). Gametes are stored in the body cavity (Fig. 14A). Reproduction typically takes place by the male stolon entangling the female with sperm. The female then releases the eggs into a brood-pouch until liberation as ciliated larvae that develop into stocks. After gamete release the stolons die. 46 species of Family Syllidae are recorded in the PMF and some examples of species found in the northern European area are given below. Keys to some species are given in Hamond, 1967 and Hayward & Ryland, 1995.

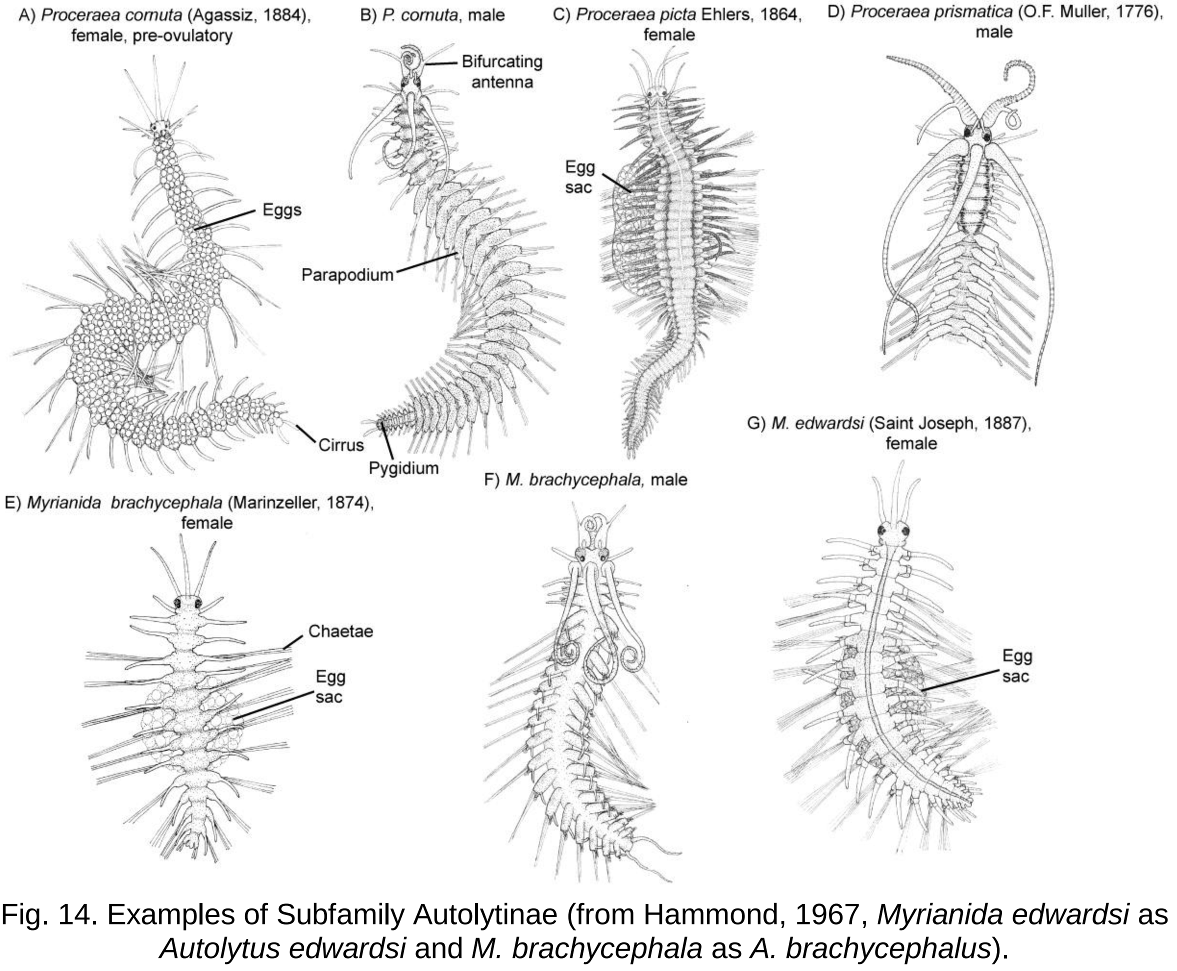

Fig. 14. Examples of Subfamily Autolytinae (from Hammond, 1967, *Myrianida edwardsi* as *Autolytus edwardsi* and *M. brachycephala* as *A. brachycephalus*).

Recorded: PMF (*Proceraea cornuta* as *Autolytus cornutus*, *P. picta* as *A. pictus*, *Myrianida brachycephala* as *A. punctatus* and *M. edwardsi* as *A. edwardsi*). L4, only recorded as Autolytinae spp. All European coastal waters.
Size: Adults ~3-12 mm.
Further information: Hamond, 1967; Hayward & Ryland, 1995; Larink & Westheide, 2011.

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PHYLUM TARDIGRADA

Tardigrades are commonly known as water bears because of the way they walk, reminiscent of a bear's gait. More than 1,000 species have been described and they occur over the entire globe, in both terrestrial and aquatic environments. They are able to survive in extreme environments that would kill almost any other animal and are one of the organisms that are capable, if environmental conditions deteriorate, of reversibly suspending their metabolism. Several species have been shown capable of surviving in a dehydrated state for around ten years. In the marine environment tardigrades are mainly found interstitially in sediments, but can also be found in association with marine algae and benthic invertebrates. None are planktonic, but they are sometimes collected in plankton samples in turbulent conditions.

Morphology

Tardigrades have no respiratory organs, gas exchange occurring over the whole of their barrel-shaped bodies. They have four pairs of unjointed, stubby legs, each terminating in claws of variable type and number (Fig.1A), although most marine species have "toes" with adhesive discs (Fig. 1B). Depending on species, plates may or may not be present on the dorsal cuticle. The cuticle contains chitin and is moulted periodically. The tubular mouth is armed with stylets that are used to pierce their food. Anteriorly, some species possess paired eye spots and appendages, and there may be numerous sensory bristles on the head and body.

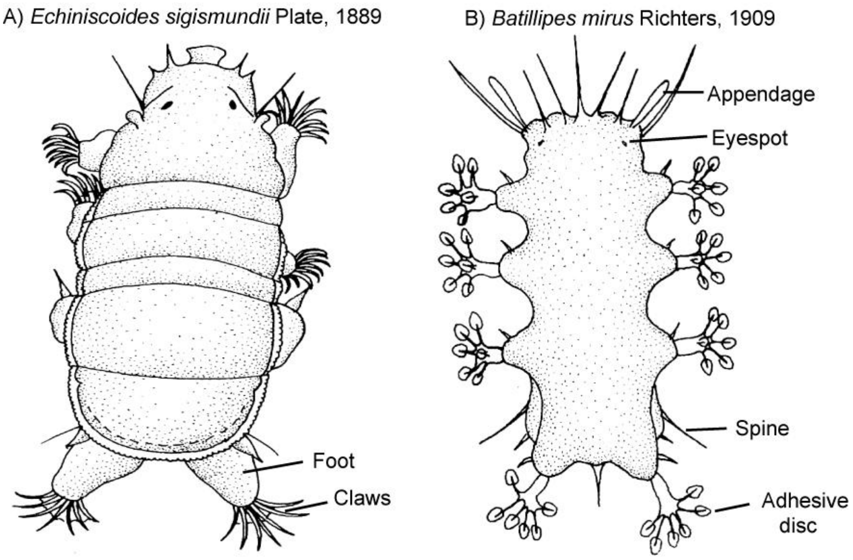

Fig. 1. Examples of tardigrades (from Morgan & King, 1976).

Reproduction and development

Although some species can reproduce without fertilisation, both sexes are usually found, each with a single gonad located above the intestine. Fertilisation is usually external and eggs are laid. Mating occurs during the moult, with the eggs being laid inside the shed cuticle of the female and then covered with sperm. A few species have internal fertilisation, with mating occurring before the female fully sheds her cuticle. The eggs are generally left inside the shed cuticle to develop, but some are attached to the substrate. The eggs hatch within a fortnight, with the young already possessing their full complement of adult cells. Growth to the adult size therefore occurs by enlargement of the individual cells (hypertrophy), rather than by cell division. They live for three to 30 months, and may moult up to 12 times.

Recorded: Not recorded in the PMF or at L4, but could occur. Widespread in coastal regions.
Size: 0.05-1.5 mm, but most ~0.3-0.5 mm.
Further information: Cuénot, 1932; Morgan & King, 1976; Morgan, 1980; King *et al*., 1981; Elliot *et al*., 1990.

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PHYLUM NEMATODA

Phylum Nematoda, after Phylum Arthropoda, contains the most described species, currently around 20,000. They occur in almost every habitat, free-living, often in bottom sediments, or as parasites of a variety of plants and animals. Around 96 nematode species are recorded in the PMF, found on seaweeds, free-living or in the guts of fish. They are occasionally found in plankton samples and may be free-living species that have been carried up from the sea bed by turbulent mixing. However, they may be present because they are in or have been dislodged from zooplanktonic organisms, many of which are an intermediate hosts to parasitic nematodes. Medusae, copepods, amphipods, cephalopods, chaetognaths, fish etc. are all known to harbor immature nematodes (Hutton *et al*., 1962) and *Anisakis* sp., a herring and seal parasite, is commonly found in euphausiids (Sluiters, 1974). Øresland (1986) found that on average 1% of the chaetognath *Parasagitta setosa* (as *Sagitta setosa*) population sampled off Plymouth were infected by the nematode *Hysterothylacium aduncum,* a common fish parasite worldwide, while chaetognaths in the Irish Sea can have a considerably higher percentage of nematode infection (personal observation). Identification of nematodes to species is a specialist task and in general zooplankton analysis they are usually only identified to phylum, so only a general description is given here.

Morphology

Nematodes have a varied morphology, so it is difficult to give a universal description. Their elongated, worm-like shape is generally quite characteristic, (Fig. 1A, B, E-G) and these are the type that are usually taken in plankton samples, but some are much broader (Fig.1C, D). One unifying characteristic that makes the phylum unique is the lack of cilia or flagellae. They are bilaterally symmetrical, usually transparent enough to see internal structure.

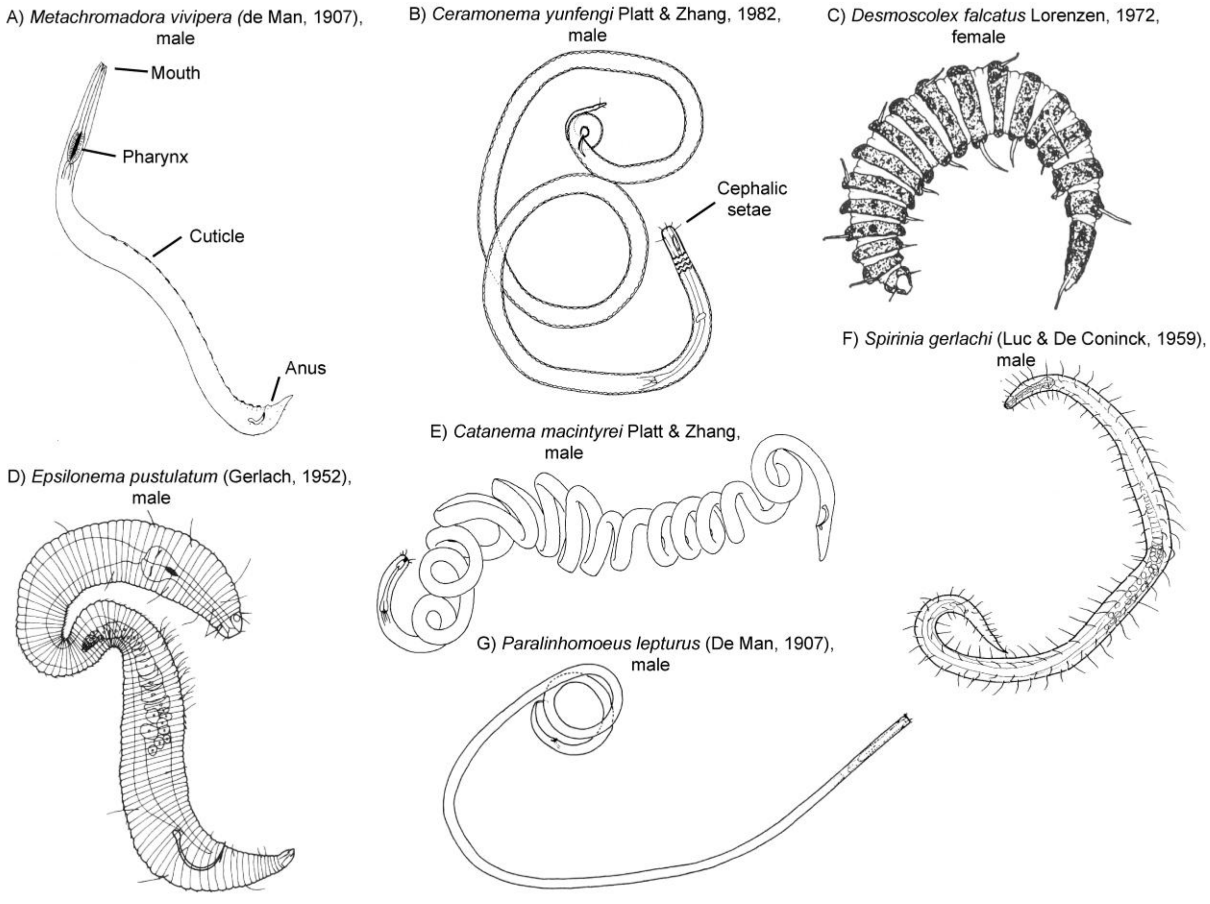

Fig. 1. Examples of variation in nematode morphology (A-F from Platt & Warwick, 1983; G from Warwick *et al*., 1998).

The body is encased in a strong, flexible non-cellular cuticle (Fig. 1A) that may be smooth, with transverse striations, or a variety of surface ornamentation that may be limited to particular areas.

Sense organs (sensilla) are present on the cuticle, typically long setae that can be numerous, or shorter papillae. Sensilla are named according to their location, so setae on the head are called cephalic (Fig. 1B). The cuticle is secreted by and covers a layer of epidermal cells, under which are muscle cells that run in a longitudinal direction only. Alternate contractions of dorsal and ventral muscle blocks resulting in locomotion. Because of high internal hydraulic pressure, contractions cause the body to flex rather than flatten and the animal moves by thrashing back and forth. Anteriorly the mouth opens into a wider buccal cavity and then a muscular oesophagus or pharynx. The buccal cavity has a very variable form, reflecting different feeding methods and may be armed with teeth or other projections. Some nematodes have paired pigment spots, or true ocelli with lens-like structures, on or in the anterior oesophagus. About half-way along the oesophagus is a nerve ring. The anus opens sub-terminally at the posterior, so there is a tail of variable length and shape beyond the anus. The tail shape and length relative to the body length is used in identification.

Reproduction and development

Between the gut and body wall is a fluid filled pseudocoelom in which the reproductive organs are situated. Most nematodes have separate sexes (dioecious) and fertilisation is by copulation. Females may have one or two ovaries and, depending on the number and arrangement, the reproductive pore may be mid-way along the body, or closer to the anus. Males usually have two testes and fertilisation takes place when males, using special copulatory spines, open the reproductive tract of the female and inject sperm. The sperm are unique in that they lack flagellae and move like amoebae, by pseudopodia. Development of fertilised eggs is usually direct and most marine species have a simple life cycle. An egg is followed by four juvenile stages, with moult between stages, before they become adult. There are developmental changes between moults and gonads and copulatory apparatus are only found in adults, so juveniles may be impossible to identify to species. A few species are viviparous, the eggs hatching in the uterus.
Parasitic species have developed a wide range of variations on the basic life cycle. The variations depend on whether there is a secondary host and the amount of time spent in one or either hosts. There is also considerable variability in the way that they transfer between host species. Many species lay eggs that pass out of the primary host with the faeces and are eaten by the secondary host, which in turn gets eaten by the primary host after the nematodes have developed. Because it is not always predictable that the secondary host will be eaten just as the nematode larvae have developed into the infective stage, many species have the ability to encyst themselves in the muscle or cuticle of their secondary hosts.

Recorded: PMF. L4. Widespread.
Size: Adults mainly ~1-2 mm.
Further information: Platt & Warwick 1983, 1988; Warwick *et al*., 1998.

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PHYLUM PHORONIDA

Phoronids are an exclusively marine group of benthic, worm-like organisms, mainly found in water depths <50 m. They secrete a chitinous tube in which they live and can be found singly or in large aggregations, encrusting rocks or among rocks or shells, but typically embedded in sand, mud or fine gravel. Most adults are around two centimetres in length and two millimetres wide, although the largest can be more than 25 centimetres long. Together with phylums Brachiopoda and Bryozoa, the Phoronida have been historically grouped as the Lophophorata, as a characteristic of adults of these three phyla is the lophophore, a food trapping organ around the mouth, but this grouping is controversial. The lophophore is a simple ring of tentacles in some species, coiled in others, or folded into a horseshoe shape, hence the common name of ‘horseshoe worms’. Ciliary tracts on the tentacles drive a water current, transporting food particles towards the mouth, but the lophophore can also be involved in protection and reproduction. While superficially resembling annelids, the gut loops around and the anus emerges near the mouth, rather than extending the length of the body.

Reproduction and development

Different phoronid species may be hermaphrodite, or have separate sexes (dioecious), although at least some can also reproduce asexually, either by dividing or by budding, but can still reproduce sexually. There are a range of reproductive strategies. At least one species retains its hatched larvae so has no pelagic phase. Of the European species, one has a slug-like larva, quite unlike other species and another releases larvae after some initial development, but the remaining species shed eggs directly into the surrounding water and have the typical larva called an actinotroch (or actinotrocha). These have an extended pelagic phase, typically two to four weeks and are often collected in coastal plankton samples, reflecting the mainly inshore distribution of the adults. The early stage larvae have a very similar morphology and are difficult to differentiate beyond recognising them as early phoronids. Only the very advanced larvae can be identified to species with any certainty.

The actinotroch larvae develop anteriorly a large hood-like lobe with a fringe of cilia, the preoral lobe (Fig. 1H). This is involved in feeding and below it is the mouth. In the mid-region of the body is a ring of tentacles that increase in number with development. The tentacles are ciliated and are used in locomotion as well as feeding. The digestive tract is more or less straight and the anus is at the posterior end of the body. Around the anus is the telotroch (or perianal ciliated ring), which is also used in locomotion. One to four solid masses of blood corpuscles or sanguinary globules, usually termed blood masses, may be visible internally, their number and position used in species identification. The larvae may also have areas of pigmentation that are also useful in identification.

Larval development can be divided into stages according to the number of tentacles. Depending on species, the final number of tentacles before metamorphosis to the adult form ranges from 10 to 42, but there can be some variation in number, determined by local environmental conditions. At a late stage of development the adult lophophore tentacles arise, either as thickenings of the wall of the larval tentacles, or as outgrowths under their bases. Actinotroch larva settles to the seabed on average after ~20 days and undergoes a radical metamorphosis in around 30 minutes, described below for *Actinotrocha branchiata* (Fig. 2).

Worldwide, there are only two phoronid genera, *Phoronis* and *Phoronopsis* and around 10 described species, but each species tends to have a very wide geographical distribution. The larvae of some of the species were originally thought to be separate organisms in their own right and were not at first associated with the adults, so larvae and adults have separate generic and sometimes also specific names.

All five adult phoronid species recorded from the northern European area (Emig, 1979) belong to the Genus *Phoronis.* If they have an actinotroch larvae, these are assigned to Genus *Actinotrocha,* but this perhaps more correctly should be called their technical name:

Phoronis muelleri Selys-Longchamps, 1903. Larva of *Actinotrocha branchiata* Müller, 1846
P. pallida Silén, 1952. Larva of *A. pallida* Silén, 1952.
P. hippocrepia Wright, 1856. Larva of *A. hippocrepia* Silén, 1954,
P. psammophila Cori, 1889. Larva of *A. sabatieri* Roule,1896
P. ovalis Wright, 1856.

P. ovalis does not have an actinotroch larva, but a short duration, slug-like larva that is unlikely to be collected in plankton samples, so is not described here. Forneris (1957) noted that all of the above actinotroch larvae, apart from *A. sabatieri*, were distributed in the western English Channel, but *P. psammophila*, the adult of *A. sabatieri* is one of the two adult phoronids recorded in the PMF, so the larvae must also occur. The second phoronid adult recorded in the PMF is *P. hippocrepia.* Although *P. muelleri* are not recorded in the PMF they must also be present, as their actinotrochs, A*. branchiata*, are the main ones sampled locally (cover image). Descriptions of the actinotroch larvae of these four species are given below.

PHYLUM PHORONIDA:

Genus *Actinotrocha:*

Actinotrocha branchiata Müller, 1846

This is the actinotroch larva of *Phoronis muelleri* Selys-Longchamps, 1903, the largest actinotroch known. Larval body transparent with numerous pigment spots; yellow pigment around the tentacle bases, around the preoral lobe and near the telotroch. From about the 20-tentacle stage, there is a pair of anteroventral blood masses (Fig. 1H). Number of tentacles increases with development to 32-42, the higher numbers resulting if the length of pelagic life is prolonged by lack of food or other unfavourable conditions. Around the 24-tentacle stage, when the larva is ~2 mm in length, it starts to prepare for metamorphosis and its appearance changes considerably. The blood masses merge and the body becomes opaque. From the 28-tentacle stage the adult definitive tentacles arise as independent protrusions under the bases of the larval ones, until the larva has around ~22. The preoral lobe contracts and a protrusion called the piriform organ appears on it (Fig. 2), thought to function in substrate selection prior to settlement. The metasomal sac, which develops in the hind body, is evaginated and pushed into the substrate where it rapidly secretes a tube in which the adult will live. The larval tentacles are absorbed, the adult lophophore is created round the mouth, and the gut becomes U-shaped so that the anus is just under and outside the lophophore.

Although *Phoronis muelleri* are not recorded in the PMF they must also be present, as their actinotrochs are the main ones sampled locally (cover image).

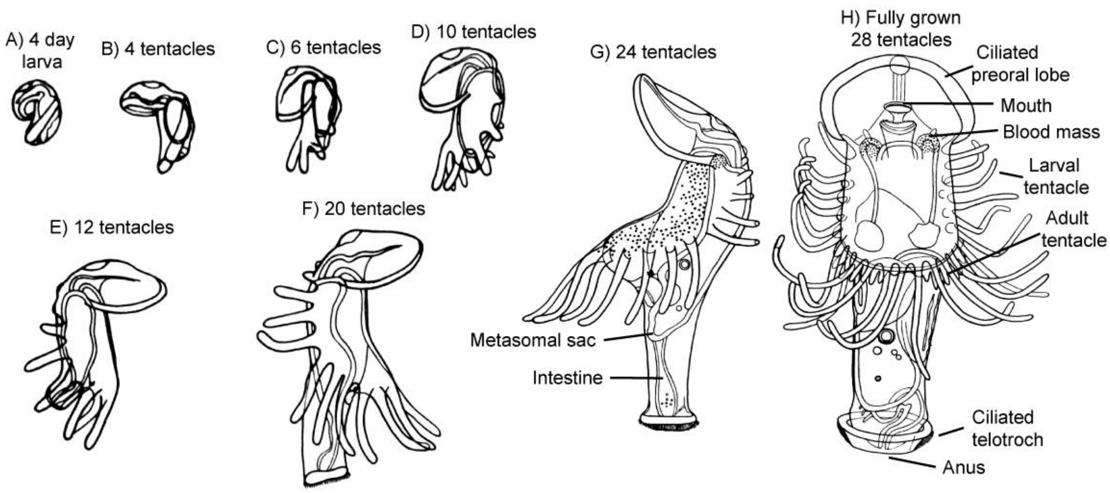

Fig. 1. *Actinotrocha branchiata* development stages (from Forneris, 1957).

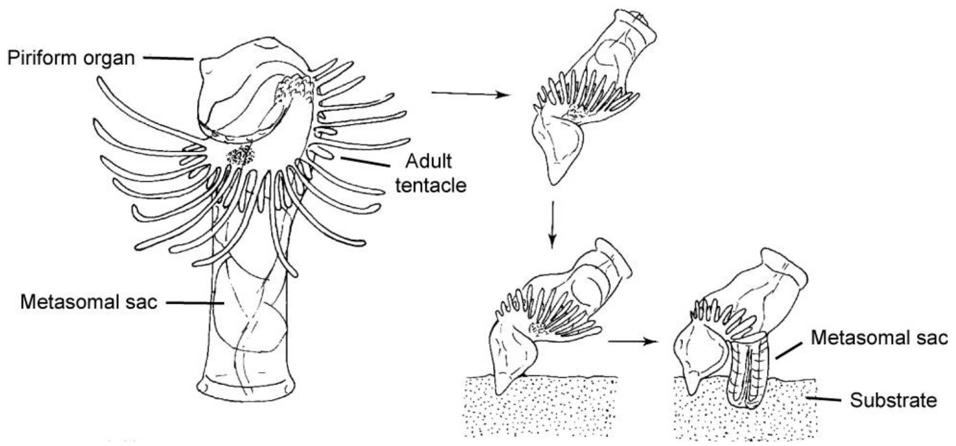

Fig. 2. *Actinotrocha branchiata* metamorphosis (from Emig, 1982).

Recorded: PMF, not recorded. L4. Millbay Marina, Plymouth. British coast. North Sea.

Size: Actinotroch up to ~2 mm.

Further information: Silén, 1954; Forneris, 1957; Emig, 1979, 1982; Johnson, 2001; Johnson & Zimmer, 2002; Larink & Westheide, 2011.

Actinotrocha pallida Silén, 1952

This is the actinotroch larva of *Phoronis pallida* Silén, 1952. Larval body relatively small, opaque and yellowish-white, no pigment spots. The colouration seems characteristic for the species. When fully developed there are 10 larval tentacles (Fig. 3H), sometimes 12 just before metamorphosis. There is a single blood mass in a double aggregation in the mid body. The larva is a very active swimmer and its pelagic life lasts 17-20 days.

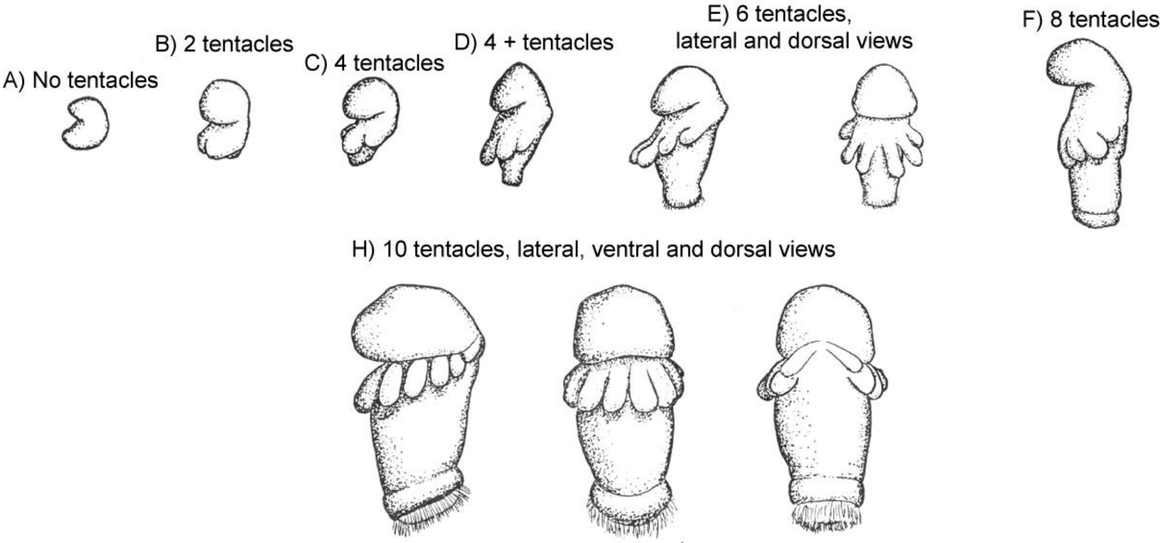

Fig. 3. *Actinotrocha pallida* (from Silén, 1954).

Recorded: PMF and L4, not recorded. Southern North Sea. English Channel.
Size: Up to 0.6 mm.
Further information: Silén, 1954; Forneris, 1957; Emig, 1979, 1982; Johnson, 2001; Johnson & Zimmer, 2002.

Actinotrocha hippocrepia Silén, 1954

This is the actinotroch larva of *Phoronis hippocrepia* Wright, 1856. The larvae develop within the adult lophophore until they reaches the four-tentacle stage, thus the adult displays a certain degree of brood protection. Larval body relatively small, opaque, with tiny, light brown pigment spots in the epidermal region, distributed in distinct patches at certain fixed points, the patches increasing in number from the four-tentacle stage. The pigment patches are characteristically located at the end of the tentacles and on the preoral lobe. A strip of pigment is present on the preoral lobe in the early stages (Fig. 4A, B) and this eventually breaks up into four circular rounded patches (Fig. 4D, E). There are two ventral blood masses that merge in older specimens. The maximum number of tentacles is 10 and adult tentacles never develop before metamorphosis. The larva is an active swimmer and its pelagic life lasts 12-14 days.

The larvae are very similar in appearance to *Actinotrocha pallida* larvae, but the characteristic pigmentation and number of blood masses in *A. hippocrepia* distinguishes it.

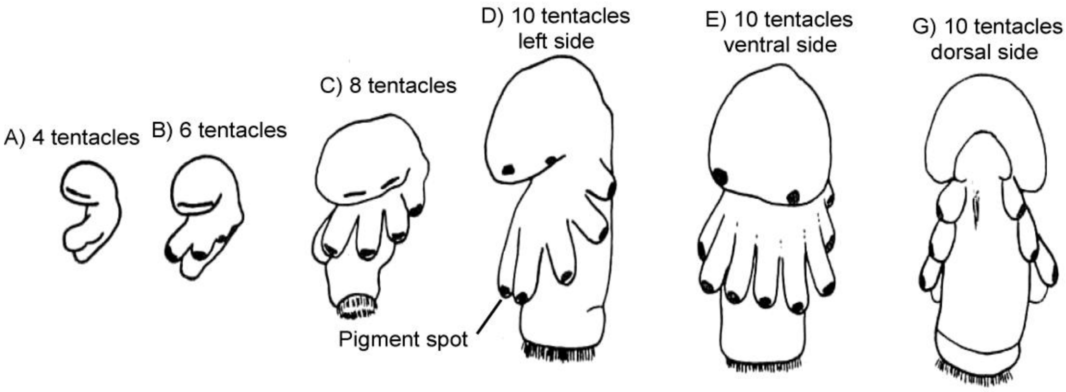

Fig. 4. *Actinotrocha hippocrepia* development stages (from Forneris, 1957).

Recorded: PMF, adults. L4, not recorded. Southern North Sea. English Channel.
Size: Up to 0.7 mm,
Further information: Silén, 1954; Forneris, 1957; Emig, 1979, 1982; Johnson, 2001; Johnson & Zimmer, 2002.

Actinotrocha sabatieri Roule, 1896

This is the actinotroch larva of *Phoronis psammophila* Cori, 1889. Larval body relatively large and transparent. From the six-tentacle stage, there are two pigment spots located on the preoral lobe and in later stages also on the end of the tentacles (Fig. 5C, D). There are no more than 12 larval tentacles. The adult definitive tentacles start to appear at the end of the 10-tentacle stage as thickenings of the wall of the larval tentacles. These were not drawn by Emig (1982; Fig. 5D), but were drawn by Herrmann (1979; Fig. 5E). From the 10-tentacle stage there are two anterior blood masses and a single mass on the ventral midline around the tentacle bases.

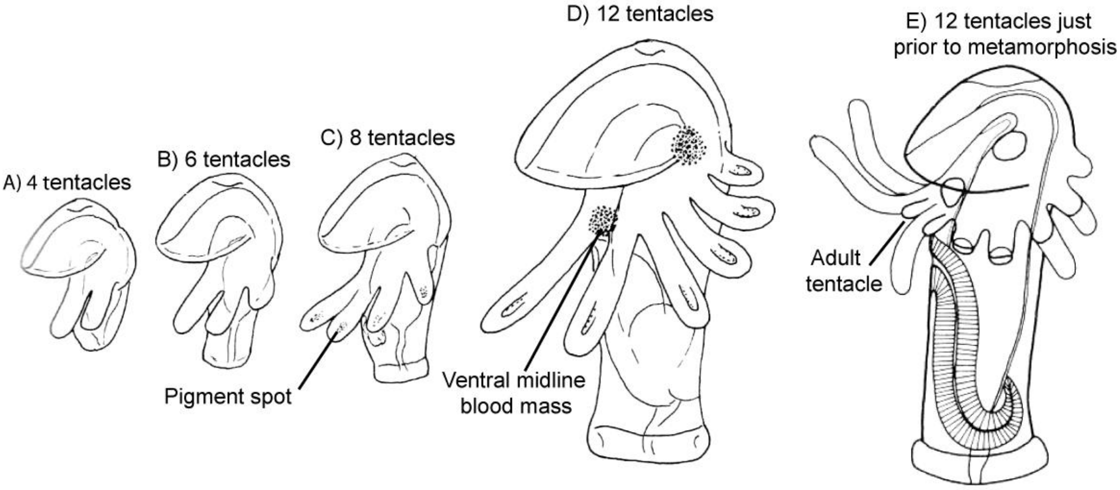

Fig. 5. *Actinotrocha sabatieri* development stages (A-D from Emig, 1982; E from Herrmann, 1979).

Recorded: PMF, adults. L4, not recorded. Southern North Sea. English Channel.
Size: Up to 0.7 mm.
Further information: Silén, 1954; Forneris, 1957; Emig, 1979, 1982; Herrmann, 1979; Johnson, 2001; Johnson & Zimmer, 2002.

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PHYLUM BRYOZOA

Bryozoa, along with the phoronids and brachiopods were historically grouped together as Lophophorates. This was based on the shared presence in the adults of a specialized feeding structure called a lophophore, an extension of the body wall into a tentaculate feeding structure that surrounds the mouth, but this grouping is controversial. The majority of bryozoans are marine and most are found in shallow waters where they can be very abundant. The adults are filter feeders, almost exclusively sessile and colonial. Colonies are composed of a few to many million individuals, forming gelatinous or rigid, encrusting mats, or raised coral-like structures on rocky surfaces, shells, sediments, algae, piers etc. Their appearance has stimulated several common names including 'sea mats', 'moss animals' or 'lace corals'. The colonies have an economic impact as fouling organisms and can range from millimetres to metres in width. Individuals in the colonies are rarely larger than a millimetre. They are called zooids, as they are not fully independent of the rest of the colony. While only fragmented parts of the adults are normally collected in plankton nets, the pelagic larvae are regularly sampled. There are two classes in Bryozoa, **Stenolaemata** and **Gymnolaemata**, with most marine representatives in the latter.

A simplified version of the current WoRMS classification is given below, but the whole classification is currently under revision. There are approximately 300 European bryozoan species and the PMF records 122 (as Phylum Polyzoa) from the Plymouth area, the number recorded in each order given in brackets as an indication of typical coastal biodiversity.

Classification:

Class Stenolaemata

- **Order Cyclostomatida** (22) - Usually calcified, elongated, tubular zooids.

Class Gymnolaemata

- **Order Cheilostomatida** (85) - Calcified zooids, rectangular, crunchy to touch.
- **Order Ctenostomatida** (15) - Uncalcified cylindrical or squat zooids, soft.
- \+ Four other lesser orders

Reproduction and development

Bryozoans can reproduce both asexually and sexually. Asexual reproduction typically occurs by budding from an 'ancestrula' that results from metamorphosis of a sexually produced larva, and is the primary way by which a colony expands in size. All bryozoans are hermaphrodite and each individual zooid may be both sexes simultaneously, but in some species they may be first male then female. Exact reproductive strategy can vary between species, but the eggs of all Stenolaemata and most Gymnolaemata are fertilised internally, while Some Gymnolaemata species broadcast their eggs. Two major larval types develop from the eggs, lecithotrophic coronate larvae (Fig. 1A, B) and planktotrophic cyphonautes larvae (Fig. 1C-E). After settling the larvae produce cocoons in which they metamorphose completely. The larval epidermis becomes the lining of the coelom, and the internal tissues are converted to a food reserve that nourishes the developing zooid until it is ready to feed.

Coronate larvae: The coronate larvae (Fig. 1A, B) of only a few species have been described. They have an obvious corona (or girdle) of short cilia, hence their name. They are small, typically with a very short pelagic existence, so the chance of them being sampled is limited. In addition they tend to be very delicate, so while they can be observed in fresh samples, they are generally altered beyond recognition in formaldehyde preserved samples and difficult to even distinguish from other similar, small larval forms. For these reasons, only brief descriptions are given below.

Cyphonautes larvae: These typically have a rigid bivalve shell, most of which are roughly triangular in outline (Fig. 1C-E). The shell survives preservation well and its morphology can be used in species identification, easiest at a late stage of development. Cyphonautes have a long pelagic duration, typically around 4-8 weeks, during which they filter feed in the plankton. Some species are taken in net samples throughout the year, often in considerable numbers in inshore regions. They share morphological features of apical organ with tuft of cilia, and corona (Fig. 1C), with some coronate larvae. The body is laterally compressed between the two chitinous shell valves, held together by an adductor muscle. The valves can be transparent or opaque, sometimes with pigmented areas, and the surface may be smooth or granulated. At their apex they are cut away and sometimes flared laterally, to accommodate the apical organ and associated cilia. At their base the valves spread apart, the opening encircled by a ciliated corona. There is an internal chamber termed the vestibule, separated by two ciliated ridges bearing current-producing and food-conveying cilia, into inhalent and exhalent chambers (Atkins, 1955a). The side of the triangle nearest the inhalant chamber is referred to as anterior, that by the exhalent chamber as posterior, although the larva actually swims with the shell apex to the front. The internal organs usually become shrunken and disrupted during preservation and the ciliated corona destroyed.

Stenolaemata

The only larvae produced by Order Cyclostomatida of Class Stenolaemata are coronate larvae. These are typically ovoid, with a slightly flattened oral pole and outer cuticle completely covered by short cilia (Fig. 1A). There are invaginations at the oral and aboral poles. The larvae of some species have pigmented areas, but there are no distinctive eye spots, apical tuft of cilia or other sensory organs as generally seen in Class Gymnolaemata larvae.

Gymnolaemata

Depending on species, orders Ctenostomatida and Cheilostomatida of Class Gymnolaemata produce either coronate or cyphonautes larvae. Most produce coronate larvae (Fig. 1B) and these are variable in morphology, but typically have an apical sensory organ (apical disc) with a tuft of apical cilia, an anterior tuft of plume cilia and an obvious corona of short cilia. Some also have eye spots.

Cyphonautes larvae of Order Cheilostomatida, Superfamily Membraniporoidea (Fig. 2) are the commonest sampled in European waters and species descriptions and the key given below are only for this superfamily.

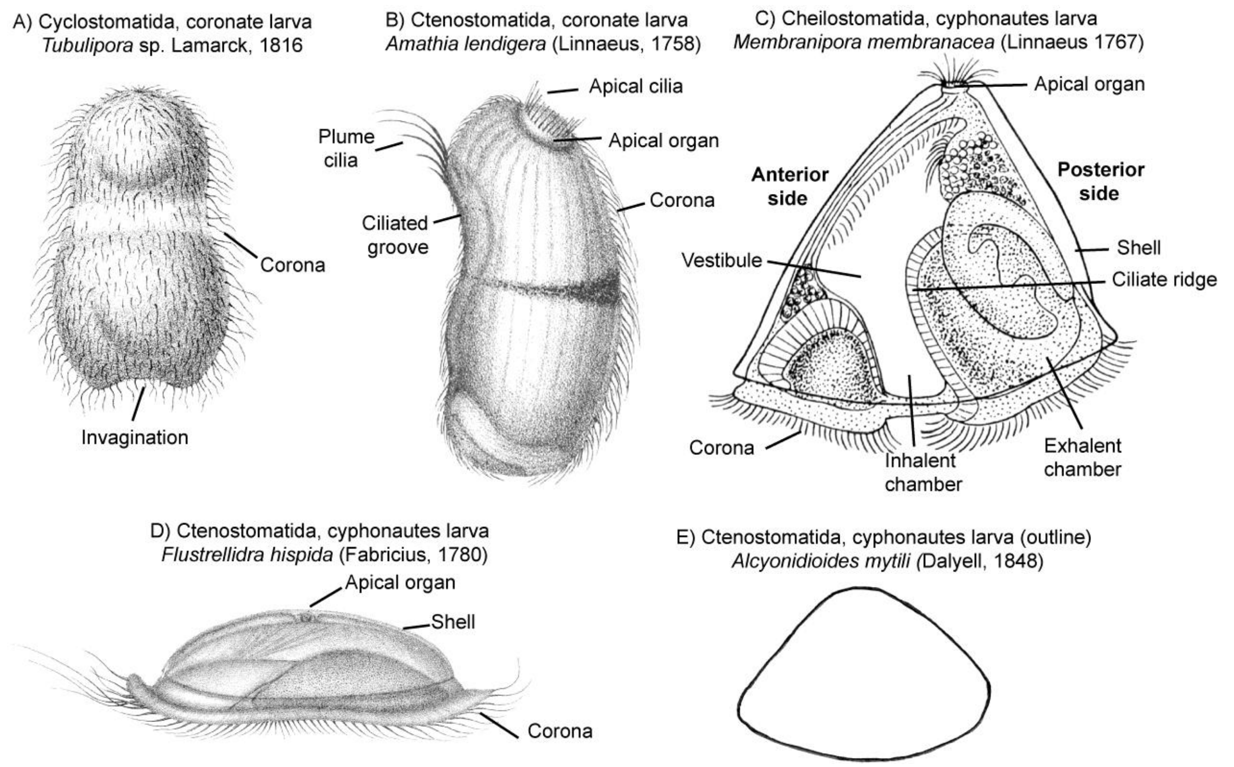

Fig. 1. Examples of bryozoan coronate and cyphonautes larvae. (A, B, D from Barrois, 1877; C from Thorson, 1946; E outline of photograph from Cadman & Ryland, 2008).

Only a few members of Order Ctenostomatida produce cyphonautes larva. These either lack a shell, or are enclosed by a rounded (Fig. 1D) or triangular (Fig. 1E) bivalved shell. There has been some disagreement in the literature as to whether some of these are actually coronate or cyphonautes larvae, but some are certainly accepted as cyphonautes. For example, Cadman & Ryland (2008) have described the larva of *Alcyonidioides mytili* (Dalyell, 1848) (as *Alcyonidium mytili*; Fig. 1E) as a cyphonautes. These are tiny larvae ~0.15-0.25 mm wide and ~0.10-0.22 mm high. The valves have a granular surface, the anterior lower corner is less rounded than the posterior corner and the apex is roughly truncated. They have no obvious lip (flange) along the edge of the posterior side of the shell.

A key to the identification of described cyphonautes larvae of Superfamily Membraniporoidea of Order Cheilostomatida is given in Ryland (1965) and Hayward & Ryland (1998) and information on species found at Plymouth by Atkins (1955b) and Ryland (1964). These common species, which are sampled over the whole northern European area, are described below. Adults of all of these are recorded in the PMF, apart from *Electra monostachys* and *Conopeum seurati*. *Membranipora membranacea* and *Electra pilosa* are the species most frequently sampled in normally saline European seas, some of the others mainly only found in brackish waters.

Key to Superfamily Membraniporoidea cyphonautes larvae (after Ryland 1965)

1. Large larva, length >0.35 mm, with quite transparent shell valves -------------------------------- **2**
- Small larva, length <0.30 mm) with granular shell valves --- **3**

2. Very large larva, length >0.50 mm, typically transparent; narrow, linear flange on posterior shell; sometimes pigment spots along lower margin --- *Membranipora membranacea* (Fig. 2A)
- Length <0.50 mm, typically slightly opaque, no pigmentation; broad flange on posterior shell, margin, behind a curved ridge descending from apex ----------- *Electra pilosa* (Fig. 2B)

3. Shell valves with distinct ridge that forms a flange on posterior shell margin ------------------- **4**
- Shell valves without ridge or flange -- **5**

4. Shell valves transparent, sometimes slightly granular, much longer than high, ridge of flange quite close to posterior shell margin ----------------------- young *Electra pilosa* (Fig. 2B)
- Shell valves opaque, encrusted with scattered dark particles, slightly longer than high, apical part of ridge of flange almost in centre of the valve ---- *Conopeum reticulum* (Fig. 2E)

5. Shell profile oval -- *Einhornia crustulenta* (Fig. 2D)
- Shell profile not oval, roughly triangular --- **6**

6. Up to 0.26 mm in length, much longer than high, at least in older larvae; anterior margin of shell straight, lower corner pointed, often with dark particles along the lower margin, --- *Electra monostachys* (Fig. 2C)
- Less than 0.20 mm in length, only slightly longer than high; anterior shell margin rounded; posterior shell margin with concave profile, accentuating the bulbous shape of lower corner; mainly in brackish waters -- *Conopeum seurati* (Fig. 2F)

PHYLUM BRYOZOA:

Order Cheilostomatida:

Superfamily Membraniporoidea:

Genus *Membranipora*:

Membranipora membranacea (Linnaeus, 1767)

A large larva, one of the most regularly sampled. Shell triangular, lower corners both quite acute (Fig. 2A); valve surfaces quite flat, transparent, especially when young, the lower margin becoming brownish with pigment when around a length of 0.70 mm, pigment sometimes forms vertical lines. Faint growth lines may be visible near the apex and down posterior margin; posterior flange linear and very narrow; notch for apical tuft deep and flared, but relatively small. Valve shape and relative lengths of the sides variable and also vary with age.

Length ~0.75-0.85 mm; height ~0.60 mm.

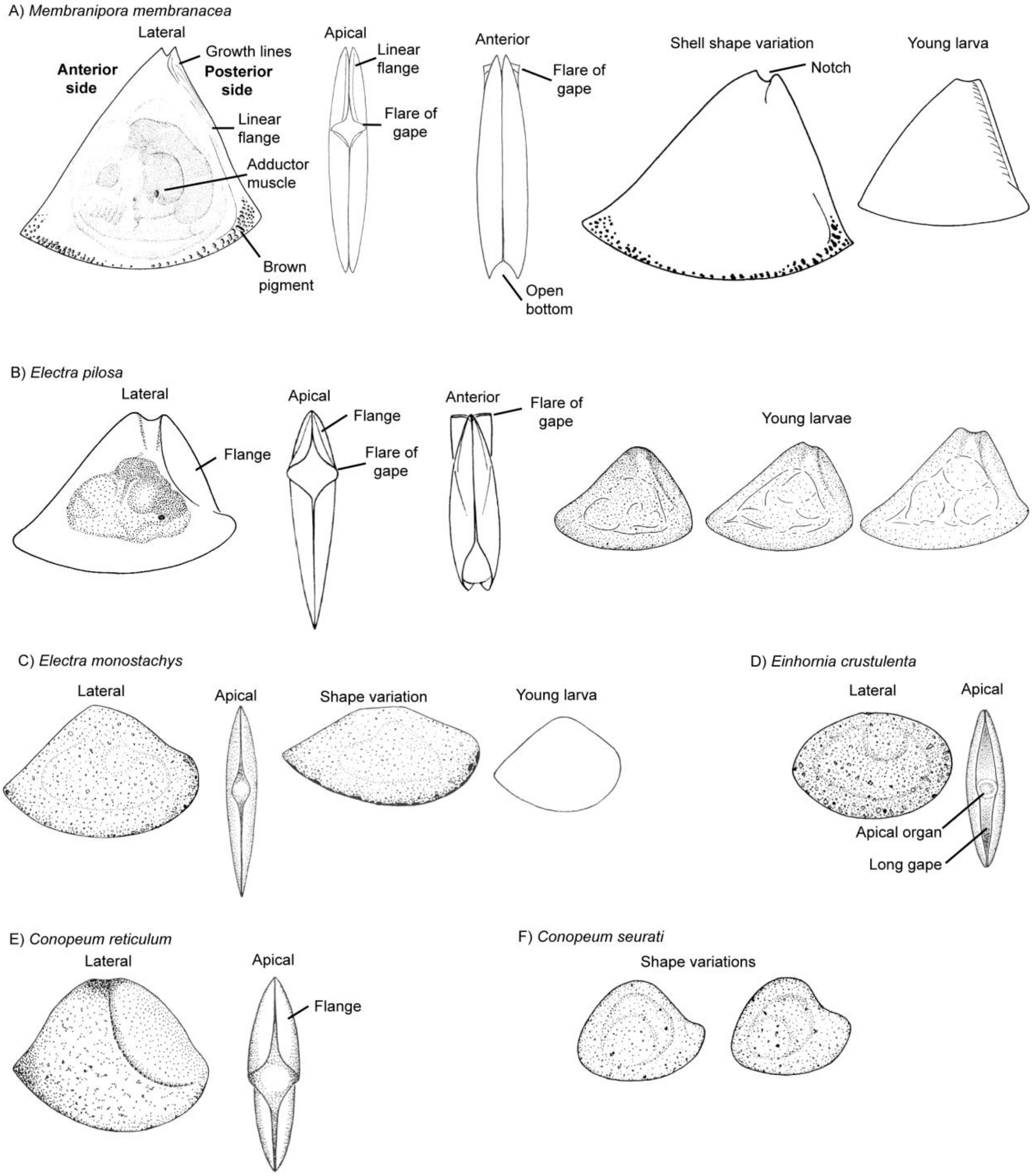

Fig. 2. Cyphonautes larvae of Superfamily Membraniporoidea commonly sampled in northern European waters (from Ryland, 1965; *Einhornia crustulenta* as *Electra crustulenta*). All orientated in the same direction.

Genus *Electra*:

Electra pilosa (Linnaeus, 1767)
Large larva, shell outline roughly triangular (Fig. 2B), the lower corners quite rounded; valve surfaces of late larva convex, translucent yellow-brown; anterior margin quite straight; on posterior border the valves flatten abruptly behind the apex to form a conspicuous flange, valves flare out towards the apex making a large cross-shaped gape for the apical organ and cilia. There is considerable variation in valve shape, but the broad flange is always obvious. The valves of young larvae may be transparent, or covered in fine particles.
Length ~ 0.40-0.50 mm; height ~0.40 mm

Electra monostachys (Busk, 1854)
Small larva, shell triangular with convex lower margin (Fig. 2C); anterior margin longer than posterior margin, quite straight, pointed at lower corner; posterior margin almost straight, sometimes slightly convex near apex, rounded or bulging at lower corner; valves at apex only slightly flared outwards for the apical organ, without notch; valves covered with fine particles, light grey, largest particles near lower margins where there may also be black particles. Distribution extending into brackish water.
Length ~0.26 mm; height ~0.17 mm

Genus *Einhornia*:

Einhornia crustulenta (Pallas, 1776) (as *Electra crustulenta* in PMF)
Very small larva, outline of shell oval (Fig. 2D), anterior margin in late larvae may be slightly straight; valve surfaces slightly convex, flared over most of the width apically, but without notch; encrusted with fine granules, giving the shell a greyish appearance. In young larvae of ~ 0.10 mm the shell is almost triangular. Brackish water species.
Length ~0.16-0.24 mm; height 0.12-0.17 mm

Genus *Conopeum*:

Conopeum reticulum (Linnaeus, 1767)
Small larva, shell profile roughly bell-shaped (Fig. 2E), lower margin very convex, anterior corner quite acute, rounded at posterior corner. Valve surfaces rather flat, apex truncated and strongly flared outwards for the apical organ, with a broad flange bordered by a prominent curved ridge running from around the centre of the apex towards the posterior margin. Shell grey in colour, lightly encrusted with small dark granules. Distribution extending into brackish water.
Length ~ 0.25-0.29 mm; height ~0.18-0.20 mm

Conopeum seurati (Canu, 1928)
Very small sub-triangular larva (Fig. 2F) with a characteristic indented profile to the posterior margin, the profile probably becoming less pronounced during growth; lower margin convex, rounded at both corners; apex rounded, without notch. Valves covered in fine granules. Brackish water species.
Length ~ 0.17 mm; height ~0.13 mm

Recorded: PMF, 120 adult species (as Phylum Polyzoa). L4, unidentified cyphonautes larvae. Cyphonautes larvae found in all European waters.
Size: Cyphonautes larvae ~0.2-0.9 mm maximum dimension; coronate larvae ~0.2-0.6 mm maximum dimension. Both are measurement ranges for fully developed larvae.
Further information: Barrois, 1877; Atkins, 1955a,b; Ryland, 1964, 1965, 1970; Zimmer & Woollacott, 1977; Hayward, 1985; Hayward & Ryland, 1985, 1998, 1999; Reed, 1991; Rafferty, 2001; Temkin & Zimmer, 2002; Larink & Westheide, 2011; Porter, 2012.

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PHYLUM ENTOPROCTA

Entoprocta are a phylum of tiny, sessile, solitary or colonial organisms, arranged taxonomically in two orders. Almost all are marine, with <200 described species worldwide, although this number will be much higher, as they are a poorly studied group. The solitary species (Order Solitaria) usually attach to larger organisms that produce feeding currents, such as sponges, bryozoans, polychaetes, sipunculans and ascidians, and are typically associated with just one or a few host species. The colonial species (Order Coloniales) are encrusting on various, mainly inanimate, surfaces. Adults range in size from 0.1-7 mm in length and their bodies are composed of a long stalk bearing a bowl-shaped top that is fringed with a crown of tentacles whose cilia generate feeding water currents towards the mouth. Entoporoct means “anus inside” as both the mouth and anus lie inside the tentacle crown. They are superficially similar to Phylum Bryozoa (previously Ectoprocta) adults, but these have the anus outside their crown of tentacles and differ in other features. Classification is very simple, with only three families. The PMF lists nine species of entoprocts (as Phylum Kamptozoa) from the Plymouth area and the number found in each of the families is given in brackets below.

Classification:
Order Solitaria
    Family Loxosomatidae (7)
Order Coloniales
    Family Pedicellinidae (1)
    Family Barentsiidae (1)

Only the larvae will be taken in plankton samples and because of their small size, only in fine mesh nets. It was not originally planned to include them in this series of guides, as they are a very small and insignificant component of the meroplankton, but several were found around different parts of the British coast over a short time period and their identity was not being recognised.

Larval morphology:
There is considerable variability between ectoproct species in trochophore morphology (Fig. 1), but because taxonomy is based on the adults, it may not be possible to identify many of the larvae to species unless cultured. Additionally, if preserved in formalin, some of the trochophore larvae will probably be so shrunken as to be indistinguishable from trochophores of other phyla.
Larvae swim and feed using various ciliated organs such as the prototroch that encircles them. They usually also have an anterior pair of brown pigment-cup ocelli, a frontal sensory organ that may be formed of a pair of whorls of cilia, a dorsal apical ciliated organ, an anteroventral foot bearing strong spinous setae and a posteroventral lobe modified as a creeping organ, reminiscent of a molluscan foot. Additionally, at least some Loxosomatidae have conspicuous, stalked vesicles on the body (Fig. 1D; 2C, D; cover image), the function of which does not appear to be known.

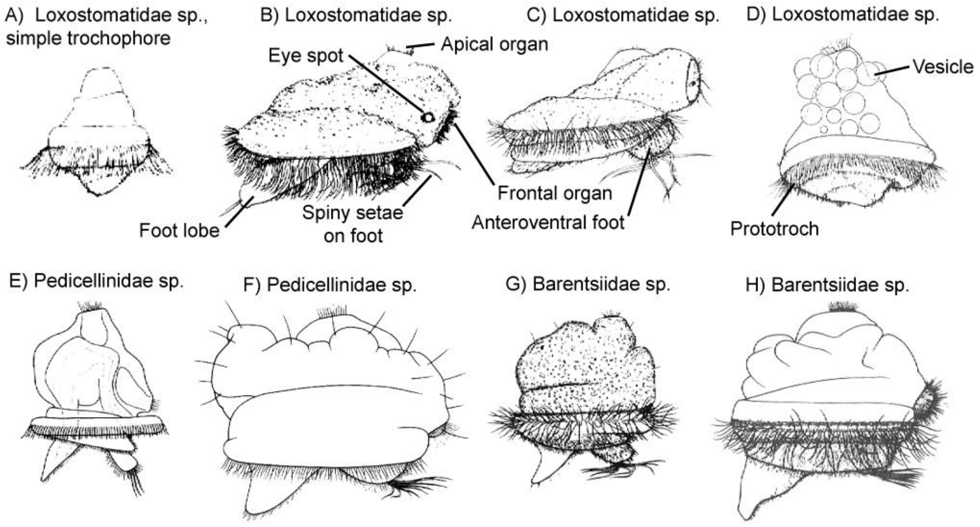

Fig. 1. Examples of entoproct larvae from the three families (From Nielsen, 1989).

Reproduction and development:
Both solitary and colonial species can reproduce asexually by budding, or sexually and all may be hermaphroditic. During sexual reproduction the eggs are fertilized internally by sperm that have been liberated into the water column. Fertilized eggs are retained internally until hatching and the larvae may be brooded for a further period prior to release. The larvae are called trochophores, the same name that is used for the larvae of a range of other phyla (Mollusca, Annelida, Echiura, Sipuncula and Nemertea), as they are all superficially similar. Some larvae are not pelagic, but bottom creepers. Pelagic larvae that are lecithotrophic will spend a short time in the plankton, but if planktotrophic may spend from weeks to, in exceptional cases, several months there. Some larvae asexually produce adult buds while pelagic, which they release and then die. Other larvae settle on a substrate and metamorphose.

In live samples from Millbay Marina, Plymouth, “heart-shaped” Loxosomatidae larvae with a deep posterior invagination were found (Fig. 2A, B), their shape changing as they swam. Initially there were some vesicles on the body, but these disappeared. Loxosomatidae larvae have also been found in preserved samples from sampling Station L4 at Plymouth (Fig. 2C) and from the Scottish west coast (cover image) also “heart-shaped”, with prominent arrays of vesicles radiation out from the body. A larvae from a preserved sample, taken off Malaysia also had many vesicles, arranged in a star-shape (Fig. 2D). These latter observations suggest that at least larvae with vesicles may be easily recognised as entoprocts in preserved samples.

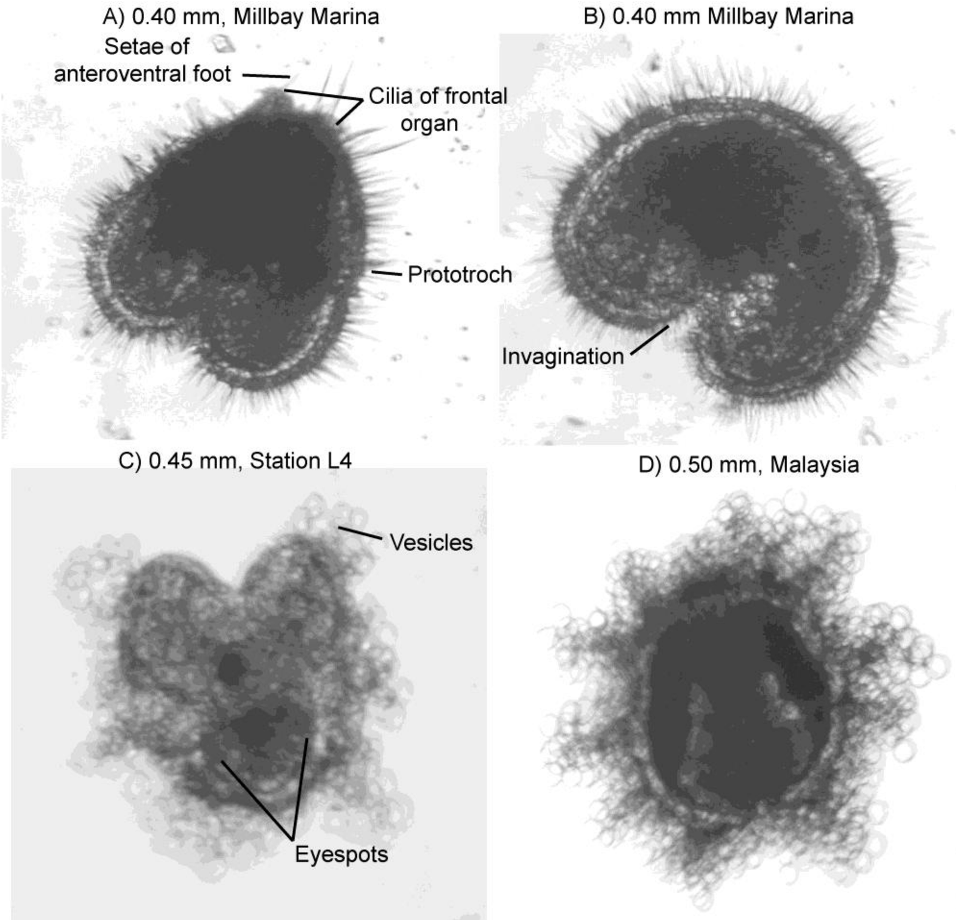

Fig. 2. Images of ectoproct Loxosomatidae larvae, A, B from live and B, C from preserved specimens.

Recorded: Adults - PMF and all the European region. Larvae - L4. Millbay Marina, Plymouth. All European coastal areas.
Size: Larvae ~0.1-0.5 mm.

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PHYLUM BRACHIOPODA

This exclusively marine phylum, along with phoronids and bryozoans, have historically been grouped together as Lophophorates, as during at least part of their development, they all have a specialized feeding structure called a lophophore, an extension of the body wall into a tentaculate structure that surrounds the mouth, but this grouping is controversial. Although they can be abundant in some areas, they are not a well-known group. The current number of species is only around 300 worldwide, but 600 million years ago, at the beginning of the Cambrian era, they dominated the benthos and around 30,000 species are described from the fossil record. They have sporadic distribution around the world, typical of remnant members of a once widespread animal group. There are at least 22 species found in northern European waters (Brunton & Curry, 1979), but are none recorded in the PMF.

Brachiopods superficially resemble bivalve molluscs as they have an external, clam-like shell, but apart from considerable anatomical difference, the shell symmetry is usually different, having dissimilar dorsal and ventral valves. Bivalve molluscs usually have a plane of approximate bilateral symmetry between the two shell valves, while brachiopods have a plane of symmetry through the shells, perpendicular to the hinge.

Adult brachiopods are benthic solitary, sessile, slow moving, suspension feeders. A few live in burrows, but most attach to rocks or other firm substrates. They are most abundant in shallow waters and have evolved to use very little energy or oxygen, so are well suited to marginal environments such as polar, deep-water, low oxygen and brackish habitats.

Phylum Brachiopoda was divided into two classes, Class Articulata with toothed shell hinges and simple muscles, and Class Inarticulata that have no shell hinge, relying upon internal muscles to hold the valves together and open and close them, but this classification has been revised and WoRMS currently lists three subphyla (below), all of which have adult representatives in European waters. Subphylum Rhynchonelliformea basically corresponds to Articulata and the other two subphyla to Inarticulata.

Classification:
Subphylum Rhynchonelliformea
Subphylum Craniiformea
Subphylum Linguliformea
- **Superfamily Discinoidea**
- **Superfamily Linguloidea**

Reproduction and development

Brachiopod sexes are usually separate, although a few species are hermaphroditic. Some have a breeding season, while others can breed throughout the year. Free-swimming larvae of four main types can be collected in plankton samples, but are generally found in low abundance.

Subphylum Rhynchonelliformea: This includes both free spawners and brooding species, both of which have larvae that are similar in appearance and lecithotrophic. The larvae of all species that have been studied resemble button mushrooms in shape (Fig. 1A) and do not develop a shell. They characteristically consists of three sections that are not true segments, an anterior apical lobe, a central mantle lobe and a posterior pedicle lobe, the latter used to anchor the larvae to the substrate on settlement. The apical lobe is covered in cilia and in some species there is a more prominent band of locomotory cilia around the circumference and a tuft of immotile cilia anteriorly. Eye spots may be present and <u>sometimes</u> there is a row of tiny circular structures around the posterior margin of the lobe, the vesicular bodies. The mantle lobe bears four bundles of setae. A metamorphosis takes place on settlement, the adult shell valves start to form and feeding starts. Larvae are probably in the plankton for less than a week.

Subphylum Craniiformea: These are free spawners and the lecithotrophic larvae are fully developed around three days after fertilisation (Fig. 1B). They are superficially similar in appearance to larvae of Subphylum Rhynchonelliformea, developing an apical lobe and a mantle lobe, but differ in having no pedicle lobe posteriorly. Additionally, the mantle lobe has six rather than four bundles of setae. A pedicle lobe is not required, as attachment to the substrate is by cementing the shell valve rather than by the pedicle. Larvae metamorphose on settlement and start feeding. Settlement taking place around four days after fertilisation, so they are in the water column for a very short period.

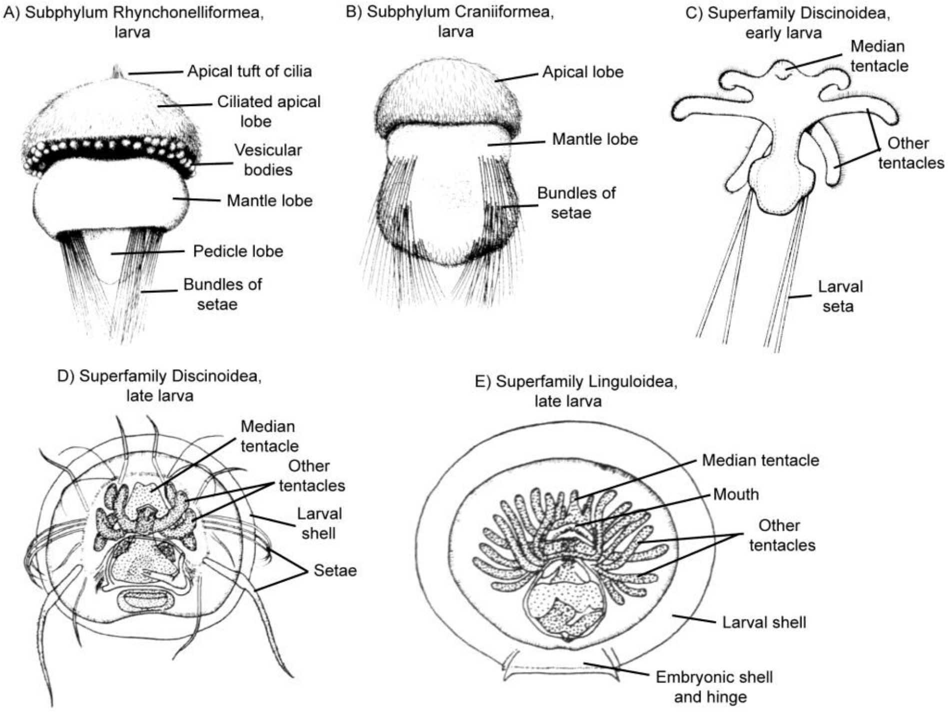

Fig. 1. Examples of brachiopod larvae. (A-C from Nielsen 1991; D, E from Wickstead 1965).

Subphylum Linguliformea: This comprises two superfamilies, each with a different larval type, but both types are pelagic and planktotrophic, with complete and functional guts. Superfamily Discinoidea release gametes into the plankton and the larvae that emerge from the eggs initially do not have a shell (Fig. 1C). Two to three pairs of ciliated tentacles develop anteriorly either side of a median tentacle, forming the lophophore. Laterally there are two bundles of very long, straight larval setae. When three to four pairs of tentacles are present a larval shell that does not have a hinge starts to form. Older larvae have up to four pairs of tentacles. The shell continues to grow, but the lophophore remains at the four pairs of tentacle stage (Fig. 1D). The early larval setae are lost, but other setae and a pedicle lobe develop. There is no striking metamorphosis on settlement. In Superfamily Linguloidea gametes are released into the plankton and before the larvae hatch from the egg membrane a half-moon shape, bivalved, hinged embryonic shell or protegulum has formed, on which an ovoid, larval shell (Fig. 1E) develops. The lophophore consists of a variable number of ciliated tentacles that develop either side of a median tentacle, a pair at a time, in increasing numbers with growth, the number present used in staging larvae. Larvae that do not encounter a suitable substrate for settlement may remain in the plankton adding additional tentacles, up to a limit. A pedicle lobe develops close to the hinge, but sometimes not until after settlement. They typically spend around three to six weeks in the plankton and there is no distinct metamorphosis when they settle. Adults of Superfamily Linguloidea do not appear to occur in the northern European area, so the larvae should not be found.

It may be possible to recognise brachiopod larvae that do not develop a shell in fresh samples, but following preservation, cilia will be destroyed and the body disrupted, making it difficult to distinguish them from other similar, small invertebrate larvae. In the brachiopod larval types that develop a shell, it is very thin, usually transparent and pale amber in colour. As they usually occur in low numbers, they are easily overlooked in samples and on superficial examination could be mistaken for mollusc bivalve larvae. In preserved material the cilia are generally destroyed, but the tentacles are usually very obvious and characteristic.

Recorded: Brachiopods adults are not recorded in the PMF or at L4, but at least 22 species are recorded from the North Sea, Irish Sea and English Channel, so larvae, apart from those of Superfamily Linguloidea, could potentially be found.
Size: Larvae ~0.1-1.5 mm.
Further information: Brunton & Curry, 1979; Nielsen, 1991; Shanks, 2001; Pennington & Stricker, 2002.

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PHYLUM ECHINODERMATA

Echinoderms are an exclusively marine group, occupying nearly all depths and habitats in the sea, typically found on or in the sea bed, where they often form a major proportion of the biomass. There are approximately 100 species recorded from the northern European area. The adults are among the most distinctive of all animal phyla and their main features are a calcitic skeleton composed of many plates (ossicles) and a water vascular system used in locomotion, respiration, feeding and some sensory functions. They also have five-fold, radially symmetrical (pentaradia) body organization at some stage in their life. They are grouped into five well-defined classes. The pelagic larvae of some of these can be very common in plankton samples, particularly those of sea urchins, sea stars and brittle stars. The larvae of many species have not been described and in many cases it is only possible to identify larvae to the level of class, or even just larval type.

Classification:

Phylum Echinodermata is divided into three subphyla and five main classes, the number in each class recorded in the PMF is given in brackets below as an indication of typical northern European coastal biodiversity.

Subphylum Crinozoa
Class Crinoidea (1) - Sea lilies and feather stars
Subphylum Asterozoa
Class Ophiuroidea (13) - Brittle stars
Class Asteroidea (11) – Sea stars
Subphylum Echinozoa
Class Echinoidea (9) - Sea urchins
Class Holothuroidea (13) - Sea cucumbers

Echinoderm larvae general

Reproductive strategy and subsequent larval development within the Echinodermata is very varied, often with a number of species in each class differing in their strategies from the others. This makes giving a concise account of larval development difficult, not helped, as pointed out by McEdward & Miner (2001), by the inconsistent terminology used between classes by different authors, especially for the non-feeding larvae with simple morphology. The various echinoderm larval types have been given individual names and while some types are particular to one class (Table 1), others are found in more than one group, making even identification to a particular class problematical to the non-specialist.

Echinoderms usually have separate sexes, with a few exceptions among the asteroids, holothurians and ophiuroids. Reproduction is generally through release of gametes into the water column and indirect development through larval stages of a variety of types (Table 1; Fig. 1). The initial, basic, ciliated larval type is called a dipleurula. Echinoderm larvae usually do not resemble the parent and are generally bilaterally symmetrical, even though they metamorphose into radially symmetrical adults. Many are planktotrophic, feeding on unicellular algae and particulates, using bands of cilia that run over their bodies. Some have spots or bands of pigment, usually only visible in fresh specimens. They generally spend a few weeks in the plankton before settling. However, in some species of each class, but particularly in holothurians and crinoids, females produce yolky eggs from which non-feeding, lecithotrophic larvae develop. Because these do not feed, they do not develop elaborate feeding and propulsion structures. Additionally, a few species, particularly ophiuroids, crinoids and some asteroids, have direct development, brooding large yolky eggs that hatch as a non-pelagic, miniature version of the adult. These are unlikely to be sample in nets so are not included here. Many early echinoderm larvae are small and delicate so will not survive sampling and preservation well, so most larvae found and recognisable in preserved plankton samples will be of a restricted number of types. Because some larval types are found in more than one group, larval types are sequentially described here, rather than giving developmental information individually for each class. Some rare larval types (barrel-shaped and schmoo; McEdward & Miner, 2001) have not been included.

Echinoderm larval types:

Larval type	Bipinnaria/ brachiolaria	Vitellaria	Doliolaria	Auricularia/ pentactula	Echinopluteus	Ophiopluteus	Mesogen
Crinoidea		✓	✓				
Ophiuroidea		✓	✓			✓	✓
Asteroidea	✓	✓					✓
Echinoidea		✓			✓		✓
Holothuroidea		✓	✓	✓			

Table 1. Summary of larval types found in echinoderms.

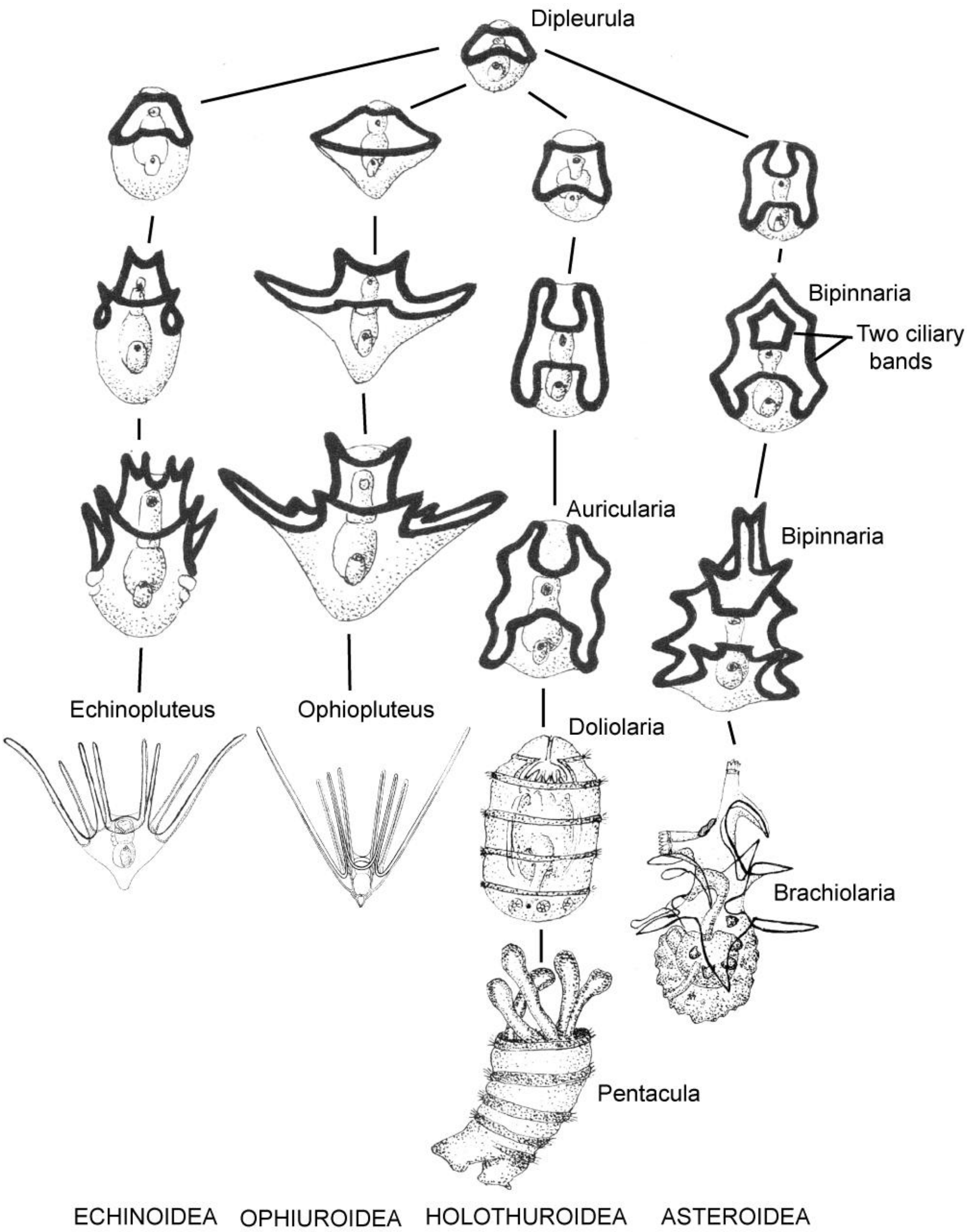

Fig.1. Typical sequence of larval development in the four main echinoderm classes (after Trégouboff & Rose 1957). Ciliary bands of early stages are highlighted.

Bipinnaria/brachiolaria (Asteroidea)

Bipinnaria and brachiolaria larvae only occur in Asteroidea (sea stars). Asteroids with small, non-yolky eggs have a free-swimming, feeding, bipinnaria larva that has two unconnected ciliary bands, extending over numerous lobes that later develop into hollow arms (Figs.1, 2A-C), unsupported by skeletal rods. One of the ciliary bands is much longer than the other and loops over most of the body, while the other is short and restricted to a small area of the body. The bipinnaria superficially resemble the auricularia larva of holothurians (Fig. 5A), but these have a single ciliary band. Some species metamorphose directly to a juvenile from the bipinnaria stage, while other bipinnaria become a brachiolaria (Fig. 2D, E; front cover), which is a further developmental stage rather than a separate larval type. *Luidia ciliaris* (Philippi, 1837) has one of the largest bipinnaria (~35 mm long; Fig. 2C) and brachiolaria larvae of European species, probably because it spends many months in the plankton before metamorphosis.

The bipinnaria/brachiolaria transformation begins with the appearance of a single dorsal and two ventral stubby brachiolar arms (Fig. 2D, E), a feature that separates the two larval types. These arms have papillae at the tips that are used by the larva to test the substrate, but also produce adhesive secretions used in temporary attachment to the substrate. There is also an adhesive disc situated between the arms for more substantial attachment. In later larvae the brachiolar arms are less obvious among the other arms.

In both bipinnaria that metamorphose directly to a juvenile and brachiolaria, metamorphosis starts in the plankton and an obvious small post-larval sea star develops (Fig. 2E). The post-larvae have different numbers of arms depending on adult number. The commonest number is five but there can be more or less. For example, the post-larvae of *Luidia ciliaris* have seven arms, while the closely related *L. sarsi* Düben & Koren, in Düben, 1845 has five. Most brachiolaria larvae need to settle and attach to the substrate before metamorphosis can continue, but some post-larvae detach from the larval body before settlement.

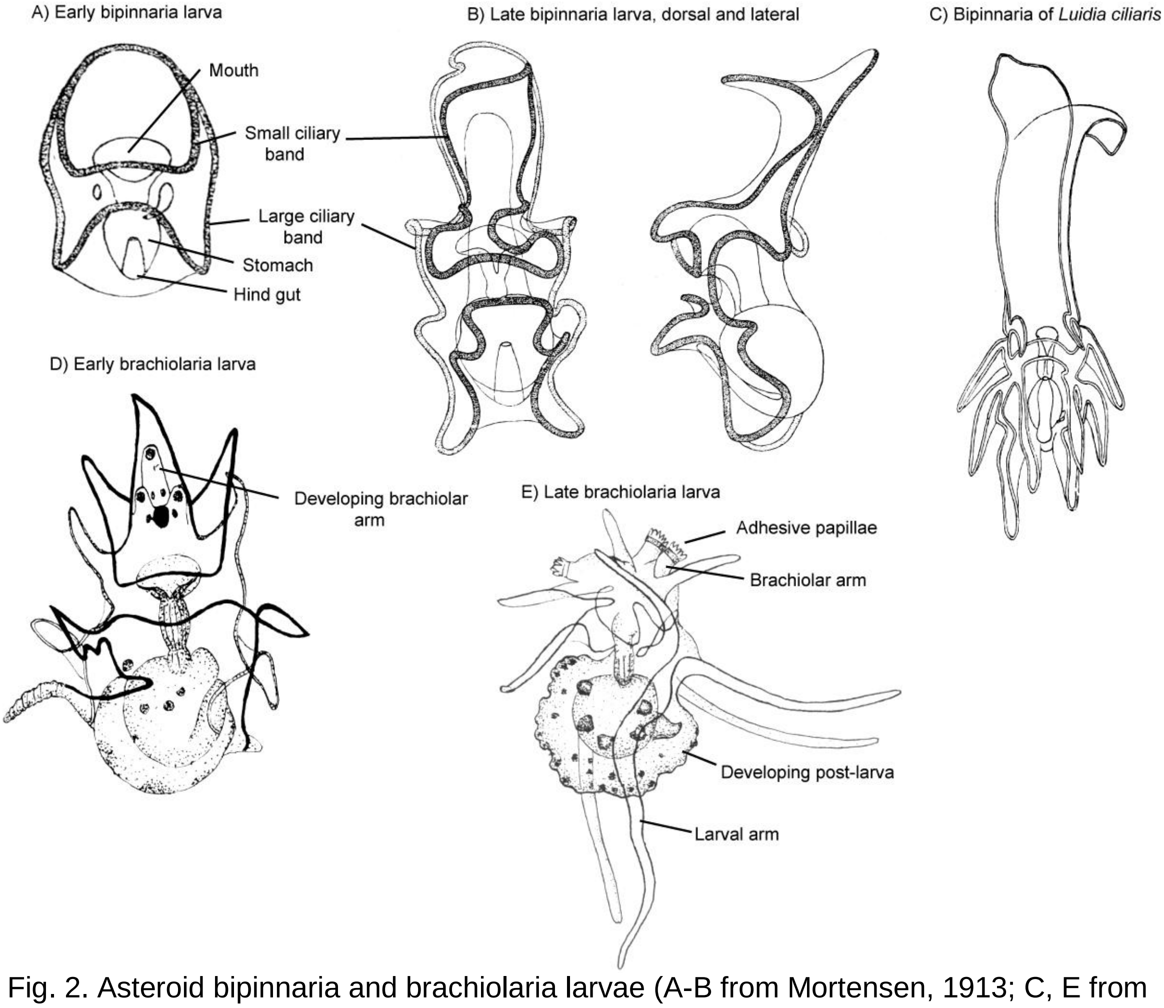

Fig. 2. Asteroid bipinnaria and brachiolaria larvae (A-B from Mortensen, 1913; C, E from Mortensen, 1901; D from Trégouboff & Rose, 1957).

Recorded: PMF, only adults recorded. L4, only as bipinnaria and brachiolaria larvae. All European area.
Size: ~0.2-35 mm.
Further information: Mortensen, 1901, 1913; Trégouboff & Rose, 1957; Larink & Westheide, 2011; McEdward *et al*., 2002; McEdward & Miner, 2001; Miller, 2001; Newell & Newell, 1963; Smith & Johnson, 1996; Southward & Campbell, 2006; Todd *et al*., 1991.

Vitellaria - barrel-shaped larvae (Asteroidea, Crinoidea, Ophiuroidea, Echinoidea and Holothuroidea)
Barrel-shaped and ovoid larvae of various types occur in all the echinoderm groups, but the nomenclature used for the different types has not been consistent among authors. McEdward & Miner (2001) suggest that all simple, non-feeding larvae, regardless of body form, be called vitellaria (Fig. 3) and those that have one or more transverse ciliary band should be termed doliolaria (Fig. 4). Most vitellaria have a simple barrel-shaped body form, typically uniformly ciliated. They are produced by some holothuroids (Fig. 3A), asteroids, echinoids, ophiuroids and crinoids. Some asteroids have a vitellaria like a simple brachiolaria larva, with stubby brachiolar arms, but lacking ciliary bands and pronounced arms (Fig. 3B). Other vitellaria are the reduced echinoplutei (Fig. 3C) and ophioplutei larvae of echinoids and ophiuroids respectively. These initially usually have a simple triangular shape (Fig. 1), or have short arms and lack ciliary bands.
Vitellaria can be brooded, benthic or free-living, with direct or indirect development. Most are small and delicate, do not survive net sampling and preservation well, so will rarely be encountered during routine plankton sampling. Identification, probably even to group, may require a specialist.

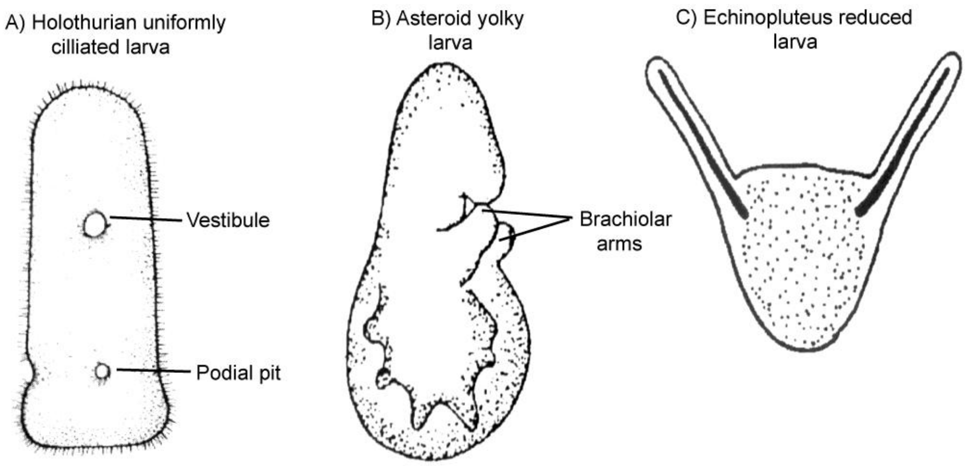

Fig. 3. Examples of vitellaria (A after Strathmann, 1987; B after Hyman, 1955; C after Raff, 1987).

Recorded: PMF, only adults recorded. L4 not recorded, but will occur. All around European area.
Size: ~0.3-1.0 mm.
Further information: Hyman, 1955; Raff, 1987; Strathmann, 1987; Balser, 2002; Byrne & Selvakumaraswamy, 2002; Emlet *et al*., 2002; McEdward & Miner, 2001; McEdward *et al*., 2002; Miller, 2001; Sewell & McEuen, 2002.

Doliolaria (Crinoidea, Ophiuroidea and Holothuroidea)
Doliolaria are barrel-shaped, non-feeding larvae with one or more transverse ciliary bands (Fig. 4A), so named because of their superficial resemblance to the pelagic tunicates of Order Doliolida. These larvae occur in Crinoidea, Ophiuroidea and Holothuroidea, but it is difficult to find information on whether the doliolaria of the three groups can be separated on morphological features. They are usually only in the plankton for two to eight days and metamorphose on settlement.
Crinoidea (sea lilies and feather stars) are the only echinoderm class that does not have planktotrophic larvae. In free-spawning species a barrel-shaped, uniformly ciliated vitellaria larva, similar to those of holothurians (Fig. 3A), emerges from the egg. The epidermis then transforms into regions with and without cilia, resulting in a single, locomotory ciliary band, looping over and

around the body, similar to that found in other echinoderm larvae, such as the auricularia (Fig. 5A). Within a few days longitudinal parts of the band disappear, leaving a series of four or five circular bands and an apical tuft (Fig. 4A). This doliolaria stage is typical of most crinoids and is probably the only crinoid larva that is likely to be caught in plankton nets. Later in larval life the first band may become interrupted in the ventral region, or displaced posteriorly, by the formation of the adhesive pit, part of the complex used in attachment to the substrate prior to metamorphosis. The second ciliary band is displaced posteriorly by formation of the vestibule, also on the ventral surface. The vestibule is an ectodermal invagination that is the future site of the mouth and emergence of the primary tube feet during the early stages of metamorphosis. Internally the skeleton can be well developed, consisting of a number of perforated calcareous plates. Some crinoid species brood eggs and embryos and release fully formed doliolaria larvae. The doliolaria attaches to the substrate by the attachment disc, which develops from the adhesive pit, and it then metamorphoses into a stalked stage termed a cystidean.
In ophiuroids, lecithotrophic development is the commonest means of reproduction, but many of the larvae produced are brooded or benthic, so will not be caught in plankton nets. However, some species produce free-swimming, non-feeding doliolaria with four, sometimes three ciliary bands.
In some holothurians the auricularia larva (Fig. 5A) transforms into a non-feeding doliolaria larva (Fig. 4B), which is a transitional, metamorphic stage prior to the protrusion of the five primary tentacles from the vestibule and transformation into the pentactula settlement stage (Fig. 5B, C). Skeletal plates or ossicles of various shapes may be seen in the body, such as wheel shapes (Figs. 4B, C). In other species with lecithotrophic development, the initial larva is a uniformly ciliated barrel-shaped vitellaria (Fig. 3A), which in some species transforms into a doliolaria with two to five transverse ciliary bands (Fig. 4D), parts of the larva sometimes retaining the uniform ciliation. These also transform into a pentactula larva.

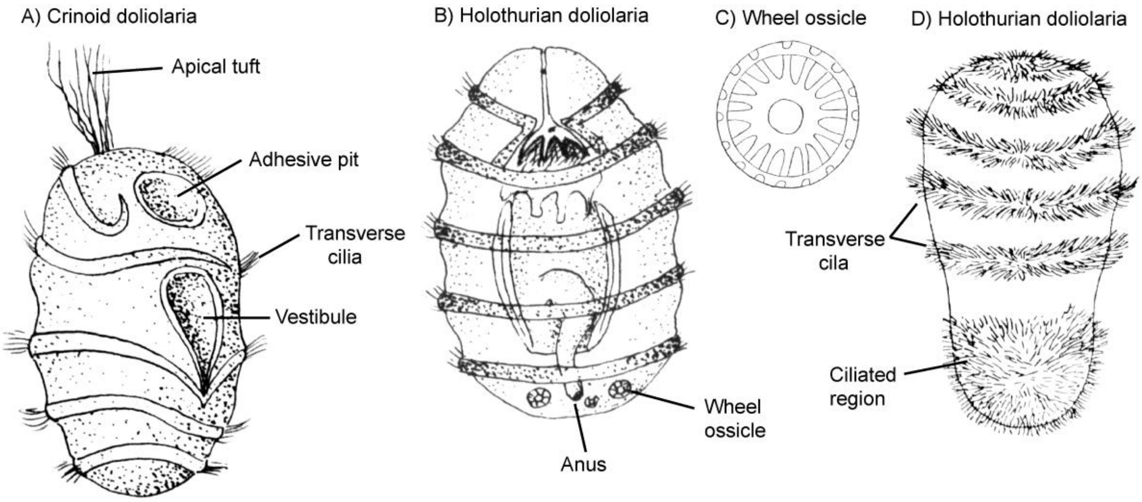

Fig. 4. Doliolaria larvae (A, B from Trégouboff & Rose, 1957; C, D from Mortensen, 1901).

Recorded: PMF, only adults recorded. L4. All European area.
Size: Doliolaria ~0.5-0.8 mm.
Further information: Mortensen, 1901; Trégouboff & Rose, 1957; Balser, 2002; Byrne & Selvakumaraswamy, 2002; Larink & Westheide, 2011; McEdward & Miner, 2001; Miller, 2001; Newell & Newell, 1963; Sewell & McEuen, 2002; Smith & Johnson, 1996; Southward & Campbell, 2006.

Auricularia/pentactula (Holothuroidea)
Some Holothurians produce small eggs that develop into a planktotrophic, bilaterally symmetrical auricularia larva with an elaborate ciliated band extending around projecting lobes (Fig. 5A). The lobes can become very numerous, but never develop into distinct larval arms as in the later bipinnaria larvae of asteroids, or plutei of echinoids and ophiuroids. The auricularia superficially resembles the bipinnaria of asteroids, but the ciliary band is a continuous loop over the body, while in the bipinnaria of asteroids there are two unconnected loops, one smaller than the other

(Figs. 1, 2A, B). Later auricularia stages may already have developed skeletal plates (ossicles) dotted all over the body (Fig. 5A). These small plates are variable in shape, in some groups resembling cart wheels (Fig. 4C), but in others are irregular perforated plates or branching structures. These ossicles would not be found in the bipinnaria larvae of asteroids. The auricularia transforms into a non-feeding doliolaria larva (Fig. 4B, D), then into a pentactula larva. This has five primary tentacles (Fig. 5B, C) that develop into the ring of tentacles surrounding the mouth in the adult. One or two primary feet may also develop. This is the settlement stage, but it may remain in the plankton for some time before metamorphosing into a juvenile.

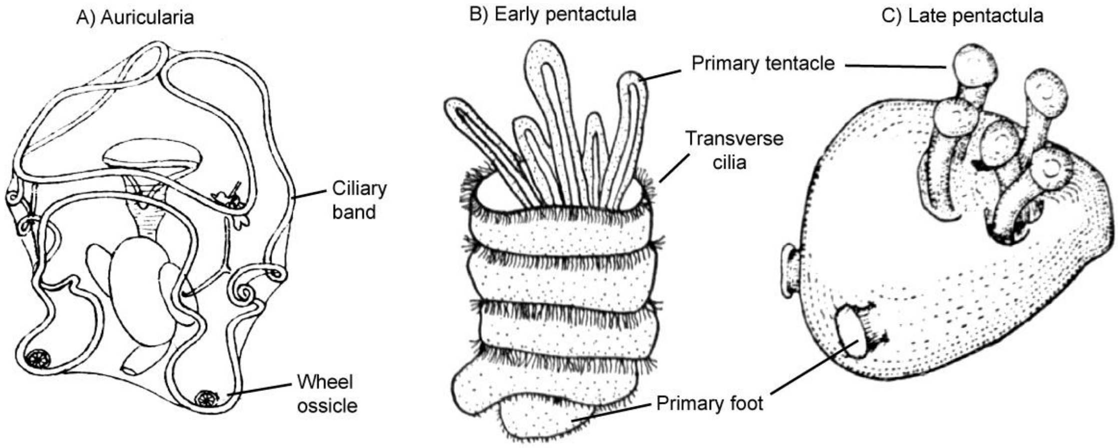

Fig. 5. Holothurian auricularia and pentactula larvae (A from Mortensen, 1901; B after Newell & Newell, 1963; C from Thorson, 1946).

Recorded: PMF, only adults recorded. L4. All around European area.
Size: Auricularia ~025-1.0 mm.
Further information: Mortensen, 1901; Thorson, 1946; Larink & Westheide, 2011; McEdward & Miner, 2001; Miller, 2001; Newell & Newell, 1963; Sewell & McEuen, 2002; Smith & Johnson, 1996; Southward & Campbell, 2006.

Echinoplutei (Echinoidea)

Sea urchins are typically broadcast spawners, producing small eggs that in the majority of species develop into a planktotrophic echinopluteus larva (Fig. 6). These are bilaterally symmetrical and have a series of paired arms. Contrary to what would be expected with their arrow-shaped body, the larvae typically swim with the arms directed forwards, so the point of the ‘arrow’ is the posterior (Fig. 6A). The arms are supported by a delicate calcareous skeleton and may be long and slender or short and broad. There is a band of cilia forming a continuous loop over the body and arms, used in feeding and locomotion. Echinoplutei initially usually develop two arms (Fig. 1), then four (Fig. 6D) and eventually generally eight (Fig. 6A, B), but sometimes ten. In the echinoplutei of two groups, the irregular urchins or heart urchins (Spatangoida) and in some members of the Diadematoida, there are 13 arms. The most posterior pair, the posterolateral arms, are directed laterally (Fig. 6C) and an unpaired arm, the posterior arm, projects backwards.
Within a few days of hatching the larva has two pairs of arms, anterolateral and postoral (Fig. 6D). A pair of posterodorsal arms then develop and then the preoral arms to form an eight-armed echinopluteus (Fig. 6E). Echinoplutei of some orders have some of their skeletal rods fenestrated (perforated along their length; Fig. 6A). In older larvae of some species, lobes called epaulettes bearing longer cilia used in locomotion may develop toward the posterior body (Fig. 6B).
Echinoplutei superficially resemble the ophioplutei larvae of ophiuroids (Fig. 7A) and similar nomenclature is used for their arms, because the arrangement appears similar. However, the arms present are not the same in both groups. Both generally have four pairs of arms, but most echinoplutei do not have arms corresponding to the pair of long posterolateral arms of ophioplutei. When these are present in echinoplutei they are either short posterolateral processes (Fig. 6A), or longer, laterally projecting posterolateral arms (Fig. 6C). The longest arms in advanced echinoplutei are usually the pairs of postorals and posterodorsals that extend dorsally and ventrally from the larval anterior/posterior axis (Fig. 6A, C). The skeleton in echinoplutei is usually

more complex than in ophioplutei. Additionally, the bodies of ophioplutei are generally more dorsoventrally compressed.
Echinoplutei may spend from weeks to months in the plankton before metamorphosis. In late larvae, tube feet may be seen forming around the skeleton (Fig. 6F). Juvenile urchins may also be taken in plankton samples, when the spherical shell, spines and tube feet are quite obvious.
Some species produce yolky, non-feeding echinoplutei larvae with simpler morphology than other echinoplutei and spend a shorter time in the plankton. These reduced plutei have one to two pairs of larval arms (Fig. 3C), lack ciliated bands and are classified as vitellaria larvae.

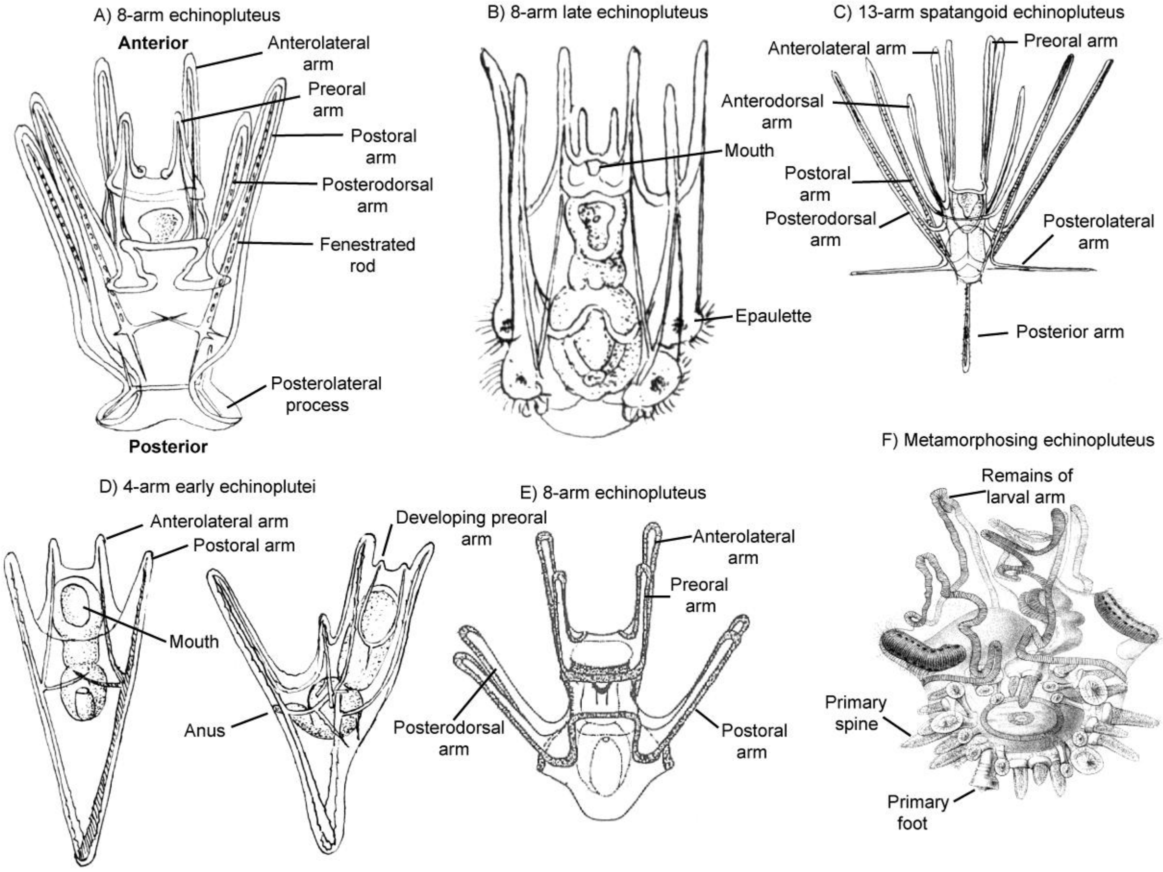

Fig. 6. Echinoplutei larvae (A, C from Mortensen, 1901; B-D from Trégouboff & Rose, 1957; E after Strathmann, 1971; F from McBride, 1903).

Recorded: PMF, only adults recorded. L4. All European area.
Size: ~0.5-6 mm in length.
Further information: Mortensen, 1901; McBride, 1903; Trégouboff & Rose, 1957; Emlet *et al.*, 2002; Geiger, 1964; Larink & Westheide, 2011; McEdward & Miner, 2001; Miller, 2001; Newell & Newell, 1963; Smith & Johnson, 1996; Southward & Campbell, 2006; Todd *et al.*, 1991.

Ophioplutei (Ophiuroidea)

Brittle stars are generally the most abundant echinoderm found in the European area. Those releasing non-yolky eggs have a planktotrophic, bilaterally symmetrical, ophiopluteus larva (Fig. 7). Ophioplutei generally have four (occasionally five or six) pairs of arms, supported by delicate, calcareous skeletal rods. A continuous band of cilia follows the contours of the arms and are used in locomotion and feeding. Like echinoplutei, the ophioplutei also typically swim with the arms pointed forwards. Some have very long thin arms and compact bodies (Fig. 7A) while others have fleshy squat arms (Fig. 7B). Red pigment cells are often present, scattered over the body.
The initial larval body is triangular (Fig. 7E) and skeletal rods can be seen internally. The two posterolateral arms develop first and extend laterally, then anterolateral, postoral and posterodorsal arms (Fig. 7F, G). The posterolateral arms are longer (Fig. 7C) to much longer (Fig. 7A) than the other arms. Each half of the larval skeleton comprises rods supporting the arms and an anchoring body rod positioned at the posterior end of the body (Fig. 7B, C), generally with end

and transverse rods connecting it to the corresponding parts on the other side of the skeleton. A few ophiuroid species have fenestrated skeletal rods in the posterolateral arms (Fig. 7C), but typically they are solid.
Ophioplutei larvae superficially resemble the echinoplutei larvae of echinoids (see comparison above) and similar nomenclature is used for their arms, because the arrangement appears similar. However, the arms are not strictly equivalent in the two groups. Both generally have four pairs of arms, but there appears to be less variation in body form and number of larval arms in ophioplutei and the skeleton is generally less complex. The pair of long posterolateral arms that extend laterally from the larval anterior/posterior axis (Fig. 7A) are not found in most echinoplutei and when present are very short. Additionally, in eight-armed ophioplutei there are no preoral arms. In ophioplutei the end and transverse skeletal rods are usually of similar size and arranged as in Figure 7, while in echinoplutei the end rods are sometimes much longer. Additionally, the bodies of ophioplutei are generally more laterally flattened.

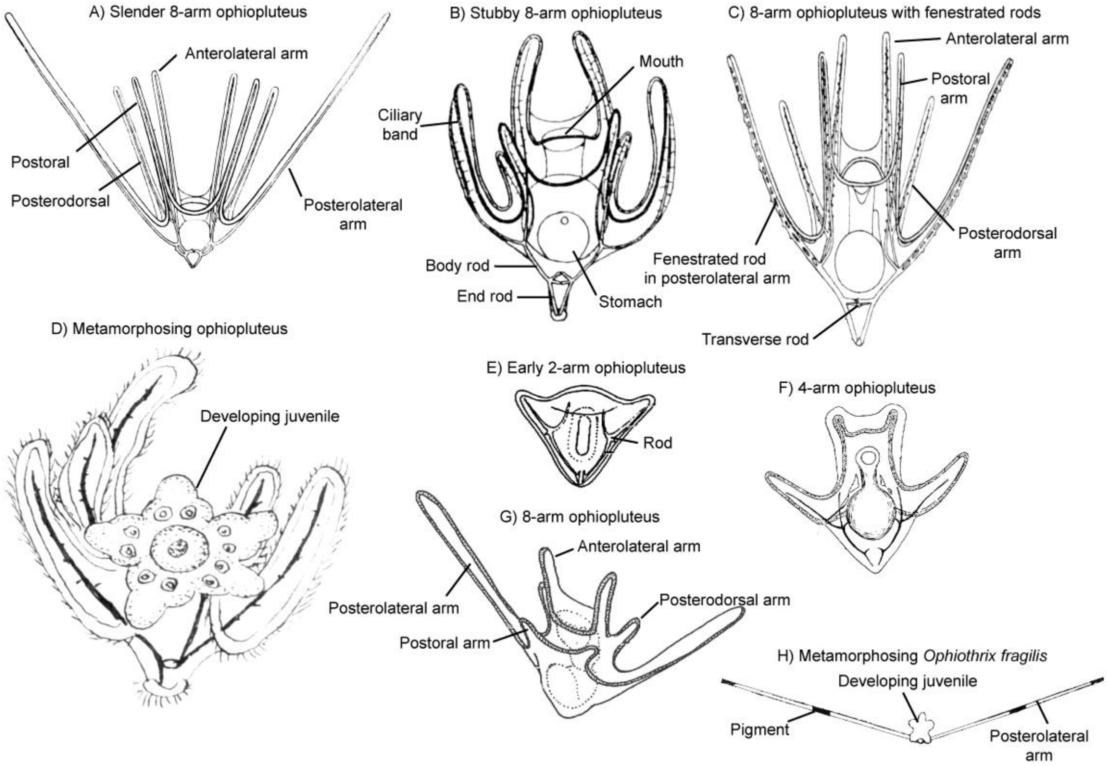

Fig. 7. Ophioplutei larvae (A-C, F from Mortensen, 1901; D from Trégouboff & Rose, 1957; E, G after Strathmann, 1987; F from Narasimhamurti, 1933).

Metamorphosis starts while still in the plankton. The minor larval arms are reabsorbed into the juvenile rudiment in the centre of the pluteus body (Fig. 7D) and eventually only the two posterolateral ones remain, very obviously in some species such as *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789)(Fig. 7H). Metamorphosis is rapid and the juvenile brittle star with well developed arms, skeletal plates and several sets of tube feet, casts off the remaining plutei arms before settling to the bottom. The arms of the juveniles tend to be more projecting and less rounded compared to juvenile asteroids. In some species the posterolateral arms remain functional and a second juvenile develops.
Lecithotrophic development is the commonest means of reproduction in ophiuroids, but many of the larvae produced are brooded or benthic, so will not be caught in plankton nets. Some of these eggs develop into non-feeding ophioplutei with one to three pairs of arms, or armless larvae with vestigial pluteus structures, all classified as vitellaria larvae.

Recorded: PMF, only adults recorded. L4. All European area.
Size: Ophioplutei ~0.3-1.0 mm.
Further information: Mortensen, 1901; Trégouboff & Rose, 1957; Byrne & Selvakumaraswamy, 2002; Geiger, 1964; Larink & Westheide, 2011; McEdward & Miner, 2001; Miller, 2001; Newell & Newell, 1963; Smith & Johnson, 1996; Southward & Campbell, 2006; Todd *et al*., 1991.

Mesogen (Echinoidea, Asteroidea and Ophiuroidea)
Mesogen larvae (Fig. 8) are a type reported from a few echinoids, asteroids and ophiuroids. They are a direct developing larva that may be brooded or pelagic, lack the typical larval body plan or metamorphosis and have unique development. They vary in appearance and at least some are not even bilaterally symmetrical. Podia, precursors of the tube feet develop around the mid-body. These larvae are rare, so are unlikely to be sampled

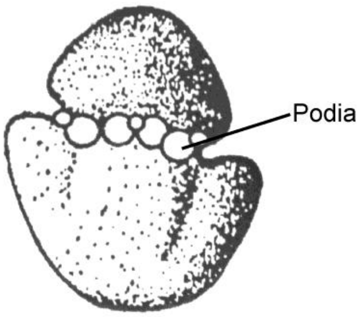

Fig. 8. Mesogen larva (After Kaufman, 1968).

Recorded: May not occur in European waters.
Size: ~0.5 mm.
Further information: Kaufman, 1968; Byrne & Selvakumaraswamy, 2002; Emlet *et al*., 2002; McEdward & Miner, 2001; McEdward *et al*., 2002; Miller, 2001.

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PHYLUM CHAETOGNATHA

Commonly called arrow worms, because of their shape and swimming action, chaetognaths can occur in very high numbers and are important predators, feeding on a range of zooplankton, mainly crustaceans, but are also noted for their cannibalism. Morphologically they are a very individual group, so occupy a phylum of their own. However, compared to other phyla, there are relatively few species, only around 120 worldwide. They range in size from a few millimetres to 12 centimetres, the largest species found in polar waters. Most are pelagic, but around a quarter are benthic. Chaetognaths are generally quite transparent, making internal infestation by parasites easy to observe, typically by protozoans, nematodes, cestodes or trematodes and are an important vector of these parasites. A wide variety of information on chaetognaths, from taxonomy to chemical composition, is given in Bone *et al*. (1991).

General body structure:

Chaetognaths have a tubular, elongated body (Fig. 1A) generally transparent, but in some species areas of them may becomes opaque when preserved. Species range from being slim and rigid when preserved, to flaccid and floppy. The head is usually separated from the trunk by a slight constriction. Some have a thickening of the epidermis on the neck, forming a collarette of tissue of varying length, sometimes present on other regions of the body. There are sometimes sensory ciliary tufts and bristles on the trunk surface, particularly obvious and usually present in certain species, but these are often destroyed during preservation.

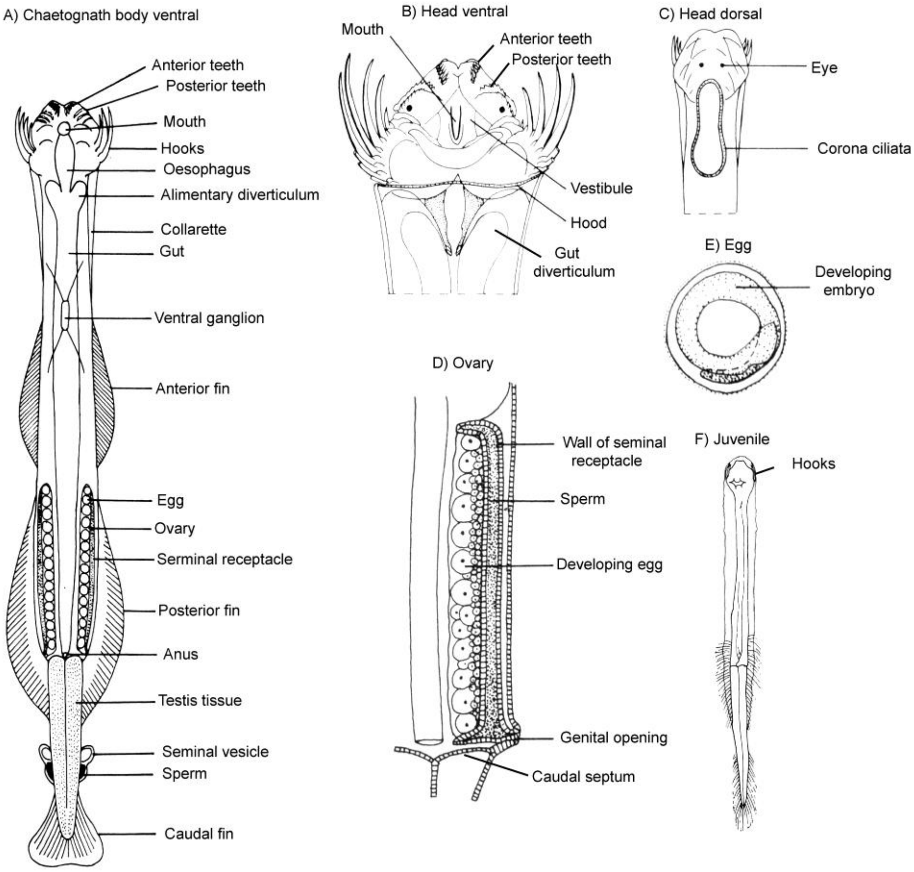

Fig. 1. Chaetognath structure (From Pierrot-Bults & Chidgey, 1988).

There are a set of long, generally brown, grasping hooks either side of the head for capturing prey. These are covered by a hood when swimming (Fig. 1B). In at least some species, venom is injected into the prey through the hooks (Thuesen *et al*., 1988). The mouth is situated, in a depression called the vestibule, ventrally between the hooks. Anterior to the mouth are rows of small teeth, usually two rows (anterior and posterior) on either side, but in some species there is only one row. Number of hooks and teeth can vary between species and this can be used in identification. However, as numbers change during development, vary slightly within the same species and can overlap between species, this is not a particularly reliable feature.

Most chaetognaths have a pair of small dorsal eyes and the shape of the pigment spot in the eyes varies between species and is sometimes used in identification. In pelagic chaetognaths, posterior to the eyes, on the head and/or anterior part of the trunk, is an oval band of ciliated cells known as the corona ciliata (Fig. 1C), thought to be sensory in function, but is difficult to see in preserved specimens. There are paired fins on either side of the body (Fig. 1A), either a single pair, two pairs, or a pair of long continuous fins, depending on species. The fins have supportive fin rays that may be continuous over the whole width of the fin, or only across part. There is a further single fin on the tail, the caudal fin. The shape and arrangement of the fins and the extent of the fin rays are all useful aids in identification. To reveal these features, staining with aniline blue is helpful (Michel, 1984). Phase contrast and dark-field microscopy can also help to show up fin structure. The position at which the anterior fin starts in relation to a nervous ganglion, an opaque patch situated on the ventral anterior surface, is another feature used in identification.

The body is divided by internal partitions into three sections – head, trunk and tail (Pierrot-Bults & Chidgey, 1988; Kapp, 1991). Central to the trunk, extending along its whole length is the gut. This terminates in the anus on the ventral surface, at the tail/trunk septum (Fig. 1A). In the neck region of certain species (e.g. *Parasagitta elegans*; Fig. 2), the gut may extend outwards into short lateral pouches or diverticulae (Figs. 1A, B; 2A, B). In some species the outer gut cells are vacuolated to such an extent that the vacuoles almost fill the coelomic cavity between the gut and inner border of the muscle layer (Dallot, 1970) in a series of indistinct, fine septae (Fig. 2C). In the species included here only *P. elegans* (Fig. 2) shows this feature.

Adult characteristics gradually develop from the time of egg hatching, so it can be difficult, using morphological characteristics to positively speciate immature individuals.

Reproductive organs:

Relatively rare among metazoa, chaetognaths are hermaphrodite. Self-fertilization has been demonstrated experimentally in some species, but in the sea cross-fertilization is probably the norm. The ovaries are situated in the posterior trunk (Fig. 1A) and are usually elongate in mature individuals, extending from the trunk/tail septum (partition) forward differing distances depending on the species and stage of maturity. Large eggs are generally visible inside the ovaries in mature specimens and are released though a lateral opening, just in front of the tail septum (Fig. 1D). In some studies chaetognaths are assigned to stages of sexual maturity, based on the size and maturity of the ovaries (e.g. Alvariño, 1967; Conway & Williams, 1986). However, chaetognaths go through cycles of egg release and egg maturation, so even large adults can appear immature immediately after spawning.

Testes are located in the tail section, one on either side, separated by a longitudinal septum (Fig. 1A). Sperm produced is stored in the seminal vesicles, which are located, one on each outer side, of the tail section. When mature, these rupture to release the spermatophores, which are attached to another chaetognath during copulation, although this transfer has rarely been seen. The transferred sperm migrates to the seminal receptacles that lie alongside the ovaries (Fig. 1D), and stored until required.

Chaetognath eggs:

The eggs of chaetognaths often occur in plankton samples, as most pelagic species release them freely into the water column and only a few species attach them to a substrate or retain them in brood pouches. Most benthic species attach the eggs to a substrate, or have floating egg masses. Eggs are typically slightly opaque when newly laid and do not have a perivitelline space. The commonest northern European species, *Parasagitta setosa* and *P. elegans*, have eggs of ~0.31 and 0.34 mm in diameter respectively, much larger than copepod eggs. As they develop the eggs become more transparent, with a small bundle of embryonic cells in the centre that gradually elongates and becomes a curved embryo (Fig. 1E). There is no discrete larval stage, the juveniles are rudimentary miniatures of the adult (Fig. 1F).

Classification:

Most chaetognaths were classified under just a few genera, most in Genus *Sagitta*, but this was revised by Bieri (1991) into around 20 genera. Following WoRMS, this classification is used here, but is still controversial.

Genus *Parasagitta***:**

Parasagitta elegans (Verrill, 1873)

The body is narrow and quite rigid (Fig. 2A). The lateral fins are separate, rounded and the fin rays extend completely across the fins. The anterior fins begin well behind the ventral ganglion. This is the only species included here in which prominent gut diverticulae are present (Fig. 2A, B), but they are often difficult to discern. There is a small, round pigment spot in the eyes. In mature specimens the ovaries are long and narrow. The seminal vesicles are either touching, or very close to the caudal fin and well separate from the posterior fins. There are 9-11 hooks, 2-8 anterior teeth and 12-18 posterior teeth.

P. elegans are morphologically very similar to *P. setosa*, but when formalin preserved are more opaque. A useful characteristic to help separate them was pointed out by Dallot (1970) and Bone *et al*. (1987). Internally in *P. elegans* the outer gut cells are vacuolated to such an extent that the vacuoles, which have very fine walls, can fill the coelomic cavity (Fig. 2C). This vacuolation is easiest to see in unpreserved or freshly preserved more mature specimens. *P. elegans* becomes opaque when preserved, apart from longitudinal areas of the body wall and the vacuoles can be observed through these windows. It is not known exactly how early the vacuoles develop, making very young *P. elegans* and *P. setosa* difficult to separate, but was observed in a *P. elegans* juvenile as small as 2.5 mm. Vacuoles are not found in any of the other species described here.

P. elegans eggs are ~0.34 mm in diameter, slightly larger but similar in appearance to *P. setosa* eggs. In the Celtic Sea, different developmental stages of *P. elegans* have been shown to adopt different seasonal depth distributions (Conway & Williams, 1986; as *Sagitta elegans*).

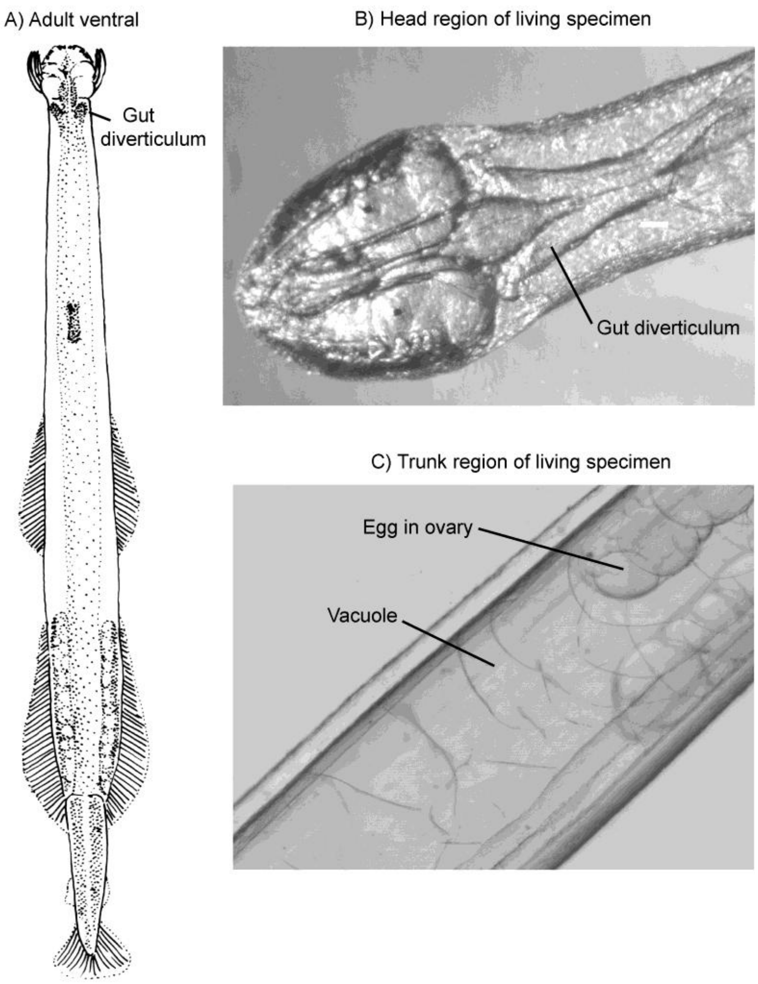

Fig. 2. *Parasagitta elegans* (A from Pierrot-Bults & Chidgey, 1988; as *Sagitta elegans*).

Recorded: PMF. L4. All European areas.

Size: Up to 30 mm in length.

Further information: Fraser, 1957; Dallot, 1970; Bone *et al*., 1987; Pierrot-Bults & Chidgey, 1988; (all as *Sagitta elegans*); Bieri, 1991.

Parasagitta setosa (Müller, 1847)
Parasagitta setosa is morphologically very similar to *P. elegans,* but is smaller, tends to be more transparent when formalin preserved, has no gut diverticula or internal vacuolation (see above) and the ovaries also tend to be shorter. The eyes have a small star-shaped pigment spot, but this is difficult to discern. There may be a small collarette. The seminal vesicles are close to or touching the posterior fins, separated from the tail fin. There are 8-9 hooks, 6-8 anterior teeth and 10-16 posterior teeth.
On average 1% of the chaetognath *P. setosa* sampled off Plymouth were infected by the nematode *Hysterothylacium aduncum* (Øresland, 1986; as *Sagitta setosa*), a common fish parasite worldwide that *P. elegans* also carry. Chaetognaths in the Irish Sea can have a considerably higher percentage infection (personal observation).
P. setosa eggs are ~0.31 mm in diameter slightly smaller, but similar in appearance to *P. elegans*.

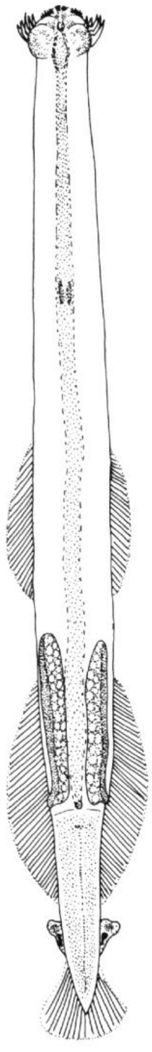

Fig. 3*. Parasagitta setosa* (from Pierrot-Bults & Chidgey, 1988; as *Sagitta setosa*).

Recorded: L4. PMF. Irish Sea. Southern North Sea.
Size: Up to 14 mm in length
Further information: Pierrot-Bults & Chidgey, 1988; Fraser, 1957 (both as *Sagitta setosa*); Bieri, 1991; Casanova, 1999.

Parasagitta friderici (Ritter-Záhony, 1911)

The body is quite firm and fairly transparent when preserved and all fins are separated and completely rayed. The anterior fins start at the rear of the ventral ganglion. More of the posterior fin is situated on the caudal segment than on the trunk and is broadest behind the septum. There is a short, small collarette on the neck and upper trunk and no gut diverticulae. This species superficially resembles *Sagitta bipunctata,* but lacks the distinctive sensitive bristles on the body. When mature the elongated, wedge-shaped seminal vesicles touch both the posterior and caudal fins. The ovaries are broad, and may extend up to the level of the ventral ganglion. There are 5-9 hooks, 6-10 anterior teeth and 12-23 posterior teeth.

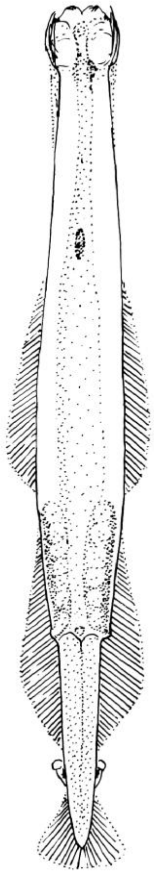

Fig. 4. *Parasagitta friderici* (from Pierrot-Bults & Chidgey, 1988; as *Sagitta friderici*).

Recorded: Not recorded in the PMF, but Pierrot-Bults & Chidgey (1988; as *Sagitta friderici*) note that it has been recorded off southwest England. L4 not recorded.
Size: Up to 15 mm.
Further information: Fraser, 1957; Michel, 1984; Pierrot-Bults & Chidgey, 1988 (all as *Sagitta friderici*); Bieri, 1991; Casanova, 1999.

Genus *Serratosagitta*:

Serratosagitta serratodentata (Krohn, 1853)

The head is small, the body needle-like, firm and opaque when formalin preserved. There is a thin collarette in the neck region. The lateral fins are separate and rounded, both described by Pierrot-Bults & Chidgey (1988) as having a small anterior, internal rayless zones (Fig. 4A). However, Lutschinger (1993) noted the anterior fins to be totally rayed and only a small inner portion of the posterior fin to be rayless (Fig. 4B). The anterior fins start at the posterior edge of the ventral ganglion. The eyes are small and oval with a T-shaped pigment spot (Fig. 4C). There are no gut diverticulae. The hooks are serrated on the inner edge (Fig. 4D), the serrations coarser than in *Serratosagitta tasmanica* (Furnestin, 1953; as *Sagitta serratodentata*). The ovaries, when mature, can extend to the ventral ganglion and be lined with large ova. The seminal vesicles almost touch the posterior fins, but are separate from the tail fin, almost touching both fins when mature. The seminal vesicles in mature and perfect specimens have two characteristic anterolateral, claw-like papillae, differing in shape from those of *Serratosagitta tasmanica*. There are 5-9 hooks, 6-11 anterior teeth and 12-20 posterior teeth.

Serratosagitta serratodentata is very similar to *Serratosagitta tasmanica* and their identification has probably been confused. In the NE Atlantic *Serratosagitta serratodentata* it is usually found in warmer waters, below latitude 50° N, while *Serratosagitta tasmanica* can have a more northerly distribution. There is only one record of *Serratosagitta serratodentata* in the PMF, but it is possible that it was a wrongly identified *Serratosagitta tasmanica*.

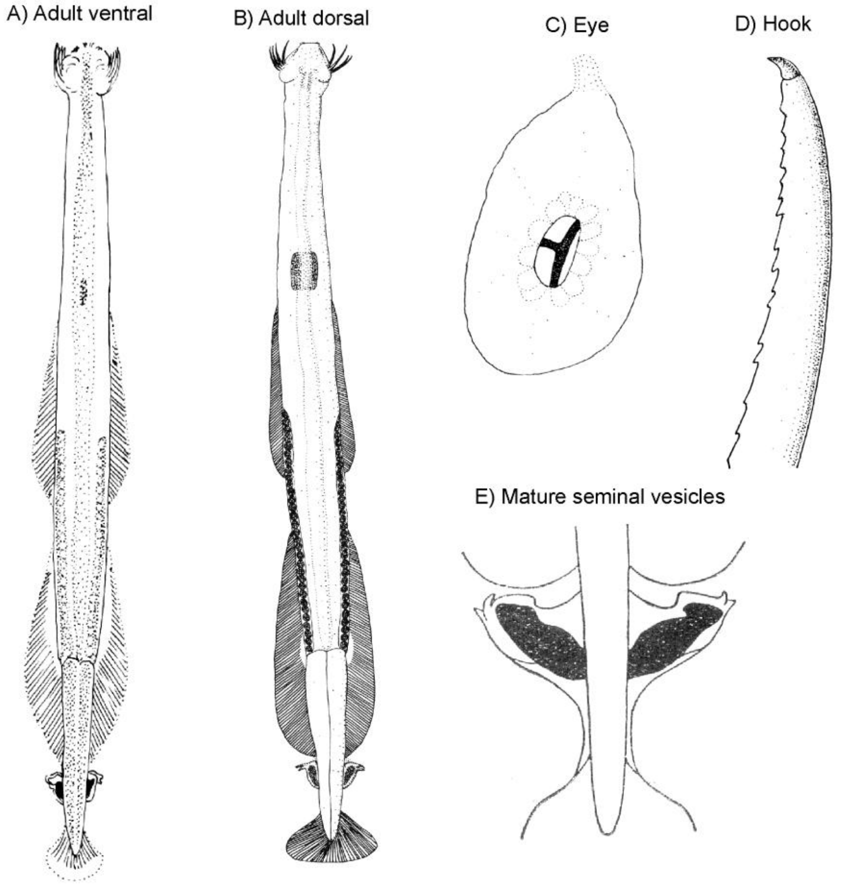

Fig. 5. *Serratosagitta serratodentata*. (A from Pierrot-Bults & Chidgey, 1988 (as *Sagitta serratodentata*); B-D from Lutschinger, 1993; E from Furnestin, 1953 (as *Sagitta serratodentata atlantica*)).

Recorded: PMF. L4 not recorded. Northeast Atlantic, warmer waters.
Size: Up to 15 mm.
Further information: Furnestin, 1953; Fraser, 1957 (both as *Sagitta serratodentata atlantica*); Michel, 1984; Pierrot-Bults & Chidgey, 1988 (both as *Sagitta serratodentata*); Lutschinger, 1993; Bieri, 1991; Casanova, 1999.

Serratosagitta tasmanica (Thompson, 1947)
The body is rigid and opaque when formalin preserved. The anterior fins start around the rear of the ventral ganglion and broaden at their posterior end. The anterior part of both fin pairs is rayless, the rayless zone in the posterior fin extending further back internally. The posterior fins are slightly longer, almost reaching the anterior pair. There are no gut diverticulae and the eyes are oval with a T-shaped pigment spot (Fig. 5B). There is a tiny collarette at the neck and between the posterior and caudal fins. The ovaries when mature reach almost to the ventral ganglion. The seminal vesicles lie closer to the lateral than the caudal fins, but do not touch them. The seminal vesicles are conspicuous when mature, and have an anterior glandular knob with protuberances (Fig. 5C), differing from those of *Serratosagitta serratodentata*. The hooks are not as coarsely serrated as in *Serratosagitta serratodentata* (Fig. 5D; Furnestin, 1953; as *Sagitta serratodentata*). There are 6-9 hooks, 2-9 anterior teeth and 3-15 posterior teeth.
This species is very similar to *Serratosagitta serratodentata* and they may have been confused in the past.

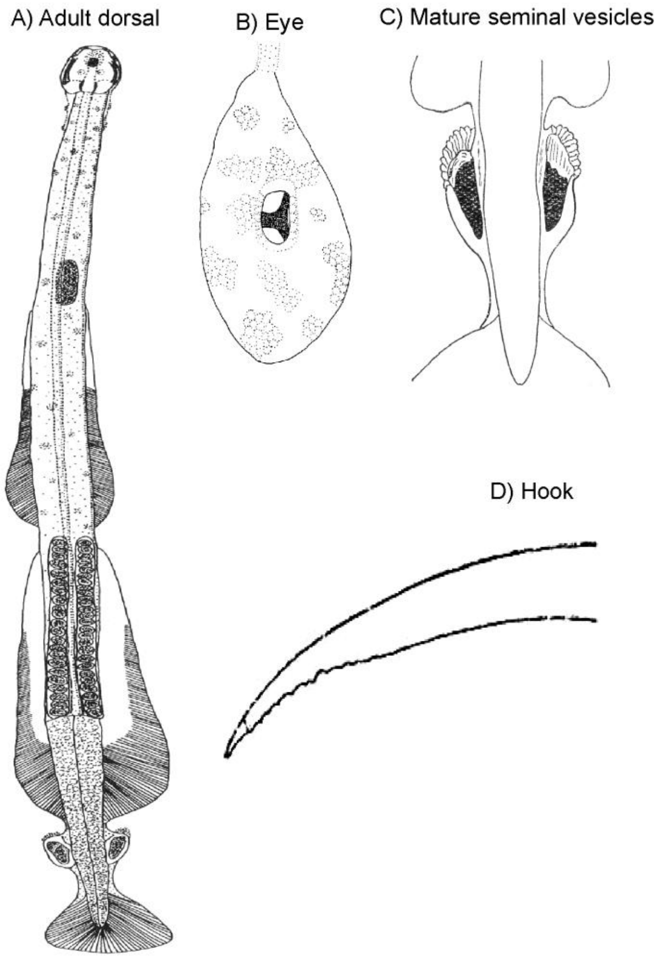

Fig. 6. *Serratosagitta tasmanica* (A, B from Lutschinger, 1993; D from Furnestin, 1953 (as *Sagitta serratodentata tasmanica*)).

Recorded: Not recorded of Plymouth, but a single record of *Serratosagitta serratodentata* (as *Sagitta serratodentata*) in the PMF may have been *Serratosagitta tasmanica*. Northeast Atlantic, colder waters.
Size: Up to 30 mm.
Further information: Furnestin, 1953; Fraser, 1957 (both as *Sagitta serratodentata tasmanica*); Pierrot-Bults & Chidgey, 1988 (as *Sagitta tasmanica*); Lutschinger, 1993; Bieri, 1991; Casanova, 1999.

Genus *Sagitta***:**

Sagitta bipunctata

Body firm and opaque when formalin preserved. There are no gut diverticulae. The anterior fins are rounded, the posterior ones more angular. The anterior fins extend to the posterior end of the ventral ganglion and are well separated from the posterior fins by a distance about the width of the body (Fig. 7A, B). The posterior fins are wider and longer than the anterior fins, reaching their maximum width at about the level of the caudal septum. Both pairs of fins are completely rayed. The eyes have a T-shaped pigment spot (Fig. 7C). There is a prominent collarette, extending from the neck to the anterior fins, thinner between the lateral fins and between the posterior fins and seminal vesicles (but may be lacking in this latter area in immature specimens). Lutschinger (1993) illustrates sensory structures on the collarette (Fig. 7A) and Fraser (1957) prominent bristles, but these were not figured by Alvariño (1967), Michel (1984), Pierrot-Bults & Chidgey (1988; Fig. 7B) or Casanova (1999). Only Fraser (1957) actually mentions these sensory structures. When mature the ovaries can reach the ventral ganglion. The seminal vesicles are separated from the posterior fins and close to the caudal fin. When mature they are pear-shaped with anterior knob-like protrusions. There are 5-10 hooks, 4-8 anterior teeth and 8-16 posterior teeth.

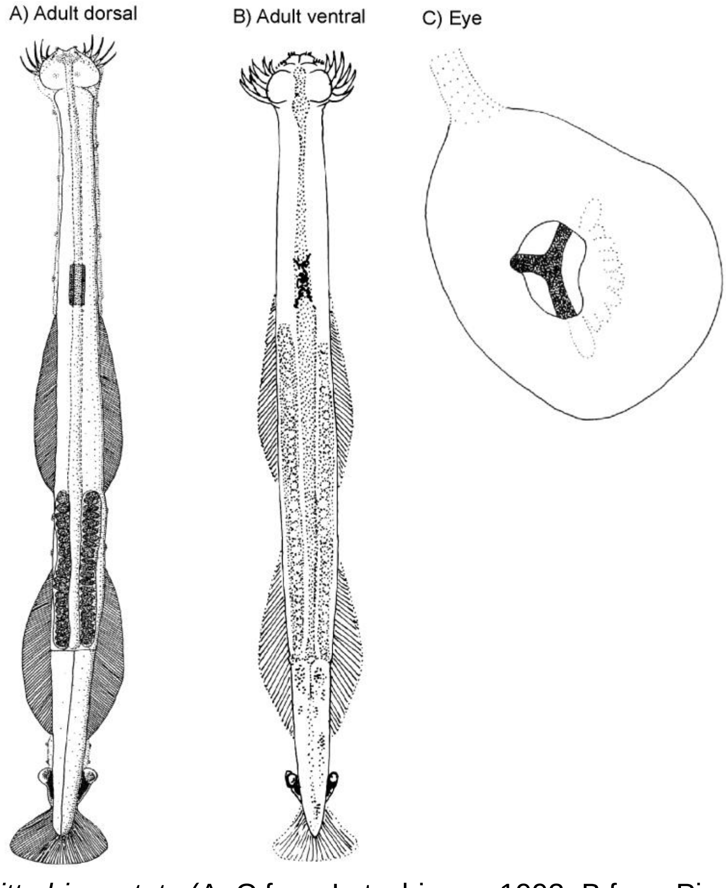

Fig. 7. *Sagitta bipunctata* (A, C from Lutschinger, 1993; B from Pierrot-Bults & Chidgey, 1988)

Recorded: Not recorded in the PMF, but found off the southern Irish coast and in the Bay of Biscay, so could possibly reach the Plymouth area.

Size: Up to 19 mm.

Further information: Fraser, 1957; Alvariño, 1967; Michel, 1984; Pierrot-Bults & Chidgey, 1988; Bieri, 1991; Lutschinger, 1993; Casanova, 1999.

Genus *Spadella***:**

Spadella cephaloptera (Busch, 1851)

This is an easily recognised small benthic species that is usually found attached to a substrate, or partially buried in sediment, but may appear in inshore plankton samples during turbulent mixing. The body is rigid and opaque with a short trunk and long tail section. There is a small head bearing pigmented eyes and a stumpy tentacle (probably vestigial) either side, which are usually held pressed against the head (John, 1933). Small gut diverticulae are present. There is one pair of lateral fins, almost entirely on the tail section, completely rayed and connecting with the tail fin. A conspicuous collarette extends from the head to the lateral fins. On certain regions of the body are cone-like protuberances with cilia at their apex. The ovaries are short and broad with large ova and the seminal vesicles are large and round, touching both lateral and tail fins. They have 7-11 hooks, 2-5 anterior teeth and 2-5 posterior teeth. The anterior teeth are longer than the posterior teeth.

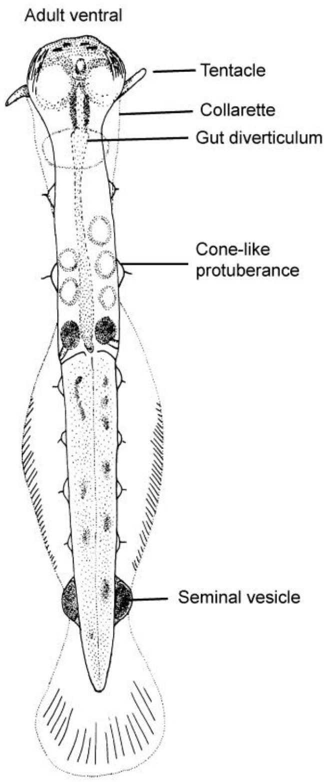

Fig. 8*. Spadella cephaloptera* (From Pierrot-Bults & Chidgey, 1988).

Recorded: PMF. L4 not recorded. Widely distributed in northern European waters.
Size: Adults 4.0-9.5 mm, usually at the lower end of the size range.
Further information: John, 1933; Fraser, 1957; Pierrot-Bults & Chidgey, 1988; Michel, 1984; Bieri, 1991.

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PHYLUM HEMICHORDATA

Hemichordata is a small marine phylum of around 120 species worldwide of worm-like, benthic deposit, or suspension feeders. They share some chordate characters, having a primitive form of notochord (at least in early development), possibly a trait they share with the common ancestor of Chordata, so are important in the study of vertebrate evolution. However, they are not classified as true chordates and DNA evidence suggests they are more closely related to echinoderms, supported by the similarity between some of their larvae.

There are two main classes of hemichordates, **Enteropneusta** and **Graptolithoidea**. These are very different, but linked by some characters. The most familiar are the Enteropneusta, commonly called acorn worms, of which there are only about 90 known species, with around four in the European area. The smallest are only a few millimetres long and the largest, can reach lengths of ~1.5 metres. They are mainly found in shallow coastal waters, but occur down to a depth of 3,000 m. They live in U-shaped burrows on the sea-bed and their casts, left exposed at low tide, are a familiar sight in the tropics. The larvae of some species are planktonic.

The Graptolithoidea, with around 20-30 species, are small tentaculate organisms, forming colonies with branching tubes and generally live in much deeper water than the Enteropneusts. They are difficult to study and little is known about their ecology. Larvae that are released have a very short pelagic existence, are ovoid, elongated, ciliated and ~400 µm in length. These unremarkable larvae are very unlikely to be caught in plankton samples, so will not be covered here.

PHYLUM HEMICHORDATA:

Class Enteropneusta:

Reproduction and development

Sexes are separate and eggs and sperm are broadcast for external fertilisation. Some species do not have a larval stage, development being directly into small juveniles, while in others the eggs develop into a free-swimming planktonic larva called a tornaria (Fig. 1)

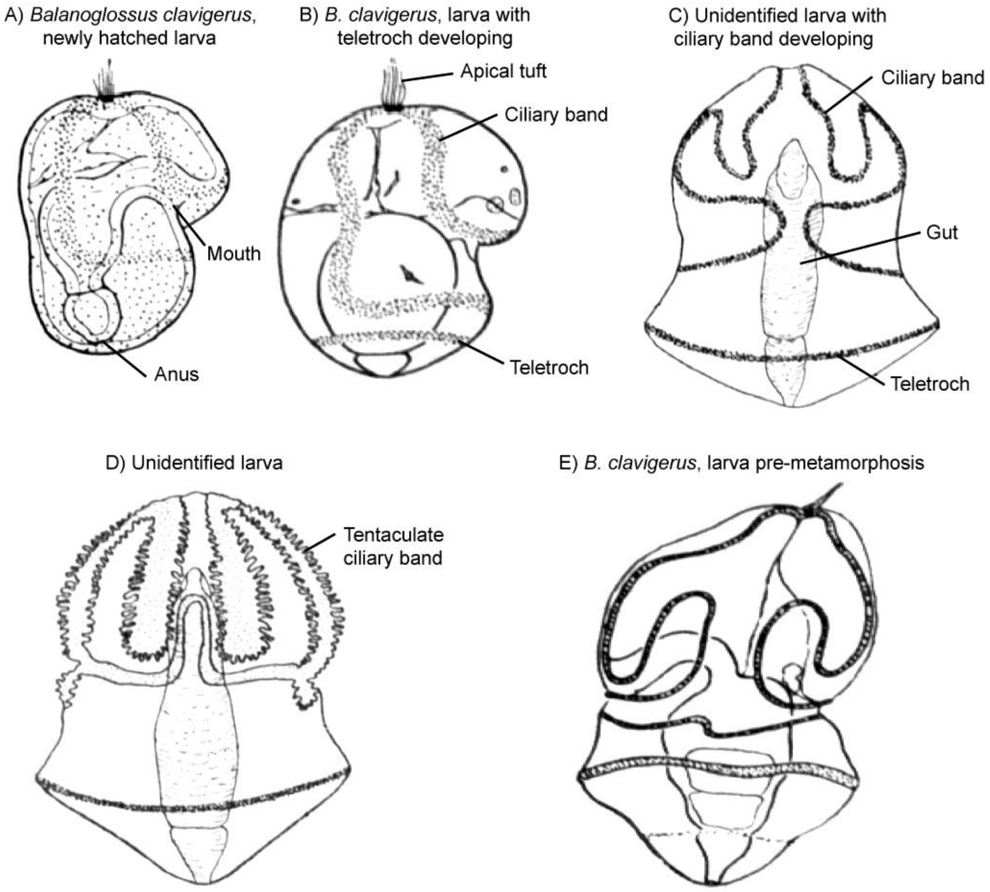

Fig. 1. Examples of developmental stages of tornaria larvae (A, B, E from Burdon-Jones, 1957; C, D from Wickstead, 1965).

The newly hatched tornaria larvae are simple and ciliated, but soon become elongated and characteristically bean-shaped (Fig. 1A, B). The mouth is situated in a midventral depression and the anus at the posterior end. There is an apical tuft of cilia and a densely ciliated band develops which rapidly forms into a series of loops (Fig. 1C). This ciliary band is used in filter feeding and develops in a very similar pattern to that seen in the early bipinnaria of asteroid echinoderms. A dense ring of cilia, the telotroch, develops round the posterior end. When this is formed, cilia over the rest of the body diminish and the telotroch takes over propulsion. During development the ciliated bands become increasingly elaborate. They surround a grove in which food particles are transported to the mouth. In some species the bands develop into rows of stubby, tiny tentacles (Fig. 1D). The tornaria may spend weeks or months in the plankton and can develop juvenile characters such as gill slits before they eventually settle to the bottom, metamorphose into tiny acorn worms and take on the adult lifestyle. Because developmental changes are continuous, identification is a specialised task, so only examples of tornaria morphology are given. Descriptions of a few larvae are given in Burdon-Jones (1957).

Distribution: The adults of two Enteropneusta species are recorded from the PMF (*Glossobalanus sarniensis* Koehler, 1886 and *Balanoglossus clavigerus* Delle Chiaje, 1829). One adult Graptolithoidea species *Rhabdopleura compacta* Hincks, 1880 has been recorded at Plymouth (Stebbing, 1970). L4, unidentified tornaria larvae. All European areas. Mainly coastal waters
Size: Eggs <0.15 mm diameter, fully developed larvae ~0.5-4.0 mm total length.
Further information: Burdon-Jones, 1957; Damas & Stiasny, 1961; Stebbing, 1979; Todd *et al*., 1991; Hadfield, 2002; Larink & Westheide, 2011; Shanks, 2001; Röttinger & Lowe, 2012.

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PHYLUM CHORDATA

Chordata includes the vertebrates, together with several invertebrates that are considered to be related. They are united by having, at some period in their life cycle, a notochord (provides skeletal support and develops into the vertebral column in vertebrates), a hollow dorsal nerve cord (develops into the central nervous system), pharyngeal slits (openings in the pharynx that develop into gill arches in bony fish, but in some chordates are part of the filter-feeding system), an endostyle (a groove in the ventral wall of the pharynx that in filter-feeding species produces mucus used in trapping and transporting food particles) and a postanal tail (a muscular tail that extends beyond the anus. There are three subphyla, **Tunicata**, **Cephalochordata** and **Craniata**.

Subphylum Tunicata:

Tunicata derive their name from their unique outer covering or "tunic”, which in some species is thin, translucent, and gelatinous, while in others it is thick, tough, and stiff. During a larval stage in their life cycle they have a primitive notochord and nerve cord that are lost in the adult. They are represented in the plankton by three main classes **Ascidiacea**, **Larvacea** and **Thaliacea**.

PHYLUM CHORDATA: Subphylum Tunicate:

Class Ascidiacea:

Adult ascidians are commonly known as sea squirts and are sac-like, solitary or colonial, sessile filter feeders, typically found on the seabed, or as fouling organisms on marine structures or ship bottoms. Some 57 species are recorded in the PMF, but the number found in the European area has increased due to introduction of alien species.

Reproduction and development

Some ascidians reproduce only sexually and these are solitary, while colonial species can reproduce both sexually and asexually (by budding). Most adults are hermaphrodite (some self-fertile) and release many eggs that are then externally fertilised with sperm from other individuals, either in the open sea (especially in colonial species) or in the body cavity, the sperm drawn into the organism in the inhalent feeding current. Some fertilised eggs develop directly into juveniles, but most into free-swimming, non-feeding (lecithotrophic) larvae. Because of their shape, the typical larvae are called “tadpole” larvae (Fig. 1) and these are often collected in finer mesh, inshore plankton samples. The larvae spend from minutes to a few days in the plankton, swimming by undulations of the tail. Species vary in size, colour and internal complexity. They generally have a simple ocellus (Fig. 1B). They select and settle on appropriate substrates using three anterior papillae, cement in place and metamorphose into juveniles. Sexual maturity can be reached within a few weeks. They superficially resemble appendicularians (Fig. 2), but the tail emerges from the rear-trunk in ascidians and from mid-trunk in post-larval appendicularians.

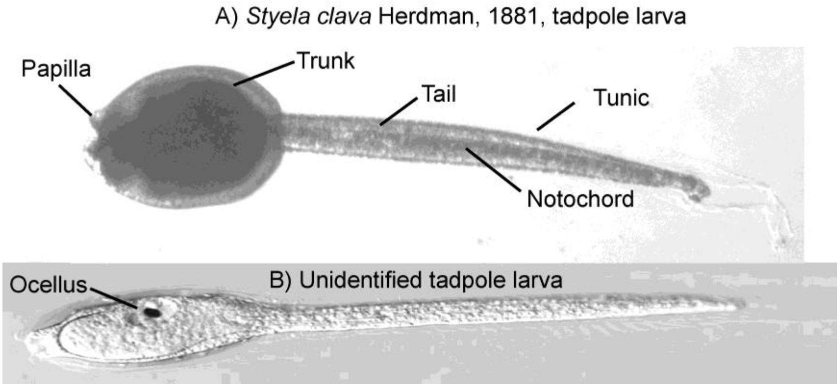

Fig. 1. Ascidian tadpole larvae.

Recorded: PMF, only adults recorded. L4, unidentified larvae. Widespread in European waters.
Size: 0.6-4.5 mm.
Further information: Sadro, 2001; Larink & Westheide, 2011.

Class Appendicularia: Order Copelata:

Appendicularia (sometimes referred to as Larvacea or Copelata) are planktonic, filter-feeding organisms, most only a few millimetres long, with a notochord (or chorda) that persists throughout their life. They can be very numerous in plankton samples in all areas and their importance in the marine ecosystem is probably not fully recognised. Their numbers present generally increases during elevated phytoplankton abundance. Only two families of appendicularians are represented in the northern European area, **Oikopleuridae** and **Fritillariidae,** with around 17 species recorded (Bückmann, 1969). However, some of these are rare visitors and probably only four of the indigenous species are common (Fraser, 1981). The seven species most likely to be sampled are in the genera *Oikopleura* and *Fritillaria* and all of these are described here. The genus *Oikopleura* is further divided into two subspecies, *Vexillaria* and *Coecaria* on the basis of presence or absence of particular tail glands.

Morphology

Appendicularia are fragile organisms and some of the features described below are difficult to observe, although at least separation into Oikopleuridae and Fritillariidae is simple. The body comprises two regions, a trunk that is rarely longer than five millimetres and a tail that is typically several times longer than the trunk (Fig. 2), frequently found detached from the trunk in plankton samples. Appendicularians have a superficial resemblance to ascidian tadpole larvae, but not to other tunicates. However, features of the basic trunk structure are similar, with pharyngo-branchial, digestive and reproductive regions, the morphology of these parts differing between families. The tail is typically flat and very thin, the epithelium covering it extending laterally forming fin-like expansions (not present in ascidian tadpoles) on both sides, of varying width depending on species (Fig. 2B, E). The tail contains a central, fluid-filled, tubular notochord, a dorsal nerve cord with several nerve ganglia and a series of striated muscle bands that flex against the notochord when beating to produce water currents.

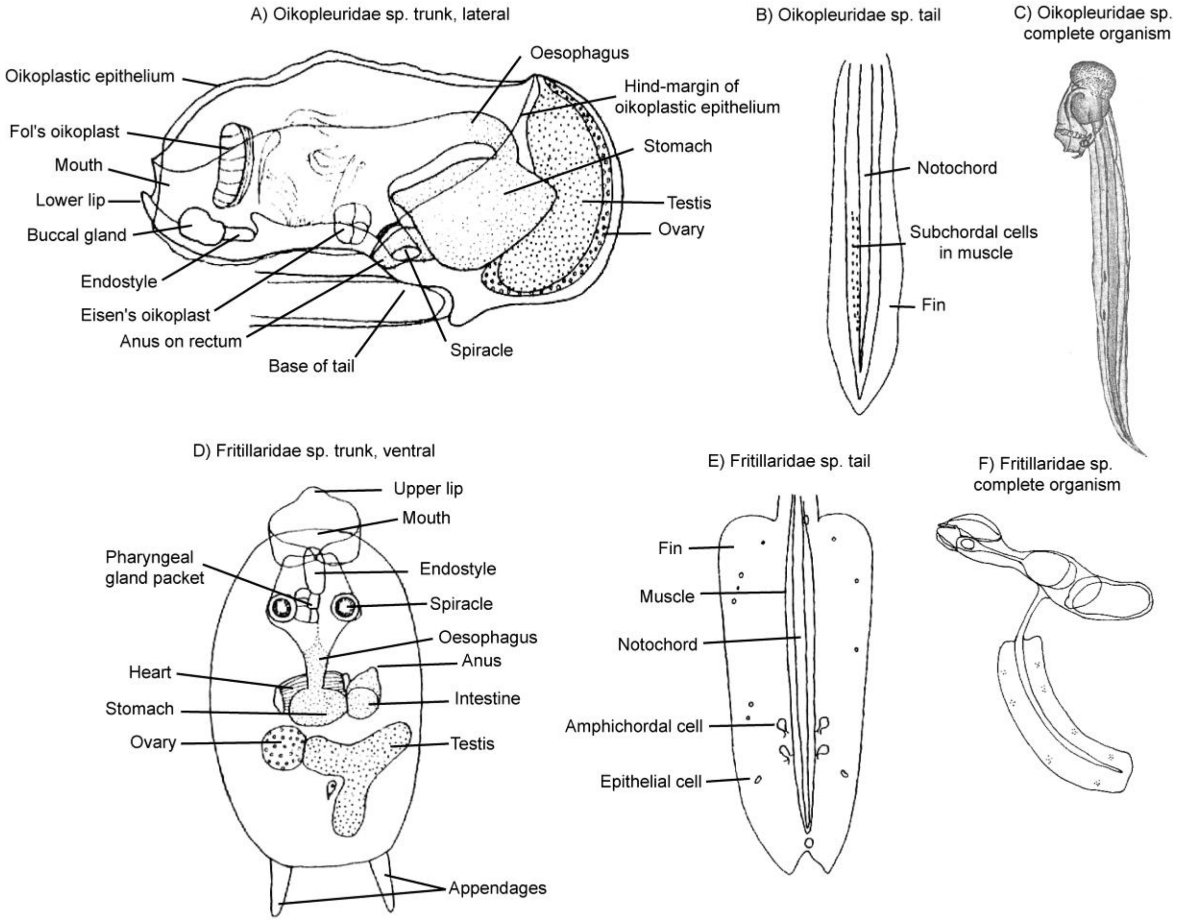

Fig. 2. General structure of Appendicularia (A, B, D, E after Bückmann & Kapp, 1975; C from Thompson, 1948; F from Fraser, 1981).

Features used in identification of appendicularians are the shape of the trunk and tail; presence or absence of lips on the mouth; shape and position of the short endostyle; presence and shape of the paired buccal glands (cells located either side of the endostyle); shape and position of the paired respiratory/feeding current openings (spiracles or gill openings), oesophagus, stomach (which may be of one or more lobes), intestine and rectum; shape, position of the generally paired testes and single ovary; presence/absence of subchordal cells (of unknown function) in the tail muscle, found only on one side of the notochord and of amphichordal cells (of unknown function) found on both sides in the fin.
The oikoplastic epithelium that covers the oral end of the trunk (Fig. 2A) secretes an almost spherical and complex, many chambered mucilaginous “house” (Fig. 3). The shape and structure of the epithelium varies between species. For Oikopleuridae it is known that regions of the epithelium known as the Fol’s and Eisen’s oikoplasts (Fig. 2A) are involved in the secretion of the feeding and inlet filters respectively. Fol’s oikoplasts are largest and usually elongated (absent in Fritillariidae), while Eisen’s oikoplasts are roughly square or round. While presence, position and shape of the oikoplasts can be used in identification, this greatly depends on the condition of the epithelium. The entire animal is enclosed by the house in Oikopleuridae and all but a small part of the trunk in Fritillariidae (Flood & Deibel, 1998). Limited information is available on the structure of the house in Fritillariidae, but in Oikopleuridae it is complex, a large part of it comprising two levels of filters (Fig. 3). There are outer coarse filters to exclude large particles and finer, inner filtering nets to trap food. Water is drawn into the house by beating of the tail and is then expelled through an exhalent aperture. The current of water through the house causes minimal locomotion and the animals are really just drifting. Food is channelled by ciliary action to the mouth and pharynx where it is trapped in mucous secreted by the endostyle (Fig. 2A, D). Behind the endostyle, on each side, there is a funnel-shaped duct provided with a ciliary ring that opens to the outside through spiracles. Beating of these and other cilia induces water circulation in the pharyngeal cavity causing an exhalent current to the spiracles, while mucous containing trapped food is channelled down the oesophagus into the stomach.
The house may be replaced several times a day as the filter becomes clogged and in some species may be replaced 46-53 times in a lifetime (Sato *et al*., 2001). When the house is discarded, or in an emergency, there is an escape exit through which the animal can leave. The house is kept inflated by flow of water and collapses when this stops. Most particles collected are ingested, but some remain in the house, making houses important as a component of marine snow and in the diet of other organisms. Unless special sampling equipment, such as a water bottle is used, appendicularians in plankton samples are usually found missing their house, or the house is badly damaged, typically reduced to a clogging slime on the inside of plankton nets.

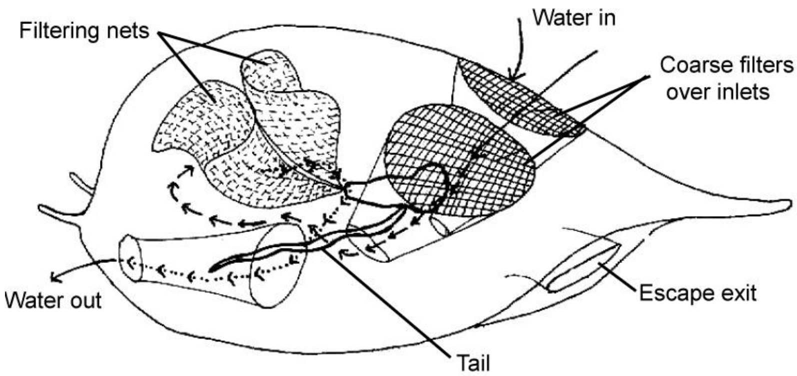

Fig. 3 The house and feeding mechanism of an *Oikopleura* sp. (from Fraser, 1981)

Reproduction and development
Appendicularia reproduce sexually and all European species are protandric hermaphrodites (born male then change sex to female), apart from, for some puzzling reason, the commonest species, *Oikopleura* (*Vexillaria*) *dioica* Fol, 1872, which has separate sexes. The gonads are in the posterior trunk (Fig. 2A, D). Oikopleuridae generally have a single ovary and paired testes, while Fritillariidae have both single ovaries and testis. Spermatozoa are released directly into the sea via a sperm

duct and sometime later the oocytes are released by rupture of the walls of the gonads and trunk, resulting in the death of the animal. Immature animals resemble the tadpole larvae of ascidians, but have developing viscera. When the trunk is fully developed, the larva undergoes "tail shift", in which the tail moves from a terminal position to a ventral orientation and twists 90°. Following tail shift, secretion of the first house begins.

Key to the Appendicularia species described here:

1. Trunk compact, pear-shaped; Fol's oikoplast present; anterodorsal oikoplastic epithelium extends to anus; oesophagus enters stomach from above or laterally, stomach composed of many small and a few large gland cells; tail several times as long as trunk, fin gradually tapering distally -- *Oikopleura* spp. -- **2**
- Trunk generally elongated; Fol's oikoplasts absent; ventral oikoplastic epithelium reduced to a small anterior area; oesophagus enters stomach from front, stomach composed of a few large cells; tail in most species broad throughout its length, usually not much longer than trunk -- *Fritillaria* spp. -- **4**

2. No subchordal cells in tail -- *O.* (*Coecaria*) *fusiformis* (Fig. 6)
- Subchordal cells in tail --- **3**

3. Two subchordal cells in tail--- *O.*(*Vexillaria*) *dioica* (Fig. 4)
- Long series of subchordal cells in tail --------------------- *O. (Vexillaria) labradoriensis* (Fig. 5)

4. Tail fin without amphichordal cells --- **5**
- Tail fin with amphichordal cells --- **6**

5. No conical appendages on genital end of trunk; tail fin tapering abruptly distally ---------------- --- *F. gracilis* (Fig. 10)
- Small conical appendages on genital end of trunk; tail fin broad distally --------------------------- --- *F. borealis* (Fig. 7)

6. Conical appendages on genital end of trunk; generally two spherical amphichordal cells on each side of tail -- *F. pellucida* (Fig. 8)
- Conical appendages on genital end of trunk; one jug-shaped amphichordal cell on each side of tail --- *F. tenella* (Fig. 9)

Family Oikopleuridae:

Genus *Oikopleura*:

Oikopleura (*Vexillaria*) *dioica* Fol, 1872

Small species; trunk ovoid, fairly compact (Fig. 4A); mouth with small lower lip; endostyle quite large, extending back, almost to rectum; rectum extending far in front of stomach; buccal glands, small and spherical; tail with narrow muscle band (Fig. 4B) and two (rarely one or three) distinct, characteristic spindle-shaped subchordal cells arranged in a line at about half to two thirds down the length (distinguishable even in unstained material). The sexes are separated in this species, while as far as is known, all other species are hermaphrodite.

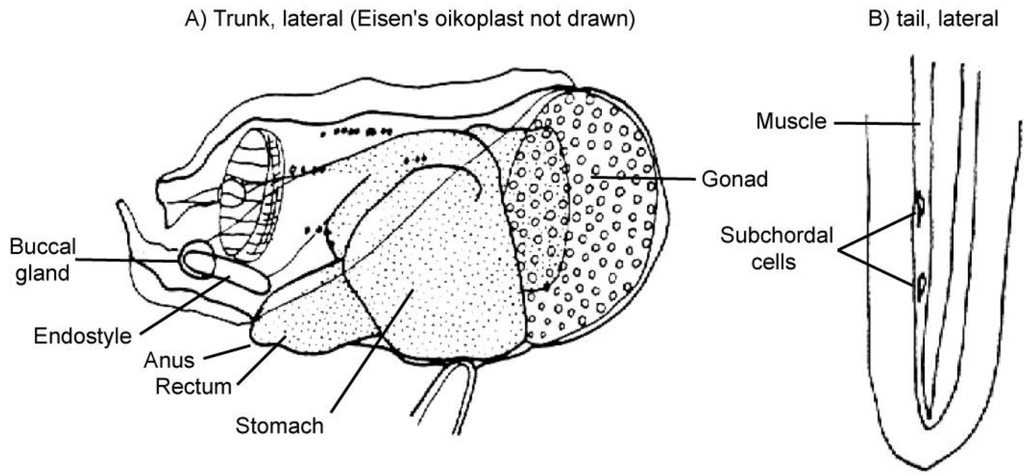

Fig. 4. *Oikopleura* (*Vexillaria*) *dioica* (after Bückmann & Kapp, 1975).

Recorded: PMF. L4. North Sea. Irish Sea. Common in coastal and brackish waters, and estuaries, as well as open sea.

Size: Trunk length usually ~ 0.5-1.0 mm, but may reach 1.3 mm; tail narrow, ~2-4 mm in length.

Further information: Thompson, 1948; Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Fenaux, 1998a; Sato *et al*., 2001; Telesh *et al*., 2009; Larink & Westheide, 2011; Marine Species Identification Portal, 2011; (all as *O. dioica*); Esnal, 1999; Richardson *et al*., 2013.

Oikopleura (Vexillaria) labradoriensis Lohmann, 1892

Medium-sized species; trunk generally larger and more elongate than in *O. dioica*; left lobe of stomach roughly five-sided (Fig. 5A); buccal glands rather large and oval in shape; single ovary and paired testes; rectum not extending far in front of stomach. Tail musculature broad and strong (Fig. 5B); a long series of sub-chordal cells in distal third of tail (a double line according to Bückmann & Kapp, 1975).

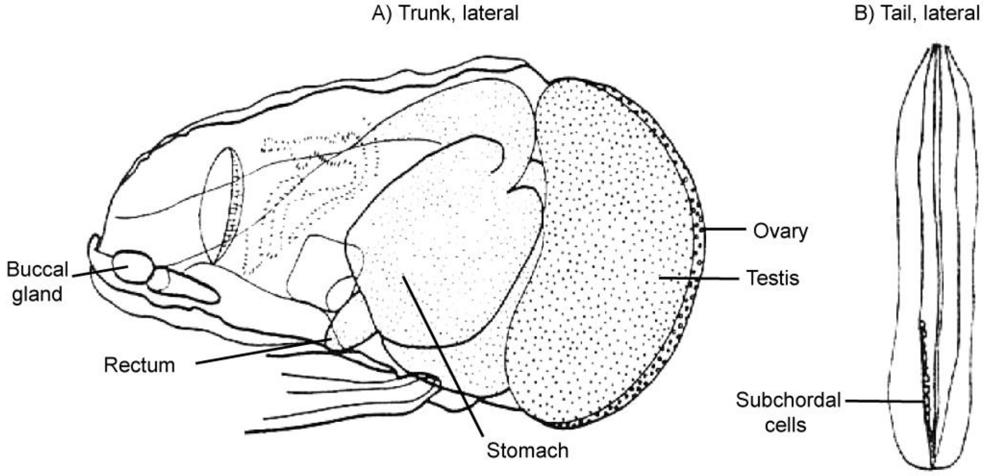

Fig. 5. *Oikopleura* (*Vexillaria*) *labradoriensis* (after Bückmann & Kapp, 1975).

Recorded: PMF and L4 not recorded. North Sea. Colder water species.

Size: Trunk length 1.4-2.4 mm (up to 2.6 mm); tail length?

Further information: Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Flood & Deibel, 1998; Marine Species Identification Portal, 2011 (all as *O. labradoriensis*).

Oikopleura (Coecaria) fusiformis Fol, 1872
Medium sized species; trunk elongated and narrow (Fig. 6A), dorsally slightly concave; a large diverticulum (caecum) extending from the left stomach lobe obliquely backwards, giving the trunk a characteristic appearance. Rectum elongated, extending far in front of stomach; mouth turned upwards so that it opens dorsally, with pronounced lower lip; no buccal glands; ovary rather flat and the paired testes are long, covering most of the stomach. Tail with narrow muscle bands, without subchordal cells (Fig. 6B).

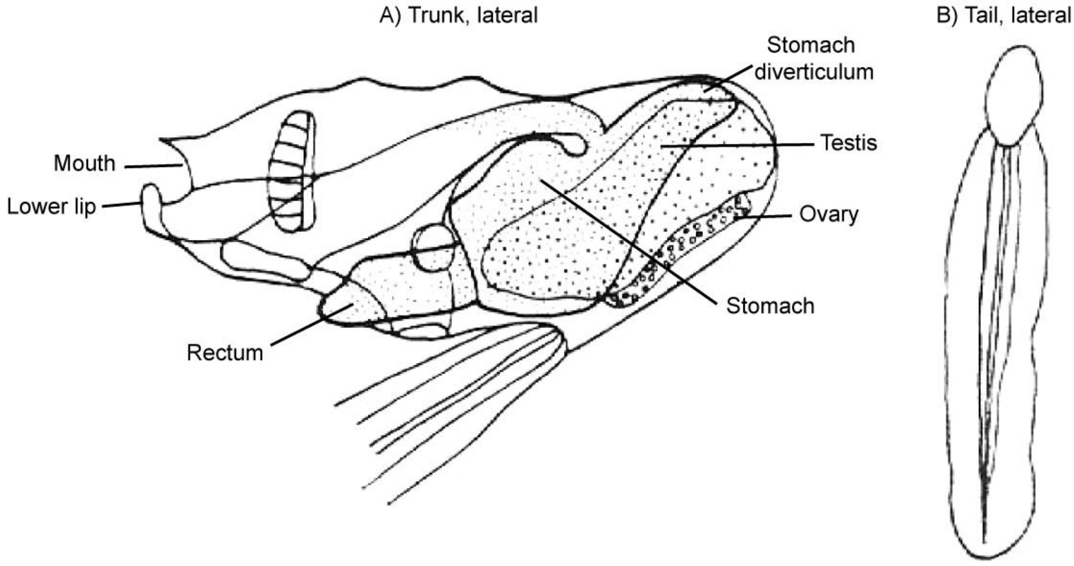

Fig. 6. *Oikopleura* (*Coecaria*) *fusiformis* (after Bückmann & Kapp, 1975).

Recorded: PMF. L4 not recorded. North Sea. Associated with influxes of oceanic, warmer water.
Size: Trunk length 1.0-1.5 mm; tail, ~5 mm in length.
Further information: Thompson, 1948; Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Marine Species Identification Portal, 2011 (all as *O. fusiformis*); Bone, 1998; Esnal, 1999.

Family **Fritillariidae:**

Genus *Fritillaria*:

Fritillaria borealis Lohmann, 1896

Trunk long and generally narrow (Fig. 7A, C); spiracles small and round; endostyle short, wider anteriorly; pharyngeal cells behind endostyle inconspicuous; oblique digestive tract axis; mouth with two lateral plates, upper lip long, truncate; gonads symmetrically arranged on median axis of trunk, single testis elongate and simple, behind spherical ovary. Tail attached to trunk mid-ventrally, short, with broad fin (Fig. 7B, D), musculature from moderately broad to narrow, no amphichordal cells.

There were originally seven forms (or subspecies) described, but these have now been reduced to three (Tokioka, 1960; Fenaux, 1998c), two of which are found in European waters. These are a cosmopolitan cold water form *F. borealis typica* Lohmann, 1900, in which the tip of the tail musculature is pointed and the tail fin is almost square-ended (Fig. 7A) and *F. borealis intermedia* Lohmann, 1905, a warmer water form in which the tip of the tail musculature is square-ended and the tail fin is distinctly bifurcate (Fig. 7B). The North Sea is the type locality of *F. borealis intermedia*.

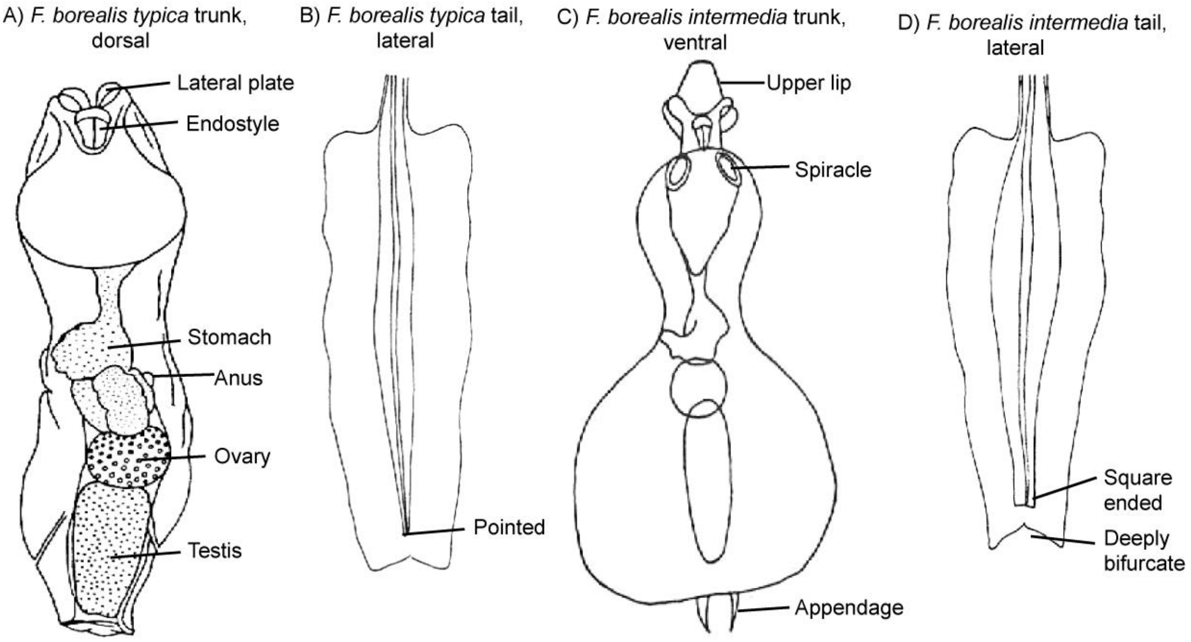

Fig. 7. *Fritillaria borealis*, A, B *F. borealis typica*; C, D *F. borealis intermedia* (after Bückmann & Kapp, 1975).

Recorded: PMF. L4. North Sea. Brackish and coastal waters as well as open sea.

Size: Trunk length 1.3 mm in *F. borealis typica* and maximum of 0.9 mm in *F. borealis intermedia*; tail length ~1.8 mm.

Further information: Thompson, 1948; Tokioka, 1960; Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Fenaux, 1998c; Esnal, 1999; Marine Species Identification Portal, 2011.

Fritillaria pellucida (Busch, 1851)

Trunk rectangular and flattened (Fig. 8A-C), with two, generally large, conical appendages at genital end; mouth with protruding upper lip; pharyngeal cells behind endostyle forming a packet that touches the left spiracle; transverse digestive tract axis; gonads asymmetrically arranged, testis behind intestine, on right side of the trunk, cylindrical and traverse in young specimens, becoming more hammer-shaped later; ovary spherical, behind stomach, on left side of body. Tail with distal V-shaped notch (Fig. 8D), musculature broad, two conspicuous, spherical amphichordal cells on each side (sometimes only three present).

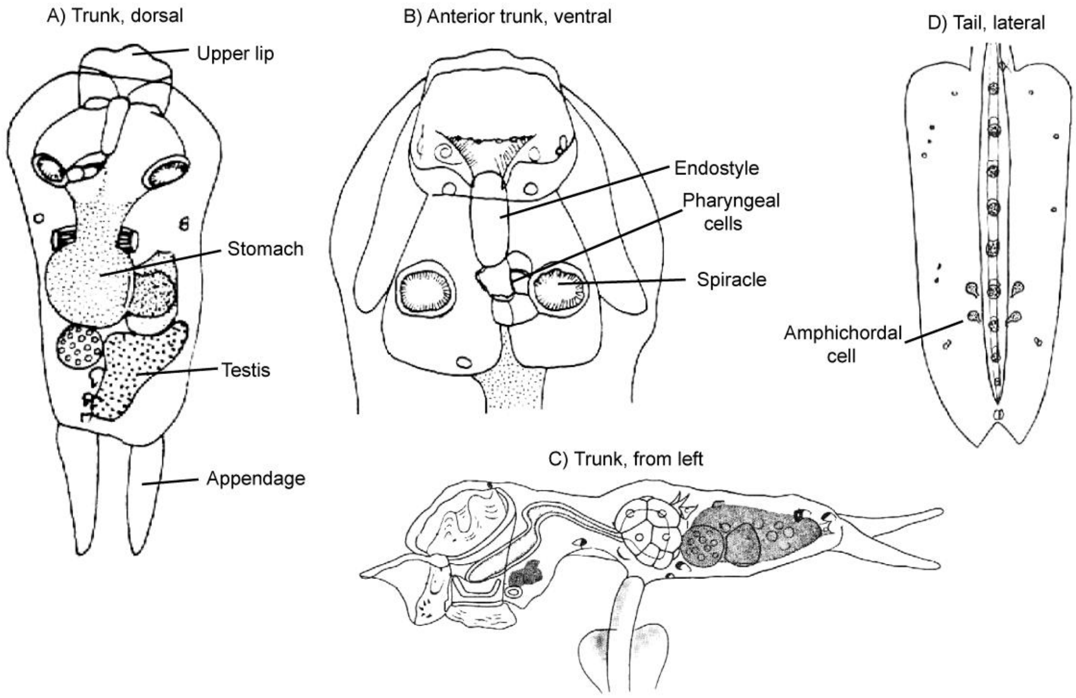

Fig. 8. *Fritillaria pellucida* (A-D after Bückmann & Kapp, 1975; C from Thompson, 1948).

Recorded: PMF and L4 not recorded. Associated with influxes of oceanic, warmer waters.
Size: Trunk up to ~2.2 mm in length; tail up to ~3 mm in length.
Further information: Thompson, 1948; Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Fenaux, 1998b; Esnal, 1999; Richardson *et al.*, 2013.

Fritillaria tenella Lohmann, 1896

Trunk rectangular, rounded anteriorly (Fig. 9A-C), with two conical appendices posteriorly; ventral part of mouth divided by a median incision into two small lips; endostyle strongly curved; pharyngeal cells behind endostyle forming a packet. Small, rounded spiracles; digestive tract compact, arranged in a straight line in an oblique axis; stomach spherical; ovary spherical or flattened; testis cylindrical, behind ovary. Tail relatively broad (Fig. 9E), with a narrow, delicate muscular band, bifurcated distally; two jug-shaped amphichordal cells around one third from the end of the tail

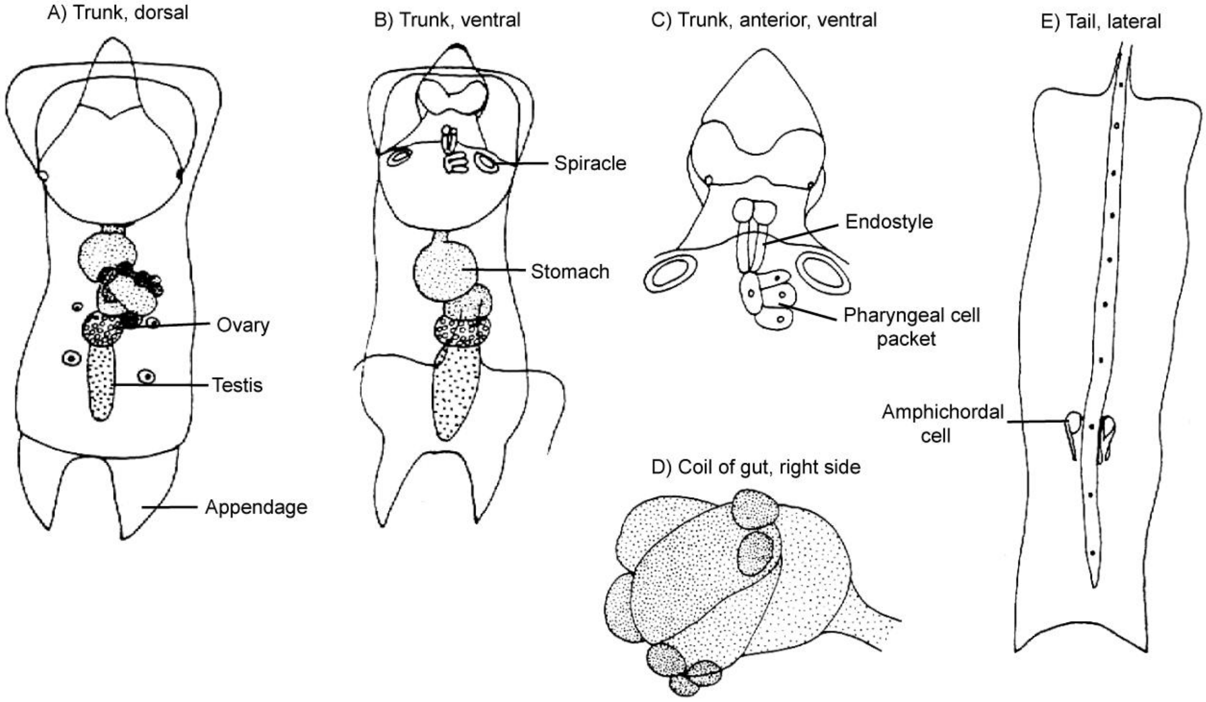

Fig. 9. *Fritillaria tenella* (after Bückmann & Kapp, 1975).

Recorded: PMF and L4 not recorded. North Sea. Associated with influxes of oceanic, warmer water.

Size: Trunk length 0.9-1.5 mm; tail length ~1.9 mm.

Further information: Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Bone, 1998; Esnal, 1999; Marine Species Identification Portal, 2011.

Fritillaria gracilis Lohmann, 1896
Small species; trunk flattened (Fig. 10A-C), almost ovoid; mouth simple, without lips, with two short lateral lobes; no pharyngeal cells; endostyle short and moderately curved in lateral view; spiracles circular; axis of alimentary tract almost transverse; testis sausage-shaped, curved along the rear and side wall of the posterior part of the body; spherical ovary masses at each end of the testis. In old specimens, the testis may be empty and invisible, while developing eggs occupy the whole of the lateral parts of the trunk. Tail tapering abruptly along the distal third, rounded distally (Fig. 10D), narrow, delicate muscle band, no amphichordal cells in the fin.

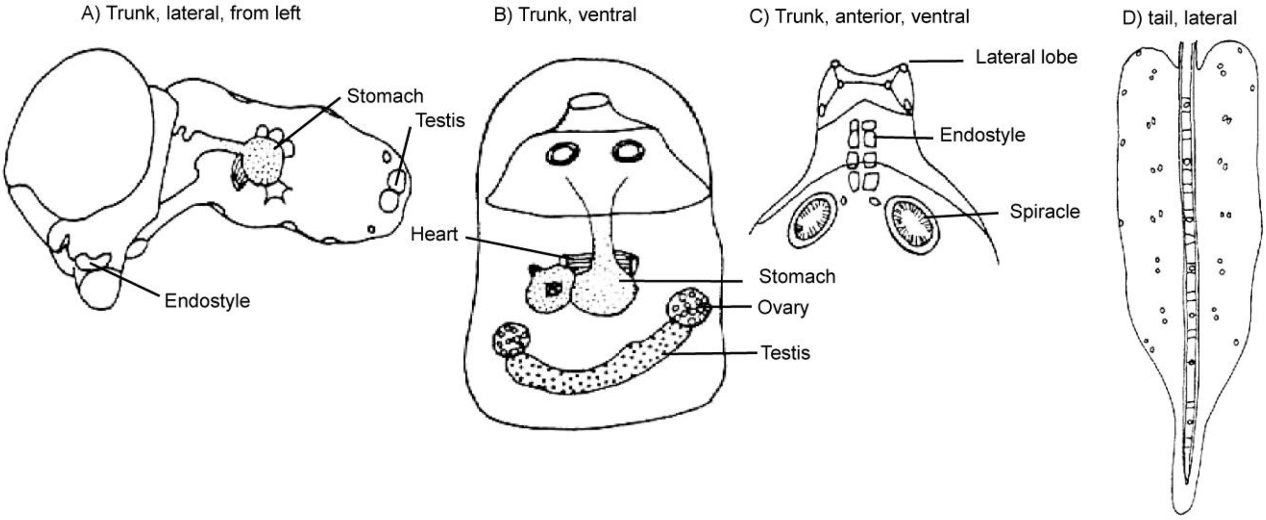

Fig. 10. *Fritillaria gracilis* (from Bückmann & Kapp, 1975).

Recorded: PMF and L4 not recorded. North Sea. Associated with influxes of oceanic, warmer water.
Size: Trunk length ~0.5-0.8 mm; tail length ~2.4 mm.
Further information: Fenaux, 1967; Bückmann, 1969; Bückmann & Kapp, 1975; Fraser, 1981; Bone, 1998; Esnal, 1999; Marine Species Identification Portal, 2011.

PHYLUM CHORDATA: Subphylum Tunicata:

Class Thaliacea:

There are two main orders of these pelagic tunicates, **Doliolida** and **Salpida**. **Pyrosomatida**, the third order, has a more oceanic distribution in the northern European area and are rare, so not included here. Thaliacea are more southern, warm water species, those found on the northern European shelf transported there in westerly oceanic currents, so are good indicators of incursions of water. They do not appear to survive the lower winter temperatures in the north, but would probably die anyway due to lack of food. Asexual reproduction can be so rapid that massive blooms can occur. Salpida in particular can clear the waters of phytoplankton and other zooplankton, so that virtually a monoculture of salps results. The dense faecal pellets of Thaliacea play an important role in the transfer of nutrition to the deeper sea and benthic layer.

PHYLUM CHORDATA: Subphylum Tunicata: Class Thaliacea:

Order Doliolida:

Morphology:

Doliolids have a complex life history, more complex than in Salpida, involving alternation of generations between oozooid and blastozooid stages, the latter arising by budding from the stolon of the asexual oozooid. Blastozooids are represented by three successive types of individuals, gonozooids, phorozooids and gastrozooids (or trophozooids), of which only the gonozooid has gonads, both ovary and testis, as they are hermaphrodite, but these are not functional at the same time.

Generally the most abundant stages in samples are the gonozooids and phorozooids (Figs. 11, 12). These are barrel-shaped and the external, thin test has eight complete and separate muscle-bands that circle the body. These are numbered consecutively (M1 etc.) from left to right in the orientation show in Figure 11. The first and last bands are narrower than the others and form sphincters to the anterior oral (inhalent) and posterior atrial (exhalent) apertures, the route of the feeding current. The sphincters have a series of rounded flaps, varying in number between species, which act as valves (Fig. 13B). Doliolida bodies are transparent so the internal organs are clearly visible. The body cavity is divided into anterior oral (or pharyngeal) and posterior atrial (or cloacal) cavities by a thin oblique partition that forms the gills (Fig. 11) and is perforated by rows of ciliated gill slits. The cilia drive the feeding current and also propels the animal along. More rapid movements are produced by contraction of the muscle bands.

In individual species the positioning of internal organs is the same in both the gonozooid and phorozooid stages. Identification is based on the position and extent of the internal organs relative to the muscle bands. Between M3 and M4 in all species is a small circular nervous ganglion. The gills extend anteriorly to different extents in different species, a useful feature in identification. The alimentary canal is situated around M5-M6 and comprises a short oesophagus, a stomach and an intestine that may be straight or coiled. A long thin endostyle that secretes mucus, used in trapping food, is situated ventrally between M2-M5. In the gonozooid stage the ovary lies posterior to the stomach and the testis originates near the anterior edge of the ovary and extends forwards in different ways, depending on the species. The phorozooid stage is easily recognised, as they lack gonads (Figs, 12F, 13B, C) and have a small ventral peduncle, although this may be missing, as in late-stage specimens it is sometimes sloughed off or reabsorbed.

Reproduction and development:

The ovaries of the sexual gonozooids mature before the testes. Eggs are laid, but only up to three, so this stage cannot produce a large population increase. The eggs are laid into the atrial cavity, fertilized internally by sperm drawn in, released by other gonozooids. The eggs are then expelled through the exhalent aperture. The oviduct then disappears and the testis matures to release sperm to fertilize the eggs of other gonozooids. Eggs develop into larvae enclosed in a membranous capsule (Fig. 12A). The larvae are typically tadpole-like, resembling those of Ascidiacea and have an elongated tail supported by a notochord, although at least the larvae of *Dolioletta gegenbauri* lack a tail, so cannot swim (Braconnot, 1970). Inside the capsule the barrel-shaped asexual oozooid stage develops, breaks out, then begins to filter feed and grow.

Oozooids, also called the nurse stage (Fig. 12B-E), are generally rare in the samples. They are distinguished by nine rather than eight muscle bands, a flat gill with only a few slits, no gonads, but have a stolon. Initially an anterodorsal process called the caudophore extends. The stolon then lengthens and strobilizes to produce a series of buds that in an amazing process migrate across the surface of the nurse to the base of the caudophore and attach to the dorsal surface in three rows. With increasing age the gills, gut and endostyle of the oozooid gradually break down until they can no longer feed, but the brain heart and stolon remain. The muscle bands gradually widen until they are almost continuous, although in some species they remain thin. The oozooids become very flabby and this stage is known as the old nurse.

The buds in the lateral rows on the caudophore of the oozooid develop into gastrozooids (Fig. 12D) and remain attached to the caudophore on short stalks. Gastrozooids have weak musculature, but an enlarged gill apparatus, extending the length of the body, as their role is feeding. They have no atrial cavity, the gut is looped on itself and the nerve ganglion lies dorsally above the gills. Because of the different types of individuals present, with different functions, the organism can now be considered a colony.

The median row of buds on the caudophore develop as phorozooids. When they are released they can feed and the posteroventral stalk by which they were attached remains as a peduncle (Fig. 12F). Buds develop on the peduncle that grow and are released as the free-living, sexual, hermaphrodite gonozooid stage (Fig. 12G). As gonozooids result from budding, they occur in much higher numbers than the other stages.

At certain periods *Doliolum nationalis* has been shown capable of a modification of the life cycle whereby the asexual phorozooid stage produces new phorozooids from the peduncle, which subsequently then produce more new phorozooid individuals, so blooms can be rapidly formed.

Genus *Dolioletta:*

Dolioletta gegenbauri (Uljanin, 1884).

This and the following species, *Dolioletta tritonis,* are very similar, and *D. tritonis* has in the past been considered a variety of *D. gegenbauri* (Fraser 1947, 1981). However Godeaux (1998) and WoRMS list them as separate species, so this separation has been followed here.

In the gonozooid stage (Fig. 11) the test is thin and delicate and the intestine is closely coiled with a median anus. The testis is very characteristic, usually sloping obliquely forwards and upwards to around M2, but its forward extension is variable and it may only reach M5 or extend to M1. As it extends forwards it bears to the left between M3 and the body wall and, if it extends far enough, also outside of M2. The ovary is ventrolateral, close to M7. Gills are attached anterodorsally just behind M3 and extend rearwards almost to M6 before turning forwards to their ventral attachment between M5 and M6, rather than between M4 and M5 as in *D. tritonis* (Fig. 12). The nerve ganglion is located just behind M3 and the long endostyle extends from behind M2 almost to M5. The oral aperture has 12 lobed flaps and the atrial aperture eight.

In the phorozooid stage, apart from the absence of gonads, the arrangement of the remaining organs are similar to the gonozooid. A ventral peduncle, from which the gonozooids are budded is present, but not always obvious.

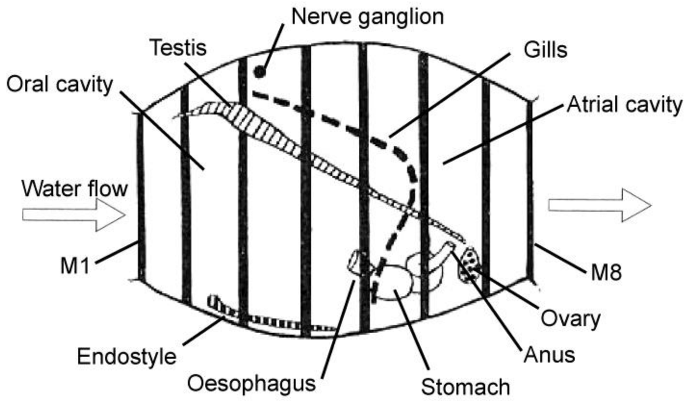

Fig. 11. *Dolioletta gegenbauri*, diagrammatic representation of the gonozooid stage (from Fraser, 1947, as *Doliolum* (*Dolioletta*) *gegenbauri*).

Recorded: PMF (as *Doliolum gegenbauri*). English Channel. Northern North Sea. South and west Ireland.

Size: Gonozooid up to ~12 mm.

Further information: Fraser, 1947, 1981 as *Doliolum* (*Dolioletta*) *gegenbauri*; Thompson, 1948; Esnal & Daponte, 1998a; Godeaux, 1998; Godeaux *et al*., 1998; Marine Species Identification Portal, 2011.

Dolioletta tritonis (Herdman, 1888).

The gonozooid, phorozooid and oozooid stages are similar to *D. gegenbauri*, the main difference being that in the phorozooid and gonozooid stages (Fig. 12F, G) the gills are attached ventrally further forwards, between M4 and M5, rather than between M5 and M6.

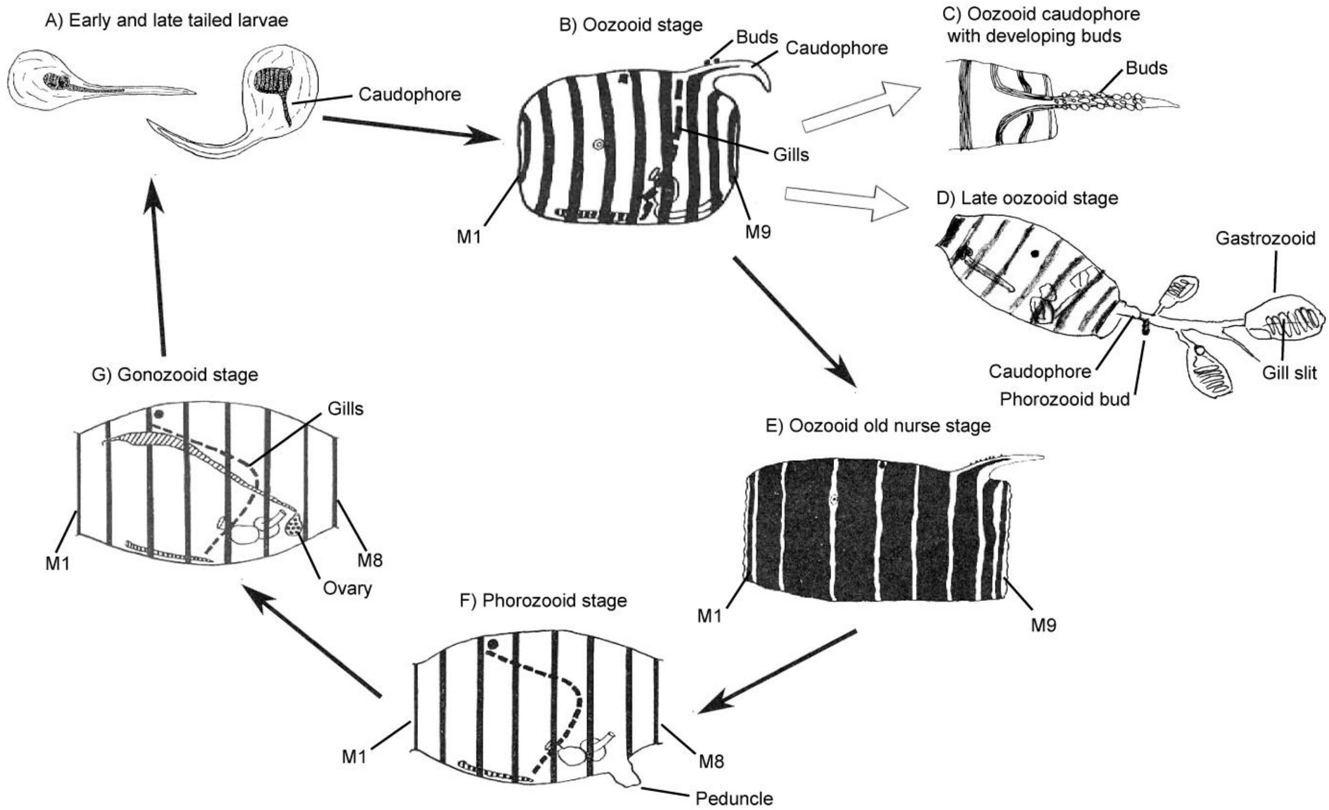

Fig. 12. Diagrammatic representation of *Dolioletta tritonis* life cycle (A-C, E-G from Fraser, 1947 as *Doliolum* (*Dolioletta*) *gegenbauri* var *tritonis*; D drawn from photograph of *Doliolina müller*i in Godeaux *et al*., 1998).

Recorded: PMF and L4, not recorded. Northern North Sea. South and west Ireland.
Size: Gonozooid up to ~17 mm.
Further information: Fraser, 1947, 1981 as *Doliolum* (*Dolioletta*) *gegenbauri* var *tritonis*; Thompson, 1948; Esnal & Daponte, 1998a; Godeaux *et al*., 1998; Godeaux, 1998.

PHYLUM CHORDATA: Subphylum Tunicata: Class Thaliacea: Order Doliolida:

Genus *Doliolum:*

Doliolum nationalis Borgert, 1894

In the small gonozooid stage (Fig. 13A) the intestine differs from that of *Dolioletta* as it forms an open arch, with the anus opening close to M6. Gills are attached anteriorly and dorsally just behind M2 and extend rearwards to between M5 and M6 before turning forwards to attach ventrally just in front of M5. The dorsal nerve ganglion is just in front of M4 and the endostyle starts close behind M2 and extends posteriorly to around M4. The testis extends horizontally on the left side and is of variable length.

In the oozooid, old nurse stage, M2-M8 are fused in a continuous sheet.

In the phorozooid stage (Fig. 13B) the gonads are absent, but the arrangement of the remaining organs are similar to the gonozooid. A ventral peduncle is present, but not always obvious.

A special type of shortened reproductive cycle has been observed in this species, when phorozooids asexually bud other phorozooids from their peduncle in large numbers, rather than sexual gonozooids. These budded phorozooids then subsequently bud more new phorozooid individuals resulting in extremely rapid bloom formation.

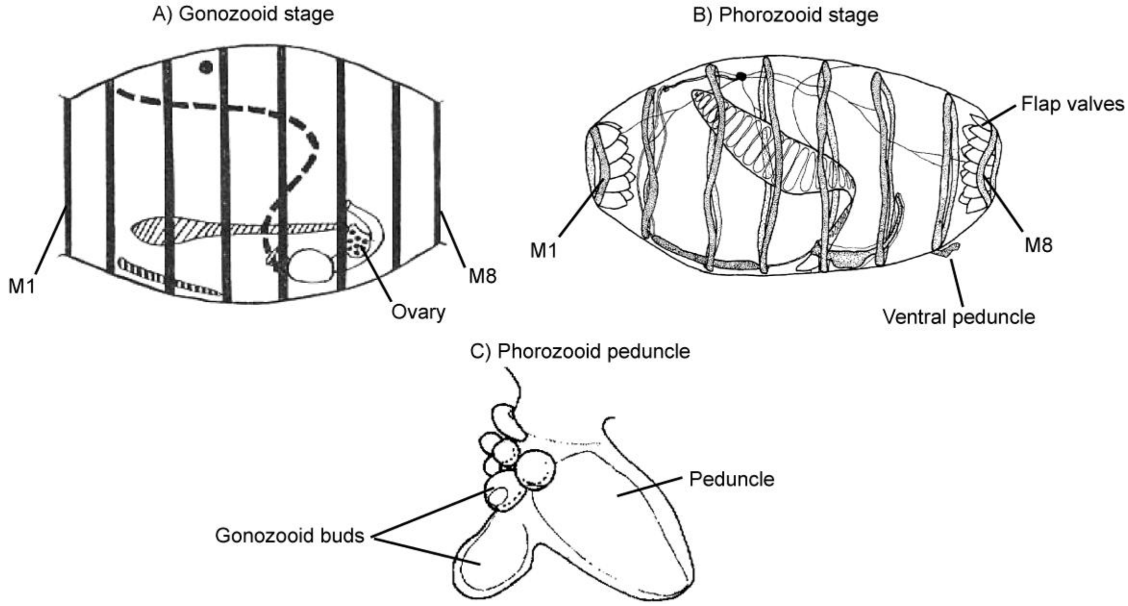

Fig. 13. Diagrammatic representation of *Doliolum nationalis* (A from Fraser, 1947 as *Doliolum* (*Doliolum*) *nationalis*; B after Terry, 1960; C from Braconnot & Casanova, 1967).

Recorded: PMF. L4. English Channel. Southern North Sea. Western UK and Ireland.

Size: Gonozooid ~4 mm

Further information: Fraser, 1947, 1981 as *Doliolum* (*Doliolum*) *nationalis*; Terry, 1960; Braconnot & Casanova, 1967; Esnal & Daponte, 1998a; Godeaux, 1998; Godeaux *et al*., 1998; Marine Species Identification Portal, 2011.

Genus *Doliolina:*

Doliolina mülleri Krohn, 1852

The gonozooid stage has an upright U-shaped intestine (Fig. 14). The gills do not extend as far forward as in other European species, being attached both dorsally and ventrally just posterior to M5 and curving only slightly to M6 or slightly beyond. The testis is not elongate as in the other species, but spherical and lies in a ventral pocket between M5 and M6. The endostyle extends from between M2 and M3 to between M4 and M5. The nerve ganglion is between M3 and M4 as in other species.

In the phorozooid stage the gonads are absent, but the arrangement of the remaining organs are similar to the gonozooid. A ventral peduncle is present, but may not be obvious.

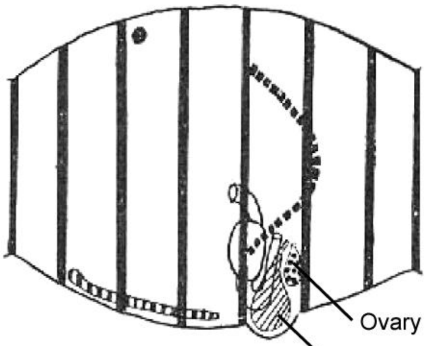

Fig. 14. *Doliolina mülleri* (from Fraser, 1947 as *Doliolum* (*Doliolina*) *mülleri*).

Recorded: A rare species found in offshore waters. It has not been positively recorded at L4, but a specimen in poor condition thought to be this species was sampled. West of Ireland.

Size: Gonozooid ~4 mm; old nurse ~ 2 mm.

Further information: Fraser, 1947, 1981 (as *Doliolum* (*Doliolina*) *mülleri*; Esnal & Daponte, 1998a; Godeaux, 1998; Godeaux *et al*., 1998; Marine Species Identification Portal, 2011.

Order Salpida:

Morphology:

Salps, are generally larger than doliolids, have more gelatinous material in their bodies, and so are usually more rigid. They are also transparent and generally barrel-shaped, but can be flattened and have terminal processes of different shapes. Similar to doliolids, they have a life cycle alternating between a sexual blastozooid generation (Fig. 15A) and an asexual oozooid generation (Fig. 15B), but the cycle is much less complex. Apart from the presence or absence of gonads, the two reproductive stages look very different, so different that earlier authors assigned them to different species.

The blastozooids are produced in chains and remain attached until wave action breaks them up, so are called aggregate. The oozooids exist singly and are called solitary. Salps also have a series of muscle bands. The anterior oral (inhalent) and posterior atrial (exhalent) apertures are controlled by small, inconspicuous muscle bands, while locomotion, feeding and respiratory currents are driven by contraction of large locomotory, body muscle bands, rather than ciliary action as in doliolids. These conspicuous bands are numbered consecutively (M1 etc.) as shown in Figure 15, the number and arrangement characteristic from the very early stages (Fig. 15C). **However, the numbering of the muscle bands is somewhat confusing, as unlike in doliolids, only the large, locomotory body bands are numbered, ignoring other, sometimes conspicuous bands.** Unlike doliolids, some of the bands can merge together at certain points and may not completely surround the body, features used in specific identification. The blastozooids have fewer muscle bands than the oozooids and the musculature is weaker.

Separating the oral and atrial cavities is a gill bar lying between two large gill slits that are not bordered with cilia as in doliolids. The gill bar is attached anterodorsally, extending backwards and is attached posteroventrally. It is covered ventrally with cilia that beat towards the oesophageal opening at its base. The endostyle is ventral and extends almost the whole length of the body. It produces a mucous filter in which food is trapped. The compact visceral mass, sometimes referred to as the ‘nucleus’, is usually circular and obvious, but elongated in some species, often tinged greenish brown or red. In the blastozooid the single ovary is on the upper right of the body while the testis is beside the visceral mass.

In oceanic samples, salps are sometimes found with the internal organs eaten out and the test occupied for protection and egg-laying by the amphipod *Phronima sedentaria* (Forskål, 1775). Often found in the same sample as salps are species of the copepod *Sapphirina* spp. that demonstrate remarkable iridescence and are symbionts/ectoparasites (Heron, 1973; Harbison, 1998; Lopes *et al*., 2007).

Reproduction and development:

The solitary oozooid stage bud off large numbers of blastozooids in a chain from the stolon. The young blastozooids, after fertilisation by sperm from older blastozooids, produce embryos (Fig. 15C) that remain attached to the walls of the atrial cavity (Fig. 15A) until large enough to be released as oozooids. While attached they are nourished through a type of placenta and when released through the atrial aperture have initial food reserves in an eleoblast. Because the oozooids are produced in low numbers, the blastozooids, which also have rapid growth rates, generally dominate the population. Unlike doliolids, the older oozooids do not develop into “nurses”, but retain their structure and function until death.

PHYLUM CHORDATA: Subphylum Tunicata: Class Thaliacea: Order Salpida:

Genus *Salpa:*

Salpa fusiformis Cuvier, 1804

This is by far the commonest salp in European waters. The aggregate blastozooid stage (Fig. 15A) is quite rigid with a smooth test that is from moderately thick to thin and has obvious large conical processes at both ends. There are six body muscle bands. M1-4 and M5-6 are fused, or come very close together mid-dorsally while M4-5 touch laterally. None of the muscle bands meet ventrally. The compact, circular visceral mass is pale green when the salp is freshly caught.

The solitary, cylindrical oozooid stage is also quite rigid and has no distinct projections. The test is smooth, moderately thick to thin. There are nine body muscle bands. M1-3 and also M8-9 are strongly fused mid-dorsally, while the intermediate bands are separate. None of the muscle bands meet ventrally. The stolon is obvious and extends forwards to between M3-4 and then turns posteriorly. The visceral mass is also green, often streaked with red.

S. fusiformis can occur in massive numbers, clearing the immediate sea of all other plankton. Warm water currents, depending on annual strength, can bring large numbers of these into the northern North Sea and English Channel, but they do not survive winter low temperatures.

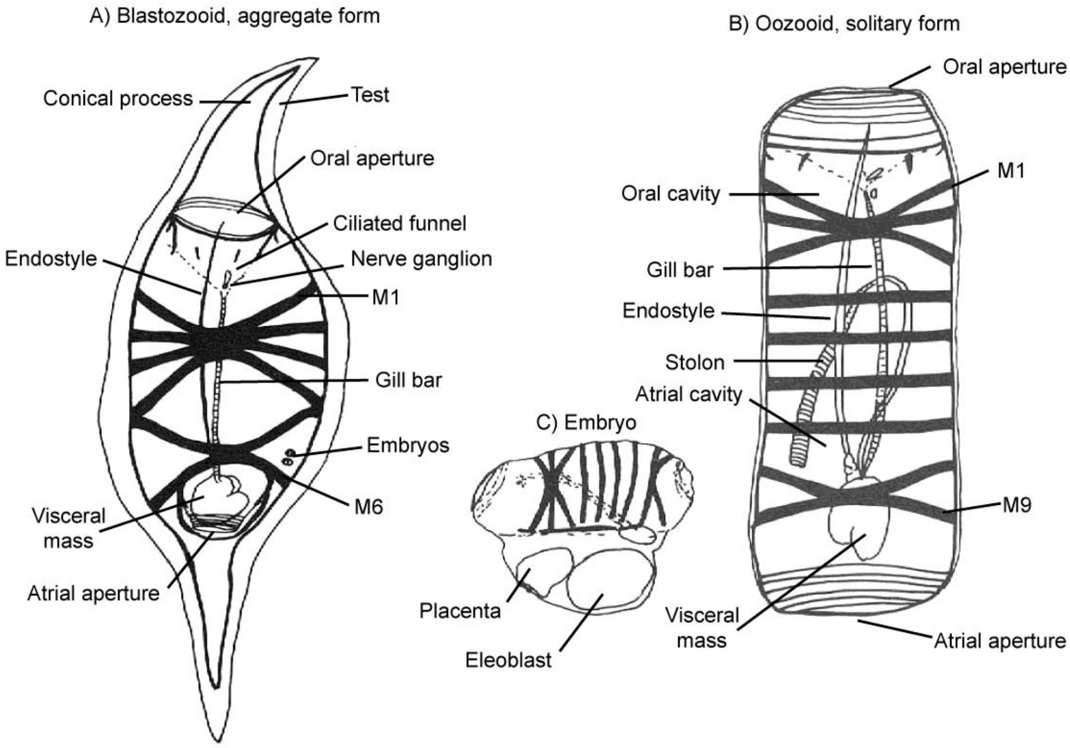

Fig. 15. *Salpa fusiformis* dorsal view (from Fraser, 1981).

Recorded: PMF. L4. Northern North Sea. Norwegian Sea. Western European shelf. English Channel.

Size: Aggregate form 7-52 mm, excluding terminal processes; solitary form 22-52 mm.

Further information: Fraser, 1947, 1981; Thompson, 1948; Godeaux, 1998; Godeaux *et al*., 1998; Esnal & Daponte, 1999b; Marine Species Identification Portal, 2011.

Genus *Thalia:*

Thalia democratica (Forskål, 1775)

The aggregate blastozooid stage (Fig. 16A) is quite rigid and somewhat pointed posteriorly while the anterior end is rounded. Body muscle bands M1-3 and also M4-5 fuse mid-dorsally, but the two groups remain quite separate laterally, compared to *Salpa fusiformis* where M4 and M5 touch laterally. M5 does not go more than halfway around the body. None of the muscle bands meet ventrally. The visceral mass is not as compact as in *S. fusiformis*. The atrial aperture is not quite central and there is a small posterolateral projection on one side only.

The solitary oozooid stage (Fig. 16B) is also quite rigid and has numerous rather asymmetrical sharp projections on the posterior end. The anterior, intermediate muscle does not meet dorsally. Body muscle bands M1-3 converge mid-dorsally, as do M4-5 (do not quite touch in some specimens). M1-4 are continuous around the body, while M5 has a narrow gap ventrally. The visceral mass lies posteriorly, inside a median projection. The short stolon curves around the visceral mass.

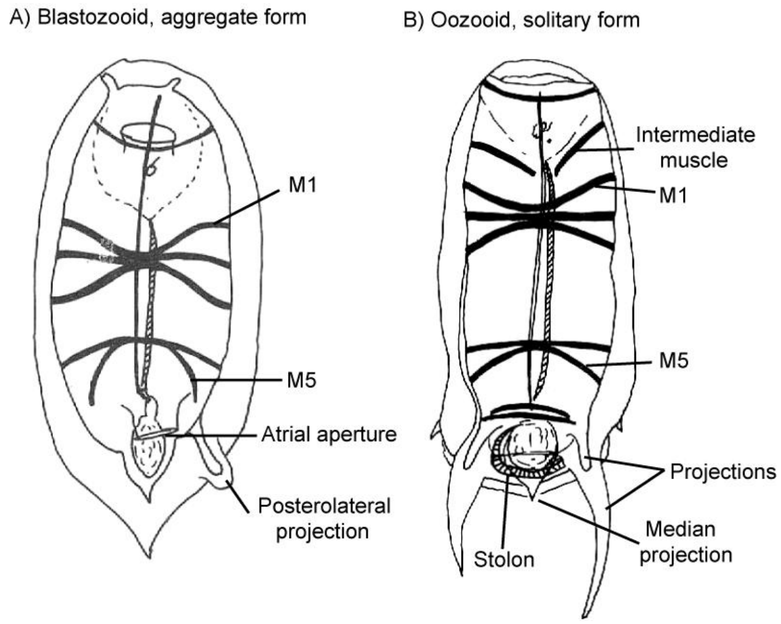

Fig. 16. *Thalia democratica*, dorsal view (from Fraser, 1981).

Recorded: PMF (as *Salpa democratica*). L4, not recorded. Western English Channel. South-western Ireland.

Size: Aggregate form 2-18 mm; solitary form 2-12 mm.

Further information: Fraser, 1947, 1981; Thompson, 1948; Esnal & Daponte, 1999b; Marine Species Identification Portal, 2011.

Genus *Soestia:*

Soestia zonaria (Pallas, 1774)

In the aggregate blastozooid stage (Fig. 17A) the very rigid test is tough and angular with deep grooves dorsally and ventrally. There is a posterior projection, located asymmetrically. The five body muscle bands are very obvious and wide and all do not meet ventrally. Only M1 does not meet dorsally. M5 is divided into two branches on the right side.

In the solitary oozooid stage the test is even more rigid and angular (Fig. 17B, C). The intermediate muscle and the five body muscles are extremely wide, almost touching laterally and do not meet either dorsally or ventrally. A very obvious posteromedian projection is present, with smaller lateral projections. The mature stolon encircles the visceral mass.

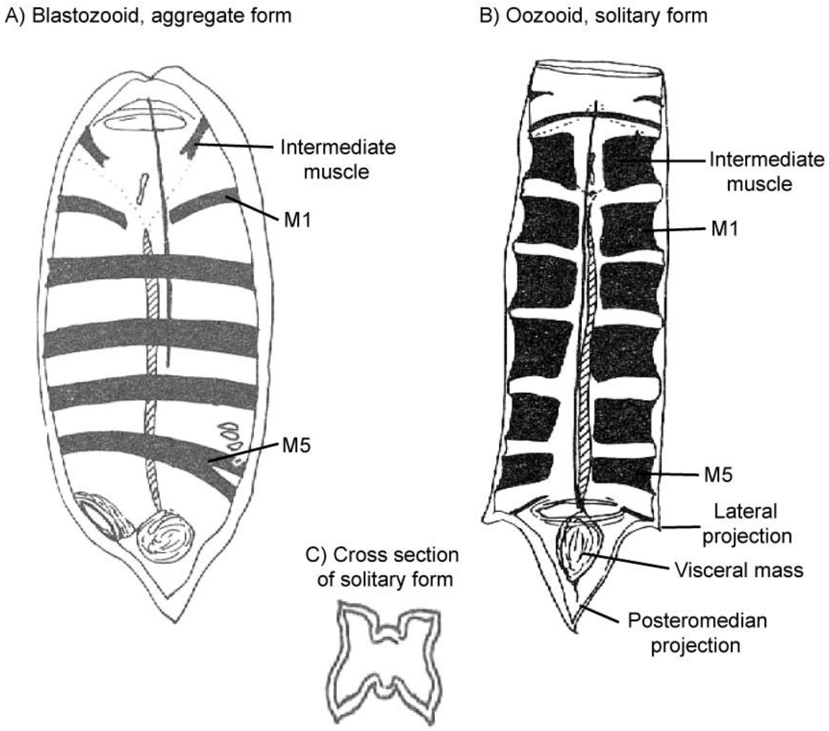

Fig. 17. *Soestia zonaria*, dorsal view (from Fraser, 1981 as *Iasis zonaria*).

Recorded: PMF (as *Salpa zonaria*). L4 not recorded. Western European shelf.

Size: Aggregate form up to ~65 mm; solitary form up to ~50 mm.

Further information: Fraser, 1947, 1981; Thompson, 1948; Godeaux, 1998; Godeaux *et al*., 1998; Esnal & Daponte, 1999b (all as *Iasis zonaria*); Marine Species Identification Portal, 2011.

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PHYLUM CHORDATA:

Subphylum Cephalochordata: Class Leptocardii: Family Branchiostomidae:

This often abundant group of benthic, exclusively marine or brackish water organisms is commonly referred to as lancelets, due to their physical resemblance to the cutting blade used by surgeons, being rigid, slender and laterally flattened. They are sometimes also referred to as "amphioxus", meaning sharp at both ends, from a now obsolete generic name. Their normal habitat is offshore beds of sand in shallow temperate and tropical regions, the distribution of suitable sites determining where they are found. They burrow into the sand and orientate with their anterior end protruding from the burrow.

Branchiostomidae may be the most basal subphylum of the chordates, possessing all four chordate characteristics: dorsal nerve cord, notochord, postanal tail, and pharyngeal gill slits (Fig. 1). However, they have a very simple circulatory system, no discrete brain or complex sense organs. The notochord extends the length of the body and above it is the nerve cord with a single anterior pigment spot, the frontal eye. Lancets collect food much like tunicates. The mouth is on the underside of the body and they filter-feed, using a tuft of oral cirri and the gill slits, trapping food inside the pharynx in mucus that is produced by an endostyle. The water then passes out through the gill slits to the surrounding atrium and out the atriopore, while the collected food is passed to the gut. The gut runs just below the notochord from the mouth to the anus, near the rear body. Co-ordination and the lateral movements used in swimming and burrowing are facilitated by the stiffness imparted by the notochord and by the segmental arrangement of the V-shaped muscles, but they can only swim, for short periods. The fins are supported by fibrous fin rays to increase their efficiency. Generally only the early stages are found in the plankton.

Reproduction and development

The sexes are usually separate, with both males and females having multiple (25-38), individual paired gonads that lie along each side of the atrial chamber. Gametes are released by internal rupture of the atrial wall and pass out through the atriopore with water that has been drawn in for feeding and respiration, Eggs are fertilised externally. Spawning in the European region is mainly in June and July.

PHYLUM CHORDATA: Subphylum Cephalochordata: Class Leptocardii: Family Branchiostomidae:

Genus *Branchiostoma*:

Branchiostoma lanceolatum (Pallas, 1774)

This is the only species recorded in the northern European area and can attain an adult length of around 60 mm.

The tiny ciliated larva that emerges from the egg elongates rapidly and starts feeding within 48 hours. At this stage the characteristic laterally flattened shape of later stages is already obvious. The larvae are thought to spend the earliest part of their lives in the bottom sediment before entering their pelagic phase. There is a unique asymmetric development, with the mouth forming laterally on the left and the first gill slit on the right (Fig. 1A). Further gill slits are added as the larva grows (Fig. 1B). The striated notochord and V-shaped body muscle blocks (up to 61) become obvious. While the body is slender, the gill region is swollen, although on preservation it usually collapses almost flat and the gut diameter shrinks (Fig. 1B).

After about four weeks a metamorphosis starts in the plankton, prior to settlement. During metamorphosis (usually between 3.5-5 mm) the mouth moves from its lateral to a more ventral position and a new adult mouth surrounded by thick oral cirri develops (Fig. 1C). A row of secondary gill slits develop and fuse with the primary slits.

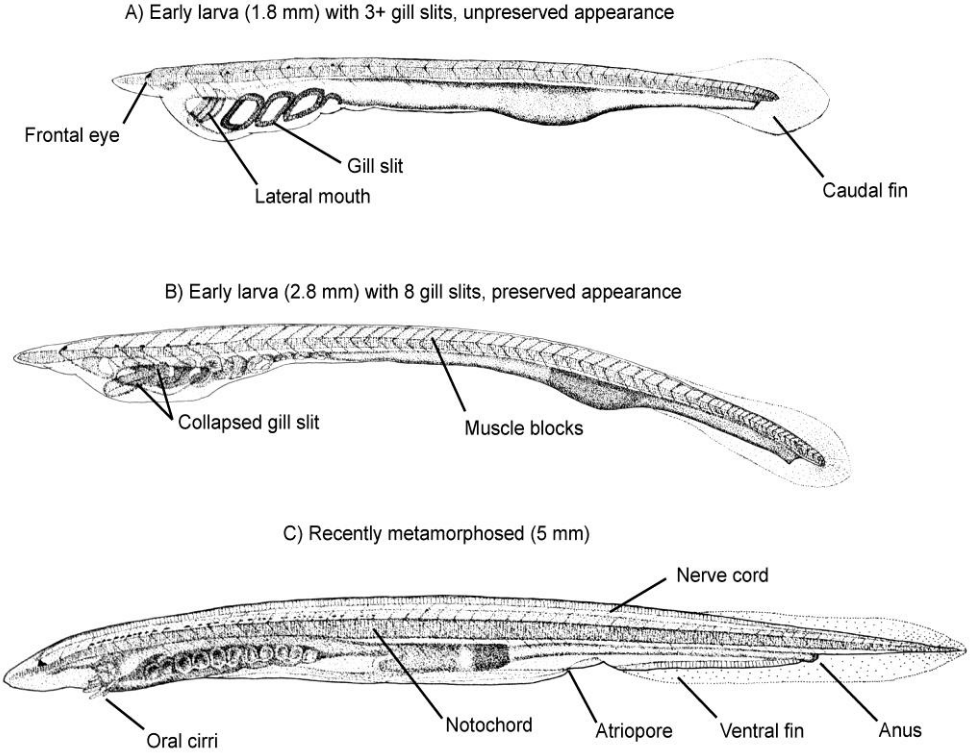

Fig. 1. *Branchiostoma lanceolatum* (from Wickstead, 1967).

Recorded: PMF (as *Amphioxus lanceolatus*). L4. Widespread in European waters.
Size: Larvae ~0.7-5.0 mm, but post metamorphosed individuals 6-8 mm may also be sampled.
Further information: Larink & Westheide, 2011; McCarthy & Young, 2002; Poss & Boschung, 1996; Wickstead, 1967.

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PHYLUM CHORDATA:

Subphylum Vertebrata: Superclass Pisces:
Class Actinopterygii:

The only fish species found in the northern European area that have planktonic eggs and early stages are all in Class Actinopterygii, the ray-finned fish. According to the WoRMS classification there are ~46 orders in this class. As an indication of typical inshore biodiversity ~148 adult species from these classes have been recorded in the PMF. However, the eggs and early stages of less than 30 of these are regularly sampled in the local plankton. The eggs of some species will not be sampled in nets because they are not planktonic, laid attached to various substrates. The commercial importance of fish makes accurate identifications of the early stages important for e.g. survival/recruitment studies, but because of the continuous morphological and pigmentation changes during egg and early development, and variable deterioration due to preservation, identification of a broad range of species is a specialised task requiring years of experience. Comprehensive descriptions of egg and early stages for the European area are given in Russell (1976), Munk & Nielsen (2005) and Ré & Meneses (2008). It is impossible to include descriptions of all the northern European early fish stages here, so only a brief description of the egg and early developmental stages of a few selected species and examples of the variety of postlarvae that may be samples is included.

The egg stage and features used in their identification:

Egg size is a useful feature in identification, as this is relatively species specific, although there may be a size reduction as the spawning season progresses. However, there are species with eggs of very similar size distribution that can only be discriminated at a late stage of development, and some not until the larva has emerged. The pelagic eggs of most species are between 0.7- 1.5 mm in diameter, but the eggs of one of the commonest fish species in the southwest of Britain, the sardine (*Sardina pilchardus* Walbaum, 1792), are ~1.7 mm (Fig. 1A, B). A few other species have even larger eggs, such as the long rough dab *Hippoglossoides platessoides* (Fabricius, 1780) that are up to 2.6 mm. Unpreserved, pelagic eggs are transparent and generally completely spherical, apart from anchovy (*Engraulis encrasicolus* (Linnaeus, 1758)), which are oblong.

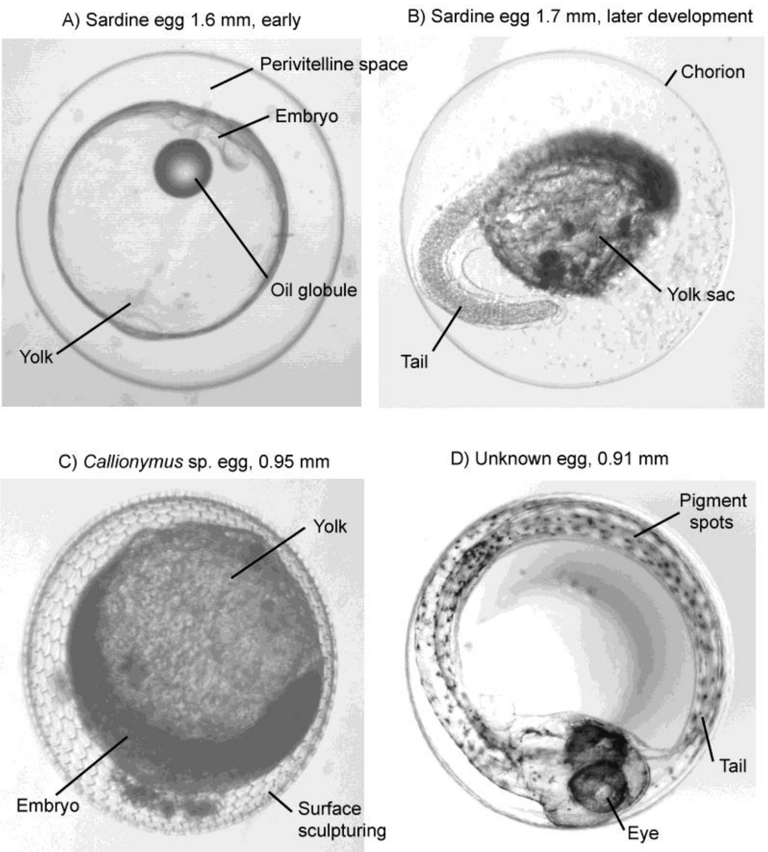

Fig. 1. Examples of some fish eggs.

The outer egg membrane, or chorion is composed of a double layer and is typically smooth, except in species such as the dragonet family (Callionymidae) in which there is fine, honeycomb-like, surface sculpturing (Fig. 1), or in the garfish (*Belone belone* (Linnaeus, 1761) in which the egg is covered in sparse filaments. In fertilized eggs the egg membrane encloses a spherical yolk mass enclosed by a thin protoplasmic membrane that in most species almost fills all the available space, leaving only a narrow outer free area, the perivitelline space. However, a few species such as the sardine (Fig. 1A) have a large perivitelline space and a small yolk mass.
The yolk may be homogeneous, but in some species is segmented by ingrowths from the outer membrane (Fig. 2A). In the eggs of different species there may be a single large (Fig. 1A) or several small or medium sized clear oil globules present, either in the yolk or spread over the surface of the yolk, evenly or in clumps. Multiple globules may coalesce into a single globule during development.
Division of the embryo continues until it is an elongated rod embedded on the surface of the yolk. Eyes, body musculature and variable amounts of pigmentation gradually become visible as the embryo extends around the yolk (Fig. 1D). Pigmentation may also be present over the yolk surface. The caudal region gradually lifts off the surface of the yolk, eye pigmentation may develop and typical fish features become obvious. Time to hatching mainly depends on temperature and initial yolk size.
Few other eggs that might be confused with fish eggs are normally taken in plankton samples. Some euphausiid eggs may be up to ~0.7 mm, but these never have oil globules, typically have a large perivitelline space and might only be misidentified before the embryo has formed.

Larval and postlarval fish identification:
Most early larvae from pelagic eggs are <4 mm in length, main exceptions being Clupeidae such as sardine (Fig. 2) or other elongated larvae (Fig. 5). In the larva the yolk sac is still present in the anterioventral region (Figs. 2A, 3A, 4A) and may extend some distance down the body. In larvae with a short incubation period the eyes may not be pigmented and the mouth and anus still closed. A marginal primordial fin, lacking fin rays typically extends around the body from behind the yolk sac to the top of the head. Presence of oil globules, pigmentation and position of the anus in relation to other features may be used in identification of this stage. In sardine, the anus is located far back in the body (Fig. 2), while in most species it is further forwards (Fig. 3). Gradually the eyes become pigmented, the yolk sac is absorbed and the larva becomes a postlarva. The alimentary tract becomes functional, so feeding can commence.

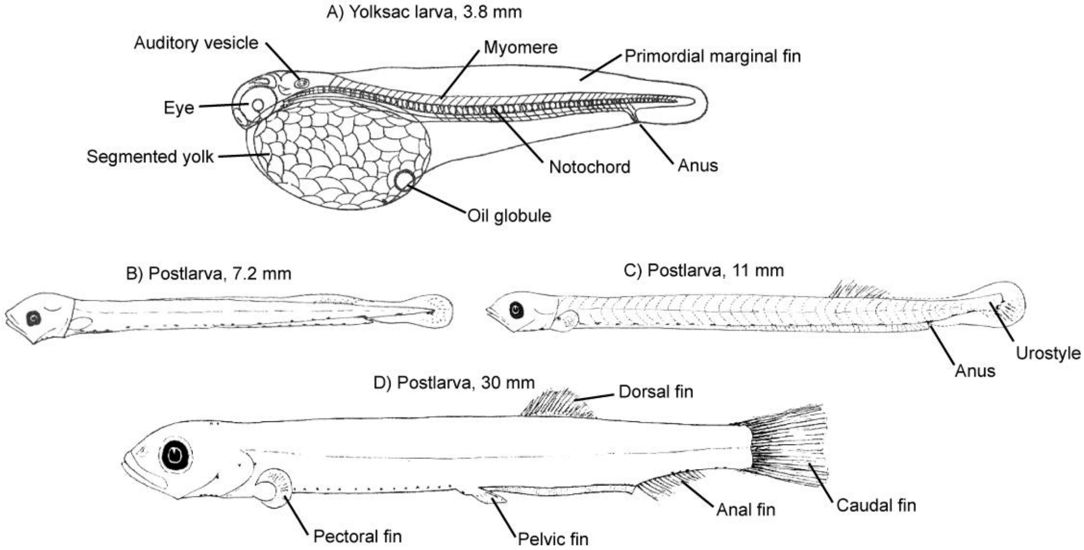

Fig. 2. Sardine, *Sardina pilchardus* larval and postlarval development (A Ehrenbaum, 1909, as *Clupea pilchardus*; B-D from Saville, 1964).

In early postlarvae the marginal primordial fin is still without rays and the end of the notochord (urostyle) is straight. The rudiments of the caudal fin rays start to appear, the urostyle bends upwards and the fin rays of the unpaired dorsal and anal fins form (Figs. 2, 3, 4). In some species such as the fivebeard rockling (Fig. 3) the pelvic fin is very well developed.

A gradually changing pigmentation pattern, typical for the species develops. The pigment cells or chromatophores may of a variety of colours, but only the black melanophores survive formalin preservation. Pigmentation pattern is one of the most important features used in species identification, but number of vertebrae, fin structure and spinal armature in the head region may also be used. In the late post larva, bones of the ribs and vertebrae ossify and the pigmentation becomes less pronounced, or silvering occurs, giving the postlarva the basic adult characteristics.

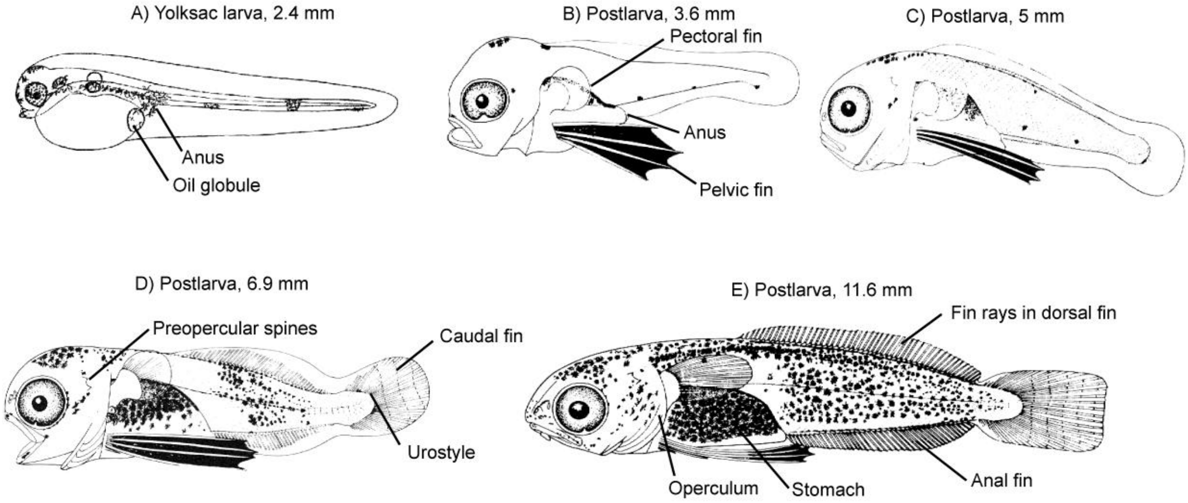

Fig. 3. Fivebeard rockling, *Ciliata mustella* larval and postlarval development (A Ehrenbaum, 1909; B-E from Demir, 1986).

Initially, flatfish larvae resemble other fish larvae, but their body gradually widens and in late stages an eye migrates, so that both are on the upper side (Fig. 4). In Scophthalmidae the right eye migrates and in Pleuronectidae (Fig. 4G-I) the left.

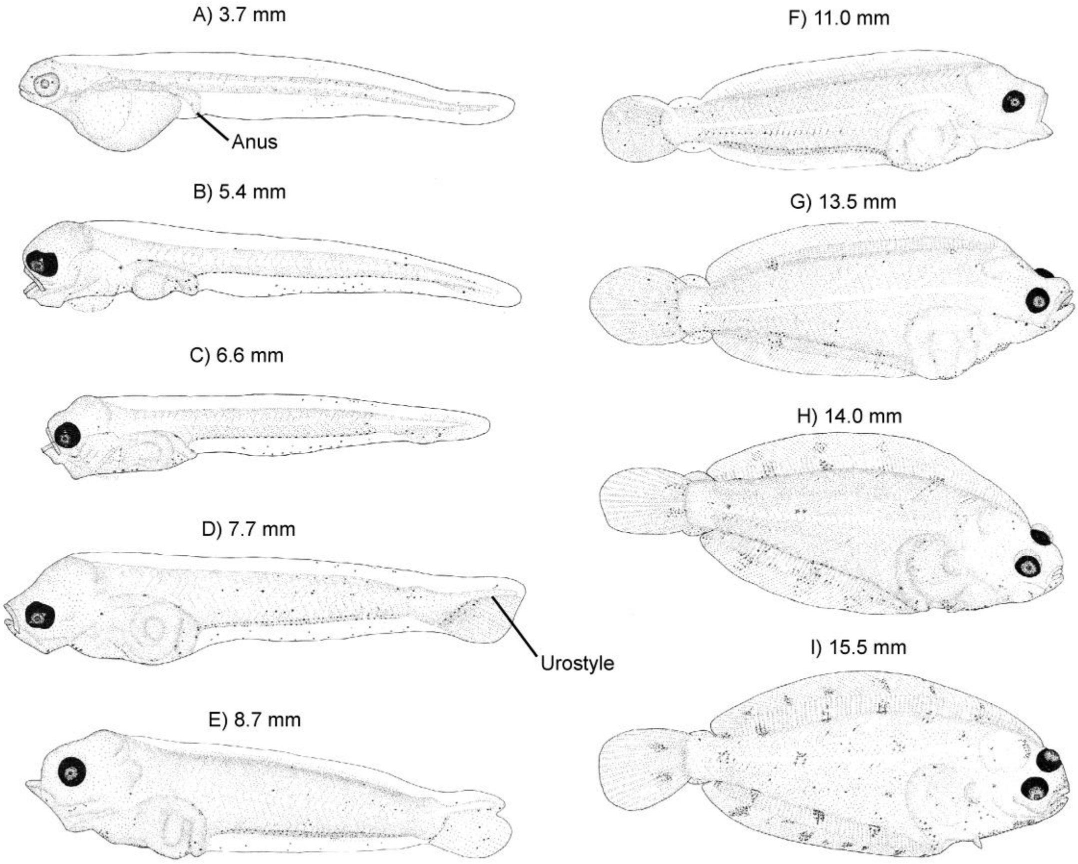

Fig. 4. Common dab *Limanda limanda* (from Nichols, 1971)

Comparison of elongated post larvae:

Several fish species have elongated, eel-like postlarvae. These include some of the commonest inshore families, so it is useful to give some information on their separation, which can be done using position of the anus.

In Clupeidae (Fig. 5A), such as sardine and sprat, the anus is very close to the end of the thin body and the head is small.

In Argentinidae (Fig. 5B) the anus also opens near the end of the body, but the body is much deeper and the pigmentation is quite different.

Ammodytidae, sandeels (Fig. 5C), have a similar body shape to Clupeidae, but the anus opens just beyond the mid-body and the head is larger.

In Stichaeidae, Genus *Chirolophis* (Fig. 5D) the anus opens around a third down the length of the body.

In Pholidae (Fig. 5E) the anus opens in a similar position to Ammodytidae, but the head shape is different, being short and rounded.

In Stichaeidae, Genus *Lumpenus* (Fig. 5F) the anus position lies between that of Pholidae and Genus *Chirolophis* of Stichaeidae.

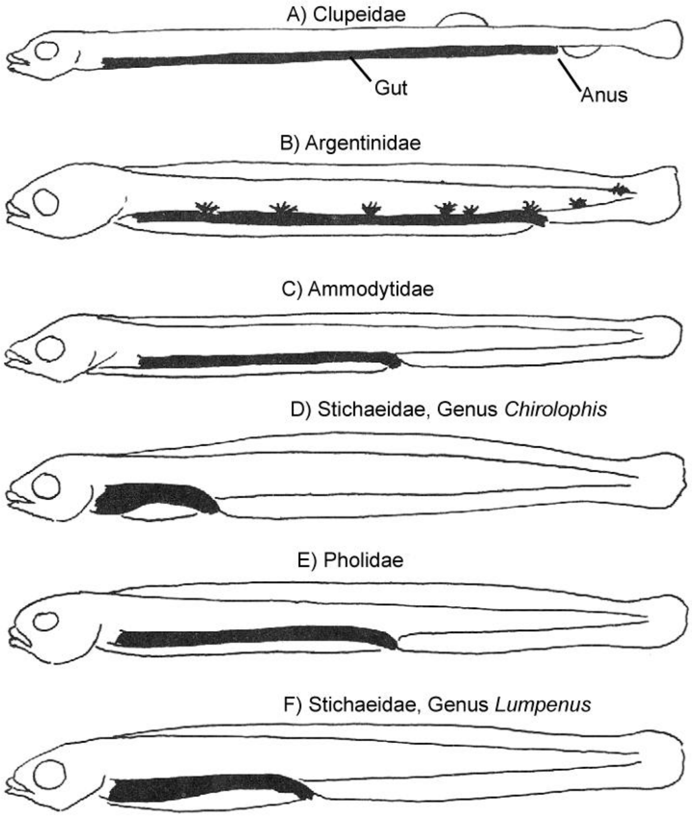

Fig. 5. Separation of elongated postlarvae (after Russell, 1976).

Fish postlarvae comparison:
To illustrate the diversity of postlarval morphology, examples from selected families are given below.

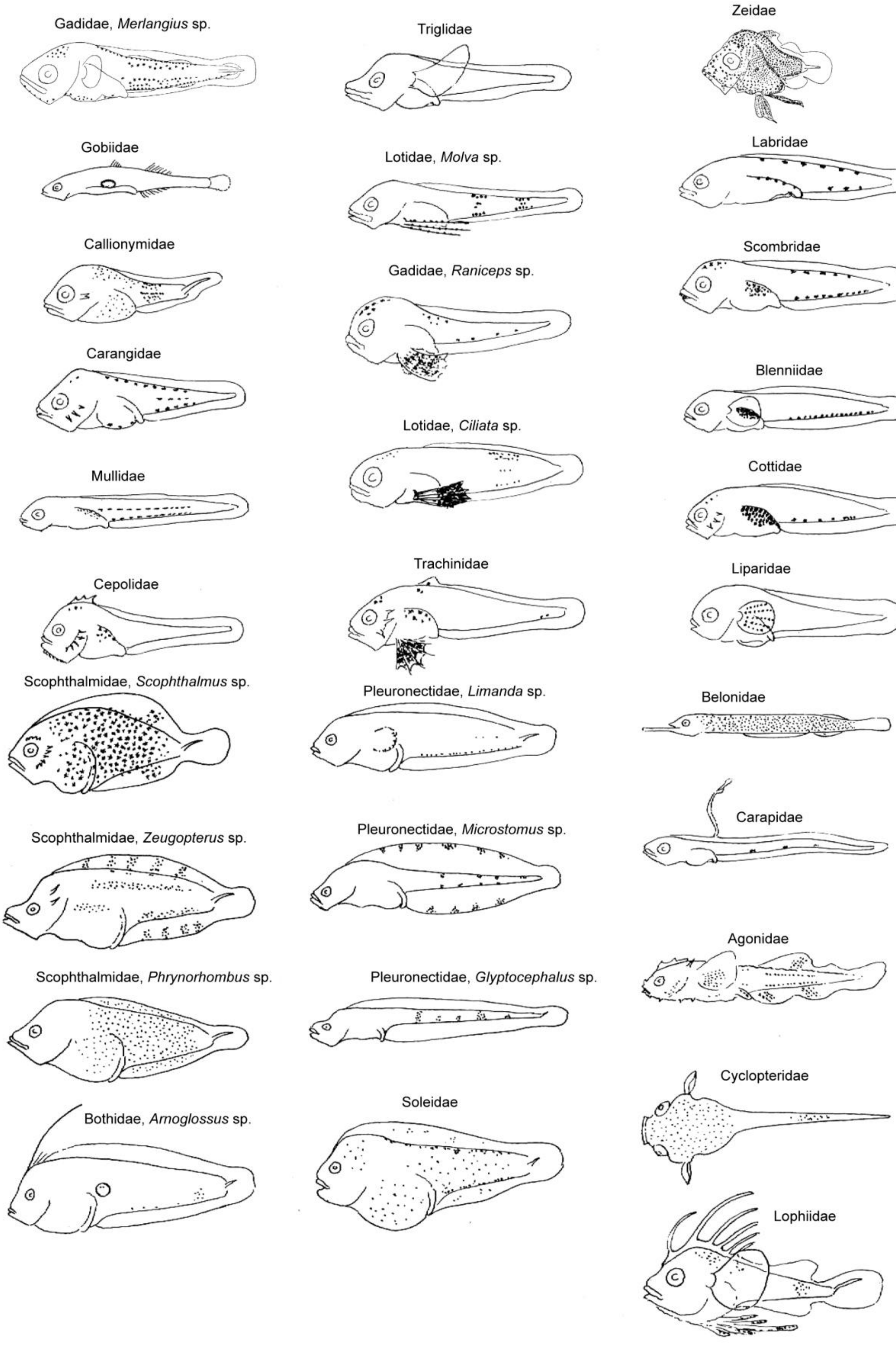

Fig. 6. Comparative examples of the postlarvae of a range of fish families (after Russell, 1976).

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Species index

(Species names in brackets are synonyms used in the PMF, or in other literature used in the guide (apart from centrally placed brackets, which indicate subgenus); bold numerals = main illustrations).

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APPENDIX TO GUIDE PART 2: ADDITIONAL COPEPODS

A few additional copepods have been recorded from southern Britain since Part 2 of the guide, which included copepods, was issued. *Rhincalanus nasutus* has been recorded at the Plymouth plankton sampling station L4, *Acartia teclae* and *Microsetella rosea* in Millbay Marina, Plymouth and *Pseudodiaptomus marinus* from the southern North Sea, the French coast of the English Channel and Milford Haven, South Wales. *M. rosea* was already included, as a species that had been found in the general area, but descriptions of the others are added here. This opportunity has also been taken to add *Bradyidius armatus* and *Pareuchaeta norvegica*, both of which are recorded from northern areas.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

Family Aetideidae:

Genus *Bradyidius*:

Bradyidius armatus (Vanhöffen, 1897)

First pedigerous somite fused with cephalosome (Fig. 1A, B, D); rostrum distinctly bifurcate (Fig. 1C)

Female: A1 as long as prosome (Fig. 1A, B); points on the last prosome somite divergent in dorsal view, straight in lateral view, reaching the end of the genital somite; urosome comparatively short, ventral genital somite not very protuberant in lateral view; furca scarcely longer than wide; no P5.

Male: Slenderer than female; points on last prosome somite shorter than in female (Fig.1D); urosome slender, anal somite short, furca often divergent; P5 simple (Fig. 1E), left limb long and pointed, with five segments, right (sometimes missing) a third the length of left, with three segments and small terminal spine

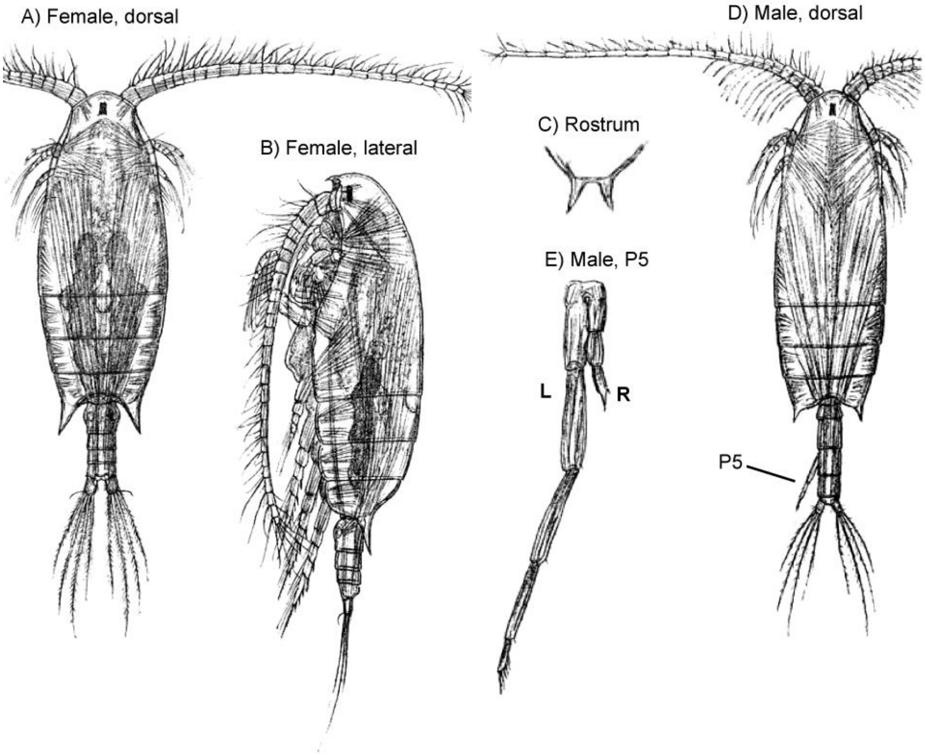

Fig. 1. *Bradyidius armatus* (From Sars, 1903).

Recorded: PMF and L4, not recorded. Irish Sea. Northwestern Scotland in deep sea lochs. Norwegian coast.

Total length: Female 2.65 mm; male 2.2 mm.

Further information: Rose, 1933; Sars, 1903 (both as *Undinopsis bradyi*); Mori, 1937.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

Family Rhincalanidae:

Genus *Rhincalanus*:

Rhincalanus nasutus Giesbrecht, 1888

Large copepod; A1 much longer than body; prosome long and slender; first pedigerous somite fused with cephalosome (Fig. 2A, E) making this cephalothorax longer than the remainder of the prosome; rostral filaments not visible from above; second to fourth pedigerous somites each with posterolateral spines and pair of posterodorsal spines (Fig. 2B, F); genital somite with pair of posterodorsal spines;

Female: Rostrum a pair of fine filaments (Fig. 2C); urosome short, of three somites (Fig. 2B), furca at least partially fused to anal somite; P5 uniramous (Fig. 2D), simple, three segments, one plumose setae on second segment and three on third.

Male: Resembles female; A1 three quarters length of female A1; P5 simple (Fig. 2G), right limb uniramous with long, thin, terminal hook, left limb biramous, exopod with long terminal hook.

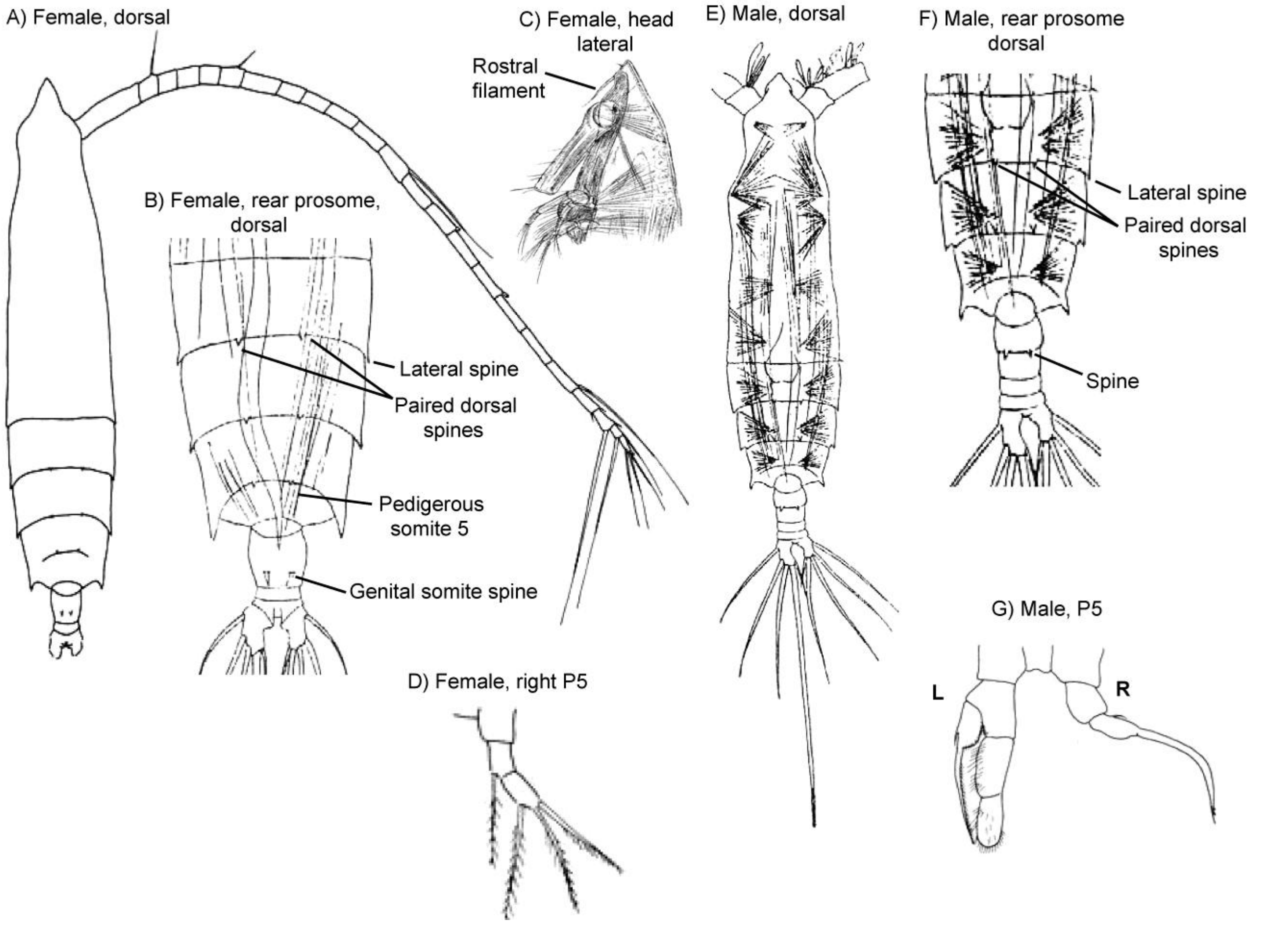

Fig. 2. *Rhincalanus nasutus* (A, D, G from Bradford-Grieve, 1994; B, E, F from Mori, 1937; C from Sars, 1903).

Recorded: PMF, not recorded. L4. Northern North Sea. West and south of Ireland.

Total length: Female 3.9-5.4 mm; male 2.7-4.3 mm.

Further information: Sars, 1903; Rose, 1933; Mori, 1937; Bradford-Grieve, 1994; Mazzocchi *et al*., 1995.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

Family Euchaetidae:

Genus *Paraeuchaeta:*

Pareuchaeta norvegica (Boeck, 1872)

Very large copepod; A1 with array of characteristic long, fine setae (Fig. 3A, B, F) that seem to survive sampling and preservation well, present even in the earliest copepodite stages; first pedigerous somite partially fused to cephalosome; both sexes with long urosomes and also very large maxillipeds, associated in the females with their carnivorous diet. In the Euchaetidae, males do not feed and some parts of the mouthparts are atrophied, their large maxillipeds probably associated with capture of females during mating. Anterior body pointed in dorsal view; in lateral view a single strong rostrum is obvious, with a frontal eminence just behind (Fig. 3C, G). Innermost (appendicular) seta on each furca well developed, much longer than other setae (Fig. 3A, B, F).

Female: A1 as long as prosome (Fig. 3A, B); last prosome somite rounded in lateral view, with tuft of long hairs (Fig. 3E); genital somite very prominent in lateral view (Fig. 3D), with small projection above swelling; anal somite very short; no P5. Often sampled carrying an egg sac (Fig. 3A).

Eggs ~0.41-0.46 mm in diameter, initially round, but irregularly shaped when nauplii are well developed. Egg sacs sometimes found detached, but usually not individual eggs. Nauplii are swollen, packed with oil and primitive in appearance. They are similar in size to euphausiid nauplii, but euphausiid nauplii have longer limbs and lack the dense oil content, so much paler in colour.

Male: A1 not geniculate (Fig. 3F); anal somite very short (Fig. 3H), middle three urosome somites with spinules around hind edge; P5 very large and characteristic (Fig. 3I), with rudimentary endopods on both legs; right leg with very elongated segment distally; left leg with a complex distal joint, the last segment short and without the long stylet found in some Euchaetidae.

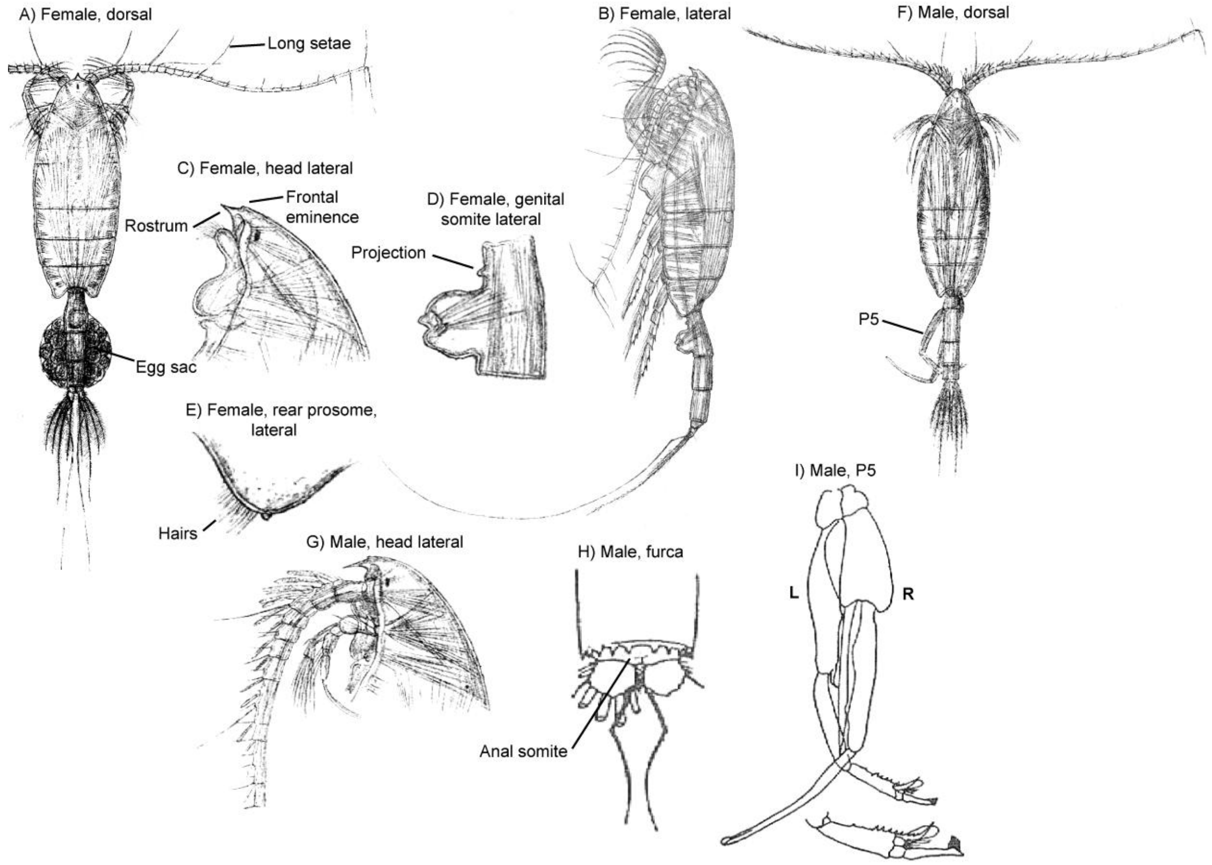

Fig. 3. *Pareuchaeta norvegica* (A-G from Sars, 1903, as *Euchaeta norvegica*; H, I from Rose, 1933 after Sars, 1903).

Recorded: PMF and L4 not recorded. Irish Sea. Northern North Sea. Northwestern Scotland in deep sea lochs. Western Norway, including fjords.

Total length: Female 7-11 mm; male 5.5-7.0 mm.

Further information: Sars, 1903; Mauchline, 1999; Nicholas & Nash, 1999 (all as *Euchaeta norvegica*); Rose, 1933; Park, 1995.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

Family Acartiidae:

Genus *Acartia:*

Acartia teclae Bradford, 1976

The smallest *Acartia* species sampled in the European area. In common with other *Acartia* species the body is coffin-shaped, there are many characteristic, fine setae on the antennules and a fan of fine setae on the furca (not illustrated). These setae seem to survive sampling and preservation better than in many other copepods, and are obvious from the earliest copepodite stages.

Female: Posterior prosome and urosome somites without hairs or spinules (Fig. 4A, B); genital somite with centrally placed swelling in lateral view, anteriorly placed in dorsal view; P5 terminal spine thick (Fig. 4C).

Male: Posterior prosome somite with ventral hairs (Fig. 4D, E), urosome somites without hairs or spinules; left P5 second basal segment with two posterior rows of medium-sized spinules (Fig. 4F) and inner border with hairs, the following segment with fine hairs on inner edge; right P5 second basal segment with conspicuous inner cleft, the second exopod segment with angular lobe internally.

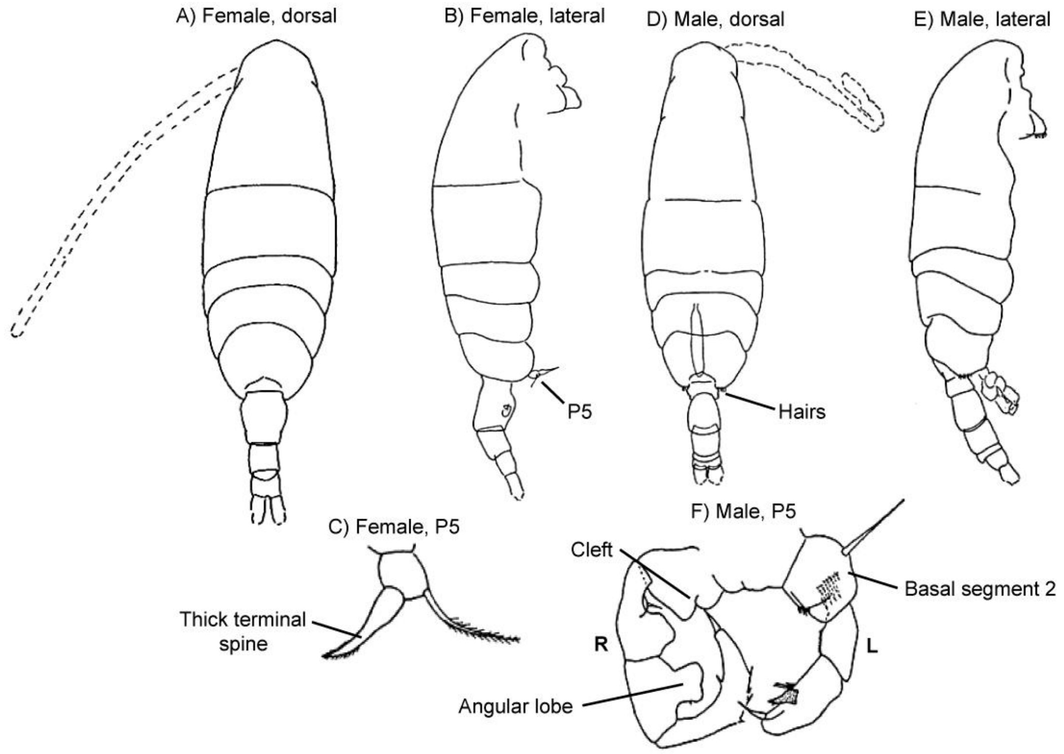

Fig. 4. *Acartia teclae* (from Bradford, 1976).

Recorded: PMF and L4, not recorded. Millbay Marina (Plymouth). Milford Haven, South Wales (K. Watts, pers. comm.). Western Norway. Northwest Scotland.

Total length: Female 0.71-0.87 mm; male 0.64-0.72 mm.

Further information: Bradford, 1976; Bradford-Grieve, 1999.

Sub-class Copepoda: Infraclass Neocopepoda: Superorder Gymnoplea: Order Calanoida:

Family Pseudodiaptomidae:

Genus *Pseudodiaptomus:*

Pseudodiaptomus marinus Sato, 1913

An alien species spread from Asia, presumably in ballast water, which seems particularly adaptable to new regions. It has been found at several sites around Europe (Olazabal & Tirelli, 2011; Brylinski *et al.*, 2012; Jha *et al*., 2013) and more records would certainly emerge if sampling in the neighbourhood of busy shipping ports were carried out. It is not restricted to inshore regions as it has been sampled in open sea in the southern North Sea (Jha *et al*., 2013).

Female: As it is not a native species, *P. marinus* females could, on cursory examination, be mistaken for females of either *Centropages hamatus* (Lilljeborg, 1853) or *Isias clavipes* Boeck, 1865, but has four rather than three free urosome somites (Fig. 5A, C). Anterior cephalosome rounded in lateral view (Fig. 5B); posterior prosome somite with lateral points (Fig. 5A, C, D); all somites of the urosome, except the anal somite, bearing a dorsoposterior row of spinules (Fig. 5F), the smallest spinules on the genital somite; genital somite slightly asymmetrical in dorsal view (Fig. 5A), swollen ventrally in lateral view, the swelling produced into a short wide acute protuberance directed backwards (Fig. 5D); P5 uniramous, four segments (Fig. 5E), distal segment with two large terminal spines and a smaller subterminal spine.

Male: Body slenderer than female; right A1 geniculate (Fig. 5H); posterior prosome somite with lateral points (Fig. 5G), less pronounced than in female; urosome of five somites, the second to fourth with spinules on dorsoposterior margin; furca slightly more than 1.5 times longer than anal somite; P5 complex and can vary slightly in morphology between sampling locations (Walter, 1986a).

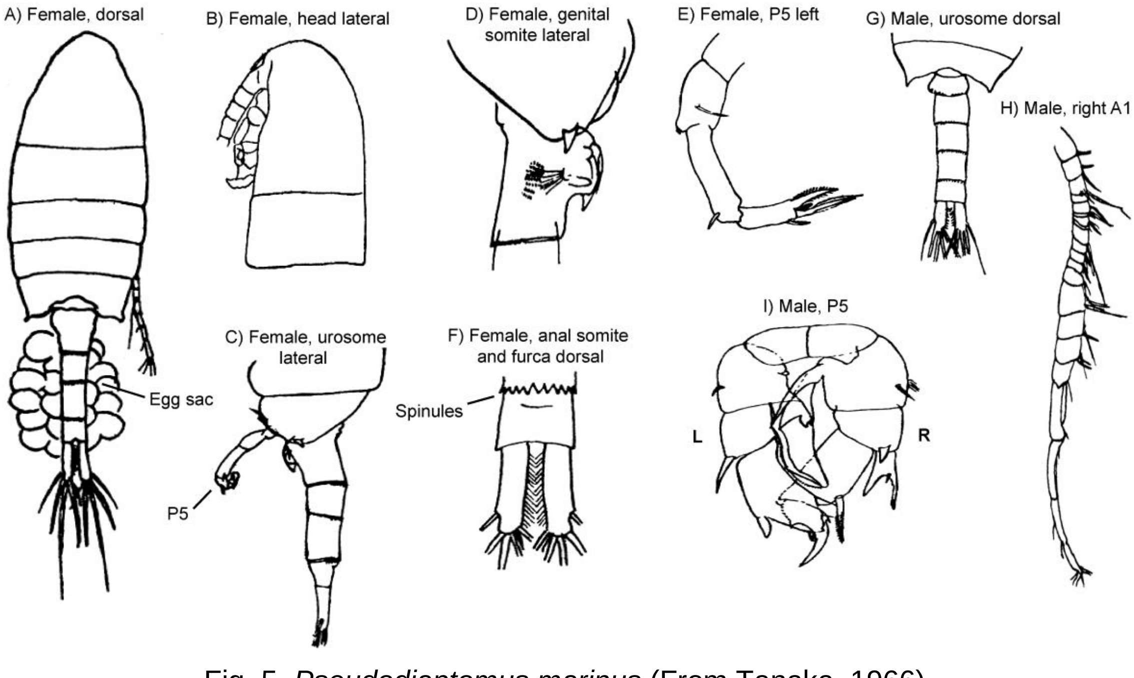

Fig. 5. *Pseudodiaptomus marinus* (From Tanaka, 1966).

Recorded: PMF and L4, not recorded. Southern North Sea. Milford Haven, South Wales (K. Watts, pers. comm.). French coast of the English Channel at Calais.

Total length: Female 1.3-1.8 mm; male 1.0-1.5 mm.

Further information: Brodskii, 1950; Tanaka, 1966; Grindley & Grice, 1969; Walter, 1986a, b; Olazabal & Tirelli, 2011; Brylinski *et al*., 2012; Jha *et al*., 2013.

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Some corrections to previous guide parts

Guide Part 1:
P. 119. Fig. 3. Replace *Littorina* spp.” with “Subfamily Littorininae”

Guide Part 2:
P. 47. Line 15. Replace “each of these is biramous (two branches)” with “each of these is biramous (two branches) apart from the latter two, which are uniramous”.

P.82. Under Recorded. Replace “PMF, upper River Tamar Estuary” with “PMF, not recorded. Upper River Tamar Estuary, Plymouth, J.A. Lindley pers. comm.”

P. 118. Fig. 65E. Replace “dorsal” with “ventral”

P. 133. Delete the first two lines of the key for males, related to *Monstrillopsis filogranarum*.